



Bioclaustration trace fossils in epeiric shallow marine stromatolites: the Cretaceous-Palaeogene Yacoraite Formation, Northwestern Argentina

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The shallow carbonate facies at the top of the Yacoraite Formation (Late Cretaceous–Early Palaeocene) in the Metán sub-basin, Salta Basin (Cretaceous-Eocene), northern Argentina, have domal stromatolitic boundstones with peculiar cavities, interpreted here as bioclaustrations. The cavities appear to have been produced by organisms that lived within the microbial mat contemporarily with its growth, producing a distinctive ichnofabric. This is the oldest reported record of bioclaustrations in stromatolites, and the first in shallow marine environments. The interpretation of the facies suggests a stressed shallow, restricted setting with variations in salinity, represented by an intertidal environment with an extensive tidal flat. *Bioclaustrations, stromatolites, endobiont Yacoraite Formation (Cretaceous-Palaeogene), Northwestern Argentina.* □ *Bioclaustrations, endobiont, Northwestern Argentina, stromatolites, Yacoraite Formation (Cretaceous-Palaeogene).*

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An interesting set of biogenic features in stromatolites are embedment structures or bioclaustrations. Their formation process was described originally by Bromley (1970) and later in more detail by Ekdale *et al.* (1984). Bioclaustrations are produced when an organism (e.g. serpulid polychaete) occupies a hard biogenic substrate that may be skeletal or stromatolitic, though not – or not only – by boring, and is then enclosed or incorporated by the substrate producer. The embedded organism can employ mechanisms to enlarge its dwelling, which is why the resulting cavities are of mixed origin, reflecting the interaction between occupant and host (Bromley 1970). This kind of cavity is identifiable in the fossil record by the deflection of the substrate producer's growth laminae around the cavities (see details in Tapanila & Ekdale 2007).

The term 'bioclaustration' was coined by Palmer and Wilson (1988) in a paper on parasitism of Upper Ordovician bryozoans, where they shared Bromley's (1970) original ideas about embedment structures: 'the biological infestation of a living host that subsequently adapted its growth to isolate and enclose the infester' (Palmer & Wilson 1988, p1). They also deduced that the infester must be soft

bodied and that the infester–host relationship is symbiotic, parasitic or possibly mutualistic. These trace fossils have been gathered into an ethological group called impedichnia (Tapanila 2005) because the infester operates as a limiting factor to the growth of the host.

There are few records of bioclaustration structures in stromatolites. Among the antecedents are the trace fossils of bioclaustration reported by Lamond and Tapanila (2003) in stromatolites from the Eocene of Wyoming (USA) and the Pleistocene-Holocene of Lodwar (Lake Turkana, Kenya). The latter had originally been studied in a first report by Ekdale *et al.* (1989), who described macroborings but did not realize that in some specimens, the cavity formation process involved interaction between the producer and the substrate, thus generating bioclaustration structures of mixed origin.

The aim of this study is to report the existence of stromatolites with bioclaustrations in the Yacoraite Formation, the epicontinental carbonate unit of the Cretaceous-Palaeogene basin of northern Argentina (Salta Group), which would mean that it is the oldest record reported. It also aims to contribute to the significance of this record in a sedimentary context of a shallow marine environment.

Geological setting

The Salta Group (Fig. 1) accumulated during the Early Cretaceous to Eocene in northwest Argentina and neighbouring regions, in an intercontinental rift-type basin (Salfty & Marquillas 1994; Viramonte *et al.* 1999; Marquillas *et al.* 2005; among others). The synrift stage corresponds to the Pirgua Subgroup dated between the Barremian and Late Campanian (Bossi & Wampler 1969; Reyes *et al.* 1976; Valencio *et al.* 1976; among others). The Balbuena Subgroup (Late Cretaceous–Early Palaeocene) is the early postrift deposit, and the Yacoraite Formation is part of

this deposit. The Santa Bárbara Subgroup represents the late postrift fill, with which the accumulation of the basin ends. The top of the Salta Group has yielded a U-Pb zircon age of 39.9 Ma (del Papa *et al.* 2010) placing it in the Middle Eocene (Bartonian). The accumulation of the Salta Group certainly crossed the K–T boundary, which may have taken place during the last part of the deposition of the Yacoraite Formation or at its top (Sial *et al.* 2001; Marquillas *et al.* 2003, 2007); the overlying Olmedo Formation belongs to the Danian (Quattrocchio & Volkheimer 2000; Quattrocchio *et al.* 2000).

The Balbuena Subgroup, which contains the Yacoraite Formation (Fig. 1), accumulated in the

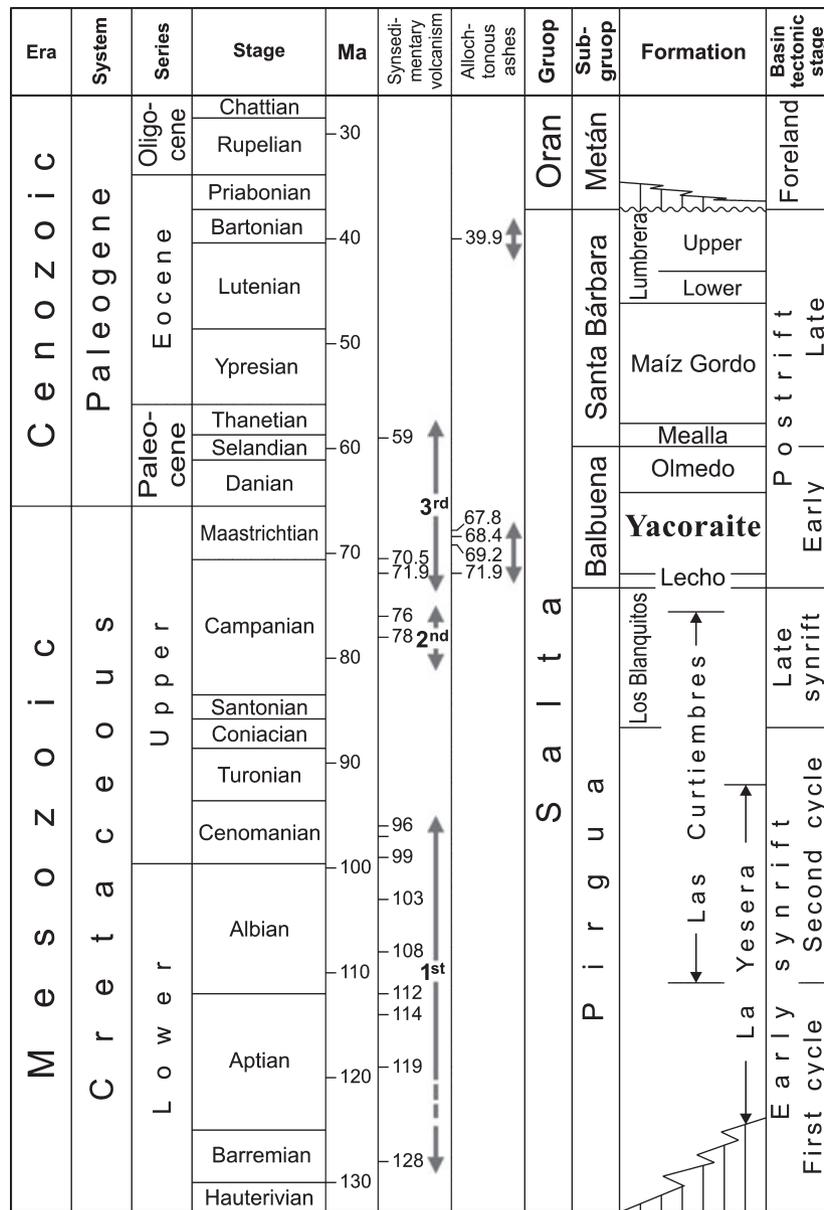


Fig. 1. Chronostratigraphy of magmatic, sedimentary and tectonic events of the Cretaceous-Paleogene Salta basin (after Marquillas *et al.* 2005, 2011).

Late Cretaceous–Early Palaeocene in a regional scenario controlled by the thermal subsidence of the postrift stage of Salta basin (Salfity & Marquillas 1994; Marquillas *et al.* 2005). At that time, the accumulation of thick red layers changed to extensive deposits of white sands (Lecho Formation) and shallow epeiric carbonates (Yacoraite Formation), probably as a result of the transgressions caused by the high global sea level (Scotese 1997; Hay *et al.* 1999; Hay 2008; Müller *et al.* 2008). The deposition of basal white sands took place upon a surface that was practically levelled by the red sands of the late synrift (Salfity 1980; Salfity & Marquillas 1994). The Yacoraite Formation carbonates accumulated on top of the Lecho Formation, with partial interdigitation between the two deposits. The set of stratigraphical, sedimentary, palaeontological-ichnological and isotopic evidence indicates restricted, shallow marine conditions for the Yacoraite Formation and a setting where fresh and brackish waters mixed (Castaños *et al.* 1975; Marquillas 1986; Marquillas & Salfity 1988; Marquillas *et al.* 2007; Cónsole-Gonella & Aceñolaza 2009, 2010).

The filling of the basin took place in several sub-basins (Reyes 1972; Salfity 1982) in one of which – the Metán sub-basin (Fig. 2) – this study was conducted. Here, in the area of the Cabra Corral dam – River Juramento (Fig. 3), the Yacoraite Formation has provided two U-Pb zircon ages using the LA-MC-ICP-MS method, which are 71.9 Ma for the

lower part and 68.4 Ma for the middle-upper part (Marquillas *et al.* 2011) (Fig. 1).

Stratigraphy and environments of the Yacoraite Formation

The Yacoraite Formation is composed mainly of grey carbonates with varied depositional textures that are largely dolomitic; in some of the proximal sections, calcareous sandstones and pelites are a major component. Exposures are generally pale orange or yellowish ochre, due to weathering of the dolomitic limestones. Stromatolite mats are characteristic and common in the deposit, predominantly in the lower part and upper third of the column; they are variable in size and shape, ranging from specimens a few centimetres high to domes measuring almost a metre. The stromatolites frequently contain ooids between the laminae; the ooids are perhaps the most plentiful allochems elements in the entire deposit, which generally indicates the presence of warm, clean, oxygenated waters, agitated by waves and currents (Illing 1954; Purdy 1963, among others). Other frequent allochems are the intraclasts, which are fragments of exposed and redeposited carbonate sediments, various bioclasts, and less frequently, pellets and grapestones.

The palaeontological record of the formation is abundant but restricted and poorly diverse (see

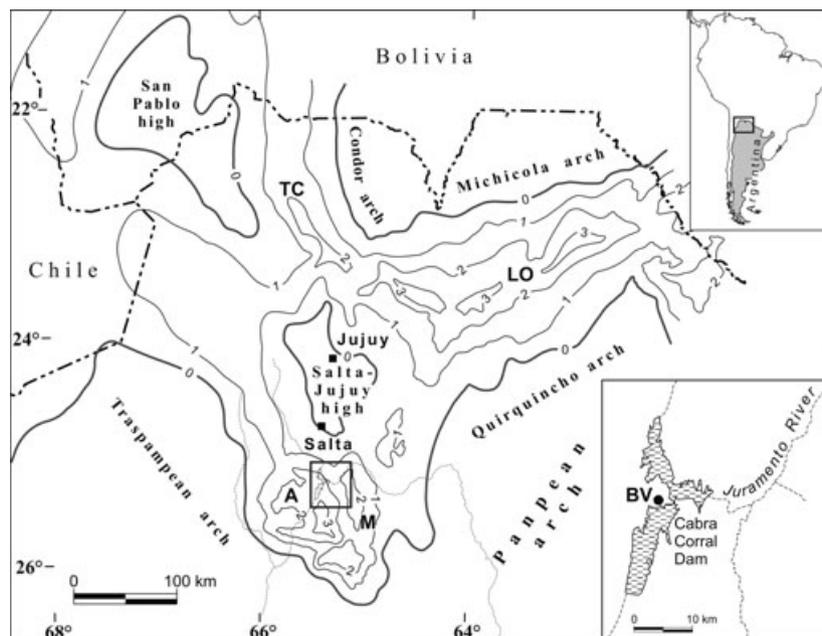


Fig. 2. Isopach map of the Yacoraite Formation. Sub-basins: TC, Tres Cruces; LO, Lomas de Olmedo; A, Alemania; M, Metán; P, Pirity. Thickness in hundreds of metres. Inset: Location of the Cabra Corral Dam and Bahía Viñuales section (BV) (after Salfity & Marquillas 1994; Marquillas *et al.* 2005, 2011).

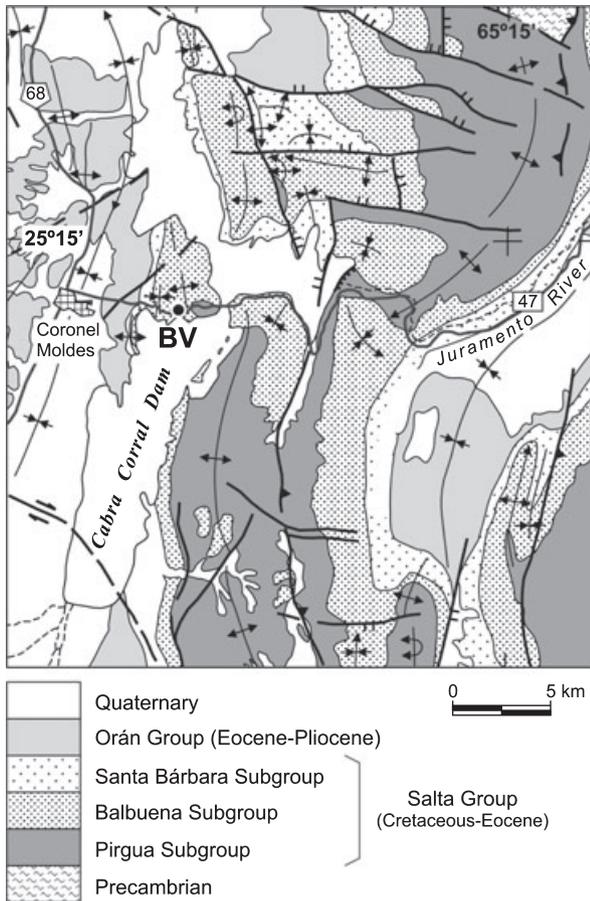


Fig. 3. Geological map of Cabra Corral region on the western side of the Metán sub-basin. BV: Bahía Viñuales section (after Marquillas *et al.* 2011).

summary in Marquillas *et al.* 2005), represented on the one hand mainly by ostracods, gastropods, bivalves, foraminifera and also fishes, and on the other hand by dinosaur and bird footprints (Alonso 1980; Alonso & Marquillas 1986) and invertebrate trace fossils (Cónsole-Gonella & Aceñolaza 2009; Cónsole-Gonella *et al.* 2009). The lack of diversity coincides with the general interpretation of an epeiric sea (Irwin 1965; Heckel 1972; Harris *et al.* 1985; Salfity & Marquillas 1994).

The Cabra Corral section

In the region of influence of the Cabra Corral dam – River Juramento, Metán sub-basin (Figs 2, 3), the Yacoraite Formation is about 200 m thick. It shows a succession of facies reflecting changes in the depositional environment and enabling the definition of four members within the formation (Fig. 4) (Marquillas 1986; Marquillas & Salfity 1989; Marquillas *et al.* 2003, 2007).

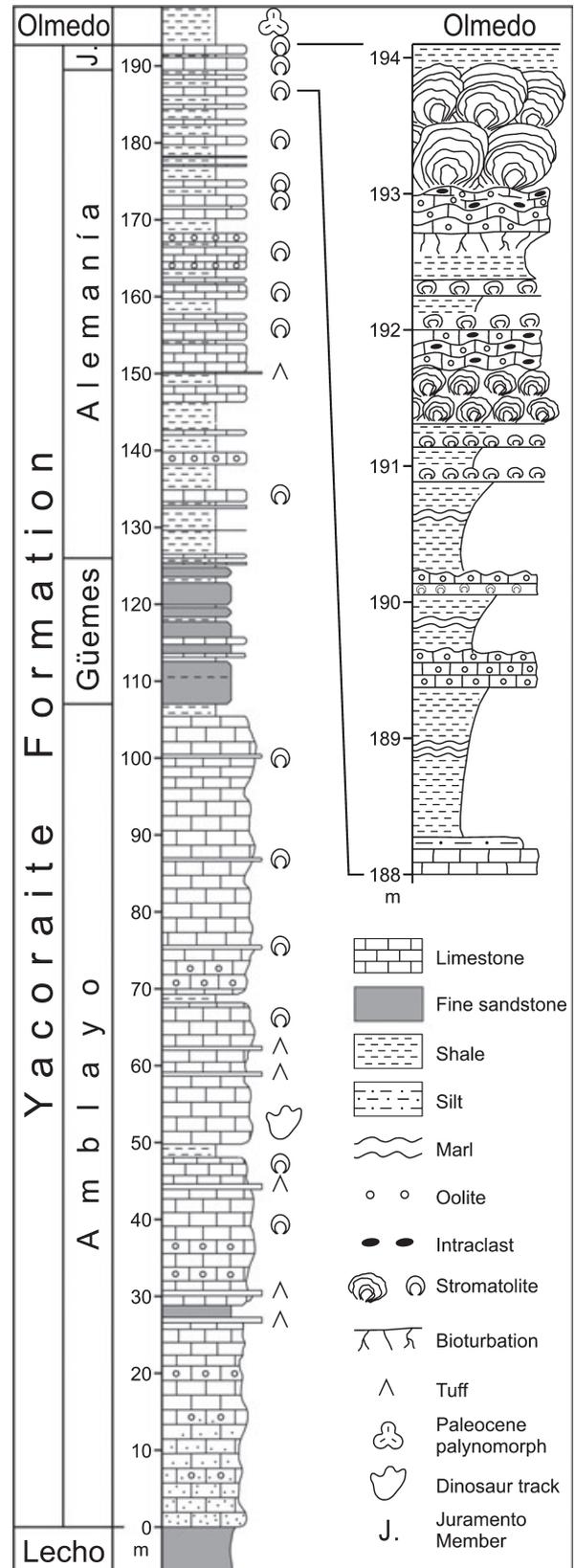


Fig. 4. Integrated stratigraphical column of the Yacoraite Formation in Cabra Corral-Río Juramento, Metán sub-basin (adapted from Marquillas *et al.* 2003, 2011).

Amblayo Member. – The basal member of the Yacoraite Formation is 100 m thick on average, calcareous-dolomitic, formed of oolitic and intraclastic grainstones, oo-intraclastic packstones, fine calcareous sandstone and fine-to-medium stromatolitic levels. It has medium stratification, frequent flaser and lenticular lamination, and hummocky cross-stratification at the top. These features suggest that the early part of the deposition of the Formation may have been dominated by intertidal activity in fair weather conditions followed by stormy weather.

Güemes Member. – This member is about 20 m thick, highly bioturbated and much of it is a distinctive reddish brown colour. It is composed of bioclastic wackestones, mudstones, siltstones and wacke. There is evidence of amalgamated strata and some levels with wave and current ripple marks, and hummocky cross-stratification. During deposition, there may have been flows of different energy and density, suggesting a situation of water mixing, storm action and perhaps some continental influence.

Alemanía Member. – Almost 70 m thick, this represents a large part of the upper section of the formation. It comprises fine heterolithic successions of green and black shale, micritic, intraclastic and oolitic limestone, sandy marls and siltstone, with strata of oolitic grainstones and/or stromatolitic boundstones at the top of each succession. Forty to 50 cm of black, grey or discoloured shales with vertical and oblique bioturbation mark the end of this member. The member has parallel, lenticular and wavy lamination, and a pattern of several metre-scale shallowing-upward sequences. Deposition may have been controlled by alternating tractive and settling processes in an environment regulated mainly by fair weather waves. The shales at the top indicate anoxic conditions, perhaps corresponding to a flood maximum, which may have preceded a shallowing event. The cyclicity of the deposit may be the response to climate variations.

Juramento Member. – Recognized at the top of the succession (Fig. 4), this member has an extensive lateral distribution but a variable thickness of only a few metres. It is composed mainly of domal stromatolitic boundstones (Fig. 5A), which contain the bioclaustrations reported herein (Fig. 6). Beneath the stromatolites (Fig. 5B) are millimetric laminae of black shale, grey shale, bioturbated shale and marls, oolitic limestone and bioclastic limestone with small phosphatized bones *incertae sedis*; there are sporadic traces of gypsum and anhydrite and levels with

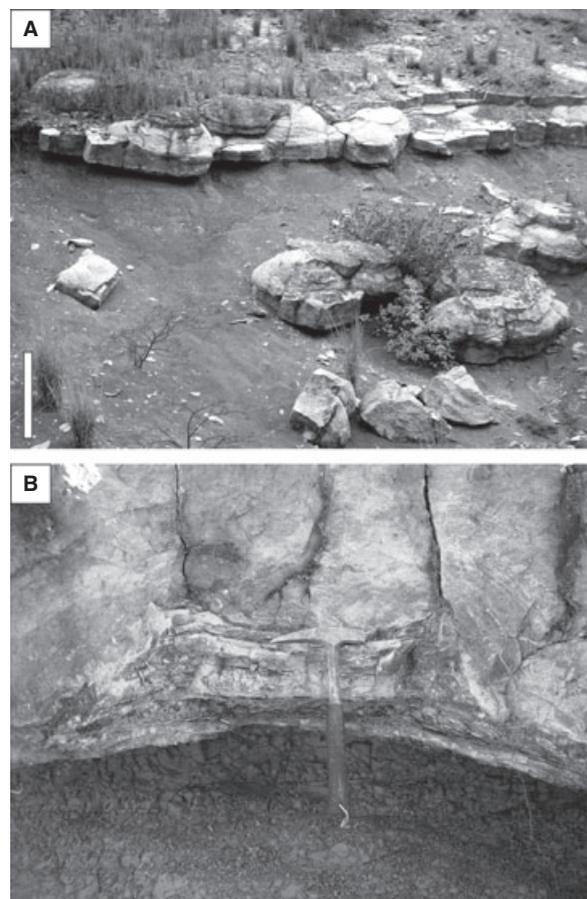


Fig. 5. Upper part of the Yacoraite Formation at Cabra Corral Dam. A, stromatolites on the top. Scale bar 1 m. B, contact between stromatolites and bioturbated shale and marls.

desiccation cracks. The ooids and small phosphatized bones are also plentiful between the laminae of the stromatolites with bioclaustration. The Juramento member represents the end of the Yacoraite Formation deposition and a situation of shallowing up from the preceding member. Within it are features indicating a high intertidal environment and locally extended tidal flat. Of particular note is the presence of a firm substrate with the development of the domal stromatolite mat, and a final episode of sedimentation that covered the stromatolites with a thin clay layer (Fig. 7A, B).

Stromatolites with bioclaustrations

Palaeogeographical, chronostratigraphical and palaeoenvironmental issues

Stromatolites with bioclaustrations have been recognized in the Bahía Viñuales section at the Cabra Corral dam, an area whose palaeogeography

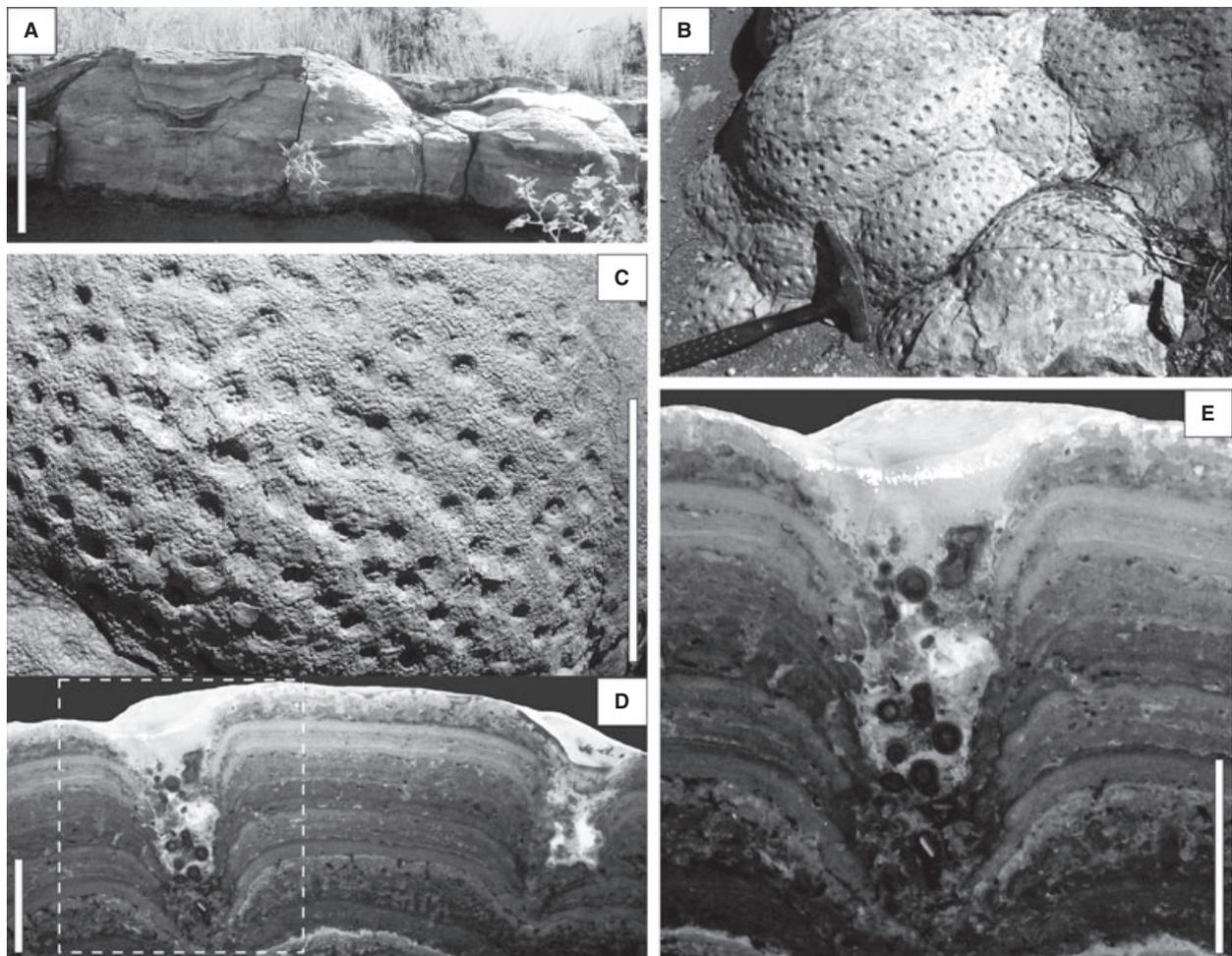


Fig. 6. Yacoraite Formation stromatolites and bioclaustrations. A, outcrop view of stromatolites at Cabra Corral section. Scale bar 1 m. B, bedding-plane view of stromatolite domes riddled with bioclaustration cavities. C, surface view of stromatolite with bioclaustrations. The cavities are filled with clayey shale and ooids. Scale bar 10 cm. D, view of two structures in cross-section. No. CC-E-37 (9). Scale bar 1 cm. E, close up of bioclaustration structure shown within dashed box in D. Note the deflection and convergence of stromatolite laminae surrounding the structure. The cavity is filled with ooids and crystalline calcite. In the upper section, the fill is finely laminated clayey shale. Scale bar 1 cm.

corresponds to the Metán sub-basin (Figs 2, 3). The Yacoraite Formation is 194 m thick here, and the stromatolites with bioclaustrations are located in a single stratigraphical position: the Juramento Member (Fig. 4). Given the high temporal resolution of the record, this stromatolitic level could represent an individual event, as no other example within the basin is known to date.

Towards the end of deposition of the Juramento Member, the environment may have become more stressful, evidence of which may be the absence or scarce presence of micro-fossils (only few ostracods), and the presence, albeit occasional, of sulphates in the form of gypsum and anhydrite, which together with the micrite and micro-spar form part of the level of the stromatolites with bioclaustrations. Variations in salinity may have occurred due both to concentration by evaporation and the arrival of

seasonal or occasional currents. On the other hand, analyses of stable isotopes show a limited variation of $\delta^{13}\text{C}$ for the carbonates of the Juramento Member and a great variation of $\delta^{18}\text{O}$ (Marquillas *et al.* 2007), which could be consistent with the assumed changes.

Morphology, composition and general features

Figure 4 is an enlarged sketch of the uppermost part of the Yacoraite Formation, where the stromatolites described herein are found. It is exposed in the surroundings of Cabra Corral dam and River Juramento, Salta Province, Argentina (Figs 3, 4). The top of this complex deposit, made up of part of the Almania Member and crowned by the Juramento Member (Fig. 4), has the domal stromatolites with bioclaustrations (Fig. 6).

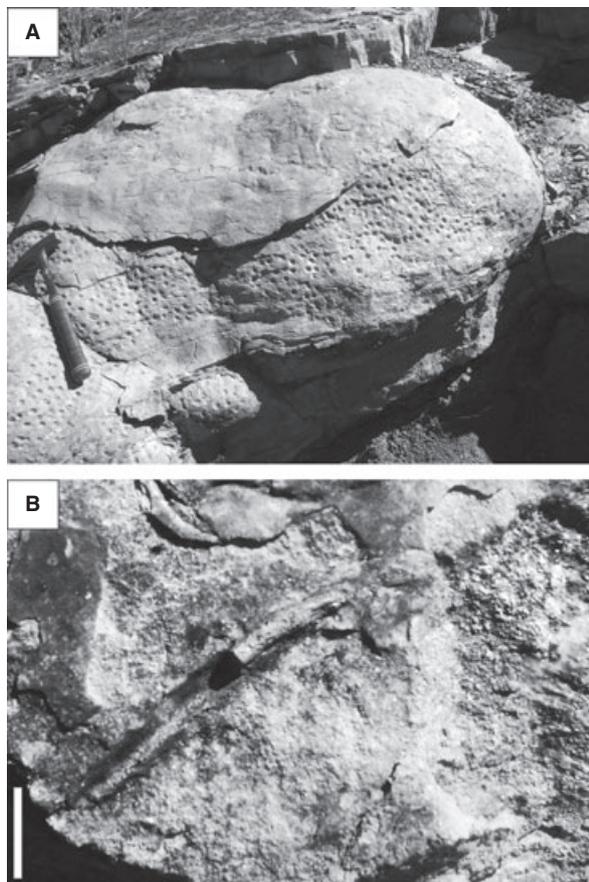


Fig. 7. Stromatolite domes at Cabra Corral section. A, bioturbated laminated shale covers the stromatolites including the cavities. B, *Planolites* isp. Scale bar 1 cm.

The stromatolites are well-defined hemispheroid domes with heights ranging from 90 to 100 cm (Fig. 6A). They are calcitic-dolomitic-ankeritic in a general proportion of 90% calcite and 10% dolomite-ankerite. Under the microscope, they are seen to be millimetrically laminate. The thickness of the laminae is variable, ranging from 0.5 to 5 mm, and they are made of dense micrite, clotted micrite, micro-spar and spar with some gypsum and anhydrite. Various elements are trapped within the stromatolite mat such as plentiful ooids, intraclasts and small fragments of phosphatized bones including whole vertebrae of millimetric dimensions; there is also a small fraction of fine silt sand of quartzofeldspathic composition with very little muscovite. The ooids are spherical, concentric and radial concentric, and averaging 1 mm in diameter; there are also composite ooids measuring 2 mm, cerebroid-shaped ooids and broken ooids. The intraclasts are micritic, 2–9 mm long, and some of them are coated. All this suggests repeated high-energy processes with sporadic sub-aerial exposures and immediate redeposition of broken material, consistent with an intertidal or high intertidal setting

(Tucker & Wright 1990). Fenestral pores or birds-eyes are frequent, filled with spar, anhydrite or fine detrital material, although some remain empty, resulting in more porous laminae. Birdseyes are characteristic of tidal flats (Shinn 1968).

Results

Repository

The material analysed in this study is deposited at the National University of Salta, Salta, Argentina: School of Natural Sciences – Department of Stratigraphy and Historical Geology – No. CC-E-37.

Description of bioclaustrations

Surface features. – Viewed from the surface, the cavities are circular to slightly oval and measure 7 mm to 12 mm in diameter (Fig. 6C), arranged homogeneously on the surface of the stromatolites, following a pattern with an average spacing of 15 mm (Fig. 6C). The density of structures per dm² ranges from 18 to 22 (Fig. 6C).

Section morphology. – In vertical section, the structures are aligned parallel to the growth axis of the domes. Their shape is regular and they are elongate within the stromatolites, which means that length is always greater than diameter, producing an elongate, predominantly conical morphology, sometimes truncate-conical (Fig. 6D, E). The maximum diameter of the structures ranges from 9 to 12 mm and decreases gradually with depth. The maximum length observed is 85 mm. The cavities do not reach the base of the stromatolites in any of the cases analysed, but are restricted to the upper section. There is no lateral connection between them, nor are there internal compartments, which is very important in the diagnosis of these trace fossils. It is worth noting that in most of the samples studied the bioclaustration structures themselves begin at a micritic lamina or very near one; the micrite is homogeneous with diffuse edges and matte yellowish brown, which distinguishes it from adjacent laminae.

The cavity walls are not lined or ornamented. Adjacent to the cavities, the stromatolitic laminae are deflected downward, which is a diagnostic element in bioclaustration (Fig. 6D, E). The angle of deflection is always acute and varies with regard to the central axis of the cavities.

Fill and taphonomic features. – In the upper section of the stromatolite, the fill is finely laminated clayey

shale up to 130 mm thick (Fig. 7A). This shale covers the stromatolites including the cavities (Fig. 6D, E); at the surface, it is bioturbated and exhibits *Planolites* isp. (Fig. 7B). The cavities are mainly filled with ooids (Fig. 6E), but there is also crystalline calcite and some cavities remain empty. The fact that all the clayey sediment settled after the oolitic filling enabled it to 'seal' the cavities, protecting the structures to a large extent from weathering and erosion; this may be the reason why significantly altered cavities have not been observed. It is deduced that the settling process must have occurred shortly after the cavities were abandoned by the endobionts that caused them.

Discussion

A general theoretical criticism of considering bio-claustration structures as trace fossils was put forward by Bertling *et al.* (2006), who argue that if the reaction of a host to 'disturbance' by an object or organism results in an embedded structure, any alteration in the growth form of unknown origin should be considered a trace fossil. Another argument against it is the unclear delimitation between processes having similar characteristics, such as bio-claustration and bioimmuration (see details in Bertling *et al.* 2006). A bioimmuration structure (*sensu* Taylor 1990) is the result of an organism that was – passively – overgrown by a skeleton-producing organism (see review in Tapanila & Ekdale 2007). Whereas bioimmurations are not endolithic domiciles and represent external moulds, bioclaustrations are dwelling structures, produced by the growth-interfering behaviour of a symbiont that lives within the growing skeleton of the host (Tapanila & Ekdale 2007; Tapanila 2008). The resultant morphology of bioclaustrations provides direct trace-fossil evidence of symbiosis, not observed in bioimmuration structures (Tapanila & Ekdale 2007; Tapanila 2008). Although we understand that many of the points observed by Bertling *et al.* (2006) are logical, we believe they are arguable and their discussion is not within the scope of this paper. Moreover, many of the points have already been extensively discussed by Tapanila and Ekdale (2007) and Tapanila (2008), particularly issues of ethology and ichnotaxonomy. Some discussion of the possibility that these structures may have been generated by processes not involving the activity of metazoans is appropriate. Cavities of inorganic origin in stromatolites and carbonates of the Upper Proterozoic have been extensively reviewed. Cloud *et al.* (1974) studied

stromatolites with tubes from the Late Proterozoic of the Noonday Dolomite in the region of Death Valley (California). Although in a first paper, Cloud (1968) considered the possibility that these tubes may have been produced by the activity of vermiform metazoans, subsequent analysis dismissed this possibility, suggesting instead that they may have been produced by fluids escaping upwards (Cloud *et al.* 1974). Corsetti & Grotzinger (2005) took up the study of Noonday Dolomite again, performing a complete background review of post-glacial Proterozoic limestones and stromatolites with tubes, providing new evidence and discussing several hypotheses for the formation of these peculiar cavities. They deduced that the origin is mixed, resulting from interaction between microbialite growth and contemporary sedimentation. They dismissed the possibility of an origin due to the escape of gases or fluids, mainly on the grounds of the absence of zones of liquefaction, and structures like sedimentary volcanoes. Moreover, the presence of unbroken bridging laminae precludes there having been vertical migration of fluids. Corsetti and Grotzinger (2005) outlined a series of analogues to these Neoproterozoic tube structures, including the Holocene stromatolites studied by Lamond and Tapanila (2003) at Lake Turkana. They rejected the claim of an origin due to metazoan activity because of the lack of evidence of the presence of metazoans, and they argued that the existence of bridging laminae and compartmentalized cavities would be incompatible with the process of bioclaustration or embedding. These characteristics indicative of inorganic origin were not observed in the record presented herein. Moreover, even though palaeobiological processes in stromatolites have only recently been tackled from an ichnological perspective, it should be noted that the scientific literature contains many references to bioturbation in general sense, and trace fossils of various types (borings, burrows and intergrowth structures) in stromatolites and microbial mats, and even of live metazoans occupying present-day stromatolites (Table 1).

In this regard, the most complete review was provided by Gerdes (2003), who presented many present-day and fossil cases, convincingly proving that both vertebrate and invertebrate macroorganisms can interact with biofilms for different reasons. These reasons may mainly relate to food, rest and shelter, and the mechanisms employed may be perforation, bioconstruction and/or excavation, depending on the type of host organism and biofilm type and consolidation. Metazoans can grow and develop together with the stromatolitic laminae. The

Table 1. Animal–stromatolite interactions and environments through time.

Age	Region	Type of stromatolite	Biogenic structure	Producer or inferred organism	Setting	Authors
Present	Shark Bay, Australia	Domal columnar	Borings and burrows	Perforating bivalves, serpulids, crustaceans and gastropods (living)	Restricted bay	Jahnert & Collins (2011)
Present	Bahamas	Domal columnar	Borings	Perforating bivalves (living)	Lagoon	Andres & Reid (2006)
Present	Bahamas	Domal columnar	Borings and burrows	Spionids polychaete worms, calcareous tube worms, harpacticoid copepods, polyps of hydroids, gastropods, bivalve pholads, encrusting bryozoans and sponges (living)	Lagoon	Riding <i>et al.</i> (1991)
Present	Persian Gulf	Planar, digitate	Bioclaustrations?	Polychaete worms (living)	Tidal flat	Shinn (1972)
Early Pleistocene	Northern Kenia	Domal	<i>Trypanites</i> , <i>Sertaterebrites</i>	Sipunculids?, Polychaeta?, Cirriped? Or perforating bivalve?	Indeterminate non-marine	Ekdale <i>et al.</i> (1989)
Cretaceous (Maastrichtian)	Northwestern Argentina	Domal	<i>Gastrochaenolites</i>	Perforating bivalve	Shallow marine	Cónsole-Gonella <i>et al.</i> (2009)
Cretaceous (Aptian-Cenomanian)	Central Switzerland	Columnar and planar	<i>Gastrochaenolites</i>	Perforating bivalve?	Shallow marine	Föllmi <i>et al.</i> (2011)
Cretaceous (Albian)	Southeast Nigeria	Irregular shape, undulate	<i>Gastrochaenolites</i>	Perforating bivalve (preserved as body fossil)	Lagoon or protected bay	Akpan (1991)
Middle-Upper Jurassic	Southern Alps, Italy	Planar, columnar and domal	<i>Thalassinoides</i>	Crustaceans?	Shallow marine	Masari & Westphal (2011)
Upper Triassic (Norian-Rhaetian)	Southwest Italy	Lenticular	Tubes and cavities	Polychaete worms	Shelf margin	Cirilli <i>et al.</i> (1999)
Lower Carboniferous (Mississippian)	Northwest Australia	Domal and planar	Diverse cavities and tubes	Encrusting bryozoans, encrusting foraminifers, corals and worms	Shallow marine	Shen & Webb (2005)
Devonian (Givetian)	Northern France	Columnar	<i>Trypanopora</i> and tube borings	Serpulid?	Shallow marine	Mistiaen & Poncet (1983)
Silurian (Ludlow-? Pridoli)	Southeast Alaska (USA) and north and south of the Ural Mountains (Russia)	Planar	Borings	Sponges and hydroid (preserved as body fossil)	Offshore carbonate shelf	Soja <i>et al.</i> (2003)
Late Ordovician	Southwest USA	Domal	Burrows	Unknown	Shallow marine	Druschke <i>et al.</i> (2009)
Lower Cambrian	Southwest USA	Wrinkle structure	Brachiopod cast and <i>Volborthella</i>	Brachiopods, probably linguliforms and polychaetes?	Shallow marine	Bailey <i>et al.</i> (2006)

resulting fabrics in these facies therefore tend to be of mixed origin, caused by the development of the biofilm and the disturbance caused by the hosted metazoan.

Tracemaker

The foregoing section has made clear that several groups of metazoans may interact with a biofilm at different stages of its consolidation and interrupt its

growth. The endobiont and the mat may also coexist and generate a fabric of mixed origin, which is the bioclaustration case presented herein.

Palmer and Wilson (1988) pointed out that by definition, the ‘infester’ (settler symbiont *sensu* Tapanila & Ekdale 2007) must have a soft body and that the relationship between infester and host may be parasitic, possibly mutualistic or simply symbiotic *s.l.* There are also examples of bioclaustration structures in which the settlers have a shell, for example,

the bivalves that colonize corals, even though they are not the most frequent cases. Unfortunately, as mentioned above, the subject has only been dealt with rather recently from an ichnological standpoint. This is why, although there are many present examples of bioclastration or embedment structures in which the hosts have a skeleton, for example corals (Tapanila & Ekdale 2007), there are hardly any analogous neoichnological cases where the host is a stromatolite or a biofilm. In this regard, Shinn (1972) documented an interesting case of interaction between microbial mats and polychaete worms on a present-day tidal flat in the Persian Gulf where mounds of laminar microbial mats develop with noticeable biogenic worm-hosting structures, which have been formed by intergrowth between the two. The structures were produced by interaction between a polychaete worm, *c.f. Marphysa sanguinea* and the growth of the biofilm lamination, producing a structure homologous to the embedment structures shown by Ekdale *et al.* (1984). The excavating worm *Marphysa sanguinea*, of the family Eunicidae, is a carnivore or omnivore (Wijnhoven & Dekker 2010) distributed at tropical latitudes around the world (Ruppert & Fox 1988) and can reach a length of 40 cm. It lives in a variety of warm benthonic environments in muddy or sandy intertidal sediments in which it creates burrows by using its muscular body; it also makes use of cavities created previously by other burrowers (Ruppert & Fox 1988; Prevedelli *et al.* 2007). It has a life cycle of about 90 days, and it is speculated that copulation takes place inside the burrows, where eggs remain until they reach the free-swimming larval stage. At this time, larvae are released from the burrows into the water column (Prevedelli *et al.* 2007). Thus, breeding of an organism can be another reason for the occupation of stromatolitic mats, in addition to shelter and food. Given the characteristics of the bioclastrations described herein for the Yacoraite Formation, and their analogy to the cases presented by Lamond and Tapanila (2003), it is probable that the endosymbiont or settler was also vermiform, probably a polychaete worm, and the group that has most often been documented as a settler symbiont in bioclastrations. It is recognized that further knowledge is needed of neoichnological cases to delimit the variety of possible producers. The morphology of a vermiform endobiont is compatible with the type of ichnofabric presented herein, which reflects the growth of an organism with a sub-cylindrical body in a central cavity, whose growth and movement are in a vertical ascending direction (see Construction, above). These features make the structures in the Yacoraite Formation very similar to the cases in

Wyoming & Kenya described by Lamond and Tapanila (2003).

Construction

The biogenic structure resulting from the bioclastration process was originally interpreted and sketched in the description of embedment structures by Ekdale *et al.* (1984), then by Lamond and Tapanila (2003) and finally reinterpreted by Tapanila and Ekdale (2007). The only contradiction to these interpretations is that of Bromley (1970) who considered in his earlier work on embedment structures that the organism's growth laminae are deflected upwards, whereas Lamond and Tapanila (2003) and Tapanila and Ekdale (2007) considered that they are deflected downwards. We believe that the difference is not substantial and that both cases reflect the same palaeobiological process; therefore, like Tapanila and Ekdale (2007), we believe that embedment structures and bioclastration structures are homologous. The basic construction alternatives are shown in Figure 8, based on the original interpretations of Bromley (1970) and Tapanila and Ekdale (2007). Based on the analysis of the material that we studied, we believe that the shape of the structures presented herein is compatible with type A in Figure 8. The resulting ichnofabric in our case is of a distinctive type because as the stromatolitic substrate grew, the body size of the infester also increased, accompanied by changes in stromatolite consolidation.

Conclusions

Bioclastration structures are recognized in domal stromatolites of the Cretaceous-Palaeogene in north-west Argentina (Yacoraite Formation). This is the oldest reported record of bioclastrations in stromatolites reported to date. The interpretation of the stromatolitic facies and their stratigraphical/sedimentological context suggests a shallow, stressed marine environment with salinity above normal, represented by an intertidal setting with an extensive tidal flat. From the standpoint of chronostratigraphy, the time at which the endobionts colonized the stromatolitic mat coincides with the end of the deposition of the Yacoraite Formation.

We believe that stromatolites are a type of substrate that should be further investigated by ichnologists. Deeper neoichnological studies of the relationship between biofilms and metazoans would probably also allow further specification of the range of possible bioclastration producers in

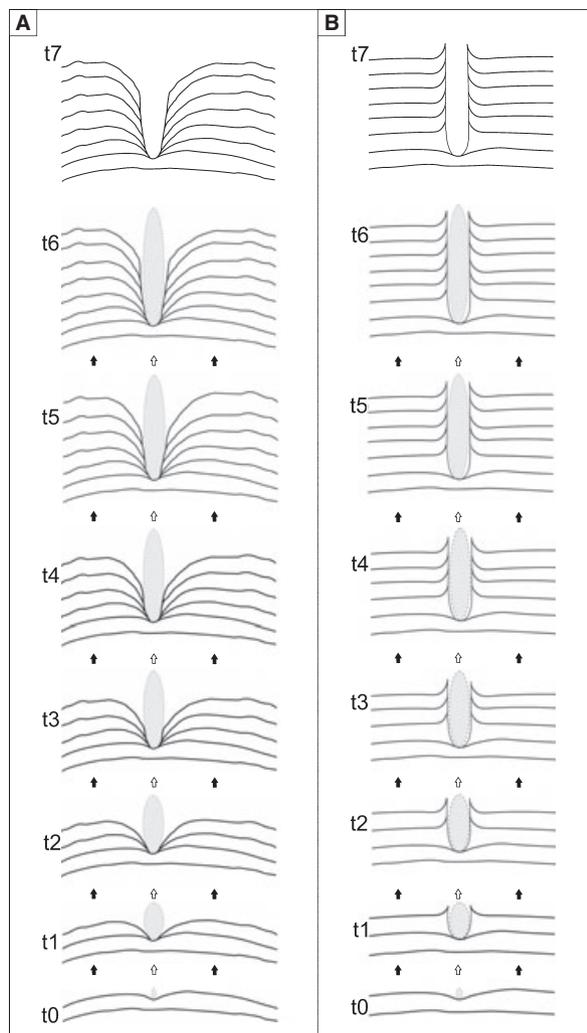


Fig. 8. Schematic illustration of bioclaustration construction alternatives (t represents time). The structures are constructed successively from the bottom to the top of the figure as result of interaction of endobionts and stromatolitic laminae through time. A, the laminae are deflected downward. This is the case reported herein (interpretation modified from Lamond & Tapanila 2003; Tapanila & Ekdale 2007). B, the laminae are deflected upward (interpretation modified from Ekdale *et al.* 1984, fig. 10-2 e). In t7, the endobionts left the cavities.

stromatolitic substrates. We also believe that the fact that there are few records of bioclaustrations in stromatolites is not due to the rarity of the palaeobiological process but rather to the fact that it has only recently been included in the field of interest of ichnology. In this regard, we support Lamond and Tapanila (2003) in expecting future reports of bioclaustrations in stromatolites, because they may be much more common biogenetic structures than have been documented to date.

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