The test wall of *?Nubeculina* Cushman 1924 (Miliolida): updates on its agglutinated-porcelaneous wall structure from entire and sectioned specimens

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ABSTRACT: There is a growing number of new foraminifera with agglutinated wall types held together by secreted crystallites of high-magnesium calcite that do not fit within the traditional definition of the Miliolida. In this study, we analysed entire and sectioned foraminiferal specimens from modern marine sediments collected off the Croatian coast (Adriatic Sea) using an Environmental Scanning Electron Microscope (ESEM) equipped with Energy-Dispersive x-ray-Spectroscopy (EDS). The investigated specimens resemble the miliolid genera *Nubeculina* Cushman 1924 and *Falsonubeculina* Amao and Kaminski 2019, but display characteristics of test morphology and an agglutinated-porcelaneous wall structure that have not been previously observed in similar miliolids. Their wall structure is more like that observed in primitive agglutinated foraminifera such as *Lagenammina* rather than in true miliolids. New taxonomical inferences regarding the nubeculinid group of genera are discussed.

Keywords: benthic foraminifera, Miliolida, test microstructure, agglutinated-porcelaneous wall, Neretva Channel, Adriatic Sea

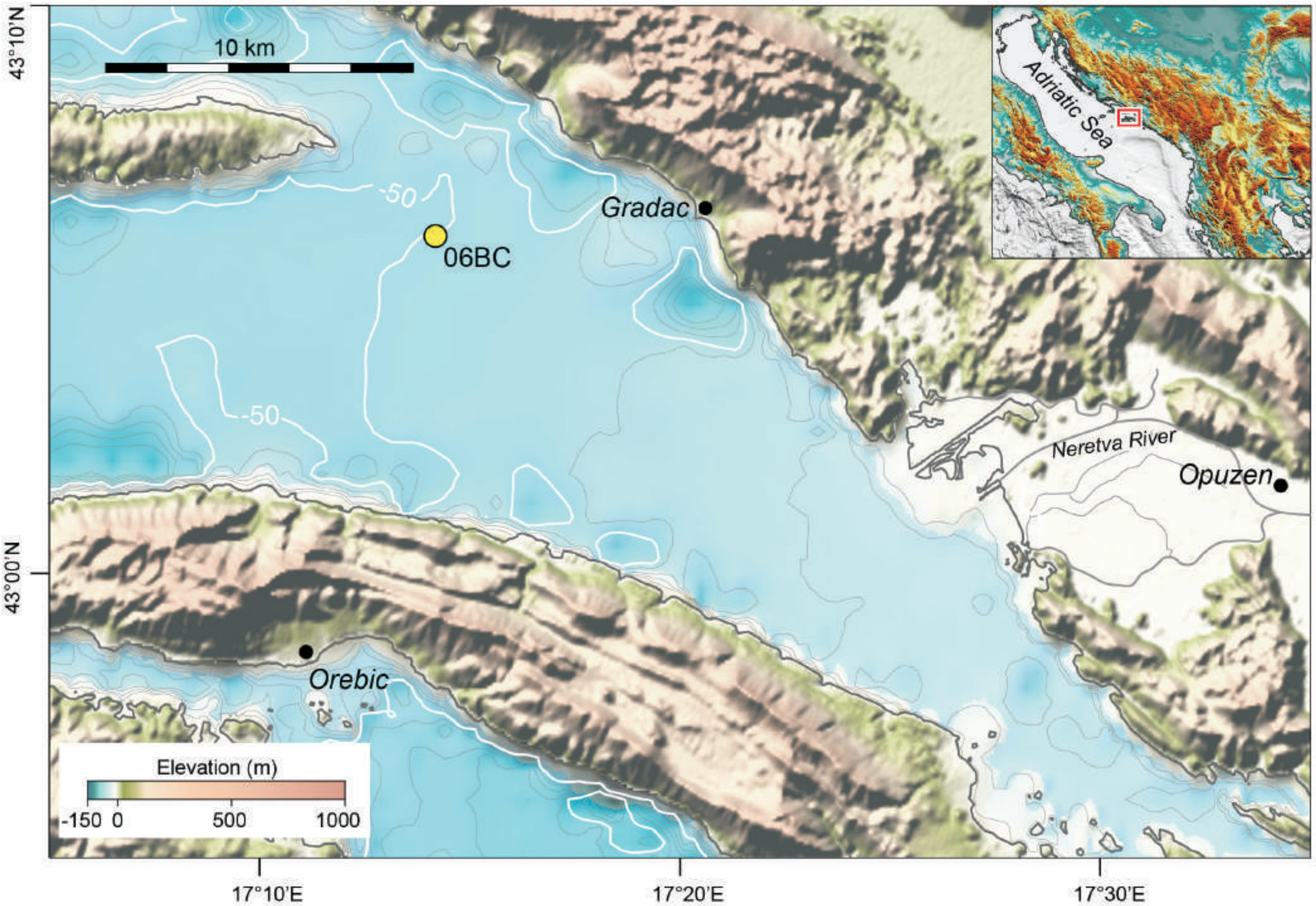
INTRODUCTION

In the Earth Sciences, the foraminifera are considered one of the most important groups of unicellular microorganisms with a mineralized shell, as they provide information for biostratigraphy and represent archives for environmental and climatic reconstructions. Traditionally, their taxonomy is primarily based on test morphology but more recently, thanks to advanced technologies in electronic microscopy, test composition and wall microstructure have also been considered (i.e., Loeblich and Tappan 1964, 1987, 1992; Sen Gupta 1999; Kaminski 2014; Parker 2017).

Among living and fossil species, the foraminiferal test wall can be either organic (of tectine), agglutinated (picking up grains from the substrate), or mineralized secreted (porcelaneous or hyaline wall made of aragonite or calcite) (Sen Gupta 1999). However, several studies have reported the existence of foraminifera showing an intermediary test wall, termed agglutinated-porcelaneous wall (Parker 2017), which seems to combine both agglutinated and porcelaneous traits (Wood 1948; El-Nakhal 1983, 1985; Loeblich and Tappan 1987; Mikhalevich and Kaminski 2008; Rigaud and Martini 2016; Amao and Kaminski 2016; Garrison 2019). In the last few years, increasing evidence of intermediary taxa (e.g., tubular foraminifera grouped in the Class Tubothalamea) has emerged, thus the exact boundary between true agglutinated and porcelaneous walls is still rather poorly defined (Rigaud and Martini 2016). Even calcareous hyaline taxa (e.g., *Melonis* and *Uvigerina*) may incorporate siliciclastic particles into their calcareous wall, secreting a significant quantity of intracellular calcitic crystallites to cement these foreign grains (Borrelli et al. 2018; Amao et al. 2022). Nevertheless, both microstructural and genetic data confirm that the test wall characteristics are of primary importance for higher-rank foraminiferal classification (e.g., Loeblich and Tappan 1992; Bowser et al. 2006; Pawlowski et al. 2013; Kaminski 2014).

In this study we used an Environmental Scanning Electron Microscope (ESEM) equipped with Energy-Dispersive x-ray-Spectroscopy device (EDS) to analyse entire and sectioned foraminiferal specimens from recent marine sediments collected off the Croatian coast (Adriatic Sea) that morphologically resemble the miliolid genus *Nubeculina* Cushman 1924.

The genus *Nubeculina* Cushman 1924 belongs to the family Nubeculariidae Jones 1875, suborder Miliolina Delage and Hérouad 1896. Currently, the genus accommodates three different species: *N. divaricata* (Brady 1879) that represents the type species, *N. advena* Cushman 1924, and *N. chapmani* Cushman 1932 (www.marinespecies.org). In the review of Clark (1993), *Nubeculina* was characterized by an elongated test, formed by coarse-grained arenaceous grains agglutinated into a calcareous wall, and a terminal complex aperture having several thick teeth and a phialine lip, placed on a long protruding neck. The test wall was layered with two distinct layers: a thicker, porcelaneous imperforate outer layer, that incorporated agglutinated grains and a thin, calcareous perforate inner layer, crossed by circular aligned pores. More recently, Parker (2017) described the test wall ultrastructure of several modern miliolids including the genus *Nubeculina*. Parker's specimens belonging to the species *N. advena* showed a porcelaneous wall formed by a layered fabric, with an intermediate thicker portion, named "porcelain", and primarily made of a matrix of needle-shape crystals that could also embed sediment particles, bounded by two surface layers: the outer extrados and the inner intrados. The intrados was of needle-shape crystals randomly oriented, whereas the extrados was of needle-shape crystals that were not aligned.



TEXT-FIGURE 1
Location of Neretva area with the investigated box core indicated (modified from Giglio et al. 2020).

The specimens analysed in this work strongly resemble the specimens reported by Cimerman and Langer (1991) from the eastern Adriatic basin and by Milker and Schmield (2012) from the Western Mediterranean, both attributed to the species *Nubeculina divaricata*, but at the same time, they display morphological characteristics that differ with respect to the previously described Mediterranean *Nubeculina* species. This study reports these new specimens, which seem to combine morphological and microstructural features of both miliolid and agglutinated foraminifera.

MATERIALS AND METHODS

The investigated foraminiferal specimens are part of an integrated study of the sediment pathways and dynamics performed along the Neretva Channel area, in the southernmost part of the Croatian coast, central Adriatic Sea (Giglio et al. 2020) (text-fig. 1). The Neretva Channel is a semi-enclosed basin characterized by a local oceanography combining the highly saline oligotrophic waters coming from the open sea and the freshwater transported by the Neretva River (Orlic et al. 2006). The seafloor is covered by fine-grained sediments, mainly clayey silts, particularly in the area in front of the river delta and in the northeast part of the channel (Giglio et al. 2020). The sediment grains are principally composed by lithic fragments of limestones and dolostones and siliciclastic minerals such as quartz, feldspar, and a significant amount of clay minerals, particularly illite, supplied from the river drainage of surrounding geological units (Jurina et al. 2010).

Sediment samples were collected using a box corer during the oceanographic cruise NERES06 onboard the R/V Bios DVA in May 2006. Analysed samples are from box core 06BC (22 cm long) collected at 46.6 m depth, NW of the Neretva Channel, at the boundary with the Korcula Channel (Lat: 43°05.946'; Long: 17°14.193') (text-fig.1). Upon recovery, cores were cut in half, visually described from a sedimentological point of view, and one half was stored for the historical archive while the other half was sub-sampled every 2 cm for subsequent sediment grain-size, micropaleontological and geochemical analyses. Radiometric data, based on ^{137}Cs and ^{210}Pb radionuclides concentration profiles *versus* depth, displayed an estimated sediment accumulation rate of about 1.9 mm/yr for the recovered sedimentary sequence, documenting the presence of recent sediments at the top (time-interval spanning 2002–2006 for the first 2 cm of the sea-floor) (Giglio et al. 2020).

For micropaleontological analyses, we prepared washed residues from the surface sediment layer (0–2 cm): sediments were dried at 50°C in an oven for one day, weighed, and washed

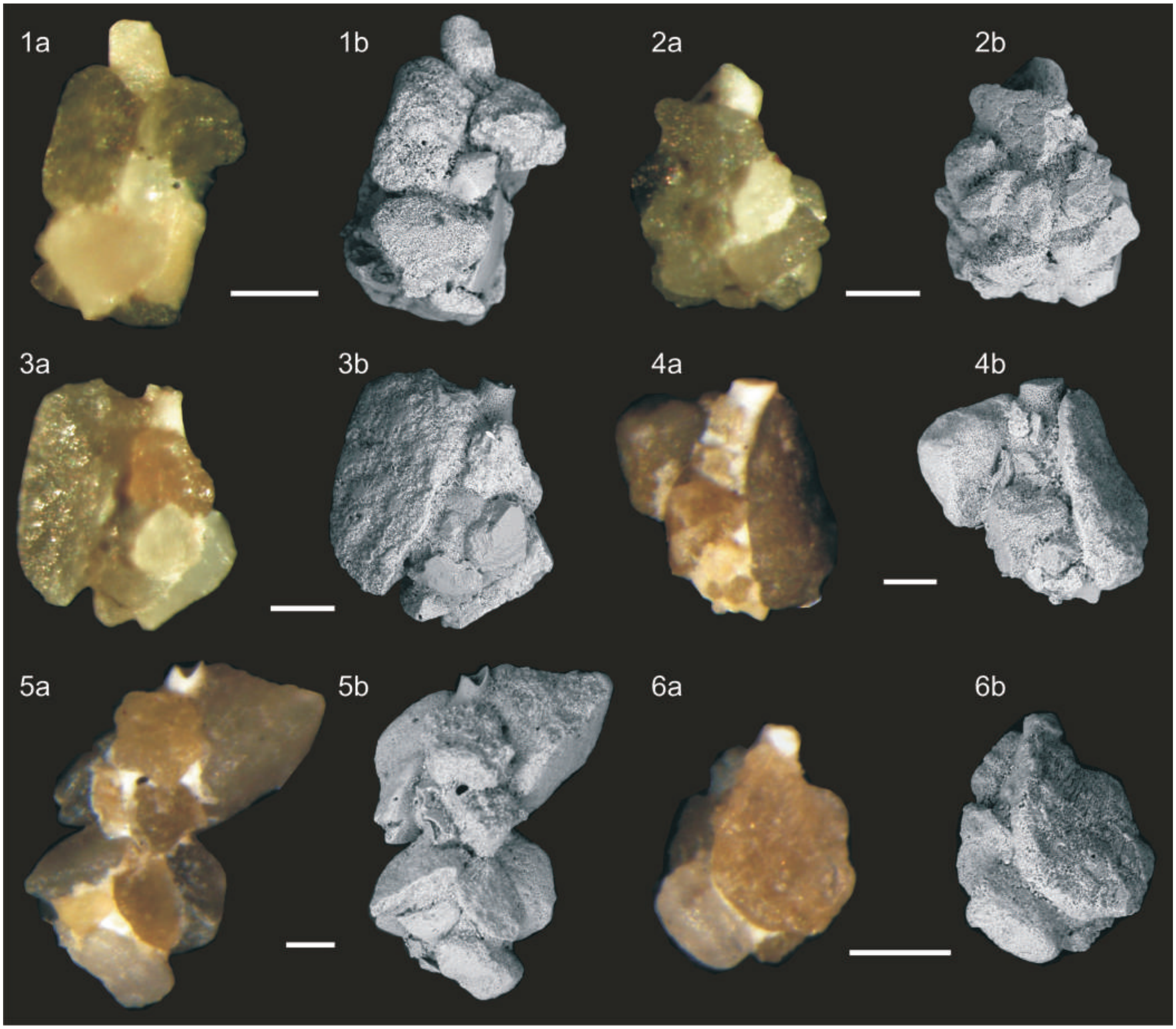


PLATE 1
Light (a) and ESEM (b) photographs of the studied specimens picked from surface sample 6BC (level 0–2cm).
Scale bars are 100 µm

through a 63 µm sieve; the residual fraction was dried again at 50°C and stored in small plastic bags for foraminiferal analyses. Taxonomical identification of benthic foraminifera was performed on the >63 µm fraction using a stereomicroscope. All specimens resembling *Nubeculina* spp. were picked and separated into micro-slides for subsequent SEM-EDS studies. Specimens were photographed using a Nikon Coolpix 4500 camera mounted on an Olimpus SzX 10 stereomicroscope. The same specimens were also mounted on stubs and analysed using an Environmental Scanning Electron Microscope (ESEM) Zeiss EVO LS10 for morphological characterizations. The chemical-mineralogical characterization of the agglutinated grains (at least 3 spot analyses per specimen) was made by means of point analyses (beam diameter: ~5 µm; accelerating voltage: 15 kV; beam current: 5 nA for calcium, and 20 nA for other elements) using the ESEM equipped with a Bruker Quantax system Energy-Dispersive Spectroscopy (EDS) device, and Esprit software at the Institute for Microelectronics and Microsystems (IMM) at CNR Research area of Bologna. The analysed material is stored at the Institute of Marine Sciences (ISMAR) at CNR Research area of Bologna - micropalaeontology collection, Adriatic section (repository number 28504).

After this first step of analyses, selected specimens were sent to the CiSRIC-ARVEDI laboratory at the University of Pavia for further SEM investigations using a Tescan FESEM, series Mira 3XMU equipped with an EDS detector. The isolated specimens were embedded in epoxy resin, sectioned and polished with diamond pastes from 0.25 to 6 µm in grain-size following the methodology described by Mancin et al. (2014). Back Scattered Electron (BSE) images of sectioned specimens highlighted compositional similarities (or dissimilarities) among agglutinated grains and secreted cement through the wall thickness, on the basis of the mean atomic number of each grain forming the test wall. The elemental composition of the single grains was provided through standardless spot microanalyses collected for 100 s at 15 mm working distance, using an accelerating voltage of 20 kV. The sectioned specimens are stored at the Laboratory of Foraminifera of the University of Pavia.

RESULTS

The studied specimens are characterised by small-sized unilocular tests (plates 1-2), more rarely rectilinear uniserial formed by two overlapping chambers, separated by a depressed suture (pl. 1, figs. 5a-b; pl. 2, fig. 1). This is in contrast with the type species of *Nubeculina*, in which the chambers are connected by narrow stolons. The test size is variable (from less than 150 µm to over 400 µm) depending on the grain size of the agglutinated material, and on the number of chambers. Chambers, mostly ovoidal or elongated, are formed by coarse-grained terrigenous particles that are highly heterometric and also compositionally heterogeneous; they are agglutinated into a milky white calcareous matrix secreted by the organism (pl. 1, figs. 1a-6a). The aperture is simple, oval or elliptical, without any internal structures (e.g., small plates or teeth) and a phialine lip, and terminal on a long protruding neck of calcite (plate 2). The neck surface is characterised by non-aligned needle-shaped crystallites, of 1-2 µm in size, arranged to around circular pits of different sizes (pl. 2, figs. 1a-b, 2a). Standardless spot microanalyses performed on both the surface of the agglutinated grains and secreted cement confirm that the grains are mainly made of calcite, dolomite, epidote, and garnet (grossular and pyrope) (Appendix 1); more rarely the grains are planktonic foraminifera or other biogenic remains (plate 2, arrows in images 2, 3; plate 3, fig. 3b). The secreted portion of the wall, about 20 µm thick, is of high-magnesium calcite (pl. 2, fig. 5; Appendix 1). This secreted part of the wall fills the space between the grains but does not coat the interior of the largest grains as in true miliolids. Where the wall was broken it displays a layered ultrastructure that can be interpreted as the extrados, the porcelain and the intrados (*sensu* Parker 2017), moving from the outside to the inside of the test (pl. 2, fig. 5a).

By observing the sectioned specimens (plate 3) these features appear more evident. All the studied specimens have unilocular or uniserial tests. The early coiled stage that characterises the genus *Nubeculina* is clearly missing. The internal chamber lumin has a pyriform shape that tapers towards the aperture (pl. 3, figs. 1-3). The agglutinated-porcelaneous wall is formed by

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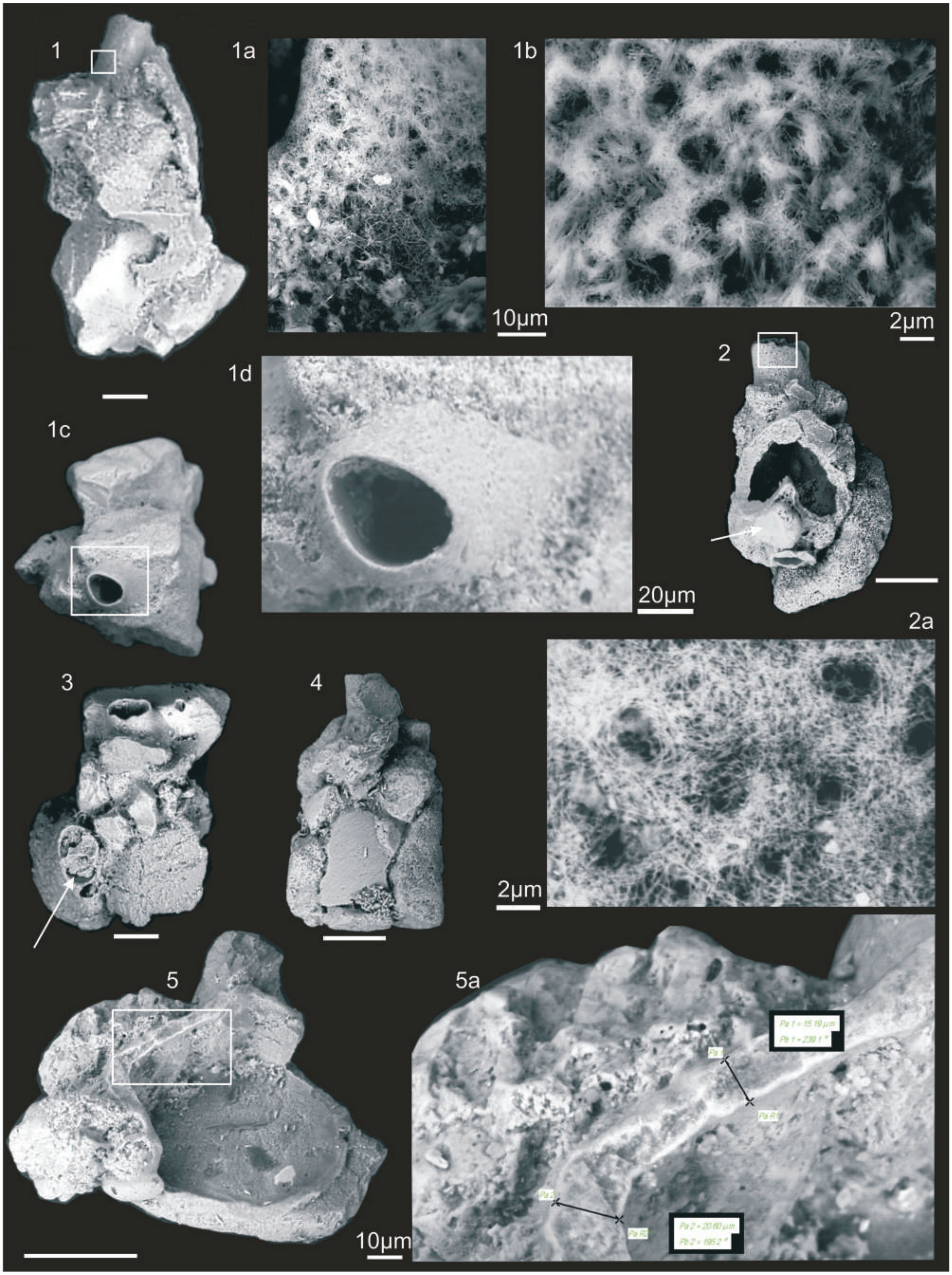
PLATE 2

ESEM magnified view of selected nubeculinid specimens.

1 Specimen showing the enlargement of the neck surface microstructure (a-b), and detail of the circular aperture lacking the phialine lip and internal complexity (c-d).

2-4 Morphological variability of the studied specimens; note on the porcelaneous neck the presence of several, small-sized, rounded pits (2a). Arrows indicate foraminiferal remains agglutinated within the test wall.

5 Fragmented specimen showing the agglutinated-porcelaneous wall; note in the enlargement (a), the porcelaneous portion which incorporates the coarse terrigenous grains. Scale bars are 100 µm unless indicated otherwise.


1
1a
1b
10µm
2µm
2
1d
1c
20µm
2a
3
4
2µm
5
5a
10µm

coarse agglutinated grains which alternate with thin secreted calcitic portions (pl. 3, figs. 1-4) that fill in the space between the grains but do not coat the interior of the grains themselves (e.g., pl. 3, figs. 1a-b). The calcitic wall displays a typical miliolid-like microstructure formed by a matrix of randomly oriented needle-shaped chrystallites (probably the thicker porcelain), however a truly lamellar fabric, with three distinct layers as the one observed by Parker (2017), is not clearly visible here. To note that where the calcitic wall is in touch with the agglutinated grains, the crystallites are small in size and partly aligned with the longer axis parallel to the grain surface (pl. 3, arrow in fig. 4a). The secreted crystallites are of high-Mg calcite; the weight percentage of Mg, semi-quantitatively estimated through spot microanalyses, varies between 7.99 and 9.69% (Table 1). These data are in line with values measured in "true" miliolids from the accompanying assemblage (plate 4, Tab. 1) and from the literature (e.g., Hover et al. 2001).

DISCUSSION

Comparison with other nubeculinids

The Croatian specimens here described displayed mostly unilocular tests, more rarely rectilinear uniserial that are much more like a primitive agglutinated foraminifer similar to *Lagenammina* or *Reophax*. The tests are very coarsely agglutinated, and externally resemble the species *Reophax bruneiensis* recently described by Goeting et al. (2021) from comparable water depths off Brunei Darussalam. However, instead of secreting organic cement they possess a high-Mg calcite wall as in true miliolids. They mainly differ from similar nubeculinid specimens reported in the literature (e.g., Cimerman and Langer 1991; Milker and Schmield 2012; Parker 2017) in: i) having a wholly uniserial serial chamber arrangement (mostly unilocular), that lacks the early spiral stage; ii) possessing a simple rounded aperture without a phialine lip and internal complexity and, iii) having an agglutinated-porcelaneous wall, that alternates agglutinated grains with secreted calcitic parts. These secreted portions, made of needle-shape crystallites randomly arranged as in true miliolids, fill the intergranular space between the agglutinated grains but do not coat the largest particles. Finally, iv) the neck surface displays pits of different size.

All these features make our specimens more similar to the ones described by Bartenstein and Brand in 1949 belonging to the extinct Cretaceous genus *Pseudonubeculina* Chapman; a genus formally deleted because considered subjective junior synonym in opinion of Loeblich and Tappan (1987), and subsequently amended into *Nodobacularia* Rhumbler 1895 (www.marinespecies.org). Recently, Amao and Kaminski (2016, 2019) proposed a new genus, *Falsonubeculina* Amao and Kaminski (2019) still of uncertain affiliation, which seems to share with our specimens the wholly uniserial chamber arrangement and the typical agglutinated-porcelaneous wall, with alternating agglutinated grains and secreted calcitic portions. However, *Falsonubeculina* clearly differs in having a slit-like aperture, marked by an imperforated rim of secreted calcite that lies on the chamber surface and is not situated on a protruding neck as in our specimens. Moreover in *Falsonubeculina* surface pits are totally lacking, on the contrary they are clearly visible on the neck of our specimens.

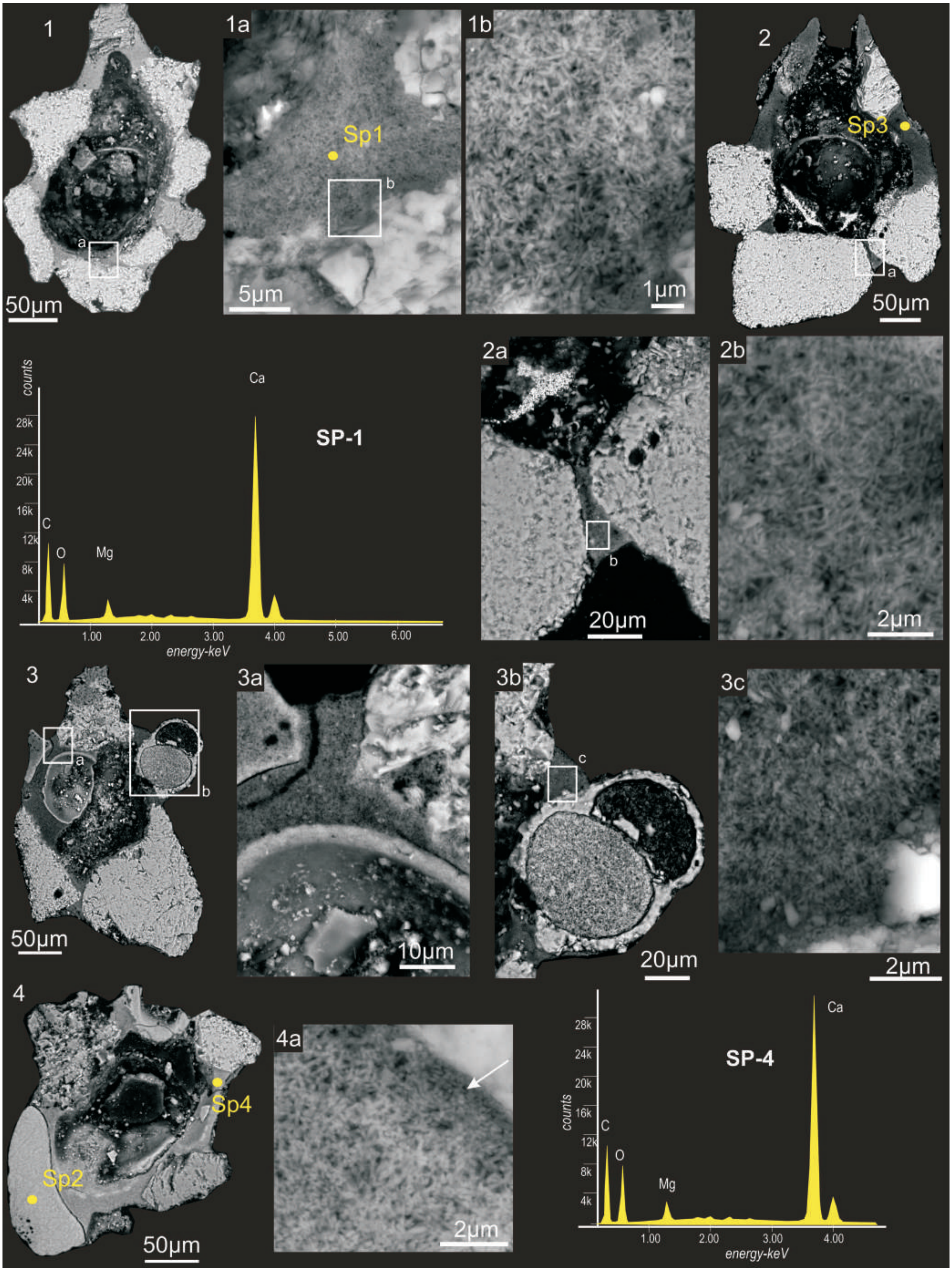
In conclusion, our specimens undoubtedly have miliolid affinities owing the structure and composition of the test wall but they also have a simple aperture and a wholly uniserial chamber arrangement, in contrast with the known species that are currently placed in the genus *Nubeculina*. Because they possess an elongated neck rather than a slit-like aperture they also differ from *Falsonubeculina*. Because of these differences in chamber arrangement, wall structure, and apertural characteristics these specimens cannot be placed in the genus *Nubeculina* or *Falsonubeculina*. They likely constitute a new taxon.

CONCLUSIONS

The nubeculinid foraminifer documented in this study combined traits of both miliolid and agglutinated foraminifera. As in the genus *Falsonubeculina*, the investigated species possesses an agglutinated-porcelaneous wall, in which agglutinates large mineral and biogenic grains cemented together using a fibrous, high-Mg calcite cement. The secreted matrix fills in the space between the grains but does not coat the interior of the grains themselves – there is no underlying continuous porcelaneous layer as observed in some other miliolid genera. The species displays morphological traits of both *Nubeculina* and *Falsonubeculina*. However, we refrain from assigning the species to *Nubeculina* because it lacks an initial coiled portion. Unlike *Falsonubeculina*, it possesses an extended porcelaneous neck with surface pits of various sizes. Because the cement between grains is composed of high-Mg calcite, the specimens doubtless belong among the miliolids. In our opinion, these agglutinated-porcelaneous forms with uniserial chamber arrangement likely constitute a new family within the Miliolida.

PLATE 3

Back scattered electron images of sectioned nubeculinid specimens showing ultrastructural details of the agglutinated-porcelaneous wall. The yellow points indicate the spots for standardless microanalyses (see Table 1); the corresponding EDS spectra are also reported.


1
50µm
1a
Sp1
b
5µm
1b
1µm
2
Sp3
a
50µm
counts
Ca
SP-1
28k
24k
20k
16k
12k
8k
4k
C
O
Mg
1.00
2.00
3.00
4.00
5.00
6.00
energy-keV
2a
b
20µm
2b
2µm
3
a
b
50µm
3a
10µm
3b
c
20µm
3c
2µm
4
Sp4
Sp2
50µm
4a
2µm
Ca
SP-4
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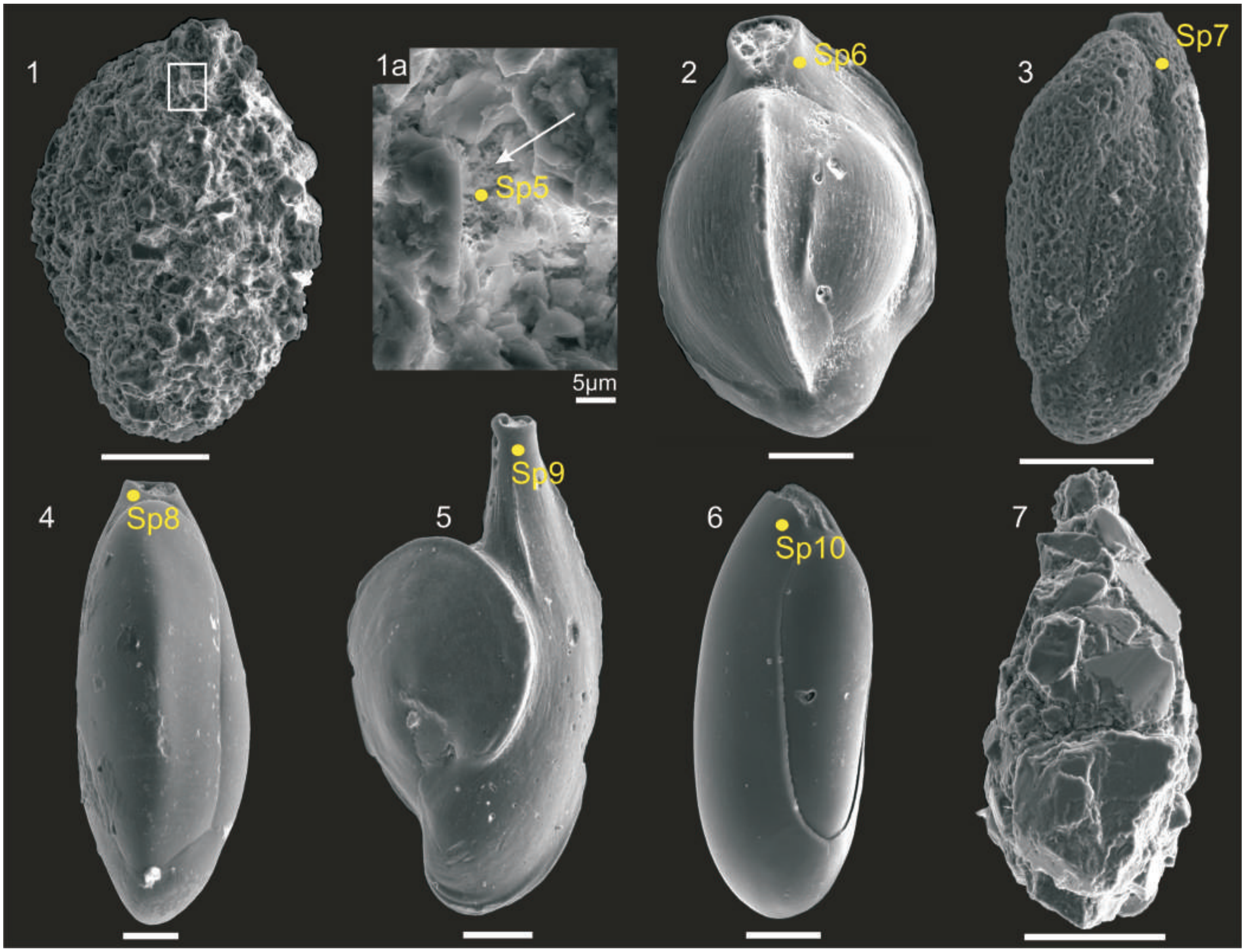

PLATE 4

SEM photographs of some miliolid and agglutinated specimens that accompany the studied nubeculinids found in the surface sample 6BC (level 0-2 cm). The yellow points indicate the spots for standardless microanalyses (see Table 1).
Scale bars are 100 µm.

1 *Sigmoilopsis schlumbergeri* (Silvestri), note in "a", among the agglutinated grains a small portion of the porcelaneous wall formed by not-aligned needle-shaped crystals (arrow).

2 *Triloculina marioni* Schlumberger.

3 *Quinqueloculina villafranca* Le Calvez and Le Calvez.

4 *Quinqueloculina seminula* (Linnaeus).

5 *Adelosina mediterranensis* Le Calvez and Le Calvez.

6 *Pseudotriloculina oblonga* (Montagu).

7 *Lagenaminna fusiformis* (Williamson).

TABLE 1
Compositional data relative to spot-microanalyses performed on single grains and cement (Plate 3 and 4). Chemical data are recalculated to 100% and expressed in weight percent.

				Weight %			
	Studied specimens	**Spot-analysis**	**Mineral**	**MgO**	**CaO**	**Fe_2O_3**	**Total**
Plate 3	nubeculinid specimens	SP-1	high-Mg calcite	8.47	91.53	0.00	100
		SP-2	Dolomite	39.00	59.57	1.43	100
		SP-3	high-Mg calcite	9.69	89.36	0.94	100
		SP-4	high-Mg calcite	7.99	91.38	0.63	100
Plate 4	*S. schlumbergeri*	SP-5	high-Mg calcite	1.71	98.29	0.00	100
	T. marioni	SP-6	high-Mg calcite	6.79	93.21	0.00	100
	Q. villafranca	SP-7	high-Mg calcite	3.30	96.70	0.00	100
	Q. seminula	SP-8	high-Mg calcite	2.38	97.62	0.00	100
	A. mediterranensis	SP-9	high-Mg calcite	5.78	94.22	0.00	100
	P. oblonga	SP-10	high-Mg calcite	4.30	95.70	0.00	100

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WoRMS-World Register of Marine species. www.marinespecies.org

APPENDIX 1
Compositional analyses of agglutinated grains and secreted cement performed on entire specimens from Croatia.