

# Corals (Anthozoa, Tabulata and Rugosa) and chaetetids (Porifera) from the Devonian of the Semara area (Morocco) at the Museo Geominero (Madrid, Spain), and their biogeographic significance

Andreas MAY

Saint Louis University - Madrid campus, Avenida del Valle 34, E-28003 Madrid, Spain  
e-mail: maya@madrid.slu.edu

**Abstract.** The paper describes the three tabulate coral species *Caliapora robusta* (Pradáčová, 1938), *Pachyfavosites tumulosus* Janet, 1965 and *Thamnopora major* (Radugin, 1938), the rugose coral *Phillipsastrea* ex gr. *irregularis* (Webster & Fenton in Fenton & Fenton, 1924) and the chaetetid *Rhaphidopora crinalis* (Schlüter, 1880). The specimens are described for the first time from Givetian and probably Frasnian strata of Semara area (Morocco, former Spanish Sahara). The material is stored in the Museo Geominero in Madrid. The tabulate corals and the chaetetid demonstrate close biogeographic relationships to Central and Eastern Europe as well as to Western Siberia. The fauna does not show any special influence of the Eastern Americas Realm.

**Key words:** Anthozoa, biogeography, Devonian, tabulate corals, Morocco, West Sahara palaeogeographic province

**Coraux (Anthozoa, Tabulata et Rugosa) et chaetétides (Porifera) du Dévonien de la région de Smara (Maroc) déposés au Museo Geominero (Madrid) et leur signification biogéographique.**

**Résumé.** L'article décrit trois espèces de coraux tabulés : *Caliapora robusta* (Pradáčová, 1938), *Pachyfavosites tumulosus* Janet, 1965, et *Thamnopora major* (Radugin, 1938), le corail rugueux *Phillipsastrea* ex gr. *irregularis* (Webster & Fenton in Fenton & Fenton, 1924) ainsi que le chaetétide *Rhaphidopora crinalis* (Schlüter, 1880). Les spécimens, entreposés au Museo Geominero de Madrid, proviennent des couches givétiennes et probablement frasnienne de différents gisements de la région de Smara (Maroc, ancien Sahara espagnol), d'où elles sont décrites pour la première fois. Les coraux tabulés et le chaetétide prouvent l'existence de relations biogéographiques proches entre l'Europe centrale et orientale mais aussi avec l'Ouest de la Sibérie. La faune ne présente pas de relations particulières avec celle du Domaine Est-Américain.

**Mots clés:** Anthozoa, biogéographie, Dévonien, coraux tabulés, Maroc, Province paléogéographique du Sahara Occidental

## INTRODUCTION

The existence of Devonian reefs and reefal limestones (including mud mounds) in the northwestern part of Africa is known since a long time. Two main phases may be distinguished concerning the palaeontological investigation of the corals and chaetetids of these reefs and mud mounds: In a first phase, some important monographs were published, e.g. Le Maître (1947) on the Tafilalet (Morocco), Termier & Termier (1950) on Morocco, and Le Maître (1952) on Erg el Djemel (Algeria).

In the second phase, which started twenty years ago, revisions of the older monographs, as well as many special investigations on particular groups of fossils and the stratigraphy and palaeoecology of the reefal limestones, have been published, for example Potthast & Oekentorp (1987), Brachert *et al.* (1992), Kaufmann (1998a,b), Pedder (1999), Schröder & Kazmierczak (1999), Coen-Aubert (2002), Döring (2002), Hüneke & Krienke (2004), Becker *et al.* (2004), Becker *et al.* (2004), Berkowski (2004, 2006), Belka & Berkowski (2005), and Coen-Aubert (2005) on Morocco; whereas the following papers of Boumendjel *et al.* (1997), Plusquellec *et al.* (1997), Wendt *et al.* (1997), Wendt & Kaufmann (1998) and Plusquellec (1998) deal with Algerian localities.

In contrast to the much more thorough research in Morocco and Algeria, the Devonian reefal limestones of West Sahara (former Spanish Sahara) always have been neglected: simultaneously with the first phase of research in the other parts of northwestern Africa, the two short papers of Rodriguez Mellado (1948) and Hernández Sampelayo

(1948) gave a first impression of the richness of the Devonian reefal faunas of West Sahara. And there are only two recent papers on the Devonian reefs of West Sahara: Königshof & Kershaw (2006) describe the growth forms of stromatoporoids in a Givetian reef from the northeastern part of West Sahara; whereas Wendt & Kaufmann (2006) give an overview on the Givetian reefs of West Sahara.

This lack of knowledge of the Devonian reefal faunas of West Sahara would not be as distressing as it is, if West Sahara would not have such a peculiar palaeogeographic position: all modern palaeogeographic maps, which are available for the Devonian, put West Sahara very close to eastern North America (e.g. Ziegler 1989, Pedder & Oliver 1990, Scotese & McKerrow 1990, Tait *et al.* 2000, McKerrow *et al.* 2000, Golonka 2002, Torsvik & Cocks 2004, Hüneke 2006). Consequently, the question raises, to which biogeographic realm the Devonian faunas of West Sahara belong: to the Eastern Americas Realm which extends over the eastern United States, eastern Canada, and northwestern South America, or to the Old World Realm which contains the western United States, western and northern Canada, Europe, northern Africa, Asia, and Australia (Boucot 1988, Oliver & Pedder 1994, Stock 2005a, p.91). Results from neighbouring areas are ambiguous in their application for West Sahara: on the one hand, different Moroccan rugose coral faunas investigated by Pedder (1999), Schröder & Kazmierczak (1999) and Coen-Aubert (2005) belong to the Old World Realm. On the other hand, the brachiopods of the Djado Sub-Basin (North Niger, SW Libya) reflect affinity to the North American faunas (Mergl *et al.* 2001).

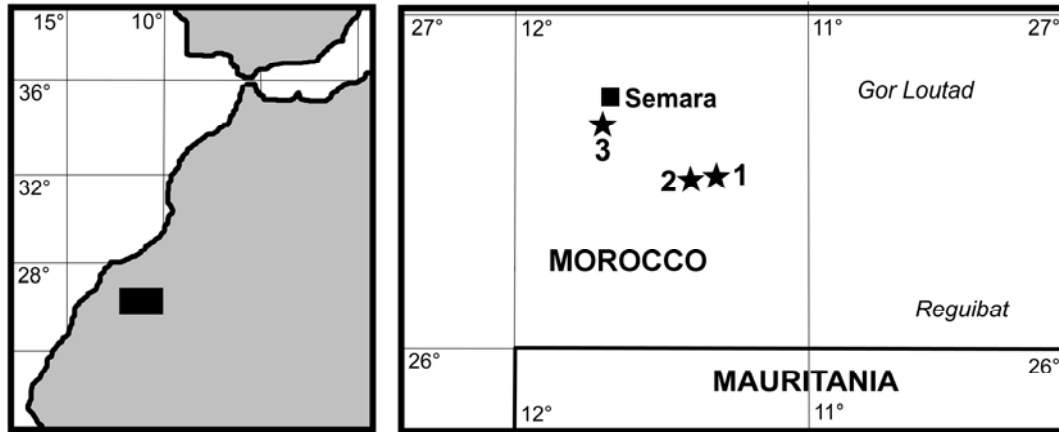


Figure 1. Approximate geographical locations of the described specimens: 1, Oued Ain Terguit; 2, between Oued Ain Terguit and Uad Miran; 3, south of Semara.

Consequently, the fact that the Museo Geominero in Madrid (Spain) houses the original material of the publication of Hernández Sampelayo (1948) and some further collections from West Sahara is of particular interest. The purpose of this investigation is to increase the knowledge of West Sahara corals by describing this important material and to uncover its palaeobiogeographic relationships.

#### MATERIALS AND METHODS

All the material investigated belongs to historical collections housed in the Museo Geominero in Madrid (Spain), but unfortunately, the information on the localities and the stratigraphic assignment is not as detailed as is customary nowadays. Furthermore, the Museo Geominero was very restrictive with permissions to prepare thin sections from the material figured by Hernández Sampelayo (1948). Only for the specimen figured by Hernández Sampelayo (1948, pl. 7, fig. 3) it was possible to get this permission. Nevertheless, finally it was possible to make thin sections from five different species (3 tabulate corals, 1 colonial rugose coral and 1 chaetetid). Fig. 1 shows the locations of these specimens.

Someone may doubt, if a publication under these circumstances is justified. However, because of the specific political situation in West Sahara, an access to the fossil bearing localities there is practically impossible (Wendt & Kaufmann 2006, p. 339). Furthermore, the material investigated is well preserved and allows many important conclusions. Finally, whereas the rugose corals in the neighbouring areas are investigated by several modern publications (Pedder 1999, Schröder & Kazmierczak 1999, Coen-Aubert 2002, 2005, Berkowski 2004, 2006, Belka & Berkowski 2005), the knowledge of the tabulate corals and chaetetids is more limited.

The systematic classification of the tabulate corals follows Birenheide (1985), whereas the systematic classification of the rugose corals follows Hill (1981). The interpretation of the Rugosa as a superorder of the subclass Zoantharia and the systematic classification of the chaetetids are taken from May (1993b).

#### SYSTEMATIC DESCRIPTION

**Phylum Cnidaria Hatschek, 1888**  
**Class Anthozoa Ehrenberg, 1834**  
**Subclass Tabulata Milne-Edwards & Haime, 1850**  
**Order Favositida Wedekind, 1937**  
**Family Favositidae Dana, 1846**

**Genus *Caliapora* Schlüter, 1889**

*Type species* – *Alveolites battersbyi* Milne-Edwards & Haime, 1851.

*Diagnosis and occurrence* – see Birenheide (1985, p. 63–64). Important additional information is given by Iven *et al.* (1997).

***Caliapora robusta* (Pradáčová, 1938)**

(Pl. II, I–J)

\* 1938 *Alveolites robustus* n. sp. – Pradáčová, p. 15–16, fig. 3–4.

1951 *Favosites endygashensis* sp. nov. – Černyšev, p. 36, pl. 12, fig. 3–4.

1963 *Caliapora endygashensis* (Tchernychev, 1951) – Dubatolov, p. 97–98, pl. 36 fig. 2.

1981 *Caliapora robusta* (Pradáčová, 1938) – Hladil, p. 161, fig. 1–2, tab. 1, pl. 1, fig. 1–3 (see for further synonymy).

*Lectotype* – See Hladil (1981, p. 161).

*Diagnosis* – A species of *Caliapora* with corallites of 1.00–1.50 mm width and 0.65–1.00 mm height. The common wall between the corallites is 0.20–0.40 mm thick. Mural pores are 0.15–0.25 mm in diameter (Pradáčová 1938, p. 15).

*Material* – A small corallum (stock no. 1789X) from which two thin sections have been made. The original label of the Museo Geominero is “*Stromatopora constellata*”. The database of the Museo Geominero states that the material comes “from the Eifelian in the south of Semara”.

*Description* – In transverse section, the outline of the corallites is kidney-shaped, oval, or long rounded polygonal. The smallest corallites have 1.0 mm width and 0.6 mm height, whereas the largest corallites have 1.9 mm width and 1.4 mm height. Most corallites have 1.2–1.5 mm width and 0.9–1.1 mm height. The transverse section shows 1–3 large, tongue-like squamulae, which are up to 0.3 mm long. Occasionally, also small true septal spines occur.

The common wall between the corallites is 0.15–0.5 mm thick (mostly about 0.25 mm thick) with a very vaguely visible dark median suture.

The mural pores are in the acute corners of the corallites and remarkably big. In this way the corallites become pseudomeandroid. Often, the mural pores are closed by pore plates, which are microcrystalline and thin.

Within the longitudinal thin section, mural pores are round or long oval and (0.15–) 0.2–0.3 mm (mostly about 0.25 mm) in diameter. Mural pores have a distance of about 0.9–1.2 mm from each other. The horizontal skeletal elements are microcrystalline and thin. Among the horizontal skeletal elements tabulae dominate, which are mostly slightly concave. Tabellae occur occasionally only. At a distance of 10 mm, the number of horizontal skeletal elements amounts to 20.

*Remarks* – The corallum from West Sahara fits very well with the original description of Pradáčová (1938). Among other aspects, also the skeletal dimensions fit very well, because the original description of Pradáčová (1938) indicates 1.0–1.5 mm width and 0.65–1.0 mm height for corallites. The skeletal dimensions of the material described by Hladil (1981) are slightly smaller (e. g.: 1.0 mm width and 0.64 mm height for corallites), but fit good enough to justify the doubtless incorporation into *Caliapora robusta*.

The statement of Hladil (1981, p. 161) that *Caliapora endygashensis* (Černyšev, 1951) is a junior synonym of *Caliapora robusta* (Pradáčová, 1938), because the original description of Černyšev (1951) and the redescription by Dubatolov (1963) are close to the description of Pradáčová (1938), is confirmed.

*Caliapora battersbyi* (Milne-Edwards & Haime, 1851), the type species of the genus, which is very common in the Givetian of Germany, Poland, Moravia, England and France (Hladil 1981; Byra 1983; Birenheide 1985; Iven *et al.* 1997; Hladil 1998), can be distinguished easily by its smaller corallite diameter of 0.6–0.8 mm (Hladil 1981, p. 159–160, tab. 1, pl. 1 fig. 3–5; Byra 1983, p. 26–28, pl. 6–7; Birenheide 1985, p. 64, pl. 16). The differences between *Caliapora robusta* and other species are explained by Hladil (1981, p. 161).

*Occurrence* – Pradáčová (1938) describes *Caliapora robusta* from bed 9 of the famous locality Čelechovice in Moravia. Ficner & Havlíček (1978, p. 50) assign a lower Givetian age to this bed, whereas Zikmundova (in Galle & Hladil 1991, p. 41–42) assumes an age close to the Eifelian/Givetian boundary for the upper part of the sequence in Čelechovice. The investigations of Hladil *et al.* (2002) allow classifying of bed 9 as early lower Givetian.

Furthermore, *Caliapora robusta* is known from the upper Eifelian of Moravia (Hladil 1981, p. 157–158, 161) and the

Shanda Formation in the Kuznetsk Basin (Western Siberia) (Černyšev 1951; Dubatolov 1963). Rzhonsnitskaya *et al.* (1985, p. 114) and Yolkin & Kim (1988) demonstrate clearly that the Shanda Formation is of upper Emsian to lower Eifelian age.

The material described here from the Devonian of West Sahara extends the known geographic distribution of the species.

### Genus *Pachyfavosites* Sokolov, 1952

*Type species* – *Calamopora polymorpha* var. *tuberosa* Goldfuss, 1829.

*Diagnosis and occurrence* – see Birenheide (1985, p. 67) and May (1993a, p. 123).

### *Pachyfavosites tumulosus* Janet, 1965

(Pl. I, fig. A–B)

\* 1965 *Pachyfavosites tumulosus* sp. nov. – Janet, p. 18, pl. 4, fig. 1.

1972 *Pachyfavosites tumulosus* Janet, 1965 – Janet, p. 49–50, pl. 15, fig. 1–2.

2005 *Pachyfavosites tumulosus?* Janet, 1965 – Stadelmaier *et al.*, p. 18–20, pl. 8, fig. 1–2.

*Holotype* – See Janet (1972, p. 49).

*Diagnosis* – A species of *Pachyfavosites* whose 5 to 7-cornered corallites are 2.0–2.65 mm in diameter (maximally 3 mm). The common wall between the corallites is 0.2–0.5 mm thick. Mural pores are 0.1–0.5 mm in diameter (Janet 1972, p. 49).

*Material* – One large corallum (stock no. 251X) from which two thin sections have been made. The original label of the Museo Geominero is “*Heliolites porosa*”. The database of the Museo Geominero states that the material comes from the Middle Devonian of Oued Ain Terguit. Wendt & Kaufmann (2006, figs 2–3) give a detailed geological map and a generalized stratigraphic section of the Givetian sequence in this area.

*Description* – The transverse thin section shows polygonal corallites with rounded corners. Large, 6 to 7-cornered corallites are 2.0–2.8 mm in diameter (mostly 2.1–2.4 mm). Between the large corallites are small corallites with 1.0–1.5 mm diameter. The common wall between the corallites is 0.2–0.42 mm thick with a well-developed dark median suture. Occasionally, very small, short, triangular septal spines occur.

Within the longitudinal thin section, mural pores are round, about 0.4 mm in diameter and ordered in one row in the middle of the side. Mural pores have a distance of about 1–1.5 mm from each other. Among the horizontal skeletal elements tabulae dominate, which are horizontal or slightly inclined. Inclined or curved tabellae occur frequently. At a distance of 10 mm, the number of horizontal skeletal elements amounts to 20.

*Remarks* – The corallum is a representative of the genus *Pachyfavosites* Sokolov, 1952, but in his skeletal

dimensions it is significantly larger than the type species *Pachyfavosites polymorphus* (Goldfuss, 1829). The cosmopolitan Givetian *Pachyfavosites polymorphus* has a corallite diameter of 1.2–1.6 mm (max. 2.0 mm) (Birenheide 1985, p. 68, pl.17; May 1993a, p. 123–125, pl. 3 fig. 1; Stadelmaier *et al.* 2005, p. 18, pl. 7).

However, the corallum from the West Sahara fits very well *Pachyfavosites tumulosus* Janet, 1965 described by Janet (1965, 1972) from the Urals as well as the corallum described by Stadelmaier *et al.* (2005, p. 18–20, pl. 8, fig. 1–2) from the Eifel Hills. Comparing the above described corallum with the material of Janet (1965, 1972) and Stadelmaier *et al.* (2005), there is no doubt that all the material belongs to the same species.

**Occurrence** – Janet (1965, 1972) describes *Pachyfavosites tumulosus* from Eifelian and Givetian beds of the Urals. Stadelmaier *et al.* (2005) found the species in the lower Givetian of the Eifel Hills. The material described here from the Devonian extends the known geographic distribution of the species of West Sahara.

### Genus *Thamnopora* Steininger, 1831

**Type species** – *Thamnopora madreporacea* Steininger, 1831.

**Diagnosis and occurrence** – See Birenheide (1985, p. 69) and May (1993c, p. 78–79).

### *Thamnopora major* (Radugin, 1938)

(Pl. I, C–D)

\* 1938 *Pachypora cervicornis* var. *major* – Radugin, p. 73–74, pl. 3, fig. 4.

1959 *Thamnopora major* (Radugin, 1938) – Dubatolov, p. 103–104, pl. 34, fig. 1–4, pl. 35, fig. 1–2 (see for further synonymy).

1964 *Thamnopora major* (Radugin, 1938) – Čudinova, p. 36–37, pl. 14, fig. 3, pl. 15, fig. 1.

**Holotype** – See Dubatolov (1959, p. 103).

**Diagnosis** – A species of *Thamnopora* whose branches are 25–35 mm in diameter. Corallites are 0.8–2.5 mm in diameter and calices are 2.5–3.0 mm in diameter. The thickness of the common wall between the corallites increases from the central part of the branch to the peripheral part of the branch from 0.1 mm to 0.5–1.0 mm (Dubatolov 1959, p. 103).

**Material** – One branch (stock no. 240X) from which two thin sections have been made. The original label of the Museo Geominero is “*Thamnopora boloniensis*”. The database of the Museo Geminero states that the branch comes from the Devonian of Oued Ain Terguit. Wendt & Kaufmann (2006, fig. 2–3) give a detailed geological map and a generalized stratigraphic section of the Givetian sequence in this area.

**Description** – The branch is 11 mm in diameter. The calices open at acute angles to the surface of the branch and some calices have a tendency to be nest-like.

Within the transverse thin section of the central part of the branch the corallites are polygonal, with 1.0–1.3 mm diameter, and the common wall between the corallites is about 0.2 mm thick. The longitudinal thin section shows that the corallites bend fan-like to the surface of the branch and run into the surface at an acute angle. In the peripheral part of the branch, the corallites are 1.5–2.5 mm in diameter (mostly about 2 mm), and the common wall between the corallites is 0.3–0.8 mm (mostly about 0.5 mm) thick.

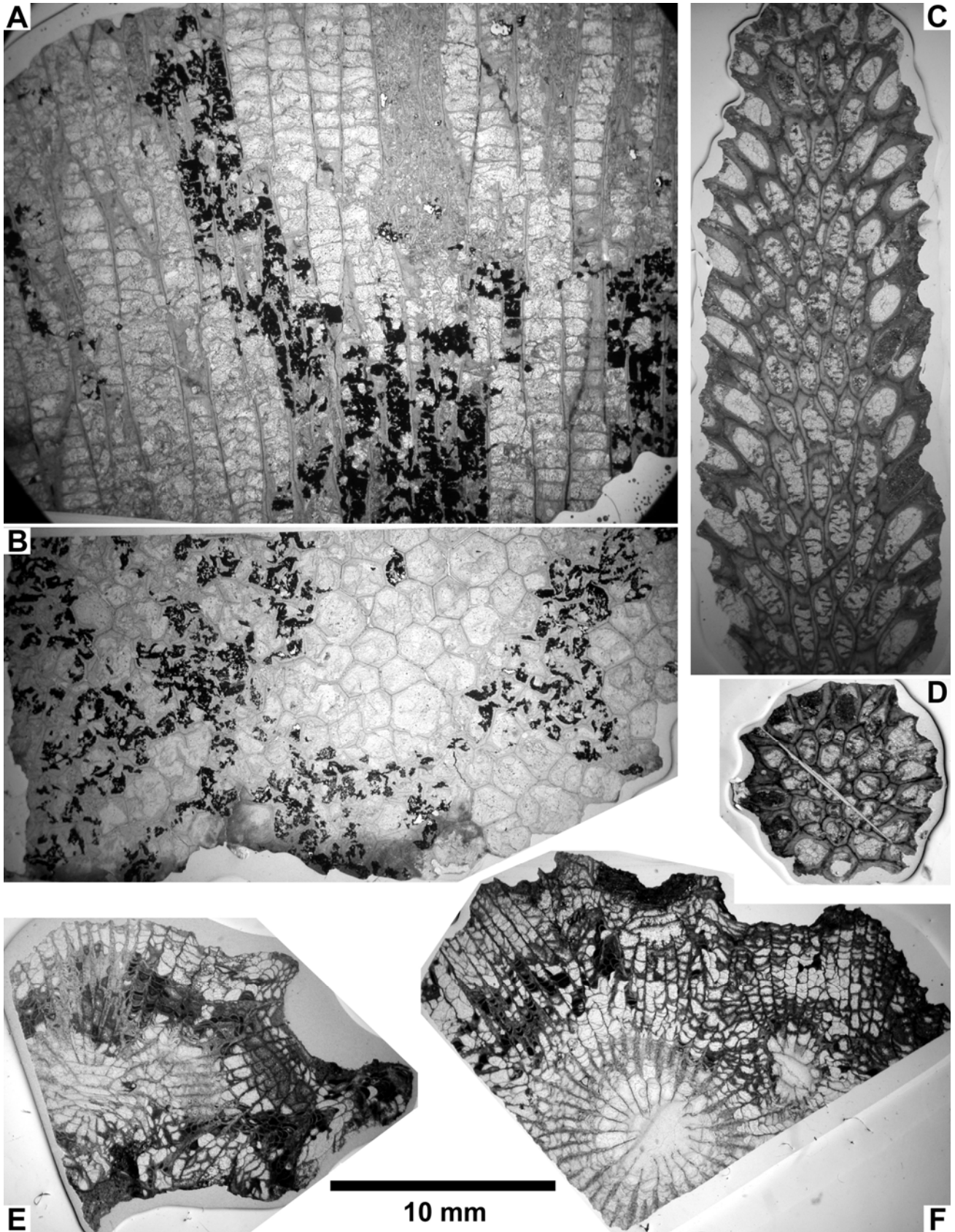
The mural pores are round and about 0.2–0.25 mm in diameter. The tabulae are thin and horizontal or slightly inclined. The distance between the tabulae in the central part of the branch varies between 0.7 mm and 1.5 mm.

In the central part of the branch the septal elements are very well developed and very frequent: tongue-like squamulae occur as well as needle-like septal spines, and septal elements are more frequent than tabulae. The septal elements are up to 0.5 mm long. The distance between the septal elements in the central part of the branch varies between 0.25 mm and 0.6 mm. In the peripheral part of the branch, the septal elements are much more weakly developed and less frequent.

**Remarks** – The corallum shows the characteristics of genus *Thamnopora* Steininger, 1831. However, the strong development of its septal apparatus, consisting of many squamulae and spines, distinguishes it from the great majority of *Thamnopora* species.

For *Thamnopora*-like species with calices like swallow's nests, often the genus *Celechopora* Pradáčová, 1938 is used. The development of nest-like calices in *Celechopora* is correlated with the fact that the calices open at very acute angles to the surface of the branch. From typical *Thamnopora* species, it is known that if the calices open at very acute angles to the surface of the branch, the calices may have a tendency to look nest-like – for example see the description of *Thamnopora boloniensis* (Gosselet, 1877) by May (1995, p. 484, pl. 2, fig. 9–11). Taking into account that within *Thamnopora* there are several species, whose calices open at very acute angles to the surface, and that this angle is correlated positively with the diameter of the branch (May 1997a, p. 219–220; May 1998, p. 144, fig. 3), the usefulness of the genus *Celechopora* Pradáčová, 1938 may be doubted. Nevertheless, any further discussion of this topic is beyond the scope of this paper. All species up to now assigned to *Celechopora* have much smaller corallite diameters than the branch described above: in *Celechopora kettnerae* Pradáčová, 1938, the type species of *Celechopora* Pradáčová, 1938, the calices are 0.75–1.05 mm in diameter (Pradáčová 1938, p. 19–21, fig. 2–3), whereas in *Celechopora devonica* Schlüter, 1885 the calices are 1.3–1.5 mm in diameter (Byra 1983, p. 29–30, pl. 15–16; Birenheide 1985, p. 76, pl. 22, fig. 1; Stadelmaier *et al.* 2005, p. 12–14, pl. 3–4).

Among the big amount of described *Thamnopora* species (see May 1997a, 1998) there are only two species which are closely comparable: *Thamnopora major* (Radugin, 1938) and *Thamnopora radugini* Dubatolov, 1959, both from the upper Givetian of the Kuznetsk Basin. In *Thamnopora major* the diameter of the branches is 25–35 mm, the diameter of the calices is 2.5–3 mm, the diameter of the



**Plate I.** A-B. *Pachyfavosites tumulosus* Janet, 1965, stock no. 251X, Oued Ain Terguit. A: longitudinal thin section. B: transverse thin section. C-D. *Thamnopora major* (Radugin, 1938), stock no. 240X, Oued Ain Terguit. C: longitudinal thin section. D: transverse thin section. E-F. *Phillipsastrea ex gr. irregularis* (Webster & Fenton in Fenton & Fenton, 1924), stock no. 2541X, between “Uin Terguit” (=Oued Ain Terguit) and Uad Miran, not figured original material of Hernández Sampelayo (1948). E: oblique thin section. F: transverse to longitudinal thin section. Scale bar represents 10 mm.

corallites in the central part of the branch is 0.8–1.8 mm and the diameter of the corallites in the peripheral part of the branch is 2–2.5 mm (Radugin 1938, Dubatolov 1959). In *Thamnopora radugini* the diameter of the branches is 15–20 mm, the diameter of the calices is 1.5–2 mm, the diameter of the corallites in the central part of the branch is 0.6–1.4 mm and the diameter of the corallites in the peripheral part of the branch is 1.6–2 mm (Dubatolov 1959, p. 104–106, pl. 36).

The diameter of the corallites in the peripheral part of the branch from West Sahara is a little bit smaller than the corallite diameter of typical *Thamnopora major*. However, taking into account, that 1) the branch from West Sahara is much thinner than a typical branch of *Thamnopora major* and that 2) in *Thamnopora* there exists a positive correlation between the corallite diameter and the branch diameter (May 1997a, p. 221, fig. 5; May 1998, p. 145, fig. 6), there is no doubt to assign the branch from West Sahara to *Thamnopora major*.

**Occurrence** – *Thamnopora major* (Radugin, 1938) was known up to now only from the upper Givetian of the Kuznetsk Basin (Western Siberia) (Radugin 1938, Dubatolov 1959, Čudinova 1964). The material described here from the Devonian of West Sahara extends the known distribution of the species.

**Subclass Zoantharia Blainville, 1830**  
**Superorder Rugosa Milne-Edwards & Haime, 1850**  
**Order Stauriida Verrill, 1865**  
**Family Phillipsastreae Hill, 1954**

**Genus Phillipsastrea d’Orbigny 1849**

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

**Diagnosis** – See Hill (1981, p. 281), McLean (1993, p. 53) and May (2006a, p. 156).

***Phillipsastrea* ex gr. *irregularis* (Webster & Fenton in Fenton & Fenton, 1924)**  
 (Pl. I, E–F)

\* 1924 *Pachyphyllum irregulare* n. sp. – Webster & Fenton in Fenton & Fenton, p. 49–50, pl. 10, fig. 1–2, pl. 11.

1948 *Acervularia goldfussi*, Vern.-Haime – Hernández Sampelayo, p. 25–26, pl. 6, fig. 1–4.

1993 *Phillipsastrea irregularis* (Webster & Fenton 1924) – McLean, p. 64–67, pl. 22, fig. 5, 6, 8, 9, pl. 23, fig. 1–7, pl. 24, fig. 1–3, 5 (see for further synonymy).

ex parte 1998 *Pachyphyllum woodmani* (White, 1870) – Sorauf, p. 78–80, pl. 47 [not pl. 2, pl. 3, pl. 43–46].

2000 *Phillipsastrea* n. sp. aff. *irregularis* (Webster & Fenton, 1924) – Schröder & Werner, p. 231–232, pl. 1–2.

**Holotype** – See McLean (1993, p. 65, pl. 23, fig. 1, 3).

**Diagnosis** – A species of *Phillipsastrea* with a predominantly thamnasterioid corallum. The tabularium has an average diameter of 5–7 mm. Horseshoe dissepiments

are variably developed (commonly weak). The number of major septa is commonly 19–23 (McLean 1993, p. 65).

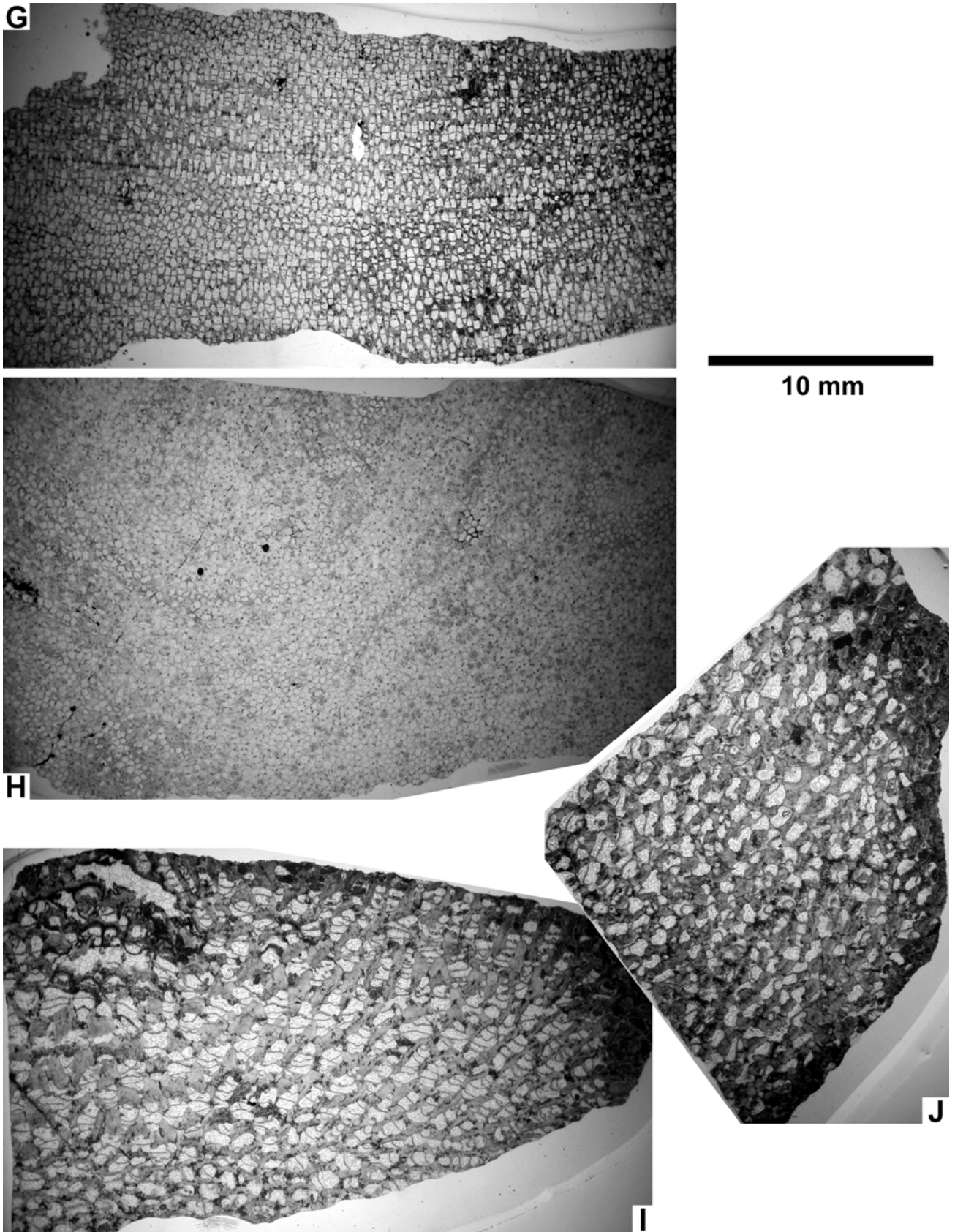
**Material** – Three small coralla which belong to the material published by Hernández Sampelayo (1948) come from the Devonian between “Uin Terguit” (=Oued Ain Terguit) and Uad Miran (Hernández Sampelayo 1948, pl. 6). All the material is labelled as “*Acervularia goldfussi*” in the Museo Geominero. The author was not allowed to make thin sections from both coralla figured by Hernández Sampelayo (1948, pl. 6, fig. 1–4) with stock no. 1360X and 1706X. However, it was possible to make two thin sections from a worn, small discus-shaped corallum (stock no. 2541X) which belongs also to the material published by Hernández Sampelayo (1948) and comes from the same locality, but had not been figured by Hernández Sampelayo (1948). Wendt & Kaufmann (2006, fig. 2–3) give a detailed geological map and a generalized stratigraphic section of the Givetian sequence in this area.

**Description** – The corallum is astreoid to thamnasterioid. Sometimes, a gap is developed between the septa of neighbouring corallites. The corallite diameter is about (8–) 13 mm and the tabularium has a diameter of 5.5–6 mm. The tabulae are weakly arched or horizontal.

Adult corallites have (19–) 20 major septa and as many minor septa. The major septa are long. However, a periaxial space of 1.2–2.2 mm diameter completely lacks septa. The minor septa are half as long as the major septa. In the inner part of the dissepimentarium the septa are dilated and 0.15–0.3 mm thick. Within the other parts of the corallum the septa are thin. The septa show weakly developed carinae. The dissepimentarium is about 0.8–1.5 mm wide. It contains an intermittently developed row of horseshoe dissepiments.

**Remarks** – The investigated corallum is only small. However, it clearly shows the characteristics of *Phillipsastrea* d’Orbigny, 1849. Its large tabularium diameter and its large corallite diameter exclude it from the majority of *Phillipsastrea* species. For example, all the three *Phillipsastrea* species described by Coen-Aubert (2002) have much smaller diameters.

The corallum from West Sahara fits well with the description of *Phillipsastrea irregularis* (Webster & Fenton in Fenton & Fenton, 1924) by McLean (1993) and the description of *Phillipsastrea* n. sp. aff. *irregularis* (Webster & Fenton, 1924) by Schröder & Werner (2000). The material described as *Phillipsastrea* n. sp. aff. *irregularis* by Schröder & Werner (2000) is very similar to the holotype of *Phillipsastrea irregularis* (see: McLean 1993, p. 65, pl. 23, fig. 1, 3; Sorauf 1998, pl. 47) and the other material described by McLean (1993). Taking into account the high variability of the material described by McLean (1993), in my opinion, the differences described by Schröder & Werner (2000, p. 232) do not justify the separation of their material from *Phillipsastrea irregularis*. Nevertheless, because of the fact, that the material described above does not give any further information to decide, whether *Phillipsastrea irregularis* and *Phillipsastrea* n. sp. aff. *Irregularis*, *sensu* Schröder & Werner (2000) are conspecific or not, and that it fits as well



**Plate II.** G-H. *Rhapsidopora crinalis* (Schlüter, 1880), stock no. 1704X, between “Uin Terguit” (= Oued Ain Terguit) and Uad Miran, specimen figured by Hernández Sampelayo (1948, pl. 7, fig. 3). G: longitudinal thin section; H: transverse thin section; I-J. *Caliapora robusta* (Pradáčová, 1938), stock no. 1789X, south of Semara; I: longitudinal thin section; J: transverse thin section; Scale bar represents 10 mm.

to both descriptions, it is determined as *Phillipsastrea* ex gr. *irregularis*.

Sorauf (1998) regards *Phillipsastrea irregularis* (Webster & Fenton in Fenton & Fenton, 1924) as a junior synonym of *Pachyphyllum woodmani* (White, 1870). However, the type material of *Phillipsastrea woodmani* has significantly smaller skeletal dimensions than the type material of *Phillipsastrea irregularis*, the other material of *Phillipsastrea irregularis* described by McLean (1993), *Phillipsastrea* n. sp. aff. *irregularis* sensu Schröder & Werner (2000) and the material described above. Consequently, I follow McLean (1993) accepting *Phillipsastrea irregularis* as an independent species.

*Occurrence* – *Phillipsastrea irregularis* (Webster & Fenton in Fenton & Fenton, 1924) is known from the Frasnian of Iowa, Nevada and Western Canada (Fenton & Fenton 1924; McLean 1993). The material described as *Phillipsastrea* n. sp. aff. *irregularis* by Schröder & Werner (2000) has been found in Morocco.

#### Phylum Porifera Grant, 1836

#### Class Sclerospongiae Hartman & Goreau, 1970

#### Order Chaetetida Okulitch, 1936

#### Family Chaetetidae Milne-Edwards & Haime 1849

#### Genus *Rhaphidopora* Nicholson & Foord, 1886

*Type species* – *Calamopora crinalis* Schlüter, 1880.

*Diagnosis and occurrence* – See Birenheide (1985, p. 35) and May (1993b, p. 71-72).

#### *Rhaphidopora crinalis* (Schlüter, 1880)

(Pl. II, G–H)

- \* 1880 *Calamopora crinalis* n. sp. – Schlüter, p. 281.
- 1948 *Stromatopora constellata*, Hall – Hernández Sampelayo, p. 27–28, pl. 7, fig. 3, (non pl. 7, fig. 1–2).
- 1983 *Rhaphidopora crinalis* (Schlüter 1880) – Byra, p. 15–16, pl. 1, fig. 1–2 (see for further synonymy).
- 1985 *Rhaphidopora crinalis* (Schlüter 1880) – Birenheide, p. 35, pl. 2.

*Lectotype* – See Byra (1983, p. 15, pl. 1, fig. 1).

*Diagnosis* – A species of *Rhaphidopora* with laminar or cylindrical growth form. Spine-like projections are infrequent. “Corallites” are 0.25–0.45 mm in diameter (average 0.3 mm). The common wall between the “corallites” is 0.05–0.12 mm thick. At a distance of 10 mm, the average number of tabulae amounts to 35–45 (Byra 1983, p. 15).

*Material* – One colony (stock no. 1704X) from which two thin sections have been made. The original label of the Museo Geominero is “*Stromatopora constellata*”. The colony belongs to the material published by Hernández Sampelayo (1948) and comes from the Devonian between “Uin Terguit” (=Oued Ain Terguit) and Uad Miran (Hernández Sampelayo 1948, pl. 7, fig. 3). Wendt & Kaufmann (2006, fig. 2–3) give a detailed geological map

and a generalised stratigraphic section of the Givetian sequence in this area.

*Description* – The colony has a laminar growth form.

In the transverse thin section, the outline of the “corallites” is irregularly polygonal. The “corallites” have 0.25–0.37 mm diameter. Centres of neighbouring “corallites” have about 0.3 mm distance from each other. The common wall between the “corallites” is 0.06–0.12 mm thick, mostly about 0.1 mm. The wall is smooth and small spine-like projections are rather infrequent.

The tabulae are microcrystalline, thin and horizontal or slightly inclined. The distance between the tabulae varies between 0.2 mm and 0.9 mm. At a distance of 10 mm, the number of tabulae amounts to 30.

*Remarks* – The above described material fits very well with the new description given by Byra (1983) of the lectotype of *Rhaphidopora crinalis* (Schlüter, 1880), the type species of *Rhaphidopora* Nicholson & Foord, 1886. *Rhaphidopora lonsdalei* (Etheridge & Foord, 1884) is similar to *Rhaphidopora crinalis*, but has somewhat thinner walls and more “septal” spines. Modern descriptions of *Rhaphidopora lonsdalei* are given by Byra (1983, p. 16–17) and May (1993b, p. 72–74, pl. 11, fig. 2, pl. 12, fig. 1–2, pl. 6, fig. 5).

*Occurrence* – Byra (1983, p. 15–16) and Birenheide (1985, p. 35) give as distribution of *Rhaphidopora crinalis* (Schlüter, 1880) the Eifelian and lower Givetian of Germany and probably the Givetian of Belgium and England. The material described here from the Devonian of West Sahara extends the known distribution of the species.

#### PALAEOBIOGEOGRAPHIC RELATIONSHIPS

Three main faunal realms are distinguished in the Devonian shallow sea: The Malvinokaffric Realm of the southern parts of Gondwana (without reefs and disappearing at the end of the Eifelian), the Eastern Americas Realm which extends over the eastern United States, eastern Canada, and northwestern South America and the Old World Realm which contains the western United States, western and northern Canada, Europe, northern Africa, Asia, and Australia (Boucot 1988; Oliver & Pedder 1994; Stock 2005a, p. 91). Their boundaries are not always known exactly. Concerning the boundary between the Eastern Americas Realm and the Old World Realm, West Sahara is a key in the puzzle, for two reasons: On the first hand, all modern palaeogeographic maps, which are available for the Devonian, put West Sahara very close to eastern North America (see for example: Ziegler 1989; Pedder & Oliver 1990; Scotese & McKerrow 1990; Tait *et al.* 2000; McKerrow *et al.* 2000; Golonka 2002; Torsvik & Cocks 2004; Hüneke 2006). On the second hand, the published data on the palaeobiogeography of neighbouring African areas are ambiguous in their application for West Sahara:

– Mergl *et al.* (2001) could demonstrate, that the brachiopods of the Djado sub-basin (North Niger, SW Libya) reflect affinity to the North American faunas.



- Pedder & Oliver (1990, p. 270) stress the similarity between the rugose coral fauna of North Africa and the Eastern Americas Realm.
- The Silurian cephalopods of the Tindouf Basin in the northeastern part of West Sahara show close relationships to different European faunas (Gnoli 2003).
- The investigation of an early Givetian rugose coral fauna from the Ma'der Basin (Morocco) by Pedder (1999) showed that this fauna had the closest relations to faunas of Western and Central Europe and that no more than 17 % of the Ma'der basin Rugosa had an Eastern Americas Realm ancestry.
- Schröder & Kazmierczak (1999, p. 105) state about the Lower Givetian rugose coral fauna of Ouhlane (Morocco) that it belongs to the Old World Realm, but shows the highest Eastern Americas Realm influx known from an area outside the Eastern Americas Realm.
- The rugose corals from the Upper Givetian of Morocco described by Coen-Aubert (2005) show affinities with faunas of Western Europe, Poland and Western Yunnan (China).
- Based on corals and brachiopods Plusquellec *et al.* (1997, p. 124) and Plusquellec & Hladil (2001, p. 43) distinguish an Ibarmaghian Domain which contains Morocco, Algeria, Libya, Spain and the Armorican Mountains in France.

Compared with this heterogeneous picture, the tabulate corals show clear relations to the Asian part of the Old World Realm: two species – *Caliapora robusta* (Pradáčová, 1938) and *Thamnopora major* (Radugin, 1938) – are known from the Kuznetsk Basin in Western Siberia, and the third species, *Pachyfavosites tumulosus* Janet, 1965, is known at least from the Urals. Furthermore, *Caliapora robusta*, *Pachyfavosites tumulosus* and the chaetetid *Rhaphidopora crinalis* (Schlüter, 1880) are known from central Europe, confirming the recognition as typical fauna of the Old World Realm.

None of the described species suggests any relationship to the Eastern Americas Realm. Not even the fact, that *Phillipsastrea irregularis* (Webster & Fenton in Fenton & Fenton, 1924) occurs in the Frasnian of Iowa and Nevada, can be taken as a hint on an Eastern Americas influence, because 1) this species is known also from Western Canada and Morocco, and 2) the genus *Phillipsastrea* is a typical member of the Old World Realm (McLean 1993, p. 57–58; May 2006a, p. 158). Furthermore, in the late Givetian the faunal barrier between the Eastern Americas Realm and the Old World Realm broke down (Oliver & Pedder 1994; May 1996, p. 41; May 1997b, p. 299–300; Stock 2005b, p. 80–81), so that a Frasnian occurrence in Iowa and Nevada doesn't contradict an affiliation to the Old World Realm.

It is noteworthy, that except from *Phillipsastrea ex gr. irregularis* none of the described species is known from any part of the Ibarmaghian Domain (Morocco, Algeria, Libya, Spain, Armorican Mountains) as defined by Plusquellec *et al.* (1997, p. 124) and Plusquellec & Hladil (2001, p. 43). Probably, this lack of Ibarmaghian faunal elements results from the groups investigated, because a similar pattern is known from the Cantabrian Mountains of Northern Spain: within the tabulate corals of the Cantabrian Mountains, the

thamnoporids and related groups show strong relations to Asia, but only weak relations to northern Africa (May 1993c, 1995), whereas the Micheliniidae and Cleistoporidae show very strong relations to other parts of the Ibarmaghian Domain and only very few relationships to Asia (May 2006b, p. 170). Obviously, different groups of corals had different biogeographic patterns in the Devonian.

## CONCLUSIONS

None of the five species described above (3 tabulate corals, 1 colonial rugose coral and 1 chaetetid) has ever been reported before from West Sahara. Wendt & Kaufmann (2006, p. 347) report some fossils from West Sahara, and among them four species of *Phillipsastrea*. However, none of the species reported by Wendt & Kaufmann (2006) is comparable with *Phillipsastrea ex gr. irregularis* (Webster & Fenton in Fenton & Fenton, 1924). Furthermore, Wendt & Kaufmann (2006, p. 347) do not report any member of the family Favositidae and do not report any chaetetid.

Furthermore, in neighbouring areas the rugose corals are relatively well known, but the knowledge of the tabulate corals and chaetetids is much smaller. In this way, the present investigation increases this knowledge substantially. For example, each of the described tabulate corals and the chaetetid represents the first record of its species from Africa.

The biogeographic analysis of the described fauna gives clear results: It is a typical fauna of the Old World Realm composed of Asian and Central European species. Even though the distance to the Eastern Americas Realm probably was small, the fauna doesn't contain any element of this last.

It is obvious, that the described fossils are coming from beds of different stratigraphic age: *Caliapora robusta* (Pradáčová, 1938), *Pachyfavosites tumulosus* Janet, 1965 and *Rhaphidopora crinalis* (Schlüter, 1880) document an Eifelian to Lower Givetian age. Taking into account, that following Wendt & Kaufmann (2006) even the oldest part of the reefs of West Sahara (“1<sup>st</sup> reef cycle”) is of Givetian age, a lower Givetian age can be assigned to these specimens. An upper Givetian age is represented by *Thamnopora major* (Radugin, 1938). The colonies of *Phillipsastrea ex gr. irregularis* probably are of Frasnian age, but a Givetian age cannot be totally excluded.

**Acknowledgements.** Without the support of the following persons this investigation would not have been possible: Antonio Perejón Rincon (Universidad Complutense, Madrid) proposed that I investigate the collections of the Museo Geominero. Isabel Rábano Gutiérrez del Arroyo, the director of the Museo Geominero, permitted me to carry out this research and supported it. Silvia Menéndez Carrasco, the custodian of the palaeontological collections of the Museo Geominero, supported my research in various ways. The reviews of Eberhard Schindler (Frankfurt) and Jean-Georges Casier (Brussels) improved the article. For all this support I am very thankful. This article is a contribution to the IGCP 499 “Devonian land-sea interaction: evolution of ecosystems and climate”.

## References

- Becker R.T., Aboussalam Z.A., Bockwinkel J., Ebbighausen V., El Hassani A. & Nübel H. 2004. The Givetian and Frasnian at Oued Mzerreb (Tata region, eastern Dra Valley). *In: El Hassani A. (ed.) - Devonian of the western Anti Atlas: Neritic-pelagic correlation and events in the Dra Valley (western Anti-Atlas, Morocco)*. *Doc. Inst. Sci.*, Rabat, 19, 37-56.
- Becker R.T., Bockwinkel J., Ebbighausen V., Aboussalam Z.A., El Hassani A. & Nübel H. 2004. Lower and Middle Devonian stratigraphy and faunas at Bou Tserfine near Assa (Dra Valley, SW Morocco). *In: El Hassani A. (ed.) - Devonian of the western Anti Atlas: Neritic-pelagic correlation and events in the Dra Valley (western Anti-Atlas, Morocco)*. *Doc. Inst. Sci.*, Rabat, 19, 90-100.
- Belka Z., & Berkowski B. 2005. Discovery of thermophilic corals in an ancient hydrothermal vent community, Devonian, Morocco. *Acta geol. Polonica*, 55, 1, 1-7.
- Berkowski B. 2004. Monospecific rugosan assemblage from the Emsian hydrothermal vents of Morocco. *Acta palaeont. Polonica*, 49, 1, 75-84.
- Berkowski B. 2006. Vent and mound rugose coral associations from the Middle Devonian of Hamar Laghdad (Anti-Atlas, Morocco). *Geobios*, 9, 155-170.
- Birenheide R. 1985. Chaetetida und tabulate Korallen des Devon. *Leitfossilien*, 3, Berlin & Stuttgart (Borntraeger), 249 p.
- Blainville H.M.D. de 1830. Zoophytes. *In: Dictionnaire Sci. natur.*, 60, 1-546, Strasbourg & Paris.
- 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, Paleocology and Biostratigraphy*. *Canadian Soc. Petroleum Geol., Mem.*, 14, 211-227.
- Boumendjel K., Brice D., Copper P., Gourvenec R., Jahnke H., Lardeux H., Le Menn J., Mélou M., Morzadec P., Paris F., Plusquellec Y. & Racheboeuf P. 1997. Les faunes du Dévonien de l'Ougarta (Sahara occidental, Algérie). *Ann. Soc. geol. Nord*, 5 (2<sup>ème</sup> sér.), 89-116.
- Brachert T.C., Buggisch W., Flügel E., Hüssner H., Joachimski M. M., Tournier F. & Walliser O.H. 1992. Controls of mud mound formation: The Early Devonian Kess-Kess carbonates of the Hamar Laghdad, AntiAtlas, Morocco. *Geol. Rundschau*, 81, 1, 15-44.
- Byra H. 1983. Revision der von Cl. Schlüter (1880–1889) beschriebenen Chaetetida und Tabulata aus dem Rheinischen Devon. *Courier Forsch.-Inst. Senckenberg*, 59, 127 p.
- Coen-Aubert M. 2002. Nouvelles espèces du genre *Phillipsastrea* D'Orbigny, 1849 près de la limite Givetien-Frasnien dans le Tafilalt et le Ma'der au Maroc et notes sur des types espagnols. *Coral Research Bull.*, 7, 21-37.
- Coen-Aubert M. 2005. Rugueux fasciculés et solitaires du Givetien supérieur dans le Tafilalt et le Ma'der (Maroc). *Bull. Inst. r. Sci. natur. Belgique*, Sci. Terre, 75, 67-85.
- Černyšev B.B. 1951. Silurijskie i devonskie Tabulata i Heliolitida okrain Kuzneckogo uglenosnogo bassejna. *Ministerstva Geologii, Vsesojuznyj naučno-issledovatel'skij geologičeskij Institut (VSEGEI)*, 160 p.
- Čudinova I.I. 1964. Tabuljaty nižnego i srednego devona Kuzneckogo bassejna. *Akademija Nauk SSSR, Trudy Paleontologičeskogo Instituta*, 101, 80 p.
- Dana J.D. 1846-1849. Structure and classification of zoophytes. *In: United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N.*, 7, x + 1-740, Philadelphia.
- Döring S. 2002. *Sedimentological evolution of the late Emsian to early Givetian carbonate ramp in the Mader (eastern Anti-Atlas, SE-Morocco)*. Dissertation, Univ. Tübingen, Bereich 16 Geowiss. Fakultät, 80 p.
- Dubatolov V.N. 1959. Tabuljaty, geliolitidy i chetetidy silura i devona Kuzneckogo bassejna. *Trudy vsesojuznogo nefljanogo naučno-issledovatel'skogo geologorazvedočnogo instituta (VNIGRI)*, 139, 472 p.
- Dubatolov V.N. 1963. Pozdnesilurijskie i devonskie tabuljaty, geliolitidy i chetetidy Kuzneckogo bassejna. *Akademija Nauk SSSR, Sibirskoe otdelenie, Institut geologii i geofiziki*, 286 p.
- Ehrenberg C.G. 1834. Beiträge zur physiologischen Kenntniß der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin*, 1832, 225-380.
- Etheridge R. jr. & Foord A.H. 1884. Descriptions of Palaeozoic Corals in the Collections of the British Museum (Nat. Hist.). *Ann. Mag. natur. Hist.*, 13, 472-476.
- Fenton C.L. & Fenton M.A. 1924. The stratigraphy and fauna of the Hackberry Stage of the Upper Devonian. *Contr. Mus. Geol. Univ. Michigan*, 1, i-xi + 260 p.
- Ficner F. & Havlíček V. 1978. Middle Devonian brachiopods from Čelechovice, Moravia. *Sborník geologických věd, paleont.*, 21, 49-106.
- Galle A. & Hladil J. 1991. Lower Paleozoic Corals of Bohemia and Moravia. *Vith International Symposium on Fossil Cnidaria; Münster, Excursion B3*, 1-83.
- Gnoli M. 2003. Northern Gondwanan Siluro-Devonian palaeogeography assessed by cephalopods. *Palaeontologia Electronica*, 5, 2, 1-19 (<http://palaeo-electronica.org>).
- Goldfuss G.A. 1826-1833. *Petrefacta Germaniae. Erster Theil*. Düsseldorf, 12 p. + 252 p.
- Golonka J. 2002. Plate-tectonic maps of the Phanerozoic. *In: Kiessling W., Flügel E. & Golonka J. (eds.) - Phanerozoic Reef Patterns. SEPM Spec. Publ. Ser.*, 72, 21-75.
- Gosselet J. 1877. Le calcaire dévonien supérieur dans le Nord-Est de l'arrondissement de Avesnes. *Ann. Soc. Géol. Nord*, 4, 238-320.
- Grant R.E. 1836. Animal kingdom. *In: Todd, R.B. (ed) - The cyclopaedia of anatomy and physiology*, London, 1, 107-118.
- Hartman W.D. & Goreau T.F. 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. *Symposium Zool. Soc. London*, 25, 205-243.
- Hatschek B. 1888. *Lehrbuch der Zoologie, eine morphologische Uebersicht des Thierreiches zur Einführung in das Studium dieser Wissenschaft*. iv p. + 144 p.
- Hernández Sampelayo P. 1948. Coralarios devonianos del Sahara Español. *Bol. Inst. Geol. Min. España*, 61, 1-45.
- Hill D. 1954. Coral faunas from the Silurian of New South Wales and the Devonian of Western Australia. *Bull. Bureau Min. Resources, Geol. Geophys., Australia*, 23, 1-51.
- Hill D. 1981. Rugosa and Tabulata. *In: Teichert C. (ed.) Treatise on Invertebrate Paleontology, Part F [Coelenterata] Suppl. 1, Boulder/Colorado & Lawrence/Kansas*, i-xl + 672 p.
- Hladil J. 1981. The genus *Caliapora* Schlüter (tabulate corals) from the Devonian of Moravia. *Věstník Ústředního ústavu geologického*, 56, 3, 157-168.
- Hladil J. 1998. Evolution of intraspecific morphological variability and its relationship to environment (*Caliapora battersbyi*, Devonian). *Věstník Českého geologického ústavu*, 73, 1, 61-74.

- Hladil J., Pruner P., Venhodová D., Hladilová T. & Man O. 2002. Toward an exact age of Middle Devonian Čelechovice corals- Past problems in biostratigraphy and present solutions complemented by new magnetosusceptibility measurements. *Coral Res. Bull.*, 7, 65-71.
- Hüneke H. & Krienke K. 2004. Toe-of-slope deposits of a Givetian reef-rimmed platform: provenance of calcareous density-flow deposits (Rabat-Tiflet-Zone, Morocco). *Facies*, 50, 2, 327-346.
- Hüneke H. 2006. Erosion and deposition from bottom currents during the Givetian and Frasnian: Response to intensified oceanic circulation between Gondwana and Laurussia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 234, 2-4, 146-167.
- Iven C., Mistiaen B. & Tourneur F. 1997. New data on the morphology and microstructure of the genus *Calipora* Schlüter, 1889 (Tabulata, Middle Devonian): systematic implications and reflections on the function of squamulae. *Bol. r. Soc. españ. Hist. natur. sec. Geol.*, 91, 261-271.
- Janet F.E. 1965. Mikrostrukturnye osobennosti sbenok ejfel'skich i živet'skich tabuljat i chetetid Urala. In: Sokolov B.S. & Dubatolov V.N. (eds.). *Tabuljatomorfnye korally devona i karbona SSSR; Akademija Nauk SSSR, Sibirskoe otdelenie, Institut geologii i geofiziki, Moskva*, 12-24.
- Janet F.E. 1972. Gruppy Chaetetida; Podklass Tabulata. In: Chodalevič, A. N. (Ed.), *Kišečnopolostnye i brachiopody živet'skich otloženiž vostočnogo sklona Urala. Ministerstvo geologii SSSR, Ministerstvo geologii RSFSR, Ural'skoe territorial'noe geologičeskoe upravlenie, Moskva*, 43-98.
- Kaufmann B. 1998a. Facies, stratigraphy and diagenesis of Middle Devonian reef- and mud-mounds in the Mader (eastern Anti-Atlas, Morocco). *Acta geol. Polonica*, 48, 1, 43-106.
- Kaufmann B. 1998b. Middle Devonian reef and mud mounds on a carbonate ramp: Mader Basin (eastern Anti-Atlas, Morocco). In: Wright, V.P. & Burchette, T.P. (eds.). *Carbonate Ramps. Geol. Soc., London, Spec. Publ.*, 149, 417-435.
- Königshof P. & Kershaw S. 2006. Growth forms and palaeoenvironmental interpretation of stromatoporoids in a Middle Devonian reef, southern Morocco (west Sahara). *Facies*, 52, 2, 299-306.
- Le Maître D. 1947. Contribution à l'étude du Dévonien du Tafilalet, II: Le récif coralligène de Ouhilane. *Notes Mém. Serv. géol. Maroc*, 67, 112 p.
- Le Maître D. 1952. La faune du Dévonien inférieur et moyen de la Saoura et des abords de l'Erg el Djemel (Sud-Oranais). *Matériaux pour la carte géologique de l'Algérie*, 1<sup>ère</sup> Série Paléontologie 12, 171 p.
- Lonsdale W. 1840. Notes on the age of limestones of south Devonshire. *Transactions Geol. Soc. London*, 5, 721-738.
- May A. 1993a. Korallen aus dem höheren Eifelium und unteren Givetium (Devon) des nordwestlichen Sauerlandes (Rheinisches Schiefergebirge). Teil I: Tabulate Korallen. *Palaeontographica, Abt. A*, 227, 87-224.
- May A. 1993b. Korallen aus dem höheren Eifelium und unteren Givetium (Devon) des nordwestlichen Sauerlandes (Rheinisches Schiefergebirge). Teil II: Rugose Korallen, Chaetetiden und spezielle Themen. *Palaeontographica, Abt. A*, 228, 1-103.
- May A. 1993c. *Thamnopora* und verwandte ästige tabulate Korallen aus dem Emsium bis Unter-Eifelium von Asturien (Devon; Nord-Spanien). *Geologica et Palaeontologica*, 27, 73-101.
- May A. 1995. *Thamnopora* (Anthozoa: Tabulata) aus dem Givetium bis Frasnium von Asturien (Devon; Nord-Spanien). *Münstersche Forsch. Geol. Paläont.*, 77, 479-491.
- May A. 1996. 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.
- May A. 1997a. Statistics on *Thamnopora* (Tabulata; Devonian). In: Perejón A. & Comas-Rengifo M. J. (eds.). Proceedings of the VII International Symposium on Fossil Cnidaria and Porifera held in Madrid, Spain, 1995, Volume I. *Bol. r. Soc. esp. Hist. natur. (Sec. Geol.)*, 91, 217-230.
- May A. 1997b. Gedanken über Zusammenhänge zwischen Meeresspiegel, Biogeographie und Bio-Events im Devon. *Coral Res. Bull.*, 5, 291-318.
- May A. 1998. Statistische Untersuchungen an der tabulaten Koralle *Thamnopora* (Anthozoa; Devon). *Geologica et Palaeontologica*, 32, 141-159.
- May A. 2006a. *Radiastraea* (Anthozoa, Rugosa) from the Emsian and Eifelian (Devonian) of Aviaños, northern Spain. *Bull. Geosci., Prague*, 81, 3, 151-162.
- May A. 2006b. *Micheliniiidae* and *Cleistoporidae* (Anthozoa, Tabulata) from the Devonian of Spain. *Bull. Geosci., Prague*, 81, 3, 163-172.
- McKerrow W.S., Mac Niocaill C., Ahlberg P.E., Clayton G., Cleal C.J. & Eagar R.M.C. 2000. The Late Palaeozoic relations between Gondwana and Laurussia. In: Franke W., Haak V., Oncken O. & Tanner D. (eds.) - *Orogenic Processes. Quantification and Modelling in the Variscan Belt. Geol. Soc., London, Spec. Publ.* 179, 9-20.
- McLean R.A. 1993. Frasnian rugose corals of Western Canada. Part 3A: The massive *Phillipsastrea* - *Phillipsastrea*, *Chuanbeiphyllum*. *Palaeontographica, Abt. A*, 230, 1-3, 39-76.
- Mergl M., Massa D. & Plauchut B. 2001. Devonian and Carboniferous Brachiopods and Bivalves of the Djado Sub-Basin (North Niger, SW Libya). *J. Czech Geol. Soc.*, 46, 3-4, 169-188.
- Milne-Edwards H. & Haime, J. 1849. Mémoire sur les polypiers appartenant aux groupes naturels des Zoanthaires perforés et des Zoanthaires tabulés. *C. R. Acad. Sci., Paris*, 29, 257-263.
- Milne-Edwards H. & Haime J. 1850. A monograph of the British fossil corals. First part. Introduction; corals from the Tertiary and Cretaceous Formations. *Monographs of the Palaeontographical Society London*, 3, 2, 7, i-lxxxv + 1-72.
- Milne-Edwards H. & Haime J. 1851. Monographie des Polypiers fossiles des terrains paléozoïques. *Archives du Muséum d'Histoire Naturelle*, 5, 502 p.
- Nicholson H.A. & Foord A.H. 1886. On a new genus of Devonian corals, with descriptions of some species of the same. *Ann. Mag. natur. Hist.*, ser. 5, 17, 389-400, 518-523.
- Okulitch V.J. 1936. On the genera *Heliolites*, *Tetradium* and *Chaetetes*. *Amer. J. Sci.*, 32, 5, 361-379.
- Oliver W.A. jr. & Pedder A.E.H. 1994. Crises in the Devonian history of the rugose corals. *Paleobiology*, 20, 2, 178-190.
- Orbigny A. d'. 1849. *Note sur des polypiers fossiles*. Paris, 12 p.
- Pedder A.E.H. 1999. Paleogeographic Implications of a Devonian (Givetian, Lower Varcus Subzone) Rugose Coral Fauna from the Ma'der Basin (Morocco). *Abh. Geol. B.-A., Wien*, 54, 385-434.
- Pedder A.E.H. & Oliver W.A. jr. 1990. Rugose coral distribution as a test of Devonian palaeogeographic models. In: McKerrow W.S., Scotese C.R. (Eds.) - *Palaeozoic Palaeogeography and Biogeography. Geol. Soc. London, Mem.* 12, 267-275.
- Plusquellec Y. 1998. *Pleurodictyidae* de l'Emsien supérieur des Monts d'Ougarta (Algérie). *Ann. Soc. geol. Nord*, 6 (2<sup>ème</sup> série), 5-23.

- Plusquellec Y., Boumendjel K., Morzadec P. & Paris F. 1997. Les faunes dévoniennes d'Ougarta dans la paléogéographie des régions Maghrébo-Européennes. *Ann. Soc. geol. Nord*, 5 (2<sup>ème</sup> série), 123-128.
- Plusquellec Y. & Hladil J. 2001. Tabulate corals of Ibarmaghian affinities in the Upper Emsian of Bohemia. *Geologica et Palaeontologica*, 35, 31-51.
- Potthast I. & Oekentorp K. 1987. Eine Favositiden-Fauna aus dem Emsium/ Eifelium des Hamar Laghdad, Tafilalt (SE-Marokko). *Münstersche Forsch. Geol. Paläont.*, 66, 57-94.
- Pradáčová M. 1938. Čeled' Favositidae z čelechovického devonu. *Rozpravy České Akademie Věd, Ř. mat. přír. Věd*, 48, 35, 1-24.
- Radugin K.V. 1938. Coelenterata srednego devona okrestnostej s. Lebedjanskogo. *Izvestija Tomskogo industr. Instituta*, 56, 6, 49-109.
- Rodriguez Mellado M. 1948. El Devónico en el Sáhara español. *Bol. r. Soc. esp. Hist. natur.*, 46, 425-442.
- Rzhonsnitskaya M.A., Kulikova V.F., Gagiev M.Kh. & Timofeeva O.B. 1985. Boundaries of Stages of the Middle Devonian in Salair. In: Ziegler W. & Werner R. (eds.) - Devonian Series Boundaries - Results of world-wide Studies. *Courier Forsch.-Inst. Senckenberg*, 75, 113-122.
- Schlüter C. 1880. *Calamopora crinalis* n. sp. *Sitzungsberichte der Niederrheinischen Gesellschaft für Natur- und Heilkunde in Bonn*, 37, 281-282.
- Schlüter C. 1885. Einige neue Anthozoen aus dem Devon. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens*, 42 (Sitzungsberichte), 144-152.
- Schlüter C. 1889. Anthozoen des rheinischen Mitteldevon. *Abhandlungen zur geologischen Special-Karte von Preussen und den thüringischen Staaten*, 8 (4), x + 259-465.
- Schröder S. & Kazmierczak M. 1999. The Middle Devonian "coral reef" of Ouhilane (Morocco) - New data on the geology and rugose coral fauna. *Geologica et Palaeontologica*, 33, 93-115.
- Schröder S. & Werner W. 2000. Eine neue rugose Stockkoralle der Gattung *Phillipastrea* ROEMER, 1883 aus dem Devon von Marokko. *Mitt. Bayer. Staatsslg. Paläont. hist. Geol.*, 40, 229-236.
- Scotese C. R. & McKerrow W.S. 1990. Revised World maps and introduction. In: McKerrow W.S. & Scotese C.R. (eds.) - Palaeozoic Palaeogeography and Biogeography; *Geol. Soc. London, Mem.*, 12, 1-21.
- Sokolov B.S. 1952. Tabuljaty paleozoja evropejskoj časti SSSR. Čast' IV: Devon ruskij platformy i zapadnogo Urala. *Trudy vsesojuznogo nefljanogo naučno-issledovatel'skogo geologo-razvedočnogo instituta (VNIGRI)*, n. S., 62, 291 p.
- Sorauf J.E. 1998. Frasnian (Upper Devonian) rugose corals from the Lime Creek and Shell Rock Formations of Iowa. *Bull. Amer. Paleont.*, 113, 355, 1-159.
- Stadelmaier M., Nose M., May A., Salerno C., Schröder S. & Leinfelder R.R. 2005. Ästige tabulate Korallen-Gemeinschaften aus dem Mitteldevon der Sötenicher Mulde (Eifel): Faunenzusammensetzung und fazielles Umfeld. *Zitteliana*, B25, 5-38.
- Steininger J. 1831. *Bemerkungen über die Versteinerungen, welche in dem Übergangskalkgebirge der Eifel gefunden werden*. Trier, 44 p.
- Stock C.W. 2005a. Biogeographical barriers. In: Lieberman B.S. & Stigall Rode A.L. (Eds.) - Paleobiogeography: generating new insights into the coevolution of the earth and its biota. *Paleont. Soc. Pap.*, 11, 89-102.
- Stock C.W. 2005b. Devonian stromatoporoid originations, extinctions, and paleobiogeography: how they relate to the Frasnian-Famennian extinction. In: Over D.J., Morrow J.R. & Wignall P.B. (eds.) - *Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach*, Amsterdam (Elsevier), 71-92.
- Tait J., Schätz M., Bachtadse V. & Soffel H. 2000. Palaeomagnetism and Palaeozoic palaeogeography of Gondwana and European terranes. In: Franke W., Haak V., Oncken O. & Tanner D. (eds.) - Orogenic Processes. Quantification and Modelling in the Variscan Belt. *Geol. Soc. London, Spec. Publ.* 179, 21-34.
- Termier G. & Termier H. 1950. Paléontologie Marocaine, II, Invertébrés de l'ère primaire, Fasc. 1, Foraminifères, spongiaires et coelentérés. *Notes Mém. Serv. géol. Maroc*, 73, 55-109.
- Torsvik T.H. & Cocks L. R.M. 2004. Earth geography from 400 to 250 Ma: a palaeomagnetic, faunal and facies review. *J. Geol. Soc.*, London, 161, 555-572.
- Verrill A.E. 1865. Classification of polyps (Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under captains Ringgold and Rodgers, U.S.N.). *Essex Institute, Proceedings*, 4, 145-149.
- Wedekind R. 1937. *Einführung in die Grundlagen der historischen Geologie. II. Mikrobiostratigraphie: Die Korallen- und Foraminiferenzeit*, 1-136. Stuttgart.
- Wendt J. & Kaufmann B. 1998. Mud buildups on a Middle Devonian carbonate ramp (Algerian Sahara). In: Wright V.P. & Burchette T.P. (eds.) - Carbonate Ramps. *Geol. Soc. London, Spec. Publ.* 149, 397-415.
- Wendt J. & Kaufmann B. 2006. Middle Devonian (Givetian) coral-stromatoporoid reefs in West Sahara (Morocco). *J. Afr. Earth Sci.*, 44, 339-350.
- Wendt J., Belka Z., Kaufmann B., Kostrewa R. & Hayer J. 1997. The world's most spectacular carbonate mud mounds (Middle Devonian, Algerian Sahara). *J. Sed. Res.*, 67, 3, 424-436.
- White C.A. 1870. *Report on the Geological Survey of the State of Iowa. Volume 1*. Des Moines, 391 pp.
- Yolkin E.A. & Kim A.I. 1988. Devonian of the Asiatic part of the USSR: Recent achievements and problems. In: McMillan N. J., Embry A.F. & Glass, D.J. (eds.) - Devonian of The World; *Canadian Soc. Petroleum Geol.*, Mem. 14, vol. III, 663-667.
- Ziegler P.A. 1989. *Evolution of Laurussia: A Study in Late Palaeozoic Plate Tectonics*. Dordrecht, Kluwer Academic Publishers, Netherlands, 102 p.

Manuscript received 8 October 2007  
Modified version accepted 7 April 2008