

# Description of some Middle Devonian rugose corals from the Ma'der (eastern Anti-Atlas, Morocco)

#### MARIE COEN-AUBERT

D.O. Terre et Histoire de la Vie (Evolution de la Paléobiosphère), Institut royal des Sciences naturelles de Belgique, rue Vautier 29, B-1000 Bruxelles, Belgium; mcoenaubert@naturalsciences.be.

#### ABSTRACT

Twelve species and four forms of Middle Devonian rugose corals from Morocco are described and illustrated. The material comes from four localities of the Ma'der Basin whose age from the Late Eifelian to the base of the middle Givetian is based on conodonts. Three taxa are new: *Marennophyllum kaufmanni* n. sp., *Stringophyllum pedderi* n. sp. and *Siphonophrentis subaequalis* n. sp. *Heliophyllum moghrabiense* Le Maître, 1947 is the only taxon common to the four outcrops and it suggests an Eastern North American influence at the level of the genus. *Siphonophrentis cantabrica* Birenheide, 1978, first described from Spain, is also a North Gondwanan species whereas *Stringophyllum acanthicum* (Frech, 1885), *Acanthophyllum heterophyllum* (Milne-Edwards & Haime, 1851), *A. vermiculare* (Goldfuss, 1826) and *Spinophyllum blacourti* (Rohart, 1988) are interesting for correlations with Western Europe and sometimes with Eastern Europe. *Enallophrentis corniformis* (Gürich, 1896) was defined in Poland, also in the Old World Realm. Farther to the east, there is a link with China where *Siphonophrentis cantabrica* is present. Finally, it must be mentioned that *Australophyllum* Stumm, 1949 is observed for the first time in Morocco.

#### Article history

Received 29.11.2023, accepted in revised form 19.02.2025, available online 27.05.2025.

#### **KEYWORDS**

Rugosa, taxonomy, stratigraphy, palaeobiogeography, Eifelian–Givetian, North Africa

#### 1. Introduction

The Ma'der Basin is a Variscan syncline situated in southeast Morocco. As mentioned by Hollard (1974), it is a wide quadrangular depression surrounded by a ridge of Devonian limestones which is nearly continuous. Among these deposits, there are various Middle Devonian levels rich in rugose corals. Le Maître (1947) was the first specialist to study these fossils in the upper Eifelian of Ouahlane (Fig. 1). Pedder (1999) described quite a lot of middle Givetian material coming from Ou Driss East. Coen-Aubert (2002, 2005) investigated in detail several localities from the upper Givetian of the northwestern part of the Ma'der.

This paper is devoted to a small collection of rugose corals across the Eifelian–Givetian boundary. The specimens have been collected by different geologists working in the field and by the author. They come from four localities: Aferdou el Mrakib and Madène el Mrakib at the southern margin of the Ma'der Basin, Ou Driss East at its southwest extremity and Ouahlane at its northern margin. The biostratigraphic data for these outcrops are due to identifications of conodonts made by several specialists. The upper Eifelian is characterized by the succession of the *Tortodus australis*, *T. kockelianus*, *Polygnathus eiflius* and *P. ensensis* conodont zones. In the lower Givetian, the *P. hemiansatus* and the *P. timorensis* zones are observed in ascending order. The base of the middle Givetian is traced at the base of the *P. rhenanus/P. varcus* Zone. Information about this biostratigraphy based on conodonts is provided among others by Becker et al. (2020, fig. 22.11) and Halamski et al. (2022a, fig. 6).

#### 2. Geological setting and localities

#### 2.1. Aferdou el Mrakib

Aferdou el Mrakib is located in the southern part of the Ma'der Basin, approximately 50 km to the south of Msissi. This reefal locality was first mentioned by Hollard (1974, p. 24). Hollard (1981, table 3) indicated the references of his fossiliferous samples for this outcrop. Some rugose corals investigated in this





**Figure 1.** Devonian outcrops of the Ma'der Basin and situation of the four localities investigated, after Bultynck & Walliser (2000, fig. 3).

paper come from these samples: MA401 with *Kuangxiastraea* sp. from TM551 and MA402 to MA404 with *Atelophyllum maximum* (Schlüter, 1882) and *Siphonophrentis subaequalis* n. sp. from TM554/1. Kaufmann (1998) described in detail the reefal facies of Aferdou el Mrakib and provided precise stratigraphic datings and correlations based on conodonts. He was also interested by the identification of some rugose and tabulate corals. During the last years, there were several papers published about the locality of Aferdou el Mrakib such as Jakubowicz et al. (2019), Majchrzyk et al. (2022) and Zatoń et al. (2023). The first of them is the most interesting for the specialist of rugose corals.

According to these different publications, the basement of the buildup from Aferdou el Mrakib consists of 20 m of bedded crinoidal limestone, close to the Eifelian-Givetian boundary (Polygnathus ensensis to P. hemiansatus conodont zones). A few metres below its top and still in the Eifelian, there is a level rich in cystiphyllid rugose corals where B. Kaufmann collected in 1995 a few solitary rugose corals assigned herein to Marennophyllum kaufmanni n. sp., Stringophyllum coenaubertae Pedder, 1999 and Heliophyllum moghrabiense Le Maître, 1947. The cystiphyllid biostrome is overlain by massive limestones characteristic of the reef core where fasciculate colonies of Thamnophyllum Penecke, 1894 are abundant. The central part of the mound is completely dolomitized so that fossils and sedimentary structures have been obliterated. The whole buildup eroded in its uppermost part measures approximately 900 m in diameter and 130 m in height. According to Kaufmann (1998), the reef development reaches the base of the middle Givetian, in the Polygnathus rhenanus/P. varcus conodont Zone.

Because of the erosion and pervasive dolomitization of the reef core, the reef builders of the former reef crest are mostly preserved as intercalations within the fore reef succession. They are represented by massive phillipsastreids and endophyllids figured by Jakubowicz et al. (2019). But other rugose corals such as those collected by Hollard (1981) are also found in this particular environment.

#### 2.2. Madène el Mrakib

Madène el Mrakib is situated in the southwestern part of the Ma'der Basin, about 8 km to the southwest of Aferdou el Mrakib. The locality has been first investigated by Hollard (1974, 1981). A simplified log of this outcrop has been figured by Kaufmann (1998, fig. 31). Recently, a more detailed lithological log has been given by Zatoń et al. (2022a, fig. 2) with interesting data about conodonts. According to these authors, the lower part of the section of Madène el Mrakib is characterized by bedded limestones with many intercalations of marls, marly clays and nodular mudstones. The Eifelian-Givetian boundary has been recognized at the transition between the Polygnathus ensensis and P. hemiansatus conodont zones. This boundary occurs 32 m below the top of this argillaceous sequence. The overlying lithological unit is represented at the end of the outcrop, by 20 m of reefal limestones with stromatoporoids and corals as mentioned by Kaufmann (1998, p. 55). In March 1984, P. Sartenaer has collected two specimens of Heliophyllum moghrabiense and Australophyllum sp. at Madène el Mrakib coming probably from this lower Givetian limestone unit. Part of the succession described by Zatoń et al. (2022a), at Madène el Mrakib, has been studied by Majchrzyk et al. (2024, fig. 2), at the top of the argillaceous sequence and at

the base of the reefal unit.

#### 2.3. Ou Driss East

The Jbel Ou Driss is a southwestern outlier of the Ma'der Basin and is located in the Zagora Graben. The Ou Driss East section investigated in detail by Hollard (1974, 1981) and Bultynck (1985, 1989, 1991) is situated 55 km northeast of Zagora and can be reached by the track to Tissemoumine. It consists of upper Emsian, Eifelian and lower to middle Givetian rocks. The diverse rugose corals identified in this paper come from the top of the section between the samples ODE 3 and ODE 2 of Hollard (1981). As mentioned by Bultynck (1989, p. 97 and 1991, p. 19), the conodonts *Polygnathus rhenanus* and *Icriodus difficilis* first occur in sample ODE 3 whereas *P. varcus* is present in sample ODE 2. This means that the interval between ODE 3 and ODE 2 belongs to the base of the middle Givetian, according among others to Halamski et al. (2022a, fig. 6).

The rugose coral fauna occurring between the samples ODE 3 and ODE 2 has been partly described by Pedder (1999). The material, which I have investigated herein in the same interval, has been collected by H. Hollard and above all by P. Bultynck. It is represented by *Marennophyllum* cf. *kaufmanni*, *Stringophyllum coenaubertae*, *S. pedderi* n. sp., *Acanthophyllum heterophyllum* (Milne-Edwards & Haime, 1851), *A. vermiculare* (Goldfuss, 1826), *Heliophyllum moghrabiense, Spinophyllum blacourti* (Rohart, 1988), *Siphonophrentis cantabrica* Birenheide, 1978 and *Enallophrentis corniformis* (Gürich, 1896).

#### 2.4. Ouahlane

The famous Middle Devonian reef of Ouahlane (or Ouihalane) is situated on the northern border of the Ma'der Basin, to the north side of the track from Msissi to Alnif. Its rich fauna of rugose and tabulate corals and stromatoporoids has been studied in detail by Le Maître (1947). This locality has also been investigated by Hollard (1974, 1981). In 1984, I had the opportunity to visit this outcrop with P. Bultynck. My material comes from the second biostrome of the Taboumakhlouf Formation, not very far from the top of the section. The conodonts identified in this level by Bultynck (1985, fig. 10, sample 25) indicate the Tortodus kockelianus Zone (upper Eifelian). In the present paper, Stringophyllum acanthicum (Frech, 1885), S. coenaubertae, Acanthophyllum heterophyllum, A. vermiculare and Heliophyllum moghrabiense are described. The collection of Schröder & Kazmierczak (1999) from Ouahlane was made at about 50 m above the second biostrome of the Taboumkhlouf Formation, in a thin bed with solitary rugose corals and tabulate corals that corresponds to the sample 27 of Bultynck (1985). The lower Givetian Polygnathus timorensis conodont Zone has been observed in this level.

#### 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 (prefixed IRScNB).

Family Cystiphyllidae Milne-Edwards & Haime, 1850

#### Genus Marennophyllum Coen-Aubert, 2022

*Type species.* By original designation, *Cystiphylloides marennense* Coen-Aubert, 2019 from the lower Givetian of southern Belgium.

Diagnosis. See Coen-Aubert (2022).

## *Marennophyllum kaufmanni* n. sp. (Plate 1A–D)

*Derivation of name.* The species is dedicated to Bernd Kaufmann from Germany who investigated the reefal locality of Aferdou el Mrakib and collected the material described herein.

*Holotype.* IRScNB a13912 (Pl. 1A–B). Specimen A1 collected by B. Kaufmann in 1995, in the Middle Devonian of the Ma'der, Morocco.

*Type locality and horizon.* Close to the top of the crinoidal basement from the Aferdou el Mrakib reef in the Ma'der, Morocco; top of the Eifelian.

*Material.* Four specimens with eight thin sections collected by B. Kaufmann: Aferdou el Mrakib A1, A3, A4 and A5.

*Diagnosis.* A species of *Marennophyllum* with a mean diameter of 27 mm to 32 mm. Corallum filled with dissepiments. At the periphery, occurrence of septal spines on inclined dissepiments. Weak septal cones in the tabularium.

*Description.* The material consists of ceratoid and conical to cylindrical coralla with growth lines and a height between 70 mm and 95 mm. The outer wall is thin and locally preserved.

The corallum is filled with globose dissepiments which are smaller at the periphery and larger in the tabularium. In transverse section, septal spines are frequent in the dissepimentarium, especially in its inner part; they may also occur against the outer wall. Partial and thin zones of stereoplasmic thickening are present at the border of the tabularium, in two specimens.

In longitudinal section, a few rows of inclined dissepiments with numerous small spines are observed. The axial vesicular tabellae have an overall concave pattern and are separated by some weak septal cones.

The diameter of the corallum ranges from 25 mm to 35 mm.

Discussion. In some features, Marennophyllum kaufmanni resembles M. radugini (Ivania, in Zheltonogova & Ivania, 1960) from the upper Givetian of the Kuznetsk Basin in Russia which has also been investigated in detail by Ivania (1965, p. 68). However, it is distinguished from M. kaufmanni by slightly smaller coralla, by sometimes a few more dissepiments which may be arranged in horizontal layers at the periphery and by the absence of spines in longitudinal section. Marennophyllum wenningi Coen-Aubert, 2022 from the lower Givetian of the Eifel Hills in Germany is more different as it is characterized by smaller dissepiments all over the corallum and more numerous in the dissepimentarium.

*Distribution.* The new species is only known in the locality of Aferdou el Mrakib (Ma'der, Morocco), at the top of the Eifelian.

### *Marennophyllum* cf. *kaufmanni* n. sp. (Plate 2C–D)

*Material.* One specimen with two thin sections collected by P. Bultynck: Ou Driss East MA44.

*Description.* The material is restricted to a ceratoid corallum with growth lines and a height of 60 mm. The diameter of the corallum ranges from 20 mm to 21 mm. The thin outer wall is locally preserved.

The corallum is filled with globose dissepiments which are smaller and limited to a few rows at the periphery and which are larger in the tabularium. In transverse section, some small septal spines are observed in the dissepimentarium whereas there is a narrow zone of stereoplasmic thickening in the centre of the tabularium.

The dissepimentarium consists of a few rows of inclined dissepiments, locally horizontal at the periphery, with some small spines. The axial vesicular tabellae have an overall concave pattern and are separated by some weak septal cones.

*Discussion.* The specimen of Ou Driss East differs mostly from *Marennophyllum kaufmanni* by the smaller diameter of the corallum. This also separates it from *M. radugini* which has also more rows of dissepiments.

*Distribution.* The form is only known at the base of the middle Givetian from Ou Driss East, in the Ma'der (Morocco).

#### Genus Atelophyllum Wedekind, 1925

*Type species.* By original designation, *Mesophyllum emsti* Wedekind, 1922 from the lower Givetian of the North Sauerland, in Germany.

Diagnosis. See Coen-Aubert (2019).

#### *Atelophyllum maximum* (Schlüter, 1882) (Plate 2A–B)

- \* 1882 Actinocystis maxima sp. n.; Schlüter, p. 207.
   1889 Mesophyllum maximum Schlüt.; Schlüter, p.70, pl. 7, fig. 1.
  - 1926 *Mochlophyllum maximum* Schlüter; Vollbrecht, pl. 15, fig. 2.
- pp. 1937 *Mesophyllum maximum* Schlüter; Ma, p. 35, pl. 14, fig. 1 (non pl. 15, fig. 1, pl. 16, fig. 1).
  - 1945 *Mochlophyllum maximum* (Schlüter); Smith p. 35, pl. 6, fig. 3, pl. 7, fig. 7.
  - 1949 Mochlophyllum maximum (Schlüter); Stumm, pl. 21, fig. 11.
- pp. 1956 Mesophyllum maximum Schlueter; Ma, p. 73, pl. 15, fig. 1, pl. 19, fig. 2, pl. 66, fig. 1 (non pl. 16, fig. 2, pl. 17, fig. 1, pl. 18, fig. 1, pl. 66, fig. 2).
  - 1964 Plasmophyllum (Mesophyllum) maximum maximum (Schlüter 1882); Birenheide, p. 43, pl. 7, figs 30–31, pl. 28, fig. 136?
- non 1964 Plasmophyllum (Mesophyllum) cf. maximum maximum (Schlüter 1882); Birenheide, pl. 8, fig. 32, pl. 15, fig. 74.
- v non 1969 Mesophyllum maximum (Schlüter), 1882; Tsien, p. 97, pl. 34, fig. 1, pl. 36, fig. 4.
- non 1977 Mesophyllum maximum Schlüter, 1882; Latypov, p. 48, pl. 11, fig. 5.
  - 1978 Mesophyllum (M.) maximum maximum (Schlüter1882); Birenheide, p. 168, fig. 105, pl. 20, fig. 3?
  - 1981 Digonophyllum (Mochlophyllum) maximum (Schlüter); Hill, p. F125, fig. 63, 2a.
- non 1981 Mesophyllum (Mesophyllum) maximum maximum (Schlüter 1882); Birenheide & Soto, p. 258, pl. 7, figs 27–28.
- non 1984 Mesophyllum (Mesophyllum) maximum maximum (Schlüter 1882); Liao & Birenheide, p. 6, pl. 1, fig. 1.
- non 1985 Mesophyllum maximum (Schlüter); Scrutton, p. 16, pl. 3.3.13.

- non 1993 Mesophyllum (Mesophyllum) maximum (Schlüter 1882); May, p. 58, pl. 10, fig. 1.
- non 1993 Digonophyllum (Mochlophyllum) cf. maximum maximum (Schlüter, 1882); Galle, p. 61, pl. 1, fig. 4, pl. 2, figs 1–2.
- ? 1998 Mesophyllum (Mesophyllum) maximum maximum (Schlüter 1882); Schröder, p. 66.
- non 2015 Mesophyllum maximum (Schlüter); Liao, pl. 2, figs 4–5.
- non 2022 Atelophyllum cf. maximum (Schlüter, 1882); Coen-Aubert, p. 59, pl. 3A–B.

*Lectotype.* Specimen WDKD 2590 selected and figured by Birenheide (1964, p. 42, pl. 7, fig. 30), stored in the Forschungsinstitut Senckenberg at Frankfurt am Main, Germany, and also illustrated by Vollbrecht (1926, pl. 15, fig. 2), Stumm (1949, pl. 21, fig. 11), Birenheide (1964, pl. 7, fig. 30), Birenheide (1978, fig. 105) and Hill (1981, fig. 63, 2a). Upper Eifelian Junkerberg Formation of Auburg in the Gerolstein Syncline, Eifel Hills in Germany.

*Material*. One specimen with two thin sections collected by H. Hollard: Aferdou el Mrakib MA 402 (his sample TM 554/1).

*Diagnosis*. A species of *Atelophyllum* with 96 to 122 septa at a diameter of 70 mm to 108 mm. Major septa thin in the outer part of the dissepimentarium, more or less dilated in its inner part and thicker in the tabularium. Slender and well developed minor septa. Occurrence of an open space in the centre of the tabularium.

*Description.* The only specimen available is a conical solitary corallum with a few growth rings and a height of 15 cm. The calice is narrow, deeply excavated and bordered by steep sides with traces of septa. The outer wall is not preserved.

The septa may be discontinuous at the periphery where there are locally yardarm carinae. They are thin in the main part of the dissepimentarium and slightly dilated at its inner border. The septa are much thicker in the tabularium where there is a wide open space; several axial ends of major septa abut against a sort of partial inner wall. The minor septa are slender and more or less long and continuous in the inner part of the dissepimentarium.

The dissepimentarium consists of numerous rows of small dissepiments arranged in horizontal layers at the periphery and inclined in its inner part. It is characterized by some longisolated trabeculae in its outer part and by zones of compact stereoplasma in its inner part. The axial tabellae are vesicular and intersected by a few segments of septa. A septal cone with traces of short septa is observed in the lower part of the corallum.

There are about 110 septa for a diameter of 60 mm to 82 mm whereas the width of the tabularium measures 13.5 mm to 17 mm.

*Discussion.* The Moroccan corallum investigated herein is remarkable by its great size with numerous septa, by the variable dilation of the septa throughout the dissepimentarium and the outer part of the tabularium and by the absence of septa in its centre. In these different characters, it is similar to the lectotype of *Atelophyllum maximum* and to the few other German specimens from the type area of Gerolstein in the Eifel Hills assigned to this species and illustrated by Schlüter (1889), Vollbrecht (1926), Ma (1937, 1956), Smith (1945), Stumm (1949), Birenheide (1964, 1978) and Hill (1981). However, all this material has never been figured in longitudinal section despite the good development of the coralla in height. Atelophyllum maximum is in fact the type species of *Mochlophyllum* Wedekind, 1923 which has not been much used by the authors. This is probably due to the incomplete knowledge of *Atelophyllum maximum* in its type area from Germany.

Coen-Aubert (2022) has ascribed to A. cf. maximum a few specimens from the lower Givetian Dreimühlen Formation of the Hillesheim Syncline also in the Eifel Hills. She has compared this sampling to several references of the list of synonymy which are excluded from A. maximum. For the rest, the holotype of A. geigeri (Wedekind & Vollbrecht, 1931, pl. 33, figs 1-4) from the lower Givetian Cürten Formation to the Binz Member of the Dreimühlen Formation, also from the Hillesheim Syncline, shows some similarities with the Moroccan specimen investigated herein. But A. geigeri is distinguished from A. maximum by the smaller diameter of the corallum, by often longer major septa and by minor septa better developed in the outer dissepimentarium. Atelophyllum geigeri was considered by Birenheide (1964, p. 44) as a synonym of A. leave (Schulz, 1883) from the lower Givetian of the same area in Germany. The differences between A. leave and A. maximum have been discussed in detail by Coen-Aubert (2022, p. 59). A comparison between Atelophyllum and Mesophyllum Schlüter, 1889 has been given by Coen-Aubert (2019, p. 127).

*Distribution.* The investigated specimen was collected in the lower Givetian of the Aferdou el Mrakib reef, in the Ma'der, Morocco. Outside this country, *Atelophyllum maximum* is certainly known in the upper Eifelian Junkerberg Formation from the Eifel Hills, Germany.

Family Stringophyllidae Wedekind, 1922

#### Genus Stringophyllum Wedekind, 1922

*Type species.* By subsequent designation of Wedekind (1925, p. 64), *Stringophyllum normale* Wedekind, 1922 from the Givetian of the Sauerland in Germany.

Diagnosis. See Coen-Aubert (2022).

### *Stringophyllum acanthicum* (Frech, 1885) (Plate 1E–F)

(1 late 1 L - 1)

- \* 1885a *Endophyllum acanthicum* nov. sp.; Frech, p. 929, pl. 41, fig. 5.
  - 1925 Schizophyllum acanthicum Frech; Wedekind, p. 60, pl. 13, fig. 78.
- v pp. 1947 'Schizophyllum' acanthicum Frech; Le Maître, p. 50, pl. 5, figs 1–2 (non pl. 5, figs 3, 10).
- v 2011 Stringophyllum acanthicum (Frech, 1885); Coen-Aubert, p. 31, pl. 1, figs 1–6, pl. 2, figs 8–9, pl. 3, fig. 4.
- v 2022 Stringophyllum acanthicum (Frech, 1885); Coen-Aubert, p. 63, pl. 5C–E.
- non 2022a Stringophyllum acanthicum (Frech, 1885); Halamski et al., fig. 13C.

*Remark*. More complete lists of synonymy for the references before 2011 and 2022 have been provided by Coen-Aubert (2011, 2022).

#### Holotype. See Coen-Aubert (2022).

*Material*. Four specimens with six thin sections collected by the author: Ouahlane MA284, MA286, MA289 and MA291.

Diagnosis. See Coen-Aubert (2022).

*Description.* The material consists of cylindrical, ceratoid and trochoid coralla often fragmentary, with longitudinal ribs and growth lines; the height varies between 30 mm and 65 mm. The outer wall is rarely preserved.

The septa are non-carinate and dilated throughout their length. They are sometimes discontinuous at the periphery, with a few presepiments and some alignments of trabeculae. Stereoplasma may be present on an inner layer of dissepiments. The major septa reach more or less the axis of the corallum where there are occasionally pseudofossulae, coarse trabeculae, fragments and curved ends of septa. The minor septa are represented by segments and spines mostly occurring in the inner part of the dissepimentarium.

The dissepimentarium consists of 2 to 7 rows of inclined dissepiments which may be horizontal at the periphery. The tabulae are strongly concave. Some thick spines and short fragments of septa are present across the dissepimentarium and the tabularium.

There are 90 to 104 septa per corallum. The diameter of the corallum ranges 22 mm to 30 mm. The width of the tabularium varies between 10.5 mm and 15 mm. In a young stage, there are 76 septa at a diameter of 13 mm to 16 mm whereas the width of the tabularium measures 8.5 mm to 9.1 mm.

*Discussion.* The material of Ouahlane is similar to that of Belgium, France and Germany investigated by Coen-Aubert (2011, 2022). The corallum from the lower Givetian of the Holy Cross Mountains illustrated by Halamski et al. (2022a) differs in having septa more continuous at the periphery and slightly dilated and by the poor development of the minor septa. Pedder (1999) has already mentioned that some specimens of *Stringophyllum acanthicum* figured by Lemaître (1947) should be better assigned to *S. coenaubertae* which is characterized by less thick septa and by only a few short segments of minor septa.

*Distribution.* The specimens investigated herein were collected in the upper Eifelian of Ouahlane from the Ma'der in Morocco. As mentioned by Coen-Aubert (2011, 2022), *Stringophyllum acanthicum* occurs across the Eifelian–Givetian boundary, on the south side of the Dinant Synclinorium, in Belgium. It is widely distributed in Germany, in the upper Eifelian and the lower Givetian from the Eifel Hills as well as in the Givetian from the Bergisches Land and the Sauerland. The species is also known in the Middle Devonian part of the Chalonnes Formation from the Southeastern Armorican Massif in France (Le Maître, 1934; Coen-Aubert, 2011) and in the Givetian from central Moravia in the Czech Republic (Kettnerova, 1932). Additionally, it may occur in the Givetian of the Urals in Russia (Shurigina, 1972).

### Stringophyllum coenaubertae Pedder, 1999

(Plate 3A–B)

- v pp. 1947 'Schizophyllum' acanthicum Frech; Le Maître, p. 50, pl. 5, figs 3, 10? (non pl. 5, figs 1–2).
- \* pp. 1999 Stringophyllum coenaubertae sp. nov.; Pedder, p. 397, pl. 5, figs 1–2, 5–9 (non pl. 5, figs 3–4, 10–11).

*Holotype.* Specimen GSC 116642 (Pedder, 1999, pl. 5, figs 6–9) stored in the Geological Survey of Canada Type Collections at Ottawa, Canada. Lower Givetian of the section Ou Driss East in the Ma'der, Morocco.

*Material.* Three specimens with five thin sections collected by B. Kaufmann, P. Bultynck and the author: Aferdou el Mrakib A2, Ou Driss East MA 703 and Ouahlane MA259.

*Diagnosis.* A species of *Stringophyllum* with 78 to 106 septa at a diameter of 18 mm to 25 mm. Septa continuous to discontinuous at the periphery. Minor septa poorly developed in the inner part of the dissepimentarium.

*Description.* The material consists of solitary rugose corals of variable shape with longitudinal ribs, growth lines and rejuvenescence for one specimen; the height of the coralla varies between 2.2 cm and 9.5 cm. The outer wall is not well preserved.

The septa are non-carinate and slightly dilated throughout their length though they are sometimes thinner in the tabularium. They may be discontinuous at the periphery with a few presepiments and alignments of trabeculae. In two coralla, a layer of inner dissepiments is locally thickened with stereoplasma. The major septa with occasionally rhopaloid ends leave a small open space in the centre of the tabularium occupied by isolated trabeculae. The minor septa are represented by a few spines and short segments in the inner part of the dissepimentarium and at the entry of the tabularium.

The dissepimentarium consists of 2 to 8 rows of inclined dissepiments sometimes horizontal at the periphery; coarse and contiguous trabeculae are locally present across them. The tabulae are closely spaced and concave or sometimes horizontal. They are intersected by spines and fragments of septa. In one specimen, a talon is observed on one side of the dissepimentarium.

There are 90 to 106 septa per corallum. The diameter of the corallum ranges from 19.5 mm to 27 mm. The width of the tabularium varies between 7.6 mm and 15 mm.

*Discussion*. My material is similar to the holotype and to the larger specimens of *Stringophyllum coenaubertae* investigated by Pedder (1999). However, this author (pl. 5, figs 3–4, 10–11) also assigned to the species smaller coralla identified in this paper as *S. pedderi. Stringophyllum coenaubertae* is related to *S. acanthicum* which is distinguished by thicker septa more discontinuous at the periphery and by more frequent minor septa in the inner dissepimentarium.

*Distribution.* The species is only known in the Middle Devonian of the Ma'der in Morocco. My material comes from the upper Eifelian of Ouahlane, the top of this stage at Aferdou el Mrakib and the base of the middle Givetian at Ou Driss East.

#### Stringophyllum pedderi n. sp.

(Plates 1G-H, 2E-H)

pp. 1999 Stringophyllum coenaubertae sp. nov.; Pedder, p. 397, pl. 5, figs 3–4, 10–11 (non pl. 5, figs 1–2, 5–9).

*Derivation of name.* The species is dedicated to Alan Pedder, a distinguished Canadian specialist of Devonian rugose corals.

*Holotype.* IRScNB a13918 (Pl. 2E–F). Specimen MA25 collected by P. Bultynck in 1975, in the middle Givetian of the Ma'der, Morocco.

*Type locality and horizon.* Between the samples ODE 3 and ODE 2 at the top of the section Ou Driss East in the Ma'der, Morocco. Base of the middle Givetian.

Material. Seven specimens with 14 thin sections collected by H.

Hollard and P. Bultynck: Ou Driss East MA25, MA40, MA365, MA711, MA712, MA722 and MA725.

*Diagnosis.* A species of *Stringophyllum* with 68 to 80 septa at a diameter of 10 mm to 16 mm. Septa slightly discontinuous at the periphery with some partial rings of stereoplasmic thickening in the disseptimentarium. Minor septa poorly developed. Disseptiments arranged in horizontal layers at the periphery.

*Description.* The material consists of conical, cylindrical and ceratoid coralla often fragmentary, with growth lines and sometimes growth rings; their height varies between 20 mm and 40 mm. The outer wall is thin and only locally preserved.

The septa are non-carinate and more or less dilated throughout their length though they may become gradually thinner in the tabularium. They are occasionally discontinuous at the periphery with a few alignments of trabeculae. In several specimens, there are complete or partial rings of stereoplasmic thickening at the inner border of the dissepimentarium and also in its outer part. The major septa reach the axis of the corallum or leave an open space in the centre of the tabularium where there are a few pseudofossulae, coarse trabeculae, fragments and rhopaloid ends of septa. The minor septa are lacking or represented by rare spines and short segments in the inner part of the dissepimentarium and even at the entry of the tabularium or against the outer wall.

The dissepimentarium consists of 2 to 6 rows of large dissepiments arranged in horizontal layers at the periphery and inclined in its inner part; locally coarse and often contiguous trabeculae are present across the dissepiments. The tabulae have a concave pattern; they are occasionally irregular and they are disrupted by trabeculae and fragments of septa.

There are 64 to 80 septa per corallum. The diameter of the corallum ranges from 10 mm to 16 mm. The width of the tabularium varies between 5.3 mm and 7.8 mm.

Discussion. Stringophyllum pedderi is distinguished from S. coenaubertae in having smaller coralla with less septa, by larger and not so numerous dissepiments and by rare presepiments. Stringophyllum *pedderi* resembles some species of Stringophyllum from the Givetian of Germany such as S. murale (Wedekind, 1922), S. acrophylloides (Wedekind, 1925) and S. primordiale Wedekind, 1922. The holotype of S. murale from the Givetian of the Bergisches Land, figured by Wedekind (1922b, figs 9-10), differs from S. pedderi by a slightly greater size, by septa more discontinuous at the periphery and by inclined dissepiments. Stringophyllum murale was considered by Engel & von Schouppé (1958) as a synonym of S. buechelense (Schlüter, 1889) also from the Givetian of the Bergisches Land. However, the lectotype of this species refigured by these two authors and by Schröder (2005, pl. 10, fig. 9a) has much thinner septa than S. pedderi. As for S. acrophylloides, its lectotype selected by Birenheide (1962, p. 118) and coming from the Givetian of the Gerolstein Syncline in the Eifel Hills has been illustrated by Engel & von Schouppé (1958, pl. 8, figs 2-3). It has no minor septa and only inclined dissepiments. This taxon has been synonymized with S. primordiale from the Givetian from the Bergisches Land by Birenheide (1978, p. 153, pl. 19, fig. 3a-b). The holotype of S. primordiale figured by the latter author is not the same corallum as the original specimen illustrated by Wedekind (1922b, fig. 7) and identified by Birenheide (1962, p. 120).

*Distribution.* The new species is only known at the base of the middle Givetian from Ou Driss East, in the Ma'der, Morocco.

Family Ptenophyllidae Wedekind, 1923

#### Genus Acanthophyllum Dybowski, 1873

*Type species.* By subsequent designation of Schlüter (1889, p. 38), *Cyathophyllum heterophyllum* Milne-Edwards & Haime, 1851 from the Devonian of the Eifel Hills in Germany.

Diagnosis. See Coen-Aubert (2017).

# Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851)

(Plate 3C-G)

- v \* 1851 *Cyathophyllum heterophyllum*; Milne-Edwards & Haime p. 367, pl. 10, figs 1, 1a–b.
- v 1947 *Acanthophyllum heterophyllum* Milne Edwards et Haime; Le Maître, p. 41, pl. 4, fig. 1.
- v 1997 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert, p. 11, pl. 1, figs 1–4, pl. 2, figs 5–7.
  - 1999 Acanthophyllum heterophyllum (Milne Edwards & Haime, 1851); Pedder, p. 403, pl. 9, figs 1–4, 6, 9.
- v 2011 *Acanthophyllum heterophyllum* (Milne-Edwards & Haime, 1851); Coen-Aubert, p. 36, pl. 2, fig. 6.
- v 2017 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert, p. 163, pl. 1A–B.
- v 2022 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert, p. 60, pl. 4C–D.
- non 2024a Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Denayer, p. 195, figs 4e, m, 11a-g, 12a, c.
- non 2024b Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Denayer, fig. 6H.

*Remarks.* More complete lists of synonymy have been provided by Coen-Aubert (1997, 2011, 2017, 2022).

Holotype. See Coen-Aubert (2017).

*Material.* Twenty-two specimens with 44 thin sections collected by H. Hollard, P. Bultynck and the author: Ou Driss East MA10, MA11, MA15, MA16, MA17, MA45, MA345, MA349, MA701, MA702, MA704 and MA705 and Ouahlane OU2, OU4, MA260, MA263, MA270, MA272, MA283, MA285, MA292 and MA294.

Diagnosis. See Coen-Aubert (2017).

*Description.* The material consists of conical, cylindrical and ceratoid coralla which are complete or fragmentary; their height varies between 3 cm and 10 cm. Longitudinal ribs and sometimes growth lines are observed. One specimen shows rejuvenescence whereas two others display an excavated calice bordered by a flat platform. The thin outer wall is preserved only locally.

The septa are dilated throughout their length though they may be thinner or even discontinuous at the periphery. The major septa are thicker than the minor ones in the main part of the dissepimentarium; sometimes, they are affected by a dark median line. Spinose carinae occur occasionally at the inner border of the dissepimentarium. In rare specimens, a little stereoplasma is present locally on an inner layer of dissepiments. In a young stage, a ring of stereoplasmic thickening occurs at the boundary with the tabularium.

The major septa reach the axis of the corallum with often vepreculae in the tabularium where they are sometimes thinner, strongly or slightly dilated. Their axial ends may be discontinuous, curved or twisted. In one specimen, a thicker and longer major septum projects beyond the centre of the tabularium where a small deposit of stereoplasma occurs locally in younger stages. The minor septa traverse the entire and wide dissepimentarium. Occasionally, they are contratingent at the inner border of the dissepimentarium or at the entry of the tabularium if they are hardly projecting into it. In young stages, the minor septa are occasionally divided into segments, short or lacking.

The dissepimentarium consists of 10 to 28 or rarely six to eight rows of dissepiments sometimes only inclined, but mostly arranged in horizontal layers in its outer part and inclined in its inner part. The tabulae are incomplete with occasionally a concave pattern; they are disrupted by thick septa and fragments of them with spinose carinae.

There are 66 to 82 or even 60 to 92 septa per corallum. The diameter of the corallum ranges frequently from 20 mm to 40 mm and rarely from 17 mm to 46 mm. The width of the tabularium varies commonly between 7 mm and 10.5 mm and more generally between 4.3 mm and 11.5 mm.

*Discussion.* The numerous Moroccan specimens investigated herein are very homogeneous and typical of *Acanthophyllum heterophyllum*. More especially, their major septa are more strongly dilated than the minor ones in the wide inner part of the dissepimentarium. This is also the case for the abundant material described from Belgium by Coen-Aubert (1997) and from Germany by Birenheide (1961, 1978), Schröder (1998) and Coen-Aubert (2022).

The two coralla figured by Denayer (2024a, figs 11, 12a and probably 12c) in thin sections come from Waha on the southern limb of the Dinant Synclinorium in Belgium, close to the Emsian-Eifelian boundary. They are distinguished from A. heterophyllum by nearly no difference between the dilation of their major and minor septa throughout the dissepimentarium and by strong septal thickenings affecting the inner part of the dissepimentarium in their young stages. In the small transverse section from the Middle Devonian of the Northern Vosges in Eastern France illustrated by Denayer (2024b), the major and minor septa are also uniformly dilated throughout the dissepimentarium with additionally weak knobbly carinae which are not characteristic of Acanthophyllum as it is a Ptenophyllidae. On the contrary, vepreculae or spinose carinae are rather frequent in the tabularium of its type species A. heterophyllum.

*Distribution.* The Moroccan material investigated herein from the Ma'der was collected in the upper Eifelian of Ouahlane and at the base of the middle Givetian from Ou Driss East. *Acanthophyllum heterophyllum* has also been observed in the lower part of the Givetian from the Zemmour in Mauritania. Outside North Africa, the species is widely distributed in the Eifelian and the lower Givetian of the Eifel Hills in Germany as well as in the upper Eifelian and the lower Givetian from the southern limb of the Dinant Synclinorium in Belgium and northern France. It is also known in the upper Emsian of the southeastern Armorican Massif in France (Le Maître, 1934; Coen-Aubert, 2011) and in the lower Eifelian of the Holy Cross Mountains in Poland (Różkowska, 1954).

#### *Acanthophyllum vermiculare* (Goldfuss, 1826) (Plate 4A–B)

- v \* 1826 *Cyathophyllum vermiculare* nobis; Goldfuss, p. 58, pl. 17, fig. 4.
- 1997 Acanthophyllum vermiculare (Goldfuss, 1826);

Coen-Aubert, p. 13, pl. 3, figs 1-8.

- v pp. 1997 Acanthophyllum heterophyllum (Milne-Edwards & Haime, 1851); Coen-Aubert, p.11 (non pl. 1, figs 1–4, pl. 2, figs 5–7).
- v 1998 Acanthophyllum vermiculare (Goldfuss, 1826); Coen-Aubert, pl. 2, fig. 1.
  - 1999 Acanthophyllum vermiculare (Goldfuss, 1826);
     Schröder & Kazmierczak, p. 102, pl. 3, figs 15– 16.
- v 2011 Acanthophyllum vermiculare (Goldfuss, 1826); Coen-Aubert, p. 37, pl. 2, figs 1–5, pl. 3, fig. 9.
- v 2022 Acanthophyllum vermiculare (Goldfuss, 1826); Coen-Aubert, p. 60, pl. 2C, pl. 3C–I.
- pp. 2024a Acanthophyllum vermiculare (Goldfuss, 1826); Denayer, p. 195, figs 4a, d, 12j-k (non fig. 12f-g).

*Remarks*. More complete lists of synonymy have been provided by Coen-Aubert (1997, 2011, 2022).

Holotype. See Coen-Aubert (2022).

*Material.* Three specimens with five thin sections collected by P. Bultynck and the author: Ou Driss East MA43 and Ouahlane MA278 and MA288.

Diagnosis. See Coen-Aubert (2022).

*Description.* The material consists of conical and fragmentary solitary coralla with longitudinal ribs and growth lines; their height varies between 4 cm and 6.5 cm. The thin outer wall is rarely preserved.

The septa are thin to slightly dilated throughout their length. The major septa reach the centre of the tabularium where they may be divided into fragments, weakly twisted or affected by spinose carinae; in one specimen, a few axial ends of septa are rhopaloid. The minor septa traverse the entire dissepimentarium. They are sometimes a little shorter, contratingent or discontinuous at the periphery.

The dissepimentarium consists of 15 to 16 rows of inclined dissepiments which are arranged in horizontal layers at the periphery in one corallum. The tabulae are closely spaced and disrupted by septa and fragments of them with spinose carinae.

There are 72 to 78 septa per corallum. The diameter of the corallum ranges from 26 mm to 31 mm. The width of the tabularium varies between 7.5 mm and 10.5 mm.

Discussion. With their slender septa, the three Moroccan specimens investigated herein are very typical of Acanthophyllum vermiculare. They can easily be compared with the abundant material described from Belgium by Coen-Aubert (1997) and from Germany by Birenheide (1961, 1978), Lütte (1984) and Coen-Aubert (2022). Le Maître (1947, p. 42) has assigned to A. torquatum orientale (Reed, 1922) two coralla from the upper Eifelian of Ouahlane which resemble A. vermiculare. However, this material is characterized by major septa strongly dilated in the tabularium with some stereoplasmic thickening and by minor septa often discontinuous in the outer part of the dissepimentarium. Therefore, it probably belongs to young stages. Acanthophyllum orientale from the Givetian of Chitral in Pakistan is very close to A. vermiculare from which it differs by the greater diameter of the corallum. As for A. torquatum (Schlüter, 1884) from the Eifelian of the Eifel Hills in Germany, it seems to be a synonym of A. vermiculare as discussed by Schröder & Kazmierczak (1999) and Coen-Aubert (2022).

It is difficult to compare the material of Denayer (2024a) illustrated in thin sections and coming from the southern limb of

the Dinant Synclinorium in Belgium, close to the Emsian– Eifelian boundary. Indeed, there seems to be some confusion between the photos of *A. heterophyllum, A. radiatum* (Wedekind, 1924) and *A. vermiculare* in his figure 12 and their captions. Such stereoplasmic thickenings affecting the young stages figured by Denayer (2024a) are more characteristic of *A. radiatum* from the lower Eifelian of the Eifel Hills, as investigated by Birenheide (1961, 1978).

Distribution. The Moroccan specimens investigated herein come from the upper Eifelian of Ouahlane and the base of the middle Givetian from Ou Driss East. At Ouahlane, *Acanthophyllum vermiculare* has also been collected in the lower Givetian by Schröder & Kazmierczak (1999). Outside Morocco, the species is common in the upper Eifelian and the lower Givetian of the Eifel Hills in Germany whereas it is abundant close to the Eifelian–Givetian boundary, on the south side of the Dinant Synclinorium, in Belgium and northern France. Additionally, *A. vermiculare* has been observed in the Middle Devonian part of the Chalonnes Formation from the Southeastern Armorican Massif in France (Le Maître, 1934; Coen-Aubert (2011). The species is perhaps present in the lower Eifelian from the southern limb of the Dinant Synclinorium.

#### Genus Australophyllum Stumm, 1949

*Type species.* By original designation, *Spongophyllum cyathophylloides* Etheridge, 1911 from the Middle Emsian of Queensland in Australia.

*Diagnosis.* Massive cerioid rugose corals. Septa of both orders often separated from the walls between adjacent corallites by several layers of presepiments. Septa rarely carinate, usually slender throughout their length. Major septa extending to or nearly to the axis of the corallites. Minor septa commonly long. Dissepimentarium composed of several rows of inclined dissepiments. Tabulae closely spaced, complete or incomplete with a concave pattern.

#### Australophyllum sp.

(Plate 4C–D)

*Material.* One colony with four thin sections collected by P. Sartenaer: Madène el Mrakib MA544.

*Description.* The only specimen available is a nodular colony with dimensions of 90 mm x 65 mm and a height of 30 mm. The walls between adjacent corallites are straight with a dark median line. Several pericalicinal offsets have been observed.

There are several layers of presepiments at the periphery of the corallites, with locally a few spines which may also be present against their walls. However, some septa are more or less continuous from these outer walls. The septa are noncarinate and thin or slightly dilated throughout their length. The major septa reach the axis of the corallites or leave sometimes a small open space in the centre of the tabularium. A few spinose carinae occur occasionally in the tabularium. The minor septa traverse all or nearly all the dissepimentarium; in some cases, they are discontinuous or lacking.

The dissepimentarium consists of 4 to 8 rows of inclined dissepiments which are frequently subhorizontal at the periphery. The closely spaced tabulae are concave, incomplete or irregular.

There are 42 to 46 septa per corallite. The diameter of the corallites ranges from 12.5 mm to 17.5 mm. In smaller corallites, there are only 34 septa whereas their diameter is restricted to 8.2 mm or 9.9 mm. The width of the tabularium

varies commonly between 3 mm and 3.8 mm and more generally between 2 mm and 5.3 mm.

Discussion. The Moroccan colony has several features in common with Australophyllum cyathophylloides. However, this Australian Middle Emsian species, which was revised among others by Jell & Hill (1970), differs by its smaller corallites with less septa. Australophyllum sp. resembles the colony from the upper Eifelian of the Yukon Territory in Canada identified by Pedder (1980, p. 608) as Psydrachophyllum new sp. which is distinguished by slightly thicker septa. It must be mentioned that *P. lonsdaleiforme* Pedder, 1971 from the upper Eifelian of the Northwest Territories in Canada and type species of Psydrachophyllum Pedder, 1971 is mostly dendroid.

*Distribution*. The colony of *Australophyllum* sp. has been collected in the lower Givetian from the reef of Madène el Mrakib, in the Ma'der, Morocco.

Family Cyathophyllidae Dana, 1846

#### Genus Heliophyllum Hall in Dana, 1846

*Type species.* By original designation, *Heliophyllum halli* Milne-Edwards & Haime, 1850 as replacement name for *Cyathophyllum helianthoides* Goldfuss, 1826 sensu Hall (1843, p. 209). Givetian of New York in the USA.

Diagnosis. See Coen-Aubert (2022).

#### *Heliophyllum moghrabiense* Le Maître, 1947 (Plates 4E–F, 5A–B)

- v \* 1947 *Heliophyllum moghrabiense* nov. sp.; Le Maître, p. 35, pl. 3, figs 2–3.
- v 1947 *Heliophyllum Halli* M. Edwards et Haime; Le Maître, p. 31, pls 1, 2, pl. 3, fig. 1.
- v 1971 *Heliophyllum halli* Milne–Edwards H. et Haime J., 1850; Brice, p. 263, pl. 18, fig. 6.
- 1987 Heliophyllum halli moghrabiense Le Maître, 1947; Coen-Aubert, p. 162, pl. 6.
  - 1999 Heliophyllum halli moghrabiense Le Maître, 1947; Pedder, p. 406.
- pp. 1999 *Heliophyllum halli* Milne Edwards & Haime, subsp. undet.; Pedder, p. 406, pl. 10, figs 6, 8, pl. 11, figs 1, 8 (non pl. 10, fig. 9, pl. 11, figs 2, 5).
  - 1999 Heliophyllum (Heliophyllum) halli moghrabiense (Le Maître, 1947); Schröder & Kazmierczak, p. 99, pl. 1, figs 3–4, pl. 2, fig. 5.

*Lectotype.* Specimen number 7 (Le Maître, 1947, pl. 3, figs 2–3) of Le Maître collection chosen by Coen-Aubert (1987) and stored in the Department of Geology from the Faculté Libre des Sciences at Lille, France. Limestone hillock to the east of the railway track, at Mechra ben Abbou, in the Moroccan Meseta. Middle Devonian limestone with calceolids.

*Material.* Fifteen specimens with 29 thin sections collected by P. Bultynck, B. Kaufmann, P. Sartenaer and the author: Aferdou el Mrakib A8 and A10, Madène el Mrakib MA 543, Ou Driss East MA7 and Ouahlane OU1, MA262, MA267, MA273, MA275, MA276, MA279, MA281, MA282, MA293 and MA296.

*Diagnosis.* A species of *Heliophyllum* with 74 to 86 septa at a diameter of 30 mm to 51 mm. Major septa reaching the centre of the tabularium or slightly shorter. Minor septa traversing all

or nearly all the dissepimentarium.

*Description.* The material consists of conical, cylindrical and ceratoid coralla which are complete or fragmentary; their height varies between 30 mm and 135 mm. Longitudinal ribs are frequent. A few specimens are compressed laterally, affected by rejuvenescence or show an excavated calice bordered by a narrow peripheral platform. The thin outer wall is only present very locally.

The septa are thin throughout their length with yardarm carinae in the dissepimentarium becoming knobbly at its inner border. In a rather young stage, the septa are slightly thicker in the main part of the dissepimentarium with yardarm and spinose carinae. In several coralla, the septa are very locally weakly dilated in the inner part of the dissepimentarium.

The major septa reach sometimes the axis of the corallum. But they often leave an open space in the centre of the tabularium where there are pseudofossulae and rarely fragments of septa and isolated trabeculae. In a rather young stage, there is an axial structure due to the fusion of some major septa as well as stereoplasmic thickenings between the septa in the outer part and the centre of the tabularium. The minor septa traverse all or nearly all the dissepimentarium. Occasionally, they are shorter, discontinuous at their inner ends, contratingent or hardly entering into the tabularium.

The dissepimentarium consists of 10 to 20 rows of small globose dissepiments arranged in horizontal layers in its outer part and inclined in its inner part. Broad asymmetrical fans of coarse and isolated trabeculae extend across the entire dissepiments; in some cases, a little stereoplasma is present between these trabeculae. The tabulae are incomplete and intersecting laterally with some intersections of septa; locally their axial part is flat-topped or convex.

There are 72 to 90 or even 114 septa per corallum. The diameter of the corallum ranges from 27 mm to 57 mm; it reaches 60 mm to 68 mm in one specimen. The width of the tabularium varies commonly between 10 mm and 20 mm and more generally between 7 mm and 25 mm.

Discussion. The Moroccan material described herein comes from different outcrops and it is very homogeneous. It is similar to *Heliophyllum chengi* Oliver & Sorauf, 1988 from the Givetian of Asturias in Spain which has stronger and more numerous yardarm carinae. The fragmentary specimen from the Givetian of the Pyrenees in France identified as *H. rhopaliseptatum* Stumm, 1968 by Joseph & Tsien (1975, pl. 3, fig. 6, non fig. 5) resembles also *H. moghrabiense*. However, the former species from the lower Givetian Tenmile Creek Formation of northwestern Ohio in USA is separated from the latter by very thin septa and a wide open space in the centre of the tabularium. Pedder (1999, pl. 11, figs 2, 5) assigned to *H. halli* subsp. undet. two small transverse sections which are characterized by slender septa with few yardarm carinae and which seem to be different from *H. moghrabiense*.

*Distribution.* The Moroccan material investigated herein in the Ma'der has been collected in the upper Eifelian of Ouahlane, at the top of the Eifelian from Aferdou el Mrakib, in the lower Givetian of Madène el Mrakib and at the base of the middle Givetian from Ou Driss East. *Heliophyllum moghrabiense* has also been described in the lower Givetian of Ouahlane. The lectotype of the species comes from Middle Devonian limestones with calceolids in the Moroccan Meseta. Outside Morocco, the species is only known in the Givetian of eastern Afghanistan.

Family Disphyllidae Hill, 1939

#### Genus Spinophyllum Wedekind, 1922

*Type species.* By monotypy, *Campophyllum spongiosum* Schlüter, 1889 from the middle Givetian of the Bergisches Land in Germany.

Diagnosis. See Coen-Aubert (2019).

#### *Spinophyllum blacourti* (Rohart, 1988) (Plates 5C–D, 6E–F)

- \* 1988 Truncicarinulum blacourti nov. sp.; Rohart, p. 277, pl. 35, figs 3–4.
  - 1999 Spinophyllum sp. nov. A; Pedder, p. 405, pl. 10, figs 1–5, 7.
  - 2001a *Temnophyllum blacourti* (Rohart 1988); Schröder, p. 65, pl. 1, figs 1–4, pl. 3, figs 15–16.
- v 2002a Spinophyllum blacourti (Rohart, 1988); Coen-Aubert, p. 16, pl. 3, figs 8–14.
- v 2004 Spinophyllum blacourti (Rohart, 1988); Barchy et al., pl. 1, figs 5–6.
  - 2011 *Truncicarinulum blacourti* Rohart, 1988; Mistiaen et al., fig. 77.
  - 2014a Spinophyllum blacourti (Rohart, 1988); Abassi et al., p. 5, pl.1, fig. 2.
  - 2014b Spinophyllum blacourti (Rohart, 1988); Abassi et al., p. 249, fig. 6A–D.

*Holotype.* Specimen GFCL 4556 (Rohart, 1988, pl. 35, fig. 3) stored in the Department of Geology from the Faculté Libre des Sciences at Lille, France. Banc Noir quarry at Ferques, Boulonnais, France. Unit c of the Griset Member, Blacourt Formation, lower Givetian.

*Material.* Four specimens with seven thin sections collected by H. Hollard and P. Bultynck: Ou Driss East MA6, MA9, MA31 and MA375.

*Diagnosis.* A species of *Spinophyllum* with 56 to 76 septa at a diameter of 15 mm to 25 mm. Septa slightly dilated and carinate in the dissepimentarium with some yardarm carinae.

*Description.* The material consists of complete or fragmentary, conical and ceratoid coralla with longitudinal ribs, growth lines and rejuvenescences; their height varies between 17 mm and 60 mm. One specimen has an excavated calice bordered by a narrow peripheral platform. The thin outer wall is only locally preserved.

The septa are slender or slightly dilated in the dissepimentarium with some knobbly, spinose and yardarm carinae especially at the periphery. The major septa are thin in the tabularium, reach the axis of the corallum or leave a small open space in its centre; their axial ends are occasionally discontinuous and very rarely rhopaloid. The minor septa traverse the entire dissepimentarium; sometimes they hardly enter into the tabularium where they may be contratingent.

The dissepimentarium consists of 10 to 13 rows of small globose dissepiments arranged in horizontal layers in its outer part and inclined in its inner part. Isolated or contiguous septal trabeculae extend across the entire dissepimentarium. The tabulae are incomplete and intersecting laterally, occasionally with horizontal or flat-topped axial parts.

There are 74 to 76 or even 86 septa per corallum. The diameter of the corallum ranges from 16 mm to 22 mm. The width of he tabularium varies between 5.3 mm and 9 mm.

Discussion. The Moroccan material investigated herein is very close to Spinophyllum blacourti from which it differs only by a slightly greater number of septa. By its locally thinner septa in the dissepimentarium, S. blacourti is related to S. arduum (Lütte, 1985) from the lower Givetian Kerpen Formation of the Eifel Hills in Germany. However, the latter species is characterized by slender septa throughout the dissepimentarium as well as by less septa and rows of dissepiments. There are some affinities between S. blacourti and S. postarduum (Birenheide & Soto, 1992) from the upper Givetian part of the Portilla Formation in the Province Leon, Spain, but the latter taxon is separated from the former by very thin septa with rare yardarm carinae and once more by less septa.

*Distribution.* The Moroccan specimens have been collected at the base of the middle Givetian from Ou Driss East in the Ma'der. Outside Morocco, *Spinophyllum blacourti* is known in the lower Givetian from the Boulonnais in France. It is frequent in the lower Givetian from the south side of the Dinant Synclinorium in Belgium where it is present at the top of the Terres d'Haurs Formation and in the lower part of the Mont d'Haurs Formation. *Spinophyllum blacourti* occurs also in the upper Givetian of the Aachen Syncline in Germany. Some coralla of the species have been observed in the Givetian of the Alborz Mountains in Iran.

#### Genus Kuangxiastraea Yu & Kuang, 1982

*Type species*. By original designation, *Haplothecia* (*Kuangxiastraea*) elegans Yu & Kuang, 1982 from the upper Givetian of Guanxi in China.

*Diagnosis.* Massive rugose corals, thamnasterioid to astreoid. Septa of two orders, variably dilated to fusiform, rarely thin. Septa moderately to heavily carinate with yardarm and zigzag carinae, sometimes with some degeneration at the periphery of the corallites. Major septa often reaching the centre of the tabularium. Minor septa traversing the entire dissepimentarium. Dissepimentarium composed of several rows of globose dissepiments arranged in flat layers and only inclined at the border of the tabularium. Incomplete or sometimes compound tabulae.

### *Kuangxiastraea* sp.

(Plate 5E–F)

*Material.* One colony with three sections collected by H. Hollard: Aferdou el Mrakib MA401 (his sample TM551).

*Description.* The only specimen available is a platy colony with an area of 130 mm x 90 mm and a height of 45 mm. The corallites are connected by confluent septa which are slender throughout their length though sometimes slightly dilated in the tabularium. The septa bear numerous small zigzag and occasionally yardarm carinae in the dissepimentarium which are less abundant in its inner part.

The major septa leave a very small space in the centre of the tabularium. Their axial ends may be carinate, discontinuous or curved. The minor septa traverse the entire and wide dissepimentarium or even enter into the tabularium where they are sometimes contratingent.

The dissepimentarium consists of numerous rows of small elongate dissepiments which are arranged in flat layers and only inclined at the border of the tabularium. Isolated and long vertical trabeculae traverse locally the dissepimentarium. The incomplete tabulae are vesicular with a more or less convex pattern. There are 48 to 56 septa per corallite. Their diameter ranges from 35 mm to 40 mm. The width of the tabularium varies from 7.8 mm to 10 mm.

Discussion. The investigated Moroccan colony is very particular due to the large size of its corallites and its slender septa with numerous yardarm and zigzag carinae. These features recall several cerioid species of Cyathophyllum Goldfuss, 1826 such as C. planum (Ludwig, 1866) and C. maecenatum Birenheide, 1963 from the Eifelian of the Eifel Hills in Germany described by Birenheide (1963), C. multicarinatum Coen-Aubert, 1990 from the upper Eifelian of the south side of the Dinant Synclinorium in Belgium and C. afghanense (Brice, 1971) from the Givetian of Afghanistan. For the rest, Kuangxiastraea sp. shows only rare affinities at the specific level. It is related to K. beichuanense (He, 1978) from the Eifelian of Sichuan in China, which has been assigned to Haplothecia Frech, 1885b by He (1978, p.136) and which is astreoid with smaller corallites and less septa. Kuangxiastraea sp. resembles also the material from the Frasnian of Nepal identified by Flügel & Tintori (1993, p. 8) as K. pengellyi (Milne-Edwards & Haime, 1851). As mentioned by Coen-Aubert (2002b, p. 31), this species known in the upper Givetian from the Devon in Great Britain is different by thicker septa with some spindle shaped dilation in the inner part of the dissepimentarium.

*Distribution.* The colony of *Kuangxiastraea* sp. has been collected in the lower Givetian from the reef of Aferdou el Mrakib, in the Ma'der, Morocco.

Family Phillipsastreidae Roemer, 1883

#### Genus Thamnophyllum Penecke, 1894

*Type species.* By subsequent designation of Lang & Smith (1935, p. 564), *Thamnophyllum stachei* Penecke, 1894 from the Eifelian of the Graz area in Austria.

Diagnosis. See Coen-Aubert, 2019.

#### *Thamnophyllum* cf. *simplex* Errenst, 1993 (Plate 7A–B)

cf. 1993 *Thamnophyllum simplex* n. sp.; Errenst, p. 25, fig. 4a-c, pl. 6, figs 1–3, pl. 7, figs 1–3.

*Holotype.* Specimen B2 C-29/Rc 3 (Errenst, 1993, fig. 4a–b, pl. 6, figs 1–3) stored in the Geologisch-Paläontologisches Institut und Museum from the University of Münster in Germany. Middle Givetian of the northeast Messinghausen quarry situated 9 km to the east of Brilon, in Northeast Sauerland, Germany.

*Material.* Two specimens with five thin sections collected by B. Kaufmann: Aferdou el Mrakib P154 and 155.

*Diagnosis.* A species of *Thamnophyllum* with 32 to 38 septa at a diameter of 4 mm to 6 mm. Major septa short or leaving a broad open space in the centre of the tabularium. Tabulae widely spaced and often complete and horizontal. No inner dissepiments.

*Description.* The material consists of two samples of limestone where corallites represented by transverse and longitudinal sections are scattered in a bioclastic matrix together with fragments of crinoids. The outer wall is thin and locally preserved.

The septa are non-carinate though a few small spinose

carinae occur in some corallites. The septa are weakly dilated in the dissepimentarium and become thinner in the tabularium or slightly beyond their entry into it when they are longer. Sometimes, they are discontinuous in the outer zone of flat dissepiments. In transverse section, the pipe of horseshoe dissepiments is easily observed and it is occasionally coated with a weak deposit of stereoplasma.

The major septa are restricted to the dissepimentarium or they are hardly projecting into the tabularium. In rare cases, they are leaving an open space in the centre of the tabularium. The minor septa are only present in the dissepimentarium.

The dissepimentarium consists of one peripheral row of flat dissepiments and one row of horseshoe dissepiments with locally narrow symmetrical fans of rhipidacanths centred over them. The sides of the horseshoe dissepiments may be weakly thickened. The tabulae are widely spaced and mostly horizontal; they are sometimes concave, a little convex or incomplete.

There are 28 to 38 septa per corallite. The diameter of the corallites ranges from 3.2 mm to 6.4 mm whereas the width of the tabularium varies between 2.2 mm and 4.1 mm.

Discussion. As mentioned by Errenst (1993), the structure of Thamnophyllum simplex is very simple. This is still more the case for the Moroccan material. Indeed, their major septa are often restricted to the dissepimentarium or hardly projecting into the tabularium whereas their tabulae are rarely concave, convex or incomplete. There are some similarities between T. cf. simplex and T. moravicum Galle, 1993 from the Eifelian of Moravia in Czech Republic, but the major septa are longer in the holotype of the latter species. The same situation concerns the holotype of T. ossalense (Joseph & Tsien, 1975) from the lower Givetian of the Pyrenees in France which is additionally not well identified. As for T. pajchelae Różkowska, 1956 from the Givetian of the Holy Cross Mountains in Poland, there is only one corallite of the holotype which has been figured and which differs from T. cf. simplex by the thickening of the two sides of the horseshoe dissepiments and by convex tabulae.

*Distribution.* The questionable Moroccan material has been collected in the lower Givetian reef of Aferdou el Mrakib. In Germany, *Thamnophyllum simplex* is only known in the middle Givetian from Northeast Sauerland.

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. Eifelian of the New York State in the USA.

Diagnosis. See Coen-Aubert (2017)

#### Siphonophrentis subaequalis n. sp.

(Plates 6A-B, 7C)

*Derivation of name.* From *subaequalis, e* (Latin) = subequal, referring to the nearly same length of the major and minor septa.

*Holotype.* IRScNB a13932 (Pl. 6A–B). Specimen MA403 collected by H. Hollard during the seventies, in the Middle Devonian of the Ma'der, Morocco.

*Type locality and horizon.* Lower Givetian of the Aferdou el Mrakib reef, in the Ma'der, Morocco.

*Material.* Two specimens with four thin sections collected by H. Hollard: Aferdou el Mrakib MA403 and MA404 (his sample TM554/1).

*Diagnosis.* A species of *Siphonophrentis* with 108 to 114 septa at a diameter of 41 mm to 51 mm. Septa weakly dilated to thin throughout their length. Both orders of septa short, the major ones being slightly longer than the minor ones. No peripheral stereozone.

*Description.* The material consists of two fragmentary ceratoid coralla with longitudinal ribs and a height between 55 mm and 105 mm. The outer wall is locally preserved.

The non-carinate septa are weakly dilated in the main part of the holotype where there is a siphonofossula. They are mostly slender in the paratype with a few small spinose irregularities. In some cases, the septa are affected by a thin dark median line. The major septa leave a wide open space in the centre of the corallum. Their axial ends may be thinner, curved or bifurcated. The minor septa are slightly shorter than the major ones and they are occasionally contratingent.

There are no dissepiments. The tabulae are characterized by a wide horizontal axial part, partly concave, but rarely convex; their narrow outermost parts are inclined towards the outer wall. In some places of the holotype, the tabulae are broken.

There are about 108 to 114 septa for diameter of 41 mm to 51 mm.

Discussion. Siphonophrentis subaequalis resembles S. subgigantea (Champernowne, 1884) whose lectotype from the upper Givetian of South Devon in Great Britain has been investigated by Smith & Thomas (1963, p. 167). However, the latter species differs by shorter minor septa and systematically thin septa. The corallum from the upper Givetian of the Sauerland in Germany assigned by May (1994, fig. 6.1) to S. subgigantea is also close to S. subaequalis, but it has only been figured by a polished transverse section and a longitudinal fragment; additionally, it has very slender septa. There are some affinities between S. subaequalis and four specimens from the middle Givetian of the Holy Cross Mountains in Poland identified by Wrzołek (2002, pl. 3, figs 1-3, 6-7) as Enallophrentis polonica (Sobolev, 1904). But the original material of Sobolev (1904) from the Givetian of the same area has longer major septa reaching the centre of the tabularium, as is recognised by Zatoń et al. (2022b, fig. 3A-B).

*Distribution.* The new species is only known in the lower Givetian from the Aferdou el Mrakib reef, in the Ma'der, Morocco.

#### Siphonophrentis cantabrica Birenheide, 1978

(Plates 6C-D, 7D)

- \* 1978 Siphonophrentis cantabrica n. sp.; Birenheide, p. 69, pl. 9, fig. 2.
- non 1991 Siphonophrentis cantabrica Birenheide 1978; May, p. 28, fig. 13.
- pp. 1994 Siphonophrentis cantabrica Birenheide, 1978; Wang, p. 374, pl. 7, figs 1, 3, pl. 8, figs 1–3, pl. 9, figs 1, 3, pl. 10, figs 1–2, pl. 11, fig. 1, pl. 12, figs 1–2, pl. 13, fig. 1 (non pl. 7, fig. 2, pl. 9, fig. 2, pl. 10, fig. 3, pl. 11, figs 2–4, pl. 12, figs 3–5).
- non 1999 Siphonophrentis cf. cantabrica; Schröder & Kazmierczak, p. 98, pl. 1, fig. 1.
- pp. 2001b *Siphonophrentis cantabrica* Birenheide 1978; Schröder, p. 259, fig. 2.5 (non fig. 2.1–2.2).

*Holotype.* Specimen SMF 30935 (Birenheide, 1978, pl. 9, fig. 2) stored in the Forschungsinstitut Senckenberg at Frankfurt am Main, Germany. Section in East-Seitental to the north of Aleje, along the road in the Esla valley, Leon Province in Spain. Lower part of the Givetian Portilla Formation.

*Material.* Two specimens with four thin sections collected by P. Bultynck: Ou Driss East MA707 and MA718.

*Diagnosis.* A species of *Siphonophrentis* with 84 to 88 septa at a diameter of 30 mm to 43 mm. Both orders of septa weakly dilated and short, the minor ones less developed than the major ones. No true peripheral stereozone.

*Description.* The material consists of two fragmentary ceratoid coralla with longitudinal ribs and growth lines. Their length varies between 35 mm and 65 mm. The outer wall is locally preserved and slightly thickened.

The non-carinate septa are weakly dilated with occasionally a dark median line. In one specimen, they are thicker in the two cardinal quadrants. The major septa leave a wide open space in the centre of the corallum; they may be thinner at their axial ends. The minor septa are shorter than the minor ones; they are sometimes reduced to spines or contratingent.

There are no dissepiments. The tabulae are characterized by a broad horizontal axial part which is occasionally incomplete or irregular; their narrow outermost parts are inclined towards the outer wall.

There are 84 to 90 septa for a diameter of 27 mm to 32 mm which may reach 42 mm in one specimen.

Discussion. Siphonophrentis cantabrica is a poorly understood species. The German specimen of May (1991) has been assigned to *S. subgigantea* by May (1994) as it is mentioned in the discussion of *S. subaequalis*. The Chinese material of Wang (1994) is a mixture of coralla with septa slightly dilated at the periphery and typical of *S. cantabrica* together with much smaller specimens and with other ones characterized by very thin septa. Siphonophrentis cantabrica is distinguished from *S. subaequalis* by its smaller septal number and diameter of the corallum, by weakly thicker septa at the periphery and by shorter minor septa. Siphonophrentis crassa Coen-Aubert, 2005 from the upper Givetian of the Ma'der in Morocco is related to *S. cantabrica*, but it has slightly more dilated and longer septa of both orders.

*Distribution.* The two investigated Moroccan specimens come from the base of the middle Givetian at Ou Driss East in the Ma'der. For the rest, *Siphonophrentis cantabrica* is known in the Givetian from Asturias and the Leon Province in Spain as well as in the upper Givetian from Western Yunnan in China.

#### Genus Enallophrentis Oliver, 1993

*Type species.* By original designation, *Strombodes simplex* Hall, 1843 from the Givetian of New York in the USA.

*Diagnosis.* Solitary rugose corals. Septa of two orders noncarinate and more or less dilated throughout their length, maybe with thickened peripheral ends to form a narrow stereozone. Major septa reaching the axis of the corallum or slightly shorter. Minor septa of variable length. Occurrence of a cardinal fossula. No dissepiments. Tabulae complete or incomplete often with a convex or irregular axial part which is sometimes flat or depressed in the centre.

#### *Enallophrentis corniformis* (Gürich, 1896) (Plate 7E–F)

- \* 1896 Blothrophyllum giganteum Les. var. corniformis; Gürich, p. 176, pl. 3, figs 3–4.
  - 2001b Blothrophyllum giganteum var. corniformis Gürich 1896; Schröder, p. 261.
  - 2002 Enallophrentis corniformis (Gürich 1896); Wrzołek, p. 236, pl. 2, figs 1–19.

*Neotype.* Specimen GIUS381 SD 21\_13 designated by Wrzołek (2002, p. 236, pl. 2, figs 11–14) and stored in the Department of Earth Sciences from the Silesian University at Sosnowiec, Poland. Lower Givetian coral banks of sets XXII/XXIII at Skały, in the Holy Cross Mountains, Poland.

*Material.* Two specimens with four thin sections collected by H. Hollard and P. Bultynck: Ou Driss East MA2 and MA351.

*Diagnosis.* A species of *Enallophrentis* with 72 to 100 septa at a diameter of 28 mm to 46 mm. Short minor septa. Tabulae with a variable pattern.

*Description.* The material consists of two fragmentary solitary coralla whose height varies between 30 mm and 90 mm. The longest of them is ceratoid with longitudinal ribs and growth lines and it is affected by rejuvenescence. The outer wall is nearly continuous.

The septa are non-carinate and slightly dilated; they may become thinner at their axial ends. A siphonofossula is observed in one specimen. Stereoplasma is locally present between the septa at the periphery of the other specimen. A few septa are characterized by a dark median line. The major septa reach more or less the centre of the tabularium where there is a deposit of stereoplasma. The minor septa are reduced to spines or short segments; they are occasionally absent.

There are no dissepiments. The close and incomplete tabulae are often broken with a wide convex or concave axial part.

There are 88 to 96 septa for a diameter of 32 mm to 38 mm.

Discussion. The two Moroccan specimens coming from Ou Driss East are very close to the Polish material of Wrzołek (2002) where the outer wall is sometimes thicker. They resemble some coralla from the same locality identified as Siphonophrentis belgebaschica (Ivania, 1955) by Pedder (1999, pl. 6, figs 1, 5, pl. 7, figs 5, 7-8). However, this sampling differs from Enallophrentis corniformis by a wide open space in the centre of the tabularium and by much simpler tabulae. It should be better assigned to Siphonophrentis kullmanni (Birenheide, 1978) from the lower to middle Givetian of the Leon Province in Spain described by Coen-Aubert (2017) in the Givetian of the Zemmour in Mauritania and considered by Pedder (1999) as one of the synonyms of S. belgebaschica. As already mentioned by Coen-Aubert (2005, 2017), the septa of the holotype of S. belgebaschica from the Givetian of the Gornyi Altai in Russia are much thicker than those of S. kullmanni. It can be added that S. belgebaschica is the type species of Altaiophyllum Ivania, 1955. At the specific level, the corallum from the upper Givetian of Asturias in Spain illustrated by Schröder (2001b, fig. 3.5) as Contophrentis sp. shows many similarities with Enallophrentis corniformis.

*Distribution.* The two investigated Moroccan specimens come from the base of the middle Givetian at Ou Driss East in the Ma'der. For the rest, *Enallophrentis corniformis* is only known in the lower Givetian from the Holy Cross Mountains in Poland.

#### 4. Stratigraphic and palaeobiogeographic conclusions

The material investigated herein comes from four middle Givetian localities of the Ma'der in Morocco, across the Eifelian–Givetian boundary (Fig. 2). It shows some biodiversity though it is not very abundant.

Heliophyllum moghrabiense is the only species common to the four localities: in the upper Eifelian Tortodus kockelianus conodont Zone of Ouahlane, at the top of the Eifelian in Aferdou el Mrakib, in the lower Givetian of Madène el Mrakib and at the base of the middle Givetian from Ou Driss East indicated by the Polygnathus rhenanus/P. varcus conodont Zone. Heliophyllum moghrabiense has also been observed by Schröder & Kazmierczak (1999), in the lower Givetian Polygnathus timorensis Zone of Ouahlane. Besides Morocco, H. moghrabiense is known in the Givetian of eastern Afghanistan (Fig. 3), according to Brice (1971) and Coen-Aubert (1987). Traditionally, the genus Heliophyllum Hall in Dana, 1846 is considered as typical of Eastern North America where it is frequent and represented by many species (Oliver & Sorauf, 1988; Oliver, 2007; Jamart & Denayer, 2020).

Stringophyllum acanthicum and Acanthophyllum heterophyllum accompanied by a few specimens of A. vermiculare are interesting for correlations with Belgium and Germany. As mentioned by Coen-Aubert (2022, figs 4 and 5), they occur across the Eifelian-Givetian boundary, on the south side of the Dinant Synclinorium in Belgium; but they have a wider stratigraphic extension in the Eifelian and in the lower Givetian of the Eifel Hills. Additionally, Stringophyllum acanthicum is also present in the Givetian from central Moravia, the Czech Republic (Kettnerova, 1932) whereas in Acanthophyllum heterophyllum has been reported by Coen-Aubert (2017) in the lower part of the Givetian from the Zemmour in Mauritania. Two other German taxa have been identified in the lower Givetian of Aferdou el Mrakib. Atelophyllum maximum, represented by a beautiful corallum, has been defined in the upper Eifelian of the Eifel Hills (Birenheide, 1964, 1978). The fragments of Thamnophyllum cf. simplex can be compared with the material of Errenst (1993) which comes from the middle Givetian of the Sauerland. Spinophyllum blacourti has been recognized at the base of the middle Givetian of Ou Driss East. This species introduced in the lower Givetian of the Boulonnais in France (Rohart, 1988) is very abundant at the top of this substage, on the south side of the Dinant Synclinorium (Coen-Aubert, 2002a). It is also known in the upper Givetian of the Aachen Syncline in Germany (Schröder, 2001a) and in the Givetian of the Alborz Mountains in Iran (Abassi et al. 2014a, 2014b).

Part of the Moroccan material is more characteristic of the Ma'der Basin. This is the case for Stringophyllum coenaubertae and S. pedderi occurring at Ouahlane and Ou Driss East whereas Marennophyllum kaufmanni has been collected at the top of the Eifelian of Aferdou el Mrakib. The genus Marennophyllum Coen-Aubert, 2022 is well represented at the base of the middle Givetian from Ou Driss East by numerous coralla of M. maderense (Pedder, 1999) and M. pegoconus (Pedder, 1999) described by Pedder (1999). I have only studied one specimen of M. cf. kaufmanni from this locality. From the same outcrop, Pedder (1999, pl. 6, figs 1, 5, pl. 7, figs 5, 7-8) has figured two coralla of Siphonophrentis belgebaschica which should be better assigned to S. kullmanni as explained in the systematic part. Siphonophrentis. kullmanni is known in the lower to middle Givetian of the Leon Province in Spain and in the middle to upper Givetian of the Zemmour in Mauritania according to Coen-Aubert (2017). Siphonophrentis cantabrica is another Spanish species from the Givetian of Asturias and the Leon Province (Birenheide, 1978; Schröder, 2001b) present at

	AFERDOU EL MRAKIB	MADENE EL MRAKIB	OU DRISS EAST	OUAHLANE	
MIDDLE GIVETIAN			* * * * * * * * * *		
LOWER GIVETIAN	x x x x	x x			
UPPER EIFELIAN	x x x			x	
LOWER EIFELIAN	Marennophyllum kaufmanni Atelophyllum maximum Stringophyllum coenaubertae Heliophyllum moghrabiense Kuangxiastraea sp. Thamnophyllum cf. simplex Siphonophrentis subaequalis	Australophyllum sp. Heliophyllum moghrabiense	Marennophyllum cf. kaufmanni Stringophyllum coenaubertae Stringophyllum pedderi Acanthophyllum heterophyllum Acanthophyllum vermiculare Heliophyllum moghrabiense Spinophyllum blacourti Siphonophrentis cantabrica Enallophrentis corniformis	Stringophyllum acanthicum Stringophyllum coenaubertae Acanthophyllum heterophyllum Acanthophyllum vermiculare Heliophyllum moghrabiense	

Figure 2. Stratigraphic distribution for the taxa of rugose corals identified in the four localities from the Ma'der investigated herein.

	BELGIUM,	POLAND			IRAN	
	FRANCE AND	AND CZECH	SPAIN	MAURITANIA	AND	CHINA
	GERMANY	REPUBLIC			AFGHANISTAN	
Atelophyllum maximum	х					
Stringophyllum acanthicum	х	х				
Acanthophyllum heterophyllum	х	х		х		
Acanthophyllum vermiculare	х					
Heliophyllum moghrabiense					х	
Spinophyllum blacourti	х				х	
Thamnophyllum cf. simplex	х					
Siphonophrentis cantabrica			х			х
Enallophrentis corniformis		х				

Figure 3. Geographic occurrences of Middle Devonian rugose corals from the Ma'der observed in different countries of Europe, North Africa and Asia.

Ou Driss East; this taxon has been well illustrated by Wang (1994), in the upper Givetian of Western Yunnan in China. Additionally, I have observed at Ou Driss East *Enallophrentis corniformis* occurring in the lower Givetian of the Holy Cross Mountains in Poland (Wrzołek, 2002). As for *Siphonophrentis subaequalis*, it is a new species of siphonophrentids present in the lower Givetian of Aferdou el Mrakib.

Among the material investigated herein, the massive rugose corals are restricted to two particular colonies: *Kuangxiastraea* sp. at Aferdou el Mrakib and *Australophyllum* sp. at Madène el Mrakib. *Kuangxiastraea* Yu & Kuang, 1982 has already been reported by Coen-Aubert (2002b, 2005), in the Ma'der where

one colony of *K. pengellyi* has been collected in the Upper *Klapperina disparilis* conodont Zone indicating the upper Givetian. The distribution of *Australophyllum* Stumm, 1949 in the Lower Devonian and the Eifelian of Canada, Australia, China, Russia and neighbouring countries has been discussed by McLean (2018). The genus is also known in the lower Givetian of Australia with the species *A. yohi* Zhen, 1994. In Belgium, *Australophyllum* has been mentioned by Denayer (2019, 2023) in the lower Eifelian Wancennes Formation, on the south side of the Dinant Synclinorium.

From a palaeogeographic point of view, the Ma'der Basin was situated during the Middle Devonian, at the northern margin of Gondwana. This was also the case for the Zemmour in Mauritania, Asturias and the Leon Province in Spain, Iran and Afghanistan (Coen-Aubert, 2017). Some species such as Heliophyllum moghrabiense, Siphonophrentis cantabrica and S. kullmanni are typical of North Gondwana. But there are other species present in the Middle Devonian of the Ma'der, such as Stringophyllum acanthicum, Acanthophyllum heterophyllum, A. vermiculare and Spinophyllum blacourti which have many affinities with Western Europe and sometimes with Eastern Europe belonging to South Laurussia. Far to the east, there is only one link between the Ma'der and the Western Yunnan in China due to the occurrence of Siphonophrentis cantabrica. For other groups of Middle Devonian fossils such as brachiopods and bryozoans, similar faunistic relations, mainly with the Old World Realm, have been emphasized at Aferdou el Mrakib and Madène el Mrakib, by Halamski & Baliński (2013), Halamski et al. (2022b) and Zatoń et al. (2022a). Finally, it must be mentioned that Australophyllum has been recognized for the first time in Morocco.

#### Acknowledgements

Henri Hollard, Paul Sartenaer, Bernd Kaufmann and Pierre Bultynck collected the Moroccan rugose corals investigated herein. P. Bultynck guided me at Ouahlane and gave me much interesting information about Ou Driss East. The thin sections have been made by René Cremers and by Joël Laval at the Laboratory of successively Eddy Poty and Valentin Fischer (Liège). Wilfried Miseur and Thierry Hubin helped me with photography of the corals. Two anonymous reviewers provided diverse and valuable comments. Anthony Wright reviewed very carefully the manuscript and improved the language. I am most grateful to all these people.

#### **Author contribution**

Collecting of some rugose corals at Ouahlane, detailed palaeontological identifications of the genera and the species, writing of the article.

#### **Data availability**

All the specimens and thin sections of rugose corals are stored in the Collection of Palaeontology of the *Institut royal des Sciences naturelles de Belgique* at Brussels.

#### References

- Abbasi, M.A., Ashouri, A. & Khaksar, K., 2014a. Solitary rugose corals from the Givetian of the Khoshyeilagh Formation (Eastern Alborz Mountains, NE Iran). Palaeodiversity, 7, 1–21.
- Abbasi, M.A. Khaksar, K & Ashouri, A., 2014b. Description of some rugose corals from the Givetian and Lower Frasnian of the Eastern Alborz Mountains, NE Iran. Geopersia, 4, 237–257.
- Barchy, L., Coen-Aubert, M., Marion, J.-M. & Coen, M., 2004. Mise en évidence de la Faille de Marenne sur la carte géologique Aye -Marche-en-Famenne. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, Supplement, 74, 59–71.
- Becker, R.T., Marshall, J.F.A. & Da Silva, A.-C., 2020. The Devonian Period. In Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (eds), Geologic Time Scale, Volume 2. Elsevier, Amsterdam, 733– 810. https://doi.org/10.1016/B978-0-12-824360-2.00022-X
- Birenheide, R., 1961. Die Acanthophyllum-Arten (Rugosa) aus dem Richtschnitt Schönecken-Dingdorf und aus anderen Vorkommen in der Eifel. Senckenbergiana lethaea, 42, 77–146.
- Birenheide, R., 1962. Die Typen der Sammlung Wedekind aus den Familien Cyathophyllidae und Stringophyllidae (Rugosa). Senckenbergiana lethaea, 43, 101–123.

- Birenheide, R., 1963. Cyathophyllum- und Dohmophyllum-Arten (Rugosa) aus dem Mitteldevon der Eifel. Senckenbergiana lethaea, 44, 363–458.
- Birenheide, R., 1964. Die « Cystimorpha » (Rugosa) aus dem Eifeler Devon. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 507, 1–120.
- Birenheide, R., 1978. Rugose Korallen des Devon. In Krömmelbein, K. (ed.), Leitfossilien begründet von G. Gürich. 2., völlig neu bearbeitete Auflage, n° 2. Gebrüder Borntraeger, Berlin-Stuttgart, 265 p.
- Birenheide, R. & Soto, F.M., 1981. "Cystimorphe" rugose Korallen aus dem Devon des Kantabrischen Gebirges, N-Spanien. Senckenbergiana lethaea, 62, 251–275.
- Birenheide, R. & Soto, F., 1992. Rugose Einzel- und Phaceloid-Korallen aus dem Ober-Givetium (Mittel-Devon) des Kantabrischen Gebirges, NW-Spanien. Palaeontographica A, 221, 95–123.
- Brice, D., 1971. Etude paléontologique et stratigraphique du Dévonien de l'Afghanistan. Contribution à la connaissance des Brachiopodes et des Polypiers Rugueux. Notes et Mémoires sur le Moyen-Orient, 11, 1–364.
- Bultynck, P., 1985. Lower Devonian (Emsian) Middle Devonian (Eifelian and lowermost Givetian) conodont successions from the Ma'der and the Tafilalt, southern Morocco. Courier Forschungsinstitut Senckenberg, 75, 261–286.
- Bultynck, P., 1989. Conodonts from a potential Eifelian/Givetian Global Boundary Stratotype at Jbel Ou Driss, southern Ma'der, Morocco. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 59, 95–103.
- Bultynck, P., 1991. Section Jbel Ou Driss (Mapsheet Tarhbalt, NH-30-XIII-4. In Walliser, O.H. (ed.), Morocco, Field Meeting of the Subcommission on Devonian Stratigraphy, Nov. 28-Dec. 5, 1991, Guide-Book. Göttingen, 17–23.
- Bultynck, P. & Walliser, O.H., 2000. Devonian boundaries in the Moroccan Anti-Atlas. Courier Forschungsinstitut Senckenberg, 225, 211–226.
- Champernowne, A., 1884. On some zaphrentoid corals from British Devonian beds. The Quarterly Journal of the Geological Society of London, 40, 497–506. https://doi.org/10.1144/GSL.JGS.1884.40.01 -04.43
- Coen-Aubert, M., 1987. Révision d'*Heliophyllum halli* Milne-Edwards et Haime, espèce-type du genre *Heliophyllum* Hall in Dana (Tétracoralliaire dévonien). Bulletin du Muséum national d'Histoire naturelle, 4<sup>e</sup> série, 9 (section C, 2), 151–180.
- Coen-Aubert, M., 1990. Description de quelques Rugueux coloniaux du Couvinien supérieur de Wellin (bord sud du Bassin de Dinant, Belgique). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 59, 15–35.
- Coen-Aubert, M., 1997. Rugueux solitaires près de la limite Eifelien-Givetien à Pondrôme (Belgique). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 67, 5–24.
- Coen-Aubert, M., 1998. Thamnophyllides et Acanthophyllides près de la limite Eifelien-Givetien à Wellin et Pondrôme (Belgique). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 68, 5–24.
- Coen-Aubert, M., 2002a. Temnophyllids and Spinophyllids (Rugosa) from the Givetian Mont d'Haurs Formation in Belgium. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 72, 5–24.
- Coen-Aubert, M., 2002b. 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 Bulletin, 7, 21–37.
- Coen-Aubert, M., 2005. Rugueux fasciculés et solitaires du Givetien supérieur dans le Tafilalt et le Ma'der (Maroc). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 75, 67–85.

- Coen-Aubert, M., 2011. Reassignment to the Middle Devonian of some rugose corals investigated by Le Maître (1934) in the Chalonnes Formation from the Southeastern Armorican Massif (France). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 81, 27–53.
- Coen-Aubert, M., 2017. Givetian rugose corals from the Zemmour in Mauritania. Geologica Belgica, 20, 161–180. http:// dx.doi.org/10.20341/gb.2017.009
- Coen-Aubert, M., 2019. Investigation of some Givetian rugose corals from the Mont d'Haurs Formation in southern Belgium. Geologica Belgica, 22, 121–138. https://doi.org/10.20341/gb.2019.008
- Coen-Aubert, M., 2022. The highly diversified rugose coral fauna from the Lower Givetian Meerbüsch quarry in the Eifel Hills (Germany). Geologica Belgica, 25, 53–81. https://doi.org/10.20341/gb.2022.003
- Dana, J.D., 1846. Genera of fossil corals of the family Cyathophyllidae. The American Journal of Science and Arts, series 2, 1, 178–189.
- Denayer, J., 2019. Revised stratigraphy of the Eifelian (Middle Devonian) of southern Belgium: sequence stratigraphy, global events, reef development and basin structuration. Geologica Belgica, 22, 149–173. https://doi.org/10.20341/gb.2019.009
- Denayer, J., 2023. From mud to limestone: Birth and growth of a giant reef in the Eifelian (Middle Devonian) of S Belgium. Palaeogeography, Palaeoclimatology, Palaeoecology, 627, 111748. https://doi.org/10.1016/j.palaeo.2023.111748
- Denayer, J., 2024a. Rugose corals across the Early-Middle Devonian boundary in southern Belgium. Palaeobiodiversity and Palaeoenvironments, 105 (pro 2025), 179–216. https:// doi.org/10.1007/s12549-024-00627-0
- Denayer, J., 2024b. Devonian corals of the Vosges Mountains, France. Acta Palaeontologica Polonica, 69, 591–605. https://doi.org/10.4202/ app.01176.2024
- Dybowski, W.N., 1873. Monographie der Zoantharia Sclerodermata Rugosa aus der Silurformation Estlands, Nord-Livlands und der Insel Gothland. Archiv f
  ür die Naturkunde Liv-, Est- und Kurlands, series 1, 5, 257–414.
- Engel, G. & von Schouppé, A., 1958. Morphogenetisch-taxionomische Studie zu der devonischen Korallengruppe Stringophyllum, Neospongophyllum und Grypophyllum. Paläontologische Zeitschrift, 32, 67–114. https://doi.org/10.1007/BF02987036
- Errenst, C., 1993. Koloniebildende Phillipsastreidae und Hexagonariinae aus dem Givetium des Messinghäuser Sattels und vom Südrand des Briloner Massenkalkes (nordöstliches Sauerland). Geologie und Paläontologie in Westfalen, 26, 7–45.
- Etheridge, R. Jr., 1911. The Lower Palaeozoic corals of Chillagoe and Clermont. Publications of the Queensland Geological Survey, 231, 1–8.
- Flügel, H.W. & Tintori, A., 1993. Late Devonian (Frasnian) corals from central Dolpo, Nepal. Rivista Italiana di Paleontologia e Stratigrafia, 99, 3–26.
- Frech, F., 1885a. Ueber das Kalkgerüst der Tetrakorallen. Zeitschrift der Deutschen geologischen Gesellschaft, 37, 928–945.
- Frech, F., 1885b. Die Korallenfauna des Oberdevons in Deutschland. Zeitschrift der Deutschen geologischen Gesellschaft, 37, 21–130.
- Galle, A., 1993. Middle Devonian Rugosa from Horni Benesov (Moravia, Czech Republic). Journal of the Czech Geological Society, 38, 59–70.
- Goldfuss, A., 1826. Petrefacta Germaniae 1. Arnz & Comp., Düsseldorf, 1–76.
- Gürich, G., 1896. Das Palaeozoicum im Polnischen Mittelgebirge. Verhandlungen der Russisch-kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg, serie 2, 32, 1–539.
- Halamski, A.T. & Baliński, A., 2013. Middle Devonian brachiopods from the southern Maïder (eastern Anti-Atlas, Morocco). Annales Societatis Geologorum Poloniae, 83, 243–307.
- Halamski, A.T., Baliński, A., Racki, G., Amler, M.R.W., Basse, M., Denayer, J., Dubicka, Z., Kilipiak, P., Kondas, M., Krawczyński, W., Mieszkowski, R., Narkiewicz, K., Olempska, E., Wrzołek, T., Wyse Jackson, P.N., Zapalski, M.K., Zatoń, M. & Kozłowski, W.,

2022a. The Pre-Taghanic (Givetian, Middle Devonian) ecosystems of Miłoszów (Holy Cross Mts, Poland). Annales Societatis Geologorum Poloniae, 92, 323–379. https://doi.org/10.14241/asgp.2022.19

- Halamski, A.T., Baliński, A. & Koppka, J., 2022b. Middle Devonian brachiopods from northern Maïder (eastern Anti-Atlas, Morocco). Annales Societatis Geologorum Poloniae, 92, 1–86. https:// doi.org/10.14241/asgp.2022.03
- Hall, J., 1843. Geology of New York. Part IV comprising the survey of the fourth geological district. Albany, 683 p.
- He, Y.X., 1978. Subclass Rugosa. In Chengdu Institute of Geology and Mineral Resources (ed.), Atlas of Fossils of Southwest China. Sichuan Volume. Part I, From Sinian to Devonian. Geological Publishing House, Beijing, 98–178.
- Hill, D., 1939. The Devonian rugose corals of Lilydale and Loyola, Victoria. Proceedings of the Royal Society of Victoria, new series, 51, 219–256.
- Hill, D., 1981. Part F, Coelenterata, Supplement 1, Rugosa and Tabulata, 2 vols. In Teichert, C. (ed.), Treatise on Invertebrate Paleontology. The Geological Society of America and The University of Kansas, Boulder (CO) and Lawrence (KS), 762 p.
- Hollard, H., 1974. Recherches sur la stratigraphie des formations du Dévonien moyen, de l'Emsien au Frasnien, dans le sud du Tafilalt et dans le Ma'der (Anti-Atlas oriental). Notes du Service géologique du Maroc, 36, 264, 7–68.
- Hollard, H., 1981. Tableaux de corrélations du Silurien et du Dévonien de l'Anti-Atlas. Notes du Service géologique du Maroc, 42, 308, 23, 5 tableaux.
- Ivania, V.A., 1955. O novom rode devonskikh korallov. Zametki po faune i flore Sibiri, 18, 85–86. [In Russian].
- Ivania, V.A., 1965. Devonskie korally Sayano-Altayskoy gornoy oblasti. Izd. Tomskogo Universiteta, Tomsk, 398 p. [In Russian].
- Jakubowicz, M., Król, J., Zapalski, M.K., Wrzołek, T., Wolniewicz, P. & Berkowski, B., 2019. At the southern limits of the Devonian reef zone: Palaeoecology of the Aferdou el Mrakib reef (Givetian, eastern Anti-Atlas, Morocco). Geological Journal, 54, 10–38. https://doi.org/10.1002/gj.3152
- Jamart, V. & Denayer, J., 2020. The Kačák event (late Eifelian, Middle Devonian) on the Belgian shelf and its effects on rugose coral palaeobiodiversity. Bulletin of Geosciences, 95, 279–311. https:// doi.org/10.3140/bull.geosci.1788
- Jell, J.S. & Hill, D., 1970. Revision of the Coral fauna from the Devonian Douglas Creek Limestone, Central Queensland. Proceedings of the Royal Society of Queensland, 81, 93–119.
- Joseph, J. & Tsien, H.H., 1975. Calcaires mésodévoniens et leurs faunes de Tétracoralliaires en Haute Vallée d'Ossau (Pyrénées-Atlantiques). Bulletin de la Société d'Histoire naturelle de Toulouse, 111, 179–203.
- Kaufmann, B., 1998. Facies, stratigraphy and diagenesis of Middle Devonian reef- and mud-mounds in the Mader (eastern Anti-Atlas, Morocco). Acta Geologica Polonica, 48, 43–106.
- Kettnerova, M., 1932. Paleontologicke studie z celechovickeho devonu, Cast IV: Rugosa. Prace geologicko-palaeontologickeho ustavu Karlovy university v Praze, 1932, 1–97.
- Lang, W.D. & Smith, S., 1935. Cyathophyllum caespitosum Goldfuss and other Devonian corals considered in a revision of that species. The Quarterly Journal of the Geological Society of London, 91, 538– 589. https://doi.org/10.1144/GSL.JGS.1935.091.01-04.19
- Latypov, Yu. Ya., 1977. Odinochnie tsistimorfnye korally Severnoy Azii. Trudy Instituta Geologii i Geofiziki, Akademiya Nauk SSSR, Sibirskoe Otdelenie, 353, 1–80. [In Russian].
- Le Maître, D., 1934. Etudes sur la faune des calcaires dévoniens du bassin d'Ancenis. Mémoire de la Société géologique du Nord, 12, 1– 267.
- Le Maître, D., 1947. Le récif coralligène de Ouihalane. Notes et Mémoires du Service des Mines et de la Carte géologique du Maroc, 67, 1–112.

- Lesueur, C.A., 1821. Description de plusieurs animaux appartenant aux polypiers lamellifères de M. le Ch<sup>er</sup> De Lamarck. Mémoires du Muséum d'Histoire naturelle, 6, 271–299.
- Liao, W.H., 2015. Two major faunal turnover events of Middle Devonian corals in South China. Acta Palaeontologica Sinica, 54, 305–315.
- Liao, W.H. & Birenheide, R., 1984. Rugose Korallen aus dem Givetium von Dushan, Provinz Guizhou, S-China. 1: "Cystimorpha". Senckenbergiana lethaea, 65, 1–25.
- Lütte, B.P., 1984. Rugose Korallen aus dem Mitteldevon (Givetium) der Sötenicher Mulde (Rheinisches Schiefergebirge, Nord-Eifel). Münstersche Forschungen zur Geologie und Paläontologie, 61, 175– 243.
- Lütte, B.P., 1985. Cyathophyllum (Cyathophyllum) arduum n. sp. (Rugosa) aus der Sötenicher Mulde (Rheinisches Schiefergebirge, Nord-Eifel). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1985/9, 542–552. https://doi.org/10.1127/ njgpm/1985/1985/542
- Ludwig, R., 1866. Corallen aus paläolithischen Formationen. Palaeontographica, 14, 133–244.
- Ma, T.Y.H., 1937. On the seasonal growth in Palaeozoic tetracorals and the climate during the Devonian period. Palaeontologia Sinica, series B, 2/3, 1–51.
- Ma, T.Y.H., 1956. A reinvestigation of climate and the relative positions of continents during the Devonian. Research on the Past Climate and Continental Drift, 9, 1–116.
- Majchrzyk, A., Jakubowicz, M., Berkowski, B., Bongaerts, P. & Zapalski, M.K., 2022. In the shadow of a giant reef: Palaeoecology of mesophotic coral communities from the Givetian of Anti-Atlas (Morocco). Palaeogeography, Palaeoclimatology, Palaeoecology, 602, 111177. https://doi.org/10.1016/j.palaeo.2022.111177
- Majchrzyk, A., Jakubowicz, M., Berkowski, B., Król, J.J., Zatoń, M. & Zapalski, M.K., 2024. Modern-type reef in ancient time – Palaeoecology of a Middle Devonian coral community from Madène el Mrakib (Anti-Atlas, Morocco). Palaeogeography, Palaeoclimatology, Palaeoecology, 633, 111876. https:// doi.org/10.1016/j.palaeo.2023.111876
- May, A., 1991. Die Fossilführung des westsauerländischen Givetiums (Devon; Rheinisches Schiefergebirge) in der Sammlung des Städtischen Museums Menden. Geologie und Paläontologie in Westfalen, 17, 7–42.
- May, A., 1993. Korallen aus dem höheren Eifelium und unteren Givetium (Devon) des nordwestlichen Sauerlandes (Rheinisches Schiefergebirge). Teil II: Rugose Korallen, Chaetetiden und spezielle Themen. Palaeontographica, Abteilung A, 228, 1–103.
- May, A., 1994. Paleoecology and paleobiogeography of corals and other reef-builders from the Middle Devonian of the Sauerland (Germany). Courier Forschungsinstitut Senckenberg, 172, 147–159.
- McLean, R.A., 2018. Fasciphyllid and spongophyllid rugose corals from the Middle Devonian of western Canada. Palaeontographica Canadiana, 37, 1–117.
- Merriam, C.W., 1973. Middle Devonian rugose corals of the Central Great Basin. U.S. Geological Survey Professional Paper, 799, 1–53. https://doi.org/10.3133/pp799
- Milne-Edwards, H. & Haime, J., 1850. A Monograph of the British Fossil Corals. Part 1, Introduction. The Palaeontographical Society, London, i–lxxxv.
- Milne-Edwards, H. & Haime, J., 1851. Monographie des Polypiers fossiles des terrains paléozoïques. Archives du Muséum d'Histoire Naturelle, 5, 1–502.
- Mistiaen, B., Brice, D., Hubert, B.L.M. & Loones, C., 2011. Field Trip 2: Classical Devonian and Carboniferous sites in the Ferques area, Boulonnais, Northern France. In Aretz, M. & Poty, E. (eds), Field Guides, 11th International Symposium on Fossil Cnidaria and Porifera, Liège, 2011. Kölner Forum für Geologie und Paläontologie, 20, 51–98.

- O'Connell, M., 1914. Revision of the genus Zaphrentis. Annals of the New York Academy of Sciences, 23, 177–192. https:// doi.org/10.1111/j.1749-6632.1914.tb56941.x
- Oliver, W.A., 1993. The Siphonophrentidae (rugose corals, Devonian) of Eastern North America. U.S. Geological Survey Bulletin, 2024, B1–B32.
- Oliver, W.A., 2007. Zaphrentis and the Zaphrentidae (Devonian; Anthozoa, Rugosa). Bulletins of American Paleontology, 373, 1–46.
- Oliver, W.A. & Sorauf, J.E., 1988. *Heliophyllum* Hall and *Charisphyllum* n. gen. (Devonian rugose corals) of the Cantabrian Mountains (NW Spain). Trabajos de Geologia, Universidad de Oviedo, 17, 3–17.
- Pedder, A.E.H., 1971. Dohmophyllum and a new related genus of corals from the Middle Devonian of northwestern Canada. Geological Survey of Canada, Bulletin, 197, 37–77.
- Pedder, A.E.H., 1980. Devonian corals of late Eifelian age from the Ogilvie Formation of Yukon Territory. Canadian Journal of Earth Sciences, 17, 594–616. https://doi.org/10.1139/e80-058
- Pedder, A.E.H., 1999. Paleogeographic implications of a Devonian (Givetian, Lower varcus Subzone) rugose coral fauna from the Ma'der Basin (Morocco). Abhandlungen der Geologischen Bundesanstalt, 54, 385–434.
- Penecke, K.A., 1894. Das Grazer Devon. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, 43, 567–616.
- Rafinesque, C.S. & Clifford, J.D., 1820. Prodrome d'une monographie des Turbinolies fossiles du Kentucky (dans l'Amériq. septentr.). Annales générales des Sciences Physiques, 5, 231–235.
- Reed, F.R.C., 1922. Devonian fossils from Chitral and the Pamirs. Memoirs of the Geological Survey of India, Palaeontologia Indica, new series, 6/2, 1–134.
- Roemer, C.F., 1883. Lethaea geognostica. I. Theil, Lethaea palaeozoica. Zweite Lieferung. Stuttgart, 324–543 and Atlas.
- Rohart, J. C., 1988. Rugueux givetiens et frasniens de Ferques (Boulonnais-France). In Brice, D. (ed.), Le Dévonien de Ferques. Bas-Boulonnais (N. France). Biostratigraphie du Paléozoïque, 7, 231–297.
- Różkowska, M., 1954. Badania wstepne nad Tetracoralla z eiflu Grzegorzowic. Acta Geologica Polonica, 4, 207–248.
- Różkowska, M., 1956. Pachyphyllinae from the Middle Devonian of the Holy Cross Mts. Acta Palaeontologica Polonica, 1, 271–322.
- Schlüter, C., 1882. Neue Korallen des Mitteldevon der Eifel. Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande und Westfalens, 39, 205–210.
- Schlüter, C., 1884. Über interessante neue Petrefakten. Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande und Westfalens, 41, 79–84.
- Schlüter, C., 1889. Anthozoen des rheinischen Mittel-Devon. Abhandlungen zur geologischen Specialkarte von Preussen und der Thüringischen Staaten, 8/4, 1–207.
- Schröder, S., 1998. Rugose Korallen und Stratigraphie des oberen Eifelium und unteren Givetium der Dollendorfer Mulde/Eifel (Mittel-Devon; Rheinisches Schiefergebirge). Courier Forschungsinstitut Senckenberg, 208, 1–135.
- Schröder, S., 2001a. Wenig bekannte rugose Korallen aus dem Mittelund Ober-Devon der Aachener Mulde (Rheinisches Schiefergebirge). Geologica et Palaeontologica, 35, 63–79.
- Schröder, S., 2001b. On some western European Siphonophrentidae. Bulletin of the Tohoku University Museum, 1, 254–264.
- Schröder, S., 2005. Stratigraphie und Systematik rugoser Korallen aus dem Givetium und Unter–Frasnium des Rheinischen Schiefergebirges (Sauerland/Bergisches Land). Zitteliana, B25, 39– 116.
- Schröder, S. & Kazmierczak, M., 1999. The Middle Devonian "coral reef" of Ouihlane (Morocco) – New data on the geology and rugose coral fauna. Geologica et Palaeontologica, 33, 93–115.
- Schulz, E., 1883. Die Eifelkalkmulde von Hillesheim. Nebst einem palaeontologischen Anhang. Jahrbuch der Königlich Preussischen

geologischen Landesanstalt und Bergakademie, Abhandlungen, 1882/3, 158–250.

- Shurigina, M.V., 1972. Podklass Tetracoralla. In Khodalevitch, A.N. (ed.), Kishechnopolostnye i brakhiopody zhivetskikh otlozheniy vostochnogo sklona Urala. Izd. Nedra, Moskva, 98–113. [In Russian].
- Scrutton, C.T., 1985. Subclass Rugosa. In Murray, J.W. (ed.), Atlas of Invertebrate Macrofossils. Longman and the Palaeontological Association, London, 13–31.
- Smith, S., 1945. Upper Devonian Corals of the Mackenzie River region, Canada. Geological Society of America, Special Papers, 59, 1–126. https://doi.org/10.1130/SPE59-p1
- Smith, S. & Thomas, H.D., 1963. On Amplexus coralloides Sowerby and some ampleximorph corals from the English Devonian. The Annals and Magazine of Natural History, series 13, 6, 161–172. https://doi.org/10.1080/00222936308651337
- Sobolev, D., 1904. Devonskie otlozheniya profilya Gregorzhevitse– Skaly–Vlokhi. Izvestiya Varshavskogo Politekhnisheskogo Instituta, 2, 3–107. [In Russian].
- Stumm, E.C., 1949. Revision of the families and genera of the Devonian tetracorals. Geological Society of America Memoirs, 40, 1–92. https://doi.org/10.1130/MEM40-p1
- Stumm, E.C., 1964. Silurian and Devonian corals of the Falls of the Ohio. Geological Society of America Memoirs, 93, 1–184. https:// doi.org/10.1130/MEM93-p1
- Stumm, E.C., 1968. The corals of the Middle Devonian Tenmile Creek Dolomite of Northwestern Ohio. Contributions from the Museum of Palaeontology, The University of Michigan, 22/3, 37–44.
- Tsien, H.H., 1969. Contribution à l'étude des Rugosa du Couvinien de la région de Couvin. Mémoires de l'Institut Géologique de l'Université de Louvain, 25, 1–174.
- Vollbrecht, E., 1926. Die Digonophyllinae aus dem unteren Mitteldevon der Eifel. Eine morphologisch–chronologische Studie. 1. Teil. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 55, Beilage–Band, Abteilung B, 189–273.
- Wang, X., 1994. The rugose coral fauna from the upper part of the Heyuanzhai Formation in Western Yunnan, China. Journal of the Faculty of Science, Hokkaido University, series 4, Geology and Mineralogy, 23, 343–552.
- Wedekind, R., 1922a. Beiträge zur Kenntnis der Mesophyllen. Palaeontologische Zeitschrift, 4, 48–63. https://doi.org/10.1007/ BF03041558
- Wedekind, R., 1922b. Zur Kenntnis der Stringophyllen des oberen Mitteldevon. Sitzungsberichte der Gesellschaft zur Beförderung der gesamten Naturwissenschaften zu Marburg, 1921/1, 1–16.
- Wedekind, R., 1923. Die Gliederung des Mitteldevons auf Grund von Korallen. Sitzungsberichte der Gesellschaft zu Beförderung der gesamten Naturwissenschaften zu Marburg, 1922, 24–35.
- Wedekind, 1924. Das Mitteldevon der Eifel. Eine biostratigraphische Studie. I. Teil. Die Tetrakorallen des unteren Mitteldevon. Schriften der Gesellschaft zur Beförderung der gesamten Naturwissenschaften zu Marburg, 14/3, 1–93.
- Wedekind, R., 1925. Das Mitteldevon der Eifel. Eine biostratigraphische Studie. II. Teil. Materialien zur Kenntnis des mittleren Mitteldevon. Schriften der Gesellschaft zur Beförderung der gesamten Naturwissenschaften zu Marburg, 14/4, 1–85.
- Wedekind, R. & Vollbrecht, E., 1931. Die Lythophyllidae des mittleren Mitteldevon der Eifel. Palaeontographica, 75, 81–110.
- Wrzołek, T., 2002. Siphonophrentidae (Rugosa) in the Devonian of Poland. Coral Research Bulletin, 7, 229–240.
- Yu, C.M. & Kuang, G.D., 1982. Late Middle Devonian rugose corals from Liujing, Heng Xian, Guangxi and their paleoecological signifiance. Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, 4, 241–278.
- Zatoń, M., Nawrot, R., Jakubowicz, M., Ernst, A., Rakociński, M., Berkowski, B. & Belka, Z., 2022a. Middle Devonian brachiopod– hosted sclerobiont assemblage from the northern shelf of Gondwana (Mader Basin, Morocco): Diversity, colonization patterns and

relation to coeval palaeocommunities. Palaeogeography, Palaeoclimatology, Palaeocology, 594, 110947. https://doi.org/10.1016/j.palaeo.2022.110947

- Zatoń, M., Malec, J., Wrzołek, T., Kubiszyn, B. & Zapalski, M.K, 2022b. Episkeletobionts of large rugose corals from the Middle Devonian mesophotic palaeoenvironment recorded in the Pokrzywianka Beds (Holy Cross Mountains, Poland). Annales Societatis Geologorum Poloniae, 92, 465–484. https:// doi.org/10.14241/asgp.2022.01
- Zatoń, M., Jakubowicz, M., Krol, J., Zapalski, M.K., Słowiński, J., Rakociński, M. & Berkowski, B., 2023. Tiny inhabitants of a large Middle Devonian reef of northern Gondwana: Sclerobionts of the coral–stromatoporoid Aferdou el Mrakib buildup, eastern, Anti– Atlas, Morocco. Palaeogeography, Palaeoclimatology, Palaeoceology, 612, 111392. https://doi.org/10.1016/j.palaeo.2023.111392
- Zheltonogova, V.A. & Ivania, V.A., 1960. Podklass Tetracoralla (Rugosa). Tetracorally. In Khalfin, L.L. (ed.), Biostratigrafiya paleozoya Sayano–Altayskoy gornoy oblasti. Trudy Sibirskogo Nauchno–issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya, 20, 368–408. [In Russian].



Plate 1. A–D. Marennophyllum kaufmanni n. sp. A–B. Holotype, IRScNB a13912, Aferdou el Mrakib A1; transverse and longitudinal sections. C–D. Paratype, IRScNB a13913, Aferdou el Mrakib A3; transverse and longitudinal sections. E–F. Stringophyllum acanthicum (Frech, 1885). IRScNB a13916, Ouahlane MA284; transverse and longitudinal sections. G–H. Stringophyllum pedderi n. sp. Paratype, IRScNB a13919, Ou Driss East MA725; transverse and longitudinal sections.



Plate 2. A–B. Atelophyllum maximum (Schlüter, 1882). IRScNB a13915, Aferdou el Mrakib MA402; transverse and longitudinal sections. C–D. Marennophyllum cf. kaufmanni n. sp. IRScNB a13914, Ou Driss East MA44; transverse and longitudinal sections. E–H. Stringophyllum pedderi n. sp. E–F. Holotype, IRScNB a13918, Ou Driss East MA25; transverse and longitudinal sections. G–H. Paratype, IRScNB a13920 Ou Driss East MA40; transverse and longitudinal sections.



Plate 3. A–B. *Stringophyllum coenaubertae* Pedder, 1999. IRScNB a13917, Aferdou el Mrakib A2; transverse and longitudinal sections. C–G. *Acanthophyllum heterophyllum* (Milne–Edwards & Haime, 1851). C–D. IRScNB a13921, Ouahlane MA263; transverse and longitudinal sections. E. IRScNB a13922, Ou Driss East MA11; transverse section. F–G. IRScNB a13923, Ou Driss East MA16; transverse and longitudinal sections.



Plate 4. A–B. Acanthophyllum vermiculare (Goldfuss, 1826). IRScNB a13924, Ou Driss East MA43; transverse and longitudinal sections. C–D. Australophyllum sp. IRScNB a13925, Madène el Mrakib MA544; transverse and longitudinal sections. E–F. Heliophyllum moghrabiense Le Maître, 1947. IRScNB a13926, Ouahlane MA281; transverse and longitudinal sections.



Plate 5. A–B. *Heliophyllum moghrabiense* Le Maître, 1947. IRScNB a13927, Aferdou el Mrakib A8; transverse and longitudinal sections. C–D. *Spinophyllum blacourti* (Rohart, 1988). IRScNB a13928, Ou Driss East MA9; transverse and longitudinal sections. E–F. *Kuangxiastraea* sp. IRScNB a13930, Aferdou el Mrakib MA401; transverse and longitudinal sections.



Plate 6. A–B. *Siphonophrentis subaequalis* n. sp. Holotype, IRScNB a13932, Aferdou el Mrakib MA403; transverse and longitudinal sections. C–D. *Siphonophrentis cantabrica* Birenheide, 1978.IRScNB a13934, Ou Driss East MA718; transverse and longitudinal sections. E–F. *Spinophyllum blacourti* (Rohart, 1988). IRScNB a13929, Ou Driss East MA6; transverse and longitudinal sections.

M. COEN-AUBERT: MIDDLE DEVONIAN RUGOSE CORALS FROM THE MA'DER 71



Plate 7. A–B. *Thamnophyllum* cf. *simplex* Errenst, 1993. IRScNB a13931, Aferdou el Mrakib P154; transverse and longitudinal sections. C. *Siphonophrentis subaequalis* n. sp. Paratype, IRScNB a13933, Aferdou el Mrakib MA404; transverse section. D. *Siphonophrentis cantabrica* Birenheide, 1978. IRScNB a13935, Ou Driss East MA707; transverse section. E–F. *Enallophrentis corniformis* (Gürich, 1896). IRScNB a13936, Ou Driss East MA351; transverse and longitudinal sections.