



# Semicosciniid bryozoans from the Middle Devonian of Rommersheim (Eifel, Germany)

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## Abstract

Two bryozoan species belonging to the Family Semicosciniidae Morozova, 1987 are described from the Middle Devonian of the Eifel—*Bigeyina winteri* (Bornemann, 1884) and *Loculipora alvearis* (Maurer, 1885). The two species are endemic to the Middle Devonian (Eifelian–Givetian) of the Eifel. Morphology and taxonomical assignment of the studied bryozoans are discussed. The Family Fenestraporidae Xia, 2002 is considered to be invalid.

**Keywords** Devonian · Bryozoa · Fenestrata · Taxonomy · Germany

## Introduction

Bryozoans represent an extant phylum of sessile aquatic animals which show an impressive fossil record from the early Cambrian to the Present. The majority of marine bryozoans possess stable carbonate skeletons which have a high potential of preservation (Smith et al. 2006) and are often abundant among fossils found in marine sediments.

Devonian bryozoans are abundant and diverse worldwide (e.g., Cuffey and McKinney 1979; Bigey 1988). The fenestrate bryozoans were especially successful during this period experiencing rapid diversification during the Early Devonian (e.g., Ernst 2013). They represent a high proportion in fossil assemblages of Devonian sediments in the Eifel area, well known for its paleontological content. Whereas the non-fenestrate bryozoan faunas of the Eifel were extensively described recently (Ernst and Schroeder 2007; Ernst 2008a, 2008b; Ernst et al. 2011, 2012, 2014a, 2014b), fenestrate taxa received only sporadic attention (Ernst 2016, 2020; Ernst and Bohatý 2009). Earlier publications on fenestrate bryozoans from the Middle Devonian of Eifel were those by Nekhoroshev (1928) and Kräusel (1953, 1954, 1956, 1957, 1981).

The Family Semicosciniidae was established by Morozova (1987: 81) for summarized fenestrate bryozoans with usually robust reticulate colonies of usually conical, rarely fan-like shape, produced by straight or undulating branches connected by dissepiments or fused together by anastomosing. The most significant character of the family are compact autozooeical chambers of predominantly rectangular shape in the mid tangential section and which lack hemisepta. Furthermore, semicosciniid bryozoans lack keel nodes; instead, usually a high and wide median keel between autozooeical rows is developed. In few genera, the median keel is low, but in the majority of representatives of Semicosciniidae, keels are high and often widened in their apical part, in some genera fusing together to form a protective superstructure. Heterozoecia in the form of rounded chambers occur in several genera which are regarded to having a reproductive function (e.g., Morozova 1987, 2001).

The Family Semicosciniidae comprises about 20 genera depending on different perceptions of taxonomists. Gorjunova (1996) did not accept the Semicosciniidae, placing the genera originally placed there by Morozova (1987, 2001) into the Family Reteporinidae Dunaeva and Morozova, 1975. However, her concept is hardly acceptable because she placed taxa with undulating branches in the Family Reteporinidae, disregarding their internal morphology. Shape of branches is an external morphological character which appears in unrelated lineages independently (homologous). Xia (2002) erected the Family Fenestraporidae based on the semicosciniid genus *Fenestrapora* Hall, 1885. However, his definition of the Family Fenestraporidae is solely based on

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the presence of heterozoecia of similar shape (like aviculomorphs in *Fenestrapora*, see McKinney 1998; Morozova and Lavrentjeva 1998; Ernst 2016) and does not consider any further internal morphological characters. Xia (2002) placed seven genera in the Family Fenestraporidae, all of them having a different internal morphology, as well as different kinds of heterozoecia (*Fenestrapora* Hall, 1885, *Ignotifenestella* Morozova, 1974, *Mirifenestella* Morozova, 1974, *Cavernofenestella* Morozova, 1974, *Permofenestella* Morozova, 1974, *Polyfenestella* Bancroft, 1986, and *Aviculofenestella* Xia, 2002). Therefore, the Family Fenestraporidae Xia, 2002 is regarded being invalid. The two species of the genus *Aviculofenestella* have been described from a loose stone block which Xia (2002) regarded being mid-Jurassic in age. However, it appears probable that this block was Palaeozoic in age and tectonically inserted within the Jurassic sediments. Fenestrate bryozoans become extinct at the end of the Permian (e.g., Morozova 2001), and the record of *Aviculofenestella* from the Jurassic appears dubious.

Devonian was the time of the main distribution of semicosciniid bryozoans. Six genera appeared in the Silurian, and three survived into the Carboniferous. Two genera, *Neoretaporina* Miller, 1962 and *Pseudounitrypa* Nekhoroshev, 1926 appeared in the Early Carboniferous, whereas the latter one survived into the Early Permian (Artinskian). However, the majority of genera and their species occurred during the Devonian, with the peak of their distribution in the interval from Emsian to Givetian.

In the Middle Devonian of the Eifel the following semicosciniid genera are known: *Schischcatella* Waschurova, 1964 (Ernst and Bohatý 2009), *Fenestrapora* Hall, 1885 (Ernst 2016), *Bigeyina* Suárez-Andrés and McKinney, 2010 (Kräusel 1953, 1954, 1956), and *Loculipora* Hall, 1885 (Kräusel 1957, 1981). Furthermore, the genus *Semicoscium* Prout, 1859 has been mentioned (in open nomenclature) by Nekhoroshev (1928) and Kräusel (1981) from the Eifel area.

The present paper extends our knowledge about fenestrate bryozoans from the Middle Devonian of the Eifel area and provides a comprehensive description of *Bigeyina winteri* (Bornemann, 1884) and *Loculipora alvearis* (Maurer, 1885) from a locality in the vicinity of Brühlborn near Rommersheim in the Eifel, Rhineland-Palatinate, Germany. Both species develop robust conical colonies and are quite common in the Middle Devonian fossil-rich limestones of the Eifel. The high median keels of *Bigeyina winteri* (Bornemann, 1884) are confined to branches and not interconnected laterally to neighboring keels, whereas those of *Loculipora alvearis* (Maurer, 1885) are fused together to a solid meshwork. Such structures in fenestrates are regarded as having a protective function (McKinney et al. 2003).

*Bigeyina winteri* and *Loculipora alvearis* are endemic to the Middle Devonian (Eifelian–Givetian) of the Eifel. Few

species of the genus *Bigeyina* are known from the Lower Devonian (Pragian) of Czech Republic and Lower to Middle Devonian of Spain (see below). The genus *Loculipora* has longer range, with several species known from the Silurian of North America and Kazakhstan. Devonian species of *Loculipora* were recorded from North America and Eurasia (Germany, Tajikistan). Both genera terminate at the end of the Givetian.

## Materials and methods

The studied locality (slope of the former planned roadwork extension of federal road "B 51") is situated in the vicinity of Brühlborn near Rommersheim, Prüm Syncline (50° 12' 27.14", 6° 27' 37.45"; Fig. 1). The outcrop contains grayish compact, thin- to medium-bedded limestones of the upper Nims Member of the Junkerberg Formation (Eifelian) (Fig. 2). These limestones are represented by rudstones and bindstones containing brachiopods, corals, stromatolites, echinoderms and abundant bryozoans. Non-fenestrate bryozoans from this locality have been studied by Ernst (2008a).

Collected material represents four separate blocks of limestones less than a fist-size each. From them, 14 randomly oriented thin sections containing fragments of fenestrate bryozoans were prepared. Thin sections were studied in a binocular microscope in transmitted light. Morphological terminology for description of bryozoans is modified from Hageman (1991a, 1991b). The following morphological characters were measured: branch width, fenestrule width, fenestrule length, distance between branch centers, autozoecial aperture width, aperture spacing along branch, aperture spacing diagonally, maximum chamber width, branch thickness including keel, branch thickness without keel (measured from reverse branch surface up to the level of aperture), number of apertures per fenestrule length.

Studied material is housed at the Research Institute and Natural History Museum Senckenberg (Frankfurt am Main, Germany), under numbers SMF 60982–SMF 60995.

## Systematic palaeontology

Phylum **Bryozoa** Ehrenberg, 1831

Class **Stenolaemata** Borg, 1926

Superorder **Palaeostomata** Ma et al., 2014

Order **Fenestellida** Elias and Condra, 1957

Suborder **Fenestellina** Astrova and Morozova, 1956

Family **Semicosciniidae** Morozova, 1987

Genus **Bigeyina** Suárez-Andrés and McKinney, 2010

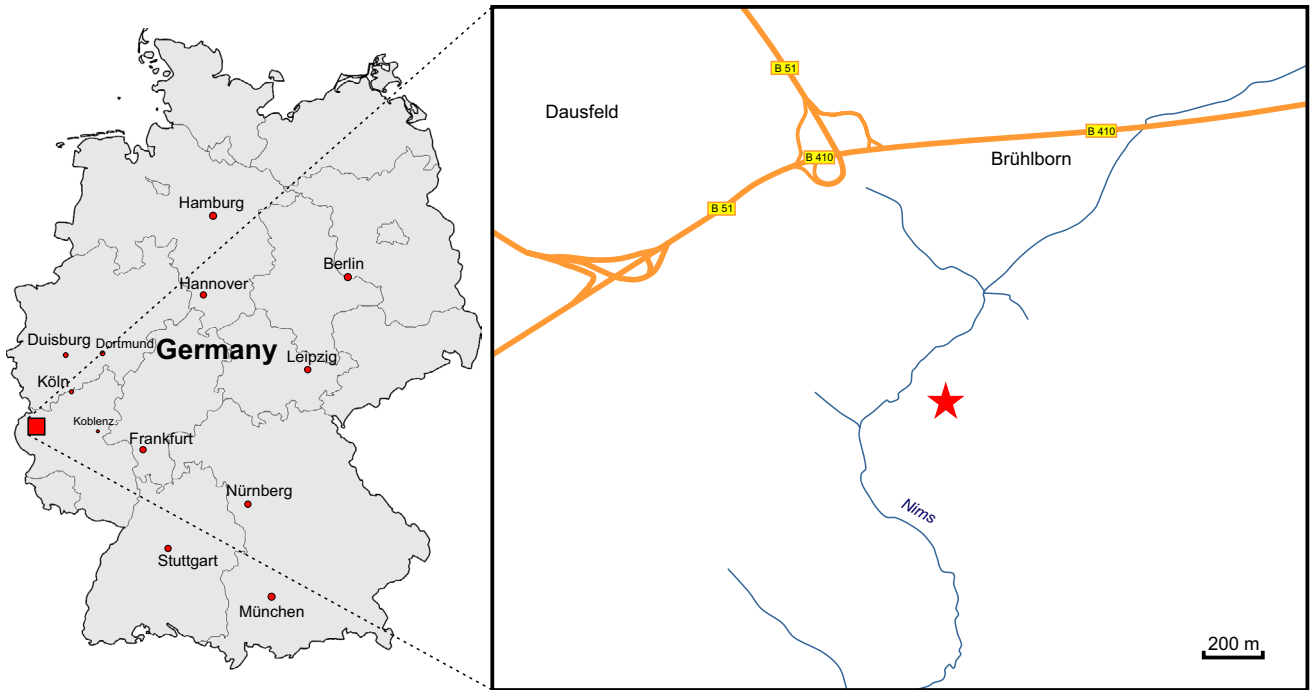


Fig. 1 Map showing the position of the studied locality at Brühlborn near Rommersheim (red asterisk)

Fig. 2 Stratigraphy of the “Type Eifelian Profile” sensu Struve and Werner (1982) reduced, showing the relation of the stratigraphic unit at the studied locality (red asterisk)

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

[= *Cyclopelta* Bornemann, 1884 (non *Cyclopelta* Amyot and Serville, 1843)].

**Type species.** *Cyclopelta winteri* Bornemann, 1884. Geeser Schichten, Eifelian, Middle Devonian; Trilobite Fields west of Gees, Eifel, Rhenish Massif, Germany.

**Diagnosis.** Colony conical, narrow to broad and flaring; rarely a set of narrow branching, tubular cones. Autozooeical apertures on outer side of cone. Branches minimally to moderately sinuous, linked at intermediate distances by lateral branch expansion and exozonal fusion or by broad, short, regularly spaced dissepiments. Linkages aligned transversely or obliquely to branches; each row of linkages and corresponding parts of branches thickened on reverse surface, forming continuous annular, rarely oblique bands that commonly project into the cone as distally deflected keels. Fenestrules elongate, oval. High keel on obverse surface of branches; granular core of keel apically bifurcated into two symmetrical or asymmetrical, divergent sheets, to form apical lath. Laminar skeleton on keel thickened apically and extending across outer side of lath. Keels not connected to one another, or with sparse to common lateral, bridge-shaped connections above points of connection between underlying branches. Autozooeicia arranged in two alternating rows per branch, axially overlapped; axial wall zigzag to sinuous; intermediate to large, cylindrical to irregularly polygonal, height greater than length or width; chamber size greater adjacent to dissepiments, where width commonly greater than length. Hemisepta and other interior structures lacking. Short, direct to laterally oblique distal tube with diameter slightly smaller than endozonal portion of autozooeicia. Peristomes thin. Autozooeicia apparently monomorphic. Basal, axial and transverse autozooeical walls granular, extremely thin or absent laterally around and near distal tube; autozooeical chambers locally lined by thin inner laminar skeleton. Basal plate flat in branch junctions to strongly concave midway along fenestrules, without longitudinal ridges on reverse side or rarely, with only one developed between branch junctions. Extrazoeical skeleton finely laminate, laminae often obscured, containing abundant, inconspicuous small microstyles. Ancestrula and two or three additional zoeicia in contact with substratum. In basal portions of colonies, vesicles also fill interior conical space, space between obverse laths and branches, and fenestrules (adapted after Suárez-Andrés and McKinney 2010).

**Comparison.** *Bigeyina* Suárez-Andrés and McKinney, 2010 differs from *Semicoscinium* Prout, 1859 in having of annular bands developed on the reverse colony surface, in the morphology of the keel with a bifurcated granular core (keel without bifurcation in *Semicoscinium*), in having a zigzag to sinuous axial wall (straight in *Semicoscinium*), and in

the absence of reproductive heterozoeicia (gonozoeicia). *Bigeyina* additionally differs from *Fenestrapora* in the absence of reproductive heterozoeicia and aviculomorphs.

**Occurrence.** Representatives of the genus *Bigeyina* Suárez-Andrés and McKinney, 2010 were found in the Lower to Middle Devonian of Europe (Czech Republic, Spain, Germany). The following species of this genus are known: *B. sacculus* (Barrande in Pošta, 1894) and *B. victrola* (McKinney and Kříž, 1986) from the Lower Devonian (Pragian) of Czech Republic, *B. cantabrica* Suárez Andrés and Wyse Jackson, 2017 and *B. spinosa* Suárez Andrés and Wyse Jackson, 2017 from the Lower Devonian (Emsian) of Spain, *B. ibera* Ernst, 2012 from the Lower/Middle Devonian (Emsian/Eifelian) of Spain, *B. concentrica* (Römer, 1852) from the Middle Devonian (Eifelian) of Germany, and *B. winteri* (Bornemann, 1884) from the Middle Devonian (Eifelian/Givetian) of Germany.

#### ***Bigeyina winteri* (Bornemann, 1884)**

Figure 3a–h; Table 1

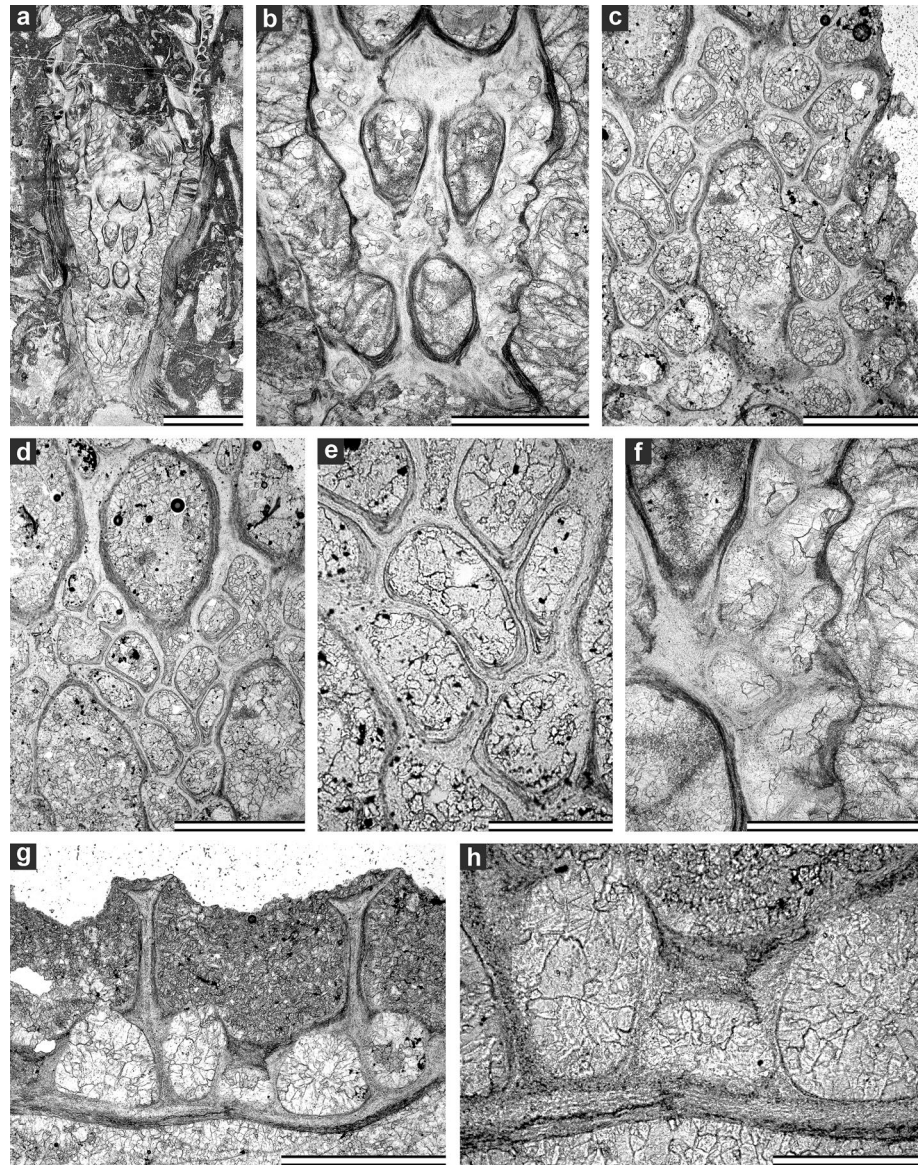
1884	<i>Cyclopelta winteri</i> Bornemann: 864–865, pl. 31.
1953	<i>Cyclopelta winteri</i> —Kräusel: 45–62, pls. 1–3, text-figs. 1–7.
non 1998	<i>Cyclopelta winteri</i> —Suárez Andrés: 190–192, pl. 1, figs. 1–3.
2001	<i>Cyclopelta winteri</i> —Morozova: pl. 20, figs. 3, 4.
2010	<i>Bigeyina winteri</i> (Bornemann, 1884)—Suárez Andrés and McKinney: 127, figs. 1, 2.

**Material.** Two colonies (6 thin sections) SMF 60982–SMF 60987.

**Exterior description.** Reticulate colonies, conical, frontal surface exterior. Branches intermediate in width, moderately sinuous, intermediately spaced, dichotomously divided, joined by short dissepiments or anastomoses. Autozooeicia arranged in two alternating rows on branches, having circular apertures with low peristomes, 4 spaced per length of a fenestrule. Fenestrules oval to lens shaped. Median keel on obverse side of branches straight to slightly sinusoid, high and wide, composed of core of granular skeleton and sheath of laminar skeleton, widening to form apical lath.

**Interior description.** Autozooeical chambers rectangular in mid tangential section, short and relatively high, with moderately short vestibules. Axial wall between autozooeical rows zigzag in tangential sections, continuing unbroken in superstructure. Hemisepta absent. Internal granular skeleton

**Fig. 3** *Bigeyina winterei* (Bornemann, 1884): **a** tangential section of the colony, SMF 60986, **b** tangential section showing branches, fenestrules and autozooeical chambers, SMF 60986, **c–e** tangential section showing autozooeical chambers, SMF 60985, **f** tangential section showing autozooeical apertures chambers, SMF 60986, **g–h** branch transverse section showing autozooeical chambers median keel with dashed nodes, SMF 60983. Scale bars 2 mm (**a**), 1 mm (**b**), 0.5 mm (**c, d, f, g**), and 0.2 mm (**e, h**)



**Table 1** Descriptive statistics of *Bigeyina winterei* (Bornemann, 1884)

	<i>N</i>	<i>X</i>	<i>SD</i>	<i>CV</i>	<i>MIN</i>	<i>MAX</i>
Branch width, mm	16	0.34	0.050	14.60	0.28	0.45
Fenestrule width, mm	15	0.38	0.038	9.96	0.31	0.44
Fenestrule length, mm	8	0.70	0.111	15.71	0.57	0.93
Distance between branch centers, mm	15	0.61	0.105	17.25	0.40	0.75
Aperture width, mm	8	0.09	0.005	5.52	0.09	0.10
Aperture spacing along branch, mm	5	0.28	0.041	14.43	0.23	0.33

*N* number of measurements, *X* mean, *SD* sample standard deviation, *CV* coefficient of variation, *MIN* minimal value, *MAX* maximal value

continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by small microstyles. Microstyles 0.005–0.010 mm in diameter. Heterozooeicia not observed.

**Comparison.** *Bigeyina winterei* (Bornemann, 1884) is similar to *Bigeyina sacculus* (Barrande in Pořta, 1894) from the Lower Devonian of the Czech Republic, but differs in having narrower branches (average branch width 0.34 mm

vs. 0.40 mm in *B. sacculus*) and longer distances between autozooeical apertures (averagely 0.28 mm vs. 0.25 mm in *B. sacculus*).

**Occurrence.** Material studied in this paper comes from the Upper Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian) at Brühlborn near Rommersheim, Prüm syncline in western Rhenish Massif, Germany. Kräusel (1953, 1954) mentioned various records of this species from various localities of Eifelian–Givetian age in the Eifel.

Genus *Loculipora* Hall, 1885

**Type species.** *Fenestella perforata* Hall, 1885. Middle Devonian; USA (New York).

**Diagnosis.** Conical or fan-shaped colonies consisting of undulating branches, anastomosing, rarely joined by wide, short or nearly reduced dissepiments with keel. Fenestrules oval to rounded. Keels connected to one another, forming reticulate meshwork connecting outgrowths on top and outgrowths of adjoined branches and dissepiments. Reticulate meshwork analogous to the structure of the main meshwork, but lacking autozoecia. Meshes in the reticulate meshwork correspond to the fenestrules in the main meshwork. Autozooeical apertures on outer side of cone. Autozoecia arranged in two alternating rows per branch, axially overlapped; rectangular to roughly triangular-pentagonal in mid tangential section; axial wall zigzag to sinuous; intermediate to large, cylindrical to irregularly polygonal, height greater than length or width. Hemisepta and other interior structures lacking. Short, direct to laterally oblique distal tube with diameter slightly smaller than endozonal portion of autozoecia. Peristomes thin. Autozoecia apparently monomorphic. Basal, axial and transverse autozooeical walls granular, extremely thin or absent laterally around and near distal tube; autozooeical chambers locally lined by thin inner laminar skeleton. Basal plate moderately to strongly concave. Extrazoeical skeleton finely laminate, laminae often obscured, containing abundant, inconspicuous small microstyles. In basal portions of colonies, vesicles also fill interior conical space, space between obverse laths and branches, and fenestrules.

**Comparison.** *Loculipora* Hall, 1885 differs from *Isotrypa* Hall, 1885 in strongly undulating branches joined mainly by anastomoses. Superstructure in *Loculipora* is produced by extensions of both median keels and dissepiments, whereas the transverse connections in the superstructure of *Isotrypa* do not contact with dissepiments. Furthermore, *Loculipora* has rectangular to roughly triangular-pentagonal autozooeical chambers and zigzag axial wall, whereas autozoecia in

*Isotrypa* are rectangular with straight axial wall. *Loculipora* differs from *Bigeyina* in superstructure morphology which represents reticulate meshwork produced by fused extensions of keels. Keels in *Bigeyina* are normally not fused together.

**Occurrence.** Middle Silurian–Middle Devonian; North America, Europe, Middle Asia.

*Loculipora alvearis* (Maurer, 1885)

Figure 4a–i; Table 2

1885 *Entopora alvearis* Maurer: 127–128, pl. 4, figs. 6, 10.

1957 *Loculipora alvearis* (Maurer, 1885)—Kräusel: 335–336, pl. 1, figs. 1–2.

1957 *Loculipora* (cf.) *alvearis* (Maurer, 1885)—Kräusel: 337–343, pl. 1, figs. 3–4.

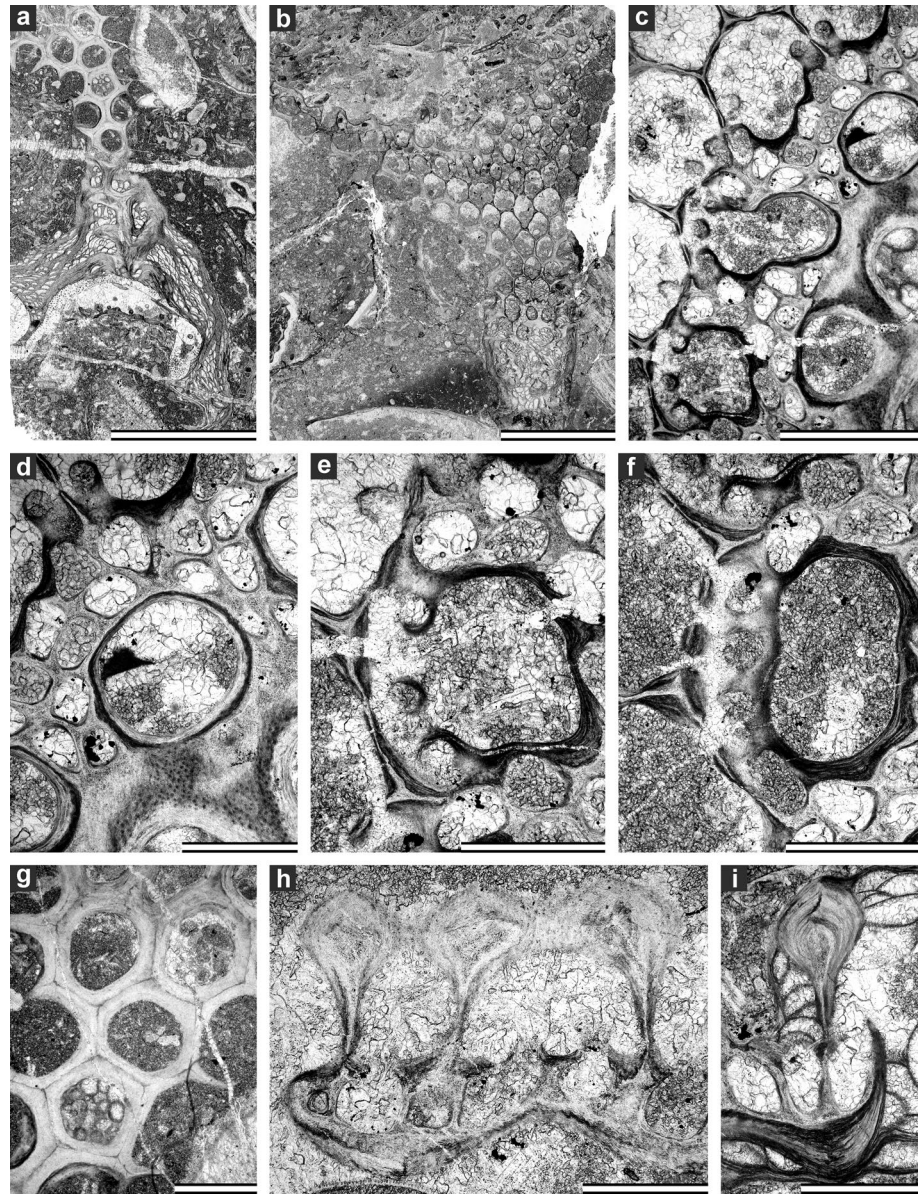
**Material.** Three colonies (8 thin sections) SMF 60988–SMF 60995.

**Exterior description.** Narrow conical colonies, consisting of strongly undulating branches, joined by anastomoses. Two rows of autozoecia on branches. Autozooeical apertures circular, with stellate structure, arranged in two alternating rows on branches, having circular apertures with low peristomes, 3–5 spaced per length of a fenestrule. Fenestrules circular to oval. Median keel on obverse side of branches straight, high and wide, composed of core of granular skeleton and sheath of laminar skeleton. Median crests on the superstructure, producing a polygonal pattern. Reverse side smooth.

**Interior description.** Autozooeical chambers rectangular to roughly triangular–pentagonal in mid tangential section, short and relatively high, with moderately short vestibules. Axial wall between autozooeical rows zigzag in tangential sections, continuing unbroken in superstructure. Hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. External laminated skeleton well developed, traversed by small microstyles. Microstyles 0.005–0.008 mm in diameter. Heterozoeecia not observed.

**Comparison.** *Loculipora alvearis* (Maurer, 1885) is similar to *L. kschtutica* (Waschurova, 1964) from the Lower Devonian of Tajikistan, but differs from it in possessing wider branches (0.31–0.46 mm vs. 0.30–0.35 mm in *L. kschtutica*), as well as in its larger fenestrules (fenestrule width 0.38–0.62 mm vs. 0.35–0.45 mm in *L. kschtutica*; fenestrule length 0.46–0.82 mm vs. 0.60–0.70 mm in *L. kschtutica*).

**Fig. 4** *Loculipora alvearis* (Maurer, 1885): **a** longitudinal section of a basal part of the colony with massive vesicular skeleton, SMF 60993. **b** tangential section showing branches with autozooezia and reticulate superstructure, SMF 60989, **c–f** tangential section showing branches, fenestrules, autozooezial chambers and apertures, SMF 60992, **g** tangential section showing reticulate superstructure, SMF 60993, **h** branch transverse section showing autozooezial chambers median keel with nodes fused to superstructure, SMF 60990, **i** branch transverse section showing autozooezial chambers median keel with nodes fused to superstructure, SMF 60994. Scale bars 5 mm (**a**, **b**), 1 mm (**b**, **g**), 0.5 mm (**d**, **e**, **f**, **h**, **i**)



**Table 2** Descriptive statistics of *Loculipora alvearis* (Maurer, 1885)

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	0.37	0.040	10.80	0.31	0.46
Fenestrule width, mm	20	0.51	0.057	11.29	0.38	0.62
Fenestrule length, mm	20	0.67	0.099	14.76	0.46	0.82
Distance between branch centers, mm	20	0.88	0.110	12.48	0.71	1.10
Aperture width, mm	20	0.10	0.006	6.47	0.09	0.12
Aperture spacing along branch, mm	20	0.30	0.034	11.44	0.25	0.38
Aperture spacing diagonally, mm	16	0.27	0.030	11.25	0.22	0.33
Maximal chamber width, mm	20	0.17	0.012	7.49	0.14	0.18
Branch thickness without keel, mm	20	0.44	0.032	7.24	0.40	0.50
Branch thickness including keel, mm	20	1.05	0.093	8.84	0.90	1.30
Apertures per fenestrule length	15	4.1	0.704	17.30	3.0	5.0

Abbreviations as for Table 1

**Occurrence.** Stringocephalen-Kalk, Middle Devonian (Givetian); Hainau, Germany. Freilingen Formation, Middle Devonian (Givetian); Dollendorf Syncline, Germany. *Calceola*-beds, Middle Devonian (Eifelian); Clausthal, Germany. Upper Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian); Brühlborn near Rommersheim, Prüm syncline.

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