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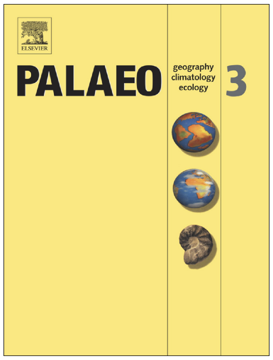

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Palaeoecology of *Chondrodonta* (Bivalvia) from the lower Aptian (Cretaceous) Apulia Carbonate Platform (Gargano Promontory, southern Italy)

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ABSTRACT

Chondrodonta is a Cretaceous oyster-like bivalve with a predominantly calcitic, dorso-ventrally elongated and slightly inequivalve shell. In the Tethyan carbonate platforms this taxon occurs commonly in rudist-bearing limestone. Often preserved with still articulated valves, the opportunistic *Chondrodonta* had a cemented and gregarious life habit. In the Apulia Carbonate Platform (Gargano Promontory, southern Italy), *Chondrodonta* beds occur within lower Aptian lagoonal to platform–basin margin deposits. The studied *Chondrodonta* concentrations, which recorded the early evolutionary phase and spreading of this bivalve, are made up of specimens ascribed to *Chondrodonta glabra* Stanton. In the inner platform the meter-thick *Chondrodonta* accumulations were originated by autochthonous bouquet-like valve aggregates, frequently preserved in living position. These aggregates constitute superimposed carpets characterised by only a few generations which were affected by mass mortality and rapid burial processes. These mass mortalities were related to repeated environmental lethal fluctuations that occurred at the onset of the early Aptian OAE 1a. The quick fluctuations of the *Chondrodonta* populations are typical of unstable and unpredictable environments characterized by significant changes in trophic resources and hyperthermal and acidification peaks. The studied *Chondrodonta* specimens show different shell preservation according to their palaeobathymetric location. In the shallow-water inner platform specimens the internal aragonite shell layer was rapidly dissolved while in deeper-water margin ones it was preserved during the early diagenetic phases. This different preservation is interpreted as related to different aragonite saturation state of shallow seawater, and tentatively connected to the acidification peak that occurred at the onset of the early Aptian OAE 1a.

Key-words:

bivalve carpets, taphonomy, functional morphology, shell microstructures, OAE1a, Tethys

1. Introduction

Chondrodonta Stanton, 1901 is a Cretaceous oyster-like bivalve with a predominant calcitic, dorso-ventrally elongated and slightly inequivalve shell. This taxon, occurring commonly in (Berriasian?) Barremian–Turonian (Campanian?) rudist-bearing limestones, inhabited marine shallow-water benthic environments of the Tethyan Realm (from the Middle East to the Mexico regions; e.g., Cox and Stenzel, 1971; Scott and Hinote, 2007; Masse et al., 2015). The valves are often found still articulated because of the dorso-ventrally elongated and tightly interlocked chondrophores, which "allowed very little motion of valves" (Stanton, 1901, p. 302). Therefore, the diagnostic taxonomical characters of the inner shell surface are generally not detectable. For this reason and despite the great abundance and wide stratigraphic and geographic distribution of *Chondrodonta*, the systematic position of this taxon is still debated.

Some authors considered *Chondrodonta* as a monomyarian (Stanton, 1901, 1947; Freneix and Lefèvre, 1967; Dhondt and Dieni, 1993) or dimyarian bivalve (Douvillé, 1902; Cox and Stenzel, 1971). The more convex and attached valve was referred to as "the right" (Freneix and Lefèvre, 1967; Dhondt and Dieni, 1993) or "the left" one (Stanton, 1901; Cox and Stenzel, 1971). *Chondrodonta* has been phylogenetically related to pectinoids (Stanton, 1901; Douvillé, 1902; Freneix and Lefèvre, 1967) or to oysters (Cox and Stenzel, 1971; Dhondt and Dieni, 1993). In the recent classification of Bivalvia (Carter et al. 2011), the family Chondrodontidae has been included within the superfamily Plicatuloidea (suborder Anomiidina, order Pectinida), which is nowadays represented by *Plicatula,* an oyster-like bivalve attached on the right valve and with a shell constituted by a thick calcitic foliated outer layer and aragonitic crossed-lamellar median and inner layers (Taylor et al., 1969). This recent classification is not yet sustained by systematic description and discussion and the microstructures of *Chondrodonta* are as yet unknown (Carter, 1990a).

The first appearance of *Chondrodonta* occurs in the Barremian–early Aptian of the Caribbean Province with *C. glabra* Stanton characterized by non-plicate shells. In this province, species with plicate shells are younger and range from early Albian (*C. youngi* Scott) to middle–late Albian (*C. munsoni* Stanton; Scott, 2007; Scott and Filkorn, 2007; Scott and Hinote, 2007). In the Mediterranean and Middle East Province the older occurrences of *Chondrodonta* are located in southern France (Leonide et al., 2012) and Oman (Immenhauser et al., 2004) and are dated respectively as to Barremian and Barremian to early Aptian. During the early Aptian *Chondrodonta* beds were very common in many shallow-water carbonate platforms bordering the Tethys Ocean (e.g., Masse, 1993; Malchus et al., 1995; Bover-Arnal et al., 2009; Skelton et al., 2010; Najarro et al., 2011; Graziano, 2013; Gili et al., 2016). These records report just species names and/or illustrations of randomly sectioned specimens in hard cemented limestones. Therefore, no detailed systematic and taphonomic/palaeoecological assessments have been so far performed on this early *Chondrodonta* forms. In these Tethyan provinces, the better-known plicated *C. joannae* (Choffat) spreads during the Cenomanian (e.g., Dhondt and Dieni, 1993; Ayoub-Hannaa and Fürsich, 2011; Ayoub-Hannaa et al., 2014).

The Mesozoic cementers predominantly inhabited shallow water environments, where some gregarious forms (e.g., lithiotids, rudists, oysters) originated highly dense aggregates (bivalve mounds, reefs, pavements, carpets), influencing the sedimentation rates and carbonate platform dynamics (e.g., Fürsich et al., 1994; Gili et al., 1995; Riding, 2002; Fraser et al., 2004; Skelton and Gili, 2012; Harper, 2012; Posenato and Masetti, 2012; Bassi et al., 2017). Despite the high abundance, widespread geographic diffusion and long-time ranging distribution, little is known about the functional morphology of the shell, taphonomy and geometries of the *Chondrodonta* accumulations. The few available data concern the late Cenomanian *C. joannae* (e.g., Ayoub-Hannaa and Fürsich, 2011; Ayoub-Hannaa et al., 2014). As already noted by Dhondt and Dieni (1993), upper Aptian *Chondrodonta* specimens from southern Italy (Accordi et al., 1990) have been referred to *Lithioperna*, another peculiar genus of the Jurassic *Lithiotis* Fauna, characterized by large and flattened shells.

In the Gargano Promontory (southern Italy), lower Aptian *Chondrodonta*-bearing beds are reported from the Apulia Carbonate Platform (ACP) in lagoonal to tidal flat settings (San Giovanni Rotondo Limestones, SGRL; Cremonini et al., 1971, Luperto Sinni and Masse, 1986; Graziano et al., 2013; Guerzoni, 2016) and in a re-sedimented pluri-decametric slab representing platform–basin margin facies (Montagna degli Angeli Limestones, MAL; Graziano et al., 2013; Guerzoni, 2016; Morsilli et al., 2017). In the SGRL the bivalve accumulations have been ascribed to the genus *Chondrodonta* (Checchia Rispoli, 1921; Cremonini et al., 1971; Luperto Sinni and Masse, 1986; Graziano, 2013; Graziano et al., 2013; Guerzoni, 2016), or as to ostreids (Claps et al., 1996; Spalluto et al., 2005). The SGRL bivalve accumulations are characterized by *Chondrodonta* and requieniids (*Chondrodonta* and requieniids member in Graziano et al., 2013). The SGRL and MAL bivalve accumulations are here analysed in terms of shell morphology, microstructures and functional morphology in order to understand their systematic position and their early evolutionary phase in the Mediterranean province, where only citations or outcrop illustrations are available in literature (e.g., Masse, 1993; Bover-Arnal et al., 2009, 2011, 2014; Najarro et al., 2011; Skelton and Gili, 2012; Graziano, 2013; Graziano et al., 2013; Gili et al., 2016).

Good exposure conditions of the lower Aptian *Chondrodonta* beds from the Gargano Promontory have enabled us to distinguish the vertical and lateral distribution and the taphonomic signatures of the bivalve accumulations, as well as their geometries. Functional shell morphology and taphonomic analyses were assessed in order to define the growth steps of the accumulations and related palaeoenvironmental constrains.

2. Stratigraphy

The Gargano Promontory (Fig. 1) represents the deformed foreland of the Southern Apennine and Dinaric thrust belts. Its structure is represented by a gentle and broad NW-SE anticline affected by reverse and direct faults, as well as by strike-slip faults (Bertotti et al., 1999; Brankman and Aydin, 2004; Billi et al., 2007). The backbone of the Gargano Promontory consists of a thick-stacked carbonate deposits belonging to the Apulia Carbonate Platform (ACP), a major palaeogeographic unit in the southern margin of the Mesozoic Tethys (Bernoulli, 2001). The Mesozoic carbonate succession has been estimated as to 5 km-thick on average, while the coeval basinal succession is up to 2 km in thickness (Morsilli et al., 2017). The outcropping part of this carbonate platform, spanning in age from Middle Jurassic to Eocene with scattered Oligocene and Miocene outcrops, consists of facies from a suite of different depositional environments ranging from those of the shallow-water inner platform to those of the relatively deep-water pelagic realm (Bosellini et al., 1999; Borgomano, 2000).

The San Giovanni Rotondo Limestones (SGRL) is a shallow-water, 500–600 m-thick carbonate succession (e.g., Luperto Sinni and Masse, 1986), which has been subdivided into the following three members by Claps et al., (1996). Member 1 (late Valanginian–Hauterivian *p.p.*, about 140 m thick; Borgo Celano Member of Luperto Sinni and Masse, 1986) consists of a monotonous and acyclic subtidal succession of lime mudstone to wackestone arranged in m-thick beds, with few dm-thick beds of skeletal or oolitic grainstone to packstone. The Member 2 (Hauterivian *p.p.*–Barremian *p.p.*, about 310 m thick; Loferitic member of Luperto Sinni and Masse, 1986) is represented by a thick cyclic unit characterized by quasi-periodic alternation of "loferitic" beds and cm-thick layers of green shales, and stromatolite layers, frequently with dinosaur footprints on the bed surfaces (Petti et al., 2008). The Member 3 (Barremian *p.p.*–early Aptian, about 100 m thick; Requieniid member of Luperto Sinni and Masse, 1986 or *Chondrodonta* and requieniids member of Graziano et al., 2013) displays a facies variety including subtidal high-energy thin-bedded calcarenites and domal stromatolites as well as *Chondrodonta* (or ostreids in Claps et al., 1996) accumulations (Graziano et al., 2013; Guerzoni, 2016). The uppermost part of

Member 2 and lower part of Member 3 have been referred to the early Aptian or early Bedoulian (Graziano, 2013, Graziano et al., 2013).

The Montagna degli Angeli Limestones (MAL), considered as an in-place depositional unit (Bosellini et al., 1993, 1999; Graziano, 2013), has been recently interpreted as a pluri-decametric succession re-deposited within slope deposits of the Mattinata Limestones (Morsilli et al., 2017). The MAL block can be considered as an "Urgonian"-type platform margin (Graziano, 2013), about 60 m thick, and consists of skeletal grainstones to packstones, with rudists, gastropods, echinoids fragments as well as textularids and miliolids and some solitary corals, alternating with *Bacinella*/*Lithocodium* rich-layers. Its upper part consists of floatstones to rudstones with disarticulated caprinids and gastropods in an orbitolinid grainstone matrix, interpreted as biostrome (Graziano, 2013), passing to skeletal floatstones with a wackestone to packstone matrix with orbitolinids, dasycladalean algae, and solitary corals. A 4–6 m thick floatstone with echinoids, *Chondrodonta* and chaetetids, microbial automicrite, *Bacinella*/*Lithocodium*, and thin pelagic beds, overlie the previous facies and has been related to lower Aptian "crisis interval" (Graziano, 2013).

3. Materials and methods

The studied material occurs in two areas (Borgo Celano and Montagna degli Angeli, Figs. 1B and C respectively) and represents two geological formations, the San Giovanni Rotondo Limestones (SGRL; Fig. 2) and the Montagna degli Angeli Limestones (MAL). Three *Chondrodonta* outcrops of the SGRL were analysed along the Borgo Celano road (SP 26) section, which is located in an extensive southward-dipping monocline (Fig. 1B). The outcrop 1 shows a *Chondrodonta* accumulation, about 0.95–1.2 m thick (Fig. 3A–D), located above a stromatolite layer, 25 to 35 cm in thickness. The *Chondrodonta* accumulation of the outcrop 2 (Fig. 4A) is located above the last shallowing-upward cycles of the Member 2 (Fig. 2). The cycles, *ca*. 1.5–2 m, are represented by bioturbated wackestone–packstone with peloids, dasycladalean algae, ostracods and foraminifers (miliolids and textulariids), with some interlayers of oncolitic or rudist floatstones, capped by planar or undulated stromatolites at the top. The *Chondrodonta* accumulation, about 1 m thick (base of the Member 3), is overlain by a subtidal interval, *ca*. 4 m thick, characterized by thick mudstones-wackestones layers, with a low bioclastic content, followed by a few dm-thick stromatolite layer (Fig. 2). The outcrop 3 is characterized by a wide exposure of the upper *Chondrodonta*-bearing bed surface (Fig. 4D–F). The *Chondrodonta* accumulations of the outcrops 1 and 2, located *ca.* 150 m each from other, are physically related, therefore they represent the same layer. The succession containing the outcrop 3 is separated by a fault from the outcrops 1 and 2, therefore a direct correlation among them is impossible, but the correspondence of the bed thickness and facies arrangement suggest that they represent the same stratigraphic bed, which probably corresponds to the *Chondrodonta* marker bed of Graziano et al. (2013). The studied material from the Monte degli Angeli area (MDA, Fig. 1C) is contained in some rock blocks collected in the debris.

Both in the Borgo Celano and in MDA areas, the *Chondrodonta* shells occur in very hard cemented limestone, which precludes isolating specimens from the matrix. The shell outline and internal shell surface are detectable, though incompletely, in very few specimens (Fig. 5). To assess the shell morphology, some specimens were sectioned applying two different methods. (A) The limestone blocks, containing dense shell accumulations and fan-like shell aggregates of individuals in living position, were sectioned with a diamond saw as parallel slabs about 10 mm thick. The slabs were then polished and reproduced by an optical scanner at 1200 dpi. This method generates randomly oriented sections in which only discontinuous images of the internal shell characters are detectable. (B) A continuous record of the internal shell characters was obtained by performing serial grinding. The sectioned surfaces, at the distance of about 500 μm apart, were polished by carborundum abrasive powder on a glass surface and reproduced on acetate peels. The shell microstructures of the lower Aptian *Chondrodonta* shells have been studied using both optical microscope on acetate peels and SEM on gold-coated fragments. Carter et al.’s (1990b, 2012) microstructure terminology is adopted.

Component, taphonomic signature and microfacies analyses were performed using a Leica MZ8 microscope on thin sections (5 x 5 cm) and acetate peels, made on polished slabs, cut perpendicular to the bedding plane. The textural classification of Dunham (1962) and Embry and Klovan (1972) was used allowing for a general component and matrix description.

4. Results

4.1. Shell morphology and preservation

The specimens from the Borgo Celano succession are generally affected by synsedimentary–early diagenetic leaching of the aragonitic shell layer, deformation and breakage, which also caused the breaking of the tightly interlocking chondrophores.

The internal shell surfaces can be observed in two valves (Fig. 5) collected from the outcrop 1. Both the specimens, with a length/height ratio ranging from 0.5 to 0.75, were collected in the upper part of the *Chondrodonta* accumulations (Fig. 3D). The valve occurring on the lower bed surface has an elongated drop-like outline, about 10 cm in height and 7.5 cm in length (Fig. 5A). The umbonal angle is acute, about 60° wide. The valve is slightly convex, with the shell leached in the central and ventral regions. Postulating that *Chondrodonta* is a pectinoid (see systematic remarks below) this convex valve is the right one, namely the lower. Only the anterior side of the hinge plate, about 20 mm long, is preserved; it is posteriorly limited by a rounded margin which marks a deep groove where the left chondrophore was wedged. The posterior side of the hinge plate and the chondrophore are missing. The inner aragonitic layers are dissolved and only the outer calcitic shell layer is preserved. The pallial line, if originally present, is therefore not detectable. A large depression, located at about one-third of valve height from the beak, where the shell is deeply corroded, could correspond to the muscle scar (Fig. 5A). The maximum shell thickness occurs along the anterior and posterior marginal regions of the dorsal valve half. The outer calcitic layer is very thin in the median and ventral regions. No trace of radial fold is detectable on the exfoliated shell surfaces or on the external surface.

The other valve, 85 mm in height and 50 mm in length (Fig. 5B), has an elongated ovoidal outline and is slightly concave, particularly in the ventral half. The hinge plate, about 20 mm long, has a shallow groove on the anterior part. Along the median part, the sharp margin of the chondrophore borders a deep groove. The posterior part of the hinge plate is infilled by sediment and the broken chondrophore of the lower valve. On the basis of chondrophore morphology and valve curvature this specimen is considered the free upper (left) valve.

Transversal serial sections obtained with the method B show the interlocking of the chondrophores until about 30 mm from the beak (Fig. 6E-SP5). The chondrophore of the upper valve has a triangular section and an edge sharper than that of the lower valve (Fig. 6B). The distance between the two chondrophores is about 1–2 mm. The sections passing through the body cavity (Figs. 6C, 6E-SP1) show a significant difference in thickness of the outer calcitic layer between the marginal and median regions. Along the shell margins, the calcitic layer is about 2–3 times thicker than that occurring along the median region.

Radial sections obtained with the method A (Fig. 6E-SP2) shows a very thin shell, about 1 mm thick. The thickness decreases towards the ventral margin, where the shell is extremely thin and sharp. The inner body space is very narrow (Fig. 6E-SP2), although it could have been reduced by the early dissolution of inner aragonitic layer and early diagenetic compaction.

In the MDA specimens, the shells are differently preserved with respect to those from Borgo Celano (Fig. 7). The inner aragonitic layer has been replaced by neomorphic sparry calcite (e.g., Fig. 7D), while in the Borgo Celano specimens, the sediment matrix is directly in contact with the inner side of the outer calcitic layer (e.g., Fig. 6C). Sparry calcite only occurs in small and strongly compressed cavities produced by the aragonite dissolution during the early sediment compaction, before the lithification (Fig. 6D). The absence of the inner shell layer in Borgo Celano specimens can be, therefore, related to this aragonite dissolution.

The marginal regions of the dorsal body cavity of MDA specimens, entirely made of calcite (Fig. 7D), are inwards interfingered with sparry calcite, which replaced the original aragonitic microstructures of the inner layer. This latter layer covered, therefore, the inner body cavity with the exclusion of the marginal regions (Fig. 7D). The chondrophores are composed of calcite, which grew in a ventral direction over the inner aragonitic layer, now replaced by neomorphic calcite. In a MDA specimen about 7 cm high, the middle shell region is very thin, only about 1.5 mm (Fig. 7E, while it is as thick as 5 mm on the marginal region. The shell thins out ventrally, where the margins are sharp. In transversal section the chondrophore of the lower valve has an internal dark-brown calcitic nodule (Figs. 7C, 7F). Such a nodule has been also drawn in the serial sections of *Chondrodonta* illustrated by Douvillé (1902). The outer shell surface is broadly plicated. In the sectioned valves, two or three irregularly spaced plicae are present. They are low, rounded and widely spaced and are likely to be restricted to the outer calcitic layer (Fig. 7A). The MDA shells show frequent processes of bioerosion (Fig. 7E) and microbial–foraminiferal encrustation.

A detailed morphological analysis of the inner umbonal cavity and hinge plates was obtained through serial sections (method B, Fig. 6) made on a specimen from Borgo Celano. These sections show an arrangement of chondrophores similar to that occurring in *Chondrodonta joannae* (Douvillè, 1902). Both the chondrophores of the latter species have tongue-like ventral extremities, which acted as ligament anchorage. In the Borgo Celano specimen, the disposition of the tongue-like extremities seems to be asymmetrical (Fig. 6E SP5, from 15 to 17 sections). However, due to the bad preservation of this specimen it is not possible to assess if this asymmetry is related to biologic or diagenetic factors.

4.2. Systematic remarks

The shell shape and morphology of the chondrophores permit the assignment of the studied ACP specimens to *Chondrodonta* Stanton, 1901. In the Borgo Celano specimens, occurring in hard-cemented limestone, the inner aragonitic layer is leached, while the MDA specimens are embedded in the sediment matrix. Such preservation cannot provide, therefore, information about the number and disposition of the adductor scars and the pallial line, precluding the orientation of the *Chondrodonta* shells. All the Borgo Celano examined specimens show a smooth shell, while the MDA shells are thicker and clearly plicated (Figs. 5–7). The ornamentation consists of low, rounded and sparse (3–4) plicae, only occurring on the outer surface. Therefore, the lower Aptian *Chondrodonta* populations from the Gargano are characterised by different shell thickness and ornamentations.

Non-plicated and thin shells are typical of *Chondrodonta glabra* Stanton, which spans from Barremian to late Albian in the Caribbean Province. The Barremian–lower Aptian populations of *C. glabra* from the Sligo Formation in Texas are characterized by small shell size (Scott and Kerans, 2004), similar to the studied lower Aptian specimens. Larger shells (up to 23 cm long) have been recorded in the upper Albian Devils River Formation of Texas (Scott and Hinote, 2007). As already noted (e.g., Dhondt and Dieni, 1993), some plicae are also detectable in a figured syntype of *C. glabra* (Stanton 1901, pl. 26, figs 1–3). This type shows three broad and irregular spaced plicae in the middle part of lower valve.

Plicated shells characterize the lower Albian *C. youngi* Scott and the middle–upper Albian *C. munsoni* (Hill), both from the Caribbean Province (Scott and Filkorn, 2007; Scott and Hinote, 2007). *Chondrodonta munsoni* differs from *C. youngi* in being smaller in size and in having larger but lesser radial plicae and costae, which are low and rounded. However, both species are characterized by a rather regular distribution of plicae and ribs, a character not present in the ACP specimens. Plicated shells also characterize the Cenomanian *C. joannae* (Choffat) from the Tethyan province. This species has a rather variable number of folds or ribs, characterized by sharp crests.

The Caribbean *C. glabra* differs from the ACP specimens with regard the length and shape of the hinge plate and the chondrophore of the lower valve. The ACP valves show a shorter (about one fifth *vs*. one third of valve height), smooth and slightly concave hinge plate, located posteriorly to the chondrophore of the lower valve. This portion of the hinge plate is grooved in *C. glabra*.

The few available isolated specimens from the Gargano Promontory and the different preservation state of Borgo Celano and MDA shells (isolated and leached valves *vs.* embedded in hard-limestone shells) hinder the analysis and comparison of the intraspecificic variability of the two groups. However, considering that *Chondrodonta* was a cemented bivalve, characterized by a wide morphological variability, and that the Texas population of *C. glabra* contains both smooth and ribbed specimens (e.g., Dhondt and Dieni, 1993), the separation at species level of the studied two lower Aptian populations from Apulia is not justified. Therefore, these populations are here both ascribed to *C. glabra*. They could represent two different ecomorphotypes, characterized by thin and smooth shells and thick and broadly plicate shells respectively. They were adapted to different hydrodynamic regimes occurring in inner platform and platform–basin margin environments. It is worth noting that the early evolutionary stage of *Chondrodonta* (Barremian–early Albian), both from Tethyan (this paper) and Caribbean provinces (Scott, 2007), is represented by predominantly smooth, small and thin shells

4.3. Shell mineralogy and microstructures

The lower Aptian *Chondrodonta* shells from the Gargano Promontory have an outer layer of foliated calcite and a wide inner layer of neomorphic sparry calcite, which suggest an original aragonitic composition. On the basis of this mineralogical shell composition and extension of the inner aragonitic layer, *Chondrodonta* does not seem phylogenetically related to Ostreoidea, because in the latter superfamily, the aragonitic microstructures are restricted to a narrow area of the myostracum (Stenzel, 1971; Carter, 1990a).

The outer layer is predominately composed by regularly foliated (RF) calcite. This microstructure is detectable along vertical radial sections (Figs. 8G, 8I). In vertical transversal sections passing through the central body of lower valve, cardinal platform and around the chondrophore, the irregular complex crossed foliated (ICCF) microstructure is also present (Fig. 8C). In the outer and inner part of the calcitic layer, the folia of the ICCF microstructure are respectively oriented at high (>15°) and low angle. The microstructure of the chondrophore nucleus consists of homogeneous calcite (Figs. 8D, 8E, 8K).

4.4. The Chondrodonta *accumulations: biogenic components, taphonomic signatures and microfacies*

In the Borgo Celano area (Fig. 1B), the *Chondrodonta* accumulations are arranged as a laterally continuous bed-set, about 100 cm thick (Figs. 3–4). These accumulations represent a rather laterally continuous sedimentary body (see above), extended over more than 150 m. In the bivalve accumulations, dominant components are represented by peloids and *Chondrodonta*. Agglutinated foraminifera, ?*Meandrospira*, microbial crusts, thin shelled bivalves, and nubeculariids are subordinate, but can be common. Undetermined ostracods are rare. Two carbonate microfacies were distinguished on the basis of component distribution: very fine peloidal wackestone-packstone (PWP) and *Chondrodonta* packstone (CP). The microfacies PWP is dominated by very fine peloids in a wackestone/packstone (Fig 9A). Locally a faint lamination is detected by peloidal accumulations in millimetre-thick laminae and clotted peloidal-micritic microfabric is also present. The microfacies CP is characterized by large *Chondrodonta* shells (Fig. 9B). These shells are often encrusted by microbial crusts, up to 2 mm-thick, and nubeculariid layers (Fig. 9D).

A microtaphonomic approach (Nebelsick et al., 2011) reveals bioerosion, encrustation, fragmentation and micritization (Fig. 9). Components are generally well preserved though bioerosion and encrustation occur in all the distinguished microfacies. Bioerosion, common on the bivalve shells, is present as (1) endolithic narrow tube-like borings assigned to the ichnogenus *Trypanites* (Fig. 9C) attributed to the activity of worms, and as (2) epilithic rounded, often connected, chambers assigned to the ichnogenus *Entobia* (Fig. 9B–C), which is known to be produced by bioeroding clionid sponges. Fragmentation and micritization affect the larger shells (Fig. 9B). Pressure solution occurs locally between *Chondrodonta* shells involving the outermost bivalve surface.

4.4.1. The Chondrodonta *accumulations of outcrops 1 and 2*

These two outcrops illustrate the *Chondrodonta* accumulations in which three main stages were distinguished. The first stage is the colonization stage of the *Chondrodonta* populations, which took place on a hard-substrate represented by the upper surface of a stromatolite layer (Fig. 3A–3C, 4A). Bouquet-like aggregates of individuals in life position occur both at the contact with the underlying stromatolite layer and in the colonization stage's upper part (see arrows in Fig. 3B). In CP microfacies the first bivalve aggregates consists of a single bivalve generation, which is followed by aggregates recording more than two generations, with the valves attached to each other. These bouquet-like aggregates, with densely packed shells, are separated by prevailing horizontally-oriented articulated valves. Local microbioturbation can be present.

The colonization stage is overlain by sub-horizontal and/or chaotically oriented valves, with subordinate bouquet-like aggregates, and PWP and CP marly lenses marking two undulated and laterally discontinuous surfaces (second stage; Fig. 3A, 4A). The third stage records at least five aborted bivalve carpets, the last of which contains bouquet-like aggregates, commonly made up by a single bivalve generation (Figs. 3D, 4B). At the last stage of outcrop 1 (Fig. 3D), in the bouquet-like aggregates the umbonal region of the individuals is cemented on horizontal-oriented, autochthonous *Chondrodonta* shells (e.g., Figs. 4B, 5A).

4.4.2. The Chondrodonta *accumulation of outcrop 3*

This accumulation is characterized by a wide exposure (*ca*. 100 m^2) of the upper bed surface, showing the lateral variability and geometry of the fossiliferous body. The *Chondrodonta* accumulation, about 90 cm in thickness, overlies a 40 cm-thick stromatolite bed (Fig. 4D). The lower part of the bed-set consists of a nodular *Chondrodonta* floatstone with a PWP matrix. The upper part of the bed-set is characterized by a *Chondrodonta* rudstone with a CP matrix. In the wide upper surface of the outcrop three sub-circular reliefs, about 20–30 cm high, were distinguished. These reliefs, 1.5–3 m in diameter, are characterised by vertical oriented valves often arranged in bouquet-like aggregates (Fig. 4F). In the flat surfaces among the reliefs, in the CP microfacies horizontal valves locally microbioturbated are frequent (Fig. 4E).

5. Discussion

5.1. Shell preservation and aragonite dissolution

The Borgo Celano *Chondrodonta* shells are thin, smooth and without any remnants of the internal aragonitic shell layer. On the contrary, the Monte degli Angeli *Chondrodonta* shells are thick, broadly plicated, with the evidence of an internal aragonitic layer, now replaced by neomorphic calcite (Fig. 7A). The matrix embedding the Borgo Celano shells does not show vadose cements or other evidences of meteoric diagenesis even related to dissolution by phreatic freshwater lenses. Moreover, the subtidal facies occurring above the *Chondrodonta* accumulations and in the upper part of the section (Fig. 2) do not show subaereal exposure evidences. The aragonite dissolution of these latter valves probably occurred before or during the early burial phase, prior the sediment lithification. The porosity originated by the aragonite dissolution was therefore filled by the unconsolidated mud (Fig. 6C). Therefore, the different shell preservation of the two localities suggest different aragonite saturation states of the surface marine waters.

The *Chondrodonta* flourishing in the Gargano Promontory has been related to the Selli Event (OAE1a; Graziano et al., 2013), which caused a biotic crisis on benthic and planktic organisms (e.g., Erba, 1994; Skelton, 2003; Weissert and Erba, 2004; Erba et al., 2010, 2015; Skelton and Gili, 2012). Some authors have related this biotic crisis to the acidification (e.g., Weissert and Erba, 2004; Erba et al., 2010, 2015), which would have also affected, for a short period (50–100 ky), the aragonite saturation state of the surface water (Bauer et al., 2017).

The different aragonite saturation state between the inner platform and platform-margin settings could be related to local environmental factors (e.g., top-down effect of acid rains in shallow and calm setting) or to a slight diachrony between the Borgo Celano and MDA *Chondrodonta*-bearing beds, as suggested by Graziano et al. (2013). These authors have correlated the *Chondrodonta* bed-set of the Borgo Celano with the acidification peak of the Cismon section (interval C4 of Menegatti et al., 1998; Malinverno et al., 2010), while the MDA *Chondrodonta* accumulations have been correlated to the top of the C2 interval in the Cismon section, slightly pre-dating the acidification peak (Menegatti et al., 1998; Malinverno et al., 2010).

5.2. Palaeoecological interpretation

Cementing bivalves appeared from different evolutionary lineages mostly during the Mesozoic, as consequence of the Mesozoic Marine Revolution (Vermeij, 1977, 1987). Their spreading has been related to the increasing of the durophagous predator pressure (Harper, 1991). Cementers predominantly inhabited shallow water environments, where some gregarious forms (e.g., lithiotids, rudists, oysters) formed highly dense aggregates (bivalve mounds, reefs and pavements), influencing the sedimentation rates and carbonate platform dynamics (e.g., Fürsich et al., 1994; Gili et al., 1995; Riding, 2002; Fraser et al., 2004; Skelton and Gili, 2012; Harper, 2012).

The cementing bivalves are characterized by high intraspecific morphological variability related to the substrate consistency and nature (e.g., rocky or shelly), wideness of the attachment area and, for gregarious species, spatial competition. Bivalves with small attachment areas and living in calm environments with high sedimentation rates show the tendency, during early ontogenetic stages, to raise the ventral margin from the substrate (e.g., Harper, 2012) and to develop an upright shell growth. Consequently, during the juvenile stage, the upright growth direction represents a secondary adaptation towards soft bottom environments. This adaptive strategy produced aberrant morphologies with spoon-, cone- or stick-shaped shells (Seilacher, 1984; Ayoub-Hannaa and Fürsich, 2011).

5.2.1. Functional morphology

The Borgo Celano *Chondrodonta glabra* individuals have a moderately elongated shell, with a spoon- to stick-like outline. The bottom was stabilised by cementation on hard substrate and the supporting muddy sediment accumulated around the valves, as already suggested for the elevator rudists (e.g., hippuritids; Skelton et al., 1995). The smooth or feebly ornamented shell did not provide any contribution to the stabilization. The common occurrence of vertically oriented valves in the outcrops 1 and 2 is likely related to the well-developed, large and stable hard substrate, the high sedimentation rate, and the low hydrodynamic energy. Local microbioturbation and no encrustation confirm these palaeoenvironmental parameters.

The lower valve of *Chondrodonta* is more convex than the upper valve (Fig. 6C, 6E SP1 and 3). This feature suggests an ancestral pleurothetic habit. However, the valves do not have significant differences in shell thickness and the adult shell is almost flat (Fig. 7E–F). *Chondrodonta*, therefore, was potentially able to develop an orthothetic life habit, which characterizes the secondary soft bottom dwellers, such as the Lower Jurassic *Lithiotis* adapted to muddy substrates under high sedimentary rate (Chinzei, 1982; Seilacher, 1984; Ayoub-Hannaa and Fürsich, 2011). The known similarities between *Chondrodonta* and the Jurassic aberrant *Lithiotis* suggested the names of some Cretaceous chondrodontids (i.e., the Albian *Lithiotis cretacea* Lörenthey, 1895, later placed in the genus *Grypheolamellotis* Horváth, 1966; Dhondt and Dieni, 1993). *Lithiotis* has a strongly specialized shell with a very elongated fixed valve, which has a flattened club- (or stick-) like shape and a very small body cavity at the ventral extremity, closed by a thin and elastic free or opercular valve. *Chondrodonta* is lesser specialised than *Lithiotis* towards the mud sticker strategy of bottom stabilization, because it has a shorter and almost equivalve shell and more elongated and wide body cavity.

Lithiotis and *Chondrodonta* are not taxonomically related because they show remarkable differences concerning the mineralogical composition, microstructures and shell morphology (*Lithiotis* is entirely aragonitic, with predominant nacreous and irregular fibrous prismatic microstructures and multivincular-like ligament; e.g., Chinzei, 1982; Savazzi, 1996).

5.2.2. Shell microstructure

The mud stickers are characterized by an opening and closure mechanism based on the flexibility of ventral region (Seilacher, 1984). In *Pinna*, a living endo-byssate and semi-infaunal bivalve, the opening and closure mechanism is allowed by the flexibility of a median dorsal carina, where the shell is fractured and joined by organic matter. The thin and elastic ventral margins close and open the mantle cavity (e.g., Seilacher, 1984). Moreover, the high ventral flexibility of *Pinna* is due to the outer shell layer microstructure consisting of simple calcitic prisms joined by organic sheaths (e.g., Taylor et al., 1969). To increase valve flexibility, the inner nacreous layer occurs very far from the ventral margin, at about half of the valve height (e.g., Taylor et al., 1969, fig. 51). A high flexibility of ventral margin has been also suggested for *Lithiotis*. Most of the ventral extremity of the free laminar valve was probably mostly organic, because it is not preserved in the fossils and the outer calcitic layer is missing (Chinzei, 1982; Seilacher, 1984; Savazzi, 1996).

In *Chondrodonta* the tight interlocking of chondrophores hindered the mechanism of valve articulation and facilitated a flexible mechanism. However, the opening mechanism of *Chondrodonta* was probably different from those of *Lithiotis* and *Pinna.* The ventral margin was very thin and less flexible than in the other two Jurassic genera. The foliated calcite of the outer shell layer is more fragile than the prismatic calcite and nacre (Taylor and Layman, 1972). Another shell constraint can be represented by the microstructure of the internal aragonitic layers. This microstructure is unknown in *Chondrodonta*. If the latter is phylogenetically related to *Plicatula*, the microstructure should be reckoned as predominantly crossed lamellar aragonite (e.g., Taylor et al., 1969), which has a lower flexibility in comparison with other aragonitic microstructures (e.g., nacre; Taylor and Layman, 1972).

The flexibility of *Chondrodonta* shell was allowed by internal morphological structures, probably related to shell thickness variations. In the dorsal internal half of the shell, *Chondrodonta* has anterior and posterior swollen marginal regions entirely made of crossed foliated calcite (Fig. 8F). These marginal crests have rounded borders which probably had two functions: i) to prevent the entry of sediment along the buried shell margins, even when the adductor muscle was relaxed; ii) to increase the shell flexibility along the middle region. For the second function, the ridges acted as fulcrum of the force exerted by the adductor muscle, transferring the deformation to the ventral margin. The absence of neomorphic calcite on the marginal crests in the MDA specimens suggests that the pallial line, if originally present, was located more inwards and during the valve closing the mantle was retracted from the crests (Fig. 10).

Probably, besides shell morphology and microstructure, other constraints have hindered the development of aberrant, mud-sticker shape. *Chondrodonta* is a fully marine bivalve, which generally formed stressed paucispecific shell concentrations (e.g., Ayoub-Hannaa and Fürsich, 2012). Its wide stratigraphic and geographic range (Dhondt and Dieni, 1993) and the occurrence both in low and high diversified benthic assemblages suggest *Chondrodonta* was as an opportunistic bivalve (Graziano et al., 2013). The trophic and reproductive strategies of

Chondrodonta, typical of r-strategist taxa, were probably not suitable to develop aberrant shell morphologies, such as those occurring in the Jurassic lithiotids.

5.3. Chondrodonta *accumulations*

The studied Gargano *Chondrodonta* accumulations contain autochthonous individuals, frequently preserved in living position, which had a gregarious behaviour and a cemented life habit.

In the Borgo Celano area, the *Chondrodonta* accumulations are characterised by three main stages, separated by undulated bed surfaces generated by the *in situ* preservation of bouquet-like shell aggregates. Each stage has been generated by the superposition of several, laterally discontinuous bivalve concentrations containing autochthonous individuals, often preserved in life position, belonging to a single or few generations. These taphonomic characters are typical of the bivalve carpets, which consist in tabular fossil concentrations recording periodic mass mortality, high sedimentation rate, and unstable environmental conditions (Bassi et al., 2015).

In the colonization stage the valves in life position have a very small, maximum 10 mm wide, cemented area. To prevent burial, the shell lifted the lower valve from the substrate very rapidly with a curvature degree related to the position of the shell inside the bouquet (Fig. 4B). The absence of deep bioturbation and the complete preservation of the thin and fragile ventral margins of adult individuals suggest a very rapid burial (Fig. 4B). The sub-horizontally and/or chaotically oriented valve stage does not show marked erosional surfaces on the underlain deposits, is laterally discontinuous and the valves are encrusted and bioturbated. This stage has been probably originated by winnowing or low energy storm events, which re-oriented the flat shells in a more stable position under low sedimentation rate, favouring the microbial and nubeculariid encrustation (e.g., Reolid et al., 2008).

The quick fluctuations of *Chondrodonta* populations are typical of unstable and unpredictable environments characterized by significant changes in trophic resources and other environmental limiting factors (e.g., Kidwell et al., 1986, p. 233; Kidwell and Bosence, 1991). In these stressed marine environments, the mass mortality events can be related to periodical or occasional eutrophication, dysoxia, temperature, salinity and turbidity fluctuations. The superimposed *Chondrodonta* carpets of the third stage represent these events that aborted the community. The ACP was far from large emerged lands, therefore significant increasing in turbidity and salinity related to nearby riverine input is not predictable (Graziano et al., 2013). In the inner platform setting of the Borgo Celano area sedimentological evidences of dysoxia/anoxia (e.g., black shales) are missing. The lethal environmental changes could have been, therefore, connected with palaeoceanographic changes of the surface water mostly related to hyperthermal and acidification peaks (Graziano et al., 2013; Graziano, 2013). The aragonite dissolution of the *Chondrodonta* inner shell layer probably can be interpreted as an evidence of shallow water acidification. Such an acidification in tropical carbonate platforms would be mitigated by the “kettle effect” (Skelton and Gili, 2012). However, in the ACP, the high evaporation predicted in this model could be limited by high acid rainfall and/or by a slight deepening originated by the crisis of the carbonate platform production.

In the MDA *Chondrodonta* shells, from the platform-slope margin setting, the preservation of the inner aragonite layer suggests a lower seawater acidification with respect to the inner platform environment (see above). However, the MDA specimens are characterized by intense bioerosion and microbial and nubeculariid encrustations which suggest the onset of upwelling nutrient-rich currents (e.g., Robin et al., 2013), pre-dating the OAE1a peak and the drowning of the platform margin (Graziano, 2013).

6. Conclusions

In the lower Aptian Apulia Carbonate Platform (ACP), during the onset of the Selli Event (OAE 1a), *Chondrodonta glabra* thrived in lagoonal to platform–basin margin settings. This species, characterised by nearly smoothed and moderately elongated shells with a relatively thick outer calcitic layer, represents the older evolutionary stage of the genus. *Chondrodonta glabra* is a cemented bivalve with a broad ecomorphic variability. The relatively large body cavity connected with the umbonal region and a shell only moderately elongated are mostly related to phylogenetic constraints. *C. glabra* developed a different mechanism of shell closure. The adductor muscle acted on the flexibility of the median and anterior shell regions whose movements were facilitated by the fulcrum of the lateral internal ridges.

The individuals living in the inner ACP (Borgo Celano, San Giovanni Rotondo Limestones) have thin and smooth shells, while those living at the ACP-slope margin (Madonna degli Angeli area, Montagna degli Angeli Limestones), have a thicker shell, covered by broad and widely spaced radial ribs. In the latter population, the internal aragonite shell layer preserved during the early diagenetic phases, while this layer has been dissolved in the shallower population of Borgo Celano. We suggest that this different preservation could be related to different aragonite saturation state of shallower settings and tentatively related to the early Aptian OAE 1a acidification peak. The *Chondrodonta* accumulations show a very wide lateral extension and were originated by autochthonous bouquet-like shell aggregates, frequently preserved in living position. These aggregates made up superimposed carpets, each containing only a few generations, affected by mass mortality and rapid burial processes. These were connected with repeated environmental lethal fluctuations occurred at the onset of the lower Aptian OAE1a. The quick fluctuations are typical of unstable and unpredictable environments characterized by significant changes in trophic resources and hyperthermal and acidification peaks.

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Figure captions

Fig. 1. A, Geographic locations of the study localities in the Gargano Promontory (southern Italy). B. The Borgo Celano outcrops illustrate a *ca*. 150 m-long *Chondrodonta* bed-set of the San Giovanni Rotondo Limestones. C. The Monte degli Angeli (MDA) outcrop of the Montagna degli Angeli Limestones.

Fig. 2. Stratigraphic column of the Borgo Celano section with the location of the studied *Chondrodonta* bed-set (mod. after Guerzoni, 2016),which marks the base of the Member 3 (*sensu* Claps et al., 1996) or the *Chondrodonta* and requieniids member (*sensu* Graziano et al., 2013) of the San Giovanni Rotondo Limestones.

Fig. 3. The *Chondrodonta* accumulations of the Borgo Celano section, outcrop 1, San Giovanni Rotondo Limestones, early Aptian. A, the three superimposed distinguished stages of the *Chondrodonta glabra* accumulation (cs, hcv, abc). B–C, details of the contact between the stromatolite layer (sl) and the base of the colonization stage; the arrows point to the oblique orientated or bouquet-like shell aggregates. D, bouquet-like shell aggregates from the upper part of the aborted bivalve carpet. cs, colonization stage; hcv, sub-horizontal and/or chaotically oriented valves; abc, aborted bivalve carpets.

Fig. 4. The *Chondrodonta* accumulations of the Borgo Celano, San Giovanni Rotondo Limestones, early Aptian. A, the distinguished three *Chondrodonta glabra* accumulation stages (cs, hcv, abc) in the outcrop 2. B–C, polished slab of a bouquet-like *Chondrodonta glabra* aggregate (from the upper part of abc, outcrop 1); B and C slabs are respectively perpendicular and horizontal (at the base) to the bed surface. D–E, outcrop 3. D, the upper surface of the *Chondrodonta* accumulations with

three low knobby reliefs formed by autochthonous shells with a prevailing bouquet-like arrangement. E, detail of the bed surface, far from the relief, with abundant horizontally oriented and broken valves. F, detail of the relief core with transversal sections of bouquet-like aggregates. cs, colonization stage; hcv, sub-horizontal and/or chaotically oriented valves; abc, aborted bivalve carpets.

Fig. 5. *Chondrodonta glabra* Stanton, internal valve surfaces, Borgo Celano section, SGRL, early Aptian. A, lower attached (?right) valve. B, upper free (?left) valve. AHP, anterior part of the hinge platform; HPB, hinge platform border; HPG, hinge platform groove; ?MS, adductor muscle scar; RC, fragment of the right chondrophore. The scale bar represents 1 cm.

Fig. 6. *Chondrodonta glabra* Stanton, Borgo Celano section, outcrop 2, San Giovanni Rotondo Limestones, early Aptian. A, polished slab illustrating the details of transversal sections through the umbonal region (B, D) and body cavity (C); arrows indicate the cavities produced by the dissolution of aragonite, crushed during the early phase of diagenetic sediment compaction and infilled by sparry calcite. E, selected transversal (SP1, SP3 and SP4) and longitudinal/radial (SP2) shell sections obtained with the method A (see text). Serial sections obtained with method B (see text) of specimen SP5; numbers refer to the section number and its distance from the umbo.

Fig. 7. *Chondrodonta glabra* Stanton, polished slabs, Monte degli Angeli, early Aptian. The shells are in vertical life position and some of them are still attached to each other (C, cemented surface). They are characterized by a thick shell with clearly detectable internal layer, now replaced by sparry calcite (NC). On the outer surface, broad undulations (F) indicate the occurrence of low folds. C, oblique radial section of the umbonal region with the upper (UC) and lower (LC) chondrophores. D, detail of the umbonal-lateral region with thick internal marginal ridges of foliated calcite

interdigitated with sparry calcite (NC). E–F, radial sections through the hinge platform (E) and chondrophores (F). LV, lower valve; UV upper valve; B, bioerosion traces.

Fig. 8. Shell microstructures of *Chondrodonta glabra* Stanton from the Monte degli Angeli (A–B, E–N) and Borgo Celano (C–D) observed on acetate-peels (A–G) and SEM (H–N). A, a longitudinal/radial and vertical section (at centre) and an oblique section through the chondrophores (on the upper left side). B, hinge platform with crossed foliated-like microstructure (?CF), which probably originated from a simple foliated structure occurring along a curved shell region. E, detail of the lower chondrophore with the homogeneous microstructure. F, transversal vertical section of the lower valve near the margin, where a crossed foliated-like (?CF) microstructure (probably originated from a simple foliated structure occurring along a curved shell region) of the lateral ridge is laterally replaced by sparry calcite (SC) infilling the void produced by the wholesale dissolution of aragonite. G, detail of lower valve radial section with the outer calcitic layer composed of regularly foliated (RF) microstructure and the inner layer consisting of sparry calcite infilling the void produced by the wholesale dissolution of aragonite; oss, outer shell surface. C, transversal vertical section of the lower valve near the centre of body cavity with the irregular complex crossed foliated (ICCF) microstructure, particularly developed on the external part of outer layer; oss, outer shell surface. D, transverse-oblique vertical section through the chondrophore of a lower valve with the calcitic core consisting of homogeneous (HOM) microstructure. H, a transversal section of the lower chondrophore and detail (K) of the regularly foliated microstructure (M) enveloping the homogeneous (HOM) microstructure of the core. I, radial section of the outer layer composed by regularly foliated (RF) microstructure (with details in J and L) and the inner layer replaced by coarse sparry calcite (SC) crystals. N, horizontal fracture through the regularly foliated (RF) microstructure of the outer layer.

Fig. 9. Photomicrographs showing the distinguished microfacies and the taphonomic signature; San Giovanni Rotondo Limestones, early Aptian, Borgo Celano, ACP, southern Italy. A, very fine peloidal wackestone–packstone (PWP), stromatolite layer, outcrop 1. B–D, *Chondrodonta* packstone (CP), outcrop 3, abc stage of the *Chondrodonta* accumulation. Bioerosion can occur on the surfaces (eb) or within (ib) the *Chondrodonta* shells. Epilithic bioerosion is represented by small rounded chambers, while the endolithic bioerosion corresponds to *Trypanites* (C). Encrusting nubeculariid successions can be up to 1 mm in thickness (D). e, encrustation; en, encrusting nubeculariids; eb, epilithic bioerosion; ib, endolithic bioerosion; ps, pressure solution.

Fig. 10. Schematic reconstruction of *Chondrodonta glabra* based on lower Aptian Borgo Celano and MDA specimens; Gargano Promontory, ACP, southern Italy. A, view of the inner surface of the lower (attached) valve. B, radial section. 1–3, transversal sections. The closure mechanism of the valves acted according to the elasticity of ventral and median shell regions, characterised by inner aragonitic and outer calcite layers. The specimen is oriented in life position. Further details in the text.

Highlights

- Lower Aptian *Chondrodonta glabra* thrived in the Apulia Carbonate Platform
- Shell closure mechanism was based on the flexibility of median and ventral regions
- Preservation of shell layers is related to early Aptian acidification peak
- *Chondrodonta* accumulations were generated by recurrent mass mortality processes
- High trophic resource level and lethal events are related to the onset of the OAE1a

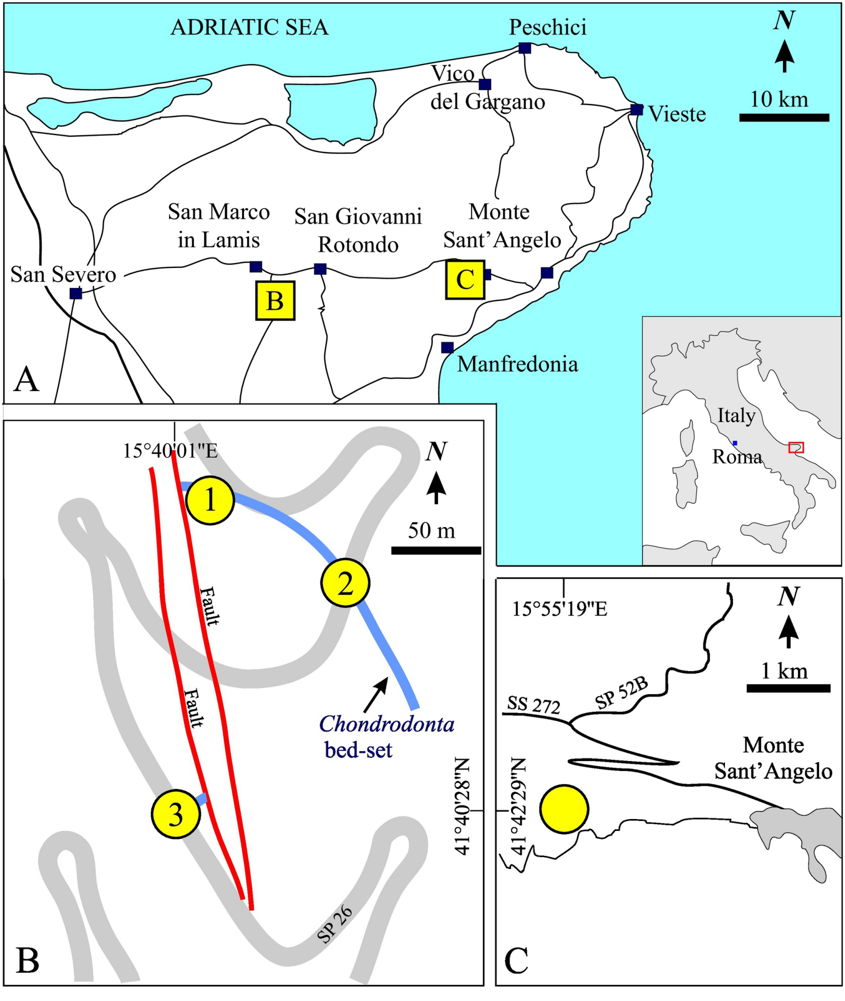

ADRIATIC SEA
Peschici
N
Vico
del Gargano
Vieste
10 km
San Marco
in Lamis
San Giovanni
Rotondo
Monte
Sant'Angelo
San Severo
B
C
Manfredonia
A
Italy
Roma
15°40'01"E
N
1
50 m
2
Fault
Fault
Chondrodonta
bed-set
3
SP 26
B
15°55'19"E
N
1 km
SP 52B
SS 272
Monte
Sant'Angelo
41°40'28"N
41°42'29"N
C

Figure 1

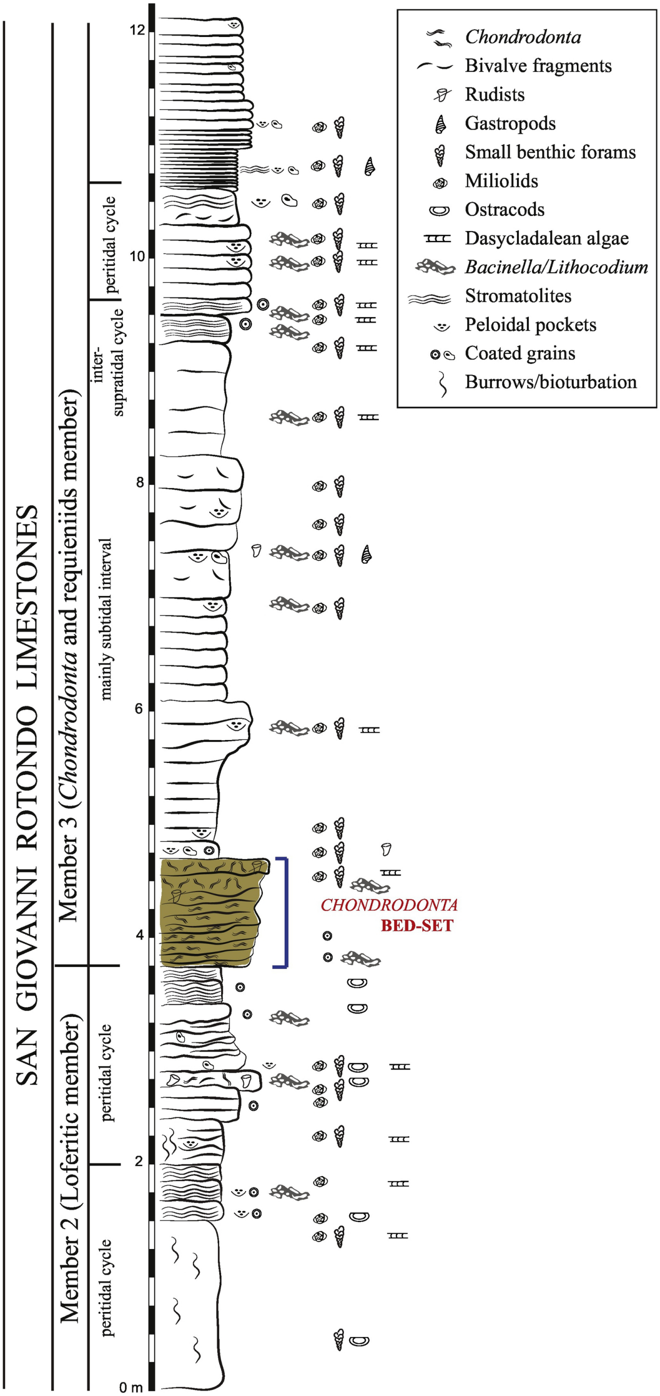

SAN GIOVANNI ROTONDO LIMESTONES
Member 3 (Chondrodonta and requieniids member)
Member 2 (Loferitic member)
peritidal cycle
inter-supratidal cycle
mainly subtidal interval
peritidal cycle
peritidal cycle
12
10
8
6
4
2
0 m
CHONDRODONTA
BED-SET
Chondrodonta
Bivalve fragments
Rudists
Gastropods
Small benthic forams
Miliolids
Ostracods
Dasycladalean algae
Bacinella/Lithocodium
Stromatolites
Peloidal pockets
Coated grains
Burrows/bioturbation

Figure 2

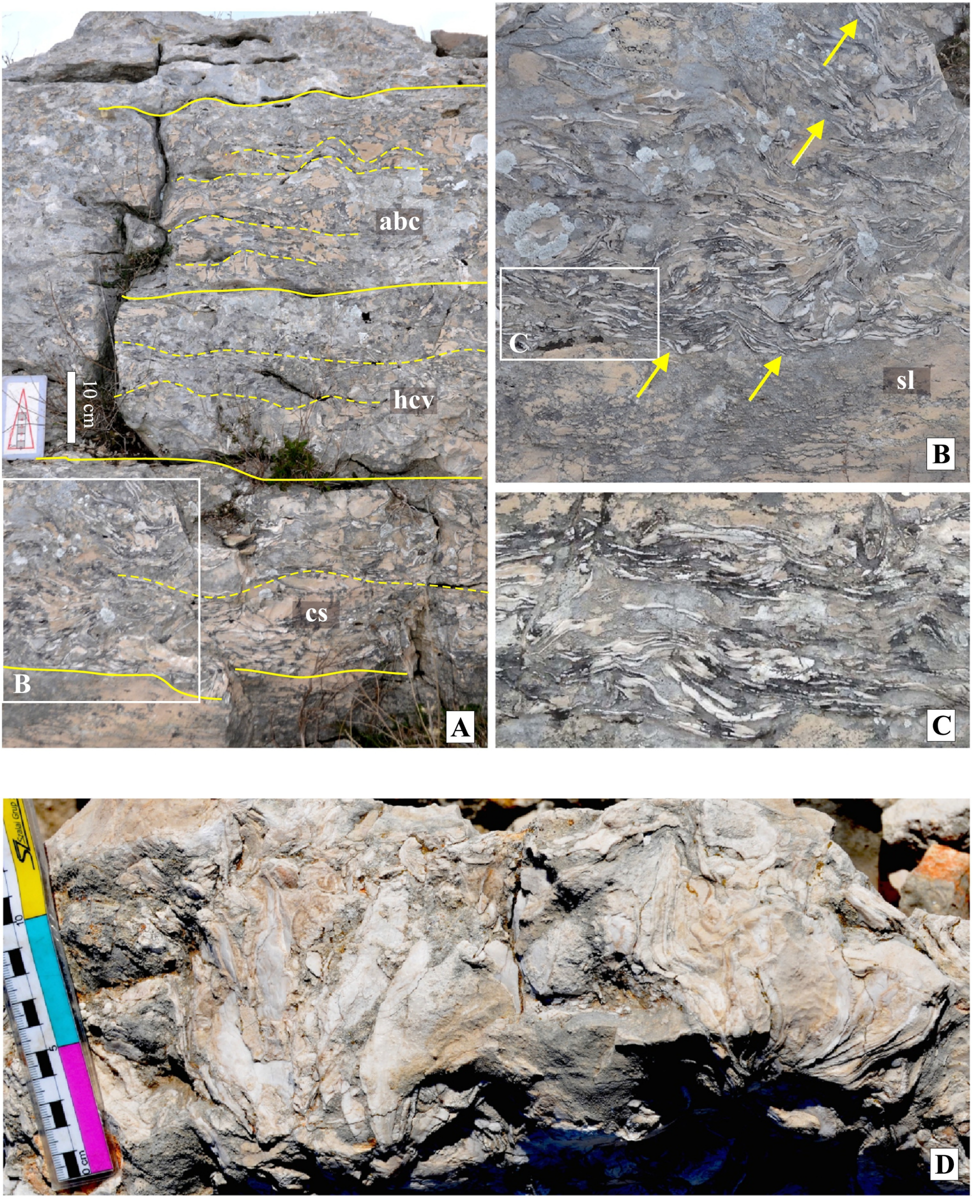


Figure 3

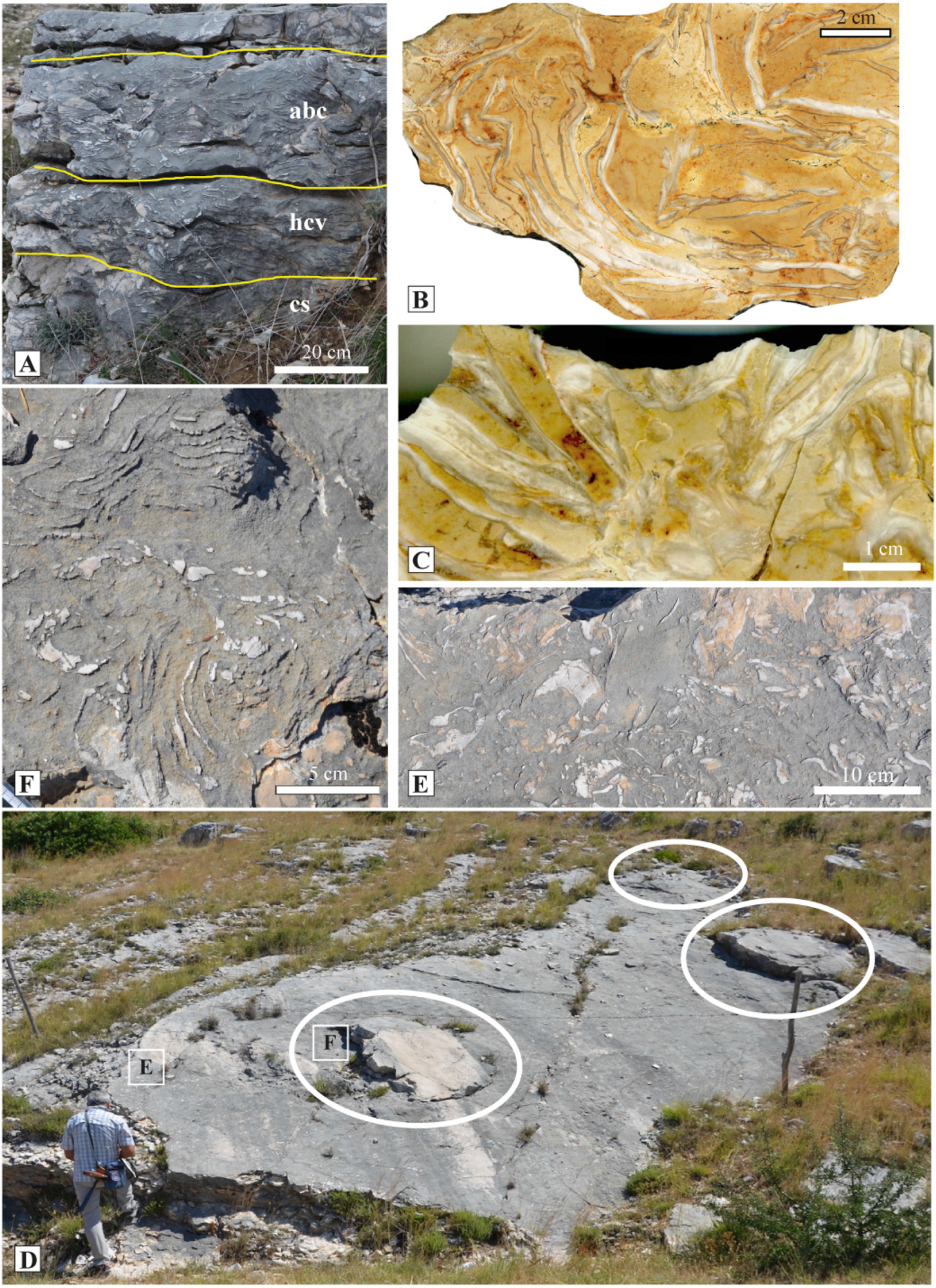


Figure 4

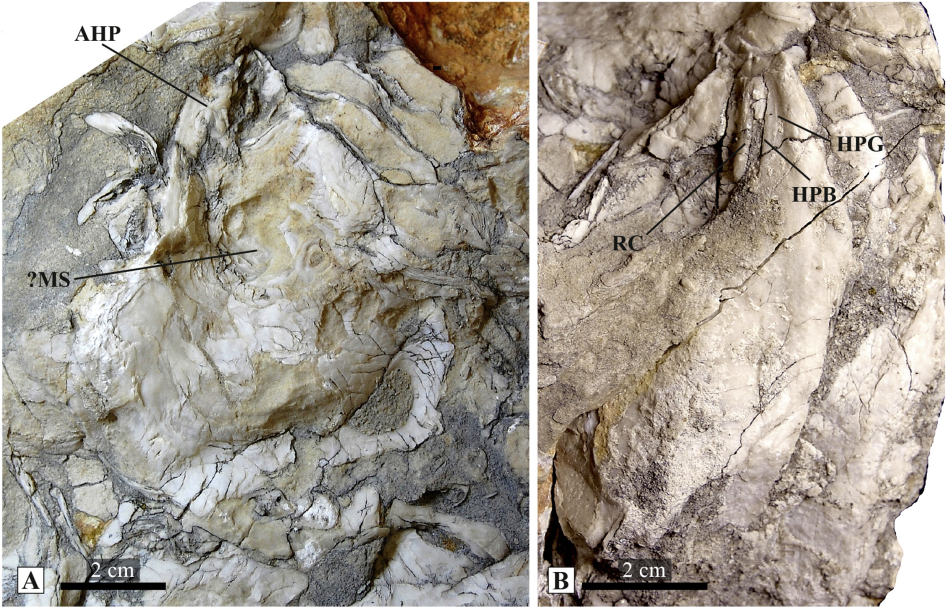


Figure 5

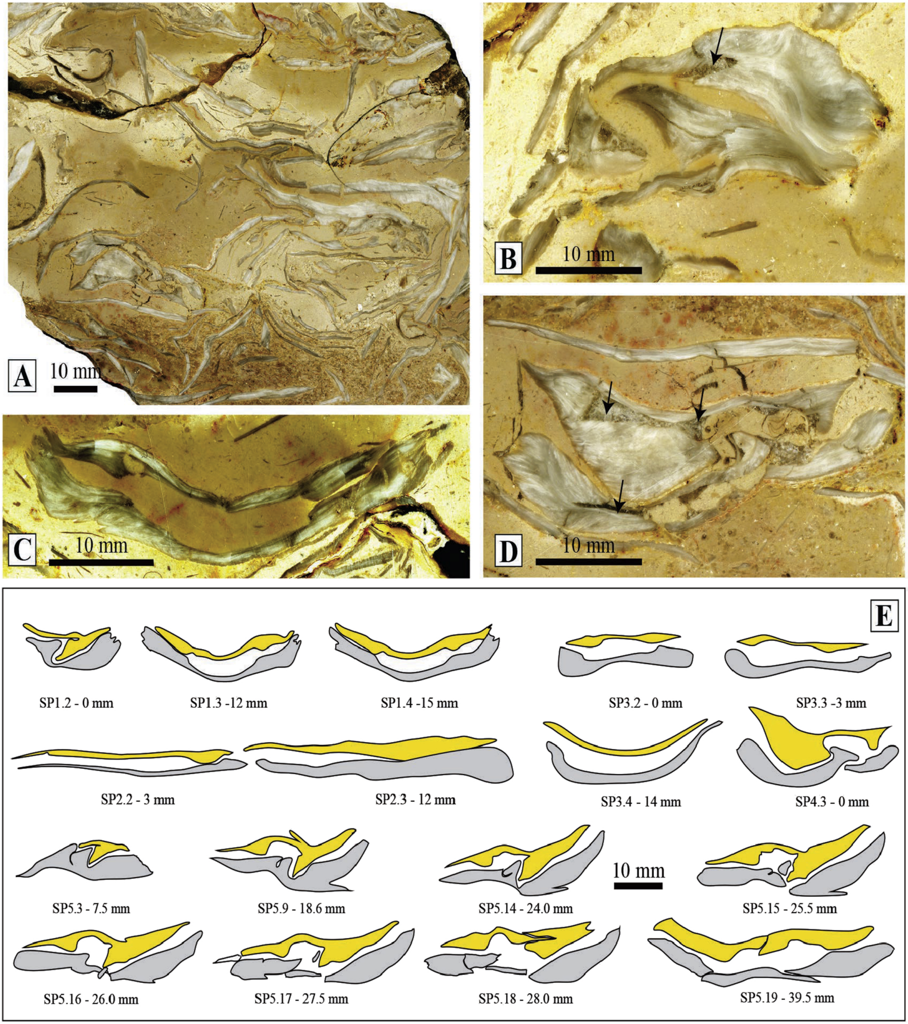

A
10 mm
B
10 mm
C
10 mm
D
10 mm
E
SP1.2 - 0 mm
SP1.3 -12 mm
SP1.4 -15 mm
SP3.2 - 0 mm
SP3.3 -3 mm
SP2.2 - 3 mm
SP2.3 - 12 mm
SP3.4 - 14 mm
SP4.3 - 0 mm
SP5.3 - 7.5 mm
SP5.9 - 18.6 mm
SP5.14 - 24.0 mm
10 mm
SP5.15 - 25.5 mm
SP5.16 - 26.0 mm
SP5.17 - 27.5 mm
SP5.18 - 28.0 mm
SP5.19 - 39.5 mm

Figure 6

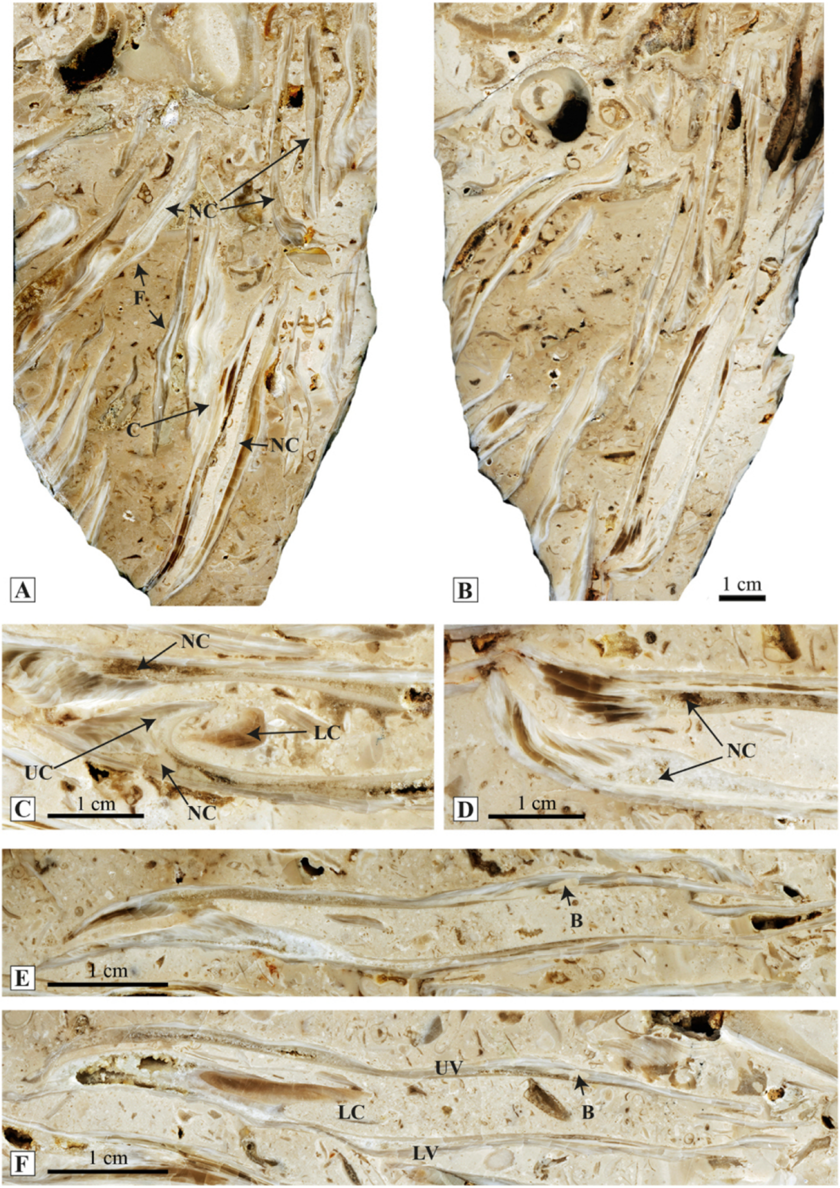
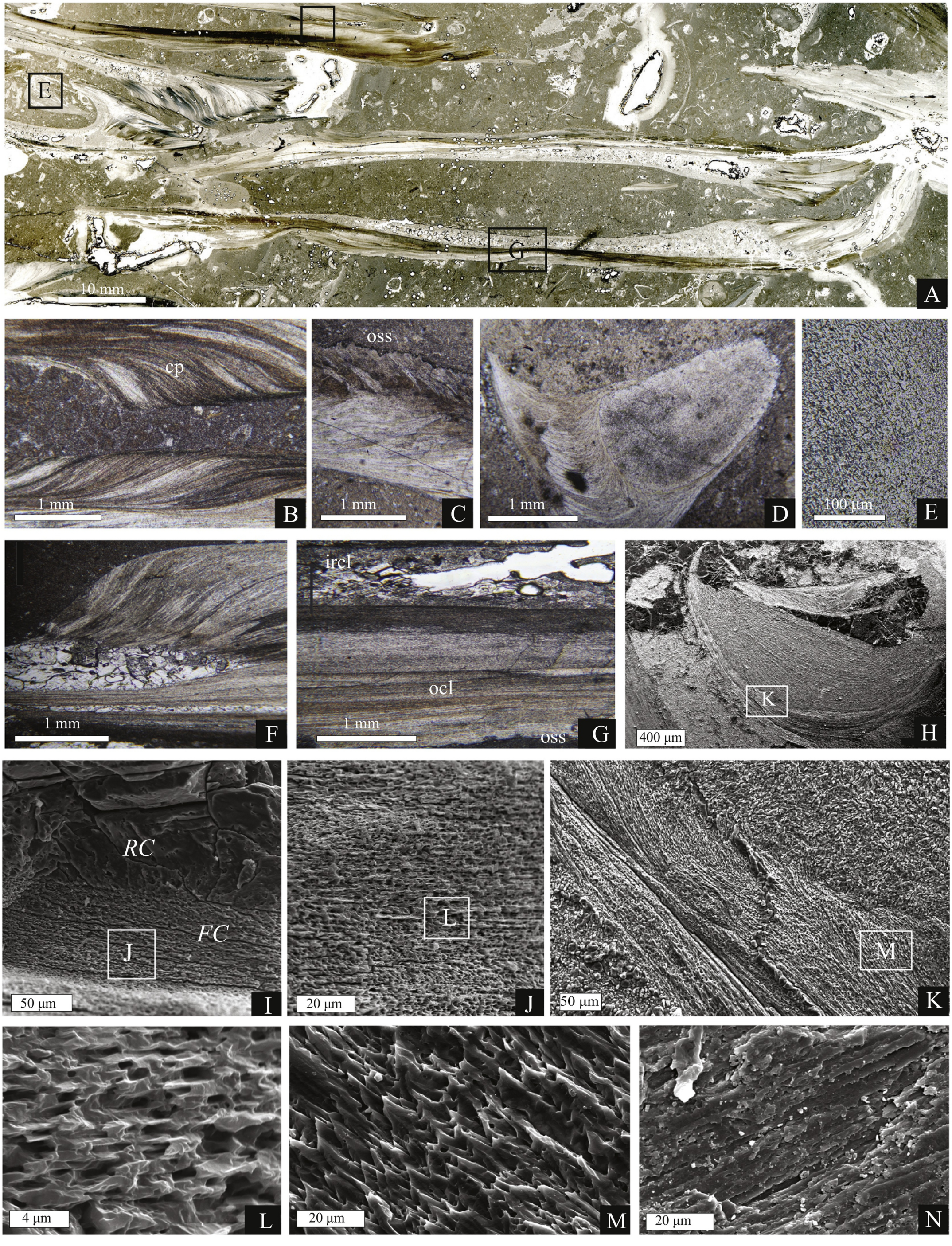


Figure 7


E
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10 mm
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C
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E
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oss
G
K
400 µm
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RC
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K
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L
20 µm
M
20 µm
N

Figure 8

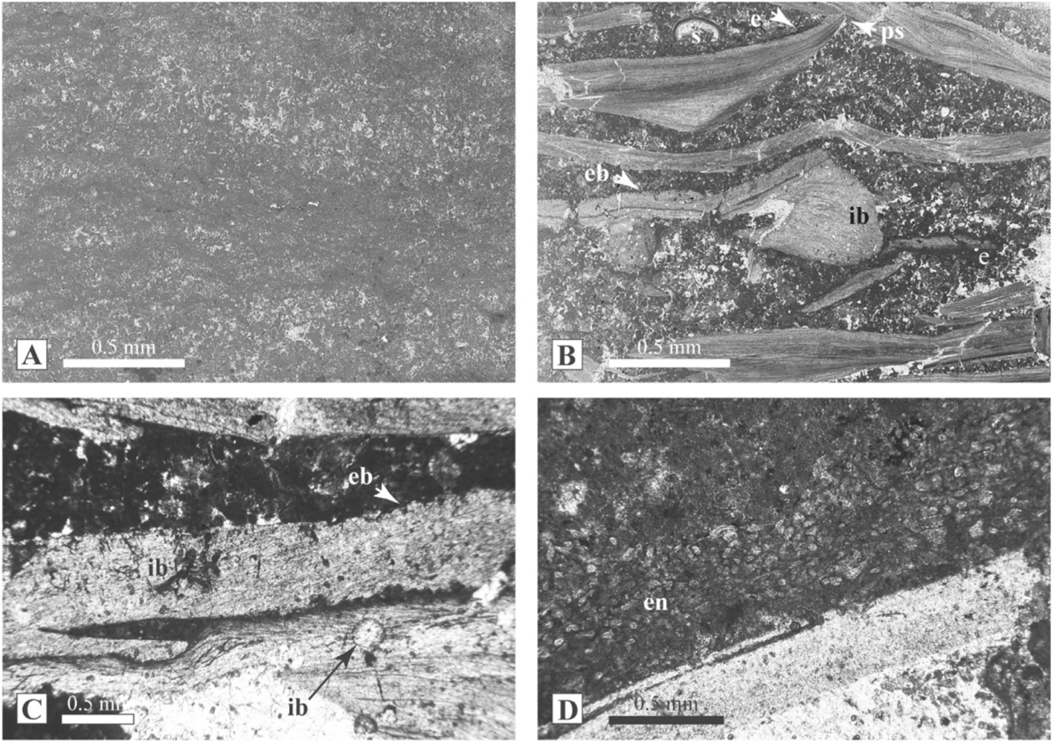

Figure 9

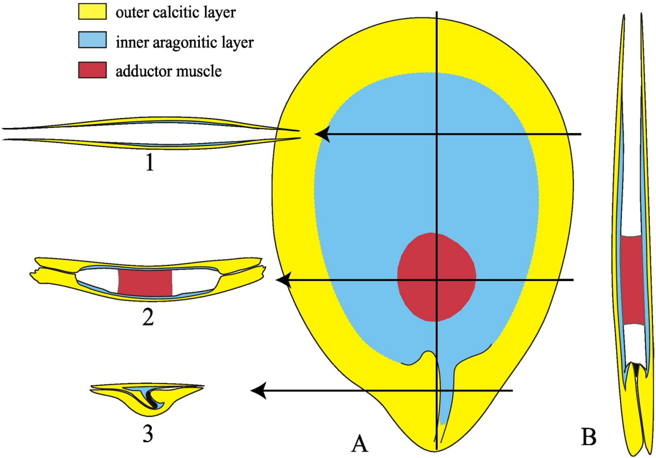
outer calcitic layer
inner aragonitic layer
adductor muscle
1
2
3
A
B

Figure 10