

The reinstated identity of agglutinated foraminifer *Campanellula capuensis* from the Lower Cretaceous of southern Italy by means of a 3D model investigation

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Campanellula capuensis was described as belonging to the Trochamminacea (trochospiral tests) and later transferred to the genus *Orbitolinopsis* of the Orbitolinidae (uniserial tests). Challenging its identity as a species of *Orbitolinopsis*, the most widely accepted classifications of agglutinated foraminifera reinstate *Campanellula* but retain its inclusion within the Orbitolinidae, subfamily Dictyoconinae. New material from the type locality and the San Lorenzello section (Matese Mountains, southern Apennines, Italy) as well as the construction of a 3D model allow to reinstate the original description as a low- to high-trochospirally (conical) coiled foraminifer with numerous chambers per whorl and to display an overall conical test morphology. An orbitolinid test construction including uniserial chambers (throughout the test or in its adult part) is absent. The conflicting opinions on taxonomic status of *Campanellula* are discussed leading to the removal from the order Loftusiina and the suborder Orbitolinina. Instead, *Campanellula* should be included into the order Lituolida and the suborder Verneuilinina. *Campanellula capuensis* represents a biostratigraphic and palaeobiogeographic marker taxon, restricted to upper Hauterivian–lower Barremian inner platform carbonates of the southern Neotethyan margin.

Key words: Foraminifera, Trochamminacea, biostratigraphy, calcareous agglutinated test, taxonomy, 3D reconstruction, Lower Cretaceous, Italy.

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*This research is dedicated to the memory
of Piero De Castro (1929–2023)*

Introduction

When it was introduced, genus *Campanellula* De Castro, 1964, was included into the family Trochamminidae, uniting forms with trochospirally coiled tests. Some years later, based on material from Algeria, the species was assigned to the orbitolinid genus *Orbitolinopsis* by Schroeder in Macoin et al. (1970), assuming adult uniserial chamber

arrangement and an internal test construction of this genus. Therefore, Schroeder in Macoin et al. (1970) considered *Campanellula* as a junior synonym of *Orbitolinopsis* Henson, 1948. Loeblich and Tappan (1987: 157), in turn, reinstated the *Campanellula* but considered it a member of family Orbitolinidae, subfamily Dictyoconinae. This supra-generic affiliation, however, has not been accepted by all subsequent workers (e.g., Arnaud-Vanneau and Sliter 1995; Gheiasvand et al. 2019). In the most recent classification

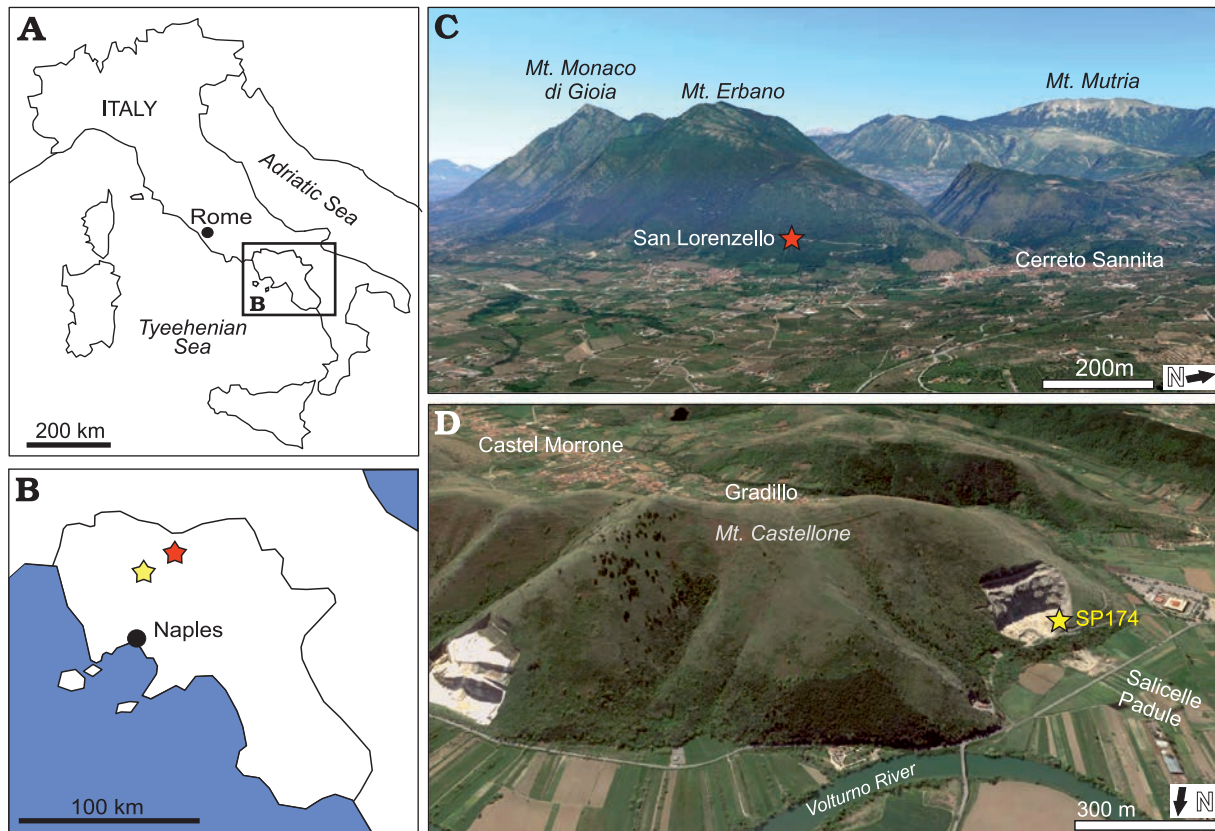


Fig. 1. Position of the studied localities. **A.** A contour map of the Italian Peninsula showing location of the Campania Region. **B.** Enlargement of the Campania Region with the two studied localities: San Lorenzello section (Benevento Province; red star) and the type locality of *Campanellula capuensis* (De Castro, 1964) near Castel Morrone village (Caserta Province; yellow star). **C.** Panoramic view of the San Lorenzello section (from Google Earth). **D.** Panoramic view of the *Campanellula capuensis* type locality along the SP174 road (from Google Earth).

of the agglutinated foraminifera, the concept of Loeblich and Tappan (1987) with *Campanellula* representing a genus of the Orbitolinidae is still followed (Kaminski 2014). New material from the upper Hauterivian–lower Barremian (Lower Cretaceous) San Lorenzello section (Mt. Monaco di Gioia, southern Apennines, Campania Region, Italy) and from the De Castro's type locality (Fig. 1), has been studied in detail.

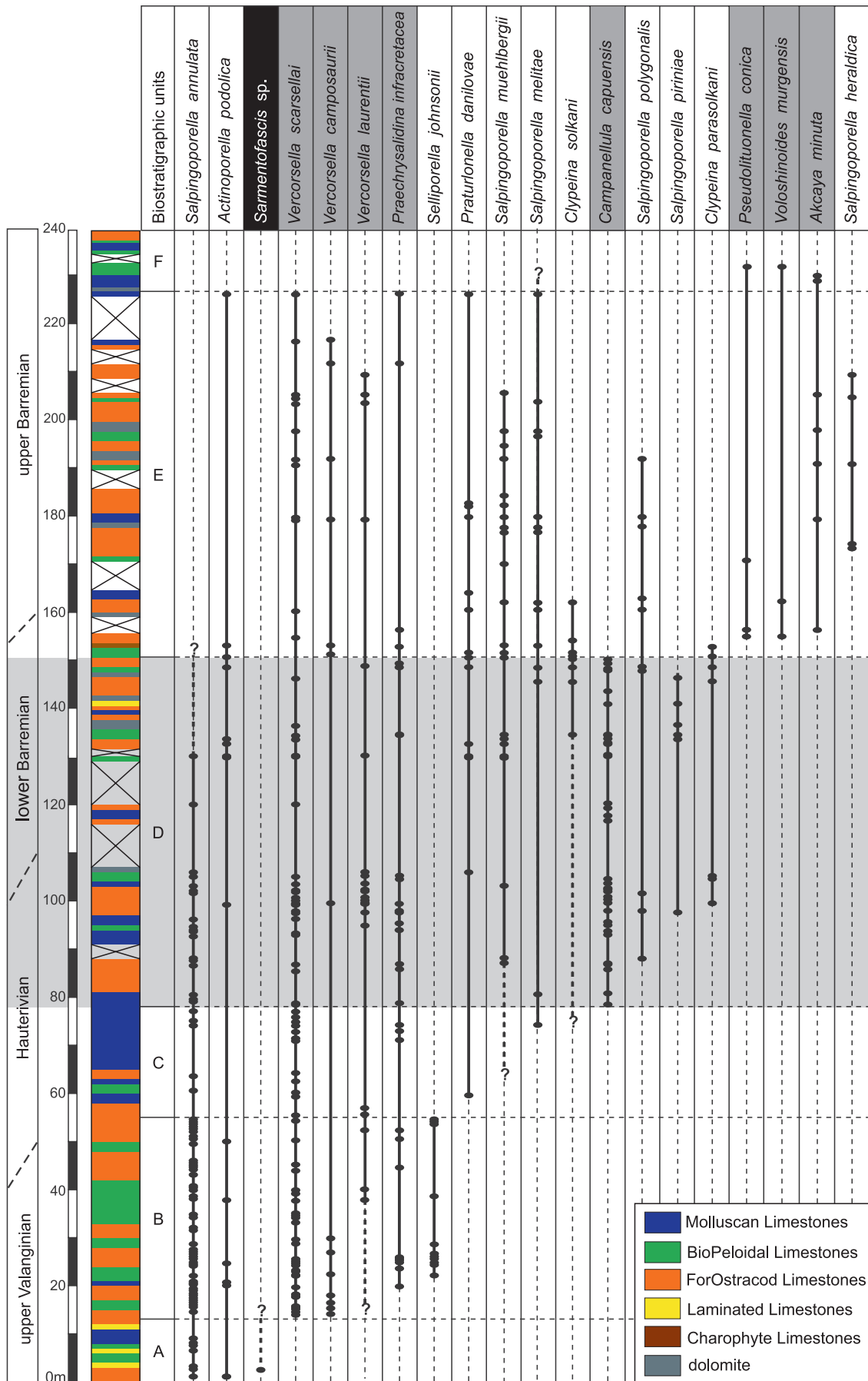
A new investigation perspective on the type species, *Campanellula capuensis* De Castro, 1964, is here offered by the reconstruction of a 3D model that can be confronted with the test structure in thin section. The application of this method allows shedding further light into the internal test construction and the implied suprageneric position. The small-sized benthic foraminifer *Campanellula capuensis* represents a biostratigraphic and palaeobiogeographic marker taxon restricted to the upper Hauterivian–lower Barremian platform carbonates of the southern Tethyan margin (De Castro 1964; Maccoin et al. 1970; Cherchi et al. 1981; Schroeder et al. 1978; Husinec and Sokač 2006, Velić 2007).

Institutional abbreviations.—DiST, Department of Science and Technology, Parthenope University, Naples, Italy; DiSTAR, Department of Earth Sciences, Environment and Resources, Federico II University, Naples, Italy; IP, Istituto di Paleontologia, Università di Napoli Federico II, Naples, Italy; Gmm, Geosciences Museum of Mashhad in the Geological Survey of North-Iran, East territory, Iran; IGZ, Institute of Geology, Zagreb, Croatia.

Geological setting

The studied locality is positioned in the San Lorenzello section ($41^{\circ}16'49.16''\text{N}$, $14^{\circ}32'23.24''\text{E}$; Fig. 1A, B), about 70 km to the north of Naples and exposed along a road-cut on the southern slope of the Monte Monaco di Gioia (Matese Mountains, Benevento Province, Italy, Fig. 1C). This mountain is a part of the southern Apennines, a N-E verging fold and thrust belt derived from Apula-Ionian composite plate migration (Malinverno and Ryan 1986;

Fig. 2. Litho-biostratigraphy of the San Lorenzello section. The columnar log is based on the predominant lithofacies associations: Molluscan Limestones are open lagoonal deposits; BioPeloidal Limestones are inner shoal deposits; ForOstracod Limestones are restricted lagoonal deposits; Laminated Limestones are tidal flat deposits; and Charophyte Limestones are coastal ponds deposits. The log is juxtaposed with upper Valanginian–upper Barremian chronostratigraphic distribution of the main benthic foraminifera and green algae recognized in the section. The grey horizontal band represents the distribution range of *Campanellula capuensis*. See Amodio et al. (2020) for a detailed description of the lithofacies and biostratigraphic units.



Patacca and Scandone 2007), caused by African-Eurasian plate collision. The shallow-water carbonates, belonging to the Apennine Carbonate Platform (e.g., Patacca and Scandone 2007), have been investigated by a high-resolution integrated stratigraphy (D'Argenio et al. 1997; Ferreri et al. 2004; Amodio 2006; Amodio et al. 2008, 2013, 2018; Martino et al. 2019; Barattolo et al. 2021; Amodio et al. 2020, 2023; Parente et al. 2022). This study focuses on the Hauterivian–Barremian interval containing the local distribution range of *Campanellula capuensis* (78–151 m interval from the base of the section), labelled as D biostratigraphic unit (Fig. 2; see also Amodio et al. 2020: fig. 8). This interval corresponds to the *Campanellula capuensis* Biozone (De Castro 1991) and to the central part of the “*Cuneolina scarsellai*” and “*Cuneolina camposaurii*” biozones of Chiocchini et al. (2008). According to De Castro (1991) and Chiocchini et al. (2008), the stratigraphic range of *Campanellula capuensis* encompasses the Hauterivian–Barremian boundary, placed in this section at 100–110 m from the base of the section, above the first occurrence of *Salpingoporella melitae* Radoičić, 1975 and *Salpingoporella muehlbergii* (Lorenz, 1902) indicated by Carras et al. (2006) as upper Hauterivian and below the appearance of *Salpingoporella piriniae* Carras and Radoičić, 1991, and the last occurrence of *Salpingoporella annulata* Carozzi, 1953, in the upper Barremian (Carras et al. 2006). *Campanellula capuensis* is considered a key marker characterising the southern Tethys bio-province (Cherchi et al. 1981; Cherchi and Schroeder 1973, 2010), but information on its stratigraphic distribution vary in the literature (see among others Macoin et al. 1970; Velić and Sokač 1983; Peybernès et al. 1984; Claps et al. 1996; Husinec and Read 2018; Gheiasvand et al. 2019).

Campanellula capuensis appears as an ubiquitous species in the San Lorenzello section where it occurs in almost all lithofacies associations (Molluscan Limestones, BioPeloidal Limestones, and ForOstracod Limestones, see for detailed description in Amodio et al. 2020: table 1), from open to restricted lagoonal facies as well as from sandy shoals. The biofacies is often very rich and diversified, including bivalves, gastropods, *Cayeuxia*-like thalli, green algae, benthic foraminifera and ostracods. The grainy textures encompass intraclasts, aggregate grains and peloids. The typical algal assemblage is characterised by *Actinoporella podolica*, *Salpingoporella annulata*, *Praturlonella danilovae*, *Salpingoporella muehlbergii*, *Salpingoporella melitae*, and *Clypeina solkani* (Fig. 2). In addition, *Salpingoporella polygonalis*, *Salpingoporella piriniae* and *Clypeina parasolkani* are also documented in this interval. The upper boundary of interval D is also marked by the last occurrence of *Salpingoporella annulata*, and roughly corresponds to the last occurrence of *Clypeina parasolkani* and *Salpingoporella piriniae*. The benthic foraminifera association includes *Vercorsella scarsellai*, *Vercorsella laurentii*, *Vercorsella camposaurii*, and *Praechrysalidina infracretacea*.

Material and methods

The San Lorenzello samples were collected during different field samplings (D'Argenio et al. 1997; Amodio 2006; Amodio et al. 2020). The material is partially hosted in the Sabrina Amodio collection (thin sections DiST/SL90–DiST/SL100), at DiST, Università degli Studi Parthenope of Naples, as well as in the Filippo Barattolo collection (thin sections DiSTAR-L8–DiSTAR-L41), at DiSTAR, Università degli Studi Federico II of Naples. We have followed the standard facies analysis for the carbonate rock classification, sequentially tabulating all the sedimentary features in a lithostratigraphic column (Fig. 2). The biostratigraphic analysis and age determination, mainly concerning benthic foraminifers and calcareous algae, were based on the biozonation schemes of the Lower Cretaceous platform carbonates (De Castro 1991; Carras et al. 2006; Chiocchini et al. 2008).

In addition, the type locality of *Campanellula capuensis* (see De Castro, 1964) was resampled in April 2022. This material is stored in the Filippo Barattolo collection (thin sections DiSTAR-BA. 4418), at DiSTAR, Università degli Studi Federico II of Naples. The original sampling site of De Castro is located at the last hairpin bend, near a quarry, on the SP174 road that leads from Gradillo locality in the municipality of Castel Morrone (Caserta Province, Campania Region, Italy) to Padule Salicelle (Fig. 1D). The samples containing *Campanellula capuensis* were also picked up from the base of the quarry wall, located on the opposite site of the roadcut, but at lower height of about 7–10 m than the original sampling site placed on the road SP174.

In this work, a high-resolution 3D model has been performed on the holotype supplemented by the analysis of numerous, variously oriented sections. The resulting 3D model was created by 3DS Max 2022 software. Afterwards, the 3D model has been sectioned and the resulting cuts compared with similar sections from the San Lorenzello material (see 3D rendering section below).

Systematic palaeontology

Phylum Foraminifera d'Orbigny, 1826

Class Globothalamea Pawlowski, Holzmann, and Tyszka, 2013

Subclass Textulariana Mikhalevich, 1980

Order Lituolida Lankester, 1885

Suborder Verneuulinina Mikhalevich and Kaminski in Kaminski, 2004

Genus *Campanellula* De Castro, 1964

Type species: *Campanellula capuensis* De Castro, 1964; Lower Cretaceous (Hauterivian–Barremian), southern Italy.

Species included: Type species and *Campanellula herishtensis* Schlagintweit, Rashidi, and Hanifzadeh, 2019 from the Gargasian, upper Aptian, Lower Cretaceous of central Iran.

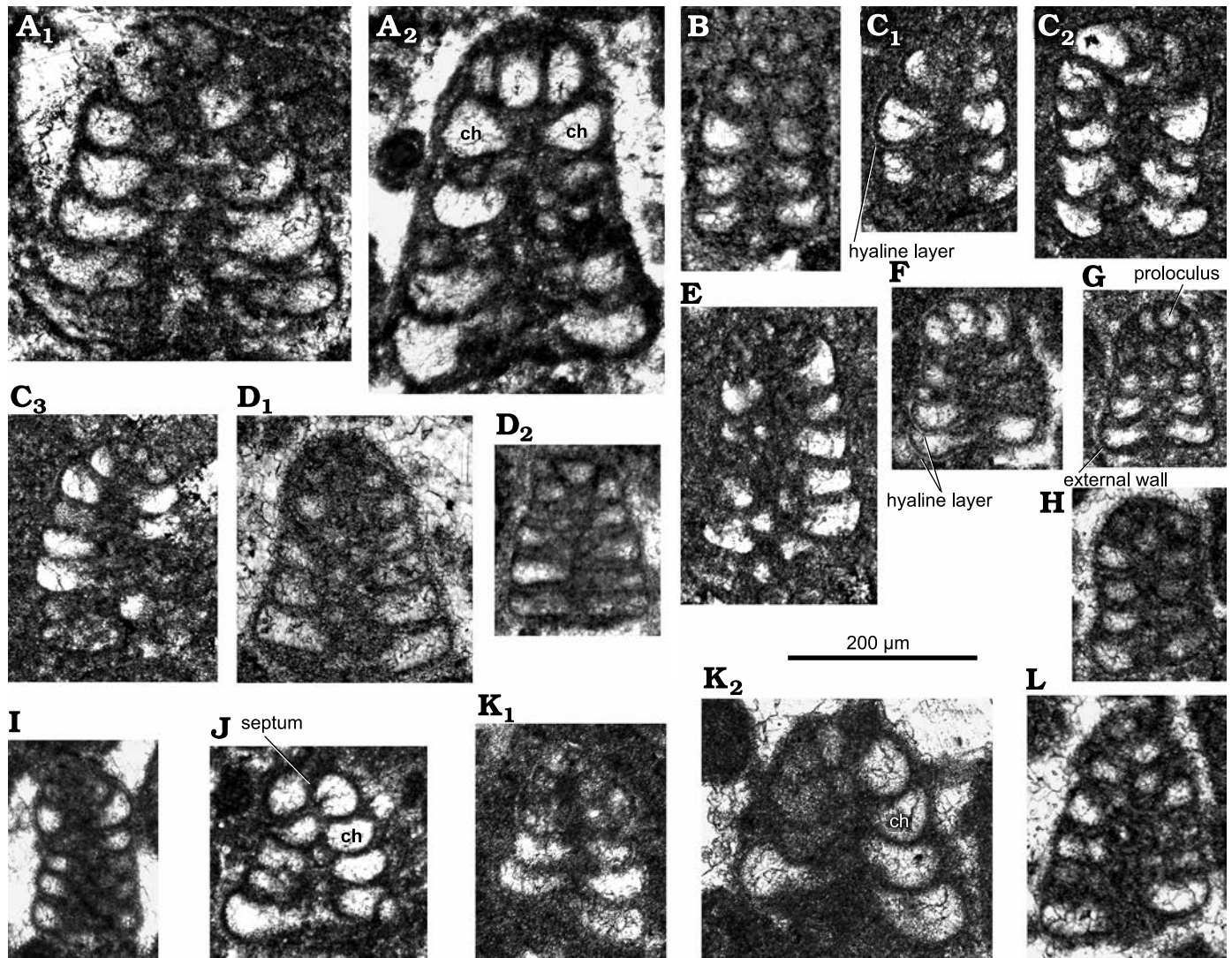


Fig. 3. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, San Lorenzello section, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous (A–J, L) and Kriz section, Mljet Island, Croatia, Lower Cretaceous (K); various (sub)axial sections. **A**. Thin section DiSTAR-L29 with two individuals (A₁, A₂). **B**. Thin section DiSTAR-L8. **C**. Thin section DiSTAR-L39-2 with three individuals (C₁–C₃). **D**. Thin section DiSTAR-L36-1 with two individuals (D₁, D₂). **E**. Thin section DiSTAR-L39-1. **F**. Thin section DiST/SL90-91.1. **G**. Thin section DiSTAR-L35. **H**. Thin section DiSTAR-L36. **I**. Thin section DiSTAR-L41. **J**. Thin section DiST/SL99C.2. **K**. Thin section IGZ-MK with two individuals (K₁, K₂), after Husinec and Sokač (2006: fig. 7J and I). **L**. Thin section DiSTAR-L37. Rather large-sized specimens (A, K₂) might belong to microspheric generation. Abbreviation: ch, chamber.

Diagnosis.—From De Castro (1964): Imperforate, microgranular calcareous test. Cylindric-conical to bellflower in shape. Trochoid coiling with rather closed tours. Simple chambers, numerous in each tour (usually from six to eight in the type species). Simple aperture placed at the base of the chamber.

Remarks.—*Campanellula* belongs to the informal group of conical agglutinated foraminifera that include both trochospiral (e.g., *Pseudochrysalidina* Cole, 1941) and orbitoliniform taxa (e.g., *Dictyoconus* Blanckenhorn, 1900) (Hottinger and Drobne 1980; Vecchio and Hottinger 2007; Cruz Abad 2018). Orbitolinids may have an initial trochospire but the main test part is formed by uniserial chambers which later may become annular (Rat 1963; Schlagintweit 2023). With its small size, distinctly less than 0.5 mm, and simple chambers (= no exoskeleton), however, *Campanellula* cannot

be regarded a larger benthic foraminifer. The microgranular-agglutinated wall exhibiting a thin outer hyaline calcareous layer is reported from the Orbitolinidae (e.g., Douglass 1960; Cherchi and Schroeder 1978; Schroeder 1985), but also from trochospirally coiled taxa such as the early Aptian *Archaeosepta coratina* Luperto Sinni and Masse, 1993, the early Cenomanian *Altamirella* Schlagintweit, Rigaud, and Wilmsen, 2015, or the Late Cretaceous *Accordiella* Farinacci, 1962, and *Gyroconulina* Schroeder and Darroian, 1977 (see Schlagintweit et al. 2016). The hyaline layer is also present in the wall of *Meyendorffina bathonica* Aurouze and Bizon (own data of MS). In *Altamirella* for example, the hyaline calcitic layers “are not involved in the chamber formation process. They are secondarily added so that one layer can cover the umbilical side of several chambers but never covers the entire septa” (Schlagintweit et al. 2015: 3),

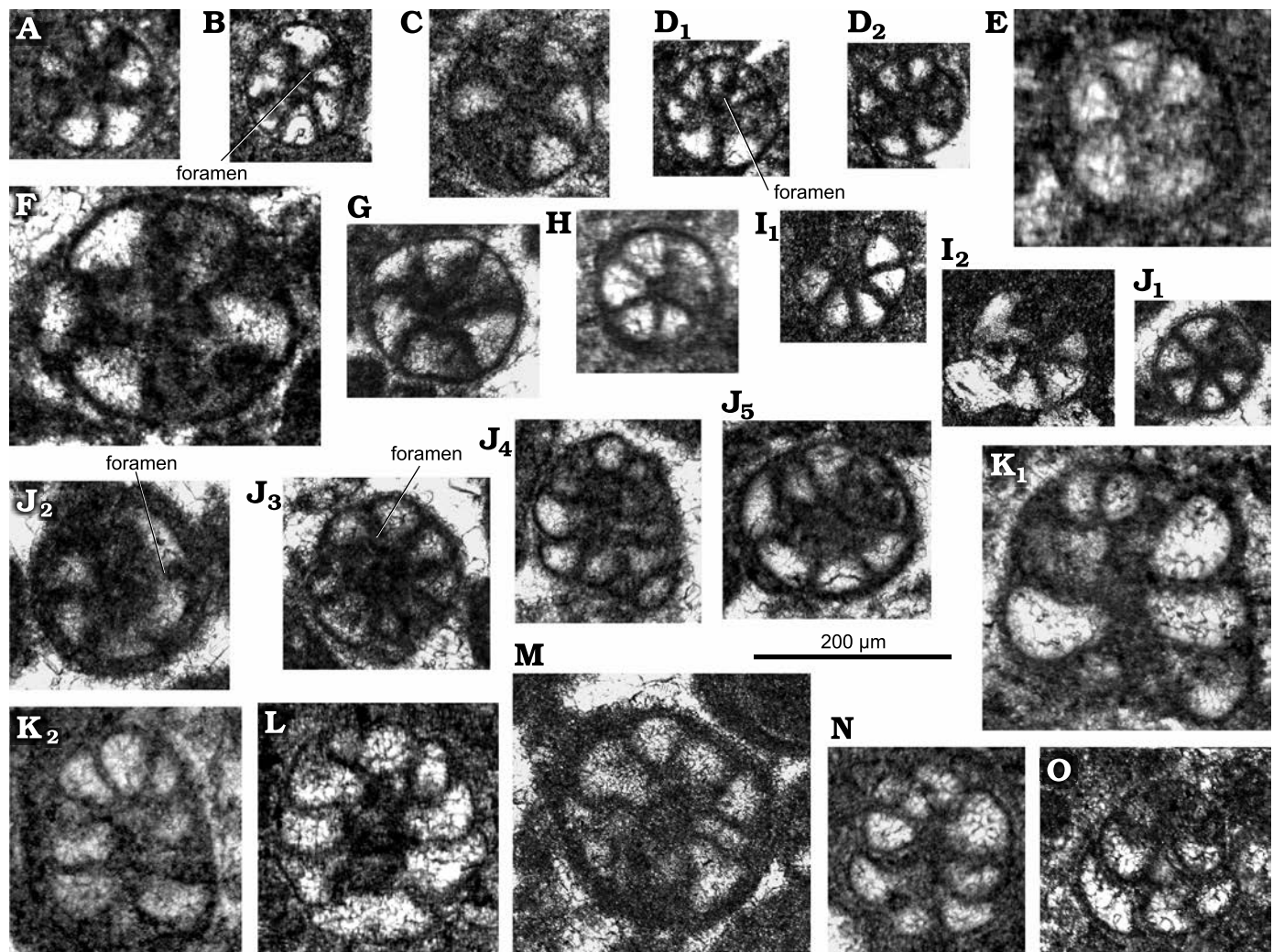


Fig. 4. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, San Lorenzello section, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous (A–L) and Križ section, Mljet Island, Croatia Hauterivian–lowermost Barremian, Lower Cretaceous (M–O); various transverse (A–J₃, J₅, M) and oblique (J₄, K, L, N and O) sections. A. Thin section DiSTAR-L28. B. Thin section DiSTAR-L33-1. C. Thin section DiSTAR-L34. D. Thin section DiSTAR-L37 with two individuals (D₁, D₂). E. Thin section DiSTAR-L36-2. F. Thin section DiSTAR-L36-2. G. Thin section DiSTAR-L36-2. H. Thin section DiSTAR-L21-2. I. Thin section DiSTAR-L39-2 with two individuals (I₁, I₂). J. Thin section DiSTAR-L36-1 with five individuals (J₁–J₅). K. Thin section DiSTAR-L29 with two individuals (K₁, K₂). L. Thin section DiSTAR-L9-2. M–O. Thin sections IGZ-MK, after Husinec and Sokač (2006: unfigured specimens from Mljet Island, Croatia). Rather large-sized specimens (F and K₁) might belong to microspheric generation.

what is also the case in *Campanellula*. The hyaline outer layer is very thin in *Campanellula* (thickness ~3–7 μm), compared to *Altamirella* (thickness ~5–20 μm) and appears functionally different. SEM observations on well preserved material would be required to decipher the nature of this “hyaline layer” (agglutinated? diagenetic induced?). For the Orbitolinidae, the finely agglutinated character of this layer has been generally assumed (e.g., Douglass 1960), and demonstrated for *Mesorbitolina* (Frijia et al. 2012).

De Castro (1964: 56) remarked that no other genus displays noteworthy similarities with *Campanellula*, an observation that appears still valid today. For an inclusion to any suprageneric category (family, superfamily, etc.) a clear morphological clarification of the internal arrangement of the chamber connections is provided by the three-dimensional model. In any case, the current tax-

onomic concept of treating *Campanellula* as a member of the Dictyoconinae (with uniserial chambers) and its subsequent inclusion into the order Orbitolinina has to be abandoned due to its trochospiral test throughout all stages, thus reinstating De Castro (1964). For the following synonymy, if not otherwise indicated, all references are from areas that were formerly parts of the southern margin of Neo-Tethys.

Campanellula capuensis De Castro, 1964

Figs. 3–10.

1964 *Campanellula capuensis* n. gen., n. sp.; De Castro 1964: 56, pl. 1, pls. 2–6 [in part].

1977 *Orbitolinopsis capuensis* (De Castro, 1964); Chiocchini and Mancinelli 1977: 127, 137, pl. 24: 2.

1978 *Orbitolinopsis capuensis* (De Castro, 1964); Garcia-Hernandez 1978: 215, pl. 25: 1, 3–5.

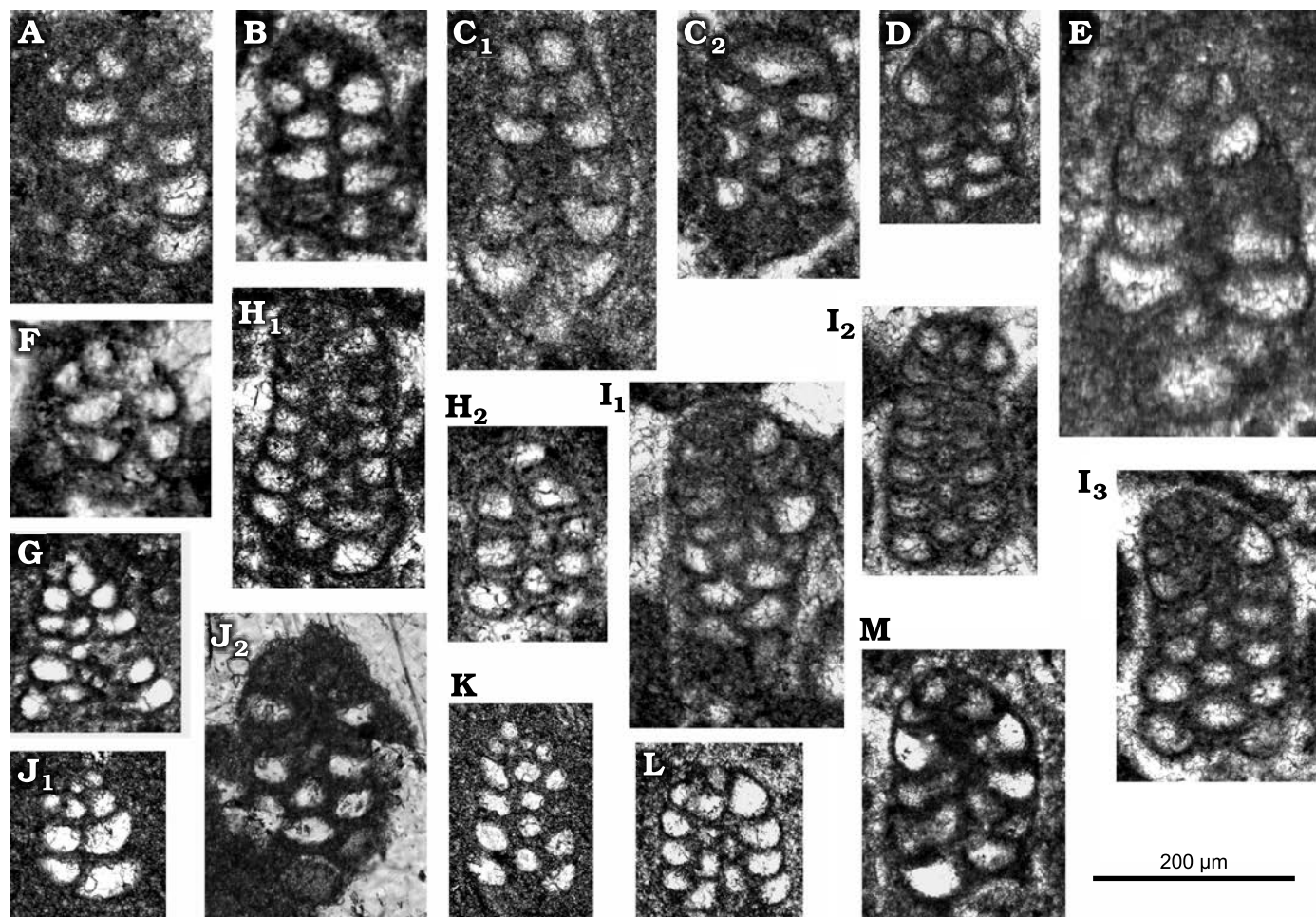


Fig. 5. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, San Lorenzello section, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous; various tangential sections. **A.** Thin section DiSTAR-L33-1. **B.** Thin section DiSTAR-L34. **C.** Thin section DiSTAR-L35 with two individuals (C_1 , C_2). **D.** Thin section DiSTAR-L38-2. **E.** Thin section DiSTAR-L21-2. **F.** Thin section DiSTAR-L13. **G.** Thin section DiSTAR-L59. **H.** Thin section DiSTAR-L37 with two individuals (explain H_1 , H_2). **I.** Thin section DiSTAR-L36-1 with three individuals (I_1 – I_3). **J.** Thin section DiSTAR-L39-1 with two individuals (J_1 , J_2). **K.** Thin section DiSTAR-L39-2. **L.** Thin section DiSTAR-L59. **M.** Thin section DiSTAR-L33-3. Rather large-sized specimen (E) might belong to microspheric generation.

1978 *Orbitolinopsis capuensis* (De Castro, 1964); Sokač and Velić 1978: 247, 249, pl. 8: 3, 4.

1982 *Orbitolinopsis capuensis* (De Castro, 1964); Peybernès 1982: pl. 2: 1, 2.

1982 *Campanellula capuensis* (De Castro, 1964); Barattolo 1982: 826–827, figs. 2, 3.

1984 *Orbitolinopsis* (?) *capuensis* (De Castro, 1964); Luperto Sinni and Masse 1984: 342, 346, 347, 350, pl. 40: 1–2.

1994 *Campanellula* cf. *C. capuensis* De Castro, 1964; Schindler and Conrad 1994: 72, pl. 5: 1.

1995 *Campanellula capuensis* De Castro, 1964; Chiocchini et al. 1995: 22, pl. 5: 16, 19, 20, 22–27.

1995 *Campanellula capuensis* De Castro, 1964; Carras 1995: 145, pl. 47: 1–3.

non 1995 *Campanellula capuensis* De Castro, 1964; Arnaud-Vanneau and Sliter 1995: 551, pl. 1: 12 (Central Pacific area).

non 1995 *Campanellula* cf. *capuensis* De Castro, 1964; Bucur et al. 1995: pl. 7: 12 (most likely an orbitolinid; Eastern Serbia = northern margin of Neo-Tethys).

1996 *Campanellula capuensis* De Castro, 1964; Claps et al. 1996: 10, 19–22, pl. 1: 9, 11–12.

2006 *Campanellula capuensis* De Castro, 1964; Husinec and Sokač 2006: 421, 425: 2, 7E, I–M.

2007 *Campanellula capuensis* De Castro, 1964; Bruni et al. 2007: 46, 49: 2, 3, pl. 3: 7–9.

2007 *Campanellula capuensis* De Castro, 1964; Velić 2007: 31, 42, pl. 11: 1–4.

2008 *Campanellula capuensis* De Castro, 1964; Chiocchini et al. 2008: 17, 42, tab.6, pl. 17: 4.

2012 *Campanellula capuensis* De Castro, 1964; Chiocchini et al. 2012: pl. 10: 8, 9.

2018 *Campanellula capuensis* De Castro, 1964; Cruz Abad 2018: 64, fig. 58.

non 2019 *Campanellula capuensis* De Castro, 1964; Gheiasvand et al. 2019: fig. 8g–h (N-Iran = northern margin of Neo-Tethys).

2020 *Campanellula capuensis* De Castro, 1964; Amodio et al. 2020: 6, 8–10, fig. 6: D–H.

Holotype: specimen in axial section (De Castro, 1964, pl. 1: 1), thin section IP-A.281.1.

Type locality: Castelmorrone, W slope of Mt. Castellone, Caserta Province, Campania Region, Italy.

Type horizon: White detritic limestone, De Castro (1964), *Campan-*

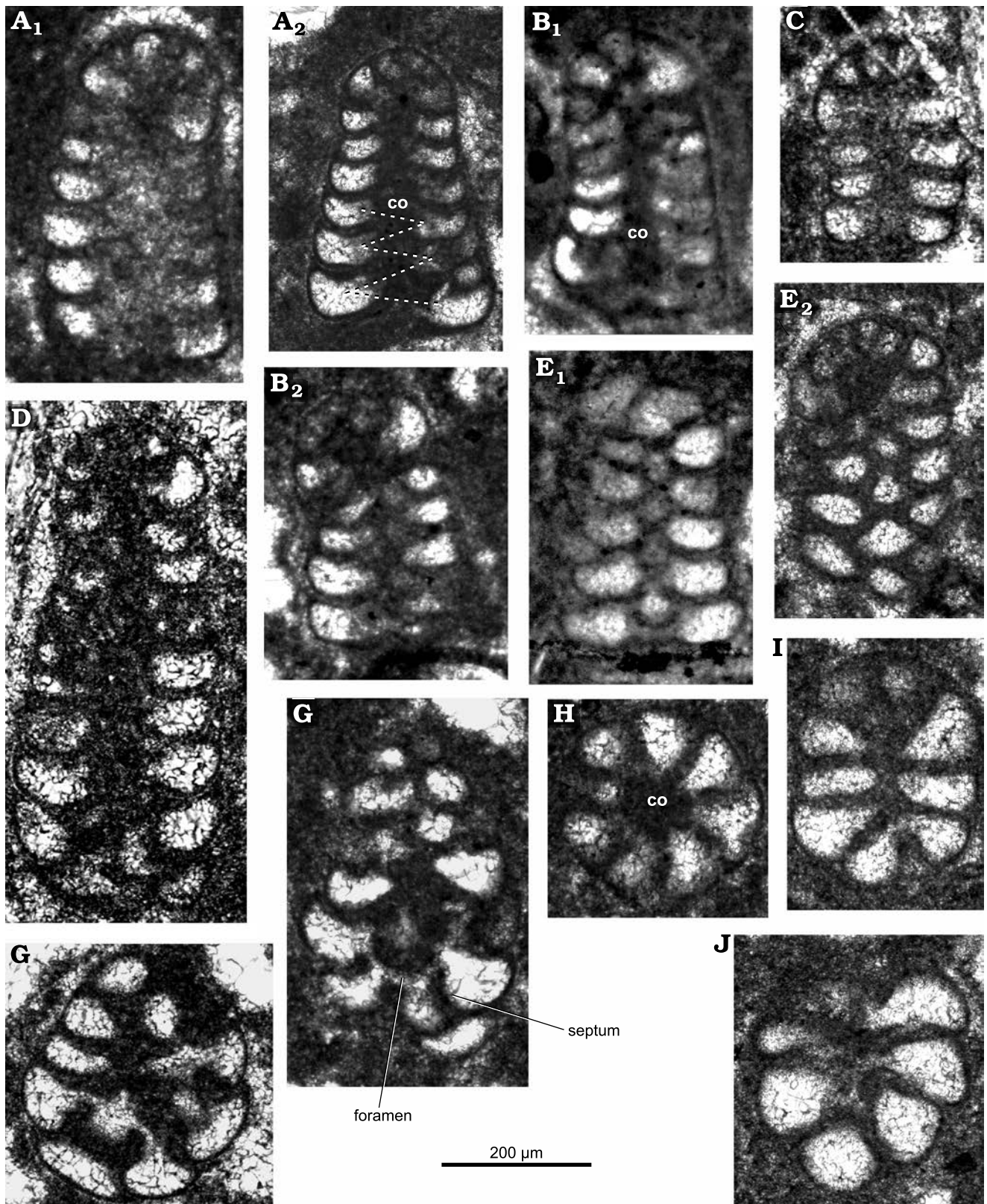


Fig. 6. Lituolimid foraminifer *Campanellula capuensis* De Castro, 1964, Castel Morrone, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous. (Sub)axial sections (A–E), oblique sections (F, G, I, J), transverse section (H). A. Thin section DiSTAR-BA.4418.2 with two individuals (A₁, A₂); the dashed line in A₂ points out alternated chambers resulting from the trochospiral arrangement. B. Thin section DiSTAR-BA.4418.3 with two individuals (B₁, B₂). C. Thin section DiSTAR-BA.4418.12. D. Thin section DiSTAR-BA.4418.15. E. Thin section DiSTAR-BA.4418.1 with two individuals (E₁, E₂). F. Thin section DiSTAR-BA.4418.13. G. Thin section DiSTAR-BA.4418.11. H. Thin section DiSTAR-BA.4418.3. I. Thin section DiSTAR-BA.4418.4. J. Thin section DiSTAR-BA.4418.2. Abbreviation: co, columella.

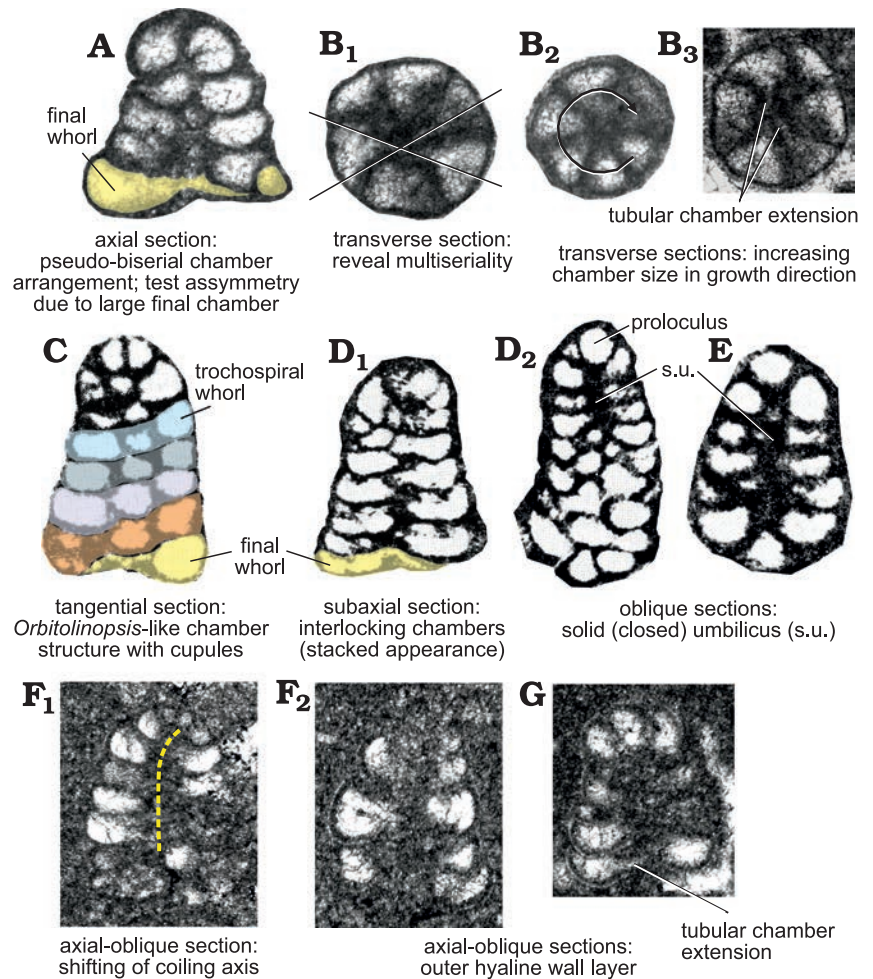


Fig. 7. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, from the Lower Cretaceous of Italy, un-angled; explanatory notes to the test structure based on different sections (not to scale). **A, B.** San Lorenzello section. **A.** Thin section DiST-SL99C.1, upper Hauterivian. **B.** Thin section DiSTAR-L36.1, lower Barremian, with three different individuals (B_1 , B_2 , B_3). **C.** Thin section IP-A.679.1 (from De Castro 1964: pl. 1: 10), paratype, Cava Grande, Punta Orlando, Hauterivian–Barremian. **D.** Thin section IP-A.281.5 with two different individuals (D_1 , D_2) (from De Castro 1964: pl. 1: 3, 5), paratype, Castel Morrone, Caserta, Hauterivian–Barremian. **E.** Thin section IP-A.85.3 (from De Castro 1964: pl. 1: 14), Monte La Foresta, Salerno, Hauterivian–Barremian. **F, G.** San Lorenzello section. **F.** Thin section DiSTAR-39.2 with two different individuals (F_1 , F_2), lower Barremian; dashed line in F_1 indicates the coiling axis; **G.** Thin section DiST-SL90/91.1, upper Hauterivian.

ellula capuensis Biozone De Castro (1991), late Hauterivian–earliest Barremian, Cretaceous.

Description.—Test rather small (height ~0.2 mm), high conical to cylindroconical, with low trochospirally enrolled chambers. Adult specimens consist of up to 10 whorls

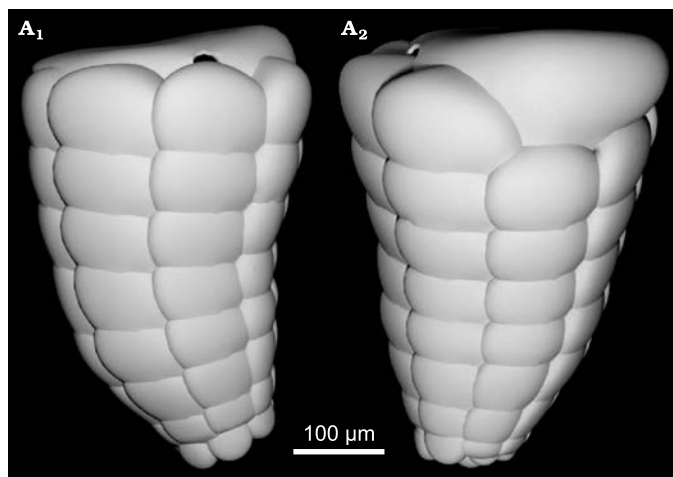


Fig. 8. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, from Castel Morrone, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous. IP-A.281.1, 3D test reconstruction of the holotype (De Castro 1964: pl. 1: 1): Left (A_1) and frontal right (A_2) views of the test.

(mostly 6–8; 6–11 [De Castro 1964]). Apical, spherical proloculus followed by up to seven trochospirally coiled whorls (Figs. 3A₂, 6A₂) each with five to eight chambers (Figs. 4H, 6H, 7B). The first whorls with a reduced number of chambers per whorl (? informal early praevalvulinid ontogenetic stage sensu Septfontaine 2020) may be slightly inclined towards the axis of the main adult stage (Figs. 5I₃, 6A₁, 7F₁). In the adult stage the plan of one whorl in side view of the test is inclined about 30° with respect to the axis of the test, sometimes sub-horizontal (Fig. 8A, B). Chambers are irregular, subtriangular in transverse sections reaching deep into the umbilical region by means of blind tubular extensions (Figs. 6J, 7B₃). The simple (= undivided) chambers only gradually increase in size as added (compare Figs. 4G, J₁, 7B₂); the ultimate chamber may occupy half to almost three-fourths of the test circumference (Figs. 3J, 6B₂, 7A, B₃, C, D₁). In tangential section, the chambers arrangement recalls a fish scales pattern, vertically aligned (Figs. 5H₁, I₂, I₃, J₂, K, 6E). The foramina connecting chambers within a whorl are positioned at the inner chamber margin. The central part of the test is filled by anastomosed (labyrinthic) calcitic extensions from the chambers (= modification of a kind of a tooth-plate?), forming either a central mass or a columella filled by calcitic material (Fig. 6A₂, B₁, H). The test wall is dark

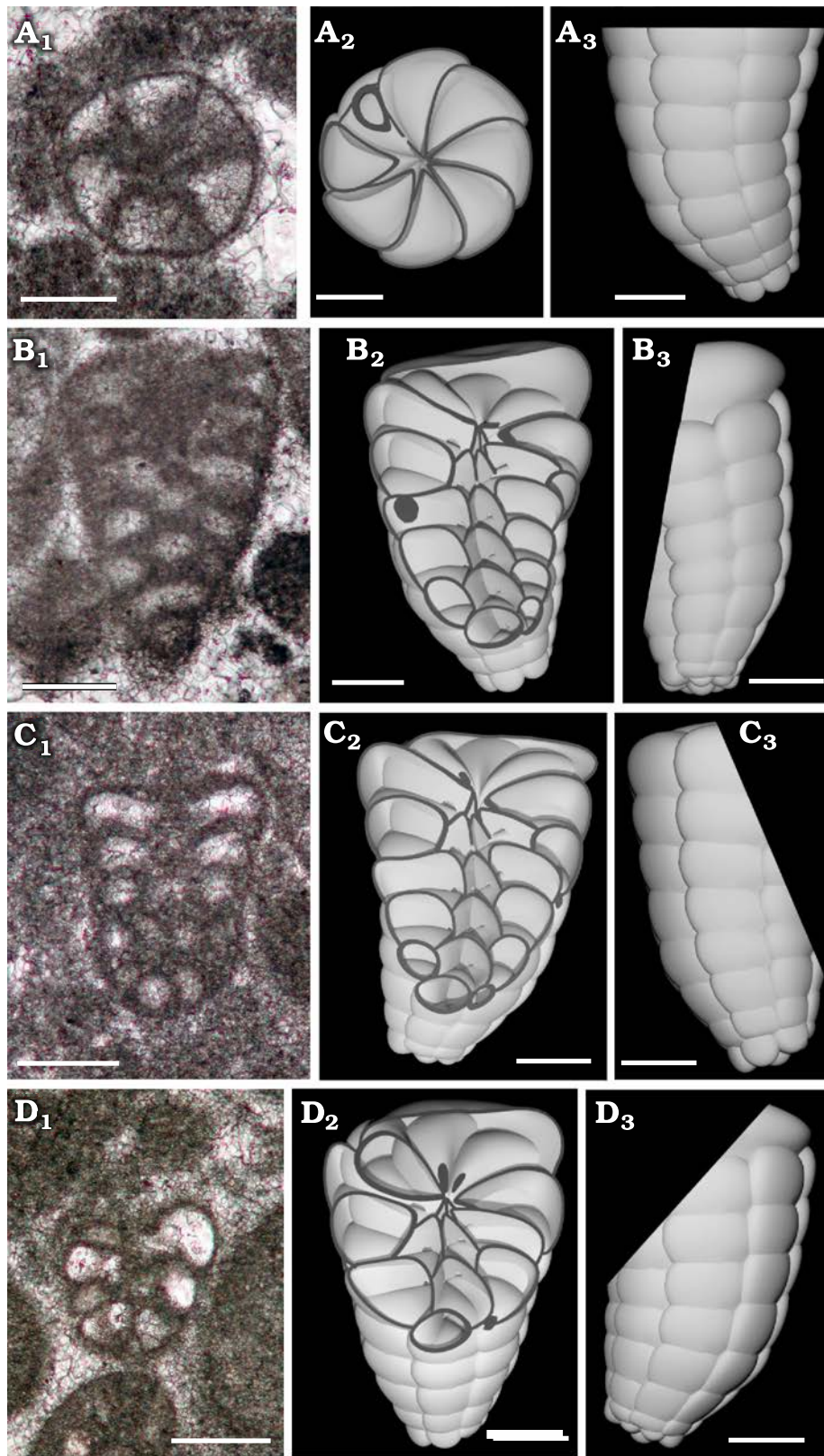


Fig. 9. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, from Castel Morrone, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous. **A.** DiSTAR-L36.1, transversal section showing six chambers per whorl (A₁), compared with the 3D model transversally cut (upper view displaying eight chamber per whorl (A₂), also represented in lateral view (A₃). **B.** DiSTAR-L36.1 tangential section (B₁), compared with the 3D model tangentially cut (frontal view of the section, B₂), also represented in lateral view (B₃). **C.** DiSTAR-L35.1, tangential-oblique section (C₁), compared with the 3D sectioned model (cut in frontal view, C₂), also represented in lateral view (C₃). **D.** DiSTAR-L34.1, oblique section through last tours (D₁), compared with the 3D sectioned model (cut in frontal view, D₂), also represented in lateral view (D₃). Scale bars 100 μ m.

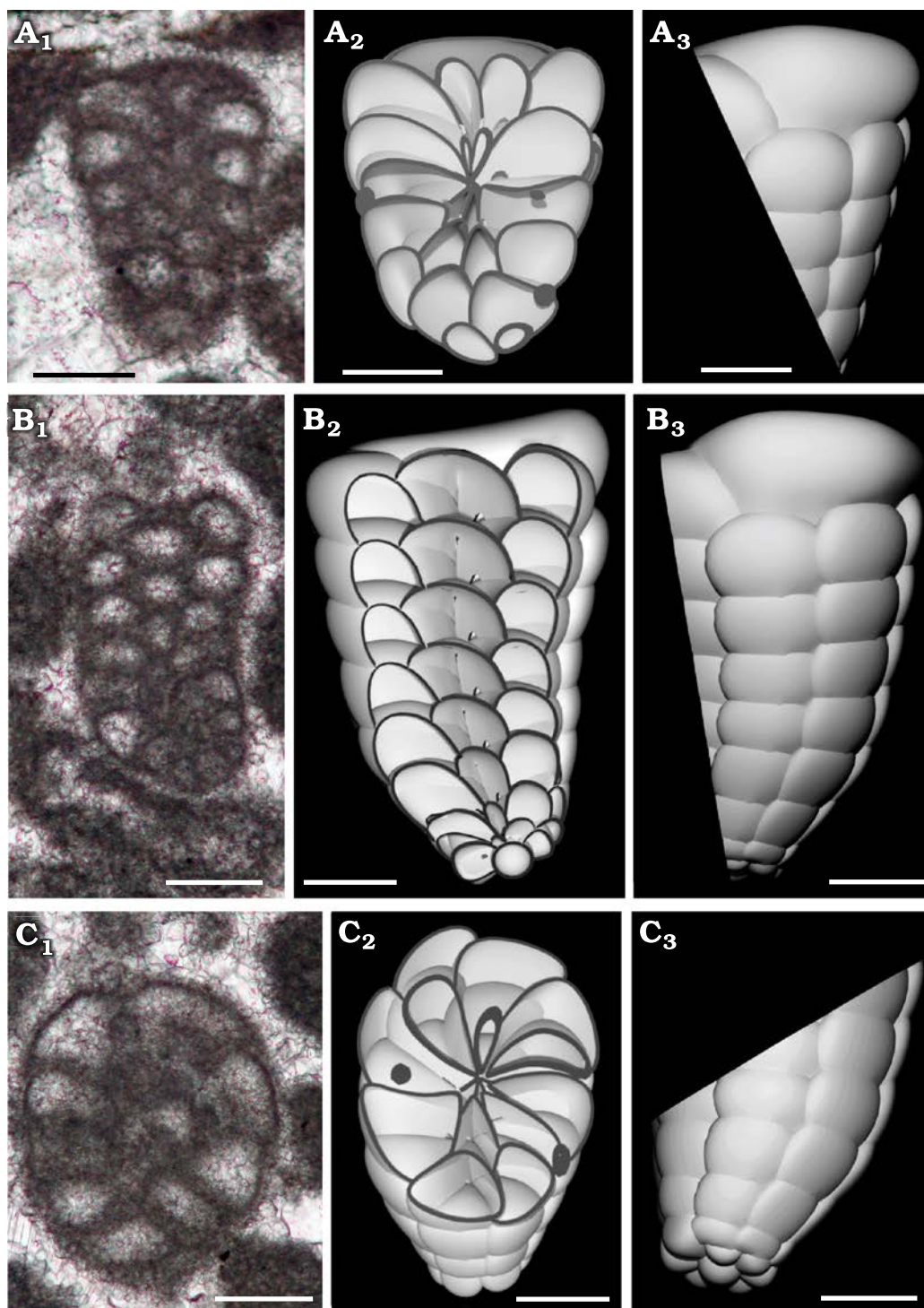


Fig. 10. Lituolinid foraminifer *Campanellula capuensis* De Castro, 1964, from Castel Morrone, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous. **A.** DiSTAR-L36.1, oblique section showing (A₁), compared with the 3D sectioned model (cut in frontal view, A₂), also represented sideways (A₃). **B.** DiSTAR-L36.1, longitudinal section (B₁), compared with the 3D sectioned model (cut in frontal view, B₂), also represented sideways (B₃). **C.** DiSTAR-L36.1, oblique section (C₁), compared with the 3D sectioned model (cut in frontal view, C₂), also represented sideways (C₃). Scale bars 100 μ m.

microgranular (?finely agglutinated) exhibiting a rather thin umbilical layer made of clear agglutinated microgranular calcite or quartz grains per whorl (Figs. 3C₁, F, 4O, 5D, 6D, F). Test most likely dimorphic expressed by specimens of bigger size assumed to belong to the microspheric generation (Figs. 3A, K₂, 4F, K₁).

3D rendering.—A three-dimensional model has been performed to obtain detailed insight of the perspective representation of the chamber arrangement. The reconstruction is based primarily on the holotype (De Castro 1964: pl. 1: 1) for the general shape in axial section. Characters such as number, shape, and size of chambers per tour are inferred by the analy-

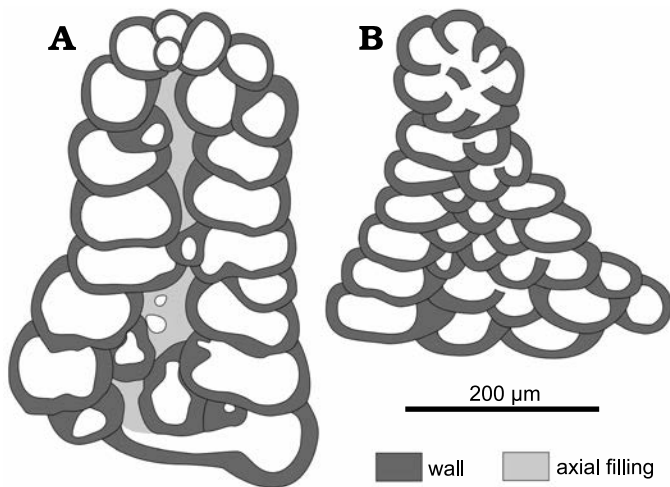


Fig. 11. Scheme of the species of *Campanellula* De Castro, 1964. A. *Campanellula capuensis* De Castro, 1964, IP-A.281.1, holotype (drawing from De Castro 1964: pl. 1: 1), Castel Morrone, Italy, upper Hauterivian–lower Barremian, Lower Cretaceous. B. *Campanellula herishtensis* Schlagintweit, Rashidi, and Hanifzadeh, 2019, T 72-6 (number Gmm 13950F110), holotype (drawing from Schlagintweit et al. 2019: fig. 5L), Ardakan, Province of Yazd, Central Iran, lower Gargasian, Aptian, Lower Cretaceous.

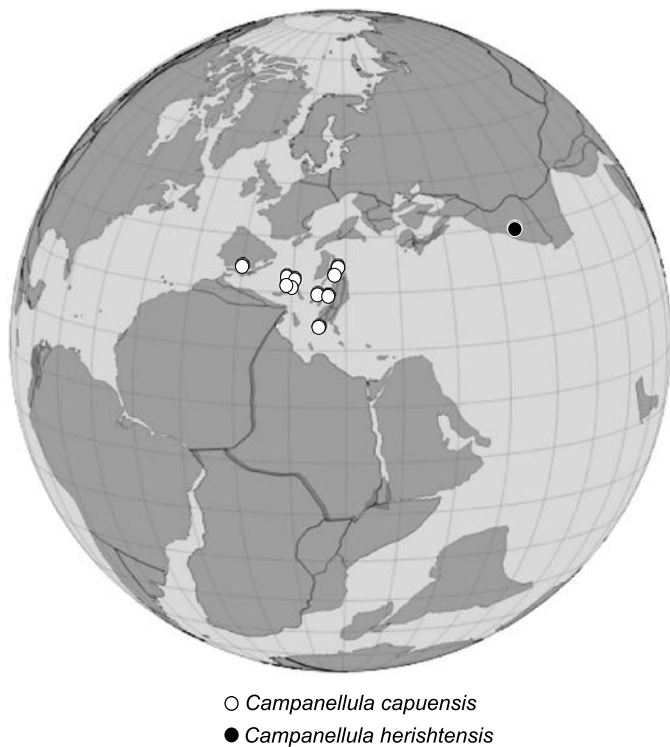


Fig. 12. Palaeobiogeographic distribution of species of *Campanellula* De Castro, 1964. Occurrence of species has been plotted on an Early Cretaceous (ca.120 Ma) paleogeographic map, after <http://portal.gplates.org/>.

sis of numerous transversal and oblique sections. In Fig. 8 the reconstruction is rendered in left view (Fig. 8A) and frontal right view (Fig. 8B), positioning the early stage downwards and inner side of the curvature to be frontal. Afterwards, the 3D model has been “sliced” and the resulting “slices” compared with similar sections from the San Lorenzello material (Figs. 9, 10). However, it is a matter of fact that variability

in size and shape of specimens will never allow a perfect correspondence between a sectioned specimen and a “slice” of a 3D model. Nevertheless, if the reconstruction accurately follows the constraints implied by specimens in thin section, the model can be rather faithful to the original and “slicing” predict internal structure of the foraminifer.

Remarks.—When describing *Campanellula*, De Castro (1964) remarked the rather low trochospirally coiled chambers in successive tight whorls and their slow increase in numbers during ontogeny. Due to this observation, De Castro (1964: 55) “did not exclude the possibility that individual whorls might exhibit uniserially-arranged chambers” (“non si esclude ... che vi possa essere qualche giro con camere disposte in serie” in the original Italian text). Further discussion on the test construction of *Campanellula* and the deriving suprageneric classification goes back to Schroeder in Macoin et al. (1970). In this work, specimens of a conical foraminifer attributed to *Campanellula capuensis* are described from the Lower Cretaceous of Algeria showing a different morphology. Its attribution to the orbitolinid genus *Orbitolinopsis* Henson, 1948, was based on an interpretation of the adult chambers that should be arranged rectilinear and not trochospirally coiled. In fact, the tangential sections illustrated by Macoin et al. (1970: pl. 2: 1–4, 5, 8) display an oblique cross-wise arrangement of the foramina connecting successive rectilinear chambers as in *Orbitolinopsis* (see also Arnaud-Vanneau 1980). Therefore, the authors introduced the new combination *Orbitolinopsis capuensis* (De Castro, 1964) included in the family Orbitolinidae and subfamily Dictyoconinae. As Schroeder in Macoin et al. (1970: 255) correctly stated, such an arrangement contradicts a trochospirally coiled test where direction of both coiling and foramina are the same. Such an arrangement of foramina has not been observed in the material studied from the type-area where a throughout trochospirally coiled chamber arrangement is obvious. Many of the transverse sections of Macoin et al. (1970) are equivalent to the Italian material indicating a trochospiral chamber arrangement often with the last and greatest chamber sectioned accounts for a slightly irregular (= not perfectly rounded) outline. The Algerian specimens are herein interpreted as being different in exhibiting a trochospirally coiled early and rectilinear adult parts, so that an investigation of the Algerian material is needed for further clarification.

The main differences between *Campanellula capuensis* De Castro, 1964, and *Campanellula herishtensis* Schlagintweit, Rashidi, and Hanifzadeh, 2019, are the morphology and size of the test. *Campanellula capuensis* displays a higher conical test and a greater size (Fig. 11).

Stratigraphic and geographic range.—*Campanellula capuensis* is mostly widespread in the Adriatic Plate (Apulian Plate sensu Stampfli and Borel 2004; Fig. 12). *Campanellula herishtensis* is restricted to the type locality (late Aptian, Central Iran).

Table 1. The *Campanellula* De Castro, 1964, in the context of current classifications of agglutinated Foraminifera (Pawlowski et al. 2013; Kaminski 2014). * not Moullade (1965) as indicated in Kaminski (2014).

| <i>Campanellula</i> De Castro, 1964 | | | |
|-------------------------------------|---|---|--|
| Classifications | Current (Kaminski 2014) | Option 1 | Option 2 |
| Phylum | Foraminifera d'Orbigny, 1826 | | |
| Class | Globothalamea Pawlowski, Holzmann, and Tyszka, 2013 | | |
| Subclass | Textulariana Mikhalevich, 1980 | | |
| Order | Loftusiida Kaminski and Mikhalevich in Kaminski, 2004 | Lituolida Lankester, 1885 | |
| Remark | An inclusion into the order Textulariida Delage and Hérouard, 1896, is excluded due to the lack of a canaliculated wall structure (see Kaminski 2004). | | |
| Suborder | Orbitolinina Kaminski, 2004 | Ataxophragmiina Fursenko, 1958 | Verneuilinina Mikhalevich and Kaminski in Kaminski, 2004 |
| Definition | Test trochospiral or conical, later stage may have reduced number of chambers per whorl, or may become uniserial and rectilinear; chamber interior of advanced taxa subdivided by vertical or horizontal exoskeletal partitions or both, by radial or transverse partitions, or with interseptal pillars (Kaminski 2004). | Test free or attached, typically high trochospiral with an asymmetrical spire, may have a conical form, or have elongated vertical chambers inclined to previous whorls; coiling may reduce to biserial or uniserial; chambers may have complex inner structure (buttresses, pillars, radial partitions, columella), or form chamberlets; wall agglutinated typically with calcareous cement; aperture basal, a wide horizontal slit at the base of the apertural face of the last chamber, may be subdivided by a median lobe (Kaminski 2014). | Test high trochospiral throughout or only in the initial part, later part may have an increased or decreased number of chambers per whorl or may become uniserial or cyclical; wall simple; aperture basal at least initially, later may become terminal, single or multiple, some genera with inner apertural structures (Kaminski 2004). |
| Remarks | “The predominantly high trochospiral to conical Ataxophragmiina and Orbitolinina possess internal partitions and interseptal pillars” (Kaminski 2004: 241). | | “The Trochamminina... comprise the low trochospirally coiled forms, while the Verneuilinina encompass the high trochospiral genera with simple walls” (Kaminski 2004: 241). |
| Superfamily | Orbitolinoidea Martin, 1890 | not assignable | not assignable |
| Remark | Orbitolinoidea do not comprise taxa with trochospiral chambers throughout (Loeblich and Tappan 1987). | no remarks | no remarks |
| Family | Orbitolinidae Martin, 1890 | not assignable | not assignable |
| Subfamily | Dictyoconinae Schubert, 1912* | not assignable | not assignable |

Discussion

With the assumed orbitolinid test morphology including uniserial adult and subdivided chambers (see Macoin et al. 1970), *Campanellula* was (Loeblich and Tappan 1987), and still is included in the order Loftusiida Kaminski and Mikhalevich, 2004, suborder Orbitolinina Kaminski, 2004, respectively (Kaminski 2014) (Table 1). Based on the throughout trochospirally coiled test with simple chambers (De Castro 1964; this work), *Campanellula* can be included into the order Lituolida Lankester, 1885, that comprises all non-canaliculate taxa with well-defined chambers (at least in the adult stage), and a simple imperforate wall (Kaminski 2004: 240). The current classification and two further options, all based on Kaminski (2004, 2014) are summarized in Table 1. These options refer to the primary importance of the wall structure, combined with the overall test morphology (e.g., coiling type), chamber arrangement, and the presence/absence of internal chamber subdivisions. Another approach, however, considers the general test architecture of

prime importance as for example proposed by Septfontaine (1988) for the Mesozoic agglutinated (larger) benthic foraminifera. With some characters (e.g., test shape and trochospiral coiling, high number of chambers per whorl) common to taxa not directly phylogenetically related like *Praechrysalidina* Luperto Sinni, 1979, *Kilianina* Pfender, 1933, *Neokilianina* Septfontaine, 1988, *Campanellula* could then also be placed within the Textulariida Delage and Hérouard, 1896.

The order Textulariida is defined by taxa that possess a canaliculate wall (Kaminski 2014). It must be noted that the presence of a pseudokeriotheca (canaliculate wall) and the related possibility for observation may be related to the size of the test and the thickness of the marginal chamber wall (Vachard et al. 2004), as very small taxa like *Campanellula* or *Kilianina* (without pseudokeriotheca) have a height (vertical axis) 5–10 times less than e.g., *Redmondoides lugeoni* (Septfontaine, 1977) or *Chrysalidina gradata* d'Orbigny, 1839, both exhibiting canaliculate (pseudokeriothecal) wall (De Castro 1981).

A suprageneric placing in a basket along with larger taxa aside *Praechrysalidina*–*Chrysalidina* (e.g., the informal morphogroup of the valvulinids, Septfontaine 1988, 2020) might only be a temporary solution. The question of the importance (and position) of the wall (canaliculate or not) is still pendant, and not obvious in the classification of Kaminski (2004) as “alveolar” or “canaliculate” or “non alveolar” (like *Kilianina* and *Campanellula*). These terms are not clearly defined and the corresponding morphotypes variously distributed in the different suprageneric taxa (order, sub-order) without evolutive justification. In conclusion, the suprageneric position of *Campanellula* is herein intentionally left open. It is concluded that *Campanellula* has to be removed from the order Loftusiina and the sub-order Orbitolinina, instead it should be included into the order Lituolida and the suborder Verneuilinina (Table 1).

Conclusions

This work presents a comparison between the *Campanellula capuensis* material from the type locality (De Castro 1964) from which an original 3D model has been reconstructed and additional material was sampled at a new site of San Lorenzello (Amodio et al. 2020). This procedure unequivocally defines that *Campanellula capuensis* exhibits a trochospiral structure that clearly persists in all stages of shell growth, thus reinstating the original description provided by De Castro (1964). One morphological question still remains open and concerns the rectilinear evolution of the adult portion of the shell, which is only present in the Algerian specimens of Macoin et al. (1970) and which appears, at present, to be the only substantial difference from the material studied in this work. This feature would be worth considering but it is beyond the scope of the present paper. Based on our results and the present taxonomic concept of agglutinated benthic foraminifera, the genus *Campanellula* is excluded from the order Loftusiina, sub-order Orbitolinina respectively, instead it is assigned to the order Lituolida, suborder Verneuilinina.

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