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ORIGINAL PAPER

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*.

This article is a contribution to the special issue "The Rhenish Massif: More than 150 years of research in a Variscan mountain chain".

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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).

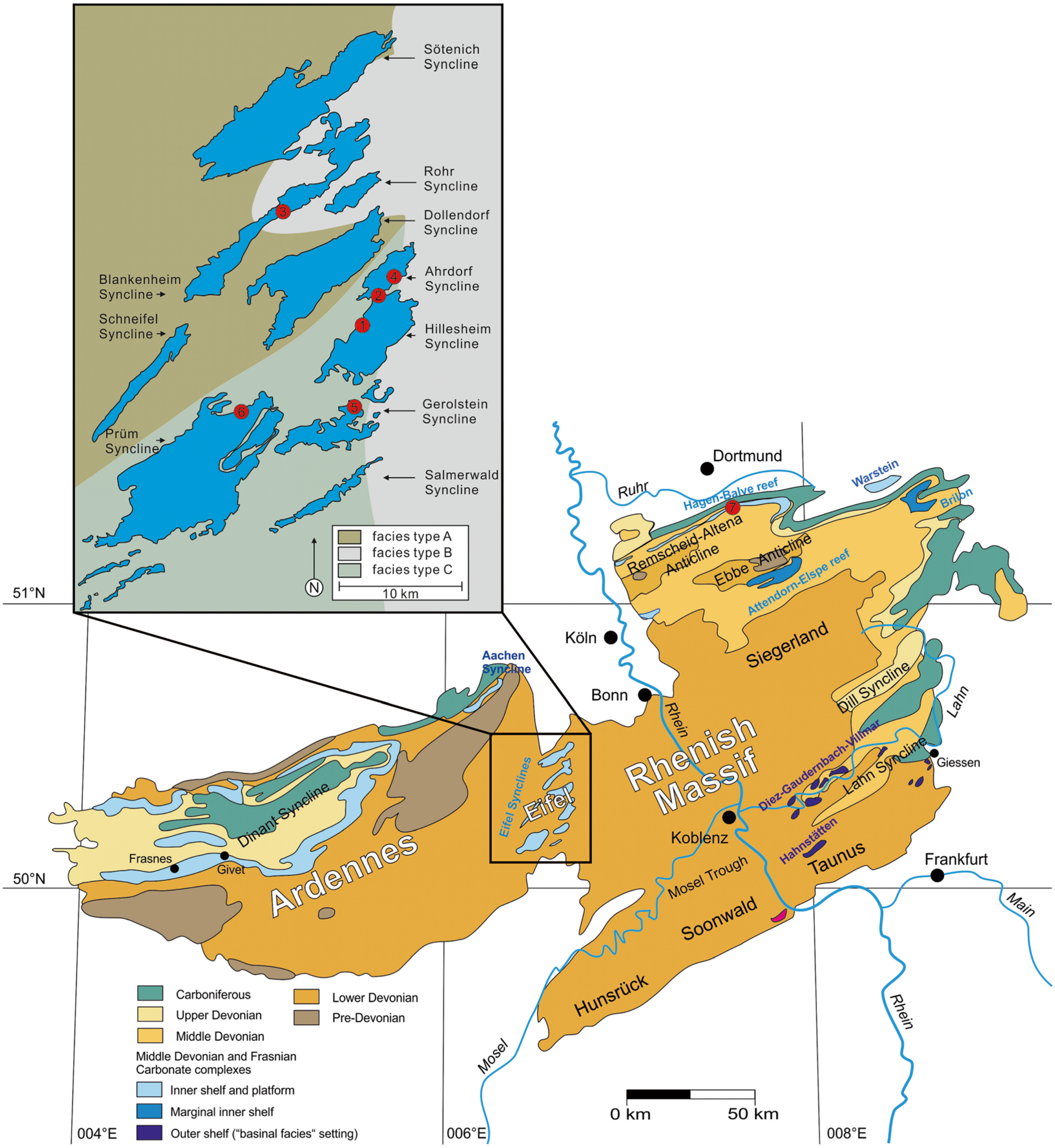


Fig. 1 Geological map with the position of studied localities: *1* Brühlborn near Rommersheim; *2* "Weinberg" Quarry near Kerpen; *3* Müllertchen Quarry; *4* Essingen-Hohenfels; *5* Schwirzheim; *6* Blankenheim; *7* Lüdenscheid (modified from Wehrmann et al. 2005 and Winter in Meyer et al. 1977)

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

Fig. 2 Stratigraphy of the "Type Eifelian Profile" sensu Struve and Werner (1982), simplified, showing the relationships of the stratigraphic units in the study area

Series	Stage	Formation	Subformation	Member	Conodont zones
Middle Devonian	Givetian	Cürten Fm.		Meerbüsch Mb.	*hemiansatus*
				Forstberg Mb.	
				Marmorwand Mb.	
				Felschbach Mb.	
		Loogh Fm.		Rech Mb.	
				Wotan Mb.	
		Ahbach Fm.	Müllert Sub. Fm.	Zerberus Mb.	
				Olifant Mb.	
				Lahr Mb.	*kockelianus & ensensis*
	Eifelian		Maiweiler Sub. Fm.	Hallert Mb.	
		Freilingen Fm.		Bohnert Mb.	
				Eilenberg Mb.	
		Junkerberg Fm.	Grauberg Sub. Fm.	Giesdorf Mb.	
				Nims Mb.	*kockelianus*
			Heinzelt Sub. Fm.	Rechert Mb.	
				Hönselberg Mb.	
				Mussel Mb.	
				Klausbach Mb.	
		Ahrdorf Fm.	Niederehe Sub. Fm.		*australis*
			Betterberg Sub. Fm.	Wasen Mb.	
				Flesten Mb.	
				Köll Mb.	
				Bildstock Mb.	

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 Honsel 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 Honsel Formation (Unterhonsel Fm.) of the Sauerland and to the Loogh Formation of the Eifel (May 1992; Andreas May, pers. comm., 2008).

Honsel Formation, lower Givetian

GZG.IN.0.010.501: Highway A45 Hagen-Siegen, access road Lüdenscheid, Geological Map sheet 4812 Herscheid (1002/38-W3).

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, autozooecial 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.

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926

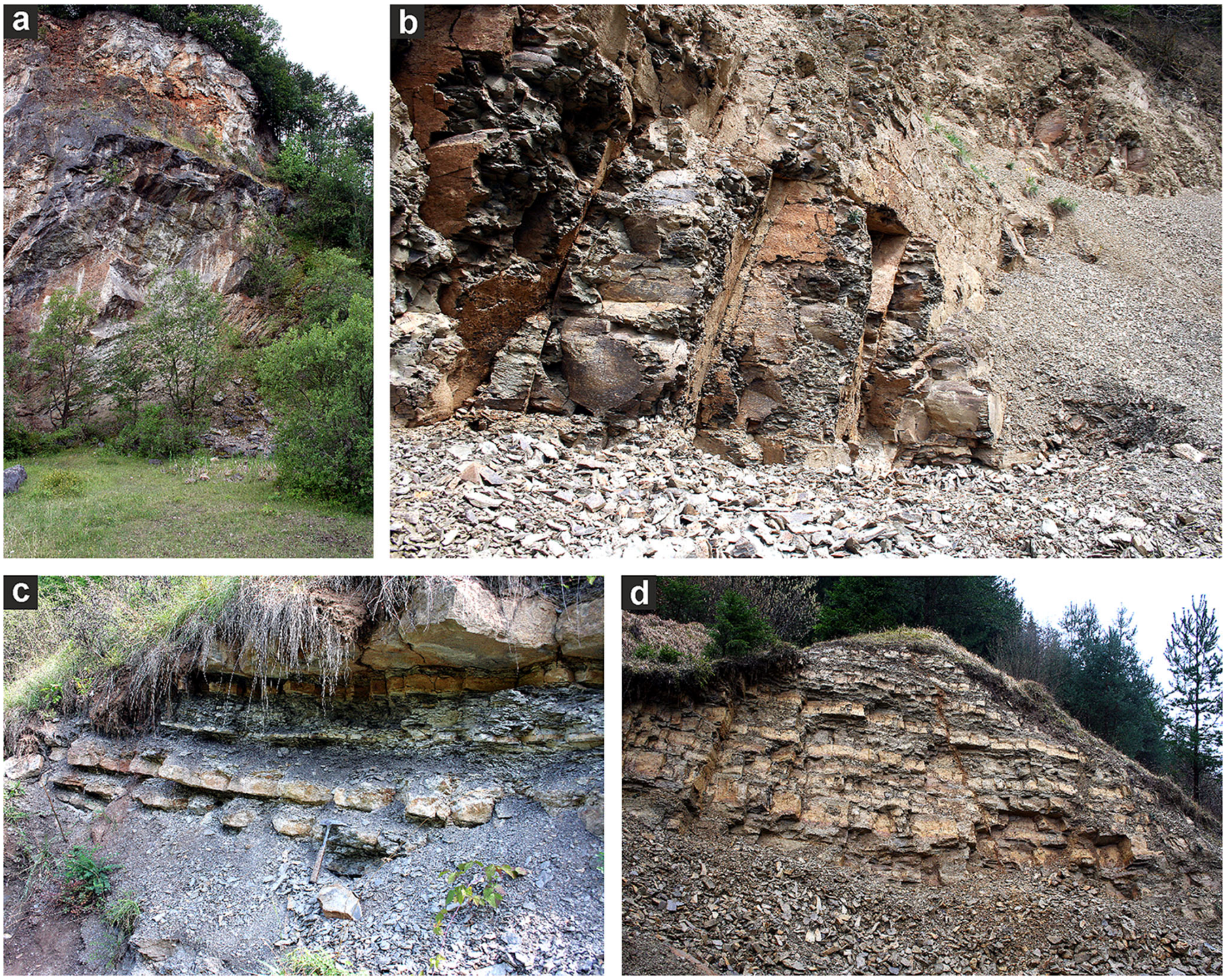


Fig. 3 Studied localities: **a** "Weinberg" Quarry near Kerpen, Hillesheim Syncline (height of the outcrop ca. 25 m); **b** Üxheim-Ahütte, abandoned Müllertchen Quarry, Hillesheim Syncline (width of the image ca. 4 m); **c** Railway cut west of Blankenheim, Blankenheim Syncline; **d** Brühlborn near Rommersheim, Prüm Syncline (height of the outcrop ca. 3.5 m)

Superorder Palaeostomata Ma, Buttler, and Taylor, 2014
Order Fenestellida Elias and Condra, 1957
Suborder Phylloporinina Lavrentjeva, 1979
Family Phylloporinidae 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 *Phylloporina* 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. Heterozooecia 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 *Hemitrypa* (?) *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–SMF 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, intermediately 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. Heterozooecia 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 formations, Eifelian, Middle Devonian; Essingen-Hohenfels, Germany. Hönselberg Member of the Junkerberg Formation, Eifelian, 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. Heterozooecia not observed.

Fig. 4 **a–e** *Prolixicella bifurcata* Ernst and Schroeder, 2007. **a** branch transverse section, GZG.IN.0.010.511b. **b–c** branch longitudinal section, GZG.IN.0.010.511g. **d** branch longitudinal section, GZG.IN.0.010.511b. **e** tangential section of an autozooecial aperture, GZG.IN.0.010.511b. **f–k** *Rectifenestella aculeata* (Sandberger and Sandberger, 1856). **f–g** sample 311, holotype of *Fenestrella aculeata* Sandberger and Sandberger, 1856, Sandberger`s Devonian collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany. **h–i** tangential section showing autozooecial apertures and chambers, SMF 62467. **j** mid tangential section showing autozooecial chambers, SMF 62467. **k** tangential section showing autozooecial apertures, SMF 62467. Scale bars: 5 mm (**f**), 2 mm (**g–h**), 1 mm (**i**), 0.5 mm (**a–e, j**), 0.2 mm (**k**)

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*).

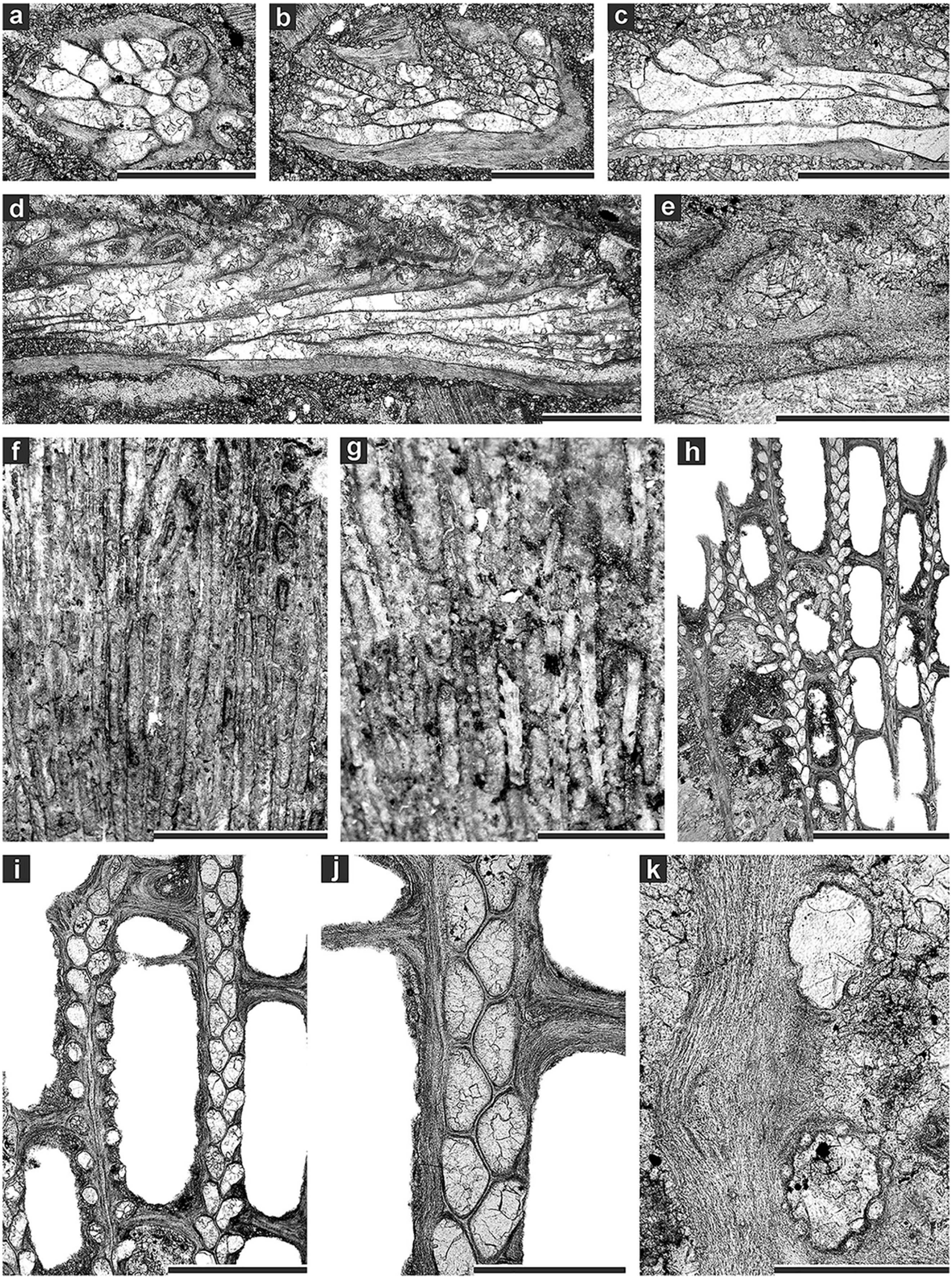
Occurrence: Bohnert Member of the Freilingen Formation, upper Eifelian, Middle Devonian; "Weinberg" Quarry near Kerpen, Hillesheim Syncline, Eifel (western Rhenish Massif), Germany.

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, intermediately 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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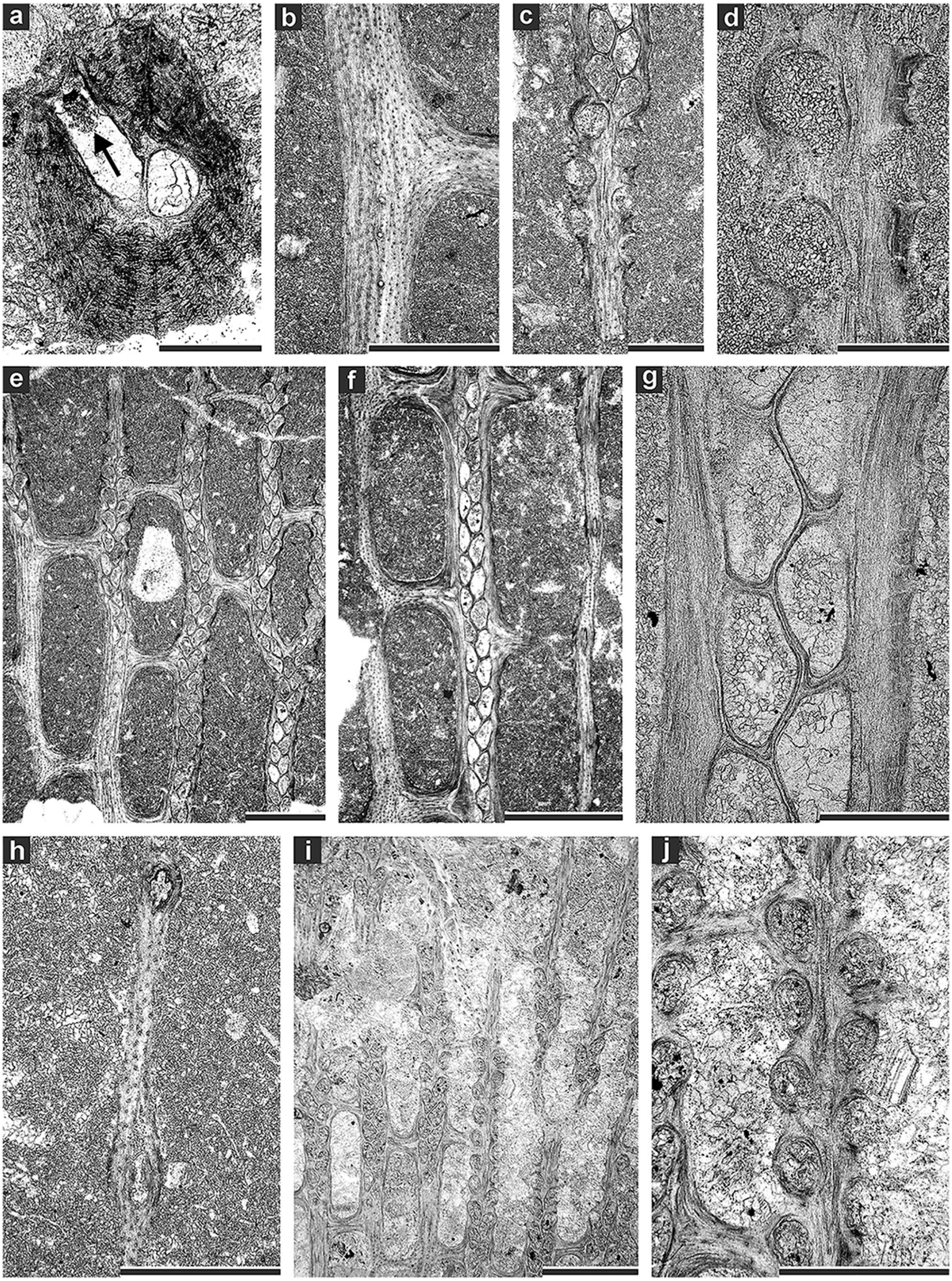
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◀ **Fig. 5** **a** *Rectifenestella aculeata* (Sandberger and Sandberger, 1856), branch transverse section (fossilised brown deposit in the vestibule of the left autozooecial chamber, arrow), SMF 62468. **b–h** *Rectifenestella* sp. 1. **b** tangential section showing branch reverse side with nodes, SMF 62471. **c** tangential section showing autozooecial apertures and chambers, SMF 62471. **d** tangential section showing autozooecial apertures, SMF 62470. **e** tangential section showing fenestrules and autozooecial chambers, SMF 62470. **f** tangential section showing fenestrules, autozooecial chambers and keel nodes, SMF 62471. **g** tangential section showing autozooecial chambers, SMF 62471. **h** tangential section showing keel nodes, SMF 62470. **i–j** *Rectifenestella* sp. 2, tangential section showing fenestrules, autozooecial apertures and chambers, SMF 62473. Scale bars: 1 mm (**e–f, i**), 0.5 mm (**b, h, j**), 0.2 mm (**a, c–d, g**)

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;

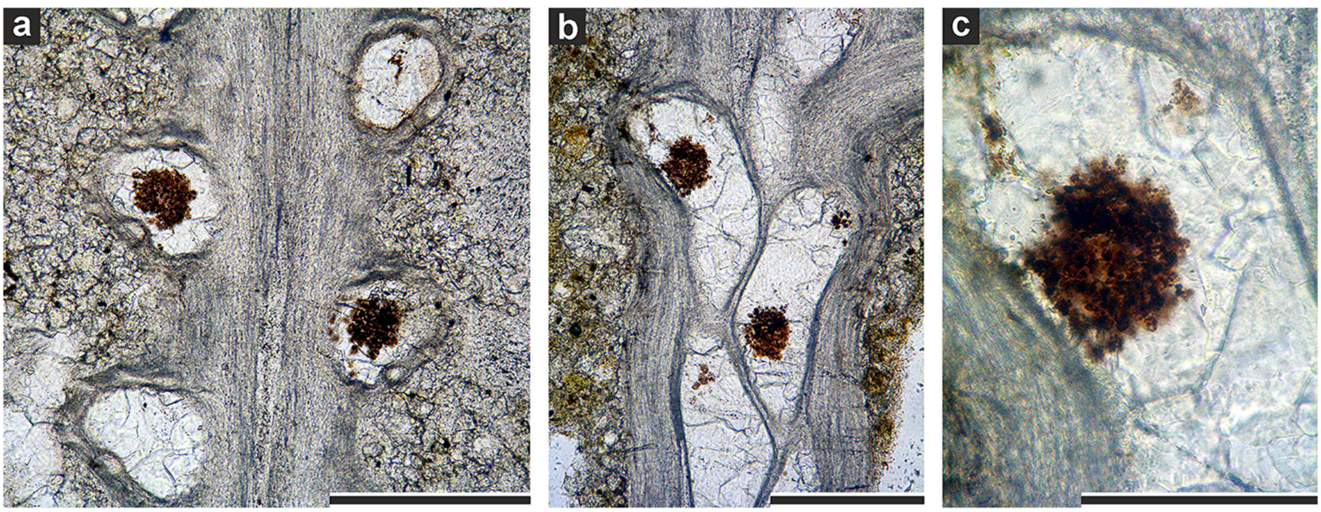


Fig. 6 **a–b** *Rectifenestella aculeata* (Sandberger and Sandberger, 1856), fossilised brown deposits in autozooecial chambers, SMF 62469. Scale bars: 0.2 mm (**a–b**) and 0.1 mm (**c**)

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 extrazooecial 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	0.046	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, intermediately 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. Heterozooecia not observed.

Comparison: *Ptylopora* sp. is similar to the species *P. nodosa* Hall, 1883 from the Givetian of USA, but differs from it in thicker branches (main branch width 0.45–0.54 mm vs. 0.33 mm in *P. nodosa*; secondary branch width 0.24–0.44 mm vs. 0.20 mm in *P. nodosa*). *Ptylopora* sp. differs from *P. 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 *P. striata*) and by presence of nodes on the median keel.

Occurrence: Olifant Member of the Müllert Subformation, of the Ahbach 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. Autozooecia 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.

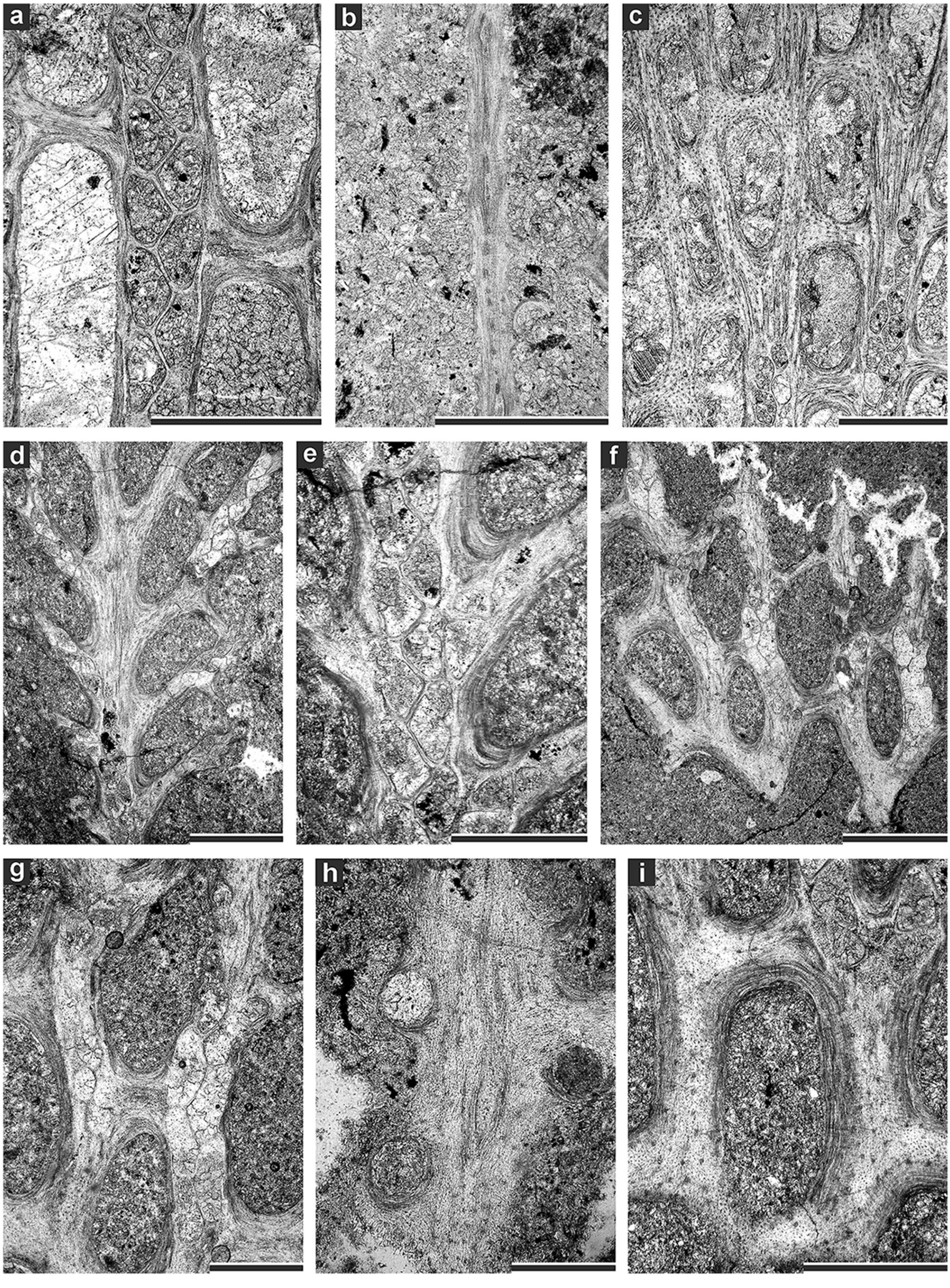
Spinofenestella antiqua (Goldfuss, 1826)
(Fig. 8a–h and Table 5)

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 *Fenestella 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). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
Branch width, mm	67	0.26	0.040	15.31	0.20	0.37
Dissepiment width, mm	74	0.17	0.044	26.02	0.10	0.28
Fenestrule width, mm	73	0.20	0.047	22.77	0.12	0.30
Fenestrule length, mm	72	0.46	0.103	22.26	0.28	0.65
Distance between branch centres, mm	75	0.46	0.063	13.71	0.35	0.66
Distance between dissepiment centres, mm	74	0.64	0.102	15.95	0.45	0.91
Aperture width, mm	81	0.08	0.007	8.40	0.06	0.10
Aperture spacing along branch, mm	75	0.22	0.036	16.15	0.14	0.32
Aperture spacing diagonally, mm	62	0.23	0.023	9.93	0.19	0.29
Maximal chamber width, mm	82	0.13	0.017	13.26	0.09	0.18
Node width, mm	62	0.044	0.010	22.09	0.025	0.070
Distance between node centres, mm	53	0.26	0.036	13.62	0.19	0.34
Apertures per fenestrule length	51	2.8	0.590	20.90	2.0	4.0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◀ **Fig. 7** **a–c** *Rectifenestella* sp. 2. **a** tangential section showing autozooecial chambers, SMF 62473. **b** tangential section showing keel nodes, SMF 62473. **c** tangential section showing branch reverse side, SMF 62474. **d–i** *Ptylopora* sp. **d–e** tangential section showing main branch and lateral branches, SMF 62477. **f–h** tangential section showing fenestrules, autozooecial apertures and chambers, SMF 62480. **i** tangential section showing branch reverse side, SMF 62477. Scale bars: 1 mm (**c–d, f**), 0.5 mm (**a–b, e, g, i**), 0.2 mm (**h**)

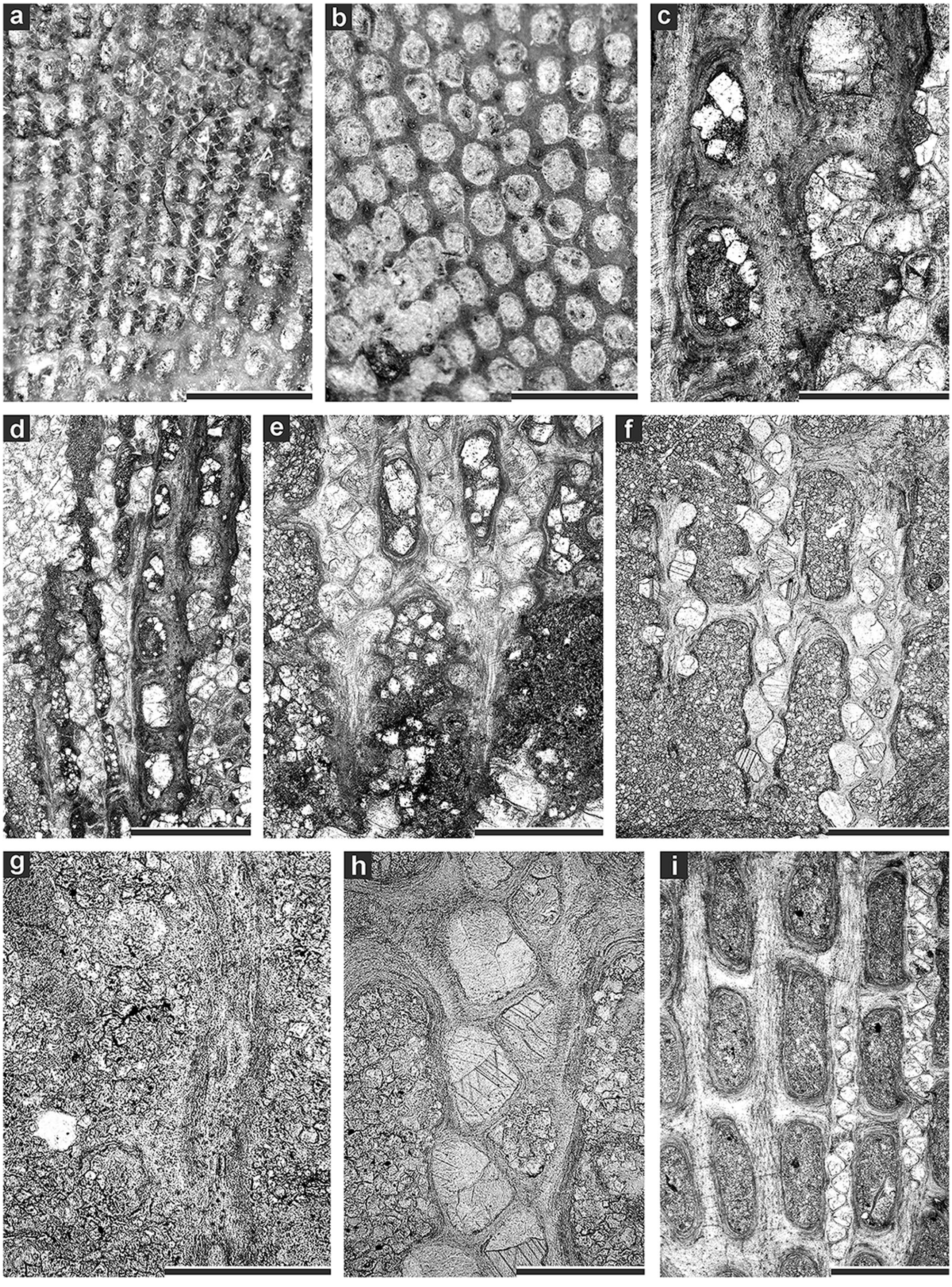
Material: Twelve thin sections GZG.IN.0.010.501a, g, i, k, 538c, SMF 62486–SMF 62493.
Additional material: 312 (lectotype of *Fenestrella subrectangularis* Sandberger and Sandberger, 1856), Sandberger`s Devonian collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany, Villmar, Stringocephalenkalk, Givetian.
Exterior description: Reticulate colony formed by straight branches joined by wide dissepiments. Fenestrules oval to rectangular, short, narrow. Autozooecia arranged in two alternating rows on branches. Autozooecial apertures circular, with stellate structure; 2–4 apertures spaced per fenestrule length. Median keel low, narrow, containing small closely spaced rounded nodes. Large nodes on the reverse side of branches positioned against dissepiments.
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. Heterozooecia not observed.
Comparison: *Spinofenestella antiqua* (Goldfuss, 1826) differs from *S. inclara* (Pǒcta, 1894) from the Lower Devonian of the Czech Republic in having wider branches (average branch width 0.27 mm vs. 0.24 mm in *S. inclara*) and in smaller distances between branch and dissepiment centres (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 autozooecial chambers. The lectotype of *Fenestrella subrectangularis* Sandberger and Sandberger, 1856, Sandberger`s Devonian collection (Wiesbaden), shows the same type of nodes and shape of autozooecia (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 autozooecia 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. Autozooecia arranged in two rows on branches. Autozooecial 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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◀ **Fig. 8** **a–h** *Spinofenestella antiqua* (Goldfuss, 1826). **a–b** 312 (lectotype of *Fenestrella subrectangularis* Sandberger and Sandberger, 1856), Sandberger`s Devonian collection, the Natural History State Collection of the Wiesbaden Museum, Wiesbaden, Germany. **c** tangential section showing reverse branch surface with microstylets and nodes, GZG.IN.0.010.501k. **d–e** tangential section showing autozooecial apertures, chambers and keel nodes, GZG.IN.0.010.501k. **f–h** tangential section showing autozooecial apertures, chambers and keel nodes, GZG.IN.0.010.538c. **i** *Spinofenestella* sp., tangential section showing autozooecial apertures and reverse branch surface, SMF 62497**.** Scale bars: 2 mm (**a–b**), 1 mm (**d, i**), 0.5 mm (**c, e–f**), 0.2 mm (**g–h**)

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

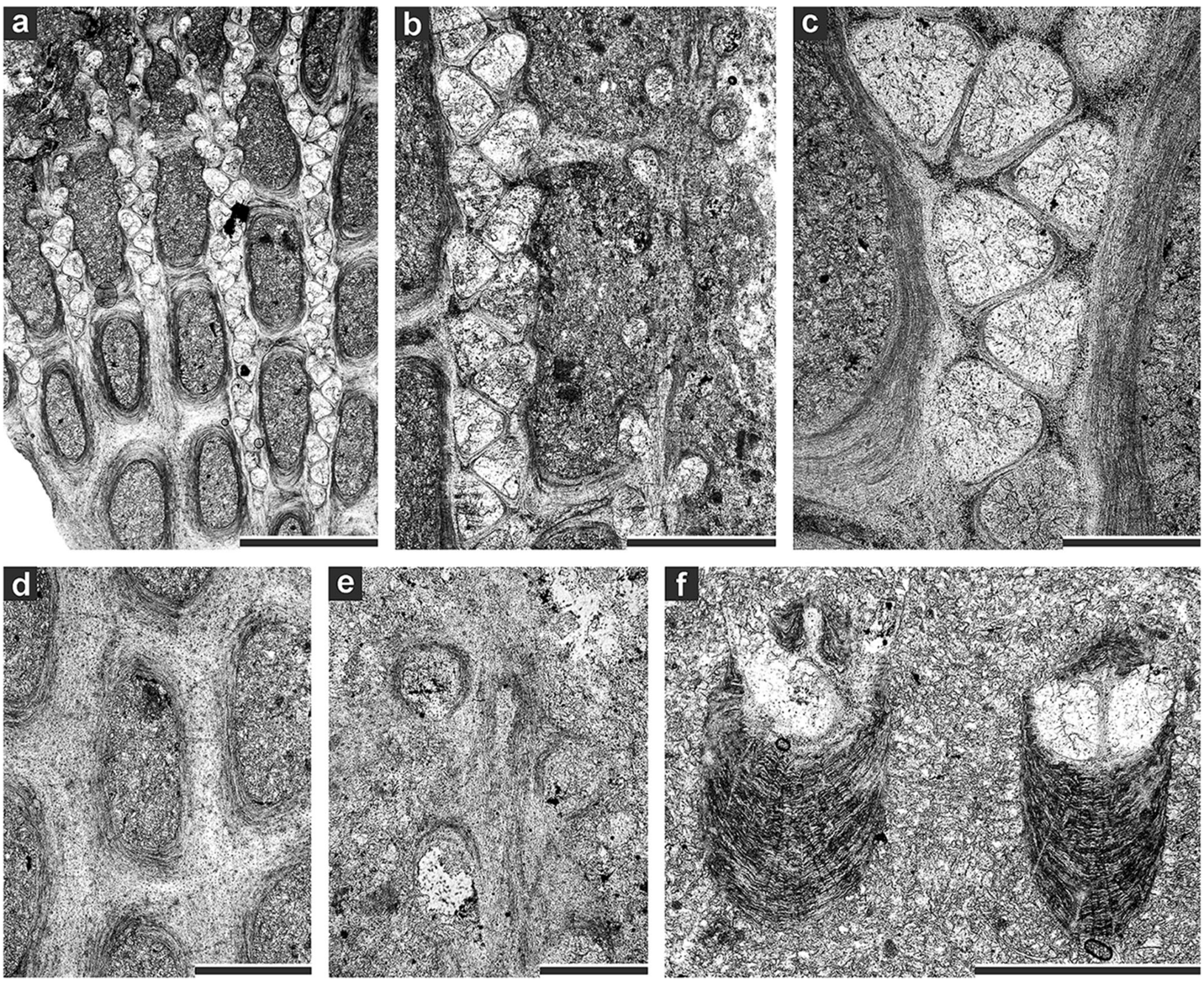

Fig. 9 **a–e** *Spinofenestella* sp. **a** tangential section showing autozooecial apertures and chambers, SMF 62496. **b** tangential section showing autozooecial apertures, chambers and keel nodes, SMF 62497. **c** tangential section showing autozooecial chambers, SMF 62496. **d** tangential section showing reverse branch surface with microstylets, SMF 62497. **e** tangential section showing autozooecial apertures and keel nodes, SMF 62497. **f** branch transverse section showing autozooecial chambers and extrazooecial laminated skeleton, SMF 60308. Scale bars: 1 mm (**a**), 0.5 mm (**b**, **d**, **f**), 0.2 mm (**c**, **e**)

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 (Eifelian) 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).

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)

	Eifelian	Givetian
Bashkirella cf. *devonica*		x
Prolixicella 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
Bigeyina winteri	x	
Schischcatella heinorum	x	
Loculipora alvearis	x	x
Fenestrapora transcaucasica	x	x
Fenestrapora tuberculata		x
Dissotrypa sincera	x	
Fenestella sp. 1		x
Fenestella sp. 2		x
Fenestella sp. 3		x

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://bryozoa.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, *Penniretepora antiqua* (Steininger, 1831), *Retepora dispar* Steininger, 1849, *R. speciosa* Steininger, 1849, *R. hexagonalis* Roemer, 1850.

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.

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. A bryozoan very close to *Bashkirella devonica* (Dessily, 1967) from the Eifelian of Belgium has been identified in the Cürten 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.

Fenestrapora transcaucasica 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 *Mucrospirifer 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 *Bigeyina* 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.

References

Astrova, G. G., & Morozova, I. P. (1956). About systematics of the order Cryptostomata. *Doklady Akademii Nauk SSSR, 110*(4), 661–664. [in Russian]

Bigey, F. P. (1988a). Devonian Bryozoa and global events: The Frasnian–Famennian extinction. In N. J. McMillan, A. F. Embry, & D. J. Glass (Eds.), *The Devonian of the World, Proceedings of the Second International Symposium of the Devonian System. Canadian Society of Petroleum Geology, Memoir 14*, 53–62.

Bigey, F. P. (1988b). Bryozoaires du Givétien et du Frasnien de Ferques (Boulonnais - France). *Biostratigraphie du Paléozoïque, 7*, 297–323.

Borg, F. (1926). Studies on Recent cyclostomatous Bryozoa. *Zoologiska Bidrag från Uppsala, 10*, 181–507.

Bornemann, J. G. (1884). *Cyclopelta winteri*, eine Bryozoe aus dem Eifeler Mitteldevon. *Zeitschrift der Deutschen Geologischen Gesellschaft, 36*, 864–865.

Condra, G. E. (1902). New Bryozoa from the Coal Measures of Nebraska. *The American Geologist, 30*, 337–358.

Crockford, J. (1944). Bryozoa from the Permian of Western Australia. Part I. Cyclostomata and Cryptostomata from the north-west basin and Kimberly district. *Proceedings of the New South Wales Linnean Society, 69*, 139–175.

Cuffey, R. J., & McKinney, F. K. (1979). Devonian Bryozoa. *Special Papers in Palaeontology, 23*, 307–311.

Dessilly, E. (1967). Les bryozoaires dévoniens de la Belgique; la présence du genre '*Phylloporina*' dans le Couvinien de la Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, 43*(3), 1–6.

Ehrenberg, C. G. (1831). Symbolae Physicae, seu Icones et descptiones Corporum Naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegiptum, Nubiam, Dongalaam, Syriam, Arabiam et Habessiniam, studia annis 1820-25, redirent. *Pars. Zoologica*, 4, Animalia Evertebrata exclusis Insectis. Berolini, 10 pls.

Elias, M. K., & Condra, G. E. (1957). *Fenestella* from the Permian of west Texas. *Geological Society of America Memoir, 70*, 1–158. https://doi.org/10.1130/mem70

Ernst, A. (2008a): Non-fenestrate bryozoans from the Middle Devonian of the Eifel (western Rhenish Massif, Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 250*(3), 313–379. https://doi.org/10.1127/0077-7749/2008/0250-0313

Ernst, A. (2008b). New data on the Middle Devonian Bryozoa of Germany. In S. J. Hageman, M. M., Jr., Key, & J. E. Winston (Eds.), *Bryozoan Studies 2007: Proceedings of the 14th International Bryozoology Conference, Boone, North Carolina, July 1-8, 2007. Virginia Museum of Natural History Special Publication, 15*, 29–36.

Ernst, A. (2012). Fenestrate bryozoan fauna from the Lower – Middle Devonian of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen, 264*(3), 205–247. https://doi.org/10.1127/0077-7749/2012/0237

Ernst, A. (2013). Diversity dynamics and evolutionary patterns of Devonian Bryozoa. *Palaeobiodiversity and Palaeoenvironments, 93*(1), 45–63. https://doi.org/10.1007/s12549-012-0086-4

Ernst, A. (2016). *Fenestrapora* (Fenestrata, Bryozoa) from the Middle Devonian of Germany. *Paläontologische Zeitschrift, 90*(1), 19–32. https://doi.org/10.1007/s12542-016-0284-x

Ernst, A. (2020). *Anastomopora* (Fenestrata, Bryozoa) from the Middle Devonian of the Rhenish Massif, Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 297*(1), 11–26. https://doi.org/10.1127/njgpa/2020/0911

Ernst, A. (2022). Semicosciniid bryozoans from the Middle Devonian of Rommersheim (Eifel, Germany). *PalZ Paläontologische Zeitschrift*. https://doi.org/10.1007/s12542-021-00602-6

Ernst, A., & Schroeder, S. (2007). Stenolaemate bryozoans from the Middle Devonian of the Rhenish Slate Massif (Eifel, Germany). *Neues Jahrbuch für Geologie und Paläontologie, 246*(2), 205–233. https://doi.org/10.1127/0077-7749/2007/0246-0205

Ernst, A., & Bohatý, J. (2009). *Schischcatella* (Fenestrata, Bryozoa) from the Devonian of the Rhenish Massif, Germany. *Palaeontology, 52*(6), 1291–1310. https://doi.org/10.1111/j.1475-4983.2009.00899.x

Ernst, A., & Königshof, P. (2010). Bryozoan fauna and microfacies from a Middle Devonian reef complex (Western Sahara, Morocco). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 568*, 1–91.

Ernst, A., Königshof, P., Taylor, P. D., & Bohatý, J. (2011). Microhabitat complexity – an example from Middle Devonian bryozoan-rich sediments. *Palaeobiodiversity and Palaeoenvironments*, *91*(4), 257–284. https://doi.org/10.1007/s12549-011-0060-6

Ernst, A., May, A., & Marks, S. (2012). Bryozoans, corals and microfacies of lower Eifelian (Middle Devonian) limestones at Kierspe, Germany. *Facies, 58*, 727–758. https://doi.org/10.1007/s10347-011-0289-6

Ernst, A., Bohatý, J., & Taylor, P. D. (2014a). *Botryllopora* (Cystoporata, Bryozoa) from the Middle Devonian of Canada and Germany. In A. Rosso, P. N. Wyse Jackson, & J. Porter (Eds.), *Bryozoan Studies 2013: proceedings of the 16th International Bryozoology Association conference, Catania, Sicily, Italy. Studi Trentini di Scienze Naturali*, *94*, 101–109.

Ernst, A., Taylor, P. D., & Bohatý, J. (2014b). A new Middle Devonian cystoporate bryozoan from Germany containing a symbiont bioclaustration. *Acta Palaeontologica Polonica*, *59*(1), 173–183. https://doi.org/10.4202/app.2010.0110

Foerste, A. F. (1887). The Clinton Group of Ohio (Bryozoa). *Bulletin of Scientific Laboratory, Denison University, 2*(1/2), 71–88, 149–176.

Goldfuss, G. A. (1826-1844). *Petrefacta Germaniae*. Düsseldorf: Arnz & Co.

Hageman, S. J. (1991a). Discrete morphotaxa from a Mississippian fenestrate faunule: Presence and implications. In F. P. Bigey (Ed.), *Bryozoaires actuels et fossil: Bryozoa living and fossil. Bulletin de la Société des Sciences Naturelles de l`Ouest de la France, Mémoire HS, 1*, 147–150.

Hageman, S. J. (1991b). Approaches to systematic and evolutionary studies of perplexing groups: an example using fenestrate Bryozoa. *Journal of Paleontology*, *65*, 630–647. https://doi.org/10.1017/S0022336000030729

Hall, J. (1883). Bryozoans of the Upper Helderberg and Hamilton groups. *Transactions of the Albany Institute, 10,* 145–197.

King, W. (1849). On some families and genera of corals. *Annals and Magazine of the Natural History, 2*, 388–390. https://doi.org/10.1080/03745485909494780

Krasnopeeva, P. S. (1935). Bryozoans of the Middle and Upper Devonian of Altai. *Materialy po geologii Zapadno-Sibirskogo Kraya, 20*, 43–84. [in Russian]

Kräusel, W. (1953). *Cyclopelta winteri* (Bryozoa) aus dem Mitteldevon der Eifel. *Senckenbergiana, 34*(1–3), 43–52.

Kräusel, W. (1954). *Cyclopelta winteri* (Bryozoa) aus der *corbis*-Bank des Oberharzer Mittel-Devons. (Bryoz.). *Senckenbergiana, 34*(4–6), 246.

Kräusel, W. (1956). Bryozoen-Arten F. A. Roemer's (Fenestellidae) aus dem deutschen Devon. *Senckenbergiana lethaea, 37*(1–2), 59–64.

Kräusel, W. (1957). *Loculipora* Hall aus dem Mittel-Devon des Rheinischen Schiefergebirges und des Harzes. *Senckenbergiana lethaea, 38*(5–6), 335–343.

Kräusel, W. (1981). Wuchsformen der Fenestelliden (Bryozoen) aus dem Mitteldevon der Eifel. *Der Aufschluss, 32*(1), 29–36.

Lavrentjeva, V. D. (1979). Phylloporinina – new Suborder of Palaeozoic Bryozoa. *Paleontologicheskii Zhurnal, 1979*(1), 59–68. [in Russian]

M'Coy, F. (1844). *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*. Dublin: Dublin University Press. https://doi.org/10.5962/bhl.title.11559

Ma, J.-Y., Buttler, C. J., & Taylor, P. D. (2014). Cladistic analysis of the 'trepostome' Suborder Esthonioporina and the systematics of Palaeozoic bryozoans. In A. Rosso, P. N. Wyse Jackson, & J. S. Porter (Eds.), *Bryozoan Studies 2013. Studi Trentini di Scienze Naturali, 94*, 153–161.

Maurer, F. (1885). *Die Fauna der Kalke von Waldgirmes bei Gießen*. Darmstadt: Bergsträsser.

May, A. (1992). Paleoecology of Upper Eifelian and Lower Givetian Coral Limestones in the Northwestern Sauerland (Devonian; Rhenish Massif). *Facies, 26*, 103–116.

Meyer, W., Stoltidis, J., & Winter, J. (1977, Eds.). Geologische Exkursion in den Raum Weyer-Schuld-Heyroth-Niederehe-Üxheim-Ahütte. *Decheniana, 130*, 322–334.

Morozova, I. P. (1974). Revision of the bryozoan genus *Fenestella*. *Paleontologicheskii Zhurnal, 1974*(2), 54–67. [in Russian]

Morozova, I. P. (2001). Bryozoans of the Order Fenestellida. *Trudy Paleontologicheskogo Instituta Rossijskoj Akademii Nauk, 277*, 1–176. [in Russian]

Morozova, I. P., & Lavrentjeva V. D. (1998). New bryozoans of the Family Semicosciniidae. *Paleontologicheskii Zhurnal, 1998*(2), 53–59. [in Russian]

Morozova I. P., Weiss O. B., & Racki, G. (2006). New Devonian and Carboniferous bryozoans of the Holy Cross Mountains (Central Poland). *Paleontological Journal, 40*, 529–540. https://doi.org/10.1134/S0031030106050078

Nekhoroshev, V. P. (1928). Über die Entdeckung der Gattung *Semicoscinium* Prout in den mitteldevonischen Ablagerungen der Eifel und über die Bedeutung dieses Fundes. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B, 1928*, 476–478.

Ochs, G., & Wolfart, R. (1961). Geologie der Blankenheimer Mulde (Devon/Eifel). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 501*, 1–100.

Počta, P. (1894). Bryozoaires, Hydrozoares et partie des Anthozoaries. In *Système Silurien du Centre de la Bohême par Joachim Barrande. Recherches Paléontologiques, 8*(1), 1–230.

Roemer, F. A. (1850). Beiträge zur geologischen Kenntniss des nordwestlichen Harzgebirges. *Palaeontographica*, *3*, 1–52.

Roemer, F. A. (1855). Beiträge zur geologischen Kenntniss des nordwestlichen Harzgebirges, Dritte Abtheilung, *Palaeontographica, 5*, 1–44.

Roemer, F. A. (1856). Kohlen-Periode (Silur-, Devon-, Kohlen- u. Zechstein-Formation). In H. G. Bronn (Ed.), *Lethaea geognostica, oder Abbildung und Beschreibung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*. (Bd. 1 u. 2, 1852–56, pp. 205–788). Schweizerbart'sche Verlagshandlung und Druckerei.

Sandberger, G., & Sandberger, F. (1850–1856). *Die Versteinerungen des Rheinischen Schichtensystems in Nassau. Mit einer kurzgefassten Geognosie dieses Gebietes und mit steter Berücksichtigung analoger Schichten anderer Länder.* Text mit vielen eingedruckten Holzschnitten, einer lithographirten Suturentafel- und einer geognostischen Uebersichtskarte in Farbendruck. XIV u. 564 Seiten. gr. 8°. Wiesbaden: Kreidel und Niedner Verlagshandlung.

Schulga-Nesterenko, M. I. (1951). Carboniferous fenestellids of the Russian Platform. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 32*, 1–161. [in Russian]

Snyder, E. M. (1991a). Revised taxonomic procedures and paleoecological applications for some North American Mississippian Fenestellidae and Polyporidae (Bryozoa). *Palaeontographica Americana, 57*, 1–275.

Snyder, E. M. (1991b). Revised taxonomic approach to acanthocladiid Bryozoa. In F.P. Bigey (Ed.), *Bryozoaires actuels et fossil: Bryozoa living and fossil*. *Bulletin de la Société des Sciences Naturelles de l`Ouest de la France, Mémoire, H.S., 1*, 431–445.

Steininger, J. (1831). *Bemerkungen über die Versteinerungen, welche in dem Übergangs-Kalkgebirge der Eifel gefunden werden*. Programm Gymnasium zu Trier 3–44, Blattau.

Steininger, J. (1849). *Die Versteinerungen des Uebergangsgebirges der Eifel.* Jahrbuch des Schul-Cursus 1848/49 Gymnasium Trier, 1–34.

Struve, W. (1982). The Eifelian within the Devonian frame, history, boundaries, definitions. *Courier Forschungsinstitut Senckenberg, 55*, 401–432.

Struve, W., & Werner, R. (1982). The Lower/Middle Devonian boundary and the Eifelian Stage in the "Type Eifelian" region. In G. Plodowski, R. Werner, & W. Ziegler (Eds.), *Field meeting on Lower and Lower Middle Devonian stages in the Ardenno-Rhenish type area, guidebook*, 81–151. Frankfurt am Main.

Suárez-Andrés, J. L., & McKinney, F. K. (2010). Revision of the Devonian fenestrate bryozoan genera *Cyclopelta* Bornemann, 1884, and *Pseusotrypa* Prantl, 1932, with a description of a rare fenestrate growth habit. *Revista Española de Paleontología*, *25(2)*, 123–138.

Suárez Andrés, J. L., & Ernst, A. (2015). Lower–Middle Devonian Fenestellidae (Bryozoa) of NW Spain: Implications for fenestrate palaeobiogeography. *Facies, 61*(415), 25 pp. https://doi.org/10.1007/s10347-014-0415-3

Termier, H., & Termier, G. (1971). Bryozoaires du Paléozoïque supérieur de l´Afganistan. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon, 47*, 1–52.

Toots, H. (1951). Über einige cryptostome Bryozoen aus dem Mitteldevon des Rheinischen Schiefergebirges. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 93*, 233–246.

Ulrich, E. O. (1890). Palaeozoic Bryozoa: III. *Geological Survey, 8*, 283–688.

Wehrmann, A., Blieck, A., Brocke, R., Hertweck, G., Jansen, U., Königshof, P., Plodowski, G., Schindler, E., Schultka, S. & Wilde, V. (2005). Paleoenvironment of an Early Devonian land-sea transition: a case study from the southern margin of the Old Red Continent (Mosel Valley, Germany). *Palaios, 20*(2), 101–120.