Lower Devonian stromatoporoids of the Sierra Morena (Southern Spain) and their palaeogeographic affinities

Andreas May

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Abstract: For the first time the stromatoporoid fauna from two locations in the Peñón Cortado Limestone (Upper Emsian) from the Sierra Moreno (Southern Spain) has been examined in detail. The fauna contains 8 stromatoporoid species. One of them, a new species, is described as *Pseudotrupetostroma anacontentoae* n. sp.

The absence of stromatoporoids with branched coenostea and the scarcity of stromatoporoids with thin-layered encrusting growth form probably served as an obstacle to reef construction. The fauna of the Sierra Morena is unrelated to that of the Eastern Americas Realm. However, it is closely related to Emsian faunas of Australia and Canada. There is no evidence to suggest that Southern Spain was a refuge for Eastern Americas stromatoporoids.

Key words: Stromatoporoidea, Devonian, Emsian, biogeography, Spain, reefs

Contents

Saint Louis University Madrid Campus, Av. Del Valle, 34, E-28003 Madrid, Spain, e-mail: maya@madrid.slu.edu

1. INTRODUCTION

Despite of some modern monographic treatments (e.g.: WEBBY, STEARN & ZHEN, 1993; WEBBY & ZHEN, 1993; PROSH & STEARN, 1996; WEBBY & ZHEN, 1997; MAY 1999a, 2002), little is known of the evolution of stromatoporoids during the Early Devonian epoch. During this epoch, in the time between the Silurian reefs and the huge Givetian-Frasnian reefs, both stromatoporoids and reefs were rather scarce.

The reefs of the Silurian and the Givetian–Frasnian were constructed mainly by stromatoporoids. We may well now pose the question whether or not stromatoporoids lost the ability to build reefs during the Early Devonian (and if so why).

Both the lower and upper parts of the Lower Devonian (Lochkovian and Emsian) in the Eastern Americas Realm contain a distinct stromatoporoid fauna, characterized by the occurrence of *Habrostroma* (STOCK 1990, 1994, 1997). However, there are no stromatoporoids known from the Pragian, the middle stage of the Lower Devonian, in the Eastern Americas Realm. Consequently, STOCK (1994, p. 26) assumed that the Eastern Americas stromatoporoids might have survived in an unknown refuge in Bohemia, France, or Spain.

Briefly, regarding Lower Devonian stromatoporoids two important questions have to be answered:

Why did the Lower Devonian stromatoporoids build very few reefs (compared to the Silurian and the Givetian–Frasnian)?

Where did the stromatoporoids of the Eastern Americas Realm reside during the Pragian age?

To answer both these questions, MAY (1999a, 2002) made a detailed investigation of the stromatoporoids of Bohemia. Near Prague a famous coral reef of Pragian age was found and this reef also contains stromatoporoids. Some important results of the research undertaken by MAY (1999a, 2002) are:

Stromatoporoids with branched coenostea are totally absent, and stromatoporoids with thin-layered encrusting growth form are very rare in the Pragian reef. However, these types of stromatoporoids occur very frequently in the Givetian–Frasnian reefs all over the world.

The Lower Devonian beds of Bohemia do not contain any species of *Habrostroma*. All of the genera found are typical of the Old World Realm. This investigation proved that the Prague Basin could not have been the refuge postulated by STOCK (1994).

On the other hand, the Sierra Morena in Southern Spain was known to contain Lower Devonian biostromal and biohermal limestones with both corals and stromatoporoids (GARCÍA-ALCALDE et al., 2002; MORENO-EIRIS et al., 1995; RODRÍGUEZ GARCÍA, 1978). However, these stromatoporoids of the Sierra Morena had never been examined in detail.

Consequently, after a first investigation by MAY (1999b), both Prof. Dr. Sergio Rodríguez (Madrid) and myself established a research project on Lower Devonian stromatoporoids of the Sierra Morena. The following are the preliminary results of our initial series of investigations.

2. STUDY AREA

The study area lies in the Sierra Morena in Southern Spain, which is a part of the Central Iberian Zone. The most recent overview of the Devonian of the Central Iberian Zone was given by García-Alcalde et al. (2002).

In the part of the Sierra Morena which was the subject of investigation, the Devonian succession commences with sandstones and shales, overlain by Emsian siltstones with calcareous beds. These calcareous beds are named "Peñón Cortado Limestone" (Moreno-Eiris et al., 1995; Rodríguez García, 1978). They contain abundant tabulate corals, common rugose corals, and stromatoporoids. Rodríguez García (1978) and Moreno-Eiris et al. (1995) assign a Late Emsian age to this limestone.

A part of these calcareous beds are biostromes. Other beds were interpreted as being products of the destruction of buildups. However, no true buildups were recorded in the study area (Moreno-Eiris et al., 1995, p. 19).

The stromatoporoid fauna of two locations, "Peñón Cortado" and "Guadámez II", in the Peñón Cortado Limestone have been investigated to date. The material is relatively good preserved and shows only very slight tectonic deformation. The exact geographical position of both locations is shown in Fig. 1. A detailed description of both locations is provided by Moreno-Eiris et al. (1995, p. 43–44).

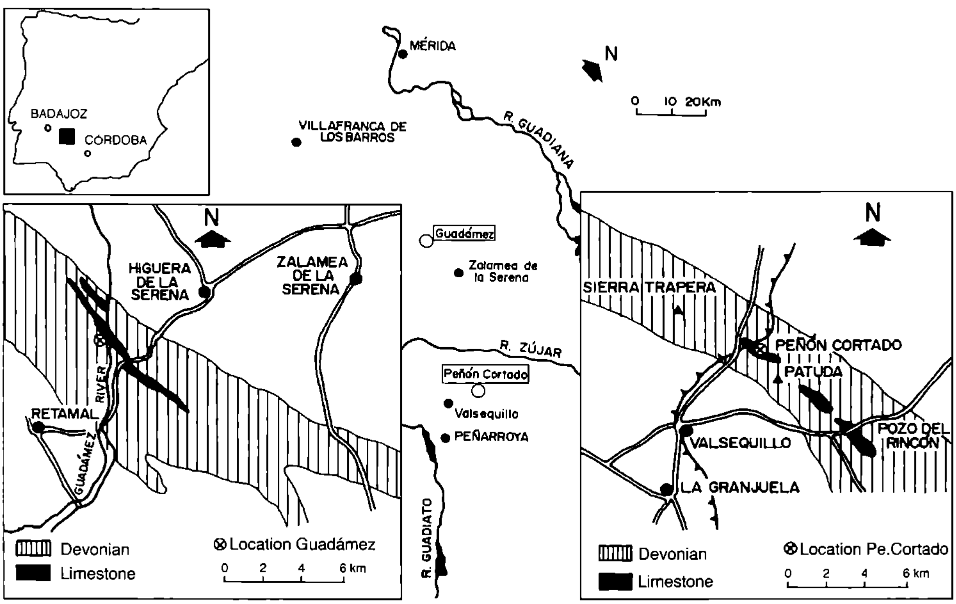

Fig. 1: Geographical positions of the investigated locations in the Sierra Morena (modified after Moreno-Eiris et al., 1995).

2.1. Location "Guadámez II"

The "Guadámez II" section is located in Badajoz Province on the western bank of the Guadámez River, two kilometres to the northwest of kilometre 12 of the road from Campillo de Llerena to Higuera de la Serena (Fig. 1). The outcropping sequence, some 85 metres thick, of fossiliferous limestones and marls was subdivided into 22 beds by Rodríguez García (1978) and Moreno-Eiris et al. (1995).

All 18 stromatoporoid coenostea were collected from bed 19 and, directly below, from the uppermost metre of bed 18. Bed 19 is a massive limestone, 3.5 metres thick, consisting of a biostrome. Bed 18 is a marlstone, 7 metres thick, which contains in its uppermost metre many *Thamnopora* layers and layered reef-builders (favositids and stromatoporoids). Favositids and stromatoporoids increase in importance upwards towards the top of bed 19 where bulbous stromatoporoids dominate.

2.2. Location "Peñón Cortado"

The "Peñón Cortado" section is located in Córdoba Province 5 kilometres north of Valsequillo, at the Córdoba-Almorchón railway cutting (Fig. 1). The outcropping se-

Species in the Sierra Morena	**Guadámez II**	**Peñón Cort.**	**Bohemia**	**Victoria**	**Canada**
Actinostroma compactum Ripper, 1933	6 coenostea	-	Genus	Species	Genus
Plectostroma salairicum (Javorskij, 1930)	-	3 coenostea	Genus	Genus	Species
Schistodictyon n. sp. aff. *amygdaloides* (Lecompte, 1951)	1 coenosteum	-	Genus	Genus	Genus
Clathrocoilona sp.	1 coenosteum	-	-	-	Genus
Stromatopora ex gr. *polaris* (Stearn, 1983)	2 coenostea	-	-	Species	Species
Pseudotrupetostroma anacontentoae n. sp.	5 coenostea	-	-	Genus	-
Syringostromella zintchenkovi (Chalfina, 1960)	-	1 coenosteum	Genus	Species	Species
Parallelostroma sinense Yang & Dong, 1979	3 coenostea	-	-	-	-

Tab: 1: Compilation of the stromatoporoid species found in the Sierra Morena. The columns "Guadámez II" and "Peñón Cortado" give the number of coenostea collected there. To the right follows a comparison of the stromatoporoid fauna of the Sierra Morena with the stromatoporoid faunas of the Middle Pragian of Bohemia (May, 1999, 2002), the Pragian to Lower Emsian of Victoria (Australia) (Webby et al., 1993) and the Lower Emsian to Lower Eifelian of Arctic Canada (Prosh & Stearn, 1996). The entry "Species" signifies that the same species as in the Sierra Morena occurs. The entry "Genus" signifies that, although not being the same species, the same genus as that of the Sierra Morena occurs.

quence, some 110 m thick, consists of fossiliferous limestones, marls, and shales. A subdivision of the site into 19 beds was made by RODRÍGUEZ GARCÍA (1978) and MORENO-EIRIS et al. (1995).

The four stromatoporoids were collected from bed 14, a 13.5 m thick, massive limestone with large colonies of favositids, stromatoporoids, and the colonial rugose coral *Hexagonaria soraufi* RODRÍGUEZ GARCÍA, 1978. MORENO-EIRIS et al. (1995, p. 44) regarded this bed as a product of the destruction of buildups.

3. MATERIAL AND METHODS

Longitudinal (= vertical) and tangential thin sections have been made from all collected stromatoporoid coenostea. The number of coenostea of each species is given in Tab. 1. The methodology, terminology, and classification (including the genus definitions) follow those of STEARN et al. (1999). The material is stored in the Departamento de Paleontología, Ciudad Universitaria, Madrid, under the stock no. DPM-00276.

4. RESULTS

4.1. Stromatoporoid species

Actinostroma compactum RIPPER, 1933

Descriptions were given by WEBBY et al. (1993, p. 123–125), WEBBY & ZHEN (1997, p. 17) and MAY (1999b, p. 99–100). Hitherto *Actinostroma compactum* has not been found outside the Pragian and Lower Emsian of Victoria and Queensland in Australia (WEBBY et al., 1993; WEBBY & ZHEN, 1997).

Plectostroma salairicum (JAVORSKIJ, 1930)

Descriptions were given by JAVORSKIJ (1930, p. 489–490) and PROSH & STEARN (1996, p. 15–16) proving the occurrence of *Plectostroma salairicum* in the uppermost Emsian and lowermost Eifelian of Western Siberia and in Arctic Canada.

Schistodictyon n. sp. aff. *amygdaloides* (LECOMPTE, 1951)

Schistodictyon n. sp. aff. *amygdaloides* (LECOMPTE, 1951) has been described by MAY (1999b, p. 100–101). It is similar to *Schistodictyon amygdaloides amygdaloides* (LECOMPTE, 1951) and *Schistodictyon amygdaloides subvesiculosum* (LECOMPTE, 1951), but has a higher number of pillars and laminae than both subspecies of *Schistodictyon amygdaloides*. The closest similarity to it shows *Schistodictyon amygdaloides amygdaloides* (LECOMPTE, 1951).

LECOMPTE (1951, p. 141–143) measured in longitudinal sections of *Schistodictyon amygdaloides amygdaloides* 7.2 to 9.6 pillars and 7.2 to 9.2 laminae over a distance of 2 mm. However, within the longitudinal section of *Schistodictyon* n. sp. aff. *amygdaloides* there occurs 9 to 13 pillars and 9 to 15 laminae over a distance of 2 mm. This difference is too great to assign the Spanish coenosteum to *Schistodictyon amygdaloides* (LECOMPTE, 1951). However, further material is necessary to be definitely sure, that it is another species.

Schistodictyon amygdaloides occurs in the Lower Eifelian to Lower Givetian beds of Belgium, Germany, and Australia (LECOMPTE, 1951, p. 141–145; AVLAR & MAY, 1997, p. 108–109).

Clathrocoilona sp.

Only one small thin-layered encrusting coenosteum was found. Several species of the encrusting stromatoporoid genus *Clathrocoilona* are distributed worldwide in the reef complexes of the Middle Devonian and Frasnian. First occurrences were reported from Emsian beds in Canada, Austria, and Russia (PROSH & STEARN, 1996; STEARN et al., 1999, p. 39).

Stromatopora ex gr. *polaris* (STEARN, 1983)

The Spanish *Stromatopora* ex gr. *polaris* is very similar to *Stromatopora polaris* (STEARN, 1983), but has more astrorhizal canals. To date, *Stromatopora polaris* (STEARN, 1983) has been found in the Emsian of Canada (STEARN, 1983, p. 551–552; STEARN, 1990, p. 507; PROSH & STEARN, 1996, p. 31). However, a very closely related form from the Lower Emsian of Victoria (Australia) was described as *Stromatopora* aff. *polaris* (STEARN, 1983) by WEBBY et al. (1993, p. 158–161).

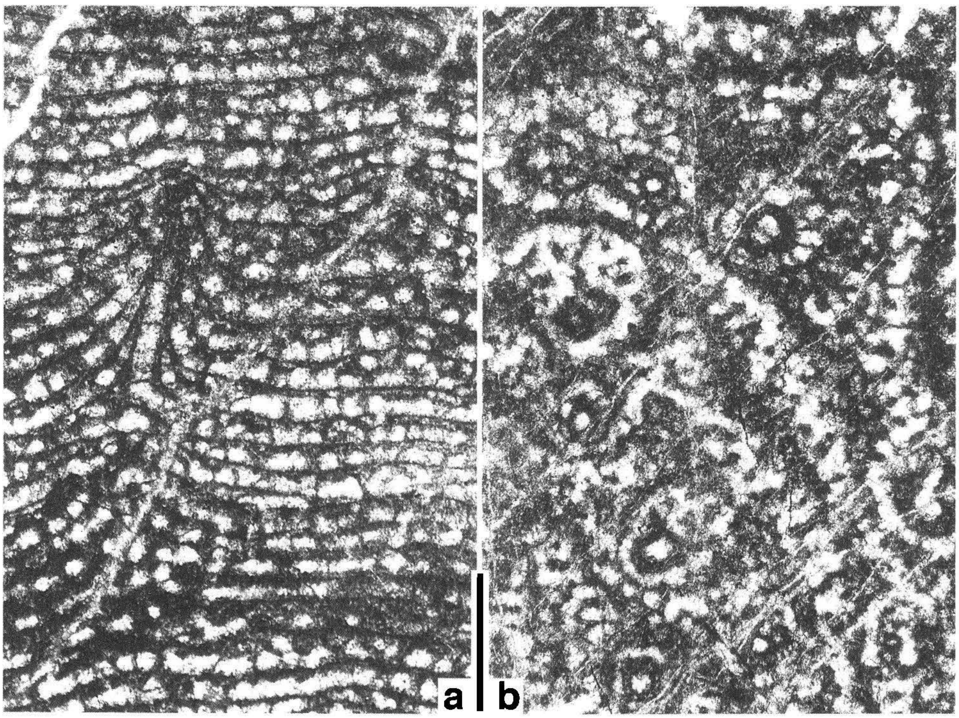

Fig. 2: *Pseudotrupetostroma anacontentoae* n. sp., holotype (DPM-00276 / S15); location "Guadámez II", Peñón Cortado Limestone (Upper Emsian). The scale is 1 mm long. a) longitudinal section; b) tangential section.

Pseudotrupetostroma anacontentoae n. sp.
(Fig. 2)

Material: The holotype (DPM-00276 / S15) and four paratypes (DPM-00276 / S8, S18, S19, S21). All coenostea are from the Peñón Cortado Limestone (Upper Emsian) of the location "Guadámez II".

Derivation of name: After Ana María Contento, my beloved wife.

Diagnosis: A *Pseudotrupetostroma* species with 8–12 pillars per 2 mm, 9–12 laminae per 2 mm, and a well developed astrorhizal system with axial canals each having 1–2.5 mm distance from each other.

Description: The 8–65 mm thick coenostea have a laminar growth form.

The longitudinal (=vertical) section shows persistent laminae, which are, more or less, at regular distances updomed to form mamelons. The mamelons have a maximum height of 0.5 mm. In the centre of each mamelon there is a longitudinally oriented axial canal with 0.145–0.185 mm diameter. The longest measured axial canal is 4 mm in length. Into the longitudinally oriented axial canals run horizontal-oriented astrorhizal canals, which are smaller than the axial canals. Axial canals and horizontal astrorhizal canals commonly contain curved dissepiments.

The laminae are 0.025–0.185 mm thick. The average thickness of the laminae is about 0.08–0.09 mm. Laminae are spaced from 9 to 12 per 2 mm. The means of laminar spacing range from 10.0 to 10.5 per 2 mm. Each lamina contain one and sometimes two microlaminae. Rarely does any lamina contain three microlaminae. The 0.01–0.03 mm thick, compact microlamina is thickened by cellular skeletal material, which looks like the skeletal material of the pillars.

The pillars are 0.035–0.165 mm thick. The average thickness of the pillars is about 0.09–0.10 mm. The pillars are spaced from (7-) 8 to 12 per 2 mm. The means of pillar spacing range from 9.5 to 9.8 per 2 mm. The pillars are of various shapes: spool, T, Y, or V-shaped. Locally the pillars are superposed through 3–8 interlaminar spaces. However, the majority of the pillars are not superposed.

The microstructure of pillars and laminae is cellular. In some places the microstructure was preserved well enough to make the following observations: It is an irregular grid of compact microelements each of which is about 0.010–0.015 mm thick, which form meshes of about 0.025–0.03 mm in size. The clear cellules in the centre of the meshes are about 0.01–0.02 mm in diameter. Clear vacuoles of about 0.03–0.04 mm in diameter commonly occur.

In the tangential section, the longitudinally oriented axial canals are relatively evenly distributed. They are at a distance of 1 to 2.5 mm from each other. The axial canals have a diameter of 0.14–0.20 mm. A concentric orientation of laminae around axial canals is visible. In the tangential section the pillars are 0.025–0.140 mm thick. Many pillars are isolated with an irregular outline. However, the pillars often fuse to become labyrinthine structures.

Comparisons: The Spanish material shows the diagnostic characters of the genus *Pseudotrupetostroma* CHALFINA & JAVORSKIJ, 1971, which were pointed out by STEARN (1993, p. 217–218) and STEARN et al. (1999, p. 48).

Stromatopora pellucida artyschensis JAVORSKIJ, 1955 from the Givetian of Siberia, the type species of *Pseudotrupetostroma*, shows some similarities with the Spanish specimens, but can be easily distinguished by either having a lower number of pillars and laminae (about 2 laminae per 1 mm, maximum 4 laminae per 1 mm) and having a stronger superposition of the pillars (JAVORSKIJ, 1955, p. 100–101). In *Stromatopora pellucida pellucida* JAVORSKIJ, 1955 from the Lower Devonian and the Givetian of Siberia, the laminae are spaced 8–9 per 2 mm and there are up to 6 pillars per 1 mm (JAVORSKIJ, 1955, p. 91–92). Therefore, the skeletal dimensions of *Stromatopora pellucida pellucida* JAVORSKIJ, 1955 resemble *Pseudotrupetostroma anacontentoae* n. sp. However, the pillars in *Stromatopora pellucida pellucida* JAVORSKIJ, 1955 are more superposed and there are not as many axial canals.

Apart from the type species, STEARN (1993, p. 218) assigns 9 other species to this genus and WEBBY & ZHEN (1993, p. 338–342) and WEBBY et al. (1993, p. 152–156) describe three other *Pseudotrupetostroma* species from the Emsian of Australia. All of these species can be distinguished from the Spanish specimens by either having a lower number of pillars and laminae or having a stronger superposition of pillars. Only the following species are similar enough to deserve to be compared with *Pseudotrupetostroma anacontentoae* n. sp.:

Pseudotrupetostroma jessiense WEBBY & ZHEN, 1993 from the Emsian of New South Wales (Australia) has a very similar appearance, but the skeletal elements are thicker and significantly more widely spaced (5–8 laminae per 2 mm and 4–7 pillars per 2 mm) and the astrorhizae are 8–10 mm apart (WEBBY & ZHEN, 1993, p. 338–340). The spacing of the unnamed *Pseudotrupetostroma* sp. described by WEBBY et al. (1993, p. 156) from the Lower Emsian of Victoria (Australia) is very similar to *Pseudotrupetostroma anacontentoae* n. sp., but the pillars of the Australian species are thicker and more superposed.

Pseudotrupetostroma cincinnatum (CHALFINA, 1960) from the Middle Devonian of the Salair (Russia) looks similar to *Pseudotrupetostroma anacontentoae* n. sp., but the pillars are thicker and more widely spaced (3–6 laminae per 1 mm and 2–3 pillars per 1 mm) (CHALFINA, 1960, p. 345). *Pseudotrupetostroma yangmeishanensis* (YANG & DONG, 1963) from the Givetian of China has 14–16 microlaminae per 2 mm and 6–8 pillars per 2 mm, but the pillars are much more uniformly superposed than the pillars of *Pseudotrupetostroma anacontentoae* n. sp.

QI & STEARN (1993, p. 723–727) and STEARN (2001, p. 23) assign *Taleastroma vitreum* GALLOWAY, 1960 to *Pseudotrupetostroma*. However, *Pseudotrupetostroma vitreum* (GALLOWAY, 1960) differs from

Pseudotrupetostroma anacontentoae n. sp. not only in the appearance, but also in the skeletal dimensons (6 laminae per 2 mm, about 5 pillars per 2 mm, and 0.1–0.34 mm pillar diameter) (GALLOWAY, 1960, p. 631).

In my opinion, *Trupetostroma cellulosum* LECOMPTE, 1952 from the Givetian and Frasnian of Belgium (LECOMPTE, 1952, p. 233–234) is also a species of *Pseudotrupetostroma*. The appearance of *Pseudotrupetostroma cellulosum* (LECOMPTE, 1952) is very similar to *Pseudotrupetostroma anacontentoae* n. sp. Both species are obviously closely related, but *Pseudotrupetostroma cellulosum* (LECOMPTE, 1952) can be distinguished by its skeletal dimensions: 19–20 laminae per 5 mm, 19–20 pillars per 5 mm, and 0.1–0.2 mm pillar diameter (LECOMPTE, 1952, p. 233). Furthermore, both species commonly contain axial canals, but they are more closely spaced in *Pseudotrupetostroma anacontentoae* n. sp.

Distribution: *Pseudotrupetostroma* was hitherto known only from the Emsian to the Givetian in Australia, Asia, and Canada. *Pseudotrupetostroma cellulosum* (LECOMPTE, 1952) and *Pseudotrupetostroma anacontentoae* n. sp. prove that this genus also occurred in Europe.

Syringostromella zintchenkovi (CHALFINA, 1960)

Descriptions are given by CHALFINA (1960, p. 327–328), WEBBY et al. (1993, p. 163), and PROSH & STEARN (1996, p. 34). Hitherto *Syringostromella zintchenkovi* has been found in the Upper Lochkovian of Russia (CHALFINA, 1960), the Pragian of Victoria (Australia) (WEBBY et al., 1993), and the Lower Emsian of Arctic Canada (PROSH & STEARN, 1996).

Parallelostroma sinense YANG & DONG, 1979

This species is described by YANG & DONG (1979, p. 73) from the Emsian of Guangxi (China). DONG & WANG (1989, p. 272, p. 290) found *Parallelostroma sinense* YANG & DONG, 1979 in the lower Middle Devonian of Guangxi (China).

4.2. Locations

It is remarkable that in neither of the two locations could any stromatoporoid with a branched coenosteum be found. Furthermore, stromatoporoids with thin-layered encrusting growth form are very rare – only one specimen of *Clathrocoilona* from "Guadámez II" has this growth form.

At location "Guadámez II" there occur *Actinostroma compactum* RIPPER, 1933, *Schistodictyon* n. sp. aff. *amygdaloides* (LECOMPTE, 1951), *Clathrocoilona* sp., *Stromatopora* ex gr. *polaris* (STEARN, 1983), *Pseudotrupetostroma anacontentoae* n. sp., and *Parallelostroma sinense* YANG & DONG, 1979. However, at "Peñón Cortado" only *Plectostroma salairicum* (JAVORSKIJ, 1930) and *Syringostromella zintchenkovi* (CHALFINA, 1960) could be found.

The differences in the faunal composition between both locations could be explained by different facies.

Compiling the known stratigraphical distributions of the species found, both faunas strongly suggest an Emsian age for the "Peñón Cortado Limestone". Indeed, the dating of the stromatoporoids is consistent with the stratigraphical assignment of RODRÍGUEZ GARCÍA (1978) and MORENO-EIRIS et al. (1995).

5. DISCUSSION

5.1. Reefs

Returning to the question posed earlier, why the Lower Devonian stromatoporoids built only very few reefs, we can state that the observations made in the Sierra Morena support the results of the investigations on the stromatoporoids of Bohemia (MAY 1999a, 2002):

Not only the both localities presented in this paper, but also some other localities, which are now under investigation, show the same picture: in the Sierra Morena, stromatoporoids with branched coenostea are totally absent and stromatoporoids with thin-layered encrusting growth form are very rare. However, these same growth forms nearly everywhere occur in the Givetian–Frasnian reefs. Perhaps these types of stromatoporoids were very important for the Givetian–Frasnian reefs, and their absence was an obstacle for reef construction.

Nevertheless, much more research on the stromatoporoid fauna will be necessary to prove this hypothesis. Furthermore, it will be necessary to investigate other fossil groups in order to gain a deeper understanding of the possible interactions between them. In addition, the possible influence of water temperature on the reef development should not be ignored. Up to now we can not exclude the possibility that upwelling cold water hindered reef development in the Sierra Morena as CARLS (1999) assumed to be the case in the Lower Devonian of Central Spain.

5.2. Biogeography

All stromatoporoid species collected in the Sierra Morena have been recorded for the first time from Spain.

All genera found in the Sierra Morena are known from beds of Emsian age in other parts of the Old World Realm (STEARN et al., 1999). The Old World Realm extended from Australia over Asia and Europe to Canada (BOUCOT, 1988; PEDDER & OLIVER, 1990; STOCK, 1990, 1997). On the species level the same pattern as on the genus level is visible: all identified species are known from beds of Emsian age in other parts of the Old World Realm. Furthermore, the closest relatives of both new species *Schistodictyon* n. sp. aff. *amygdaloides* (LECOMPTE, 1951) and *Pseudotrupetostroma anacontentoae* n. sp. lived in the Old World Realm.

Table 1 compares the stromatoporoid fauna of the Sierra Morena with the following recently investigated sites in the Old World Realm:

Middle Pragian of Bohemia (MAY, 1999a, 2002);

Pragian to Lower Emsian of Victoria (Australia) (WEBBY et al., 1993);

Lower Emsian to Lower Eifelian of Arctic Canada (PROSH & STEARN, 1996).

The stromatoporoid fauna of the Sierra Morena displays the least amount of conformity with the Middle Pragian of Bohemia, in spite of the small geographical distance between them. This is probably a result of the stratigraphical distance between them.

However, the stromatoporoid fauna of the Sierra Morena displays a high level of conformity with the synchronous faunas in Victoria (Australia) and Arctic Canada. Such close connections between very distant sites are most remarkable because the Emsian was the time of the strongest faunal provincialism during the Devonian period (BOUCOT, 1988, p. 211–212, p. 219; PEDDER & OLIVER, 1990, p. 267; OLIVER & PEDDER, 1994, p. 185; MAY, 1995, p. 39).

Now we should prove the relations between the stromatoporoid fauna of the Sierra Morena and the stromatoporoid fauna of the Eastern Americas Realm: the stromatoporoid fauna of the Eastern Americas Realm is characterized by the occurrence of *Habrostroma* and by the absence of species of the order Actinostromatida (STOCK, 1990, p. 258; STOCK, 1994; STOCK, 1997, p. 285). However, the stromatoporoid fauna of the Sierra Morena does not contain any *Habrostroma*, but with *Actinostroma compactum* RIPPER, 1933 and *Plectostroma salairicum* (JAVORSKIJ, 1930) two species of the order Actinostromatida. Consequently, the fauna of the Sierra Morena does not show any relation to that of the Eastern Americas Realm.

6. CONCLUSION

The presented research contributed to both questions mentioned in the introduction. However, to date, we have been unable to answer either of the questions fully. Further investigations will be required in order to confirm the presented, preliminary results.

Concerning the reef building potential of Lower Devonian stromatoporoids, the observations in the Sierra Morena support the observations made in Bohemia. In this way, more evidence has emerged to suggest that stromatoporoids with branched coenostea and stromatoporoids with thin-layered encrusting coenostea may have played a crucial role in the construction of the Devonian stromatoporoid reefs.

The stromatoporoids collected hitherto in the Sierra Morena bear a strong relationship to the Emsian fauna of Victoria (Australia) and Arctic Canada, but are unrelated to those of the Eastern Americas Realm. However, to date, we can not state definitely that there was no refuge for American stromatoporoids in Southern Spain, but the probability is low.

The exclusion of Bohemia together with these preliminary results from the Sierra Morena have caused us to doubt whether or not there was any refuge for stromatoporoids of the Eastern Americas Realm in Europe. However, it still remains a possibility, that we might find such a refuge in other parts of Spain or, indeed, France (e. g. Armorican Massif).

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References

AVLAR, H. & MAY, A., 1997: Zur Fauna und Stratigraphie der *cultrijugatus*-Schichten (Wende Unter-/Mittel-Devon) im West-Sauerland (Rheinisches Schiefergebirge). – Coral Research Bulletin, **5**: 103–119, Dresden.

BOUCOT, A.J., 1988: Devonian Biogeography: An Update. – In: MCMILLAN, N.J., EMBRY, A.F. & GLASS, D.J. (Eds.): Devonian of The World, Volume III: Paleontology, Paleoecology and Biostratigraphy. – Canadian Society of Petroleum Geologists, Memoir, **14**: 211–227, Calgary.

CARLS, P., 1999: El Devónico de Celtiberia y sus fósiles. – In: GÁMEZ VINTANED, J.A., & LIÑÁN, E. (Eds.): Memorias de las VI Jornadas Aragonesas de Paleontología "25 años de Paleontología Aragonesa". – 101–164, Zaragoza (Institución "Fernando el Católico").

CHALFINA, V.K., 1960: Otrjad Stromatoporoidea. [Devonskaja sistema]. – In: CHALFIN, L.L. (Ed.): Biostratigrafija paleozoja Sajano-Altajskoj gornoj oblasti, Tom II, Srednij paleozoj. – Trudy sibirskogo naučno-issledovatel'skogo Instituta Geologii, Geofiziki i mineral'nogo Syr'ja (SNIIG-GIMS), **20**: 323–349, 602–633, Novosibirsk.

DONG, D. & WANG, S., 1989: Devonian stromatoporoid biota of northern Guangxi and mountlike superimposed bioherm of Huanjiang county – with remarks on the distribution of the Devonian and sedimentary paleogeography in this area. – Memoirs of Nanjing Institute of Geology and Palaeontology, **26**: 235–290, Nanjing (Science Press).

GALLOWAY, J.J., 1960: Devonian stromatoporoids from the lower Mackenzie valley of Canada. – Journal of Paleontology, **34**: 620–636, Tulsa.

GARCÍA-ALCALDE, J.L., CARLS, P., PARDO ALONSO, M.V., SANZ LÓPEZ, J., SOTO, F., TRUYOLS-MASSONI, M. & VALENZUELA-RÍOS, J.I., 2002: Devonian. – In: GIBBONS, W. & MORENA, T. (Eds.): The Geology of Spain., 67–91, London (Geological Society).

JAVORSKIJ, V.I., 1930: Actinostromidae iz devonskich otlozenij okrain Kuzneckogo bassejna i Urala. – Izvestija geologiškovo komiteta, **49** (4): 473–496, Moskva, Leningrad.

JAVORSKIJ, V.I., 1955: Stromatoporoidea Sovetskogo Sojuza. Cast' pervaja. – Trudy vsesojuznogo naučno-issledovatel'skogo geologičeskogo Instituta (VSEGEI), Novaja Serija, **8**: 173 p., Moskva.

LECOMPTE, M., 1951: Les stromatoporoides du Dévonien moyen et supérieur du bassin de Dinant. Première Partie. – Institut royal des Sciences naturelles de Belgique, Memoires, **116**: 1–216, Bruxelles.

LECOMPTE, M., 1952: Les stromatoporoides du Dévonien moyen et supérieur du bassin de Dinant. Deuxième Partie. – Institut royal des Sciences naturelles de Belgique, Memoires, **117**: 217–359, Bruxelles.

MAY, A., 1995: Relationship among sea-level fluctuation, biogeography, and bioevents of the Devonian: an attempt to approach a powerful, but simple model for complex long-range control of biotic crises. – Geolines, **3**: 38–49, Praha.

MAY, A., 1999a: Revision of the Silurian and Devonian stromatoporoids of Bohemia described by Pocta (1894). – Journal of the Czech geological Society, **44** (1–2): 167–180, Prague.

MAY, A., 1999b: Stromatoporen aus dem Ober-Emsium (Unter-Devon) der Sierra Moreno (Süd-Spanien). – Münstersche Forschungen zur Geologie und Paläontologie, **86**: 97–105, Münster.

MAY, A., 2002: Bisher noch nicht bekannte Stromatoporen aus dem Pragium (Unterdevon) von Koneprusy (Böhmen). – Coral Research Bulletin, **7**: 115–140, Dresden.

MORENO-EIRIS, E., PEREJÓN, A., RODRÍGUEZ, S. & FALCES, S., 1995: Paleozoic Cnidaria and Porifera from Sierra Morena. – VII International Symposium on Fossil Cnidaria and Porifera, Field Trip D: 68 p., Madrid.

OLIVER, W.A. & PEDDER, A.E.H., 1994: Crises in the Devonian history of the rugose corals. – Paleobiology, **20** (2): 178–190, Ithaca / New York.

PEDDER, A.E.H. & OLIVER, W.A., 1990: Rugose coral distribution as a test of Devonian palaeogeographic models. – In: MCKERROW, W.S. & SCOTESE, C.R. (Eds.): Palaeozoic Palaeogeography and Biogeography. – Geological Society, Memoir, **12**: 267–275, London.

PROSH, E. & STEARN, C.W., 1996: Stromatoporoids from the Emsian (Lower Devonian) of Arctic Canada. – Bulletins of American Paleontology, **109** (349): 5–66, Ithaca / New York.

QI, W. & STEARN, C.W., 1993: Stromatoporoids from the Slave Point Formation (Givetian) at Evie Lake, Northeastern British Columbia. – Acta Scientiarium Naturalium Universitatis Pekinensis (Pei-ching ta hsueh hsueh pao), **29** (6): 715–728, Beijing.

RODRÍGUEZ GARCÍA, S., 1978: Corales rugosos del Devónico de la sierra del Pedroso. – Estudios geologicos, **34**: 331–350, Madrid (Institut de investigaciones geologicas Lucas Mallada).

STEARN, C.W., 1983: Stromatoporoids from the Blue Fiord Formation (Lower Devonian) of Ellesmere Island, Arctic Canada. – Journal of Paleontology, **57** (3): 539–559, Tulsa.

STEARN, C.W., 1990: Stromatoporoids from the allochthonous reef facies of the Stuart Bay Formation (Lower Devonian), Bathurst Island, Arctic Canada. – Journal of Paleontology, **64** (4): 493–510, Lawrence.

STEARN, C.W., 1993: Revision of the order Stromatoporida. – Palaeontology, **36** (1): 201–229, London.

STEARN, C.W. (2001): Biostratigraphy of Devonian stromatoporoid faunas of Arctic and Western Canada. – Journal of Paleontology, **75** (1): 9–23, 3 Abb.; Lawrence.

STEARN, C.W., WEBBY, B.D., NESTOR, H. & STOCK, C.W., 1999: Revised classification and terminology of Palaeozoic stromatoporoids. – Acta Palaeontologica Polonica, **44** (1): 1–70, Warszawa.

STOCK, C.W., 1990: Biogeography of the Devonian stromatoporoids. – In: MCKERROW, W.S. & SCOTESE, C.R. (Eds.): Palaeozoic Palaeogeography and Biogeography. – Geological Society, Memoir, **12**: 257–265, London.

STOCK, C.W., 1994: Stromatoporoid paleobiogeography of the Eastern Americas Realm during the Lochkovian Age (Early Devonian). – In: SOEST, R.W.M. van, KEMPEN, T.M.G. van & BRAEKMAN, J.-C. (Eds.): Sponges in Time and Space: Biology, Chemistry, Paleontology. – 23–27, Rotterdam (Balkema).

STOCK, C.W., 1997: Paleobiogeographical range of North American Devonian stromatoporoids: roles of global and regional controls. – In: PEREJÓN, A. & COMAS-RENGIFO, J. (Eds.): Proceedings of the VII International Symposium on Fossil Cnidaria and Porifera held in Madrid, Spain, 1995, Volume II. – Boletín de la Real Sociedad Española de Historia Natural (Seccíon Geológica), **92** (1–4): 281–288, Madrid.

WEBBY, B.D. & ZHEN, Y.Y., 1993: Lower Devonian stromatoporoids from the Jesse Limestone of the Limekilns area, New South Wales. – Alcheringa, **17** (2): 327–352, Brisbane.

WEBBY, B.D. & ZHEN, Y.Y., 1997: Silurian and Devonian clathrodictyids and other stromatoporoids from the Broken River region, north Queensland. – Alcheringa, **21** (1): 1–56, Brisbane.

WEBBY, B.D., STEARN, C.W. & ZHEN, Y.Y., 1993: Lower Devonian (Pragian–Emsian) stromatoporoids from Victoria. – Proceedings of the Royal Society of Victoria, **105** (2): 113–185, Melbourne.

YANG, K.-C. & DONG, D.-Y., 1963: Stromatoporoids from the Jiwozhai Member, upper part of the Middle Devonian of Dushan District, Gueizhou (Kueichow). – Acta palaeontologica sinica, **11** (2): 148–177, Beijing.

YANG, J. & DONG, D., 1979: Devonian stromatoporoids from central and eastern parts of Guangxi, China. – Palaeontologia sinica, new series B, **14** [whole number 157]: 89 p., Beijing (Science Press).