Distinguishing core and flank facies based on shell fabrics in Lower Jurassic lithiotid shell beds

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ABSTRACT

Lower Jurassic larger bivalves, mostly represented by the monospecific lithiotid genera *Lithiotis*, *Cochlearites* and *Lithioperna*, formed large shell accumulations in the shallow-water carbonate Tethyan and Panthalassa margins. A quantitative analysis of lithiotid accumulations from the Trento Platform (northern Italy) was carried out in order to solve the conundrum of distinguishing the distribution of autochthonous and parautochthonous forming lithiotids in the core and flanks of these bivalve accumulation. Various representative accumulations are characterized with respect to taxonomic make up systematic content, shell cover, shell density, orientation and disarticulation of individual shells allowing for autochthonous, parautochthonous or allochthonous individuals to be distinguished within core and flank deposits. *Lithioperna* shows a high shell cover within the accumulation core while that of *Cochlearites* is variable and *Lithiotis* is rare. All three lithiotids occur in high densities in the accumulation flanks. As expected, autochthonous individuals of all

three genera are frequent in the accumulation cores where they are preserved in life position. In the flanks, most bivalves are parautochthonous except for *Lithioperna* which can grow in life position. Bivalves in allochthonous shell beds are highly fragmented and disarticulated. The studied traits are potentially useful as proxies for distinguishing core or flank facies when the accumulation does not crop out as a whole.

1. Introduction

Abundant and well-diversified in different marine habitats, the bivalves are a key-group involved in the biotic recovery after the end-Triassic mass extinction event (e.g., Bambach, 2006; Wignall and Bond, 2008; Mander et al., 2008; Ros and Echevarría, 2012). Their recovery and diversification was very rapid and not geographically homogeneous in comparison with other marine invertebrates (e.g., corals). For instance, they show high origination rates in Argentina already since the uppermost latest early Hettangian (Damborenea et al., 2017), while a nearly instantaneous recovery has been reported in Tibet (Hautmann et al., 2008). Significant diversification is observed among Hettangian marine invertebrates, culminating in the Pliensbachian reappearance of reef organisms/reef biotas/reef habitats/reef ecosystems (Hallam and Wignall, 1997). These organisms/biotas/habitats/ecosystems recorded biotic turnovers, changes in abiotic ocean and regional perturbations (e.g., Dera et al., 2010; Martindale et al., 2019).

Sinemurian–lower Toarcian tropical shallow-water communities are distinguished by a unique evolutionary phase of aberrant and frame-building constratal-growth forms (*sensu* Skelton et al., 1995) represented by the lithiotid bivalves. These include several, not systematically related, gregarious taxa such as *Cochlearites*, *Gervilleioperna*, *Lithiotis*, *Lithioperna*, *Mytiloperna* and *Opisoma*. They thrived along the Tethyan and Phanthalassa margins from northern Africa, through southeast Asia to western America (e.g., Bosellini, 1972; 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). Well known lithiotids occur in the Formazione di Rotzo, a shallow-water carbonate succession deposited on the Jurassic Trento Platform of northeastern Italy (e.g., Gümbel, 1871; Tausch, 1890; Böhm, 1891; Reis, 1903; Bosellini and Broglio Loriga, 1971; Clari, 1975; Masetti et al., 1998), the objects of this study.

Modern accumulations of larger bivalve shells constructed by oysters play an important ecological role on marine substrates, providing habitats for other organisms (e.g., Coen and Grizzle, 2016). These accumulations affect in different terms turbidity and nutrient recycling by their filter feeding (Gutiérrez et al., 2003). When the balance between oyster recruitment and mortality rate is higher than the carbonate loss, the accumulations attain vertical relief (e.g., Waldbusser et al., 2011). Reef-building oysters have thus been considered ecosystem engineers (Parras and Casadío, 2006; Gutiérrez et al., 2011). Similar ecological conditions have been reconstructed for the Lower Jurassic lithiotids which formed large shell accumulations in shallow-water carbonate depositional systems (e.g., Bosellini, 1972; Broglio Loriga and Neri, 1976; Chinzei, 1982; Fraser et al., 2004; Posenato and Masetti, 2012; Brame et al., 2019).

Studies on these faunas have been focused mostly on systematics (Accorsi Benini and Broglio Loriga, 1977; Accorsi Benini, 1979), functional morphology (i.e., Chinzei, 1982; Seilacher, 1984; Accorsi Benini and Broglio Loriga, 1982; Seilacher, 1984; Accorsi Benini, 1985; Broglio Loriga and Posenato, 1996; Savazzi, 1996) and palaeobiogeography (Broglio Loriga and Neri, 1976; Fraser et al., 2004) of these faunas. Recent investigations have shown that the lower Pliensbachian faunal distribution took place after the Sinemurian–Pliensbachian eutrophic, poorly oxygenated water phase (Franceschi et al., 2014), and that the extinction of these largest aberrant bivalves occurred at the onset of the early Toarcian oceanic anoxic event (Trecalli et al., 2012; Franceschi et al., 2014; Posenato et al., 2018).

Difficulties in distinguishing the lithiotids preserved in indurated limestone have hampered the detailed descriptions of their accumulations and related architecture (i.e., core and flanks), as well as the distinction of autochthonous and parautochthonous individuals. At the outcrop scale, randomly sectioned shells often do not show the diagnostic characters at genus level. Furthermore, the entire accumulation shape rarely crops out completely and the architectural features (i.e., core, flanks as described by Posenato and Masetti, 2012) are poorly known (e.g., Posenato et al., 2018). Although a suite of quantitative methods to describe the rudist accumulations has been so far applied and discussed (e.g., Vilardell and Gili, 2003; Gili et al., 2016), little has been performed for the lithiotid accumulations as far as quantitative methodology is concerned (Posenato et al., 2018). The conundrum of Lower Jurassic lithiotids lies, therefore, in the distinction of (1) the autochthonous and parautochthonous individuals and (2) the accumulation architecture (i.e., core and flanks).

Various accumulations containing the monospecific taxa *Lithiotis problematica* Gümbel, 1871, *Cochlearites loppianus* (Tausch, 1890) and *Lithioperna scutata* (Dubar, 1948) from the Trento Platform are studied in detail in order to: (1) document different lithiotid accumulations with respect to taxonomic diversity of large bivalves, sedimentary fabric and taphonomy; (2) identify different accumulation types including cores and flanks by quantitative various sedimentary and taphonomic attributes; and (3) distinguish and interpret different taxonomic systematic presence and preservation of autochthonous, parautochthonous or allochthonous bivalves within the architectural features of the accumulations.

2. Jurassic lithiothid bivalves

The taxonomic identification of lithiotid bivalves at the outcrop scale is difficult because specific shell sections showing diagnostic characters are usually very rare (e.g., Posenato et al., 2018). The most recognizable characters are found in transversal sections of the dorsal body cavity (e.g., Berti Cavicchi et al., 1971; Chinzei, 1982; Broglio Loriga and Posenato, 1996). *Lithiotis* and *Cochlearites* have dorso-ventrally elongated shells, with a thick attached valve and a thinner free valve. In *Lithiotis,* the free valve is very thin and thus rarely preserved. *Cochlearites* is characterized by an umbonal area with a median large furrow on the thicker valve and a median ridge on the thinner valve. *Lithiotis* is distinguished from *Cochlearites* in having a body cavity with a sub-central ridge in the thicker valve and a furrowed median plate (a possible multivincular ligament area) on the umbonal area. *Lithioperna* is characterized by large, flattened to concavo-convex shells with roundish to subrectangular outline. In radial longitudinal sections, the articulated shells of *Lithioperna* have a flattened shape with the a couplet of lens-shaped articulated pair valves which seemingly reflect one another.

Cochlearites and *Lithiotis* were semi-infaunal suspension-feeders, which developed a “mud-sticker” strategy for stabilization in soft substrates in calm environments with relatively high sedimentation rates (Chinzei, 1982; Seilacher, 1984). These taxa were cemented in the early life stage to hard substrates. *Lithiotis* and *Cochlearites* shells are rarely found as bouquet-like aggregates suggesting that their life position was basically up-right (Göhner, 1980; Chinzei, 1982; Posenato et al., 2018). Their accumulations are characterized by a mud-supported core with a loosely packed shells fabric with embedded congregation of forms (constratal *sensu* Skelton et al., 1995) and few shells in vertical position. These build-ups, lacking a wave-resistant rigid framework, have been defined as bivalve mounds (*sensu* Riding, 2002; Posenato and Masetti, 2012).

Lithioperna had an epifaunal to semi-infaunal mode of life. Two main morphotypes were recognized in adult shells (Seilacher, 1984): an orthothetic, mud-sticker (morphotype A of Broglio Loriga and Posenato, 1996), with a flat and thin shell contributing to crowded, book-like vertically embricated colonies. and a pleurothetic morphotype, cup-shaped recliner (morphotype B of Broglio Loriga and Posenato, 1996) with thick and roundish shells which lived in more sparse populations. The morphotype B had either heavyweight shells for bottom stabilization in skeletal supported substrates or corresponding lightweight strategies in mud-supported substrates (Broglio Loriga and Posenato, 1996).

3. Geological and stratigraphic setting

The Calcari Grigi Group represents a Hettangian–Pliensbachian carbonate shallow water succession of the Trento Platform (Fig. 1), a palaeogeographic unit resulting from rifting associated with the opening of central North Atlantic Ocean (e.g., Winterer and Bosellini, 1981; Castellarin et al., 2005). In the study area, the Calcari Grigi Group consists of the (in stratigraphic order): Formazione di Monte Zugna, Calcare Oolitico di Loppio, Formazione di Rotzo, and the Oolite di Massone (e.g., Castellarin et al., 2005).

The Formazione di Rotzo is characterized, in the lower part, by decimetre-thick grey peloidal wackestone/packstone and marlstone alternations followed, in the upper part, by prevailing packstone/grainstone calcarenites of packstone/grainstone with peloids or coated grains. It extends from the Adige Valley to the Asiago area with the maximum thickness (ca. 250 m) in the Altopiano di Tonezza–Folgaria area. The Formazione di Rotzo represents a tropical lagoon protected from the open sea by oolitic shoals and from the emerged land by marshes (Bosellini and Broglio Loriga, 1971; Clari, 1975). Due to the scarcity of ammonoids, the biostratigraphy of the Formazione di Rotzo has been essentially based on benthic foraminifera (e.g., Bosellini and Broglio Loriga, 1971; Fugagnoli, 2004). The Formazione di Rotzo has been divided into three foraminiferal biostratigraphic units (Fig. 2): *Lituosepta recoarensis* Zone, *Orbitopsella* Zone and *Lituosepta compressa* Zone, ranging in age from the late Sinemurian to the late Pliensbachian (e.g., Fugagnoli, 2004).

The stratigraphic and geographical distribution of lithiotids in the Formazione di Rotzo were controlled by various environmental factors (e.g., salinity, oxygen, hydrodynamic and trophic regimes; Posenato and Masetti, 2012). *Lithiotis* is common in the middle part of the formation (*Orbitopsella* Zone), where the foraminiferal assemblage suggests prevailing mesotrophic conditions (Fugagnoli, 2004). The acme of lithiotid occurrence, mainly represented by *Cochlearites*, occurs in the upper part of the formation, where prevailing oligotrophic conditions occurred (Fugagnoli, 2004; Posenato and Masetti, 2012; Franceschi et al., 2014). *Lithioperna*, widespread throughout the Formazione di Rotzo, is considered to be the most eurytopic lithiotid adapted to more stressed (e.g., low oxygenation) environments in comparison to *Lithiotis* and *Cochlearites* (Posenato et al., 2000; Fraser et al., 2004; Posenato and Masetti, 2012). Several studies dealt with the facies characterising of this lithostratigraphic unit (Fugagnoli, 1999, 2004; Boomer et al., 2001; Monaco and Giannetti, 2002; Bassi et al., 2008, 2015; Posenato et al., 2013a, 2013b).

The studied lithiotid shell deposits are defined as accumulations to indicate bivalve deposits with no structural and dynamic implications (e.g., Riding 2002). Eighteen lithiotid accumulations cropping out in the Verona, Vicenza and Trento areas (northeast Italy) were studied (Fig. 1, Table 1): one accumulation in the Vaio dell'Anguilla (Monti Lessini, Verona), seven accumulations in the

Altopiano di Tonezza (Vicenza; six in the Monte Toraro succession, one near Monte di Campoluzzo), four accumulations in the Altopiano di Asiago (Vicenza), an isolated outcrop near Passo Vezzena (Trento) with four lithiotid accumulations and a huge accumulation near Contrada Dazio (Folgaria, Trento).

4. Methods

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The studied accumulations, characterised by the three most aberrant taxa (*Lithiotis*, *Cochlearites, Lithioperna*), occur in six different successions, within the Formazione di Rotzo and range from the *Orbitopsella* Zone to the *Lituosepta compressa* Zone (Fugagnoli 2004; Fig. 2, Table 1). These accumulations were selected for their distinctive characteristics which represent the suite of the larger bivalve accumulations. The Monte Toraro, Monte di Campoluzzo and Vaio dell'Anguilla outcrops, located in the middle-upper Formazione di Rotzo, show the accumulation shapes in which all lithiotid morphotypes occur (Figs. 3–5). The Formazione di Rotzo accumulation case shows horizontally oriented shell accumulations, with no defined general shape. The largest accumulation occurs in Contrada Dazio outcrop (Göhner 1980), where the lithiotid shells are chaotically arranged, while The Passo Vezzena outcrop has never been examined in detail.

The examined bivalve accumulations were described in terms of stratigraphic location, dominant lithiotid taxa, shell fabrics and taphonomic attributes. These attributes are (1) percentage of shell cover (% of area covered by shells), (2) shell density (number of individuals/400 cm^2 occurring in perpendicular sections to the bedding or on the bedding surface), (3) percentage of articulated and (4) complete shells, and (5) occurrence relative proportion of autochthonous/parautochthonous or allochthonous individuals. Some representative randomly-sectioned shell specimens allowed for the taxonomic identification of the dominating bivalve taxa (see Posenato et al. 2018). Large rock samples were also sectioned and polished in order to identify enclosed specimens. The sedimentary fabric and taphonomic attributes of the lithiotid accumulations were quantitatively assessed using field macro-photographs of exposed natural rock surfaces oriented either parallel or perpendicular to the bedding and analysed by using the graphic software package AutoCAD 2004.

Each outcrop was mapped by quadrants (Fig. 3) in order to analyse the sedimentary and taphonomic attributes of the lithiotids within the accumulations. Whenever possible, representative quadrants were taken from the core and flanks of accumulations. In outcrops with undetermined accumulation architecture (i.e., Rotzo, Contrada Dazio), randomly distributed quadrants were taken from different parts of the accumulation. Depending on maximum shell size, quadrants ranging in size from 7.5x7.5 cm to 40x40 cm were analysed. In all, a total of 150 quadrants were analysed (Table 1) with the average values reported in Figs. 6–8.

5. Results

5.1. Monte Toraro accumulation A (TorA1–A2, Figs 4A–B, 5, 6A)

Lithiotis characterises two superimposed bivalve accumulations consisting of peloidal-bioclastic rudstones/floatstones with a wackestone/packstone matrix containing rare undetermined lituolid larger foraminifera: TorA1 and TorA2. TorA1 accumulation is ca. 1 m high and ca. 10 m wide (Fig. 6A). The thick *Lithiotis* shells ranging from 5 mm to 25–30 mm in thickness and up to 30 cm high, are easily recognizable by the transversal sections of the body cavity of the attached valve. The free valve, thinner than the attached one, cannot be identified at the outcrop scale. Vertical and strongly inclined individuals are mostly preserved as moulds and casts due to aragonite dissolution (Posenato and Masetti 2012, fig. 7g, k, l). In the TorA1 accumulation core the shell density is relatively low (7–15 ind./400 cm^2), but higher in the accumulation flanks (19–27 ind./400 cm^2; Fig. 4B). The percentage of shell cover increases toward the accumulation flanks, where rare sponges, brachiopods, *Pseudopachymytilus*, *Opisoma* and solitary corals occur. The core is characterized by abundant autochthonous *Lithiotis* and brachiopod shells. The lithiotid shells have an inclination ranging from 25°–30° to 80°; some bouquet-aggregates are also present (Fig. 4A). In the periphery of the flanks, the shells are sub-horizontal (at most inclined ca. 15°; Fig. 4B).

The smaller lens-shaped A2 accumulation (Figs. 5, 6A), *ca.* 4 m wide and 30 cm high, is dominated by wide, short and articulated *Lithiotis* shells (ca. 10 cm high and ca. 8 cm wide; Fig. 5). Subordinate components are represented by brachiopods, larger foraminifera, oncoids and peloids. The *Lithiotis* shells are sparse and sub-vertical in orientation.

5.2. Monte Toraro accumulation B (TorB, Fig. 6B)

This accumulation, 30 cm high in the core and ca. 10 m wide, consist of small *Cochlearites* shells (up to 10–15 cm in height) in a bioclastic wackestone sediment matrix (Fig. 6B). Locally few gastropods, rare solitary corals and rare thin-shelled bivalves are present (Posenato and Masetti 2005, 2012, fig. 7o).

In the core, the *Cochlearites* shells show complete dissolution while those occurring in the accumulation flanks are re-crystallised. The shells occur in sub-vertical position, with rare bouquet-like aggregates. In the core, because the bad preservation of the shells, articulated individuals were not recognised. The shell density ranges from 60 ind./400 cm^2 in the core to 100 ind./400 cm^2 towards the flanks (Fig. 6B). The flanks are characterized by a lower percentage of whole shells (24.2%) than in the accumulation core (44.4%).

5.3. Monte Toraro accumulation C (TorC, Fig. 6D)

This accumulation, lying on a storm deposit with thin-shelled bivalves and gastropods, is ca. 15 m wide and ca. 1.5 m thick. *Cochlearites*, up to 2 cm thick and 10–15 cm up to 30 cm in height, dominates. In the wackestone matrix, the shells are completely recrystallized. At the outcrop scale (about 5 m wide), this accumulation shows a tabular shape (Fig. 6D). The accumulation flanks are not clearly detectable. The shell fabric varies within the accumulation and most of the individuals show an apparently chaotic arrangement with shell inclination ranging from few degrees to more than 50°. Shell density and shell cover are highly variable (17–46 ind./400 cm^2 and 17–30%, respectively). Two bouquet-like aggregates were also identified. The morphoplasticity (i.e., ontogenetic shell adaptation to the substrate) of the shells is shown by autochthonous individuals, with the lowermost part of the shell sub-parallel and the uppermost part sub-vertical to bedding.

5.4. Monte Toraro accumulation D (TorD, Figs 4E, 6C)

This accumulation is tabular in shape, occurring at the bottom of a lens-shaped *Cochlearites* accumulation, consists of decimetre-thick undulated packstone beds separated by erosional surfaces (Fig. 4E, 6C). Dominating *Lithioperna* occurs as small (up to 8 cm in size) fragmented and disarticulated shells. These are frequently iso-oriented and sub-parallel (10°) to the bedding. Low percentage of articulated (ca. 5%) and whole shells (2–17%) and high shell density (220–252 ind./400 cm^2) characterize this accumulation. Rare oncoids, brachiopods and gastropods are also present.

5.5. Monte Toraro accumulation E (TorE, Fig. 7A)

This lens-shaped shell accumulation is dominated by recrystallized *Cochlearites* shells. In the central accumulation area these shells, up to 20 cm long, are apparently sub-horizontally arranged because they are transversally sectioned. Along the flanks the shells are longitudinally sectioned and show an inclination of more than 30° (Fig. 7A). Locally rare individuals of *Lithioperna* occur. Small brachiopods, rare solitary corals and gastropods are also present. The shell density increases toward the lateral areas (from 10 to 27 ind./400 cm^2). The same trend is followed by the percentage of shell cover (from ca. 10% to 36%; Fig. 7A).

5.6. Monte di Campoluzzo accumulation (Cm, Figs 4F, 7B)

This accumulation is made up by *Lithioperna* morphotype A, with flattened, sub-equivalve and slightly undulated shells (Figs. 4F, 7B). These are preserved as coarse calcitic prisms. Rare individuals of *Cochlearites* occur as very small, disarticulated and sub-horizontal shells. Rare brachiopods, gastropods and thin-shelled bivalves are also present.

Shell inclination varies from mainly sub-horizontal, to ca. 30° in the central part of the outcrop, up to 70° in its outermost part. The shell density ranges from ca. 39–66 ind./400 cm^2 in the central part to >100 ind./400 cm^2 in its periphery. The central area is characterized by high percentage of articulated individuals (ca. 82%; even if recorded in some restricted areas) and the occurrence of some whole shells (8–25%). The abundant lithiotid fragments contribute, therefore, to the high shell density.

5.7. Vaio dell'Anguilla accumulation (Va, Fig. 7C–D*)*

The two lithiotid accumulations located ca. 6 m and ca. 20 m above the base of the formation (Posenato and Masetti, 2012, fig. 5). Both accumulations are dominated by *Lithioperna* morphotype A with densely packed vertically-subvertically arranged shells. In the first accumulation, because the lower part is poorly preserved, the shell density and percentages of whole and articulated shells were tentatively calculated (Fig. 7C). In the middle to upper part of the accumulation, closely-packed, large shells are sub-horizontally arranged with a high percentage of articulated and whole individuals. The second accumulation is similar to the the first with high shell densities (ca. >30 ind./400 cm^2) and a high percentage of articulated and whole shells (ca. >55% and >30% respectively; Fig. 7D). Rare shell fragments locally occur.

5.8. Rotzo accumulations (Ro)

In this succession, the lithiotid bearing outcrops are some tens of meters in width. The studied accumulations correspond to the Ro22, Ro27 and Ro34 units of Bosellini and Broglio Loriga (1971). These beds are characterized by *Lithiotis*, *Cochlearites* and individuals tentatively assigned to *Lithioperna* (Table 2).

The lower part of unit Ro22 contains *Lithiotis*, with a maximum shell size of ca. 20 cm long and up to 1 cm thick. Shell density (13 ind./400 cm^2) and shell cover (28.56%) are relatively low (Table 2). Shells are randomly arranged ranging from sub-horizontal individuals to inclined shells. Only larger individuals are articulated.

A tripartite subdivision is present in unit Ro27, 3 m in total thickness (Bosellini and Broglio Loriga, 1971). In the micritic lower subunit (1.5 m thick), *Cochlearites* dominates with subordinate *Lithioperna*. Rare gastropods are also present. The lithiotid shells are small in size (ca. 5–6 cm in height high and only a few millimetres thick). Shell inclination ranges from 30°–40° in the lower part to subhorizontal in the upper part. Shell density and shell size increase both laterally and vertically. The average shell density is high (112 ind./400 cm^2). The middle subunit (in total 1.45 m thick), consist of several lithiotid bearing layers intercalated with bioclastic micritic beds, about 20–40 cm thick with rare lithiotid shells. Each lithiotid layer is marked by undulated surfaces interpreted as synsedimentary erosional events. The uppermost subunit (ca. 40 cm thick) contains highly concentrated, iso-oriented ?*Lithioperna* shells, with shell inclinations changing laterally from 25° up to horizontal. Taphonomic attributes are difficult to assess in the middle and upper subunit due to poor preservation.

The Ro34 (ca. 10 m in thickness) was subdivided in four parts by Bosellini and Broglio Loriga (1971; Table 2). The unit consists of thick lithiotid accumulations with a micritic matrix (Bosellini and Broglio Loriga, 1971). The muddy intervals Ro34.1 and Ro34.2 (lower part) are dominated by *Cochlearites* with rare *Lithioperna*. The shell density is high (30–52 ind./400 cm^2; Ro34-section in Table 2) and the shells arrangement is chaotic. Sub-horizontal individuals and rare bouquet-like aggregates are also present. Some bouquet-like aggregates were identified. Ro34-section and Ro34-surface show the same shell density (Table 2), while the shell covered is biased by the poor shell surface preservation.

5.9. Contrada Dazio accumulation (Da)

In the Contrada Dazio, lithiotid accumulations occur crop out in an extensive outcrop, ca. 30 m wide and high (Göhner, 1980). The analysed sedimentary body is wedge-shaped and only the lower 2 m were previously described (i.e., Interval A of Göhner, 1980). In this accumulation, the lithiotid shells are recrystallized and the core and flanks are not clearly distinguishable. *Lithiotis* dominates and is associated with subordinate *Cochlearites*. Both *Lithiotis* and *Cochlearites* are randomly arranged, with some individuals in an up-right position. Random shell sections and poor exposure conditions did not allow for the assessment of articulation. In the analysed quadrants, the percentage of complete shells does not show significant changes, while shell density increases towards the periphery (Da3–4; Table 2).

5.10. Passo Vezzena accumulations (Ve, Figs 4C–D,8)

The studied lithiotid outcrop is located along the road connecting Asiago (Vicenza) to Lavarone (Trento; Fig. 1). The outcrop, about 20 m wide and 3 m high, is composed of four superimposed accumulations with packstone matrix dominated by *Cochlearites* (Ve1–4; Fig. 8A). In Ve1 *Cochlearites* shells are chaotically to sub-vertically arranged (Figs. 4C, 8B). Rare gastropods are also present. The percentage of articulated and complete shells is relatively low (ca. 2.13% and 8.91% respectively). Ve2 is characterized by vertical or slightly inclined *Cochlearites* shells. The estimation of the shell covered areas and the complete shells is highly influenced by the bad preservation of the outcrop (Fig. 8C). The shells are densely packed with complete, articulated individuals, up to 20 cm in height and up to ca. 1 cm in thickness. The *Cochlearites* dominated accumulations Ve3 and Ve4 show sub-horizontally and sub-vertically arranged large shells (up to 35 cm in height) with high percentage of complete, articulated individuals (>40%). *Lithioperna* is subordinated. These last two accumulations are characterized by high densities of shells (ca. 48%; Figs. 4D, 8D–E).

6. Discussion

Autochthonous *Cochlearites* and *Lithioperna* can occur both in the accumulation core and flanks while autochthonous *Lithiotis* only occurs in the accumulation cores (es. Figs. 4A, 6A, 9; Table 3). Among the studied accumulations, TorA1–A2 represents the best example of an accumulation core where dominating autochthonous *Lithiotis* occurs in sub-vertical position or in bouquet-like aggregates (Figs 4A–B). The high percentage of complete *Lithiotis* shells (i.e., ca. 87%; Table 2) and their sub-vertical arrangement in the accumulation core of Contrada Dazio is also an indication for the autochthonous position of these bivalves.

Cochlearites typically occurs upright within dense thickets and bouquets, whereby the commissure planes are oriented in various directions (Debeljak and Buser, 1998; Brame et al., 2019). Bouquet aggregates of *Cochlearites* were found in the cores of TorC, TorB and Ve1–2.

These aggregates along with sub-vertical individuals are interpreted to be in life position (Chinzei 1982; Seilacher 1984). Similar as that described for rudists (Skelton et al., 1995) this arrangement suggests a relative sparse availability of suitable attachment substrates. The best examples of autochthonous *Cochlearites* shells are present in the Ve1–2 accumulations where they are complete, articulated and in a vertical or slightly inclined orientation (Fig. 4C–D). Sparse, small *Cochlearites* bouquets were also identified along the Ro34 accumulation flanks.

Autochthonous *Lithioperna* morphotype A showing the classic, highly-packed, book-like vertically embricated accumulations (e.g., Seilacher, 1984; Broglio Loriga and Posenato, 1996) were encountered in the core of the Vaio dell'Anguilla accumulation. The highly-packed aggregation together with the semi-infaunal life habits are highly conducive to burial and preservation and show corresponding high numbers of complete and articulated shells (Fig. 7C–D). This type of preservation is common in the Trento Platform (Posenato and Masetti, 2012) and Apennine Carbonate Platform of southern Italy (Posenato et al., 2018). In some cases, imbricated autochthonous shells acted as hard substrates for the larval settlement of *Cochlearites* accumulations (Posenato and Masetti, 2012, fig. 7c).

Inclined lithiotid shells found along the accumulation flanks are interpreted as parautochthonous shells which have been displaced from their life position. These shells are often correspondingly disarticulated and re-orientated, though they can remain complete (Table 3; Fig. 9). The misplacement of the life position is likely due to a decrease of sedimentation rate and an increase in water energy before final burial (e.g. Chinzei, 1982; Seilacher, 1984; Posenato and Masetti, 2012). Encrusted and bioeroded shells of the lithiotid fauna are very rare. This suggests that (1) sedimentation rates were high enough to hamper encrusting epifauna and bioeroding endofauna and (2) parautochthonous to allochthonous lithiotid shells, which could have been exposed for longer, to show increased encrustation and bio-erosion. The only detailed study on the occurrence of bioerosion in a member of the lithiotid fauna suggested seasonal or temporal mesotrophic conditions within an overall oligotrophic regime as a factors for this rare occurrence in Pliensbachian larger bivalves (Bassi et al., 2017).

In the Ve3–4 accumulation, parautochthonous *Cochlearites* and *Lithioperna* individuals are distinguished by high percentages of articulated shells along with large sizes and sub-horizontal positions (Figs. 8D–E). These occurrences are interpreted as the flanks of two accumulations whose cores are likely located lateral to the studied outcrop. The sub-horizontally arranged *Cochlearites* of TorE are also interpreted as parautochthonous (Fig. 4E). If the accumulation core is surrounded by radially arranged parautochthonous shells, their transversal sections appear as sub-horizontal. The original inclination of the shells is undetectable since it depends to the randomly oriented section of the outcrop. The increase in parautochthonous specimens may, therefore, suggest a change in the above mentioned environmental parameters, which influenced the shell stability on the muddy substrate.

Abundant parautochthonous forms are present in the accumulation flanks of the Monte di Campoluzzo accumulation (Fig. 7B). The shell density (> 39 ind./400 cm^2) and the flat and ventrally elongated shell morphology are characteristics of the *Lithioperna* morphotype A (Fig. 4F, 7B). This morphotype, which lived vertically in life position, was adapted to high sedimentation rates and contributed to very dense aggregates showing the typical vertically embricated book-like (book-like in Seilacher, 1984) or bouquet-like (e.g., Fraser et al., 2004) packing arrangement. Although shell inclination varies in the studied outcrops, the high percentage of articulated individuals lying sub-horizontally and the occurrence of fragmented and disarticulated shells (Table 3, Fig. 9) suggest that accumulation flanks could be subjected to a higher water turbulence and lower sedimentation rate than the autochthonous *Lithioperna* accumulations from the Vaio dell'Anguilla (Figs. 7C–D). A weaker substrate anchorage (byssate at the juvenile stage) with respect to the other lithiotids which are cemented as juveniles together with a reduced sedimentation rate could have allowed *Lithioperna* to grow sub-horizontally (e.g., Broglio Loriga and Posenato, 1996, fig. 4F) thus reducing the possibilities of preserving shells in an up-right position.

6.1. Taphonomic attributes of the lithiotid accumulations

The analysis of the studied lithiotid accumulations allowed taphonomic attributes of bivalves within the cores and flanks of bivalve accumulations to be assessed. The lithiotid accumulations would have been exposed to processes of erosion, reworking and winnowing before final burial (e.g., Nauss and Smith, 1988; Posenato and Masetti, 2012). These parautochthonous/allochthonous accumulations show a high degree of spatial and temporal mixing, and thus represent within-habitat, time-averaged assemblages (Kidwell et al., 1986). Despite the fact that the taxonomic ascription of randomly sectioned specimens can be problematic, some general trends in preservation of these bivalves can be recognized. Furthermore, the Monte Toraro, Monte di Campoluzzo, Passo Vezzena and Vaio dell'Anguilla accumulations show nearly entire accumulation shapes (with both core and flanks) and can thus be used as comparative models for the other outcrops such Rotzo and Contrada Dazio which are not as well exposed. Distinctive sedimentary fabrics as well as taphonomic features of the studied *Lithiotis*, *Cochlearites* and *Lithioperna* within the accumulation core and flanks (Table 3; Fig. 9) can thus be compared.

The lithiotid accumulations with a tabular shape (Fig. 6C–D) yield both reworked allochthonous shells (e.g., *Lithioperna*, TorD; Figs. 4E, 6C, 9) as well as parautochthonous/autochthonous shells (e.g., *Cochlearites*, TorC; Fig. 6D). Allochthonous shell accumulations are characterised by low shell cover (< ca. 18%), high shell density (>200 ind./cm^2) and very low percentages of articulated (< 6%) and complete bivalves (<17%) suggesting physical reworking. This is the case for *Lithioperna* accumulation which represented the hard substrate for the settlement of cemented or byssally attached bivalves. The tabular *Cochlearites* accumulation (Fig. 6D) is comparable to those from the Apennine Carbonate Platform (Posenato et al., 2018).

Although adult specimens can also occur in the flanks, most lithiotid individuals in the core represent the largest-sized adults. In the *Lithiotis* accumulations, the core is mud-supported, with loosely packed shells of dominating autochthonous individuals (complete shells >15%) associated with subordinate parautochthonous ones (e.g., Da, TorA1; Figs. 4A, 9). The muddy flanks show higher shell cover and density, with well-preserved dominating sub-horizontal individuals (e.g., Ro22, TorA1; Fig. 4B). In the studied accumulation flanks, disarticulated *Lithiotis* shows a sub-horizontal to inclined orientation (Table 3). These are interpreted as parautochthonous because their interpreted life position was vertical to subvertical (e.g., Chinzei, 1982; Seilacher, 1984; Nauss and Smith, 1988).

The *Cochlearites* accumulation core and flanks show a high variability of shell fabrics and taphonomic attributes (e.g., Ve1–4; Table 3; Fig. 9). Only in Passo Vezzena outcrop (Ve1–2; Figs. 4C, 8B–C), is the core of the *Cochlearites* accumulation well preserved, with individuals in life position (vertical/sub-vertical) with high shell densities. The flanks are characterized by inclined or sub-horizontal shells whose taphonomic attributes vary according to the distance from the core area (Ve3–4; Figs. 4D, 8D–E). As already noted in other localities (Posenato and Masetti, 2012), the flanks constitute the most conspicuous part of the accumulation. The peripheral area shows higher shell cover (>20%; TorE) and shell density (ca. > 17 ind./400 cm^2; TorE; Fig. 7A) than the core area. In the *Cochlearites* tabular bodies (e.g., TorC; Fig. 6D), the shell arrangement and taphonomic attributes vary without a specific trend. In these bodies, sparse bouquet-like aggregates are present. With regard to the Rotzo accumulations, the Ro27 (dominated by *Cochlearites*) and the Ro34 (dominated by *Cochlearites*) are interpreted as the accumulation flanks because their taphonomic attributes (Table 2). *Cochlearites* records have been reported for southern Italy, Slovenia, Maorocco and western USA (Debeljak and Buser, 1998; Fraser et al., 2004; Posenato et al., 2018; Brame et al., 2019).

The single studied example of *Lithioperna* morphotype A accumulation core in the Vaio dell'Anguilla accumulation, is characterized by highly dense packed shells with sub-vertical/vertical arrangement. The accumulation core shows a high shell cover (ca. >47%), a high percentage of articulated (ca. >55%) and complete shells (ca. >30%; Fig. 9). In the Monte di Campoluzzo, the *Lithioperna* accumulation flanks show high shell cover (> 15%) and density (h > 15 ind./400 cm^2), along with abundant parautochthonous individuals (Figs. 4F, 9; Table 3). In both core and flanks, articulated shells occur in variable amounts (up to ca. 90%; Fig. 9). *Lithioperna* accumulations described in the literature show generally a tabular shape (Posenato and Masetti 2012; Posenato et al. 2018), which can be related to the *Lithioperna* life habit (e.g., weak bottom anchorage and shell instability), and environmental conditions (high hydrodynamic setting and low sedimentary rate; Debeljak and Buser, 1998; Posenato and Masetti, 2012).

7. Conclusions

In the Pliensbachian shallow-water carbonate successions of the Southern Alps, northern Italy, different types of lithiotid accumulations are present. Although the accumulations are often characterized by wide lateral extension, only a limited number of outcrops allow for the recognition of architectural features such as core and flanks. A quantitative taphonomic analysis was performed in order to characterize these lithiotid accumulations and to explore the possibility of using sedimentary fabrics and taphonomic features to distinguish accumulation core and flanks.

Based on taxonomic systematic composition, the accumulations can be dominated by a single lithiotid species or be composed of the three species (i.e., *Lithiotis problematica*, *Cochlearites loppianus*, *Lithioperna scutata*). When *Lithiotis* is the dominant taxon, it is rarely associated with subordinate *Cochlearites*. Dominant *Cochlearites* is associated with subordinate *Lithioperna*. When *Lithioperna* dominates, it occurs only with flat and thin shells and is rarely associated with subordinate *Cochlearites*.

In the studied outcrops, autochthonous individuals in a vertical position or in a bouquet-like aggregates are recognizable in the accumulation core, while the flanks are characterized by high percentage of flat lying, toppled parautochthonous shells.

Shell bed characteristics and taphonomic attributes in the core and flanks vary according to the dominating lithiotid bivalves: 1) in the core, the shell cover is highest for *Lithioperna*, variable for *Cochlearites* and low for *Lithiotis*, while in the flanks these attributes show an opposite trend; 2) shell densities are high in the core for *Cochlearites* and *Lithioperna* and low for *Lithiotis*, while in the flanks it is high for all the taxa with more variability in *Cochlearites*; 3) articulated and complete shells vary conspicuously in both the core and the flanks; 4) *Cochlearites* shows the higher variability of taphonomic features; 5) a relative high percentage of articulated individuals (>35%) of *Lithioperna* in the accumulation flanks suggests that autochthonous individuals also thrived in these areas.

Supplementary data to this article can be found online at http://doi.org/…..

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References

Accorsi Benini, C., Broglio Loriga, C., 1977. *Lithiotis* Gümbel, 1971 e *Cochlearites* Reis, 1903 I–Revisione morfologica e tassonomica. Boll. Soc. Paleontol. Ital. 16, p15–60.

Accorsi Benini, C., 1979. *Lithioperna*, un nuovo genere fra i grandi Lamellibranchi della facies a "*Lithiotis*". Morfologia, tassonomia ed analisi morfofunzionale. Boll. Soc. Paleontol. Ital. 18, 221–257.

Accorsi Benini, C., 1985. The large Liassic bivalves: symbiosis or longevity. Palaeogeogr. Palaeoclimatol. Palaeoecol. 52, 21–33.

Accorsi Benini, C., Broglio Loriga, C., 1982. Microstrutture, modalità di accrescimento e periodicità nei lamellibrachi liassici (facies a "*Lithiotis"*). Geol. Rom. 21, 795–823.

Bambach, R.K., 2006. Phanerozoic biodiversity mass extinction. Ann. Rev. Earth Plan. Sci. 34, 127–155.

Bassi, D., Fugagnoli, A., Posenato, R., Scott, D.B., 2008. Testate amoebae from the Early Jurassic of the western Tethys, North-East Italy. Palaeontology 51, 1335–1339.

Bassi, D., Posenato, R., Nebelsick, J.H., 2015. Paleoecological dynamics of shallow-water bivalve carpets from a Lower Jurassic lagoonal setting, northeast Italy. Palaios 30, 758–770, doi: 10.2110/palo.2015.020.

Bassi, D., Posenato, R., Nebelsick, J.H., Owada, M., Domenicali, E., Iryu, Y., 2017. Bivalve borings in Lower Jurassic *Lithiotis* fauna from northeastern Italy and its palaeoecological interpretation. Hist. Biol. 29, 937–946.

Berti Cavicchi, A., Bosellini, A., Broglio Loriga, C., 1971. Calcari a *Lithiotis problematica* Gumbel o calcari a "*Lithiotis*". Mem. Geopaleontol. Univ. Ferrara 3, 41–53.

Böhm, G., 1891. Über *Lithiotis problematica* Gümbel. Z. Dtsch. Geol. Ges. 43, 531–532.

Boomer, I., Whatley, R.C., Bassi, D., Fugagnoli, A., Broglio Loriga, C., 2001. An Early Jurassic oligohaline ostracod assemblage within the marine carbonate platform sequence of the Venetian Prealps, NE Italy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166, 331–344.

Bosellini, A., 1972. Paleoecologia dei Calcari a "*Lithiotis*" (Giurassico Inferiore, Prealpi Venete). Riv. Ital. Paleontol. 78 (3), 441–464.

Bosellini, A., Broglio Loriga, C., 1971. I “Calcari Grigi” di Rotzo (Giurassico inferiore, Altopiano di Asiago) e loro inquadramento nella paleogeografia e nell’evoluzione tettonico-sedimentaria delle Prealpi Venete. Ann. Univ. Ferrara N. Ser. 9 (5/l), 1–61.

Brame, H.M.R., Martindale, R.C., Ettinger, N.P., Debeljak, I., Vasseur, R., Lathuilière, B., Kabiri, L., Bodin, S., 2019. Stratigraphic distribution and paleoecological significance of Early Jurassic (Pliensbachian–Toarcian) lithiotid-coral reefal deposits from the Central High Atlas of Morocco. Palaeogeogr. Palaeoclimatol. Palaeoecol. 514, 813–837.

Broglio Loriga, C., Neri, C., 1976. Aspetti paleobiologici e paleogeografici della facies a “*Lithiotis*” (Giurese inf.). Riv. Ital. Paleontol. Stratigr. 82 (4), 651–706.

Broglio Loriga, C., Posenato, R., 1996. Adaptive strategies of Lower Jurassic and Eocene multivincular bivalves. Boll. Soc. Paleontol. Ital. spec. vol. 3, 45–61.

Buser, S., Debeljak, I., 1994. Lower Jurassic beds with bivalves in south Slovenia. Geologija 37, 23–62.

Castellarin, A., Picotti, V., Cantelli, L., Claps, M., Trombetta, L., Selli, L., Carton, A., 2005. Note Illustrative della Carta Geologica D'Italia, foglio 080 Riva del Garda. APAT, Serv. Geol. Italia, Firenze, pp. 1–145.

Chinzei, K., 1982. Morphological and structural adaptations to soft substrates in the Early Jurassic monomyarians *Lithiotis* and *Cochlearites*. Lethaia 15, 179–197.

Clari, P., 1975. Caratteristiche sedimentologiche e paleontologiche di alcune sezioni dei Calcari Grigi del Veneto. Mem. Ist. Geol. Min. Univ. Padova 31, 1–63.

Coen, L.D., Grizzle, R.E., 2016. Bivalve molluscs. In: Kennish, M.J. (ed.), Encyclopedia of Estuaries. Springer, Netherlands, pp. 89–109.

Coletta, S., 2012. I bivalvi aberranti e microbiofacies della Formazione di Rotzo (Giurassico Inferiore) dell’area del Valico di Valbona (Altopiano di Tonezza, Vicenza). Unpubl. M.Sc. thesis, Univ. Ferrara, Ferrara, 87 pp.

Damborenea S.E., Echevarría J., Ros-Franch, S., 2017. Biotioc recovery after the end-Triassic extinction event: evidence froom marine bivalves of the Neuquén Basin, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 487, 93–104.

Debeljak, I., Buser, S., 1998. Lithiotid bivalves in Slovenia and their mode of life. Geologija 40, 11–64.

Dera, G., Neige, P., Dommergues, J.-L., Fara, E., Laffont, R., Pellenard, P., 2010. High-resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian Ammonites (Cephalopoda). J. Geol. Soc., 167, 21–33, 10.1144/0016-76492009-068

Dubar, G., 1948. La faune domerienne du Lias marocain (domaine atlasique). Notes Mem. Serv. Géol. Maroc (Rabat) 68, 250 pp.

Franceschi, M., Dal Corso, J., Posenato, R., Roghi, G., Masetti, D., Jenkyns, H.C., 2014. Early Pliensbachian (Early Jurassic) C-isotope perturbation and the diffusion of the *Lithiotis* Fauna: insights from the western Tethys. Palaeogeogr. Palaeoclimatol. Palaeoecol. 410, 255–263.

Fraser, N.M., Bottjer, D.J., Fischer, A.F., 2004. Dissecting "*Lithiotis*" Bivalves: implications for the Early Jurassic Reef Eclipse. Palaios 19, 51–67.

Fugagnoli, A., 1999. *Cymbriaella lorigae*, a new foraminiferal genus (Textulariina) from the Early Jurassic of the Venetian Prealps (Northeastern Italy). Rev. Micropaléontol. 42 (2), 99–110.

Fugagnoli, A., 2004. Trophic regimes of benthic foraminiferal assemblages in Lower Jurassic shallow water carbonates from northeastern Italy (Calcari Grigi, Trento Platform, Venetian Prealps). Palaeogeogr. Palaeoclimatol. Palaeoecol. 205, 111–130.

Geyer, O.F., 1977. Die "Lithiotis-Kalke" im Bereich der unterjurassischen Tethys. Neues Jahrb. Geol. Paläontol. Abh. 153 (3), 304–340.

Gili, E., Skelton, P. W., Bover-Arnal, T., Salas, R., Obrador, A., Fenerci-Masse, M., 2016. Depositional biofacies model for post-OAE1a Aptian carbonate platforms of the western Maestrat Basin (Iberian Chain, Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 453, 101–114.

Göhner, D., 1980. „Covel dell'Angiolono"- ein mittelliassisches *Lithiotis*-Schlammbioherm auf der Hochebene von Lavarone (Provinz Trento, *Norditalien). Neues Jahrb.* Geol. *Paläontol.* Abh. 10, 600–619.

Gümbel, C.W., 1871. Die sogennanten Nulliporen, *Lithiotis problematica*. Abh. Königl. Bayer Akad. Wiss. Cl. 2 (1), 38–52.

Gutiérrez, J.L., Jones, C.G., Byers, J.E., Arkema, K.K., Berkenbusch, K., Commito, J.A., Duarte, C.M., Hacker, S.D., Lambrinos, J.G., Hendriks, I.E., Hogarth, P.J., Andpalomo, M.G.. 2011. Physical ecosystem engineers and the functioning of estuaries and coasts. In: Wolanski, E., McLusky, D.S. (Eds.), Treatise on estuarine and coastal science. Academic Press, Waltham, vol. 7, pp. 53–81.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystems engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90, doi: 10.1034/j.1600-0706.2003.12322.x.

Hallam, A., Wignall, P.B., 1997. Mass extinctions and their aftermath. Oxford Univ. Press, Oxford, 320 pp.

Hautmann, M., Stiller, F., Cai, H., Sha, J., 2008. Extinction-recovery pattern of level-bottom faunas across the Triassic-Jurassic boundary in Tibet: implications for potential killing mechanisms. Palaios 23, 711–718.

Kidwell, S.M., Fürsich, F.T., Aigner, T., 1986. Conceptual framework for the analysis and classification of fossil concentrations. Palaios 1, 228–238.

Lee, C.W., 1983. Bivalve mounds and reefs of the Central High Atlas, Morocco. Palaeogeogr. Palaeoclimatol. Palaeoecol. 43, 153–168.

Leinfelder, R., Schmid, D.U., Nose, M., Werner, W., 2002., Jurassic reef patterns – the expression of a changing globe. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. SEPM Spec. Publ. 72, 465–520.

Mander, L., Twitchett, R.J., Benton, M.J., 2008. Palaeoecology of the Late Triassic extinction event in the SW UK. J. Geol. Soc. Lond. 165, 319–332.

Martindale, R.C., Foster, R.J., Velledits, F., 2019. The survival, recovery, and diversification of Metazoan reef ecosystems following the End-Permian mass extinction event. Palaeogeogr. Palaeoclimatol. Palaeoecol. 513, 100–115.

Masetti, D., Claps, M., Giacometti, A., Lodi, P., Pignatti, P., 1998. I Calcari Grigi della Piattaforma di Trento (Lias inferiore e Medio, Prealpi Venete): Atti Ticinesi di Scienze della Terra, v. 40, p. 139–183.

Monaco, P., Giannetti, A., 2002. Three-dimensional burrow systems and taphofacies in shallowing-upward parasequences, lower Jurassic carbonate platform (Calcari Grigi, Southern Alps, Italy). Facies 47, 47–57.

Nauss, A.L., Smith, P.L., 1988. *Lithiotis* (Bivalvia) bioherms in the Lower Jurassic of east-central Oregon, U.S.A. Palaeogeogr. Palaeoclimatol. Palaeoecol. 65, 253–268.

Parras, A., Casadío, A., 2006. The oyster *Crassostrea*? *hatchery* (Ortmann, 1897), a physical ecosystem engineer from the upper Oligocene–lower Miocene of Patagonia, Southern Argentina. Palaios 21, 168–186.

Posenato, R., Masetti, D., 2005. Stop 3. The ?*Cochlearites* micromound of monte Toraro. In Masetti at al. (Eds), The Rotzo Formation (Lower Jurassic at the Val Bona Pass (Vicenza Province). Field Excusion book, 5th Reg. Symp. Int. Fossil Algae Ass., St. Trent. Sci. Nat. Acta Geol. 80 suppl., 23–25.

Posenato, R., Masetti, D., 2012. Environmental control and dynamics of Lower Jurassic bivalve build-ups in the Trento Platform (Southern Alps, Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 361–362, 1–13.

Posenato, R., Masetti, D., Broglio Loriga, C., 2000. I banchi a bivalvi del Giurassico Inferiore (Piattaforma di Trento): dinamica deposizionale, modalità di insediamento e sviluppo. In: Cerchi, A., Corradini, C. (Eds.), Crisi biologiche, radiazioni adattative e dinamica delle piattaforme carbonatiche. Acc. Naz. Sci. Lett. Arti Modena 21, 211–214.

Posenato, R., Bassi, D., Avanzini, M., 2013a. Bivalve pavements from shallow-water black-shales in the Early Jurassic of northern Italy: a record of salinity- and oxygen-depleted environmental dynamics. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 262–271.

Posenato, R., Bassi, D. and Nebelsick, J.H., 2013b, *Opisoma excavatum* Boehm, a Lower Jurassic photosymbiotic alatoform-chambered bivalve: Lethaia, v. 46, p. 424–437.

Posenato, R., Bassi, D., Nebelsick, J., 2014. Field Trip Guide – Tonezza del Cimone (VI) 13/09/2014. 7th Int. Meeting on Taphonomy and Fossilization, Taphos 2014, 10th–13th/09/2014, Ferrara, Italy, 28 pp.

Posenato, R., Bassi, D., Trecalli, A., Parente, M., 2018. Taphonomy and evolution of Lower Jurassic lithiotid bivalve accumulations in the Apennine Carbonate Platform (southern Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 489, 261–271.

Reis, O., 1903. Über Lithiotiden. Abh. K.-K. Geol. Reich. 17 (6), 1–44.

Riding, R., 2002, Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. Earth-Sci. Rev. 58, 163–231.

Ros, S., Echevarría, J. 2012. Ecological signature of the end-Triassic biotic crisis: what do bivalves have to say? Hist. Biol. 24, 489–503.

Savazzi, E., 1996. Preserved ligament in the Jurassic bivalve *Lithiotis*: adaptive and evolutionary significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 120, 281–289.

Seilacher, A., 1984. Constructional morphology of bivalves evolutionary pathways in primary versus secondary soft dwellers. Palaeontology 27, 207–237.

Skelton, P.W., Gili, E., Vicens, E., Obrador, A., 1995. The growth fabric of gregarious rudist elevators (hippuritids) in a Santonian carbonate platform in the southern Central Pyrenees. Palaeogeogr. Palaeoclimatol. Palaeoecol. 119, 107–126.

Tausch, L., 1890. Zur Kenntnis der Fauna der "Grauen Kalke". Abh. K.-K. Geol. Reich. 15 (2), 1–40.

Trecalli, A., Spangenberg, J., Adatte, K., Föllmi, K.B., Parente, M., 2012. Carbonate platform evidence of ocean acidification at the onset of the early Toarcian oceanic anoxic event. Earth Planet. Sci. Lett. 357–358, 214–225.

Vilardell, O., Gili, E., 2003. Quantitative study of a hippuritid rudist lithosome in a Santonian carbonate platform in the southern Central Pyrenees. Palaeogeogr. Palaeoclimatol. Palaeoecol. 200, 31–41.

Waldbusser, G.G., Steenson, R.A., Green, M.A., 2011. Oyster shell dissolution rates in estuarine waters: effects on pH and shell legacy. J. Shellfish Res. 30, 659–669.

Wignall, P.B., Bond, D.P.G., 2008. The end-Triassic and Early Toarcian mass extinction records in the British Isles. Proc. Geol. Assoc. 119, 73–84.

Winterer, H., Bosellini, A., 1981. Subsidence and sedimentation on Jurassic passive continental margin, southern Alps, Italy. Am. Assoc. Pet. Geol. Bull. 42, 394–419.

Figure and table captions

Fig. 1. Geographic locations of the studied lithiotid accumulations in the Trento Platform, northern Italy. 1, Monte Toraro; 2, Monte di Campoluzzo; 3, Vaio dell'Anguilla; 4, Rotzo; 5, Contrada Dazio; 6, Passo Vezzena. Palaeogeographic map from Posenato and Masetti (2012, modified).

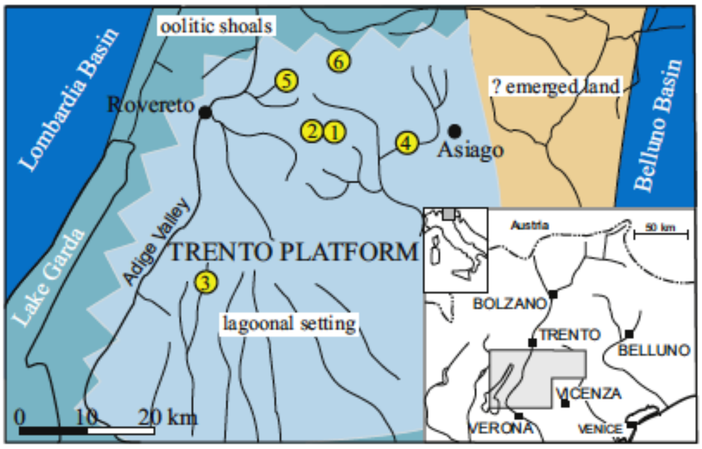

Fig. 2. Schematic stratigraphic setting of the Formazione di Rotzo with the biostratigraphic location of the studied accumulations. Numbers refer to the geographic areas of Fig. 1. Si, upper Sinemurian; A, *Lituosepta recoarensis* Zone; *L. compressa* Z., *Lituosepta compressa* Zone; OM, Oolite di Massone.

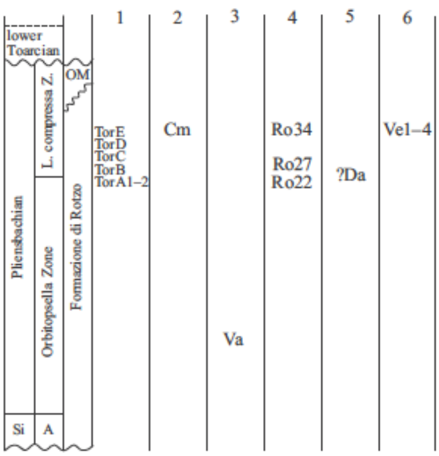

Fig. 3. Example of analysed quadrants in each of which with digitally analyzed photos in which the randomly sectioned lithiotid shells preserved within indurated limestone were traced (e.g.,

Lithioperna, TorD). In the digitally analyzed photos sedimentary fabrics and taphonomic attributes such as percentage of shell cover, shell density, percentage of articulated and complete shells were calculated.

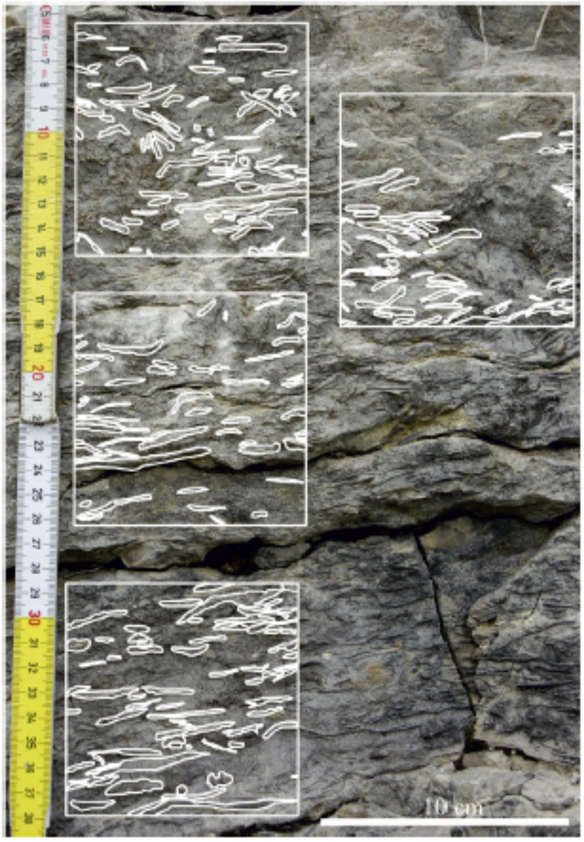

Fig. 4. Examples of randomly-sectioned lithiotid specimens characterising the studied accumulations. A–B, *Lithiotis problematica* (A, core with bouquet-like aggregate, circle inset white rectangle; B, parautochthonous specimens in the accumulation flanks; TorA). C–D, *Cochlearites loppianus* (C, core; D, flanks; Passo Vezzena), white arrows points to a cross-section of an articulated shell which shows the free right valve (R.V.) with the internal median ridge (above) and the thicker left valve (L.V.) characterized by a median wide furrow (below); e.g., Chinzei, 1982). E–F, *Lithioperna scutata* (E, base of the accumulation, TorD; F, flank, Monte di Campoluzzo); white arrow points to an articulated specimen with the characteristic shape resembling a couple of lenses (e.g., Broglio Loriga and Posenato, 1996). White arrows point to random sections of *Cochlearites* (C) and *Lithioperna* (F) showing the taxonomic diagnostic characters (see e.g., Chinzei, 1982).

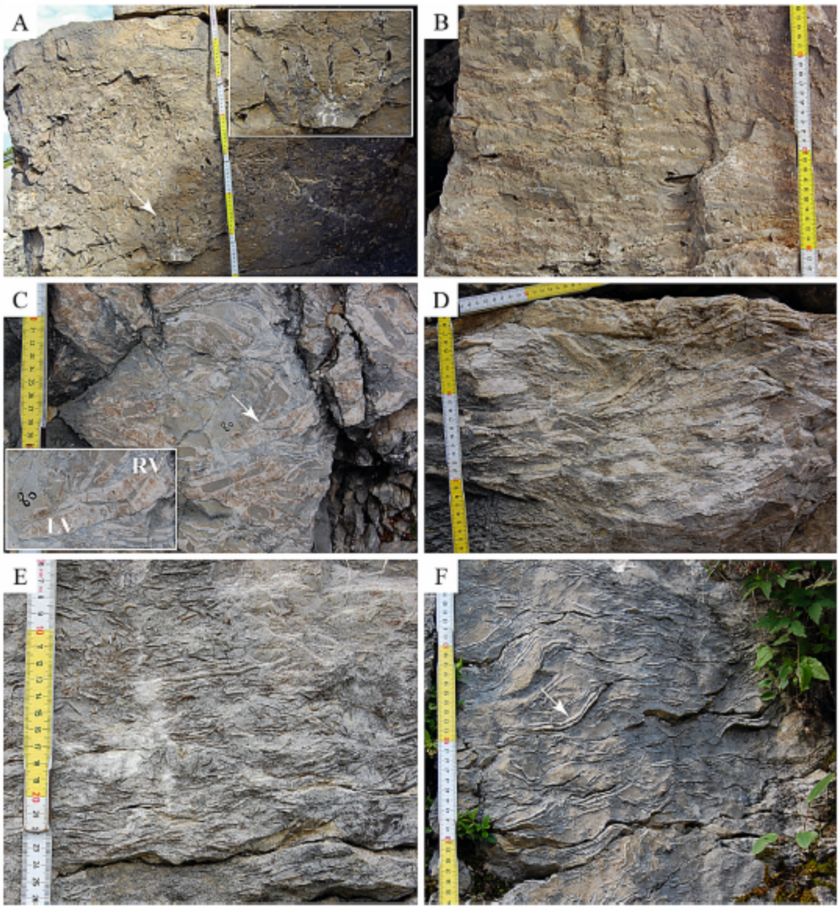

Fig. 5. Two rock samples representing mostly articulated and autochthonous *Lithiotis problematica* specimens from the accumulation TorA2. A) Upper bed surface with sub-transversal sections of the *Lithiotis* massive umbonal region. B) Polished surface of a perpendicular bedding section showing some articulated shells; two representative specimens are depicted with free (F.V.) and attached (A.V.) valves. B.C., body cavity; U.C., umbonal body cavity.

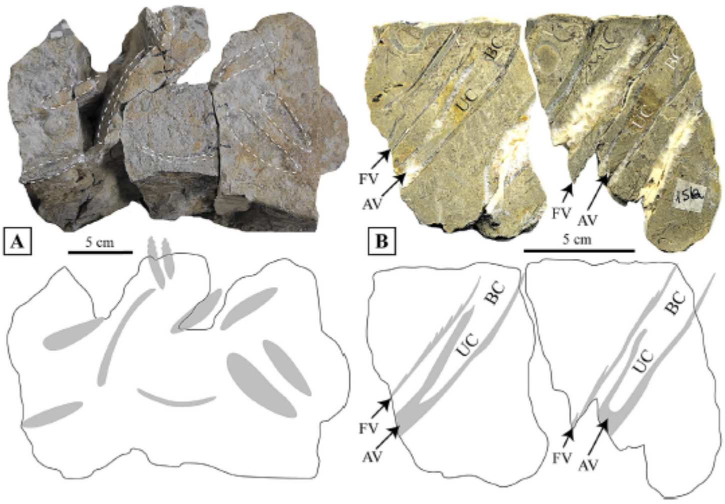

Fig. 6. Distribution of distinguished features in the Monte Toraro succession. The accumulations are marked by solid lines. A) TorA1–2. B) TorB. C) TorD. D) TorC. The TorD (C), characterized by *Lithioperna* shells, represents a tabular bioclastic, coarse-grained hard substrate for the overlying lithiotid accumulation.

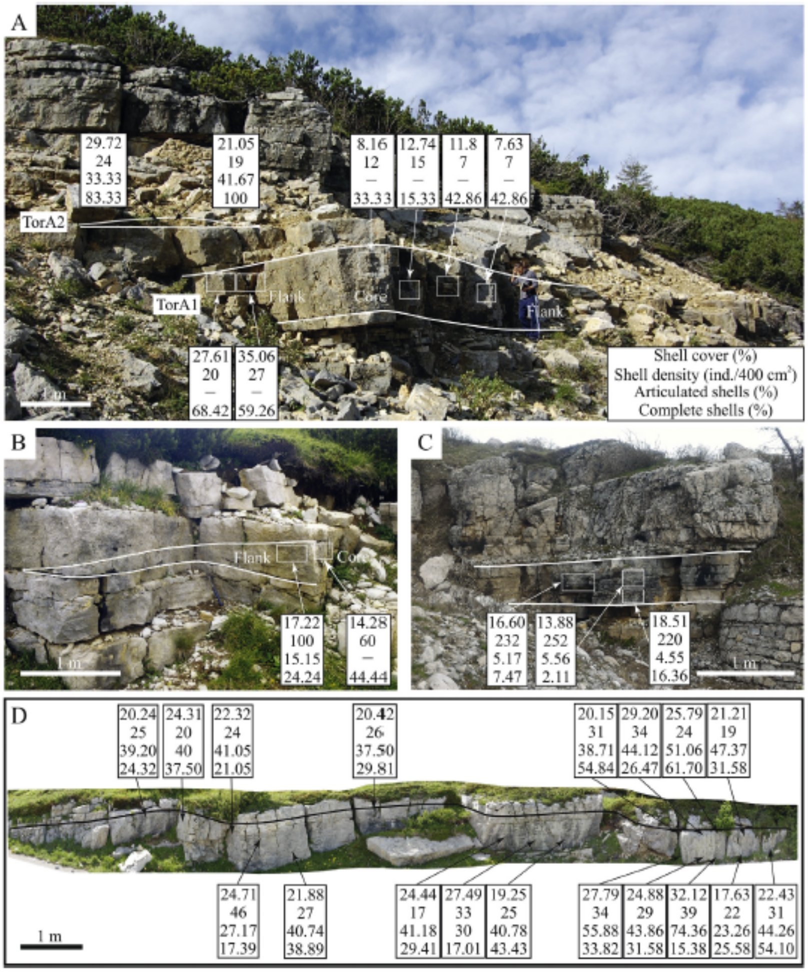

Fig. 7. Distribution of distinguished features in the studied lithiotid accumulations in the Monte Toraro (A, TorE), Monte di Campoluzzo (B) and Vaio dell'Anguilla (C–D) successions which are marked by solid lines. The studied TorE (A) represents a section of a *Cochlearites* accumulation passing only through the accumulation flank. The Monte di Campoluzzo (B) accumulation consist of parautochthonous *Lithioperna* individuals, while that of Vaio dell'Anguilla (C, D) consists of autochthonous *Lithioperna* individuals.

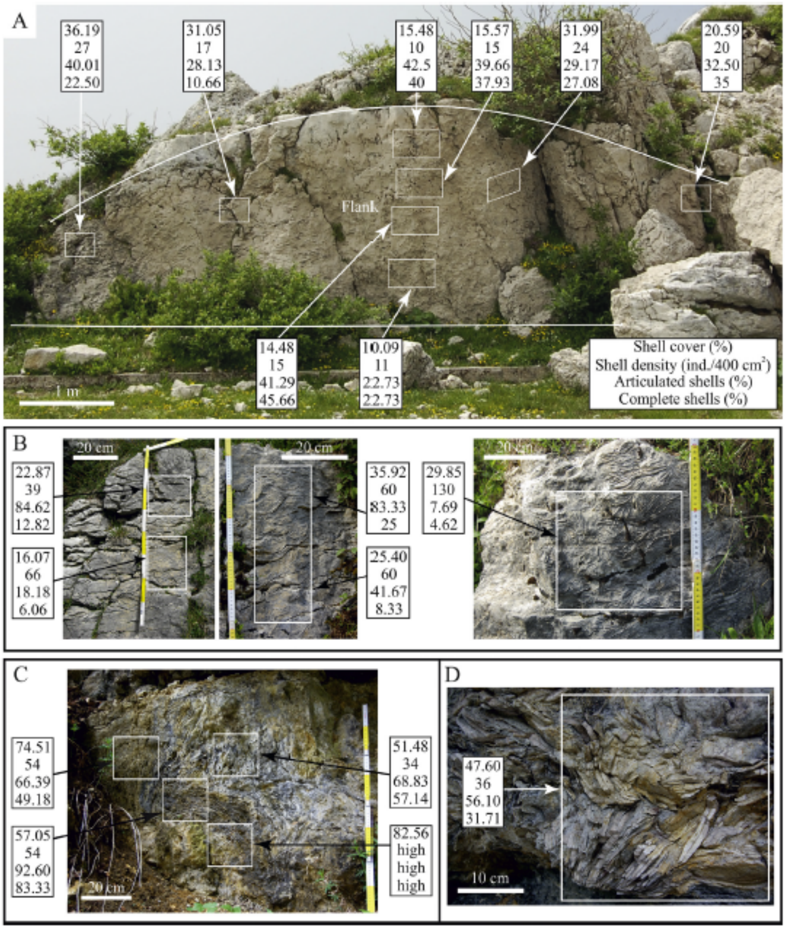

Fig. 8. Distribution of distinguished taphonomic features in the studied lithiotid accumulations in the Passo Vezzena (A–E) outcrop. The accumulations are marked by solid lines. White arrows point to random sections of *Cochlearites* showing diagnostic characters (see e.g., Chinzei 1982).

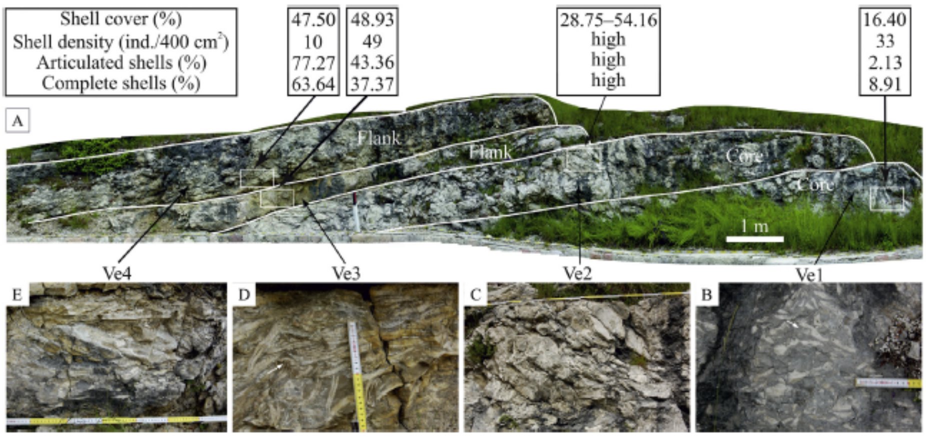

Fig. 9. Schematic model of the studied lithiotid accumulations showing the dominant distribution of the assessed fabric and taphonomic attributes of autochthonous (autoch), parautochthonous

(parautoch) and allochthonous (alloch) individuals. The tabular bioclastic hard-substrate (TorD), produced by physical reworking, is the representative study case made up of allochthonous *Lithioperna* shells (1; Fig. 6C). Autochthonous *Lithiotis* was found articulated in the level TorA2 overlying the TorA1, whereas parautochthonous *Lithiotis* characterise the accumulation flank (Fig. 6A). Autochthonous *Lithioperna* was recorded in the Vaio dell'Anguilla (2; Fig. 7C–D), while parautochthonous individuals of the Monte di Campoluzzo occur in the accumulation flank (3; Fig. 7B). Not to scale. Lithiotid shells are simply depicted and do not reflect the complex shell morphology. SC, shell cover; SD, shell density; AI, articulated individuals; CS, complete shells.

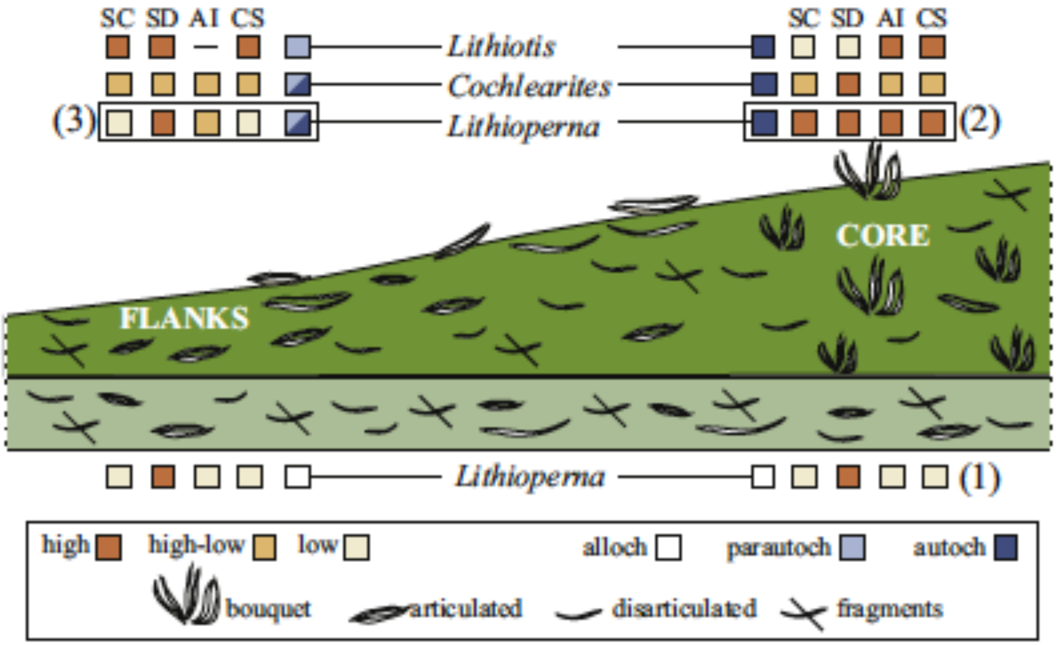

Table 1.

Summary data of the studied lithiotid accumulations with the geographic and biostratigraphic locations, number of the total analysed quadrants and areal extension for each analysed quadrant. The distance of the studied accumulations from the base of the stratigraphic section refers to Coletta (2012; Monte Toraro, Monte di Campoluzzo), Posenato and Masetti (2012; Vaio dell'Anguilla) and Bosellini and Broglio Loriga (1971; Rotzo). Details of the shell accumulations in the text. Z., Zone.

Stratigraphic section	Accumulation		Distance from the base	Biozone	Total analysed quadrants	Areal extension for each quadrant
Monte Toraro (45°52′08.9″N, 11°16′20.2″E)	TorA1		−120 m	*Orbitopsella* Zone	15	400 cm²
	TorA2		−120 m	*Orbitopsella* Zone	4	100 cm² (1), 56.25 cm² (3)
	TorB		160 m	*L. compressa* Z.	2	100 cm²
	TorC		172 m	*L. compressa* Z.	42	400 cm²
	TorD		177 m	*L. compressa* Z.	9	100 cm²
	TorE		180 m	*L. compressa* Z.	26	400 cm²
Monte di Campoluzzo (45°52′17.9″N, 11°15′34.4″E)	Cm		−1–2 m	*L. compressa* Z.	5	400 cm²
Vaio dell'Anguilla (45°39′26.3″N 11°00′58.5″E)	Va		−15 m	*Orbitopsella* Z.	5	900 cm² (3), 400 cm² (2)
Rotzo (45°51′06.7″N, 11°22′15.8″E)	Ro22		−60 m	*Orbitopsella* Z.	3	400 cm²
	Ro27		−68 m	*L. compressa* Z.	10	100 cm²
	Ro34.1		−81 m	*L. compressa* Z.	1	400 cm²
	Ro34.2		−82 m	*L. compressa* Z.	1	100 cm²
	Ro34	Ro34-section	−87 m	*L. compressa* Z.	1	400 cm²
		Ro34-surface	−89 m	*L. compressa* Z.	10	400 cm² (9), 1600 cm² (1)
Contrada Dazio (45°55′40.1″N, 11°15′31.8″E)	Da		Isolated outcrop	? *L. compressa* Z.	4	900 cm²
Passo Vezzena (45°57′05.1″N, 11°21′36.3″E)	Ve1		Isolated outcrop	*L. compressa* Z.	3	400 cm²
	Ve2		Isolated outcrop		6	1600 cm² (4), 400 cm² (1), 900 cm² (1)
	Ve3		Isolated outcrop		2	400 cm² (1), 225 cm² (1)
	Ve4		Isolated outcrop		1	900 cm²

Table 2.

Dominating lithiotid genera and average values of shell bed characteristics and taphonomic attributes for the studied accumulations located in the Rotzo stratigraphic section (Ro) and Contrada Dazio (Da). The percentages of articulated and complete shells in the Ro34-surface are tentatively calculated (?) because the difficult in assessing articulated and/or whole individuals on bedding surface. In Da1–4 the articulated individuals cannot be identified at the outcrop scale. *Cochl*, *Cochlearites*; *Lithiop*, *Lithioperna*; –, no entry.

Shell beds	Dominating taxa	Shell cover (%)	Shell density (ind./400 cm²)	Articulated shells (%)	Complete shells (%)
Ro22	*Lithiotis*	28.56	13	69.99	62.39
Ro27 (lower part)	*Cochlearites* (rare *Lithiop*)	52.95	112	16.24	21.44
Ro34.1	*Cochlearites* (rare *Lithiop*)	68.28	30	100	100
Ro34.2	*Cochlearites* (rare *Lithiop*)	61.41	52	83.33	36.67
Ro34-section	*Cochlearites* (rare *Lithiop*)	63.57	32	84.38	78.13
Ro34-surface	*Cochlearites* (rare *Lithiop*)	55.58	32	?	?10.56
Da1	*Lithiotis* (rare *Cochl*)	27.56	7	–	87.50
Da2	*Lithiotis* (rare *Cochl*)	22	11	–	87.50
Da3	*Lithiotis*	38.82	17	–	86.84
Da4	*Lithiotis*	31.95	17	–	86.84

Table 3.

Distinctive attributes for the core and flanks in the lithiotid accumulations. Autochthonous individuals were preserved in life position, while parautochthonous were reworked to some degree, but not transported out of the original life habit.

The obtained mean values differ among the dominating genera as follow (h, high): *Lithiotis*: shell cover, h > 25%; shell density, h > 17 ind./400 cm^2; articulated individuals, h > 35%; whole individuals, h > 15%. *Cochlearites*: shell cover, h > 15%; shell density, h > 17 ind./400 cm^2;

articulated individuals, h >35%; complete shells, h > 35%. *Lithioperna* A (morphotype *sensu* Broglio Loriga and Posenato 1996): shell cover, h > 40%; shell density, h > 17 ind./400 cm^2; articulated individuals, h > 35%; whole shells, h > 25%.

	Shell cover (%)	Shell density (ind./400 cm^2)	Articulated shells (%)	Complete shells (%)	Autochthonous individuals	Parautochthonous individuals
Core						
Lithiotis	Low	High–low	High	High	High	Low
Cochlearites	High-low	High	High–low	High-low	High	Low
Lithioperna A	High	High	High	High	High	Low
Flanks						
Lithiotis	High	High	–	High	–	High
Cochlearites	High-low	High-low	High–low	High-low	Low	High
Lithioperna A	Low	High	High–low	Low	Low	High