Radiastraea (Anthozoa, Rugosa) from the Emsian and Eifelian (Devonian) of Aviados, northern Spain

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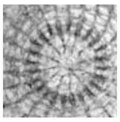

This paper describes a colonial rugose coral from the upper Emsian or lower Eifelian of Aviados (Provincia León, northern Spain). This colony, which has been figured as *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) by Almela & Revilla (1950), belongs in fact to *Radiastraea arachne* Stumm, 1937. It is the first reported occurrence of the genus *Radiastraea* from Europe, and an example of close palaeobiogeographical relationships between the Cantabrian Mountains and North America during the Emsian. *Cantabriastraea* Schröder & Soto, 2003 is probably only a marginal case of *Radiastraea* Stumm, 1937. The lectotype of *Phillipsastrea torreana* var. *minuta* Almela & Revilla, 1950 from the upper Emsian to lower Eifelian or upper Givetian of Aviados (Provincia León, northern Spain) is designated and described in detail. It is a subspecies of *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) with 10–12 major septa and a tabularium diameter of 1.9–2.1 mm. • Key words: Anthozoa, biogeography, Devonian, systematics, rugose corals, Spain.

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The Museo Geominero in Madrid holds very important historical collections of fossils from Spain and the Western Sahara that are registered in an exemplary manner in a well developed database (Rabano & Arribas 1997). This enables a revision of the Spanish Devonian corals in the Museo Geominero, which has been initiated by May (2005). As part of this work, the present author revises the original material of Almela & Revilla (1950).

Among other fossils, Almela & Revilla (1950) described and figured two distinct, but very similar colonial rugose corals of the genus *Phillipsastrea* from the "Couvinian" of Aviados on the southern slope of the Cantabrian Mountains. Both colonies are stored in the collections of the Museo Geominero. The fact that Almela & Revilla (1950) gave clear information about the localities where the corals were found, but neither made any thin section of the corals, nor gave sufficient descriptions of them, motivated the present author to prepare thin sections of these colonies. Surprisingly, the thin sections show that these very similar looking corals are not closely related, and that only the colony named *Phillipsastrea torreana* var. *minuta* by Almela & Revilla (1950, p. 58, p. 60, pl. 3, fig. 5) belongs to *Phillipsastrea*.

The other colony (Almela & Revilla 1950, pl. 3, fig. 4) belongs to *Radiastraea*, an American genus which was not previously known from Europe and most of Asia. The finding of a *Radiastraea* species in the collections of the Museo Geominero is of particular interest, because it provides evidence of a close relationship between the Cantabrian Mountains and North America during the Emsian, which was the time of strongest faunal provincialism during the Devonian period. Consequently, the present paper gives a detailed description of the *Radiastraea*. Furthermore, to facilitate the distinction of this *Radiastraea* from superficially similar species of *Phillipsastrea*, *Phillipsastrea torreana minuta* Almela & Revilla, 1950 is also described in detail.

Provenance of the material

The investigated colonies came from two different localities in the vicinity of Aviados (Provincia León). Both are classified as "Couvinian" by Almela & Revilla (1950). Aviados is a very small village near La Vecilla de Curueño, on regional road LE-626 from La Robla to Boñar. The Aviados area has been famous since the nineteenth century for its wealth of fossil deposits, which occur in the Santa Lucía Formation (Méndez-Bedia *et al*. 1994, Fernández *et al*. 1995, p. 41). The Santa Lucía Formation belongs mainly to the upper Emsian, while only the uppermost part belongs to the lower Eifelian (García-López 1986, Méndez-Bedia *et*

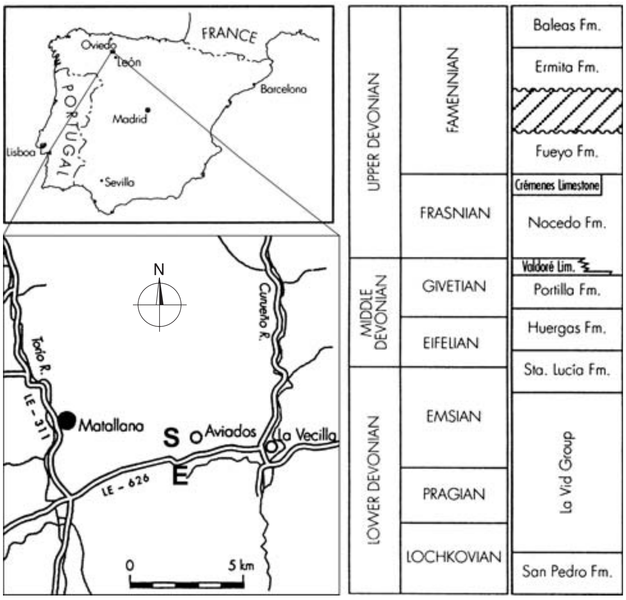


Figure 1. The geographical position of the localities and the stratigraphy of the Devonian in the area. E = outcrop "El Cueto", S = outcrop "Sierra Carro". Modified after Fernández *et al*. (1995, figs 1, 8).

al. 1994, Fernández *et al*. 1995, García-Alcalde *et al*. 2002). It consists of a 250 m thick series of limestones and argillaceous limestones with interbedded thin shaly levels (Méndez-Bedia 1976; Méndez-Bedia *et al.* 1994, p. 164; Fernández *et al*. 1995, p. 16; Hofmann & Keller 2006). Furthermore, the Portilla Formation, an upper Givetian limestone (Fernández *et al.* 1995, García-Alcalde *et al.* 2002), also crops out in the vicinity of Aviados. The geographical position of the localities and the stratigraphy of the Devonian in this area are shown in Fig. 1.

The colony now described as *Radiastraea arachne* (stock No. 1519D) comes from an outcrop on El Cueto hill, which lies one km southwest from Aviados, and whose top is comprised of grey limestones (Almela & Revilla 1950, p. 50). Almela & Revilla (1950, pp. 50–51) collected their fossils from the top, the northern slope, and the western slope of the hill up to the cliff that limits El Cueto.

Almela & Revilla (1950, p. 51) reported brachiopods from the limestones of the El Cueto outcrop, including *Spirifer cultrijugatus.* Regardless of whether this was a true *Paraspirifer cultrijugatus* (F. Roemer, 1844) or only another species of *Paraspirifer,* the stratigraphical information is evident: *Paraspirifer* originated in the lower upper Emsian and became extinct in Europe and Northern Africa at the end of the lower Eifelian (Godefroid 1980, pp. 85–92, May 1996, pp. 39–40, May & Avlar 1996, p. 51, May 1997, pp. 295–296, García-Alcalde *et al.* 2002, p. 75, p. 80). It is important to note that no brachiopod exists in the Givetian and Frasnian that could be confused with *Paraspirifer cultrijugatus*. Consequently, the El Cueto outcrop is upper Emsian or lower Eifelian in age and belongs (based on the lithology described by Almela & Revilla 1950) to the Santa Lucía Formation.

Almela & Revilla (1950) found the lectotype of *Phillipsastrea torreana minuta* (stock No. 1520D) in the "Sierra Carro" outcrop on a 1,197 m high hill with a limestone band at its summit, one km west from Aviados (Almela & Revilla 1950, p. 51). They collected the fossils from the top and the uppermost part of the southern slope of the hill, but unfortunately did not include any useful index brachiopods in their fossil list from the limestones of the Sierra Carro outcrop (Almela & Revilla 1950, pp. 51–52). Therefore, we cannot be sure that this locality belongs to the upper Emsian or (lower) Eifelian as assumed by Almela & Revilla (1950), or to the upper Givetian.

Systematic description

Class Anthozoa Ehrenberg, 1834
Subclass Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verrill, 1865
Family Disphyllidae Hill, 1939
Subfamily Paradisphyllinae Jell, 1969

Genus *Radiastraea* Stumm, 1937

Type species. – *Radiastraea arachne* Stumm, 1937.

Diagnosis. – See Hill (1981, pp. 272–275).

Remarks. – *Cantabriastraea* Schröder & Soto, 2003, with the type species *Cantabriastraea cantabrica* Schröder & Soto, 2003 from the Emsian of the Cantabrian Mountains (Schröder & Soto 2003, pp. 552–553), is very similar to *Radiastraea* Stumm, 1937. Schröder & Soto (2003, p. 553) mention only a few differences of *Radiastraea*, such as "differently structured tabularium" and "generally complete septa". The arched tabulae of *Cantabriastraea* makes it even more similar to *Radiastraea*. Furthermore, the septal development of *Radiastraea verrilli* (Meek, 1867), redescribed by Pedder (1980, pp. 598–600, pl. 2, figs 5–8), shows some similarities to the septal development of *Cantabriastraea cantabrica* Schröder & Soto, 2003. Consequently, it is very doubtful that *Cantabriastraea cantabrica* Schröder & Soto, 2003 deserves to be distinguished on a generic level from *Radiastraea arachne* Stumm, 1937. It is probably only a marginal case of *Radiastraea*. However, an investigation of the different species of *Radiastraea* and their variability would be necessary before making a definitive decision.

Occurrence. – Hill (1981, p. 275) gave the geographical and stratigraphical distribution of *Radiastraea* as the upper Silurian of the Canadian Arctic, the Emsian of Nevada and

Australia, and the lower Middle Devonian of North America. Subsequently, Hou (1988, pp. 187–188) described two species of *Radiastraea* from the *serotinus* conodont zone (upper Emsian) of Sichuan in China, Yu & Cai (1983, p. 44) described another from the Early Middle Devonian of Gansu (Northwest China), and the Xi'an Institute of Geology and Mineral Resources (1983, pp. 86–87) described four species of *Radiastraea* from the Devonian of Northwest China. However, up to now *Radiastraea* had not been known from Europe or other parts of Asia.

***Radiastraea arachne* Stumm, 1937**
Figure 2A–C

* 1937 *Radiastraea arachne* Stumm, n. sp.; Stumm, pp. 439–440, pl. 53, fig. 13, pl. 55, fig. 8.
1940 *Radiastraea arachne* Stumm. – Merriam, p. 53, 105, pl. 13, fig. 5.
v 1950 *Phillipsastrea torreana* Edw. Haime. – Almela & Revilla, p. 58 (14), p. 60 (16), pl. 3, fig. 4.
non 1956 *Radiastraea arachne* Stumm. – Warren & Stelck, pl. 1, fig. 8.
1964 *Radiastraea arachne* Stumm, 1937. – Pedder, p. 447, pl. 72, figs 1–3, pl. 73, figs 1–5.
1974 *Billingsastraea nevadensis* subsp. *arachne* (Stumm). – Merriam, p. 64, pl. 24, fig. 4 (see for further synonymy).
1976 *Radiastraea arachne* Stumm, 1937. – Oliver, p. 90, pl. 66, figs 1–4.

Holotype and diagnosis. – See Stumm (1937, pp. 439–440, pl. 53, fig. 13, pl. 55, fig. 8).

Material. – The complete colony figured by Almela & Revilla (1950, pl. 3, fig. 4) is stored in the palaeontological collection of the Museo Geominero (Madrid) under stock No. 1519D. One transversal and one longitudinal thin section have been prepared from it.

Description. – The corallum is flat discus-shaped with a width of 140 mm and a thickness of 23 mm. The holotheca on the underside of the corallum shows pock-like bulges that correspond to the corallites of the upper (distal) surface. The holotheca also shows fine growth wrinkles.

The distal surface of the corallum is slightly domed, with calical rims slightly raised (maximum one mm raised) above the calicular platform. The calicular pit is crater-shaped, 1–2 mm deep, typically circular in outline, and has a diameter of 2.6–3.6 mm (mostly 3.1–3.4 mm). The distances between neighbouring calical centres range between 6.0–12.5 mm (mostly 8.0–10.5 mm).

The transversal section shows that the corallum is normally thamnasterioid. Parts of the corallum are only rarely aphroid, where a gap is developed between the septa of neighbouring corallites. In the transversal section the corallite diameter is about 10 mm, the distances between neighbouring corallite centres are 7.5–10 mm, and the tabularia have diameters of 2.6–3.1 mm.

All measured corallites have 16 major septa and as many minor septa. The major septa are long and reach deep into the tabularium, but only in places reach the middle of the tabularium. In some corallites a few of the major septa touch each other in the middle of the tabularium. In other corallites, a periaxial space of 0.3–0.5 mm diameter completely lacks septa. Within the tabularium the major septa are 0.02–0.04 mm thick. They are straight or slightly wavy. At the margin of the tabularium the septa are wedge-shaped dilated.

Minor septa normally extend into the peripheral edge of the tabularium. But in rare cases the minor septa are slightly shorter and do not reach the peripheral edge of the tabularium.

In a part of the dissepimentarium that is close to the tabularium, all septa are remarkably thickened: Major septa are 0.12–0.2 mm (mostly 0.15–0.18 mm) thick and minor septa are 0.06–0.14 mm thick. In the peripheral part of the corallites there is no distinction between major and minor septa, they are all 0.04–0.10 mm thick.

The septa are usually smooth, but occasionally they develop very weak carinae that reach up to 0.04 mm into the lumen.

The longitudinal section shows a tabularium of 2.5–2.9 mm diameter, which is very clearly separated from the dissepimentarium. Complete tabulae occur only rarely. The complete tabulae are generally horizontally oriented. The vast majority of the tabulae are incomplete (= tabellae). Significantly, the tabellae are axially domed, which is typical for *Radiastraea* (Pedder 1964, p. 446). Periaxially elevated tabellae may be present. In the middle of the tabularium the tabellae are separated 0.06–0.6 mm from each other. Over a vertical distance of 5 mm the number of tabellae amount to 25.

The dissepiments are curved (globose to elongate). They are oriented vertically within the first row at the boundary to the tabularium. From there to the periphery, the orientation of the dissepiments rapidly becomes horizontal. Normally the dissepiments are approximately horizontally oriented. However, a very slight downward inclination from the inner boundary of the dissepimentarium to the periphery of the corallite is visible.

Remarks. – Without the use of thin sections it is difficult to distinguish this species from *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851; see below). Perhaps the occurrence of pock-like bulges on the underside of the corallum may serve as a distinctive mark, as neither *Phillipsastrea torreana* var. *minuta* Almela & Revilla, 1950, nor a colony of *Phillipsastrea torreana torreana* (Milne-Edwards & Haime, 1851) in the Museo Geominero show these bulges (see below).

However, the longitudinal and transversal sections show the typical characteristics of the genus *Radiastraea* Stumm, 1937, and fit well with the descriptions and figures of its type species *Radiastraea arachne* Stumm, 1937 by Stumm (1937), Pedder (1964), Merriam (1974), and Oliver (1976). Pedder (pers. comm. 2005) considers the existence of periaxially elevated tabellae as a diagnostic feature of *Radiastraea arachne*. The Spanish material also shows periaxially elevated tabellae, although they are not as well developed as in the holotype (Oliver 1976, pl. 66, fig. 4).

Radiastraea nevadensis (Stumm, 1937) shows some similarities to *Radiastraea arachne* Stumm, 1937, but has larger corallites with more septa (Stumm 1937, pp. 438–439, pl. 53, fig. 12, pl. 55, fig. 9; Merriam 1974, pp. 63–64, pl. 24, figs 1–3, 5–8). The decision of Merriam (1974) to reduce *arachne* to a variety of *nevadensis* is not valid, because *arachne* was proposed as a species, whereas the name *nevadensis* pertains to a variety.

Cantabriastraea cantabrica Schröder & Soto, 2003 from the Emsian of the Cantabrian Mountains (Schröder & Soto 2003, pp. 553–556, figs 6–9) can be distinguished easily from *Radiastraea arachne* Stumm, 1937 by the higher number of septa and the much more strongly developed carinae in *C. cantabrica*.

Radiastraea verrilli (Meek, 1867) from the late Eifelian of Canada, redescribed by Pedder (1980, pp. 598–600, pl. 2, figs 5–8), is also very similar to *Radiastraea arachne* Stumm, 1937, but has more strongly developed carinae. *Radiastraea norrisi* Pedder, 1980, from the late Eifelian of Canada (Pedder 1980, pp. 600–602, pl. 3, figs 3–6, pl. 4, figs 1–4), is very similar to *Radiastraea arachne* Stumm, 1937, but has somewhat thicker and less numerous septa, somewhat more strongly developed carinae, and contains more frequent gaps between the septa of neighbouring corallites. *Radiastraea tapetiformis* (Crickmay, 1960), also from the late Eifelian of Canada (Pedder 1980, p. 598, pl. 2, figs 1–4), has a much smaller corallite diameter and less numerous septa than *Radiastraea arachne* Stumm, 1937.

Hill (1978, p. 16) classified *Phillipsastrea aperta* Hill, 1942 from the Emsian of New South Wales with *Radiastraea*. Nevertheless, *Phillipsastrea aperta* Hill, 1942 is not comparable with the described corallum, because it has a corallite diameter of 12–15 mm and 19–20 septa of each order (Hill 1942, p. 154, pl. 2, fig. 7; Strusz 1965, pp. 547–549, pls 74, 75).

Radiastraea regularis Yu & Cai, 1983 from the Early Middle Devonian of Gansu (northwest China) can be easily distinguished from *Radiastraea arachne* Stumm, 1937 by its corallite diameter of 4.3–8.2 mm and 11–14 septa of each order (Yu & Cai 1983, pp. 44–45, pl. 10, fig. 2, pl. 11, fig. 4).

Among the four species of *Radiastraea* described by the Xi'an Institute of Geology and Mineral Resources (1983, pp. 86–87, pl. 26–27) from the Devonian of northwest China, only *Radiastraea xiawuraensis* Cao (in Xi'an Institute of Geology and Mineral Resources, 1983) is comparable to *Radiastraea arachne* Stumm, 1937. *Radiastraea xiawuraensis* Cao is in all dimensions a little smaller (6–7 mm corallite diameter, 2–2.3 mm tabularium diameter, 14–15 septa of each order) and the septa are slightly thicker (Xi'an Institute of Geology and Mineral Resources 1983, pp. 86–87, pl. 26, fig. 3). Apparently, *Radiastraea xiawuraensis* Cao is closely related to *Radiastraea verrilli* (Meek, 1867) and *Radiastraea norrisi* Pedder, 1980.

He (*in* Hou 1988) described two species of *Radiastraea* from the *serotinus* conodont zone (upper Emsian) of Sichuan (China) that are clearly distinct from *Radiastraea arachne* Stumm, 1937: *Radiastraea longmenshanensis* He with corallites of 6 mm diameter (*in* Hou 1988, pp. 187–188, pl. 18, fig. 4), and *Radiastraea? ertaiziensis* He *in* Hou 1988 with cerioid astreoid (!) corallites of 6–8 mm diameter and 12–14 septa of each order (Hou 1988, p. 188, pl. 18, fig. 6).

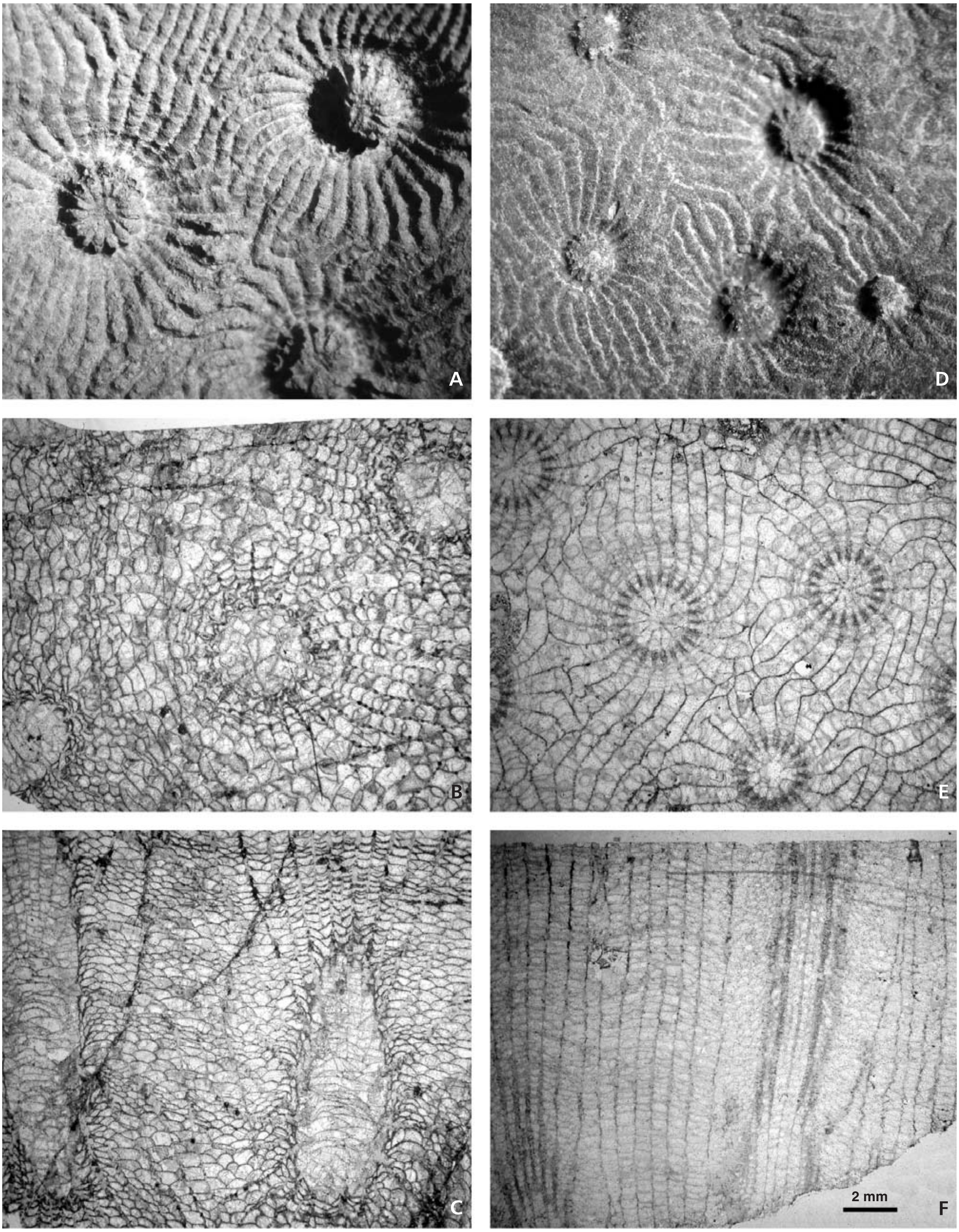
Pedder (pers. comm. 2005) believes that the corallum from the Devonian of western Canada figured by Warren & Stelck (1956, pl. 1, fig. 8) as *Radiastraea arachne* is a specimen of *Taimyrophyllum stirps* (Crickmay, 1960), which is a common late Eifelian species in the Norman Wells region of western Canada. *Taimyrophyllum stirps* is restricted to the Hume Formation in western Canada; it does not occur in the Hare Indian Shale according to Warren & Stelck (1956, pl. 1) (Pedder, pers. comm. 2005).

Occurrence. – The type stratum of *Radiastraea arachne* Stumm, 1937 occurs in the Bartine Member, *Eurekaspirifer pinyonensis* Zone (Zlichovian, early Emsian) of Nevada (Pedder 1980, p. 598).

All specimens of *Radiastraea arachne* Stumm, 1937 described or figured by Stumm (1937), Pedder (1964), and Merriam (1974) come from localities in central Nevada.

Following Johnson & Oliver (1977, p. 1466), *Radiastraea arachne* Stumm, 1937 is a characteristic coral of the coral zone D_2 within the Bartine Member of Nevada. Pedder & Murphy (2003, p. 602) gave the biostratigraphical

Figure 2. A–C – *Radiastraea arachne* Stumm, 1937, stock No. 1519D, outcrop "El Cueto", upper Emsian or lower Eifelian limestones (Santa Lucía Formation) of Aviados (Provincia León). • A – calices. • B – transversal thin section. • C – longitudinal thin section. • D–F – *Phillipsastrea torreana minuta* Almela & Revilla, 1950, lectotype, stock No. 1520D, outcrop "Sierra Carro", upper Emsian to lower Eifelian limestone (Santa Lucía Formation) or upper Givetian linestones (Portilla Formation) of Aviados (Prov. León). • D – calices. • E – transversal thin section. • F – longitudinal thin section. Scale bar represents 2 mm.


A
D
B
E
C
2 mm
F

range of the Bartine Member from an upper part of the *lenzi* conodont zone (lower Emsian) to a lower part of the *inversus* conodont zone (lower upper Emsian). Pedder & Murphy (2004, pp. 840, 841) restricted the occurrence of *Radiastraea arachne* from an upper part of the *lenzi* conodont zone to a lower part of the *gronbergi* conodont zone (upper lower Emsian).

Up to now, *Radiastraea arachne* Stumm, 1937 had only been known from the Emsian of North America. The above described corallum from the upper Emsian or lower Eifelian of Northern Spain does not only expand the geographical distribution of *arachne*, but also constitutes the first description of the genus *Radiastraea* in Europe. Remarkably, the European occurrence is only slightly younger than that of the material from Nevada.

Family Phillipsastreidae Hill, 1954

Genus *Phillipsastrea* d'Orbigny, 1849

Type species. – *Astrea (Siderastrea) hennahii* Lonsdale, 1840.

Diagnosis. – See Hill (1981, p. 281) and McLean (1993, p. 53).

Remarks. – There currently exists no full consensus about the definition of the genus *Phillipsastrea* d'Orbigny, 1849. Since the investigation of Scrutton (1968), most authors have accepted the existence of a pipe of horseshoe dissepiments as an important diagnostic criterion of *Phillipsastrea*. However, some recent authors refute this: e.g. Birenheide (1978, p. 99) and Sorauf (1998, pp. 70–73). Following Scrutton (1968, pp. 210–214), Hill (1981, p. 281), Coen-Aubert (1986, p. 46; 2002, p. 26), McLean (1989, pp. 239–240; 1993, p. 53; 1994), Errenst (1993, pp. 21–22), and Wang (1994, p. 408), the present author only includes species into this genus that contain an intermittently to completely developed pipe of horseshoe dissepiments.

Occurrence. – For geographical and stratigraphical distribution see Hill (1981, p. 281) and McLean (1993, pp. 57–58). Lists of synonymous genera and assigned species are given by McLean (1993, pp. 53–58) and Wang (1994, pp. 408–414).

***Phillipsastrea torreana torreana* (Milne-Edwards & Haime, 1851)**

1850 *Phillipsastrea Torreana*, n. s.; Verneuil & Haime, p. 162. (no description, only citation in a fossil list)

* 1851 *Syringophyllum? torreanum*; Milne-Edwards & Haime, p. 452.

non 1950 *Phillipsastrea torreana* Edw. Haime. – Almela & Revilla, p. 58 (14), p. 60 (16), pl. 3, fig. 4.

2002 *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851). – Coen-Aubert, pp. 30–31, pl. 4, figs 1, 2 (see for further synonymy).

non 2005 *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851). – Wrzołek, p. 178, fig. 9, tab. 3.

Lectotype. – See Coen-Aubert (2002, p. 30, pl. 4, figs 1, 2).

Diagnosis. – A species of *Phillipsastrea* with always smooth septa, 11–14 major septa, a tabularium diameter of 2.1–2.7 mm, and an astreoid corallum (Coen-Aubert 2002, p. 30).

Material. – A complete colony from the "Couvinian" of Sierra Carro (Provincia León) stored in the palaeontological collection of the Museo Geominero (Madrid) under the stock No. 1521D. It is probably from the type locality of *Phillipsastrea torreana minuta* Almela & Revilla, 1950 or its vicinity.

Description. – The flat discus-shaped corallum 1521D is mostly astreoid and only subordinately thamnasterioid. The corallite diameter is about 6–10 mm, the distance between neighbouring corallite centres is 7.0–9.5 mm, and the tabularium has a diameter of 2.1–2.3 mm. The corallites have 12–13 (usually 12) major septa and as many minor septa. The septa are smooth and lack carinae. The holotheca on the underside of the corallum shows only bulge-like concentric growth zones, which are spaced about 5 mm apart, and a radial striation produced by the septa. The corallum lacks pock-like bulges or similar structures.

Remarks. – Without the use of thin sections it is difficult to distinguish this species from *Radiastraea arachne* Stumm, 1937. The observed differences in the development of the holotheca could perhaps be used to distinguish them. However, the longitudinal and transversal sections show the typical characteristics of the genus *Phillipsastrea* d'Orbigny, 1849.

As explained below, *Phillipsastrea torreana minuta* Almela & Revilla, 1950 can be separated only on a subspecific level from *Phillipsastrea torreana torreana* (Milne-Edwards & Haime, 1851).

Phillipsastrea torreana torreana (Milne-Edwards & Haime, 1851) is very similar to *Phillipsastrea hennahi hennahi* (Lonsdale, 1840) from the Givetian of England, which was redescribed by Scrutton (1968, pp. 214–221, pls 1, 2). Both species are not only very similar in appearance, but also have comparable skeletal dimensions. Possible distinctive criteria may be the slightly stronger tendency to thamnasterioid growth and sometimes longer major septa in *Phillipsastrea hennahi hennahi.* Considering the high variability that Wrzołek (1993) described for *Phillipsastrea*, these criteria could never justify separation on a specific level if it were not for the fact that the septa of *Phillipsastrea hennahi hennahi* are not always smooth, but sometimes show roughened sides or rudimentary carinae (Scrutton 1968, p. 216; Errenst 1993, pp. 22, 23, fig. 3). The investigation of more material with known stratigraphical positions (see below) would be necessary for estimating the taxonomic importance of this difference in the development of the septa. However, *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) is currently accepted as an independent species.

The material from the upper Givetian of the Cantabrian Mountains classified by Wrzołek (2005, p. 178, fig. 9, tab. 3) with *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) does not belong to *torreana.* In the material of Wrzołek (2005), the septa are not smooth like in *torreana*, but have weakly developed carinae like in *Phillipsastrea hennahi* (Lonsdale, 1840). Furthermore, the material of Wrzołek (2005) has remarkably more septa (12.2–18.2 major septa at 7.6–10.5 mm corallite diameter).

Occurrence. – The corallum 1521D described above is of late Emsian to early Eifelian age, or of late Givetian age. Coen-Aubert (2002, p. 30) assumed that the lectotype of *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) from the Cantabrian Mountains probably comes from the Portilla Formation of the upper Givetian. However, considering that the original label of the lectotype states “Sabero, Leon” (Coen-Aubert 2002, p. 30) and that the well known Sabero fossils came from the Emsian of Colle (Fernández *et al*. 1995, p. 43; García-Alcalde 1999), an (upper) Emsian age of the lectotype of *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) is at least possible.

***Phillipsastrea torreana minuta* Almela & Revilla, 1950**
Figure 2D–F

*v 1950 *Phillipsastrea torreana* Edw. Haime var. *minuta* nov. var.; Almela & Revilla, p. 58 (14), p. 60 (16), pl. 3, fig. 5.

Lectotype. – Almela & Revilla (1950) did not define a holotype for *Phillipsastrea torreana* var. *minuta*. Furthermore, they reported it from both the El Cueto and the Sierra Carro outcrops. Consequently, it is possible, that they had more than one specimen of *Phillipsastrea torreana* var. *minuta*. However, the complete colony figured by Almela & Revilla (1950, pl. 3, fig. 5), which is stored in the palaeontological collection of the Museo Geominero (Madrid) under stock No. 1520D, is the only extant specimen. Herewith, this colony (stock No. 1520D), figured by Almela & Revilla (1950, pl. 3, fig. 5), is chosen as lectotype. One transversal and one longitudinal thin section have been prepared from it.

Diagnosis. – A subspecies of *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) with 10–12 (usually 12) major septa, a tabularium diameter of 1.9–2.1 mm, a distance between neighbouring calical centres of 4.5–10.0 mm (mostly 6.0–7.5 mm), and a thamnasterioid to astreoid corallum.

Description. – The corallum is flat discus-shaped with a width of 155 mm and a thickness of 45 mm. It has calices on the upper and underside surfaces. However, only the well developed and preserved calices of the upper surface are described in what follows.

On the upper surface, the calical rims are raised 0.5–2 mm above the calicular platform. The calicular pit is crater-shaped, typically circular in outline and has a diameter of 1.6–2.3 mm (mostly 1.9–2.1 mm). The distance between neighbouring calical centres is 4.5–10.0 mm (mostly 6.0–7.5 mm).

The transversal section shows that the corallum is thamnasterioid to astreoid. The astreoid parts, in which there is a false wall built by the bent endings of the septa separating neighbouring corallites, have a similar frequency as the thamnasterioid parts. Within the transversal section, the corallite diameter is 7–8 mm, the distance between neighbouring corallite centres 6.5–9.0 mm, and the diameter of the tabularium is 1.9–2.1 mm.

The septa are smooth and lack carinae. The measured corallites have 10–12 (mostly 12) major septa and as many minor septa. The major septa are long and reach deep into the tabularium, but in the middle there always remains a space of 0.1–0.6 mm diameter without any septa. Within the tabularium, the major septa are 0.03–0.04 mm thick. Minor septa end at the peripheral edge of the tabularium or extend up to 0.1 mm into the tabularium.

The part of the dissepimentarium which is close to the tabularium consists of a pipe of horseshoe dissepiments. Within the area of this pipe all septa and dissepiments are remarkably thickened, building a kind of inner wall. Here the major septa are 0.14–0.20 mm thick and the minor septa are 0.10–0.18 mm thick.

In the peripheral part of the corallites there is no distinction in thickness between major and minor septa, all of which are 0.02–0.06 mm (mostly 0.03–0.04 mm) thick.

The dissepiments are normally very thin (0.01–0.02 mm thick). However, they are thickened within the inner part of the dissepimentarium, and their thickness varies between 0.02 mm and 0.22 mm. The thickening of the dissepiments is most intensive within the pipe of horseshoe dissepiments.

The longitudinal section shows a tabularium in which the tabulae are weakly arched and spaced 0.15–0.4 mm from each other.

The innermost part of the dissepimentarium consists of one row of horseshoe dissepiments of 0.4–0.6 mm width. The dissepiments are curved (globose to elongate) towards the periphery. They show a downward inclination from the outer boundary of the row of horseshoe dissepiments to the periphery of the corallite. The dissepiments are more or less horizontally oriented at the periphery of the corallite.

Remarks. – The lectotype of *Phillipsastrea torreana* var. *minuta* Almela & Revilla, 1950 has the typical characteristics of the genus *Phillipsastrea* d'Orbigny, 1849, and shows many similarities with the description of the lectotype of *Phillipsastrea torreana* (Milne-Edwards & Haime, 1851) given by Coen-Aubert (2002, pp. 30, 31, pl. 4, figs 1, 2). However, the lectotype of *minuta* is somewhat smaller in all skeletal dimensions, and, furthermore, the thamnasterioid parts have a higher frequency in *minuta* than in *torreana.*

Two facts suggest that the differences between the lectotypes of *torreana* and of *minuta* are not only the normal variation expected within one population: 1) in the present article a corallum is described that fits very well with the lectotype of *Phillipsastrea torreana*, and 2) Almela & Revilla (1950) reported *minuta* from two different outcrops. However, considering the high variability that Wrzołek (1993) described from *Phillipsastrea*, *Phillipsastrea torreana minuta* Almela & Revilla, 1950 can be separated only on a subspecific level from *Phillipsastrea torreana torreana* (Milne-Edwards & Haime, 1851).

Phillipsastrea torreana minuta Almela & Revilla, 1950 shows some similarities to *Phillipsastrea hennahi hennahi* (Lonsdale, 1840) from the Givetian of England, which was redescribed by Scrutton (1968, pp. 214–221, pls 1, 2). *Phillipsastrea hennahi hennahi* has somewhat larger skeletal dimensions than *Phillipsastrea torreana minuta*, and its septa sometimes have roughened sides or rudimentary carinae (Scrutton 1968, p. 216; Errenst 1993, pp. 22, 23, fig. 3).

Phillipsastrea hennahi ussheri Scrutton, 1968 from the lower Frasnian of England has a comparable tabularium diameter and number of septa, but is distinguished from *Phillipsastrea torreana minuta* Almela & Revilla, 1950 by its strongly dilated septa, which form a dense inner wall (Scrutton 1968, pp. 221–226, pl. 3).

Phillipsastrea hennahi ranciae Coen-Aubert, 1986 from the upper Frasnian of Belgium (Coen-Aubert 1986, pp. 48–49, pl. 2) is very similar to *Phillipsastrea hennahi ussheri* Scrutton, 1968. *P. hennahi ranciae* has a dense inner wall, a slightly smaller number of septa, and a smaller tabularium, distinguishing it from *Phillipsastrea torreana minuta* Almela & Revilla, 1950.

Phillipsastrea torreana minuta Almela & Revilla, 1950 shows strong similarities to *Phillipsastrea tafilaltensis* Coen-Aubert, 2002 from the upper Givetian of Marocco (Coen-Aubert 2002, pp. 28, 29, pl. 1, fig. 8, pl. 2). However, in *Phillipsastrea tafilaltensis* the major septa leave a broad free space within the tabularium and the septa have some rudimentary carinae.

Phillipsastrea liujingensis Yu & Kuang, 1982 from the late Middle Devonian of Guangxi, China (Yu & Kuang 1982, pp. 258–259, pl. 2, fig. 4, pl. 3, fig. 1), and from the early Frasnian of Yunnan, China (Wang 1994, pp. 416–418, pls 61, 62) are very similar to *Phillipsastrea torreana minuta* Almela & Revilla, 1950. However, there are small carinae present on the sides of the septa of *P. liujingensis* that distinguish it from *Phillipsastrea torreana minuta* Almela & Revilla, 1950. *Phillipsastrea liujingensis* Yu & Kuang, 1982 is probably only a subspecies of *Phillipsastrea hennahi* (Lonsdale, 1840).

Phillipsastrea linearis Hill, 1942 from the late Emsian (Pedder, pers. comm. 2005) of New South Wales (Hill 1942, pp. 153–154, pl. 3, fig. 6) has similar skeletal dimensions as *Phillipsastrea torreana minuta* Almela & Revilla, 1950. However, in *P. linearis* the major septa are shorter and may be developed as discrete trabeculae.

Some colonies of *Pachyphyllum minutissimum* Webster, 1905 from the Frasnian of Iowa (Sorauf 1998, pp. 73–75, pl. 36, fig. 5, pls 37, 38) have skeletal dimensions similar to those of *Phillipsastrea torreana minuta* Almela & Revilla, 1950. However, the former are distinguished by the shorter major septa and the stronger thickening within the ring of horseshoe dissepiments.

Occurrence. – *Phillipsastrea torreana minuta* Almela & Revilla, 1950 is currently known only from the upper Emsian to lower Eifelian or the upper Givetian of Northern Spain.

Palaeobiogeographical relationships

The Lower and Middle Devonian shallow marine fauna has been divided into three marine faunal realms: the 1) Malvinokaffric Realm (central and southern South America, South Africa, Antarctica); 2) Eastern Americas Realm (eastern United States and eastern Canada, and northwestern South America); and 3) Old World Realm (western United States and western and northern Canada, Europe, northwestern Africa, Asia, and Australia) (Boucot 1988; Stock 2005a, p. 91). All parts of Spain clearly belong to the Old World Realm. One example of a rugose coral typical for the Old World Realm is *Phillipsastrea.*

The Eastern Americas Realm and the Old World Realm were separated by a land barrier in what is now North America. This barrier was composed of the Canadian Shield and the Transcontinental Arch (Oliver 1977; Stock

2005a, p. 93, fig. 3). In this context it is very interesting to look for evidence of a breach in the barrier. Findings of Eastern Americas faunal elements in Spain provide such evidence.

Several examples of migration between the Eastern Americas Realm (or America in general) and Spain are known from the Devonian. However, two restrictions must be noted:

1. Almost all examples come from the Cantabrian Mountains. The only exception is the rugose coral *Synaptophyllum oliveri* Rodríguez García, 1978 from the Emsian of the Sierra Morena in southern Spain (Rodríguez García 1978, p. 344–346). It is not entirely clear if this difference in the amount of examples results only from the lower degree of investigation in the Devonian of the Sierra Morena, or if it reflects a different degree of connection to the Eastern Americas Realm. However, the stromatoporoid fauna of the Sierra Morena is a typical fauna of the Old World Realm and shows no relation to the Eastern Americas fauna (May 2006).

2. Many of the known cases refer to the Middle Devonian of the Cantabrian Mountains. Examples of this include the rugose corals described by Oliver & Sorauf (1988) and Plusquellec (2005), and the rugose corals and tabulate corals cited by Oekentorp (1975, pp. 76–78) and Soto (1979, p. 404).

The increase of faunal migration in the Middle Devonian is not surprising, as the sea-level rise during the Middle Devonian gradually weakened this barrier until its final breakdown in the Givetian in the Taghanic Event (May 1996, 1997, Stock 2005b).

On the other hand, close palaeobiogeographical relationships between Spain and the Eastern Americas Realm during the Emsian and lower Eifelian would be remarkable because the Emsian was the time of strongest faunal provincialism during the Devonian period (Boucot 1988, pp. 211–212, p. 219; Pedder & Oliver 1990, p. 267; Oliver & Pedder 1994, p. 185; May 1996, p. 39). Nevertheless, these palaeobiogeographical relationships are supported by the finding of the *Radiastraea arachne* Stumm, 1937 described above.

That this finding is not an anomaly, but part of a common pattern, is demonstrated by the publications of Soto (1979; 1981; 1986, p. 34), Fernández-Martínez & Tourneur (1995), and May (2005), all of whom discerned close palaeobiogeographical relationships between the Cantabrian Mountains and America during the Emsian in different groups of rugose and tabulate corals.

Furthermore, observations in North America suggest the existence of connections between the Eastern Americas Realm and the Old World Realm during the Emsian. For example, a breach in the Transcontinental Arch is thought to have occurred from lower Pragian through lower Emsian, when Eastern Americas taxa invaded the Great Basin of the southwestern United States (Stock 2005b, p. 77). Another case involves four stromatoporoid species that occur in North America on both sides of the barrier in close proximity to the Emsian-Eifelian boundary (Stock 2005a, p. 95). However, it remains unclear whether the migration of *Radiastraea arachne* occurred via one of these breaches or by another breach. For example, in the case of the four stromatoporoid species it is assumed that this migration only was possible because stromatoporoids probably possessed unique ecological tolerances that allowed them to traverse the Devonian transcontinental barrier (Prosh & Stearn 1993, p. 2473; Stock 2005a, p. 95). Consequently, *Radiastraea arachne* probably wouldn't have been able to use this breach.

Conclusions

The finding of *Radiastraea arachne* Stumm, 1937 in the Cantabrian Mountains is remarkable for two reasons: it is the first reported occurrence of the genus *Radiastraea* from Europe, and it is an example of close palaeobiogeographical relationships between the Cantabrian Mountains and North America. Comparable patterns have been reported by Soto (1979; 1981; 1986, p. 34), Fernández-Martínez & Tourneur (1995), and May (2005), all of whom were able to discern close palaeobiogeographical relationships between the Cantabrian Mountains and America during the Emsian in different groups of rugose and tabulate corals. These close palaeobiogeographical relationships are remarkable because the Emsian was the time of strongest faunal provincialism during the Devonian period (Boucot 1988, pp. 211, 212, p. 219; Pedder & Oliver 1990, p. 267; Oliver & Pedder 1994, p. 185; May 1996, p. 39). It is also remarkable that the European occurrence of *Radiastraea arachne* Stumm, 1937 is only slightly younger than the material from Nevada. *Radiastraea arachne* Stumm, 1937 may prove to be a useful index fossil for Emsian (and possibly early Eifelian) age.

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