Givetian rugose corals from the Zemmour in Mauritania

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ABSTRACT. Ten species and three forms of rugose corals from the Givetian of the Zemmour in Northern Mauritania are described and illustrated, confirming the age of the coral levels intercalated in a succession of mainly detrital deposits more than 300 m thick. Five taxa are new: Acanthophyllum filiforme n. sp., A. sougyi n. sp., Charactophyllum soraufi n. sp., C. mauritanicum n. sp. and Macgeea tourneuri n. sp. The coral fauna of the Zemmour is characterized by some North Gondwanan species such as Siphonophrentis kullmanni (Birenheide, 1978). However, there are also several species defined in the Givetian of Western and Eastern Europe which are useful for stratigraphic correlations, especially Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851), Sociophyllum isactis (Frech, 1886), Spinophyllum spongiosum (Schlüter, 1889) and Argutastrea briceae (Rohart, 1988). Farther to the east, the relationships with the Givetian of Russia, China and Australia are only occasional. Additionally, the fauna of the Zemmour is unusual due to the occurrence of the rather rare genera Moravophyllum Kettnerova, 1932, Charactophyllum Simpson, 1900 and Iowaphyllum Stumm, 1949.

KEYWORDS: Rugosa, taxonomy, stratigraphy, Givetian, palaeobiogeography, Gondwana.

1. Introduction

The Givetian of the Zemmour is well exposed to the north of Bir Moghreim (formerly Fort Trinquet), in the northern part of Mauritania (Fig. 1). It was investigated in great detail, from a lithologic and biostratigraphic point of view, by Sougy (1964) who gathered among others a large collection of rugose corals in the early Sixties. Part of these specimens was sent to Professor Marius Lecompte of the Catholic University of Louvain in Belgium and is now stored in the Collection of Palaeontology of the Institut royal des Sciences naturelles de Belgique at Brussels.

Three Givetian species of massive rugose corals have been identified in the Zemmour by Coen-Aubert (2013); these are Phillipsastrea torreana (Milne-Edwards & Haime, 1851), P. kergarvanensis Coen-Aubert & Plusquellec, 2007 and P. sobolevi (Rozkowska, 1956). Besides two massive colonies belonging to Argutastrea Crickmay, 1960 and Iowaphyllum Stumm, 1949, a diverse fauna of mostly solitary rugose corals is described in this paper. Unfortunately, the Givetian of the Zemmour is not dated or subdivided with much precision as there are nearly no recent studies on other groups of fossils and as there are no block samples available for the extraction of microfossils such as conodonts.

2. Geological setting and material

The Givetian of the Zemmour has been summarized with some detail by Coen-Aubert (2013), on the basis of the three main sections investigated by Sougy (1964): sections E4 of Tighirt, F5 of Aguel Nebka and Amgli el Harra and F6 of Amgli el Harra and Amgli Zguilma (Fig. 2). Additionally, some rugose corals studied herein come from the sections of Douik el Akhdar and D13 of Aguelt Oudiate el Khyam where only the base of this succession is exposed.

Lithologically, the Givetian of the Zemmour can be subdivided into two parts above unit 81 of Sougy (1964) which was named Cabrieroceras Limestone as it contains the goniatite C. crispiformis (Fig. 3). For Sougy (1964), this level corresponds to the base of the Givetian. However, as mentioned by Tourneur (1987), C. crispiformis occurs in the middle part of the Tortodus kockelianus conodont Zone, that is to say below the start of the Givetian defined at the base of the Polygnathus hemiansatus Zone. Therefore, the Eifelian-Givetian boundary is not known with precision.
The lower part of the succession between units 82 and 90 of Sougy (1964) consists of 208 m of marls with several intercalations of limestone. Two of these intercalations are coralliferous and named by Sougy (1964) Lower Coral Beds for unit 87 and Upper Coral Beds for unit 90. In unit 87, the following taxa have been observed:

- Argutastrea briceae (Rohart, 1988) in the section of Douik el Akhdar;
- Acanthophyllum heterophyllum (Mine-Edwards & Haime, 1851), A. filiforme n. sp. and Moravophyllum cf. ptenophyloides Kettnerova, 1932 in section D13 of Aguelt Oudiate el Khyam;
- Phillipsastrea sobolewi and Iowaphyllum cf. crassozonalum Kettnerova, 1932 in section E4 of Tighirt.

In the latter section, only a few specimens of Sociophyllum isactis (Frech, 1886) and Siphonophrentis sp. have been identified in unit 90.

The upper part of the Givetian from the Zemmour has been investigated less precisely by Sougy (1964), in section F6 of Amgli el Harra and Amgli Zguilma. Between units 91 and 100, there are 209 m of siltstones and clays with again a few intercalations of limestone. Rugose corals have been collected by Sougy (1964) a few metres above unit 90 as well as in units 96, 98 and 100. Charactophyllum mauritanicum n. sp., Phillipsastrea sobolewi, P. torreana and Macgeea tourneuri n. sp. are present at the base of unit 91. M. tourneuri and Phillipsastrea torreana have also been recorded slightly higher in sample 2392 (Fig. 4) of Sougy (1964). Samples 2396, 2398 and 2413 of this author come probably from units 96, 98 or 100 whereas his sample 2381C and D comes probably from units 98 or 100. For a few samples such as 2443, there is no geographic and stratigraphic information provided by the letters and specimen labels of J. Sougy. Despite this imprecision, the diversified rugose coral fauna of units 96, 98 and 100 is represented by Acanthophyllum sougyi n. sp., Charactophyllum soraufi n. sp., C. mauritanicum, Spinophyllum spongiosum (Schlüter, 1889), Phillipsastrea kergarvanensis and Siphonophrentis kullmanni (Birenheide, 1978).

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**Figure 3.** Schematic lithologic column for the Givetian of the Zemmour according to the detailed data provided by Sougy (1964), with the distribution of rugose corals.

**Figure 4.** Relations between the coralliferous units, sections and samples of Sougy (1964) from the Givetian of the Zemmour, investigated herein and by Coen-Aubert (2013).
At the top of section F6 f Amgli el Harra and Amgli Zguilma, unit 100 of Sougy (1964) is overlain first by 43 m of clays and siltstones with brachiopods (unit 101) and then by 100 m of silty clays with rare fossils (unit 102). No appropriate arguments are available in these deposits to recognize the Givetian-Frasnian boundary.

As noted by Coen-Aubert (2013), the Givetian succession of the Zemmour has been compared by Dumestre & Illing (1967) and Wendt & Kaufmann (2006) with that situated about 100 km to the north, close to Smara in the northern part of Western Sahara. The correlations proposed by these authors are based on several levels of coralliferous limestone as well as on the key bed of oolitic limestone occurring at the top of unit 94 (Fig. 3) of Sougy (1964). According to Wendt & Kaufmann (2006), the lower and upper boundaries of the Givetian are also not clearly defined in Western Sahara.

3. Systematic Palaeontology

The types of the new species and the figured specimens are stored in the Collection of Palaeontology of the Institut royal des Sciences naturelles de Belgique at Brussels (IRScNB). All the material investigated herein was collected by J. Sougy in the Zemmour during the early Sixties.

Family Ptenophyllidae Wedekind, 1923

Genus Acanthophyllum Dybowski, 1873

Type species. By subsequent designation of Schlüter (1889, p. 38), Cyathophyllum heterophyllum Milne-Edwards & Haime, 1851.

Diagnosis. Large solitary rugose corals. Septa of two orders, rarely discontinuous at the periphery, thin to more or less dilated throughout their length. Major septa, sometimes thicker in the outer or in the inner part of the dissepimentarium, carinate in the tabularium and reaching usually the axis of the corallum. Minor septa traversing the entire dissepimentarium. Wide dissepimentarium composed of numerous rows of inclined dissepiments which are occasionally subhorizontal at the periphery. Tabulae incomplete and closely spaced, forming concave floors.

Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851)

(Plate 1A-B)

v * 1851 Cyathophyllum heterophyllum; Milne-Edwards & Haime: 367, pl. 10, figs 1, la-b.

v 1997 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert: 11, pl. 1, figs 1-4, pl. 2, figs 5-7.

non 2005 Acanthophyllum heterophyllum (Milne-Edwards & Haime); Jin: 118, pl. 17, figs 1-8.

v 2011 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert: 36, pl. 2, fig. 6.

Remarks. More complete lists of synonymy with the references before 1997 and 2011 have been provided by Coen-Aubert (1997; 2011).

Holotype. Specimen Z47a or MNHN LP S 11670 from the collection Milne-Edwards stored in the Laboratory of Palaeontology, Muséum National d’Histoire naturelle in Paris, France. Devonian of the Eifel Hills in Germany; locality details mentioned by Birnheide (1961) are unsatisfactory as he thought that the type of the species was probably lost. Pl. 10, figs 1, la and 1b in Milne-Edwards & Haime (1851) and pl. 1, figs 1-2 in Coen-Aubert (1997).

Material. 1 specimen with 2 thin sections: Zemmour 5544B l. 9160-I.

Diagnosis. A species of Acanthophyllum with 70 to 90 septa at a diameter of 20 mm to 42 mm. Major septa strongly dilated in the inner dissepimentarium. Dissepiments often arranged in horizontal layers at the periphery.

Description. The only corallum available is 8 cm high and is cylindrical with longitudinal ribs. The outer wall is not preserved.

The septa are non-carinate and strongly dilated throughout their length. The major ones are thicker in the dissepimentarium than the minor ones. Locally, both orders of septa may be divided longitudinally into two parts, at the periphery where there are a few dissepiments like abutments. The major septa bear vepreculae in the tabularium and reach its centre where a few fragments of them are also present. The minor septa traverse the entire and wide dissepimentarium.

The dissepimentarium consists of 19 to 26 rows of dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. Some spots of stereoplasma occur in the dissepimentarium. The tabulae are closely spaced and vesicular; they are disrupted by axial ends of thick major septa with vepreculae.

There are 86 septa for a diameter of 32 mm to 43 mm whereas the width of the tabularium measures 14.5 mm to 17 mm.

Discussion. The Mauritanian specimen is typical of the species Acanthophyllum heterophyllum though its major septa are rather strongly dilated in the main part of the dissepimentarium. The Emsian material of Yunnan in China illustrated by Jin (2005) is different as it is characterized by slightly smaller coralla with all their septa thickened in the dissepimentarium and locally a peripheral stereozone.

Distribution. The Mauritanian specimen comes from the lower part of the Givetian in the Zemmour. Acanthophyllum heterophyllum is widely distributed in the Eifelian and the Lower Givetian of the Eifel Hills in Germany, in the Upper Emsian of the Eifel and the Lower Givetian from the south side of the Dinant Synclinorium in Belgium and the North of France as well as from the Ma’der in Morocco. It is also known in the Upper Emsian of the Southeastern Armorican Massif in France and in the Lower Eifelian of the Holy Cross Mountains in Poland.

Acanthophyllum filiforme n. sp.

(Plate 1C-D; Plate 2F-G)

Derivation of name. From filiformis, e (Latin) = threadlike, referring to the thin septa of the species.

Holotype. IRScNB a13143 (= Plate 1C-D). Specimen 5544B l. 9160-II collected during the early Sixties by J. Sougy in the Zemmour, Mauritania.

Type locality and horizon. Sample 5544 collected at the top of section D13 described by Sougy (1964) at Aguelt Oudiate el Khyam, in the Zemmour, Mauritania. Unit 87 named Lower Coral Beds by Sougy (1964), lower part of the Givetian.

Material. 3 specimens with 6 thin sections: Zemmour 5544B l. 9160-II and 1. 9163-I; Zemmour 5544F l. 9168-II.

Diagnosis. A species of Acanthophyllum with 74 to 86 septa at a diameter of 24 mm to 44 mm. Septa thin throughout their length. Wide dissepimentarium with numerous dissepiments often arranged in horizontal layers at the periphery.

Description. The material consists of conical and ceratoid coralla with longitudinal ribs and growth lines whose height varies between 4 cm and 8.5 cm. In one of them, an excavated calice border is bordered by a flat platform whereas another one belongs to a young stage. The outer wall is very rarely preserved.

The septa are non-carinate and thin throughout their length. Occasionally, the major septa are weakly dilated in the inner part of the dissepimentarium. They reach the axis of the
corallum where they are slightly twisted. In the centre of the tabularium, a few fragments of them, a pseudofossil, a little stereoplasma or a few vepraculae are locally observed. The minor septa traverse the entire and wide dissepimentarium; they are sometimes discontinuous at the periphery in the young stage.

In adult coralla, the dissepimentarium consists of 22 to 30 rows of globose dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. There are only 12 to 14 rows of inclined dissepiments at the tip of the young corallum. The tabulae are incomplete or vesicular with an overall concave pattern. They are disrupted by axial ends of septa often bearing vepraculae. A little stereoplasma is present close to the base of the corallum.

In the adult specimens, there are 86 septa for a diameter of 35 mm to 44 mm whereas the width of the tabularium measures 8.5 mm to 10 mm. In the young stage, there are only 74 septa for a diameter of 20 mm to 26 mm and the tabularium is 6.5 mm to 7 mm wide.

Discussion. By its slender septa, Acanthophyllum filiforme is related to A. verniculare (Goldfuss, 1826) from the Upper Eifelian and the Lower Givetian of the Eifel Hills in Germany. However, the latter species is separated from the former by slightly smaller coralla, by mostly inclined dissepiments and by septa weakly dilated throughout their length though they are sometimes thinner at the periphery. The abundant Belgian material of A. verniculare close to the Eifelian-Givetian boundary has been investigated by Coen-Aubert (1997). As discussed by Schröder & Kazmierczak (1999) and Coen-Aubert (2011), A. torquatum (Schlüter, 1884) from the Eifelian of the Eifel Hills is probably conspecific with A. verniculare. Thin septa characterize also Grypophyllum mirabile Birenheide, 1972 renamed G. frechi Birenheide, 1974. But this taxon from the Upper Eifelian of the Eifel Hills is distinguished from Acanthophyllum filiforme by septa often discontinuous at the periphery and by its tabularium much better separated from the dissepimentarium. Grypophyllum frechi has also been described by Birenheide (1978).

Distribution. The species is only known in the lower part of the Givetian from the Zemmour in Mauritania.

Acanthophyllum sougyi n. sp. (Plate 1G-H; Plate 2D-E; Plate 4F)

Derivation of name. The species is dedicated to Jean Sougy, a distinguished French geologist who collected during the Sixties and from 19 mm to 20 mm in the young stages. The width of the tabularium varies between 10.5 mm and 20 mm.

Discussion. Acanthophyllum sougyi is related to A. heterophyllum by its quantitative data, by the thickness and the length of the septa and by numerous dissepiments often arranged in horizontal layers at the periphery. It is different in having major and minor septa nearly equally dilated throughout the dissepimentarium, some stereoplastic thickenings in the tabularium and more vesicular tabulae. Such stereoplastic thickenings affect the tabularium of A. radiatum (Wedekind, 1924) and A. filosum (Wedekind, 1923) from the Eifelian of the Eifel Hills in Germany. They are weak in A. filosum and more strongly developed in A. radiatum. However, these two taxa have rather thin septa at the periphery as shown by the illustrations of Birenheide (1961, 1978). A. sougyi resembles more in transverse section the corallum from the Eifelian of Northwest Turkey assigned to A. cf. filosum by Birenheide & Kaya (1987); but this specimen is distinguished in longitudinal section by wider incomplete tabulae and fewer inclined dissepiments. Finally, A. sougyi has some affinities with A. baculoides (Pocta, 1902) from the Pragian of Bohemia in the Czech Republic, which has been revised by Olivier & Galle (1971). In the lectotype selected by these authors, the septa are more or less discontinuous at the periphery whereas in the rest of their material, all the septa are much thicker throughout the dissepimentarium.

Distribution. The species is only known in the Middle to Upper Givetian from the Zemmour in Mauritania.

Family Cyathophyllidae Dana, 1846

Genus Moravophyllum Kettnerova, 1932

Type species. By original designation, Moravophyllum ptenophylloides Kettnerova, 1932.

Diagnosis. Large solitary rugose corals. Septa of two orders, non-carinate and thin in the dissepimentarium. Major septa more or less thickened within the tabularium, up to rather late growth stages. Major septa reaching the axis of the corallum or leaving an open space in the centre of the tabularium. Minor septa traversing the entire dissepimentarium. Narrow dissepimentarium composed of globose dissepiments arranged in horizontal layers in its outer part and inclined towards the axis of the corallum in its inner part. Broad tabularium with usually incomplete tabulae.
**Moravophyllum cf. ptenophylloides** Kettnerova, 1932

(Plate 2-B-C)

cf. 1932 *Moravophyllum ptenophylloides* n. sp.; Kettnerova: 29, figs 8-12.

cf. 1932 *Ptenophyllum celechovicense* n. sp.; Kettnerova: 24, figs 3-5, pl. 3, figs 7-8.

cf. 1932 *Ptenophyllum irregularare* n. sp.; Kettnerova: 26, figs 6-7.

cf. 1978 *Moravophyllum ptenophylloides* Kettnerova 1932; Birenheide: 82, fig. 44.

cf. 1981 *Moravophyllum ptenophylloides*; Hill: F303, figs 197, 1a-c.

? 2005 *Moravophyllum ptenophylloides* Kettnerova; Jin: 130, pl. 20, figs 9-12, pl. 21, figs 1-7.

**Holotype.** Specimen PrFUK No 19 from the Remes collection stored in the Geological Institute of the Charles University at Prague, Czech Republic. Lower Givetian Celechovic Limestone at Celechovice in Moravia, Czech Republic according to Galle (2007). Figs 8-12 in Kettnerova (1932), fig. 44 in Birenheide (1978) and figs 197, 1a-c in Hill (1981).

**Material.** 1 specimen with 2 thin sections: Zemmour 5544G I. 9166.

**Diagnosis.** A species of *Moravophyllum* with 90 to 124 septa at a diameter of 25 mm to 50 mm. Major septa reaching the axis of the corallum and thin to slightly thicker within the tabularium. Long minor septa.

**Description.** The only corallum available is 8.5 cm high and is ceratoid with longitudinal ribs and a deep calice. The transverse section is faintly elliptical whereas the outer wall is not preserved.

The septa are non-collinear or bear rare small nodes at the periphery. They are thin or locally slightly dilated in the dissepimentarium. They are frequently thicker at its inner border or within the tabularium. The major septa leave a small open space in the centre of the corallum where there are a few fragments of them; one pseudofossula is also present. The minor septa are traversing all or nearly all the dissepimentarium and they are rather often contragredient; they are rarely shorter or discontinuous at their inner ends.

The dissepimentarium consists of 10 rows of globose dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. The tabulae are closely spaced, incomplete and intersecting laterally. At the base of the corallum, there are thickened and more or less contiguous septa which become discontinuous upwards, in later ontogenetic stages and finally disappear.

There are 118 septa for a diameter of 38 mm to 60 mm whereas the width of the tabularium measures 18 mm to 21 mm.

**Discussion.** By comparing the descriptions and illustrations of *Moravophyllum ptenophylloides*, *M. celechovicense* (Kettnerova, 1932) and *M. irregularare* (Kettnerova, 1932) given by Kettnerova (1932), it is clear that these three species from the Lower Givetian of Celechovice in Moravia are synonymous. For Birenheide (1978), *M. tenuiseptatum* Kettnerova 1932 from the same locality belongs also to this taxon; however, it is not so well known as its longitudinal section has not been figured by Kettnerova (1932). Additionally, Birenheide (1987) had already assigned *M. irregularare* to the genus *Moravophyllum* Kettnerova, 1932.

The Mauritanian specimen differs from *M. ptenophylloides* and its two synonyms by a small open space in the centre of the tabularium and occasionally shorter minor septa which do not traverse systematically the entire dissepimentarium. The abundant material of Jin (2005) does not show any septal thickening within the tabularium. *Moravophyllum oliveri* Birenheide, 1987 from the Upper Eifelian Freilingen Formation of the Eifel Hills in Germany is very close to *M. ptenophylloides*; however, the former species is separated from the latter by its septa which are slightly fewer and much more dilated throughout their length, during the young ontogenetic stages. The corallum also from the Upper Eifelian of the Eifel Hills identified as *M. cf. oliveri* by Schröder (1995) resembles more the Mauritanian specimen.

**Distribution.** Besides the questionable specimen from the lower part of the Givetian in the Zemmour (Mauritania), *Moravophyllum ptenophylloides* is only known in the Lower Givetian from Moravia in the Czech Republic. It may be present in the Lower to Middle Devonian from Yunnan in China.

Family Stringophyllidae Wedekind, 1922

**Genus Sociophyllum** Birenheide, 1962

1962 *Stringophyllum (Sociophyllum)* Birenheide: 53.

1978 *Parasociophyllum* Kong in Kong & Huang: 111.

1981 *Stringophyllum (Gaofengophyllum)* Kong: 55.

**Type species.** By original designation, *Spongophyllum elongatum* Schlüter, 1881.

**Diagnosis.** Fasciculate rugose corals. Septa of two orders, rather thick and consisting of coarse monacanthine trabeculae. Septa sometimes continuous from the wall to the axis of the corallites, but more often disrupted at the periphery by presepiments. Major septa bilaterally arranged and reaching or not the centre of the tabularium where they are occasionally breaking up into isolated trabeculae. Minor septa lacking or poorly developed. Dissepimentarium composed of a few rows of elongate dissepiments. Tabulae complete or incomplete, normally concave.

**Sociophyllum isactis** (Frech, 1886)

(Plate 1-E-F)

* p. 1886 *Cyathophyllum isactis* n. sp.; Frech: 75, pl. 1, fig. 7, pl. 2, figs 13-18 (non fig. 19).

1911 *Cyathophyllum isactis* Frech; Frech: 52, pl. 8, fig. 5.

1925 *Grypophyllum isactis* Frech; Wedekind: 14, 16-17, pl. 4, figs 12-14.

v 1958 *Stringophyllum? isactis* (Frech, 1886); Engel & Von Schouppé: 90, figs 13-14, pl. 8, figs 7-8.

1974 *Neospingophyllum isactis* (Frech); Song: 167, pl. 78, fig. 5.

? 1998 *Stringophyllum cf. isactis* Frech (1886); Birenheide, 179, pl. 10, fig. 4.

v 1999 *Sociophyllum isactis* (Frech, 1886); Coen-Aubert: 33, pl. 1 figs 8-10, pl. 2, figs 10-12, pl. 3, figs 5-10.

v 2000 *Sociophyllum isactis* (Frech, 1886); Coen-Aubert: pl. 3, fig. 10.

2002 *Sociophyllum isactis*; Coen-Aubert: 11.

2005a *Stringophyllum isactis* (Frech, 1886); Schröder: 104, pl. 10, figs 5-6.

v 2016 *Sociophyllum isactis* (Frech, 1886); Coen-Aubert in Brice: figs 110, H-I.

non 2017 *Parasociophyllum isactis* (Frech), 1886; Liao & Ma: 73, figs 4, 1-4.

**Remark.** A complete list of synonymy for the references before 1998 has been provided by Coen-Aubert (1999).

**Lectotype.** Specimen SMF WDKD 2584 chosen by Wedekind (1925, p. 16) and stored in the Forschungsinstitut Senckenberg at Frankfurt am Main, Germany. Givetian Büchel Formation at Schladetal, close to Bergisch Gladbach in the Bergisches Land, Germany. Pl. 2, fig. 15 in Frech (1886) and pl. 4, fig. 12 in Wedekind (1925). For a long time, the lectotype was presumed lost and a neotype was selected by Engel & Von Schouppé (1938). However Birenheide (1998, p. 179) claimed that he has found again the lectotype of Wedekind (1925).
Material. 1 specimen with 2 thin sections: Zemmour 5552K-MAU45.

Diagnosis. A species of Sociophyllum with 25 to 30 major septa at a diameter of 8 mm to 13 mm. Major septa commonly continuous from the outer wall to the axis of the corallite. Minor septa lacking.

Description. The only corallite available, which is 3 cm high, is cylindrical with longitudinal ribs. The outer wall is not preserved.

The non-carinate septa are dilated throughout their length though they may be progressively less thick within the tabularium. The septa are locally discontinuous at the periphery with a few lonsdaleoid dissepiments. The major septa more or less reach the axis of the corallite where there are a few trabeculae; their axial ends are sometimes rhopaloid. The minor septa are lacking or represented by rare small spines. Some layers of dissepiments are occasionally affected by a weak stereoplasmic thickening.

The dissepimentarium consists of 1 to 3 rows of large inclined dissepiments. The more or less incomplete tabulae with a concave pattern are disrupted by coarse trabeculae and fragments of septa.

There are 34 major septa for a diameter of 10 mm to 14 mm whereas the width of the tabularium measures 8 mm to 8.2 mm.

Discussion. Sociophyllum isactis is the type species of Parasociophyllum Kong in Kong & Huang (1978). However, the Chinese genus is based on the specimen of S. isactis figured by Frech (1911) and coming from the Givetian of Tien Shan in China. Several authors such as Hill (1981, p. F248) consider that this corallite is conspecific with the Givetian German material of Frech (1886). As S. isactis is mostly represented by fragments of slender cylindrical corallites with some lateral buds suggesting a fasciculate growth form, Parasociophyllum is here placed in synonymy with Sociophyllum Birenheide, 1962. Coen-Aubert (2000) has indeed figured a fasciculate colony of Sociophyllum isactis from the Givetian of Belgium.

Though the Mauritanian specimen of S. isactis is characterized by some discontinuity of the septa at the periphery, it falls within the wide variability of the species illustrated in the Givetian of Belgium and Germany (Coen-Aubert, 1999; Wedekind, 1925). Concerning the list of synonymy, it is difficult to identify the fragmentary longitudinal section assigned to S. cf. isactis by Birenheide (1998) and occurring in the Givetian of the Viersen 1001 borehole from Northwest Germany. The Givetian material from Northeast Yunnan in China figured by Liao & Ma (2017) is variable, but typically fasciculate. More particularly, it has horizontal layers of small dissepiments and sometimes mesa-shaped tabulae. Therefore, it does not belong to the genus Sociophyllum.

Distribution. Besides the Mauritanian specimen from the Givetian of the Zemmour, Sociophyllum isactis is widely distributed in the Givetian of the Old World Realm. In Belgium, the species is present at the top of the Lower Givetian, mainly on the south side of the Dinant Synclinorium. In Germany, it comes from the Givetian Büchel Formation in the Bergisches Land and from the Givetian of Stötenich in the Eifel Hills without more precision. S. isactis also occurs in the Givetian of Moravia in the Czech Republic, from the Russian Platform and the Urals in Russia, from Tien Shan, Guizhou and Yunnan in China and from New South Wales and North Queensland in Australia.

Family Disphyllidae Hill, 1939

Genus Charactophyllum Simpson, 1900

Type species. By original designation, Campophyllum nunum Hall & Whitfield, 1873.

Diagnosis. Solitary rugose corals. Septa of two orders, non-carinate to faintly carinate and more or less dilated in the dissepimentarium. Major septa commonly with weak to strong additional dilation within the tabularium, in some or all stages of corallite growth. Major septa reaching the axis of the tabularium or leaving an open space in the centre of the tabularium. Minor septa traversing the entire dissepimentarium. Dissepimentarium composed of several rows of globose dissepiments, often arranged in horizontal layers in its outer part and inclined towards the axis of the corallum in its inner part. Tabulae usually incomplete or compound.

Charactophyllum soraufi n. sp.

(Plate 2A; Plate 3E-H; Plate 5F-G)

Derivation of name. The species is dedicated to James Sorauf, a distinguished American specialist of Devonian rugose corals.

Holotype. IRScNB a13150 (= Plate 3E-F). Specimen 2381D-MAU34 collected during the early Sixties by J. Sougy in the Zemmour, Mauritania.

Type locality and horizon. Sample 2381 collected close to the section F6 of Amgh el Harra and Amgh Zguilma described by Sougy (1964) in the Zemmour, Mauritania. Probably unit 98 or 100 of Sougy (1964), Middle to Upper Givetian.

Material. 18 specimens with 31 thin sections: Zemmour 2381D-MAU34, MAU35, MAU36, MAU37, MAU38, MAU39, MAU41, MAU42, MAU79, MAU82, l. 9144-II, IV, VI and X; Zemmour 2398-MAU30, l. 7169-1 and IV, l. 8195-VII.

Diagnosis. A species of Charactophyllum with 62 to 74 septa at a diameter of 15 mm to 25 mm. Septa rarely carinate and slightly dilated in the dissepimentarium. Major and minor septa more or less long. Rather wide dissepimentarium.

Description. The material consists of conical, trochoid and ceratoïd coralla with longitudinal ribs whose height varies between 1.5 cm and 6 cm. In some specimens, an excavated calice is bordered by a flat peripheral platform whereas a few others are affected by rejuvenescence. The outer wall is rarely preserved and the coralla may be abraded at the periphery.

The septa are non-carinate or bear a few spinose, knobbly and even yardarm carinae in the outer dissepimentarium of some specimens. The septa are slightly dilated in the dissepimentarium with occasionally the major ones thicker than the minor ones. They are sometimes thinner at the periphery or in the tabularium. However, the septa are often dilated throughout their length, thicker or less thick in the tabularium. In a few coralla, a stereoplasmic thickening is present within the dissepimentarium whereas a more or less continuous inner wall occurs at the border of the tabularium, in some juvenile transverse sections.

The major septa reach the axis of the corallum or leave an open space in the centre of the tabularium. Their axial ends are sometimes rhopaloid, forming pseudofossulae or breaking into fragments. In a few specimens, some stereoplasma is present in the tabularium, between the septa or at its centre. The minor septa traverse the entire dissepimentarium. They are occasionally shorter, contragenting, discontinuous especially at their inner ends or hardly projecting into the tabularium.

The dissepimentarium consists of 3 to 12 or even 17 rows of small globose dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. Some spots of coarse and usually contiguous septal trabeculae occur in the dissepimentarium whereas an inner stereozone may be present at the base of the corallum and in the longitudinal sections of young stages. The tabulae are incomplete and intersecting laterally, often with a flat-topped or horizontal axial part which is locally affected by a stereoplasmic thickening; the tabulae are rarely concave or horizontal.

There are 60 to 80 septa per corallum. The diameter of the corallum ranges from 13.5 mm to 27 mm. The width of the
tabularium varies between 8.2 mm and 13.5 mm.

Discussion. Charactophyllum Simpson, 1900 and its type species C. nanum (Hall & Whitfield, 1873) from the Upper Frasnian of Iowa in USA have been well revised by Sorauf (1998) and McLean (2014). The latter author restricted the genus to a few Frasnian species and to C. burdekinense Zhen & Jell, 1996 from the Lower Givetian of North Queensland in Australia. Qualitatively, C. burdekinense which shows notably septa more or less thick in the tabularium, looks similar to C. soraufi, but differs from it by smaller septal number and diameter of the corallum. According to McLean (2014), Spinophyllum complicatum (Wang, 1948) from the Givetian of Yunnan in China could possibly be referred to Charactophyllum. However, this species is more carinate than C. soraufi. As described by Soshkina (1952, p. 68) and Sytova et al. (1974, p. 37), C. armenicum (Soshkina, 1952) from the Givetian of Armenia resembles the new species though it is characterized by a narrower dissepimentarium, more septa and larger coralla. On the contrary and as mentioned by McLean (2014), the species figured by Soshkina et al. (1962, pl. 6, fig. 5) as C. armenicum does not belong to the same genus and species as it has carinate and weakly dilated septa.

At first view, there are some affinities between C. soraufi and Spinophyllum blacourti (Rohart, 1988) from the Givetian of the Boulonnais in France. However, the latter is easily separated from Charactophyllum by its septa becoming systematically thin in the tabularium and is also well known in the Givetian of Belgium (Coen-Aubert, 2002).

Distribution. The species is only known in the Middle to Upper Givetian from the Zemmour in Mauritania.

Charactophyllum mauritanicum n. sp.

(Plate 3A-D; Plate 4A-C)

Derivation of name. From mauritanicus, a, um (Latin) referring to the country where the new species has been collected.

Holotype. IRScNB a13154 (= Plate 3A-B). Specimen 2398 l. 7168-III collected during the early Sixties by J. Sougy in the Zemmour, Mauritania.

Type horizon and locality. Sample 2398 collected in the section F6 of Amghi el Harra and Amghi Zguiulma described by Sougy (1964) in the Zemmour, Mauritania. Probably between units 96 and 100 of Sougy (1964), Middle to Upper Givetian.


Diagnosis. A species of Charactophyllum with 70 to 80 septa at a diameter of 20 mm to 30 mm. Major septa more or less reaching the axis of the corallum and commonly very thickened in the tabularium. Incomplete tabulae intersecting laterally.

Description. The material consists of conical and ceratoid coralla whose height varies between 2 cm and 6 cm; longitudinal ribs and growth lines are sometimes present. In one specimen, a weakly excavated calice is bordered by a flat peripheral platform. The coralla may be abraded at the periphery and the outer wall is locally preserved in a few of them.

The septa are non-carinate or bear a few small spinose, knobly or even yardarm carinae. They are dilated throughout their length and they are often thicker in the tabularium. Occasionally, the major septa are much dilated in the dissepimentarium than the minor ones. A little stereoplasma may occur in the tabularium where the septa may also be thinner locally.

The major septa reach more or less the axis of the corallum and they are rarely shorter. Their axial ends are sometimes rhopaloid, curved, discontinuous or fusing to form pseudofossulae. In one specimen, a longer major septum is bent as a hook whereas in a few other ones, septa are locally broken in the dissepimentarium and the tabularium. The minor septa traverse the entire dissepimentarium; occasionally, they are slightly shorter, contractant or hardly projecting into the tabularium.

The tip of the corallum is full of stereoplasma or of thick and contiguous septa. The dissepimentarium consists of 5 to 12 or even 18 rows of small globose dissepiments arranged in horizontal layers in its outer part and inclined in its inner part. The tabulae are incomplete and intersecting laterally; they are sometimes disrupted by axial ends of thick septa or affected by stereoplastic thickenings.

There are 70 to 82 septa per corallum. The diameter of the corallum ranges from 17 mm to 32 mm. The width of the tabularium varies between 8.7 mm and 14.5 mm.

Discussion. Charactophyllum soraufi differs from C. mauritanicum by slightly smaller septal number and diameter of the corallum, by major septa less thickened in the tabularium and by tabulae often compound with a flat-topped axial part. Quantitatively, C. mauritanicum is similar to C. armenicum which is slightly more carinate and whose dissepimentarium is much narrower.

In transverse section, C. mauritanicum resembles Glossophyllum salmense Wedekind, 1924 and G dohmi Wedekind, 1924 from the Eifelian of the Eifel Hills in Germany. In longitudinal section, G. salmense is characterized by very few dissepiments and flat-topped tabulae. As for G. dohmi, type species of Glossophyllum Wedekind, 1924, its lectotype is only represented by a few transverse sections figured among others by Birenheide (1978). So the genus Glossophyllum is inadequately known as mentioned already by Pedder (1982) and Coen-Aubert (1997). Charactophyllum mauritanicum has also some affinities with Thoulelasma yukonanum Pedder, 1984 from the Lower Emsian of the Yukon Territory in Canada. However, the latter species is distinguished from the former by fewer dissepiments and by vesicular tabulae with a convex pattern. Thoulelasma loewei Pedder, 1983 from the Upper Emsian of the Northwest Territories in Canada, type species of Thoulelasma Pedder, 1983, is much larger than Charactophyllum mauritanicum and has on the other hand more vesicular tabulae as noted by Lütte (1987) in his comparison with Glossophyllum.

Distribution. The species is only known in the Middle to Upper Givetian from the Zemmour in Mauritania.

Genus Spinophyllum Wedekind, 1922

1922 Spinophyllum Wedekind: 5.
1982 Truncicarinulum Yu & Kuang: 253.

Type species. By monotypy, Campophyllum spongiosum Schütler, 1889.

Diagnosis. Solitary rugose corals. Septa of two orders, highly and irregularly carinate in the dissepimentarium with yardarm and zigzag carinae. Septa more or less dilated in the dissepimentarium and thin in the tabularium. Major septa reaching the axis of the corallum or leaving an open space in the centre of the tabularium. Minor septa traversing the entire dissepimentarium. Dissepimentarium composed of several rows of globose dissepiments arranged in horizontal layers in its outer part and inclined towards the axis of the corallum in its inner part. Tabulae incomplete or compound.

Spinophyllum spongiosum (Schütler, 1889)

(Plate 6H-I)
Schröder: 66, pl. 1, fig. 5.  

v 2002 Spinophyllum spongiosum (Schütler, 1889); Coen-Aubert: 15, pl. 2, figs 11-12, pl. 3, figs 3-7.  

2002 Spinophyllum spongiosum (Schütler 1889); Schröder: 180, pl. 2, fig. 13.  

v 2004 Spinophyllum spongiosum (Schütler, 1889); Barchy et al.: pl. 1, figs 8-9.  

non 2005 Spinophyllum cf. spongiosum Schütler; Jin: 127, pl. 18, figs 5-19.  

2005a Spinophyllum spongiosum (Schütler, 1889); Schröder: 64, pl. 2, fig. 6, pl. 3, figs 2-7.  

v 2007 Spinophyllum spongiosum (Schütler, 1889); Galle: fig. 2.  

v 2016 Spinophyllum spongiosum (Schütler, 1889); Coen-Aubert in Bricé: fig. 110J.  

**Remark.** A complete list of synonymy for the references before 2001 has been provided by Coen-Aubert (2002).

**Lectotype.** Specimen Nr 174a of the Schlüter collection chosen by Birenheide & Lütte (1990, p. 4) and stored in the Paläontologisches Institut from the University of Bonn in Germany. Givetian Büchel Formation of the disused Büchel quarry near Herrenstruden and Bergisch Gladbach in the Bergisches Land in Germany. Specimen Nr 174a of the Schlüter collection chosen by Birenheide & Lütte (1990, p. 4) and stored in the Paläontologisches Institut from the University of Bonn in Germany. 

**Material.** 1 specimen with 2 thin sections: Zemmour 2381D-MAU33.

**Diagnosis.** A species of Spinophyllum with 60 to 70 septa at a diameter of 13 mm to 21 mm. Yardarm and zigzag carinae rather strong and numerous. No stereoplasmic thickening between the septa in the adult stage.

**Description.** The only corallum available is 3 cm high and is conical with longitudinal ribs; its calice is excavated and bordered by steep sides. The outer wall is not preserved. The septa with strong yardarm carinae are dilated in the disseppimentarium and thinner in the tabularium; locally they are slender at the periphery. The major septa leave a small open space in the centre of the tabularium. The minor septa traverse the entire disseppimentarium; sometimes they are hardly projecting into the tabularium where they are constrictingent. The disseppimentarium consists of 6 to 8 rows of small globose dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. The tabulae are incomplete and intersecting laterally, occasionally with a narrow flat-topped axial part.

There are 68 septa for a diameter of 18 mm to 20 mm whereas the width of the tabulium measures 8.9 mm to 9.5 mm.

**Discussion.** Despite its septa being rather slender in the disseppimentarium, the Mauritanian specimen falls within the variability of Spinophyllum spongiosum. Indeed, this feature appears also in some Belgian and German coralla of the Givetian. In Belgium, it is present at the top of the Lower Givetian, mainly on the south side of the Dinant Synclinorium. In Germany, S. spongiosum is known in the Middle Givetian from the Aachen Syncline, the Eifel Hills, the Bergisches Land and the Sauerland.  

**Genus Argutastrea Crickmay, 1960**

Type species. By original designation, Argutastrea arguta Crickmay, 1960.

**Diagnosis.** Massive cerioid rugose corals. Septa of both orders, non-carinate or sometimes faintly carinate, dilated in the disseppimentarium or at least in its outer part and becoming thin in the tabularium. Major septa extending to or nearly to the axis of the corallites. Minor septa variable in length. Disseppimentarium moderately wide with commonly several series of small inclined dissepiments. Tabulae incomplete, occasionally complete or compound.

**Argutastrea briceae (Rohart, 1988)** (Plate 5A-C)

1988 Cyathophyllum briceae sp. nov.; Rohart: 282, pl. 31, fig. 15, pl. 36, figs 1-2.  

2011 Cyathophyllum briceae Rohart, 1988; Mistiaen et al.: 94, fig. 78.

**Holotype.** Specimen GFCL 4558 stored in the Department of Geology from the Faculté Libre des Sciences at Lille, France. 

**Material.** 1 specimen with 3 thin sections: Zemmour 417 l. 9137.

**Diagnosis.** A species of Argutastrea with 40 to 56 septa at a diameter of 15 mm to 25 mm. Septa weakly carinate and slender to slightly dilated in the disseppimentarium. Septa of both orders long, the minor ones traversing the entire disseppimentarium. Numerous rows of dissepiments often arranged in horizontal layers at the periphery.

**Description.** The only colony available is tabular and fragmentary with an area of 10 cm x 7 cm and a height of 6 cm. The large corallites are separated by a straight wall with locally a dark median line. The septa are non-carinate or bear a few small carinae. They are slightly dilated or rather slender in the disseppimentarium. They are often becoming thin in the tabularium. The major septa reach the axis of the corallites or leave a small open space in the centre of the tabularium where a few pseudofossulae are observed. The minor septa traverse the entire and wide disseppimentarium. The disseppimentarium consists of 6 to 12 rows of globose dissepiments which are arranged in horizontal layers in its outer part and inclined in its inner part. The tabulae are incomplete and intersecting laterally with flat-topped axial parts. There are 48 to 52 sepa per corallite. The diameter of the corallites ranges between 12.5 mm and 22 mm or even 25 mm. The width of the tabulium varies between 4.2 mm and 6 mm.

**Discussion.** Argutastrea briceae was assigned by Rohart (1988) to Cyathophyllum Goldfuss, 1826 whose type species is C. dianthus Goldfuss, 1826 from the Lower Givetian of the Eifel Hills in Germany. As mentioned already by Rohart (1988), Argutastrea briceae is not a typical representative of Cyathophyllum which is characterized by very thin septa with strongly zigzag carinae. Cyathophyllum was revised by Birenheide (1963) and discussed by Coen-Aubert (1990) who considered Argutastrea briceae as a somewhat extreme taxon of Argutastrea. Indeed, A. briceae is characterized by poorly carinate and faintly dilated septa in the disseppimentarium. Due to its large corallites, the species has a wide disseppimentarium whose outer dissepiments are often arranged in horizontal layers. Nevertheless, Rohart (1988) also observed among his numerous colonies of A. briceae some weakly inclined dissepiments at the periphery. Additionally, he placed in the synonymy list of A. briceae the Givetian material from the Boulozmons in France identified by Smith (1945, pl. 25, figs
1-3) as *Prismatophyllum bolonense* (Milne-Edwards & Haime, 1851) and showing in longitudinal section only inclined dissepiments, which is the common situation for *Argutastrea*. In fact, *Argutastrea briceae* is closely related to *A. tenuiseptata* Coen-Aubert & Lütte, 1990 from the Lower Givetian of Belgium and Germany. The latter species is separated from the former by slightly smaller septal number and diameters of the corallites and by mostly inclined dissepiments. However, in Belgian colonies of *A. tenuiseptata* with some large corallites, the dissepiments are locally arranged in horizontal layers at the periphery.

Despite the overall pattern of the dissepimentarium, *A. briceae* cannot be referred to *Hexagonaria* Gürich, 1896 whose type species is *Cythophyllum hexagonum* Goldfuss, 1826 from the Frasnian of the Bergisches Land in Germany. Indeed, *Hexagonaria* is characterized in transverse section by spindle-shaped dilated septa in the inner part of the dissepimentarium as it is mentioned among others in the diagnosis of the genus given by McLean (2010). This feature is certainly not present in the colony of *Argutastrea briceae* from the Zemmour. On the contrary and as noted herein, *Argutastrea* has septa uniformly thickenened in the dissepimentarium or at least in its outer part.

**Distribution.** Besides the colony from the lower part of the Givetian in the Zemmour, *Argutastrea briceae* is only known in the Lower Givetian from the Boulonnais in France.

Family Phillipsastreidae Roemer, 1883

**Genus Macgeea Webster, 1889**

**Type species.** By subsequent designation of Fenton & Fenton (1924, p. 54), *Pachyphyllum solitarium* Hall & Whitfield, 1873.

**Diagnosis.** Solitary rugose corals with a deep calice and the epitheca not quite extending to the rim of the calice so that the peripheral edges of the septa are exposed distally. Septa of two orders, non-carinate or sometimes faintly carinate, more or less long and dilated in the dissepimentarium, thin in the tabularium. Dissepimentarium with one outer row of flat dissepiments, a median pipe of horseshoe dissepiments and a few inner rows of small inclined dissepiments. Symmetrical fans of rhipidacanths centred over horseshoe dissepiments. Wide tabularium with incomplete or compound tabulae. Occurrence of stereome in early corallum growth stages.

**Macgeea tourneuri** n. sp.

(Plate 4D-E; Plate 5D-E)

**Derivation of name.** The species is dedicated to Francis Tourneur, a distinguished specialist of tabulate corals and Belgian marbles.

**Holotype.** IRSnC NB a13160 (= Plate 4D-E). Specimen 2391 l. 7108-V collected during the early Sixties by J. Sougy in the Zemmour, Mauritania.

**Type locality and horizon.** Sample 2391 collected close to the section F6 of Amgeli el Harra and Amgeli Zguilma described by Sougy (1964) in the Zemmour, Mauritania. A few metres above unit 90 of Sougy (1964), Middle to Upper Givetian.

**Material.** 7 specimens with 14 thin sections: Zemmour 2391 l. 7108-I, III, IV, V and VI; Zemmour 2392 l. 7165-II and III.

**Diagnosis.** A species of *Macgeea* with 78 to 88 septa at a diameter of 19 mm to 31 mm. Major septa affected by stereoplastic thickenings within the tabularium, rather late in the ontogeny. Occurrence of few rows of inner dissepiments.

**Description.** The material consists of often fragmentary, conical and ceratoid coralla with some longitudinal ribs and growth lines; their height varies between 2 cm and 6 cm. The coralla are usually abraded at the periphery and the outer wall is only locally preserved in one of them.

The septa are non-carinate and dilated throughout their length though they become thinner in the tabularium of a few adult specimens. More or less stereoplastic is frequently present between the septa in the tabularium where these skeletal elements are very thick and contiguous in the young stages. Locally, the septa are slender or discontinuous in the outer zone of flat dissepiments. In transverse section, the pipe of horseshoe dissepiments is occasionally coated with stereome on both sides and bordered by some inner dissepiments.

In the young stages, the major septa reach the axis of the corallum. Later in the ontogeny, the same situation is still present or the major septa leave an open space in the centre of the tabularium where are observed pseudofossulae, isolated trabeculae, discontinuous or twisted septa. The minor septa traverse all or nearly all the dissepimentarium; sometimes, they are restricted to the ring of the horseshoe dissepiments or they are hardly projecting into the tabularium where they may be contracting.

The dissepimentarium consists of:
- one peripheral row of flat dissepiments occasionally concave or intersecting laterally, which are rarely preserved;
- one row of horseshoe dissepiments with narrow symmetrical fans of rhipidacanths centred over them;
- 0 to 4 rows of inner inclined dissepiments.

In one specimen, one or two rows of external inclined dissepiments occur between the flat and horseshoe dissepiments. The tabulae are incomplete and intersecting laterally; sometimes, they are vesicular or their axial parts are flat-topped. The tabulae may be affected by local stereoplastic thickenings or disrupted by discontinuous and mostly thick septa especially at the base of the corallum which is nearly full of stereoplastic.

There are 78 to 88 sepa per corallum; their number is restricted to 68 in a juvenile specimen. The diameter of the corallum ranges from 18 mm to 31 mm, but it is only 15 mm or 16 mm in young stages. The width of the tabularium varies between 12 mm and 19 mm.

**Discussion.** *Macgeea tourneuri* is a peculiar species as it is represented by rather large coralla with poorly developed inner dissepiments and stereoplastic thickenings still present within the tabularium, in rather late growth stages. A more or less similar situation characterizes *M. sorafii* McLean, 2005 from the Middle Frasnian of the Northwest Territories in Canada. However, this taxon differs from the Mauritanian material by a slightly smaller diameter, by major septa often reaching the axis of the corallum and by stereoplastic less abundant in the young stages and mostly affecting the axial ends of the major sepa later in the ontogeny. McLean (2005) compared *M. sorafii* with *M. ponderosa* Stumm, 1960 from the Middle Frasnian of New York in USA, which has been revised by Sorauf (1987). *M. ponderosa* is separated from *M. tourneuri* by stereome always occurring in the tabularium even of adult specimens and by less constant inner dissepiments.

**Distribution.** The species is only known in the Middle to Upper Givetian from the Zemmour in Mauritania.

Family Siphonophrentidae Merriam, 1973

**Genus Siphonophrentis O’Connell, 1914**

**Type species.** By original designation, *Caryophyllia gigantea* Lesueur, 1821 placed in synonymy with *Siphonophrentis elongata* (Rafinesque & Clifford, 1820) by Stumm (1964, p. 23) and Oliver (1993, p. B26) after revision of the neotypes of both species.

**Diagnosis.** Large ceratoïd to cylindrical rugose corals. Septa of two orders non-carinate. In the young stages, septa dilated in the two cardinal quadrants. In the adult stages, septa thin to more or less dilated throughout their length, maybe with thickened peripheral ends to form a narrow stereosome.
Short major septa and still more reduced minor septa. Occurrence of a siphonofossula. No dissepiments. Tabulae often with a mesa-shaped pattern.

*Siphonophrentis kullmanni* (Birenheide, 1978)  
(Plate 6F-G)  

* 1978 *Breviphrentis kullmanni* n. sp. ; Birenheide: 69, pl. 9, fig. 3.  
non 2001b *Contophrentis kullmanni* (Birenheide, 1978) ;  
Schröder: 259, fig. 2.6.  

Holotype. Specimen SMF 50 936 stored in the Forschungsinstitut Senckenberg at Frankfurt am Main, Germany. Road between Verdiago and Valdore in the Esla valley, Leon Province in Spain. Lower part of the Givetian Portilla Formation. Pl. 9, fig. 3 in Birenheide (1978).

Material. 1 specimen with 2 thin sections: Zemmour 2381D I. 9144-III.

**Diagnosis.** A species of *Siphonophrentis* with 90 to 100 septa at a diameter of 30 to 40 mm. Septa more or less dilated to thin throughout their length. Rather long major septa and shorter minor septa. No peripheral stereozone.

**Description.** The only corallum available, which is 5 cm high, is conical with longitudinal ribs and a broad excavated calice. The transverse section is elliptical whereas the outer wall is partly preserved.

The non-carinate septa are more or less dilated throughout their length and are locally affected by a dark median line; they are occasionally thinner at their axial ends. The major septa leave a wide open space in the centre of the corallum where some fragments of septa are broken. The minor septa are rather short, but always present.

The tabulae are often broken with some broad flat-topped axial parts. At the base of the corallum, the septa are thick and nearly contiguous.

There are 94 septa for a diameter of 23 x 37 mm.

**Discussion.** The Mauritanian specimen is very close to the Spanish holotype figured by Birenheide (1978) which is characterized by a circular transverse section. The Spanish corallum illustrated by Schröder (2001b) as *Contophrentis kullmanni* comes from the Givetian Candas Formation in Asturias and is different in having a nearly continuous peripheral stereozone. The same specimen was identified by Altevogt (1967, pl. 1, fig. 8) as *Heterophrentis prolifica* (Billings, 1858). This taxon was chosen as type species of the genus *Metaxiphyrentis* Oliver, 1993 and its lectotype was revised by Oliver (1993). *M. prolifica* from the Eifelian of Ontario in Canada is in fact represented by coralla with long and thick septa which are commonly contiguous in a wide peripheral stereozone.

As mentioned by Schröder (2001b) and Coen-Aubert (2005), *Siphonophrentis kullmanni* was synonymized by Pedder (1999) with *S. belghebaschika* (Ivania, 1955) from the Givetian of the Gornyi Altai in Russia, which is the type species of *Altaiphyllum* Ivania, 1955. However, the septa of the holotype of *Siphonophrentis belghebaschika* figured by Ivania (1958, pl. 1, fig. 1) are much more dilated than those of *S. kullmanni*.

**Distribution.** Besides the Mauritanian specimen which comes from the Middle to the Upper Givetian of the Zemmour, *Siphonophrentis kullmanni* is known in the Lower to Middle Givetian from the Leon Province in Spain.

**Siphonophrentis sp.**  
(Plate 6C-E)

Material. 3 specimens with 5 thin sections: Zemmour 5552K-MAU43, MAU44 and I. 9186-I.

**Diagnosis.** The material consists of cylindrical and ceratoid coralla whose height varies between 3.5 cm and 6.5 cm. The outer wall is more or less continuous, but not very thick.

The non-carinate septa are thin or slightly dilated throughout their length. However, they may also be much thicker in the two cardinal quadrants or in all the transverse section of a rather young stage. The cardinal fossula is observed in the three specimens. The major septa leave a wide open space in the centre or the corallum where their axial ends are sometimes discontinuous or weakly rhopaloid. The minor septa are short, but always present. The tabulae are incomplete and often show a convex or more or less flat-topped axial part.

There are 66 to 76 septa for a diameter of 21 mm to 29 mm.

**Discussion.** Based on its quantitative data and some other features, *Siphonophrentis* sp. is related to *S. wangii* Coen-Aubert, 2005 from the Upper Givetian of the Tafilalt in Morocco. Nevertheless, the latter species is separated from the Mauritanian form by shorter major septa and by minor septa which are not always developed as they appear rather late during the ontogeny; additionally, the septa of *S. wangii* may be thicker in the adult stages. There are also some similarities between *Siphonophrentis* sp. and *S. laskovae* Wrzolek, 2002 which is known in the Upper Givetian from the Holy Cross Mountains in Poland and from the Ma’der in Morocco. However, *S. laskovae* is characterized by greater septal number and diameter of the corallum and once more by very short major septa.

**Distribution.** The form has only been observed in the Givetian of the Zemmour in Mauritania.

Family Endophyllidae Torley, 1933

**Genus Iowaphyllum** Stumm, 1949

**Type species.** By original designation, *Smithia johanni* Hall & Whitfield, 1873.

**Diagnosis.** Massive aphroid rugose corals. Non-carinate septa thin in the tabularium, more or less thick in the inner dissepimentarium and continuing across the outer dissepimentarium as dilated septal ridges or crests on the top surfaces of large presepiments arranged in horizontal layers. Major septa reaching the axis of the corallites or leaving an open space in the centre of the tabularium. Minor septa restricted to the dissepimentarium. Tabulae usually incomplete with an elevated axial part.

*Iowaphyllum cf. crassozonatum* He, 1978  
(Plate 6A-B)  

(cf. 1978 *Iowaphyllum crassozonatum* He (sp. nov.); He: 156, pl. 78, fig. 3.  
v 1993 *Iowaphyllum* sp. ; Coen-Aubert & Lüttke: 49, figs 5b-c.

Holotype. Specimen Scr 705 stored in the Chengdu Institute of Geological and Mineral Resources at Chengdu, Sichuan Province in China. Givetian Guanwushan Formation in the Longmenshan Mountains to the north of Chengdu City, Beichuan County, Sichuan Province in China. Pl. 78, fig. 3 in He (1978).

Material. 1 specimen with 2 thin sections: Zemmour 5314 I. 9112.

**Diagnosis.** A species of *Iowaphyllum* with 54 to 66 septa at tabularial diameters of 6.5 mm to 8 mm. Adjacent corallite axes 13 mm to 18 mm apart. Major septa reaching the axis of the corallites, strongly dilated and contiguous in the inner dissepimentarium.
Description. The only colony available is tabular with an area of 17 cm x 9 cm and a height of 9 cm. The septa are continuous in the inner dissepimentarium and in the tabularium. They are very thick and often contiguous in the inner dissepimentarium. The major septa are much less dilated in the tabularium and reach the axis of the corallites; their axial ends may be rhopaloid, fusing to form pseudofossilae or bearing a few spinose carinae. The minor septa are restricted to the inner dissepimentarium and they barely project into the tabularium where they are sometimes contrangent. Outside the inner dissepimentaria, the corallites are separated by large presepiments where incomplete rings of stereoplasmic thickenings are developed, consisting of more or less short segments of thick septa.

In longitudinal section, the presepiments are arranged in horizontal layers alternating with thin zones of stereoplasmic thickenings characterized by some spines. The dissepiments are only inclined at the border of the tabularium where there is nearly no inner wall. The tabulae are incomplete with occasionally a more or less flat-topped axial part. They are interrupted by the axial ends of rather slender septa with a few spinose carinae.

There are 60 septa per corallite. The diameter of the tabularium varies between 11 cm and 12 cm. The distances between the centres of adjacent corallites range from 33 mm to 55 mm.

Discussion. The Mauritanian colony resembles the holotype of *Iowaphyllum crassozonalum* from which it differs by larger tabularia and greater distances between the centres of adjacent corallites. Additionally, the minor septa are restricted to the dissepimentarium in *I. crassozonalum* whereas its tabulae are typically compound with flat-topped axial parts. The Mauritanian form assigned to *I. cf. crassozonalum* resembles also *I. schlueteri* (Etheridge, 1898) which comes from the Givetian of New South Wales and North Queensland in Australia and which has been revised by Pedder et al. (1970), figs 6, 9) and Zhen (1994, p. 312). However, *I. schlueteri* is more separated from the Mauritanian specimen by shorter distances between adjacent corallites and slightly smaller septal number and diameter of the tabularium. Moreover, *I. schlueteri* is characterized by thicker zones of stereoplasmic thickenings between the horizontal layers of dissepiments.

Distribution. Besides the questionable colony from the lower part of the Givetian in the Zemmour (Mauritania), *Iowaphyllum crassozonalum* is only known in the Givetian from the Sichuan Province in China.

4. Stratigraphic and palaeobiogeographic conclusions

The Givetian rugose coral fauna of the Zemmour is highly diversified though several species are only represented by a few specimens in the collection of Sougy (1964). At the specific level, there are curiously not many affinities with the Givetian material of the Tafilalt and the Ma'der in Morocco (Fig. 5) investigated recently by Pedder (1999), Schröder & Kazmierzczak (1999) and Coen-Aubert (2005, 2013). From a stratigraphic point of view, all the species of the Zemmour identified between units 87 and 100 of Sougy (1964) are typical of the Givetian stage.

In unit 87, *Acanthophyllum heterophyllum*, *A. filiforme* and *Moravophyllum cf. ptenophyloides* have been recognized in section D13 of Aguelt Oudiam el Khayam. *M. ptenophyloides* was originally described from the Lower Givetian of Moravia in the Czech Republic. *Acanthophyllum heterophyllum* is well known in the Upper Eifelian and the Lower Givetian from Belgium and France as well as from the Ma’der in Morocco where it has been described among others by Pedder (1999).

As mentioned in the systematic part, *A. filiforme* is related to *A. vermiculare* which is associated with *A. heterophyllum* in Belgium and Germany and which has also been reported in the Lower Givetian of the Ma’der by Schröder & Kazmierzczak (1999). *Argutastrea briceae* is present in unit 87 from the section of Douik el Akhdar. All the original material of Rohart (1988) from the Boulonnais in France comes from the base of the Griset Member, in the lower part of Blacourt Formation. This level with *A. briceae* is still Lower Givetian on the basis of conodonts (Mistiaen et al., 2011). According to Coen (1985), the main part of the Griset Member in the Boulonnais can be correlated with the Mont d’Haur Formation, on the south side of the Dinant Synclinorium in Belgium. This lithostratigraphic unit has been described among others by Coen-Aubert (1999, 2002). Finally, *Phillipsastrea sobolewi* and *Iowaphyllum cf. crassozonalum* have been recorded in unit 87 from section E4 of Tighirt. The *Iowaphyllum* form of the Zemmour resembles the Givetian species *I. crassozonalum* and *I. schlueteri* collected respectively in the Sichuan Province in China and in New South Wales and North Queensland in Australia. *Phillipsastrea sobolewi* occurs also at the base of unit 91 of Sougy (1964) and has been defined in the Middle Givetian of the Holy Cross Mountains in Poland (Coen-Aubert, 2013).

In section E4 of Tighirt, *Siphonophrentis* sp. and *Sociophyllum isacis* have been observed in unit 90 of Sougy (1964). The latter species is widely distributed in the Givetian of the Old World Realm (Fig. 5) and it is a good stratigraphic marker for this stage (Coen-Aubert, 1999).

More precisely, *S. isacis* is common in the lower part of the Mont d’Haur Formation, on the south side of the Dinant Synclinorium (Coen-Aubert, 1999, 2002) and it is associated with *Iowaphyllum schlueteri* in the Givetian of New South Wales (Pedder et al., 1970).

All the rest of the rugose coral fauna from the Zemmour comes from section F6 of Amgli el Harra and Amgli Zguilma, above unit 90 of Sougy (1964). At the base of this succession, *Macgeea tourneuri* and *Phillipsastrea torreana* are restricted to samples 2391 and 2392 (Fig. 4). As mentioned by Coen-Aubert (2013), *P. torreana* is known in the Givetian Portilla Formation from the Leon Province in Spain. *Macgeea tourneuri* is characterized by large coralla with stereoplasmic thickenings still developed in the tabularium of rather adult stages. Therefore, it is very different from other *Macgeea* such as *M. cressisepata* Schröder, 2005 described from the Upper Givetian of the Ma’der by Schröder (2005b).

In the other samples of section F6, *Acanthophyllum sougyi*, *Charactophyllum soraufi*, *C. mauritanicum* and *Phillipsastrea kergarvanensis* are more or less frequent whereas *Spinophyllum spongiosum* and *Siphonophrentis kulkmanni* are only represented by one specimen. *S. kulkmanni* has also been introduced in

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Figure 5. Occurrences of Givetian rugose corals from the Zemmour in different areas of the Old World Realm.
the Givetian Portilla Formation of the Leon Province. As for *Spinophyllum spongiosum*, it is another species characteristic for the top of the Lower Givetian in Belgium. Indeed, it is present in the lower part of the Mont d’Haur Formation and at the top of the underlying of the Terres d’Haur, on the south side of the Dinant Synclinorium (Coen-Aubert, 2002). Besides the Zemmour, *Phillipsastrea kergarvanensis* is abundant in the Upper Givetian of the Armorican Massif (Coen-Aubert, 2013). As discussed in the systematic part, the relations of the new species *Acanthophyllum sougyi*, *Chactophyllum soraufi* and *C. mauritanicum* with taxa of other countries are not very clear.

From a palaeogeographic point of view, the Zemmour was situated during the Givetian at the northern margin of Gondwana. This was also the case for the Ma’der in Morocco, the Leon Province in Spain and the Armorican Massif in France as explained by Coen-Aubert & Plusquellec (2007) and Coen-Aubert (2013). This means that *Phillipsastrea torearea*, *P. kergarvanensis* and *Siphophonentis kullmanni* are typically North Gondwanan species. Among the Givetian rugose corals from the Zemmour, there are additionally several species introduced in Eastern Europe and in other countries of Western Europe (Fig. 5) belonging to South Laurussia (Coen-Aubert & Plusquellec, 2007). More particularly, *Acanthophyllum heterophyllum*, *Sociophyllum inacis*, *Spinophyllum spongiosum* and *Argustrea briceae* are very useful for precise correlations between the Givetian of the Zemmour with that of Belgium, Germany and the Boulonnais in France. Farther to the east, there are only a few links with the Givetian of Russia, China and Australia (Fig. 5). These palaeogeographic relations for the Givetian rugose corals of the Zemmour are the same as those mentioned by Coen-Aubert (2005, 2013) for the Mauritanian Adrar and for the Ma’der and the Taifilait in Morocco. Finally, it must be emphasized that the rather rare genera *Moravophyllum*, *Chactophyllum* and *Iowaphyllum* have been observed in the Givetian of the Zemmour.

5. Acknowledgements

Through the kindness of Dominique Laduron and Francis Tourneur, the rugose coral collection of Jean Sougy from the Zemmour in Mauritania, which was previously stored in the Institute of Geology at Louvain-la-Neuve, has been moved to the Collection of Palaeontology from the Institut royal des Sciences naturelles de Belgique in Brussels. Jean Sougy provided me stratigraphic data about several samples of the Zemmour, during the years 1991 and 1992. Weihua Liao (Nanjing) gave me interesting information about the holotype of *Iowaphyllum crassozonalum* He, 1998. Some recent thin sections have been made by Joel Laval at the Laboratory of successively Eddy Poty and Valentin Fischer (Liège). Wilfried Miser and Thierry Hubin helped me with photography of the corals. Ross McLean and Anthony Wright reviewed very carefully the manuscript and improved the language. I am most grateful to all these persons.

6. References


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Plate 2. A: Charactophyllum soraufi n. sp. Paratype, IRScNB a13151, Zemmour 2381D-MAU35; transverse section. B-C: Moravophyllum cf. ptenophylloides Kettnerova, 1932. IRScNB a13148, Zemmour 5544G l. 9166; transverse and longitudinal sections. D-E: Acanthophyllum sougyi n. sp. Paratype, IRScNB a13146, Zemmour 2396 l. 7167-II; transverse and longitudinal sections. F-G: Acanthophyllum filiforme n. sp. Paratype, IRScNB a13144, Zemmour 5544F l. 9168-II; transverse and longitudinal sections. Magnification x 2 for figures B-G and x 3 for figure A.
Plate 4. A-C: Charactophyllum mauretanum n. sp. A: Paratype, IRScNB a13156, Zemmour 2389-MAU21; transverse section. B-C: Paratype, IRScNB a13157, Zemmour 2389-MAU25; transverse and longitudinal sections. D-E: Macgeea tourneuri n. sp. Holotype, IRScNB a13160, Zemmour 2391 l. 7108-V; transverse and longitudinal sections. F: Acanthophyllum sougyi n. sp. Paratype, IRScNB a13147, Zemmour 2413 l. 7170-IV; transverse section. Magnification x 2 for figure F and x 3 for figures A-E.