

Intergrowth of chaetetids, *Girvanella* and *Donezella* in Pennsylvanian mounds in the Valdeteja Formation, NW Spain

Intercrecimiento entre quetétidos, *Girvanella* y *Donezella* en montículos del Pensilvánico en la Formación Valdeteja, Noroeste de España

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Abstract: Multiple types of mounds have been described in the Pennsylvanian of the Cantabrian Mountains. In many of them the main component is *Donezella* Maslov, 1929. This organism was first described as an alga, but its occurrence in dysphotic and aphotic facies led to its inclusion in the order Algospongia, which includes organisms of doubtful affinity. Most of the mounds with *Donezella* from the Cantabrian Mountains previously described in the San Emiliano, Valdeteja and Picos de Europa formations have been identified in ramp or slope facies in dysphotic or aphotic conditions, confirming that it was not an alga. However, mounds 1 to 2 metres thick and 3 to 5 metres in diameter have been located in outcrops near the town of Truébano. The main component is *Donezella*, but unlike other occurrences, these mounds also contain chaetetids and *Girvanella* as important components. The latter is considered to be a cyanobacteria and clearly indicative of shallow waters in the photic zone. Chaetetids are typical reef builders and frequent on Devonian and Carboniferous shallow platforms. In the studied mounds, chaetetids occur in association with *Donezella*, *Girvanella*, *Masloviporidium*, *Claracrusta* and other components, proving that these mounds developed in the photic zone, unlike those when the main component is *Donezella*.

Resumen: En el Pensilvánico de la Cordillera Cantábrica se han descrito múltiples tipos de montículos, de entre los cuales destacan aquellos cuyo componente principal es *Donezella* Maslov, 1929. Este organismo fue inicialmente descrito como un alga, pero su aparición en facies disfóticas y afóticas llevó a su inclusión en el orden Algospongia, que engloba organismos de afinidad dudosa. La mayor parte de los montículos con *Donezella* descritos en la Cordillera Cantábrica en las formaciones San Emiliano, Valdeteja y Picos de Europa se han identificado en facies de rampa o talud en condiciones disfóticas o afóticas, confirmando que no era un alga. Sin embargo, en afloramientos próximos a la localidad de Truébano se han localizado montículos de 1 a 2 metros de espesor y 3 a 5 metros de diámetro cuyo componente principal es *Donezella*, pero que contrariamente a lo habitual contienen como componentes importantes quetétidos y *Girvanella*. Esta última está considerada como una cianobacteria y claramente indicadora de aguas someras en la zona fótica. Por su parte, los quetétidos son típicos bioconstructores de arrecifes y frecuentes en plataformas someras del Devónico y especialmente del Carbonífero. En estos montículos están en asociación con la propia *Donezella*, y con *Girvanella*, *Masloviporidium*, *Claracrusta* y otros componentes. La presencia de organismos fotosintéticos prueba que dichos montículos, a diferencia de lo habitual cuando el componente principal es *Donezella*, se desarrollaron en la zona fótica.

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INTRODUCTION

Mounds composed mainly of algae or algospongia are common in the Pennsylvanian of the Cantabrian Mountains (Bowman, 1979; Eichmüller, 1985; Samankassou, 2001, 2003; Della Porta *et al.*, 2002; Chesnel *et al.*, 2016, 2017; Rogers, 2018; Rodríguez-Castro *et al.*, 2020). The algospongia *Donezella* is the main component in several types of mounds, combined with siliceous sponges (Choh & Kirkland, 2000,

2006), *Petschoria*, *Komia* and *Archaeolithophyllum* (Rácz, 1964; Eichmüller, 1985), *Komia*, *Ungdarella* and phylloid algae (Bowman, 1979), *Tubiphytes* (Samankassou, 2001; Cook *et al.*, 2007), *Rothpletzella* and *Claracrusta* (Rogers, 2018), and chaetetids and *Girvanella* (Rodríguez-Castro *et al.*, 2020). Most of these mounds have been recorded in the Bashkirian or Moscovian of the Cantabrian Mountains,

representing different ecological or climatic conditions, including deep-water facies. Some of the components associated to *Donezella* are algae, which require light and therefore demonstrate that these mounds were built in shallow waters within the photic zone. However, some of the mentioned components are algaespongioids (*Clarachrasta*, *Komia*, *Ungdarella*) that could grow in deeper waters. Accordingly, most mounds described in the Pennsylvanian from the Cantabrian Mountains (Valdeteja, San Emiliano and Picos de Europa Formations) have been recorded in ramps or slopes, in dysphotic or aphotic conditions (Della Porta *et al.*, 2002).

Rodríguez-Castro *et al.* (2020) described a different type of mound in the Valdeteja Formation at the Rosario Mine; the mounds were also composed mainly of *Donezella* but associated with chaetetids and *Girvanella*. The presence of *Girvanella*, which is generally interpreted as a photosynthetic organism, indicates that these mounds were built in the photic zone (Riding, 1975; Zhang *et al.*, 2024). In addition, chaetetids were typical reef-builders in the Devonian and Carboniferous, and they also developed predominantly in shallow waters (Kershaw & West, 1991). These organisms lived intimately related in the mounds from the Rosario Mine, forming bulbous structures that appear to be chaetetids, but are actually a consortium that lived together or in ecologic successions.

The objective of this paper is elaborating on the information on the outcrops at the Rosario Mine presented by Rodríguez-Castro *et al.* (2020), with the detailed description of the ecologic relationships between the components of the mentioned mounds.

GEOLOGICAL SETTING

The Valdeteja Formation (Bashkirian) crops out in the Cantabrian Zone of the Iberian Massif, which contains a thick succession of Palaeozoic rocks that was deformed into a set of thrust sheets during the Variscan Orogeny (Bahamonde *et al.*, 2007; Alonso *et al.*, 2009). The thrust faults divide the zone into several structural units (Bastida, 2004) (Fig. 1). The studied outcrop belongs to the Sobia-Bodón Unit, in its south-western area, where the Valdeteja Formation, otherwise a completely calcareous formation, contains siliciclastic beds and coals. The outcrop is part of the abandoned Rosario Mine, which is located in the Babia Valley in the León Province (Fig. 1). The Valdeteja Formation overlies the Barcaliente Formation (mainly Serpukhovian) and underlies the San Emiliano Formation (mainly Moscovian).

METHODS

Field work included measurement of stratigraphical log (Fig. 2), analysis and description of the rock structures and textures and sampling in several parts of three different mounds. The laboratory tasks included examination of thin sections and hand specimens, including several bulbous chaetetids. Five hand specimens and one thin section have been added to the samples described and studied in Rodríguez-Castro *et al.* (2020). The hand specimens were cut and polished, showing similar structures to the thin section, which has been studied with optical binocular microscope Olympus SZ61.

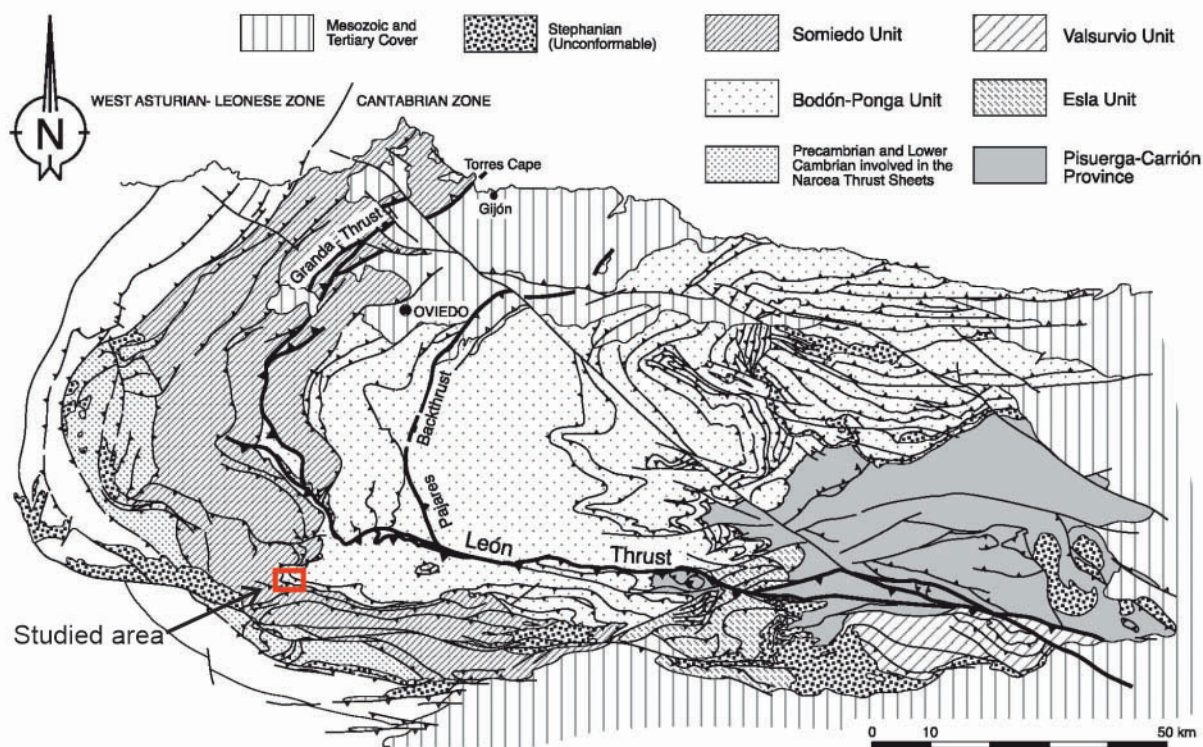


Figure 1. Location of the studied area in the structural map of the Cantabrian Mountains (after Alonso *et al.*, 2009).

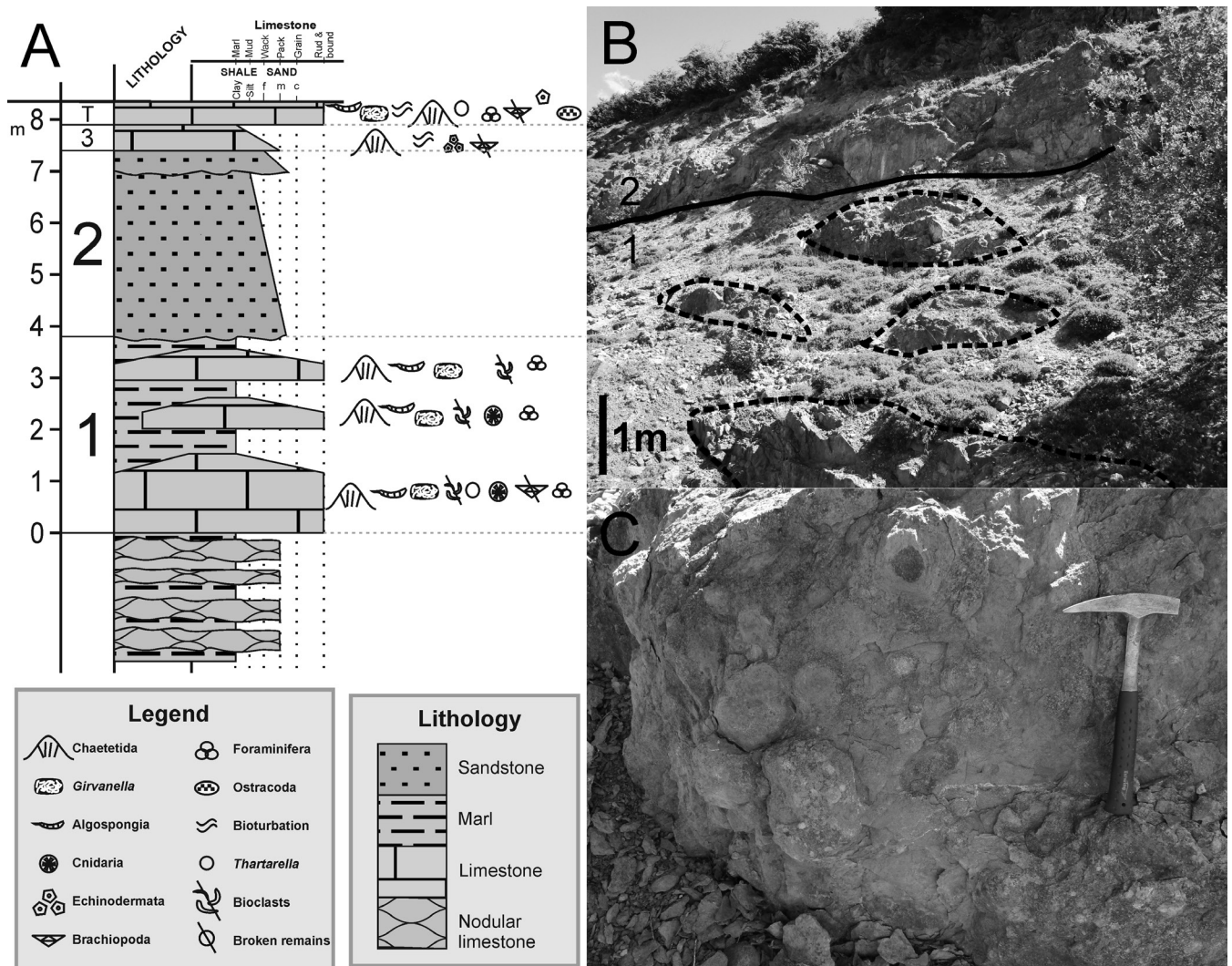


Figure 2. A, Stratigraphic log, modified from Rodríguez-Castro *et al.* (2020), from the first mounds to the top (T) of the outcrop; **B**, field picture, depicting the first unit of the stratigraphic log and its contact with the second. The dotted lines limit some of the mounds; approximate scale = 1m; **C**, detail picture of the base of unit 1 of the stratigraphic log, showing the bulbous structures described in the text.

CHAETETIDS

The most conspicuous feature of the studied mounds is the presence of bulbous structures (Figs. 2, 3) identified as chaetetids (Rodríguez-Castro *et al.*, 2020), but actually containing several components. Chaetetids are Porifera related to and probably belonging to the Demospongiae (Kershaw & West, 1991). They range from Ordovician to Miocene (Hill, 1981), and possibly to the present if we include *Acanthochaetetes*, ceratoporellids and *Merlia* (Kershaw & West, 1991). They are especially abundant in the Bashkirian and Moscovian strata from North America, the Palaeotethys (Stanton *et al.*, 2016) and the Panthalassa Ocean (Sano, 2006; Ezaki *et al.*, 2024). They possess a massive skeleton composed of small tubules oriented parallel to the growth direction. Thin laminae, called tabulae, are perpendicular to the tubules and irregularly spaced. Unlike corallites in corals, which are independent individuals, tubules are part of a single sponge skeleton (Stanton *et al.*, 2016).

There are two types of growth: laminar, composed of tubules radiating horizontally and growing later upward from the basal surface; and axial, composed of tubules that radiate from a central axis of growth (Stanton *et al.*, 2016). Chaetetids may have many different shapes: tabular, hemispherical, columnar and branching, and many variants in each category (Stearn, 1982; Stanton *et al.*, 2016). The shape and growth form are controlled by the environmental factors during their growth, and they have been used as environmental indicators (Miller & West, 1996; Stanton *et al.*, 2016).

Kershaw and West (1991) demonstrated that the laminar growth is produced by the stacking of laminar units, which may be separated by growth interruption surfaces that record depositional or winnowing events during the life of the chaetetids. The distribution of these units produces the different shapes. Miller and West (1996) described five types of growth-interruptions, pictured in Figure 4:

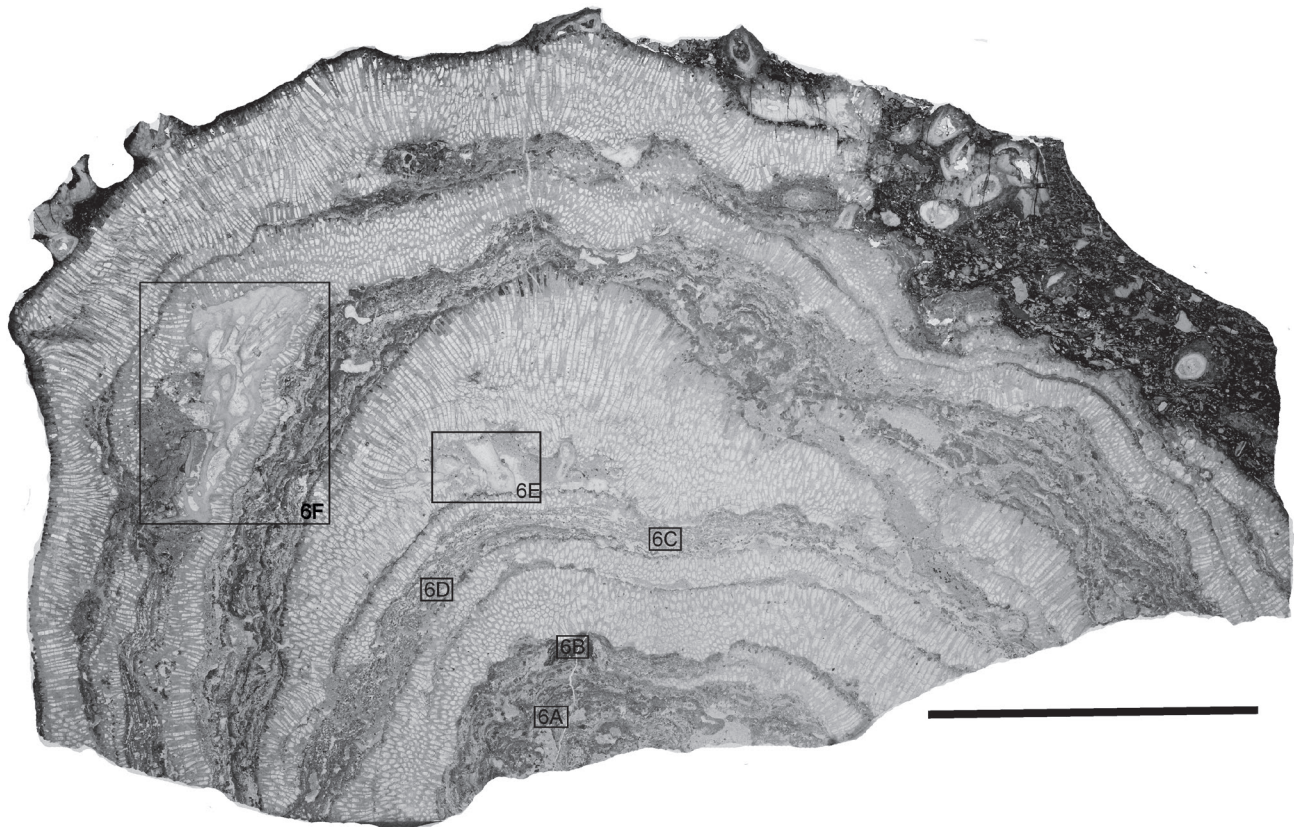


Figure 3. Example of a bulbous structure composed of chaetetids and other components. The location of the different components is shown with rectangles, each labelled with the corresponding Figure in the main text; scale bar = 1 cm.

- Type 1, the tubules show apparent continuity across the break.
- Type 2, the tubules are discontinuous across the break, and they usually radiate or diverge above the break.
- Type 3, the surfaces have either thin 'sediment' separations trapped within the skeleton or 'sediment'-filled tubules.
- Type 4, the surfaces were colonised by encrusting organisms either coincident with or preceding renewed chaetetid growth.
- Type 5, the surfaces are locally corroded with evidence of skeletal destruction.

DESCRIPTION OF THE BULBOUS STRUCTURES

Bulbous structures, from 3 to 20 cm in height and 8 to 30 cm in diameter, occur at the base of some mounds (Fig. 3). Their external appearance at first seems to be massive chaetetids, however a fresh cut shows the intergrowth of several components and the presence of all the types of growth interruption described by Miller and West (1996) (Fig. 4A–4E).

The major component of the mounds is the alga *Donezella*, which is found as accumulations of fragmented branches in some zones, and in growth position in others, typically showing dichotomous branching (Fig. 5A, 5B). However, the initial stage of the bulbous structures is composed of masses of *Girvanella*

and, less frequently, *Masloviopodium* (Fig. 6A, 6B) that encrust debris of *Donezella*. Laminar beds of chaetetids grew on the masses of *Girvanella* (Fig. 3). They extend laterally and develop hemispherical forms that show higher relief if they reach large size.

There are common interruptions in the growth of the chaetetids, and the layers between them usually reach 2 to 10 mm in thickness. The most common interruption is the type 4 (Fig. 4D), where the surfaces are colonised by diverse organisms including algae, algaespongia and invertebrates. The most common encrusters are *Girvanella* and *Claracrusta* (Fig. 6C, 6D). The tabulate coral *Multithecopora* is also common (Fig. 6E). Some solitary rugose corals, both dissepimented (*Kionophyllum*, *Semenophyllum*) and undissepimented (*Cyathaxonia*, *Rotiphyllum*), are attached on the chaetetid laminae (Fig. 6F). These encrusters were subsequently overgrown by the chaetetid's skeleton. Bushy *Donezella* grew on the bulbous chaetetids to build the main part of the mounds.

DISCUSSIONS

Ecological factors

The effects of the events preserved in the chaetetid's growth interruptions, their shape, and the different colonising organisms associated to them provide valuable information on many environmental factors

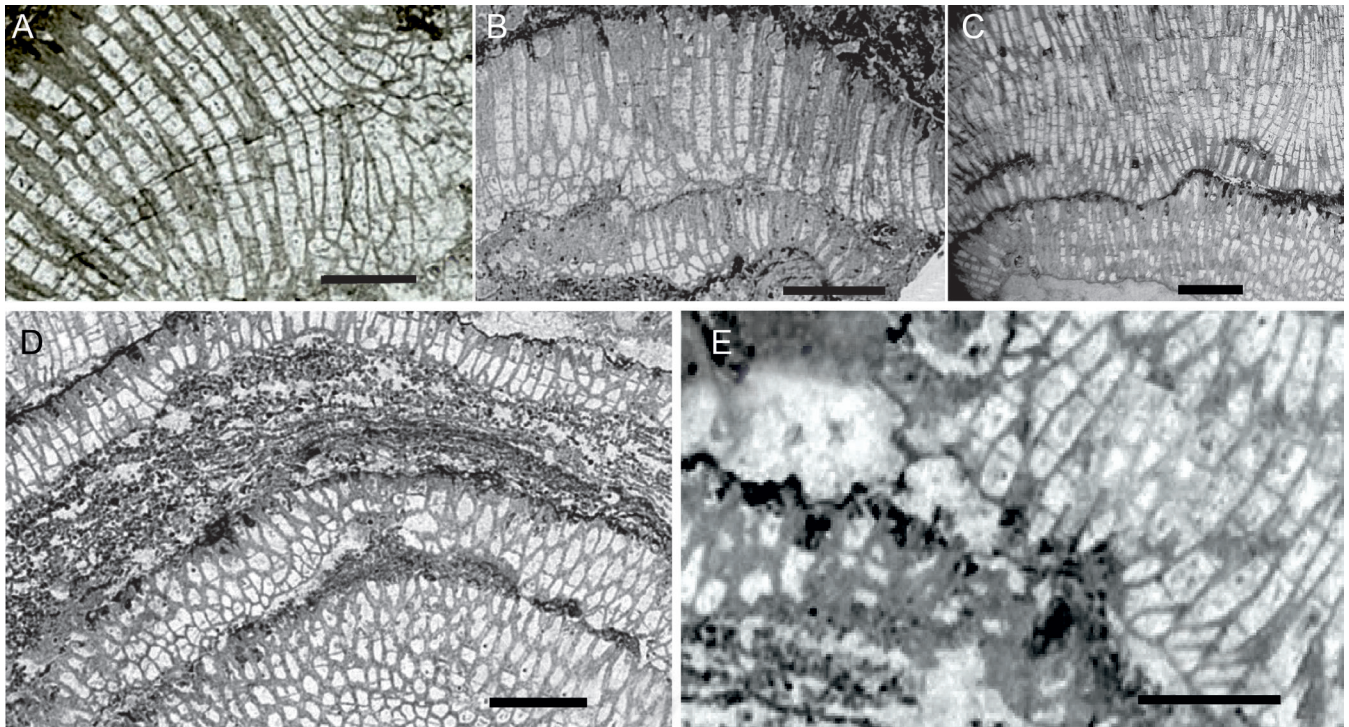


Figure 4. Types of interruptions in the growth of the chaetetids after Miller and West (1996). **A**, Type 1, the chaetetid tubules show continuity across the break; **B**, type 2, the tubules are discontinuous across the break; **C**, type 3, the surfaces have thin sediment separations and some filled tubules; **D**, type 4, the surfaces were colonised by encrusting organisms (laminose or sheet-like algae) preceding renewed chaetetid growth; **E**, type 5, the surfaces are locally corroded; scale bars = 2 mm.

and on the sedimentation rates (Kershaw & West, 1991; Miller & West, 1996).

Salinity

All the recorded chaetetids occur in typical marine facies. In many cases they are associated with crinoids, brachiopods or corals, which indicate a normal marine salinity. Such is the case in the Rosario Mine, where auloporids and rugose corals are attached to the chaetetids.

Substrate

Chaetetids are usually found in carbonate rocks, but they tolerated both muddy substrates as well as clean carbonate sands (Kershaw & West, 1991). Usually, their basal surfaces are established on surfaces with high skeletal content. In the Rosario Mine, the chaetetids mostly grew on skeletal debris composed mainly of fragments of *Donezella* and or masses of *Girvanella*. This demonstrates the need of a hard substrate for their settling and attachment.

Sedimentation

Sedimentation is one of the main influences on the morphology of the chaetetids (Kershaw, 1984; Stanton *et al.*, 2016). Low and high domical chaetetids occur in the mounds from the Rosario Mine. Low domes indicate no sedimentation, whereas high domes indicate slow and continuous sedimentation (Kershaw & West,

1991). The presence of both types and the presence on numerous surfaces of growth interruption indicate a slow sedimentation with interruptions, which provided opportunity to different types of encrusters to colonise the chaetetid's surface.

Turbulence

Water turbulence had clear interactions with the morphology of the chaetetids. Kershaw and West (1991) suggested that in many localities some chaetetids show evidence of having been moved during their growth, indicating an intermittent high turbulence and that they probably were not attached to the substrate. This is not the case in the Rosario Mine, where all observed chaetetids are not reworked. The reasons for that could be multiple; a solid attachment to the *Donezella* debris, and/or a low level of turbulence. The presence of partially eroded upper surfaces on some chaetetid laminae (type 5 interruption), although not common, indicates that at least some intervals of high turbulence could have occurred. Such a turbulence seems to be sporadic, because *Donezella* has quite fragile branches and usually lived in calm environments (Riding, 1975).

Water depth

Chaetetids clearly grew in shallow water marine environments, but the precise depth cannot be determined only based on their presence. It must be determined by the associations with other organisms. Connolly *et al.* (1989) suggested very shallow water

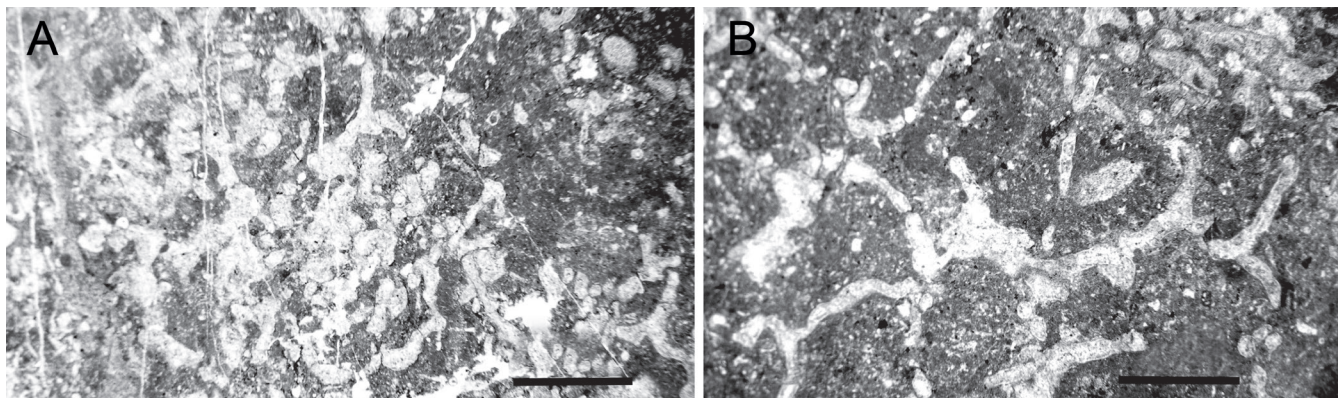


Figure 5. *Donezella* in the mounds. **A**, *Donezella* debris, usually located at the base of the mounds and being the substratum for the growth of *Girvanella* and the chaetetids; **B**, bushes of *Donezella* growing on the chaetetids; scale bars = 1 mm.

depth for most chaetetids because they found chaetetid biostromes with flat-topped skeletons similar to the rugose coral colonies found in many Mississippian outcrops that resemble lagoonal microatolls in modern reefs (Rodríguez *et al.*, 1992, 1994). This is not the case in the Rosario Mine, where all chaetetids show quicker growth in the centre, resulting in typical domal forms (Fig. 3). The association with *Girvanella* and other photosynthetic organisms indicates shallow waters (Riding, 1975), but the absence of flat-topped skeletons shows at least a depth of several decimetres. The domal morphology of the mounds where the chaetetids occur indicates a depth of several metres. The sporadic turbulence points to a zone below the base of fair-weather waves and above the base of storm waves.

Ecological relationships

These mounds, composed of *Donezella*, *Girvanella*, chaetetids, and others, show a narrow association of several organisms that lived together and/or in ecological succession. They started their growth with the development of chaetetids that grew on a hard substrate constituted of bioclastic beds composed mainly of *Donezella* debris, probably generated by the destruction of previous *Donezella* mounds by high turbulence events, such as storms. Masses of *Girvanella* proliferated on the debris and, together with the *Donezella* branches, provided a good substrate for the chaetetids.

The growth of the chaetetids was frequently interrupted. The interruption surfaces are partly covered by micrite and by masses or layers of *Girvanella*, *Clara crusta* and *Donezella* that grew directly on them (Fig. 3). Some other encrusters, such as *Masloviporidium* or *Multithecopora* are less frequent (Fig. 3). Rarely, small rugose corals, both dissepimented and undissepimented, used the chaetetids to settle, but they usually reached small sizes and had irregular shapes, hardly competing with the chaetetids.

The chaetetids repeatedly restarted their growth, producing structures ranging from 3 to 20 cm in height

and 8 to 30 cm in diameter, which, together with the *Donezella* bushes, formed mounds that reach 1 to 2 metres in thickness and 3 to 5 metres in diameter. The development of these mounds took place in the photic zone, below the fair-weather wave base and above the storm wave base. The irregular presence of high hydrodynamic energy and inputs of micritic sediment produced interruptions in the growth of the chaetetids and facilitated the colonisation by the encrusters, but the restoration of the normal environmental conditions stimulated new growth of the chaetetids.

Comparison to other Pennsylvanian mounds

These mounds are similar in some ways to others present in the Cantabrian Mountains but showing several peculiarities. The Pennsylvanian mounds from the Cantabrian Mountains were summarized by Rogers (2018); they are diverse and have been described by many authors (Rácz, 1964; Bowman, 1979; Riding, 1979; Eichmüller, 1985; Dingle *et al.*, 1993; Barba & Colmenero 1994; Hensen *et al.*, 1995; Samankassou, 2001; Della Porta *et al.*, 2003; Bahamonde *et al.*, 2007; Coronado & Rodríguez, 2009; Chesnel *et al.*, 2016; Rogers, 2018). Some of the mounds show main components other than *Donezella* and have very different origin. However, the most frequent dominant component is that algaespongia. The mounds described by Kenter *et al.* (2002) in northern Cantabrian Mountains and by Samankassou in the Cármenes area from southern Cantabrian Mountains show larger sizes (6–12 m thick and 10 to 30 m in diameter) and are also composed of worm tubes (*Thartharella*) and calcisponges. The absence of photosynthetic organisms and their occurrence in slope facies (Kenter *et al.*, 2002; Della Porta *et al.*, 2002) indicates probably deeper facies, below the storm wave base. On the contrary, the mound complexes described by Samankassou *et al.* (2013) in south-eastern Cantabrian Mountains contain also clotted microbial peloids and phylloid algae and grew in palaeohighs into the photic zone. The mound complexes developed

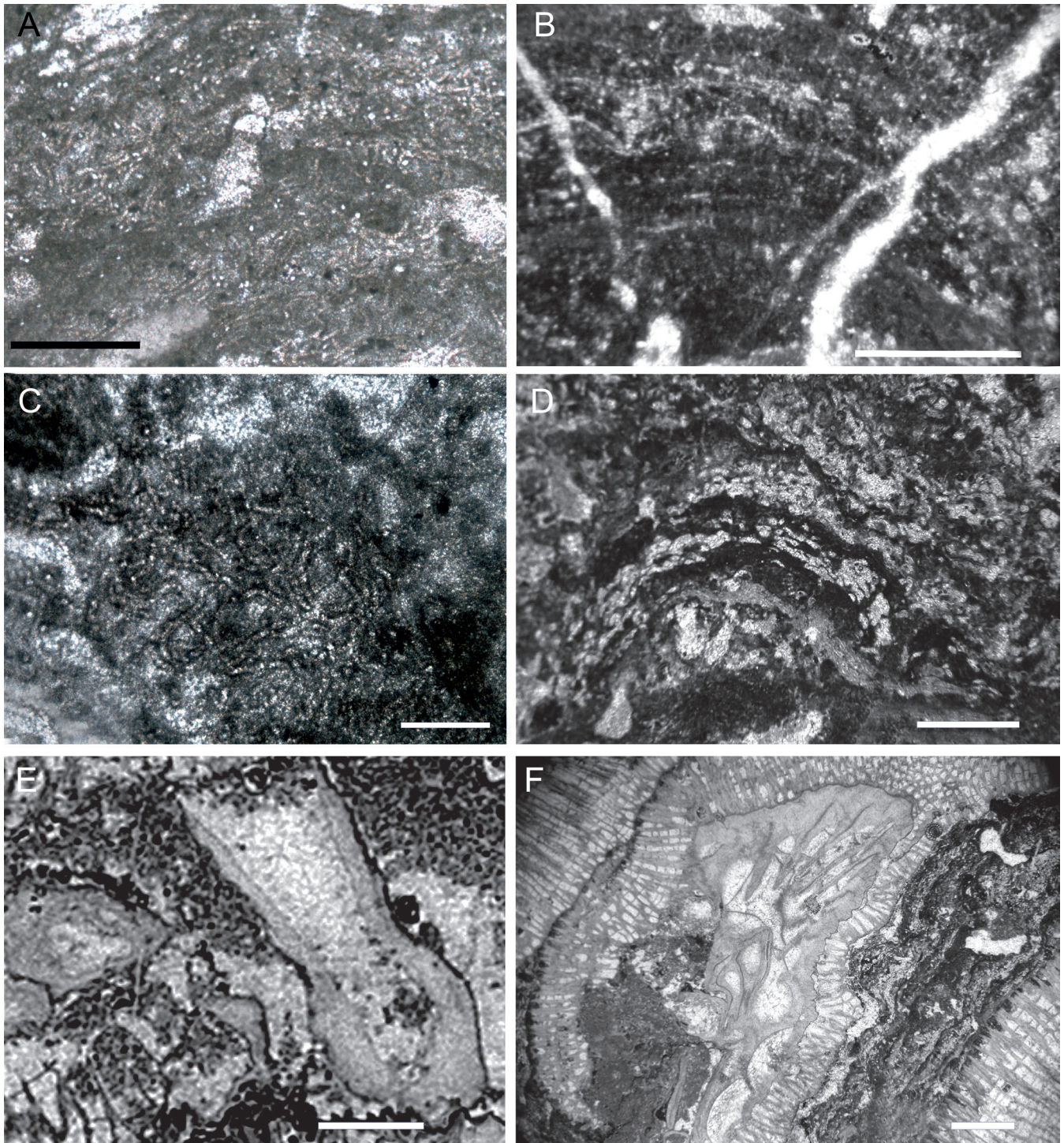


Figure 6. Different components of the bulbous structures that are mainly composed of chaetetids. **A**, *Girvanella* at the basis of the chaetetids; **B**, *Masloviporidium*; **C**, *Girvanella* growing on the chaetetids; **D**, *Claracrusta*; **E**, *Multithecopora*; **F**, Young specimen of *Kionophyllum* encrusted by chaetetids; scale bars = 1 mm (B, D, E), 2 mm (F), 100 μ m (C), 200 μ m (A).

in the Valdorría platform and in the type area of San Emiliano Formation, also in the southern Cantabrian Mountains, show diverse components including other algaespongia (*Komia*, *Ungdarella*, etc.), red and green algae, corals, bryozoans, etc. Chaetetids are mentioned as minor components but *Girvanella* is not mentioned (Bowman, 1979; Chesnel *et al.*, 2016). However, these mounds also seem to have developed partly in the photic zone. In Picos de Europa, Merino-

Tomé *et al.* (2009) described small mounds very similar to those from the Rosario Mine, composed of chaetetid sponges, syringoporids, branching rugose corals, *Anthracoporella* and phylloid algae, but *Girvanella* is, again, not present in the assemblage. Finally, Rogers (2018) described mounds dominated by *Donezella*, *Claracrusta*, *Rothpletzella* and *Girvanella*. However, in this case chaetetids were completely absent.

Similar mounds, composed of *Donezella* in association with other components, have been described in other realms such as the Midcontinent Province (Rich, 1967; Choh & Kirkland, 2000, 2006; Lambert & Stanton, 1988), the Maritime Province and Canada (Davies & Nassichuk, 1989; Watkins, 1999) in North America, in Kazakhstan (Cook *et al.*, 2007) and in Western Urals (Proust *et al.*, 1998). In all cases, either *Girvanella*, chaetetids or both are absent from the mound communities.

CONCLUSIONS

The mounds located at the Rosario Mine are a variant of the *Donezella* mounds that occur typically in the Cantabrian Mountains and other tropical regions during the Pennsylvanian.

Their special feature is the unique combination of *Donezella*, chaetetids, and *Girvanella*, which is not found in any other previously described mound. It means that these mounds developed in the photic zone, probably below the fair-weather wave-base but above the storm wave-base.

The bulbous structures are mostly composed of chaetetids and show an ecological succession. *Girvanella* grew on bioclastic beds, mainly consisting of *Donezella* branches. The chaetetids used the *Girvanella* masses as a substrate for attachment. When the growth of the chaetetids stopped for different reasons, several types of encrusters (including *Clarachusta*, *Girvanella*, *Multithecopora* and rugose corals) covered the upper surface of the chaetetids, providing new surfaces for their growth when conditions were favourable for them.

Supplementary information. This article has no additional data.

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