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

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Abstract. Seven bryozoan species are described from the shallow-water Aisemont and Lambermont formations (upper *rhenana* 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: *Triznotrypa potii* n. sp. and *Isostylus veserensis* n. sp. In addition, the following species were identified in this assemblage: *Fistulipora pavimenta* Bigey, 1988, *Canutrypa hemispheroidea* (Yang, 1954), *Eostenopora conspersa* Volkova, 1974, *Leptotrypella radiata* Bigey, 1988, and *Anastomopora 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 (Dessilly 1961, 1967; Dessilly & Kräusel 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 overturn thrust sheets (former 'southern limb of the Namur Synclinorium'), as well as the eastern extension of the later, the Vesdre area (Fig. 1). In the southern part of the Namur-Dinant Basin (southern limb of the Dinant Synclinoirum 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

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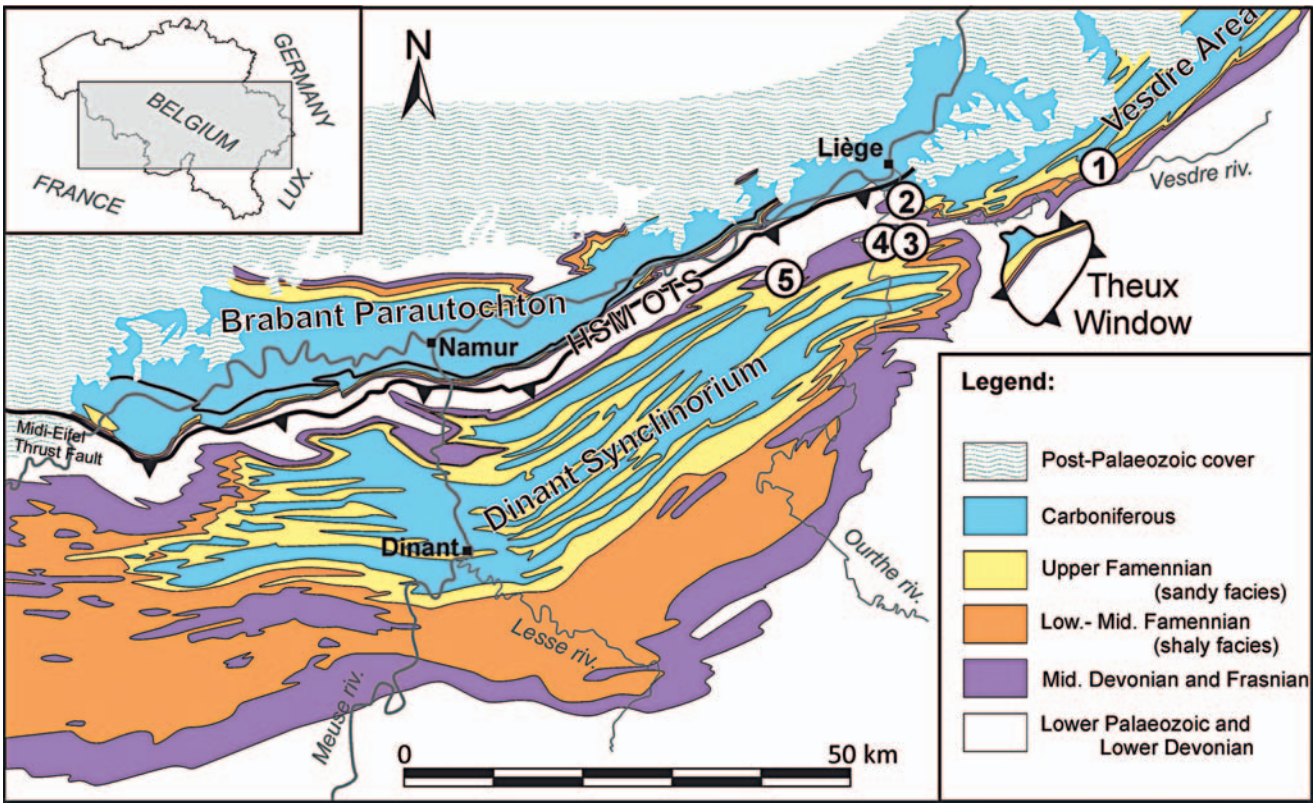


Fig. 1 - Location and schematic geological map of southern Belgium (redrawn after de Béthune 1954) with indication of the sampled localities: 1) Lambermont section, 2) Fond-des-Cris disused quarry, 3) Dolembreux section, 4) Hony section, 5) Baugnée section (see Denayer & Poty 2010 for description of the sections).

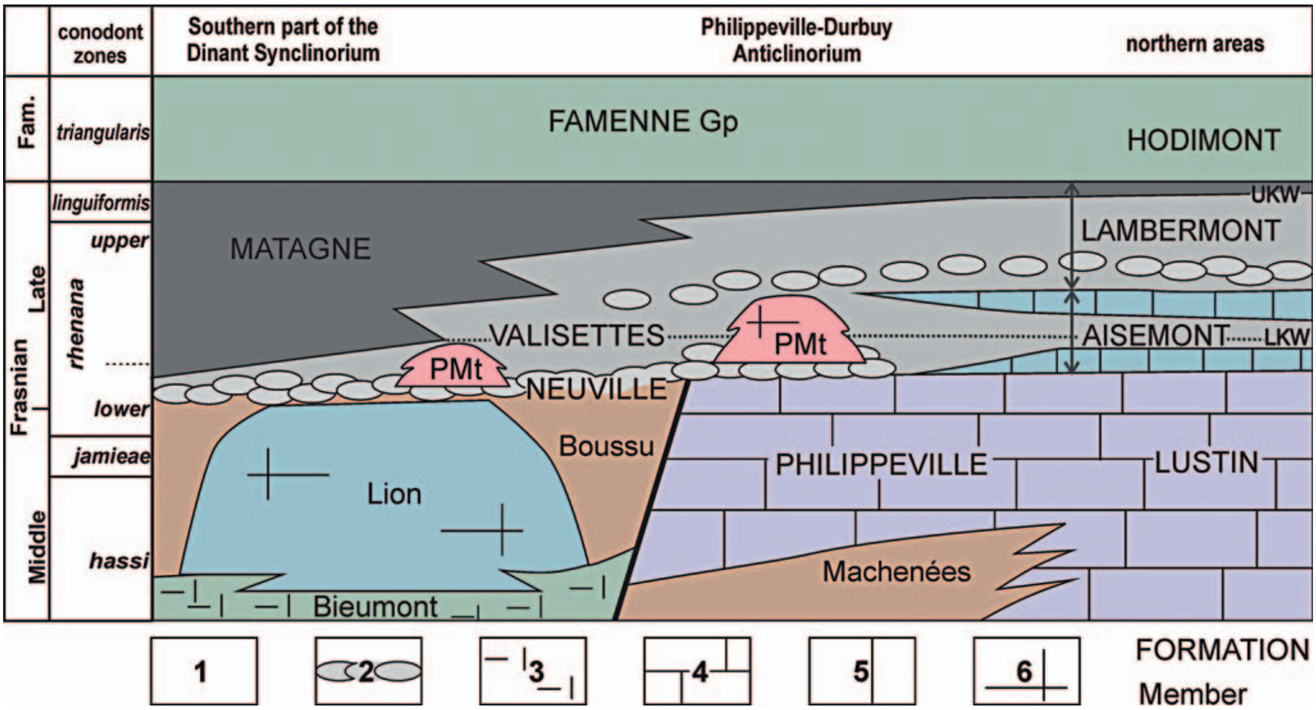


Fig. 2 - Upper Frasnian lithostratigraphy of the Namur-Dinant Basin (modified after Boulvain et al. 1999, updated by Mottequin & Poty, submitted), conodont zonation after Bultynck et al. (1998). Legend: 1) shale, 2) nodular calcareous shale, 3) argillaceous limestone, 4) thinly-bedded limestone, 5) thickly-bedded 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 Aisemont Formation that consists of three members, and the Lambermont Formation, both within the upper *rhenana* Conodont Zone. Detailed descriptions of the sections are available in Denayer & Poty (2010). The lower carbonate member of the Aisemont Formation varies from argillaceous limestone with coquina beds to a biostrome with *Alveolites* and phillipstastreid rugose corals or stromatoporoids (Poty & Chevalier 2007). The middle member is a fossiliferous shaly unit in which a dysoxic level containing numerous pterinopectinids, lingulid brachiopods and bryozoans – that has been identified as the lower Kellwasser event (Mottequin 2008a). The upper member is a bioclastic limestone unit, with phillipsastreid rugose corals and oncoids (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 phillipsastreid and *Iowaphyllum* 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 Kellwasser event. The Frasnian-Famennian boundary is situated above the dark shales (Bultynck et al. 1998; Gouwy & Bultynck 2000). The Aisemont 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 Aisemont Formation, known in the Belgian literature as the 'second biostrome with *Phillipsastrea*' (Coen 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 Kellwasser 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 Aisemont Formation and before the generalized argillaceous sedimentation characterizing the upper Frasnian and lower Famennian.

Material and methods

The present study is based two collections of thin sections. The first collection includes thin sections from samples taken from Lambermont, Baugnée, Dolembreux, 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 Hageman (1991, 1993) for cryptostomes, and Snyder (1991) for fenestrates. The studied material is deposited at the Department of Animal Palaeontology of the University of Liège (prefix: PAULg).

Systematic palaeontology

Phylum **Bryozoa** Ehrenberg, 1831

Class **Stenolaemata** Borg, 1926

Superorder **Palaeostomata** Ma et al., 2014

Order **Cystoporata** Astrova, 1964

Suborder **Fistuliporina** Astrova, 1964

Family Fistuliporidae Ulrich, 1882

Genus *Fistulipora* M'Coy, 1849

Type species: *Fistulipora minor* M'Coy, 1849. Carboniferous; England.

Diagnosis: Massive, encrusting or ramose colonies. Cylindrical autozooecia with thin walls and complete diaphragms. Apertures rounded, possessing horse-shoe shaped lunaria. Autozooecia separated by the extrazooecial vesicular skeleton.

Comparison. *Fistulipora* M'Coy, 1849 differs from *Eridopora* Ulrich, 1882 in having rounded, horseshoe-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

1988 *Fistulipora pavimentum* Bigey, p. 300-301, pl. 37, fig. 3-6.

2002 *Fistulipora pavimenta* Bigey, 1988 – Morozova et al., p. 309, fig. 3A-B.

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. Autozooecia growing from 0.04-0.05 mm thick epitheca, bending sharply at their bases towards colony surface. Autozooecial apertures circular to oval.

Basal diaphragms common, thin, horizontal or inclined. Lunaria well developed, triangular to horseshoe-shaped. Vesicles moderate in size, separating autozooecia in 1-2 rows, polygonal in tangential section, box-like to hemispheric, with plane or slightly concave roofs, 5-11 arranged around each autozooecial aperture. Autozooecial 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 autozooecial 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 autozooecial apertures (aperture width 0.16-0.26 mm vs. 0.25-0.27 mm in *F. volynica*).

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

Genus *Canutrypa* Bassler, 1952

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

Canutrypa Bassler 1952, p. 382; Dessilly 1961, p. 2-3; Utgaard 1983, p. 383; Bigey 1988, p. 301-302; 1991, p. 27; Ernst 2008, p. 332; Ernst et al. 2012, p. 2.

Fistuliporid Bigey 1980, pl. 56, figs 1, 5; 1991: 27.

Fistulipora Yang 1954, p. 210; Yang & Lu 1962, p. 11-12.

Diagnosis: Branched and encrusting colonies. Secondary overgrowths common. Autozooecia long, tubular, curving gently to the colony surface, having circular to oval apertures. Autozooecial diaphragms few to common, thin, straight or inclined. Lunaria poorly defined. One or rarely two hemicylindrical cyst-like structures with axes perpendicular to autozooecial axis in many autozooecia 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 cystoporates in the presence of cyst-like structures.

Occurrence. Two species are known: *Canutrypa francqana* 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 (Dessily 1961) and Poland (Morozova et al. 2002); *C. hemispheroidea* (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 Shishtu 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.

1991 *Canutrypa francqana* Bassler, 1952. – Bigey, p. 27, pl. 1, figs 12-13 [non figs 1-8],

1991 Fistuliporid. – 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. Autozooecia tubular, having circular to oval apertures; long to short, originating from a thick epitheca, curving gently to the colony surface. Autozooecial diaphragms few to abundant throughout the colony, thin, straight or inclined. Lunaria indistinct, triangular to horseshoe-shaped, occurring only in outermost parts of autozooecia. Vesicles polygonal in cross section; wide, high and irregularly shaped in endozones and maculae, becoming narrow and flat at colony surface, sealed by granular skeleton at colony surface, 9-17 surrounding each autozooecial aperture. Hemicylindrical cyst-like structures in many autozooecia in exozone, positioned directly on autozooecial walls, usually at distal parts of autozooecial chambers in exozone, rare to absent in endozones, 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 autozooecia and vesicular skeleton. PAULg.Hony/II-1, Hony section.

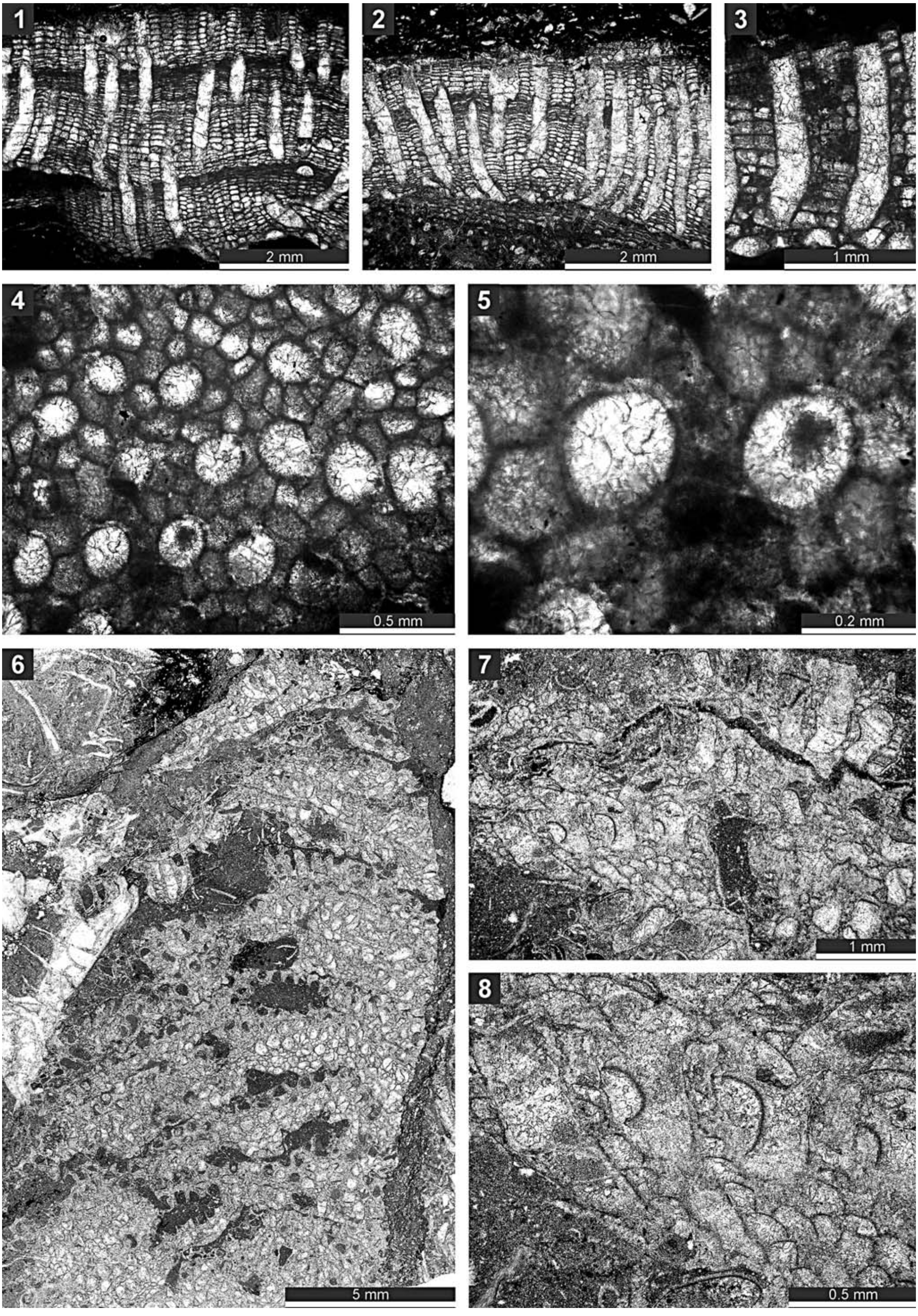
Fig. 3 - Longitudinal section showing autozooecia with diaphragms and vesicular skeleton. PAULg.Baugnée/37, Baugnée section.

Figs 4-5 - Tangential section showing autozooecial apertures and vesicles. PAULg.Baugnée/37, Baugnée 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 autozooecia with diaphragms and hemiphragms and vesicular skeleton. PAULg.Fond-des-Cris/9-1A-7, Fond-des-Cris disused quarry.


1
2 mm
2
2 mm
3
1 mm
4
0.5 mm
5
0.2 mm
6
5 mm
7
1 mm
8
0.5 mm

the wall plane, 0.03-0.04 mm thick. Autozooecial 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 autozooecia, 1.00-1.35 mm in diameter regularly spaced on the colony surface.

Comparison. Both species of *Canutrypa* developed encrusting and solid ramose growth forms. *Canutrypa hemispheroidea* (Yang, 1954) differs from *C. francqana* Bassler, 1952 in possessing larger autozooecial 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 *Canutrypa 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. Dessily (1961) gives 0.18-0.24 mm for the aperture width of *Canutrypa 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. Shishtu Formation, Upper Devonian (Frasnian); Niaz section, northeast Iran. Base of the Lambermont Formation, upper *rhenana* Conodont zone, upper Frasnian; Vesdre area, southern Belgium.

Order **Trepostomata** Ulrich, 1882

Suborder **Amplexoporina** Astrova, 1965

Family Eridotrypellidae Morozova, 1961

Genus *Eostenopora* Duncan, 1939

[= *Paratrachytoechus* Hu, 1980]

Type species: *Eostenopora picta* Duncan, 1939. Middle Devonian; Michigan, USA.

Diagnosis: Encrusting, massive or rarely branched colonies. Autozooecial apertures irregularly polygonal. Autozooecial walls laminated, without distinct zooecial boundaries, irregularly thickened, containing spherulites. Diaphragms complete, varying in number. Exilazooecia rare. Acanthostyles varying in size and number.

Comparison. *Eostenopora* Duncan, 1939 differs from *Eridotrypella* Duncan, 1939 in colony form (encrusting or massive colonies vs. ramose branched).

Occurrence. Upper Silurian – Upper Devonian; Europe, USA, Russia, Kazakhstan, Uzbekistan, Mongolia and China.

Eostenopora conspersa Volkova, 1974

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

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

Material: Seven specimens from Baugnée and Fond-des-Cris. PAULg.Fond-des-Cris/9-1A-2, 9-1E-(1, 2), 9-1B-2, 9-1F-(1-5), PAULg.Baugnée/ 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. Autozooecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozooecial apertures polygonal. Autozooecial 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 macrozooecia, 1.75-2.90 mm in diameter, often with the central core of thicker skeleton.

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

PLATE 2

Canutrypa hemispheroidea (Yang, 1954). Upper Devonian (Frasnian); southern Belgium.

Fig. 1 - Longitudinal section showing autozooecia with diaphragms and hemiphragms and vesicular skeleton. PAULg.Fond-des-Cris/9-1A-6, Fond-des-Cris disused quarry.

Fig. 2 - Tangential section showing autozooecial apertures with lunaria. PAULg.Fond-des-Cris/9-1A-6, Fond-des-Cris disused quarry.

Fig. 3 - Tangential section showing autozooecial aperture with lunaria. PAULg.Fond-des-Cris/9-1A-7, Fond-des-Cris disused quarry.

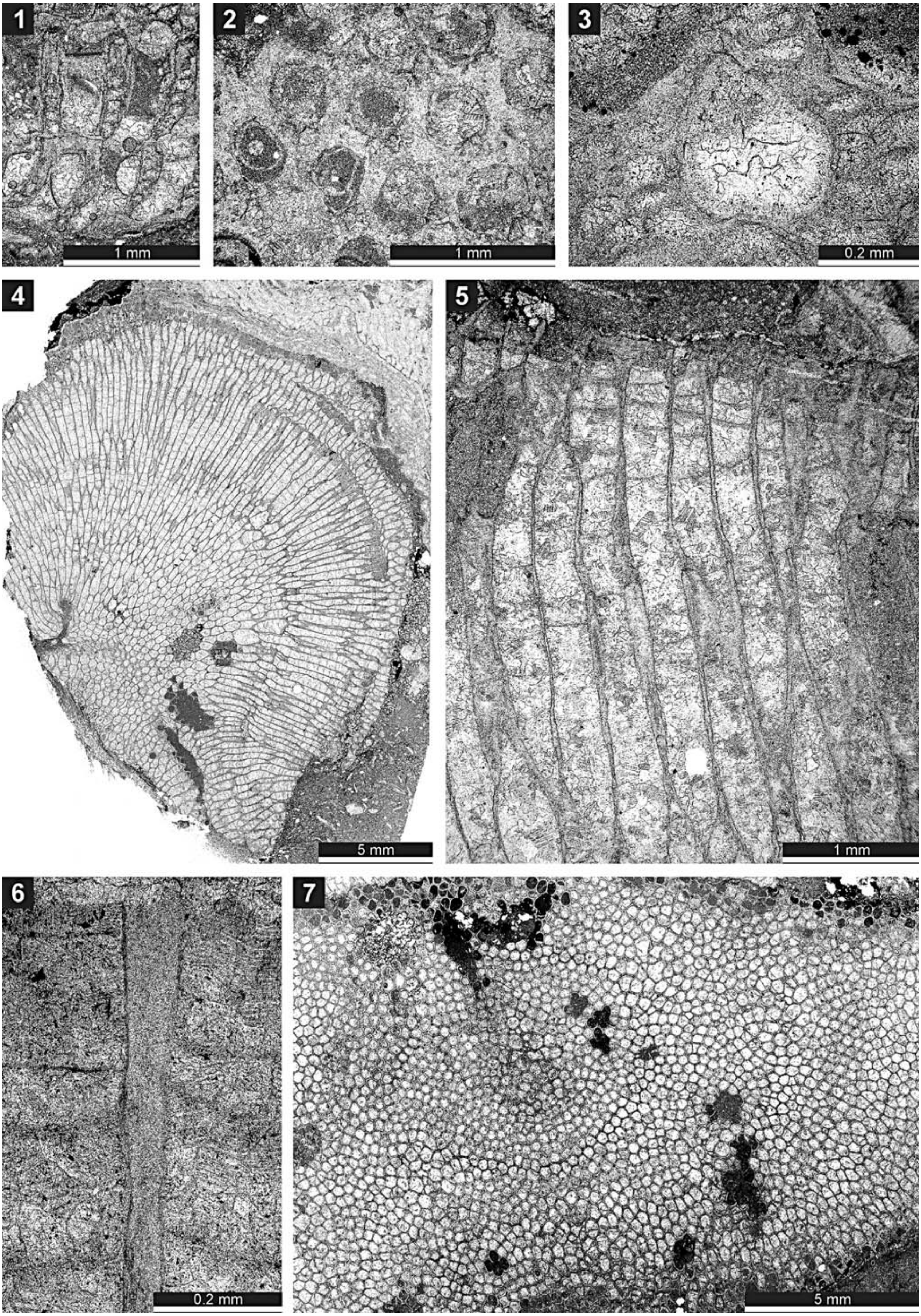
Eostenopora conspersa Volkova, 1974. Upper Devonian (Frasnian); southern Belgium.

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

Fig. 5 - Longitudinal section showing autozooecial chambers and diaphragms. PAULg.Fond-des-Cris/9-1F-5. Fond-des-Cris disused quarry.

Fig. 6 - Longitudinal section showing autozooecial wall microstructure. PAULg.Fond-des-Cris/9-1F-4. Fond-des-Cris disused quarry.

Fig. 7 - Tangential section showing autozooecial apertures and maculae. PAULg.Fond-des-Cris/9-1D-1. Fond-des-Cris disused quarry.


1
1 mm
2
1 mm
3
0.2 mm
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5 mm
5
1 mm
6
0.2 mm
7
5 mm

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 seiromuralis* 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 Atactotoechidae Duncan, 1939

Genus *Leptotrypella* Vinassa de Regny, 1921

Type species: *Chaetetes barrandei* Nicholson, 1874. Middle Devonian; Ontario, Canada.

Diagnosis: Branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Autozooecial diaphragms lacking in endozones; rare to common in exozones. Exilazooecia rare. Acanthostyles long, common to abundant. Autozooecial walls granular, thin in endozones; laminated, mainly merged but sometimes serrated, irregularly thickened in exozones (modified after Astrova 1978).

Comparison. *Leptotrypella* 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 endozones.

Occurrence. Middle Silurian to Lower Carboniferous; worldwide.

Leptotrypella radiata Bigey, 1988

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

1988 *Leptotrypella radiata* Bigey, p. 308, pl. 38, figs 13-16.

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

Description. Branched colonies. Branch diameter 1.64-2.65 mm, endozone 0.56-0.92 mm wide and exozone 0.54-0.86 mm wide. Autozooecia prismatic. Autozooecial diaphragms absent in endozone; abundant in outermost parts of exozone, straight, thin. Autozooecial apertures polygonal. Exilazooecia rare to common, 0.02-0.05 mm in diameter. Acanthostyles common, 2-3 surrounding each autozooecial aperture, 0.02 mm in diameter. Autozooecial walls finely laminated, 0.02 mm thick in endozone; laminated, merged without visible autozooecial boundaries, 0.06-0.10 mm thick in exozone.

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

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 subtomiensis* Lavrentjeva, 1997. Lower Carboniferous (Viséan); Russia (Kuznetsk Basin).

Diagnosis: Colonies encrusting and frondose, consisting of bifoliate branches. Autozooecia prismatic, growing from mesotheca or laminated epitheca. Mesotheca straight, undulating or zigzag-folded. Autozooecial diaphragms thin, rare to common. Autozooecial apertures rounded to sub-polygonal. Exilazooecia rare, small. Autozooecial walls laminated, integrate with well defined boundary zone. Tubules in exozone wall present, forming a regular pattern around autozooecial apertures. Styles absent. Maculae consisting of macrozooecia or exilazooecia.

Comparison. *Triznotrypa* Lavrentjeva, 1997 differs from *Amplexoporella* Morozova, 1959 in regular arrangement tubules, presence of diaphragms only in exozone 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 autozooecial apertures and acanthostyles. PAULg.Fond-des-Cris/9-1F-3. Fond-des-Cris disused quarry.

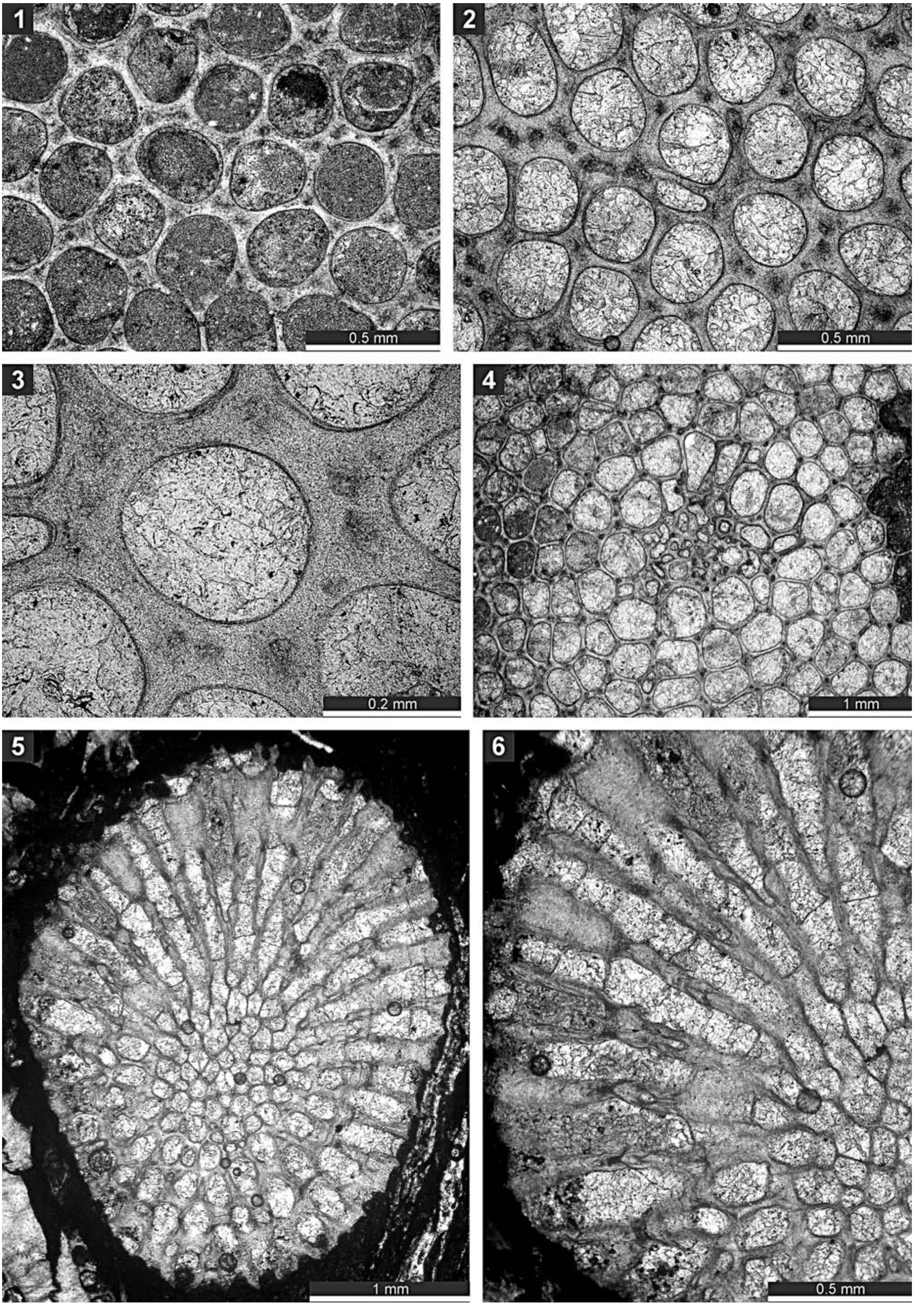
Figs 2-3 - Tangential section showing autozooecial apertures and acanthostyles. PAULg.Fond-des-Cris/9-1F-1. Fond-des-Cris disused quarry.

Fig. 4 - Tangential section showing macula. PAULg.Fond-des-Cris/9-1F-3. Fond-des-Cris disused quarry.

Leptotrypella 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.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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, Vesdre Valley, southern Belgium.

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

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

Description. Encrusting colony, 0.75-1.10 mm thick. Autozooecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozooecial apertures rounded-polygonal. Autozooecial diaphragms common, 2-5 occurring in each autozooecium, straight, thin. Acanthostyles absent. Tubules present, arranged in a single row around autozooecial apertures. Exilazooecia rare. Autozooecial walls laminated, 0.015-0.020 mm thick in the endozone and 0.07-0.10 mm thick in the exozone. 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 autozooecial 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* (Trizna, 1958) from the Viséan of Kuznetsk Basin in encrusting colony instead of bifoliate frondose one and in smaller autozooecial 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 Rhomboporidae Simpson, 1897

Genus *Isostylus* Ernst et al., 2011a

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

Diagnosis: Colony branched; bifurcation common. Autozooecia tubular, short, growing in spiral pattern from the distinct median axis, abruptly bending in exozones; triangular to rhombic, tear-drop shaped in transverse section of endozone. Autozooecial diaphragms rare to absent. Hemisepta absent. Styles represented only by paurostyles, usually abundant. Mural spines absent. Heterozooecia absent. Autozooecial walls finely laminated in exozones.

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

Occurrence. *Isostylus abelgasensis* 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 Rhenish Slate Mountains, Germany, and *Isostylus veserensis* n. sp. of the Lambermont Formation, upper *rhenana* Conodont zone, upper Frasnian, Vesdre area, southern Belgium.

Isostylus veserensis n. sp.

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

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

Holotype: PAULg.Fond-des-Cris/9-1A-5.

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, Vesdre Valley, southern Belgium.

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

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

PLATE 4

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

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

Figs 2-3 - Tangential section showing autozooecial apertures and acanthostyles. PAULg.Baugnée/40. Baugnée section.

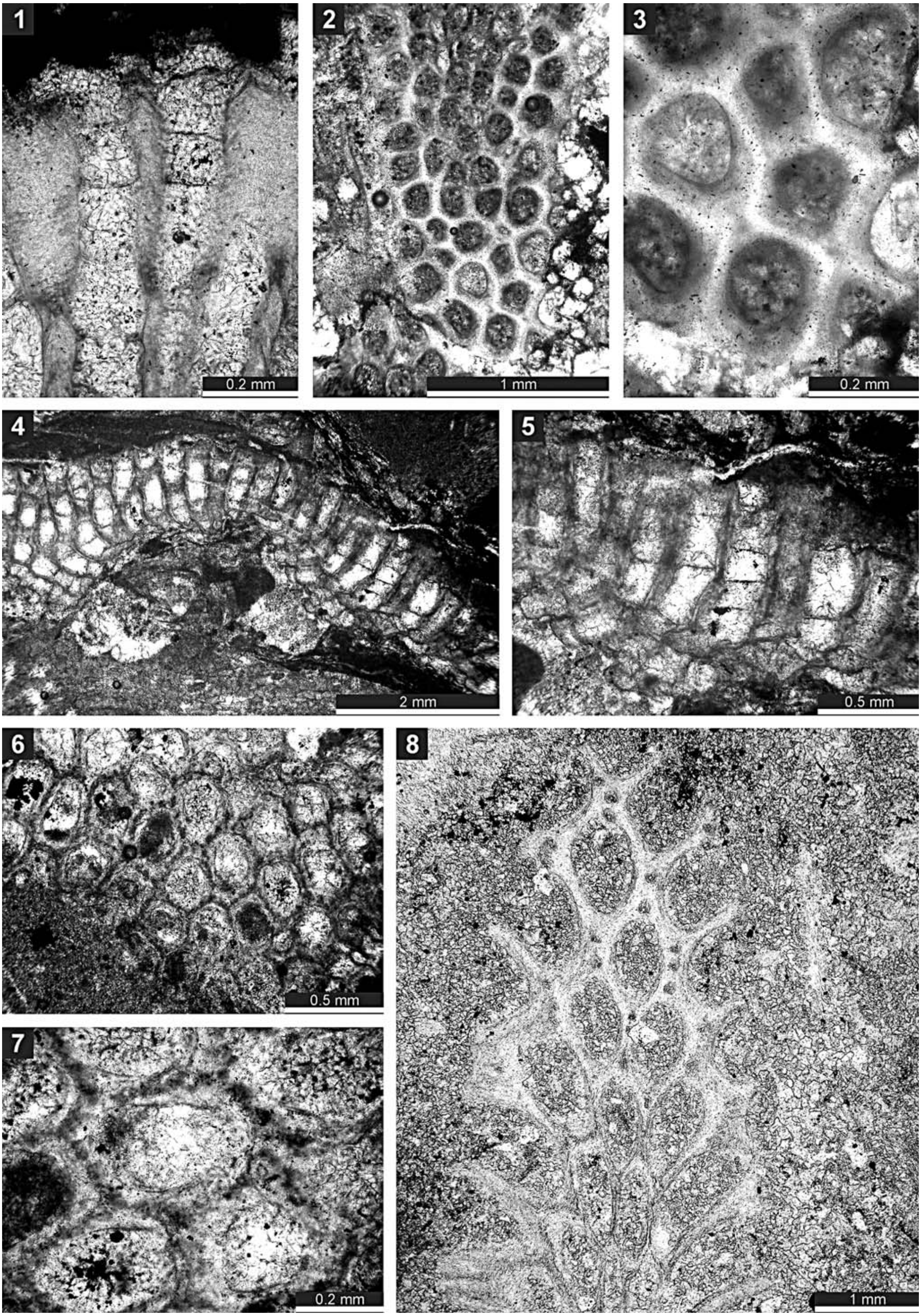
Triznotrypa potii n. sp. Upper Devonian (Frasnian); southern Belgium.

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

Figs 6-7 - Tangential section showing autozooecial 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 autozooecial apertures and paurostyles. Holotype PAULg. Fond-des-Cris/9-1A-5, Fond-des-Cris disused quarry.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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. Autozooecia short, growing in spiral pattern from the distinct median axis, abruptly bending in exozones; having a triangular to rhombic, tear-drop shape in transverse section of endozone. Autozooecial diaphragms absent. Hemisepta absent. Autozooecial 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. abelgasensis* Ernst et al., 2011a in having larger colonies, larger autozooecial apertures (average autozooecial width 0.11 mm vs. 0.07 mm in *I. abelgasensis*), and less abundant paurostyles.

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

Order **Fenestrata** Elias & Condra, 1957

Suborder **Fenestellina** Astrova & Morozova, 1956

Family Reteporinidae Dunaeva & Morozova, 1975

Genus *Anastomopora* Simpson, 1897

[= *Reteporidra* Nickles & Bassler, 1900]

Type species: *Fenestella cinctuta* 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 sinuous, bifurcating, branch spacing and anastomoses at intermediate distance; keels and superstructure absent; autozooecia 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; hemisepta and diaphragms absent; elevated peristome present in well preserved specimens. Tubes connecting the endozonal zooecial chambers with the obverse surface present, few or abundant, varying in size. Autozooecial walls of thick 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 autozooecia on branches. Both genera possess exozonal tubes, which number and size varies between species.

Occurrence. Lower – Upper Devonian; North America, Europe, Asia.

Anastomopora inflata (Bigey, 1988)

Pl. 5, figs 4-8; Appendix

1988 *Reteporidra inflata* Bigey, p. 312, pl. 39, figs. 3-5.

2007 *Reteporidra inflata* Bigey, 1988 – Ernst & Schroeder, p. 224, fig. 10B-E.

Material: Seven specimens from Baugnée, Dolembreux, Fond-des-Cris and Hony. PAULg.Fond-des-Cris/14-0, 14-20, 91B-4, -5, PAULg.Dolembreux/47, PAULg.Baugnée/40-12, 40-12.2, PAULg.Hony/II-1

Exterior description. Reticulate colonies, composed of undulating branches and joined by wide and short dissepiments. Fenestrules circular to oval. Autozooecia arranged in 2 to 3 rows on the branches. Autozooecial 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, 0.003-0.005 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. Autozooecial 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 distoabaxial end of chamber; with moderately long vestibule. Hemisepta absent. Tubes connecting endozonal zooecial chambers with the obverse surface present, 0.012-0.015 mm in diameter. Heterozooecia not observed.

PLATE 5

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

Fig. 1 - Tangential section of a branched colony showing autozooecial apertures and paurostyles. Holotype PAULg. Fond-des-Cris/9-1A-5, Fond-des-Cris disused quarry.

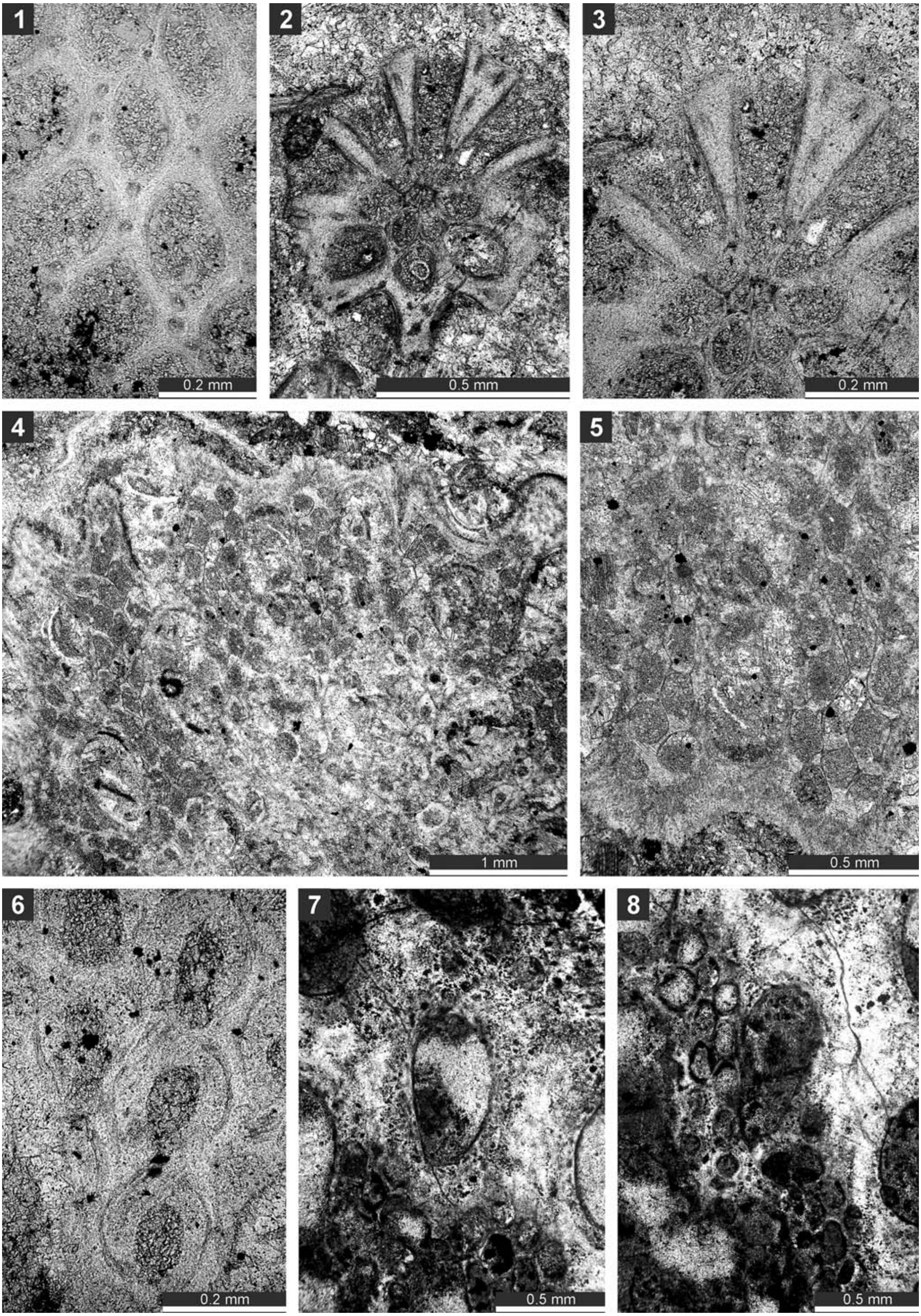
Figs 2-3 - Oblique section of a branched colony showing autozooecial chambers and paurostyles. Holotype PAULg. Fond-des-Cris/9-1F-1, Fond-des-Cris disused quarry.

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 autozooecial apertures. PAULg. Fond-des-Cris/9-1B-5, Fond-des-Cris disused quarry.

Figs 7-8 - Tangential section. PAULg. Dolembreux/47. Dolembreux section.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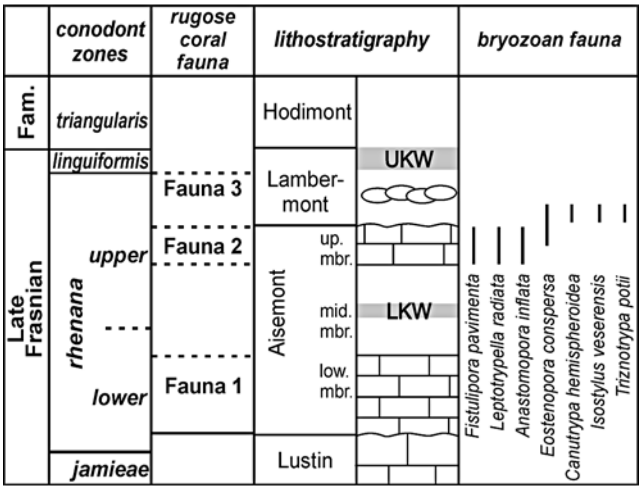

Fig. 3 - Synthetic stratigraphic column of the investigated area (modified after Denayer & Poty 2010) with distribution of the discussed bryozoan species. Conodont zonation after Bultynck et al. (1998), rugose coral faunas after Coen et al. (1976) and Coen-Aubert (2012). Legend: LKW: lower Kellwasser event, low. mbr.: lower member, mid. mbr: middle member, UKW: upper Kellwasser event, up. mbr.: upper member.

Comparison. The present material is similar to *Anastomopora inflata* (Bigey, 1988) from the Frasnian of the Pas-de-Calais (northern France). This species has also been recorded in the Givetian of the Rhenish Slate Massif (Germany). *Anastomopora inflata* differs from *A.* cf. *quebecensis* Fritz, 1938 described from the Frasnian of Iran (Ernst et al. 2012) in narrower branches (average branch width 0.49 mm vs. 0.67 mm in *A.* cf. *quebecensis*) and in shorter distances between aperture centres (average aperture spacing 0.23 mm vs. 0.29 mm in *A.* cf. *quebecensis*). *Anastomopora inflata* differs from *A. recta* Ernst & Königshof, 2010 from the upper Givetian of Morocco in shorter distances between aperture centres (average aperture spacing 0.23 mm vs. 0.28 mm in *A. recta*).

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 *rhenana* 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). *Canutrypa hemispheroidea* (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 Gornyi 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,

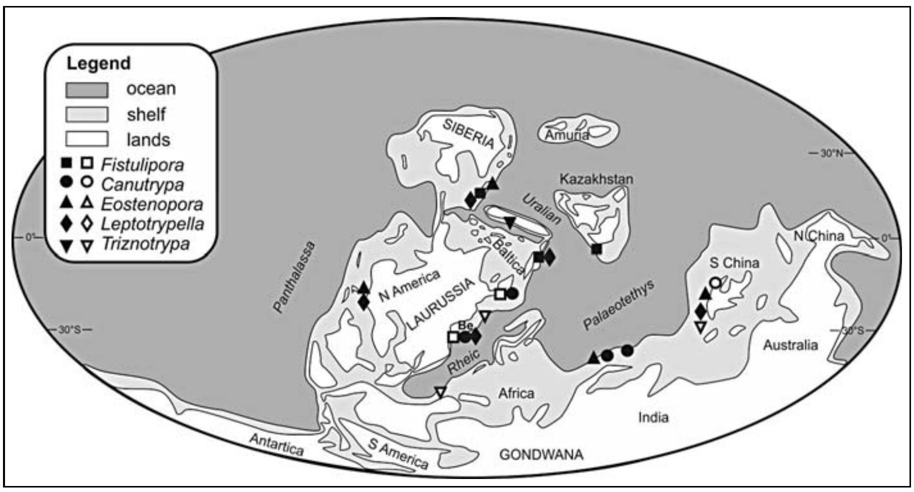

Fig. 4 - Palaeogeographic reconstruction (modified after Golonka et al. 1994) with occurrences of some taxa described in the main text. Full polygons indicate Frasnian occurrences, white polygons indicate middle Devonian occurrences. Be: Position of the Belgian Namur-Dinant Basin.

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 *Leptotrypella*, are cosmopolitan in general, but restricted to some few localities during the Frasnian. Representatives of the genus *Fistulipora* are known the Frasnian of Russia (Altai, Kuznetsk Basin) and Kazakhstan. Species of the genus *Leptotrypella* 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 *Eostenopora* and *Anastomopora* are known from the Frasnian of Canada, Russia (Gornyi Altai) and Iran (Astrova 1972; Volkova 1974; Ernst et al. 2012). *Eostenopora* is also known from the Frasnian of China (Yang et al. 1988). Genus *Canutrypa* 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 Gornyi Altai and displays continuity of development of bryozoans within France-Belgian Basin in the Middle and Late Devonian. On the generic level, palaeobiogeographical connections with the Frasnian deposits of France, Poland, Russia, Kazakhstan, China and Northern America are recognizable.

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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, 1988

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.22	0.029	13.43	0.16	0.26
Aperture spacing, mm	40	0.37	0.047	12.81	0.29	0.53
Vesicle width, mm	40	0.11	0.024	21.00	0.07	0.18
Vesicles per aperture	25	7.6	1.381	18.07	5.0	11.0
Vesicle spacing, mm	30	0.07	0.015	21.08	0.05	0.10

Canutrypa hemispheroidea (Yang, 1954)

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

Eostenopora conspersa Volkova, 1974

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.26	0.025	9.39	0.20	0.31
Aperture spacing, mm	40	0.31	0.036	11.44	0.25	0.42
Aperture width, mm (maculae)	20	0.39	0.026	6.75	0.33	0.44
Aperture spacing, mm (maculae)	20	0.48	0.072	15.01	0.40	0.65
Acanthostyle diameter, mm	30	0.035	0.006	18.25	0.025	0.050
Acanthostyles per aperture	40	5.7	0.687	12.05	4.0	7.0
Exilazooecia width, mm	30	0.08	0.023	29.05	0.05	0.13
Exozonal wall thickness, mm	20	0.04	0.010	27.04	0.02	0.06
Autozooecial diaphragm spacing, mm	20	0.22	0.066	29.51	0.11	0.36

Leptotrypella radiata Bigey, 1988

	N	X	SD	CV	MIN	MAX
Aperture width, mm	31	0.14	0.027	20.01	0.09	0.19
Aperture spacing, mm	22	0.22	0.023	10.36	0.18	0.25
Exilazooecia width, mm	5	0.04	0.019	44.73	0.02	0.06
Acanthostyle diameter, mm	2	0.025	0.007	28.28	0.020	0.030
Exozonal wall thickness, mm	6	0.07	0.012	16.90	0.06	0.09

Triznotrypa potii n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	15	0.16	0.017	10.62	0.13	0.19
Aperture spacing, mm	15	0.25	0.017	6.91	0.23	0.28

Isostylus veserensis n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	6	0.79	0.161	20.49	0.60	1.08
Exozone width, mm	6	0.22	0.046	21.36	0.15	0.29
Endozone width, mm	6	0.36	0.082	23.03	0.30	0.50
Aperture width, mm	20	0.11	0.017	15.73	0.09	0.13
Aperture spacing along branch, mm	10	0.35	0.040	11.39	0.29	0.40
Aperture spacing diagonally, mm	10	0.18	0.020	10.94	0.15	0.22
Acanthostyle width, mm	20	0.03	0.004	16.96	0.02	0.04

Anastomopora inflata Bigey, 1988

	N	X	SD	CV	MIN	MAX
Branch width, mm	19	0.49	0.074	14.89	0.35	0.62
Branch thickness, mm	10	0.58	0.089	15.41	0.45	0.72
Dissepiment width, mm	6	0.43	0.014	3.24	0.40	0.44
Fenestrule length, mm	12	0.59	0.075	12.71	0.44	0.75
Fenestrule width, mm	12	0.33	0.046	13.98	0.26	0.40
Distance between branch centres, mm	8	0.69	0.096	13.94	0.60	0.84
Distance between dissepiment centres, mm	8	0.93	0.030	3.21	0.87	0.96
Aperture width, mm	12	0.07	0.005	7.44	0.06	0.08
Aperture spacing along branch, mm	12	0.23	0.017	7.66	0.20	0.25
Aperture spacing diagonally, mm	12	0.18	0.010	5.51	0.16	0.20
Maximal chamber width, mm	12	0.13	0.014	11.47	0.11	0.15