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: Trepostoma sp. indet., Nikiforovella sp., and Rhomboporidai sp. indet. Middle Famennian Trepostoma sp. indet. shows morphology not previously recorded in Palaeozoic bryozoans.

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 (Saillé 1919; Dessilly 1961, 1967; Dessilly & Kräusel 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 Famenn 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}
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...
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 biostratigraphy 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°30´17.15˝; E 5°35´47.31˝) has been described in great detail 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 Hastorian age (basal Tournaisian). Only the bryo-

zoans 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*, quaesendothyrids) 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 *Trepostomata* 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 exilazoecia. Autozoecia parallel to longitudinal direction of the colony in endozone; gradually bending outward in exozone. Diaphragms in autozoecia lacking or very rare; lacking in exilazoecia.
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 epiphyllous 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 exozones. Maculae not observed.

Remarks. – Dyscritella perforata sp. nov. differs from D. clara (Trizna 1958) from the Tournaisian of the Kuznetsk
Basin in colony form (encrusting vs branched ramose), possessing more abundant exilazooecia and in smaller autozoecial 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). 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 autozoecial 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. Autozoecial 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 autozoecial budding pattern, the presence of diaphragms and regularly sized acanthostyles.

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; autozoecial apertures rounded; autozoecial diaphragms rare; 1–5 exilazooecia surrounding each autozoecial aperture; 3–8 acanthostyles surrounding each autozoecial 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. Autozoecia long in endozones, bending at low angles in exozones. Autozoecial apertures rounded. Autozoecial diaphragms rare. Autozoecial walls lamellated, 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 autozoecial aperture. Acanthostyles abundant, 0.015–0.045 mm in diameter, with narrow hyaline cores and wide laminated sheaths, 3–8 surrounding each autozoecial aperture. Maculae not observed.

Remarks. – 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.

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.

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

Occurrence. – Upper Devonian to Upper Permian; worldwide.

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.
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 endozones. 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 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 autozoocoeal 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.

<table>
<thead>
<tr>
<th>Measurements of Pseudobatostomella parva sp. nov.</th>
<th>Abbreviations as in Table 1.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>F</strong></td>
<td><strong>N</strong></td>
</tr>
<tr>
<td>-----------------</td>
<td>-------</td>
</tr>
<tr>
<td>Branch width, mm</td>
<td>5</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>5</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>5</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>6</td>
</tr>
<tr>
<td>Autozooecial aperture spacing, mm</td>
<td>6</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>6</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>6</td>
</tr>
<tr>
<td>Exilazooecia width, mm</td>
<td>6</td>
</tr>
<tr>
<td>Exilazooecia per aperture</td>
<td>6</td>
</tr>
<tr>
<td>Exozone wall thickness, mm</td>
<td>5</td>
</tr>
</tbody>
</table>

Family uncertain

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

Material. – ULg PDB 5-21a-d.

Description. – Branched colonies, 0.28–3.25 mm in diameter, with 0.30–0.45 mm wide exozones and 1.48–2.55 mm wide endozones. 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 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 autozoecoeal 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 endozones. 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,
merged without visible zoocelial 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 outhensis 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 zoocelial boundaries. Few metazoecia 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 metazoecia and aktinotostyles and in the more regular shape of autozooecia.

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

Nikiforovastylus outhensis gen. et sp. nov.

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. Metazoecia 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 zoocelial boundaries in exozone.

Remarks. – As for genus.

Occurrence. – As for genus.

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

<table>
<thead>
<tr>
<th></th>
<th>F</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>6</td>
<td>0.69</td>
<td>0.089</td>
<td>12.82</td>
<td>0.54</td>
<td>0.80</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>6</td>
<td>6</td>
<td>0.20</td>
<td>0.030</td>
<td>15.10</td>
<td>0.16</td>
<td>0.25</td>
</tr>
<tr>
<td>Endozoecial width, mm</td>
<td>6</td>
<td>6</td>
<td>0.30</td>
<td>0.044</td>
<td>14.87</td>
<td>0.22</td>
<td>0.35</td>
</tr>
<tr>
<td>Autozoecial aperture width, mm</td>
<td>7</td>
<td>20</td>
<td>0.09</td>
<td>0.011</td>
<td>12.94</td>
<td>0.06</td>
<td>0.10</td>
</tr>
<tr>
<td>Autozoecial aperture spacing, mm</td>
<td>7</td>
<td>17</td>
<td>0.19</td>
<td>0.021</td>
<td>10.85</td>
<td>0.15</td>
<td>0.23</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>7</td>
<td>25</td>
<td>0.03</td>
<td>0.007</td>
<td>18.83</td>
<td>0.02</td>
<td>0.05</td>
</tr>
<tr>
<td>Exozonal wall thickness, mm</td>
<td>5</td>
<td>5</td>
<td>0.047</td>
<td>0.011</td>
<td>23.04</td>
<td>0.035</td>
<td>0.063</td>
</tr>
</tbody>
</table>

Figure 7. Nikiforovastylus outhensis 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.
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).

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**Table 4. Measurements of *Nikiforovystylus ourthensis* gen. et sp. nov.**

<table>
<thead>
<tr>
<th></th>
<th>F</th>
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<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch width, mm</td>
<td>4</td>
<td>4</td>
<td>0.88</td>
<td>0.098</td>
<td>11.22</td>
<td>0.75</td>
<td>0.96</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>4</td>
<td>4</td>
<td>0.24</td>
<td>0.033</td>
<td>13.61</td>
<td>0.20</td>
<td>0.28</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>4</td>
<td>4</td>
<td>0.40</td>
<td>0.055</td>
<td>13.21</td>
<td>0.35</td>
<td>0.47</td>
</tr>
<tr>
<td>Autozooecial aperture width, mm</td>
<td>4</td>
<td>25</td>
<td>0.10</td>
<td>0.020</td>
<td>19.41</td>
<td>0.07</td>
<td>0.13</td>
</tr>
<tr>
<td>Autozooecial aperture spacing along branch, mm</td>
<td>4</td>
<td>21</td>
<td>0.34</td>
<td>0.030</td>
<td>8.66</td>
<td>0.27</td>
<td>0.39</td>
</tr>
<tr>
<td>Autozooecial aperture spacing diagonally, mm</td>
<td>4</td>
<td>21</td>
<td>0.20</td>
<td>0.015</td>
<td>7.51</td>
<td>0.18</td>
<td>0.23</td>
</tr>
<tr>
<td>Aktinotyle diameter, mm</td>
<td>4</td>
<td>25</td>
<td>0.04</td>
<td>0.012</td>
<td>26.17</td>
<td>0.02</td>
<td>0.07</td>
</tr>
<tr>
<td>Metazooecia width, mm</td>
<td>4</td>
<td>25</td>
<td>0.027</td>
<td>0.009</td>
<td>34.09</td>
<td>0.013</td>
<td>0.045</td>
</tr>
<tr>
<td>Acanthostyle per aperture</td>
<td>4</td>
<td>20</td>
<td>1.5</td>
<td>0.513</td>
<td>34.20</td>
<td>1.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Metazooecia per aperture</td>
<td>4</td>
<td>20</td>
<td>1.6</td>
<td>0.503</td>
<td>31.41</td>
<td>1.0</td>
<td>2.0</td>
</tr>
</tbody>
</table>

---

**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.
Nikiforovella is a species of bryozoan that has distinctly larger apertures than the Mississippian of Altai, Russia. In its larger autozoecial apertures (autozoecial 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 autozoecial apertures (autozoecial 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 geographical range from the 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 and Kazakhstan (Nekhoroshev 1956, 1958, 1969). 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 and Kazakhstan (Nekhoroshev 1956, 1969).

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 1958, 1959, 1979), can be undertaken due to the lack of recent data. Dehée (1929) briefly discussed and illustrated some species present in the Etreugnt 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.

| Table 5. Measurements of Nikiforovella dinantia sp. nov. Abbreviations as in Table 1. |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 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      |
| Autozoecial aperture width, mm| 6 24 0.11 | 0.014     | 13.47     | 0.08      | 0.13      |
| Autozoecial aperture spacing   | 6 8 0.27  | 0.033     | 12.18     | 0.23      | 0.33      |
| 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        | 1.0       | 1.0       |
| Metazooecia per aperture       | 6 6 1.5   | 0.548     | 36.52     | 2.0       |

| Table 6. Measurements of Nikiforovella sp. Abbreviations as in Table 1. |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Autozoecial aperture width, mm | 2 40 0.19 | 0.022     | 11.94     | 0.14      | 0.23      |
| Autozoecial aperture spacing   | 2 40 0.32 | 0.037     | 11.46     | 0.25      | 0.40      |
| Acanthostyle diameter, mm      | 2 40 0.22 | 0.029     | 12.95     | 0.15      | 0.30      |
| Metazooecia width, mm          | 2 40 0.03 | 0.006     | 15.22     | 0.025     | 0.050     |
| Acanthostyles per aperture     | 2 40 0.03 | 0.009     | 25.60     | 0.018     | 0.050     |
| Metazooecia per aperture       | 2 25 2.0  | 0.889     | 45.35     | 1.0       | 3.0       |

**Description.** – Branched colonies, branch width unknown. Autozoecial apertures oval to circular, arranged in regular diagonal rows. Autozoecial diaphragms absent. Metazooecia 0.018–0.050 mm wide, originating at the base of exozone, 1–2 arranged between longitudinally successive autozoecial apertures. Acanthostyles 0.025 to 0.050 mm in diameter, 1–3 arranged between longitudinally successive autozoecial apertures, having distinct hyaline cores and laminated sheaths. Autozoecial 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 autozoecial apertures implying spiral budding of autozoecia. 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 autozoecial apertures (autozoecial width 0.14–0.23 mm vs. 0.08 to 0.12 mm in N. alternata).}

References:

- Ernst & Herbig, 2010.
- Tolokonnikova, 2011.
- Ernst & Herbig, 2010.
- Ernst et al., 2014.
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.

Acknowledgements

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