



Palaeoecology of calcified microfossils from the Lower Devonian (Pragian-Emsian) of Sierra Morena (SW Spain)

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Abstract

Lower Devonian (Pragian-Emsian) reefal deposits of Sierra Morena (SW Spain) contain locally abundant calcified cyanobacteria, calcareous algae, and various microfossils including foraminifers. Calcified cyanobacteria are represented by *Girvanella* spp. A–C, which form crusts and clumps of various shapes. Supposed green algae (?Dasycladales) are represented by a new genus with one new species, *Bediaella hispanica* gen. et sp. nov. Algospongia include *Vasicekia margaritula* (Saltovskaya, 1986) n. comb. Microproblematica are represented by *Rothpletzella* sp. The studied assemblages indicate photic and warm conditions in a shallow and well-agitated environment with normal salinity, and probably mirror episodes of shallowing due to eustatic sea level fluctuations.

Keywords Cyanobacteria · Microproblematica · Green algae · Taxonomy · Palaeoecology · Lower Devonian · SW Spain

Introduction

Among the typical reef-building organisms such as corals and stromatoporoids, various calcified cyanobacteria and calcareous algae were involved in the reef growth during the Palaeozoic (e.g., Chuvashov and Riding 1984; Adachi et al. 2006, 2007). Their role in Palaeozoic reefs has been repeatedly highlighted (e.g., Antoshkina 1996; Wood 2000, 2004; Stephens and Sumner 2003; Antoshkina and Königshof 2008; Liu et al. 2016, 2017, 2021). However, the diversity and palaeoecology of calcified microfossils from Lower Devonian reefal sediments is still poorly understood. Development of Early Devonian reefs was suppressed by various factors, e.g., low sea level and increase in terrigenous influx

(e.g., Flügel and Flügel-Kahler 1992; Boulvain and Wood 2007), apparently linked to the closing of the Iapetus ocean, uplift and retreat of large shallow seas, and plate motion reorganizing sea-surface current patterns in the tropics (Copper 2002) with consequent climatic impacts (e.g., Joachimski et al. 2009). Few Lower Devonian reefs have been reported with significant involvement of calcified cyanobacteria and calcareous algae (e.g., Flajs and Hüßner 1996; Antoshkina and Königshof 2008; Hubmann and Suttner 2007; Hubmann and Messner 2013; Koeshidayatullah et al. 2016).

Reefal sediments from the Lower Devonian of Spain were not previously known containing calcified cyanobacteria and/or calcareous algae. Lower to Middle Devonian rocks crop out in the mountains located between the rivers Zújar and Guadamez and to the southeast of them in the Ossa-Morena Zone (SW Spain). These outcrops are part of a long band of Palaeozoic outcrops 200 km long between Badajoz and Córdoba (Fig. 1). The Devonian succession comprises more than 600 m of shales and sandstones that are interbedded with some limestones and marls. The limestones show reefal features of limited lateral and vertical extent. Some of the best outcrops of the reefal facies are, from northwest to southeast, the sections called Guadamez-2, Arroyo del Lobo, Zújar, Peñón Cortado, and Arroyo del Pozo del Rincón (Rodríguez-García 1978). Most of these localities contain Pragian reefal facies and are best exposed in the Peñón Cortado section. Only the Guadamez-2 section contains Emsian

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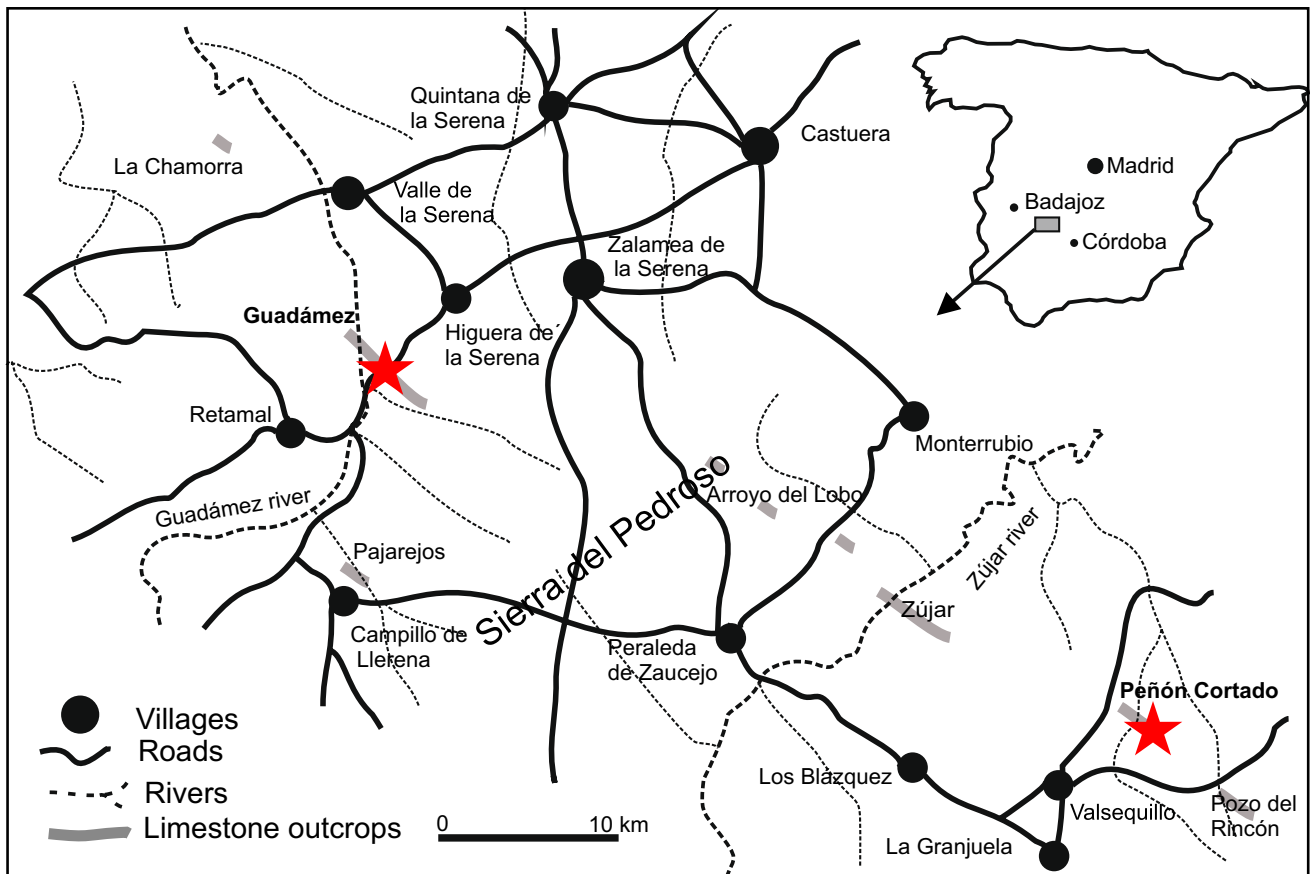


Fig. 1 Outcrops of the Lower to Middle Devonian rocks in the Ossa-Morena Zone (SW Spain) (coordinates: Guadamez 2 ($38^{\circ}37'26''$ N, $5^{\circ}48'07''$ W), Peñón Cortado ($38^{\circ}26'08''$ N, $5^{\circ}48'07''$ W))

reefs. During a field trip in 2007, abundant material from the reefal and peri-reefal facies was collected. These samples were used for description of the rich bryozoan fauna (Ernst and Rodríguez 2023). However, the study of ca 200 thin sections showed the presence of rich calcified microfossils, among them cyanobacteria, green algae, and various microproblematica. The present paper aims to provide an overview and taxonomic description of calcified microfossils from the Peñón Cortado and Guadamez-2 sections at the Ossa-Morena Zone.

Geographical and geological settings

The studied sections reveal the best exposed Lower Devonian sediments in the Sierra Morena. The Peñón Cortado section was named by Herranz (1970). It is located along the railway from Córdoba to Almorchón, in the Angostura valley, 5 km northeast of the village of Valsequillo (Fig. 1; $38^{\circ}26'08''$ N, $5^{\circ}48'07''$ W). The lower part of the section is composed of shales and marls containing brachiopods, bryozoans, solitary rugosans and tabulate corals. The middle

part of the section (units 12–14) contains massive limestones yielding rugose and tabulate corals, stromatoporoids and bryozoans. The upper part of the section comprises again an alternation of limestones and marls containing ramose rugose and tabulate corals, bryozoans, brachiopods, etc. (Fig. 2). The old section was modified to introduce more accurate units. So, the old units 14b to 17 of Rodríguez-García (1978) are changed to units 15–20. The age of the reefal facies is Pragian. The old samples taken in this part of the section are marked in grey and the new samples are marked in black and a B letter in Fig. 3. A fault above the old unit 17 (new 20) repeats a segment of the section in less calcareous facies.

Two main sections were studied at the bank of the Guadamez River close to the road from Higuera de la Serena to Campillo de Llerena in Badajoz province (Fig. 1) by Rodríguez-García (1978) who named them Guadamez-1 and Guadamez-2 ($38^{\circ}37'26''$ N, $5^{\circ}48'07''$ W). The Guadamez-1 section shows monotonous facies composed of calcareous shales and crinoidal limestones. The Guadamez-2 shows interbedded limestones and marly limestones containing a rich fossil biota including corals, brachiopods, bryozoans,

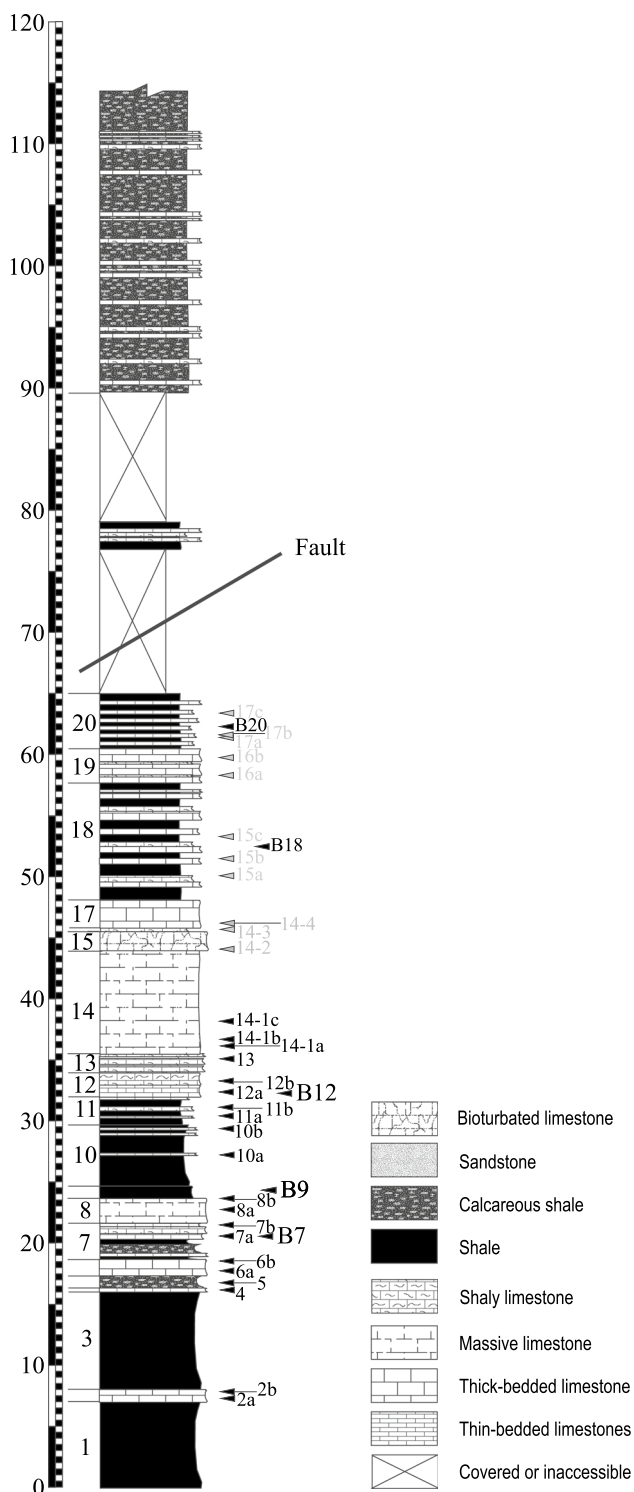


Fig. 2 Lithostratigraphic succession at the Peñón Cortado section (thickness of the profile in meters)

crioconarids, stromatoporoids, ostracods, conodonts, etc. (Fig. 3). The upper part of the section (units 15–19) is composed mainly of stromatoporoids, tabulate corals and bryozoans that built middle-sized (15–20 m wide, 2–3 m

thick) bioherms (Rodríguez et al. 2010). The main facies containing bryozoans are tabulate coral rudstones and stromatoporoid–tabulate coral boundstones of Emsian age (Rodríguez et al. 2010).

Several species of foraminifers were found in the studied thin sections including representatives of two unidentified genera, Gen. indet. 1 (Fig. 8k–l) and Gen. indet. 2 (Fig. 8m) from unit 18 of the Guadámex-2 section. *Vicinesphaera* sp. (Fig. 8n) from unit 18 and *Sphaeroporella* sp. were identified from unit 20 of the Guadámex-2 section, whereas *Parathurammina* sp. (Fig. 8p) was found in unit 20 of the Peñón Cortado section.

Materials and methods

The material for the study was collected in autumn 2007 and represents a series of samples taken from the Peñón Cortado and Guadámex-2 sections. From these rock samples, more than 200 thin sections were made (24 × 48 mm, 50 × 50 mm). Some of the thin sections were provided by SR. In 74 thin sections (29 and 46 from Peñón Cortado and Guadámex-2 sections, respectively) calcified cyanobacteria and algae were found. This material is housed at the Senckenberg Museum (Frankfurt am Main, Germany), under the numbers SMF 40580–SMF 40692. The thin sections were studied using an Olympus SZX7 binocular microscope.

In the Emsian Peñón Cortado section, samples collected from units 1, 12, and 17–19 contained various *Girvanella* species, the calcified microproblematicum *Rothpletzella* sp., and the green alga *Bediaella hispanica* gen. et sp. nov. (units 17–19).

The samples from units 1 and 12 comprise floatstones with micritic cements containing bryozoans, tabulate corals, echinoderms, brachiopods and a few gastropods as macro-components (Fig. 4b). Unit 14 is a boundstone composed mainly of massive and fasciculate rugose corals, favositids and stromatoporoids. Units 13, 15 and 16 are rudstones composed of the same bioconstructors plus diverse bryozoans, ostracods, echinoderms and brachiopods. The samples from units 17–19 represent rudstones and in part boundstones (Fig. 4a). The matrix contains abundant fragments of bryozoans, ostracod carapaces, echinoderms, brachiopods and microbial mats. Cements are mainly sparitic, locally dolomitized. Larger components are represented by bryozoans, brachiopods and echinoderms. Notable is the presence of large gastropods with calcitic shells and only a few corals. The majority of fragments are enveloped in microbial crusts.

The Pragian Guadámex-2 section also contained calcified cyanobacteria (*Girvanella*) and microproblematica (*Rothpletzella*). The green alga *Bediaella hispanica* gen. et sp. nov. was not found in this section. The samples from units G 18–G 20 contain numerous crusts of *Girvanella*

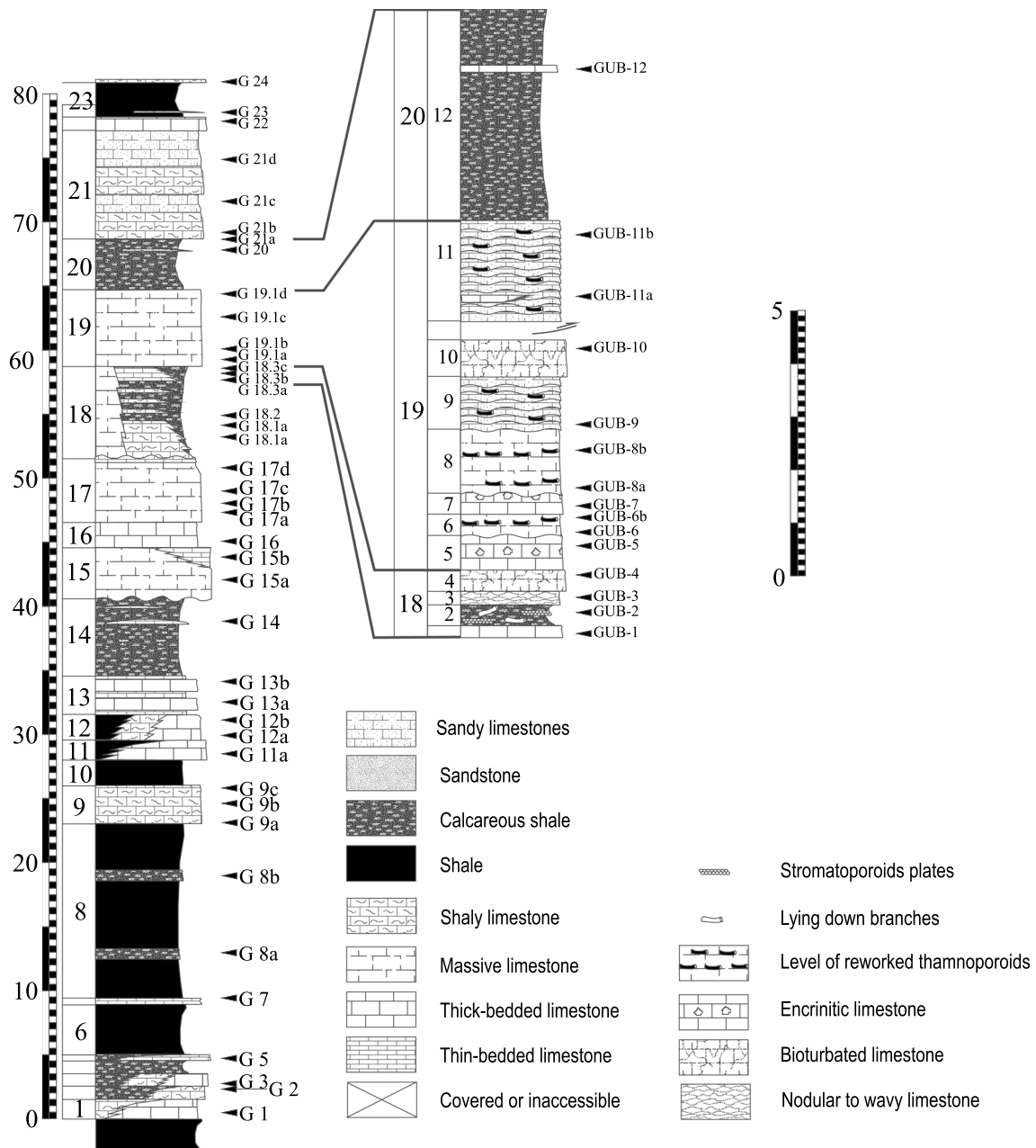


Fig. 3 Lithostratigraphic succession at the Guadamez-2 section (thickness of the profile in meters)

spp. and less abundant *Rothpletzella* sp. In addition, various other calcified microproblematica and algae were found in these units, among them *Vasicekia margaritula* (Saltovskaya, 1986) (former *Rhabdoporella*, see below).

The microfacies of units G 18–G 20 are represented by rudstones with abundant bryozoans, brachiopods, crinoids and a few corals (Fig. 4d). Smaller components include numerous ostracods, smaller bryozoans and diverse skeletal fragments. Cements are predominantly sparitic.

Systematic descriptions

Phylum: Cyanobacteria Stanier, 1974.

Order: Osillatoriales Elenkin, 1949.

Genus: *Girvanella* Nicholson and Etheridge, 1878.

Type species: *Girvanella problematica* Nicholson and Etheridge, 1878 emend. Wood, 1957; Upper Ordovician, Scotland.

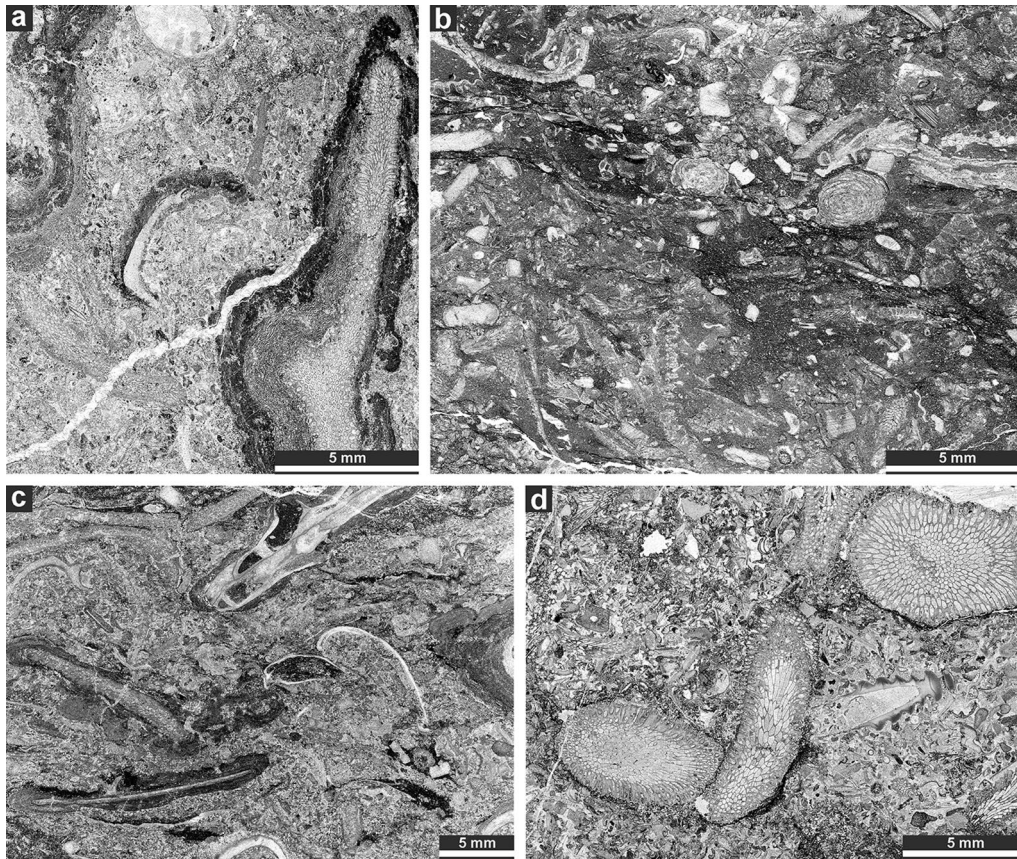


Fig. 4 Microfacies of the studied rocks at the Peñón Cortado section. **a** bryozoan-rich marly limestone, between units 17 and 20, SMF 40580; **b** bryozoan–crinoid rudstone, unit 12, SMF 40581. Microfa-

cies of the studied rocks at the Guadámex-2 section. **c** SMF 40582, microbial boundstone with corals, molluscs, and bryozoans, unit G 19, **d** SMF 40583, bryozoan–crinoid rudstone, unit G 18

The studied samples from units 12 and 17–19 of the Peñón Cortado section and units G 18–G 21 of the Guadámex-2 section contain crusts and globular masses, which are formed by tube-shaped remains placed in the genus *Girvanella* Nicholson and Etheridge, 1878. This fossil is described as calcareous tubular filaments forming nodules and encrusting masses with uniform external diameter. The filaments are long, sinuous to irregularly tangled and have thin micritic walls (e.g., Feng et al. 2010). *Girvanella* resembles *Subtifloria* Maslov, 1956 but differs in the disordered arrangement of the filaments. It is regarded as a cyanobacterium (e.g., Riding 1977).

In the studied samples at least three forms can be distinguished. All encrust various components such as bryozoans, brachiopod and gastropod shells, as well as ephemeral objects resulting in the formation of tubular structures after the decay of these soft-bodied organisms (e.g., Fig. 5a, l). Separate sheets and globular masses also occur (e.g., Fig. 5e–h).

Girvanella sp. A

Description: Relatively loosely arranged tubes with uniform wall thickness (Fig. 5a–e) forming crusts 0.18–1.00 mm in thickness. Tubes 23–30 μm in diameter with 5–8 μm thick walls.

Remarks: *Girvanella* sp. A is similar to *G. kasakiensis* Maslov, 1949.

Girvanella sp. B

Description: Compact masses measuring 0.16–0.81 mm in thickness (Fig. 5f–k), formed by tubes 15–20 μm in diameter with 2–5 μm thick walls.

Remarks: The masses of this species look darker than those of *Girvanella* sp. A, apparently because of denser packing of the micritic tubes. Alternatively, the presence of fine micrite between the tubes, precipitated within the microbial mat, may be responsible for the dark color of these masses. The difference between the two species of *Girvanella* is especially evident in Fig. 5l. *Girvanella* sp. B is similar to *G. problematica* Nicholson and Etheridge, 1878, as described in Liu et al. (2021).

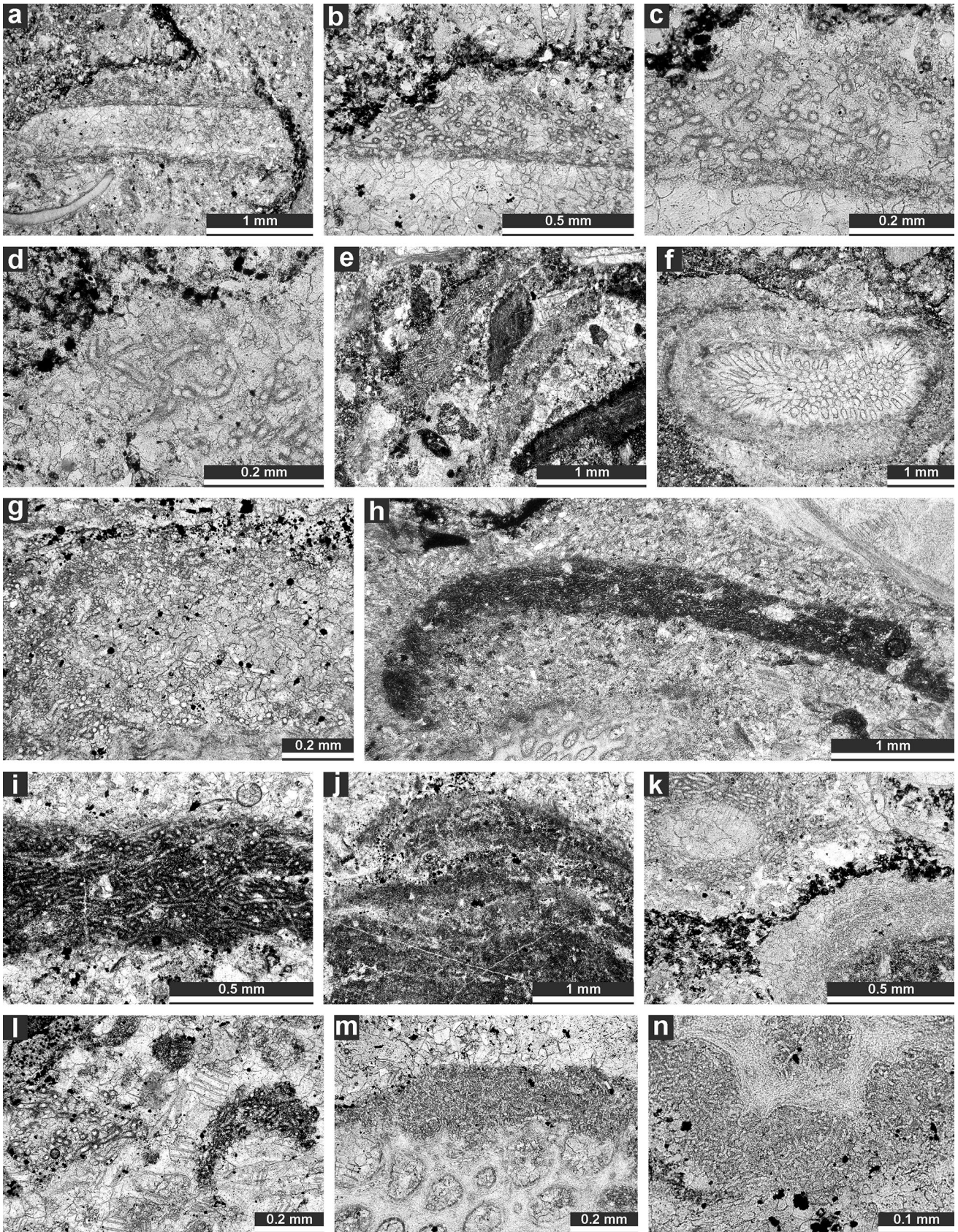


Fig. 5 Calcified cyanobacteria from the Lower Devonian (Pragian) of SW Spain (all from the unit 20 of the Peñón Cortado section). **a–d** *Girvanella* sp. A, tubular encrusting of filaments, SMF 40594; **e** separate crust of *Girvanella* sp. A and other microbial mats in the sparitic matrix, SMF 40592; **f, g** transverse section of the trepostome bryozoan *Leptotrypella armata* Ernst et al., 2012, encrusted by *Girvanella* sp. B, SMF 40603; **h, i** crust formed by *Girvanella* sp. B, SMF 40595; **j** crust formed by an assemblage of various *Girvanella* tubes and microbial crusts, SMF 40604; **k** crusts of *Girvanella* sp. A encrusting an ephemeral object (left top) and *G. sp. B* (right bottom), SMF 40601; **l** crusts of *Girvanella* sp. A (left) and *G. sp. B* (right) in the sparitic matrix, SMF 40606; **m, n** crust of *Girvanella* sp. C on bryozoan *Leptotrypella armata* Ernst et al., 2012, SMF 40591

Girvanella sp. C

Description: Dense masses of small tubes (Fig. 5m–n). Tubes 8–13 µm in diameter with walls of ca 2 µm thickness.

Remarks: *Girvanella* sp. C differs from *G. sp. A* and *G. sp. B* by its smaller tubes (8–13 µm vs. 23–30 µm in *G. sp. A* and 15–20 µm in *G. sp. B*).

Calcified microproblematica

Genus: *Rothpletzella* Wood, 1948

Thin sections from units 12 and 19 of the Peñón Cortado section as well as those from the units G 18–G 20 of the Guadamez-2 section contain fossils which are placed in the genus *Rothpletzella* Wood, 1948. This microfossil is regarded as a cyanobacterium (Wood 1948), or a microproblematicum (Riding 1991) as no modern analogues are known.

Rothpletzella sp.

Description: Calcareous tubular filaments with micritic walls bifurcating to form sheet-like flat to undulose layers, resembling strings of beads in transverse section. Layers 0.18–0.63 mm in thickness (Fig. 6a–e), rarely concentric in structure (Fig. 6f). Filament internal short dimension (tube height) 20–40 µm, thickness of vertical walls 3–8 µm, and that of horizontal walls (between layers) 10–15 µm.

Calcareous algae

Kingdom: Plantae sensu Copeland, 1956.

Division: Chlorophyta Reichenbach, 1828, emend. Pascher, 1914, emend. Lewis and McCourt, 2004.

Class: Ulvophyceae Stewart and Mattox, 1978.

Order: Dasycladales Pascher, 1931.

Genus: *Bediaella* gen. nov.

Type species: *Bediaella hispanica* gen. et sp. nov.

Etymology: The new genus is dedicated to Isabel Méndez Bedia from Oviedo University in Spain.

Occurrence: Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Diagnosis: Subcylindrical thallus not bifurcated with rounded ends. Central cavity relatively broad. Calcareous wall of sparry calcite, probably originally aragonitic, with subspherical, vesiculifer, aspondylous laterals.

Remarks: *Bediaella* gen. nov. differs from *Nigrella* Mamet and Préat, 1994 by the presence of elongate vesiculiform (barrel-shaped) laterals. *Bediaella* differs from *Amicus* Maslov, 1956, which has only one narrow central siphon. Due to its apparent uniaxial construction, *Amicus* was attributed to the primitive Dasycladales. Other Devonian taxa have similarities with Dasycladales: *Zeapora* Penecke, 1894 emend. Hubmann, 2000 (= *Litanaella*; see also Hubmann and Reuter 2013, 2017; Hubmann and Messner 2013); *Coelotrochium* Schlüter, 1879; *Scribroporella* Spriesterbach, 1935; and *Hoegenites* Nitecki and Spjeldnæs, 1989 (see discussion about this latter genus in Nitecki and Spjeldnæs 1989; Mamet and Préat 2005; Khodjanyazova and Mamet 2003; Mamet and Khodjanyazova 2006; Vachard and Cózar 2010; Rhebergen 1997, 2009; van Keulen and Rhebergen 2017).

Furthermore, *Bediaella* differs from *Wagonella* Mamet and Préat, 1994, a very poorly known genus, by the more irregular calcification of the interpores. *Bediaella* differs from *Gyroporella* Gümbel, 1872, by its more spherical laterals (not drum-shaped) and more aspondylous arrangement (this of *Gyroporella* is sometimes denominated mesospondylous, because it is almost euspondylous). Moreover, *Gyroporella* appears in the Moscovian (Racz 1966; Kochansky-Devidé 1970). In addition, two contiguous specimens in our material display a growth entirely unknown in *Gyroporella* (Fig. 7).

The new genus differs also from *Uragiellopsis* Vachard in Vachard and Montenat, 1981 by the absence of intercalated acrophorous laterals, and from *Megaporella* Deloffre and Beun, 1986 by the presence of a narrow extremity in the laterals, inconspicuous in our material.

***Bediaella hispanica* gen. et sp. nov.**

Figures 6g–n and 7a–c.

Etymology: The new species is named after Spain where it was found.

Holotype: Thin section SMF 40643 (Fig. 6g–i).

Paratypes: Seven thin sections (SMF 40644–SMF 40650).

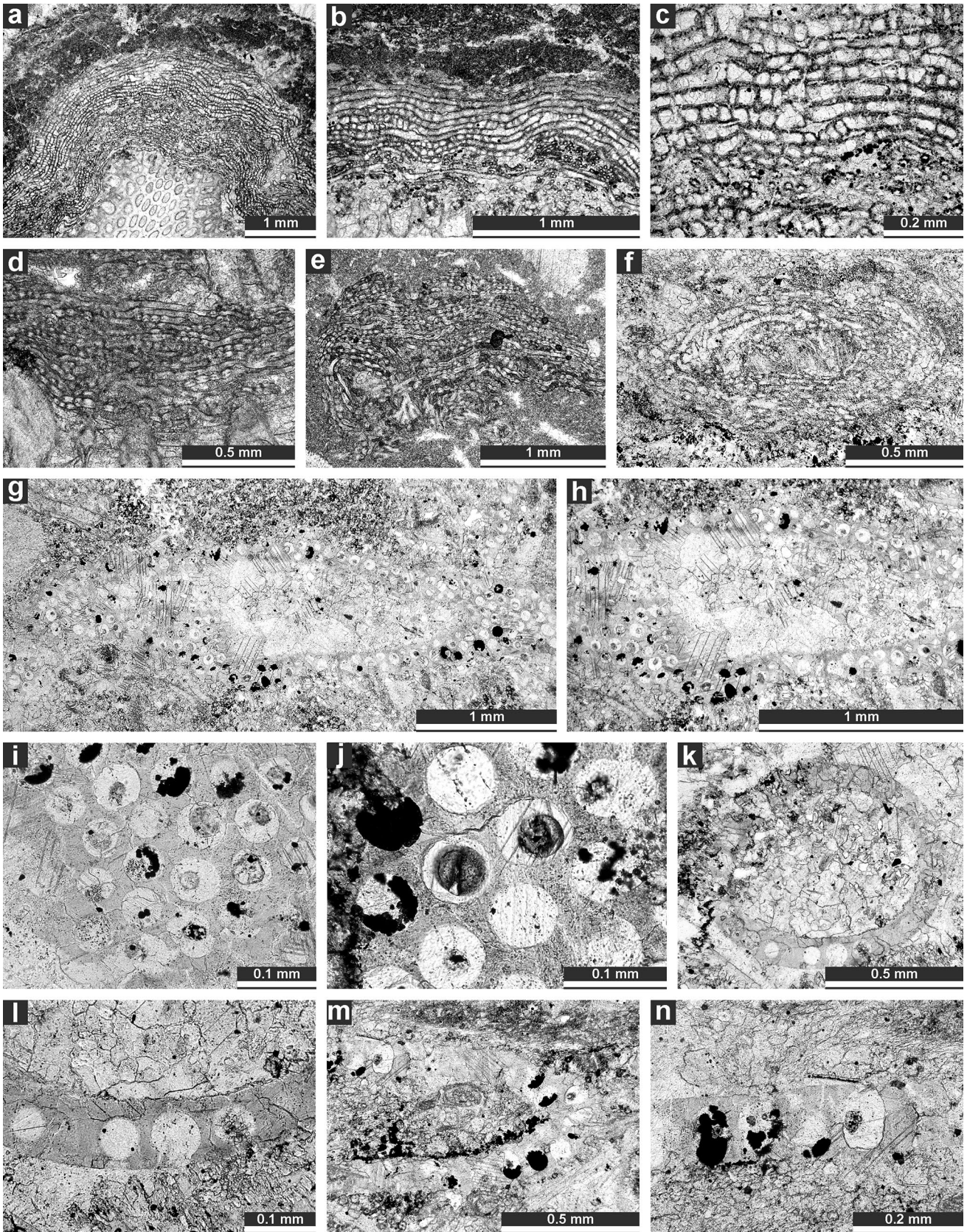


Fig. 6 Calcified microproblematica and *Bediaella hispanica* gen. et sp. nov., new green alga from the Lower Devonian (Pragian) of SW Spain (a–c, f–n from the unit 20, d, e from the unit 12 of the Peñón Cortado section). **a–c** crust of *Rothpletzella* sp. (with intercalations of *Girvanella* sp. A), SMF 40614; **d** crust of *Rothpletzella* sp. on a trepostome bryozoan *Anomalotoechus* sp., SMF 40620; **e** globular mass of *Rothpletzella* sp., SMF 40622; **f** oncoid of *Rothpletzella* sp., SMF 40619; **g, h** *Bediaella hispanica* gen. et sp. nov., oblique axial section of the thallus; holotype SMF 40643; **i** *Bediaella hispanica* gen. et sp. nov., tangential section of the wall with chambers containing apparent cysts, holotype SMF 40643; **j** *Bediaella hispanica* gen. et sp. nov., tangential section of the wall with chambers containing apparent cysts, paratype SMF 40645; **k, l** *Bediaella hispanica* gen. et sp. nov., transverse section of the thallus, holotype SMF 40643; **m, n** *Bediaella hispanica* gen. et sp. nov., longitudinal section, paratype SMF 40648

Repository of the types: Senckenberg Museum (Frankfurt am Main, Germany).

Type locality: Peñón Cortado, Ossa-Morena Zone (SW Spain).

Type horizon: Lower Devonian (Pragian).

Material: More than ten specimens identified in eight thin sections, in longitudinal, oblique and transverse orientations.

Diagnosis: As for the genus, by monotypy.

Description: Seven thin sections from unit 20 contain remnants of an apparent green alga (Dasycladales). This fossil comprises a tubular, probably tapering body with a recrystallized wall 0.08–0.11 mm in thickness. The tubes are 0.54–0.97 mm in diameter. The wall contains densely spaced oval laterals, 0.05–0.09 mm in width (Fig. 6g–n; Table 1). The laterals were not observed with openings either internally or externally. Majority of chambers contain mostly spherical, sometimes collapsed, thin-walled bodies, which may represent cysts (Fig. 6i, j). This fossil is interpreted as possibly belonging to the green algae (Dasycladales) because of its general shape and recrystallized walls that suggest an original aragonitic mineralization. Two contiguous specimens display a growth rarely observed among the Dasycladales (Fig. 7a–c).

Occurrence: As for the genus.

Algae incertae sedis

Class: Algospongia Termier et al., 1977 ex Vachard and Cózar, 2010.

Order: Moravamminales Pokorny, 1951 ex Vachard in Termier et al., 1975.

Family: Issinellaceae Deloffre, 1987 emend. Vachard and Cózar, 2010.

Genus: *Vasicekia* Pokorny, 1951.

Type species: *Vasicekia moravica* Pokorny, 1951.

Diagnosis: Thallus cylindrical to claviform, simple or once or several times bifurcated. Numerous thin radiate, aspondylous, cylindrical laterals. Wall calcitic, yellowish.

Description: The morphological diversity may be described following the work of Saltovskaya (1986) in which the genus is misinterpreted as *Rhabdoporella*.

Included species: *Vasicekia moravica* Pokorny, 1951; *Vasicekia?* sp. of Mamet et al. (1999, pl. 4, Figs. 1–3); *Parmacaulis hulgensis* Shuysky and Shirshova in Chuvashov et al., 1987; *Rhabdoporella perfecta* Saltovskaya, 1986; *Rhabdoporella fragile* Saltovskaya, 1986; *Rhabdoporella elongata* Saltovskaya, 1986; *Rhabdoporella clavaeformis* Saltovskaya, 1986; *Rhabdoporella margaritula* Saltovskaya, 1986.

Remarks: These taxa differ from true *Rhabdoporella* by their cylindrical and not acrophore laterals, yellowish and probably originally calcitic wall, and not aragonitic as in the true dasycladales. Hence, they are comparable with *Issinella*, *Serrisinella*, *Issinellina*, etc. rather than *Rhabdoporella*.

Rhabdoporella sensu Vachard and Gélard 1980 is a primitive dasycladale Seletonellaceae relatively similar to the Dasyporelleae. *Rhabdoporella* sensu Pia 1920, and perhaps Poncet (1986), is another taxon with an aspondylous arrangement of acrophore laterals. *Vasicekia* differs by its typical issinellacean laterals (cylindrical, very thin, aspondylous) and the yellowish, calcitic wall (never recrystallized microsparite). *Issinella*, *Issinellina* and *Serrisinella* are cylindrical thalli; *Vasicekia* being claviform.

Moreover, *Rhabdoporella* is bifurcated and segmented (*Serrisinella* is also weakly segmented). *Vasicekia* has a thin wall and a proportionally large axial cavity. Even if *Vasicekia* was initially described as a foraminifer by Pokorny (1951). Subsequently, Mamet et al. (1999), Vachard and Cózar (2010), and Mamet and Pr eat (2013) considered *Vasicekia* as an alga.

Occurrence: Upper Ordovician–Lower Silurian of Tajikistan, Caucasus, England, Gotland, Prebaltica (Saltovskaya 1986). It is noteworthy that this dating is disputable in Russia and has been revised as Lower Devonian (Vachard et al. 2010; Nestell et al. 2011). Lower Devonian of Spain (present publication). Lower to Middle Devonian of Northern and Prepolar Urals. Eifelian of Morocco. Givetian of Moravia. Givetian of western France (Vachard and Cózar 2010). Middle Devonian of Poland (Halamski et al. 2022; Gajewska 2022).

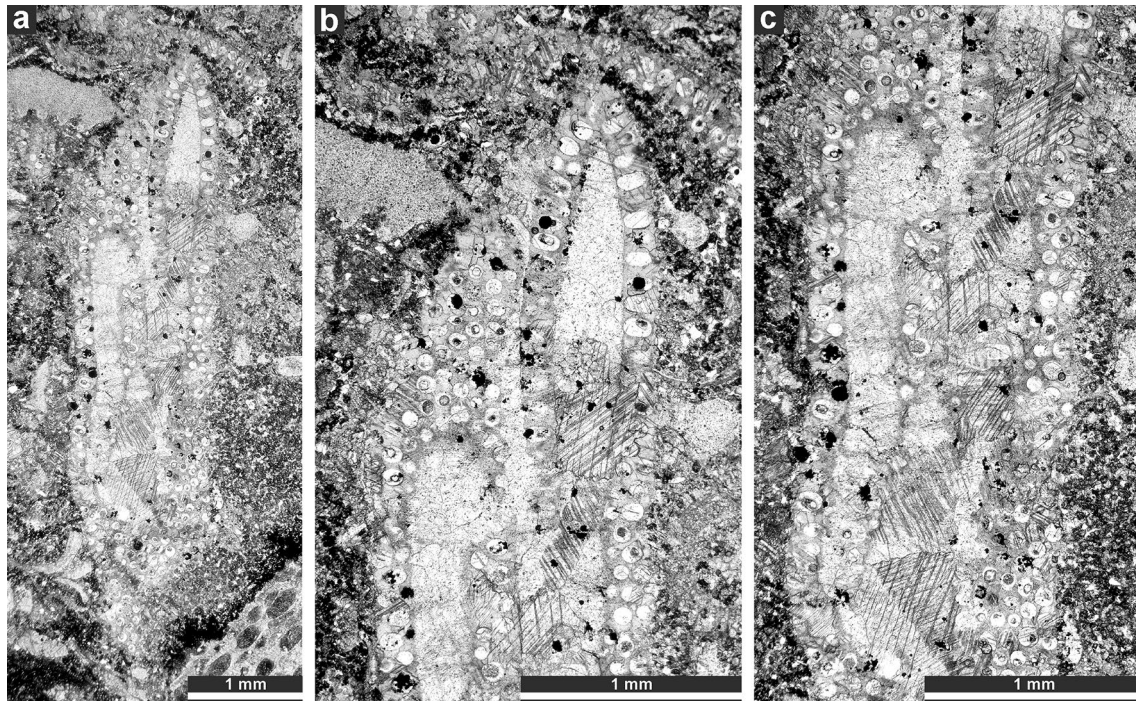


Fig. 7 *Bediaella hispanica* gen. et sp. nov., **a–c** longitudinal section, paratype SMF 40650

Table 1 Width of laterals of *Bediaella hispanica* gen. et sp. nov., holotype (SMF 40643) and two paratypes (SMF 40645 and SMF 40650)

	<i>N</i>	<i>X</i>	<i>MIN</i>	<i>MAX</i>	<i>SD</i>	<i>CV</i>
SMF 40643	20	0.065	0.050	0.080	0.007	10.59
SMF 40645	20	0.071	0.050	0.080	0.008	11.65
SMF 40650	20	0.068	0.050	0.090	0.010	14.17

N number of measurements, *X* mean, *MIN* minimal value, *MAX* maximal value, *SD* standard deviation, *CV* coefficient of variation

Vasicekia margaritula (Saltovskaya, 1986) n. comb.

Figures 8a–j

Material: More than 50 specimens identified in 36 thin sections, in longitudinal, oblique and transverse sections (SMF 40651–SMF 40686).

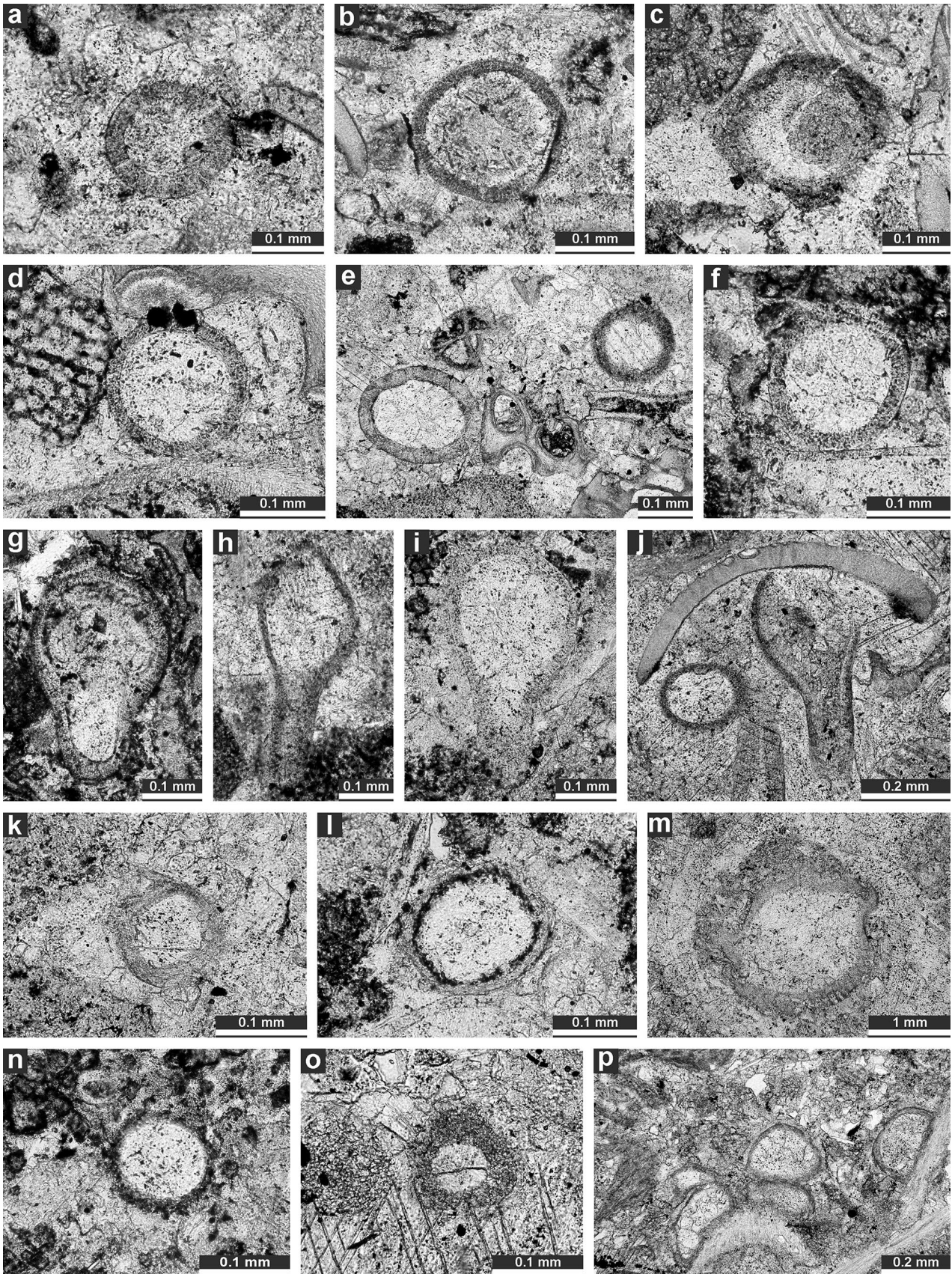
Diagnosis: Thallus claviform with well-preserved wall.

Description: Thirty-six thin sections in the sample from unit G 18 of the Guadamez-2 section contain remnants of an apparent issinellacean (incertae sedis algae). This fossil is tubular, probably claviform, with well-preserved walls, and 0.35–0.43 mm in length. The tubes are 0.20–0.29 mm in diameter. The wall, 0.025–0.050 mm thick, contains densely spaced cylindrical laterals, 0.05–0.12 mm in width

(Fig. 8g–j). The laterals are all open either internally or externally (Fig. 9).

Occurrence: Upper Ordovician of Tajikistan (Saltovskaya 1986). Discovered in the Lower Devonian of Spain (unit G 18 of the Guadamez-2 section).

Fig. 8 *Vasicekia margaritula* (Saltovskaya, 1986) n. comb., from the Lower Devonian (Emsian) of SW Spain, Guadamez-2 section, unit G 18. **a–f** transverse sections showing the very fine aspondylous, acrophore, radiate perforations in the wall (8a—SMF 40659, 8b—SMF 40656, 8c—SMF 40661, 8d—SMF 40664, 8e—SMF 40664, 8f—SMF 40677); **g–j**, oblique axial sections showing the claviform thallus and the very fine aspondylous, acrophore, radiate perforations in the wall (8g—SMF 40658, 8h—SMF 40653, 8i—SMF 40664, 8j—SMF 40655). Foraminifers found in the studied profiles of the Lower Devonian of SW Spain: **k–l** Gen. indet. 1 (8k—SMF 40687, 8l—SMF 40688); **m** Gen. indet. 2 (SMF 40689); **n** *Vicinesphaera* sp. (SMF 40690); **o** *Parathuramina* sp. (SMF 40691); **p** *Sphaeroporella* sp. (SMF 40692)



Discussion

Calcified cyanobacteria and algae were found only within narrow intervals in two localities of the Lower Devonian in SW Spain: Peñón Cortado (Pragian) and Guadamez-2 (Emsian). From the total sequence of these two localities, more than 200 thin sections were made for study of bryozoans (Ernst and Rodríguez 2023).

Distribution within studied sections

Girvanella spp. A–C occur in units 1, 12 and 17–19 of the Peñón Cortado section and units G 18–G 21 of the Guadamez-2 section, whereas *Rothpletzella* sp. was found in units 12 and 19 of the Peñón Cortado section, and in units G 18–G 20 of the Guadamez-2 section (Table 2). Units G 18–G 21 represent a succession deposited on a protected shallow platform with patch reefs, normal salinity and moderate water energy (Rodríguez et al. 2010).

Three types of *Girvanella* sp. were identified within the studied units. They differ in size and arrangement of filaments. *Girvanella* sp. A produced larger relatively loosely arranged filaments, whereas those of *G.* sp. B and C are smaller and more densely packed (see description above). All three varieties appear as masses and crusts, *Girvanella* sp. A and B were observed in tubular congregations, apparently around ephemeral objects (e.g., algae).

Rothpletzella sp. produces crusts on bryozoans and corals, as well free-lying globular masses which can reveal

a concentric arrangement (oncoïd, Fig. 6f). *Rothpletzella* sp. is often intercalated with *Girvanella* sp. A. Similar co-occurrences of *Girvanella* and *Rothpletzella* are quite common in reefal sediments (e.g., Tsien 1979; Liu et al. 2016, 2017, 2021).

The green alga *Bediaella hispanica* gen. et sp. nov. is restricted to units 18–20 of the Peñón Cortado section. *Vasicekia margaritula* (Saltovskaya, 1986) was found only in unit G 18 of the Guadamez-2 section. This unit (and the succeeding G 19) represents patch reefs built mainly by thamnoporoids and stromatoporoids (Rodríguez et al. 2010).

Furthermore, various laminated micritic structures of apparently microbial origin are abundant in unit 20 of the Peñón Cortado section (e.g., Figs. 4a, 5e, j, 6b). and in unit G 19 of the Guadamez-2 section (Fig. 4c). They often show indistinct relicts of tubular structures.

Palaeoecology and environmental interpretation

The crusts produced by *Girvanella* spp. A–C and *Rothpletzella* sp. often cover bryozoans sealing their apertures (e.g., Figs. 5m–n, 6a–b, d–e). The temporal succession of these overgrowths is indistinct, however. The encrusted bryozoans were probably already dead before the apertures were sealed by crusts of calcareous microorganisms. However, the sealing of living biotic substrates causing death cannot be completely excluded as no unequivocal evidence for either alternative was found in the studied material.

Abundant tubular aggregations (e.g., Fig. 5a, k–l) of *Girvanella* spp. A–B indicate the presence of ephemeral

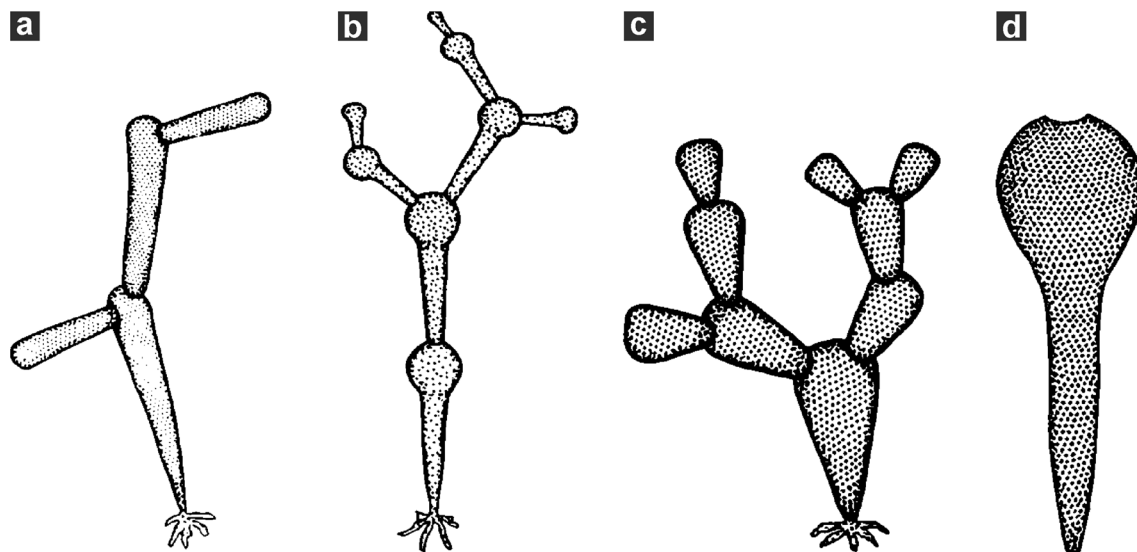


Fig. 9 Life reconstruction of *Vasicekia*. **a** *Vasicekia elongata* (Saltovskaya, 1986); **b**, **c** *V. clavaeformis* (Saltovskaya, 1986); **d** *V. margaritula* (Saltovskaya, 1986)

organisms, probably cyanobacteria. Such bioclastrations are especially abundant in unit 18 of the Peñón Cortado section, and in unit G 21 of the Guadáméz-2 section. These tubes are unbranching and may have represented uncalcified cyanobacteria.

The abundance and diversity of calcified microbial structures observed in the studied units suggests a relatively shallow and agitated environment within the photic zone, as confirmed by the presence of green algae (*Bediella*) and algae of uncertain affinity (*Vasicekia*). The high level of fragmentation of most components in many beds indicates a considerable hydrodynamic energy. The accompanying fauna, including abundant rugose corals, brachiopods and echinoderms, indicates a normal marine salinity and well-oxygenated waters.

Cyanobacterial calcification is believed to require high overall seawater carbonate saturation (e.g., Riding 1992, 2011). Such conditions normally occur during evaporation in restricted lagoons or soda lakes. Although abundant and diverse in marine environments (Hoffman 1999), modern calcimicrobes experience intensive calcification mostly in fresh water and rarely in subtidal marine environments (e.g., Flügel 2010). In contrast, the fossil representatives of this group are found in tidal and subtidal biotopes, often in reefs, as, for example, shown for some Ordovician (Liu et al. 2021) and Devonian occurrences (Stephens and Sumner 2003). *Rothpletzella* is suggested to occur in shadowed, protected environments like lagoons, but also in reefs and open platform habitats (e.g., Chuvashov and Riding 1984; Antoshkina 1996; Wood 2000, 2004).

Calcareous microfossils and Lower Devonian depositional history

Studied assemblages of calcareous microfossils from the Lower Devonian of the Sierra Morena might mirror regional and global sea level changes. The two main occurrences in the Pragian Peñón Cortado section (units 17–20) and in the Emsian Guadáméz-2 section (units G 18–G 20) probably mark peaks of regressive cycles observed during the Pragian and Emsian, which were separated by the transgression near the Pragian/Emsian transition (e.g., Johnson et al. 1985, 1996; Chlupáč and Kukul 1986; Flajs and Hüssner 1996; Keller 1997). Reefal sediments in the Lower Devonian are relatively rare being mainly restricted to lower latitudes and deposition in normal marine conditions (e.g., Copper 2002; Kiessling 2002; Vennin et al. 2007). There are various explanations for this reef reduction including such abiotic factors as high water temperature as well as certain developments in reef-forming biotas (e.g., Joachimski et al. 2009; May 2022). The Lower Devonian was postulated to be an episode of reduced cyanobacterial calcification (Riding 1992). Nevertheless, cyanobacteria and calcareous algae have been

Table 2 Distribution of calcified microfossils in Peñón Cortado and Guadáméz-2 sections

Unit		<i>Girvanella</i> sp. A	<i>Girvanella</i> sp. B	<i>Girvanella</i> sp. C	<i>Rothpletzella</i> sp.	<i>Bediella hispanica</i>	<i>Vasicekia margaritula</i>
Guadáméz-2	base of unit G21 (40 cm above)						
	retransition between units G19 and G20	●	●	●	●		
	top of G18.1	●	●	●	●		●
	base of G18 (small channels)						●
	unit G10 (~1 m below the top)						
	unit G8a						
Peñón Cortado	bed 19	●	●	●	●	●	
	bed 18	●	●	●	●	●	
	bed 17, middle	●	●	●	●	●	
	bed 14						
	bed 12, top				●		
	bed 12						
	1.5 m from top	●			●		
	bed 12						
	3 m from base						
	bed 12						
	2 m from base						
	bed 12, base						
	bed 11 (3 m from base)						
	bed 11, base						
top of bed 10							
top of bed 9 (10-15 cm)							
bed 9							
top of bed 7							
bed 1	●						

reported from different reefal constructions, e.g., in the Lower Devonian of Belgium (Tsien 1979), Austria (Hubmann and Suttner 2007), Prague Basin (e.g., Flajs and Hüssner 1996), Russia (Antoshkina and Königshof 2008), and Saudi Arabia (Koeshidayatullah et al. 2016). Such occurrences of calcified cyanobacteria, alongside other calcified microorganisms and algae, may indicate short intervals of increased carbonate saturation, probably because of basin shallowing and increased temperature.

Conclusion

Certain horizons of the reefal deposits of two Lower Devonian sections in Sierra Morena (SW Spain) contain abundant calcified cyanobacteria, calcareous algae, and various microfossils including the problematicum *Rothpletzella* and foraminifers. Calcified cyanobacteria (*Girvanella* spp. A–C) form crusts and clumps of various shapes, notably tubular structures.

A new genus with one new species, *Bediaella hispanica* gen. et sp. nov., apparently belonging to Dasycladales (green algae), is described from the Lower Devonian (Pragian) sediments of the Peñón Cortado section.

A new combination *Vasicekia margaritula* (Saltovskaya, 1986) n. comb. (Algospongia) is described from the Lower Devonian (Emsian) deposits of the Guadamez-2 section.

Microproblematica are represented by *Rothpletzella* sp., which often occurs intercalated with *Girvanella* sp. A.

Horizons with calcified cyanobacteria and calcareous algae were apparently deposited during brief episodes with higher carbonate saturation as supposed for the Lower Devonian (e.g., Riding 1992). These temporal environmental changes might be linked to regressions due to eustatic sea level fluctuations (e.g., Johnson et al. 1985, 1996). The studied assemblages contain predominantly autotrophic organisms and indicate photic and warm conditions in a shallow and well-agitated environment with normal salinity.

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Author contributions AE designed the research, made the thin sections (in part), measured the material, and described the cyanobacteria and calcified microproblematica. DV provided descriptions of the algae and IDs of foraminifers. SR wrote introduction parts and provided thin sections (in part). AE, DV, and SR contributed to discussion and conclusions.

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Data availability Studied material is housed at the Senckenberg Museum (Frankfurt am Main, Germany).

Code availability Not applicable.

Declarations

Conflict of interest None.

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