Palaeogeography, Palaeoclimatology, Palaeoecology 648 (2024) 112262

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Success and demise of exceptionally preserved terebratulide brachiopod accumulations in a Jurassic (early Pliensbachian) tropical lagoonal setting (Southern Alps, Italy): brachiopod response to environmental changes

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ARTICLE INFO

Editor: Dr. Howard Falcon-Lang

Keywords:
Brachiopods
Taphonomy
Shell accumulations
Palaeoecology
Pliensbachian
Southern Alps

ABSTRACT

During the Early Jurassic, the shallow marine carbonate platforms of the western-Tethys margins were characterized by highly diverse benthos including larger foraminifera, sponges, bivalves, gastropods, brachiopods, echinoderms, and dasycladalean calcareous algae. In this paper, we document examples of such assemblages within the lower Pliensbachian part of the Rotzo Formation (upper *Orbitopsella* Zone) of the Southern Alps, Italy. This carbonate succession was deposited in a complex mosaic of marine and brackish habitats within a tropical lagoon of the Trento Platform area. Large terebratulide brachiopod shells form autochthonous accumulations comprising exceptionally well-preserved monospecific assemblages of *Lychnothyris rotzoana*. These brachiopod-bearing successions were analysed in terms of biotic components, microfacies analysis, shell biofabric (three-dimensional arrangement of skeletal elements), and taphonomic signatures to understand brachiopod response to changing conditions within a highly variable lagoonal palaeoecosystem. Findings show that terebratulide shell accumulations are dominated by adult specimens and juveniles are rare. The brachiopods thrived during low energy conditions that resulted in the accumulation of highly temporally-condensed shell beds. Stabilized by microbialite encrustations, the shells were not re-oriented during the subsequent rapid burial. The abrupt demise of these communities was possibly related to rapid environmental change, and causal factors are discussed. The medium-term response of brachiopods to the relatively instable ecosystem of the tropical lagoon shows that they were not able to adapt to continuous perturbations, and that continuing stress severely compromised the resilience of benthic taxa.

1. Introduction

During the Early Jurassic, the western Tethyan margins were characterized by diversified marine habitats ranging from tidal to shallow-water carbonate platform settings and shallow bathyal pelagic plateaux. After the end-Triassic mass extinction (e.g., Alroy, 2010; Schoepfer et al., 2022), the Early Jurassic witnesses the appearance of a number of new biotic groups. These include larger lituolid foraminifera showing complex shell architectures as well as the peculiar large lithiotid bivalves, which thrived along the shallow-water carbonate Tethyan and Panthalassa margins from southern Europe, northern Africa, through southeast Asia to western America (Broglio Loriga and Neri, 1976; Geyer, 1977; Lee, 1983; Nauss and Smith, 1988; Buser and Debeljak, 1994; Leinfelder et al., 2002; Fraser et al., 2004; Posenato and Masetti, 2012). Extraordinary examples of these benthic faunas are found in the unique Lower Jurassic carbonate platform succession of the Trento Platform in the Southern Alps (Bosellini, 1989). These faunas thrived in a complex mosaic of habitats within a highly variable lagoonal palaeoecosystem (Bosellini and Broglio Loriga, 1971; Clari, 1975; Broglio Loriga and Neri, 1976; Beccarelli-Bauck, 1988; Posenato and Masetti, 2012; Posenato et al., 2013a, 2013b). The successions are characterized by a highly diverse flora and fauna which thrived in tropical lagoonal settings (Bosellini and Broglio Loriga, 1971; Posenato and Masetti, 2012).

Within the well-studied Pliensbachian succession of the Trento Platform (Fig. 1A), known as the Rotzo Formation, especial interest has

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https://doi.org/10.1016/j.palaeo.2024.112262
Received 12 April 2024; Received in revised form 10 May 2024; Accepted 10 May 2024
Available online 12 May 2024

been devoted to bivalve mass occurrences consisting of autochthonous lithiotid accumulations and isognomonid-like bivalve carpets. These have been interpreted with respect to bottom oxygenation levels, accumulation patterns among different bivalve taxa, functional significance and climatic control on shell microstructures (Posenato and Masetti, 2012; Bassi et al., 2015; Brandolese et al., 2019; Posenato et al., 2022; Posenato and Crippa, 2023).

The common occurrence of larger benthic foraminifera (*sensu* Hottinger, 2006) and dasycladalean algae in the Rotzo Formation points to upper euphotic marine conditions (Hottinger, 1997; Hohenegger, 2004). The larger benthic foraminifera belong to Tethyan lituolid faunas characterized by *Orbitopsella* spp. along with *Bosniella oenensis* Gušić, 1977, *Everticyclammina praevirguliana* Fugagnoli, 2000, *Lituosepta compressa* Hottinger, 1967, *Lituosepta recoarensis* Cati, 1959, *Paleomayncina termieri* (Hottinger, 1967), *Pseudocyclammina liasica* Hottinger, 1967, *Pseudopfenderina butterlini* (Brun, 1962) (Fugagnoli, 2004; BouDagher-Fadel and Bosence, 2007; Fugagnoli and Bassi, 2015; Gale and Kelemen, 2017; Sevillano et al., 2020). These larger foraminifera represent forms

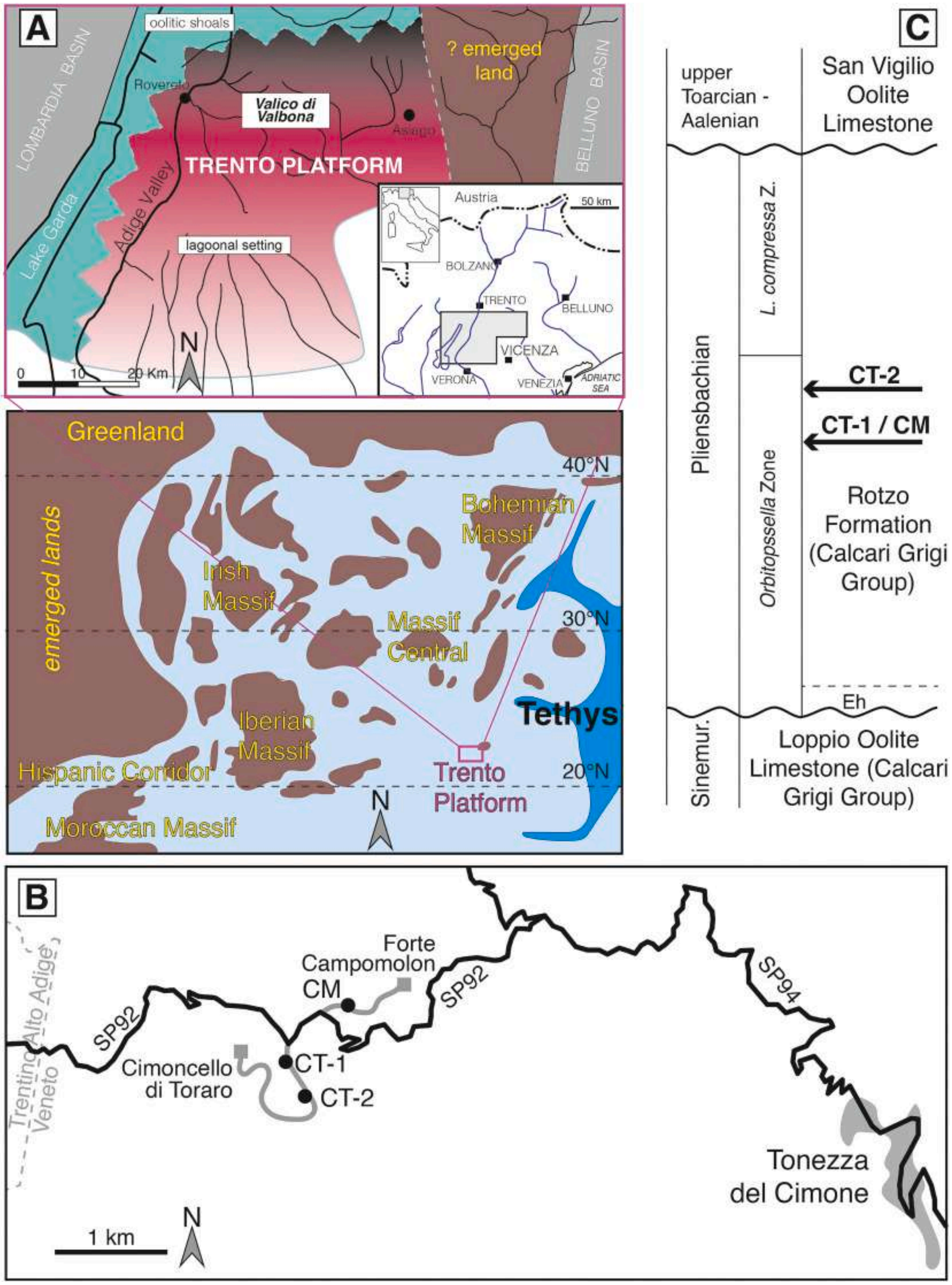

Fig. 1. The study area (Valico di Valbona, Vicenza) is located in the Lower Jurassic Trento Platform (Southern Alps, northern Italy), a palaeogeographic unit of the western Tethyan margin (A; modified from Posenato and Masetti, 2012; palaeomap from Dercourt et al., 2000). (B) The three studied stratigraphic sections crop out in Campomolon (CM) and Cimoncello di Toraro (CT-1, CT-2). (C) The studied terebratulide accumulations are located in the middle part of the Rotzo Formation, within the *Orbitopsella* Zone. Eh: *Eomiodon* horizon. Biostratigraphic setting after Fugagnoli (2004).

which have a narrow tolerance to environmental change (Bassoullet and Bergougnan, 1981; Hottinger, 1996) and their occurrence in the Rotzo Formation thus points to a generally stable marine environment (Fugagnoli, 2004). Often associated with these larger benthic foraminifera is the Pliensbachian dasycladalean alga *Palaeodasycladus mediterraneus* (Pia) Pia, 1927. This alga, considered a biostratigraphic marker (Sokač, 2001; Barattolo et al., 1994), has been identified in Tethyan shallow-water carbonate platforms in lagoonal and tidal flat settings (Flügel, 1983; Sokač, 2001; Mancinelli et al., 2005; Posenato et al., 2018; Rychliński et al., 2018; Bucur and Reolid, 2024), and in the Rotzo Formation co-occurs with the photosymbiotic alatoform-chambered bivalve *Opisoma* and isognomonid bivalve carpets (Posenato et al., 2013b; Bassi et al., 2015).

Brachiopods also constitute important faunal elements of this succession and are found not only as common isolated specimens, but also form mass occurrences at discrete intervals (Schauroth, 1865; Tausch, 1890; Bosellini and Broglio Loriga, 1971; Clari, 1975; Vörös, 2009). Brachiopods have, however, yet to be studied in detail with respect to faunal and sedimentary associations, taphonomic signatures and bed form characteristics. The most common rhynchonelliformean brachiopod of the succession is represented by *Lychnothyris rotzoana* (Schauroth, 1865). This terebratulide occurs in the middle part of the formation, in a c. 70 m-thick stratigraphic interval. The *Lychnothyris rotzoana*-bearing interval is characterized by stable positive δ^{13}C values of the bulk rock, corresponding to the proliferation of stenotopic marine benthic communities (Franceschi et al., 2014).

Actualistic investigations concerning the taphonomic signatures of recent and sub-recent shells and their applications to conservation biology have been dominated by studies concerning bivalves (e.g., Fürsich and Flessa, 1991; Kowalewski et al., 1994; Cutler, 1995; Best and Kidwell, 2000; Schneider-Storz et al., 2008; Tsolakos et al., 2021; Edelman-Furstenberg, 2023; Meadows et al., 2023 among others). There have been fewer studies concerning recent brachiopod taphonomy and in particular the compositional fidelity of brachiopod death assemblages. This is in part due to their relatively sparse occurrence in accessible modern settings (Noble and Logan, 1981; Carroll et al., 2003; Tomašových, 2004; Tomašových and Rothfus, 2005; Simões et al., 2005, 2009; Tomašových et al., 2022, 2023). Tomašových et al. (2022, 2023) underscored the contrast between modern brachiopod death assemblages of continental shelves, which are poorly preserved and disarticulated, and the abundant articulated shells record in Paleozoic and Mesozoic shallow-water successions. The authors attributed this pattern to relative low predation, bioturbation and organic carbon recycling prior to the main Cretaceous phase of the Mesozoic Marine Revolution. In fact, present day brachiopod death assemblages show high articulation even in millennial time averaged assemblages, but in bathyal settings only, where alteration processes (bioerosion, predation) are less intensive (Tomašových et al., 2022, 2023). Although brachiopods and their preservation in the fossil record have also attracted attention (Boucot et al., 1958; Alexander, 1984, 1986; Holland, 1988; Alexander and Gibson, 1993; Velbel and Brandt, 1989; Collins, 1991; Ratcliffe, 1991; Baeza-Carratalá, 2011; Lazăr et al., 2011; Nebelsick et al., 2011; Zabini et al., 2012; García Joral et al., 2023), little is known about Mesozoic lagoonal brachiopod assemblages and their palaeoecology.

The purpose of this paper is to describe and interpret Pliensbachian large terebratulide accumulations of the Trento Platform in terms of biogenic components, shell biofabric (i.e., three-dimensional arrangement of skeletal elements), and taphonomic signatures. Two principal palaeoecological aspects of Lower Jurassic terebratulides are addressed: (1) the formation of autochthonous terebratulide mass accumulations, and (2) the effects of environmental changes on these large terebratulide populations.

2. Stratigraphic setting of the brachiopod beds

In the Early Jurassic, the southern Tethyan margin was characterized by a wide shallow-water carbonate platform known as the Trento Platform, represented by two thick sedimentary successions: the Calcari Grigi Group (Hettangian–Pliensbachian) and the San Vigilio Oolite Limestone (upper Toarcian–Aalenian) (Winterer and Bosellini, 1981; Castellarin et al., 2005; Fig. 1). These successions extended from the Adige Valley in the west to the Asiago area in the east (Castellarin et al., 2005; Fig. 1A). The Calcari Grigi Group is subdivided in the Monte Zugna Formation, the Loppio Oolite Limestone, and the Rotzo Formation (Castellarin et al., 2005). The Rotzo Formation has been interpreted as representing a tropical lagoon, with remarkable lateral and vertical facies variability, protected seawards by oolithic shoals and bars and bordered landwards by marshes (Bosellini and Broglio Loriga, 1971; Clari, 1975; Fig. 1A). In the Rotzo Formation, two biostratigraphic units have been distinguished: the *Orbitopsella* Zone (lower–middle part) and the *Lituosepta compressa* Zone (upper part) (Fugagnoli and Loriga Broglio, 1998; Fugagnoli, 2004; Fugagnoli and Bassi, 2015; Fig. 1C).

The stratigraphic interval of the *Orbitopsella* Zone differs from that of the *Lituosepta compressa* Zone in being characterized by higher marlstone abundance and thicker limestone–marl alternations, along with higher abundance of infaunal bivalves (e.g., *Gresslya elongata* Benecke, 1868, *Pholadomya athesiana* Tausch, 1890) and terebratulide brachiopods (*Lychnothyris rotzoana*) (Posenato and Masetti, 2012). Large lithiotid bivalve accumulations are rare (Posenato and Masetti, 2012; Brandolese et al., 2019). In the *L. compressa* Zone, the thin limestone–marlstone and thick biocalcarenite alternations yield bivalve assemblages dominated by epifaunal free-living species (e.g., *Protodiceras pumilum* (Gümbel, 1862), *Pachyrisma* spp.), whereas terebratulide brachiopods are rare and lithiotid accumulations become very abundant (Posenato and Masetti, 2012; Posenato and Crippa, 2023).

The studied large terebratulide beds occur in the Rotzo Formation within the upper Calcari Grigi Group. This study was carried out on the sedimentary successions cropping out in the Altopiano di Tonezza–Folgaria area where the Rotzo Formation attains its maximum thickness (c. 210 m). In this area, the base of the formation is characterized by laminated mudstone and fissile, dark grey and black organic-rich marlstone and claystone (c. 10 m in thickness), yielding abundant pavements of the thin-shelled bivalve *Eomiodon serradensis* (Tausch, 1890) (i.e., *Eomiodon* horizon; Posenato et al., 2013a; Fig. 1). These monotypic to paucispecific pavements recorded salinity- and oxygen-depleted environments during a short-term warm-humid climatic phase (Boomer et al., 2001; Posenato et al., 2013a). The overlain lithologies of the Rotzo Formation consist of mudstone-wackestone and marls alternations (c. 40 m in thickness), nodular wackestone-packstone and marl alternations (c. 100 m in thickness), and c. 60 m-thick biocalcarenites with large-lithiotid accumulations.

3. Material and methods

Three stratigraphic sections containing the studied terebratulide brachiopod shell accumulations were measured: Cimoncello di Toraro 1 (CT-1), Cimoncello di Toraro 2 (CT-2) and Campomolon (CM; Figs. 1–2). The Cimoncello di Toraro sections crop out along the military road at the Valico Valbona (SP92; N 45°51′44.536“, E 11°16’8.133”), whereas the Campomolon section is located along the road to Forte Campomolon (N 45°52′20.413“, E 11°17’5.831”; Fig. 1B). These sections, analysed with respect to biogenic composition including microbialites, carbonate microfacies and taphonomic features, are stratigraphically located in the middle part of the Rotzo Formation corresponding to the upper *Orbitopsella* Zone, spanning the early Pliensbachian (Fugagnoli and Loriga Broglio, 1998; Fugagnoli, 2004; Fig. 1C).

Facies analysis was based on field observations as well as thin sections (c. 5 × 5 cm). Larger rock samples including the studied terebratulide accumulations were sectioned perpendicular to the bedding plane and polished. Each brachiopod assemblage was defined by the brachiopod shell size, shell orientation and number of articulated specimens, along with a qualitative assessment of associated bioclasts.

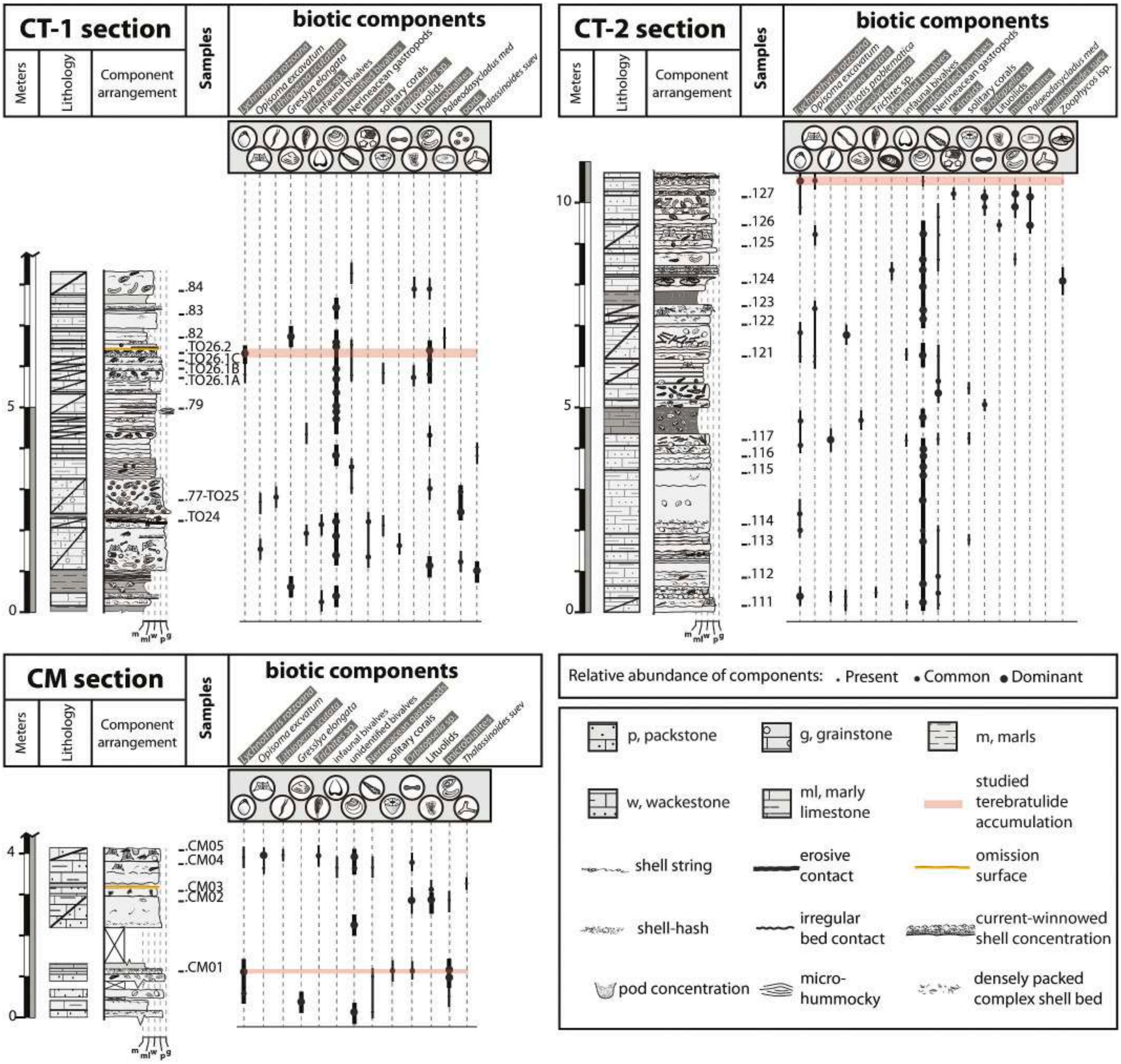

Fig. 2. Stratigraphic sections and biogenic component distributions. The studied terebratulide accumulations (pink horizons) occur in three outcrops (CM, Campomolon; CT, Cimoncello di Toraro) representing the Pliensbachian Rotzo Formation. The accumulations are illustrated in Fig. 3. *Palaeodasycladus med*: *Palaeodaycladus mediterraneus*; *Thalassinoides suev*: *Thalassinoides suevicus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The following shell orientations were considered which are either consistent with life position (life assemblage *sensu* Brenchley and Harper, 1998) umbo-down vertical, umbo-down oblique with hidden foramen, umbo-down oblique with visible foramen, and concordant to bedding ventral valve-up; or indicative of post-mortem disturbance (neighbourhood assemblages *sensu* Brenchley and Harper, 1998): umbo-up vertical, umbo-up oblique, and concordant to bedding with the ventral valve down.

4. Terebratulide assemblages: biotic components, taxonomic composition and taphonomy

4.1. Biotic components

The studied terebratulide successions are locally characterized by larger lithiotid bivalves represented by *Lithioperna scutata* (Dubar, 1948), *Lithiotis problematica* Gümbel, 1871, and the astartid *Opisoma excavatum* Boehm, 1884 (Fig. 2). Benthic foraminifera are represented by scattered larger (*Paleomayncina* cf. *termieri*, *Everticyclammina praevirguliana*, *Orbitopsella* sp., *Pseudocyclammina liasica*) and smaller forms (*Duotaxis metula* Kristan, 1957, *Glomospira* sp., *Glomospirella* sp., *Planiinvoluta* sp., textulariids) (Fig. 4). Dasycladalean algae are generally rare and were found abundantly only in sample CT126 (*Palaeodasycladus mediterraneus* (Pia) Pia; Fig. 4G–H).

Various unidentified disarticulated thin-shelled bivalves are also represented either by small shells (< 2 mm long) or by larger shells (2–5 mm long) usually replaced by sparry calcite. Large turritelliform gastropods (up to 10 cm long) are present along with sponge spicules, echinoid spines and crinoid columnals. Ostracods are locally abundant. Solitary corals (< 2 cm in transversal section) also occur. Fecal pellets can be locally very abundant. Sub-spheroidal peloids, up to 0.5 mm in diameter, are also common. Subordinate nerineacean gastropods, as well as bivalves represented by *Gresslya elongata* Benecke, 1868, *Pholadomya athesiana* Tausch, 1890, *Pteria volanensis* (Lepsisus, 1878), *Trichites* sp., and unidentified modioliform bivalves were also found (Fig. 2). Larger biotic components (bivalves, brachiopods, gastropods) are well preserved and rarely abraded or fragmented. Locally, thin-shelled bivalves are encrusted by microbialites (Fig. 5). The ichnites *Thalassinoides suevicus* (Rieth, 1932) and *Zoophycos* isp. were identified exclusively in the section CT-2.

4.2. Terebratulide assemblages: taxonomic composition and taphonomy

The terebratulide accumulations, consisting of wackestone and packstone with small-scale lateral and vertical variations (Figs. 2–3), show a distinct shell fabric type (see below). The brachiopod assemblages are monospecific, with the single terebratulide species *Lychnothyris rotzoana* (Vörös, 1983, 2009; Siblík, 2003). The specimens are 20–58 mm in length and 25–46 mm in width, a size range comparable to that reported for coeval populations described from the Vajo dell'Anguilla area (southern Trento Platform; Vörös, 2009; Fig. 6; Supplementary data). Juveniles, below c. 25 mm in length and c. 20 mm in width, are very rare. Outer, posterior shell surfaces of the terebratulide specimens show rare microboring (ovoidal traces c. 0.4 mm long and 0.15 mm in diameter) and are locally encrusted by microbialites (Fig. 5). The microborings, infilled by micrite, are nearly perpendicular to the punctae of the shells. The outer shell surfaces can also show shallow micritization (< 50 μm in thickness). Several articulated specimens preserve geopetal structures with blocky calcite and body cavities floored by micropeloids or only blocky calcite within the body cavities (Figs. 8–9).

The CT-1 stratigraphic section is characterized by two shell concentrations (Fig. 3). The first concentration (at c. 1.5 m from the section base) is c. 0.5 m-thick and contains highly diverse components. Common chaotically-oriented articulated bivalve specimens of *Lithioperna scutata* and *Opisoma excavatum* along with coated-bioclast microbialites were distinguished. The second bed, occurring at c. 7 m from the base of the section, contains the studied terebratulide assemblage, overlying centimetre-thick wackestone with thin-shelled bivalve concentrations. The *Lychnothyris rotzoana* assemblage occurs in a 1.20 m-thick bed which passes upward into centimetre-thick wackestone alternated to marly layers, topped by a 70 cm-thick packstone. The CT-1 terebratulide assemblage is composed mostly of articulated specimens showing umbo-down vertical, through umbo-down oblique to concordant valve up orientations (in all 95.8%; Figs. 3A–B, 7A–B). The assemblage is overlain by c. 0.30 m-thick barren wackestone and coated-bioclast microbialite wackestone-packstone.

The CT-2 stratigraphic section, c. 11 m in thickness, is stratigraphically located 50 m above the CT-1 section (Fig. 1B). At c. 4 m from its base, this section yields a 0.5 m-thick packstone with common articulated bivalves *Lithioperna scutata*, *Lithiotis problematica*, and *Opisoma excavatum* specimens and local concentrations of decimetre-thick packstone with turritelliform and nerineacean gastropods. The studied *Lychnothyris rotzoana* accumulation, occurring at 7 m from the base of the section, is 0.5 m-thick and overlies a 1.5 m-thick bioclastic packstone with common *Opisoma excavatum*, *Orbitopsella* sp. and coated-bioclast microbialites (Fig. 3C–D). A *Zoophycos* isp. horizon, 0.3 m-thick, occurs just 1 m below the *Opisoma excavatum* packstone (Fig. 2).

The terebratulide assemblage in the CT-2 stratigraphic section contains articulated specimens with consistent life position (i.e., umbo-down vertical, through umbo-down oblique to concordant valve up orientations, 75.8%; Figs. 3E, 7C–D). Subordinate ventral valve down specimens (21.2%) are present. *Opisoma excavatum* shell fragments and undetermined bioclasts are subordinate. The articulated terebratulids show geopetal structures (Fig. 6). The terebratulide assemblage is overlain by bioclastic packstone characterized by wackestone-filled tubular burrows (*Thalassinoides suevicus* type I of Monaco, 2000) preserved as endichnia (Fig. 8). These burrows, up to 3 cm in diameter, are sub-horizontal and locally can show Y-shaped branching points. The infilling sediment consists of structureless wackestone, with small biotic components commonly oriented nearly tangentially to the burrow wall.

The CM stratigraphic section contains a *Lychnothyris rotzoana* assemblage exposed as a prominent pavement c. 20 m^2 in area. This assemblage stratigraphically corresponds to the above described CT-1 terebratulide assemblage which is about 500 m distant (Fig. 1B). The c. 5-m thick succession consists of decimetre-thick limestone beds. The first c. 1 m in thickness of the succession consists of 10–20 cm-thick bioclastic packstone, with rare sparse brachiopod specimens, passing into *Gresslya* bivalve pavements, < 1 cm in thickness. These pavements are overlain by a decimetre bedded coated-bioclast microbialite with turritelliform/nerineacean gastropods. The studied *Lychnothyris rotzoana* assemblage, with solitary corals and the larger foraminifer *Orbitopsella* sp., occurs at c. 1.2 m from the base of the succession (sample CM-01; Figs. 2, 3F–H). Above a 1 m-thick of non-exposed section, a 80 cm-thick bed consists of *Orbitopsella* wackestone-packstone with disarticulated bivalves and floating microbialite-coated bioclasts. The *Orbitopsella* wackestone-packstone is overlain by a bioclastic wackestone-packstone characterized by common *Opisoma excavatum* and a coated-bioclast microbialite wackestone-packstone.

The excellent exposure of the terebratulide assemblage allows for the orientation in cross-section to be assessed. The assemblage is composed of articulated terebratulids dominated by specimens in life position (umbo-down vertical, through umbo-down oblique to concordant valve up orientations, 84%; Figs. 3F–H, 7). A subordinate cohort of specimens with ventral valve-down specimens (17.9%) is also present. The smallest *Lychnothyris rotzoana* specimens were found in the assemblages CT-1 and CM (< c. 3 cm in length, < 2.5 cm in width; Fig. 6; Supplementary data). Terebratulide shells are infilled by peloidal packstone-grainstone (Fig. 9).

4.3. Microbialite components

Microbialites are recognizable in thin sections and on polished slabs (Figs. 5, 8–9). In the CT-1 section, microbialites dominated within the *Opisoma excavatum* packstone at the base and within the *Lychnothyris rotzoana* accumulation (samples TO26; Fig. 2). In the CT-2 section, dominant microbialites are overlain and overlie the terebratulide accumulation (sample 127). Microbialites also characterize the CM terebratulide accumulation (sample CM01). The microbialites occur along with various amounts of bioclasts which themselves can be encrusted by microbialites and other epibionts including *Planiinvoluta* sp. The small agglutinated benthic foraminifer *Glomospirella* sp. is also present. Bioclasts, dispersed within the wackestone, are represented by local abundant sponge spicules, fragments of thin-shelled bivalves (< 1 mm long) as well as common smaller textulariid benthic foraminifera. Densely packed grain-supported microfabrics (packstone) are locally present. The microbialites consists of micrite/microspar with both clotted and homogeneous patterns (Fig. 5). The clotted areas show aggregates, < 20 μm in diameter, within wackestone, packstone or floatstone. These differences in microfabric density are reflected by the varying degrees of opaqueness under the optical microscope.

Following the different components and proportions of micrite/microspar, two microbialite fabrics are distinguished: structureless microbialites and coated-bioclast microbialites. Structureless

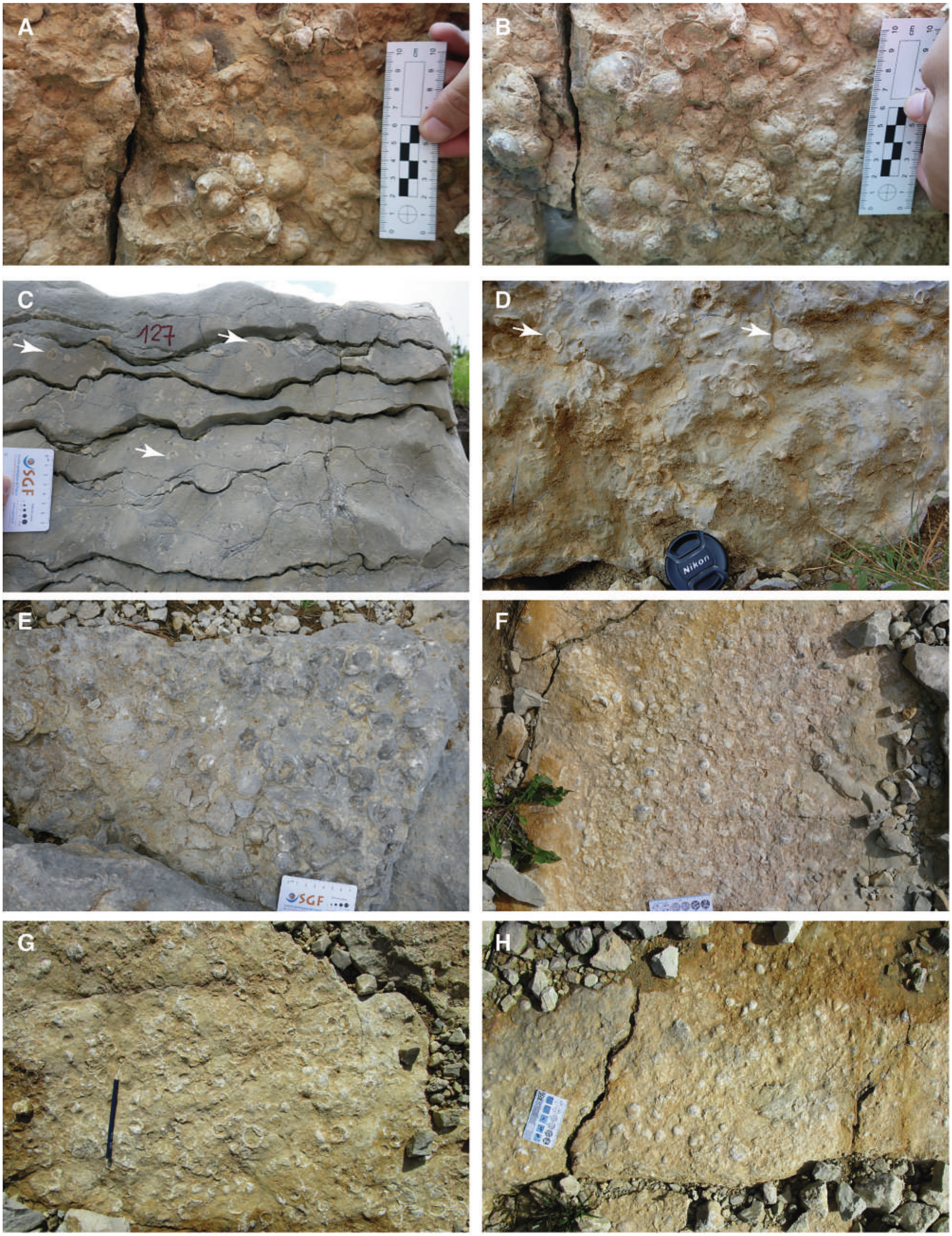

Fig. 3. Outcrop photographs of the three studied terebratulide accumulations; Pliensbachian, northern Italy. (A—B) CT-1; bottom view of the terebratulide accumulation occurring at c. 7 m from the base of the section, dominated by specimens from umbo-down vertical, through umbo-down oblique to concordant valve up oriented. (C—E) CT-2; bedding 127, bioclastic packstone overlain by the studied terebratulide accumulation (E, bedding top), is characterized by coated-bioclast microbialites (arrows) whose nuclei are often represented by large (B-forms) *Orbitopsella* specimens. (F—H) CM; terebratulide accumulation top showing the large specimens. CM: Campomolon; CT: Cimoncello di Toraro. For stratigraphic details see Fig. 2.

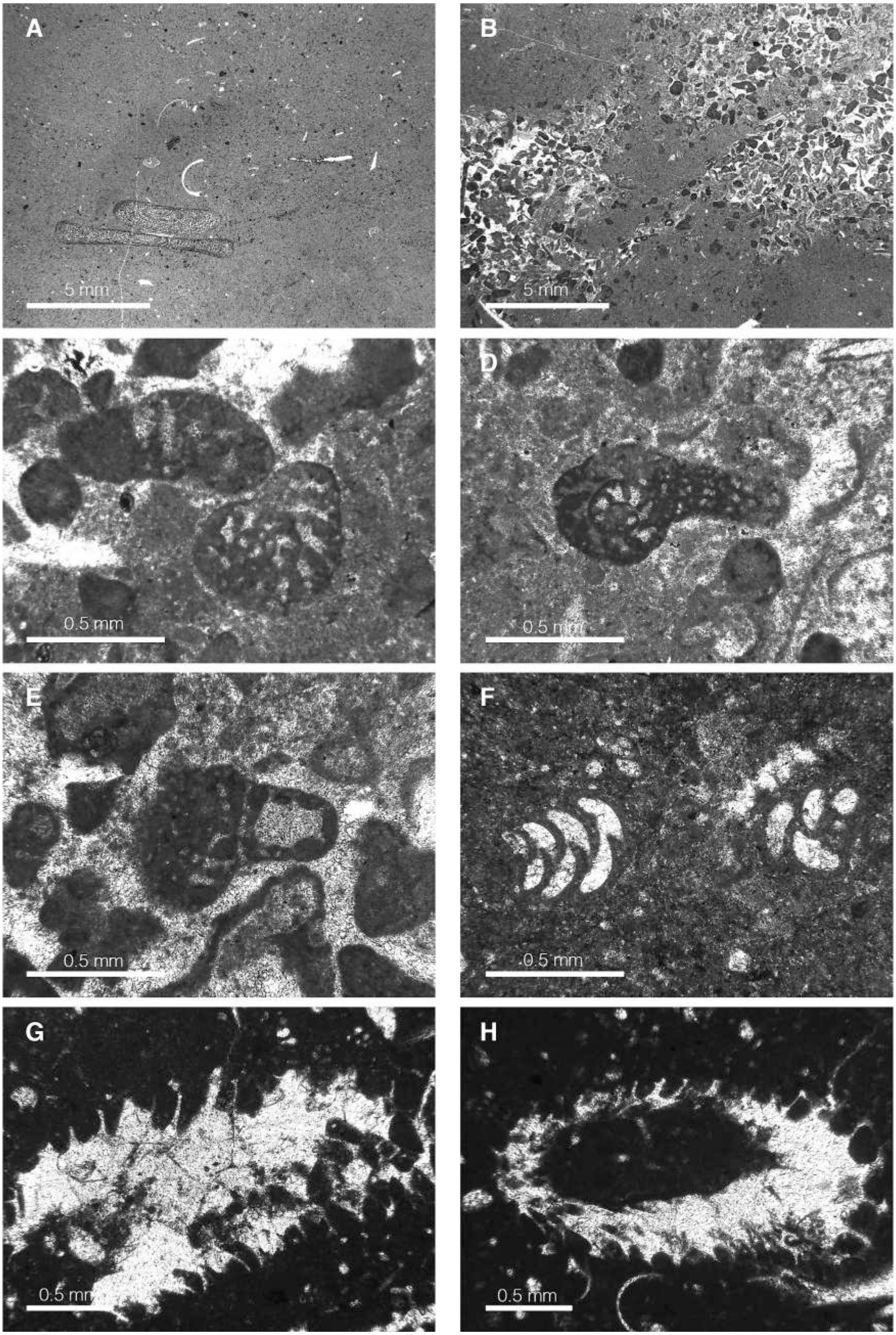

Fig. 4. Benthic foraminifera and dasycladalean algae characterizing the studied sedimentary successions; Pliensbachian, northern Italy. (A) *Orbitopsella* sp.; (B—C) *Paleomayncina* cf. *termieri*; (D) *Pseudocyclammina liasica*; (E) *Everticyclammina praevirguliana*; (F) *Duotaxis metula*; (G—H) *Palaeodasycladus mediterraneus* (Pia).

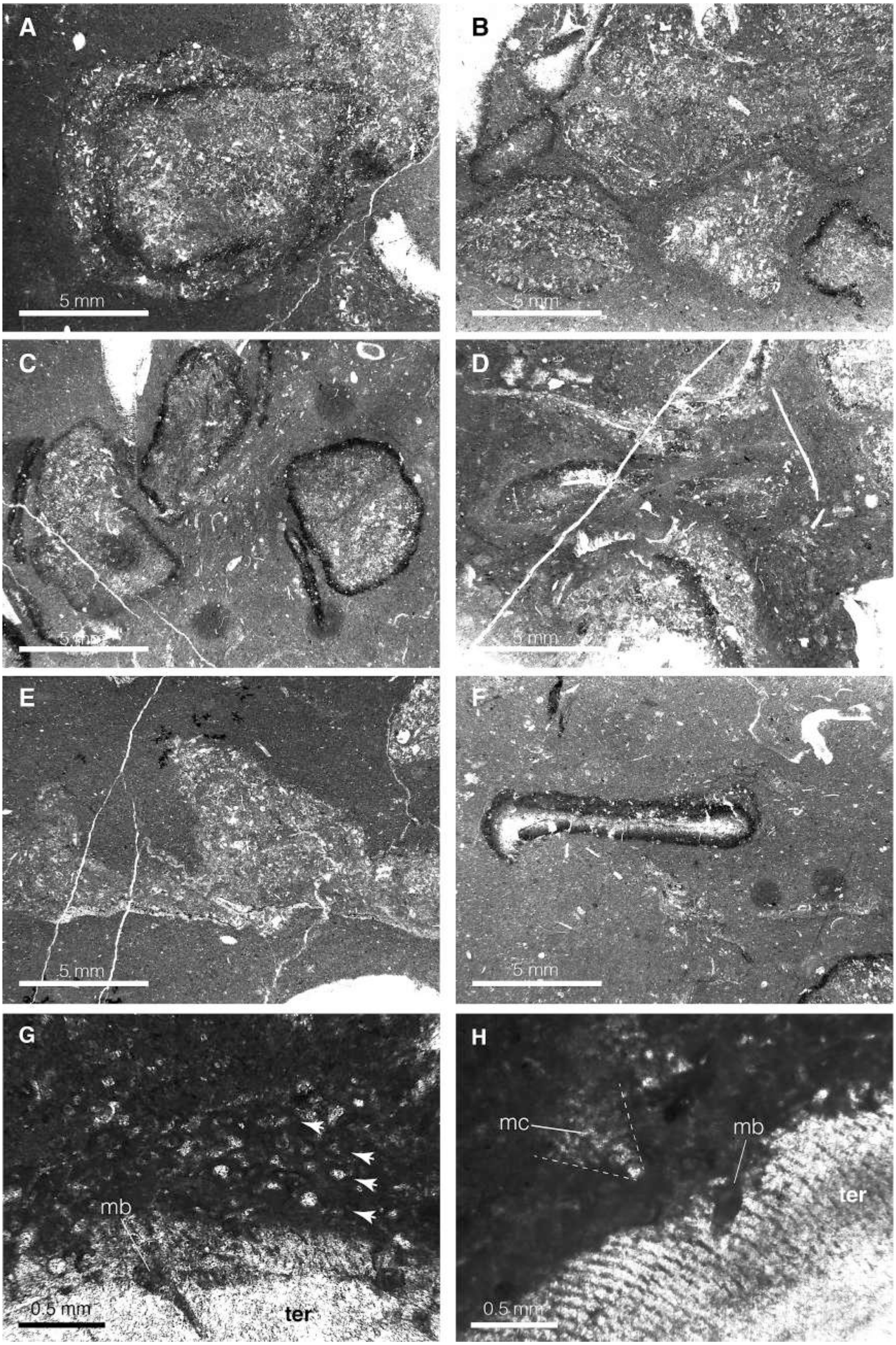

Fig. 5. The distinguished structureless microbialite forms sub-spheroidal and sub-ellipsoidal grains (A—E). Most of the grains show asymmetrical growths, whereas rare grains (A) show changes in micrite/microspar microfabric and density. Superimposed microbialite growths, made up of peloidal microfabric tubular features, coat bioclasts usually represented by bivalve shells (F). (G—H) In rare outer shell surface of terebratulides (ter) ovoidal microborings (mb) are nearly perpendicularly the punctae and are covered by microbialite with microspar sub-conical clusters (mc, dashed lines).

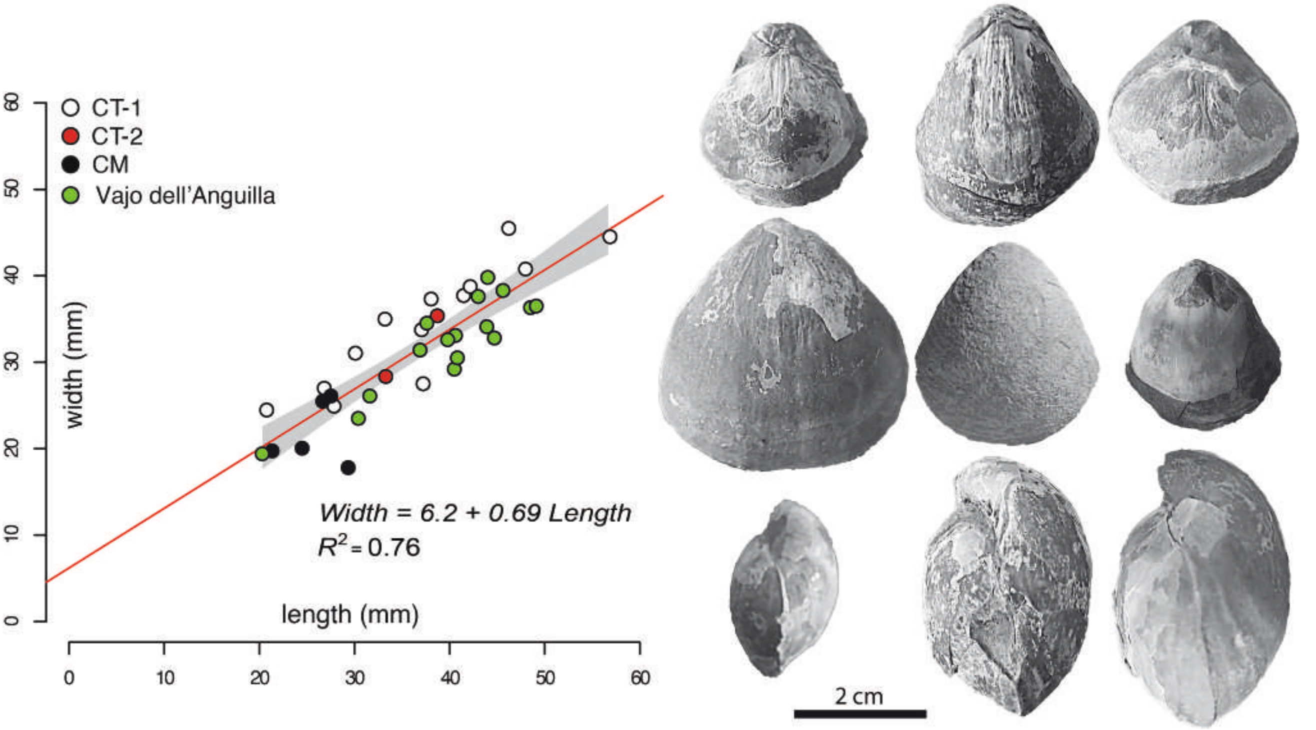

Fig. 6. Shell size comparison between the specimens of *Lychnothyris rotzoana* (Schauroth, 1865) from Vajo dell'Anguilla (southern Trento Platform; specimens collected by A. Vörös in 1988 and deposited in the Hungarian Natural History Museum, Budapest; Vörös, 2009) and the specimens identified in the studied terebratulide accumulations (CM, CT-1, CT-2).

microbialites constitute indistinct grains formed by irregularly sized micrite/microspar areas in which tubular features are locally bifurcating and co-aggregate (Fig. 5A–E). These filamentous areas usually resemble tiny crusts, some millimetres long and < 1 mm in thickness. The microbialites are present as sub-spheroidal and sub-ellipsoidal grains up to 1 cm width, and range from aggregated micritic clots in the inner part of the grains to homogeneous microfabrics in the outer growth stage. Structureless microbialites form grains with usually an asymmetrical inner arrangement (Fig. 5A–C), although rare symmetrical specimens were also found. Changes in micrite microfabric and density are recognizable especially on polished slabs. Bioclasts do not usually occur within these structureless microbialites.

Coated-bioclast microbialites are represented by well-preserved bioclastic grains coated by superimposed microbialite growths often characterized by hemispherical chambers with micritized walls (Fig. 5F–H). The common peloidal microfabric, with tubular features locally bifurcating and co-aggregating, shows locally poorly defined internal lamination and microspar sub-conical clusters. Identified bioclasts include disarticulated thin-shelled bivalves, larger foraminifera (*Orbitopsella*; Fig. 3C–D) and small brachiopod shells. On some disarticulated thin bivalve shells, the coating microbialite forms laminar growths which can develop undulated to lumpy morphologies, < 0.5 mm height.

5. Discussion

The presence of dense accumulations of terebratulides suggests phases of fully marine well-oxygenated conditions with sufficient nutrient input to support these filter-feeding organisms. These environmental conditions characterize the middle part of the Rotzo Formation with scattered and disarticulated terebratulide shells present in the *Opisoma excavatum* beds of the Toraro succession (Posenato et al., 2013b). *Lychnothyris rotzoana* shells and *Opisoma excavatum* are associated with solitary corals, sponges and larger foraminifera, suggesting an interval of fully marine conditions with low sedimentary rate (Posenato et al., 2013b). In the terebratulide accumulations, the prevalence of adult specimens with only rare juveniles points to the predominance of a single cohort. This population structure indicates a short-term favourable environment which promoted brachiopod colonization and growth.

5.1. Autochthonous shell accumulations

The *Lychnothyris rotzoana* accumulations are composed of well-preserved shells dominated by either umbo-down, oblique and concordant to bedding, ventral valve-up orientations (Fig. 7). The brachiopod accumulations represent therefore primarily autochthonous to parautochthonous shell accumulations (e.g., Kidwell and Jablonski, 1983) or life assemblage (*sensu* Brenchley and Harper, 1998). The lack of abrasion, sorting and fragmentation provides further evidence of autochthony. The occurrence of dominant umbo-down, oblique, and concordant to bedding, ventral valve-up specimens (Fig. 7), and shells infilled by blocky calcite (Figs. 8–9) indicates absence of transport and wave-induced reworking.

5.2. Benthic assemblages and environmental conditions prior the colonization

In the stratigraphic interval containing the CT-1 and CM accumulations, the underlying bed consists of grey to black marlstones with infaunal (e.g., *Gresslya, Pholadomya, Pleuromya),* epi- or endobyssate (*Camptonectes, Musculus, Pteria, Trichites*) and cemented epibiont (*Placunopsis*) bivalves. This assemblage suggests muddy, both soft and semi-consolidated, bottom substrates. Byssate and cemented epibiont bivalves support low sedimentation rates (Padovese, 2000; Posenato et al., 2002). The absence of stenotopic benthic marine taxa (e.g., terebratulides, *Opisoma*) in these beds suggests stressed environmental conditions probably corresponding to a restricted environment of the lagoonal setting with low oxygenation and/or salinity fluctuations. This

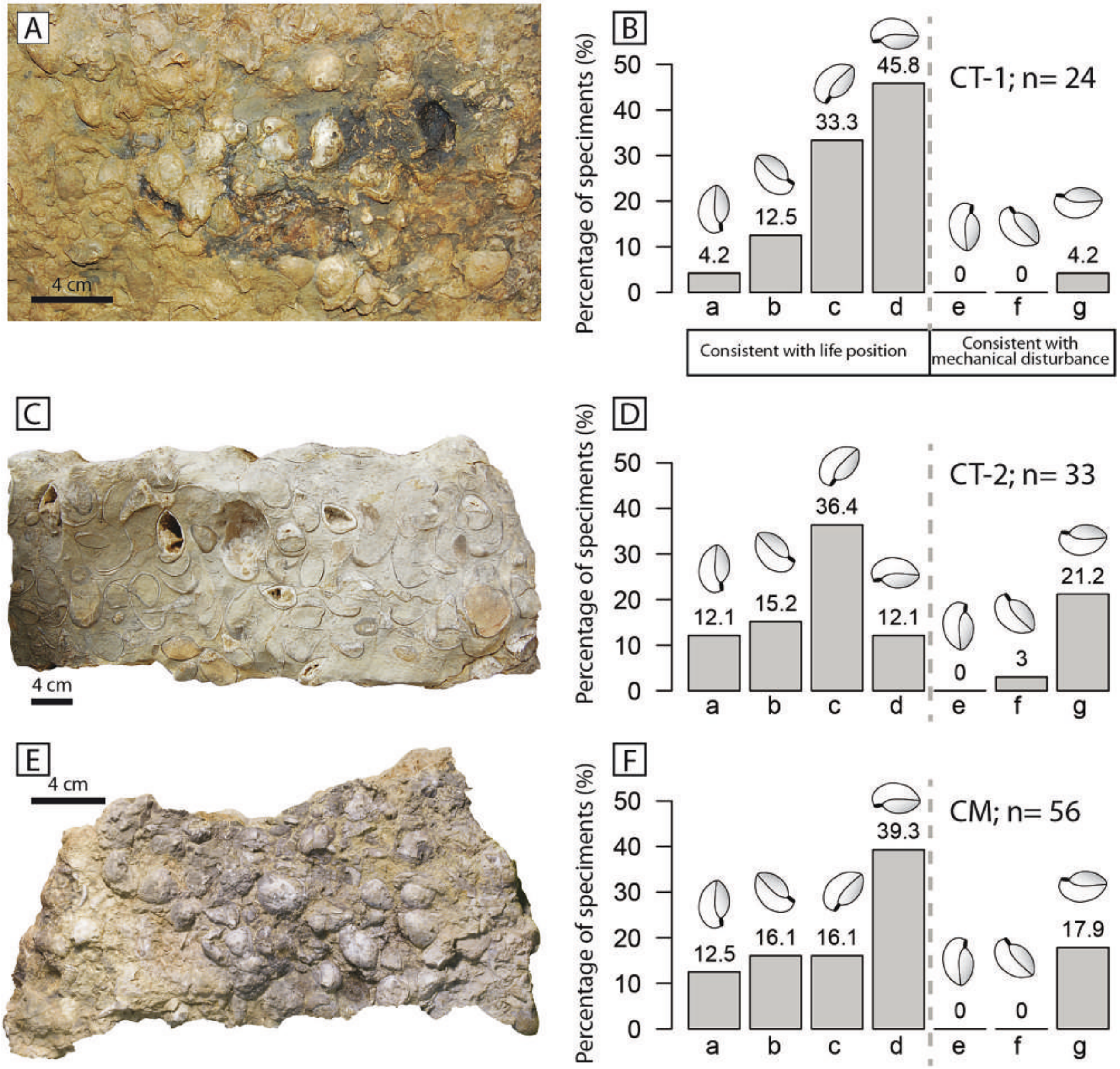

Fig. 7. Shell orientations in the three studied terebratulide accumulations (CM, CT-1, CT-2) from the Pliensbachian of northern Italy. Outcrop view (A, lower bed surface, CT-1; C, bed-cross section, CT-2; E, lower bed surface, CM) and related cross-section orientation versus percentage of specimens (B, D, E). The accumulations are dominated by specimens oriented from umbo-down vertical, through umbo-down oblique to concordant to bedding valve up pointing out their autochthonous preservation. The excellent exposition of the CM accumulation surface shows that the terebratulids have no preferred posterior-anterior axis orientation. Compare with Fig. 3. a, umbo-down, vertical; b, umbo-down, oblique, hidden foramen; c, umbo-down, oblique, visible foramen; d, concordant to bedding, ventral valve-up; e, umbo-up, vertical; f, umbo-up, oblique; g, concordant to bedding, ventral valve-down.

bivalve assemblage characterizes the TF3s winnowed bivalve taphofacies (see Monaco and Giannetti, 2002), which has been interpreted as the upper and regressive part of a shallowing-up parasequence originated in restricted and anoxic ponds (Monaco and Giannetti, 2001).

5.3. Environmental conditions allowing the larval substrate colonization

The larval attachment occurred during a transgressive phase and was promoted by normal marine conditions (e.g., well oxygenated marine waters with no significant salinity and trophic resource fluctuations). Low hydrodynamic energy conditions coupled with low sedimentation rates facilitated the settling of *Lychnothyris rotzoana* larvae which could attach to sparsely distributed shell material on the muddy substrate. Shell growth was facilitated by elevated input of suspended organic matter, which characterized the lagoonal environment (Posenato et al., 2002). Shell stabilization was possibly attained by pedicle rootlets at the water-substrate interface, as observed in free living pediculate modern species (Richardson, 1997). Larvae attached to dead shells or adult pedicle rootlets forming a dense network, as observed for modern *Terebratulina septentrionalis* (Couthouy, 1838; Logan et al., 1984), which is able to provide the substrate for further settlement and thus enhance brachiopod survival in a generally mud-dominated environment with limited available hard-substrates (Curry, 1981). Low sedimentation rates and low hydrodynamic energy conditions favoured population growth and successive in situ recruitments.

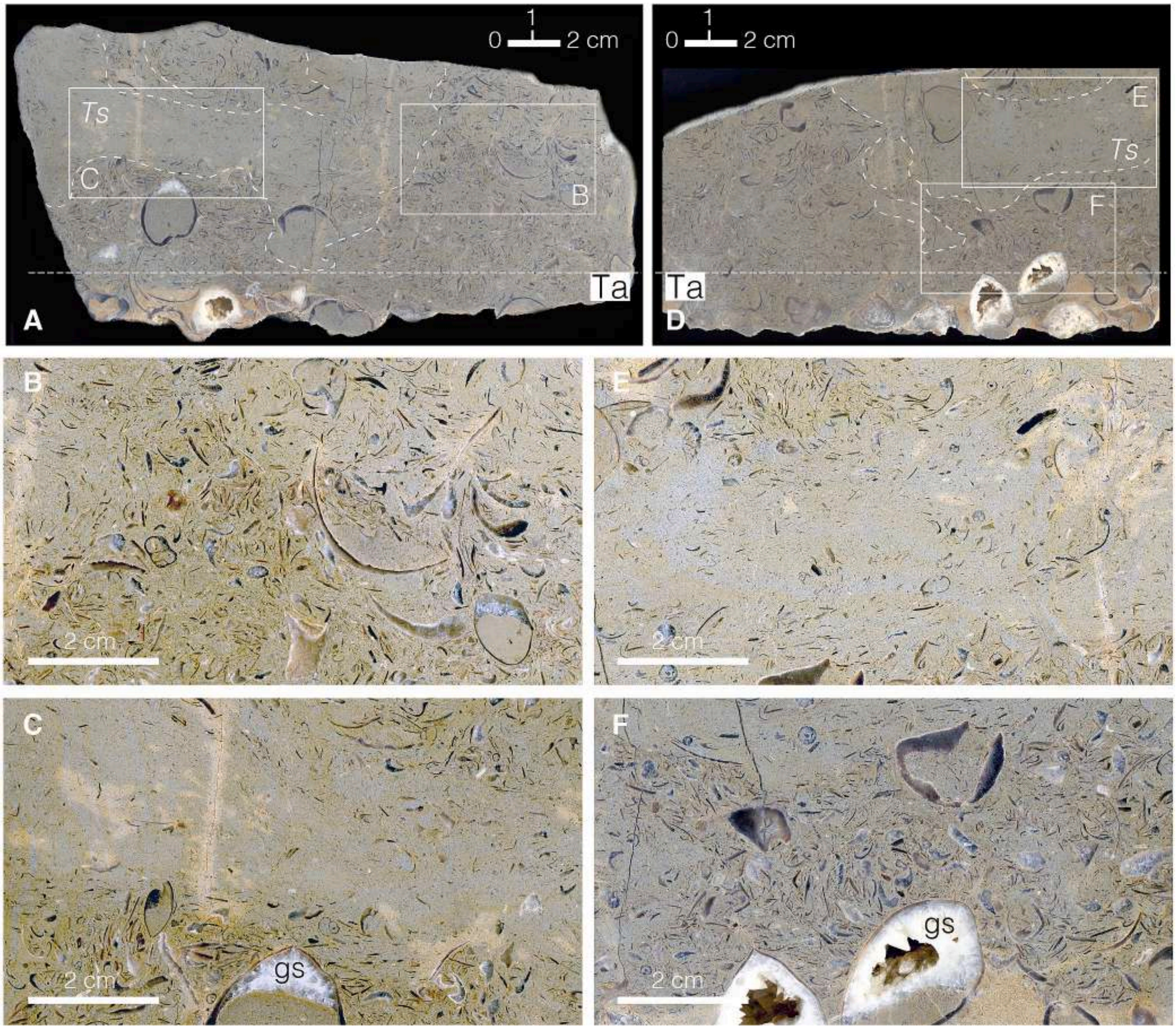

Fig. 8. Parallel polished slabs (A, D) oriented perpendicularly to the bedding surface, Cimoncello di Toraro stratigraphic section (CT-2); Pliensbachian, northern Italy. Wackestone-filled tubular burrows (dashed lines; *Ts*, *Thalassinoides suevicus*), with small biotic components commonly oriented nearly tangentially to the burrow wall, occur in chaotically oriented-bioclastic packstone overlying the terebratulide accumulation (Ta). Articulated terebratulides show preserved geopetal structures (gs). (B—C, E—F) Details of the slabs showing the arrangement of the bioclasts inside and outside the tubular burrows.

5.4. Growth and death of brachiopod populations

The size distributions of shells indicate that the *Lychnothyris rotzoana* populations mostly belong to a single cohort. This population structure suggests a short-term duration of the favourable environmental conditions promoting brachiopod colonization and survival. The presence of mostly autochthonous/parautochthonous assemblages suggests a rapid environmental change which induced a mass mortality event and the demise of the population. The causes of mass mortality can be related to various rapid environmental changes, such as eutrophy and anoxia, freshwater input, strong temperature change, water poisoning, and/or burial.

Lethal anoxic events are recorded in the *Eomiodon* horizon at the base of the Rotzo Formation. These events caused the mass mortality of the infaunal bivalve *Eomiodon serradensis* (Tausch), an interpretation supported by several lines of evidence with respect to lithology (black shales; total organic carbon is 1.48 wt%, oxygen and hydrogen indices are 344 mgHC/gCorg and 102 mgCO$_2$/gCorg respectively; Bassi et al., 1999), taphonomy (butterfly position of articulated shells stunt growth of individuals), and the presence of eurytopic taxa (Bassi et al., 1999, 2008; Posenato et al., 2013a). Short dysoxic or anoxic events are highly probable in the lagoonal environment recorded by the Rotzo Formation, where seasonal peaks of nutrient inputs related to rainfalls or upwelling events have been recognized (Bassi et al., 2017; Posenato et al., 2022). An exceptional and stronger nutrient and freshwater input triggered by a heavy and prolonged rainy phase could have been the cause of the mass mortality of the studied brachiopods.

In the terebratulide accumulations the occurrence of small microgranular and porcelaneous foraminifera such as *Duotaxis metula* and *Glomospira/Planiinvoluta* spp. points to occasional dysoxic conditions (Fugagnoli, 2004; Bassi et al., 2015). These events possibly affected the shallow infauna (thin-shelled bivalve and small gastropods) with their shells being successively concentrated on the sediment/water interface by weak storms and winnowing (e.g., at the base of the CT-1 section and beds near the sample 79; beds near the samples 117, 123–124 in the CT-2 section; Fig. 2). Increased run-off into the lagoon is shown by the

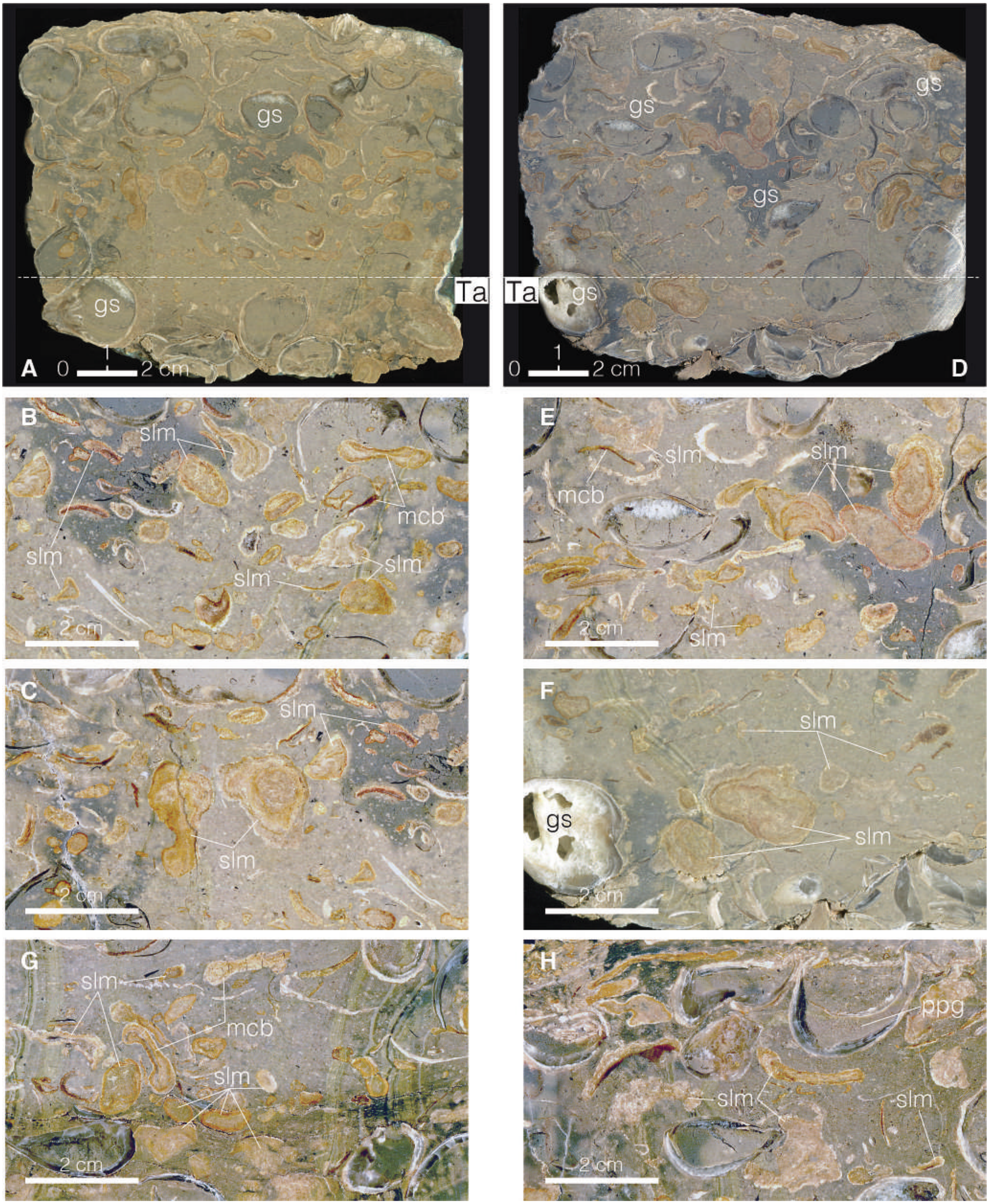

Fig. 9. Parallel polished slabs (A, D) oriented perpendicularly to the bedding surface, Campomolon stratigraphic section (CM); Pliensbachian, northern Italy. (B—H) Details of the slabs showing the different microbialite fabrics (compare with Fig. 5). gs, geopetal structure; mcb, microbialite-coated bioclasts; ppg, peloidal packstone–grainstone; slm, structureless microbialite; Ta, terebratulide accumulation.

presence of abundant textulariids (Fugagnoli, 2004). In present-day Bora Bora (French Polynesia) and Eniwetok Atoll (Marshall Islands), an abundance of textulariids in lagoons is associated to the run-off of fine sediments along with volcanic soil-derived nutrients, which likely enhanced the microbialite development (Gischler et al., 2020; Parker and Gischler, 2021). These explanations, including eutrophy and anoxia, however, remain speculative because they are not supported by robust evidence and could have mainly affected the infauna, rather than the terebratulide epifauna.

With respect to possible rapid temperature changes, the Rotzo lagoon was located in the tropical belt, at about 20°–25° lat. N, with low temperature seasonality (c. +8 °C; Posenato et al., 2022). A scenario with strong temperature changes is therefore highly improbable, apart from a process involving a rapid decrease in water temperature caused by an intense phase of upwelling due to the breaching of the lagoon's protective barrier island, which may possibly have been induced by active tectonics which affected the Pliensbachian Trento Platform (Franceschi et al., 2014).

Lychnothyris rotzoana was a sessile and filter feeding brachiopod unable to survive burial events. A rapid burial as a lethal cause is, however, precluded by the sedimentary record in which the brachiopods are found. In addition, the presence of encrusting and microboring on the inner shell surface must have been produced after the death of the brachiopod thus suggesting generally low sedimentation rates.

Toxic shocks induced by water poisoning events are also an intriguing possibility, though such necrolytic events have little or no chance of being discerned in the fossil record. Although pathogenic bacteria found in modern brachiopods are indicative of toxic infections (e.g., Chistyulin et al., 2017), little is known about the parasites affecting fossil counterparts (Vinn et al., 2014; Zhang et al., 2020). Cyanobacterial blooms usually comprise both toxin and non-toxin producing species (Baker and Humpage, 1994). In fact, 50% of these blooms are commonly expected to contain toxic species (Carmichael, 1992). Toxic Cyanobacterial Harmful Algal Blooms (CHABs) and their impact on water quality are well documented. Recent studies suggest that climate change (i.e., coastal nutrient supply, increasing rainfall and temperature) may promote the proliferation and expansion of present-day CHABs (O'Neil et al., 2012; Anderson et al., 2021; Kalaitzidou et al., 2021). The Florida CHABs brought about acute exposure impacts on larval and juvenile stages of many marine benthic biota suffering the brevetoxin influence (e.g., Heil and Muni-Morgan, 2021; Pouil et al., 2021). The CHABs have been associated to weather and physical conditions, and local nutrient supply (Ingle and Martin, 1971; Slobodkin, 1953; Curren et al., 2019). Although cyanobacterial blooms could have had toxic effects, cyanobacterial carbon is known to support the benthic food web (Zepernick et al., 2023) and thus it could have sustained benthic taxa. In fact, some present-day suspension feeding clams and mussels are able to filter toxic cyanobacteria (e.g., Bolam et al., 2019; Oliveira et al., 2020).

5.5. Post-mortem stabilization by encrustation

The microbialites point to short-term encrusting events which stabilized the *Lychnothyris rotzoana* shells, preventing significant reorientation during burial. The occurrence of micropeloids in the geopetal structures suggests bioperforation of the shells (i.e., ovoidal microborings). These are consistently slightly tilted, indicating that the specimens were re-oriented when the body cavity was infilled with sediment (Figs. 8–9). The terebratulide shells could have been reoriented either by biogenic agents or by currents after exposure by winnowing (e.g., Monaco and Giannetti, 2002). Tilting by biological activity is corroborated by the common occurrence of wackestone-filled tubular burrows in associated sediments ascribed to *Thalassinoides suevicus* type I (Fig. 8), interpreted as being produced by endobenthic decapod crustaceans (Monaco, 2000; Monaco and Garassino, 2001; Monaco and Giannetti, 2002; Carvalho et al., 2007).

The microboring traces (< 50 μm in thickness) occurring in the brachiopod shells are similar to those produced by coccoid cyanobacteria, fungal hyphae, and eukaryotic algae. In particular, the ovoidal borings are likely to be bag-like reproductive structures of fungi found to proliferate within the organic lamellae of present-day bivalves (Golubic et al., 2005). The occurrence of ovoidal microborings, being nearly perpendicularly to the punctae of the studied *Lychnothyris rotzoana* shells and thus nearly parallel to the shell vault (Fig. 5G–H), suggests that the endolithic fungi were not hampered by the organic parts of the shells (Golubic et al., 2005). Low hydrodynamic energy conditions allowed for the activity of bioeroders and encrusters after the death of the brachiopods (Kidwell, 1991).

The structureless microbialites and the coated-bioclast microbialites are interpreted to originate from cyanobacteria. Comparable encrusting microbialite microcolonies are those referred as to *Koskinobullina socialis* (Cherchi and Schroeder, 1979) and recorded in Jurassic shallow-water coral-microbial facies (Pleş et al., 2013). The sub-spheroidal and sub-ellipsoidal grains of the structureless microbialites originated as superimposed microbialite growth which became detached and were successively coated by further microbialite growth (Fig. 5A–C). Considering that microbialite grains are porous with a relative low bulk density (Alshuaibi et al., 2012), movement of the bioclasts was minimal under low hydrodynamic energy conditions and overturning was most probably facilitated by burrowing and grazing organisms (e.g., Gebelein, 1976). In marine environments off Grand Cayman Island, Bahamas and Florida, present-day oncoids with bioclasts as nuclei form in lagoonal settings where occasional storms detach the grains coated by mucilaginous microbialites (Monty and Hardie, 1976; Jones and Goodboy, 1985; Flügel, 2004).

5.6. Burial and environmental conditions

In the CT2 section, the bioclastic packstone overlying the *Lychnothyris rotzoana* accumulations is interpreted to reflect low hydrodynamic energy condition and extended quiescent fair-weather intervals favouring bioturbation. This packstone consists of chaotically oriented bioclastic grains and very small, disarticulated thin-shelled bivalves (< 1 cm in length) lacking encrustation. The terebratulides are confined to the lower third of the bed (Figs. 8–9). The upper two thirds of this section show an increasing amount of very small thin-shelled bivalves, structureless microbialites and coated-bioclast microbialites. Incorporation of shelly bioclasts (e.g., sponge spicules, echinoid spines and crinoid columnals) and peloids indicates that trapping of detrital sediment was involved in its origin of the microbialites.

A rapid burial and an equally rapid/early lithification of the substrate are evidenced by the preservation of wackestone-filled tubular burrows (*Thalassinoides suevicus*) as well as the presence of blocky calcite within the terebratulide shells. Despite the high bioturbation characterizing the sedimentary succession of the Rotzo Formation (Monaco, 2000; Monaco and Giannetti, 2001, 2002), the burrows were preserved and not early bioturbated suggesting a rapid burial and an early lithification. After their rapid burial, the soft parts of the articulated *Lychnothyris rotzoana* shells started decaying. Early lithification after burial slowed down aerobic biodegradation and the decay of soft parts, allowing for the growth of blocky calcite (Figs. 8–9; Fernández-López, 1997). A similar process has been suggested for the common gastropods occurring within the studied succession (Monaco and Giannetti, 2001, 2002). The occurrence of the larger benthic foraminifer *Orbitopsella* associated with textulariids, *Glomospira/Planiinvoluta* spp., and valvulinids have also been related to high rate of micrite production and supply of organic matter (Fugagnoli, 2004).

6. Conclusions

In the Pliensbachian, the Trento Platform (Southern Alps) along the western Tethyan margin is distinguished by a mud dominated, complex shallow-water environmental mosaic containing a wide variety of organisms including lithiotid bivalve assemblages, highly diversified larger benthic foraminifera, sponges, infaunal bivalves, gastropods, brachiopods, echinoderms, crustaceans, dasycladalean algae, and microbialites. The patchy facies distribution of the Rotzo Formation is reconstructed with some components pointing to restricted lagoonal conditions, while other, such as the brachiopods, are more characteristic of more open water, stenohaline conditions. Although brachiopods constitute common faunal elements within these benthic assemblages, they only form rare mass occurrences at discrete intervals. During low sedimentation rate, stable marine conditions, and low hydrodynamic energy phases terebratulides form localized autochthonous monospecific (*Lychnothyris rotzoana*) biotic accumulations, occurring within the upper *Orbitopsella* Zone. These accumulations are characterized by rare juvenile and abundant large adult specimens. Larvae attached to dead shells or laid on adult pedicle rootlets forming a dense network, thus enhancing brachiopod survival in a generally mud-dominated environment. After death, the terebratulide shells were further stabilized by microbialites which point to short-term encrusting events, hampering the possible re-orientation of the shells during the subsequent burial. The accumulations underwent occasional heavy stormy events, rapid burial and rapid lithification.

The *Lychnothyris rotzoana* populations were affected by unpredictable environmental change which brought about the demise of the community. Changes in water temperature, variations on oxygenation and nutrient supply, and water poisoning events were considered. Even if toxic shocks induced by water poisoning events may be a plausible cause, further studies are needed to decipher the possible sources of the sudden mass mortality of the studied brachiopod accumulations. The response of terebratulide brachiopods to palaeoenvironmental changes provides a reconstruction of the effects on marine ecosystem resilience.

CRediT authorship contribution statement

Davide Bassi: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lucia Angiolini:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **James H. Nebelsick:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Renato Posenato:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This investigation was financially supported by local research funds (FAR 2018–2022) at the University of Ferrara (DB). This paper is a scientific contribution of the PRIN 2017RX9XXXY (*Biota resilience to global change: biomineralization of planktic and benthic calcifiers in the past, present and future*). This study was partly financially supported by the MIUR-Dipartimenti di Eccellenza 2018–2022 Project. The authors would like to thank Diego Antonio García-Ramos for field and laboratory analyses. Dr. A. Dulai provided shell measurements of *Lychnothyris rotzoana*, specimens collected by A. Vörös in 1988 from Vajo dell'Anguilla and deposited in the Hungarian Natural History Museum, Budapest. Reviews and comments by the Editor and three reviewers (D. Macfarlan, M. Reolid, A. Vörös) are much appreciated.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112262.

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