

# Selective mineral composition, functional test morphology and paleoecology of the agglutinated foraminiferal genus *Colominella* Popescu, 1998 in the Mediterranean Pliocene (Liguria, Italy)

NICOLETTA MANCIN<sup>1</sup>✉, ELENA BASSO<sup>2</sup>, CAMILLA PIRINI<sup>3</sup> and MICHAEL A. KAMINSKI<sup>4,5</sup>

<sup>1</sup>Earth and Environment Sciences, University of Pavia, via Ferrata 1, 27100 Pavia, Italy; ✉nicoletta.mancin@unipv.it

<sup>2</sup>Arvedi Laboratory-CISRIc, University of Pavia, via Ferrata 1, 27100 Pavia, Italy

<sup>3</sup>via Europa 28, 20097 San Donato (MI), Italy

<sup>4</sup>Earth Sciences Department, Research Group of Reservoir Characterization, King Fahd University of Petroleum & Minerals, P.O. Box 701 KFUPM, 31261 Dhahran, Saudi Arabia

<sup>5</sup>Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, U.K.

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**Abstract:** Specimens of *Colominella* (agglutinated Foraminifera) from a Pliocene Mediterranean succession were analysed through a scanning electron microscope (SEM) equipped with an energy-dispersive X-ray spectrometer (EDX) to document their test microstructure. *Colominella* develops a complex large test with a mostly biserial chamber arrangement, but with the internal chamber lumens partitioned by vertical and horizontal plates that form a labyrinthine structure of alveoles. This internal partition occurs from the first chambers but is completely masked from the outside by the thick wall. The test-wall microstructure is characterized by canaliculi (parapores) that are externally covered by a pavement of agglutinated grains. The mineralogical characterization of the agglutinated grains and the secreted cement shows that the grains are strongly selected as regards to size, arrangement and composition, with the coarse grains placed close to the outer wall. Moreover, these coarse grains, forming a pavement, are made of monocrystalline quartz, whereas the inner part of the skeleton is mostly composed of dolomite. The carbonate cement is less abundant and appears as cloudy light grey areas among the detrital grains. These shell features can be interpreted as functional adaptations to perform kleptoplastidy and/or to house functional photosymbionts, probably induced by stable environmental conditions as in warm shallow waters characterized by low nutrient flux.

**Key words:** Mediterranean Pliocene, photosymbiont, SEM-EDX analysis, grain selectivity, functional morphology, shell architecture, agglutinated Foraminifera.

## Introduction

Over the past two decades, a number of studies have emphasized the importance of wall structure and cement composition as important criteria for agglutinated foraminiferal taxonomy, leading to recognition of four principal orders: Textulariida, Astrorhiziida, Lituoliida and Loftusiida (e.g. Desai & Banner 1987; Loeblich & Tappan 1987, 1989; Brönnimann & Whittaker 1990; Hottinger et al. 1990; Banner et al. 1991; Bertram & Cowen 1998; Kaminski 2004a and references therein; Bartholdy et al. 2005). Currently, however, there is less agreement regarding the taxonomic level at which wall microstructure and cement composition ought to be used (e.g. Mikhalevich 2004), even though modern researchers do agree that modern microstructural and compositional studies on agglutinating tests can be used for future taxonomic and paleo-environmental studies.

The genus *Colominella* Popescu, 1998 was first described from the Paratethyan Middle Miocene (Badenian) Kostej (Costei) succession, outcropping in Transylvania (Popescu et al. 1998; Kaminski 2004b), and is based on a species first described by Cushman (1936) from the same locality (type spe-

cies *Textulariella paalzowi*). The same species was subsequently reported from the Miocene (Badenian) of the Rauchstallbrunngraben, Vienna Basin (Popescu et al. 1998). The type species is characterized by a very large, elongated, mostly biserial test, with the inner part subdivided by secondary septa forming a typical labyrinthine structure and by its canaliculate test wall. *Colominella* likely evolved from the genus *Matanzia* (which is also canaliculate) during the Oligocene to Middle Miocene (Kaminski & Cetean 2011). *Colominella* and *Matanzia* have recently been placed in the subfamily Colominellinae Popescu, 1998 together with other two additional closely-related genera: *Colomita* Gonzales-Donoso, 1968 and *Cubanina* Palmer, 1936 (Kaminski & Cetean 2011).

In spite of this recent systematic review, not much is known about the test wall microstructure of *Colominella* as regards the arrangement and chemical-mineralogical composition of the agglutinated grains and the occurrence of other functional adaptive morphologies probably selected from the environment in which it lived. This work aims to provide new insights into *Colominella*'s test features and to better clarify the relationship between such a complex test structure and its mode of life. Moreover we report for the first time the occurrence of

*Colominella* in a Pliocene succession of the Mediterranean area, thereby extending the known stratigraphical and geographical range of the genus. Direct comparisons with the type species from the Badenian of Transylvania were beyond the scope of this study, therefore, we only tentatively assign the Mediterranean specimens to the species *C. paalzowi* (Cushman) 1936.

### Rationale and methods

The studied section, about 20 m thick, crops out along the Torsero rivulet in the easternmost portion of the Albenga Basin (western Liguria) (Fig. 1). This Pliocene Mediterranean outcrop has been well known since the end of the 19<sup>th</sup> century because of its rich mollusc faunas (mainly gastropods) as documented by several papers (e.g. Bernasconi & Robba 1984, 1994; Solsona 1999; Solsona & Martinell 1999; Andri et al. 2005 and references therein; Harzhauser & Kronenberg 2008). At its base, the Pliocene succession is composed of Lower

Pliocene light grey silty marls belonging to the upper part of the “Argille di Ortovero” Formation (MPL3 foraminiferal Biozone of the biostratigraphic scheme of Sprovieri 1992), overlain by Middle–Lower Pliocene coarse-grained biogenic sands, sandstones and conglomerates of the Monte Villa Formation (MPL4 Zone) (Violanti 1987). Analyses of both mollusc and foraminiferal associations clarified the depositional environment of the Argille di Ortovero, which was probably represented by the deeper portion of the circalittoral zone, close to the shelf edge (Violanti 1987; Bernasconi & Robba 1994). The Pliocene succession rests transgressively on a Mesozoic substratum belonging to the Monte Galero Formation, a monogenic breccia mostly formed by dolostones and dolomitic limestones (Fig. 1).

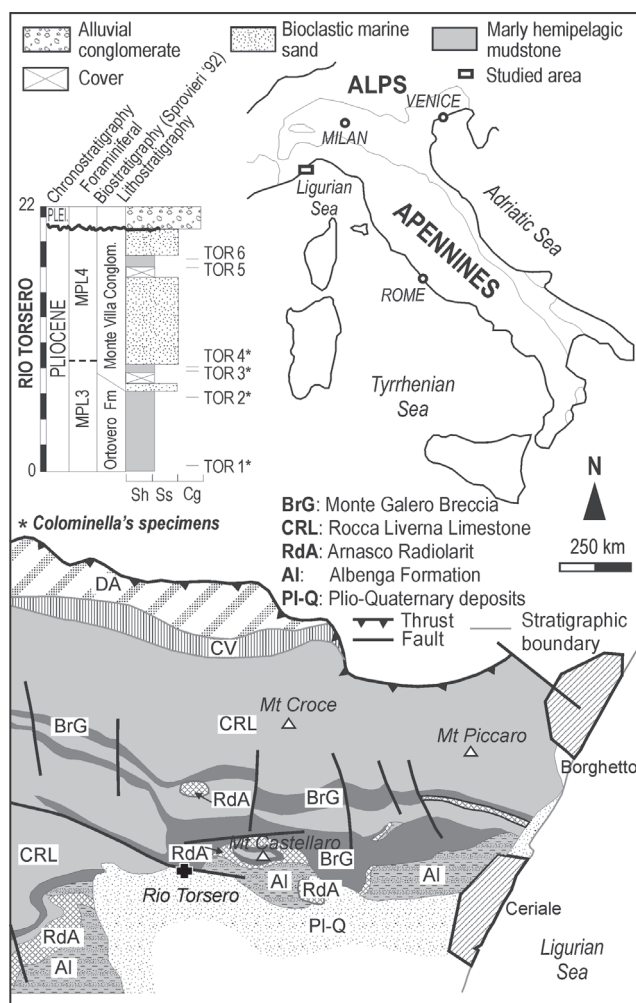
For the investigation of foraminiferal assemblages, standard analytical techniques were used. Six sediment samples, gathered from the marly portions of the succession (Fig. 1), were washed through sieves with mesh sizes of 425, 180 and 63  $\mu\text{m}$ , respectively. The residue retained on each sieve was analysed quantitatively under a stereo-microscope by counting ca. 300 specimens from each fraction, as done in the study by van Hinsbergen et al. (2005). About 50 individuals (also including fragments) of *Colominella* from the >425 and 425–180  $\mu\text{m}$  fractions were isolated and prepared for scanning electron microscope (SEM) observations.

In order to assess the internal morphological and compositional features, SEM analyses were performed on the isolated individuals that had been first embedded in epoxy resin. Resin mountings were cut in order to obtain a longitudinal section of the individual. The exposed test surfaces were mechanically ground with silicon carbide papers and polished with diamond pastes at 6, 3, 1 and 0.25  $\mu\text{m}$ , in order to obtain a smooth surface. Samples were then mounted on aluminium stubs using carbon tapes and carbon-coated, using a Cressington 208HR splutterer. Analyses were performed using a Tescan FE-SEM, series Mira 3XMU, equipped with an EDAX energy dispersive spectrometer. Spot microanalyses for standardless elemental composition were performed at 15 mm working distance, using an accelerating voltage of 20 kV, with counts of 100 s per analysis. X-ray mapping (stage mapping) for Silicon, Magnesium, and Calcium was also done on representative portions of each individual. EDX elemental maps were acquired at 20 kV, using a matrix of 256 $\times$ 200 with a DWELL TIME of 200 ms, 16 frames, 1 ADC and 3 ROIs. The EDX measurements were processed with the EDAX Genesis software. For each specimen, SEM-EDX analyses were focussed on:

- 1) documenting the internal morphological features of the chambers;
- 2) measuring the shell thickness and the grain distribution;
- 3) emphasizing the presence of canaliculi penetrating the test walls;
- 4) detecting the chemical composition of the grains and the cement.

Paleoenvironmental interpretations were based on the characteristics of foraminiferal assemblage composition recorded in the Rio Torsero succession as proposed by Murray (2006) and Jorissen et al. (2007). The utilized proxy methods were:

- a) proxies of paleobathymetry: the ratio of planktonic to benthic foraminiferal tests  $\{P = (P/P + B)\}$  as in van Hinsbergen



**Fig. 1.** Location and stratigraphic log of the Pliocene Rio Torsero section cropping out in the Albenga Basin (western Liguria). A geological sketch map of the Albenga Basin, with the Mesozoic substratum mostly formed by carbonate formations, is also reported (redrawn and simplified by Dallagiovanna & Seno 1986).

**Table 1:** Synthesis of the bathymetric distribution and of the ecological and environmental preferences of some benthic foraminifera observed in the modern Mediterranean Sea and used in this work as paleoenvironmental proxies (Jorissen et al. 1992, 1995, 2007; de Stigter et al. 1998; de Rijk et al. 1999; Schmiedl et al. 2000; Donnici & Serandrei Barbero 2002; Murray 2006). The paleobathymetric subdivision follows van Morkhoven et al. (1986).

BENTHIC TAXA	WATER DEPTH (ranges in m)							LIFE MODES		FOOD SUPPLY	OXYGEN CONTENT	SUBSTRATE	OTHER
	CONTINENTAL SHELF			CONTINENTAL SLOPE			ABYS.	Infaunal	Epifaunal				
	NERITIC		BATHYAL	ABYSSAL		PLAIN							
	0-50	50-100	100-200	200-600	600-1000	1000-2000	2000-4000						
<i>Ammonia beccarii</i>	X								X			muddy to sandy	
<i>Anomalinooides helacinus</i>		X	X						X				similar to <i>C. incrassatus</i>
<i>Asterigerinata planorbis</i>	X								X (fixed epiphytic)		high	sandy	similar to <i>A. mamilla</i> and <i>A. adriatica</i>
<i>Bolivina apenninica, B. cistina</i>		X	X	X	X			intermediate to deep		usually high with also refractory organic matter	can tolerate low oxygen content	muddy	typical of sapropelitic layers
<i>Bulimina costata</i> gr.					X	X		shallow		usually high	can tolerate low oxygen content	muddy	typical of sapropelitic layers
<i>B. exilis</i>					X	X		shallow		high (mostly fresh labile organic matter)		muddy	
<i>Cassidulina neocarinata</i>		X	X					shallow	X	usually high	high	mixed	similar to <i>C. carinata</i> . It can tolerate intermediate to slightly dysoxic conditions. Typical of strong bottom currents
<i>Cibicides pseudoungerianus</i>				X					X	low	high	sandy and elevated, with strong and persistent near-bottom currents	similar to <i>C. pachyderma</i>
<i>C. ungerianus</i>				X	X				X	low	high	sandy and elevated, with strong and persistent near-bottom currents	Intolerant to low oxygen condition
<i>C. wuellerstorfi</i>						X	X	shallow	X	low (mostly pulsed)	high	elevated	high-energy environments
<i>Cibicides lobatulus</i>	X								X (mainly fixed epiphytic)		high	coarse-grained and elevated, with strong and persistent near-bottom currents	
<i>C. refulgens</i>	X								X (mainly fixed epiphytic)		high	vegetated substrata with high sediment content ( <i>Posidonia</i> rhizomes)	
<i>Elphidium</i> spp.	X								X (free epiphytic)	low	high	sandy, mainly vegetated	
<i>Florilus boueanum</i>	X							shallow				muddy to sandy	
<i>Globocassidulina subglobosa</i>					X	X	X	facultative	X	low	high	sandy and elevated, with strong and persistent near-bottom currents	mainly cold bottom-water
<i>Gyroidinoides soldanii</i>				X	X	X				high			
<i>Heterolepa bellincionii</i>			X	X					X				similar to <i>C. dutemplei</i>
<i>H. floridana</i>		X	X	X					X				similar to <i>C. matanzasensis</i>
<i>Lenticulina</i> spp.					X	X		shallow	X	low	high	muddy	
<i>Melonis affinis</i>			X	X	X			shallow		high			
<i>M. soldanii</i>			X	X	X			shallow					
large <i>Quinqueloculina</i> with <i>costae</i> ( <i>Q. mediterraneis</i> )	X								X (mostly free epiphytic)		high	sandy vegetated	Intolerant to oxygen stress
<i>Neoponoides schreibersi</i>				X					X				similar to <i>N. campester</i>
<i>Oridorsalis umbonatus</i>						X	X	X	X	quite low, also pulsed fluxes	high		corrosive cold deep waters
<i>Planulina ariminensis</i>			X	X	X				X			elevated	max. abundance 300-500 m
<i>Praeglobobulimina</i> spp.			X	X				deep		high (refractory organic matter)	low		
<i>Pullenia bulloides</i>					X	X	X	intermediate		intermediate	low	muddy	
<i>Reussella</i> spp.			X	X	X			shallow					
<i>Rosalina globularis</i>	X								X (free epiphytic)		high	sandy, mainly vegetated	
<i>Sigmoilopsis schlumbergeri</i>		X	X	X	X	X							
<i>Siphonina reticulata</i>					X								similar to <i>S. pozonensis</i>
<i>Sphaeroidina bulloides</i>					X	X		shallow			high		Intolerant to oxygen stress
<i>Textularia</i> spp.	X	X	X	X				shallow				sandy	
<i>Trifarina</i> spp.					X	X		shallow				coarse-grained	<i>T. angulosa</i> occurs on the shelf
<i>Uvigerina peregrina</i>			X	X	X			shallow		high (mostly fresh labile organic matter)	rather high, but can tolerate low oxygen conditions	muddy	



et al. (2005), completed by the relative abundances of water-depth benthic indexes;

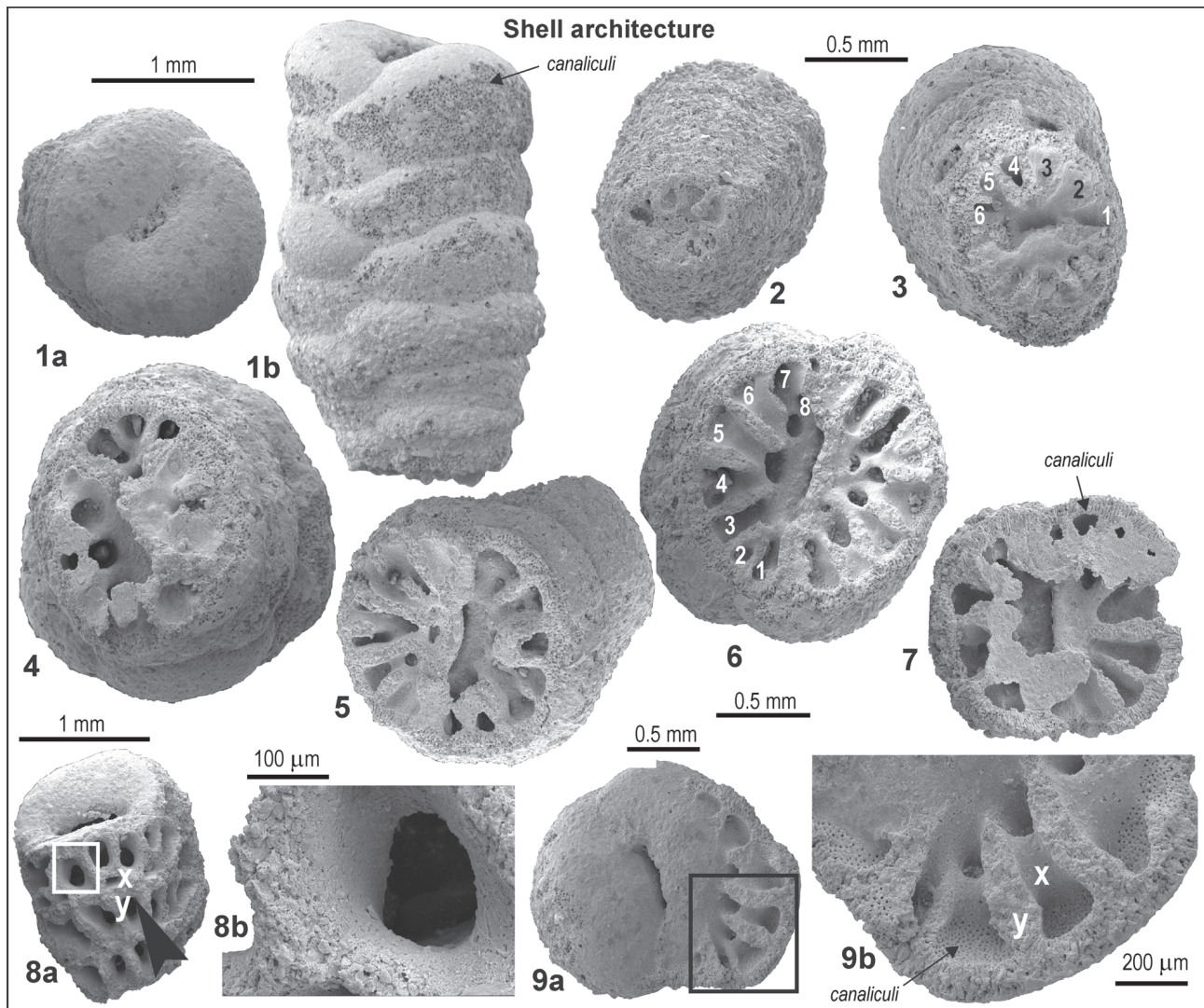
b) proxies of food availability to the sea floor: Epifaunal/ Infaunal ratio (E/I) and relative abundance of deep and shallow infaunal taxa;

c) proxies of substrate: relative abundance of benthic species indicative of the sediment type (muddy, sandy, mixed), hard and vegetated surface (epifaunal and phytal taxa) integrated by lithology and facies variations throughout the succession.

A synthesis of the ecological and environmental preferences of some benthic foraminifera observed in the Mediterranean Sea and used in this work as paleoenvironmental proxies (Jorissen et al. 1992, 1995, 2007; de Stigter et al.

1998; de Rijk et al. 1999; Schmiedl et al. 2000; Donnici & Serandrei Barbero 2002; Murray 2006) are reported in Table 1. The preservation, transport and reworking of benthic foraminiferal tests in a mostly terrigenous succession were also carefully evaluated in order to improve the ecological interpretation.

Benthic foraminiferal taxonomic identifications were mainly based on the Agip S.p.a.'s Atlas (1982), supplemented by the works of Cimerman & Langer (1991) and Hottinger et al. (1993). The benthic foraminiferal terminology used in this work follows the glossary reported in Hottinger et al. (1993). Foraminiferal species abundances are reported in Table 2a,b (available in the data repository).



**Fig. 2.** Details of the test architecture of *Colominella* Popescu, 1998. **1** — Specimen of *Colominella* from the Rio Torsero section, sample TOR1; magnification  $\times 36$ ; a — apertural face, b — longitudinal view. Note that the internal chamber subdivision into alcoves and the presence of canaliculi are masked from the outside. Here they are made partly visible by the erosion of the external surface. **2–7** — Details of the internal partition in alcoves. They are present from the first whorl (2–4) to the last chamber (7); magnification  $\times 50$ . Note that the number of the alcoves formed by the interposition of vertical plates increases with test growth. **8** — Details of the alcove structure, sample TOR2; a — alcoves formed by the interposition of horizontal (x) and vertical (y) plates; b — enlargement of “a” showing an alcove with its typical ovoidal shape. **9** — a — alcoves with trapezoidal shapes, sample TOR1; b — enlargement of “a”: note that also in this case alcoves are formed by the interposition of two orthogonal plates (x and y, respectively).

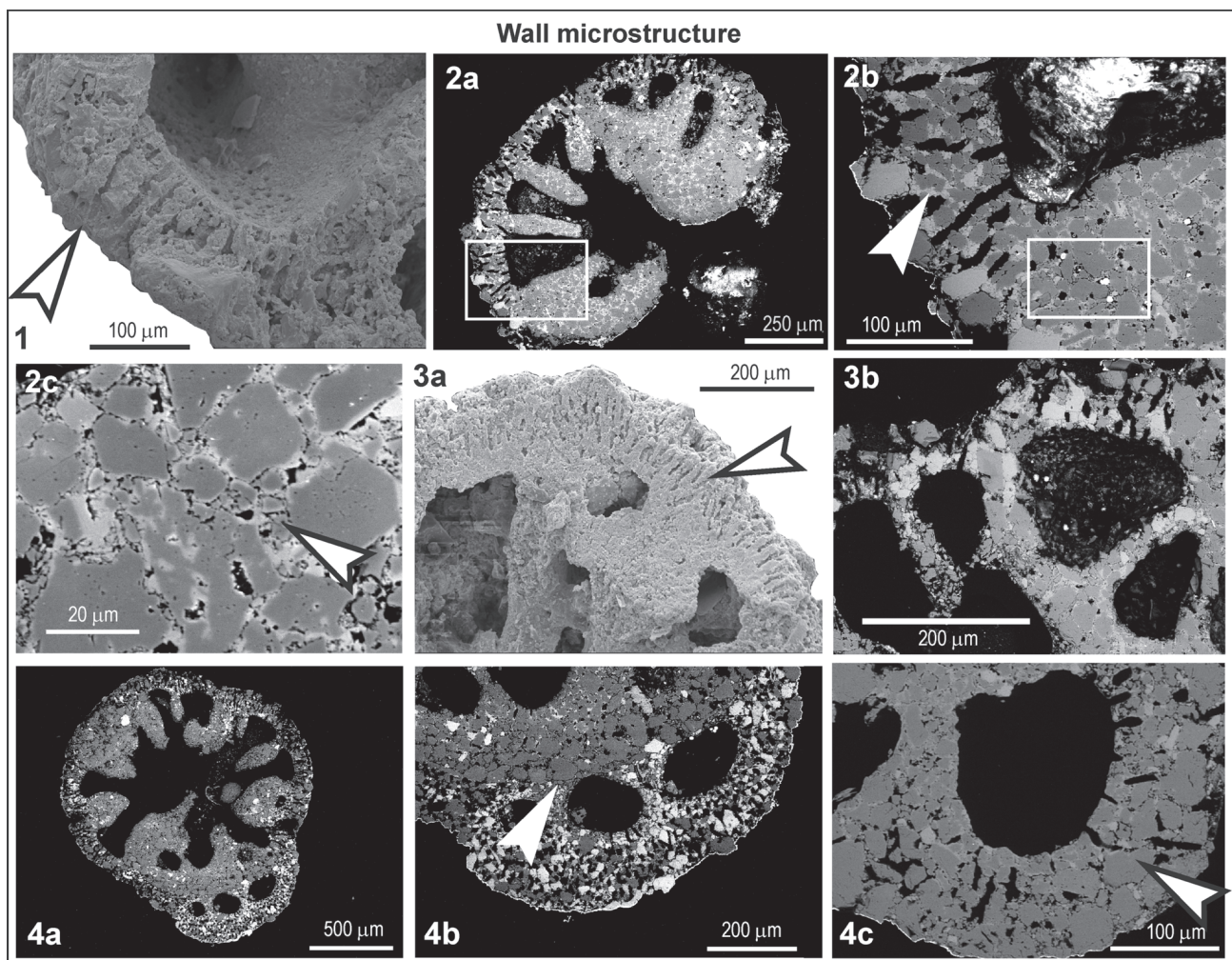


## Results

### Shell architecture

The studied *Colominella* has a quite large, elongate to fusiform, free test, usually characterized by a circular outline in equatorial section; the average test dimensions span from 2.5 to 3 mm in length and 1.4 to 1.8 mm in width. The test shows a mostly biserial chamber arrangement, reported as triserial in the early stage. The aperture face is formed by the penultimate and ultimate chamber; the aperture is an internal marginal slit at the base of the last chamber (Fig. 2.1a–b).

Chambers are partitioned into alcoves, which occur from the beginning of the shell and continue to the last stage, making a typical internal labyrinthine structure (Fig. 2.2–7). Alcoves, ovoidal or trapezoidal, are formed by the interposition of vertical (y) and horizontal (x) plates (Fig. 2.8–9). In the early stages of the test, alcoves are mostly constituted by the interposition of vertical plates that form 5 to 6 “chamberlets”, whereas the interposition of horizontal plates, which increases the compartmentalization of chambers, occurs later during test construction (Fig. 2.2,3,5). Nevertheless, the number of alcoves formed by the interposition of vertical plates increases throughout the test, reaching the number of 7 to 8 for each



**Fig. 3.** Detail of the wall microstructure in *Colominella*. Note that the test wall is crossed by canaliculi with the agglutinated grains selected in size and distribution. **1** — Detail of the test wall crossed by canaliculi; note that they are externally covered by a pavement, sample TOR2. **2** — a — Equatorial section of a specimen of *Colominella* (SEM-BSE image, sample TOR2) showing the typical internal subdivision into alcoves. Note that canaliculi are limited to the upper portion of alcoves towards the external surface and are missing on the secondary septa. b — Enlargement of “a”: note that the wall is crossed by canaliculi that are externally covered by a pavement; note also that the larger grains are arranged close to the external edge forming the pavement. c — Detail of “b” showing the wall microstructure formed by coarse-grained particles that are embedded by numerous small detrital granules, cemented by calcite that appears as cloudy grey areas among the grains. **3** — Detail of the wall crossed by canaliculi in a specimen of *Colominella* sample TOR3. a — Note that canaliculi are mostly straight and radial internally but become branching in the outer portion of the wall. b — Transverse section of *Colominella* (SEM-BSE image) showing the grain arrangement and the occurrence of canaliculi. **4** — a — Equatorial section of a specimen of *Colominella* (SEM-BSE image, sample TOR3). b–c — Details of “a” showing the grains selected in size and disposition with the largest ones located near the external margin while the smallest grains are in the inside. Also in this case canaliculi mostly occur towards the external margin of the alcove.

chamber in the last growing stages (Fig. 2.5,6). All these features are masked from the outside by the rough test surface.

### Wall microstructure

The test wall is crossed by canaliculi (“parapores” of Hottinger et al. 1990, 1993) whose presence, just below the surface, is revealed only in broken tests or where the wall has been partly abraded (e.g. Fig. 2.1b,7; Fig. 3.1,3a). Canaliculi are straight and radial in the inner portion of the wall but become branching in the outer part (Fig. 3.1,2b,3a). Moreover, they are present mostly in the upper portion of alcoves towards the external margin and are missing on the secondary septa (Fig. 2.9b; Fig. 3.1,2a–b). Canaliculi do not open onto the outer wall surface, because this surface is covered by an external pavement of agglutinated grains (Fig. 3.2b,3b,4c); however, their open entrances are clearly visible in the inner surface (Fig. 3.1).

The agglutinated grains are strongly selected in terms of size and distribution. The largest ones (about 30–50 µm in diameter) are arranged close to the external surface forming a pavement, while the smallest grains are set in the inner part of the wall (Fig. 3.2b,4b–c). Moreover, the coarse-grained particles are embedded in an aggregate of very small detrital granules, 3 to 5 µm in size, cemented by a calcite cement that appears as cloudy light grey areas among the detrital grains (Fig. 3.2c). The grain selectivity seems to persist through the whole test.

### Chemical-mineralogical characterization

The agglutinated grains are strongly selected not only in terms of size and distribution, but also on the basis of their mineralogical composition (Fig. 4). The external particles are mainly composed of quartz grains (Qz), whereas the internal ones are made of dolomite (Dol) and a minor amount of calcite (Cc), as indicated by the EDX spectra (Fig. 4a,b,f). In rare individuals the last chamber is almost totally formed by calcite grains (Fig. 4g,h). All the granules are sub-angular to angular in shape, and the size of quartz and carbonate grains do not exceed 30 and 50 µm, respectively.

Elemental maps of some major elements were obtained from a representative portion of the test, in order to observe their distribution from the outer to inner part of the wall. Silicon (Si) and Magnesium (Mg) maps, the discriminating elements of quartz and dolomite respectively, provide further evidence for the placement of different mineral grains in different parts of the test wall. It clearly appears that Si is concentrated only in the external portion of the shell, forming a thin pavement that covers the canaliculi (Fig. 4d,l). On the other hand, Mg is concentrated towards the inner part of the wall (Fig. 4e,m). These features are stable during test growth, occurring from the beginning of the shell to the last chamber.

### Characteristics of foraminiferal assemblage composition

Foraminiferal assemblages are abundant, diverse, and well preserved. They occur together with frequent remains of molluscs, echinoids, bryozoans, ostracods, fish teeth and otoliths. Toward the top of the studied section in the coarse-grained

Monte Villa Conglomerate, crushed and abraded specimens increase in number. Foraminiferal associations are very similar in the first three samples (TOR1 to TOR3, Fig. 1) where they are strongly dominated by benthic taxa; the plankton percentages range from 10 to 15 % (Fig. 5a). Toward the top of the section (samples TOR4 to TOR6) planktonic foraminifera slightly increase in abundance reaching values of ca. 25–30 %. *Globigerinoides* (*G. obliquus*, *G. trilobus*, *G. sacculifer*, *G. gomitolus*) is the most common planktonic genus with average percentages of ca. 50 % in the planktonic assemblages, followed by *Globigerina* (particularly *G. decoraperta* and *G. bulloides*) and by the species *Orbulina universa* and *Globorotalia puncticulata* (Fig. 5i, Table 2a).

Benthic assemblages are mostly composed of calcareous taxa, while agglutinated species usually do not exceed 10–15 % (Fig. 5h, Table 2b); the latter slightly decrease in abundance from bottom to top. The most frequent agglutinated species are: *Lagenammina* sp., *Textularia pseudorugosa*, *Dorothia gibbosa* and *Spiroplectammina wrighti*. *Colominella* is present in very low abundances in samples TOR1 to TOR4, with a maximum abundance in sample TOR3 (Table 2b). Calcareous benthic foraminifera are particularly abundant and well diversified throughout the entire succession, with over 80 species recognized (Table 2b). In particular, phytal and epifaunal taxa (Fig. 5f–g) strongly dominated the benthic assemblages recording an Epifaunal/Infaunal ratio always >2, with peaks of 4 and 6 in sample TOR3, respectively for the 425–180 and >425 µm fractions (Fig. 5c). Shallow infaunal species (particularly *Melonis*) are frequent (Fig. 5e), while deep-infaunal taxa (mostly *Bolivina* and *Brizalina* genera) usually do not exceed 12 % throughout the succession (Fig. 5d). The most abundant benthic specimens belong to the shallow-water genera *Ammonia* (*A. beccarii* and *A. inflata*), *Elphidium* (*E. crispum*, *E. macellum*), large *Quinqueloculina* with an ornamentation composed by longitudinal costae (*Q. mediterraneensis* and *Q. vulgaris* and less abundant *Q. colomi*, *Q. lamarkiana*, *Q. disparilis*) and to the species *Cibicides lobatulus*, *Cibicides refulgens*, *Asterigerinata planorbis* and *Neoeponides screibersi* (Fig. 5l–q, Table 2b). Other important components of the benthic assemblage are: *Lenticulina* (mostly *L. calcar*), *Heterolepa bellincionii*, *Melonis affinis* and *Melonis soldanii*. Deep-water species (indicative of water depths deeper than 200–400 m; Table 1), such as *Cibicoides pseudoungerianus*, *Gyroidinoides neosoldanii*, *Oridorsalis umbonatus* and *Trifarina* spp., also occur but in very low abundances (e.g. < 10 %); they slightly increase in abundance toward the top of the section (Fig. 5b).

## Discussion

The genus *Colominella* developed an agglutinated test that is structurally and compositionally very complex. This prompts the following questions: 1) what is the functional significance of the complex structural and compositional features of the *Colominella* test and 2) what kind of environmental drivers are they associated with?

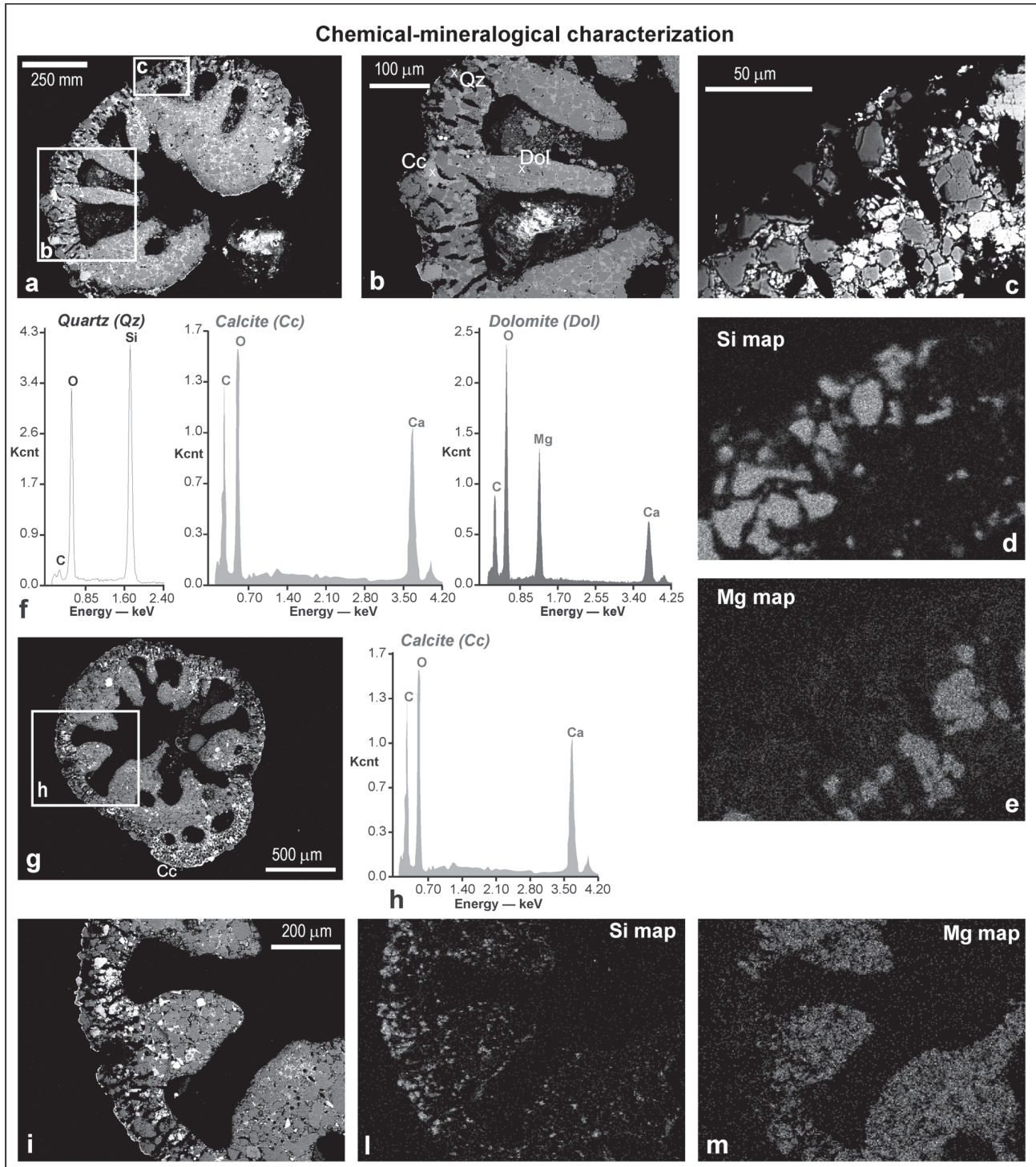
In the following discussion we address these questions even if in some cases further investigations will be needed.



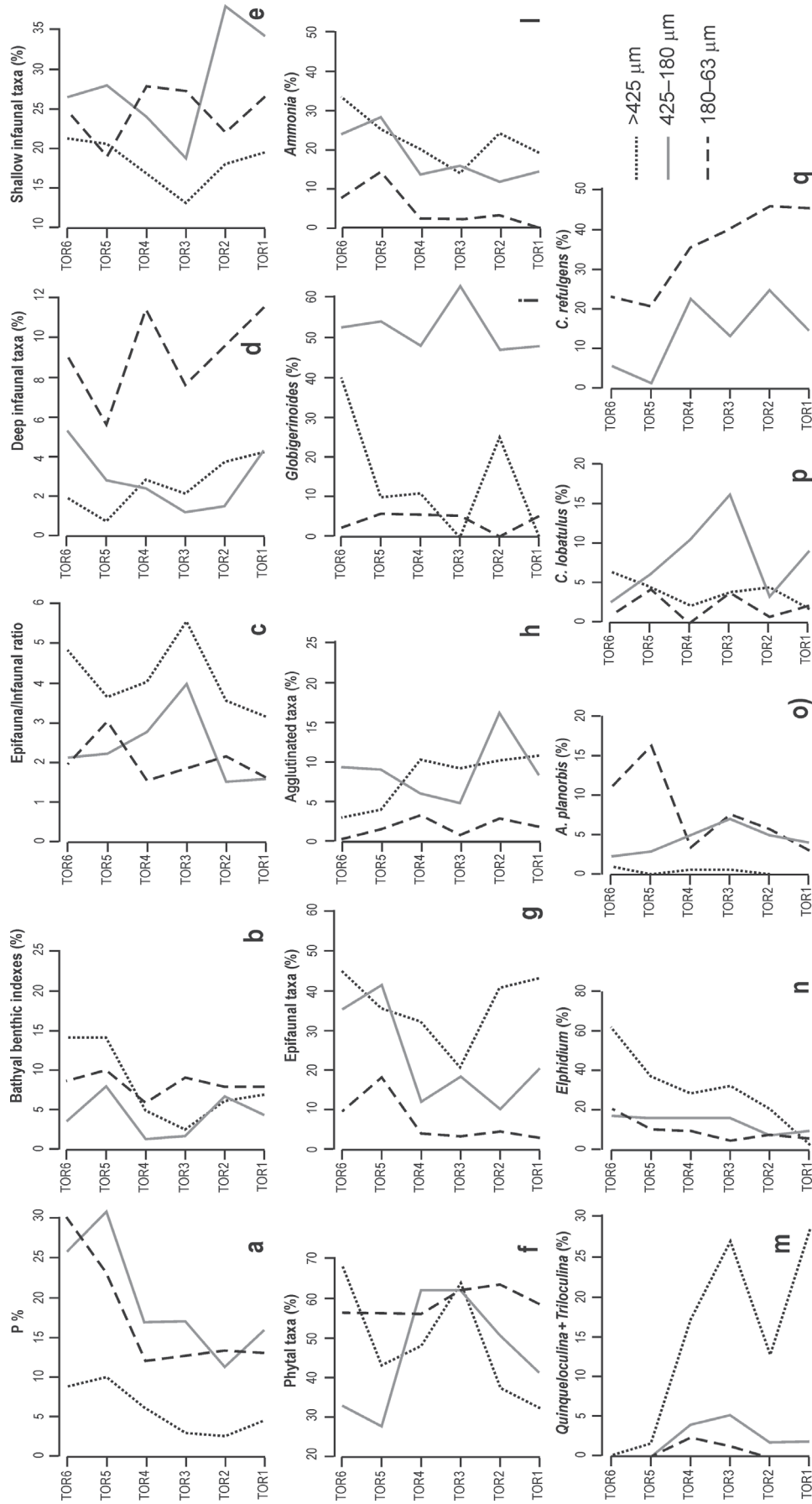
**Functional morphologies**

Most of the morphological features characterizing the test of *Colominella* could be interpreted as a direct expression of

a strong relationship with the environment. These are: the large free test; its aperture face, chambers internally partitioned by secondary septa forming alcoves, the caniculate test wall; the complex wall microstructure with grains selected



**Fig. 4.** SEM images of equatorial sections of *Colominella* and EDX spectra of the agglutinated grains. **a-c** — BSE images at different magnifications; **d-e** — elemental maps showing the distribution of Si and Mg respectively in the portion of the *Colominella* test recorded in image c; **f** — EDX spectra of quartz, calcite and dolomite grains; **g-i** — BSE images of another *Colominella* individual; **h** — EDX spectrum of a calcite grain; **l-m** — elemental maps showing the distribution of Si and Mg respectively in the portion of the *Colominella* test corresponding to image i.



**Fig. 5.** Characteristics of the foraminiferal assemblage composition recorded in the Pliocene Rio Torsero succession. See the text for further explanations.



in terms of size, distribution and composition with an external pavement mostly made of quartz.

The large size of *Colominella* (ca. 3 mm in length and ca. 1.5 mm in width) could represent the first important morphological evidence of its interaction with the life environment. Larger individuals can be considered as distinctive expression of an environmental selection applied for longer times, as in the case of environments characterized by stable ecological conditions and by k-strategist relationships. Hottinger (2000) maintained that the larger an organism, the longer its exposure to the environment during its life time, the more important are the functions guiding permanent morphologies that become necessary for the individual's survival. Moreover its aperture face is characterized by a smoothed surface that is not a plane, but it shows a difference of level between the penultimate and ultimate chamber. We think that *Colominella* could live attached to a substrate by its apertural end extruding its pseudopods from the gap between the substrate and its penultimate chamber (Fig. 2.1a). According to Hottinger (2006) as well, this feature is indicative of an adaptation to a sessile or poorly motile life-style, as documented by the occurrence of this kind of aperture face in some modern textulariids that live attached to firm substrates in the Red Sea.

Another important piece of morphological evidence is the internal chamber subdivision into alcoves (Fig. 2). These spaces within the test are usually utilized to compart the protoplasm producing marginal or lateral "quiet zones" in the protoplasm itself (Hottinger 2000). It is noteworthy that in numerous modern calcareous foraminifera, similar compartments usually host algal photo-symbionts (green-house structures), even though similar structural elements also occur in deep-sea species (e.g. *Cyclammina*) living at too great a depth to host algal symbionts. In the latter case, alcoves and alveoles have been interpreted as functional to better facilitate gas exchange with the exterior (Hottinger et al. 1990; Hottinger 2000). However, in the deep-water species *Cyclammina apenninica*, the test wall is never crossed by canaliculi (Plate 1: fig. 1b in Mancin 2001), on the contrary a caniculate test wall is well developed in the studied specimens of *Colominella* (Fig. 3).

Agglutinated foraminiferal canaliculi (parapores) have been compared with the test-wall pores in hyaline foraminifera probably because they serve the same function (Murray 1994). At present, their function is not so clear, but agglutinated canaliculi and hyaline pores may be functional for enhancing gas exchange, for taking and distributing organic matter inside the test, and/or for accumulating food items in the cytoplasm (Hottinger 2000). In hyaline foraminifera, gas exchange becomes very useful when they enter into endosymbiosis with algal cells; in this case pores are also used to irradiate symbionts by sunlight. For further details on endosymbiosis in foraminifera see Lee et al. (2010 and references therein). Canaliculi could serve for the internal diffusion of nutrients, since modern agglutinated foraminifera lack photo-symbionts and therefore have no requirement for the uptake of carbon dioxide or sunlight irradiation (Hottinger et al. 1990).

The studied specimens of *Colominella* also show a very complex wall microstructure with the agglutinated grains selected in terms of size and mineralogical composition. Mancin (2001) documented in Paleogene deep-sea species of *Vulvulina*

and *Karreriella* a similar grain arrangement and a marked selectivity in grain composition (e.g. albite in *Vulvulina*). However, those deep-sea species did not develop a caniculate test wall, with canaliculi covered by a distinct pavement made of quartz (Plate 3: fig. 3c in Mancin 2001). In *Colominella* the test wall is mostly composed of dolomite and a minor amount of calcite and quartz (Fig. 4). The choice of these minerals could be simply related to their presence and/or abundance in the sea floor. The substratum on which the Pliocene succession deposited is a dolomitic breccia, interbedded with micaeous-quartzitic sandstones (Fig. 1). We believe that the grain selection cannot be merely a matter of chance or related to the mineral availability and abundance. Using large quartz grains to build the external pavement, *Colominella* could improve its test robustness with an increase in protective function, an adaptation that would be very useful in a high energy environment or in an area with heavy predatory pressure. Because quartz is transparent, sunlight would be transmitted across the pavement and *via* canaliculi to irradiate the alcoves, above all in shallow water where the light intensity is higher. Other studies documented preferential grain selection in modern and fossil agglutinated foraminifera and a strong relationship with the environment (e.g. Heron-Allen & Earland 1909; Allen et al. 1998; Tuckwell et al. 1999; Tyszka & Thies 2001; Armynot du Chatelet et al. 2008; Thomsen & Rasmussen 2008; Makled & Langer 2010; Gooday et al. 2010). However, *Colominella* shows a grain selectivity in terms of arrangement within the test wall as well as the choice of particular minerals to build the shell, that appears to be stable during its test growth, supporting the idea of genetic control on grain selection.

In the studied Pliocene specimens of *Colominella*, different functional adaptations co-exist. They are the expression of adaptive responses to persisting environmental selection, as in the case for hosting photo-symbionts, superimposed on a genetic basis. At least one modern agglutinated foraminiferal genus (*Reophax*) is reported to perform chloroplast sequestration, also known as kleptoplastidy (Bernhard & Bowser 1999); that is the ability of heterotrophic organisms to preserve photosynthetically active chloroplasts of algal prey they eat and partially digest (Lee et al. 1988; Stoeker et al. 2009; Pillet et al. 2010). We hypothesize that the Pliocene Mediterranean *Colominella* could have performed kleptoplastidy or engaged in some other kind of photosymbiotic relationship. To check this possibility, the paleoecological parameters that probably affected the benthic foraminiferal distribution in the studied succession and also influenced the test morphology of *Colominella* are discussed below.

#### *Paleoenvironmental limiting factors*

The characteristics of the foraminiferal assemblages previously described (Fig. 5), enable us to gain some insight into the paleoenvironmental conditions in the Rio Torsero area during the Early Pliocene. These are:

1) **Oligotrophic warm surface waters:** these conditions can be hypothesized considering the strong abundance in the planktonic assemblages of the warm-water, surface dwelling *Globigerinoides*, *O. universa*, and *G. puncticulata* (Hemleben et al. 1989, 1991) throughout the entire succession. These

surface conditions seem to persist for the whole studied interval. Warm surface stable conditions are also consistent with literature data that report a warm stable climate for the Early Pliocene Mediterranean, the so called “Pliocene climate optimum”, till about ca. 3.2 Myr (Thunell 1979); a time-span characterized by the development of faunas and floras with subtropical affinities (e.g. Monegatti & Raffi 2001; Triantaphyllou et al. 2009; Marques da Silva et al. 2010; Bertini 2010; Por 2010).

2) **Outer shelf environment:** the strong abundance of free and fixed mostly epiphytal taxa such as large *Quinqueloculina* with longitudinal costae (*Q. mediterraneensis* and *Q. vulgaris*), *E. crispum* and *E. macellum*, *A. planorbis* and the fixed epifaunal species *C. lobatulus* and *C. refulgens* in association with other shallow-water indexes (*A. beccarii* and *A. inflata*) is indicative of upper neritic bathymetries as in the vegetated inner shelf environment (*Posidonia oceanica* seagrass; Table 1). However, the co-occurrence of deep-water species (*Cibicidoides pseudoungerianus*, *Gyroidinoides neosoldanii*, *Lenticulina calcar*, *Oridorsalis umbonatus* and *Planulina ariminensis*), even if with quite low abundances (Fig. 5b), is probably indicative of a deeper bathymetry (lower neritic to uppermost portion of the upper bathyal, ca. 100–300 m), consistent with an outer continental shelf environment. The marked abundance of upper neritic taxa is therefore interpreted as due to their transport from shallower environments. Higher in the studied section an increase of water depth, probably toward the upper slope (below 200–300 m), is hypothesized. An increase in both the P % and the relative abundance of deep-water indexes is recorded in sample TOR4 (Fig. 5a–b). Contemporaneously, a marked decrease or disappearance of some inner-shelf indexes, as *Quinqueloculina* (mostly *Q. mediterraneensis*), *A. planorbis*, *C. lobatulus*, *C. refulgens* and the large-size agglutinated foraminifera (*Textularia ponderosa*, *T. pseudorugosa*, *Dorothia gibbosa*, *Reophax* spp. and *Colominella*), occurred together with an increase of crushed and abraded specimens, above all in those with the largest sizes (Table 2b — available in the data repository). These data indicate a rapid deepening within the upper part of the section (Monte Villa Conglomerate). Similar paleoenvironmental conditions have been previously proposed by Violanti (1987) and Bernasconi & Robba (1994 and references therein) on the basis of both foraminifera and gastropod faunas.

3) **Mainly mesotrophic conditions on the sea floor:** benthic assemblages are characterized by a very high E/I ratio and a low percentage of deep infaunal taxa (Fig. 5c–d). Both these proxies are commonly used as indicative of low food supplies to the sea floor, typical of mesotrophic environments and well-oxygenated conditions (e.g. Murray 2006; Jorissen et al. 2007). This interpretation is supported by the low abundance in the studied samples of opportunistic benthic species, such as buliminids and uvigerinids (Table 2b), that proliferate when abundant organic flux reaches the sea floor (Jorissen et al. 1992, 1995) and also by the absence of typical oligotrophic larger foraminifera (*Amphistegina*). These are common in oligotrophic conditions of coeval shallow-water successions in the Mediterranean area and still persist today in the Aegean Sea and Levantine Basin (Checconi et al. 2007; Mancin et al. 2009; Triantaphyllou et al. 2009).

4) **Substrate with a high terrigenous content, vegetated in the neighbouring inner-shelf portions:** these features are supported by the high occurrence of the species *Quinqueloculina mediterraneensis*, *Elphidium crispum* and *E. macellum* that usually lived in the vegetated zone and, by other shallow-water indexes that preferred muddy to sandy substrates, such as *Ammonia* and textulariids, and by the high percentage of shallow infaunal species, which need soft substrates (Table 1). Towards the top of the section, an increase of terrigenous input could be hypothesized mostly on the basis of facies variations and also by the rapid turnover in foraminiferal assemblages, recording a progressive deepening toward upper slope environments. The overlying deposits belonging to the Monte Villa Conglomerate are characterized by redeposited sediments mostly composed of coarse-grained sediments with abundant bioclastics intercalated with pelitic levels.

#### *The mode of life of Colominella*

The depositional environment reconstructed for the Pliocene Rio Torsero section probably comprised the most external portion of a warm-water continental outer shelf, where downslope currents transported shallow-water detritus (mostly biogenic remains and benthic foraminifera) from the shallower inner portions. The strong abundance of transported sediment with well preserved biogenic remains that are not size-selected implies that the coast line was not far away, indicating a narrow continental shelf similar to the present-day shelf around the Ligurian coast. The innermost shelf was probably vegetated, hosting a large variety of epiphytal taxa, such as in the modern Mediterranean *Posidonia* sea-grass communities (Murray 2006), but also characterized by a high terrigenous content. In the studied assemblages, epifaunal taxa that lived attached or encrusted to firm substrates are quite rare, while free-living epiphytal and shallow infaunal taxa are very abundant.

Nutrient supplies were probably low, typical of an oligo-mesotrophic environment. This ecological parameter, together with the occurrence of substrates with high terrigenous content and the lack of widely extended hard surfaces, probably limited the development of *Amphistegina* assemblages that frequently occurred in open oligotrophic carbonate environments in coeval Mediterranean successions (e.g. Checconi et al. 2007).

We can conclude that *Colominella* was an upper neritic species, living in the vegetated parts of the inner shelf and that it could live attached to macrofaunal remains. It was a minor constituent of the foraminiferal associations that usually develop in environments with stable conditions (Jorissen et al. 1992; Murray 2006; Lee et al. 2010). We also speculate that it could perform kleptoplastidy. Its attached life habitat within the photic zone and association with epiphytal forms in an environment with mostly oligo-mesotrophic conditions to the sea floor further implies that *Colominella* could have housed functional internal symbionts within its chamber alcoves. By analogy with Early Jurassic larger agglutinated foraminifera from Tethyan carbonate platforms which are believed to have harboured photosymbionts (BouDagher-Fadel 2008; p. 204), the alcoves of *Colominella* could have been used for such a pur-

pose. Its transparent quartz outer pavement would have allowed sunlight to be transmitted *via* the canaliculi to irradiate the alveoles, especially in shallow waters with high light intensity.

### Final remarks

Pliocene specimens of *Colominella* develop an agglutinated test that is more complex in comparison to those described by Popescu et al. (1998) from the Middle Miocene of Transylvania. The complexity of the agglutinated test, in terms of both internal shape and wall microstructure and composition, is interpreted as an adaptative response to ecological limiting factors that persisted for a long time, as probably occurred during the warm Early Pliocene interval in the Mediterranean basin. In particular the co-occurrence of different functional morphologies, such as: the large size, the sessile style-life, the compartmentalized shell with a caniculate wall and a transparent test surface, are here interpreted as adaptations to perform kleptoplastidy and/or to harbour symbionts in order to establish k-strategist relationships that usually develop in stable environments such as in shallow warm waters with a scarce food supply.

In many lineages of larger agglutinated foraminifera, the development of complex inner structure is accompanied by a phylogenetic size increase. The supposed ancestor of *Colominella* was *Matanzia*, which was a deep-water form that became larger once it evolved a canaliculated wall structure. The Middle Miocene type species of *Colominella* from Transylvania probably inhabited a deep neritic to upper bathyal environment. If indeed our Pliocene *Colominella* housed kleptoplasts, then this behavior represents a modification of pre-existing structures.

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Table 2: Numerical database reporting the abundances and distributions of the foraminiferal species detected in the Rio Torsero section. a — Planktonic species; b — Benthic species.

180 μm										P % = 100xP/(P+B)	
Planktonics									total count		
SAMPLES											
TOR 6	8	12	41	0	0	13	0	1	3	78	25.7
TOR 5	16	15	53	0	0	10	1	0	3	98	30.7
TOR 4	11	6	24	1	1	5	2	0	0	50	16.7
TOR 3	10	4	32	0	1	3	1	0	0	51	17
TOR 2	12	2	16	1	0	3	0	0	0	34	11.3
TOR 1	7	13	23	0	2	2	0	0	1	48	15.9

63 μm									P % = 100xP/(P+B)	
Planktonics								total count		
SAMPLES										
TOR 6	63	2	0	0	6	5	13	0	89	30
TOR 5	55	4	0	4	4	3	0	0	70	23.1
TOR 4	31	2	1	1	1	1	0	0	36	12
TOR 3	28	2	1	2	1	4	0	0	38	12.6
TOR 2	36	0	0	1	3	0	0	0	40	13.3
TOR 1	29	2	2	1	2	2	1	1	39	13

b

425 μm																								P % = 100xP/(P+B)																																
CALCAREOUS																							Total count																																	
SAMPLES																																																								
TOR 6	26	43	3	1	2	0	13	0	0	0	2	0	123	3	3	1	7	0	0	0	2	23	0	0	6	1	1	0	12	0	0	0	0	199	0	0	2	0	1	1	0	0	2	0	6	205										
TOR 5	31	38	0	0	1	0	12	0	0	0	0	0	79	2	2	1	6	0	0	1	29	1	0	8	0	0	0	9	1	10	0	0	0	0	0	3	0	1	1	259	0	0	7	0	0	1	1	11	270							
TOR 4	2	56	1	1	3	0	6	0	0	0	0	0	97	0	0	1	7	0	0	0	1	9	0	1	4	3	2	1	13	1	5	1	1	48	0	6	0	0	0	0	0	16	4	0	0	1	2	29	282							
TOR 3	2	39	1	1	2	0	11	1	0	0	0	1	88	1	0	2	2	1	0	0	1	4	1	0	2	1	1	2	9	2	2	0	72	0	1	0	2	0	0	4	0	1	257	0	2	3	0	1	4	0	0	12	4	26	283	
TOR 2	4	68	5	0	2	0	13	0	0	0	0	0	57	2	0	2	10	1	0	1	1	9	2	0	7	5	1	2	24	0	4	0	37	0	4	2	0	0	0	0	0	0	0	0	0	2	6	30	293							
TOR 1	2	54	7	0	2	2	5	0	1	2	0	0	4	2	0	0	6	0	1	0	5	13	0	0	6	7	0	1	22	0	15	0	3	70	2	4	3	3	2	0	11	0	0	255	1	3	6	1	8	5	0	4	3	0	31	286

180 μm																								P % = 100xP/(P+B)																													
CALCAREOUS																							Total count																														
SAMPLES																																																					
TOR 6	26	22	0	5	1	3	0	1	0	0	0	4	6	13	2	0	2	3	2	0	4	22	7	12	0	3	1	2	1	15	0	1	0	0	0	0	1	0	0	0	5	0	6	15	0	0	21	225					
TOR 5	30	29	0	6	0	0	1	0	0	0	5	13	3	10	1	0	0	1	0	1	7	24	18	0	0	5	0	0	0	0	8	3	1	0	1	0	1	0	0	0	0	0	3	0	0	0	2	1	194	213			
TOR 4	6	10	0	12	1	3	1	1	3	0	0	5	26	56	0	0	0	0	0	8	5	0	0	0	0	1	0	4	0	1	0	0	0	0	0	7	17	0	3	0	0	0	1	1	1	0	0	0	3	15	249		
TOR 3	0	24	1	17	2	2	0	0	0	0	1	0	40	33	0	0	0	1	13	2	2	8	13	0	0	0	0	4	0	0	0	9	10	0	0	9	10	0	0	1	0	1	3	2	0	0	0	0	8	0	237	249	
TOR 2	1	9	0	13	1	3	0	0	3	0	0	4	23	66	2	0	0	3	6	0	0	0	9	0	4	0	0	6	0	6	0	2	1	0	0	1	0	0	3	2	0	0	0	0	0	2	1	0	0	9	0	224	267
TOR 1	2	17	0	10	6	7	0	0	0	2	0	1	23	37	3	0	0	0	11	1	2	0	9	1	0	0	6	0	7	1	3	0	2	0	0	16	12	0	0	0	0	0	0	0	5	1	1	0	3	2	232	253	

63 μm																								P % = 100xP/(P+B)																								
CALCAREOUS																							Total count																									
SAMPLES																																																
TOR 6	16	1	0	23	0	6	5	0	4	0	0	11	4	2	48	0	7	13	0	2	0	16	0	0	5	11	2	0	2	1	3	1	0	4	0	2	0	1	10	1	0	0	0	0	5	207		
TOR 5	33	1	0	38	0	4	5	0	0	2	0	3	7	9	48	3	6	6	5	0	0	7	0	0	7	6	5	2	0	0	4	1	1	5	0	0	1	0	2	7	1	0	0	4	0	5	228	232
TOR 4	7	0	0	9	0	5	20	0	0	0	5	9	8	3	0	93	0	11	8	0	1	0	5	2	0	2	9	3	1	0	1	0	3	5	0	0	13	10	1	0	2	0	0	6	254	263		
TOR 3	6	1	0	20	1	4	13	1	0	0	0	8	7	9	105	0	0	0	0	0	3	0	0	0	19	3	0	0	0	0	1	3	0	1	0	5	10	2	0	0	1	0	3	259	262			
TOR 2	9	0	1	15	0	8	14	1	0	0	2	7	1	2	119	0	4	9	0	0	7	0	0	2	10	4	1	0	0	5	2	0	2	0	0	13	2	0	0	5	0	7	252	260				
TOR 1	2	0	0	8	0	5	22	0	1	2	0	0	12	12	5	118	0	2	10	0	1	0	2	0	1	1	16	0	1	0	0	8	7	1	4	0	0	0	2	0	2	1	2	7	256	261		