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New results on the hydrodynamic behaviour of fossil Nummulites tests from two nummulite banks from the Bartonian and Priabonian of northern Italy

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KEY WORDS - Settling velocity, Eocene, taphonomy, Larger Foraminifera, test density, nummulite banks.

ABSTRACT - Settling velocities of 58 well-preserved tests of fossil Nummulites *were experimentally determined using a settling tube. The tests were collected from the nummulite banks of Pederiva di Grancona (A forms of* N. lyelli *and* N. striatus*, Middle Eocene) and San Germano dei Berici (A and B forms of* N. fabianii*, Late Eocene), both in the Berici Mts. (Veneto, northern Italy). The data were compared with estimated settling velocities that the same specimens might have had in life conditions. This was done by reconstructing their densities simulating water-filled condition and, to simulate post-diagenetic effects, under calcite-filled condition. These simulations show that A and B forms, even if they greatly diverge in shape, volume and size, still possess comparable settling velocities, and that each nummulite bank is characterized by specific hydrodynamic parameters. The use of settling velocity as a parameter to quantify the hydrodynamic behaviour of particles in seawater enables estimation of palaeoenvironmental conditions such as depth, substrate and the energy scenario. Such information is useful in obtaining further insights into the genesis of nummulite banks, the autochthony or allochthony of which is still being debated. Our results point to an autochthonous interpretation.*

RIASSUNTO - [Nuovi risultati sul comportamento idrodinamico dei gusci fossili di *Nummulites* da due banchi a nummuliti del Bartoniano e Priaboniano dell'Italia settentrionale] - *La genesi delle strutture bio-sedimentarie note come banchi a nummuliti è tuttora dibattuta. Sono state proposte sostanzialmente due interpretazioni: genesi autoctona, dovuta a particolari condizioni paleoecologiche e genesi alloctona, determinata da trasporto passivo ed accumulo per rideposizione.*

Questo studio ha lo scopo di fornire dati sulle proprietà idrodinamiche dei gusci fossili di Nummulites*. Su 58 esemplari fossili ben conservati di tre diverse specie di questo genere sono state determinate sperimentalmente le velocità di sedimentazione in acqua marina, utilizzando un tubo di decantazione. I fossili sono stati raccolti dai banchi a nummuliti di Pederiva di Grancona (forme A di* N. lyelli *e* N. striatus*, Bartoniano, Eocene Medio) e San Germano dei Berici (forme A e B di* N. fabianii*, Priaboniano, Eocene Superiore), entrambi nei Monti Berici (Veneto, Italia settentrionale).*

I dati sono stati elaborati e confrontati con le velocità di sedimentazione stimate che gli stessi esemplari potrebbero aver avuto in vita. Le densità sono state ricostruite simulando la condizione del guscio pieno d'acqua e, per tener conto degli effetti post-diagenetici, simulando condizioni di riempimento delle cavità da parte della calcite. Le simulazioni mostrano che le forme A e B della stessa specie, anche se differiscono fortemente per forma, volume e dimensioni, possiedono velocità di sedimentazione comparabili, e che ogni banco a nummuliti è caratterizzato da specifiche classi di parametri idrodinamici.

Le velocità stimate per i due casi in esame permettono di ipotizzare una diversa profondità di sviluppo per il banco di Pederiva di Grancona, più profondo rispetto a quello di San Germano dei Berici.

L'uso della velocità di sedimentazione come unico parametro per valutare il comportamento idrodinamico delle particelle in acqua di mare, permette la stima di condizioni paleoambientali quali profondità e substrato e consente di delineare lo scenario energetico.

Nel complesso, i risultati di questo studio fanno propendere per una genesi autoctona dei banchi a nummuliti.

INTRODUCTION

Shallow-water Eocene carbonate deposits are often represented by nummulite-rich limestones. Among them, some are characterized by a striking abundance of large specimens of the genus *Nummulites*, and have been referred to as "nummulite banks" by Arni (1965). He observed that these sedimentary bodies are composed of one or two species of *Nummulites*, with an unusual abundance of large B forms. He explained that these species flourished only in environments where test production was faster than the sedimentation rate. This yielded gentle reliefs rising above the sea floor and forming structures partially resembling modern coral reefs.

Nummulite banks were re-interpreted by Aigner (1982, 1983, 1985), who pointed out the sedimentological features suggesting that accumulations were mainly produced by transport and selective removal of the smaller A forms. Accordingly, he defined four categories of nummulite accumulations: 1) parautochthonous (A>>B), 2) relatively enriched in B forms (A>B), 3) residual (B), and 4) allochthonous (A). In this view, the nummulite banks could belong essentially to the second category, whereas the residual and allochthonous accumulations should be retrieved in the original life environment and in the final deposition site, respectively. He therefore questioned the former interpretation of Arni (1965), who considered the nummulite banks as substantially autochthonous.

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In more recent years the Aigner model was followed by several workers, among which are Anketell & Mriheel (2000), Racey (2001), Jorry et al. (2003, 2006), Beavington-Penney et al. (2005, 2006), and Swei & Tucker (2012). Mateu-Vicens et al. (2012) interpreted some nummulite banks as accumulations from mass flows, triggered by the action of internal waves. The autochthonous interpretation was instead followed by Loucks et al. (1998) and Wielandt (1999). Based on outcrop observations, Papazzoni (2008) pointed out that the presence of very fine micritic or clayey sediments preserved among the nummulite tests might indicate autochthonous deposition, as originally suggested by Arni. The presence of intraclastic fine sediments could occur by sheltering due to the nummulite tests, which functioned as a barrier against water motion.

The relationship between transport and depth distribution of modern foraminifera has been investigated extensively in the last decades, with researchers tackling foraminifera redeposition in different ways (e.g., Martin & Liddell, 1991; Hohenegger & Yordanova, 2001a, b; Yordanova & Hohenegger, 2002). One conclusion is that foraminiferal tests may be easily transported even by very weak currents. Transport and deposition mechanisms under water motion have been studied for a long time by coastal engineers (Soulsby, 1983), sedimentologists (Le Roux, 1997) and palaeontologists (Allen, 1994). The latter were interested in studying the hydrodynamic behaviour of particles (molluscs or foraminifera can also be considered as particles of a specific size, density and shape) under effects of seawater motion. The main result of such efforts led to the definition of one parameter which best represents and quantifies the transportability of the particle itself: the settling velocity (Fütterer, 1978; Baba & Komar, 1981; Komar, 1981; Allen, 1984; Komar & Cui, 1984; Davaud & Septfontaine, 1995; Li et al., 1998; Hughes, 1999; Paphitis et al., 2002; Yordanova & Hohenegger, 2007 and references therein; Briguglio & Hohenegger, 2011). All these studies evidenced the positive correlation between settling velocity and hydrodynamic resistance to transport. In shallow-water environments, where larger foraminifera commonly live, water energy and turbulence play an important role and may cause particle transport by different mechanisms: entrainment, saltation and transport in suspension. These processes can be inferred from the test preservation of nummulitids (Beavington-Penney, 2004) and in the deposit geometry (i.e., imbrication, orientation, etc.; Racey, 2001). In such a complex hydrodynamic scenario, in which multiple transport mechanisms occur, the use of the settling velocity is justified as the only mathematical parameter that quantifies the hydrodynamic response (i.e., the behaviour) of each single particle (i.e., nummulite test) in the sea. In fact, the equations to estimate the settling velocity include numerous morphological parameters such as nominal diameter, shape entropy, density and drag coefficient. An alternative approach to study the reaction of nummulite tests to water energy takes into account the diameter/thickness ratio (Larsen, 1976; Larsen & Drooger, 1977; Hallock, 1979; Hallock & Hansen, 1979; Hallock, 1981; Renema, 2005). The rationale of this approach is simple: the lower the ratio, the shallower the environment. However, this parameter, which has been proven to be quite reliable, is actually more directly linked to light and seawater transparency (Renema, 2005; Mateu-Vicens et al., 2009) and only secondarily to hydrodynamic energy.

The interpretation of settling velocity and a correct determination of autochthonous vs. allochthonous sediments is a major issue in sedimentology. For larger foraminifera, test geometry and structure (i.e., density, size, shape) and the settling velocity that ensues from these parameters, point to specific scenarios (i.e., depths) at which the organisms might have lived. All larger foraminifera tend to avoid downslope transport in order to get enough light for their symbionts. Accordingly, their tests are well adapted to the particular hydrodynamic environment they inhabit. Transport evidence is recognisable in the settling parameters whenever a shallow-living test (i.e., with a high settling velocity) is found with other tests possessing lower settling velocities (Briguglio & Hohenegger, 2011).

Estimating the settling velocity of tests embedded into nummulite banks thus helps to reveal the hydrodynamic regime in which they were or were not transported.

Except for some studies on the hydrodynamic behaviour of fossil larger foraminifera (Jorry et al., 2006; Briguglio & Hohenegger, 2009), most publications concern the hydrodynamics and depth transport of modern larger foraminifera (e.g., Beavington-Penney & Racey, 2004; Yordanova & Hohenegger, 2007). The investigation of fossil tests is typically hampered by several issues, key among them the estimation of density, which is pivotal for correctly determining the settling velocity. Settling velocity values obtained on fossil materials - where recrystallization effects, fillings and mineralogical alteration may be prominent and influence the densities - are difficult to interpret. Nonetheless, several recent studies proposed new ways to approach such problems, yielding, at least theoretically, reliable data on the density of fossil foraminifera (Hohenegger & Briguglio, 2012). The present study was designed to investigate the genesis of nummulite banks by studying the settling velocity of the larger foraminifera; this is a first step in identifying whether such sedimentary bodies had an autochthonous, parautochthonous or allochthonous origin.

We have to point out that the few previous studies on nummulites did not describe in detail the localities, outcrop features, full assemblage and taxonomy. Even the seminal paper by Jorry et al. (2006) considered specimens coming from different samples, for which no geological/outcrop data were provided. Therefore, this is probably the first comprehensive study of the hydrodynamic behaviour for selected nummulite banks.

GEOLOGICAL AND STRATIGRAPHIC SETTING

The samples used for this research come from the Berici Mts., which during the Paleogene were part of the Lessini Shelf (Bosellini, 1989), a palaeogeographic unit roughly coincident with the present-day Lessini and Berici Mts. The distribution of Paleogene sediments in this area was influenced by the Alpone-Chiampo Graben (Zampieri, 1995; Bassi et al., 2008), a tectonic structure extending along a NNW-SSE axis, encompassing the eastern part of the Lessini Mts. and the main portion of

Fig. 1 - Location map of the Pederiva and San Germano nummulite banks in the Berici Mts., northern Italy.

the Berici Mts. In this structural low, a great amount of carbonate sediments, mainly made up of nummulite-rich limestone, accumulated during Eocene-Oligocene times.

The Paleogene formations of the Lessini Shelf are quite homogeneously distributed in the Lessini and Berici Mts. (e.g., Bosellini et al., 1967; Mietto et al., 1981). In the Berici Mts., the Middle and Upper Eocene succession is composed of two formations: the 'Calcari nummulitici' ('Nummulitic limestone') of Early-Middle Eocene age (e.g., Bosellini et al., 1967) and the 'Marne di Priabona' (Upper Eocene; e.g., Suess, 1868; Cita, 1969; Ungaro, 1969). The 'Calcari Nummulitici' Fm. consists of shallow-water carbonate limestone deposits characterized by the widespread presence of nummulite accumulations (Bassi et al., 2001). This formation includes quite different facies and ages and still requires thorough revision despite having been extensively investigated (Fabiani, 1915; Schweighauser, 1953; Papazzoni, 1994; Papazzoni & Sirotti, 1995; Bassi et al., 2001; Nebelsick et al., 2005). The Marne di Priabona Fm. is represented by marls and marly limestones, usually with a rich fossil content consisting of larger foraminifera (nummulitids, orthophragminids, etc.), smaller benthic foraminifera, planktonic foraminifera, bryozoans, bivalves, calcareous algae, etc.

The samples collected for this work come from two localities, both in the southwestern Berici Mts., Vicenza Province, north-eastern Italy (Fig. 1): Pederiva di Grancona and San Germano dei Berici, about two km apart from each other. Pederiva di Grancona is well known for the nummulite bank cropping out directly below the so-called "Cava Zengele" (Schweighauser, 1953: the correct name is indeed "Cava Cengelle"), on the northern side of the Liona Valley, near the village of Grancona. Here the nummulite bank is at least 6 m thick (the base is not visible), made up of large nummulite tests with high abundance of B forms of *N. lyelli* d'Archiac & Haime, 1853. The A/B ratio of *N. lyelli* is about 35. This species represents more than 75% of the whole assemblage, which also includes (in order of decreasing abundance): *N. striatus* (Bruguière, 1792), *N. discorbinus* (Schlotheim, 1820), *N. biarritzensis* d'Archiac, 1837 emend. d'Archiac, 1852, and *N. beaumonti* d'Archiac & Haime, 1853. Large assilinas and bivalve shells are common. The sediment is marly, with fine clayey matrix infilling the broad spaces among the large nummulite tests. Imbricated contacts among large *N. lyelli* B forms are present in the Pederiva bank, indicating water movement (Papazzoni & Sirotti, 1995; Papazzoni, 2008). The age of this bank is early Bartonian (SBZ 17 of Serra-Kiel et al., 1998).

In San Germano dei Berici, on the eastern side of the Liona Valley, another nummulite bank crops out (Papazzoni & Sirotti, 1995). The bank, about 4 m thick, is composed mainly of A and B forms of *N. fabianii* (Prever in Fabiani, 1905). The A/B ratio of *N. fabianii* is about 28. This species represents more than 85% of the whole assemblage, which includes (in order of decreasing abundance) *N. stellatus* Roveda, 1961, *N. incrassatus* de la Harpe, 1883, *N. cunialensis* Herb & Hekel, 1975, *N. garnieri* de la Harpe in Boussac, 1911, and *N. chavannesi* de la Harpe, 1878. Here, too, fine-grained marly sediment is present among the nummulite tests. Coralline red algae and bivalve shells are also present. Arni (1965) suggested that encrusting coralline algae help stabilize the sediment, but in this case the extent of encrustation is evidently insufficient to bind the grains together. The age of this bank is early Priabonian (SBZ 19 of Serra-Kiel et al., 1998).

MATERIALS AND METHODS

For this study, 58 specimens of nummulites were used (Tab. 1). They were collected from the nummulite banks of Pederiva di Grancona (N 45°25'18.18", E 11°28'02.67") and San Germano dei Berici (N 45°24'15.16", E 11°28'35.83") in Veneto, NE Italy. From Pederiva di Grancona we selected A forms of *N. lyelli* and *N. striatus* (Fig. 2). From San Germano dei Berici we selected A and B forms of *N. fabianii* (Fig. 2). The measurements made on each specimen are largest diameter (L) and thickness (S), measured by a calliper. In this work the intermediate diameter has not been measured, since it is practically the same as L. After overnight drying, the weight of each specimen was measured on a precision balance Mettler UM 3/mg (Mettler-Toledo, Greifensee, Switzerland). Then, the maximum sinking velocity was experimentally measured using a settling tube with transparent glass walls, filled with artificial seawater. The height of the settling tube is 90 cm and the squared base is 12 x 12 cm; the artificial seawater used for this experiment had a measured density of 1.06 g/cm^3 and was provided by the Department of Limnology and Bio-Oceanography at the University of Vienna. The settling velocity was measured by calculating the time for passing through the last 60 cm of the settling tube (the settling pattern during the first 30 cm is commonly affected by acceleration effects and the turbulence caused by the starting position of the settling specimen).

Each test was released directly beneath the water/air interface in stagnant water at room temperature (23°-25°C) and the fall was filmed by a digital camera.

Settling measurements in cases of collision between specimen and tube walls were not considered and the procedure was repeated. The very large B forms of *N. lyelli* were also preliminarily tested to determine their settling velocity, but they always bumped against the walls of the settling tube. This yielded inaccurate measurements, and they were therefore not considered in this study.

N°	Origin	Taxon	Gen.	Weight (g)	ρ_m (g/cm^3)	Volume (cm^3)	*TND* (cm)	Observed *v* (cm/s)	*v* with ρ_m (cm/s)	*v* with ρ_c (cm/s)	*v* with ρ_w (cm/s)
1	Ped	*N. lyelli*	A	0.0848	2.23	0.0380	0.42	20.4	26.5	28.5	21.4
2	Ped	*N. lyelli*	A	0.1028	2.17	0.0473	0.45	20.0	23.8	26.1	19.4
3	Ped	*N. lyelli*	A	0.0675	2.13	0.0317	0.39	20.8	23.7	26.6	20.3
4	Ped	*N. lyelli*	A	0.0691	2.24	0.0308	0.39	21.5	25.4	27.3	20.5
5	Ped	*N. lyelli*	A	0.0556	2.37	0.0234	0.36	22.2	26.0	26.7	19.5
6	Ped	*N. lyelli*	A	0.1426	5.24	0.0272	0.37	23.8	40.5	26.4	19.8
7	Ped	*N. lyelli*	A	0.0797	1.92	0.0416	0.43	24.4	23.4	28.8	22.0
8	Ped	*N. lyelli*	A	0.0781	2.55	0.0307	0.39	26.3	30.0	29.3	22.0
10	Ped	*N. lyelli*	A	0.0704	2.24	0.0314	0.39	20.4	25.3	27.2	21.5
11	Ped	*N. lyelli*	A	0.0945	1.92	0.0492	0.45	21.3	22.4	27.4	21.0
12	Ped	*N. lyelli*	A	0.0961	2.09	0.0460	0.44	24.4	24.9	28.2	21.6
13	Ped	*N. lyelli*	A	0.0734	2.50	0.0294	0.38	24.4	27.0	26.7	20.3
14	Ped	*N. lyelli*	A	0.0943	2.46	0.0383	0.42	25.6	28.1	28.1	21.9
15	Ped	*N. lyelli*	A	0.071	1.81	0.0392	0.42	21.7	21.5	28.1	21.4
16	Ped	*N. lyelli*	A	0.0757	2.87	0.0264	0.37	22.7	30.0	26.9	20.1
17	Ped	*N. lyelli*	A	0.0935	2.11	0.0443	0.44	20.8	24.5	27.5	21.0
1	Ped	*N.striatus*	A	0.0502	1.93	0.0261	0.37	20.0	20.5	25.1	18.2
2	Ped	*N.striatus*	A	0.0384	2.28	0.0169	0.32	21.3	23.5	24.7	18.8
4	Ped	*N.striatus*	A	0.0342	1.72	0.0199	0.34	20.0	17.0	24.2	17.3
5	Ped	*N.striatus*	A	0.0435	1.74	0.0250	0.36	21.7	18.8	26.0	18.2
6	Ped	*N.striatus*	A	0.04111	1.33	0.0308	0.39	22.7	12.3	26.2	21.2
7	Ped	*N.striatus*	A	0.0517	1.73	0.0299	0.39	22.5	18.8	26.0	18.9
8	Ped	*N.striatus*	A	0.052	2.13	0.0244	0.36	20.5	23.6	26.2	18.2
9	Ped	*N.striatus*	A	0.0366	1.87	0.0195	0.33	21.3	20.1	25.6	17.6
10	Ped	*N.striatus*	A	0.0465	2.08	0.0224	0.35	22.7	21.3	24.3	20.3
12	Ped	*N.striatus*	A	0.0417	1.70	0.0245	0.36	20.2	18.1	25.9	17.9
13	Ped	*N.striatus*	A	0.0301	1.58	0.0190	0.33	20.0	15.7	24.9	19.2
14	Ped	*N.striatus*	A	0.044	1.73	0.0254	0.36	21.5	20.0	27.5	19.2
15	Ped	*N.striatus*	A	0.0524	1.62	0.0324	0.40	22.2	18.7	27.9	20.6
16	Ped	*N.striatus*	A	0.0564	1.92	0.0293	0.38	22.0	22.0	26.9	20.3
18	Ped	*N.striatus*	A	0.0332	2.14	0.0155	0.31	20.8	21.7	24.2	18.5
1	SG	*N. fabianii*	A	0.0131	2.44	0.0054	0.22	16.1	16.0	15.6	10.5
2	SG	*N. fabianii*	A	0.0261	2.32	0.0113	0.28	16.7	17.5	18.0	12.0
3	SG	*N. fabianii*	A	0.0203	3.15	0.0064	0.23	14.1	20.5	16.8	12.3
4	SG	*N. fabianii*	A	0.0131	2.45	0.0053	0.22	15.1	15.9	15.5	11.6
5	SG	*N. fabianii*	A	0.0204	2.26	0.0090	0.26	15.9	16.5	17.3	13.1
6	SG	*N. fabianii*	A	0.0128	2.02	0.0063	0.23	13.8	13.8	16.4	13.5
7	SG	*N. fabianii*	A	0.00581	1.67	0.0035	0.19	12.2	9.1	13.9	10.0
8	SG	*N. fabianii*	A	0.0209	2.26	0.0092	0.26	18.0	17.5	18.4	14.7
9	SG	*N. fabianii*	A	0.0161	2.05	0.0078	0.25	15.7	14.3	16.7	13.0
10	SG	*N. fabianii*	A	0.0205	2.21	0.0093	0.26	19.4	16.2	17.5	13.6
12	SG	*N. fabianii*	A	0.0187	2.50	0.0075	0.24	16.7	17.5	16.8	13.2
13	SG	*N. fabianii*	A	0.0166	2.13	0.0078	0.25	15.9	14.9	16.7	13.1
14	SG	*N. fabianii*	A	0.0214	2.43	0.0088	0.26	16.7	17.0	16.8	12.9
16	SG	*N. fabianii*	A	0.0175	2.00	0.0088	0.26	15.9	14.1	16.9	12.5

Tab. 1 - Weight/volume measurements and hydrodynamic parameters calculated on 58 specimens of fossil *Nummulites*. N° = progressive number distinctive for each specimen; Origin: Ped = Pederiva bank; SG = San Germano bank; *TND* = True Nominal Diameter; ρ_m = measured density; Observed *v* = settling tube observed velocity; *v* with ρ_m = velocity calculated with volumetric mass density (ρ_m); *v* with ρ_c = velocity calculated with calcite-filled condition; *v* with ρ_w = velocity calculated with water-filled condition.

N°	Origin	Taxon	Gen.	Weight (g)	ρ_m (g/cm³)	Volume (cm³)	*TND* (cm)	Observed *v* (cm/s)	*v* with ρ_m (cm/s)	*v* with ρ_c (cm/s)	*v* with ρ_w (cm/s)
17	SG	*N. fabianii*	A	0.0128	2.03	0.0063	0.23	14.0	13.2	15.6	12.7
1	SG	*N. fabianii*	B	0.3261	2.14	0.152275254	0.66	25.6	28.5	30.8	21.4
2	SG	*N. fabianii*	B	0.4195	2.06	0.203152974	0.73	22.6	32.5	36.1	25.6
3	SG	*N. fabianii*	B	0.2218	2.29	0.096735879	0.57	20.8	27.7	28.3	19.2
4	SG	*N. fabianii*	B	0.1759	2.92	0.060224451	0.49	21.5	32.6	26.1	17.6
5	SG	*N. fabianii*	B	0.3552	2.44	0.145746514	0.65	23.0	33.3	32.1	22.2
6	SG	*N. fabianii*	B	0.1747	2.37	0.073705859	0.52	19.6	27.5	27.1	18.3
7	SG	*N. fabianii*	B	0.1068	2.11	0.050618246	0.46	20.4	22.2	24.5	16.4
8	SG	*N. fabianii*	B	0.2051	2.36	0.086769596	0.55	23.3	27.6	27.4	18.6
9	SG	*N. fabianii*	B	0.2563	2.44	0.105133343	0.59	21.0	29.1	28.1	19.1
13	SG	*N. fabianii*	B	0.3036	2.05	0.14815979	0.66	19.6	26.8	31.3	21.3
15	SG	*N. fabianii*	B	0.1235	2.08	0.059378533	0.48	21.7	22.3	25.2	17.0
16	SG	*N. fabianii*	B	0.1307	1.88	0.069642672	0.51	22.7	19.7	25.4	17.2

Tab. 1 - Continuation.

After the laboratory analyses were performed on all tests, the data were used to run three calculations to estimate mathematically the settling velocity of the same tests under three conditions. The first calculation (named volumetric mass density) was made using the measured density of each test obtained by the weight-to-volume ratio. The second calculation (named water filled) involved computing the density as if the tests were filled with sea water (or cytoplasm because its density is approximately the same) and the third one (named calcite filled) as if they were completely filled with calcite. These last two calculations simulate hydrodynamic behaviour of the tests during their life (or directly after death) and after they had undergone diagenesis, respectively.

The calculations of water-filled and calcite-filled densities were conducted by means of the "half-tori" geometric method based on axial sections proposed by Hohenegger & Briguglio (2012). Density for the water-filled condition (ρ_w) represents the density of a test whose lumen is filled with seawater (ρ = 1.07), while density for the calcite-filled condition (ρ_c) is when the lumen is filled with calcite (ρ = 2.71) after diagenetic effects. According to Jorry et al. (2006), the calculation of a gas-filled condition might be also important to estimate test density during the decay of the cytoplasm. However, due to the hyaline (i.e., porous) wall of the foraminifera we investigated, gas produced by organic matter decay would quite suddenly leave the porous test and be replaced by seawater in freshly dead tests. We therefore did not include the gas-filled condition in this work. Furthermore, the value obtained for ρ_w can also be used to estimate the hydrodynamic behaviour of a test when it is living because the difference between cytoplasm and seawater density is very small (0.04).

The density value of calcite for simulating a calcite-filled test was assumed as 2.46 and used in the TORICALC program (Hohenegger & Briguglio, 2012), because we considered all lumina of the specimen as filled with calcite, but retained a residual porosity proportion of 0.15 (i.e., 15%) as not filled. The use of this slightly reduced value (instead of 2.71) changes the calculation only minimally but probably gives more reliable results. This is because it considers details such as small test fractures, spacing between growing calcite crystals and incompletely filled microporosity, typical for nummulitids possessing a very complex canal system. The settling velocities in all calculations were obtained according to the procedures used by Le Roux (1996, 1997), Jorry et al. (2006), and Briguglio & Hohenegger (2009, 2011). In the present work, the settling velocity (W_s) - see eq. (18) of Le Roux (1996) - was used for the *N. lyelli* and *N. striatus* specimens, whereas the settling velocity (W_e) of eq. (19) of Le Roux (1996) was used for *N. fabianii* A and eq. (3) of Allen (1984) (v) for *N. fabianii* B. The use of different formulas reflects the different shape entropy parameter measured on each test according to Briguglio & Hohenegger (2011).

To allow the comparison of the hydrodynamic behaviour of specimens belonging to different species and with different sizes, the True Nominal Diameter (*TND*) has been chosen as a shape-independent dimensional parameter representing the size of the specimen. Moreover, *TND* parameter neglects the shape of the investigated objects (Briguglio & Hohenegger, 2009). It has been firstly introduced by Wadell (1932), then commonly used as linear variable representing the diameter of a sphere with the same volume as the investigated specimen (Jorry et al., 2006; Briguglio & Hohenegger, 2009).

Statistical analyses were done using the program package PAST 3.08 and Microsoft Excel 2013.

Illustrated specimens are deposited in the "Inventario Paleontologia Università di Modena e Reggio Emilia" (IPUM) at the Dipartimento di Scienze Chimiche e Geologiche, Modena, Italy, under repository numbers IPUM 28777 - IPUM 28780.

RESULTS

During settling, the sinking pattern of each test is a combination of rotations and glides; the test wobbles along the horizontal plane while rotating along its vertical axis.

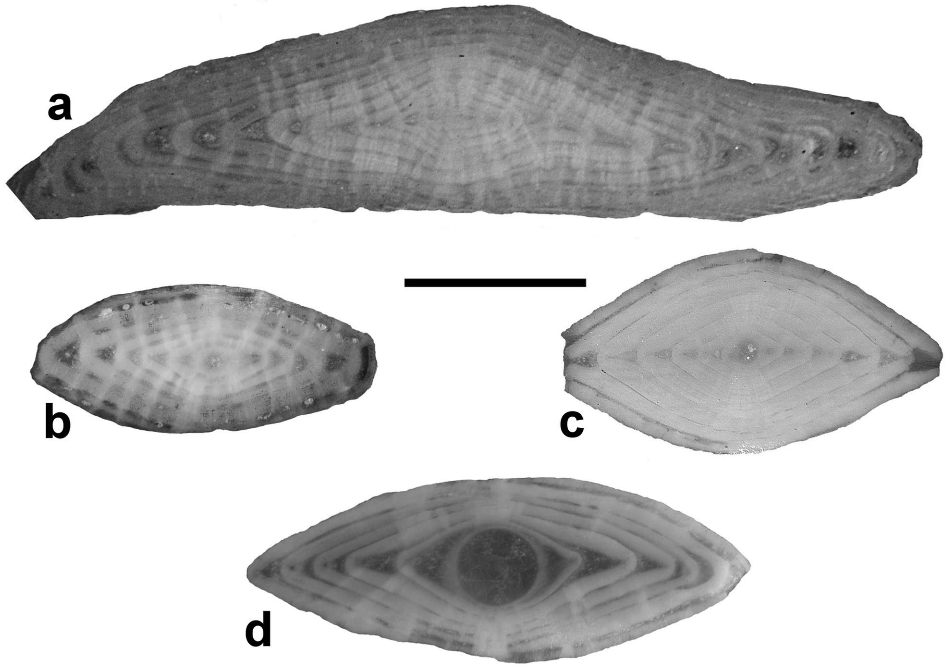

Fig. 2 - Axial sections of *Nummulites* specimens. a) *N. fabianii* B form, specimen No. 13, IPUM 28777; b) *N. fabianii* A form, specimen No. 2, IPUM 28778; c) *N. striatus* A form, specimen No. 9, IPUM 28779; d) *N. lyelli* A form, specimen No. 2, IPUM 28780. Scale bar corresponds to 2 mm.

The data we obtained are reported in Tab. 1, while the experimental and theoretical settling velocities using different density estimations are shown in Fig. 3.

There are clear differences in settling velocities between the experiments using the settling tube and the theoretical calculations based on densities obtained by the volume/weight ratio or the half-tori method; this pertains both to water- and calcite filled tests either filled with water or calcite (Fig. 3, Tab. 2).

Velocity variances (expressed as standard deviations in Tab. 2) based on densities obtained by the half-tori method filled with water and calcite are statistically identical in all A-generations. In the investigated taxa, variances (standard deviations) of settling velocities based on volumetric mass densities are always much higher than experimental velocities (>2 times) and theoretical velocities (>4 times) based on the half-tori methods (Tab. 2).

The variance in the settling tube observations for the *N. lyelli* A-generation is significantly higher than in both half-tori methods, while it is significantly lower in the experimental investigation of the *N. fabianii* B-generation compared to both half-tori methods (Tab. 2).

Comparing settling velocities obtained by different methods confirms the strong discrepancy of velocities based on volumetric mass densities from the other methods. This is documented in insignificant, sometimes negative correlations between paired measurements (Tab. 3). Such high and uncorrelated variability of values obtained by volumetric mass densities, compared to the other data, makes any further comparisons involving these specific datasets irrelevant.

Correlations are positive and significant in all species and generations between both half-tori methods, whereas they are positively correlated, but not significant, among settling tube observations and the half-tori methods (Tab. 3).

Within all species, the water-filled method shows the lowest settling velocities, followed by the settling tube observations, whereas calcite-filled data are the highest (Tabs 2-3).

The comparison of settling velocities among species and generations obtained by settling tube observations and both half-tori methods is shown in Tab. 4.

The comparison with the weakest (but almost significant) mean differences in settling velocity is the one between the A-generations of *N. lyelli* and *N. striatus*.

Surprisingly, the comparison between the two generations of *N. fabianii* shows a highly significant mean difference, whereas both other comparisons (between the *N. fabianii* B-generation and the A-generation of *N. lyelli* and *N. striatus*) have barely significant mean differences (Tab. 4).

Settling velocities depend on test size; thus, a simple comparison of tests with different sizes may lead to erroneous results when using means and variances. Therefore, dependencies of settling velocities on test size were studied using power regressions (Fig. 3). No size-dependent relations were detected for the *N. lyelli* A-generation in the experimental data or for both A-generations of *N. lyelli* and *N. striatus* in the volumetric mass density calculation. In contrast, in both half-tori methods the regressions are - except for the *N. lyelli* A-generation - significant (Fig. 3).

Comparing the curved regression lines of each single taxon in both half-tori methods, the differences in the multiplicative constant *a* are significant for all investigated species and generations, whereas they are insignificant in the power constant *b* (Tab. 5). This indicates a similar shape (parallelism) of the curved regression lines, but with different reaction intensities to the substrate (water) during settling.

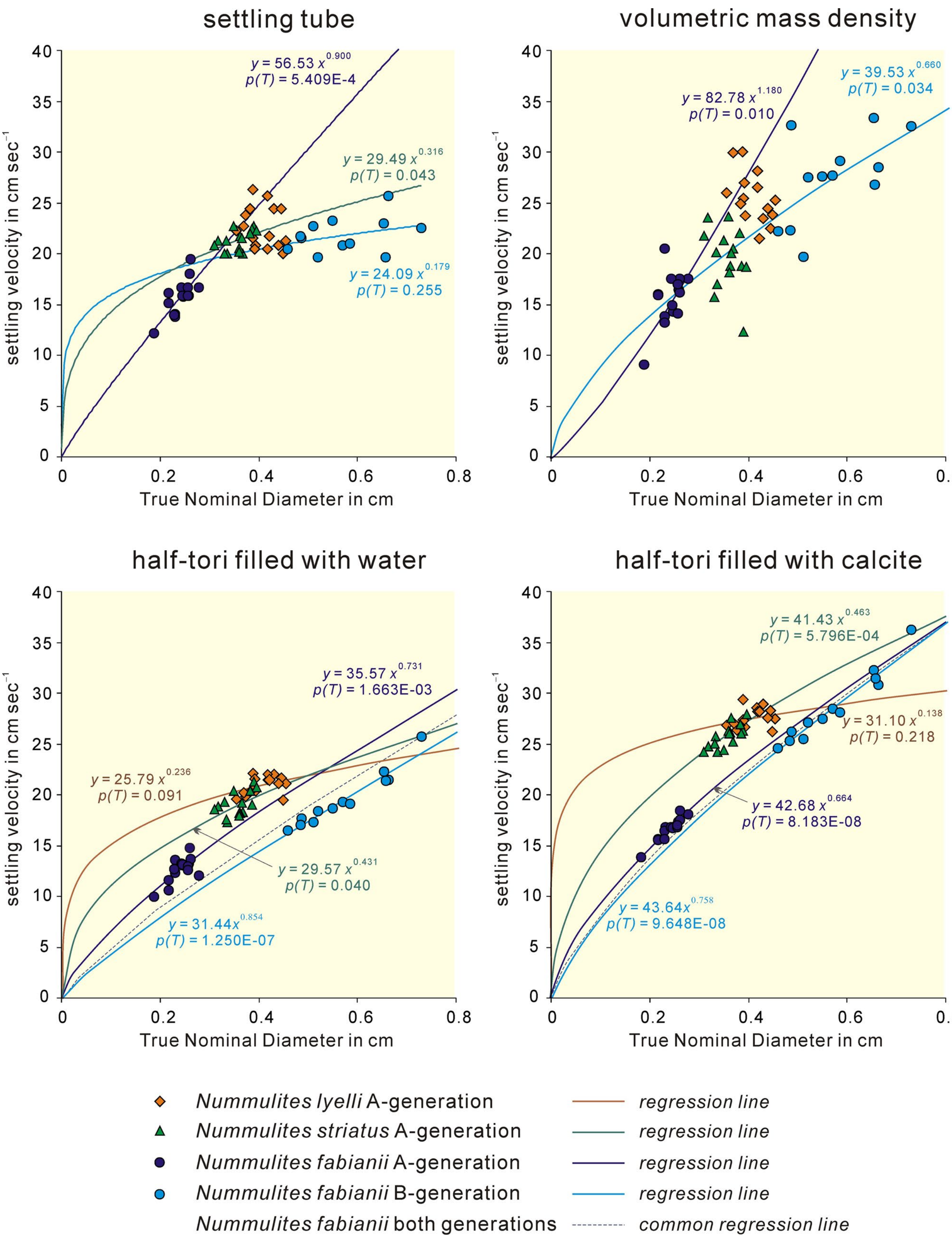

Fig. 3 - Settling velocities obtained through experiments in settling tubes and calculated using densities of theoretical settling functions gained by the volume/weight ratio and the half-tori method (tests theoretically filled with water or calcite). Fit by power regressions; *p(T)* marks the probability accepting the H_0 hypothesis (no correlation).

		experimental		mass/volume		water filled		calcite filled	
	number	mean	standard deviation	mean	standard deviation	mean	standard deviation	mean	standard deviation
***Nummulites lyelli* A**	16	22.544	2.010	26.438	4.467	20.856	0.883	27.488	0.927
***Nummulites striatus* A**	15	21.293	1.001	19.052	3.341	18.960	1.169	25.707	1.156
***Nummulites fabianii* A**	15	15.747	1.771	15.600	2.590	12.580	1.194	16.593	1.111
***Nummulites fabianii* B**	12	21.817	1.731	27.483	4.314	19.492	2.673	28.533	3.431

Tab. 2 - Distribution parameters of settling velocities obtained by experiments (settling tube), volumetric mass densities (mass/volume) and density calculations based on the half-tori methods using chamber volumes filled by water or calcite.

We compared the regression line parameters *a* and *b* of each taxon with the others to check if any species behave similarly to others (Tab. 6). For both parameters, the smallest differences are between the taxa collected in the same outcrops: the A-generations of *N. lyelli* and *N. striatus* are separated by the smallest difference, followed by both generations of *N. fabianii*, whose difference is also very small.

Other comparisons indicate that some forms (shapes) might be more similar to others under specific conditions (e.g., *N. fabianii* A-generation is more similar to the A-generations of *N. lyelli* and *N. striatus* under the water-filled than under the calcite-filled condition).

Interestingly, the differences in the multiplicative constant *a* are in most cases less significant than those of the power constant *b*. This could indicate similar sinking velocities in the investigated taxa, only differentiated due to size differences (Fig. 2). The most highly significant differences are, as expected, between the B-generation of the *N. fabianii* and the A-generations of *N. lyelli* and *N. striatus*. In these cases the multiplicative constant is also significantly different.

DISCUSSION

For a more accurate and realistic interpretation of the data, a brief discussion of the mathematical model used here and its reliability are necessary. The key issue here is the calculation of density and size.

The calculation of density is an easy task if the weight and the volume are known. Both measurements, however, can lead to major misevaluations of density values in hyaline foraminifera. Volume measurements can be made by mercury immersion (Jorry et al., 2006) because mercury is a not wetting liquid and it does not fill the pores (if open). This technique can yield very good data if microporosity (which can be very high in hyaline foraminifera possessing extended canal systems as all nummulitids) quantification is not requested and if well-preserved (i.e., unbroken) tests are used. However, mercury immersion data from fossil tests (where breakage or mechanical stress might have affected test shape) might underestimate the original test volume; this volume is pivotal for test reconstructions for hydrodynamic models. Original test volume can therefore be estimated using complex but precise geometrical methods such as computed tomography (Benedetti & Briguglio, 2012; Ferràndez-Cañadell et al., 2014; Kędzierski et al., 2015) or simple equations (e.g., see eq. 1 in Yordanova & Hohenegger, 2007). In this study we used this latter approach, which has already been tested on larger foraminifera (Jorry et al., 2006; Yordanova & Hohenegger, 2007; Briguglio et al., 2011). This approach was verified by comparisons with computed tomography results, providing good results (Briguglio et al., 2013; Briguglio & Hohenegger, 2014). For well-preserved specimens, such as those used in this study, geometric calculations are clearly the easiest, the fastest and probably the most accurate way to determine the volume of geometric shapes.

Concerning weight measurements, recent forms are very easy to handle, but major problems may arise for fossil forms. Weight in fossil tests might be overestimated either due to external particles calcified on the test or to different infilling material (e.g., some compartments might be filled with calcite or pyrite or both). Conversely, underestimates can arise due to incomplete tests, e.g., if the test is affected by breakage and microboring, which is sometimes hard to detect from the outer appearance. These problems can lead to density estimations that poorly represent original test density. Such problems are visible in some of the present data on the smallest specimens of *N. lyelli* and the largest of *N. striatus*: they deviate strongly from the expected results, possibly due to weight anomalies (Fig. 3). Density estimations can also be problematic in those forms in which test shape is not symmetrical, which the geometric calculation assumes. All these factors might have affected the calculations based on volumetric mass density: it showed the broadest range of variability, a negative correlation between size and settling velocity, and the weakest correlation with the other data.

Furthermore, the large size spectrum covered by the A and B forms investigated here might lead to additional misevaluation in the dataset. The observed settling velocity for larger specimens (i.e., B forms) might be partially underestimated because a much longer settling distance (or time) is needed to reach the maximum settling velocity. This problem might explain the lower settling velocity of the B-generation of *N. fabianii* in the settling tube in comparison to the other values obtained by calculation (as reported in Tab. 2). Similarly, the data obtained for the two calculations water- and calcite-filled showed good correlations because the mathematical approach used is consistent for all taxa and merely the densities are modified; the correlations are therefore always significant (Tab. 3).

Concerning size, the mathematic calculation requires specific modification of some additive (or multiplicative)

***Nummulites lyelli* A**

		experimental	mass/volume	water filled
mean difference	mass/volume	**-3.894**		
p(T)		*0.002*		
correlation		0.422		
p(T)		*0.104*		
mean difference	water filled	**1.688**	**5.581**	
p(T)		*0.002*	*0.000*	
correlation		0.398	-0.246	
p(T)		*0.127*	*0.357*	
mean difference	calcite filled	**-4.944**	-1.050	**-6.631**
p(T)		*0.000*	*0.388*	*0.000*
correlation		0.468	-0.179	**0.905**
p(T)		*0.068*	*0.507*	*0.000*

***Nummulites striatus* A**

		experimental	mass/volume	water filled
mean difference	mass/volume	**1.856**		
p(T)		*0.047*		
correlation		-0.084		
p(T)		*0.767*		
mean difference	water filled	**2.333**	0.513	
p(T)		*0.000*	*0.576*	
correlation		**0.729**	-0.258	
p(T)		*0.002*	*0.353*	
mean difference	calcite filled	**-4.413**	**-6.233**	**-6.747**
p(T)		*0.000*	*0.000*	*0.000*
correlation		0.389	-0.079	0.412
p(T)		*0.152*	*0.781*	*0.127*

***Nummulites fabianii* A**

		experimental	mass/volume	water filled
mean difference	mass/volume	0.147		
p(T)		*0.803*		
correlation		**0.528**		
p(T)		*0.043*		
mean difference	water filled	**3.167**	**3.020**	
p(T)		*0.000*	*0.000*	
correlation		**0.557**	0.397	
p(T)		*0.031*	*0.134*	
mean difference	calcite filled	**-0.847**	-0.993	**-4.013**
p(T)		*0.014*	*0.074*	*0.000*
correlation		**0.761**	**0.691**	**0.771**
p(T)		*0.001*	*0.004*	*0.001*

***Nummulites fabianii* B**

		experimental	mass/volume	water filled
mean difference	mass/volume	***-5.667***		
p(T)		*0.001*		
correlation		0.175		
p(T)		*0.587*		
mean difference	water filled	**2.325**	**7.992**	
p(T)		*0.012*	*0.000*	
correlation		0.322	**0.660**	
p(T)		*0.308*	*0.020*	
mean difference	calcite filled	**-6.717**	-1.050	**-9.042**
p(T)		*0.000*	*0.288*	*0.000*
correlation		0.288	**0.668**	**0.998**
p(T)		*0.365*	*0.018*	*0.000*

Tab. 3 - Differences between experimental and theoretical settling velocities tested by paired *T*-tests; interdependence tested by correlation; *p(T)* marks the probability of accepting the H_0 hypothesis (no differences, no correlation); bold numbers indicate significant difference or correlation.

constants to achieve reliable results. For larger specimens, whose parameter D_d (representing the size of a sphere possessing the same volume as the investigated test) is higher than 134.9, different equations must be used (Le Roux, 1997; Jorry et al., 2006). All these methodological difficulties should not inhibit researchers from attempting theoretical approaches; on the contrary these are the only verified methods to compare taxa on a shape-independent basis. Accordingly, even if the absolute value of each single velocity might not be accurate, its comparison with the values obtained on different taxa can provide interesting hidden information.

The obtained data and their statistical analyses enable us to discuss a number of issues which are essential to interpret the nummulite banks as autochthonous or allochthonous.

The first analysis, regarding the quality of the data collected, (Tab. 2) is fundamental to check which data are worth for further discussion and which are not. Accordingly, the settling velocity data obtained by using the so called mass/volume calculation shows very high standard deviation values, which reach 20% of the mean values. There are a number of factors which lead to this consequence and they will be thoroughly discussed later in this work but mainly connected to fossilization processes which commonly alter the data for this kind of analyses.

The results displayed in Tab. 3, where the comparison among different settling velocities is reported, confirm the mass/volume calculation is not reliable. For this kind of analysis, good comparisons between two settling velocity data should be given by mean differences ~0, both *p(T)* < 0.04 and always positive correlations with high values. The negative correlations of mass/volume data and their low significance point to their irrelevance for the current analysis. On the contrary, positive correlations coupled with very low *p(T)* point to good comparisons between the different methods used. Due to the mathematical calculation used, there are good correlations between the half tori methods although the mean differences are high because of the different densities used. Good correlations

***Nummulites lyelli* A - *Nummulites striatus* A**

	experimental	water filled	calcite filled
mean difference	**1.251**	**1.896**	**1.781**
df	*22.314*	*29*	*29*
p(T)	*0.037*	*0.000*	*0.000*

***Nummulites lyelli* A - *Nummulites fabianii* A**

	experimental	water filled	calcite filled
mean difference	**6.797**	**8.276**	**10.894**
df	*29*	*29*	*29*
p(T)	*0.000*	*0.000*	*0.000*

***Nummulites lyelli* A - *Nummulites fabianii* B**

	experimental	water filled	calcite filled
mean difference	0.727	1.365	-1.046
df	*26*	*12.812*	*12.812*
p(T)	*0.325*	*0.113*	*0.324*

***Nummulites striatus* A - *Nummulites fabianii* A**

	experimental	water filled	calcite filled
mean difference	**5.647**	**6.380**	**9.113**
df	*28*	*28*	*28*
p(T)	*0.000*	*0.000*	*0.000*

***Nummulites striatus* A - *Nummulites fabianii* B**

	experimental	water filled	calcite filled
mean difference	-0.423	-0.532	**-2.827**
df	*25*	*14.356*	*13.005*
p(T)	*0.334*	*0.531*	*0.017*

***Nummulites fabianii* A - *Nummulites fabianii* B**

	experimental	water filled	calcite filled
mean difference	**-6.070**	**-6.912**	**-11.940**
df	*25*	*14.502*	*12.851*
p(T)	*0.000*	*0.000*	*0.000*

Tab. 4 - Differences in settling velocities between species and generations checked by *T*-tests. Integers in degrees of freedoms (*df*) mark *T*-tests based on equal variances, while fraction numbers mark unequal variances; *p(T)* indicates the probability of accepting the H_0 hypotheses (no differences); bold numbers indicate significant difference.

are visible for *N. striatus* experimental vs. water filled, *N. fabianii* A experimental vs. both calcite and water filled.

The results listed in Tab. 4 show that the settling velocities of the A-generations of *N. lyelli* and *N. striatus* are very similar. This similarity confirms that they possessed similar hydrodynamic behaviour and might have lived under the same hydrodynamic scenario. Therefore, differential transport or reworking can be excluded. These results were somewhat expected because both species are present and abundant in the same outcrop and therefore must have had a comparable depositional environment. Additional sedimentological observations, such as the presence of abundant fine-grained sediment (clay) together with the large nummulite tests, suggest the preservation of an autochthonous assemblage (Papazzoni, 2008). The observation of some imbricated tests, considered by Aigner (1983) as one of the evidences of transport, can indeed be the necessary consequence of the densely packed large B tests, possibly transported for short distances because they are at hydrodynamic near-equilibrium conditions. In the banks here studied no clear bedding planes and/or tractive structures were observed.

Even if we speculate a mass transport, which could be also consistent with the hydrodynamic data, we are required to assume the original assemblage had the same characters we can observe now.

Due to the limited outcrop exposure, it was not possible to determine whether the nummulite banks had or not a positive relief in comparison to the neighbouring stratification.

These results are also very surprising because these two species are characterized by very different external

***Nummulites lyelli* A**

	constant *a*	constant *b*
water filled	**25.790**	0.236
calcite filled	**31.104**	0.138
p(T)	*0.000*	*0.577*

***Nummulites striatus* A**

	constant *a*	constant *b*
water filled	**29.567**	0.431
calcite filled	**41.425**	0.463
p(T)	*0.000*	*0.890*

***Nummulites fabianii* A**

	constant *a*	constant *b*
water filled	**35.569**	0.731
calcite filled	**42.675**	0.664
p(T)	*0.000*	*0.741*

***Nummulites fabianii* B**

	constant *a*	constant *b*
water filled	**31.442**	0.854
calcite filled	**43.638**	0.758
p(T)	*0.000*	*0.300*

Tab. 5 - Comparison of multiplicative and power constants in power regressions of chamber volumes theoretically filled by water or calcite; probability of H_0 hypothesis (insignificant differences) checked by *T*- test; bold numbers indicate significant difference.

water filled

		***N. striatus* A**	***N. fabianii* A**	***N. fabianii* B**
multiplicative constant *a*	***N. lyelli* A**	**0.0297**	**0.0032**	**0.0003**
power constant *b*		0.4136	0.0554	**2.068E-09**
multiplicative constant *a*	***N. striatus* A**		0.3014	**0.0385**
power constant *b*			0.0079	**2.056E-07**
multiplicative constant *a*	***N. fabianii* A**			0.5380
power constant *b*				**0.0043**

calcite filled

		***N. striatus* A**	***N. fabianii* A**	***N. fabianii* B**
multiplicative constant *a*	***N. lyelli* A**	**0.0830**	**0.0003**	**6.440E-05**
power constant *b*		0.0449	**9.503E-07**	**1.162E-05**
multiplicative constant *a*	***N. striatus* A**		0.1078	**0.0242**
power constant *b*			**1.139E-08**	**9.638E-08**
multiplicative constant *a*	***N. fabianii* A**			0.3018
power constant *b*				**0.0393**

Tab. 6 - Probabilities *p(T)* of H_0 hypothesis (insignificant differences; checked by *T*- test) comparing multiplicative and power constants in power regressions (Tab. 5) between species and generations with chambers filled either by water or calcite; bold numbers indicate significant difference.

and internal morphologies, which would normally lead to different settling velocity data. As evident in Fig. 2, they differ in longest diameter, proloculus size, thickness of the marginal cord, and lumen extensions within their alar prolongation (sensu Hottinger, 2006). Such differences apparently compensate themselves, yielding similar settling velocities. The A-generation of *N. striatus* is smaller (therefore slower-sinking) but thicker, and the whorls are densely packed (therefore faster-sinking), while the A-generation of *N. lyelli* is larger (therefore faster-sinking) but thinner and with much larger internal empty volume (therefore slower-sinking). The D/T ratio of these two taxa is only slightly different (2.14 mm for *N. lyelli*, 2.04 mm for *N. striatus*). Accordingly, not only might morphologically similar tests have lived in similar environments, but also quite different shapes might still be perfectly adapted to the same hydrodynamic scenario. The relation of sinking velocity to size as expressed in power regressions can also explain the similar mean sinking velocities of *N. lyelli* and *N. striatus* A-generations (Fig. 2). The form of the regression line is strongly curved in *N. lyelli* as expressed in weaker power constants *b* compared to *N. striatus* (0.236 versus 0.431 in water-filled tests and 0.138 versus 0.463 in calcite-filled tests). The extremely large proloculus of *N. lyelli* (Fig. 3) and its broad alar prolongations can largely affect the settling velocity and explain this weak increase in sinking velocity with size, while the small proloculus and the tight alar prolongation in *N. striatus* (Fig. 3) lead to a stronger increase in sinking velocity with size. The size ranges of both species overlap exactly at the intersection of both regression lines (Fig. 3), explaining the similar sinking velocities despite different shape.

The comparisons of the multiplicative and the power constants (Tab. 5) provide further interesting results. The large B forms of *N. fabianii* show regression line parameters that are, surprisingly, quite similar with those of the regression line of the A-generation (Fig. 3). This result is very important: it confirms that both generations with similar morphology but large size differences follow similar (water-filled) or the same (calcite-filled) regression lines (see common regression lines in Fig. 3). The much smaller A-generations can be more easily entrained than the large B-generations. When the generations appear together, then the sinking velocity of the A-generation is indicative in determining the hydrodynamic parameters during settling conditions.

A further insight is possible by comparing the settling velocity to the energetic scenario where the tests lived (i.e., the bottom orbital velocity sensu Briguglio & Hohenegger, 2011). Taking into consideration such velocity relations, the living environment for *N. fabianii* (both A- and B-generations) is less energetic than for the A-generations of *N. lyelli* and *N. striatus*. According to Briguglio & Hohenegger's (2011) estimate, where the settling velocity is compared with the orbital bottom velocity (which is depth dependent), possible depth estimations for *N. fabianii* (both A- and B-generations) are between 40 to 60 m. For the A forms of *N. lyelli* and *N. striatus* the values range between 30 to 50 m.

CONCLUSIONS

There is a good agreement between the sinking velocities obtained experimentally using a settling tube and the mathematical results obtained by studying the axial sections of the tests to calculate their density (Fig. 2). Moreover, the calculated settling velocities confirm that the equations proposed by Allen (1984) and Le Roux (1996) give good results on the settling velocities of fossil tests, as Jorry et al. (2006) firstly pointed out. Eventually, this mathematical approach will enable calculating the settling velocities for fossil nummulitids even without the settling tube, which might have some limitations for very large specimens. The results from the half-tori methods seem quite reliable to determine the fossil densities and the hydrodynamic behaviour of nummulitids much better than by measuring test density by the volume-to-weight ratio.

The most important result of this study is that, at least in nummulitids, species that have different shapes and different internal structures could still have exhibited similar hydrodynamic behaviour during their life. This has been stated also by Jorry et al. (2006), but the authors did not compare different species and did not examine homogeneous samples. Here we can point out that species with similar hydrodynamic properties most probably lived together in the same palaeoenvironment.

The diameter-to-thickness ratio can be a good approximation to discriminate "hydrodynamically" similar forms, even if it is to some extent linked to the light intensity.

The comparison of settling velocities for the A and B forms of the same species (*N. fabianii* in this case) is particularly important. On the one hand, it confirms the two generations could live together in equilibrium with environmental water energy, reinforcing the arguments for the autochthonous origin of nummulite banks. On the other hand, it is reasonable to assume that the B forms could be also adapted to slightly higher water motion (i.e., shallower palaeoenvironment). This could explain the positive relief of the nummulite banks: the A forms colonized the sea bottom and stacked vertically, approaching the upper limit of their equilibrium zone. At this stage, the B forms developed over them, giving shelter to the A tests in the large spaces among B tests. This could explain the unusual proportion of B tests as being due to a hydrodynamic advantage.

It is worth mentioning what Racey (2001, p. 92) observed: "The lower part of the nummulite banks are dominated by A forms, while erosional bedding contacts and B form "lags" are more common in the upper parts". This is exactly expected when the rapid accumulation brings the tests to reach shallower depths and increasing hydrodynamic energy, until equilibrium is no more possible and erosion becomes preponderant.

The results from our analyses support the hypothesis of nummulite banks as being autochthonous deposits, as Arni (1965) suggested. In fact, according to Aigner (1985) interpretation, the original life environment could not allow the contemporary presence of A and B forms of the same species. Instead, our observations support the co-occurrence of the two generations. Therefore, the first two of his four categories (parautochthonous and relatively enriched in B) are probably representing two autochthonous facies, the second one being the nummulite bank. The remaining categories (residual and allochthonous) could instead account for the transported tests, given this phenomenon for sure occurred.

Imbricate structures could be regarded as consistent with an energetic palaeoenvironment, close to the upper limit of equilibrium. Here, some tests could be occasionally entrained for very short distances, orienting the tests in hydrodynamically convenient positions.

Higher settling velocities calculated for the tests of the A-generation of *N. lyelli* and *N. striatus* versus *N. fabianii* also suggest that the *Nummulites* species in Pederiva bank possibly lived in a more energetic environment than those in San Germano bank. As noted above, we were unable to perform the settling tube measurements on the B forms of *N. lyelli* and *N. striatus* because they bumped against the walls and because the settling tube was not large enough to give reliable results. Further investigations are still required from different nummulite banks and from more B forms collected from different localities to improve the methods and the values obtained.

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REFERENCES

Aigner T. (1982). Event stratification in nummulite accumulations and shell beds from the Eocene of Egypt. *In* Einsele G. & Seilacher A. (eds), Cyclic and Event stratification. Springer, Berlin Heidelberg NewYork: 248-262.

Aigner T. (1983). Facies and origin of nummulitic buildups: an example from the Giza Pyramids Plateau (Middle Eocene, Egypt). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 166: 347-368.

Aigner T. (1985). Biofabrics as dynamic indicators in nummulite accumulations. *Journal of Sedimentary Petrology*, 55: 131-134.

Allen J.R.L. (1984). Experiments on the settling, overturning and entrainment of bivalve shells and related models. *Sedimentology*, 31: 227-250.

Allen J.R.L. (1994). Fundamental properties of fluids and their relation to sediment transport processes. *In* Pye L. (ed.), Sediment Transport and Depositional Processes, Blackwell Scientific Publications, Oxford: 25-60.

Anketell J.M. & Mriheel I.Y. (2000). Depositional environment and diagenesis of the Eocene Jdeir Formation, Gabes-Tripoli Basin, Western Offshore, Libya. *Journal of Petroleum Geology*, 23: 425-447.

Archiac A. d' (1837). Mémoire sur la formation crétacée du Sud-Ouest de la France. *Mémoires de la Société géologique de France*, 2: 157-192.

Archiac A. d' (1852). Nummulites. *In* Bellardi L. (ed.), Catalogue raisonné des fossiles nummulitiques du Comté de Nice, *Mémoires de la Société géologique de France*, 4: 205-300.

Archiac A. d' & Haime J. (1853). Description des animaux fossiles du groupe Nummulitique de l'Inde. Précédée d'un resume géologique et d'une monographie des Nummulites. 373 pp. Gide & Baudry, Paris.

Arni P. (1965). L'évolution des Nummulitinae en tant que facteur de modification des dépots littoraux. *Mémoirs du Bureau de Recherches Géologiques et Minières*, 32: 7-20.

Baba J. & Komar P.D. (1981). Measurements and analysis of settling velocities of natural quartz sand grains. *Journal of Sedimentary Petrology*, 51: 631-640.

Bassi D., Bianchini G., Mietto P. & Nebelsick J.H. (2008). Southern Alps in Italy: Venetian Pre-Alps. *In* McCann T. (ed.), The Geology of Central Europe. The Geological Society, London: 1087-1092.

Bassi D., Cosovic V., Papazzoni C.A. & Ungaro S. (2001). The Colli Berici. *In* Bassi D. (ed.), Shallow water benthic communities at the Middle-Upper Eocene Boundary. Southern and North-Eastern Italy, Slovenia, Croatia, Hungary. Field trip guidebook of the 5th meeting IGCP 393 IUGS-UNESCO, *Annali dell'Università di Ferrara, Scienze della Terra, Supplemento*: 43-57.

Beavington-Penney S.J. (2004). Analysis of the effects of abrasion on the test of *Palaeonummulites venosus*: Implications for the origin of nummulithoclastic sediments. *Palaios*, 19: 143-155.

Beavington-Penney S.J. & Racey A. (2004). Ecology of extant nummulitids and other larger benthic foraminifera: applications in palaeoenvironmental analysis. *Earth-Science Reviews*, 67: 219-265.

Beavington-Penney S.J., Wright V.P. & Racey A. (2005). Sediment production and dispersal on foraminifera-dominated early Tertiary ramps: the Eocene El Garia Formation, Tunisia. *Sedimentology*, 52: 537-569.

Beavington-Penney S.J., Wright V.P. & Racey A. (2006). The Middle Eocene Seeb Formation of Oman: an investigation of acyclicity, stratigraphic completeness, and accumulation rates in shallow marine carbonate settings. *Journal of Sedimentary Research*, 76: 1137-1161.

Benedetti A. & Briguglio A. (2012). *Risananeiza crassaparies* n. sp. from the Late Chattian of Porto Badisco (southern Apulia). *Bollettino della Società Paleontologica Italiana*, 51: 167-176.

Bosellini A. (1989). Dynamics of Tethyan carbonate platforms. *In* Crevello P.D., James L.W., Sarg J.F.& Read J.F. (eds), Controls on Carbonate Platform and Basin Development. *SEPM Special Publication*. 44: 3-13.

Bosellini A., Carraro F., Corsi M., De Vecchi G.P., Gatto G.O., Malaroda R., Sturani C., Ungaro S. & Zanettin B. (1967). Note illustrative della Carta Geologica d'Italia, Foglio 49 "Verona". *Servizio Geologico d'Italia*, Roma: 1-61.

Boussac J. (1911). Études paléontologiques sur le Nummulitique Alpin. *Mémoires pour servir à l'explication de la Carte géologique détaillée de la France*: 1-437.

Briguglio A. & Hohenegger J. (2009). Nummulitids hydrodynamics: an example using *Nummulites globulus* Leymerie, 1846. *Bollettino della Società Paleontologica Italiana*, 48: 105-111.

Briguglio A. & Hohenegger J. (2011). How to react to shallow water hydrodynamics: The larger benthic foraminifera solution. *Marine Micropaleontology*, 81: 63-76.

Briguglio A. & Hohenegger J. (2014). Growth oscillation in benthic foraminifera. *Paleobiology*, 40: 494-509.

Briguglio A., Hohenegger J. & Less G. (2013). Paleobiological applications of three-dimensional biometry on larger foraminifera: a new route of discoveries. *Journal of Foraminiferal Research*, 43: 72-87.

Briguglio A., Metscher B. & Hohenegger J. (2011). Growth rate biometric quantification by x-ray microtomography on larger benthic foraminifera: three-dimensional measurements push nummulitids into the fourth dimension. *Turkish Journal of Earth Sciences*, 20: 683-699.

Bruguière J.G. (1792). Histoire naturelle des Vers. *In* Encyclopédie méthodique. Vol. 1 (2): 345-757.

Cita M.B. (1969). Le Paléocène et l'Eocène de l'Italie du Nord. *Mémoirs du Bureau de Recherches Géologiques et Minières*, 69: 417-429.

Davaud E. & Septfontaine M. (1995). Post-mortem onshore transportation of epiphytic foraminifera: recent example from the Tunisian coastline. *Journal of Sedimentary Research,* 65: 136-142.

Fabiani R. (1905). Studio geo-paleontologico dei Colli Berici. *Atti del Regio Istituto Veneto di Scienze, Lettere ed Arti,* 64: 1797-1839.

Fabiani R. (1915). Il Paleogene del Veneto. *Memorie dell'Istituto Geologico della Regia Università di Padova*, 3: 1-336.

Ferràndez-Cañadell C., Briguglio A., Hohenegger J. & Wöger J. (2014). Test fusion in adult foraminifera: a review with new observations of an Early Eocene *Nummulites* specimen. *Journal of Foraminiferal Research*, 44: 316-324.

Fütterer E. (1978). Untersuchungen über Sink- und Transportgeschwindigkeit biogener Hartteile. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 155: 318-359.

Hallock P. (1979). Trends in test shape with depth in large, symbiont-bearing foraminifera. *Journal of Foraminiferal Research*, 9: 61-69.

Hallock P. (1981). Light dependence in *Amphistegina*. *Journal of Foraminiferal Research*, 11: 42-48.

Hallock P. & Hansen H.J. (1979). Depth adaptation in *Amphistegina*: change in lamellar thickness. *Geological Society of Denmark, Bulletin*, 27: 99-104.

Harpe P. de la (1878). Note sur les Nummulites des Alpes occidentales. *Actes de la Société Helvétique des Sciences Naturelles*, 60: 227-232.

Harpe P. de la (1883). Étude des Nummulites de la Suisse et révision des espèces éocènes des genres *Nummulites* et *Assilina* -3ème et dernière partie. *Schweizerische Paläontologische Abhandlungen*, 10: 141-180.

Herb R. & Hekel H. (1975). Nummuliten aus dem Obereocaen von Possagno. *Schweizerische Paläontologische Abhandlungen*, 97: 113-135.

Hohenegger J. & Briguglio A. (2012). Axially oriented sections of nummulitids: a tool to interpret larger benthic foraminiferal deposits. *Journal of Foraminiferal Research*, 42: 134-142.

Hohenegger J. & Yordanova E. (2001a). Displacement of larger foraminifera at the western slope of Motobu peninsula (Okinawa, Japan). *Palaios*, 16: 53-72.

Hohenegger J. & Yordanova E. (2001b). Depth-transport functions and erosion-deposition diagrams as indicators of slope inclination and time-averaged traction forces: applications in tropical reef environments. *Sedimentology*, 48:1025-1046.

Hottinger L. (2006). Illustrated glossary of terms used in foraminiferal research. *Carnets de écologie/ Notebooks on Geology-Memoir* 2006/02 (CG2006-M02). 126 pp.

Hughes T.P. (1999). Off-reef transport of coral fragments at Lizard Island, Australia. *Marine Geology*, 157: 1-6.

Jorry S.J., Hasler C.A. & Davaud E. (2006). Hydrodynamic behaviour of *Nummulites*: implications for depositional models. *Facies*, 52: 221-235.

Kędzierski M., Uchman A., Sawlowicz Z. & Briguglio A. (2015). Fossilized bioelectric wire – the trace fossil *Trichichnus*. *Biogeosciences*, 12: 1-9.

Komar P.D. (1981). The applicability of the Gibbs equation for the grain settling velocities to conditions other than quartz grains in water. *Journal of Sedimentary Petrology*, 51: 1125-1132.

Komar P.D. & Cui B. (1984). The analysis of grain-size measurements by sieving and settling-tube techniques. *Journal of Sedimentary Petrology*, 54: 603-614.

Larsen A.R. (1976). Studies of recent *Amphistegina*: taxonomy and some ecological aspects. *Israel Journal of Earth Sciences*, 25: 1-26.

Larsen A.R. & Drooger C.W. (1977). Relative thickness of the test in *Amphistegina* species from the Gulf of Elat. *Utrecht Micropaleontological Bulletins*, 15: 225-239.

Le Roux J.P. (1996). Settling velocity of ellipsoidal grains as related to shape entropy. *Sedimentary Geology*, 101: 15-20.

Le Roux J.P. (1997). An Excel program for computing the dynamic properties of particles in Newtonian fluids. *Computers & Geosciences*, 23: 671-675.

Li C., Jones B. & William B.C. (1998). Carbonate sediment transport pathways based on foraminifera: case study from Frank Sound, Grand Cayman, British West Indies. *Sedimentology*, 45: 109-120.

Loucks R.G., Moody R.T.J., Bellis J.K. & Brown A.A. (1998). Regional depositional setting and pore network systems of the El Garia Formation (Metlaoui Group, Lower Eocene), offshore Tunisia. *In* MacGregor D.S., Moody R.T.J. & Clark-Lowes D.D. (eds), Petroleum Geology of North Africa, *Geological Society, London, Special Publication*, 132: 355-374.

Martin R.E. & Liddell W.D. (1991). Taphonomy of foraminifera in modern carbonate environments. *In* Donovan S.K. (ed.), The processes of fossilization, Belhaven Press, London: 170-193.
Mateu-Vicens G., Hallock P. & Brandano M. (2009). Test shape variability of *Amphistegina* d'Orbigny 1826 as a paleobathymetric proxy: application to two Miocene examples. *In* Demchuk T. & Gary A. (eds), Geologic problems solving with microfossils, *SEPM Special Publication* 93: 67-82.
Mateu-Vicens G., Pomar L. & Ferràndez Cañadell C. (2012). Nummulitic banks in the upper Lutetian "Buil level", Ainsa Basin, South Central Pyrenean Zone: the impact of internal waves. *Sedimentology*, 59: 527-552.
Mietto P., Sedea R. & Ungaro S. (1981). Note illustrative del Foglio 50 "Padova". *In* Castellarin A. (ed.), Carta tettonica delle Alpi Meridionali (1:200.000). Servizio Geologico d'Italia, Roma: 99-103.
Nebelsick J.H., Rasser M.W. & Bassi D. (2005). Facies dynamics in Eocene to Oligocene circumalpine carbonates. *Facies*, 51: 197-216.
Papazzoni C.A. (1994). Macroforaminifera and paleoenvironments near the Middle-Upper Eocene boundary in the Mossano section (Berici Mts., Vicenza, northern Italy). *In* Matteucci R., Carboni M.G. & Pignatti J.S. (eds), Studies on Ecology and Paleoecology of Benthic Communities. *Bollettino della Società Paleontologica Italiana*, Vol. Spec. 2: 203-212.
Papazzoni C.A. (2008). Preliminary palaeontological observations on some examples of "nummulite banks": sedimentary or biological origin? *In* Ciarapica G., Masetti D., Nardon S. & Ronchi P. (eds), 3° Meeting Annuale del Gruppo Italiano Carbonati (San Donato Milanese, 28-30 Aprile 2008). *Rendiconti online della Società Geologica Italiana*, 2: 135-138.
Papazzoni C.A. & Sirotti A. (1995). Nummulite biostratigraphy at the Middle/Upper Eocene boundary in the northern Mediterranean area. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 63-80.
Paphitis D., Collins M.B., Nash L.A. & Wallbridge S. (2002). Settling velocities and entrainment thresholds of biogenic sands (shell fragments) under unidirectional flow. *Sedimentology*, 49: 211-225.
Racey A. (2001). A review of Eocene Nummulite accumulations: structure, formation and reservoir potential. *Journal of Petroleum Geology*, 24: 79-100.
Renema W. (2005). Depth estimation using diameter-thickness ratios in larger benthic foraminifera. *Lethaia*, 38: 137-141.
Roveda V. (1961). Contributo allo studio di alcuni macroforaminiferi di Priabona. *Rivista Italiana di Paleontologia*, 67: 153-224.
Schlotheim E.F. von (1820). Die Petrefactenkunde. LXXII + 437 pp. Becker, Gotha.
Schweighauser J. (1953). Mikropaläontologische und stratigraphische Untersuchungen im Paleocaen und Eocaen des Vicentin (Norditalien) mit besonderer Berücksichtigung der Discocyclinen und Asterocyclinen. *Schweizerische Paläontologische Abhandlungen*, 70: 1-97.
Serra-Kiel J., Hottinger L., Caus E., Drobne K., Ferràndez C., Jauhri A.K., Less G., Pavlovec R., Pignatti J., Samsó J.M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998). Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société géologique de France*, 169: 281-299.
Soulsby R.L. (1983). The bottom boundary layer of shelf seas. *In* Johns B. (ed.), Physical Oceanography of Coastal and Shelf Seas, Elsevier, Amsterdam: 189-266.
Suess E. (1868). Ueber die Gliederung des Vicentinischen Tertiärgebirges. *Sitzungsberichte der K. Akademie der Wissenschaften, mathematisch-naturwissenschafliche Classe*, 58: 265- 279.
Swei G.H. & Tucker M.E. (2012). Impact of diagenesis on reservoir quality in ramp carbonates: Gialo Formation (Middle Eocene), Sirt Basin, Libya. *Journal of Petroleum Geology*, 35: 25-48.
Ungaro S. (1969). Étude micropaléontologique et stratigraphique de l'Éocène supérieur (Priabonien) de Mossano (Colli Berici). *Mémoires du Bureau de Recherches Géologiques et Minières*, 69: 267-280.
Wadell H. (1932). Volume, shape, and roundness of rock particles. *Journal of Geology*, 40: 443-451.
Wielandt U. (1999). Early progressive evolutionary features in *Nummulites luterbacheri* from the Western Desert of Egypt. *Journal of Foraminiferal Research*, 29: 130-142.
Yordanova E.K. & Hohenegger J. (2002). Taphonomy of larger foraminifera: Relationships between living individuals and empty tests on flat reef slopes (Sesoko Island, Japan). *Facies*, 46: 169-203.
Yordanova E.K. & Hohenegger J. (2007). Studies on settling, traction and entrainment of larger benthic foraminiferal tests: implications for accumulation in shallow marine sediments. *Sedimentology*, 54: 1273-1306.
Zampieri D. (1995). Tertiary extension in the southern Trento Platform, Southern Alps, Italy. *Tectonics*, 14: 645-657.

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