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RESEARCH PAPER

Fenestrapora (Fenestrata, Bryozoa) from the Middle Devonian of Germany

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Abstract Two species of the fenestrate genus *Fenestrapora* Hall, 1885 are described from the Middle Devonian (middle Eifelian-lower Givetian) of the Rhenish Massif, Germany. The species *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998 is known from the Middle Devonian (Eifelian) of Transcaucasia, Azerbaijan, and from the Middle Devonian (Eifelian) of Sauerland, Germany. One species is new: *Fenestrapora tuberculata* sp. nov. Numerical statistics were tested for species discrimination of the studied material of three *Fenestrapora* species from the Lower Devonian of Spain and Middle Devonian of Germany. Discrepancies in the taxonomical and numerical assignment of the studied samples are explained by restriction of the involved characters and their affection by environmental conditions.

Keywords Devonian · Bryozoa · Taxonomy · Evolution · Eifel (Rhenish Massif, Germany)

Kurzfassung Zwei Arten der fenestraten Bryozoen-Gattung *Fenestrapora* Hall, 1885 werden aus dem Mitteldevon des Rheinischen Schiefergebirges beschrieben. Die Art *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998 ist aus dem Mitteldevon (Eifelium) von Transkaukasien (Aserbaidschan) und dem Sauerland (Deutschland) bekannt. Die neue Art *Fenestrapora tuberculata* sp. nov. wird vorgestellt und beschrieben. Eine numerische statistische Analyse zur Art-Abgrenzung innerhalb des untersuchten Materials (drei *Fenestrapora*-Arten) aus dem Unter- (Spanien) und Mitteldevon (Deutschland) wurde durchgeführt. Abweichungen in der taxonomischen und numerischen Zuordnung der untersuchten Proben können durch die geringe Anzahl der herangezogenen Merkmale und deren Beeinflussung durch Umweltverhältnisse erklärt werden.

Schlüsselwörter Devon · Bryozoa · Taxonomie · Evolution · Eifel (Rheinisches Schiefergebirge, Deutschland)

Introduction

Genus *Fenestrapora* Hall, 1885, existed for a short period from the Lower Devonian (Emsian) to the Middle Devonian (Givetian) of the USA and Europe. This genus includes only a few species: *Fenestrapora biperforata* Hall, 1885, from the Lower to Middle Devonian of New York, USA, *F. infraporosa* (Ulrich, 1886), *F. occidentalis* Ulrich, 1890, from the Middle Devonian (Givetian) of the USA and *F. transcaucasica* Morozova and Lavrentjeva, 1998, from the Middle Devonian (Eifelian) of Transcaucasia. The species *Fenestrapora occidentalis* Ulrich, 1890, has been recently identified from the Lower to Middle Devonian (Emsian-Eifelian) of NW Spain (Ernst 2012; Fig. 7f–h), whereas *F. transcaucasica* Morozova and Lavrentjeva, 1998, has been found in the Middle Devonian (lower Eifelian) of Sauerland, Germany (Ernst et al. 2012). The new species *F. tuberculata* sp. nov. is described from the Middle Devonian (Eifelian-Givetian) of the Rhenish Massif, Germany.

The genus *Fenestrapora* differs from other fenestrates by the presence of aviculomorphs, which are regarded being functionally analogous with avicularia of the

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cheilostome bryozoans (McKinney 1998; Morozova 2001). These structures are situated in the outer laminated skeleton, mainly on the reverse side of branches, widened crests of keels on the obverse side, or in the thickened skeleton around colony bases. Similar structures occur in *Mirifenestella* Morozova, 1974, which represent paired aviculomorphs situated on dissepiments and opened to the reverse side. In contrast to avicularia, aviculomorphs are not interpreted as heterozooecia (modified zooecia), but as colonial structures (McKinney 1998). The contrasting hypothesis regards aviculomorphs as remnants of avicularia-like heterozooecia (Morozova and Lavrentjeva 1998; Morozova 2001). The function of aviculomorphs must have been the same as of avicularia: protection and (or) cleaning (Winston 1984). The whole contents of the function of avicularia of cheilostomes is not well understood (McKinney and Jackson 1989).

The aim of this article is to provide a description of a new *Fenestrapora* species from the Middle Devonian (Eifelian-Givetian) of the Rhenish Massif, Germany, and a numerical comparison of three species from the Devonian of Europe: *Fenestrapora occidentalis* Ulrich, 1890, *F. transcaucasica* Morozova and Lavrentjeva, 1998, and *F. tuberculata* sp. nov.

Geological setting

The material for this study comes from five localities in the western Rhenish Massif, Germany (Fig. 1).

The first locality is situated in the vicinity of Brühlborn near Rommersheim, Prüm Syncline (50°22′, 6°47′). The locality is a road cut in which limestones of the upper Nims Member of the Junkerberg Formation (Eifelian) crop out. These limestones are represented by rudstones and bindstones containing brachiopods, corals, stromatolites, echinoderms and abundant bryozoans.

The second locality is an abandoned Müllertchen quarry in the vicinity of Üxheim-Ahütte, Hillersheim Syncline (50°21′, 6°46′). This quarry contains muddy limestone containing corals, brachiopods, crinoids, sponges and bryozoans. These limestones belong to the Olifant Member of the Ahbach Formation (lowermost Givetian) and the Müllert Subformation of the Ahbach Formation (lowermost Givetian).

The third locality is the well-known abandoned “Weinberg” quarry near Kerpen (50°19′, 6°42′), which reveals the Middle Devonian carbonate succession. The studied material from the “Weinberg” Quarry comes from the Bohnert Member of the Freilingen Formation (upper Eifelian).

The fourth locality lies southwest of the village Gondelsheim, Prüm Syncline (50°14′, 6°28′). Muddy limestones of the Nims Member of the Upper Junkerberg Formation (Eifelian) at this locality contain corals, brachiopods, echinoderms and bryozoans.

The fifth locality is situated in the vicinity of the village Essingen-Hohenfels, eastern Gerolstein Syncline (50°15′, 6°44′), and contains muddy limestones of relatively uncertain stratigraphic position. These sediments represent a transition between the Ahrdorf and Junkerberg formations (Jan Bohatý, pers. comm. 2009).

The stratigraphic nomenclature of the Middle Devonian of the Eifel carbonate synclines follows Struve (1961, 1992, 1996). The terms “formation,” “subformation” and “member” are considered independent and hierarchic, respectively Fig. 2.

Materials and methods

Colonies of *Fenestrapora* species were studied in thin sections using a binocular microscope in transmitted light. Additionally, a scanning electron microscope was used to study an external morphology. The morphological terminology is modified from Hageman (1991a, b). The following morphological characters were measured: branch width, dissepiment width, fenestrule width, fenestrule length, distance between the branch centers, distance between the dissepiment centers, aperture spacing along the branch, diagonal aperture spacing, autozooecial aperture width, maximum chamber width, thickness of the reverse wall granular layer, thickness of the reverse wall laminated layer, branch thickness including the keel, branch thickness without the keel (measured from the reverse branch surface up to the level of the aperture), aviculomorph length, aviculomorph width, reproductive heterozooecium diameter and reverse surface node diameter (Fig. 3; Tables 1, 2, 3).

The studied material is housed at the Senckenberg Museum in Frankfurt am Main, Germany, under numbers SMF 21.687–SMF 21.736.

Systematic palaeontology

Phylum **Bryozoa** Ehrenberg, 1831
Class **Stenolaemata** Borg, 1926
Superorder **Palaeostomata** Ma et al., 2014
Order **Fenestrata** Elias and Condra, 1957
Suborder **Fenestellina** Astrova and Morozova, 1956

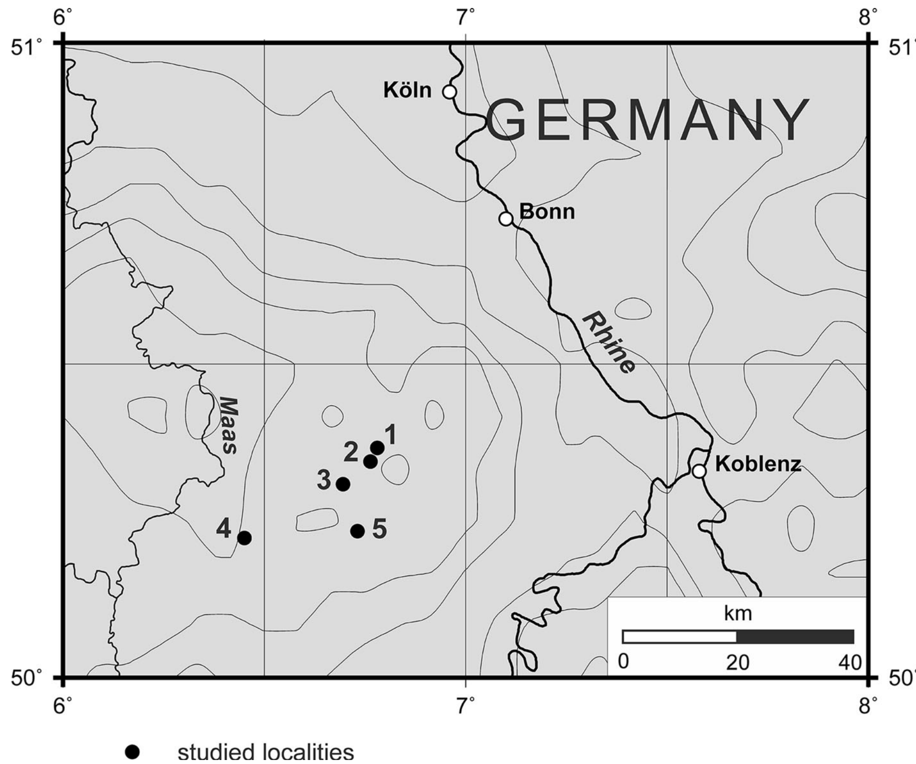


Fig. 1 Map of Devonian bryozoan localities in the Rhenish Massif: *1* Brühlborn near Rommersheim; *2* abandoned Müllertchen quarry near Üxheim-Ahütte; *3* "Weinberg" quarry near Kerpen; *4* Gondelsheim; *5* Essingen-Hohenfels

Fig. 2 Stratigraphy of the "Type Eifelian Profile" sensu Struve and Werner (1982) reduced, showing the relation of the stratigraphic units mentioned in the article Numbers in *circles* refer to the bryozoan localities (see Fig. 1)

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. ②	Müllert Sub. Fm.	Zerberus Mb.	
				Olifant Mb.	
				Lahr Mb.	
	Eifelian		Maiweiler Sub. Fm.	Hallert Mb.	*kockelianus & ensensis*
		Freilingen Fm. ③		Bohnert Mb.	
				Eilenberg Mb.	
		Junkerberg Fm. ① ④	Grauberg Sub. Fm.	Giesdorf Mb.	
				Nims Mb.	*kockelianus*
			Heinzelt Sub. Fm.	Rechert Mb.	
				Hönselberg Mb.	
				Mussel Mb.	
				Klausbach Mb.	
		Ahrdorf Fm. ⑤	Niederehe Sub. Fm.		*australis*
			Betterberg Sub. Fm.	Wasen Mb.	
				Flesten Mb.	
				Köll Mb.	
				Bildstock Mb.	

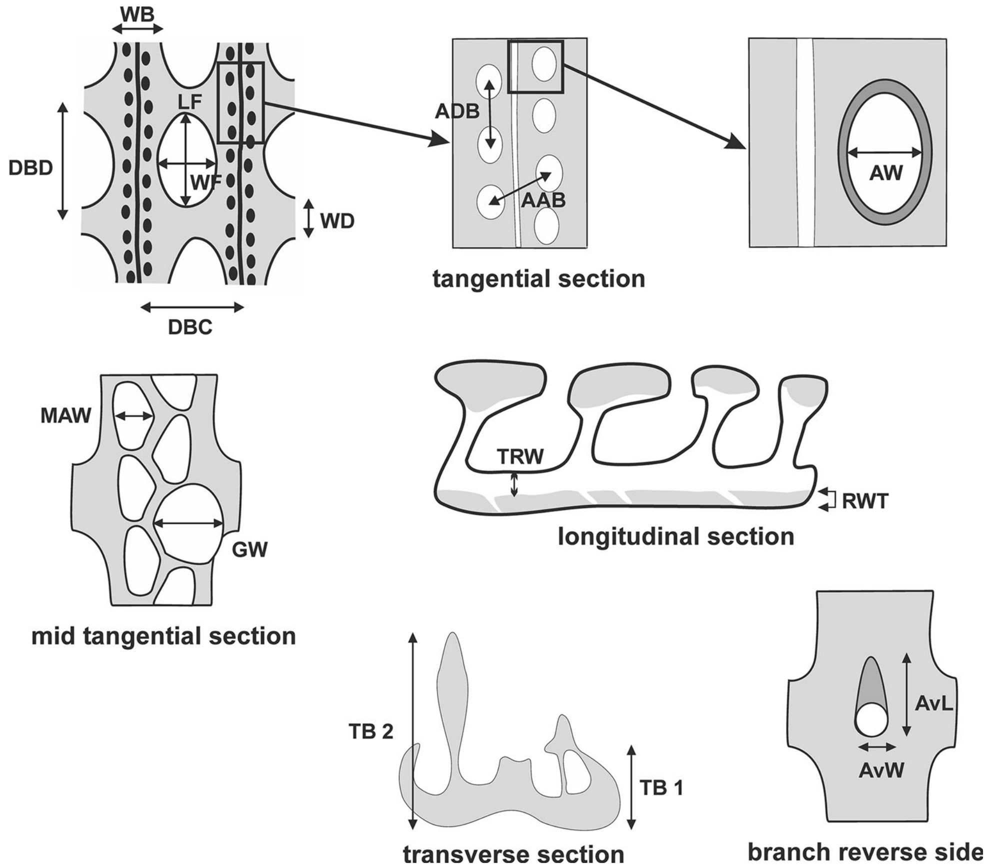


Fig. 3 Overview of the morphology of *Fenestrapora* and important measurements. *WB* branch width, *WD* dissepiment width, *WF* fenestrule width, *LW* fenestrule length, *DBC* distance between the branch centers, *DBD* distance between the dissepiment centers, *ADB* aperture spacing along the branch, *AAB* diagonal aperture spacing, *AW* autozooecial aperture width, *MAW* maximum chamber width, *TRW* thickness of the reverse wall granular layer, *RWT* thickness of the reverse wall laminated layer, *TB 1* branch thickness including the keel, *TB 2* branch thickness without the keel (measured from the reverse branch surface up to the level of the aperture), *AvW* aviculomorph length, *AvL* aviculomorph width, *GW* reproductive heterozooecium diameter

Table 1 *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998 (Middle Devonian, Rhenish Massif)

	N	X	SD	CV	MIN	MAX
Branch width (mm)	34	0.39	0.051	13.25	0.30	0.53
Dissepiment width (mm)	35	0.38	0.055	14.44	0.28	0.48
Fenestrule width (mm)	35	0.43	0.055	12.86	0.32	0.56
Fenestrule length (mm)	36	0.76	0.114	14.94	0.60	1.05
Distance between branch centers (mm)	36	0.78	0.088	11.28	0.63	1.00
Distance between dissepiment centers (mm)	36	1.09	0.096	8.80	0.90	1.35
Aperture width (mm)	36	0.10	0.010	9.38	0.08	0.12
Aperture spacing along branch (mm)	36	0.31	0.018	5.87	0.28	0.35
Aperture spacing diagonally (mm)	34	0.31	0.043	14.10	0.24	0.40
Maximal chamber width (mm)	36	0.16	0.023	13.82	0.12	0.20
Apertures per fenestrule length	35	3.8	0.646	17.12	3.0	5.0
Thickness of reverse wall granular layer (mm)	20	0.016	0.004	25.42	0.010	0.025
Thickness of reverse wall laminated layer (mm)	20	0.111	0.023	20.56	0.080	0.165
Branch thickness without keel (mm)	20	0.44	0.027	6.15	0.38	0.48
Branch thickness including keel (mm)	20	0.75	0.043	5.72	0.69	0.84
Aviculomorph width (mm)	26	0.14	0.015	10.47	0.11	0.16
Aviculomorph length (mm)	26	0.27	0.049	18.44	0.22	0.40
Reproductive heterozooecia diameter (mm)	10	0.31	0.037	11.65	0.26	0.37
Reverse surface node diameter (mm)	10	0.048	0.017	35.18	0.025	0.070

Summary descriptive statistics (measurements in mm) of three colonies

Statistics: number of measurements (N), arithmetic mean (X), sample standard deviation (SD), coefficient of variation (CV), and minimum (MIN) and maximum (MAX) values

Table 2 *Fenestrapora tuberculata* sp. nov

	N	X	SD	CV	MIN	MAX
Branch width (mm)	70	0.44	0.058	13.32	0.31	0.54
Dissepiment width (mm)	55	0.38	0.082	21.65	0.23	0.60
Fenestrule width (mm)	65	0.55	0.124	22.51	0.30	0.78
Fenestrule length (mm)	65	1.07	0.173	16.18	0.66	1.50
Distance between branch centers (mm)	65	0.93	0.169	18.22	0.60	1.29
Distance between dissepiment centers (mm)	65	1.45	0.206	14.22	1.17	1.95
Aperture width (mm)	60	0.10	0.011	11.36	0.07	0.12
Aperture spacing along branch (mm)	60	0.30	0.033	10.85	0.25	0.36
Aperture spacing diagonally (mm)	60	0.31	0.038	12.34	0.24	0.42
Maximal chamber width (mm)	70	0.19	0.023	12.18	0.14	0.25
Apertures per fenestrule length	70	4.8	0.754	15.70	3.0	6.0
Thickness of reverse wall granular layer (mm)	45	0.020	0.007	34.95	0.010	0.035
Thickness of reverse wall laminated layer (mm)	45	0.16	0.069	43.33	0.05	0.35
Branch thickness without keel	50	0.47	0.061	12.95	0.34	0.60
Branch thickness including keel	50	0.96	0.175	18.30	0.66	1.50
Aviculomorph width (mm)	4	0.14	0.024	17.18	0.12	0.17
Aviculomorph length (mm)	4	0.27	0.024	8.98	0.25	0.30
Reproductive heterozooecia diameter (mm)	20	0.30	0.042	13.66	0.22	0.38
Reverse surface node diameter (mm)	20	0.13	0.025	19.77	0.08	0.17

Summary descriptive statistics (measurements in mm) of seven colonies

Abbreviations as for Table 1

Table 3 Raw measurements (arithmetic means of 10 measurements, respectively) of 12 specimens of 3 *Fenestrapora* species (*FO F. occidentalis*, *FTR F. transcaucasica* and *FTU Fenestrapora tuberculata*)

	WB	WD	WF	LF	DBC	DBD	AW	ADB	AAB	AF
FO 1	0.52	0.46	0.41	0.74	0.82	1.22	0.12	0.27	0.30	4.7
FO 2	0.45	0.41	0.52	0.86	0.86	1.26	0.10	0.26	0.32	4.4
FO 3	0.48	0.48	0.40	0.80	0.79	1.27	0.12	0.26	0.37	4.9
FO 4	0.45	0.60	0.30	0.79	0.74	1.37	0.11	0.26	0.31	5.1
FO 5	0.42	0.38	0.44	0.81	0.76	1.24	0.10	0.29	0.27	4.5
FTR 1	0.39	0.41	0.43	0.71	0.76	1.05	0.11	0.30	0.33	3.6
FTR 2	0.36	0.33	0.42	0.90	0.78	1.17	0.11	0.32	0.27	4.2
FTR 3	0.40	0.40	0.33	0.57	0.70	1.02	0.10	0.25	0.25	4.1
FTU 1	0.43	0.43	0.69	1.28	1.12	1.70	0.10	0.33	0.33	5.2
FTU 2	0.39	0.33	0.50	0.97	0.80	1.31	0.09	0.28	0.29	4.8
FTU 3	0.44	0.37	0.44	1.09	0.92	1.43	0.10	0.33	0.31	4.6
FTU 4	0.46	0.34	0.56	0.95	0.89	1.31	0.10	0.32	0.31	4.6

Abbreviations for morphological characters in the Fig. 3

Family **Semicosciniidae** Morozova, 1987
Genus ***Fenestrapora*** Hall, 1885

Type species *Fenestrapora biperforata* Hall, 1885. Middle Devonian; NY, USA.

Diagnosis Reticulate funnel-shaped colonies consisting of sinusoid, relatively wide and thick branches jointed by wide and short dissepiments, sometimes tending to anastomosing. Autozooecia arranged in two rows on the branches, opening onto outer surface of the cone. High median keel widening apically. Autozooecial chambers rectangular in mid-tangential section, short and relatively high, with moderately short vestibules. Autozooecial apertures circular, stellate structures occurring. Axial wall straight to slightly sinusoid, projecting in the median keel. Hemisepta absent. Apparent reproductive heterozooecia represented enlarged zooecia, situated preferably near dissepiments. Aviculomorphs representing circular to oval chambers with triangular projections, positioned on the reverse and obverse colony side, on dissepiments and keels. External laminated skeleton usually well developed, traversed by abundant microstyles. Vesicular skeleton (kenozooecia) often developed. Branch reverse side often with nodes of different sizes.

Comparison *Fenestrapora* Hall, 1885 differs from *Semicoscinium* Prout, 1859, in possessing aviculomorphs, and from *Tectulipora* Hall, 1888, in possessing aviculomorphs and the absence of a reticulate protecting superstructure. *Fenestrapora* differs from *Mirifenestella* Morozova, 1974, in absence of paired aviculomorphs (parazooecia), which open to the reverse side of the colony.

Occurrence Lower—Middle Devonian (Emsian-Givetian) of the USA, Germany, Spain; Middle Devonian (Eifelian) of Azerbaijan.

Fenestrapora transcaucasica Morozova and Lavrentjeva, 1998.
Figures 4a–i, 5a–h.

1998 *Fenestrapora transcaucasica* n. sp. Morozova and Lavrentjeva: p. 56–57, text-figs. 1–2, pl. 4, figs. 4–5, pl. 5, figs. 1–2.
2001 *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998—Morozova: pl. 24, fig. 1, pl. 25, fig. 1.
2008 *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998—Ernst: figs. 3.8–9.
2012 *Fenestrapora caucasica* Morozova and Lavrentjeva, 1998—Ernst et al.: p. 749, figs. 11a–h [wrong subsequent spelling].

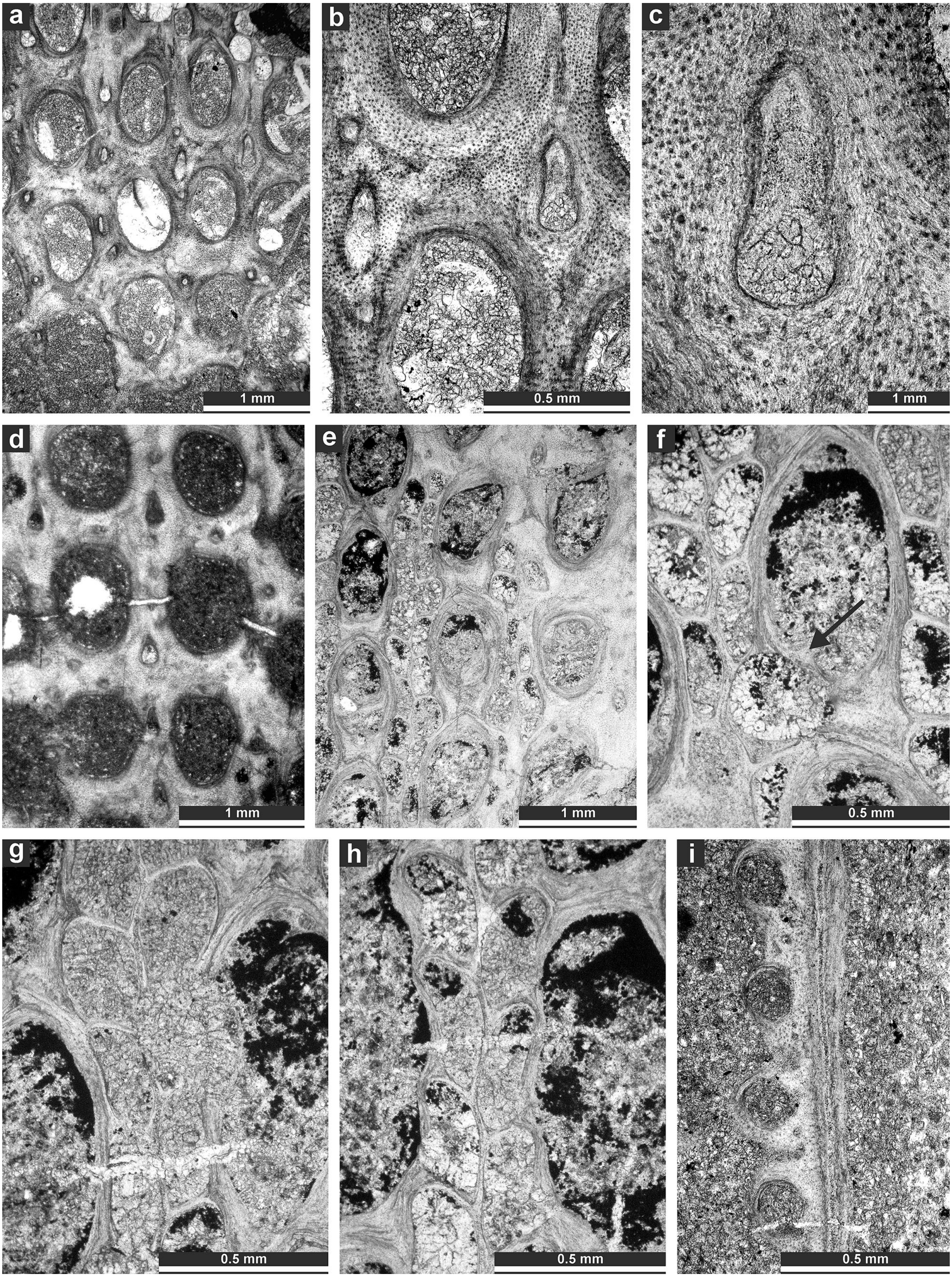
Material SMF 21.687, SMF 21.690, SMF 21.693–SMF 21.705.

Exterior description Reticulate colonies in the form of flaring cones, composed of moderately wide branches jointed by wide and short dissepiments. Autozooecia arranged in two rows on branches, situated on the outer colony side, 3–6 spaced on the length of a fenestrule. Fenestrules oval to lens-shaped sharpened toward colony growth direction. Narrow, high median keel present, often club-shaped because of apical widening. Locally lateral projections on keels developed. Vesicular skeleton locally well developed, concentrated near the base of colonies. Nodes on the reverse branch surface present, 0.025–0.070 mm in diameter.

Interior description Autozooecial chambers rectangular in mid-tangential section, short and relatively high, with moderate vestibules. Axial wall straight, thick, projecting in the median keel. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, microstyles, peristome and across dissepiments, 0.010–0.025 mm thick on the reverse wall. Basal granular wall in autozooecia straight, protruding laterally into fenestrule space and continuous across dissepiments. External laminated skeleton well developed, 0.08–0.165 mm thick on the reverse wall, coarsely laminated and traversed by microstyles. Microstyles 0.005–0.010 mm in diameter. Aviculomorphs occurring only on reverse side of branches, usually arranged in single longitudinal row, 0.11–0.16 mm wide and 0.22–0.40 mm long (Fig. 4a–d). Apparent reproductive heterozooecia representing rounded chambers (enlarged zooecia) occurring preferably on dissepiments (Figs. 4f, 5f–h), 0.26–0.37 mm in diameter. Nodes on the reverse branch surface present, 0.025–0.070 mm in diameter.

Comparison *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998 is similar to *F. occidentalis* Ulrich, 1890, from the Middle Devonian of the USA and Lower Devonian of Spain. However, it differs in having 3–5 apertures per fenestrule length vs. 4–7 in *F. occidentalis* and in shorter distances between dissepiment centers (average 1.09 vs. 1.23 mm in *F. occidentalis*). *Fenestrapora transcaucasica* differs from *F. tuberculata* sp. nov. in having 3–5 apertures per fenestrule length vs. 4–6 in *F. tuberculata* sp. nov and in shorter distances between dissepiment centers (average 1.09 vs. 1.45 mm in *F. tuberculata*). *Fenestrapora transcaucasica* is similar to *F. biperforata* Hall, 1885, from the Middle Devonian of the USA, but differs from it in having longer fenestrules (0.60–1.05 vs. 0.60–0.70 mm in *F. biperforata*). Moreover, aviculomorphs in *F. transcaucasica* are arranged in regular rows on the branch reverse side, whereas aviculomorphs in

Fig. 4 *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998. **a–c** SMF 21.687, tangential section showing the reverse colony side with aviculomorphs and nodes. Brühlborn near Rommersheim, Germany; Upper Nims Member of the Junkerberg Formation, Middle Devonian, middle Eifelian. **d** SMF 21.696, tangential section showing reverse colony side with aviculomorphs and nodes. Üxheim-Ahütte, Germany; Müllert Subformation of the Ahbach Formation, Middle Devonian, lowermost Givetian. **e–h** SMF 21.701, tangential section showing fenestrules, autozooecial chambers and reproductive heterozooecia (*arrow*). Üxheim-Ahütte, Germany; Müllert Subformation of the Ahbach Formation, Middle Devonian, lowermost Givetian. **i** SMF 21.697, tangential section showing autozooecial apertures. Üxheim-Ahütte, Germany; Müllert Subformation of the Ahbach Formation, Middle Devonian, lowermost Givetian ▶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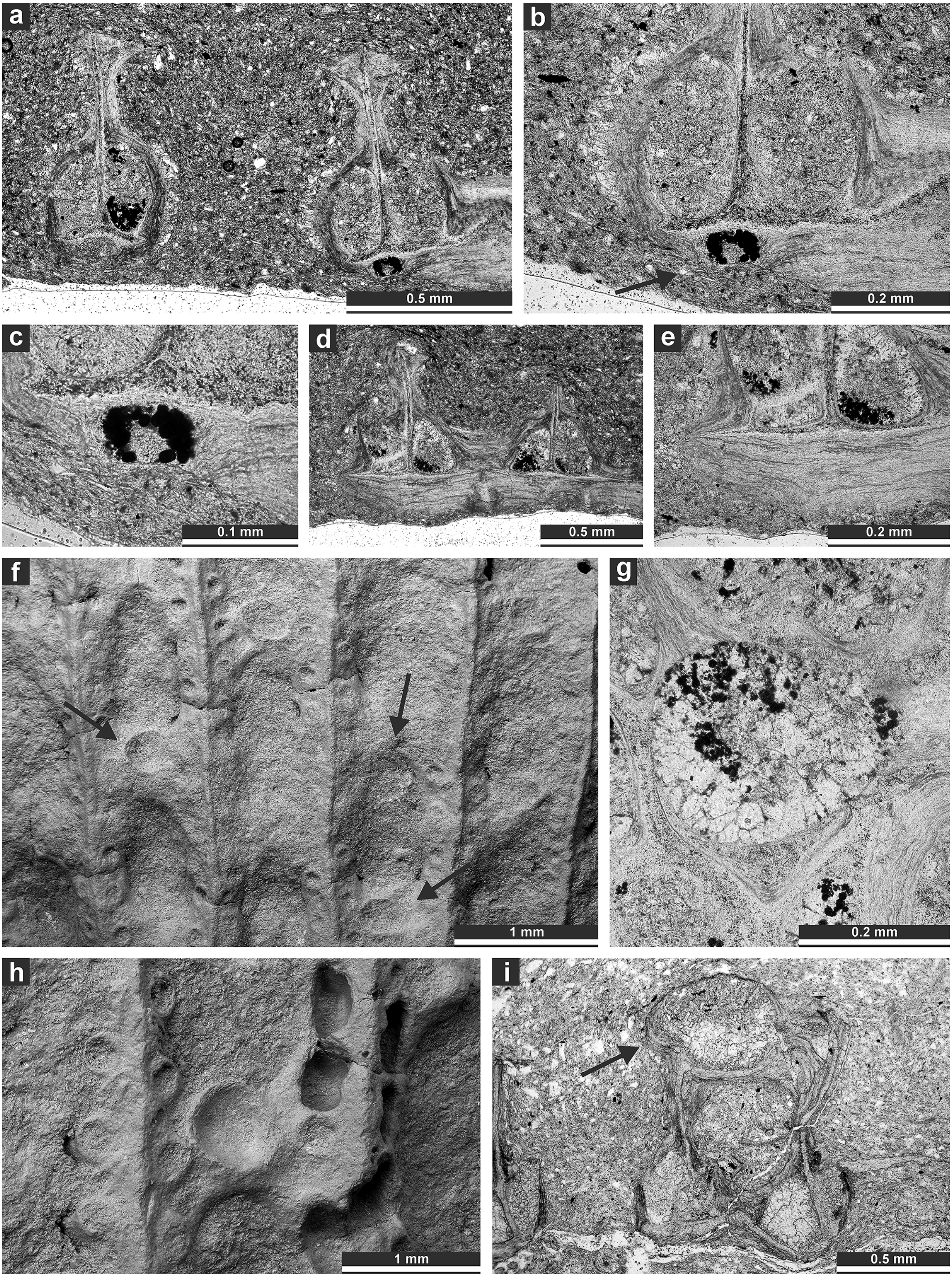
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◀**Fig. 5** **a–h** *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998. Üxheim-Ahütte, Germany; Müllert Subformation of the Ahbach Formation, Middle Devonian, lowermost Givetian. **a–c** SMF 21.695, transverse section showing high keels, autozooecial chambers, internal granular and external laminated skeleton, and aviculomorph (*arrow*). **d–e** SMF 21.705, transverse section showing distribution of the internal granular and external laminated skeleton. **f, h** SMF 21.690, colony obverse surface showing autozooecial apertures and reproductive heterozooecia (*arrows*). **g** SMF 21.701, tangential section of reproductive heterozooecium. **i** *Fenestrapora tuberculata* sp. nov. Essingen-Hohenfels, Germany; Middle Devonian, middle Eifelian, paratype SMF 21.714, transverse section showing branches and keel with bioimmurated symbiont (*Caupokeras calyptos* McKinney 2009)

F. biperforata are more abundant and spaced irregularly on the reverse branch and dissepiment surface.

Remark One colony of *Fenestrapora transcaucasica* contains the symbiont *Caupokeras calyptos* McKinney, 2009, which was apparently a bioimmurated worm-like organism (Fig. 5i).

Occurrence Meinerzhagener Korallenkalk (=upper *Cultrijugatus* Beds), lower Eifelian and Upper Nims Member of the Junkerberg Formation, middle Eifelian; Müllert Subformation of the Ahbach Formation, lowermost Givetian, Middle Devonian; Germany; *Mucrospirifer diluvianoides–Radiomena irregularis* brachiopod zone, upper Eifelian, Middle Devonian, Azerbaijan.

Fenestrapora tuberculata sp. nov.
Figures 5i, 6a–i, 7a–e.

Etymology The species name refers to the presence of large nodes on the reverse branch surface.

Holotype SMF 21.710.

Paratypes SMF 21.688, SMF 21.691–SMF 21.692, SMF 21.706–709, SMF 21.711–SMF 21.736.

Locality and horizon Essingen-Hohenfels, eastern Gerolstein syncline, Rhenish Slate Massif, Germany; transition from the Ahrdorf Formation to the Junkerberg Formation, middle Eifelian, Middle Devonian.

Diagnosis Reticulate colony composed of moderately wide sinusoid branches jointed by wide and short dissepiments; autozooecia in two rows on the branches, situated on the outer colony side, 3–6 spaced on the length of a fenestrule; fenestrules oval to lens-shaped or sub-rectangular; median keel high, often widened apically; autozooecial chambers rectangular in mid-tangential section, short and relatively high, with moderate vestibules; axial wall straight; hemisepta absent; external laminated skeleton well developed, traversed by microstyles and nodes on the reverse branch side; aviculomorphs and apparent reproductive heterozooecia present; giant aviculomorphs occurring.

Exterior description Reticulate colonies in form of flaring cones, composed of moderately wide branches jointed by wide and short dissepiments. Autozooecia arranged in two rows on the branches, situated on outer colony side, 3–6 spaced on the length of a fenestrule. Fenestrules oval to sub-rectangular or lens-shaped sharpened toward colony growth direction. Narrow, locally very high median keel present, often widening apically. Vesicular skeleton locally well developed, concentrated near the base of colonies. Nodes on the reverse branch surface present, 0.08–0.17 mm in diameter.

Interior description Autozooecial chambers rectangular in mid-tangential section, short and relatively high, with moderate vestibules. Axial wall straight, projecting in the median keel. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, microstyles, peristome and across dissepiments, 0.010–0.035 mm thick on the reverse wall. Basal granular wall in autozooecia straight, protruding laterally into fenestrule space and continuous across dissepiments, often overlapping with basal wall of neighboring branch (Fig. 7b). External laminated skeleton well developed, 0.05–0.35 mm thick on the reverse wall, coarsely laminated, and traversed by microstyles. Microstyles 0.005–0.010 mm in diameter. Aviculomorphs of two sizes present. Normal aviculomorphs occurring on reverse side of branches, occasionally arranged in single longitudinal row, on the obverse side of the colony on dissepiments and on keels, 0.12–0.17 mm wide and 0.25–0.30 mm long. Giant aviculomorphs regularly occurring on the reverence branch surface near fenestrules, triangular shaped, 0.25–0.35 mm wide and 0.54–0.69 mm long (Fig. 6d–f). Apparent reproductive heterozooecia representing rounded chambers (enlarged zooecia) occurring preferably on dissepiments or opening into fenestrules, 0.22–0.38 mm in diameter (Fig. 6i).

Comparison *Fenestrapora tuberculata* sp. nov. is similar to *F. occidentalis* Ulrich, 1890, from the Middle Devonian of the USA and Lower Devonian of Spain. However, the new species differs in the presence of large nodes on the reverse branch surface, in having giant aviculomorphs and in larger distances between dissepiment centers (average

1.45 vs. 1.23 mm in *F. occidentalis*). *Fenestrapora tuberculata* differs from *F. transcaucasica* Morozova and Lavrentjeva, 1998 in having more apertures per fenestrule length (average 4.8 apertures vs. 3.8 apertures in *F. transcaucasica*) and in larger nodes on the reverse surface (average node diameter 0.13 vs. 0.048 mm in *F. transcaucasica*). *Fenestrapora tuberculata* differs from *F. biperforata* Hall, 1885, from the Middle Devonian of the USA in having giant aviculomorphs and longer fenestrules (0.66–1.50 vs. 0.60–0.70 mm in *F. biperforata*).

Occurrence Nims Member of the upper Junkerberg Formation, middle Eifelian; Bohnert Member of the Freilingen Formation, upper Eifelian, Middle Devonian; Germany.

Numerical statistics

Fenestrate bryozoans reveal complex external and internal morphology, which allows various approaches to numerical statistics (e.g., Hageman 1991a, b; Snyder 1991a, b; Holdener 1994; Hageman and McKinney 2010). The aim of the statistical analysis was to estimate relations between species of *Fenestrapora* from the Devonian of Europe. Measurements on 12 colonies of three species were included in the analysis. Two colonies of *Fenestrapora transcaucasica* Morozova and Lavrentjeva, 1998, come from the Middle Devonian of the western Rhenish Massif: FTR 1 (locality 2) and FTR 2 (locality 1). The third sample comes from the Middle Devonian (lower Eifelian) of Kierspe, Sauerland (Ernst et al. 2012): FTR 3. Four colonies of *Fenestrapora tuberculata* sp. nov. come from the Middle Devonian (Eifelian) of the western Rhenish Massif: FTU 1 (locality 5), FTU 2 (locality 4), FTU 3 (locality 3) and FTU 4 (locality 3). Five colonies of *Fenestrapora occidentalis* Ulrich, 1890, come from the Lower Devonian (Emsian) of the Cantabrian Mountains, NW Spain (Ernst 2012; Fig. 7f–h): FO 1, FO 2, FO 3, FO 4, and FO 5.

The following ten characters were involved in the analysis: branch width (WB), dissepiment width (WD), fenestrule width (WF), fenestrule length (LF), distance between branch centers (DBC), distance between dissepiment centers (DBD), aperture width (AW), aperture spacing along branch (ADB), aperture spacing diagonally (AAB) and number of apertures per fenestrule length (AF) (Fig. 3). Each character was measured ten times (raw measurements). This set of measurements was chosen because of its availability and the biological importance of individual characters for a bryozoan.

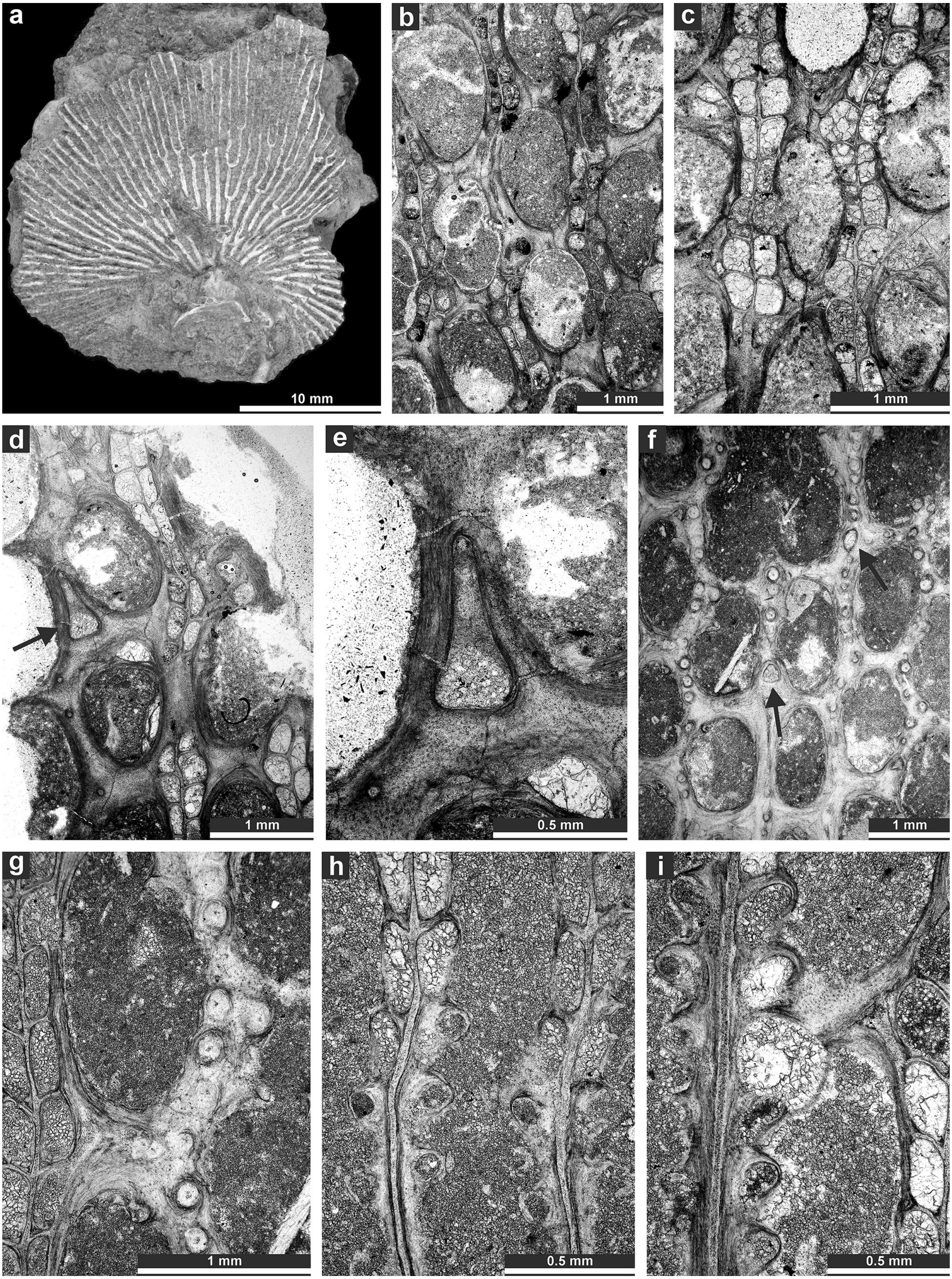
Cluster analysis was performed using PAST software (Hammer et al. 2001). The numerical statistics was carried out using an unweighted pair-group average method (UPGMA), in which clusters are joined based on the average distance between all members in the two groups (Fig. 8). Distances were measured using the Euclidean distance metric. Euclidean distance is the most common use of distance and examines the root of square differences between coordinates of a pair of objects. This method is useful for raw data rather than for standardized ones.

Fig. 6 *Fenestrapora tuberculata* sp. nov. **a** Paratype SMF 21.688, ▶ external view of a colony with wide base and wide keels as protective structure. **b** holotype SMF 21.710, tangential section showing branches, fenestrules and autozooecial chambers. Essingen-Hohenfels, Germany; Middle Devonian, middle Eifelian. **c** Paratype SMF 21.712, tangential section showing branches, fenestrules, and autozooecial chambers. Essingen-Hohenfels, Germany; Middle Devonian, middle Eifelian. **d–e** Paratype SMF 21.711, tangential section showing branches, fenestrules, autozooecial chambers and giant aviculomorph (*arrow*). Essingen-Hohenfels, Germany; Middle Devonian, middle Eifelian. **f–g** Paratype SMF 21.723, tangential section showing reverse branch side with large nodes and giant aviculomorph (*arrow*). Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian. **h** Paratype SMF 21.721, tangential section showing autozooecial apertures. Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian. **i** Paratype SMF 21.717, tangential section showing autozooecial apertures and a reproductive heterozooecium. Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian

Discussion

The computed dendrogram (Fig. 8) is based on characters of different taxonomic value. Branch width reflects the size of autozooecia chambers and surrounding extrazooecial material. The latter character can vary strongly with the age of the colony or its part. Younger colonies are usually thinner than the older ones. Dissepiment width corresponds mainly with the thickness of the outer laminated skeleton. Both these characters can affect the fenestrule width and length (wider branches and dissepiments would automatically narrow the fenestrule space). Fenestrule width and length as well as the distances between branch centers and between dissepiment centers reflect the filtering capacity of the colony meshwork (Cowen and Rider 1972; Hageman 1991a, b).

Aperture width, aperture spacing along the branch and diagonally as well as the number of apertures per fenestrule length are characters related to the size and spacing of feeding structures of bryozoans, lophophores (Winston 1977, 1978; McKinney and Jackson 1989; Hageman 1991a, b). These characters usually show the highest stability (low variation) within the colony.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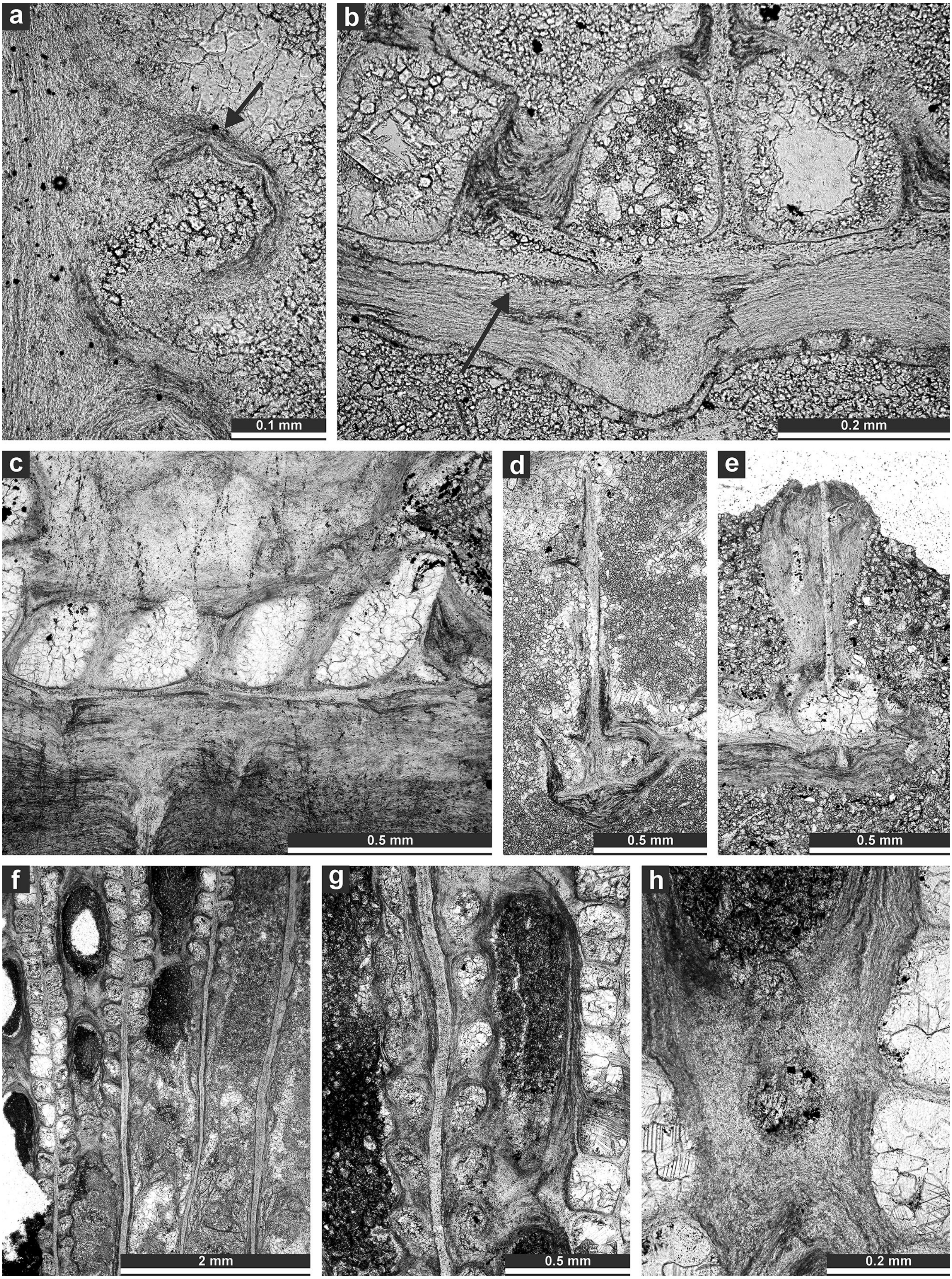
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◀**Fig. 7** **a–e** *Fenestrapora tuberculata* sp. nov. **a** Paratype SMF 21.717, tangential section showing autozooecial aperture with nodes (*arrow*). Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian. **b** Paratype SMF 21.719, transverse section showing distribution of internal granular and external laminated skeleton (*arrow*: overlapping of the basal walls of two neighboring autozooecia). Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian. **c** Paratype SMF 21.734, branch longitudinal section showing autozooecial chambers. Gondelsheim, Germany; Nims Member of the upper Junkerberg Formation, Middle Devonian, middle Eifelian. **d** Paratype SMF 21.722, branch transverse section showing high keel. Quarry Weinberg near Kerpen, Germany; Bohnert Member, Freilingen Formation, Middle Devonian, upper Eifelian. **e** Paratype SMF 21.731, branch transverse section showing high keel widened apically. Gondelsheim, Germany; Nims Member of the upper Junkerberg Formation, Middle Devonian, middle Eifelian. **f–h** *Fenestrapora occidentalis* Ulrich, 1890, mid-tangential section showing autozooecial chambers, apertures and aviculomorphs (h), GZG.IN.0.010.523a; Llama de Colle near Villayandre, Rio Esla Region, Cantabrian Mountains, NW Spain; lower part of the upper Emsian, Lower Devonian

The computed dendrogram shows that the measured specimens produce more or less distinct clusters. Specimen FTU 1 (holotype of *Fenestrapora tuberculata* sp. nov.) is separated from the rest of the specimen set (clusters 1–4). Cluster 1 is built by two specimens of *F. transcaucasica* (FTR 1 and FTR 2) and neighbors cluster 2, formed by three specimens of *F. occcidenatlis* (FO 1, FO 3 and FO4). Three remnant specimens of *F. tuberculata* are clustered together in cluster 3 (FTU 2, FTU 3 and FTU 4), which neighbors cluster 4, consisting of one specimen of *F. transcaucasica* (FTR 2) and two specimens of *F. occidentalis* (FO 2 and FO 5).

The reason for such a discrepancy may be that the feature set does not reflect the whole morphological characteristic of a fenestrate bryozoan. It also shows that at least some of the features are affected by the ecological situation. Spanish material on *Fenestrapora occidentalis* produces two distinct clusters (material comes from various sources, but seems to be quite homogeneous, see Ernst 2012). Two specimens from locality 3 (FTU 3 and FTU 4) are clustered together within cluster 3. Sample FTU 1 comes from the oldest locality with muddy limestones reflecting low water energy conditions with quite high precipitation rates of fine sediment. Such environments are extreme for bryozoans, which suffer under high levels of sedimentation. Analysis of the character set shows that this sample differs in having the largest fenestrules: average fenestrule width 0.69 mm and fenestrule length 1.28 mm. The second largest fenestrule width is in FTU 4 (0.56 mm) and the second largest fenestrule length in FTU 3 (1.09 mm). This difference could be explained by the effect of the muddy environment in which larger

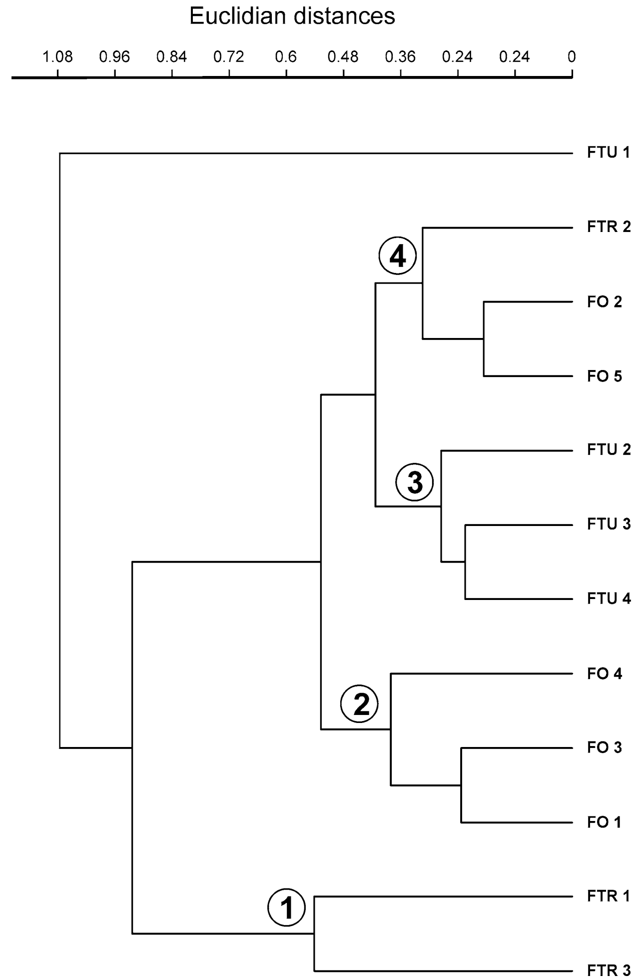

Fig. 8 Cluster diagram showing similarities between *Fenestrapora* species from the Devonian of Europe (UPGMA, unweighted pair group method with arithmetic mean, Euclidean distances metric, PAST ver. 2.01, Hammer et al. 2001)

fenestrules gained an advantage in order to avoid occluding the fenestrules by sediment.

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