Fenestrate bryozoan fauna from the Middle Devonian of the Eifel (western Rhenish Massif, Germany)

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Abstract
Seven fenestrate bryozoans are described from the Middle Devonian of the Eifel. Three species were identified as Prolixicella bifurcata Ernst and Schroeder, 2007, Rectifenestella aculeata (Sandberger and Sandberger, 1856), and Spinofenestella antiqua (Goldfuss, 1826). Four species are described in open nomenclature: Rectifenestella sp. 1 and sp. 2, Ptylopora sp., and Spinofenestella sp. Analysis of the distribution of the fenestrate bryozoans from the Middle Devonian of the Eifel shows their relatively high level of endemism revealing some few connections to the Devonian of Europe and Asia. The studied association shows similarities to the contemporary fauna from Sauerland.

Keywords Bryozoans · Fenestrates · Taxonomy · Eifelian · Givetian · Eifel · Palaeobiogeography

Introduction
Fenestrate bryozoans represent an important group of Palaeostomata, which became dominant during the Devonian (e.g. Cuffey and McKinney 1979; Bigey 1988a; Morozova 2001; Ernst 2013). They are found in marine deposits of Devonian age including the well-known localities in the Eifel, Germany. Some very early palaeontological studies included descriptions of Devonian fenestrate bryozoans from this area (e.g. Goldfuss 1826; Steininger 1849; Roemer 1850, 1856; Sandberger and Sandberger 1856; Bornemann 1884; Maurer 1885). Important later investigations have been presented by Nekhoroshev (1928), Toots (1951), and Kräusel (1953, 1954, 1956, 1957, 1981).

The evaluation of self-collected material and museum bryozoan collections from the Middle Devonian (Eifelian–Givetian) of the Eifel revealed the presence of diverse fenestrate taxa: phylloporines Prolixicella and Bashkirella as well as fenestellid genera Fenestella, Spinofenestella, Rectifenestella, Dissotrypa, Anastomopora, Bigeyina, Loculipora, Fenestrapora, Schischcatella, Ptylopora, and Hemitrypa. The majority of these bryozoans were treated in recent studies (Ernst and Schroeder 2007; Ernst and Bohatý 2009; Ernst et al. 2012; Ernst 2016, 2020, 2022). From this fauna, the genus Hemitrypa is currently excluded for a later investigation, whereas the present paper deals with the study of the representatives of the genera Prolixicella, Rectifenestella, Ptylopora, and Spinofenestella.

Localities and stratigraphy
The material for this study comes from various localities in the Rhenish Massif (Fig. 1). Material was collected by the author in years 2008–2010. Further samples from Essingen-Hohenfels and Schwirzheim were provided by Jan Bohatý, Wiesbaden. All these specimens are deposited at the Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany (SMF-numbers). Material from Lüdenscheid, Sauerland, was collected by Frank Langenstrassen, Göttingen, and deposited at the Geological Centre Göttingen, Germany (GZG-numbers). Type material of Sandberger and Sandberger (1856) is deposited in Sandberger’s Devonian Collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany.

The stratigraphy of Devonian sedimentary rocks at studied localities has been adopted from Struve and Werner (1982), with corrections by Jan Bohatý (pers. comm., 2008; Figs. 2 and 3).
The locality "Weinberg" Quarry near Kerpen (50°52', 6°41') contains the fossiliferous limestones of the Bohnert Member of the Freilingen Formation (upper Eifelian) (Fig. 3a).

The abandoned Müllertchen Quarry is situated in the vicinity of Üxheim-Ahütte, Hillesheim Syncline (50°21', 6°46'). This quarry contains muddy limestones of the Olifant Member of the Müllert Subformation of the Ahbach Formation (lowermost Givetian) (Fig. 3b).

The Blankenheim locality is a railway cut west of the village Blankenheim, Blankenheim Syncline (50°26', 6°39'). In this locality silty limestones with a rich fauna of the Grauberg

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Fig. 1 Geological map with the position of studied localities: 1 Brühlborn near Rommersheim; 2 "Weinberg" Quarry near Kerpen; 3 Müllertchen Quarry; 4 Essingen-Hohenfels; 5 Schwirzheim; 6 Blankenheim; 7 Lüdenscheid (modified from Wehrmann et al. 2005 and Winter in Meyer et al. 1977)
Subformation (lowermost *Latistriatus* Member sensu Ochs and Wolfart 1961) of the Junkerberg Formation (Eifelian) are exposed (Struve 1982; Struve and Werner 1982) (Fig. 3c).

In the locality at Brühlborn near Rommersheim, Prüm Syncline (50°22', 6°47'), rudstones and bindstones of the Upper Nims Member of the Junkerberg Formation (Eifelian) crop out (Fig. 3d).

Locality Essingen-Hohenfels (50°15′ N, 6°44′) reveals strata, which are estimated as the transition between the Ahrdorf and Junkerberg formations, Eifelian (Jan Bohatý, pers. comm. 2008).

In the locality Schwirzheim (50°14′, 6°32′), limestones of the Hönselberg Member of the Junkerberg Formation (Eifelian) are exposed (Jan Bohatý, pers. comm., 2008).

The localities near Lüdenscheid in the Sauerland (51°09, 7°33) include a series of outcrops of silty and richly fossiliferous limestones of the Hönsel and Werdohl formations (Givetian). Most of these outcrops are no longer accessible (Frank Langenstrassen, pers. comm., 2006). The Werdohl Formation corresponds to the lower part of the Hönsel Member of the Junkerberg Formation (Eifelian) are exposed (Jan Bohatý, pers. comm., 2008).

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**Systematic palaeontology**

Phylum Bryozoa Ehrenberg, 1831

Class Stenolaemata Borg, 1926

GZG.IN.0.010.511: Highway A45 Hagen-Siegen, Geological Map sheet 4812 Herscheid (1002/68-W3). Coll. F. Langenstrassen (KA 06)

Werdohl Formation, Givetian

GZG.IN.0.010.538: Highway A45 Hagen-Siegen, km 53.42, Geological Map sheet 4711 Lüdenscheid (1002/30-W2).

**Methods**

Bryozoans were investigated in thin sections using a binocular microscope in transmitted light. Morphologic character terminology is partly adopted from Snyder (1991a, b) and Hageman (1991a, b). The following morphologic characters were measured and used for statistics in the studied material: aperture spacing along branch, aperture spacing diagonally, autotetraspinal aperture width, branch width, branch thickness, dissepiment width, fenestrule width, fenestrule length, distance between branch centres, distance between dissepiment centres, maximum chamber width, keel node width, and distance between node centres.
Superorder Palaeostomata Ma, Buttler, and Taylor, 2014
Order Fenestellida Elias and Condra, 1957
Suborder Phyllopornina Lavrentjeva, 1979
Family Phyllopornidae Ulrich, 1890
Genus Prolixicella Ernst and Schroeder, 2007

Type species: Prolixicella bifurcata Ernst and Schroeder, 2007. Cürten Formation (Givetian, Middle Devonian); Dollendorf Syncline, Rhenish Massif (Germany).

Diagnosis: Branched, bifurcating colonies. Autozooecia long, bending sharply at the base of exozone, irregularly polygonal in transversal section in endozone, becoming rounded in the exozone, arranged in 3–4 rows on branches. Hemisepta absent; autozooecial diaphragms present. Heterozooecia absent.

Comparison: Prolixicella Ernst and Schroeder, 2007 is similar to Phylloporna Ulrich in Foerste, 1887 in having long autozooecia, but differs in having bifurcating instead of anastomosing colonies and in the absence of heterozooecia.

Occurrence: Lower–Middle Devonian of Europe: Prolixicella bifurcata Ernst and Schroeder, 2007, Eifelian–lower Givetian, Germany. Prolixicella lata Ernst and Königshof, 2010, Givetian, Morocco. Prolixicella parva Ernst, 2012 and P. ibera Ernst, 2012, Emsian, NW Spain.

Prolixicella bifurcata Ernst and Schroeder, 2007
(Fig. 4a–e)

2007 Prolixicella bifurcata Ernst and Schroeder, 2007, p. 216–217, fig. 5f–i

Holotype: SMF 2233, Research Institute and Natural History Museum, Frankfurt am Main, Germany. Cürten Formation, lower Givetian, Middle Devonian; Dollendorf Syncline, Rhenish Massif.
Material: GZG.IN.0.010.511a–b, f–g.

Description: Branched, regularly dichotomising colonies, 0.5–0.6 mm wide and 0.6–0.7 mm thick. Autozooecia long, in endozone polygonal to rounded-polygonal in transverse section becoming round at colony surface, originating along the reverse branch side and continuing at low angles through the exozone, bending sharply into the exozone and opening on the obverse branch side. Autozooecial and terminal diaphragms present. Autozooecial apertures circular, arranged in 3–5 rows on colony surface, 0.09–0.13 mm wide (0.11 mm at average). Autozooecial walls hyaline, 0.003–0.005 mm thick in endozone. External laminated walls 0.03–0.15 mm thick, containing thin microstyles. Heterozoecia not observed.

Comparison: Prolixicella bifurcata Ernst and Schroeder, 2007 differs from P. parva Ernst, 2012 in larger autozooecia (average aperture width 0.11 mm vs. 0.067 mm in P. parva). Prolixicella bifurcata differs from P. lata Ernst and Königshof, 2010 in narrower branches (0.50–0.60 mm vs. 0.58–1.50 mm in P. lata).

Occurrence: Devonian (Givetian); Germany.

Suborder Fenestellina Astrova and Morozova, 1956
Family Fenestellidae King, 1849
Genus Rectifenestella Morozova, 1974

Type species: Fenestella medvedkensis Schulga-Nesterenko, 1951. Pennsylvanian (Kasimovian); Russian Platform.

Diagnosis: Reticulate colonies consisting of fine to intermediately robust branches and straight dissepiments. Autozooecia triangular to pentagonal in mid tangential section. Superior hemisepta present; inferior hemisepta absent. Low keel carrying one row of intermediate nodes (modified after Morozova 2001, p. 45).

Comparison: Rectifenestella differs from Laxifenestella Morozova, 1974 in having a pentagonal shape of autozooecia and in the absence of inferior hemisepta, from Minilya Crockford, 1944 in having a single row of nodes on the keel instead of two alternating rows in Minilya.

Occurrence: Devonian to Permian; worldwide.

Rectifenestella aculeata (Sandberger and Sandberger, 1856) (Figs. 4f–k, 5a, 6a–c and Table 1)

v1856 Fenestrella aculeata Sandberger and Sandberger, p. 376, pl. 36, fig. 2
1951 Hemitrype (?) aculeata (Sandberger and Sandberger, 1856)–Toots, p. 243–245, pl. 15, fig. 1

Holotype: 311, Sandberger’s Devonian collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany. Stringocephalenkalk, Givetian, Middle Devonian; Villmar, Germany.

Material: Nine thin sections of three colonies SMF 62460–62469.

Exterior description: Reticulate colonies with straight branches, bifurcating, joined by moderately wide dissepiments. Autozooecia arranged in two alternating rows on branches, having circular apertures with moderately high peristomes, 3–8 spaced per length of a fenestrule. Peristomes containing nodes. Apertural nodes 0.010–0.015 mm in diameter. Fenestrules oval to rectangular, long and narrow. Median keel low. Keel nodes small, intermittently spaced, granular core stellate in shape. Nodes on reverse side present, 0.023–0.045 mm in diameter.

| Table 1 Summary of descriptive statistics for Rectifenestella aculeata (Sandberger and Sandberger, 1856). |
|------------------------------------------------------------------------------------------------|
| Abbreviations: N number of measurements; X mean; SD sample standard deviation; CV coefficient of variation; MIN minimal value; MAX maximal value |
|------------------------------------------------------------------------------------------------|
| **N** | **X** | **SD** | **CV** | **MIN** | **MAX** |
|-------|-------|--------|--------|--------|--------|
| Branch width, mm | 30 | 0.28 | 0.043 | 15.17 | 0.21 | 0.38 |
| Branch thickness, mm | 16 | 0.35 | 0.043 | 12.30 | 0.30 | 0.46 |
| Dissepiment width, mm | 30 | 0.14 | 0.031 | 21.93 | 0.08 | 0.22 |
| Fenestrule width, mm | 30 | 0.46 | 0.086 | 18.74 | 0.32 | 0.66 |
| Fenestrule length, mm | 30 | 1.41 | 0.331 | 23.51 | 0.80 | 2.13 |
| Distance between branch centres, mm | 30 | 0.75 | 0.127 | 16.95 | 0.53 | 0.96 |
| Distance between dissepiment centres, mm | 30 | 1.61 | 0.319 | 19.78 | 1.05 | 2.25 |
| Aperture width, mm | 30 | 0.09 | 0.008 | 8.60 | 0.07 | 0.11 |
| Aperture spacing along branch, mm | 30 | 0.27 | 0.030 | 10.95 | 0.20 | 0.32 |
| Aperture spacing diagonally, mm | 30 | 0.25 | 0.026 | 10.74 | 0.20 | 0.30 |
| Maximal chamber width, mm | 30 | 0.10 | 0.010 | 10.22 | 0.08 | 0.13 |
| Node width, mm | 30 | 0.05 | 0.012 | 22.97 | 0.03 | 0.08 |
| Distance between node centres, mm | 30 | 0.57 | 0.128 | 22.46 | 0.37 | 0.82 |
| Apertures per fenestrule length | 35 | 5.0 | 1.339 | 26.63 | 3.0 | 8.0 |
**Interior description:** Autozooecia triangular to pentagonal in mid-tangential section; with well-developed long vestibule; axial wall zigzag; aperture positioned at distal end of chamber. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by abundant microstyles. Microstyles regularly arranged in longitudinal rows on colony reverse surface, 0.008–0.010 mm in diameter. Heterozoocia not observed.

In some autozooecia brown deposits are present, which represent sack-shaped accumulations of brown material, 0.05–0.07 mm in diameter (Figs. 5a and 6a–c).

**Comparison:** Rectifenestella aculeata (Sandberger and Sandberger, 1856) differs from *R. exilis* (Počta, 1894) in larger distances between branches (on average 0.75 mm vs. 0.474 mm in *R. exilis*), and larger distances between dissepiment centres (averagely 1.61 mm vs. 0.648 mm in *R. exilis*). Rectifenestella aculeata differs from *R. elongata* (Krasnopeeva, 1935) from the Middle–Upper Devonian of Russia in longer fenestrules (fenestrule length 0.80–2.13 vs. 0.30–0.90 mm in *R. elongata*), and more widely spaced keel nodes (node spacing 0.37–0.82 mm vs. 0.28–0.30 mm in *R. elongata*).

**Occurrence:** Stringocephalenkalk, Givetian, Middle Devonian; Villmar, Germany. Transition Ahrdorf / Junkerberg formation, Eifelian; Villmar, Germany. Bohnert Member of the Freilingen Formation, Lower Devonian of Spain; Massif, Germany. Honseberg Member of the Junkerberg Formation, Eifel, Middle Devonian; Schwirzheim, Germany.

**Rectifenestella sp. 1** (Fig. 5b–h and Table 2)

**Material:** Two thin sections of a single colony SMF 62470–SMF 62471.

**Exterior description:** Reticulate colonies with straight branches, bifurcating, joined by moderately wide dissepiments. Autozooecia arranged in two alternating rows on branches. Autozooecial apertures circular, surrounded by a row of small nodes; 6–10 apertures spaced per fenestrule length. Fenestrules oval to rectangular, long and wide. Median keel low. Keel nodes moderately large, widely spaced, granular core stellate in shape. Nodes on reverse side present, widely and irregularly spaced, 0.015–0.030 mm in diameter.

**Interior description:** Autozooecia triangular to pentagonal in mid-tangential section; with well-developed long vestibule; axial wall zigzag; aperture positioned at distal end of chamber. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by abundant microstyles. Microstyles regularly arranged in longitudinal rows on colony reverse surface, 0.005–0.010 mm in diameter. Heterozoocia not observed.

**Comparison:** Rectifenestella sp. 1 is similar to *R. elegantula* Ernst, 2012 from the Lower Devonian (Emsian) of Spain, but differs from it in larger fenestrules (average fenestrule width 0.65 mm vs. 0.31 mm in *R. elegantula*; average fenestrule length 1.86 mm vs. 1.03 mm in *R. elegantula*), and in larger spacing of keel nodes (average distance between node centres 0.87 mm vs. 0.49 mm in *R. elegantula*). Rectifenestella sp. 1 differs from *R. covae* Suárez-Andrés and Ernst, 2015 from the Lower–Middle Devonian of Spain in longer fenestrules (average fenestrule length 1.86 mm vs. 1.31 mm in *R. covae*) and in wider spacing of autozooecial apertures (average distance between centres of autozooecial apertures 0.27 mm vs. 0.24 mm in *R. covae*).

**Occurrence:** Bohnert Member of the Freilingen Formation, upper Eifelian, Middle Devonian; ”Weinberg” Quarry near Kerpen, Hillesheim Syncline, Eifel (western Rhenish Massif), Germany.

**Rectifenestella sp. 2** (Figs. 5i–j, 7a–c and Table 3)

**Material:** Four thin sections of a single colony SMF 62472–SMF 62475.

**Exterior description:** Reticulate colonies with straight branches, bifurcating, joined by moderately wide dissepiments. Autozooecia arranged in two alternating rows on branches. Autozooecial apertures circular, surrounded by apertural nodes; 3–5 apertures spaced per fenestrule length. Apertural nodes 0.015–0.020 mm in diameter. Fenestrules oval to rectangular, moderately long and narrow. Median keel low. Keel nodes small, moderately spaced, granular core stellate in shape. Nodes on reverse side present, 0.020–0.025 mm in diameter.

**Interior description:** Autozooecia triangular to pentagonal in mid-tangential section; with well-developed long vestibule; axial wall zigzag; aperture positioned at distal end of chamber. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by abundant microstyles. Microstyles regularly arranged in...
longitudinal rows on colony reverse surface, 0.02–0.03 mm in diameter. Heterozooecia not observed.

Comparison: Rectifenestella sp. 2 is similar to R. villayandrensis Ernst, 2012 from the Lower Devonian (Emsian) of Spain, but differs from its closer spacing of apertures (average distance between centres of autozooecial apertures 0.24 mm vs. 0.27 mm in R. villayandrensis), and in having 3–5 apertures per fenestrule length vs. 2–4 in R. villayandrensis. Rectifenestella sp. 2 is similar to R. localis Morozova and Weiss, in Morozova et al., 2006 from the Middle Devonian (Eifelian) of Poland, but differs from it in wider branches (branch width 0.25–0.40 mm vs. 0.20–0.25 mm in R. localis).

Occurrence: Junkerberg Formation, Grauberg Subformation, lowermost Latistriatus Member, Eifelian, Middle Devonian;

Table 2 Summary of descriptive statistics for Rectifenestella sp. 1. Abbreviations as for Table 1

|                          | N  | X     | SD  | CV  | MIN | MAX |
|--------------------------|----|-------|-----|-----|-----|-----|
| Branch width, mm         | 15 | 0.38  | 0.026 | 6.73 | 0.34 | 0.42 |
| Dissepiment width, mm    | 15 | 0.29  | 0.034 | 11.95 | 0.21 | 0.33 |
| Fenestrule width, mm     | 15 | 0.65  | 0.149 | 22.75 | 0.44 | 0.93 |
| Fenestrule length, mm    | 15 | 1.86  | 0.289 | 15.58 | 1.28 | 2.40 |
| Distance between branch centres, mm | 15 | 1.03  | 0.163 | 15.91 | 0.77 | 1.38 |
| Distance between dissepiment centres, mm | 15 | 2.13  | 0.293 | 13.77 | 1.63 | 2.75 |
| Aperture width, mm       | 14 | 0.13  | 0.011 | 8.41  | 0.11 | 0.14 |
| Aperture spacing along branch, mm | 18 | 0.27  | 0.017 | 6.02  | 0.24 | 0.30 |
| Aperture spacing diagonally, mm | 7  | 0.27  | 0.023 | 8.65  | 0.24 | 0.30 |
| Maximal chamber width, mm| 20 | 0.12  | 0.010 | 8.38  | 0.10 | 0.14 |
| Node width, mm           | 20 | 0.09  | 0.011 | 12.84 | 0.06 | 0.10 |
| Distance between node centres, mm | 20 | 0.87  | 0.094 | 10.91 | 0.69 | 1.02 |
| Apertures per fenestrule length | 7  | 7.6   | 1.512 | 19.97 | 6.0  | 10.0 |
railway cut west of Blankenheim, Blankenheim Syncline, Eifel (western Rhenish Massif), Germany.

Genus *Ptylopora* M'Coy, 1844

**Type species:** *Ptylopora pluma* M'Coy, 1844. Mississippian (Carboniferous); Ireland.

**Diagnosis:** Fan-shaped colonies, pinnate, with linear main branch(es), and linear to slightly sinuous, infrequently bifurcating lateral branches connected by narrow dissepiments; main branch(es) typically thickened on reverse and widened by more lamellar skeleton than is present on lateral branches; two rows of autozooecia on main and lateral branches; median keel with regularly spaced nodes consisting of axial core of granular skeleton; autozooecia elongate box-shaped, pentagonal in section parallel to chamber base, with lateral sides planar or only slightly inflated; vestibule short to intermediate, erect, oval in transversal section, oriented toward obverse surface with little distal or lateral tilt; axial wall strongly zigzag at basal plate, becoming straighter towards obverse side; hemisepta and other internal structures absent; granular autozooecial walls may be lined interiorly by thick laminated skeleton; laminar extrazoecial skeleton traversed by abundant small styles.

**Comparison:** *Ptylopora* M'Coy, 1844 differs from *Rectifenestella* Morozova, 1974 in having pinnate colony with main and secondary branches instead of regularly shaped reticulate colony.

**Occurrence:** Lower Devonian–Permian (Lopingian); Europe, USA, and Australia.

*Ptylopora* sp. (Fig. 7d–i and Table 4)

### Table 3
Summary of descriptive statistics for *Rectifenestella* sp. 2.
Abbreviations as for Table 1

|                            | N  | X  | SD  | CV  | MIN | MAX |
|---------------------------|----|----|-----|-----|-----|-----|
| Branch width, mm          | 18 | 0.31 | 0.46 | 14.96 | 0.25 | 0.40 |
| Dissepiment width, mm     | 22 | 0.17 | 0.029 | 16.63 | 0.13 | 0.23 |
| Fenestrule width, mm      | 22 | 0.28 | 0.058 | 20.73 | 0.20 | 0.44 |
| Fenestrule length, mm     | 24 | 0.76 | 0.153 | 20.26 | 0.52 | 1.10 |
| Distance between branch centres, mm | 21 | 0.56 | 0.062 | 11.11 | 0.47 | 0.70 |
| Distance between dissepiment centres, mm | 26 | 0.95 | 0.131 | 13.74 | 0.70 | 1.28 |
| Aperture width, mm        | 23 | 0.10 | 0.009 | 8.80  | 0.09 | 0.12 |
| Aperture spacing along branch, mm | 27 | 0.25 | 0.016 | 6.58  | 0.22 | 0.28 |
| Aperture spacing diagonally, mm | 25 | 0.23 | 0.014 | 6.09  | 0.20 | 0.27 |
| Maximal chamber width, mm | 27 | 0.12 | 0.011 | 8.97  | 0.10 | 0.14 |
| Node width, mm            | 10 | 0.04 | 0.006 | 15.06 | 0.03 | 0.05 |
| Distance between node centres, mm | 7  | 0.55 | 0.044 | 7.93  | 0.47 | 0.62 |
| Apertures per fenestrule length | 15 | 3.7  | 0.724 | 19.74 | 3.0  | 5.0  |

### Table 4
Summary of descriptive statistics for *Ptylopora* sp.
Abbreviations as for Table 1

|                            | N  | X  | SD  | CV  | MIN | MAX |
|---------------------------|----|----|-----|-----|-----|-----|
| Secondary Branch width, mm | 63 | 0.33 | 0.043 | 12.95 | 0.24 | 0.44 |
| Dissepiment width, mm     | 60 | 0.23 | 0.046 | 19.61 | 0.14 | 0.34 |
| Fenestrule width, mm      | 60 | 0.33 | 0.084 | 25.43 | 0.20 | 0.52 |
| Fenestrule length, mm     | 60 | 0.83 | 0.138 | 16.64 | 0.52 | 1.06 |
| Distance between branch centres, mm | 60 | 0.68 | 0.129 | 18.95 | 0.45 | 1.00 |
| Distance between dissepiment centres, mm | 60 | 1.09 | 0.126 | 11.57 | 0.77 | 1.35 |
| Aperture width, mm        | 60 | 0.09 | 0.009 | 9.94  | 0.07 | 0.11 |
| Aperture spacing along branch, mm | 54 | 0.32 | 0.031 | 9.69  | 0.26 | 0.43 |
| Aperture spacing diagonally, mm | 53 | 0.30 | 0.035 | 11.91 | 0.24 | 0.38 |
| Maximal chamber width, mm | 60 | 0.15 | 0.012 | 7.93  | 0.12 | 0.17 |
| Apertures per fenestrule length | 40 | 3.2  | 0.549 | 17.31 | 2.0  | 4.0  |
| Node width, mm            | 10 | 0.05 | 0.005 | 9.11  | 0.05 | 0.06 |
| Distance between node centres, mm | 2  | 0.34 | 0.064 | 19.00 | 0.29 | 0.38 |
Material: Ten thin sections of four colonies SMF 62476–SMF 62485.
Exterior description: Reticulate, pinnate colonies with straight main branches and straight to slightly sinuous secondary branches. Main branches 0.45–0.54 mm wide. Secondary branches bifurcating, joined by moderately wide dissepiments, 0.24–0.44 mm wide. Autozooecia arranged in two alternating rows on branches. Autozooecial apertures circular, with stellate structure; 2–4 apertures spaced per fenestrule length. Fenestrules oval to rectangular, moderately long and narrow. Median keel low. Keel nodes small, moderately spaced, granular core oval in shape. Nodes on reverse side present, 0.010–0.035 mm in diameter.
Interior description: Autozooecia triangular to pentagonal in mid-tangential section; with well-developed long vestibule; axial wall zigzag; aperture positioned at distal end of chamber. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by abundant microstyles. Microstyles regularly arranged in longitudinal rows on colony reverse surface, 0.003–0.005 mm in diameter. Heterozoecia not observed.
Comparison: Ptylopora sp. is similar to the species Ptylopora nodosa Hall, 1883 from the Givetian of USA, but differs from it in thinner branches (main branch width 0.45–0.54 mm vs. 0.33 mm in Ptylopora nodosa; secondary branch width 0.24–0.44 mm vs. 0.20 mm in Ptylopora nodosa). Ptylopora sp. differs from Ptylopora striata Hall, 1883 from the Givetian of USA, in thinner branches (main branch width 0.45–0.54 mm vs. 1.0–1.25 mm in Ptylopora striata) and by presence of nodes on the median keel.
Occurrence: Olifant Member of the Müllert Subformation, of the Abbach Formation, lowermost Givetian; Üxheim-Ahütte, Müllertchen Quarry, Hillesheim Syncline, Eifel (western Rhenish Massif), Germany.

Genus Spinofenestella Termier and Termier, 1971
[= Alternifenestella Termier and Termier, 1971]

Type species: Fenestella spinosa Condra, 1902. Cisuralian (Wolfcampian, Permian); North America.
Diagnosis: Reticulate colonies with relatively wide and thick branches and relatively thin dissepiments. Autozooecia arranged in two rows on the branches. Autozooecial triangular in mid-tangential section, triangular to pentagonal proximal to bifurcations. Narrow keel with single row of nodes developed.
Comparison: Spinofenestella Termier and Termier, 1971 differs from the genus Rectifenestella Morozova, 1974 by the triangular shape of the autozooecia in mid-tangential section.

Spinofenestella antiqua (Goldfuss, 1826)
(Fig. 8a–h and Table 5)

1826 Retepora antiqua Goldfuss, p. 27, pl. 9, fig. 10.
1856 Fenestrella subrectangularis Sandberger and Sandberger, p. 376, pl. 36, figs. 2, 2a, 2b and 3, 3a, 3b
1951 Fenestrella antiqua (Goldfuss, 1826) – Toots, p. 236–237, pl. 14, fig. 2, text-fig. 1
2007 Spinofenestella antiqua (Goldfuss, 1826) – Ernst and Schroeder, p. 220–222, fig. 8B–H

Holotype: IGPB-Goldfuss-106a & IGPB-Goldfuss-106b, Institut für Geowissenschaften, Paläontologie, Bonn, Germany. Heisterstein, Eifel, Germany; upper part of the Middle Devonian.

| Table 5 | Summary of descriptive statistics for Spinofenestella antiqua (Goldfuss, 1826). |
|---------|---------------------------------|
| N Branch width, mm | 67 | 0.26 | 0.040 | 15.31 | 0.20 | 0.37 |
| N Dissepiment width, mm | 74 | 0.17 | 0.044 | 26.02 | 0.10 | 0.28 |
| N Fenestrule width, mm | 73 | 0.20 | 0.047 | 22.77 | 0.12 | 0.30 |
| N Fenestrule length, mm | 72 | 0.46 | 0.103 | 22.26 | 0.28 | 0.65 |
| N Distance between branch centres, mm | 75 | 0.46 | 0.063 | 13.71 | 0.33 | 0.66 |
| N Distance between dissepiment centres, mm | 74 | 0.64 | 0.102 | 15.95 | 0.45 | 0.91 |
| N Aperture width, mm | 81 | 0.08 | 0.007 | 8.40 | 0.06 | 0.10 |
| N Aperture spacing along branch, mm | 75 | 0.22 | 0.036 | 16.15 | 0.14 | 0.32 |
| N Aperture spacing diagonally, mm | 62 | 0.23 | 0.023 | 9.93 | 0.19 | 0.29 |
| N Maximal chamber width, mm | 82 | 0.13 | 0.017 | 13.26 | 0.09 | 0.18 |
| N Node width, mm | 62 | 0.044 | 0.010 | 22.09 | 0.025 | 0.070 |
| N Distance between node centres, mm | 53 | 0.26 | 0.036 | 13.62 | 0.19 | 0.34 |
| N Apertures per fenestrule length | 51 | 2.8 | 0.590 | 20.90 | 2.0 | 4.0 |

Abbreviations as for Table 1
S. inclara branch width 0.27 mm vs. 0.24 mm in of the Czech Republic in having wider branches (average branch spacing 0.43 mm vs. 0.71 mm in S. inclara; average dissepiment spacing 0.61 mm vs. 1.23 mm in S. inclara).

**Remarks:** Toots (1951) described and depicted the original material of Goldfuss (1826) for Retepora antiqua. He noted the presence of tubercles (nodes) on the reverse branch side which are characteristic for this species, as well as triangular shape of autozoocelial chambers. The lectotype of Fenestrella subrectangularis Sandberger and Sandberger, 1856, Sandberger’s Devonian collection (Wiesbaden), shows the same type of nodes and shape of autozoocelia (Fig. 8a-b). Their dimensions are similar, so Fenestrella subrectangularis is acknowledged as a junior synonym of Retepora antiqua, which is assigned here to the genus Spinofenestella because of triangular shape of autozoocelia and presence of nodes on the median keel.

**Occurrence:** Cürten Formation (lower Givetian, Middle Devonian); Dollendorf Syncline, Rhenish Massif, Germany. Honsel and Werdohl formations, Givetian, Middle Devonian; Lüdenscheid, Sauerland, Germany. Upper Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian); Brühlborn near Rommersheim, Prüm Syncline, Germany. Villmar, Stringocephalenkalk, Middle Devonian, Givetian.

**Spinofenestella sp.**
(Figs. 8i, 9a-e and Table 6)

**Material:** Five thin sections of a single colony SMF 60308, SMF 62494–SMF 62497.

**Exterior description.** Reticulate colony formed by straight branches joined by wide dissepiments. Fenestrules oval to rectangular, moderately long, narrow. Autozoocelia arranged in two rows on branches. Autozoocelial apertures circular, with stellate structure; 3–5 apertures spaced per fenestrule length.

| Table 6 | Summary of descriptive statistics for Spinofenestella sp. | Abbreviations as for Table 1 |
|---------|----------------------------------------------------------|-----------------------------|
| N       | X            | SD           | CV          | MIN       | MAX          |
| Branch width, mm | 20 | 0.31 | 0.032 | 10.36 | 0.25 | 0.35 |
| Dissepiment width, mm | 20 | 0.30 | 0.051 | 16.82 | 0.23 | 0.39 |
| Fenestrule width, mm | 20 | 0.32 | 0.040 | 12.57 | 0.25 | 0.40 |
| Fenestrule length, mm | 20 | 0.82 | 0.095 | 11.63 | 0.67 | 1.01 |
| Distance between branch centres, mm | 20 | 0.61 | 0.076 | 12.63 | 0.50 | 0.76 |
| Distance between dissepiment centres, mm | 20 | 1.09 | 0.076 | 6.93 | 1.00 | 1.25 |
| Aperture width, mm | 20 | 0.08 | 0.006 | 7.02 | 0.07 | 0.09 |
| Aperture spacing along branch, mm | 20 | 0.29 | 0.040 | 13.99 | 0.22 | 0.36 |
| Aperture spacing diagonally, mm | 20 | 0.26 | 0.029 | 11.10 | 0.20 | 0.30 |
| Maximal chamber width, mm | 20 | 0.16 | 0.009 | 5.38 | 0.15 | 0.18 |
| Node width, mm | 20 | 0.054 | 0.006 | 11.64 | 0.045 | 0.065 |
| Distance between node centres, mm | 10 | 0.42 | 0.073 | 17.53 | 0.32 | 0.55 |
| Apertures per fenestrule length | 10 | 3.8 | 0.789 | 20.76 | 3.0 | 5.0 |
Median keel low, narrow, containing small closely spaced rounded nodes.

**Interior description.** Autozooecia short, triangular to trapezoid in mid-tangential section; with short to moderately long vestibule in longitudinal section. Axial wall between autozooecial rows strongly zigzag; aperture positioned at distal end of chamber. Superior hemisepta weakly developed; inferior hemisepta absent. External laminated skeleton well-developed on both obverse and reverse sides, traversed by small microstyles. Microstyles of two sizes regularly spaced on the reverse colony surface. Smaller styles (tubules) 0.003–0.005 mm in diameter, larger ones 0.010–0.015 mm in diameter. Heterozooecia not observed.

**Comparison:** *Spinofenestella* sp. differs from *S. antiqua* (Goldfuss, 1826) in larger fenestrules (average fenestrule width 0.32 mm vs. 0.20 mm in *S. antiqua*; average fenestrule length 0.82 mm vs. 0.46 mm in *S. antiqua*) as well as in wider spacing of autozooecial apertures (average distance between...
aperture centres along branch 0.29 mm vs. 0.22 mm in S. antiqua). Spinofenestella sp. differs from S. genuina Morozova and Weiss, in Morozova et al., 2006 from the Middle Devonian (Eifel) of Poland, in shorter fenestrules (fenestrule length 0.67–1.01 mm vs. 1.90–2.50 mm in S. genuina).

**Occurrence:** Olifant Member of the Müllert Subformation of the Ahbach Formation, lowermost Givetian, Middle Devonian; Üxheim-Ahütte, Müllertchen Quarry, Hillesheim Syncline, Eifel (western Rhenish Massif), Germany.

### Discussion

**Distribution of fenestrate bryozoans in the Devonian of the Eifel**

As shown by recent studies, Devonian bryozoans of the Eifel are abundant and diverse (Ernst and Schroeder 2007; Ernst 2008a, b, 2016, 2020; Ernst and Bohatý 2009; Ernst et al. 2011, 2012, 2014a, b, 2016, 2020). According to these results, the non-fenestrate bryozoans (orders Cystoporata, Trepostomata, and Cryptostomata) are represented by forty-seven species. In contrast, the fenestrate bryozoan fauna contains twenty-seven fenestrate species identified during the author's own studies. Of these, nine species occur in the Eifelian, fifteen species are restricted to the Givetian, whereas three species occur throughout the Middle Devonian of the Eifel (Table 7).

A significant number of taxa established in older publications still need re-study. Type material from the collections is often unavailable for study or cannot be used for the preparation of thin sections. Moreover, the type localities do not exist anymore or are not accessible. The homepage of the International Bryozoology Association (IBA, http://bryozoan.net) lists following fenestrate species from the Devonian of the Eifel, whose assignment needs clarification:

**Fenestella angusta** Steininger, 1849, *F. fastuosa* Steininger, 1849, *F. purpurea* Steininger, 1849, *F. sanguinea* Steininger, 1849, *F. textilis* Steininger, 1849, *F. conica* Roemer, 1850, *F. explanata* Roemer, 1850, *F. bifurca* Roemer, 1850, *F. micropora* Roemer, 1855, *F. bischoffi* Roemer, 1855, *F. bifurcata* Roemer, 1856, *F. tubulipora* Roemer, 1856, *Fenestrellina dichotoma* Roemer, 1855, *Hemitrypa elegans* Steininger, 1849, *H. striata* Steininger, 1849, *Ptylopora* Steininger, 1849, *Prolixicella bifurcata* Steininger, 1849, *Loculipora alvearis* Steininger, 1849, *Spinofenestella antiqua* (Goldfuss, 1826). The species *Spinofenestella antiqua* differs from *Spinofenestella* sp. 1.

Bryozoans described by Sandberger and Sandberger (1856) from the Stringocephalenkalk (Middle Devonian, Givetian) of Villmar, Germany, were studied in the Sandberger’s Devonian collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany (samples 311–314). The species *Polypora striatella* Sandberger and Sandberger, 1856 (sample 313) has been assigned to the genus *Anastomopora* (Ernst 2020). In the present paper, species *Fenestrella aculeata* Sandberger and Sandberger, 1856 (sample 311) has been placed in the genus *Rectifenestella* and the species *Fenestrella subrectangularis* Sandberger and Sandberger, 1856 (sample 312) was found being a junior synonym of the species *Spinofenestella antiqua* (Goldfuss, 1826). The species *Polypora laxa* Sandberger and Sandberger, 1856 (sample 314) belongs probably to *Anastomopora*; however, this specimen is badly preserved.

**Table 7** Distribution of fenestrate species in the Middle Devonian of the Eifel based on own research (*Spinofenestella* sp. – from the present paper; *Spinofenestella* sp. 1 and 2 – from Ernst and Schroeder 2007; *Fenestella* sp. 1–3 – from Ernst and Schroeder 2007; *Hemitrypa* sp. 1–4 – unpublished data)

| Species                                | Eifelian | Givetian |
|----------------------------------------|----------|----------|
| *Bashkirella cf. devonica*             | x        |          |
| *Proliticea bifurcata*                 | x        |          |
| *Rectifenestella aculeata*             | x        |          |
| *Rectifenestella sp. 1*                | x        |          |
| *Rectifenestella sp. 2*                | x        |          |
| *Ptylopora sp.*                        | x        |          |
| *Spinofenestella antiqua*              | x        | x        |
| *Spinofenestella sp.*                  | x        |          |
| *Spinofenestella sp. 1*                | x        |          |
| *Spinofenestella sp. 2*                | x        |          |
| *Hemitrypa sp. 1*                      | x        |          |
| *Hemitrypa sp. 2*                      | x        |          |
| *Hemitrypa sp. 3*                      | x        |          |
| *Hemitrypa sp. 4*                      | x        |          |
| *Anastomopora inflata*                 | x        |          |
| *Anastomopora blankenheimensis*        | x        |          |
| *Anastomopora minor*                   | x        |          |
| *Anastomopora striatella*              | x        |          |
| *Bigequina winteri*                    | x        |          |
| *Schischcatella heinorum*              | x        |          |
| *Loculipora alvearis*                  | x        | x        |
| *Fenestrapora transcaucasica*          | x        |          |
| *Fenestrapora tuberculata*             | x        |          |
| *Disotrypa sincera*                    | x        |          |
| *Fenestella sp. 1*                     | x        |          |
| *Fenestella sp. 2*                     | x        |          |
| *Fenestella sp. 3*                     | x        |          |

Palaeobiogeographic relations of fenestrate bryozoans from the Middle Devonian of the Eifel

The fenestrate bryozoan species from the Middle Devonian of the Eifel seem to be quite endemic. From the published data, few connections to the Devonian of Europe can be detected.
bryozoan very close to *Bashkirella devonica* (Dessily, 1967) from the Eifelian of Belgium has been identified in the Čurten Formation (Givetian) of the Eifel (Ernst and Schroeder 2007). In the same locality, the species *Anastomopora inflata* (Bigey, 1988b), previously known from the Frasnian of France, was found.

*Fenestrupora transcaucasia* Morozova and Lavrentjeva, 1998 is quite common in the Eifelian to Givetian of the Eifel (Ernst 2016), whereas the original record of this species comes from the *Microspirifer diluvianoides-Radiomena irregularis* brachiopod Zone (upper Eifelian, Middle Devonian) of Azerbaijan. The species *Dissotrypa sincera* Ernst and Königshof, 2010 was originally described from the Givetian of Western Sahara.

The majority of fenestrate genera from the Middle Devonian of the Eifel are cosmopolitan (*Fenestella, Rectifenestella, Spinofenestella, Hemitrypa, Anastomopora, and Loculipora*). The others show some restrictions in their distribution. The genus *Bigeypina Suárez-Andrés* and McKinney, 2010 is restricted to the Lower–Middle Devonian of Europe (Czech Republic, Spain, and Germany). The genus *Prolixicella* was identified besides German localities in the Lower–Middle Devonian (Emsian–Eifelian) of Spain (Ernst 2012) and in the Givetian of Western Sahara (Ernst and Königshof 2010). The genus *Schischcatella* Waschurova, 1964 is originally known from the Lower Devonian (Emsian) of Tajikistan. Two species of the genus *Dissotrypa* Ernst and Königshof, 2010 are known from the Lower–Middle Devonian (Emsian–Eifelian) of Spain (Ernst 2012).

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**Data availability** The studied specimens (thin sections and rock material) are deposited at the Research Institute and Natural History Museum, Frankfurt am Main, Germany (SMF-numbers), the Geological Centre Göttingen, Germany (GZG-numbers), and the Sandberger’s Devonian Collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany.

**Declarations**

**Conflict of interest** The author declares that he has no conflict of interest.

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