UPPER FRASNIAN (UPPER DEVONIAN) BRYOZOANS IN PROXIMAL FACIES OF SOUTHERN BELGIUM

ANDREJ ERNST¹, ZOYA TOLOKONNIKOVA² & JULIEN DENAYER³

Received: January 13, 2015; accepted: February 27, 2015

Key words: Frasnian, Kellwasser events, bryozoans, taxonomy, extinctions, Belgium.

Abstract. Seven bryozoan species are described from the shallow-water Aisemont and Lambergstein formations (upper Phenoma Conodont zone, upper Frasnian) in southern Belgium. The studied interval is situated between the lower and upper Kellwasser events. Among the recognized taxa two species are new: Transitorya rotis n. sp. and Isotrypa praeferens n. sp. In addition, the following species were identified in this assemblage: Fultulina pannonica Bigey, 1988, Canistrochaeta hemispheridea (Yang, 1954), Eostenospora conchera Volkov, 1974, Leptostrygia radae Bigey, 1988, and Anostomopora inflata (Bigey, 1988). The studied bryozoan assemblage of the Frasnian age shows palaeogeographic connections to Iran, Russia (Altai) and Afghanistan. Most of them are documented for the first time in this area and it provides important knowledge of the distribution of bryozoans in the late Frasnian and near the Frasnian-Famennian boundary.

Introduction

Records of Devonian bryozoans from Belgium are very scarce – only a small number of species have been described from the Middle to Upper Devonian deposits to date (Dessily 1961, 1967; Dessily & Krausel 1963). However the majority of these species remains inadequately characterized and described only externally, without use of thin sections. No information about internal morphology has ever been provided by earlier authors, what is tremendously important for the accurate systematic treatment and taxonomic identifications in Palaeozoic Bryozoa. Despite their abundance and a priori diversity in the late Frasnian, the effects of the crisis and extinctions associated with the Frasnian-Famennian boundary on the bryozoan fauna remain largely unknown. Hence, this paper aims to provide a taxonomic description of the bryozoan association from the upper Frasnian formations in the proximal part of the Namur-Dinant Basin (southern Belgium).

Geological and stratigraphic settings

In southern Belgium, the upper Frasnian formations are exposed in several Variscan structural elements that formed the Namur-Dinant Basin developed along the southeastern margin of Laurussia during Devonian and Carboniferous times. These structures are: the Dinant Synclinorium and the Philippeville-Durbuy Anticlinorium south of the Midi-Eifel Thrust Fault, the Brabant Parautochton (former ‘northern limb of the Namur Synclinorium’, Belanger et al. 2012) and Haine-Sambre-Meuse overthrust sheets (former ‘southern limb of the Namur Synclinorium’), as well as the eastern extension of the latter, the Vesdre area (Fig. 1). In the southern part of the Namur-Dinant Basin (southern limb of the Dinant Synclinorium and Philippeville-Durbuy Anticlinorium) the upper Frasnian is characterized by the development of carbonate mudmounds (see Boulvain et al. 2011 for recent summary) in a dominant argillaceous succession. In the proximal part of the basin, the sedimentation is mainly carbonate with repeated episodes of dysoxic to anoxic shaly facies linked to third-order transgressions (Mottequin & Poty, submitted). The upper part of the upper Frasnian and the transition to the Famennian is entirely argillaceous. This

¹ Institut für Geologie, Universität Hamburg, Bundesstr. 55, 20146 Hamburg, Germany. E-mail: Andrej.Ernst@uni-hamburg.de
² Kuban State University, 353235 Aphipskii, Post box 30, Krasnodar, Russia. E-mail: zalato@yandex.ru
³ Evolution and Diversity Dynamics Lab, Geology Department, University of Liège, Allée du Six-Août, B18, Sart Tilman, B4000 Liège, Belgium. E-mail: julien.denayer@ulg.ac.be
Fig. 1 - Location and schematic geological map of southern Belgium (redrawn after de Bèthune 1954) with indication of the sampled localities: 1) Lambermont section, 2) Fond-des-Crns disused quarry, 3) Dolembreux section, 4) Hony section, 5) Baugnée section (see Denayer & Poty 2010 for description of the sections).

Fig. 2 - Upper Frasnian lithostratigraphy of the Namur-Dinant Basin (modified after Boulvain et al. 1999, updated by Mottequin & Poty, submitted), conodont zonation after Bulyńczyk et al. (1998). Legend: 1) shale, 2) nodular calcareous shale, 3) argillaceous limestone, 4) thinly-bedded limestone, 5) thickly-bedded limestone, 6) massive limestone; Gp: Group, LKW: lower Kellwasser event, PMt: Petit-Mont Member, UKW: upper Kellwasser event.
paper focuses only on the northern part of the Dinant Synclinorium and the Vesdre area (Figs 1, 2), hence the lithostratigraphic description is given only for these areas. Further information is available in Poty & Chevalier (2007), Denayer & Poty (2010), Mottequin (2008a, b).

In the studied area, the upper Frasnian is represented by the Aiseomant Formation that consists of three members, and the Lambermont Formation, both within the upper *brenana* Conodont Zone. Detailed descriptions of the sections are available in Denayer & Poty (2010). The lower carbonate member of the Aiseomant Formation varies from argillaceous limestone with coquina beds to a biostrome with *Alveolites* and phillipsistesrid rugose corals or stromatoporoids (Poty & Chevalier 2007). The middle member is a fossiliferous shaly unit in which a disyocyst level containing numerous pterinopectinids, lingulid brachiopods and bryozoans – that has been identified as the lower Kelwasser event (Mottequin 2008a). The upper member is a bioclastic limestone unit, with phillipsistesrid rugose corals and oncoinds (Denayer & Poty 2010). The Lambermont Formation begins with a greenish and reddish shaly member including, at its base, several centimetre-thick bioclastic lenses rich in bryozoans, corals and brachiopods.

In the Vesdre area, a middle member formed of argillaceous limestone with colonies of phillipsistesrid and *Iasaphylus* rugose corals (Mottequin & Poty submitted) is developed. The upper part of the formation is dominated by greenish shales with dark-grey intercalations corresponding to the upper Kelwasser event. The Frasnian-Famennian boundary is situated above the dark shales (Bultynck et al. 1998; Gouwy & Bultynck 2000). The Aiseomant Formation recorded a transgressive-regressive cycle corresponding to a single third order sequence (Poty & Chevalier 2007; Denayer & Poty 2010) while the Lambermont Formation corresponds to the transgressive and highstand system tracts the following third-order sequence (Mottequin & Poty submitted).

The bryozoans studied in the present paper are from the upper member of the Aiseomant Formation, known in the Belgian literature as the 'second biostrome with *Phillipsistesra*' (Coe et al. 1976; Coen-Aubert 1974, 1982, 2012) and from bioclastic lenses at the very base of the Lambermont Formation (Fig. 3), thus from the interval between the lower and upper Kelwasser horizons. The first unit recorded the last shallow-water carbonate facies of the Frasnian in the Namur-Dinant Basin and is separated from the next one by a disconformity and a short-term hiatus. The bioclastic lenses of the Lambermont Formation correspond to a short-living recolonization event following the sea-level fall recorded at the top of the Aiseomant Formation and before the generalized argillaceous sedimentation characterizing the upper Frasnian and lower Famennian.

**Material and methods**

The present study is based on two collections of thin sections. The first collection includes thin sections from samples taken from Lambermont, Baugnée, Dolembrunx, and Hony localities (collected by JD in 2006 and 2007) and from Fond-des-Cris (collected by JD in 2007 and additional material collected in 2013 by AE and ZT).

Bryozoans were investigated in thin sections using a binocular microscope in transmitted light. Morphologic character terminology is partly adopted from Anstey & Perry (1970) for trepostomes and from Haegeman (1991, 1993) for cryptostomes, and Snyder (1991) for fenestrate. The studied material is deposited at the Department of Animal Palaeontology of the University of Liége (prefix PAULg).

**Systematic palaeontology**

*Phylum Bryozoa* Ehrenberg, 1831

*Class Stenolaemata* Borg, 1926

*Superorder Palaeostomata* Ma et al., 2014

*Order Cystoporata* Astrowa, 1964

*Suborder Fistuloporina* Astrowa, 1964

*Family Fistuliporidae* Ulrich, 1882

*Genus Fistulipora* M'Coy, 1849


*Diagnosis:* Massive, encrusting or ramose colonies. Cylindrical autozoecia with thin walls and complete diaphragma. Apertures rounded, possessing horse-shoe shaped lunaria. Autozoecia separated by the extrazoecial vesicular skeleton.

*Comparison.* *Fistulipora* M'Coy, 1849 differs from *Eridopora* Ulrich, 1882 in having rounded, horse-shoe-shaped lunaria instead of triangular ones. Furthermore, *Eridopora* develops persistently encrusting colonies, whereas *Fistulipora* may also develop massive and branched colonies.

*Occurrence.* Ordovician to Permian; worldwide.

*Fistulipora pavimenta* Bigey, 1988

Pl. 1, figs. 1-5; Appendix


*Material:* Four specimens from Lambermont, Fond-des-Cris, Hony and Baugnée. PAULg.Fond-des-Cris/9-1A-7, PAULg.Lambermont/7, PAULg.Baugnée/37, PAULg.Hony/II-1

*Description.* Encrusting multi-layered colonies up to 3.5 mm thick, separate sheets 0.66 to 2.34 mm in thickness. Autozoecia growing from 0.04-0.05 mm thick epitheca, bending sharply at their bases towards colony surface. Autozoecial apertures circular to oval.
Basal diaphragms common, thin, horizontal or inclined. Lunaria well developed, triangular to horseshoe-shaped. Vesicles moderate in size, separating autozoecia in 1-2 rows, polygonal in tangential section, box-like to hemispheric, with plane or slightly concave roofs, 5-11 arranged around each autozoecial aperture. Autozoecial walls thick, laminated.

**Comparison.** Fistulipora pavimenta Bigey, 1988 differs from F. galinae Morozova, 1961 from the Middle Devonian (Givetian) of Kuznetsk Basin in having larger autozoecial apertures (aperture width 0.16-0.26 mm vs. 0.10 mm in F. galinae). Fistulipora pavimenta differs from F. volynica Dunaeva, 1970 from the Middle Devonian (Givetian) of Ukraine in smaller autozoecial apertures (aperture width 0.16-0.26 mm vs. 0.25-0.27 mm in F. volynica).

**Occurrence.** Couderousse Member (Blacourt Formation, upper-middle varicus Conodont Zone, uppermost Givetian); Pas-de-Calais, France. Upper Member of Aisemont Formation, upper rhenana Conodont zone, upper Frasnian; Dinant Syncrinium and Vesdre area, southern Belgium.

**Genus Canutrypa Bassler, 1952**
Type species: Canutrypa franciana Bassler, 1952. Upper Devonian (Frasnian); Ferques, France.

*Fistulipora* Bigey 1980, pl. 56, figs 1, 5; 1991, p. 27.

**Diagnosis.** Branched and encrusting colonies. Secondary overgrowths common. Autozoecia long, tubular, curving gently to the colony surface, having circular to oval apertures. Autozoecial diaphragms few to common, thin, straight or inclined. Lunaria poorly defined. One or rarely two hemicylindrical cyst-like structures with axes perpendicular to autozoecial axis in many autozoecia in exozone, having a wall consisting of prismatic calcite crystals. Vesicles wide at the base of exozone, becoming narrow at the colony surface. Colony surface covered with a thick layer of granular skeleton.

**Comparison.** Canutrypa Bassler, 1952 differs from other cystopores in the presence of cyst-like structures.

**Occurrence.** Two species are known: Canutrypa franciana Bassler, 1952, from the Middle Devonian (Eifelian-Givetian) of Germany and Poland (Morozova et al. 2002); Upper Devonian (Frasnian) of France (Bassler 1952; Bigey 1980, 1985, 1988, 1991), Belgium (Desilvly 1961) and Poland (Morozova et al. 2002); C. hemiosperoidea (Yang, 1954) from the Wutsun Shale, Middle Devonian of Kwangsi, and Devonian of Qilianshan, both China, from the Hajigak Formation (Upper Devonian, Frasnian) of Hajigak, central Afghanistan, and Shishau Formation (Upper Devonian, Frasnian) of Iran (Ernst et al. 2012).

**Canutrypa hemispheroidea** (Yang, 1954)
Pl. 1, figs 6-8, Pl. 2, figs 1-3, Appendix

1954 *Fistulipora hemispheroidea* Yang, p. 210, pl. 1, figs 4a-b.
1962 *Fistulipora hemispheroidea* Yang, 1954. – Yang & Lu, p. 11-12, pl. 2, figs 1a-c.
1989 *Canutrypa franciana* Bassler, 1952. – Bigey, p. 27, pl. 1, figs 12-13 [non figs 1-8].
1991 Fistulipora. – Bigey, p. 27, pl. 1, figs 9-11.
2012 *Canutrypa hemispheroidea* (Yang, 1954) – Ernst et al., p. 3, pl. 1, figs 1-12.

**Material.** Four specimens from Fond-des-Cris. PAULg.Fond-des-Cris/9-1A-3, -5, -6, -7.

**Description.** Encrusting colonies consisting of single or multilayered sheets, 0.56-1.25 mm thick. Autozoecia tubular, having circular to oval apertures; long to short, originating from a thick epitheca, curving gently to the colony surface. Autozoecial diaphragms few to abundant throughout the colony, thin, straight or inclined. Lunaria indistinct, triangular to horseshoe-shaped, occurring only in outermost parts of autozoecia. Vesicles polygonal in cross section; wide, high and irregularly shaped in endozone and maculae, becoming narrow and flat at colony surface, sealed by granular skeleton at colony surface, 9-17 surrounding each autozoecial aperture. Hemicylindrical cyst-like structures in many autozoecia in exozone, positioned directly on autozoecial walls, usually at distal parts of autozoecial chambers in exozone, rare to absent in endozone, 0.13-0.21 mm wide. Cyst wall consisting of prismatic calcite crystals oriented with their axes perpendicular to

---

**PLATE 1**

*Fistulipora pavimenta* Bigey, 1988. Upper Devonian (Frasnian); southern Belgium.
Fig. 1 - Longitudinal section of a multilayered colony. PAULg.Hony/II-1, Hony section.
Fig. 2 - Longitudinal section showing autozoecia and vesicular skeleton. PAULg.Hony/II-1, Hony section.
Fig. 3 - Longitudinal section showing autozoecia with diaphragms and vesicular skeleton. PAULg.Baunée/37, Baunée section.
Figs 4-5 - Tangential section showing autozoecial apertures and vesicles. PAULg.Baunée/37, Baunée section.

*Canutrypa hemispheroidea* (Yang, 1954). Upper Devonian (Frasnian); southern Belgium.
Fig. 6 - Longitudinal section of a multilayered colony. PAULg.-Fond-des-Cris/9-1A-3 Fond-des-Cris disused quarry.
Figs 7-8 - Longitudinal section showing autozoecia with diaphragms and hemispheres and vesicular skeleton. PAULg.Fond-des-Cris/9-1A-7, Fond-des-Cris disused quarry.
the wall plane, 0.03-0.04 mm thick. Autozoocentral walls granular-prismatic, 0.010-0.015 mm thick in endozones; granular, 0.03-0.05 mm thick in exozones. Colony surface covered with thick layer of granular skeleton. Maculae consisting of elevated central cluster of large and irregularly shaped vesicles surrounded by larger autozoocia, 1.00-1.35 mm in diameter regularly spaced on the colony surface.

**Comparison.** Both species of *Camuntrypa* developed encrusting and solid ramose growth forms. *Camuntrypa hemispheroides* (Yang, 1954) differs from *C. francqana* Bassler, 1952 in possessing larger autozoocentral apertures (average aperture width 0.29 mm vs. 0.21 mm in *C. francqana*) and larger distance between aperture centres (average distance between aperture centres 0.41 mm vs. 0.31 mm in *C. francqana*). Measurements for *C. francqana* Bassler, 1952 (encrusting growth form, Eifelian of Germany) are from Ernst (2008). Measurements from the type material of *Camuntrypa francqana* (photographs in Utgaard 1983: fig. 175, 1a) result in aperture width by 0.16-0.25 mm and aperture spacing by 0.33-0.41 mm. Dersily (1961) gives 0.18-0.24 mm for the aperture width of *Camuntrypa francqana* from the Frasnian of Belgium (ramose growth form).

**Occurrence.** Wutsun Shale, Middle Devonian; Kwangsi, China. Devonian; Qilianshan, China. Hajigak Formation, Upper Devonian (Frasnian); Hajigak, central Afghanistan. Shishbu Formation, Upper Devonian (Frasnian); Niaj section, northeast Iran. Base of the Lambrmont Formation, upper *rhenana* Conodont zone, upper Frasnian; Veesde area, southern Belgium.

**Eostenopora conspersa** Volkoa, 1974

*Pl. 2, figs 4-7, Pl. 3, figs 1-4; Appendix*

1974 *Eostenopora conspersa* Volkoa, p. 42, pl. 14, fig. 2, pl. 15, fig. 3.

**Material.** Seven specimens from Baugné and Fond-des-Cris. PAUL.g.Fond-des-Cris/9/1A-2, 9-1E-(1, 2), 9-1B-2, 9-1F-(3), PAUL.g.Baugné/ 40-12.2.

**Description.** Massive hemispheric and encrusting colonies. Massive colonies 12-20 mm high and 12-23 mm wide. Encrusting colonies 2-8 mm thick. Autozoecia budding from a thin eptheica, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozoocentral apertures polygonal. Autozoocentral diaphragms common, straight, thin. Acanthostyles abundant, 4-7 surrounding each aperture, originating in the outermost exozone, having distinct calcite cores and dark, laminated sheaths. Walls laminated, 0.010-0.012 mm thick in the endozone and 0.02-0.06 mm thick in the exozone, containing spherules. Spherules distributed irregularly within skeletal material. Maculae consisting of macrozoocia, 1.75-2.90 mm in diameter, often with the central core of thicker skeleton.

**Comparison.** The present material is similar to *Eostenopora conspersa* Volkoa, 1974 from the Upper Devonian (Frasnian) of Altai, Russia. However, it possesses more abundant autozoocentral diaphragms and in

**PLATE 2**

*Camuntrypa hemispheroides* (Yang, 1954). Upper Devonian (Frasnian); southern Belgium.

**Fig. 1** - Longitudinal section showing autozoecia with diaphragms and hemizaphgms and vesicular skeleton. PAUL.g.Fond-des-Cris/9/1A-6, Fond-des-Cris disused quarry.

**Fig. 2** - Tangential section showing autozoocentral apertures with kanana. PAUL.g.Fond-des-Cris/9/1A-6, Fond-des-Cris disused quarry.

**Fig. 3** - Tangential section showing autozoocentral aperture with kanana. PAUL.g.Fond-des-Cris/9/1A-7, Fond-des-Cris disused quarry.

**Eostenopora conspersa** Volkoa, 1974. Upper Devonian (Frasnian); southern Belgium.

**Fig. 4** - Longitudinal section of a hemispherical colony. PAUL.g.Fond-des-Cris/9/1A-4. Fond-des-Cris disused quarry.

**Fig. 5** - Longitudinal section showing autozoocentral chambers and diaphragms. PAUL.g.Fond-des-Cris/9/1F-3. Fond-des-Cris disused quarry.

**Fig. 6** - Longitudinal section showing autozoocentral wall microstructure. PAUL.g.Fond-des-Cris/9/1F-4. Fond-des-Cris disused quarry.

**Fig. 7** - Tangential section showing autozoocentral apertures and maculae. PAUL.g.Fond-des-Cris/9/1D-1. Fond-des-Cris disused quarry.
smaller acanthostyles (0.025-0.050 mm vs. 0.030-0.075 mm in *E. conspersa*). The present species differs from *E. grandis* Volkova, 1974 from Givetian of Altai by its massive colony instead of the branched ramose form, and from *Eostenopora serrotralis* Yang et al., 1988 from the Upper Devonian (Frasnian) of Yunnan (China) by the presence of one type of acanthostyles (the latter species possesses both smaller and larger acanthostyles).

**Occurrence.** Upper member of Aisemont Formation and base of Lambermont Formation, upper *rhenana* Conodont zone, upper Frasnian; Dinant Synclinorium and Vesdre area, southern Belgium.

Family Acticetoehidae Duncan, 1939

Genus Leptotrypa Vinassa de Regny, 1921

Type species: *Chactetes barnardii* Nicholson, 1874. Middle Devonian; Ontario, Canada.


**Comparison.** *Leptotrypa* Vinassa de Regny, 1921 differs from *Leptotrypa* Ulrich, 1883 in having branched colony, and from *Anomalotoechus* Duncan, 1939 in having branched colonies and absence of diaphragms in endocones.

**Occurrence.** Middle Silurian to Lower Carboniferous; worldwide.

*Leptotrypa radiata* Bigey, 1988

Pl. 3, figs 5-6, Pl. 4, figs 1-3; Appendix


**Material.** Two specimens from Baugné and Fond-des-Cris. PAULg.Fond-des-Cris/14, PAULg.Baugnée/40.

**Description.** Branched colonies. Branch diameter 1.64–2.65 mm, endzone 0.56–0.92 mm wide and exzone 0.54–0.86 mm wide. Autozooecia prismatic. Autozooecial diaphrags absent in endzone; abundant in outermost parts of exzone, straight, thin. Autozooeal apertures polygonal. Exilazoecia rare to common, 0.02–0.05 mm in diameter. Acanthostyles common, 2-3 surrounding each autozooeal aperture, 0.02 mm in diameter. Autozoecial walls finely laminated, 0.02 mm thick in endzone; laminated, merged without visible autozoocoeal boundaries, 0.06–0.10 mm thick in exzone.

**Comparison.** *Leptotrypa radiata* Bigey, 1988 differs from *L. mira* Volkova, 1974 from the Frasnian of Gorny Altai in smaller autozoocoeal apertures (aperture width 0.09–0.19 mm vs. 0.25–0.27 mm in *L. mira*). *Leptotrypa radiata* differs from *L. zitaqaoensis* Yang et al., 1988 from the Frasnian of China, in less abundant acanthostyles (2–3 vs. 3–5 per autozooolcal aperture) and smaller colony (branch diameter 1.64–2.65 mm vs. 4.5 mm in *L. zitaqaoensis*).

**Occurrence.** La Parisienne Member (Ferques Formation, Frasnian); Pas-de-Calais, France. Upper member of Aisemont Formation, upper *rhenana* Conodont zone, upper Frasnian; Dinant Synclinorium and Vesdre area, southern Belgium.

Family Amplexoporidae Miller, 1889

Genus *Triznotrypa* Lavrentjeva, 1997

Type species: *Triznotrypa subtemens* Lavrentjeva, 1997. Lower Carboniferous (Viséan); Russia (Kuznets Basin).

**Diagnosis.** Colonies encrusting and frondose, consisting of bifoliate branches. Autozooeal prismatic, growing from mesotheca or laminated epiheca. Mesotheca straight, undulating or zigzag-folded. Autozooecial diaphragms thin, rare to common. Autozooolcal apertures rounded to sub-polygonal. Exilazoecia rare, small. Autozoocoeal walls laminated, integrate with well defined boundary zone. Tubules in exzone wall present, forming a regular pattern around autozooeal apertures. Styles absent. Maculae consisting of macrozooecia or exilazoecia.

**Comparison.** *Triznotrypa* Lavrentjeva, 1997 differs from *Amplexoporella* Morozova, 1959 in regular arrangement tubules, presence of diaphragms only in exzone and absence of acanthostyles.

**Occurrence.** Middle Devonian (Givetian) of China; Upper Devonian (Frasnian) of Altai and Europe; Lower Carboniferous (Tournaisian – Viséan) of Russia.

PLATE 3

*Eostenopora conspersa* Volkova, 1974. Upper Devonian (Frasnian); southern Belgium.

Fig. 1 - Tangential section showing autozooeal apertures and acanthostyles. PAULg.Fond-des-Cris/9-IF-3. Fond-des-Cris disused quarry.

Figs 2-3 - Tangential section showing autozooolcal apertures and acanthostyles. PAULg.Fond-des-Cris/9-IF-1. Fond-des-Cris disused quarry.

Fig. 4 - Tangential section showing macula. PAULg.Fond-des-Cris/9-IF-3. Fond-des-Cris disused quarry.

*Leptotrypa radiata* Bigey, 1988. Upper Devonian (Frasnian); southern Belgium.

Fig. 5 - Oblique branch section. PAULg.Fond-des-Cris/14-2. Fond-des-Cris disused quarry.

Fig. 6 - Longitudinal branch section. PAULg.Fond-des-Cris/14-2. Fond-des-Cris disused quarry.
**Triznotrypa potii** n. sp.

Pl. 4, figs 4-7; Appendix

**Etymology.** The species is named in honour of Edouard Poty, who greatly contributed to the knowledge of Devonian and Carboniferous palaeontology.

**Holotype:** PAULg.Fond-des-Cris/1-6.

**Type locality:** Fond-des-Cris disused quarry near Chaudfontaine, Vedre Valley, southern Belgium.

**Type stratum:** Base of Lambmont Formation, upper *rhenana* Conodont zone, upper Frasnian.

**Diagnosis:** Encrusting colony; autozoecial diaphragms common; tubules arranged in a single row around apertures; exilazoecia rare; maculae not observed.

**Description.** Encrusting colony, 0.75-1.10 mm thick. Autozoecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms common, 2-5 occurring in each autozoecium, straight, thin. Acanthostyles absent. Tubules present, arranged in a single row around autozoecial apertures. Exilazoecia rare. Autozoecial walls laminated, 0.015-0.20 mm thick in the endzone and 0.07-0.10 mm thick in the exozoic. Maculae not observed.

**Comparison.** The present specimen represents the only known species of *Triznotrypa* in the Frasnian of Europe. *Triznotrypa potii* n. sp. differs from *T. kossmati* (Nikiforova, 1933) from the Mississippian of Kazakhstan and Altai in encrusting colony instead of bifoliate frondose one and in smaller autozoecial apertures (aperture width 0.13-0.16 mm vs. 0.30-0.38 mm in *T. kossmati*). *Triznotrypa potii* n. sp. differs from *T. praetomiensis* (Trznava, 1958) from the Viséan of Kuznetsk Basin in encrusting colony instead of bifoliate frondose one and in smaller autozoecial apertures (aperture width 0.13-0.16 mm vs. 0.24-0.30 mm *T. praetomiensis*).

**Occurrence.** To date, the species is only known in the type area.

---

**Order Cryptostomata** Vine, 1884

**Suborder Rhabdomesina** Astrova & Morozova, 1956

**Family Rhombopodidae** Simpson, 1897

**Genus Isostylus** Ernst et al., 2011a

**Type species:** *Isostylus abelgasiensis* Ernst et al., 2011a. Santa Lucia Formation, Lower-Middle Devonian (upper Emsian – upper Eifelian); Abelgas, Cantabrian Mountains, NW Spain.

**Diagnosis:** Colony branched; bifurcation common. Autozoecia tubular, short, growing in spiral pattern from the distinct median axis, abruptly bending in exoxones; triangular to rhombic, tear-drop shaped in transverse section of endzone. Autozoecial diaphragms rare to absent. Hemisepa absent. Styles represented only by paurostyles, usually abundant. Mural spines absent. Heterozoecia absent. Autozoecial walls finely laminated in exoxones.

**Comparison.** *Isostylus* Ernst et al., 2011a is similar to *Saffordotaxis* Bassler, 1952 in autozoecial shape and budding pattern, but differs in the style of type present (paurostyles vs. aktinotyostyles). *Isostylus* differs from *Pamirellia* Gorjunova, 1975 in the shape of the autozoecia, which are longer in *Pamirellia*.

**Occurrence.** *Isostylus abelgasiensis* Ernst et al., 2011a, Santa Lucia Formation, Lower – Middle Devonian (upper Emsian – lower Eifelian); Abelgas, Cantabrian Mountains, NW Spain. *Isostylus simplex* (Ernst, 2011) from the Lower Devonian (? Emsian) of Spain, *Isostylus vulgaris* Ernst et al., 2011b from the Middle Devonian (Eifelian) of Rheinishe Slate Mountains, Germany, and *Isostylus veserensis* n. sp. of the Lambmont Formation, upper *rhenana* Conodont zone, upper Frasnian, Vedre Valley, southern Belgium.

**Isostylus veserensis** n. sp.

Pl. 4, fig. 8, Pl. 5, figs 1-3; Appendix

**Etymology:** The specific name refers to Vedre Valley (*Voëra* in Latinized Gallic) flowing the area where this bryozoan was discovered.

**Holotype:** PAULg.Fond-des-Cris/9-1A-3.

**Paratypes:** PAULg.Fond-des-Cris/14-20, 9-1B-2, 9-1B-4, 9-1F-1, 9-1F-3.

**Type locality:** Fond-des-Cris disused quarry near Chaudfontaine, Vedre Valley, southern Belgium.

**Type stratum:** Lower part of Lambmont Formation, upper *rhenana* Conodont zone, upper Frasnian.

**Diagnosis:** Branched colony with relatively wide exozones; autozoecial diaphragms absent; paurostyles abundant, arranged in one row between autozoecial apertures.

---

**PLATE 4**

*Leptotrypella radiata* Bigey, 1988. Upper Devonian (Frasnian); southern Belgium.

Fig. 1 - Longitudinal branch section showing autozoecial chambers with diaphragms. PAULg.Fond-des-Cris/14-2. Fond-des-Cris disused quarry.

Figs 2-3 - Tangential section showing autozoecial apertures and acanthostyles. PAULg.Baunée/40. Baunée section.

*Triznotrypa potii* n. sp. Upper Devonian (Frasnian); southern Belgium.

Figs 4-5 - Longitudinal section showing autozoecial chambers with diaphragms. Holotype PAULg.Fond-des-Cris/1-6, Fond-des-Cris disused quarry.

Figs 6-7 - Tangential section showing autozoecial apertures and tubules. Holotype PAULg.Fond-des-Cris/1-6, Fond-des-Cris disused quarry.

*Isostylus veserensis* n. sp. Upper Devonian (Frasnian); southern Belgium.

Fig. 8 - Oblique section of a branched colony showing autozoecial apertures and paurostyles. Holotype PAULg.Fond-des-Cris/9-1A-3, Fond-des-Cris disused quarry.
Description. Colony branched, branches 0.60-1.08 mm in diameter, with 0.30-0.50 mm wide endozone and 0.15-0.29 mm wide exozone; branch bifurcation not observed. Transverse sections of branches circular. Autozoocoea short, growing in spiral pattern from the distinct median axis, abruptly bending in exozone; having a triangular to rhombic, tear-drop shape in transverse section of endozone. Autozoocoeal diaphragms absent. Hemisepa absent. Autozoocoeal apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.010-0.015 mm thick; finely laminated, 0.04-0.06 mm thick in exozone. Paurostyles abundant, prominent, arranged in a single longitudinal row between apertures, originating at the base of endozone.

Comparison. Isostylus veserensis n. sp. differs from I. abelgaseis Ernst et al., 2011a in having larger colonies, larger autozoocoeal apertures (average autozoocoeal width 0.11 mm vs. 0.07 mm in I. abelgaseis), and less abundant paurostyles.

Occurrence. To date, the new species is only known in the type area.

Order Fenestra Elias & Condra, 1957
Suborder Fenestellina Astrova & Morozova, 1956
Family Reteporinidae Dunaeva & Morozova, 1975
Genus Anastomopora Simpson, 1897
 [= Reteporina Nickles & Bassler, 1902]
Type species: Fenestella circumata Hall, 1884; Middle Devonian (Erian); Canada and USA.

Diagnosis: Fan-shaped colonies, some with heavy extrazooidal calcification covering proximal portion of colony; branches broad, strongly anisous, bifurcating, branch spacing and autozoocoeae at intermediate distance; keels and superstructure absent; autozoocoeae arranged in 2-8 rows on branches, large-end intermediate-sized, elongate perpendicular to curved obverse surface, chambers nearly circular oval in tangential section deep in endozone, elongate oval in shallower endozone; transverse wall at high angle to reverse wall; hemisepa and diaaphrags absent; elevated peristome present in well preserved specimens. Tubes connecting the endozooidal zoocoeal chambers with the obverse surface present, few or abundant, varying in size. Autozoocoeal walls of thin granular material may be lined by laminar skeleton in both the distal tube and the inflated chamber; reverse wall flat or minimally curved transversely, longitudinal ridges on reverse side minimally developed; extrazooidal skeleton finely laminated, traversed by closely spaced small microstyles, a gently sloped median keel commonly present on reverse surface, locally forming cystose structures bridging fenestrules where broad expanse of extrazooidal skeleton is deposited as continuous sheet over multiple branches.

Comparison. Anastomopora Simpson, 1897 differs from the similar genus Reteporina d’Orbigny, 1849 in having more than 2 rows of autozoocoea on branches. Both genera possess exozonal tubes, which number and size varies between species.


Anastomopora inflata (Bigey, 1988)
Pl. 5, figs. 4-8; Appendix
1988 Reteporina inflata Bigey, p. 312, pl. 39, figs. 3-5.
2007 Reteporina inflata Bigey, 1988 – Ernst & Schroeder, p. 224, fig. 10B-E.

Material: Seven specimens from Baugné, Dolembreux, Fond-des-Cris and Hony. PAULg.Fond-des-Cris/14-0, 14-20, 91B-4, -5, PAULg.Dolembreux/47, PAULg.Baugné/L-12, 40-12, PAULg.Hony/II-1

Exterior description. Reticulate colonies, composed of undulating branches and joined by wide and short disseipments. Fenestrules circular to oval. Autozoocoea arranged in 2 to 3 rows on the branches. Autozoocoeal apertures circular, 4-7 spaced per length of a fenestrule. Microstyles on the reverse surface common, irregularly and densely spaced, originating from interior granular skeleton, 0.003-0.055 mm in diameter. Inner granular skeleton variable in thickness, well-developed, continuous in microstyles. Extrazooidal skeleton finely laminated, well-developed on reverse side. Branch reverse side carrying distinct striation.

Interior description. Autozoocoeal chambers relatively short, deep, displaying rhombic to hexagonal or pentagonal shape in mid tangential section; elongate parallel to branch length; aperture positioned at distal to distoaxial end of chamber; with moderately long vestibule. Hemisepa absent. Tubes connecting endozooidal zoocoeal chambers with the obverse surface present, 0.012-0.015 mm in diameter. Heterozoocoea not observed.

PLATE 5
Isostylus veserensis n. sp. Upper Devonian (Frasnian); southern Belgium.

Fig. 1 - Tangential section of a branched colony showing autozoocoeal apertures and paurostyles. Holotype PAULg. Fond-des-Cris/9-1A-3, Fond-des-Cris disused quarry.
Figs 2-3 - Oblique section of a branched colony showing autozoocoeal chambers and paurostyles. Holotype PAULg. Fond-des-Cris/9-1F-1, Fond-des-Cris disused quarry.

Anastomopora inflata Bigey, 1988. Upper Devonian (Frasnian); southern Belgium.

Figs 4-5 - Tangential section. PAULg. Fond-des-Cris/9-1B-5, Fond-des-Cris disused quarry.
Fig. 6 - Tangential section showing autozoocoeal apertures. PAULg. Fond-des-Cris/9-1B-5, Fond-des-Cris disused quarry.
Figs 7-8 - Tangential section. PAULg. Dolembreux/47. Dolembreux section.
Occurrence. La Parisienne Member (Ferques Formation, Frasnian); Pas-de-Calais, France. Cürten Formation (Early Givetian, Middle Devonian); Dollendorf Syncline, Rhenish Slate Massif (Germany). Upper member of the Aisemont Formation, upper *rhena* Conodont zone, upper Frasnian; Dinant Synclinorium and Vesdre area, southern Belgium.

Discussion and conclusions

The late Frasnian bryozoan association of southern Belgium comprises seven species: two cystoporates, three trepostomes, one rhabdomesine cryptostomes and one fenestrate. Two species are new: trepostome *Triznotrypa potii* n. sp. and cryptostome *Isostylus veserensis* n. sp. (Fig. 3).

The studied association contains species known from the Givetian and Frasnian of Europe and Asia (Fig. 4). *Fistulipora pavimenta* Bigey, 1988 is characteristic for the Givetian of France and Poland (Bigey 1988; Morozova et al. 2002). *Canotrypa hemispheroides* (Yang, 1954) displays wide stratigraphic and geographical range. This species has been found in the Givetian of China and Frasnian of Afghanistan and Iran (Yang 1954; Bigey 1991; Ernst at al. 2012). The trepostome species *Eostenopora conspersa* Volkova, 1974 was described from the lower Frasnian sediments of Gomyi Altai, Russia (Volkova 1974). *Leptotrypella radiata* Bigey, 1988 and *Anastomopora inflata* (Bigey, 1988) are also known from the Frasnian of France.

The discovery of *Isostylus veserensis* n. sp. and *Triznotrypa potii* n. sp. widens our knowledge about phylogeny, stratigraphic and geographic distribution of the genera *Isostylus* and *Triznotrypa*. Besides the species from the Frasnian of Belgium, three species of this genus are known from the Emsian and Eifelian of Spain and Germany (Ernst et al. 2011a, b). The genus *Triznotrypa* is known from the Middle Devonian of China,
Upper Devonian (Frasnian) of Russia and Lower Carboniferous of Kazakhstan and Russia (Kuznetsk Basin).

The bryozoan genera of the studied fauna display various geographical and temporal distribution (Figs 3, 4). Two genera, Fistulipora and Leptotriphella, are cosmopolitan in general, but restricted to some few localities during the Frasnian. Representatives of the genus Fistulipora are known from the Frasnian of Russia (Altai, Kuznetsk Basin) and Kazakhstan. Species of the genus Leptotriphella are known from the Frasnian of Russia (Altai, Kuznetsk Basin), Northern America and China (e.g., Morozova 1961; Volkova 1974; Fritz 1944; Yang et al. 1988). Species of the genera Eosthenopora and Anatomopora are known from the Frasnian of Russia (Gornyi Altai) and Iran (Astrova 1972; Volkova 1974; Ernst et al. 2012). Eosthenopora is also known from the Frasnian of China (Yang et al. 1988). Genus Cantrypa occurs in the Frasnian of France, Poland, Iran and Afghanistan.

Moreover, the bryozoan assemblage from the Frasnian of southern Belgium shares species with contemporaneous sediments of Iran, Afghanistan and Gorny Altai and displays continuity of development of bryozoans within France-Belgium Basin in the Middle and Late Devonian. On the generic level, palaeobiographical connections with the Frasnian deposits of France, Poland, Russia, Kazakhstan, China and North America are recognizable.

Acknowledgements. Zoya Tolokonnikova and Andrei Ernst are grateful to Edouard Poty and Bernard Mottequin for an interesting field excursion in 2013. Andrei Ernst thanks the Deutsche Forschungsgemeinschaft (DFG) for financial support (project ER 278/6-1). This study is a contribution to the IGCP 596 "Mid-Paleozoic climate and biodiversity": Caroline Butliner (Cardiff) and Hans Arne Nækrem (Oslo) are thanked for their constructive and helpful reviews.

REFERENCES


Coen M., Coen-Aubert M. & Cornet P. (1976) - Distribution et extension stratigraphique des récifs à Phillipsa-


Mottequin B. (2008a) - Late Middle to Late Frasnian Atrypida, Pentamerida, and Terebratulida (Brachiopods) from southern Belgium. Geobios, 41: 493-513.
Mottequin B. (2008b) - New observations on Upper Devonian brachiopods from the Namur-Dinant Basin (Belgium). GeoDiversitas, 30: 455-537.
Vine G.R. (1884) - Fourth report of the Committee consisting of Dr. H. R. Sorby and Mr. G. R. Vine, appointed for the purpose of reporting on fossil Polyzoa. In: Reports of the 53rd Meeting of the British Association for the Advancement in Sciences: 161-209.

Appendix

Descriptive statistics

Abbreviations: N = number of measurements, X = mean, SD = sample standard deviation, CV = coefficient of variation, Min = minimal value, Max = maximal value.

Fistulipora pavimenta Bigey, 1888

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>40</td>
<td>0.22</td>
<td>0.029</td>
<td>13.43</td>
<td>0.16</td>
<td>0.26</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>40</td>
<td>0.37</td>
<td>0.047</td>
<td>12.81</td>
<td>0.29</td>
<td>0.33</td>
</tr>
<tr>
<td>Vesicle width, mm</td>
<td>40</td>
<td>0.11</td>
<td>0.024</td>
<td>21.00</td>
<td>0.07</td>
<td>0.18</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
<td>25</td>
<td>7.6</td>
<td>1.381</td>
<td>18.07</td>
<td>5.0</td>
<td>11.0</td>
</tr>
<tr>
<td>Vesicle spacing, mm</td>
<td>30</td>
<td>0.07</td>
<td>0.015</td>
<td>21.08</td>
<td>0.05</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Cuntrypa hemispheroidea (Yang, 1954)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>39</td>
<td>0.29</td>
<td>0.036</td>
<td>12.43</td>
<td>0.22</td>
<td>0.36</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>39</td>
<td>0.41</td>
<td>0.048</td>
<td>11.87</td>
<td>0.31</td>
<td>0.50</td>
</tr>
<tr>
<td>Vesicle width, mm</td>
<td>30</td>
<td>0.09</td>
<td>0.024</td>
<td>25.55</td>
<td>0.03</td>
<td>0.12</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
<td>6</td>
<td>11.3</td>
<td>1.366</td>
<td>12.06</td>
<td>9.0</td>
<td>13.0</td>
</tr>
<tr>
<td>Vesicle spacing, mm</td>
<td>30</td>
<td>0.08</td>
<td>0.016</td>
<td>19.75</td>
<td>0.05</td>
<td>0.11</td>
</tr>
<tr>
<td>Autozooidal diaphragm spacing, mm</td>
<td>25</td>
<td>0.14</td>
<td>0.041</td>
<td>29.57</td>
<td>0.08</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Eostenopora compacta Volkova, 1974

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>40</td>
<td>0.26</td>
<td>0.025</td>
<td>9.39</td>
<td>0.20</td>
<td>0.31</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>40</td>
<td>0.31</td>
<td>0.036</td>
<td>11.44</td>
<td>0.25</td>
<td>0.42</td>
</tr>
<tr>
<td>Aperture width, mm (macula)</td>
<td>20</td>
<td>0.39</td>
<td>0.026</td>
<td>6.75</td>
<td>0.33</td>
<td>0.44</td>
</tr>
<tr>
<td>Aperture spacing, mm (macula)</td>
<td>20</td>
<td>0.48</td>
<td>0.072</td>
<td>13.01</td>
<td>0.40</td>
<td>0.65</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>30</td>
<td>0.035</td>
<td>0.006</td>
<td>18.25</td>
<td>0.025</td>
<td>0.050</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>40</td>
<td>5.7</td>
<td>0.687</td>
<td>12.05</td>
<td>4.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Exilozoecia width, mm</td>
<td>30</td>
<td>0.08</td>
<td>0.023</td>
<td>29.05</td>
<td>0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>Exozon wall thickness, mm</td>
<td>20</td>
<td>0.04</td>
<td>0.010</td>
<td>27.04</td>
<td>0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Autozooidal diaphragm spacing, mm</td>
<td>20</td>
<td>0.22</td>
<td>0.066</td>
<td>29.51</td>
<td>0.11</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Leptocyrtella radiata Bigey, 1988

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>31</td>
<td>0.14</td>
<td>0.027</td>
<td>20.01</td>
<td>0.09</td>
<td>0.19</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>22</td>
<td>0.22</td>
<td>0.023</td>
<td>10.36</td>
<td>0.18</td>
<td>0.28</td>
</tr>
<tr>
<td>Exilozoecia width, mm</td>
<td>5</td>
<td>0.04</td>
<td>0.019</td>
<td>44.73</td>
<td>0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>2</td>
<td>0.025</td>
<td>0.007</td>
<td>28.28</td>
<td>0.02</td>
<td>0.03</td>
</tr>
<tr>
<td>Exozon wall thickness, mm</td>
<td>6</td>
<td>0.07</td>
<td>0.012</td>
<td>16.90</td>
<td>0.06</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Tnapostrype poiti n. sp.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>15</td>
<td>0.16</td>
<td>0.017</td>
<td>10.62</td>
<td>0.13</td>
<td>0.19</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>15</td>
<td>0.25</td>
<td>0.017</td>
<td>6.91</td>
<td>0.23</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Isocyrtella veereensis n. sp.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>6</td>
<td>0.79</td>
<td>0.161</td>
<td>20.49</td>
<td>0.60</td>
<td>1.08</td>
</tr>
<tr>
<td>Exozon width, mm</td>
<td>6</td>
<td>0.22</td>
<td>0.046</td>
<td>21.36</td>
<td>0.15</td>
<td>0.29</td>
</tr>
<tr>
<td>Endozon width, mm</td>
<td>6</td>
<td>0.36</td>
<td>0.082</td>
<td>23.03</td>
<td>0.30</td>
<td>0.50</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>20</td>
<td>0.11</td>
<td>0.017</td>
<td>15.73</td>
<td>0.09</td>
<td>0.13</td>
</tr>
<tr>
<td>Aperture spacing along branch, mm</td>
<td>10</td>
<td>0.35</td>
<td>0.040</td>
<td>11.39</td>
<td>0.29</td>
<td>0.40</td>
</tr>
<tr>
<td>Aperture spacing diagonally, mm</td>
<td>10</td>
<td>0.18</td>
<td>0.020</td>
<td>10.94</td>
<td>0.15</td>
<td>0.22</td>
</tr>
<tr>
<td>Acanthostyle width, mm</td>
<td>20</td>
<td>0.03</td>
<td>0.004</td>
<td>16.96</td>
<td>0.02</td>
<td>0.04</td>
</tr>
</tbody>
</table>

Anastomopora inflata Bigey, 1988

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>19</td>
<td>0.49</td>
<td>0.074</td>
<td>14.89</td>
<td>0.35</td>
<td>0.62</td>
</tr>
<tr>
<td>Branch thickness, mm</td>
<td>10</td>
<td>0.58</td>
<td>0.089</td>
<td>15.41</td>
<td>0.45</td>
<td>0.72</td>
</tr>
<tr>
<td>Dissepiment width, mm</td>
<td>6</td>
<td>0.43</td>
<td>0.014</td>
<td>3.24</td>
<td>0.40</td>
<td>0.44</td>
</tr>
<tr>
<td>Fenestral length, mm</td>
<td>12</td>
<td>0.59</td>
<td>0.075</td>
<td>12.71</td>
<td>0.44</td>
<td>0.75</td>
</tr>
<tr>
<td>Fenestral width, mm</td>
<td>12</td>
<td>0.33</td>
<td>0.046</td>
<td>13.98</td>
<td>0.26</td>
<td>0.40</td>
</tr>
<tr>
<td>Distance between branch centres, mm</td>
<td>8</td>
<td>0.69</td>
<td>0.096</td>
<td>13.94</td>
<td>0.60</td>
<td>0.84</td>
</tr>
<tr>
<td>Distance between dissepiments centres, mm</td>
<td>8</td>
<td>0.93</td>
<td>0.030</td>
<td>3.21</td>
<td>0.87</td>
<td>0.96</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>12</td>
<td>0.07</td>
<td>0.009</td>
<td>7.44</td>
<td>0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>Aperture spacing along branch, mm</td>
<td>12</td>
<td>0.23</td>
<td>0.017</td>
<td>7.66</td>
<td>0.20</td>
<td>0.25</td>
</tr>
<tr>
<td>Aperture spacing diagonally, mm</td>
<td>12</td>
<td>0.18</td>
<td>0.010</td>
<td>5.51</td>
<td>0.16</td>
<td>0.20</td>
</tr>
<tr>
<td>Maximal chamber width, mm</td>
<td>12</td>
<td>0.13</td>
<td>0.014</td>
<td>11.47</td>
<td>0.11</td>
<td>0.15</td>
</tr>
</tbody>
</table>