***Carnets Geol.* 19 (18)**

E-ISSN 1634-0744
DOI 10.4267/2042/70538

New data on the intergrowth of Rugosa-Bryozoa in the Lower Devonian of North Gondwana

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Abstract: Numerous and generally well-preserved examples of the intergrowth Rugosa-Bryozoa from the Upper Pragian and Lower Emsian of the Armorican Massif (Châteaulin and Laval synclinoria), France, and from the Upper Emsian of the Ougarta Mountains, Erg Djemel, Algeria, are described. In the Armorican Massif, the corallites of a rugosan Tryplasmatidae? are intergrown with Ceramoporidae bryozoan close to *Crepipora*, exceptionally with an unidentified Fistuliporidae (likely a new genus), whereas in Ougarta the coral is not identifiable and is associated with a Fistuliporidae assigned to *Fistulipora*. Although mainly left in open nomenclature, the material is fully described (structure and microstructure) and illustrated (calcitic skeleton and natural moulds) for the first time. In addition, the presence of Ceramoporidae in the Lower Devonian is clearly established. The evaluation of the association is briefly discussed and a mutualistic relationship supported.

Key-words:

- intergrowth;
- Rugosa;
- Bryozoa;
- Pragian-Emsian;
- Armorican Massif;
- Algerian Sahara

Citation : PLUSQUELLEC Y. & BIGEY F.P. (2019) - New data on the intergrowth of Rugosa-Bryozoa in the Lower Devonian of North Gondwana.- *Carnets Geol.*, Madrid, vol. 19, no. 18, p. 421-437.

Résumé : *Données nouvelles sur l'intercroissance Rugosa - Bryozoa dans le Dévonien inférieur du Nord Gondwana.* - Des exemples nombreux et généralement bien conservés d'intercroissance Bryozoa-Rugosa, collectés dans le Praguien supérieur et l'Emsien inférieur du Massif Armoricain (synclinoria de Châteaulin et de Laval), France, et dans l'Emsien supérieur des Monts d'Ougarta, Erg Djemel, Algérie, sont décrits. Dans le Massif Armoricain, les corallites d'un tétracoralliaire Tryplasmatidae? sont associés à un bryozoaire Ceramoporidae proche de *Crepipora*, exceptionnellement à un Fistuliporidae probablement nouveau, tandis que dans l'Ougarta le coralliaire - mal ou partiellement préservé - n'est pas identifiable et se développe en association avec un Fistuliporidae du genre *Fistulipora*. Bien que laissé en nomenclature ouverte pour l'essentiel, le matériel est décrit en détail (structure et microstructure) et, des images du squelette calcitique et des moulages naturels sont fournies pour la première fois. Accessoirement, la présence des Ceramoporidae dans le Dévonien inférieur est incontestablement établie. Les modalités de l'intercroissance sont brièvement discutées et une relation de type mutualiste est retenue.

Mots-clefs :

- intercroissance ;
- Rugosa ;
- Bryozoa ;
- Praguien-Emsien ;
- Massif Armoricain ;
- Sahara Algérien

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Published online in final form (pdf) on November 11, 2019
[Editor: Bruno GRANIER; language editor: Stephen EAGER]

1. Introduction

Vinn *et al*. (2016, 2017a, 2018) describe some cases of intergrowth between Rugosa and Bryozoa in the Katian of Estonia and stated that this association is only known from the Upper Ordovician of Baltica and Laurussia. Shortly after, Sendino *et al.* (2019) publish a "*new rugose coral-cystoporata association from the Devonian of NW Spain*" and stated that it is "*the first evidence of intergrowths between Devonian rugose corals and bryozoans*". In fact some cases of intergrowths were previously reported in an abstract published on the occasion of the Congrès national de Paléontologie held in Paris in 1990 (Plusquellec & Bigey, 1990), but not illustrated and the aim of this work is to provide new accurate data about these cases known from the Devonian of the Armoricain Massif (France) and the Ougarta Mountains (Algeria).

As far as we know, no other example of rugose coral - bryozoan intergrowths have been published. However, a similar association involving the bryozoan *Celleporaria palmata* (Michelin, 1847) and the scleractinian corals referred either to *Culicia parasitica* (Michelin, 1847) or *Cryptangia woodii* Milne-Edwards & Haime, 1850, is well known from the Neogene of northwestern Europe (Cadée & McKinney, 1994).

2. Geographical and geological settings and material

The Devonian material described in this paper has been collected in four localities of the Armorican Massif belonging to the Central Armorican domain and in one locality of the Ougarta area. These two areas are situated during the Devonian time on the northern margin of the paleocontinent Gondwana.

In the Western part of the Armorican Massif, Châteaulin Synclinorium, three fossiliferous localities, located in the rade de Brest and Crozon peninsula, have yielded the association.

1 - Pointe de l'Armorique, Northern section, West of Plougastel-Daoulas (Finistère), upper part of the Le Faou Formation in the level called "Banc des monstres", Lower Emsian, *dehiscens* Conodont Zone (six specimens in natural moulds, LPB 17 257 - 17 258.a-e).

2 - Seillou section, left bank of the Le Faou River (Finistère), upper part of the Le Faou Formation, level LF 7 *sensu* Le Menn (1985), "Banc des monstres", Lower Emsian, *dehiscens* Conodont Zone (one specimen in natural mould, LPB 17 259).

3 - Batterie de Pont-Scorff section, Eastern coast of Roscanvel area, Crozon peninsula (Finistère), calcareous level in the Le Faou Formation, Upper Pragian or Lower Emsian (one specimen with preserved skeleton, LPB 17 256).

In the Eastern part of the Armorican Massif, Laval Synclinorium, old quarries located in the NW of Loué (Sarthe) known as "carrières de la station de pompage de Monfoulon" (Plusquellec *et al*., 1993, fig. 22) have yielded very well-preserved specimens with calcitic skeletal material in an horizon called Monfoulon Limestones, roughly middle part of the Montguyon Formation. The material was collected from two levels, respectively 4.50 m ("niveau à Tabulés branchus") and 10 m ("niveau à Blastoïdes") above a level which has provided the Upper Pragian conodont *Polygnathus pireneae.* (Plusquellec *et al.*, 1993, p. 28, fig. 22). *Caudicriodus angustoides angustoides* and *Caudicriodus curvicauda* are known from two levels, one between the "niveau à Tabulés branchus" and the "niveau à Blastoïdes", and a second one about 10 m above the "niveau à Blastoïdes" (Weyant and Morzadec unpublished data). According to Weyant *et al*. (2010), *C. curvicauda* occurs well below the Lower Emsian *P. dehiscens* in the Guadarrama and in the Upper part of the Pragian in different sections from the Barrandian area.

Thus, in the quarry of Monfoulon, the Rugosa-Bryozoa intergrowths are Upper Pragian (*pireneae* Zone) in age, including the following material: one specimen probably from the "niveau à Tabulés branchus", LPB 17 252; five specimens from the "niveau à Blastoïdes", LPB 17 248.a-b, 17 249, 17 250, 17 253, 17 254 and two specimens for which the level is unknown, LPB 17 251 and 17 259bis.

In the Ougarta Mountains, the material is from the Erg Djemel section, Chefar El Ahmar Formation, level ED 29 ("niveau coralligène"), Upper Emsian (Paris *et al.*, 1997). One specimen with preserved skeleton, LPB 17 255.

As a result, the material consists in 18 specimens, 35 thin sections (including 13 polished ultra-thin sections, the so-called "LFP"), 46 acetate peels (including 30 serial acetate peels in LPB 17 249) and is deposited in the collections of the Laboratoire de Paléontologie, Université de Bretagne Occidentale, Brest (France), with the prefix LPB.

3. General features of the intergrowth

The rugosan corallites, tentatively assigned to the Tryplasmatidae, occur embedded in bryozoan belonging to n.gen. 1 cf. *Crepipora* Ulrich, 1882 (Cystoporata, Ceramoporidae), *Fistulipora* McCoy, 1849 (Cystoporata, Fistuliporidae), and to a third unidentified genus (n.gen. 2) of the family Fistuliporidae.

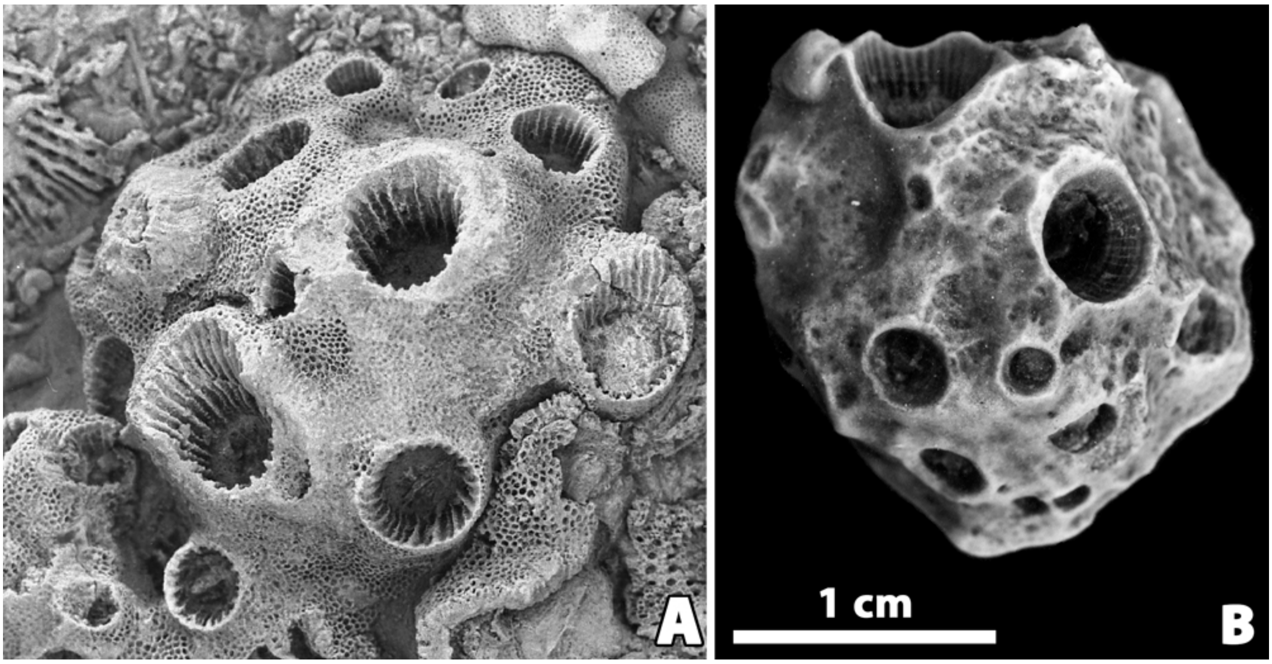


Figure 1: A, Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth, distal side; LPB 17 248. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian. **B**, *Fistulipora* sp. - Rugosa indet. intergrowth, distal side; LPB 17 255. Ougarta, Algeria, Erg Djemel section, Chefar El Ahmar Fm., Upper Emsian.

The association with the *Crepipora*-like is the most frequent (Figs. 1.A, 2 - 3) and is recorded in the material from Monfoulon: LPB 17 248 - 252, LPB 17 253 ?, 17 259bis and from the Batterie de Pont-Scorff: LPB 17 256. It is very likely that the specimens preserved in natural moulds (Pointe de l'Armorique and Seillou) belongs to the same association owing to the characteristics of the apparently contiguous moulds of autozooecia: LPB 17 257 - 259. The association with the Fistuliporidae n.gen. 2 is only known in Monfoulon: LPB 17 254 (Figs. 12.C-D, 14), the one involving *Fistulipora* in Ougarta: LPB 17 255 (Figs. 4 - 5).

The zooarium of all the bryozoan material is massive and more or less hemispherical. In the specimen from Ougarta the proximal side of the colony is rather well preserved: concave with concentric growth ridges and no indication of the presence of coral. The distal side is generally irregularly convex and shows the numerous zooecial apertures as well as the calical apertures of the associated coral (Fig. 1).

The rugosan corallites are regularly spaced over the colony surface leaving only their calical aperture free. Moreover, although coated by the zooecia on their external side, the apertures of the corallites are elevated above the growth surface of the bryozoan. The size of the corallites at the surface level is highly variable indicating various growth stages. In addition, the longitudinal sections as well as the natural moulds show that the corals began to grow after the bryozoan became established on the substrate.

As in the rugosan-stromatoporoid association (Vinn *et al.*, 2015) and rugosan-tabulate association (Vinn *et al.*, 2017b) the rugosan corallites are arranged perpendicularly to the growth surface of the bryozoan. The longitudinal section in the association shows that the bryozoan grew by frontal budding and according to Cadée and McKinney (1994) "*the growth of the corallites was nicely balanced, keeping the corallites always at the colony surface*".

In longitudinal section, around each corallite, the zooecia appear upwards diverging with an angle of about 25-45° and the virtual laminations within the bryozoan (shown by the diaphragms) are upturned when they meet corallites (Figs. 2.B, 3.A, 3.C).

Frequently, it can be seen that, at the contact between the bryozoan and the coral, the wall of the zooecia is lacking (Figs. 3, 12.A). This feature is seen in both transverse and longitudinal sections and indicates that the growth of the coral precedes that of the bryozoan. Similar features have been described and well-illustrated by Sorauf and Kissling (2012) in a *Streptelasma* anchored within the skeleton of *Paleofavosites*: usually, the ventral wall of this solitary Rugosa is absent or very thin.

Rarely, necroses of the surface are recorded within the bryozoans; in the illustrated example it is located around the calicinal edge of the Rugosa (Fig. 3.A).

Figure 2: A, Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth. **A**, transverse section, note in the Bryozoa the numerous maculae; LPB 17 251, thin section a. **B**, longitudinal section; LPB 17 251, thin section b. **C**, longitudinal section showing a case of parricidal increase; LPB 17 250, thin section b. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

Despite the appearances the intergrowth occurs between the bryozoan and solitary corals. The branching pattern is widely missing as shown by transverse and longitudinal sections, and also by the natural moulds. A unique pattern of parricidal increase has been noted, where an adult corallite split into two offsets of the same diameter occupying the whole calice of the parent (LPB

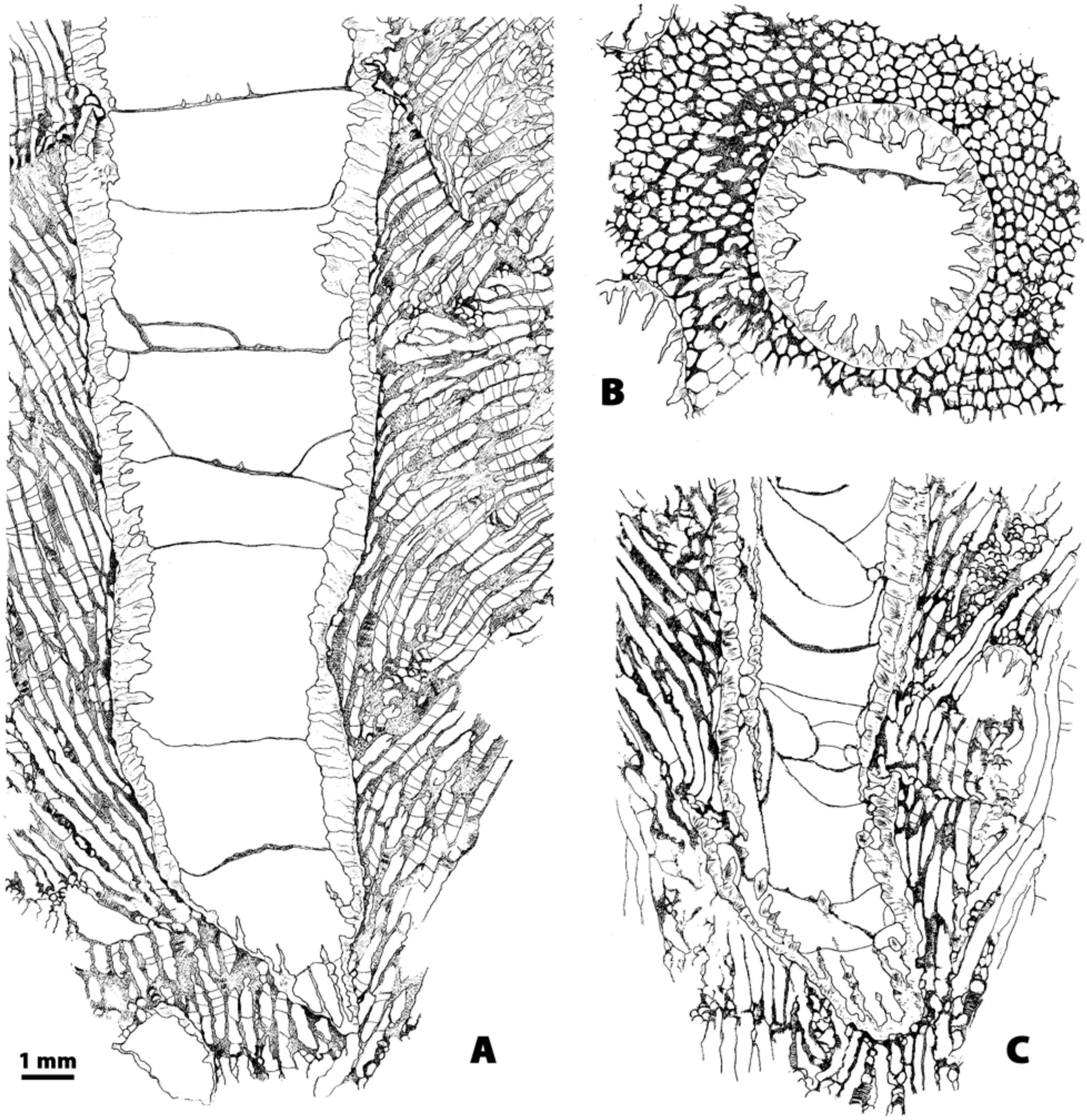


Figure 3: A, Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth. **A**, longitudinal section, note in the upper part of the section a surface of necrosis in the bryozoan linked with irregularities in the growing of the coral; LPB 17 251, thin section b. **B**, transverse section; LPB 17 251, thin section a. **C**, longitudinal section, LPB 17 251, thin section b. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian-Lower Emsian.

17 250, thin section b, Fig. 2.C). It is obvious too, taking into account the various sizes and length of the corallites and the very scarce case of budding, that the settlement of the young corals on the surface of the bryozoan was an ongoing process.

As a result, the association involves a bryozoan and a gregarious solitary coral giving rise - due to the "cement" provided by the bryozoan - to a pseudo-colony of Rugosa. The collected material does not allow us to say if the bryozoan occurs with or without the coral (but it is very likely) neither if the coral can be found solitary.

4. Cases of immuration

In addition to the intergrowth, some corallites are found to be overgrown by the bryozoan in specimens from Monfoulon (LPB 17 250, LPB 17 254, LPB 17 259bis) and Pont-Scorff (LPB 17 256, Fig. 6).

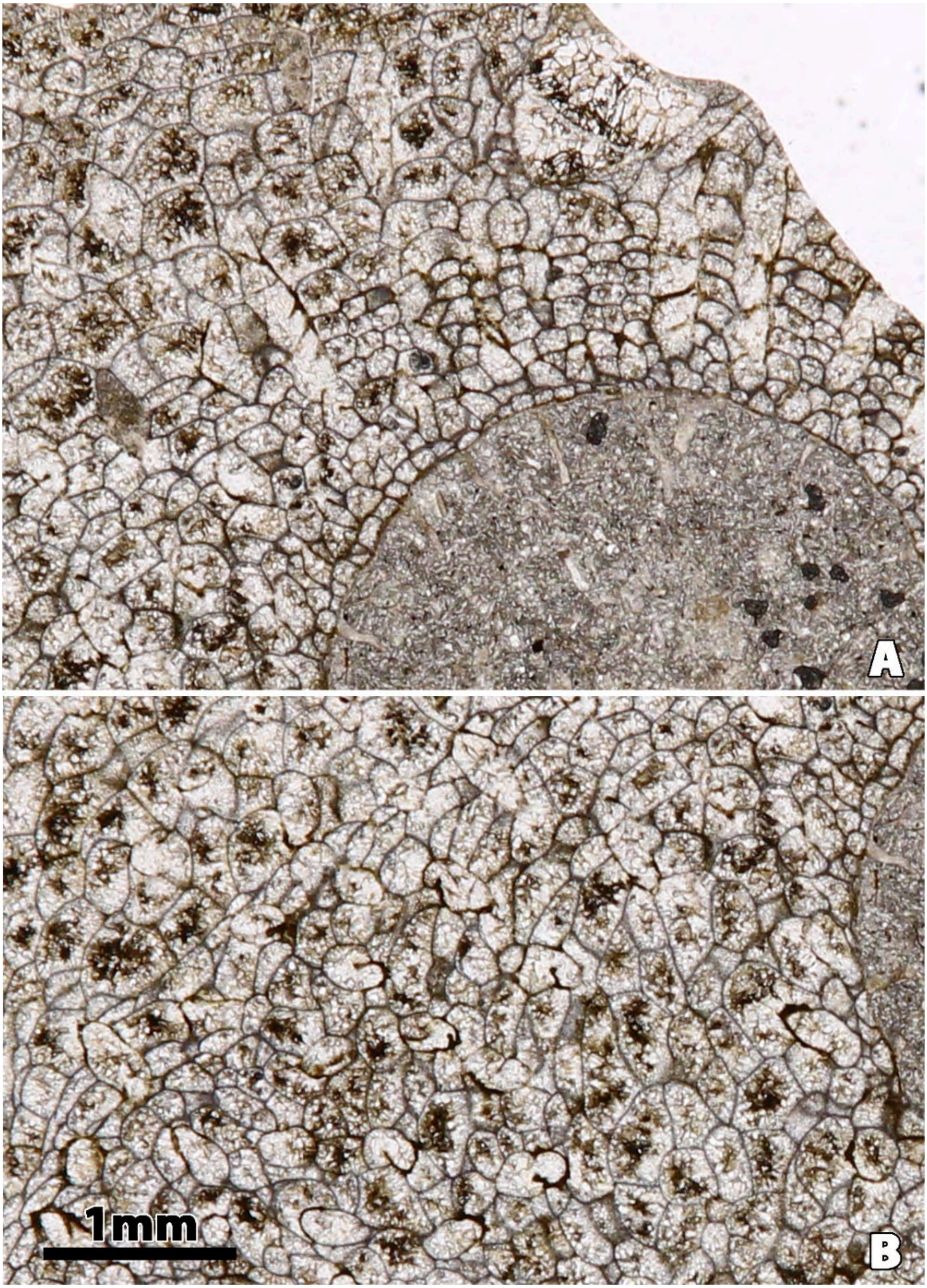


Figure 4: *Fistulipora* sp. - Rugosa indet. intergrowth. **A**, transverse section in the Rugosa, oblique in the Bryozoa. **B**, transverse section; both LPB 17 255, thin section B 35 142-a (same specimen as Figs. 1.B, 3). Ougarta, Algeria, Erg Djemel section, Chefar El Ahmar Fm., Upper Emsian.

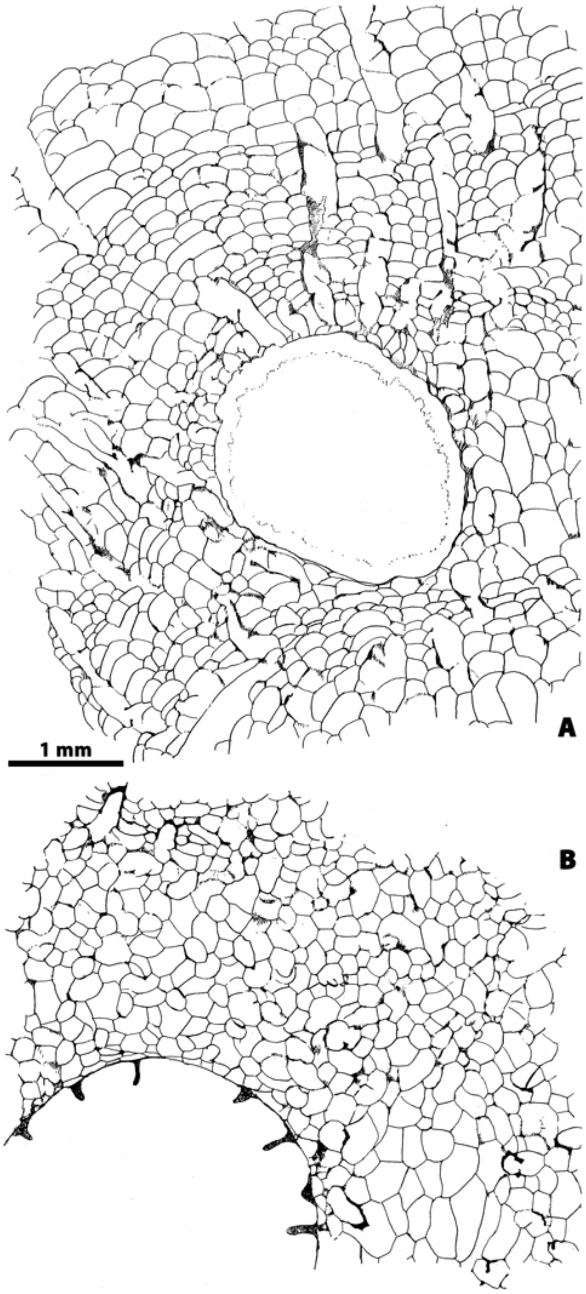


Figure 5: *Fistulipora* sp. - Rugosa indet. intergrowth (same specimen as Fig. 1.B). **A**, transverse section in the coral, here very bad preserved, and mainly longitudinal in the bryozoan; thin section B 35 142-b. **B**, transverse section; thin section B 35 142-a. Ougarta, Algeria, Erg Djemel section, Chefar El Ahmar Fm., Upper Emsian.

This may be caused by active overgrowth but more likely, passively after death of the corallite (cf. Kershaw, 1987). According to Sorauf and Kissling (2012), dealing with the immuration of *Streptelasma* by *Paleofavosites*, the death of the corallite appears to have preceded overgrowth as the calices of some specimens seem to be filled with sediments prior to be immured. Moreover, overgrowth only occurs on corallites reaching a large diameter, *i.e.*, adult or gerontic specimens.

Figure 6: Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth overgrown by *Fistulipora* sp., longitudinal section; loose hatching as *Crepipora*, close hatching as *Fistulipora*, X as (late) boring; LPB 17 256, thin section B 35 145. Pont-Scorff, Roscanvel peninsula, Armorican Massif, Le Faou Fm., Upper Pragian-Lower Emsian.

The overgrowth is either located at the calicinal margin level or spread more or less deeply on its inner side. In the specimen from Pont-Scorff, the inner side of the calice is occupied by a "foreign" bryozoan (*Fistulipora* sp.) prior to be overlapped by its "own" *Crepipora*-like (Fig. 6).

5. Systematic palaeontology

Subclass Rugosa Milne-Edwards & Haime, 1850

Order Cystiphyllidae Nicholson, 1889

Family ?Tryplasmatidae Etheridge, 1907

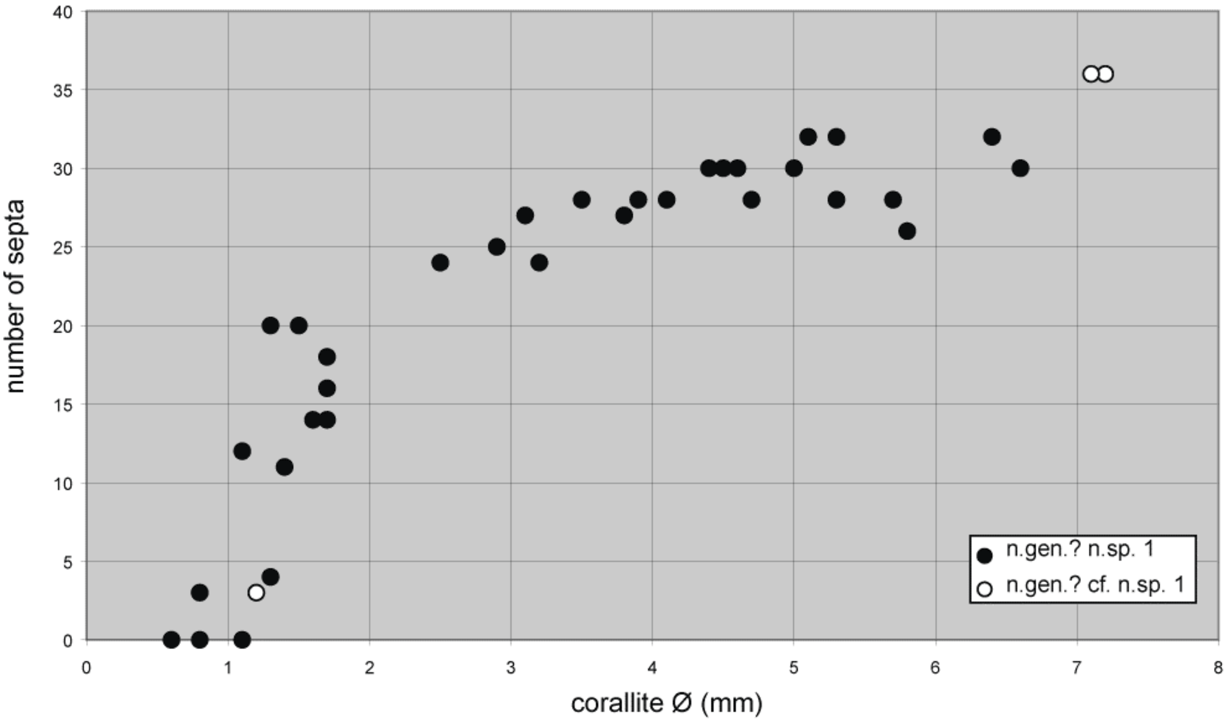
Genus ?n.gen.

See discussion below.

n.gen.? n.sp. 1

Morphology. Corallum solitary or with very scarce parricidal offsets (Fig. 2.C); corallites ceratoid to cylindrical. Apical region conical, strongly curved to geniculate in some cases (Fig. 7) and devoid of septa (Fig. 8.A) but "ornamented" by delicate transverse growth striae visible on the natural cast of the inside of corallite. This unusual feature shows some similarity with that illustrated (on the external surface) by Fedorowski (1991) in *Paraduplophyllum*. Calices having carinate septa differentiated in two orders (Fig. 8.C-I). External surface not exposed due to the intergrowth.

Diagram 1



Transverse sections. In the juveniles sections, close to the aseptate apical region, only few septa are recorded (3 to 4). They are short and likely major ones (Fig. 8.B, 8.D), whereas in the adult or gerontic sections the number of septa reaches up to 32 (major and minor septa). In fact, the number of septa increases quickly but does not exceed 20 in the corallites the diameter of which is less than 2 mm, whereas the number only varies from 24 to 32 in the corallites the diameter of which is between 2 and 7 mm (Diagram 1).

The protosepta cannot be identified although the sections (especially the adult sections) generally show an area where major and minor septa are less prominent, less thick, and in some cases difficult to distinguish from each other (Fig. 8.C, 8.F-G, 8.I).

Overall, the major septa are short, thicker than the minor ones, with an inner margin rather smooth or bearing a small tooth (Fig. 8.I). In some sections, the outline of the lateral side of the septa appears irregular due to the presence of carinae (Fig. 8.G). The minor septa are shorter and usually triangular in section.

Longitudinal sections. The tabulae, thin, mainly flat, appear widely spaced, generally between 0.4 to 2.8 mm, some being as much as 3.6 to 4.2 mm, even 6.8 mm apart. Rare tabulae show slight thickening and bear short spines. Some incomplete, convex and rather deeply inclined peripheral tabellae are recorded; dissepiments are absents (Fig. 3.A, 3.C).

Microstructure. The septa exhibit a trabecular microstructure consisting of parallel and contiguous rather short bundles of fibres, free at inner ends, sloping upwards and inwards from the periphery at angle ca. 25° (Figs. 3.A, 3.C, 9). The trabeculae are devoid of true axis as in the monacanths and thus are assigned to water-jet trabeculae (see CUIF & GAUTRET, 1993, fig. 4).

The wall (studied as well as the septa by ultrathin sections, the so-called "LFP") consists of two parts:

1) a very thin outer layer (0.05 - 0.07 mm) of fibroids not organized into trabeculae and oriented inwards and upwards (=true epitheca?) (Fig. 9.B-C). A similar structure is known in *Siphonodendron* and probably in *Disphyllum* (see respectively SEMENOFF-TIAN-CHANSKY, 1984, text-fig. 2F, and COEN-AUBERT *et al.*, 2013, fig. 7).

2) an inner thick layer (0.2 - 0.3 mm) built of the thickened outer parts of the radial elements (major and minor septa) (Fig. 9.A). In addition, supernumerary bundles of fibres occupy spaces between major and minor septa but are confined to the stereozone although their inner margin - seen in transverse section - could be slightly prominent (Fig. 9.A). Thus, the wall seems to be better interpreted as trabeculotheca (or a structure close to this category) than to septotheca (see STOLARSKY, 1996, fig. 7).

Remark. One specimen from Monfoulon (LPB 17 253), although associated with *Crepipora*, differs from the material described above, only by having longer major septa in all the stages of growth (Fig. 10, Diagram 1); it is provisionally assigned to n.gen.? cf. n.sp. 1. As for that of Ougarta (Figs. 1.B, 4 - 5), very poorly preserved in some sections, even wall possibly lacking (Fig. 5.A), the coral remains unidentified; it is associated with *Fistulipora*.

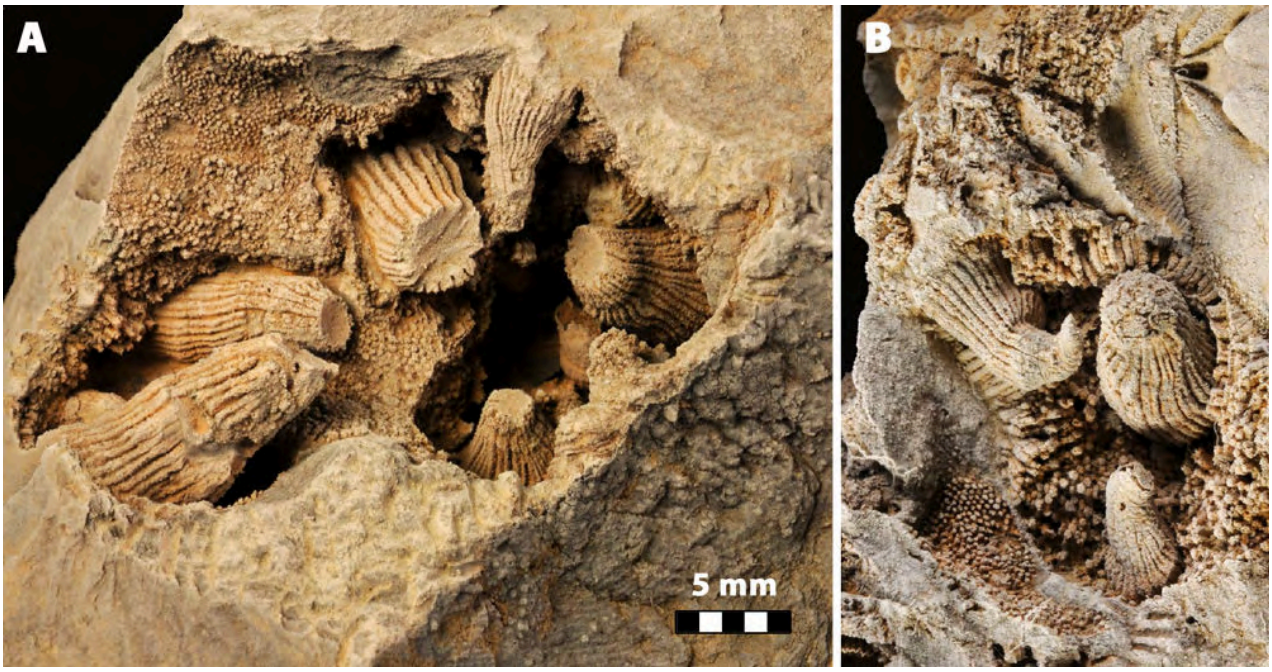


Figure 7: Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth preserved in natural moulds, note the curved tip of the corallites and the development of transverse striae; LPB 17 258.e. Pointe de l'Armorique section, W. of Plougastel-Daoulas, Armorican Massif, Le Faou Fm., "Banc des monstres", Lower Emsian.

Discussion. The material shares some generic features with *Tryplasma* LONSDALE, 1845 (see diagnosis *in* HILL, 1981, p. F98), but according to PEDDER (pers. comm., 1990) it probably represents a new genus and the family assignment is also problematical.

It is obvious that, by the use of "LFP", the level of knowledge of our specimens is better than that of *Tryplasma* (description of layer of fibroids, supernumerary bundles of fibres in the wall) and thus the comparison is uncertain as such details are not available for *Tryplasma*. Moreover, the septa of *Tryplasma* are said to be rhabdacanthine, holacanthine or dimorphacanthine - strange in our opinion - whereas the Armorican material is undoubtedly water-jet.

Preliminary remarks about the generic assignment of the Bryozoa

Case 1 - In the Treatise on Invertebrate Paleontology, Bryozoa revised, BOARDMAN *et al.* (1983) stated that Ceramoporina primarily have a laminated skeletal microstructure (p. 342) and show the presence of "tabular crystallites" in the Ordovician *Ceramophylla vaupeli* (fig. 149) and *Ceramoporella flabellata* (fig. 150). They also provide numerous and nice photos, at lower magnification, showing the lamellar nature of most of the genera of the family such as *Acanthoporella* (fig. 157), *Ceramophylla* (fig. 158), *Ceramoporella* (fig. 159) and *Crepipora* (fig. 160), all from Ordovician.

These authors give less clear data about the microstructure of the lunaria deposits but pointed out their light colored hyaline appearance under a light microscope and indistinct, distantly spaced laminations in some forms (p. 344).

On the other hand, they did not indicate the occurrence of Ceramoporidae in the Devonian except that of the poorly known genus *Ganiella* whose "*microstructure* (is) *indistinct, questionably laminated*" and "*the lunaria with shorter radius of curvature, indistinct*" (p. 368). They did not mention the very poorly illustrated species of *Crepipora ferganensis* ORLOVSKY, 1982, and *C. subglobosa* ORLOVSKY, 1982, from the Lower Devonian of Asia (MODZALEVSKAJA & ORLOVSKY, 1968).

Ultra-thin sections ("LFP") prepared from the specimens LPB 17 250 and 17 251 from Monfoulon and formerly assigned to *Crepipora* (PLUSQUELLEC & BIGEY, 1990) show that the wall of the autozoecia is made of short and rather strong fibres 12-13 µm x 3 µm) displayed on both sides of a median plate (Fig. 11.B, 11.C left). This plate is made of tiny granular crystals (3 µm), appearing as a dark line in transverse sections of usual thickness (Fig. 11.A). In transverse section the fibres appear normal to the median line, whereas in longitudinal one they show their slightly upwards diverging setting (Fig. 11.C left). The microstructure of the lunaria, well exposed in longitudinal sections, consists of large fibroids radiating upward and outward (Fig. 11.C right). The size of these crystallites (40-100 µm x 5-10 µm) gives rise to their light coloured appearance in sections of usual thickness. In transverse section, the main visible feature of the lunaria (in natural light) is the presence of more or less scattered tiny dark granules such as those described in the large biocrystals of the tabulate coral *Thamnopora* by LAFUSTE and TOURNEUR (1991).

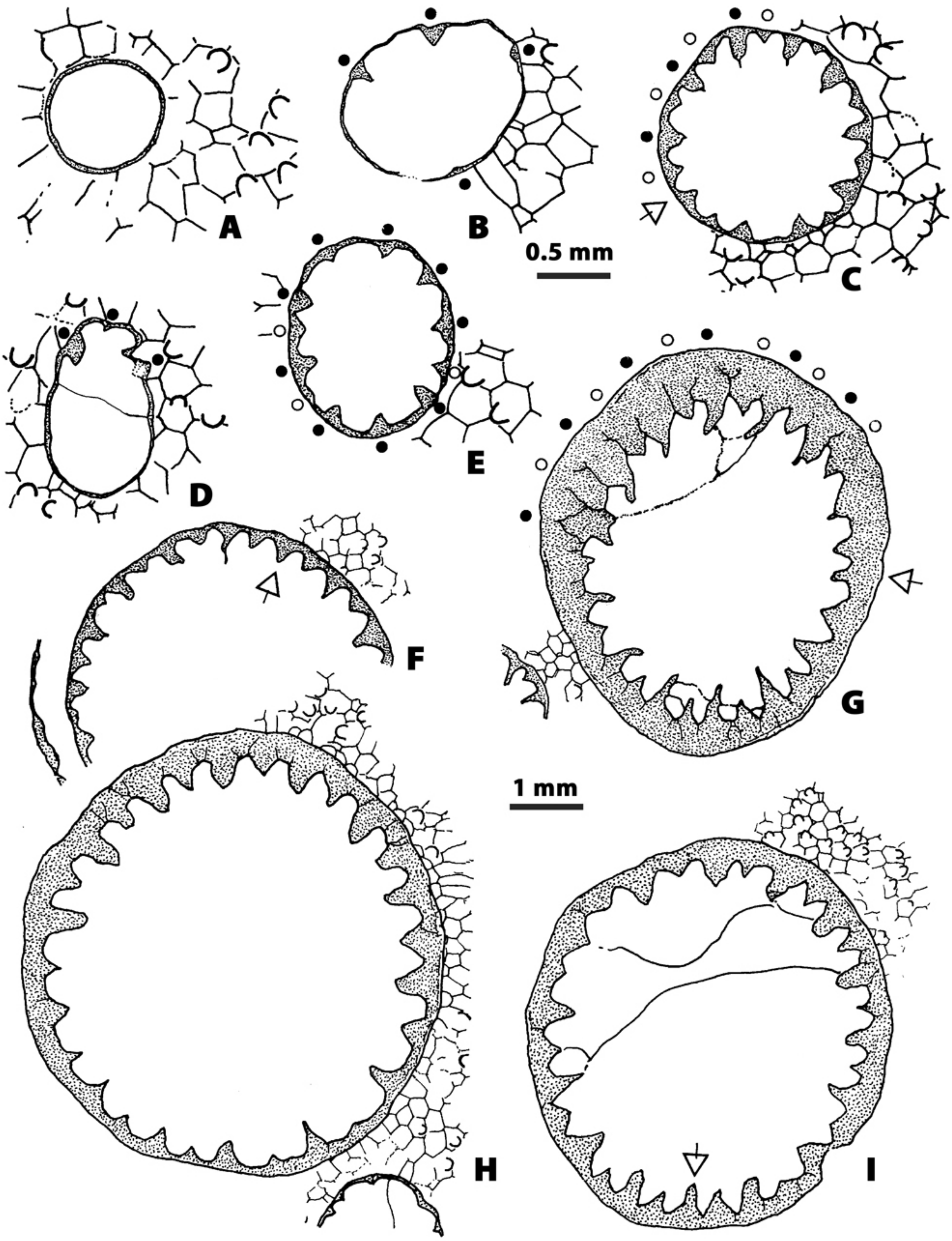


Figure 8: Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? n.sp. 1) intergrowth. Transverse sections in the corallites at various growth stages. Black circle as major septum, open circle as minor septum, open arrow as area where major and minor are few differentiated. Note the lack of septa in earliest stage (**A**) and only three or four major septa in juvenile stages (**B**, **D**). **A**, LPB 17 259 bis, thin section B 36 854. **B**, LPB 17 259 bis, thin section B 36 854. **C**, LPB 17 254, thin section a. **D**, LPB 17 252, thin section a. **E**, LPB 17 252, thin section c. **F**, LPB 17 252, thin section c. **G**, LPB 17 250, thin section b. **H**, LPB 17 259 bis, thin section B 36 854. **I**, note a small tooth on the margin of the major septum situated on top of figure, LPB 17 252, thin section a. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

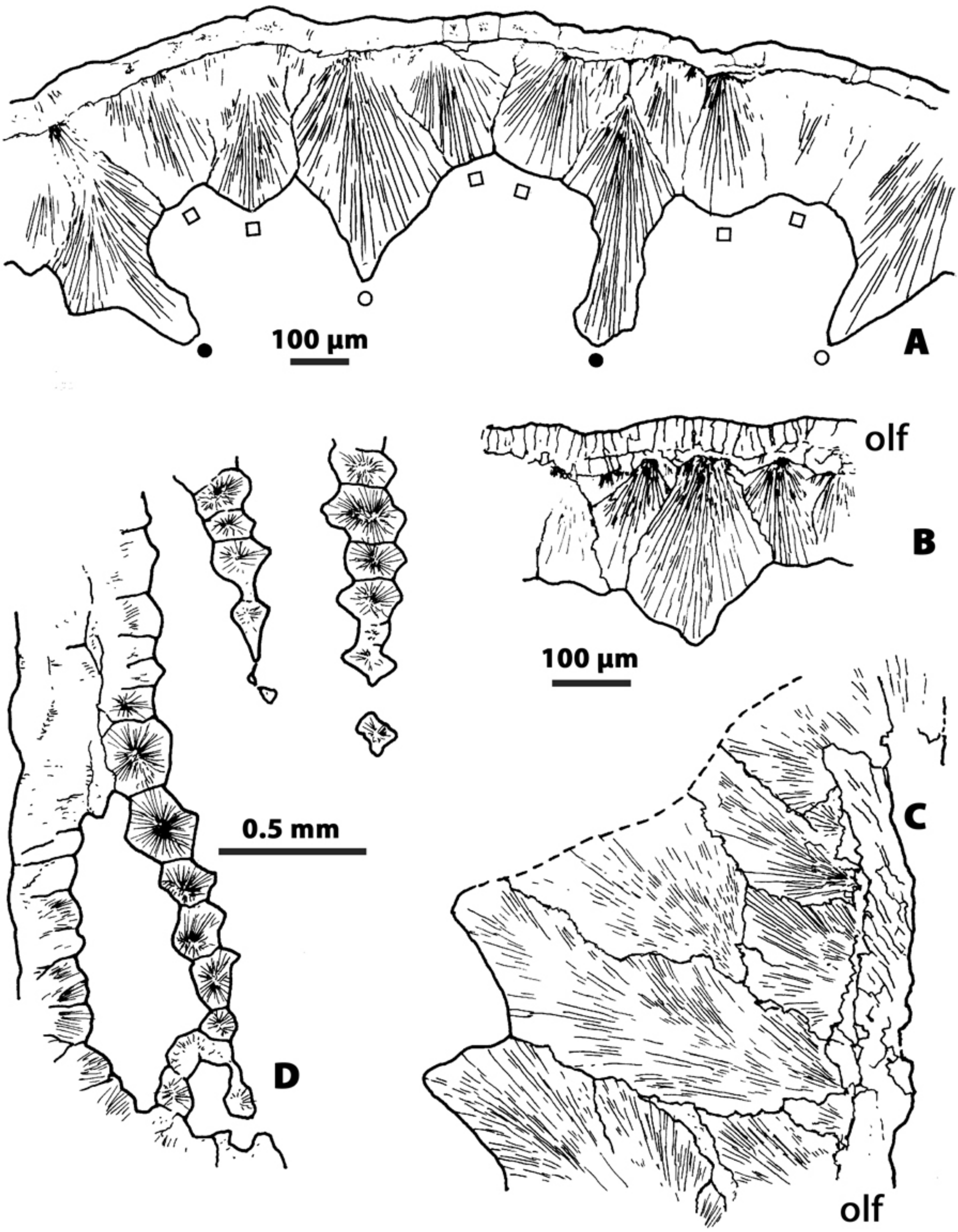


Figure 9: Rugosa Tryplasmatidae?, n.gen.? n.sp. 1. Microstructure of the wall and septa. Black circle as major septum, open circle as minor septum, open square as supernumerary bundles of fibres, "olf" as outer layer of fibroids. **A**, transverse section; LPB 17 250, thin section a (standard thickness). **B**, idem; LPB 17 250, "LFP" thin section l. **C**, longitudinal section within the plane of septa; LPB 17 250, "LFP" thin section i. **D**, longitudinal section at right angle to the plane of septa showing how the trabeculae give rise to carinae; LPB 17 259 bis, thin section B 36 856 (standard thickness). Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

Hence, it appears that the microstructure of the autozooecial wall of the Devonian *Crepipora*-like forms clearly differs from that of the Ordovician forms. In addition, taking into account the light-coloured appearance of the lunaria of the Ordovician genera their microstructure could be similar to that of the Devonian representatives.

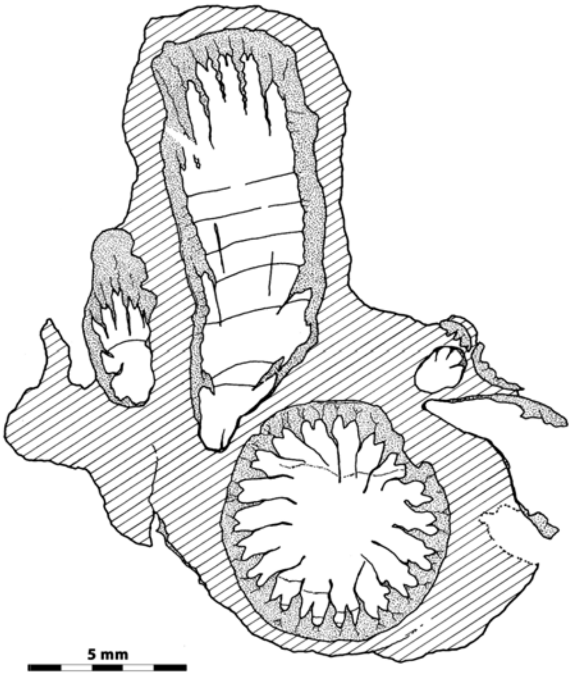


Figure 10: Bryozoa (n.gen. 1 cf. *Crepipora* n.sp. 1).- Rugosa (n.gen.? cf. n.sp. 1) intergrowth, note that the septa are longer than usual in the other specimens of this locality; note also a juvenile section with three major septa located in one side of the section. LPB 17 253, thin section a. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

As a result, their microstructural characteristics indicate that the Devonian *Crepipora*-like forms belong to a new genus and they are herein provisionally assigned to n.gen. 1 cf. *Crepipora* ULRICH, 1882.

Remarks: SPJELDNEAS (1963, p. 66), dealing with the type species of *Crepipora*, indicated that "the pores are numerous in the exozone"; these are not recorded in the Devonian material.

Moreover, it can be noted that the evolution of the skeleton of the Ceramoporidae from Middle Ordovician to Lower Devonian is somewhat similar to that of the tabulate corals. For example, as early as 1962, LAFUSTE pointed out that the wall of the genus *Favosites* is microlamellar in Silurian forms but fibrous in Devonian ones, and that, accordingly, it should be split into two distinct genera.

Case 2 - Another member of the Cystoporata is recorded from the Monfoulon Limestones in association with a species of the Rugosa. The only available specimen is small and only a section of petrographic thickness was possible. It is characterized by: 1) strongly thickened lunaria probably made of fibroids (light coloured appearance) and 2) by well-developed extrazooidal vesicular tissue. The microstructure of the wall of the autozooecia is indistinct (owing to the lack of "LFP") whereas the alleged fibroids of the lunaria are strongly oblique to the growth direction of the lunaria itself, parallel to each other, and upwards sloping from a dark line shifted close to their inner (concave) side (Fig. 14).

The specimen clearly belongs to the Fistuliporidae and differs from all genera of the family by its significantly thickened and strongly curved lunaria. Thus it is herein provisionally assigned to n.gen. 2. It recalls *Buskopora* ULRICH, 1886.

In addition, note that the microstructure of the lunaria of n.gen. 2 differs from that of n.gen. 1 cf. *Crepipora* and, as a result, examples of two kind of lunarial microstructure are provided: "water jet-like" (in sections normal to the flattening of the lunaria) in some Ceramoporidae, clinogonally fibrous in some Fistuliporidea.

Case 3 - The specimen from Ougarta is assigned to the large genus *Fistulipora* MCCOY, 1849.

The recorded Bryozoa are thus as listed below.

Class Gymnolaemata ALLMAN, 1856

Order Cystoporata ASTROVA, 1964

Family Ceramoporidae ULRICH, 1882

Genus n.gen. 1
cf. *Crepipora* ULRICH, 1882

n.gen. 1 cf. *Crepipora* n.sp. 1

(Figs. 1.A, 2 - 3, 12.A-B, 13)

Remark: The species is not described herein but, owing to the lack of dependable data about the so-called Devonian *Crepipora*, it is likely a new species. Its description is in progress.

Family Fistuliporidae ULRICH, 1882

Genus *Fistulipora* MCCOY, 1849

***Fistulipora* sp.**

(Figs. 1.B, 4 - 5)

Remark: The only known specimen is not described but illustrated.

Genus n.gen. 2

n.gen. 2 n.sp. 2

(Fig. 12.C-D, 14)

Remark: The well preserved but unique specimen is provisionally not described but illustrated.

6. Evaluation of the association

The modalities of the association coral-bryozoan, involving for example Ordovician (VINN *et al.*, 2017a), Devonian (SENDINO *et al.*, 2019) or Neogene (CADÉE & MCKINNEY, 1994) species, have been discussed and it appears that the true nature of the association is difficult to assess.

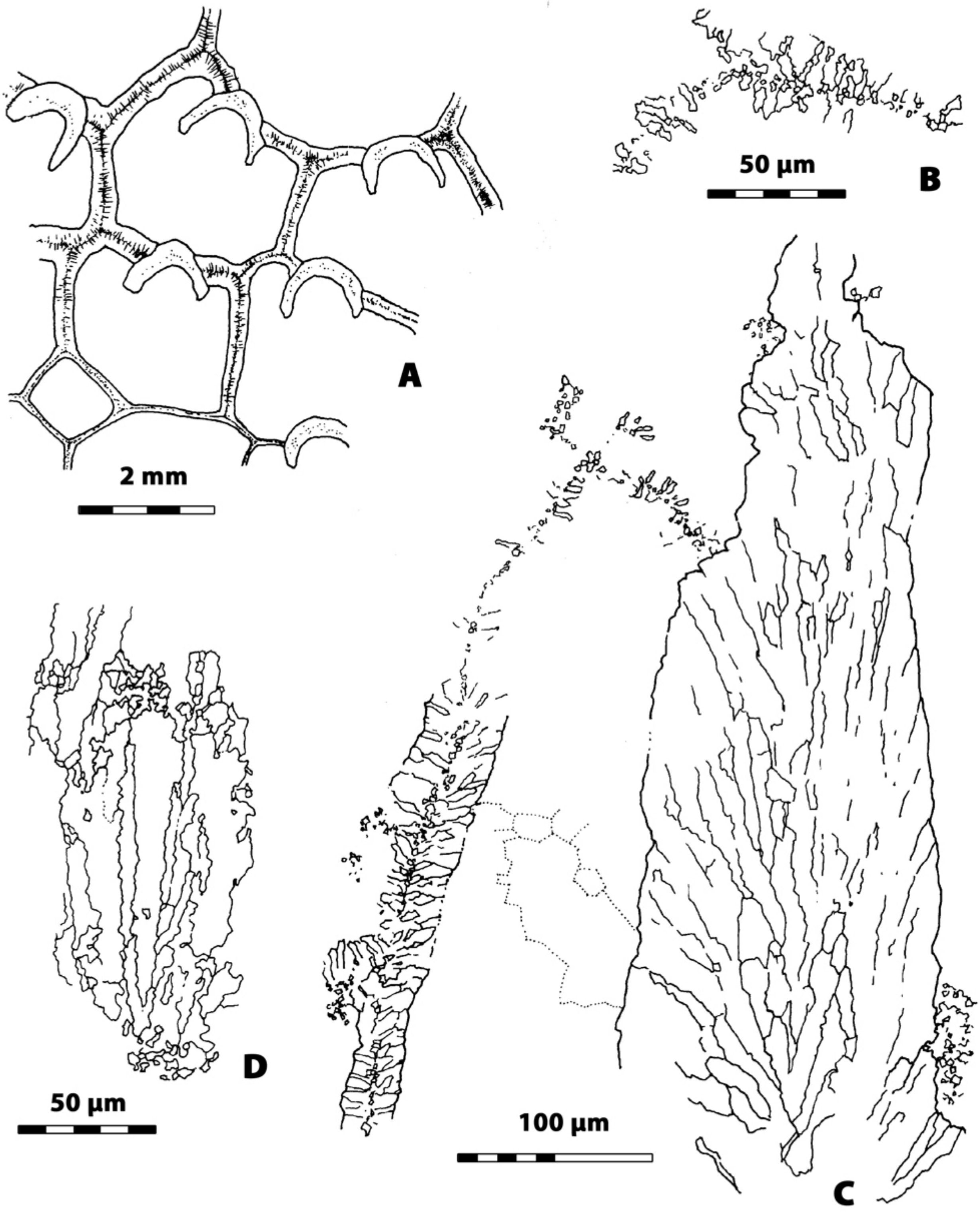


Figure 11: n.gen. 1 cf. *Crepipora* n.sp. 1. Microstructure of specimen LPB 17 250. **A**, transverse section showing the median dark line of the autozoecial wall; note that this feature is only visible rarely in some areas of the section; thin section LPB 17 250-b (standard thickness). **B**, transverse section in the autozoecial wall, explanation in text; "LFP" thin section 17 250-l. **C**, longitudinal section in the autozoecial wall (left) and in the lunaria (right), explanation in text; "LFP" thin section 17 250-h. **D**, longitudinal section in a lunaria showing the morphology of the fibroids; "LFP" thin section 17 250-k. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

CADÉE and MCKINNEY (1994) dealing with the intergrowth *Celleporaria palmata* - *Culicia woodii* discussed possible beneficial and negative effects for the coral and the bryozoan and concluded that "*the association is a commensal or, more likely, a mutualistic relationship, probably obligatory for the coral, but non-obligatory for the bryozoan*". These conclusions largely apply to our material but as to whether or not the association is obligatory for the coral remains uncertain.

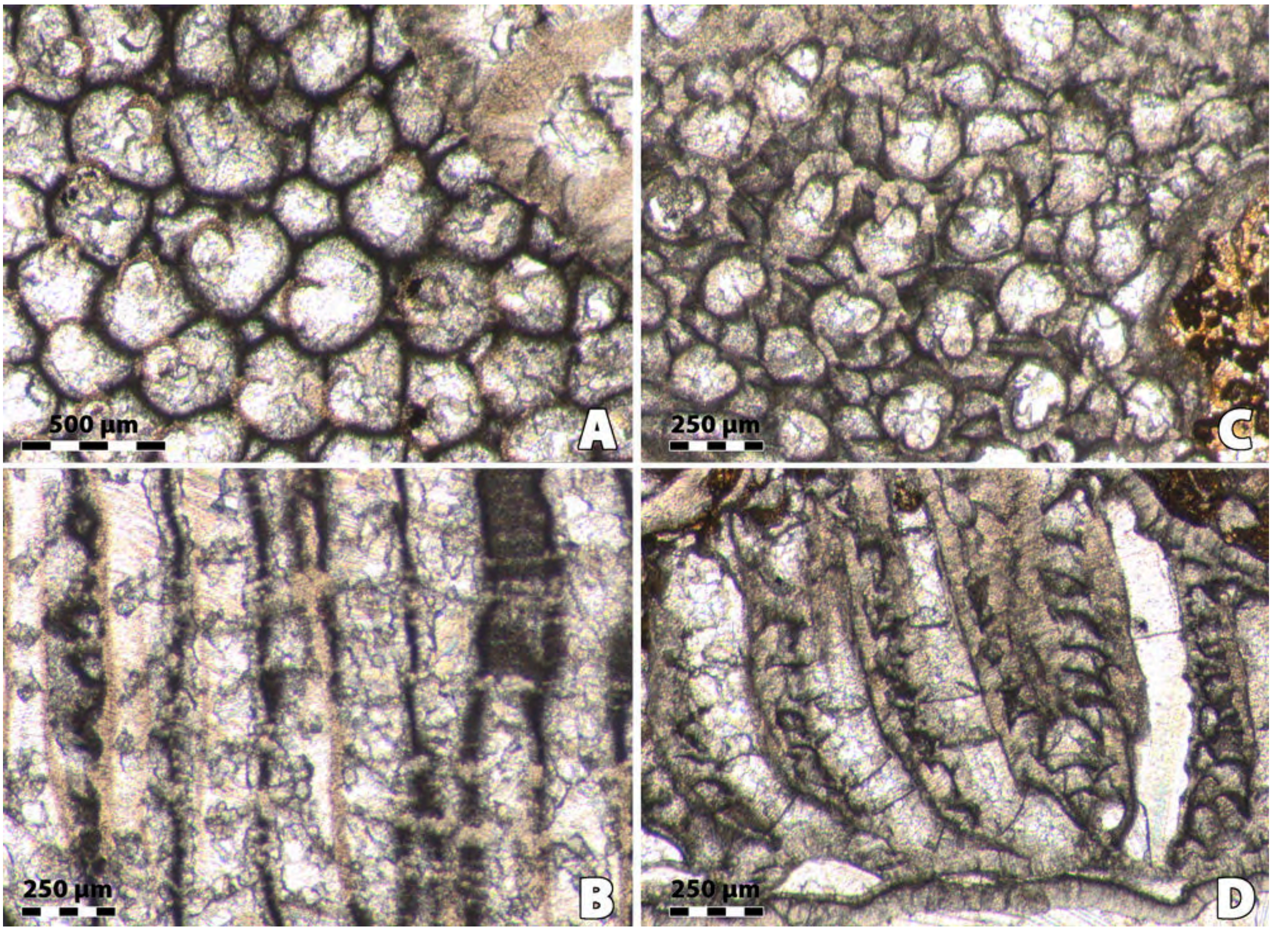


Figure 12: A-**B**, n.gen. 1 cf. *Crepipora* n.sp. 1, respectively transverse and longitudinal section (same specimen as Fig. 13); LPB 17 251, thin section a, and LPB 17 351, thin section b. **C**-**D**, n.gen. 2 n.sp. 2, respectively transverse and longitudinal section (same specimen as Fig. 14). Section in Rugosa: A, upper right (note the lack of zooecial wall at its contact); C, lower right; D, upper right and bottom. Both Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

Vinn *et al.* (2017a) stated that the so-called symbiotic association of *Stigmatella massalis* - *Lambelasma* sp. is "*presumably purely accidental*". It can be true, but in the Armorican and the Ougarta material - taking into account the rather numerous cases of the same kind of association - it seems that the corals selected most suitable organisms for their growth and that massive Cystoporata provided a convenient place.

An example of intergrowth between likely the same kind of coral and a Chaetetida from the Lower Emsian of the Middle Harz Mountains (locality Grosses Mühlental, South of altenbrak, coll. D. Weyer, LPB 17 259ter, not described herein) supports this idea. In this example the general morphology of the chaetetid is similar to that of the bryozoan and their small tubular units similar by their size to the zooecia of the bryozoan. The locality belongs to the Giessen-Harz Nappes and thus, probably to North Gondwana (Plusquellec & Jahnke, 1999).

On the other hand, as far as we know the symbiosis concerns two organisms physiologically connected and unable to live one without the other (Pouyet, 1978), thus the somewhat atypical example ("*large rugosan partially embedded within the bryozoan colony*") provided by Vinn *et al*. (2017a) belongs more likely to commensalism than to symbiosis.

7. Conclusions

- The presence of rugosan - bryozoan intergrowth in the Lower Devonian of North Gondwana (Armorican Massif and Ougarta area) is documented and widely illustrated. This association is not unusual.
- The Armorican association involves an unidentified Triplasmatidae? assigned herein to n.gen.? n.sp. 1 and some Cystoporata: n.gen. 1 cf. *Crepipora*, rarely *Fistulipora* sp. or to another unidentified Fistuliporidae.
- The wall of the bryozoan zooecia is generally lacking where the bryozoan is in direct contact with the Rugosa.

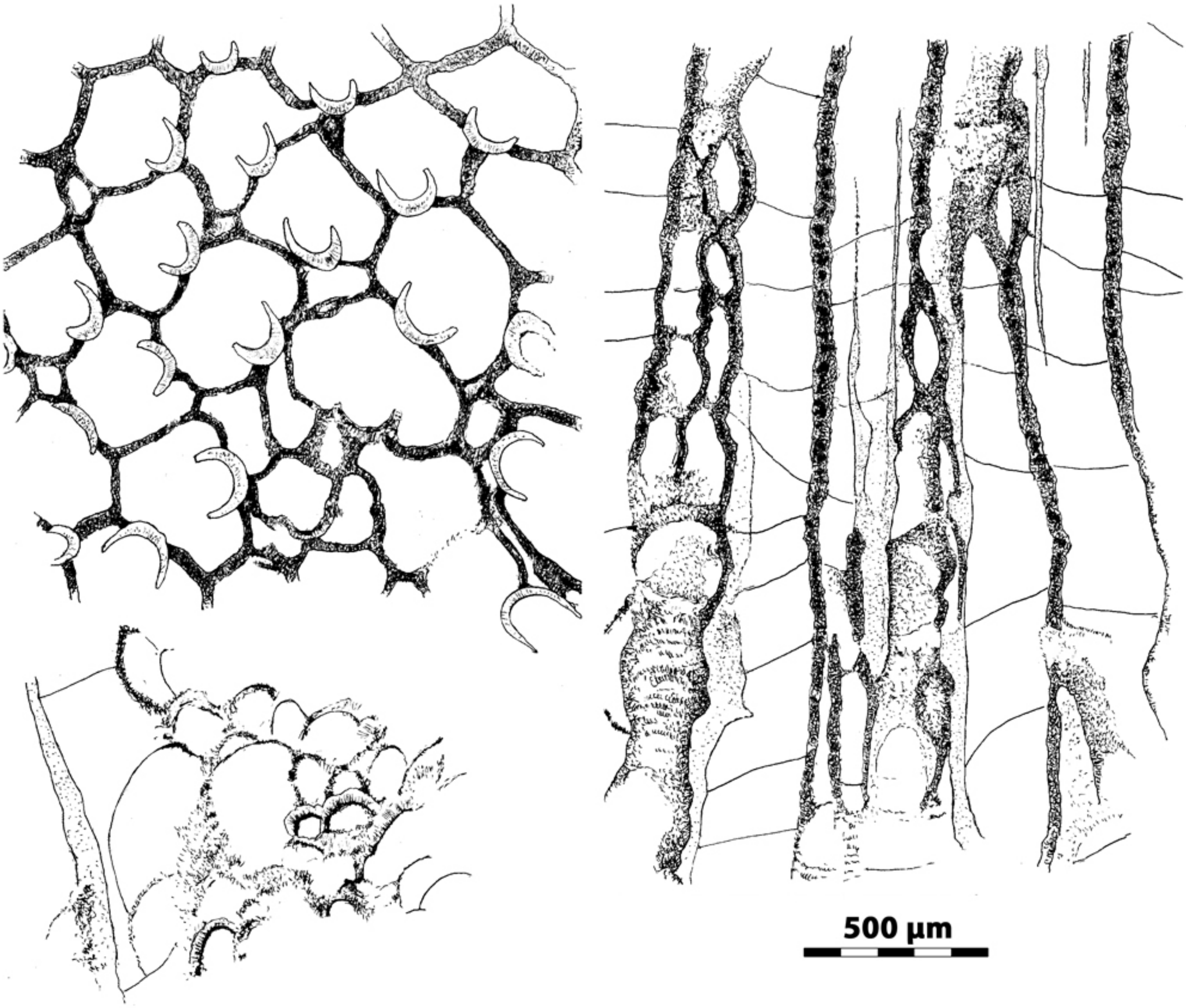


Figure 13: n.gen. 1 cf. *Crepipora* n.sp. 1. **A**, transverse section showing the well- developed lunaria clearly projecting into autozooecial cavity; LPB 17 251, thin section a. **B**, longitudinal section showing long lunarial deposit (in light grey) reaching herein up to 1.2 mm, and numerous diaphragms; LPB 17 251, thin section b. **C**, longitudinal section, lunarial deposit on left and thickened vesicular heterozooecia on bottom and right; LPB 17 251, thin section c. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

- The rugosan-bryozoan intergrowth can be followed by immuration of (very likely) dead corallites.
- The intergrowth gives rise to a pseudo-colony of Rugosa.
- The presence of rugosan-bryozoan intergrowth is not restricted to the Ordovician of Baltica and Laurentia being now well documented in the Lower Devonian of Gondwana (Armorican Massif, Cantabrian Mountains and Ougarta Mountains).
- The association of Triplasmatidae-like corals with chaetetids is briefly indicated in the lower Emsian of Harz Mountains.
- The association is very likely a mutualistic relationship if, as stated by CADÉE and MCKINNEY, "*the stinging cells of the coral provided protection against predator*" and the bryozoan provided substrate and "*the surrounding of the corallites by the bryozoan strength and lateral protection*".
- Except for the possible inclusion of the genus *Ganiella* (poorly known and family placement uncertain) and of two very doubtful *Crepipora* from Asia, the Ceramoporidae have not been indisputably recorded in the Devonian. The present paper provides an example of their presence in the Lower Devonian of the Armorican Massif. However, the Upper Ordovician *Crepipora* with lamellar microstructure are replaced in the Devonian by *Crepipora*-like forms with fibrous autozooecial wall, belonging consequently to a new genus.

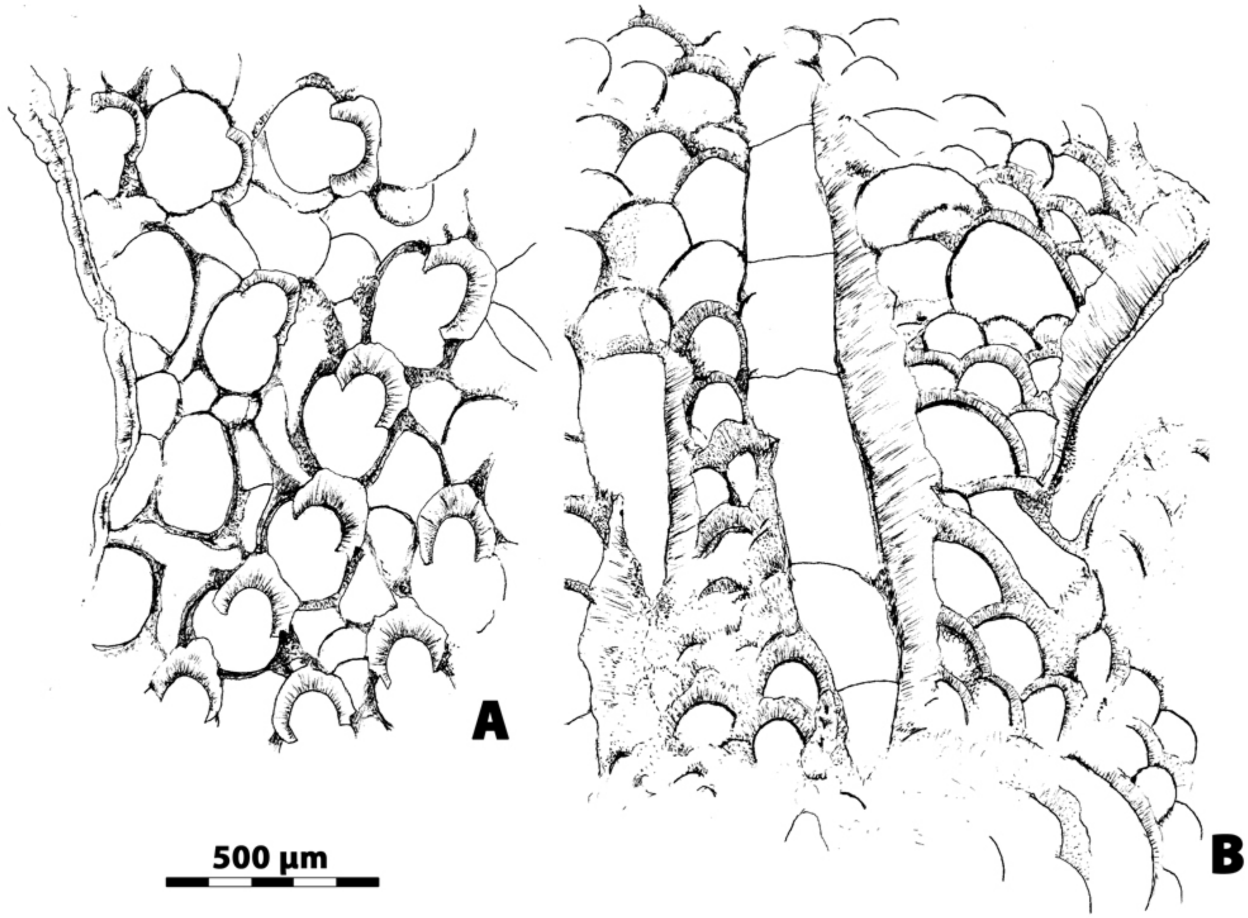


Figure 14: n.gen. 2 n.sp. 2. **A**, transverse section showing the strongly thickened lunaria and, on left, section in the wall of an indet. Rugosa (note the presence of a median dark line not recorded in Rugosa n.gen.? n.sp. 1; LPB 17 254, thin section a. **B**, longitudinal section showing extrazooidal vesicular tissue and some section of lunaria which fibrous microstructure is well exposed; LPB 17 254, thin section a. Monfoulon, Armorican Massif, Monfoulon Limestones, Upper Pragian.

Acknowledgments

The manuscript was critically read by O. Vinn, University of Tartu, Estonia and P. Fedorov, St. Petersburg State University, Russia. . The "LFP" thin sections were made by M. Lemoine of the Muséum National d'Histoire Naturelle, Paris. The photography of the thin sections was done by J.-P. Cuif in the same institution, the Photoshop © matters by B. Granier, Université de Bretagne Occidentale, Brest, and the linguistic review as well as some scientific suggestions by A.J. Wright, University of Wollongong, N.S.W., Australia. The authors are deeply indebted to the above persons for their help and assistance.

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