

Research Article

**PALEOECOLOGICAL DYNAMICS OF SHALLOW-WATER BIVALVE CARPETS  
FROM A LOWER JURASSIC LAGOONAL SETTING, NORTHEAST ITALY**

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**ABSTRACT: Shell beds are products of complex biological, taphonomic and sedimentological factors. Paleocological analysis of Pliensbachian shell accumulations from northeast Italy, Southern Alps, records successive phases of colonization and demise, each of which characterized by specific taphonomic features and sedimentary fabrics. Field studies were augmented by serial sectioning and thin sections revealing microfacies and microtaphofacies, as well as scanning electro-microscopy (SEM) and electron backscatter diffraction (EBSD). The term bivalve carpet is introduced to describe the original geometry of the bivalve accumulation colonizing the substrate. Within a lagoonal depositional setting, small, thin-shelled Isognomonidae-like bivalves lived as endo-byssate, non-siphonate suspension feeders. These bivalves, interpreted as juveniles, constructed bivalve carpets with a primary lateral extension while lacking a distinct vertical growth. Bivalves colonized firm, dysoxic carbonate substrates consisting of a mixture of peloids, bioclasts, and chemolithotrophic iron-oxidising bacteria. Oxygen-rich bottom currents and microbial activity stabilized the lagoon floor thus allowing for the episodic settlement of fixosessile bivalves and their autochthonous preservation. Short-term anoxic phases interpreted to reflect seasonal decreases in water energy resulted in the mass mortalities of the juvenile bivalves. The abundance of articulated, vertical orientated valve pairs in the shell accumulations document that the bivalve carpets were embedded soon after the death of the organisms without prior physical disturbance.**

## INTRODUCTION

This study of Pliensbachian bivalve assemblages aims to reconstruct the formation, demise and preservation of a unique biotic assemblage here defined as a bivalve carpet. This study is conducted by analyzing the constituent components, shell fabrics, taphonomic features and associated microfacies as well as by using scanning electron microscopy (SEM) and electron backscatter diffraction (EBSD). Due to the exceptional preservation at small scale, the role of peloidal micritic substrates and microbial crusts in supporting and preserving this shallow water lagoonal bivalve assemblage as well as the role of variation in oxygen content in their demise are explored.

Lower Jurassic shallow-water carbonate deposits of the Southern Alps record a unique Pliensbachian facies platform succession at the northern Tethyan margin in the Venetian area of Northern Italy. These deposits occur within the paleogeographic unit of the Trento Platform (Bosellini, 1989) and represent a widespread lagoonal setting characterized by a high diversity of marine benthic communities with exceptional preservation of biogenic components and shell accumulations within fine-grained sediments. The most prominent components of the Trento Platform are the aberrant giant bivalves of the *Lithiotis* fauna (e.g., Broglio Loriga and Neri, 1976; Posenato and Masetti, 2012). The benthic communities also include calcareous algae, larger foraminifera, sponges, solitary corals, gastropods, brachiopods, echinoderms, as well as plant remains (e.g., Broglio Loriga and Neri, 1976; Beccarelli Bauck, 1988; Avanzini and Broglio Loriga, 1996; Fugagnoli, 2004; Posenato and Masetti, 2012; Posenato et al., 2013a and references therein). These components were deposited in a complex mosaic of shallow-water habitats within a lagoonal setting (e.g., Bosellini and Broglio Loriga, 1971; Clari, 1975; Broglio Loriga and Neri, 1976).

Mass occurrence of bivalves in both fossil and Recent settings are known to represent either *in situ* deposits or transported assemblages. Autochthonous bivalve deposits include not only the above mentioned Jurassic *Lithiotis* fauna, but also various Cretaceous rudist accumulations (e.g., Gili et al., 1995; Skelton and Gili, 2012) as well as Recent and past oyster, *Mytilus* and *Mya* beds (e.g., Markert et al., 2010; Hertweck and Liebezeit, 2002). Transported bivalve accumulations have been described from the fossil record (e.g., Jiménez and Braga, 1993; Mandic and Piller, 2001; Yesares-García and Aguirre, 2004; Mandic et al., 2004; Fürsich et al., 2009). Present-day bivalve accumulations are present in subtidal (e.g., Sørensen and Surlyk, 2013; Zonneveld and Gingras, 2013), intertidal (e.g., Herlyn et al., 2008; Schneider-Storz et al., 2008) and supratidal settings (e.g., Flessa and Kowalewski, 1994). Shell-beds are the products of a complex interplay of biological, taphonomic and sedimentological processes (e.g., Fürsich and Kirkland, 1986; Kidwell et al., 1986; Kidwell, 1991; Fürsich and Oschmann, 1993; Flessa and Kowalewski, 1994; Brett, 1995; Fürsich and Pandey, 1999; Schneider-Storz et al., 2008).

In the case study presented here, bivalve assemblages are exceptionally preserved *in situ* and characterized by shells arranged more or less continuously in a lateral pattern. These deposits are hereby defined as “bivalve carpets” following the term “coral carpet” defined by Geister (1983) as “fairly coherent coral growths forming a reef framework by successive colonizations of several generations of reef corals that remain in growth position”. The coral carpets cover large surfaces compared with their thickness and do not rise appreciably above the general level of sedimentation. There is no active formation of a reef topography. Reiss and Hottinger (1984) used the term to describe coral frameworks lacking distinct zonation under the reach of longshore current systems. Riegl and Piller (1999, 2000a, b) applied the term to frameworks showing a primarily lateral growth component without a distinct vertical ecological zonation. The above circumscribed term “carpet” is extended to those of bivalve origin, thus the term ‘bivalve carpet’ is applied to densely packed bivalve aggregates in growth position and in rock-forming quantities. The investigated bivalve carpets are mud-

supported with a peloidal matrix as described in both fossil and Recent mollusk assemblages (see Riding, 2000; Folk and Chafetz, 2000; Reitner et al., 2000).

## STRATIGRAPHIC SETTING

The study area lies in the Altopiano di Tonezza del Cimone (Vicenza, northeast Italy; Fig. 1). The bivalve carpet succession occurs within the Monte di Campoluzzo section first described by Fugagnoli (1999). The *ca.* 25-m-thick section consists of bioclastic limestones with a few thin silty carbonate mudstone intercalations and embraces the upper part of the formation named Formazione di Rotzo, above the *Orbitopsella* Zone (Fig. 2). The biostratigraphic position of the studied section is based on the larger foraminifera *Cymbriella lorigae* Fugagnoli, *Haurania deserta* Henson, *Haurania* sp., *Everticyclammina* sp., *Pseudocyclammina* sp., and *Bosniella oenensis* Gusic (Fugagnoli 1999). *Siphovalvulina variabilis* Septfontaine, *Duotaxis metula* Kristan, *Earlandia* sp., *Glomospira* sp., *Planiinvoluta* sp., textulariids, valvulinids, dasycladales, and *Thaumatoporella parvovesiculifera* (Raineri) are also present. This assemblage indicates a Late Pliensbachian age (Fugagnoli and Loriga Broglio, 1998; Fugagnoli, 2004).

## MATERIAL AND METHODS

The examined bivalve carpet is found in the well exposed Formazione di Rotzo, the facies of this lithostratigraphic unit have been described in a number of publications (Bassi et al., 1999, 2008; Fugagnoli, 1999, 2004; Monaco and Giannetti, 2002; Posenato et al., 2013a, b). The studied locality is located *ca.* 25 m below the boundary between the Formazione di Rotzo and the San Vigilio Oolite formation (45° 52' 48" N, 11° 15' 28" E, elev. 1713 m; Figs. 1–2). Field analysis included detailed measurement and sampling as well as macroscopic analysis of biotic content. Taphonomic data were collected with respect to biofabrics including packing, size-sorting, shell orientation patterns, fragmentation, disarticulation, and encrustation (e.g., Fürsich and Kirkland, 1986; Kidwell and Holland, 1991; Fürsich et al., 2012).

Shell orientation patterns of shells in cross-sectional view were recorded in the field as well as on larger blocks transported to the laboratory which were first sectioned parallel and then perpendicular to the bedding plane. These blocks were then successively ground down in 5 mm thick intervals. The resulting surfaces (n= 20) were polished and studied with reflected-light microscopy. Scanning electron microscopic analysis (using a FEI Quanta 400, located at the Centro de Instrumentación Científica, Universidad de Granada) was performed on polished samples etched by diluted HCl and sputtered by carbon. Pyrite was initially detected on the basis of crystal morphology and its presence verified by electron backscatter diffraction (EBSD). Component, microfacies and microtaphofacies analyses were performed using a Leica MZ8 microscope on thin sections (5 x 5 cm) cut perpendicular to the bedding plane. The textural classification of Embry and Klovan (1972) was used allowing for a general component and matrix description.

## RESULTS

### Stratigraphic section

The bivalve carpet horizon occurs within a *ca.* 7-m-thick succession consisting of decimeter- to meter-thick, locally nodular limestone beds interbedded with silty carbonate mudstone layers up to 3 cm thick (Fig. 2). The basal part of the succession (1.50 m-thick) consists of 20-to-40 cm-thick beds of packstones and grainstones containing bivalves, oncoids, and small gastropods which are often associated with the shell layers. The following

ca. 70 cm-thick bed consisting of peloidal, bioclastic and bivalve packstones contains a number of well preserved bivalve carpets (Fig. 2) which are the object of this study (Fig. 3). This bed is overlain by a thick bioclastic peloidal packstone layer. A bivalve mound occurs at about 5.50 m from the base of the section. The mound, constructed by the bivalve *Cochlearites*, is 1 to 3 m thick at the core and rapidly dwindles laterally to a decimeter-thick bed. Decimeter-thick packstone beds overlie the bivalve mound and pass upward into nodular packstones containing small, thin-shelled bivalves.

Post-depositional stylolites are common in the section mostly follow bed boundaries, but can also cut through the beds. Component relationships were studied in areas within carbonate beds not crossed by stylolites. In other cases, variation in microfacies types as well as the temporal successions of microfacies and shell beds can also be assessed between distinct horizontal beds bounded by the stylolites.

### Components, microtaphofacies and EBSD analysis

The dominating thin-shelled bivalves are equivalved with thin sub-parallel valves as seen in longitudinal section. Shells are small, with a maximum height of 30 mm, and thin, with a maximum shell thickness of about 1 mm. They possess bi-mineralic shells consisting of an originally aragonitic, but now recrystallized, inner hyaline layer and an outer calcitic, prismatic layer. The bivalves have a narrow and elongated body cavity and lack a very broad internal contact area, which is a distinctive taxonomic character for the adult individuals of *Lithioperna* (Accordi Benini, 1979). The ventral margin is very thin and commonly slightly patulous. This species most likely is an isognomonid-like bivalve (see Discussion below). It is mostly represented by articulated specimens, commonly with the commissural plane in an upright or inclined position. Sparse disarticulated valves as well as small fragments are also present, but subordinate. A further subordinate bivalve taxon has a heart-shaped morphology with a wide body cavity and a thick shell. These shells are completely re-crystallized and were presumably aragonite in origin. This bivalve can be ascribed to megalodontids (see Discussion below).

Small and larger benthic foraminifera are common, including small benthic forms (valvulinids, miliolids) and micro-agglutinated litiolids (*Lituolipora termieri*, *Everticyclammina*). Locally abundant dasycladalean algae can occur as millimeter-sized fragments, which are often micritized and abraded. *Palaeodasycladus mediterraneus* (Pia) and *Thaumatoporella parvovesiculifera* (Ranieri) were identified; *Rivularia* sp. is also present. Fragmented bioclasts up to 20 mm in size are abundant and include unidentified bivalves, gastropods and echinoderm fragments, the latter often represented by cross-sections of echinoid spines. Ostracods are locally common. Common oncoids, with a distinct bioclastic nucleus and a micritic, occasionally layered envelope, reach up to 3 mm in diameter (Fig. 4A). Sub-spheroidal peloids, less than 0.5 mm in diameter, are common and often clotted together. Fecal pellets can be very abundant.

Although components are generally well preserved, microtaphofacies analysis (Brachert et al., 1998; Nebelsick et al., 2011) reveals disarticulation, fragmentation, bioerosion and encrustation. Disarticulation and fragmentation affect bivalves, dasycladaleans and echinoderms. Bivalve shells show rare bioerosion present locally as narrow, tunnel-shaped borings. Encrustation identified on outer and inner surfaces of bivalve shells is present as (1) thin microbial crusts coating small bioclasts which act as nuclei for small oncoids (< 1 mm in diameter; Fig. 5A), (2) thin, superimposed microbial laminae on isolated bivalve shells and shell fragments, and (3) small, uniserial encrusting foraminifera (Fig. 5A). Bivalve shells and oncoids often show micritization. Primary aragonitic shells or shell layers of bivalves, gastropods and dasycladalean skeletons are replaced by calcite.

Light to dark grey packstones within the bivalve carpets are often characterized by

light-red to orange veins (< 1mm thick) and pockets (up to some millimeter in size) filled by very fine micritic sediment. Black (amorphous), light-red and orange minerals are present within these packstones. EBSD analysis reveals the black minerals as pure amorphous organic matter and that the light-red and orange minerals consist of detrital pyritic grains (0.01–0.40 mm in size) composed of pyrite framboids. Pits on the surface of these pyrite grains (Fig. 4E) suggest pyrite dissolution.

### Microfacies

Carbonates consist of light to dark-grey packstones with local grainstone pockets (Table 1). Thin silty carbonate mudstone layers are also locally present. Five different carbonate microfacies were distinguished on the base of lithology, component distribution and biofabric (Fig. 2): fine bioclastic packstone (FBP), peloidal packstone (PL), bivalve packstone (BP), coarse bioclastic packstone (CBP), and peloidal grainstone (PG). The microfacies FBP, PL, BP and CBP are common, while PG is only locally present. Small-scale lateral and vertical microfacies variations are present within individual beds and also within the single thin-sections. Most of the microfacies types are dominated by packstones (FBP, PL, BP, CBP). The bivalve carpets as such are not distinguished as separate microfacies, but are differentiated with respect to shell concentration types (see below). Isolated pockets of pure micrite are also present.

*Fine Bioclastic packstone (FBP).*—The dominating undeterminable fine bioclasts (<60 µm in size) are associated with subordinate small benthic (*Duotaxis metula*, *Meandrovoluta asiagoensis* Fugagnoli and Rettori in Fugagnoli et al. 2003) and larger foraminifera (?*L. termieri*), rare dasycladaleans (*T. parvovesiculifera*), peloids and ostracods. The bioclasts can be abraded.

*Peloidal packstone (PL).*—Peloids consist of single micritic sub-spheroidal coccooids or as small clusters of coccooids. Small benthic foraminifera (*Glomospira*, *Planiinvoluta*) are rare. Bioclasts are abraded and fragmented. Small bioclasts are covered by thin layers of micrite. Micritization can also be present.

*Bivalve packstone (BP).*—Isolated bivalve shells are covered by thin microbial layers and by small encrusting foraminifera (Fig. 5A). Coccooids and clotted peloids are also present. Rare bioerosion and micritization were recognized in bivalve shells.

*Coarse bioclastic packstone (CBP).*—Larger foraminifera and poorly preserved dasycladaleans are rare, coccooids (irregular micritic micro-sub-spherulites) and clotted peloids also occur. Biogenic components are abraded, fragmented and encrusted. In some cases, bioerosion is present in bivalve shells (Fig. 5B).

*Peloidal grainstone (PG).*—Abundant laminar and homogeneous oncoids, up to 1 mm in diameter, show a core (usually a small bioclast) and an envelope of superimposed laminae. Benthic foraminifera are represented by *Lituolipora termieri* associated with undeterminable small forms. Abraded small fragments of undeterminable bioclasts are present.

### Bivalve shell concentrations

Two types of bivalve shell concentrations are distinguished based on taxonomic content, sedimentary fabric and taphonomic features (Table 2) in the *ca.* 70 cm-thick bed (Fig. 2) in the middle of the studied section.

*Type 1: Bivalve carpet with articulated bivalve shells.*—The bivalve carpet consist of densely-packed articulated isognomonid-like bivalve shells which are predominantly vertically oriented (*ca.* 75%) with subordinate sub-horizontal valves. The bivalves show rare fragmentation and disarticulation, encrustation is absent. Interstices between the bivalves are filled with bioclasts and peloidal packstone. The vertically oriented bivalves can be found either attached to horizontal single valves or their umbonal/dorsal part is totally immersed into the sediment matrix. In this latter case, the rest of the bivalve chamber is fill-in by sediment matrix and cement.

*Type 2: Partly disarticulated bivalve concentration.*—Type 2 bivalve concentration are characterized by loosely packed, commonly disarticulated (*ca.* 65 %) bivalve shells floating in the matrix. The shells are dominated by isognomonid-like bivalves with subordinate megalodontid-like bivalves. Fragments of large prismatic bivalves are also present. Shells show a wide size range, from few millimeters up to 5 cm in length. The orientation of shells is predominantly horizontal and mostly convex-up (*ca.* 40 %) with subordinated vertically orientated specimens (*ca.* 35 %; Fig. 6). Fragmentation is poor and disarticulation is common, bioerosion can be present (Fig. 5B). This type of shell concentration occurs together with abundant densely to loosely packed, poorly sorted bioclasts such as ostracods, gastropods, and oncoids. The matrix is formed by bioclasts and peloidal packstone and grainstone.

*Spatial relationships of shell concentration types.*—The spatial relationships of the two shell concentration types are illustrated in Fig. 3. The basal succession of the studied bivalve horizon is formed by the Type 1 concentration which either grades upwardly into or passes abruptly into the Type 2 concentration.

Type 1 concentration constructs characteristically thin tabular veneers, 3 to 10 cm in thickness and around 2 m in width before laterally pinching (Fig. 3). This concentration does not create any significant topographic reliefs. Individual shell concentrations can be densely stacked, separated by only several millimeters of shell-poor sediment (Fig. 3) or be separated by a vertical distances of up to 20 mm in parts of the section. The base of Type 1 concentration is usually sharp (Fig. 3F). Over a vertical distance of 15 cm, three Type 1 concentrations were counted, each bed ranging from 2 to 3 cm in thickness. However, distances between shell beds may reach up to 20 mm in parts of the section.

Sedimentary bodies with Type 2 bivalve concentrations are lenticular with a thickness varying between 2.5 to 4 cm and laterally pinch out.

## DISCUSSION

### Composition of the bivalve fauna

Taxonomic identification of the dominating bivalves taxa is hampered due to their occurrence in highly indurated limestone on the one hand, and re-crystallization of aragonitic shell material on the other. The very thin ventral margins of the small, thin shelled bivalves, commonly slightly patulous, suggest an original elasticity of the shell margins with a mechanism of closure similar to that of the Recent Pinnidae and of most of the semi- or quasi-infaunal bivalves of the *Lithotis* fauna (e.g., Chinzei, 1982; Seilacher, 1984). The systematic identification of these bivalves is problematic due to the fact that diagnostic taxonomic features (e.g., hinge, ligamental area) have not been recognized in the field or in polished rock sections.

The studied isognomonid-like bivalves are characterized by small-sized shells with few incremental growth sublayers suggesting juvenile individuals. According to Accorsi Benini (1985), the bivalves of the Formazione di Rotzo have a growth rate of shell thickness ranging from 2.5 to 3 mm per year in the intertidal taxa (small byssate and semi-infaunal), to about 10 mm per year in the *Lithiotis* fauna. The small size (2–3 cm high) and reduced thickness (<1 mm thick) of the isognomonid-like bivalves suggest mass mortality of juvenile individuals. A question arises whether these bivalves represent juveniles of the equivalved isognomonid *Lithioperna*, a prominent member of the *Lithiotis* fauna of the Calcari Grigi group. *Lithioperna* occasionally also has a prismatic outer layer (Broglia Loriga and Posenato, 1996). This genus, however, has a strongly reduced body cavity and a very broad internal area of contact, which is located at the plane of the multivincular ligamental area (e.g., Broglia Loriga and Posenato, 1996). This morphology has been described in adult and large-sized isognomonid *Lithioperna*, while no information is available for the small-sized juveniles. *Lithioperna* is considered a mud-sticker semi-infaunal bivalve with a juvenile byssate stage (Accorsi Benini, 1979; Seilacher, 1984). The life position, shell structure and mineralogy, and available morphological traits for the studied specimens are close to isognomonid-like bivalves which have a semi-infaunal and endo-byssate life habit. The rare encrustation and bioerosion on studied bivalves hamper the assessment of their buried depth below the sediment-water interface.

Another possible taxonomic affinity as suggested by the upright living position is the pinnid *Trichites*. The shell of this genus, however, is almost completely composed of prismatic calcite (e.g., Alencáster et al., 2009), while the studied small shells show a bi-mineralic composition with the possible inner aragonitic layer as thick as the outer prismatic calcitic layer. The subordinated heart-shape shells show similarities to epifaunal, free-living megalodontids (e.g., *Protodicerias*), which commonly occur in the upper Formazione di Rotzo (e.g., Posenato and Masetti, 2012).

#### Development and demise of the bivalve carpets

The Type 1 shell concentration is interpreted to represent *in situ* bivalve carpets (the bivalve carpet as such) preserved as autochthonous articulated shells, while the Type 2 shell concentration represents physical disturbance of the bivalve carpet. The rare occurrence of boring and encrustation on *in situ* bivalve shells points to a rapid burial and a high sedimentation rate (e.g., Kidwell et al., 1986; Rivas et al., 1997; Hauser et al., 2008). Partial reworking of the bivalve carpet is indicated by the: 1) rare occurrence of articulated bivalves, 2) sub-horizontal or loose arrangement of disarticulated bivalve shells, and 3) irregular distribution of muddy matrix. In the overlying packstone microfacies, coated grains (Fig. 4A) indicate low sedimentation rates during which the biogenic packstone sediments were influenced by moderate bioturbation and occasional currents.

The transition from Type 1 to Type 2 shell concentrations is accompanied by (1) a shift from coarser (FBP, CBP) to finer (PL common) microfacies, (2) the presence of encrustation and bioerosion in the bivalve shells, and (3) a decrease in articulated bivalve shells. The Type 2 shell concentration thus represents parautochthonous disarticulated shells originating from the bivalve carpet which occasionally became encrusted and weakly bioeroded.

The studied skeletal assemblages are interpreted to have been deposited (1) within the upper euphotic zone as indicated by the occurrence of larger lituolid foraminifera and dasycladalean algae, and (2) in a low-energy environment where a fine-grained sedimentary matrix was retained. This environment was punctuated by brief periods of moderate water energy leading to sediment transport and grainstone production. This led to the observed variations in microfacies and shell bed types as well as to variation in oxygenation of the

sediment.

*Microfacies and bivalve carpet.*—The Type 1 shell concentration contains isognomonid-like bivalves, which colonized the muddy sediments of an upper euphotic lagoonal setting. The preferred arrangement of their commissural plane perpendicular to the bedding reflects their original life position. It represents an orthothetic life position characteristic of many isognomonids (e.g., Fürsich, 1980; Seilacher, 1984). The Type 1 shell concentration is thus interpreted to represent autochthonous assemblage representing a bivalve carpet of semi-infaunal, endo-byssate, suspension-feed non-siphonate bivalves. Fine sediments deposited between the upright baffling specimens resulted in the bivalves being entombed in a packstone matrix protecting the specimens from post-mortem reworking and transport. The homogeneous fine peloidal types of the PL microfacies show no evidence of biological and/or physical reworking and are interpreted as primary automicrites (e.g. Rodríguez-Martínez et al., 2010). The occurrence of automicritic peloids in the matrix of the bivalve carpet and the presence of coated grains in the overlying packstone microfacies supports the autochthony of the bivalve carpet. The peloidal grainstone (PG microfacies) represents intermittent moderate water-energy events and is only locally present at the top of the analyzed bivalve carpet horizon (Fig. 3).

In summary, depositional textures of the investigated horizon suggest soft substrates (*sensu* Reiss and Hottinger, 1984) containing fine and coarse bioclasts associated with peloids. These sediments were occasionally swept by currents, giving rise to coarser, grain-supported patches. These autochthonous bivalve carpets are overlain by the parautochthonous Type 2 shell concentration caused by a change in sedimentation rate and water energy. In the Type 2 shell concentration, the oncoids formed under low sedimentation rates and calm conditions favoring microbial growth leading to common oncoids and coated skeletal grains (e.g., Reolid et al., 2005, 2010; Reolid, 2011; Figs. 4A, 5A).

Episodic events is evident throughout the studied horizon with alternation of shell beds and relatively barren packstone. Two successive phases of (1) colonization and (2) demise are reconstructed, each of which reflected by changes in shell fabrics, microfacies and taphonomic signatures (Table 3, Fig. 7).

1. Colonization phase. The isognomonid-like bivalves were semi-infaunal, endo-byssate, non-siphonate, gregarious organisms that settled on the firm muddy substrates. Due to their orientation with vertical commissure (Type 1 concentration) the bivalves were able to keep up with high sedimentation rates. The bivalve carpets consisted of juvenile isognomonid-like bivalves suggesting recurrent, perhaps seasonal, mass mortalities. These bivalves probably represent juvenile individuals of the *Lithiotis* fauna, which is characterized by highly specialized bivalves adapted to mobile bottom conditions, with a mud-sticker stabilization strategy (Seilacher, 1984). The lithiotids are characterized by a fast ventral growth, resulting in spoon- or stick-like shells, as a response a relatively high sedimentation rates (e.g., Chinzei, 1982). Rare bioerosion and encrustation point to relatively short exposure before rapid burial.

The carpets followed the contour of the lagoon floor with a primary lateral growth without a distinct vertical ecological zonation. This is reflected by the dominance of a single taxon. The associated megalodontid-like bivalves are rare and do not show any appreciable concentration (Fig. 7A).

*Production of micrite and seasonal variation of sedimentation rates.*—The gregarious bivalves of the carpets along with microbial colonies produced peloids consisting of autochthonous primary micrite. Present-day suspension-feeding bivalves produce pseudo-faeces, which can contribute substantially to bivalve biodeposits (e.g., Beninger et al., 1999; Kooijman, 2006). Variations in the amount of sediment caused by both the trapping activity of the aggregates and microbial colonies probably had no effect on the bivalve carpets since



their adaptation to a relatively high sedimentary rate. In present-day mussel beds, the mean accretion rates are high (>0.5 mm/d) during the summer season, whereas in the winter season net deposition decreases to zero or shows erosional trends (Flemming and Delafontaine, 1994). Long-term sediment budgets are thus composed of highly variable mean annual rates which, in turn, comprise highly variable seasonal and even monthly rates, depending on the local weather pattern (e.g., Flemming and Delafontaine, 1994; Hertweck and Liebezeit, 2002).

2. Decline and demise of the bivalve carpets. Mass mortality events could in principle be related to (A) rapid burial events, and (B) lowering of oxygenation levels.

A) *Rapid burial events*.—Occasional storms are not supported by sedimentological evidences as transported bivalve accumulations are missing. The articulation of the shells occurring in the bivalve carpets and the Type 2 accumulations (*ca.* 75 % and *ca.* 35 % respectively; Fig. 6) rules out possible event transportation. The absence of abrasion, poor fragmentation, poor or no sorting, and the concave-up orientation of the shells constitute a further evidence that storm event did not affect the shell accumulations.

B) *Variation in oxygenation levels*.—The change in sedimentation regimes as reflected in the shell accumulation types can be explained by changes in the degree of oxygenation in or on the floor of the lagoon. A lowering in oxygenation is supported by the high amount of pyrite grains and rounded framboids that range in size from *ca.* 5 to *ca.* 30  $\mu\text{m}$ , which occur in the bivalve carpets. Sedimentary pyrite forms when bacterial sulfate production provides sulfide ions ( $\text{HS}^-$ ) and  $\text{H}_2\text{S}$  that react with dissolved iron to form pyrite either directly or via an iron monosulfide precursor (Berner, 1984; Schoonen, 2004). Pyrites may form in sediments in two different manners. One is the oxidation of iron monosulphides by hydrogen sulphide, a fast reaction (days; e.g., Rickard, 1997; Butler and Rickard, 2000). This process has been reported as responsible for the formation of framboids just below the redox boundary of strictly anoxic sediments. The other is the polysulphide pathway, which is relatively slow and leads to the formation of isolated crystals over a period of years, usually at greater depths than those typical of framboids (e.g., Wilkin and Barnes, 1997; Butler and Rickard, 2000; Álvarez-Iglesias and Rubio, 2012). The former reaction predominates in anoxic marine sediments with a pH of around 7, and the latter in sediments with a low pH (Yücel et al., 2010).

Studies of modern environments show that pyrite framboids form by chemolithotrophic iron-oxidizing bacteria (e.g., Knoll, 2003; Planavsky et al., 2009) immediately beneath the redox boundary, be it within the sediment or within the water column in the case of euxinic conditions (Wilkin et al., 1996). Framboids reach larger sizes and show a broader size distribution if they grow within the sediment during early diagenesis (Wilkin et al., 1996). The occurrence of larger framboids in the thin veins and laminae (*ca.* 500  $\mu\text{m}$  thick) suggests the occurrence of a redox boundary below the sediment surface that was subject to earlier diagenesis. Following the presence of large framboids (several tens of microns in diameter; Fig. 4E) in the studied sediments, the fast mechanism of pyrite formation is assumed. Thus, the bivalve carpet most likely suffered short anoxic phases.

Once pyrites has been formed, its preservation depends on factors affecting oxidation rates, including water energy (e.g., Raiswell and Canfield, 1998). When surface sediments are remobilized, whether by natural processes (hydrodynamic process) or biotic activity (bioturbation), pyrites can be oxidized. In the present study, the large framboids feature partially oxidized pyrite microcrystals, pointing to sediment remobilization. Oxidation of iron sulfides causes formation of iron hydroxides and substantial lowering of pH. The newly formed iron hydroxides would form coatings on surface sediment grains (Berner, 1969; Schieber and Riciputi, 2005; Schieber, 2007). This process can explain the common orange to light-red colos of veins and of coatings of several oncoids which are a common feature

throughout the Formazione di Rotzo packstone sediments.

Studies on larger benthic foraminifera of the Formazione di Rotzo demonstrated that the degree of oxygenation of the near-surface sediment, along with the nutrient availability, were the most important benthic ecological drivers. Seasonal phytoplankton blooms in the Rotzo lagoonal system played an important role in the production of organic matter (Fugagnoli, 2004), which could have promoted short anoxic phases in the inner lagoon. In fact, amorphous organic matter and small vegetal remains have also been recorded in other facies of the formation (Boomer et al., 2001). Thus, the occurrence of the interpreted dysoxic bottom water, where the bivalve carpets thrived, most likely lies in the seasonal eutrophic nature of the Rotzo lagoonal basin. Lowering of pH in fossil lagoonal settings have been illustrated from southern Patagonia where variations in salinity and pH conditions generated Upper Cretaceous pavements composed by conchostracans, gastropods and corbulids; these pavements represent episodes of mass mortality (Varela et al., 2011). An example of seasonal mass mortality caused by anoxic conditions during the summer in a Lower Cretaceous lake in China was illustrated by Fürsich et al. (2007).

Dysoxic conditions are interpreted to have occurred at the sediment/water interface (Fig. 7). Chemolithotrophic microbial colonies contributed to the production of a firm substrate on which the bivalves settled and baffled the muddy carbonate sediment. The small size of the bivalves (2–3 cm high) suggest a brief existence.

Short-term, possible seasonal anoxic events are interpreted, in connection with occasional decreases in water energy brought about a lowering in oxygenation causing the mass mortality of the juvenile bivalves. The anoxic conditions, below the sediment/water interface, preserved the autochthonous carpets. Consequently, once the baffling action of the carpet ceased, sediment starvation (and early diagenetic changes within the substrate) concomitant with destructive taphonomic processes occurred. The periodicity of the bivalve carpets might be related to repeated phases of bottom stabilization induced by oxygen-rich bottom currents and microbial activity, which allowed the settlement of fixosessile isognomonid-like bivalves.

Our ability to diagnose natural environmental changes based on dissimilarities between life and death assemblages is contingent on the existence of a time lag between changes in the life assemblage and their manifestations in the time-averaged death assemblage (i.e. taphonomic inertia of Kidwell, 2008). Here, we utilized a unique set of serial sectioning, thin section, and scanning electro-microscopic records of Lower Jurassic, Pliensbachian marine bivalves from shallow-water lagoonal deposits to assess a low magnitude of taphonomic inertia in this setting. Although we see distinct taphonomic changes in the bivalve carpets and bivalve accumulations through the sampled interval, the clear lack of change in taxonomic composition (macro- and micro-fossils) suggests that the temporal dynamics observed here have not been driven by fundamental changes to the environment. In any case, the temporal dynamics of these bivalve carpets signals seasonal tracking of ecological changes.

## CONCLUDING REMARKS

Highly diverse Pliensbachian benthic communities living in the Formazione di Rotzo lagoonal settings of the Trento Platform, Venetian area, northeast Italy, were characterized by several bivalve assemblages. Among these, small-sized, thin-shelled bivalves, Isognomonidae-like bivalves, formed bivalve carpets in which individuals occur in growth position and in rock-forming quantities. Bivalve carpets do not generate a significant topographic relief, but rather tabular sedimentary bodies. Environmental drivers (physical and biological factors) constrained the colonization and the demise of the carpets. The following conclusions underscore the unusual paleoecological dynamic aspects of the bivalve carpets under study:

1. The colonization and growth of the bivalve carpets, made up by semi-infaunal, possibly endo-byssate, non-siphonate suspension-feeding forms, took place under a high

sedimentation rate which produced, together with microbial activity, a firm muddy substrate in low hydrodynamic conditions, occasionally swept by higher water energy events.

2. The bivalve carpets grew with a primary lateral growth without a distinct vertical ecological zonation and followed the underlying floor morphology with a maximum thickness above the surrounding lagoonal floor of 10 to 20 cm.

3. Short-term anoxic phases led to a dysoxic carbonate substrate, consisting of a mixture of peloids, bioclasts, amorphous organic matter, small vegetal remains, and chemolithotrophic iron-oxidising bacteria.

4. The bivalve carpets recorded unstable environmental conditions with seasonal phases of reduced oxygenation which caused the mass mortality of juvenile individuals of a single generation.

5. The abundance of nearly-articulated valve pairs in the shell accumulations documents that burial of the bivalve carpets took place soon after the death of the organisms without prior physical disturbance.

6. Successively, repeated phases of bottom stabilization, induced by oxygen-rich bottom currents and microbial activity, and low sedimentation rate allowed the settlement of a new generation of fixosessile isognomonid-like bivalves.

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## FIGURE AND TABLE CAPTIONS

**FIGURE 1**—Geographic location of the study area (Tonezza del Cimone) on the Pliensbachian Trento Platform, a paleogeographic unit in the Southern Alps. The studied bivalve carpets occur toward the top of the Formazione di Rotzo which represents a tropical lagoon closed seawards by oolitic shoals and bars and bordered landwards by marshes (see text for details; from Posenato and Masetti, 2012, modified).

**FIGURE 2**—Schematic stratigraphic setting of the Formazione di Rotzo in the Tonezza del Cimone area (Trento Platform, Early Jurassic) and the section studied. The bivalve carpet succession (ca. 7 m-thick) is located in the upper part of the formation, within the *Lituosepta compressa* Zone, about 25 m below the boundary between the Formazione di Rotzo and the San Vigilio Oolite formation. The bivalve carpets are illustrated in Fig. 3. A, *Lituosepta recoarensis* Zone; Microfacies: 1, peloidal grainstone; 2, fine bioclastic packstone; 3, peloidal packstone; 4, bivalve packstone; 5, coarse bioclastic packstone. Biozonation after Fugagnoli (2004).

**FIGURE 3**—Outcrop photographs and schematic interpretations of the bivalve carpet horizon. Bedding surfaces are indicated. The bivalve carpets are characterized by sub-vertical and vertical shell arrangements constituting a closely packed cluster-framework (shell accumulation Type 1). The carpets pass into floatstone with articulated and disarticulated, thin valves and fragments of prismatic large valves (shell accumulation Type 2).

**FIGURE 4**—Backscatter (SSD) and secondary electron (ETD) SEM images from the bivalve packstone facies, Early Jurassic, northeast Italy.

**A)** Polished cross-section. Thin-shelled articulated bivalves (ab) in living position (shell concentration Type 1; T1) are overlain by partially disarticulated bivalve shell concentration (Type 2; T2); the red pockets are characterized by pyrite grains (py). Note the occurrence of coated grains (oncooids; on), encrustation (en) and bioerosion (bo) just above the T1/T2 boundary.

**B)** Panoramic view of the fine packstone with pyrite clusters (Py), organic matter (black vegetal remains, V), and euhedral authigenic potassium feldspar (F).

**C)** Details of pyrite grains, framboids and remnant spherical shapes (interpreted as degraded pyrite framboids) with corroded surfaces.

**D)** Framboids with non-corroded pyrite crystallites.

**E)** Smooth surface of a large corroded framboid with a tight packing of pyrite crystallites

**FIGURE 5**—**A)** Different encrustations on shells represented by thin, superimposed microbial laminae (tl, arrows) and small, uniserial encrusting foraminifera (ef).

**B)** Rare bioerosion on bivalve shells is present locally as narrow tunnel-shaped borings (arrow) Scale bars = 500  $\mu$ m.

**FIGURE 6**—Cross-section orientation of the thin-shelled bivalves occurring in the bivalve horizon. See Fig. 2 for stratigraphic details. The shell concentration Type 1 (solid-line rectangles on photographs) represents the densely packed bivalve carpet. Shell concentration Type 2 (dashed-line rectangles on photographs) is composed of disarticulated and partly articulated shells floating in a packstone matrix. Shell orientations assessed on equal areas of both types.

**FIGURE 7**—Schematic summary of the development of the Pliensbachian bivalve carpet. Environmental drivers such as sedimentation rate, water energy, oxygenation of the substrate

produced small-scale seasonal variations. Trento Platform, northeast Italy. Not to scale.

**A)** Colonization of thin-shelled bivalves on a firm muddy substrate composed of amorphous organic matter and microbial colonies.

**B)** Bivalve carpet, following the contour of the floor, thrived during high microbial production and sedimentation rates. Bb, close-up view of the position of the oxic (Ox)–dysoxic (Dysox) interface,

**C)** The demise of the bivalve carpets through anoxic conditions promoted by seasonal phytoplankton blooms. The dead shells still act as bafflers and the carpet is buried.

**D)** 3-D sketch showing the patchy distribution of the bivalve carpet. Note the autochthonous (Type 1) and parautochthonous (Types 2) shell concentrations (compare Fig. 3). Not to scale.

**TABLE 1**—Distinctive characteristics of the main microfacies from the Lower Jurassic bivalve carpet succession of the Altopiano di Tonezza del Cimone, northeast Italy (Figs. 2–6): sedimentological features, bioclastic components, water turbulence, sedimentation rate and substrate. LBF, larger foraminifera; FBP, fine bioclastic packstone; PL, peloidal packstone; BP, bivalve packstone; CBP, coarse bioclastic packstone; PG, peloidal grainstone.

**TABLE 2**—Sedimentary and taphonomic features of the two shell concentration types distinguished in the Lower Jurassic succession from the Altopiano di Tonezza del Cimone, northeast Italy. \*in cross-section; \*\* of the deposit.

**TABLE 3** — Summary of the paleoecological dynamics and environmental drivers responsible for the densely packed bivalve carpets, which thrived in the Lower Jurassic Rotzo lagoon of the Trento Platform, Venetian area, northeast Italy.

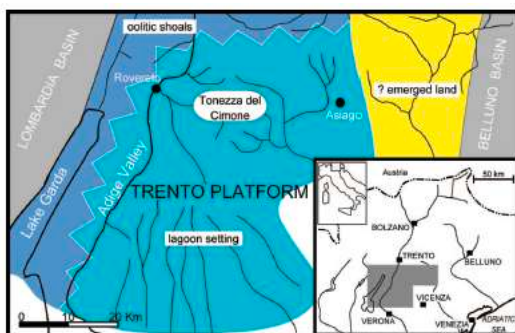


FIG. 1.—Geographic location of the study area (Tonezza del Cimone) on the Pliensbachian Trento Platform, a paleogeographic unit in the Southern Alps. The studied bivalve carpets occur toward the top of the Formazione di Rotzo which represents a tropical lagoon closed seaward by oolitic shoals and bars and bordered landwards by marshes (see text for details). Modified from Posenato and Masetti (2012).

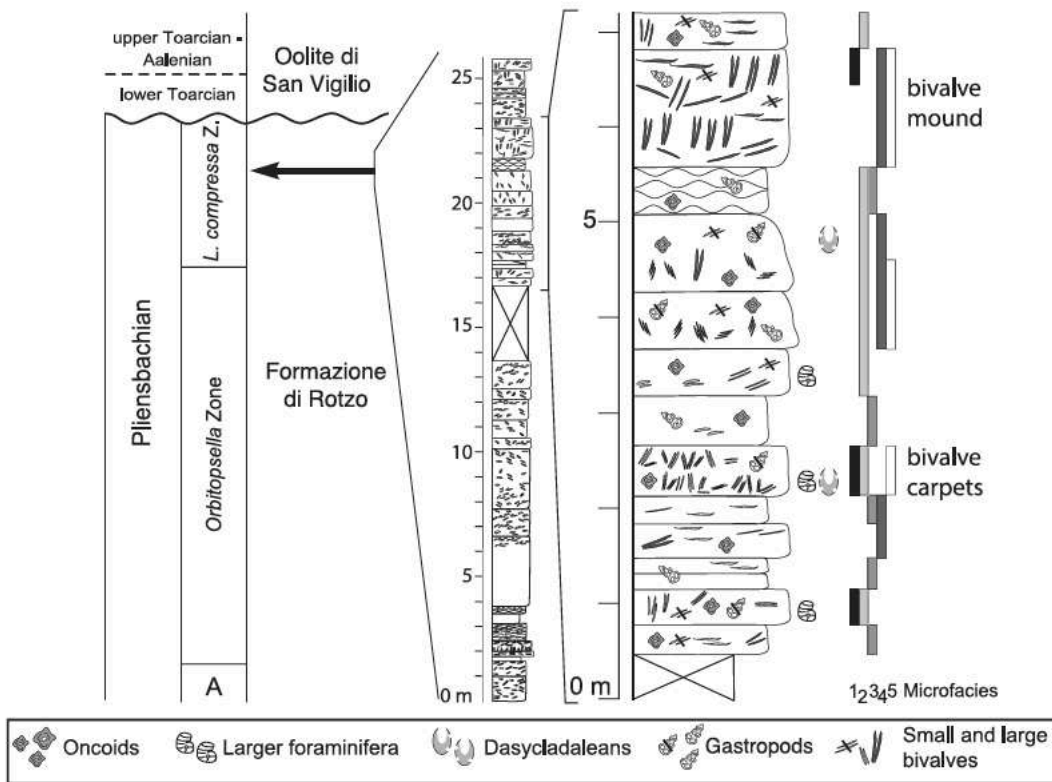


FIG. 2.—Schematic stratigraphic setting of the Formazione di Rotzo in the Tonzella del Cimone area (Trento Platform, Early Jurassic) and the section studied. The bivalve carpet succession (~7 m-thick) is located in the upper part of the formation, within the *Litosepta compressa* Zone, about 25 m below the boundary between the Formazione di Rotzo and the San Vigilio Oolite formation. The bivalve carpets are illustrated in Figure 3. A, *Litosepta recoarensis* Zone; Microfacies: 1, peloidal grainstone; 2, fine bioclastic packstone; 3, peloidal packstone; 4, bivalve packstone; 5, coarse bioclastic packstone. Biozonation after Fugagnoli (2004).

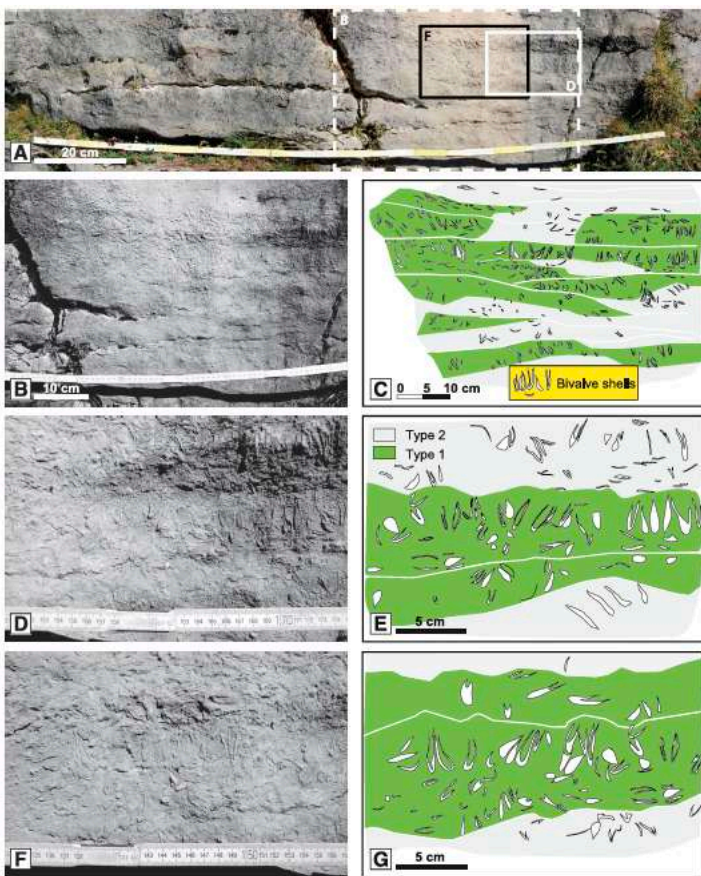


FIG. 3.—Outcrop photographs and schematic interpretations of the bivalve carpet horizon. Bedding surfaces are indicated. The bivalve carpets are characterized by sub-vertical and vertical shell arrangements constituting a closely packed cluster-framework (shell accumulation Type 1). The carpets pass into float stone with articulated and disarticulated, thin valves and fragments of prismatic large valves (shell accumulation Type 2).

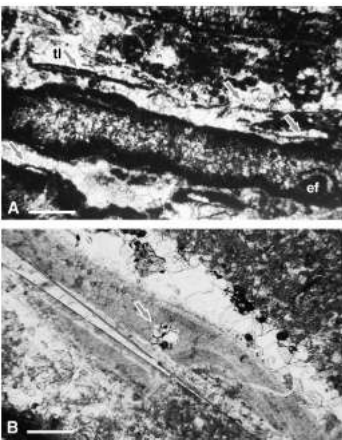
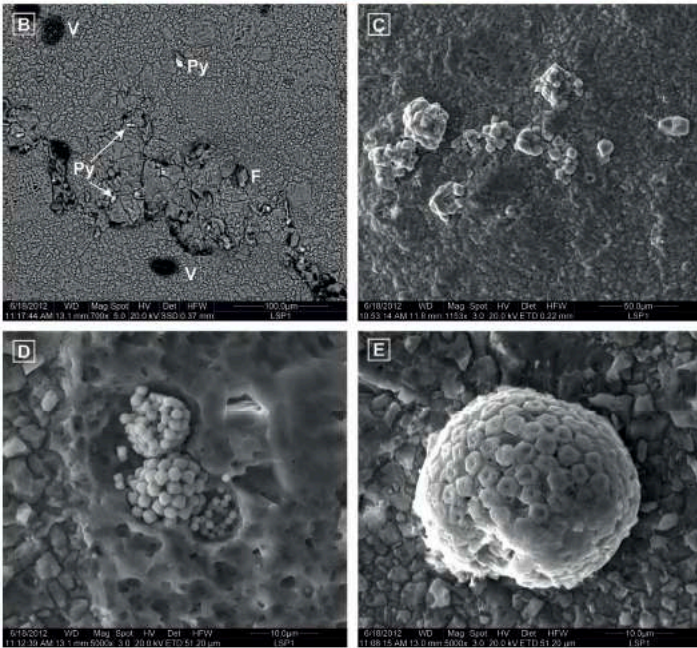
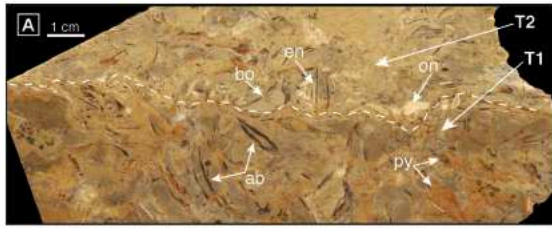


FIG. 5.—A) Different encrustations on shells represented by thin, superimposed microbial laminae (d, arrows) and small, uniserial encrusting foraminifera (f). B) Rare bioerosion on bivalve shells is present locally as narrow tunnel-shaped borings (arrow). Scale bars = 500  $\mu$ m.

TABLE 1.—Distinctive characteristics of the main microfacies from the Lower Jurassic bivalve carpet succession of the Altopiano di Toncetta del Cimone, northeast Italy (Figs. 2–6): sedimentological features, bioclastic composition, water turbulence, sedimentation rate and substrate. Abbreviations: LBF, larger foraminifera; FBP, fine bioclastic packstone; PL, peloidal packstone; BP, bivalve packstone; CBP, coarse bioclastic packstone; PG, peloidal grainstone.

Microfacies	Texture	Dominant components	Subordinate components	LBF	Water turbulence	Sedimentation rate	Substrate
FBP	fine packstone	bioclasts	small benthic foraminifera, gastropods, bivalves, ostracods, dacycladactans	<i>Litellipora tenuis</i>	occasionally very low	high	fine, muddy mobile
PL	packstone	peloids	small benthic foraminifera, bioclasts, fecal pellets	absent	occasionally very low	high	fine, mobile
BP	packstone	bivalves	small benthic foraminifera, dacycladactans, small peloids, gastropods	rare, undetermined	occasional	high	fine mobile
CBP	coarse packstone	bioclasts	prismatic bivalves, small peloids, fecal pellets, gastropods, ostracods, dacycladactans	rare, poorly preserved	frequent	low	coarse, muddy mobile
PG	grainstone	peloids	oncoids, larger foraminifera	<i>Litellipora tenuis</i>	occasionally moderate	low	fine, mobile

TABLE 2.—Sedimentary and taphonomic features of the two shell concentration types distinguished in the Lower Jurassic succession from the Altopiano di Tonèzza del Canone, northeast Italy. Single asterisk indicates feature in cross-section; double asterisk indicates feature of the deposit.

Shell concentration properties	Type 1	Type 2
packing	dense	loosely
sorting	absent	poor
orientation (in cross section)	sub-horizontal/vertical	absent/random
geometry (of deposit)	tubular/lens	absent
internal structure/arrangement	cluster/frame	absent
fragmentation	rare	poor
disarticulation	rare	rare, common
bioerosion	absent	rare
encrustation	absent	absent
final burial	very rapid	late
interpretation	autochthonous	parautochthonous

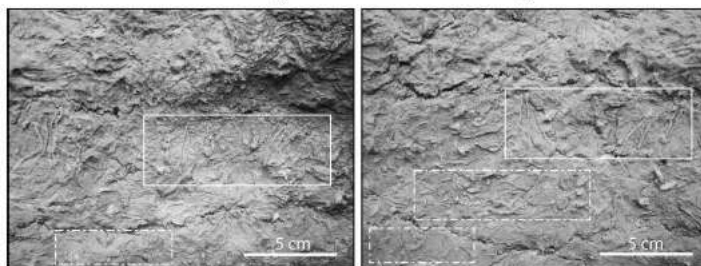
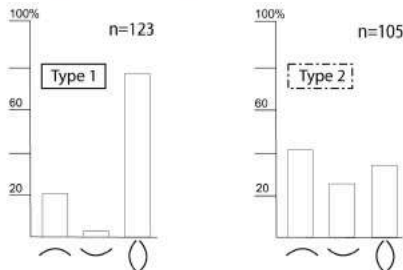


FIG. 6.—Cross-section orientation of the thin-shelled bivalves occurring in the bivalve horizon. See Figure 2 for stratigraphic details. The shell concentration Type 1 (solid-line rectangles on photographs) represents the densely packed bivalve carpet. Shell concentration Type 2 (dashed-line rectangles on photographs) is composed of disarticulated and partly articulated shells floating in a packstone matrix. Shell orientations assessed on equal areas of both types.

TABLE 3.—Summary of the paleoecological dynamics and environmental drivers responsible for the densely packed bivalve carpets, which thrive in the Lower Jurassic Rotzo lagoon of the Trento Platform, Venetian area, northeast Italy.

Paleoecological dynamics	Environmental drivers	Evidences	Effects/outcome
colonization	Firm muddy substrate	packstone microfacies	semi-infusunal, byssate, nonsiphonate bivalves
demise	High sedimentation rate	rare bioerosion and encrustation	rapid burial
	Seasonal anoxic events	organic matter, large-sized pyrite framboids	mass mortality of bivalves and overproduction of microbial colonies
	Decrease in sedimentation rate	oncoids, bioerosion, and encrustation	shells are rapidly buried or re-worked, early substrate lithification and preservation of <i>in situ</i> bivalve carpets

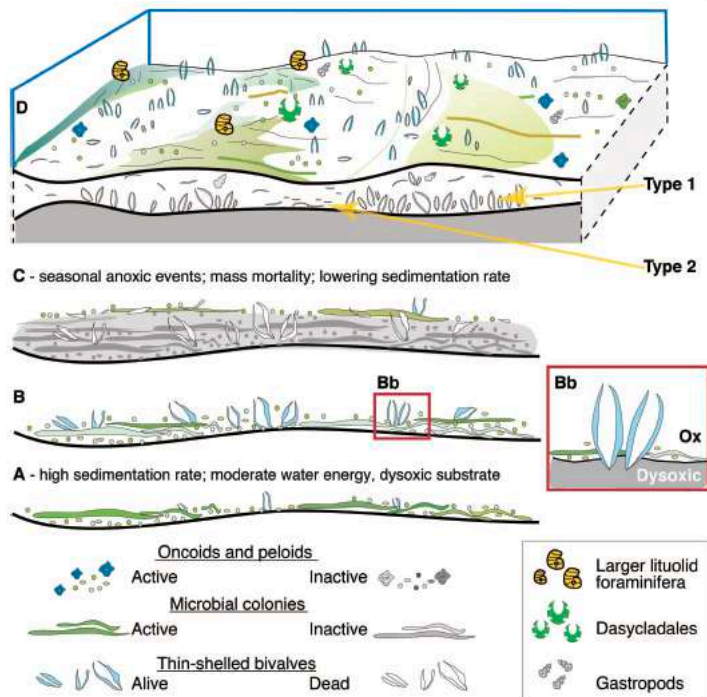


FIG. 7.—Schematic summary of the development of the Pleistocene bivalve carpet. Environmental drivers such as sedimentation rate, water energy, oxygenation of the substrate produced small-scale seasonal variations. Trento Platform, northeast Italy. A) Colonization of thin-shelled bivalves on a firm muddy substrate composed of amorphous organic matter and microbial colonies. B) Bivalve carpet, following the contour of the floor, thrived during high microbial production and sedimentation rates. Bb, close-up view of the position of theoxic (Ox)/dysoxic (Dysox) interface. C) The demise of the bivalve carpets through anoxic conditions promoted by seasonal phytoplankton blooms. The dead shells still act as buffers and the carpet is buried. D) 3D sketch showing the patchy distribution of the bivalve carpet. Note the autochthonous (Type 1) and parautochthonous (Types 2) shell concentrations (compare Fig. 3). Not to scale.