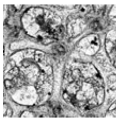
Middle and uppermost Famennian (Upper Devonian) bryozoans from southern Belgium

ZOYA TOLOKONNIKOVA, ANDREJ ERNST, EDOUARD POTY & BERNARD MOTTEQUIN



A stenolaemate bryozoan fauna from the Upper Devonian (middle and uppermost Famennian) of the Dinant Synclinorium, southern Belgium, contains seven species (three trepostomes and four cryptostomes). One genus and four species are new: *Nikiforovastylus ourthensis* gen. et sp. nov., *Dyscritella perforata* sp. nov., *Pseudobatostomella parva* sp. nov., and *Nikiforovella dinantia* sp. nov. Three species are described in open nomenclature: Trepostomata sp. indet., *Nikiforovella* sp., and Rhomboporidae sp. indet. Middle Famennian Trepostomata sp. indet. shows morphology not previously recorded in Palaeozoic bryozoans. • Key words: Upper Devonian, Famennian, Belgium, Bryozoa, taxonomy.

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Knowledge of Devonian–Carboniferous bryozoans from Belgium is based mainly on lists of fossils devoid of illustration (*e.g.* Maillieux 1933, Demanet 1958). Information about Devonian bryozoans from this region is thus very scarce: only a small number species from the Middle Devonian and the Frasnian have been described to date (Salée 1919; Dessilly 1961, 1967; Dessilly & Kraüsel 1962, 1963). Their Mississippian counterparts are known from two dozen species, which are placed in the Orders Fenestrida and Cryptostomida, and were described by de Koninck (1842–1844), Demanet (1938), and Kaisin (1942). However the majority of these species remain inadequately characterised and thus has an historical value only because the descriptions were made on the external colony shape. No information about internal morphology was provided by earlier authors, and it is this that is tremendously important for the provision of detailed and accurate systematic treatments and taxonomic identifications.

Despite their great abundance in several levels of the Devonian and Carboniferous succession of Belgium (Namur–Dinant Basin), notably within the Waulsortian buildups of Tournaisian age (Lees 1988, 2006; Wyse Jackson 2006) and in some small Livian reefs (middle Viséan) (Lauwers 1992, Chevalier & Aretz 2005), bryozoans from this area have received scant attention from specialists. As recently stressed by Ernst & Herbig (2010), Famennian bryozoans from Western Europe remain poorly known in spite of some papers published recently (*e.g.* Weber & Wyse Jackson 2006, Tolokonnikova *et al.* 2014). Therefore, until now, only a partial view of their diversity is available whereas there is urgent need to improve the quality of information of the evolution and renewal of bryozoan associations during this significant time interval in geological history. The Famennian was indeed marked, at its base, by the post-Kellwasser recovery and, at its top, by the Hangenberg Event that took place just below the Devonian–Carboniferous boundary (*e.g.* Kaiser *et al.* 2011).

Belgium is the historical type area of the Famennian Stage (Thorez *et al.* 2006), which is the youngest of the Upper Devonian. Its name originated from the Famenne region in southern Belgium and was first proposed by Dumont (1855). Although the bryozoans have been neglected so far, the other marine faunas from the area and horizon have been widely studied, notably those that can be used for regional and global biostratigraphy (Thorez *et al.* 1977, Poty *et al.* 2006), such as brachiopods (*e.g.* Sartenaer 1972, Mottequin 2008), conodonts (*e.g.* Bouckaert *et al.* 1965, Dreesen 1978), corals (*e.g.* Poty 1999, Poty *et al.* 2006, Denayer *et al.* 2012), and the foraminifers (Conil *et al.* 1986, Poty *et al.* 2006).

The present paper is the first systematic study of bryozoans from the middle and uppermost Famennian of the

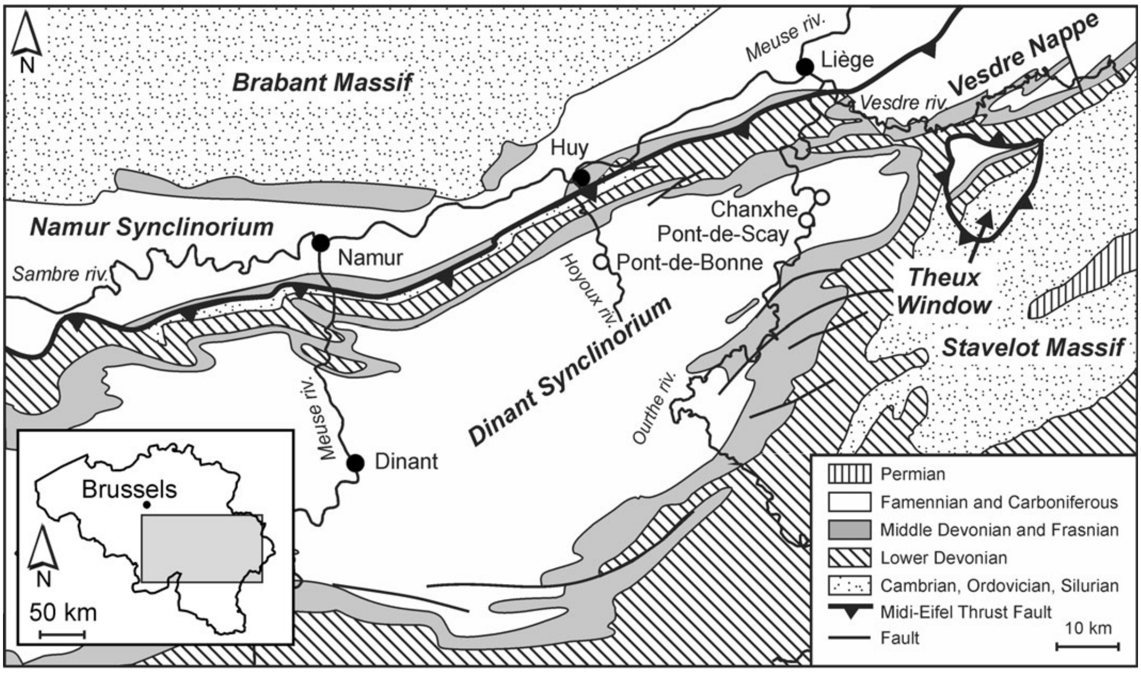

Figure 1. Location and schematic geological map of southern Belgium with indication of the sampled localities (modified from de Béthune 1954).

Dinant Synclinorium (southern Belgium). They are of interest for biodiversity studies and allow for comparisons with other Famennian bryozoan faunas from Eurasia.

Material and methods

The studied material comes from three localities situated in the northern (Pont-de-Bonne) and the eastern (Chanxhe and Pont-de-Scay) parts of the Dinant Synclinorium (Fig. 1). All the localities were sampled during the summer 2013 and 23 thin sections were prepared: four sections from Pont-de-Bonne (PDB), 13 sections from Pont-de-Scay (PDS), and six from Chanxhe (Ch). This material was complemented by the study in 2013 of the E. Poty collections of lithological and coral thin sections.

The investigated bryozoans were studied in thin sections using a transmitted light binocular microscope. Morphological character terminology is adopted from Anstey & Perry (1970) for trepostomes, and Hageman (1993) for cryptostomes. All the studied material is housed at the Department of Palaeontology of the University of Liège (prefix: ULg).

Geological setting

The Dinant Synclinorium is a Variscan structural element, along with the "Namur Synclinorium" (see Belanger *et al.* 2012 for discussion about the this structural unit), the Vesdre area and the Theux Window, constituted the Namur–Dinant Basin (Fig. 1), which developed along the southeastern margin of Laurussia during Devonian and Mississippian times. The Famennian is particularly well developed in the Dinant Synclinorium where it comprises a 600 m-thick sequence, which is predominantly dominated by siliciclastic sediments with some carbonate levels (Thorez *et al.* 2006). The depositional setting approximately corresponds to a ramp with an accentuation of the marine influence and a southward deepening setting (Thorez *et al.* 2006). Therefore, the northern proximal facies, which frequently show a continental influence, are dominantly sandy, silty and shaly, whereas the southern distal facies are essentially shaly with some carbonate intercalations.

Bryozoans were recovered from three distinct lithostratigraphic units, namely the Souverain-Pré, Comblain-au-Pont and Hastière formations (Fig. 2). The middle Famennian Souverain-Pré Formation comprises to thick layers (pluridecimetric to plurimetric) of nodular, bioclastic (crinoids, brachiopods, bryozoans) limestones with shaly to silty cement and intercalations of calcareous sandstones (*e.g.* Dreesen 1978, Bultynck & Dejonghe 2002, Thorez *et al.* 2006). Locally, in the Vesdre area, red-stained carbonate mudmounds are developed and these make up to the Baelen Member (Dreesen *et al.* 1985, 2013). Material from the Souverain-Pré Formation has been collected in the Pont-de-Bonne section (N 50°27´ 03.38˝; E 5°16´ 57.48˝) in the Hoyoux valley, which was previously described by Bouckaert *et al.* (1965) and Dreesen (1978). This lithostratigraphic unit reaches at least 10 m in thickness in this section (its top is not exposed) and is

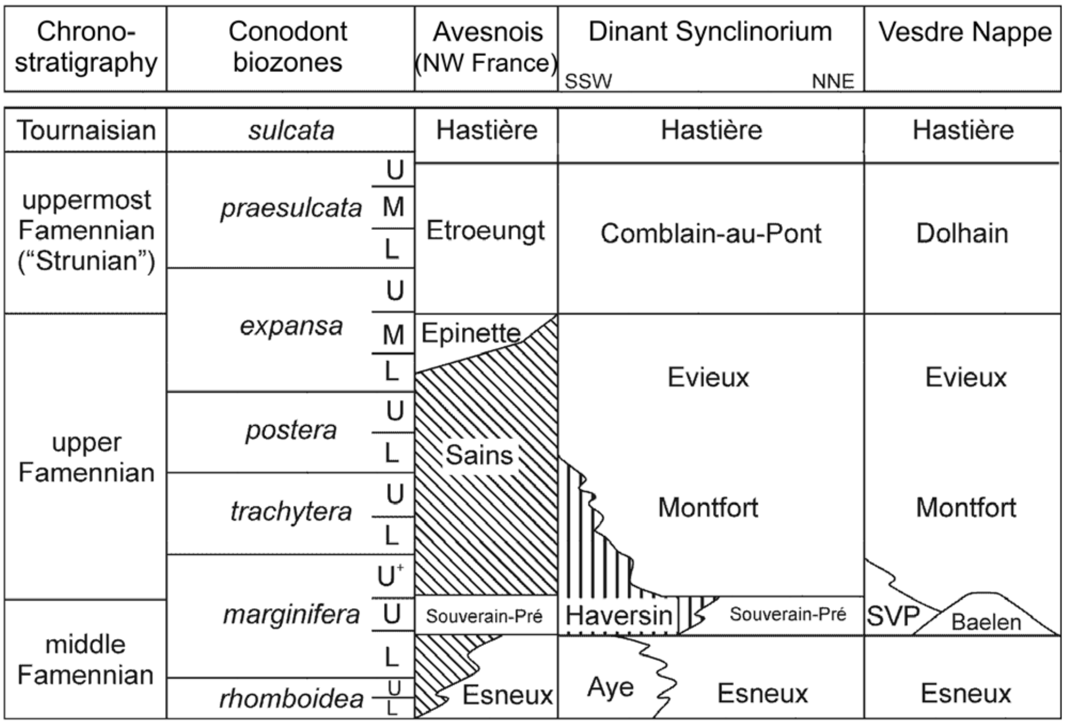

Figure 2. Partial lithostratigraphical scheme of the middle Famennian to the base of the Tournaisian in some tectonic units of southern Belgium (Dinant Synclinorium, Vesdre Nappe) and northern France (Avesnois) (modified from Thorez *et al.* 2006)

included in the *Palmatolepis marginifera* conodont Zone (Dreesen 1978).

The uppermost Famennian ("Strunian") Comblain-au-Pont Formation is composed of green shales and siltstones interbedded with argillaceous or calcareous, micaceous sandstones, and limestones. The latter are frequently crinoidal and become more abundant at the top of the formation (Bultynck & Dejonghe 2002). The presence of stromatoporoid biostromes is characteristic of this unit. Bryozoans from the Comblain-au-Pont Formation come from the Chanxhe (Ch.) and Pont-de-Scay sections, both are situated in the Ourthe valley. The Chanxhe section (N 50°30′ 17.15″; E 5°35′ 47.31″) has been described in great detail by several authors (*e.g.* Conil 1964, Maziane *et al.* 1999, Casier *et al.* 2005, Maziane-Serraj *et al.* 2007). We refer here to Conil (1964)'s bed numbers (*e.g.* Ch-127) that were used by subsequent workers. The Pont-de-Scay section (N 50°29′ 02.63″; E 5°34′ 58.67″) was previously described by several authors for its Tournaisian and Viséan succession (*e.g.* Conil 1968, Groessens 1975, Poty *et al.* 2011). Figure 3 illustrates the contact between the Comblain-au-Pont and the Hastière Formation in this section.

The Hastière Formation is essentially calcareous with thin shaly intercalations (see Poty *et al.* 2002 for a complete description). The bottom part of the formation is of uppermost Famennian age and yields typical elements of a Devonian fauna, but they are generally reworked; the rest of the formation is of Hastarian age (basal Tournaisian). Only the bryozoans from the basal bed (No. 101) of the Hastière Formation exposed in the Pont-de-Scay (see above) section have been studied. According to Poty *et al.* (2011), who placed the base of the Hastière Formation at the first occurrence of a metre-thick limestone bed, the facies is unchanged between the limestones of the top of the Comblain-au-Pont and those of the base of the Hastière Formation, but the last uppermost Famennian faunas (*Cryptophyllus*, quasiendothyrids) are found in the first bed (bed No. 101) of the latter (Fig. 3).

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Trepostomida Ulrich, 1882
Suborder Amplexoporina Astrova, 1965
Family Dyscritellidae Dunaeva & Morozova, 1967

Genus *Dyscritella* Girty, 1911

Type species. – *Dyscritella robusta* Girty, 1911. Mississippian (Lower Carboniferous); Arkansas, USA.
Diagnosis. – Dendroid and encrusting colony with abundant acanthostyles and exilazooecia. Autozooecia parallel to longitudinal direction of the colony in endozone; gradually bending outward in exozone. Diaphragms in autozooecia lacking or very rare; lacking in exilazooecia.

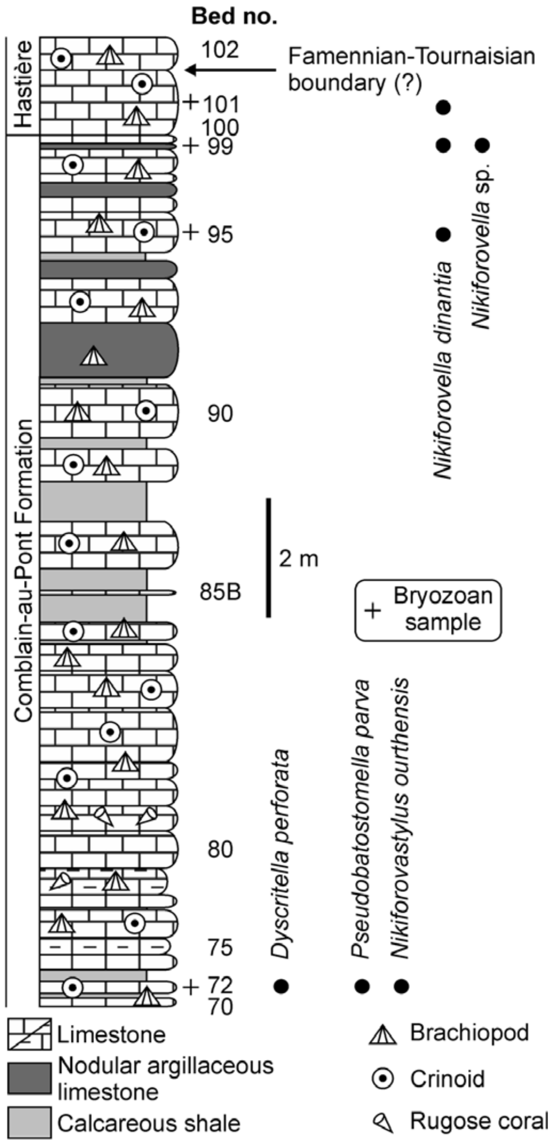

Figure 3. Schematic log of the upper part of the Comblain-au-Pont Formation and the base of the Hastière Formation in the Pont-de-Scay section (modified from unpublished data of R. Conil and M. Sautois).

Exilazooecia circular to angular in cross section and separated from the autozooecia and from each other by thick walls. Two sizes of acanthostyles may be present. Zooecial walls thin in endozone, rapidly thickening in the exozone (modified after Ernst & Gorgij 2013).

Remarks. – *Dyscritella* Girty, 1911 generally lacks diaphragms which are commonly developed in the similar genus *Dyscritellina* Morozova *in* Dunaeva & Morozova, 1967. Furthermore, *Dyscritellina* has extremely large acanthostyles, which are absent in *Dyscritella*.

Occurrence. – Devonian to Triassic; worldwide.

Dyscritella perforata **sp. nov.**
Figure 4A–H, Table 1

Type horizon and locality. – Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation; Pont-de-Scay, Belgium.

Holotype. – ULg PDS-72a.

Paratypes. – ULg PDS-72 (2007), PDS-72d, e, f, h, j, k, l, m, ULg Ch-113a.

Etymology. – The species name refers to the presence of abundant exilazooecia (from Latin "*perforata*" – porous).

Diagnosis. – Encrusting colonies; autozooecial diaphragms rare to absent; exilazooecia abundant, 5–11 surrounding each autozooecial aperture, 0.015–0.07 mm wide; acanthostyles abundant 0.015–0.045 mm in diameter, 2–6 surrounding each autozooecial aperture; maculae not observed.

Description. – Colonies encrusting often cylindrical ephemeral substrates, therefore, appearing tubulose. Encrusting sheets 0.20–0.45 mm thick. Autozooecia growing from 0.003–0.006 mm thick epitheca, for the short distance parallel to the substrate, then bending sharply to the colony surface. Autozooecial diaphragms rare to absent, thin. Autozooecial apertures rounded to slightly polygonal. Exilazooecia abundant, 0.015–0.07 mm wide, 5–11 surrounding each autozooecial aperture, with polygonal apertures. Acanthostyles abundant 0.015–0.045 mm in diameter, locally indenting autozooecial apertures, having distinct hyaline cores and wide laminated sheaths, 2–6 surrounding each autozooecial aperture. Autozooecial walls laminated, 0.005–0.010 mm thick in endozones; laminated, merged without zooecial boundaries, 0.02–0.05 mm thick in exozone. Maculae not observed.

Remarks. – *Dyscritella perforata* sp. nov. differs from *D. clara* (Trizna 1958) from the Tournaisian of the Kuznetsk

Figure 4. A–H – *Dyscritella perforata* sp. nov. • A, B – longitudinal section, holotype ULg PDS-72a. • C – tangential section, holotype ULg PDS-72a. • D – tangential section, paratype ULg PDS-72d. • E–G – longitudinal section, paratype ULg PDS-72h. • H – tangential section, paratype ULg PDS-72f. • I–K – *Pseudobatostomella parva* sp. nov. • I – oblique section of the branch, paratype ULg PDS-72g. • J – branch transverse section, paratype ULg PDS-72g. • K – tangential section, holotype ULg PDS-72c.

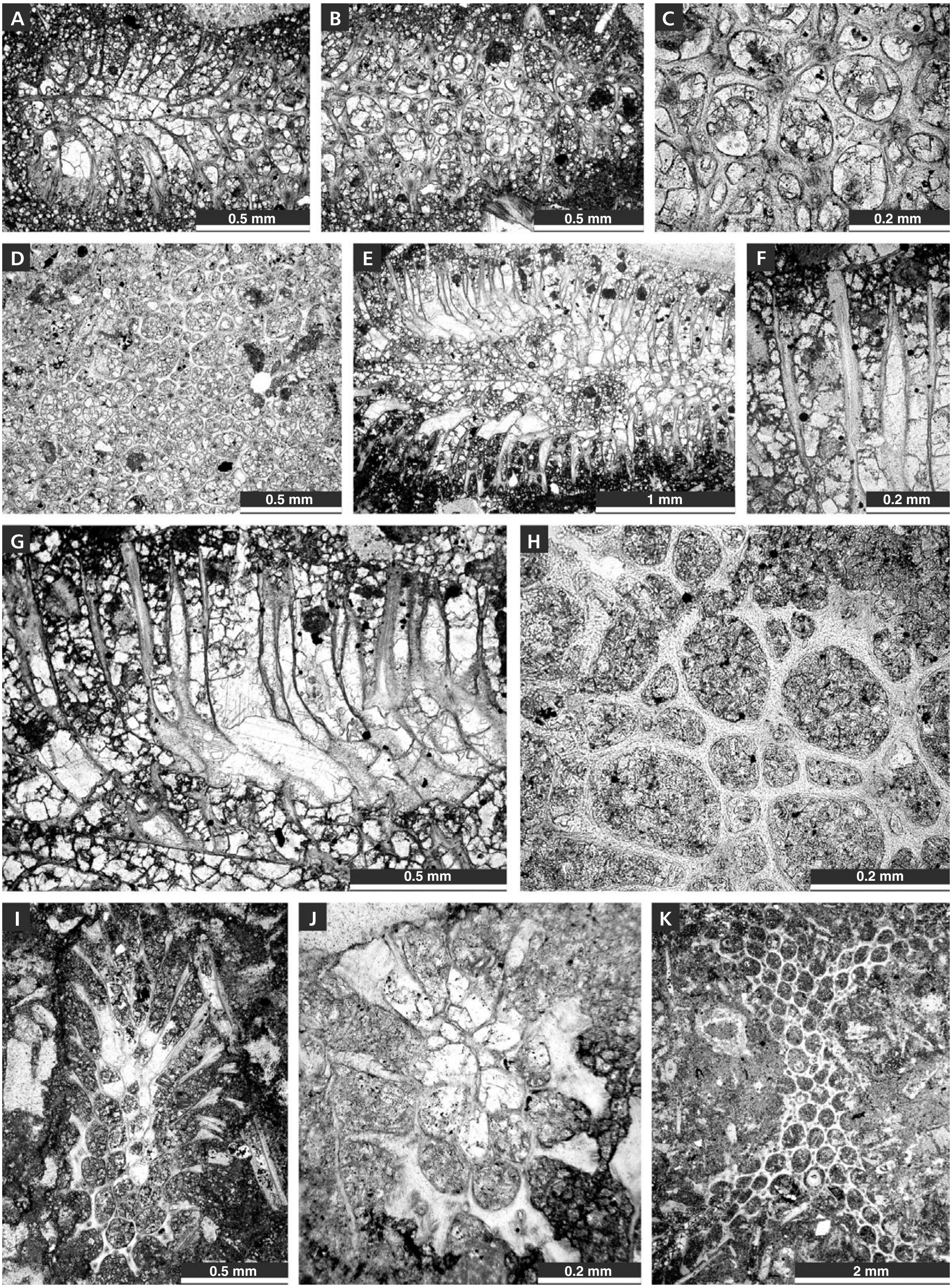
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Table 1. Measurements of *Dyscritella perforata* sp. nov. Abbreviations: F = number of measured fragments; N = number of measurements; X = mean; SD = standard deviation; CV = coefficient of variation; MIN = minimal value; MAX = maximal value.

	F	N	X	SD	CV	MIN	MAX
Colony thickness, mm	9	10	0.45	0.173	38.82	0.20	0.75
Autozooecial aperture width, mm	12	50	0.14	0.016	12.00	0.10	0.17
Autozooecial aperture spacing, mm	12	50	0.20	0.032	15.78	0.14	0.28
Exilazooecia width, mm	12	54	0.041	0.012	28.93	0.015	0.070
Acanthostyle diameter, mm	12	45	0.031	0.009	27.57	0.015	0.045
Exilazooecia per aperture	12	30	7.6	1.632	21.47	5.0	11.0
Acanthostyles per aperture	12	30	2.7	0.884	33.15	2.0	6.0
Exozonal wall thickness, mm	12	10	0.03	0.009	34.88	0.02	0.05

Basin in colony form (encrusting *vs* branched ramose), possessing more abundant exilazooecia and in smaller autozooecial apertures (0.10–0.17 mm *vs* 0.16–0.24 mm in *D. clara*). *Dyscritella perforata* sp. nov. differs from *D. multifida* Lee, 1912 from the Tournaisian of Ireland in colony form (encrusting *vs* branched ramose). No measurements are given for the latter species, except of arrangement of 40 apertures per 10 mm (Lee 1912, p. 180). This value produces an average autozooecial aperture spacing of 0.25 mm, which is larger than in *D. perforata* (0.20 mm in average).

Occurrence. – Pont-de-Scay, Chanxhe, Belgium; uppermost Famennian.

Genus *Pseudobatostomella* Morozova, 1960

Type species. – *Batostomella spinulosa* Ulrich, 1890. Mississippian (Lower Carboniferous); Kentucky, U.S.A.

Diagnosis. – Ramose cylindrical colonies. Autozooecial apertures irregularly rounded or oval, arranged in more or less regular diagonal rows. Diaphragms complete, thin, most abundant in the transition between endozones and exozones. Exilazooecia usually rare, short. Acanthostyles small, abundant, regularly sized. Walls irregularly thickened.

Remarks. – The genus *Pseudobatostomella* Morozova, 1960 differs from the genus *Dyscritella* Girty, 1911 in its autozooecial budding pattern, the presence of diaphragms and regularly sized acanthostyles.

Occurrence. – Upper Devonian to Upper Permian; worldwide.

Pseudobatostomella parva sp. nov.
Figures 4I–K, 5A–E, Table 2

Type horizon and locality. – Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation; Pont-de-Scay, Belgium.

Holotype. – ULg PDS-72c.

Paratypes. – ULg PDS-72b, h, m.

Etymology. – The species name refers to the small size of this species (from Latin "*parva*" – small).

Diagnosis. – Thin branched colonies; autozooecial apertures rounded; autozooecial diaphragms rare; 1–5 exilazooecia surrounding each autozooecial aperture; 3–8 acanthostyles surrounding each autozooecial aperture; maculae not observed.

Description. – Branched colonies, 0.40–0.80 mm in diameter, with 0.13–0.20 mm wide exozones and 0.10–0.40 mm wide exozones. Autozooecia long in endozones, bending at low angles in exozones. Autozooecial apertures rounded. Autozooecial diaphragms rare. Autozooecial walls laminated, 0.005–0.075 mm thick in endozone; merged without visible zooecial boundaries, 0.025–0.040 mm thick in exozone. Exilazooecia 0.018–0.045 mm wide, short, common to abundant, 1–5 surrounding each autozooecial aperture. Acanthostyles abundant, 0.015–0.040 mm in diameter, with narrow hyaline cores and wide laminated sheaths, 3–8 surrounding each autozooecial aperture. Maculae not observed.

Remarks. – *Pseudobatostomella parva* sp. nov. differs from *P. amazagensis* Modzalevskaya, 1960 from the Famennian of Transbaikalia in having narrower branches (0.40–0.80 mm *vs* 2.0 mm in *P. amazagensis*) and larger autozooecial apertures (0.11–0.19 mm *vs* 0.10–0.12 mm in *P. amazagensis*). *Pseudobatostomella parva* sp. nov. differs from *P. abrupta* (Ulrich, 1890) from the Mississippian of the USA in its narrower branches (0.40–0.80 mm *vs* 2.0–3.0 mm in *P. abrupta*).

Occurrence. – Pont-de-Scay, Belgium; uppermost Famennian.

Figure 5. A–E – *Pseudobatostomella parva* sp. nov. • A, B – tangential section, holotype ULg PDS-72c. • C–E – longitudinal section, holotype ULg PDS-72c. • F–H – Trepostomata sp. indet. • F, G – branch transverse section, ULg PDB-5-21b. • H – branch transverse section, ULg PDB-5-21a.

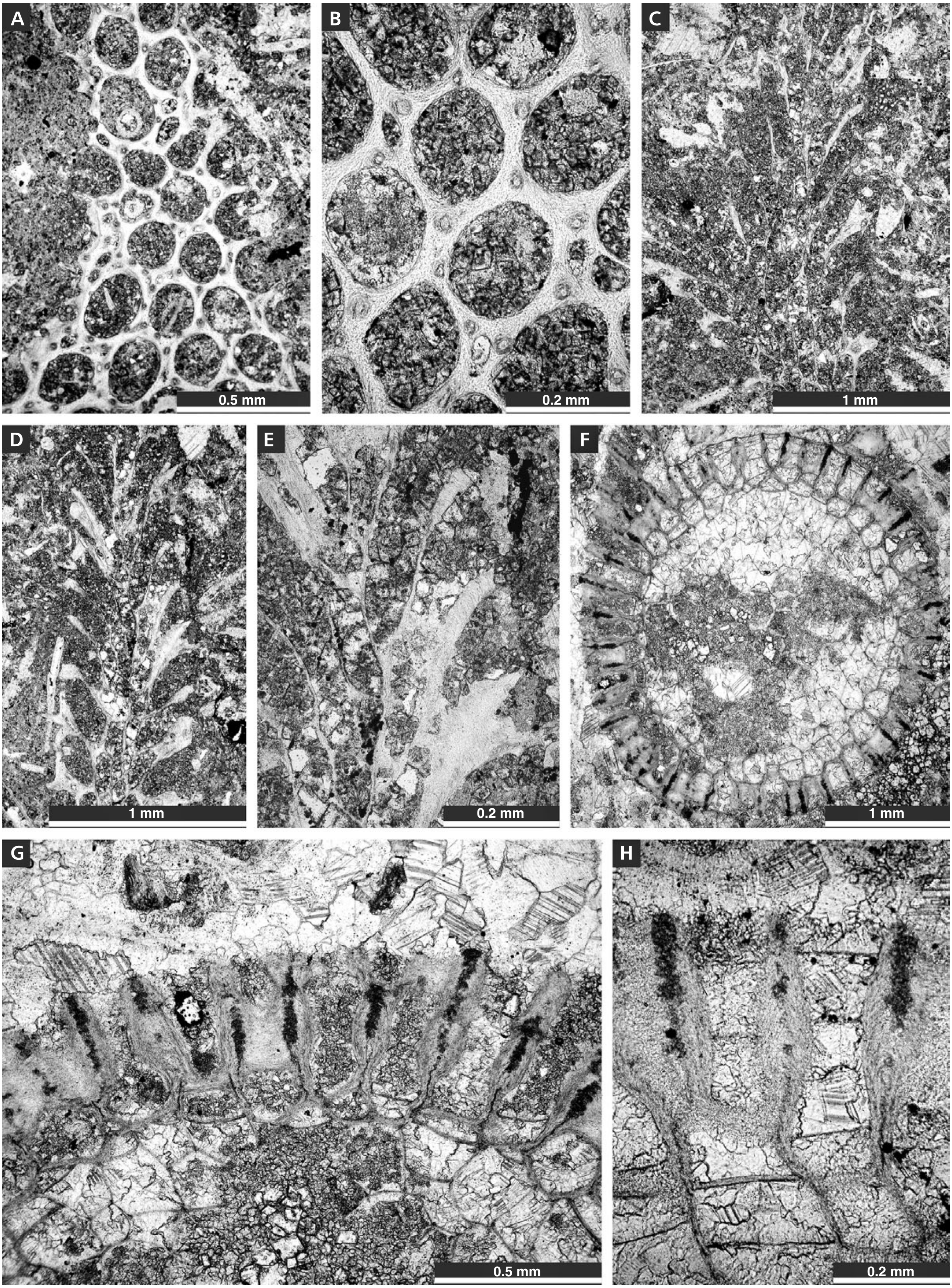
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Table 2. Measurements of *Pseudobatostomella parva* sp. nov. Abbreviations as in Table 1.

	F	N	X	SD	CV	MIN	MAX
Branch width, mm	5	5	0.60	0.146	24.30	0.40	0.80
Exozone width, mm	5	5	0.16	0.026	16.72	0.13	0.20
Endozone width, mm	5	5	0.29	0.114	39.54	0.10	0.40
Autozooecial aperture width, mm	6	25	0.14	0.020	14.20	0.11	0.19
Autozooecial aperture spacing, mm	6	25	0.20	0.029	14.70	0.16	0.26
Acanthostyle diameter, mm	6	30	0.028	0.006	21.86	0.015	0.040
Acanthostyles per aperture	6	25	5.04	1.136	22.54	3.0	8.0
Exilazooecia width, mm	6	30	0.028	0.008	28.41	0.018	0.045
Exilazooecia per aperture	6	21	2.81	1.030	36.68	1.0	5.0
Exozone wall thickness, mm	5	5	0.03	0.006	19.08	0.025	0.040

Family uncertain

Trepostomata sp. indet.
Figures 5F–H, 6A–C

Material. – ULg PDB 5-21a-d.

Description. – Branched colonies, 2.38–3.25 mm in diameter, with 0.30–0.45 mm wide exozones and 1.48–2.55 mm wide exozones. Secondary overgrowth occurring, 0.40–0.65 mm thick. Autozooecia long in endozones, bending abruptly in exozones. Autozooecial apertures rounded-polygonal, 0.11–0.15 mm in diameter. Autozooecial diaphragms common to abundant in the transition between endozone and exozone, straight, thin to moderately thick. Autozooecial walls laminated, 0.025–0.075 mm thick in endozone; with serrated dark zooecial boundaries at the base of exozone and merged in the outer part of exozone, 0.03–0.11 mm thick in exozone. Heterostyles abundant, consisting of dark granulated material, irregularly shaped, restricted to exozone and not protruding above the colony surface, 0.03–0.04 mm in diameter. Maculae not observed.

Remarks. – The present material displays a type of heterostyles, which is hitherto unknown in Palaeozoic bryozoans. They bear slight resemblance to cryptostyles of the cryptostome genus *Cryptostyloecia* Ernst, Königshof & Schäfer, 2009, from the Middle Devonian of Western Sahara. However, those styles have smooth outlines in longitudinal section, whereas heterostyles in the present material are irregularly shaped (Fig. 5G, H). The usual type of styles in Palaeozoic bryozoans are acanthostyles, which represent cylindrical bodies with a distinct hyaline core jacketed by laminated sheath (Armstrong 1970; Blake 1973, 1983; see *Dyscritella perforata* sp. nov., Fig 4C, H, and *Pseudobatostomella parva* sp. nov., Fig. 5A, B). Acanthostyles usually protrude above the colony surface, often implying a protective function. Alternative opinion regards acanthostyles as supporting structures of the surficial tissue (Tavener-Smith 1975). Such structures are unknown in living bryozoans, therefore we do not know their function. Some modern bryozoans can produce spines as a reaction to the presence of predators (nudibranchs) (*e.g*., Harvell 1984, 1992). The truth may be that the function of acanthostyles depends on their morphology and position in the colony (*e.g*., Blake 1983). Some trepostome genera have heterostyles, which consist of granular material and have irregular shape. The most similar genus *Nikiforopora* Dunaeva, 1964 from the Mississippian of Ukraine and Russia, has normal acanthostyles and smaller heterostyles without cores, which resemble the styles of the present material. However, *Nikiforopora* possesses hemiphragms, which are absent in the present species. Besides the styles, the present species shows characteristic morphology of autozooecial walls (serrated in the basal exozone and merged in the outer exozone), which makes it similar to amplexoporine trepostomes, especially stenoporids.

Occurrence. – Pont-de-Bonne, Belgium; Upper Devonian, middle Famennian, base of the Souverain-Pré Formation.

Order Cryptostomida Vine, 1884
Suborder Rhabdomesina Astrova & Morozova, 1956
Family Rhomboporidae Simpson, 1895

Rhomboporidae sp. indet.
Figure 6D–I, Table 3

Material. – ULg Ch-127a-b, Ch-150c, PDS-72a, b, h, m.

Description. – Branched colonies, 0.54–0.80 mm in diameter, with 0.16–0.25 mm wide exozones and 0.22 to 0.35 mm wide exozones. Autozooecia growing from the distinct median axis, long in endozones, bending at low angles in exozones. Autozooecial apertures rounded. Autozooecial diaphragms rare. Autozooecial walls laminated, 0.005 to 0.0075 mm thick in endozone; laminated,

Figure 6. A–C – Trepostomata sp. indet., ULg PDB-5-21d. • A – branch longitudinal section. • B – longitudinal section of exozone. • C – oblique tangential section. • D–I – Rhomboporidae sp. indet. • D, E – longitudinal section, ULg PDS-72a. • F – tangential section, ULg PDS-72a. • G, H – longitudinal section, ULg Ch-127. • I – branch oblique section, ULg Ch-127.

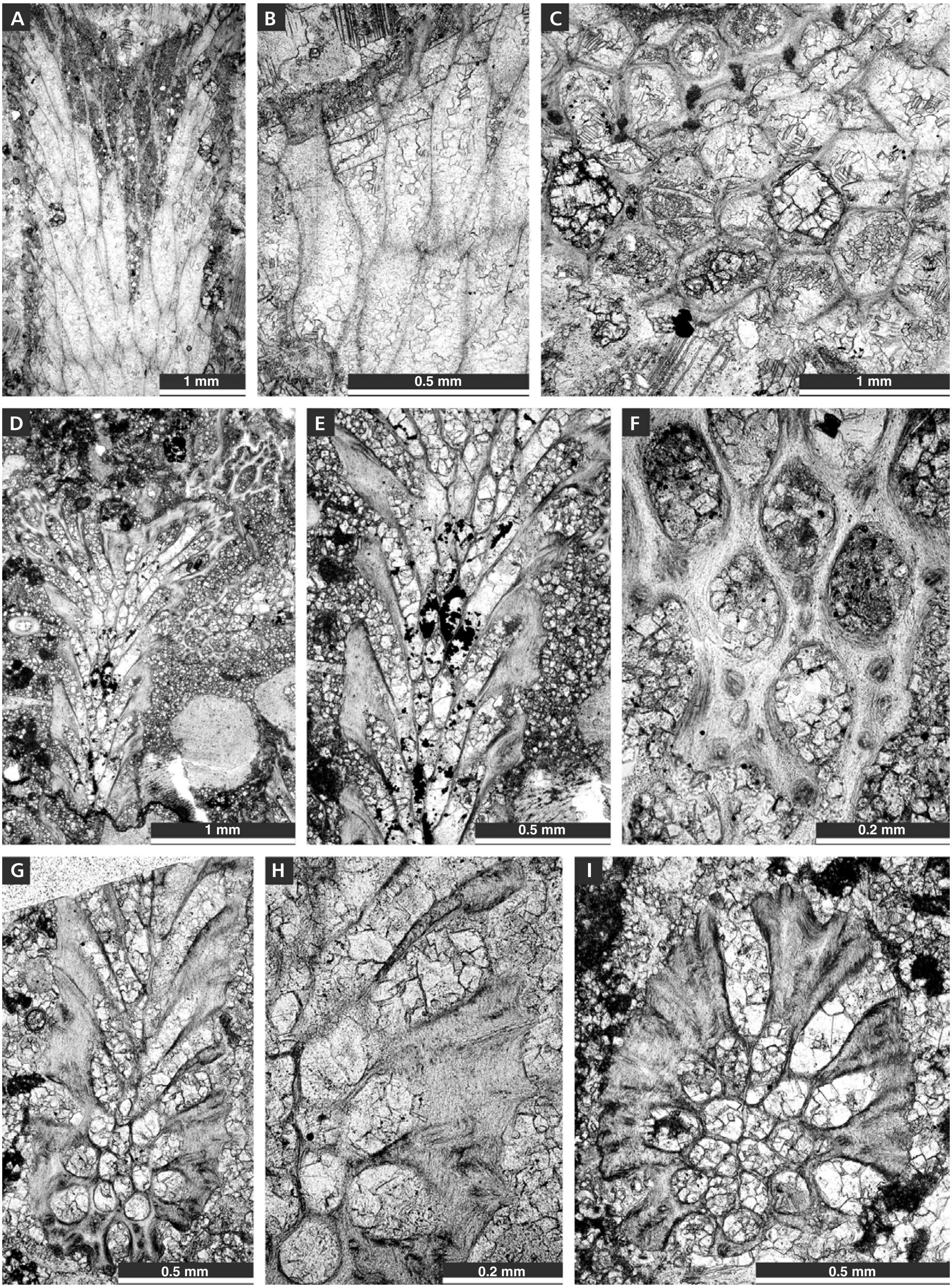
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Table 3. Measurements of Rhomboporidae sp. indet. Abbreviations as in Table 1.

	F	N	X	SD	CV	MIN	MAX
Branch width, mm	6	6	0.69	0.089	12.82	0.54	0.80
Exozone width, mm	6	6	0.20	0.030	15.10	0.16	0.25
Endozone width, mm	6	6	0.30	0.044	14.87	0.22	0.35
Autozooecial aperture width, mm	7	20	0.09	0.011	12.94	0.06	0.10
Autozooecial aperture spacing, mm	7	17	0.19	0.021	10.85	0.15	0.23
Acanthostyle diameter, mm	7	25	0.03	0.007	18.83	0.02	0.05
Exozonal wall thickness, mm	5	5	0.047	0.011	23.04	0.035	0.063

merged without visible zooecial boundaries, 0.035 to 0.063 mm thick in exozone. Acanthostyles common to abundant, 0.02 to 0.05 mm in diameter. Heterozooecia absent. Maculae not observed.

Remarks. – The present material resembles *Klaucena* (*Spira*) Trizna, 1958 from the Tournaisian of the Kuznetsk Basin in Russia. It differs in more abundant acanthostyles [4–8 *vs* 1–2 in *Klaucena* (*Spira*)] and forming median axis only [*vs* median axis and mesotheca in *Klaucena* (*Spira*)].

Occurrence. – Pont-de-Scay, Chanxhe, Belgium; Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation.

Family Nikiforovellidae Goryunova, 1975

Genus *Nikiforovastylus* gen. nov.

Type species. – *Nikiforovastylus ourthensis* sp. nov., by original designation. Upper Devonian, uppermost Famennian; Pont-de-Scay, Belgium.

Etymology. – The genus is named in honour of Alexandra I. Nikiforova (1894–1939), Russian bryozoologist in acknowledgement of her contribution to the study of Palaeozoic bryozoans.

Diagnosis. – Branched colonies. Autozooecia diverging at low angles from distinct median axis, polygonal at their bases in endozone, with rounded apertures at colony surface. Hemisepta absent, diaphragms rare. Autozooecial walls laminated, with dark zooecial boundaries. Few metazooecia and aktinotostyles between longitudinally successive autozooecial apertures. Longitudinal ridges absent.

Remarks. – *Nikiforovastylus* gen. nov. differs from *Nikiforovella* Nekhoroshev, 1948 in possessing of aktinotostyles rather than acanthostyles as in the latter genus. *Nikiforovastylus* differs from *Pinegopora* Shishova, 1965 in this regular arrangement of metazooecia and aktinotostyles and in the more regular shape of autozooecia.

Occurrence. – Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation; Pont-de-Scay, Belgium.

***Nikiforovastylus ourthensis* gen. et sp. nov**.
Figure 7A–I, Table 4

Type horizon and locality. – Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation; Pont-de-Scay, Belgium.

Holotype. – ULg PDS-72i.

Paratypes. – ULg PDS-72b, g, k.

Etymology. – The species name refers to the river Ourthe, in the vicinity of the type locality Pont-de-Scay.

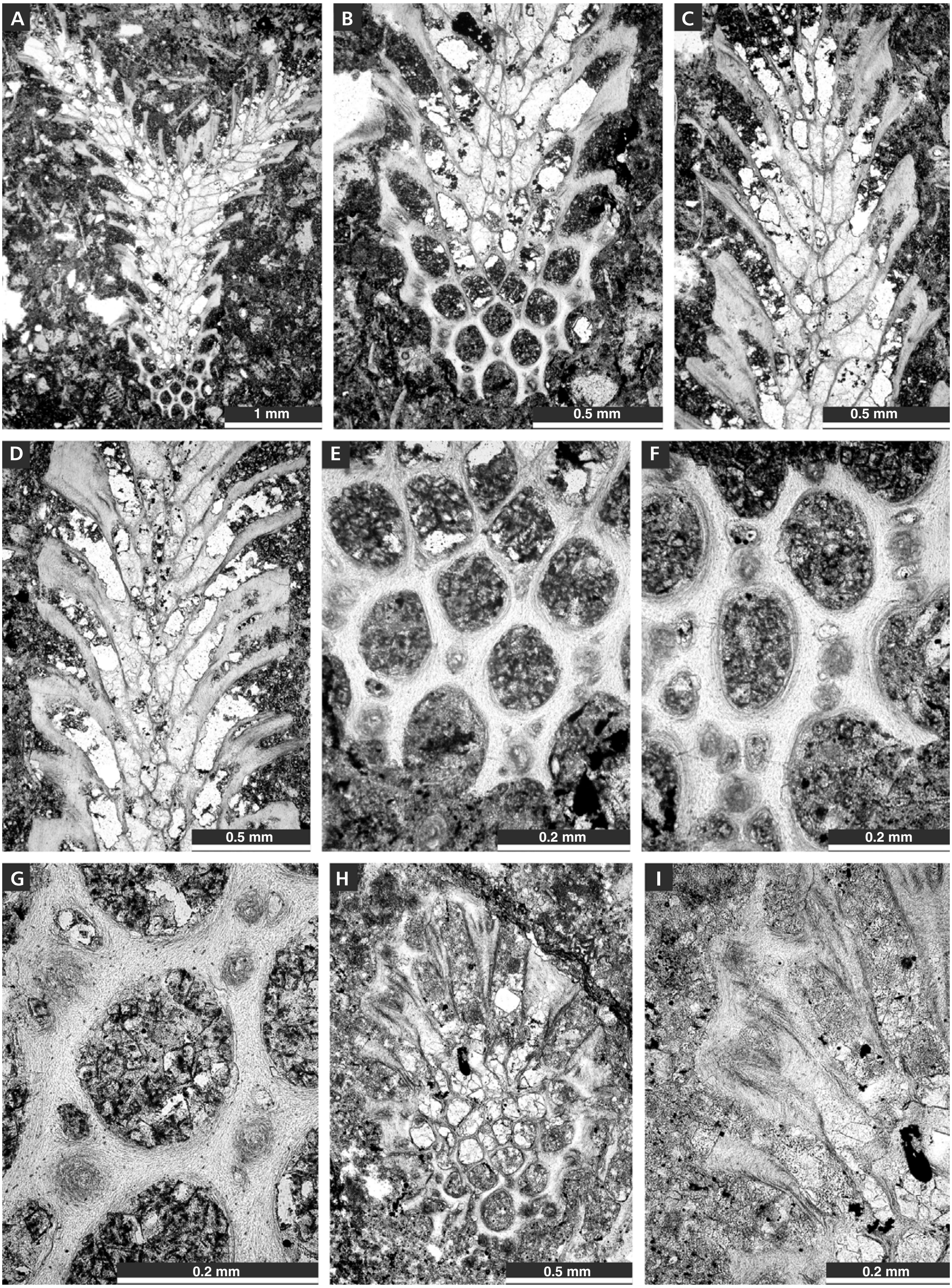
Diagnosis. – As for genus.

Description. – Branched colonies, 0.75–0.96 mm in diameter, with 0.20–0.28 mm wide exozones and 0.35–0.47 mm wide endozones. Autozooecia growing in spiral pattern from the median axis, rhombic in the transverse section of endozone, abruptly bending in exozone. Autozooecial apertures oval to circular, arranged in regular diagonal rows. Autozooecial diaphragms absent. Metazooecia originating at the base of exozone, 1–2 arranged between longitudinally successive autozooecial apertures, 0.013 to 0.045 mm wide. Aktinotostyles 0.02–0.07 mm in diameter, 1–2 arranged between longitudinally successive autozooecial apertures, having distinct hyaline cores and laminated sheaths. Autozooecial walls granular, 0.005–0.010 mm thick in endozone; finely laminated, without visible zooecial boundaries in exozone.

Remarks. – As for genus.

Occurrence. – As for genus.

Figure 7. *Nikiforovastylus ourthensis* sp. nov. • A–D – longitudinal sections, holotype ULg PDS-72i. • E–G – tangential section, holotype ULg PDS-72i. • H–I – branch oblique section, paratype ULg PDS-72b.


A
1 mm
B
0.5 mm
C
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D
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E
0.2 mm
F
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G
0.2 mm
H
0.5 mm
I
0.2 mm

Table 4. Measurements of *Nikiforovastylus ourthensis* gen. et sp. nov. Abbreviations as in Table 1.

	F	N	X	SD	CV	MIN	MAX
Branch width, mm	4	4	0.88	0.098	11.22	0.75	0.96
Exozone width, mm	4	4	0.24	0.033	13.61	0.20	0.28
Endozone width, mm	4	4	0.40	0.053	13.21	0.35	0.47
Autozooecial aperture width, mm	4	25	0.10	0.020	19.41	0.07	0.13
Autozooecial aperture spacing along branch, mm	4	21	0.34	0.030	8.66	0.27	0.39
Autozooecial aperture spacing diagonally, mm	4	21	0.20	0.015	7.51	0.18	0.23
Aktinotostyle diameter, mm	4	25	0.04	0.012	26.17	0.02	0.07
Metazooecia width, mm	4	25	0.027	0.009	34.09	0.013	0.045
Acanthostyles per aperture	4	20	1.5	0.513	34.20	1.0	2.0
Metazooecia per aperture	4	20	1.6	0.503	31.41	1.0	2.0

Genus *Nikiforovella* Nekhoroshev, 1948

Type species. – *Nikiforovella alternata* Nekhoroshev, 1948, by original designation. Mississippian (Lower Carboniferous); Altai, Russia.

Diagnosis. – Branched colonies. Autozooecia diverging at low angles from distinct median axis. Hemisepta absent, diaphragms rare. Autozooecial walls laminated, with dark zooecial boundaries. Metazooecia few between longitudinally successive autozooecial apertures; acanthostyles common to abundant. Longitudinal ridges absent.

Remarks. – *Nikiforovella* Nekhoroshev, 1948 is similar to *Streblotrypella* Nikiforova, 1948, but differs from it mainly in the shape of autozooecia, which bend at higher angles in exozone, and in the absence of longitudinal ridges. Moreover, styles can be absent in *Streblotrypella*.

Occurrence. – Devonian to Permian; worldwide.

Nikiforovella dinantia sp. nov.

Figure 8A–E, Table 5

Type horizon and locality. – Upper Devonian, uppermost Famennian, Comblain-au-Pont Formation; Pont-de-Scay, Belgium.

Holotype. – ULg PDS 95 (19.5–25).

Paratypes. – ULg PDS 99 (base), ULg PDS 95 (30.5–35), ULg PDS 101 (6–10), ULg PDS 99 (45.5–49).

Etymology. – The species is named after the Dinantian synclinorium, in which this species was found.

Diagnosis. – Branched colonies; autozooecial apertures oval to circular, arranged in regular diagonal rows; autozooecial diaphragms absent; 1–2 metazooecia and one acanthostyle arranged between longitudinally successive autozooecial apertures.

Description. – Branched colonies, 0.90–1.26 mm in diameter, with 0.23–0.36 mm wide exozones and 0.42–0.54 mm wide endozones. Autozooecia growing in spiral pattern from the median axis, rhombic in the transverse section of endozone, abruptly bending in exozone. Autozooecial apertures oval to circular, arranged in regular diagonal rows. Autozooecial diaphragms absent. Metazooecia 0.02–0.04 mm wide, originating at the base of exozone, 1–2 arranged between longitudinally successive autozooecial apertures. Single acanthostyle situated between longitudinally successive autozooecial apertures, having distinct hyaline cores and laminated sheaths, 0.025–0.050 mm in diameter. Autozooecial walls granular, 0.003–0.005 mm thick in endozone; finely laminated, without visible zooecial boundaries, 0.025–0.035 mm thick in exozone.

Remarks. – *Nikiforovella dinantia* sp. nov. differs from *N. nitida* Troizkaya, 1979 from the Famennian of Central Kazakhstan in possessing thicker branches (0.90–1.26 mm *vs* 0.60–0.65 mm in *N. nitida*). Furthermore, autozooecial apertures are spaced in *Nikiforovella dinantia* sp. nov. less closely than in *Nikiforovella nitida* (average aperture spacing along the branch 0.27 mm *vs* 0.22 mm in *N. nitida*). The new species differs from *N. gracilis* Ernst & Herbig, 2010 in that it has fewer metazooecia and acanthostyles (1–2 *vs* 1–5 metazooecia between apertures in *N. gracilis*, and one *vs* 1–3 acanthostyles between apertures in *N. gracilis*).

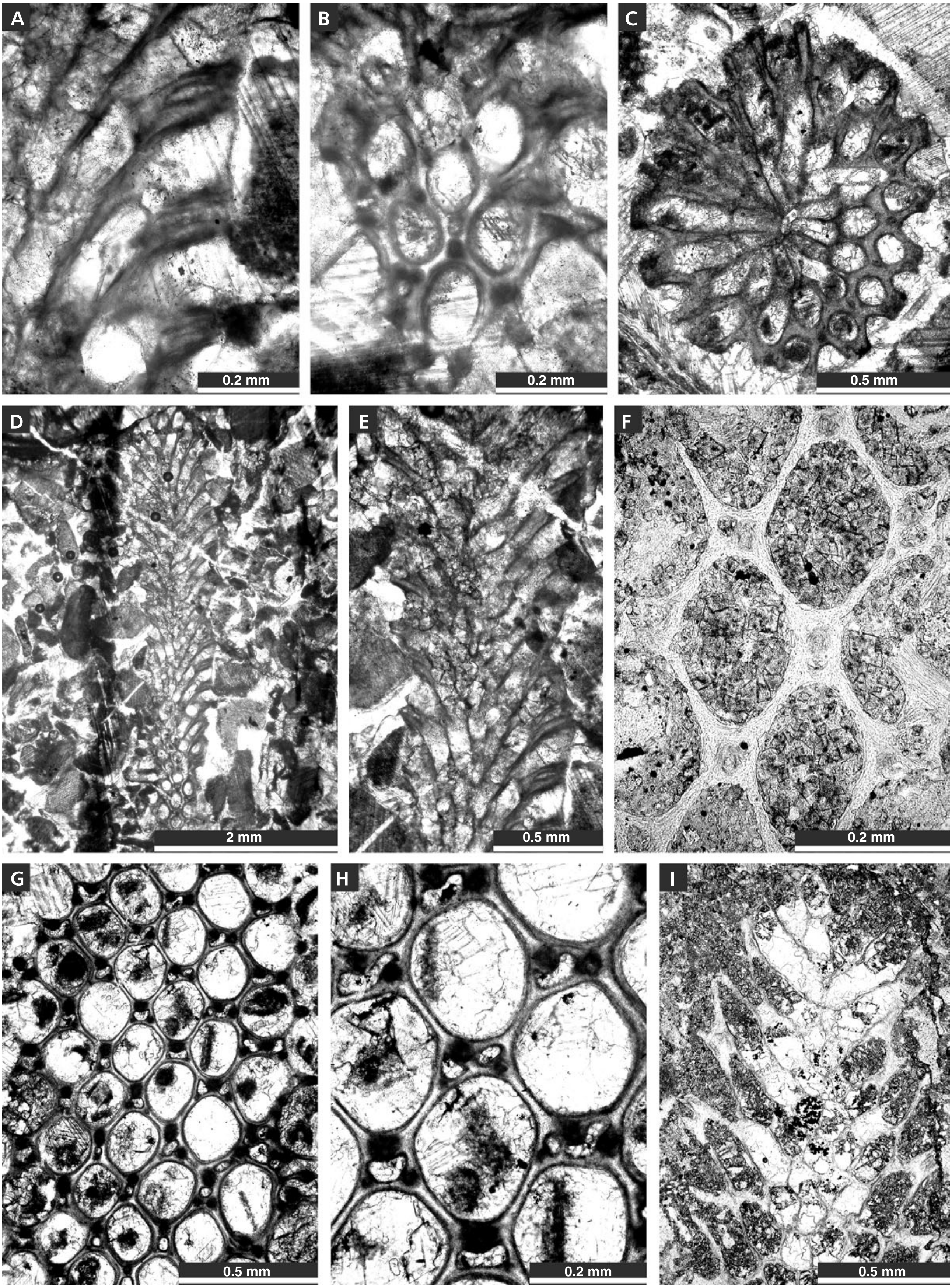
Occurrence. – Pont-de-Scay, Belgium; uppermost Famennian, Comblain-au-Pont Formation.

Nikiforovella sp.

Figure 8F–I, Table 6

Material. – ULg PDS-72c, ULg PDS 99 (base) (two tangential sections of two colonies).

Figure 8. A–E – *Nikiforovella dinantia* sp. nov. • A, B – longitudinal section, holotype ULg PDS-95 (19,5-25). • C – branch oblique section, paratype ULg PDS-99 (45.5–49). • D, E – longitudinal section, holotype ULg PDS-95 (19.5–25). • F–I – *Nikiforovella* sp. • F – tangential section, ULg PDS-72c. • G–H – tangential section, ULg PDS-99. • I – longitudinal section, PDS-72c.


A
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B
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C
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D
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E
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F
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G
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H
0.2 mm
I
0.5 mm

Table 5. Measurements of *Nikiforovella dinantia* sp. nov. Abbreviations as in Table 1.

	F	N	X	SD	CV	MIN	MAX
Branch width, mm	6	6	1.04	0.144	13.85	0.90	1.26
Exozone width, mm	6	6	0.29	0.052	18.40	0.23	0.36
Endozone width, mm	6	6	0.47	0.043	9.23	0.42	0.54
Autozooecial aperture width, mm	6	24	0.11	0.014	13.47	0.08	0.13
Autozooecial aperture spacing along branch, mm	6	8	0.27	0.033	12.18	0.23	0.33
Autozooecial aperture spacing diagonally, mm	6	8	0.19	0.020	10.53	0.15	0.22
Acanthostyle diameter, mm	6	14	0.03	0.007	20.20	0.025	0.05
Metazooecia width, mm	6	18	0.03	0.007	23.28	0.02	0.04
Acanthostyles per aperture	6	6	1.0	0	0	1.0	1.0
Metazooecia per aperture	6	6	1.5	0.548	36.52	1.0	2.0

Table 6. Measurements of *Nikiforovella* sp. Abbreviations as in Table 1.

	F	N	X	SD	CV	MIN	MAX
Autozooecial aperture width, mm	2	40	0.19	0.022	11.94	0.14	0.23
Autozooecial aperture spacing along branch, mm	2	40	0.32	0.037	11.46	0.25	0.40
Autozooecial aperture spacing diagonally, mm	2	40	0.22	0.029	12.95	0.15	0.30
Acanthostyle diameter, mm	2	40	0.037	0.006	15.22	0.025	0.050
Metazooecia width, mm	2	40	0.034	0.009	25.60	0.018	0.050
Acanthostyles per aperture	2	25	2.0	0.889	45.35	1.0	3.0
Metazooecia per aperture	2	25	1.2	0.408	34.02	1.0	2.0

Description. – Branched colonies, branch width unknown. Autozooecial apertures oval to circular, arranged in regular diagonal rows. Autozooecial diaphragms absent. Metazooecia 0.018–0.050 mm wide, originating at the base of exozone, 1–2 arranged between longitudinally successive autozooecial apertures. Acanthostyles 0.025 to 0.050 mm in diameter, 1–3 arranged between longitudinally successive autozooecial apertures, having distinct hyaline cores and laminated sheaths. Autozooecial walls granular, 0.005 to 0.010 mm thick in endozone; finely laminated, without visible zooecial boundaries in exozone.

Remarks. – The present material belongs to the genus *Nikiforovella* because of regular distribution of metazooecia and acanthostyles and regular arrangement of autozooecial apertures implying spiral budding of autozooecia. This species has distinctly larger apertures than the Mississippian species of *Nikiforovella*. However, the restricted material prevents establishing a new species, therefore this material is described in open nomenclature here. *Nikiforovella* sp. differs from *N. alternata* Nekhoroshev, 1956 from the Mississippian of Altai, Russia in its larger autozooecial apertures (autozooecial width 0.14–0.23 mm *vs* 0.08 to 0.12 mm in *N. alternata*). *Nikiforovella* sp. differs from *N. gracilis* Ernst & Herbig, 2010 in its larger autozooecial apertures (autozooecial width 0.14–0.23 mm *vs* 0.08 to 0.14 mm in *N. gracilis*), and in having 1–2 metazooecia rather than 1–5 metazooecia between apertures in the latter species.

Occurrence. – Pont-de-Scay, Belgium; uppermost Famennian, Comblain-au-Pont Formation.

Discussion

The bryozoan fauna from the middle and uppermost Famennian deposits of southern Belgium is very specific. It presents seven bryozoans from that four species and one genus are new. Middle Famennian Trepostomata sp. indet shows morphology not previously recorded in Palaeozoic bryozoans. Nonetheless, further material is required to reach a better identification.

Analysis of the generic composition shows predominance of cosmopolitan taxa over endemic taxa. The bryozoan genera *Pseudobatostomella* and *Nikiforovella* show a significant geological range from the Devonian to Permian. The genus *Dyscritella* is known from Devonian to Triassic strata worldwide. Among these genera, *Nikiforovella* displays the widest geographic distribution during the Famennian. Representatives of this genus are known from the upper Famennian of Germany, Transbaikalia, Kuznetsk Basin, Southern Urals and from the lower part of Famennian of Kazakhstan (Nekhoroshev 1932, Trizna 1958, Troizkaya 1979, Popeko 2000, Ernst & Herbig 2010, Tolokonnikova 2011, Tolokonnikova *et al*. 2014, Ernst *et al.* submitted).

Dyscritella occurs in the upper Famennian deposits of Germany and Mongolia (Ariunchimeg 2000, Ernst & Herbig 2010, Tolokonnikova *et al*. 2014), whereas *Pseudobatostomella* is known from the upper Famennian of Transbaikalia and Kazakhstan (Nekhoroshev 1956, Popeko 2000).

Comparison between the uppermost Famennian bryozoans faunas occurring in the Dinant Synclinorium and those from the Avesnois (northern France), which is the historical type area of the Strunian (Streel *et al.* 2006), cannot be undertaken due to the lack of recent data. Dehée (1929) briefly discussed and illustrated some species present in the Etrœugnt Formation (*e.g*. Mistiaen *et al.* 2013), which is the westernwards time-equivalent of the Comblain-au-Pont Formation, but modern studies are required to give a full account of the bryozoan diversity in this formation.

Conclusions

The present paper provides the first data on middle to uppermost Famennian bryozoans of southern Belgium. The studied fauna is represented by seven bryozoans, including three new species of cosmopolitan genera *Pseudobatostomella*, *Nikiforovella* and *Dyscritella*, and one new genus *Nikiforovastylus*. In the upper Famennian close palaeobiogeographical connections can be traced between Belgium and Germany. Further studies are needed to assess the diversity of the Devonian bryozoans of the Namur–Dinant Basin, notably those from the lower Famennian but especially from the Middle Devonian and Frasnian mixed siliciclastic–carbonate succession of this area in which facies favourable to bryozoans are more developed.

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