Pennsylvanian bryozoans from the Cantabrian Mountains (northwestern Spain)

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Key words - Bryozoa, Pennsylvanian, Cantabrian Mountains, Spain.

Bryozoans from six Pennsylvanian localities in the Cantabrian Mountains (northwestern Spain) are described. The faunas include 54 species, of which two are new, *Streblotrypa* (*Streblotrypa*) *peculiaris* sp. nov. and *Bashkirella minor* sp. nov. Bryozoans are represented mainly by fenestrates (27 species), followed by rhabdomesine cryptostomes (eleven species), cystoporates (ten species) and trepostomes (six species). Some species were known previously from the Pennsylvanian of northern Spain and the Carnic Alps, others from the Carboniferous of the Russian Platform and North America.

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Introduction

Carboniferous bryozoans are commonly abundant and diverse. However, our knowledge about them is very uneven. Whereas Carboniferous rocks of North America, certain parts of Australia, the British Isles, and the European part of Russia and Ukraine contain well studied bryozoan faunas, they are scarcely investigated in other regions such as Asia, Africa and Antarctica. Except for the British Isles, Carboniferous bryozoans in Western Europe are poorly known. Existing publications give only a superficial impression of the Carboniferous faunas of Spain, France, Germany, Hungary and Austria (Kodsi, 1967; Ceretti, 1963, 1964, 1967; Delvolvé & McKinney, 1983; Zágoršek, 1993; Ernst 2003, 2005; Ernst *et al.*, 2005; Wyse Jackson & Weber, 2005). Revision of many of the taxa is necessary. Carboniferous rocks of the Cantabrian Mountains, northern Spain, contain locally abundant bryozoans (Barrois, 1882; Winkler Prins, 1968; González & Suaréz Andréz, 1999; Elias Samankassou, pers. comm. 2005). However, our knowledge of them is very limited and needs to be expanded (Ernst *et al.*, 2005).

When discussing the stratigraphic and geographic range of the species, the international subdivision of Mississippian and Pennsylvanian is used, apart from the Russian and Ukrainian occurrences where the regional subdivisions of Lower, Middle and Upper Carboniferous is used instead; the Lower Carboniferous equates to the Mississippian and the Middle-Upper Carboniferous equals the Pennsylvanian.

The second author has, during the last 40 years, collected marine invertebrate faunas from the Carboniferous of the Cantabrian Mountains (mainly brachiopods and molluscs, but other fossil groups as well), partly in projects together with Dr R.H. Wagner (see Martínez Chacón & Winkler Prins, 2005). Also, limestone samples were collected for conodont studies by Dr M. van den Boogaard (e.g., van den Boogaard & Bless, 1985). The residues provided also silicified fossils, including bryozoans, which are, however, far from perfect due to partial silicification.

Geological setting

The Palaeozoic core of the Cantabrian Mountains in northwestern Spain (Cantabrian Zone of Lotze, 1945) represents an arcuate fold belt (see, for example, Wagner & Winkler Prins, 2000, fig. 1) which consists of thrust slices and small nappes caused by diastrophic movements during the Carboniferous (Pennsylvanian), resulting from a tightening of the arcuate basin. The further subdivision of the Cantabrian Zone, as proposed by Julivert (1971), reflects major faults in the area which constituted a single palaeogeographical region. The thrust structures have been moulded around a foreland spur which became more and more restricted to the east as time went on (Wagner & Martínez García, 1974; Wagner, 2004; Wagner & Winkler Prins, unpublished data). This foreland massif was called the Cantabrian Block by Radig (1962). The general region of the Picos de Europa represents the more permanently stable area in which carbonate sedimentation was the norm throughout the Carboniferous. A strongly subsident basinal area was situated in the West Asturian-Leonese Zone (Lotze, 1945) during the Early Palaeozoic, receiving sediment from an enveloping hinterland to the west and south. It moved to the Cantabrian Zone during the Pennsylvanian, where four different basins can be recognised, separated by well dated folding phases (e.g., Wagner, 1966; Kullmann et al., 2007). The Palaeozoic edifice is covered by an unconformable succession of highest Pennsylvanian (Stephanian C), Permian, Mesozoic and Cenozoic sedimentary rocks (Wagner & Martínez García, 1982). A discussion of the different views on the complicated tectonics of the Cantabrian Mountains is beyond the scope of this paper.

Carboniferous stratigraphy of the Cantabrian Mountains

For a complete overview of the Carboniferous stratigraphy of the Cantabrian Mountains (Fig. 1), the reader is referred to Truyols & Sánchez de Posada (1983), Wagner *et al.* (1983), Sánchez de Posada *et al.* (1996, 2002a, b) and Colmenero *et al.* (2002). The Carboniferous of the Cantabrian Mountains is exceptional in Western Europe since it was deposited in a tectonically active area (e.g., Wagner & Winkler Prins, 1985) and is largely marine well into the Stephanian, but also containing coal layers with associated fossil plants, thus allowing correlation with both the northwest European and Russian time scales. The following discussion is centred on the formations with the bryozoan-bearing samples described in this paper.



Fig. 1. Sketch map of the Cantabrian Mountains with localities indicated.

Two different areas of stratigraphic development can be distinguished in the Devonian and Carboniferous, the Asturian-Leonese and Palentian Domains (Brouwer, 1964; Wagner & Winkler Prins, 2000, unpublished research), respectively, separated by an important faultline (thrustplane) generally referred to as the Ruesga Fault or León Line. In the Carboniferous a third domain, the Picos de Europa unit, can be distinguished (Fig. 2).

The Cantabrian Mountains were a stable region during the Mississippian with deposition of a thin succession of mainly black shales (Vegamián Formation) and nodular limestones (Genicera - or Alba – Formation; see Wagner et al., 1971) in the Asturian-Leonese Domain, with mainly pelagic faunas indicating quiet water conditions (Amler & Winkler Prins, 1999) unsuitable for bryozoans. During the late Serpukhovian the region started to subside and the black, turbiditic limestones of the Barcaliente Formation were deposited, which continued into the Bashkirian (Sanz-López et al., 2006; Nemyrovska et al., unpublished research). The Barcaliente Limestone is poorly fossiliferous and no bryozoans were found.

Further subsidence in the Asturian-Leonese Domain (Fig. 2) lead to the deposition of light grey limestones of the Valdeteja Formation (originally described as a member of the Escapa Formation; see Winkler Prins, 1968, 1971, 2007; Eichmüller & Seibert, 1984; Eichmüller, 1985), whilst in other areas a condensed succes-

	R	ussia	Asturian- Leonese	Picos de Europa	Palencia	NW Europe
	GZHELIAN			Cavandi Fm.	Peña Cilda Em	(B) (C)
54	IAN	v- Dorogo- milovsky		Puente- Ilês Fm.		Barruelian (A)
	KASIMOVI	Krevya- Khamov kinsky nichsky		enas Fm. ©	S Braño- n. serra Fm.	HANJAN tabrian
		hkovsky		Las Llac	a Ver- S. deña Fm Fm	STEP
		Myac	ROUP		aario Ojos. Fm.	Asturian (D)
		Podolsky	SAMA G	pa Fm.	Vañes Ver Fm B	olsovian (C)
	NAINC	Kashirsky	GROUP	cos de Euro		LIAN skman B (B)
	MOSCO	Vereisky		Pi	Car- Cu men vao Fm. Fm	restpHA ngset- Duo n (A) lian
12		Asatausky	0		Pera-	ta N
		Tashas- tinsky	aldeteja Fm	aldeteja Fn		Yeadonian
	7	Askyn- bashsky	× 13			
	HKIRIAN	H Aka-			1.00-1	- Mars-
18	BASH	Syurar sky	F	F	é.,	Kinde
	SERPU-	CHOVSKY	Barcaliente Fr	Barcaliente Fr	Barcaliente Fr (+ equvalents)	Alportian

tions see Wagner & Winkler Prins (1994, 1997); the numeric ages (in millions of years) are according to Davydov *et al.* (2004)

sion of shales was deposited (Ricacabiello Formation; see Martínez Chacón et al., 1985). The rich faunas of the Valdeteja Formation include partly silicified bryozoans (Localities 1a, b, 2). Its age is Bashkirian, ranging locally into the earliest Moscovian (Villa, 1982; Villa et al., 2001). It is followed by the mainly clastic San Emiliano Formation, which contains some limestone layers with rich faunas (e.g., Winkler Prins, 1968; Martínez Chacón, 1979; Martínez Chacón & Winkler Prins, 1986), including bryozoans (Locality 2). In the Cármenes syncline the San Emiliano Formation is poorly represented due to a hiatus on top of the Valdeteja Limestone marked by a pronounced palaeokarst (clearly visible near the road north of Cármenes). The age of the San Emiliano Formation in its type area ranges from (upper) Bashkirian to Vereisky. Near Cármenes, the possible San Emiliano Formation is followed by a massive limestone and the Villamanín beds (shales, sandstones, and some thin limestones and coals; see Moore et al., 1971; Truyols & Sánchez de Posada, 1983). The latter are locally abundant in fossils, including bryozoans (Locality 3), and early Moscovian (Vereisky) in age (Villa et al., 1988; Fernández, 1993; van Ginkel & Villa, 1996). In the Asturian-Leonese region, sedimentation became more clastic, less marine and with an increasing amount of coal (Asturian coal basin; e.g., Bless & Winkler Prins, 1973). The marine fossils are usually moulds and thus unfavourable for bryozoan studies.

More to the east, in the Province of Palencia, marine deposits prevailed in the Moscovian and Kasimovian, interbedded with some coal-bearing intervals (Heredia *et al.*, 1990; Wagner & Winkler Prins, 2002; Kullmann *et al.*, 2007). Marine fossils are abundant, both in clastic mudstones and limestones, the latter containing well-preserved bryozoans (Localities 4, 5a-c).

On the stable platform of the Picos de Europa Domain, the Valdeteja Formation is followed by the Moscovian Picos de Europa Formation, which is rather similar to the Barcaliente and Valdeteja Limestones (Sánchez de Posada *et al.*, 1993). It is succeeded by the Kasimovian sedimentary rocks varying locally from clastic to calcareous, which can be rich in fossils (e.g., Las Llacerias and Puentellés formations; see Villa & van Ginkel, 2000; Mamet & Villa, 2004; Locality 6).

Materials and methods

The material used for the present study comes from different localities of the Pennsylvanian in the Cantabrian Mountains, Spain (see Fig. 2).

Locality 1a – 1.5 km east of Valdeteja, León; Valdeteja Formation, Bashkirian: A = *Cladochonus* Band; B = 10 m above *Cladochonus* Band (see map of Evers, 1967; Winkler Prins, 1968, 1971).

Locality 1b – 1.2 km east of Valdeteja, León; Valdeteja Formation, *Fenestrellina-Composita* Band, Bashkirian (see map of Evers, 1967; Winkler Prins, 1968, 1971).

Locality 2 – Section Villafeliz (Ernst *et al.*, 2005): uppermost part of Valdeteja Formation or lower part of San Emiliano Formation (Marsdenian–Langsettian, upper Bashkirian to lowermost Vereisky); see map of van den Bosch (1969); for a discussion of the age see Villa (1982), Villa *et al.* (1988) and van Ginkel & Villa (1996). *Locality* 3 – Immediately north of Barrio de la Tercía, León; Villamanín beds, Lower Moscovian (probably Vereisky) (see map of Evers, 1967; Moore *et al.*, 1971).

Locality 4 – Celada Syncline (in valley), 3 km northeast of Celada de Roblecedo, Palencia; Vergaño Formation, Villar Limestone, Upper Moscovian (Podolsky/Myachkovsky) (see map of de Sitter & Boschma, 1966; Wagner *et al.*, 1984; for detailed stratigraphic information see van de Graaff, 1971, enclosure 1, section 8).

Locality 5a – 2 km northeast of Herreruela de Castillería, Palencia; Vergaño Formation, Coterraraso Limestone, Upper Moscovian (Podolsky/Myachkovsky) (see map of de Sitter & Boschma, 1966; Wagner *et al.*, 1984; for detailed stratigraphic information see van de Graaff, 1971, fig. 3 and enclosure 1, section 5).

Locality 5b – 2.5 km northeast of Herreruela de Castillería, Palencia; Vergaño Formation, Coterraraso Limestone, Upper Moscovian (Podolsky/Myachkovsky) (see map of de Sitter & Boschma, 1966; Wagner *et al.*, 1984; for detailed stratigraphic information see van de Graaff, 1971, enclosure 1, section 5).

Locality 5c – 1 km southeast of Herreruela de Castillería, Palencia; Vergaño Formation, Sierra Corisa Limestone, Upper Moscovian (Podolsky/Myachkovsky) (see map of de Sitter & Boschma, 1966; Wagner *et al.*, 1984; for detailed stratigraphic information see van de Graaff, 1971, enclosure 1, section 5).

Locality 6 – 3 km southeast of Sotres, below Pico Grajal, Asturias; strata probably attributable to the Las Llacerias Formation, Kasimovian (= U-252 in Martínez Chacón & Winkler Prins, 1985; see map in Marquínez, 1978).

Bryozoans were investigated both through transmitted light microscopy using thin sections and by SEM. Thin sections were made from the hand specimens. The terminology of the morphological characters is adopted from Anstey & Perry (1970) for trepostomes, and Snyder (1991a, b) and Hageman (1991a, b) for cryptostomes. The inner diameter was measured for hollow features such as apertures or autozooecial chambers. Spacing of morphological characters at the colony surface was measured from centre to centre (e.g., aperture spacing along (across) branch). Additional quantitative characters were the number of mesozooecia, exilazooecia and acanthostyles surrounding each autozooecial aperture. Spacing of horizontal structures such as diaphragms or cystiphragms were quantified either by counting the number in 1 mm steps of the length of the host autozooecium or mesozooecium, or by measuring the distance between two successive diaphragms or cystiphragms. Statistics were summarized in tables with the descriptions of the species with arithmetic mean, sample standard deviation, coefficient of variation, minimum and maximum value. Abbreviations: N = number of measurements; X = mean; SD = sample standard deviation; CV = coefficient of variation; MIN = minimal value; MAX = maximal value.

Institutional abbreviations — Material from the Villafeliz section (Ernst *et al.*, 2005) is housed at the Senckenberg Museum (Frankfurt am Main, Germany; SMF 2641-2700). The remainder of the material (thin sections and SEM samples) is housed at the Nation-

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aal Natuurhistorisch Museum (Leiden, The Netherlands), registered under numbers RGM 211 494-211 536.

Systematic palaeontology (A. Ernst)

Phylum Bryozoa Ehrenberg, 1831 Class Stenolaemata Borg, 1926 Order Cystoporida Astrova, 1964 Suborder Fistuliporina Astrova, 1964 Family Fistuliporidae Ulrich, 1882 Genus *Fistulipora* M'Coy, 1849

Type species — *Fistulipora minor* M'Coy, 1849, by subsequent designation (Milne-Edwards & Haime, 1850, p. lix), Mississippian, British Isles.

Fistulipora multivesiculata Morozova, 1955 Pl. 1, figs. 1, 2.

1955 *Fistulipora multivesiculata* Morozova, pp. 16, 17, pl. 1, fig. 2a, b., pl. 2, fig. 1, text-figs. 1, 2. 2005 *Fistulipora* cf. *multivesiculata* Morozova; Ernst *et al.*, p. 303, pl. 1, fig. 1.

Material – Single colony, RGM 211 499a.

Description — Almost circular encrusting colony, measuring 6.4 × 7.5 mm. Apertures circular. Lunaria weakly developed. Vesicles large, rounded to polygonal in tangential section, separating the autozooecia in 1-2 rows, usually two.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	10	0.30	0.033	11.20	0.25	0.35
aperture spacing, mm	10	0.67	0.074	11.15	0.53	0.77

Remarks — The present specimen displays a close similarity to *Fistulipora multivesiculata* Morozova, 1955, from the Kasimovian Stage of the Middle Don, Russia, and to *F. cf. multivesiculata* Morozova 1955, described from the San Emiliano Formation (Westphalian B) near Villamanín by Ernst *et al.* (2005). The material described by Morozova (1955) possesses colonies in the form of tubular, sometimes multilaminar encrustations.

Stratigraphic and geographic range — Kasimovian Stage of the Middle Don, Russia. Spain, Villamanín, Villamanín beds, Pennsylvanian (Vereisky, Westphalian B); Locality 6 herein.

Fistulipora micidolamina McKinney, 1972 Pl. 1, figs. 3-5.

1972 Fistulipora micidolamina McKinney, pp. 24-26, pl. 4, figs. 1-6. 2005 Fistulipora micidolamina McKinney; Ernst et al., p. 303, pl. 1, fig. 2. Material – Five colonies, SMF 2641-2642, RGM 211 508a, b, 211 517b.

Description — Thin encrusting colony, reaching 0.48-0.54 mm in thickness. Apertures circular. Lunaria well developed. Rare planar diaphragms occurring in autozooecia. Vesicles small, rounded-polygonal in tangential section, separating the autozooecia in 1-2 rows, spaced 10-11 in 1 mm of the longitudinal section.

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	25	0.21	0.021	10.23	0.17	0.26
aperture spacing, mm	25	0.43	0.044	10.35	0.34	0.51
lunarium width, mm	20	0.16	0.015	9.42	0.13	0.19
lunarium length, mm	17	0.12	0.018	15.63	0.09	0.14

Measurements (three colonies) -

Remarks — *Fistulipora micidolamina* McKinney, 1972, is superficially similar to *F. distincta* Schulga-Nesterenko, 1955, from the Podolsky horizon of the Russian Platform, but differs in aperture width (0.17-0.26 mm in present material vs. 0.30-0.35 mm in *F. distincta*).

Stratigraphic and geographic range — Bangor Limestone (Late Mississippian), Alabama, U.S.A. Localities 2 and 6 herein.

Fistulipora cf. *elegans* Schulga-Nesterenko, 1955 Pl. 1, figs. 6, 7.

cf. 1955 Fistulipora elegans Schulga-Nesterenko, p. 69, pl. 6, figs. 2, 3, text-fig. 3b.

Material — Three colonies, RGM 211 505a, d, 211 516c.

Description — Circular colonies, 2.8-3.0 mm in diameter. Apertures circular to oval. Lunaria long, prominent, oriented towards the colony centre. Vesicular skeleton sealed by a layer of extrazooidal material.

Measurements —						
	Ν	Х	SD	CV	MIN	MAX
autozooecial aperture width, mm	16	0.20	0.021	10.49	0.16	0.24
aperture spacing, mm	15	0.45	0.051	11.51	0.38	0.57

Remarks — The internal morphology of this species is unknown. Externally, this species is similar to *Fistulipora elegans* Schulga-Nesterenko, 1955, from the Myachkovsky horizon (Pennsylvanian) of the Russian Platform. The aperture width in the present material is between 0.16-0.24 mm, that in the material of Schulga-Nesterenko (1955) 0.15-0.30 mm. Aperture spacing (centre to centre) is between 0.38-0.57 mm in the present material and 0.40-0.50 mm in *F. elegans* from Russia (measured from the images of Schulga-Nesterenko, 1955).

Stratigraphic and geographic range — Locality 6.

Genus Eridopora Ulrich, 1882

Type species — *Eridopora macrostoma* Ulrich, 1882, by original designation; Mississippian of Kentucky, U.S.A..

Eridopora sp. 1

Pl. 1, fig. 8; Pl. 2, figs. 1-3.

Material — Three colonies, RGM 211 511a, 211 521a, 211 497 (thin sections).

Description — Encrusting colonies, 0.72-0.75 mm thick. Autozooecial apertures rounded to oval, with well developed triangular lunaria. Lunaria large, prominent, containing single node in the central part. Autozooecial diaphragms absent. Vesicles angular, separating autozooecia in 1-2 rows, spaced 8-13 in 1 mm of longitudinal section.

Measurements (two colonies) —

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.26	0.045	17.12	0.19	0.34
aperture spacing, mm	20	0.47	0.053	11.27	0.36	0.58
lunarium width, mm	15	0.28	0.045	16.13	0.19	0.38
lunarium length, mm	15	0.27	0.043	15.83	0.17	0.31
vesicle diameter, mm	10	0.07	0.018	24.63	0.04	0.10

Remarks — The present material is similar to *Eridopora macrostoma* Ulrich, 1882, in having large lunaria, but differs in its smaller apertures (aperture width 0.26 mm vs. 0.39 mm in *E. macrostoma* on average).

Stratigraphic and geographic range — Localities 4 and 6.

Eridopora **sp. 2** Pl. 2, fig. 4.

Material — Single colony, RGM 211 517a.

Measurements -

Description — Thin encrusting colony. Apertures circular to oval. Lunaria large, prominent, triangular in shape. Vesicles apparently large. Extrazooidal material weakly developed.

1110000000000000						
	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	8	0.16	0.013	8.14	0.14	0.18
aperture spacing, mm	7	0.45	0.029	6.54	0.41	0.49
lunarium width, mm	5	0.13	0.022	16.42	0.11	0.16
lunarium length, mm	5	0.20	0.059	30.31	0.14	0.27

Remarks — This specimen differs from *Eridopora* sp. 1 in having smaller apertures (aperture width 0.16 mm vs. 0.26 mm in *E*. sp. 1 on average).

Stratigraphic and geographic range – Locality 6.

Fistuliporid sp. indet.

Pl. 2, figs. 5, 6.

Material - Two colonies, RGM 211 505b (89594-95), 211 520e.

Description — Thin encrusting colony. Autozooecial apertures polygonal. Hemiphragms restricting one-third to one-half of autozooecial tube. Lunaria large, cap-like. Rare small vesicles spaced between autozooecia, polygonal in shape.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	10	0.20	0.020	10.18	0.17	0.23
aperture spacing, mm	10	0.27	0.030	11.10	0.22	0.31
lunarium width, mm	5	0.17	0.014	8.32	0.15	0.19
lunarium length, mm	5	0.17	0.008	4.86	0.16	0.18
vesicle diameter, mm	5	0.05	0.012	24.50	0.04	0.07

Remarks — Only a few fistuliporid genera have hemiphragms, like *Cliotrypa* Ulrich *in* Bassler, 1929, and *Strotopora* Ulrich *in* Miller, 1889, from the Lower Mississippian of North America. However, both genera have a branched colony form and numerous alternating hemiphragms in the autozooecia, and *Strotopora* has prominent acanthostyles, features not found in the present species.

Stratigraphic and geographic range — Locality 6.

Suborder Hexagonellina Morozova, 1970 Family Hexagonellidae Crockford, 1947 Genus *Prismopora* Hall, 1883

Type species — *Prismopora triquetra* Hall & Simpson, 1887, by subsequent designation. Middle Devonian, North America.

Prismopora digitata Crockford, 1957

Pl. 2, figs. 7, 8; Pl. 3, figs. 1-3.

1957 Prismopora digitata Crockford, pp. 23, 24, pl. 5, figs. 1-4. 2000 Prismopora digitata Crockford; Ernst, pp. 84-86, pl. 17, fig. 6, pl. 18, figs. 1-5, text-fig. 4.

Material — Five colonies, RGM 211 498a, 211 501b, c, 211 503a, 211 533a.

Description — Colony erect-trilobate, with bifoliate lobes, arising from an encrusting base. Lobes diverging radially at angles of 108-115°, 119-122° and 124-130°. Autozooecia long, tubular, growing from an encrusting base or mesotheca. Autozooecial diaphragms and hemisepta not observed. Lunaria large, prominent, horse-shoe shaped. Vesicular skeleton consisting of large vesicles, completely separating autozooecia.

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	40	0.16	0.029	17.60	0.10	0.22
aperture spacing, mm	40	0.36	0.042	11.62	0.30	0.50
lunarium width, mm	10	0.18	0.018	9.80	0.16	0.21
lunarium length, mm	10	0.15	0.023	15.07	0.13	0.19

Remarks — The present material is similar to that described as *Prismopora digitata* Crockford, 1957, from the Lower Permian of the Carnic Alps (Ernst, 2000).

Stratigraphic and geographic range — Australia, Fitzroy Basin; Lower Permian. Carnic Alps, Austria; Lower Permian. Locality 6 herein.

Family Goniocladiidae Nikiforova, 1938 Genus *Cystocladia* Ernst & Minwegen, 2006

Type species — *Cystocladia hispanica* Ernst & Minwegen, 2006, by original designation. Picos de Europa Formation, Moscovian, Pennsylvanian; La Hermida, Spain.

Cystocladia hispanica Ernst & Minwegen, 2006

Pl. 3, figs. 4-6.

2006 Cystocladia hispanica Ernst & Minwegen, pp. 573-575, fig. 4C-E.

Material — Three colonies, RGM 211 511c, 211 520a, 211 521c.

Description — Ramose branched colonies. Branches rounded to slightly flattened, commonly ramifying dichotomously, 0.71-0.81 mm in diameter. Apertures oval, arranged in a quincunxial pattern, spaced four per 2 mm longitudinally. Lunaria large, occupying more than half of the autozooecial diameter, consisting of moderately thick calcitic skeleton. Vesicles relatively small, in 1-2 rows separating autozooecia. Colony surface covered by granular calcitic material.

Ν	X	SD	CV	MIN	MAX
20	0.16	0.024	14.66	0.13	0.21
20	0.40	0.054	13.30	0.32	0.58
	N 20 20	N X 20 0.16 20 0.40	N X SD 20 0.16 0.024 20 0.40 0.054	N X SD CV 20 0.16 0.024 14.66 20 0.40 0.054 13.30	N X SD CV MIN 20 0.16 0.024 14.66 0.13 20 0.40 0.054 13.30 0.32

Remarks — The present material was investigated only on silicified casts. However, it fits completely with the type material from the Picos de Europa Formation of La Hermida.

Stratigraphic and geographic range — Spain, La Hermida, Picos de Europa Formation, Moscovian, Pennsylvanian. Locality 6 herein.

Genus Ramiporidra Nikiforova, 1938

Type species — *Ramipora uralica* Stuckenberg, 1895, by original designation. Lower Permian of northern Urals, Russia.

Ramiporidra minuta (Schulga-Nesterenko, 1933) Pl. 4, figs. 1-6.

1933 Ramipora minuta Schulga-Nesterenko, p. 57, pl. 8, figs. 6, 9, 11, 14-15.
1941 Ramiporidra minuta (Schulga-Nesterenko); Schulga-Nesterenko, p. 213, pl. 58, figs. 2-5.
1994 Ramiporidra cf. minuta (Schulga-Nesterenko); Nakrem, p. 62, fig. 8A.
2005 Ramiporidra minuta (Schulga-Nesterenko); Ernst et al., p. 304, pl. 1, figs. 3-5.

Material — SMF 2643-2646 (thin sections).

Description — Branched, pinnate bifoliate colony. Branches oval in cross section, flattened laterally. Secondary stems branch off from the main stem at angles of 70°-80°. Autozooecia long, budding from the vertical mesotheca, arranged in 3-4 rows on each side of the medial ridge (protruding mesotheca), hemispherical shape in cross section at their bases, bending gently to the colony surface and becoming circular in cross section. Autozooecial apertures circular. Lunaria indistinct. Rare diaphragms slightly curved distally. Vesicles small, flat, partly separating autozooecia. Outer skeleton well developed. Mesotheca 0.02 mm thick, three-layered, slightly undulating, protruding as a low carina on the obverse side and as a high sharp ridge on the reverse side of the branch.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	6	0.99	0.149	15.10	0.81	1.26
branch thickness, mm	9	0.60	0.151	25.08	0.42	0.84
autozooecial aperture width, mm	20	0.15	0.024	15.74	0.12	0.22
aperture spacing along branch, mm	6	0.54	0.059	11.07	0.43	0.6

Measurements (two colonies) -

Remarks — *Ramiporidra minuta* (Schulga-Nesterenko, 1933) differs from other species of the genus *Ramiporidra* in having its thinner branches and 3-4 rows of autozooecia on each side of the carina. In contrast, other species of *Ramiporidra* have four or more rows of autozooecia on each colony side. The type species *R. uralica* (Stuckenberg, 1895) has thicker stems (2.33 mm vs. 0.81-1.26 mm in present form) and 5-6 rows of apertures on both sides of the medial ridge.

Stratigraphic and geographic range — Upper Carboniferous (Gzhelian), northern Russia (Petchora region); Lower Permian, Urals. Pennsylvanian (Late Gzhelian), Spitzbergen. Locality 2 herein.

Family Cystodictyonidae Ulrich, 1884 Genus Sulcoretepora d'Orbigny, 1849 [= Arcanopora Vine, 1884; Acanthopora Vine in Morozova, 1960 (incorrect subsequent spelling); Mstania Schulga-Nesterenko, 1955]

Type species — *Flustra*? *parallela* Phillips, 1836, by original designation; Mississippian of Whitewell, Yorkshire, England.

Sulcoretepora lophodes (Condra, 1902)

Pl. 4, figs. 7-9; Pl. 5, figs. 1-3.

1902 Cystodictya lophodes Condra, p. 356, pl. 25, figs. 6, 7.
1903 Cystodictya lophodes Condra; Condra, p. 106, pl. 21, figs. 6-9
1929 Cystodictya lophodes Condra; Moore, p. 153, pl. 18, figs. 23-26.
1955 Sulcoretepora virgata Schulga-Nesterenko, pp. 171-173, pl. 31, figs. 3-5, text-fig. 55.
1967 Sulcoretepora modesta Moore; Ceretti, pp. 291, 292, pl. 32, figs. 6, 7.
2005 Sulcoretepora lophodes (Condra); Ernst et al., p. 304, pl. 1, fig. 6, pl. 3, figs. 1, 2.

Material – Four colonies, RGM 211 501a, 211 528a, 211 533b, 211 534a.

Description — Branched bifoliate colonies. Branches oval in cross section, 0.79-1.84 mm wide and 1.3 mm thick in the thickest portion of cross section. Autozooecia long, budding from a horizontal mesotheca, hemispherical to quadrate in cross section at their bases, becoming rounded in the exozone. Curved hemisepta present in autozooecia. Autozooecial apertures circular, arranged in 3-6 alternating rows on the colony surface. Vesicles small, developed mostly in the exozone and near lateral protrusions of mesotheca.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	6	1.23	0.399	32.55	0.79	1.84
autozooecial aperture width, mm	20	0.14	0.019	13.62	0.11	0.17
aperture spacing along branch, mm	19	0.68	0.057	8.25	0.61	0.83
aperture spacing across branch, mm	18	0.43	0.066	15.40	0.34	0.59

Measurements -

Remarks — *Sulcoretepora lophodes* (Condra, 1902) is similar to the species *S. magnistriata* Schulga-Nesterenko, 1955, from the Steshevsky horizon (Lower Carboniferous, Serpukhovian) of Russia. It differs from the latter in having slightly larger apertures (0.11-0.17 mm vs. 0.10-0.15 mm in *S. magnistriata*).

Stratigraphic and geographic range — Pennsylvanian of Texas and Nebraska, U.S.A.. Auernig, Carnic Alps (Udine, Italy); Auernig Formation (Lower Gzhelian). Spain, Valverdín section, Villamanín beds, Pennsylvanian (Vereisky?, Westphalian B/C). Localities 1a, 6 herein.

Order Trepostomata Ulrich, 1882 Suborder Halloporina Astrova, 1965 Family Heterotrypidae Ulrich, 1890 Genus *Leioclema* Ulrich, 1882 [= *Lioclema* Ulrich, 1882]

Type species — *Callopora punctata* Hall, 1858, by original designation; Mississippian of U.S.A. (Iowa).

Leioclema? sp. Pl. 5, figs. 4, 5.

Material – Five colonies, RGM, 211 511b, 211 517c, d, 211 521b, 211 536c.

Description — Thin encrusting colonies. Autozooecial apertures oval to petaloid, surrounded by moderately thick peristome. Acanthostyles large, 2-5 surrounding each aperture, often indenting autozooecia, restricted to distal parts of autozooecial peristomes and usually absent in areas between autozooecia. Diaphragms not observed. Heterozooecia (mesozooecia?) small, polygonal, abundant, separating autozooecial apertures in 1-3 rows, 11-17 surrounding each autozooecial aperture.

Measurements —						
	Ν	Х	SD	CV	MIN	MAX
autozooecial aperture width, mm	30	0.16	0.023	14.25	0.12	0.21
aperture spacing, mm	30	0.40	0.036	8.96	0.33	0.47
acanthostyle diameter, mm	20	0.065	0.016	25.10	0.040	0.095
mesozooecia width, mm	15	0.048	0.010	20.61	0.033	0.066
number of acanthostyles per aperture	30	3.3	0.758	22.74	2.0	5.0
number of mesozooecia per aperture	15	14.4	2.131	14.80	11.0	17.0

Remarks — The internal morphology of this taxon is unknown. The general appearance suggests the genus *Leioclema* or *Hinaclema* Sakagami & Sugimura, 1987, because of the presence of abundant heterozooecia and acanthostyles. *Hinaclema* differs from *Leioclema* mainly in the absence of diaphragms in their heterozooecia. Unfortunately, heterozooecia cannot be observed in the present material. The arrangement of acanthostyles on only one side of the aperture is unusual for trepostome bryozoans and implies also a certain similarity to the cystoporates.

Stratigraphic and geographic range — Locality 6.

Suborder Amplexoporina Astrova, 1965 Family Crustoporidae Dunaeva & Morozova, 1967 Genus *Crustopora* Dunaeva, 1964

Type species — *Crustopora tuberculata* Dunaeva, 1964, by original designation; Lower Carboniferous (Serpukhovian), Ukraine.

Crustopora? sp. Pl. 5, fig. 6; Pl. 6, figs. 1, 2.

Material – Two colonies, RGM 211 518a, 211 532a.

Description — Ramose branched colonies. Branches 1.4-2.0 mm in diameter. Autozooecial apertures rounded. Acanthostyles abundant, large, 5-6 surrounding each autozooecial aperture. Heterozooecia (mesozooecia?) abundant, varying in size, polygonal in shape, covered by calcitic skeleton, separating autozooecia. Small maculae consisting of mesozooecia and acanthostyles.

Measurements —						
	Ν	Х	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.17	0.026	16.04	0.12	0.23
aperture spacing along branch, mm	20	0.38	0.044	11.81	0.30	0.45
exilazooecia width, mm	15	0.07	0.017	25.37	0.04	0.10

Remarks — The internal morphology of this species is not known. Its external morphology (abundant heterozooecia separating autozooecia and abundant acanthostyles) suggests the genus *Crustopora* Dunaeva, 1964.

Stratigraphic and geographic range — Locality 6.

Family Anisotrypidae Dunaeva & Morozova, 1967 Genus *Stenophragmidium* Bassler, 1952

Type species — *Stenophragma lobatum* Munro, 1912, by original designation; Mississippian (Viséan) of England.

Stenophragmidium paramirandum Ernst, Schäfer & Reijmer, 2005 Pl. 6, figs. 3-5.

2005 Stenophragmidium paramirandum Ernst et al., p. 306, pl. 1, fig. 7, pl. 2, fig. 1, pl. 3, fig. 4.

Material — Three colonies, RGM 211 505e, 211 519a, 211 522a.

Description — Thin encrusting colonies. Autozooecial apertures polygonal. Macroacanthostyles moderately large, 4-5 surrounding each autozooecial aperture. Microacanthostyles small, needle-like, 1-2 between neighbouring macroacanthostyles. Exilazooecia not observed. Hemiphragms restricting one-third to two-third of the autozooecial space, positioned at proximal wall.

Measurements –

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.20	0.029	14.77	0.14	0.25
aperture spacing, mm	20	0.28	0.044	15.43	0.21	0.37
acanthostyle diameter, mm	8	0.06	0.011	19.14	0.04	0.08

Remarks — The present material fits well with the description of *Stenophragmidium paramirandum* in Ernst *et al.* (2005). It differs from *S. mirandum* Dunaeva, 1964, from the Lower Carboniferous (Serpukhovian) of Ukraine by its thinner colonies and strongly differentiated acanthostyles as well as smaller apertures (0.14-0.25 mm vs. 0.27-0.30 mm in *S. mirandum*).

Stratigraphic and geographic range — Spain, Villamanín section, San Emiliano Formation, Pennsylvanian (Bashkirian, Westphalian A). Locality 6 herein.

Family Stenoporidae Waagen & Wentzel, 1886 Genus *Tabulipora* Young, 1883

Type species — *Tabulipora scotica* Lee, 1912 (*Tabulipora urei* Young, 1883, in part) by subsequent designation of Lee (1912); Carboniferous, Scotland.

Tabulipora cf. demissa Trizna, 1961

Pl. 6, figs. 6, 7; Pl. 7, fig. 1.

cf. 1961 Tabulipora demissa Trizna, pp. 38, 39, pl. 2, fig. 7, pl. 3, figs. 4, 5, text-fig. 5.

Material — Seven colonies, RGM 211 500b, 211 501d, 211 505c, 211 510c, 211 513a, 211 521d, 211 522c.

Description — Thin encrusting colonies, 0.8-1.5 mm thick. Autozooecial apertures polygonal. Macroacanthostyles positioned in junctions of apertures, 3-6 surrounding each aperture. Microacanthostyles arranged in one row between macroacanthostyles. Heterozooecia absent. Ring septa abundant to rare, restricting more than a half of the autozooecial space.

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	58	0.22	0.035	15.78	0.17	0.32
aperture spacing, mm	51	0.32	0.045	14.20	0.23	0.43
acanthostyle diameter, mm	34	0.066	0.010	15.66	0.050	0.085
number of acanthostyles per aperture	18	3.4	0.784	22.76	3.0	6.0

Measurements (seven colonies) —

Remarks — The present material is similar to *Tabulipora demissa* Trizna, 1961, from the Myachkovsky horizon (Middle Carboniferous) of the Urals. Microacanthostyles are not mentioned in the description of the Uralian species and it has fewer ring septa in autozooecia. However, the absence of microacanthostyles can be explained by the thin sections being too deep and the number of ring septa being variable within the colony. In the arrangement of macro- and microacanthostyles, the present material is similar to *T. carbonaria* (Worthen *in* Worthen & Meek, 1875). However, it differs in having a thin encrusting colony instead of a thick ramose one and smaller apertures (0.22 mm vs. 0.29 mm in *T. carbonaria*; measurements from Cuffey, 1967).

Stratigraphic and geographic range – Locality 6.

Trepostomata sp. indet. 1 Pl. 7, figs. 2-6; Pl. 8, figs. 1, 2.

Material – Five colonies, RGM 211 514a, SMF 2648-2652.

Description — Encrusting colonies, 0.48-0.54 mm thick. Colonies usually attached on cylindrical ephemeral substrates, apparently algal stems. Autozooecial apertures rounded-polygonal. Acanthostyles large, abundant, 4-7 surrounding each autozooecial aperture. Exilazooecia short, rounded-polygonal, abundant. Autozooecial diaphragms absent. Spoon-shaped (hook-shaped in longitudinal thin sections) hemiphragms present, commonly one or rarely two in each autozooecium, positioned in the distal middle part of the autozooecium. Autozooecial walls granular, 0.020-0.025 mm thick in endozone; regularly thickened, laminated, 0.040-0.055 mm thick in exozone.

Measurements —						
	Ν	Х	SD	CV	MIN	MAX
autozooecial aperture width, mm	40	0.15	0.027	18.41	0.11	0.22
aperture spacing, mm	35	0.24	0.045	19.12	0.17	0.34
acanthostyle diameter, mm	35	0.05	0.013	27.94	0.03	0.09
number of acanthostyles per aperture	17	5.88	0.928	15.77	4.00	7.00
exilazooecia width, mm	9	0.05	0.017	34.59	0.02	0.07

Remarks — The present material shows the general characters of stenoporid bryozoans – acanthostyles, thickened laminated walls and exilazooecia. However, it has spoon-shaped hemiphragms, which are similar to those of some Devonian eridotrypellids, like *Eridocampylus* Duncan, 1939. Some species of *Stenophragmidium* Bassler, 1952, can reveal similar hemiphragms. However, the hemiphragms of the present material differ in their regular arrangement in distal middle part of the autozooecium, whereas the hemiphragms of *Stenophragmidium* are situated in one row in the proximal exozonal part of the autozooecium.

Stratigraphic and geographic range – Localities 2 and 6.

Trepostomata sp. indet. 2

Pl. 8, figs. 3-6.

Material — SMF 2653-2659.

Description — Encrusting and ramose colonies. Encrusting sheets 0.48-0.53 mm thick, single ramose colony 1.38 mm in diameter, with 0.36 mm wide endozone and 0.51 mm wide exozone. Autozooecial apertures rounded-polygonal, 0.16-0.22 mm wide. Acanthostyles abundant, 5-7 surrounding each autozooecial aperture, 0.025-0.030 mm in diameter. Exilazooecia short, rounded polygonal, abundant, 0.04-0.06 mm in diameter. Autozooecial diaphragms not observed. Thick hemiphragms present. Autozooecial walls granular, 0.020-0.025 mm thick in endozone; regularly thickened, laminated, 0.030-0.050 mm thick in exozone. Abundant small styles (tubules of some authors) protruding from autozooecial walls in exozone, 0.005-0.010 mm in diameter.

Remarks — The wall structure of this bryozoan is similar to those of eridotrypellid bryozoans in the presence of 'rods.' The species *Stenopora signata* Ulrich, 1890, from the Pennsylvanian of North America superficially resembles the present material, but differs in having fewer acanthostyles (2-3 around each aperture vs. 5-7 in the present material). *Stenopora signata* was placed by Astrova (1978) in the genus *Permopora* Romantchuk, 1967, which shows similar morphological characters. This genus is known from the Upper Permian of the Russian Far East.

Stratigraphic and geographic range — Locality 2.

Order Cryptostomata Vine, 1884 Suborder Rhabdomesina Astrova & Morozova, 1956 Family Rhabdomesidae Vine, 1885 Genus *Pseudorhabdomeson* Gorjunova, 2002

Type species — *Rhabdomeson polygonum* Gorjunova, 2002, by original designation. Upper Carboniferous (Kasimovian), Russian Platform.

Pseudorhabdomeson bispinatum (Schulga-Nesterenko, 1955) Pl. 8, figs. 7, 8; Pl. 9, figs. 1, 2.

1955 Rhabdomeson bispinatum Schulga-Nesterenko, p. 145, pl. 23, figs. 7-9, text-fig. 40.

Material – SMF 2660-2666 (thin sections).

Description — Ramose colony with small axial cylinder and distinct exozone, branches 0.66-0.93 mm in diameter. Axial cylinder 0.17-0.25 mm in diameter. Autozooecia growing in spiral pattern, arranged in ten rows around axial cylinder, rhomboidal in cross-section. Autozooecia inclined at angles of 24-29° to axial cylinder and intersecting colony surface at angles of 62-70°. Autozooecial apertures oval, arranged in regular diagonal rows. Macroacanthostyles large, a single row of two between apertures longitudinally. Usually 1-3 small microacanthostyles between macroacanthostyles. Hemisepta and diaphragms absent.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	7	0.77	0.094	12.24	0.66	0.93
axial cylinder diameter, mm	7	0.20	0.026	12.95	0.17	0.25
aperture width, mm	17	0.07	0.009	13.53	0.06	0.08
aperture spacing along branches, mm	15	0.51	0.060	11.93	0.38	0.63
aperture spacing diagonally, mm	15	0.28	0.042	14.87	0.23	0.40
macroacanthostyle diameter , mm	15	0.044	0.007	16.75	0.030	0.055
microacanthostyle diameter, mm	12	0.024	0.003	13.09	0.020	0.030

Measurements (three colonies) -

Remarks — *Pseudorhabdomeson bispinatum* (Schulga-Nesterenko, 1955) differs from the similar species *P. binodosum* (McKinney, 1972) from the Mississippian of Alabama in

the arrangement of paired macroacanthostyles. The macroacanthostyles of *P. bispinatum* are arranged in one row in the interspaces between apertures, whereas in *P. binodosum* they are arranged in two rows.

Gorjunova (2002) separated species of *Rhabdomeson* with a polygonal axial cylinder in her new genus *Pseudorhabdomeson*. The diagnosis of this genus includes well-developed superior and inferior hemisepta, which, however, are absent in *P. bispinatum* (Schulga-Nesterenko, 1955).

Stratigraphic and geographic range — Upper Carboniferous (Kasimovian); Russian Platform and Ukraine. Locality 2 herein.

Family Hyphasmoporidae Vine, 1885 Genus Ascopora Trautschold, 1876

Type species — *Ceriopora nodosa* Fischer von Waldheim, 1837 (International Commission on Zoological Nomenclature, 1994). Carboniferous, Russia.

Ascopora **sp.** Pl. 9, figs. 3, 4; Pl. 10, figs. 1, 2.

Material — One colony, RGM 211 495a-f (thin sections).

Description — Ramose branched colonies. Branches 1.80-2.26 mm in diameter. Axial bundle 0.30-0.60 mm in diameter, consisting of 4-5 axial zooecia. Autozooecia tubular-prismatic, rhombic in cross section in endozones, inclined to the axial bundle at angles of 37-39°. Autozooecial apertures oval, arranged in regular diagonal rows around branches. Two to three long hemisepta in each autozooecial aperture, arranged in pairs side by side longitudinally; microacanthostyles arranged haphazardly, 0.01-0.20 mm in diameter. Autozooecial walls granular, 0.010-0.015 mm thick in endozone; laminated, 0.09-0.13 mm thick in exozone.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
branch width, mm	6	1.99	0.167	8.38	1.80	2.26
axial bundle diameter, mm	6	0.48	0.111	23.09	0.36	0.60
autozooecial aperture width, mm	10	0.13	0.017	12.77	0.11	0.17
aperture spacing along branch, mm	10	0.40	0.066	16.62	0.30	0.48
aperture spacing across branch, mm	10	0.29	0.017	5.81	0.26	0.32
macroacanthostyle diameter, mm	10	0.060	0.011	20.03	0.045	0.075

Remarks — The best known species of *Ascopora* have one macroacanthostyle between autozooecial apertures or they are arranged in a row, but not side by side like in this species. Similar species are *Ascopora graemei* Fritz, 1970, from the Pennsylvanian of Canada, which has, however, only two acanthostyles sporadically between apertures, and

A. nesviti Trizna, 1961, from the Moscovian of the Urals. The latter species has smaller autozooecial apertures (aperture width 0.09-0.10 mm vs. 0.11-0.17 mm in the present material).

Stratigraphic and geographic range — Locality 5a.

Genus Streblotrypa Ulrich in Vine, 1884 Subgenus Streblotrypa (Streblotrypa) Ulrich in Vine, 1884

Type species — Streblotrypa nicklesi Ulrich *in* Vine, 1884, by original designation; Mississippian, England.

Streblotrypa (Streblotrypa) peculiaris sp. nov. Pl. 10, figs. 3-7; Pl. 11, fig. 1.

2006 Streblotrypa (Streblotrypa) sp.; Ernst & Minwegen, p. 577, fig. 5E, F.

Derivation of the name — The name refers to the peculiar morphology of the new species, the budding axis being shifted to one side.

Type material — Holotype, RGM 211 513b; paratypes, SMF 2669, 2671.

Type locality and horizon - 3 km southeast of Sotres, below Pico Grajal, Asturias, northern Spain. Strata probably attributable to the Las Llacerias Formation, Kasimovian (Locality 6)

Diagnosis — Thin branched colonies; autozooecia growing from an indistinct budding axis which is usually shifted to one side; autozooecial apertures arranged around the stem or only on one side of it, the opposite side bearing only metazooecia; 15-21 metazooecia in interapertural areas.

Material — Apart from the type material, there are nine specimens, SMF 2667-2668, 2670, RGM 211 504a, b, 211 518c, 211 523d, 211 529a, 211 534b.

Description — Ramose colony, 0.40-0.73 mm in diameter. Axial bundle not clearly defined. Autozooecia long, growing in spiral pattern from an indistinct budding axis at angles of 28-35°. The budding axis situated in the centre of the stem or more usually shifted aside. Autozooecial apertures oval, arranged around stems in diagonal rows in colonies with central budding axis. In colonies with excentic budding axis apertures occurring only on one side, the opposite side bearing metazooecia. Stems with excentic budding axis distinctly flattened in the plane of obverse/reverse side. Metazooecia rounded to polygonal, arranged in 3-4 longitudinal rows between autozooecia, 15-21 in the interapertural areas. Diaphragms not observed; superior hemisepta absent, inferior hemisepta short.

	Ν	X	SD	CV	MIN	MAX
branch diameter	11	0.52	0.093	17.89	0.40	0.73
aperture width	10	0.10	0.010	9.29	0.09	0.12
aperture spacing along branches	20	0.46	0.091	19.84	0.32	0.62
metazooecia width	10	0.027	0.010	36.73	0.015	0.045
metazooecia number	6	16.8	2.401	14.27	15.0	21.0

Measurements (ten colonies) —

Remarks — Rhabdomesine cryptostomes are characterized by having cylindrical stems, with a more or less symmetrical pattern of autozooecia in cross section. In a few Lower Palaeozoic genera (e.g., *Heminematopora, Hemiulrichostylus*), the budding axis is excentric, which results in opening of autozooecial apertures not all around the stem, but on one side only. A similar pattern is here observed in a new species of *Streblotrypa* (*Streblotrypa*) for the first time which makes it different from other species of the genus. *Streblotrypa* (*S.*) *angulatum* Karklins, 1986, from the Late Mississippian of Utah, U.S.A., is similar to *S.* (*S.*) *peculiaris*, especially in the presence of an inferior hemisepta. However, this American species has thicker branches (0.82-1.02 mm vs. 0.40-0.73) and fewer metazooecia between the apertures (8-16 vs. 15-21).

Stratigraphic and geographic range — Spain, La Hermida (Ernst & Minwegen, 2006), Picos de Europa Formation, Moscovian, Pennsylvanian. Localities 1b and 6 herein.

Subgenus Streblotrypa (Streblascopora) Bassler, 1929

Type species — *Streblotrypa fasciculata* Bassler, 1929, by original designation; Upper Permian, Indonesia.

Streblotrypa (Streblascopora) cf. densa Morozova, 1955 Pl. 11, figs. 2-4.

cf. 1955 Streblotrypa densa Morozova, pp. 63, 64, pl. 9, fig. 3.

Material – Two colonies, RGM 211 516d, 211 536a.

Description — Ramose colony, branches 0.9-1.2 mm in diameter. Axial bundle 0.28 mm in diameter. Autozooecial apertures oval. Metazooecia rounded, arranged in 2-3 longitudinal rows between autozooecia, 7-11 spaced in interapertural areas.

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.085	0.009	10.10	0.075	0.100
aperture spacing along branch, mm	20	0.48	0.064	13.25	0.35	0.62
aperture spacing across branch, mm	20	0.30	0.038	12.65	0.24	0.38
number of metazooecia	11	8.6	1.206	13.97	7.0	11.0

Measurements –

Remarks — The internal morphology of the present material is unknown. Externally, it is similar to *Streblotrypa* (*Streblascopora*) *densa* Morozova, 1955, from the Upper Carboniferous (Gzhelian) of Ukraine. The latter has, however, larger autozooecial apertures (autozooecial aperture width 0.10-0.13 mm vs. 0.075-0.100 mm in the present material). *Streblotrypa* (*S.*) *nikiforovae* Morozova, 1955, from the Middle Carboniferous of Ukraine differs in having 6-7 metazooecia in interapertural areas instead of 7-11 in the present material.

Stratigraphic and geographic range — Ukraine?; Upper Carboniferous, Gzhelian Stage. Locality 6 herein.

Streblotrypa (Streblascopora) sp. 1 Pl. 11, figs. 5, 6.

Material - Two colonies, RGM 211 524c, 211 530b.

Description — Ramose colony, branches 0.90-0.95 mm in diameter. Autozooecial apertures oval. Metazooecia rounded, arranged in 3-4 longitudinal rows between autozooecia, 13-19 spaced in interapertural areas.

Measurements -

3.1

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.09	0.010	11.31	0.07	0.10
aperture spacing along branch, mm	25	0.41	0.042	10.15	0.35	0.50
aperture spacing across branch, mm	20	0.26	0.030	11.70	0.20	0.30
number of metazooecia	10	15.7	2.111	13.45	13.0	19.0

Remarks — The internal morphology of this species is unknown. *Streblotrypa* (*Streblascopora*) sp. 1 is superficially similar to *S*. (*S*.) *germana* Bassler, 1929, but differs by having more metazooecia in interapertural areas, 13-19 vs. 9-11 in S. (*S.*) *germana*.

Stratigraphic and geographic range — Locality 6.

Streblotrypa (Streblascopora) sp. 2 Pl. 11, figs. 7, 8.

Material – Two colonies, RGM 211 520d, 211 523a.

Description — Ramose colony, branches 0.75-0.90 mm in diameter. Autozooecial apertures oval. Metazooecia rounded, arranged in 3-4 longitudinal rows between autozooecia, 18-27 spaced in the interapertural area.

Measurements —						
	Ν	Х	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.09	0.014	15.14	0.07	0.12
aperture spacing along branch, mm	20	0.50	0.070	13.84	0.40	0.68
aperture spacing across branch, mm	16	0.29	0.055	18.79	0.20	0.36
number of metazooecia	12	22.2	2.588	11.68	18.0	27.0

Remarks — Internal morphology of this species is unknown. *Streblotrypa* (*Streblascopora*) sp. 2 is superficially similar to *S*. (*S*.) *striatopora* Rogers, 1900, but differs in having smaller autozooecial apertures (autozooecial width 0.07-0.10 mm vs. 0.2 mm in S. (S.) *striatopora*).

Stratigraphic and geographic range — Locality 6.

Family Nematotrypidae Spjeldnaes, 1984 Genus *Clausotrypa* Bassler, 1929

Type species — *Clausotrypa separata* Bassler, 1929, by original designation; Lower Permian, Timor, Indonesia.

Clausotrypa monticola (Eichwald, 1860)

Pl. 12, figs. 1-3.

1860 Myriolithes monticola Eichwald, p. 452, pl. 25, fig. 6a, b.
1938 Clausotrypa monticola (Eichwald); Nikiforova, p. 181, pl. 14, figs. 4-7, pl. 15, figs. 7-10.
1941 Clausotrypa monticola (Eichwald); Schulga-Nesterenko, p. 219, pl. 13, figs. 3-6.
1986 Clausotrypa monticola (Eichwald); Morozova & Krutchinina, p. 67, pl. 20, figs. 3, 4.
2003 Clausotrypa monticola (Eichwald); Ernst, p. 60, pl. 3, figs. 2-5.
2006 Clausotrypa monticola (Eichwald); Ernst & Minwegen, pp. 578, 579, fig. 6D-I.

Material — Five colonies, SMF 2700, RGM 211 497b (thin sections), 211 516a, 211 518d, 211 528d.

Description — Cylindrical branches, 0.52-1.45 mm in diameter. Autozooecia long, cylindrical, growing parallel to the branch axis for a long distance, turning at low angles to the colony surface in exozone. Autozooecial apertures oval. Diaphragms rare in autozooecia. Heterozooecia (tectitozooecia after Kopaevich, 1975) numerous, restricted to exozone, in 1-3 rows separating autozooecial apertures, having common diaphragms. Acanthostyles abundant, originating in the endozone, having clear calcite cores, 5-7 around each aperture.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
branch width, mm	5	0.96	0.364	38.07	0.52	1.45
autozooecial aperture width, mm	20	0.12	0.019	15.18	0.09	0.17
aperture spacing along branch, mm	10	0.81	0.118	14.46	0.63	0.98
aperture spacing across branch, mm	10	0.43	0.041	9.43	0.36	0.48
metazooecia width, mm	10	0.06	0.015	25.52	0.04	0.09
acanthostyle diameter, mm	10	0.04	0.007	17.76	0.03	0.05
number of acanthostyles per aperture	10	5.9	0.876	14.84	5.0	7.0

Remarks — *Clausotrypa monticola* (Eichwald, 1860) is similar to *C. conferta* Bassler, 1929, from the Lower Permian of Indonesia and Thailand. However, the latter species

has smaller acanthostyles and larger autozooecial apertures (0.15-0.25 mm vs. 0.09-0.17 in *Clausotrypa monticola*).

Stratigraphic and geographic range — Pennsylvanian to Lower Permian of Russia and the Arctic. This species is known from the following Pennsylvanian localities in Europe: Carnic Alps (Austria); Pennsylvanian, Lower *Pseudoschwagerina* Formation (Upper Gzhelian). Spain, La Hermida, Picos de Europa Formation, Moscovian, Pennsylvanian. Localities 1b, 2, 4 and 6 herein.

Family Rhomboporidae Simpson, 1895 Genus *Rhombopora* Meek, 1872

Type species — *Rhombopora lepidodendroides* Meek, 1872, by original designation; Pennsylvanian, U.S.A..

Rhombopora lepidodendroides Meek, 1872 Pl. 12, figs. 4-6.

Material - Three colonies, RGM 211 522d, 211 528b, c.

Description — Ramose colony, branches 1.2-1.5 mm in diameter. Autozooecial apertures oval, arranged in irregular diagonal rows. Paurostyles about 0.02 mm in diameter, arranged usually in a single, sometimes a double row between autozooecia. Large single macroacanthostyle positioned in interspaces between apertures in angles of the hexagons of smaller paurostyles, 0.03-0.05 mm in diameter.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	15	0.12	0.020	16.71	0.08	0.15
aperture spacing along branch, mm	20	0.39	0.048	12.16	0.30	0.46
aperture spacing across branch, mm	20	0.25	0.025	9.83	0.20	0.30

Remarks — *Rhombopora lepidodendroides* Meek, 1872, is similar to *R. corticata* Moore, 1929, but differs in the smaller diameter of its autozooecia and in having smaller colonies.

Stratigraphic and geographic range — This species apparently had a wide distribution (Newton, 1971; Sakagami, 1995). The investigated material comes from Localities 1b and 6. It is also known from the Villamanín beds (Pennsylvanian, Vereisky?, Westphalian B/C) of Valverdín, and from the Picos de Europa Formation (Moscovian, Pennsylvanian) of La Hermida, Cantabrian Mountains (Ernst *et al.*, 2005; Ernst & Minwegen, 2006).

Rhombopora corticata Moore, 1929

Pl. 12, figs. 7, 8.

1929	Rhombopora	corticata	Moore,	p. 137,	text-fi	g. 4i,	j, pl	. 17,	figs	. 3, 4	
1005	Phowhonorg	conticata	Moore	Salvage	min	262	fige	1 7	1 0	21	2.2

1995 Rhombopora corticata Moore; Sakagami, p. 262, figs. 1-7, 1-8, 2-1, 2-2.

2005 Rhombopora corticata Moore; Ernst et al., pp. 307-309, pl. 2, fig. 2, pl. 3, fig. 6.

2006 Rhombopora corticata Moore; Ernst & Minwegen, pp. 579-581, fig. 6B, C.

Material — Single colony, RGM 211 515a.

Measurements -

Description — Ramose colony, branches 1.6 mm in diameter. Autozooecial apertures oval, arranged in regular diagonal rows, paurostyles 0.03-0.05 mm in diameter, arranged in a single row between autozooecia forming a regular rhombic pattern. Single large acanthostyles positioned in interspaces between apertures at angles of hexagons of smaller paurostyles, having pale sheaths and dark cores, 0.063-0.075 mm in diameter.

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	Ν	X	SD	CV	MIN	MA
autozooecial aperture width, mm	10	0.17	0.021	12.93	0.12	0.19
aperture spacing along branch, mm	7	0.72	0.050	6.86	0.62	0.78
aperture spacing across branch, mm	10	0.36	0.060	16.81	0.30	0.50

Remarks — *Rhombopora corticata* Moore, 1929, is similar to *R. lepidodendroides* Meek, 1872. It differs from the latter species in having larger colonies with a wider exozone as well as larger and more widely spaced apertures.

Stratigraphic and geographic range — Graham Formation (Pennsylvanian) of Texas, U.S.A.. *Pseudoschwagerina* zone (Permian) of Bolivia. Spain, La Hermida, Picos de Europa Formation, Moscovian, Pennsylvanian; Valverdín, Villanueva beds, Pennsylvanian, (Vereisky?, Westphalian B/C). Locality 6 herein.

Rhombopora cf. tenuirama Ulrich, 1890

Pl. 12, fig. 9; Pl. 13, figs. 1-4.

cf. 1890 Rhombopora tenuirama Ulrich, p. 660, pl. 70, fig. 8.

Material — SMF 2672-2682, RGM 211 513c, 211 521e, 211 522e, 211 526c, 211 527a.

Description — Ramose branched colonies. Branches dichotomizing, 0.23-1.00 mm in diameter. Autozooecia tubular, growing from a central axis. Autozooecial apertures oval, arranged in regular diagonal rows. Superior hemisepta weakly developed; inferior hemisepta absent. Diaphragms lacking. Six macroacanthostyles surrounding each autozooecial aperture; microacanthostyles arranged in a single row between macroacanthostyles.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	14	0.54	0.261	48.39	0.23	1.00
autozooecial aperture width, mm	26	0.08	0.019	22.42	0.06	0.12
aperture spacing along branch, mm	18	0.40	0.065	16.11	0.30	0.53
aperture spacing across branch, mm	15	0.25	0.045	17.92	0.20	0.35
macroacanthostyle diameter, mm	15	0.04	0.008	18.71	0.03	0.06

Measurements (fourteen colonies) -

Remarks — The present material is superficially similar to *Rhombopora tenuirama* Ulrich, 1890, from the Chester Group of the U.S.A., especially in the arrangement of acanthostyles and branch diameter. However, the internal morphology of the American species is unknown. Another similar species is *R. angustata* Ulrich, 1890, which has, however, numerous small paurostyles instead of the macro- and microacanthostyles of *R. cf. tenuirama*.

Stratigraphic and geographic range — Localities 1a, 2 and 6.

Family Nikiforovellidae Gorjunova, 1975 Genus Nikiforovella Nekhoroshev, 1956

Type species — *Nikiforovella alternata* Nekhoroshev, 1956, by original designation. Lower Carboniferous, Russia.

Nikiforovella sp.

Pl. 13, fig. 5; Pl. 14, figs. 1-4.

Material — SMF 2683-2685, RGM 211 526a, d.

Description — Ramose branched colonies. Branches 0.77-1.05 mm in diameter, with 0.18-0.21 mm wide exozones. Autozooecia tubular-prismatic, growing from a central axis, bending sharply in exozones. Autozooecial apertures rounded to oval, arranged in irregular diagonal rows. Superior hemisepta blunt; inferior hemisepta absent. Diaphragms not observed. Paurostyles abundant, originating in the outermost exozone. Autozooecial walls granular in exozones; thick, laminated in endozones. Metazooecia common, rounded, varying in size.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	3	0.93	0.144	15.51	0.77	1.05
autozooecial aperture width, mm	14	0.10	0.014	13.87	0.08	0.12
aperture spacing along branch, mm	14	0.70	0.068	9.66	0.60	0.80
aperture spacing across branch, mm	16	0.38	0.059	15.40	0.26	0.48
macroacanthostyle diameter, mm	15	0.04	0.006	14.78	0.03	0.05
metazooecia width, mm	10	0.030	0.013	40.48	0.015	0.050

Measurements (four colonies) -

Remarks — The present material is similar to *Nikiforovella vera* Romantchuk, 1975, from the Middle Carboniferous of Khabarovsk Territory, but has thinner branches (branch diameter 0.77-1.05 mm vs. 1.20 mm in *N. vera*) and smaller autozooecial apertures (aperture width 0.08-0.12 mm vs. 0.13-0.15 mm in *N. vera*).

Stratigraphic and geographic range — Localities 1a and 2.

Ernst & Winkler Prins. Pennsylvanian bryozoans. Scripta Geol., 137 (2008)

Order Fenestellida Astrova & Morozova, 1956 Suborder Fenestellina Astrova & Morozova, 1956 Family Fenestellidae King, 1849 Genus Laxifenestella Morozova, 1974

Type species — Fenestella sarytshevae Schulga-Nesterenko, 1951, by original designation, Carboniferous, Russia.

Laxifenestella? filistriata (Ulrich, 1890)

Pl. 14, fig. 5; Pl. 15, figs. 1-6; Pl. 16, figs. 1, 2.

- ? 1890 Fenestella filistriata Ulrich, p. 535, pl. 49, fig. 2
- ? 1906 Fenestella filistriata Ulrich, var. nodosa; Johnsen, pp. 144, 145, pl. 10, fig. 6.
- ? 1963 Fenestella gortanii Ceretti, p. 270, pl. 24, fig. 1a, b, pl. 26, fig. 1.
- ? 1967 Fenestella (Fenstella) filistriata Ulrich; Kodsi, pp. 4-65, pl. 2, figs. 8-10.

Material — SMF 2686-2687 (thin sections), RGM 211 506a, 211 509a, 211 524a, 211 529b.

Description — Reticulate colonies with straight branches joined by moderately thick dissepiments. Branch bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, 6-7 spaced per length of a fenestrule. Shape of fenestrules varying from oval to slightly rectangular, often irregular. Keel low; nodes absent. Outer lamellar skeleton moderately thick. Heterozooecia in form of ovicells present. Ovicells produce spherical chambers, 0.35-0.41 mm in diameter, with 0.025-0.029 mm thick wall, situated on autozooecial apertures, with openings positioned lateraly.

Interior: autozooecia rectangular in tangential section; aperture positioned at distal to distal-abaxial end of chamber. Hemisepta long, positioned mid-length of autozooecial chamber. Internal granular skeleton thin.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	10	0.39	0.060	15.34	0.30	0.45
dissepiment width, mm	8	0.22	0.061	28.27	0.13	0.30
fenestrule width, mm	7	0.58	0.071	12.22	0.50	0.69
fenestrule length, mm	8	1.84	0.285	15.54	1.56	2.30
autozooecial aperture width, mm	5	0.08	0.004	5.39	0.08	0.09
aperture spacing along branch, mm	15	0.32	0.046	14.50	0.22	0.40
aperture spacing across branch, mm	10	0.25	0.019	7.38	0.23	0.28
distance between dissepiment centres, mm	8	2.01	0.360	17.92	1.64	2.60
distance between branch centres, mm	7	0.91	0.128	14.11	0.72	1.05
zooecial chamber width, mm	10	0.11	0.008	6.90	0.10	0.13
apertures per fenestrule length	4	6.75	0.500	7.41	6.00	7.00

Measurements (four colonies) -

Remarks — The present material is very similar to *Fenestella filistriata* Ulrich, 1890, from the Mississippian of Iowa, U.S.A. The most characteristic features are the low

keel without nodes and the number of autozooecia per fenestrule. However, the internal morphology of this species is unknown, as well as that of species described by Johnsen (1906), Ceretti (1963) and Kodsi (1967) (see synonymy list). Morphologically, the present material is similar to *"Fenestella" octonicellata* Schulga-Nesterenko, 1952, from the Lower Permian of the Urals (Schulga-Nesterenko, 1952, p. 34, pl. 2, fig. 4). Confusingly, Schulga-Nesterenko did not mention any hemisepta in her description and did not illustrate them in her text-fig. 14, but her pl. 2, fig. 4 shows distinct hemisepta in autozooecia that are rectangular to slightly pentagonal in mid-tangential section. *"Fenestella" octonicellata* has low triserial keel without nodes and larger fenestrules (fenestrule length 3.9-4.0 mm vs. 1.56-2.30 mm and fenestrule width 1.30 mm vs. 0.50-0.69 mm) compared with the species described here. Otherwise, the present material shows morphological similarities to the genus *Lyrocladia* Schulga-Nesterenko, 1930, in shape of autozooecia and presence of hemisepta, but differs in lacking keel nodes.

Stratigraphic and geographic range — Mississippian? of North America and Pennsylvanian of the Carnic Alps. Localities 2 and 6 herein.

Genus Spinofenestella Termier & Termier, 1971

Type species — Fenestella spinulosa Condra, 1902, by original designation; Lower Permian, Nebraska, U.S.A..

Spinofenestella subspeciosa (Schulga-Nesterenko, 1955) Pl. 16, figs. 3-9.

1955 Fenestella subspeciosa Schulga-Nesterenko, pp. 121, 122, pl. 19, fig. 3.

Material - Three colonies, RGM 211 494 (thin sections), 211 532b, 211 536b.

Description — Reticulate colonies with straight branches joined by moderately thick dissepiments. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, bearing eight nodes, 4-6 spaced per length of a fenestrule. Shape of fenestrules varying from oval to slightly rectangular, often irregular. Keel low, carrying prominent nodes. Internal granular skeleton thin, continuous with obverse keel, nodes, rods, peristome and across dissepiments. Outer lamellar skeleton moderately thick. No heterozooecia observed. Reverse side bearing irregularly shaped large nodes, arranged usually in a single row.

Interior: autozooecia triangular to trapezoid in mid tangential section, moderately high and elongated, with well developed vestibule; aperture positioned at distal to distalabaxial end of chamber. Hemisepta absent.

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	Ν	X	SD	CV	MIN	MAX
branch width, mm	20	0.30	0.041	13.67	0.25	0.42
dissepiment width, mm	25	0.23	0.029	12.87	0.17	0.28
fenestrule width, mm	25	0.53	0.105	19.93	0.34	0.72
fenestrule length, mm	25	1.23	0.179	14.53	1.05	1.80
autozooecial aperture width, mm	15	0.08	0.016	20.18	0.06	0.10
aperture spacing along branch, mm	20	0.31	0.024	7.82	0.27	0.36
aperture spacing across branch, mm	17	0.28	0.034	12.11	0.23	0.35
distance between dissepiment centres, mm	20	1.55	0.224	14.49	1.29	2.10
distance between branch centres, mm	20	0.82	0.110	13.46	0.63	0.99
zooecial chamber width, mm	20	0.150	0.008	5.73	0.135	0.170
apertures per fenestrule length	17	4.8	0.636	13.18	4.0	6.0
branch thickness, mm	4	0.37	0.029	7.71	0.34	0.41
node width, mm	6	0.12	0.023	19.58	0.10	0.16
node spacing, mm	8	0.51	0.076	14.86	0.41	0.66

Remarks — *Spinofenestella verrucosa* (Trizna, 1950) from the Lower Permian of the Urals is similar to *S. subspeciosa* (Schulga-Nesterenko, 1955), but differs in having smaller fenestrules (fenestrule length 1.38-1.48 mm vs. 1.05-1.80 mm and fenestrules width 0.55-0.65 mm vs. 0.34-0.72 in *S. subspeciosa* and *S. verrucosa*, respectively). Furthermore, *Fenestella compressa* and *F. compressa* var. *nodosa* Ulrich, 1890 (pp. 539, 540, pl. 50, fig. 2, 2a), from the Mississippian of North America are superficially similar to *S. subspeciosa* (Schulga-Nesterenko, 1955). Especially characteristic are nodes on the reverse side of *F. compressa* var. *nodosa* Ulrich, 1890 (pl. 50, fig. 2). However, the internal morphology of these bryozoans is unknown.

Stratigraphic and geographic range — Russian Platform; Gzhelian, Upper Carboniferous. Localities 5c and 6 herein.

Genus Fabifenestella Morozova, 1974

Type-species — Fenestella praevirgosa Schulga-Nesterenko, 1951, by original designation; Upper Carboniferous, Russian Platform.

Fabifenestella praevirgosa Schulga-Nesterenko, 1951 Pl. 17, figs. 1-5.

1951 Fenestella praevirgosa Schulga-Nesterenko, p. 28, pl. 2, fig. 6, pl. 4, fig. 1. 1955 Fenestella praevirgosa Schulga-Nesterenko; Morozova, p. 28, pl. 3, fig. 1. 1967 Fenestella (Minilya) praevirgosa Schulga-Nesterenko; Kodsi, pp. 74-76, pl. 2, figs. 11, 12.

Material — Two colonies, RGM 211 520b and SMF 2688 (thin sections).

Description — Reticulate colonies with straight branches joined by relatively thick dissepiments. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, with eight peristomal nodes, 3-4 spaced per length of a

fenestrule. Shape of fenestrules varying from oval to slightly rectangular. Keel low, carrying two alternating rows of nodes. Internal granular skeleton thin, continuous with obverse keel, nodes, rods, peristome and across dissepiments. Outer lamellar skeleton moderately thick. No heterozooecia observed.

Interior: autozooecia rectangular to kidney-shaped in mid tangential section, low and elongated, with well developed vestibule; aperture positioned at distal to distal-abaxial end of chamber. Superior hemisepta long; inferior hemisepta long, separating the proximal third of the chamber.

	Ν	Х	SD	CV	MIN	MAX
branch width, mm	8	0.39	0.049	12.75	0.32	0.48
dissepiment width, mm	5	0.29	0.048	16.24	0.21	0.32
fenestrule width, mm	8	0.34	0.107	31.82	0.23	0.48
fenestrule length, mm	8	0.78	0.089	11.36	0.62	0.90
autozooecial aperture width, mm	4	0.09	0.005	5.55	0.08	0.09
aperture spacing along branch, mm	20	0.30	0.016	5.38	0.28	0.35
aperture spacing across branch, mm	10	0.36	0.021	5.76	0.32	0.37
distance between dissepiment centres, mm	5	1.06	0.098	9.22	0.92	1.15
distance between branch centres, mm	5	0.64	0.041	6.45	0.60	0.69
node width, mm	15	0.06	0.009	15.78	0.05	0.07
node spacing, mm	15	0.17	0.028	16.27	0.14	0.22
apertures per fenestrule length	8	3.38	0.518	15.34	3.00	4.00

Measurements -

Remarks — The present material is superficially similar to *Fenestella binodata* Condra, 1902, from the Pennsylvanian of Nebraska. However, the internal morphology of Condra's species is unknown.

Stratigraphic and geographic range — Russian Platform and Ukraine; Upper Carboniferous (Gzhelian). Localities 2 and 6 herein.

Fabifenestella? plummerae Moore, 1929

Pl. 17, figs. 6-8; Pl. 18, figs. 1, 2.

cf. 1929 Fenestella plummerae Moore, p. 19, pl. 2, figs. 11, 12.

cf. 1967 Fenestella (Minilya) plummerae Moore; Kodsi, p. 74, pl. 1, fig. 7.

Material - Two colonies, RGM 211 514b, 211 515b.

Description — Reticulate colonies with straight branches joined by relatively thick dissepiments. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, with eight peristomal nodes, two spaced per length of a fenestrule. Shape of fenestrules varying from oval to slightly rectangular. Keel low, carrying two weakly alternating rows of nodes. Heterozooecia in form of ovicells present (incomplete), spherical chambers, 0.18-0.23 mm in diameter.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	20	0.24	0.054	22.84	0.16	0.33
dissepiment width, mm	20	0.13	0.021	16.22	0.10	0.17
fenestrule width, mm	20	0.23	0.032	13.74	0.17	0.29
fenestrule length, mm	20	0.38	0.037	9.72	0.33	0.44
autozooecial aperture width, mm	10	0.06	0.006	11.10	0.05	0.07
aperture spacing along branch, mm	25	0.27	0.032	11.954	0.23	0.33
aperture spacing across branch, mm	25	0.23	0.043	18.74	0.18	0.30
distance between dissepiment centres, mm	20	0.53	0.060	11.22	0.44	0.66
distance between branch centres, mm	20	0.44	0.067	15.25	0.33	0.55
node width, mm	10	0.06	0.008	13.07	0.05	0.07
node spacing, mm	20	0.14	0.029	20.26	0.10	0.19

Remarks — The internal morphology of this species is unknown. Superficially, the present material is identical to *Fenestella (Minilya) plummerae* Moore, 1929, as redescribed by Kodsi (1967). It is also similar to the original description of Moore (1929). However, no ovicells were mentioned by either of the previous authors.

Stratigraphic and geographic range — Carnic Alps; Austria; Pennsylvanian. Texas, U.S.A.; Graham Formation, Pennsylvanian. Locality 6 herein.

Genus Ptiloporella Hall, 1885

Type species — Fenestella laticrescens Hall & Simpson, 1887, by original designation. Lower Devonian (Upper Heidelberg), U.S.A.

Ptiloporella? irregularis Nikiforova, 1938 Pl. 19, figs. 1-4.

cf. 1938 Ptiloporella irregularis Nikiforova, pp. 148-151, pl. 34, figs. 4-6, pl. 36, figs. 4, 5.

Material — Three measured colonies, RGM 211 507a, 211 519b, 211 535a, and numerous unmeasured fragments.

Description — Reticulate colonies consisting of wide main branches and frequently diverging secondary branches. Main branches 0.7-1.0 mm wide, secondary branches 0.28-0.45 mm wide. Secondary branches joined by dissepiments building oval fenestrules or fused together building trapezoid fenestrules. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular. Keel absent; two alternating rows of nodes on both main and secondary branches. No heterozooecia observed. Internal morphology unknown.

	Ν	X	SD	CV	MIN	MAX
secondary branch width, mm	10	0.37	0.048	13.10	0.28	0.45
fenestrule length, mm	10	0.95	0.174	18.37	0.56	1.20
fenestrule width, mm	10	0.69	0.158	22.10	0.48	0.94
distance between dissepiment centres, mm	8	1.27	0.149	11.77	1.06	1.47
distance between branch centres, mm	6	1.26	0.208	16.55	1.00	1.47
autozooecial aperture width, mm	20	0.08	0.009	10.78	0.07	0.09
aperture spacing along branch, mm	20	0.35	0.020	5.65	0.31	0.38
aperture spacing across branch, mm	20	0.38	0.022	5.72	0.33	0.42
node width, mm	15	0.08	0.009	11.14	0.07	0.09
node spacing, mm	15	0.19	0.029	14.77	0.16	0.26

Remarks — The present material is externally similar to *Ptiloporella irregularis* Nikiforova, 1938, from the Upper Carboniferous of the Urals, but the internal morphology cannot be compared as it is unknown in the present material. The diagnosis of *Ptiloporella* Hall, 1885, as given by Morozova (2001, p. 59) includes a single row of nodes on branches, which contradicts the description of *P. irregularis* by Nikiforova (1938).

Stratigraphic and geographic range – Lower Permian of Russia. Locality 6 herein.

Incertae familiae Genus *Cervella* Chronic *in* Newell, Chronic & Roberts, 1949

Type species — *Cervella cervoidea* Chronic *in* Newell *et al.*, 1949, by original designation; Lower Permian of Peru.

Cervella sp.

Pl. 18, figs. 3-6.

Material – Four colonies, RGM 211 515c, 211 520c, 211 524d, 211 530a.

Description — Reticulate colonies with straight branches joined by relatively thick dissepiments. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, with eight large peristomal nodes, two spaced per length of a fenestrule. Shape of fenestrules varying from oval to slightly rectangular. Keel wide and low, carrying a single row of large nodes, transformed to crucifix-shaped protecting structures. Heterozooecia absent. Reverse side covered by nodes arranged in 1-3 rows.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	20	0.26	0.052	20.43	0.17	0.36
dissepiment width, mm	20	0.13	0.022	17.24	0.08	0.18
fenestrule width, mm	30	0.33	0.044	13.68	0.18	0.39
fenestrule length, mm	30	0.44	0.049	10.95	0.36	0.54
aperture spacing along branch, mm	35	0.32	0.035	10.78	0.27	0.4
aperture spacing across branch, mm	20	0.27	0.032	11.91	0.22	0.34
distance between dissepiment centres, mm	25	0.57	0.058	10.15	0.48	0.69
distance between branch centres, mm	20	0.58	0.081	13.97	0.37	0.69
node width, mm	20	0.08	0.018	21.68	0.05	0.11
node spacing, mm	20	0.30	0.022	7.40	0.27	0.34

Remarks — The internal morphology of the present material is unknown. The genus *Cervella* was described on the basis of external characters (dendroid, crucifix-shaped protecting structures) and its internal morphology has never been studied. *Fenestella cruciformis latespinata* Ceretti, 1963, from the Pennsylvanian of the Carnic Alps is similar in the form of the protecting structures. However, it differs from the present material in having smaller fenestrules (average length 0.38 mm vs. 0.44 mm and width 0.26 mm vs. 0.33 mm).

Stratigraphic and geographic range — Locality 6.

"Fenestella" modesta Ulrich, 1890 Pl. 18, figs. 7, 8.

1890 Fenestella modesta Ulrich, p. 550, pl. 52, fig. 3.1906 Fenestella modesta Ulrich; Johnsen, p. 148, pl. 10, fig. 12.1963 Fenestella modesta Ulrich; Ceretti, pp. 267-269, pl. 23, fig. 1a, b.

Material - Single colony, RGM 211 514c.

Description — Reticulate colonies with straight branches joined by relatively thick dissepiments. Bifurcation common. Autozooecia arranged in two alternating rows on branches. Apertures circular, with eight peristomal nodes, 3-4 spaced per length of a fenestrule. Shape of fenestrules varying from oval to slightly rectangular. Keel narrow and moderately high, carrying a single row of moderately large nodes. Heterozooecia absent.

	NI	v	SD	CV	MIN	ΜΑΥ
	1	Λ	30	CV	IVIIIN	IVIAA
branch width, mm	5	0.23	0.041	17.54	0.20	0.28
dissepiment width, mm	10	0.14	0.011	7.92	0.13	0.16
fenestrule width, mm	10	0.41	0.039	9.54	0.35	0.46
fenestrule length, mm	8	0.64	0.042	6.56	0.58	0.70
autozooecial aperture width, mm	5	0.06	0.013	20.82	0.05	0.08
aperture spacing along branch, mm	10	0.25	0.021	8.22	0.21	0.28
aperture spacing across branch, mm	10	0.24	0.023	9.67	0.22	0.30
distance between dissepiment centres, mm	7	0.79	0.048	6.05	0.75	0.85
distance between branch centres, mm	5	0.62	0.027	4.42	0.6	0.65
node width, mm	5	0.06	0.011	17.67	0.05	0.07
node spacing, mm	5	0.35	0.018	5.25	0.32	0.37
apertures per fenestrule length	10	3.5	0.527	15.06	3.0	4.0

Remarks — The present specimen resembles superficially bryozoans described as *"Fenestella" modesta* Ulrich, 1890, from the Pennsylvanian of Illinois, Texas and the Carnic Alps. However, the internal structure in all of these specimens, including the present material, is unknown.

Stratigraphic and geographic range – Locality 6.

Family Septoporidae Morozova, 1962 Genus Septopora Prout, 1859

Type species — *Septopora cestriensis* Prout, 1859, by original designation; Mississippian, Illinois, U.S.A..

Septopora robusta Ulrich, 1890 Pl. 19, figs. 5-9.

1890 Septopora robusta Ulrich, p. 633, pl. 56, figs. 9, 9a-c, pl. 64, figs. 3, 3a-b.

Material — One colony, RGM 211 496 (thin sections).

Description — Reticulate colonies with straight branches joined by dissepiments. New branches appearing by transformation of dissepiments to new branches or by bifurcation of branches. Autozooecia arranged in two alternating rows on branches and dissepiments, opening on inside of the colony. Apertures circular to slightly oval, with low and thin peristomes, usually 4-5 spaced per length of a fenestrule. Shape of fenestrules varying from oval, narrow oval to rectangular and V-shaped. Obverse keel low, bearing small nodes. Abundant microacanthostyles on the reverse surface of the colony arranged in regular rows. Internal granular skeleton thick, well developed, continuous with obverse keel, nodes, microacanthostyles, rods, peristome and across dissepiments. Outer lamellar skeleton sometimes extremely thick, containing small hyaline rods. Cyclozooecia abundant, spaced throughout the colony, often overgrown by the outer lamellar skeleton. Interior: autozooecia rectangular in mid tangential section, relatively high and short in longitudinal section, with well developed vestibule; elongate, parallel to branch length; aperture positioned at distal to distal-abaxial end of chamber. Hemisepta absent.

Measurements —								
	Ν	X	SD	CV	MIN	MAX		
branch width, mm	15	0.74	0.114	15.409	0.60	0.90		
dissepiment width, mm	15	0.65	0.112	17.093	0.48	0.90		
fenestrule width, mm	15	0.52	0.185	35.466	0.22	0.90		
fenestrule length, mm	15	0.64	0.126	19.727	0.32	0.78		
autozooecial aperture width, mm	20	0.13	0.008	6.536	0.11	0.14		
aperture spacing along branch, mm	20	0.29	0.015	5.22	0.26	0.34		
aperture spacing across branch, mm	20	0.26	0.024	8.97	0.22	0.31		
distance between dissepiment centres, mm	15	1.09	0.106	9.66	0.93	1.35		
distance between branch centres, mm	14	1.13	0.256	22.72	0.81	1.44		
node width, mm	10	0.06	0.008	14.29	0.05	0.07		
node spacing, mm	7	0.35	0.042	12.11	0.29	0.42		
zooecial chamber width, mm	20	0.12	0.009	7.30	0.11	0.13		
apertures per fenestrule length	10	4.5	0.527	11.71	4.0	5.0		
branch thickness, mm	9	0.81	0.077	9.48	0.69	0.93		
cyclozooecia diameter, mm	20	0.080	0.007	8.45	0.070	0.095		

Remarks — *Septopora robusta* Ulrich, 1890, is similar to *S. luterkensis* Shishova, 1952, from the Podolsky horizon of the Moscow region, but differs in having thicker branches (0.60-0.90 mm vs. 0.35-0.60 mm).

Stratigraphic and geographic range — Illinois, U.S.A.; Pennsylvanian. Locality 5b herein.

Family Acanthocladiidae Zittel, 1880 Genus *Penniretepora* d'Orbigny, 1849 [= Acanthopora Young & Young, 1875; *Pinnatopora* Vine, 1884]

Type species — *Retepora pluma* Phillips, 1836, by original designation; Mississippian, Ireland.

Remarks — The genus *Penniretepora* generally includes pinnate bryozoans with two rows of autozooecia both on the main and lateral branches. Morozova (2001) specified the diagnoses of the genera *Penniretepora* and *Filites* with similar pinnate colony form and arrangement of autozooecia, but they are characterized by different internal morphology. However, there are many pinnate species which do not fit within these concepts and many others which were described without thin sections. Therefore, all the species described below are placed in the genus *Penniretepora*, albeit tentatively.

Penniretepora sp. 1 Pl. 20, figs. 1-4.

Material - Six colonies, SMF 2689-2692, RGM 211 516b, 211 534d.

Description — Straight main branch with commonly diverging secondary branches. Main branches 0.34-0.41 mm wide, secondary branches 0.28-0.35 mm wide. Apertures circular, arranged in two rows both on the main and secondary branches; 3-4 apertures in the space between the two neighbouring secondary branches. Keel low, undulating, developed on both the main branch and secondary branches. Small nodes present on the keel.

Interior: autozooecia rectangular to pentagonal in the mid tangential section. Long hemiseptum present, dividing distal third to half of the autozooecial chamber.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	6	0.37	0.033	8.99	0.34	0.41
lateral branch width, mm	10	0.31	0.031	10.28	0.28	0.35
lateral branch spacing, mm	10	1.07	0.087	8.21	0.94	1.20
lateral branch diverging angle	10	83.3	3.466	4.16	78.0	90.0
autozooecial aperture width, mm	10	0.090	0.006	7.52	0.075	0.095
aperture spacing along branch, mm	10	0.35	0.018	5.34	0.30	0.36
aperture spacing across branch, mm	11	0.28	0.026	9.18	0.23	0.30
zooecial chamber width, mm	6	0.13	0.008	6.37	0.12	0.14

Measurements (three colonies) -

Remarks — The present species is similar to *Penniretepora inconstans* Shishova, 1959, from the Podolsky horizon of the Moscow region in the shape of the autozooecia and the presence of long hemisepta. However, it differs in the presence of a monoserial keel with nodes, whereas *P. inconstans* possesses a triserial keel without nodes. Superficially, the present species is similar to the species *P. pluma* (Phillips, 1836) described by Olaloye (1974) from the Lower Carboniferous (Viséan) of Ireland. However, no internal structure of this species is known. It differs from the present species in having larger autozooecial apertures (on average 0.126 mm vs. 0.090 mm in present species) and more closely spaced lateral branches (on average 0.748 mm vs. 1.07 mm).

Stratigraphic and geographic range — Localities 2 and 6.

Penniretepora sp. 2

Pl. 20, figs. 5, 6.

Material — Single colony, RGM 211 524b.

Description — Straight main branch with frequently diverging secondary branches. Main branches 0.6 mm wide, secondary branches 0.38-0.45 mm wide. Apertures circular, arranged in two rows on both the main and secondary branches; three apertures in the space between the two neighbouring secondary branches. Keel low, undulating, developed only on the main branch. Large circular nodes present on the keel, closely spaced.

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	Ν	X	SD	CV	MIN	MAX
lateral branch width, mm	5	0.43	0.034	7.89	0.38	0.45
lateral branch spacing, mm	7	1.05	0.050	4.75	1.00	1.11
lateral branch diverging angle	8	68.88	6.534	9.49	59.00	80.00
autozooecial aperture width, mm	5	0.10	0.015	15.79	0.075	0.11
aperture spacing along branch, mm	10	0.34	0.009	2.77	0.33	0.35
aperture spacing across branch, mm	10	0.33	0.017	5.14	0.3	0.35
node width, mm	5	0.23	0.034	14.87	0.18	0.25
node spacing, mm	6	0.55	0.052	9.40	0.50	0.63

Remarks — The internal morphology of this species is unknown. No species of *Penniretepora* with similar morphology of the keel and nodes is known, but the available material is insufficient for establishing a new species.

Stratigraphic and geographic range — Locality 6.

Penniretepora sp. 3

Pl. 21, figs. 1, 2.

Material – Three colonies, RGM 211 502a, 211 509c, 211 522b.

Description — Straight main branch with frequently diverging secondary branches. Main branches 0.30-0.45 mm wide, secondary branches 0.20-0.30 mm wide. Apertures circular, arranged in two rows both on the main and secondary branches; two apertures in the space between the two neighbouring secondary branches. Keel low, triserial, undulating, developed only on the main branch. Nodes absent.

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	Ν	X	SD	CV	MIN	MAX
branch width, mm	3	0.37	0.076	20.83	0.30	0.45
lateral branch width, mm	11	0.25	0.041	16.66	0.20	0.30
lateral branch spacing, mm	15	0.76	0.045	6.00	0.70	0.83
lateral branch diverging angle	10	75.2	7.315	9.73	66.0	85.0
autozooecial aperture width, mm	6	0.05	0.004	8.45	0.04	0.05
aperture spacing along branch, mm	20	0.39	0.026	6.60	0.33	0.43
aperture spacing across branch, mm	20	0.31	0.038	12.39	0.23	0.38

Measurements –

Remarks — The present species is similar to *Penniretepora inconstans* Shishova, 1959, and *P. trilineata* Meek, 1872, in the shape of the keel and dimensions of the colony. However, the internal structure of the present material is unknown, prohibiting a closer comparison.

The present material is also similar to the species described as "*Penniretepora geometrica* Shishova (in coll.)" by Morozova (1955). However, there is confusion about this species. Morozova mentioned that the species was found by Shishova and should have a low triserial keel without nodes (Morozova, 1955, pp. 42, 43, pl. 6, fig. 4). However, Shishova (1959, p. 24, text-fig. 7) described the species as *"Penniretepora geometrica* (Morozova)," noting the monoserial keel with small nodes. The illustrations of both Morozova (1955) and Shishova (1959) fail to demonstrate the morphology of the keel because their tangential thin sections are too deep.

Stratigraphic and geographic range – Locality 6.

Penniretepora sp. 4 Pl. 22, figs. 1, 2.

Material — Two colonies, RGM 211 509d, 211 511d.

Description — Straight main branch with commonly diverging secondary branches. Main branches 0.41-0.50 mm wide, secondary branches 0.24-0.35 mm wide. Apertures circular, arranged in two rows both on the main and secondary branches; two apertures in the space between the two neighbouring secondary branches. Keel high, straight, 0.12-0.15 mm wide, developed on both main and secondary branches. Nodes long, thick, widely spaced on main branch; long and thin, closely spaced on secondary branches.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
branch width, mm	4	0.46	0.038	8.25	0.41	0.50
lateral branch width, mm	7	0.29	0.034	11.91	0.24	0.35
lateral branch spacing, mm	19	0.83	0.072	8.63	0.75	1.00
lateral branch diverging angle	9	72.89	7.623	10.46	60.00	86.00
aperture spacing along branch, mm	9	0.42	0.037	8.85	0.35	0.45
aperture spacing across branch, mm	5	0.30	0.035	11.79	0.25	0.35
node width, mm	4	0.14	0.017	12.83	0.12	0.15
node spacing, mm	11	0.84	0.050	5.96	0.75	0.91

Remarks — The internal morphology of this species is unknown. Superficially, the present material is similar to *P. oculata* (Moore, 1929) from the Graham Formation (Pennsylvanian) of Texas, especially because of high keel and relatively large nodes in the latter species. Another similar species is *P. normalis* Olaloye, 1974, from the Lower Carboniferous (Viséan) of Ireland. The internal structure of this species is also unknown. *Penniretepora frondiformis* differs from the present species in having wider lateral branches (0.428 mm vs. 0.290 mm on average in *P.* sp. 4), more closely spaced lateral branches (0.747 mm vs. 0.830 mm on average in *Penniretepora* sp. 4) and more closely spaced nodes on keel (0.445 mm vs. 0.840 mm on average in *Penniretepora* sp. 4).

Stratigraphic and geographic range – Locality 6.

Penniretepora sp. 5 Pl. 22, figs. 3, 4.

Material — Two colonies, RGM 211 525a, c.

Description — Frequently dichotomosing colonies with alternating secondary branches. Main branches 0.23-0.35 mm wide, secondary branches 0.17-0.30 mm wide. Apertures circular, arranged in two rows on both the main and secondary branches; 2-3 apertures in the space between the two neighbouring secondary branches. Keel high, straight, 0.07-0.10 mm wide, developed on both main and secondary branches. Nodes small, present on both main and secondary branches.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
branch width, mm	7	0.30	0.044	14.90	0.23	0.35
lateral branch width, mm	5	0.22	0.053	23.71	0.17	0.30
autozooecial aperture width, mm	4	0.080	0.020	25.27	0.067	0.110
aperture spacing along branch, mm	10	0.38	0.030	7.88	0.33	0.43
aperture spacing across branch, mm	10	0.26	0.035	13.42	0.22	0.33
node spacing, mm	3	0.24	0.023	9.49	0.23	0.27

Remarks — The internal morphology of this species is unknown. The present material is superficially similar to *P. bellula* (Ulrich, 1890) from the Pennsylvanian of Illinois (Ulrich, 1890, pp. 362, 619, pl. 66, figs. 8, 8a-b), which, however, differs in having a lower keel and more regular branching.

Stratigraphic and geographic range — Locality 1a.

Penniretepora cf. beresovensis Morozova, 1955 Pl. 21, figs. 3, 4.

cf. 1955 Penniretepora beresovensis Morozova, pp. 43, 44, pl. 6, fig. 1; text-figs. 14, 15.

cf. 1959 Penniretepora beresovensis Morozova; Shishova, text-fig. 8.

Material – Two colonies, RGM 211 501e, 211 509b.

Description — Straight main branch with frequently diverging secondary branches. Main branches 0.33-0.55 mm wide, secondary branches 0.23-0.35 mm wide. Apertures circular to oval, with eight nodes on a horseshoe-shaped peristome; arranged in two rows on both the main and secondary branches; two apertures in the space between the two neighbouring secondary branches. Keel high, straight, 0.11-0.17 mm wide, developed on both main and secondary branches. Nodes prominent, present on both main and secondary branches; spaced more closely on secondary branches.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	3	0.41	0.119	28.86	0.33	0.55
lateral branch width, mm	12	0.29	0.038	13.23	0.23	0.35
lateral branch spacing, mm	15	0.73	0.046	6.37	0.65	0.80
lateral branch diverging angle	10	78.8	6.161	7.82	72.0	89.0
autozooecial aperture width, mm	10	0.05	0.006	10.32	0.05	0.07
aperture spacing along branch, mm	13	0.31	0.019	6.18	0.27	0.34
aperture spacing across branch, mm	13	0.27	0.017	6.21	0.25	0.31
node width, mm	5	0.11	0.008	7.75	0.10	0.12
node spacing, mm	12	0.55	0.048	8.76	0.50	0.60

Remarks — The present species is superficially similar to *Penniretepora beresovensis* Morozova, 1955, from the Upper Carboniferous (Kasimovian) of Ukraine. Especially striking characters are the morphology of the medial keel with widely spaced nodes and peristomal nodes. *Penniretepora geometrica* Shishova *in* Morozova, 1955 (see 'Remarks' for *Penniretepora* sp. 3), from the Podolsky horizon (Pennsylvanian) of the Russian Platform (Moscow region) and *P. oculata* (Moore, 1929) from the Graham Formation (Pennsylvanian) of Texas are also similar in the shapes of keel and nodes as well as in colony dimensions. However, the internal morphology of the present material is unknown, preventing a closer comparison. Another similar species is *Penniretepora frondiformis* Olaloye, 1974, from the Mississippian (Viséan) of Ireland. The internal structure of this species is also unknown. *Penniretepora frondiformis* differs from the present species in having wider main branches (on average 0.734 mm vs. 0.410 mm in *P. cf. beresovensis*) and more closely spaced lateral branches (on average 0.655 mm vs. 0.730 mm).

Stratigraphic and geographic range – Locality 6.

Penniretepora cf. nodocarinata Richards, 1959 Pl. 23, figs. 1, 2.

cf. 1959 Penniretepora nodocarinata Richards, pp. 1116-1118, text-figs. A9, 10.

Material – Two colonies, RGM 211 510a, 211 533c.

Description —Main branches sinuous, zigzaging and with frequently diverging secondary branches. Main branches 0.41-0.50 mm wide, secondary branches 0.24-0.35 mm wide. Apertures circular, arranged in two rows both on the main and secondary branches; two apertures in the space between the two neighbouring secondary branches. Keel high, sharp, straight, 0.04-0.06 mm wide, developed on both main and secondary branches. Nodes prominent, observed only on main branches.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	5	0.42	0.039	9.23	0.37	0.46
lateral branch width, mm	7	0.31	0.016	5.05	0.30	0.34
lateral branch spacing, mm	8	1.09	0.084	7.66	0.96	1.23
aperture spacing along branch, mm	15	0.37	0.016	4.36	0.33	0.38
aperture spacing across branch, mm	15	0.29	0.022	7.62	0.27	0.35
node width, mm	9	0.13	0.008	6.07	0.12	0.14
node spacing, mm	12	0.59	0.028	4.67	0.53	0.64

Remarks — The present material is superficially similar to *Penniretepora nodocarinata* Richards, 1959, from the Lower Permian (Lower Wolfcampian) of Kansas. The latter species has rectangular autozooecia and possesses hemisepta. As the internal morphology of the investigated specimens is unknown, a closer comparison between the two species is not possible. Another similar species is *Penniretepora elegantula* (Etheridge, 1877) described by Olaloye (1974) from the Lower Carboniferous (Viséan) of Ireland. The internal structure of this species is also unknown, superficially it shows the same zigzag pattern and prominent nodes. However, the keel is absent in *P. elegantula*. *Penniretepora* cf. *nodocarinata* differs from *P. elegantula* also in having narrower lateral branches (on average 0.31 mm vs. 0.385 mm in *P. elegantula*).

Stratigraphic and geographic range — Locality 6.

Genus Polypora M'Coy, 1844

Type species — Polypora dendroides M'Coy, 1844, by subsequent designation (Vine, 1884, p. 194); Mississippian, Ireland.

Polypora remota Condra, 1902

Pl. 23, figs. 2-5; Pl. 24, figs. 1-5.

1902 Polypora remota Condra, pp. 353, 354, pl. 24, figs. 1, 2. 1963 Polypora triangularis subpolita Ceretti, p. 304, pl. 24, fig. 6a, b. 1999 Polypora sp. A; González & Suárez Andréz, p. 605, pl. 2, figs. 4-6. 2006 Polypora cf. remota Condra; Ernst & Minwegen, p. 582, fig. 6J-L.

Material — Two colonies, RGM 211 497, 211 525b (thin sections).

Description — Reticulate colony. Branches commonly bifurcating, 0.59-0.96 mm wide, joined by dissepiments. Autozooecia arranged in 3-4 rows on branches. Autozooecial apertures rounded, 6-9 spaced on fenestrule length. Autozooecia rhombic in mid tangential section. Both superior and inferior hemisepta absent. Fenestrules oval to rectangular in shape. Outer laminated skeleton moderately developed, containing abundant microstylets. Nodes absent; weak keels developed on obverse surface; microacanthostyles spaced irregularly on reverse surface.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	21	0.76	0.104	13.68	0.59	0.96
dissepiment width, mm	20	0.37	0.072	19.31	0.29	0.56
fenestrule width, mm	20	0.85	0.087	10.24	0.71	1.05
fenestrule length, mm	16	2.39	0.435	18.17	1.76	2.96
autozooecial aperture width, mm	20	0.11	0.011	10.78	0.09	0.13
aperture spacing along branch, mm	30	0.36	0.029	8.13	0.31	0.44
aperture spacing across branch, mm	30	0.27	0.023	8.75	0.22	0.30
distance between dissepiment centres, mm	20	2.84	0.477	16.84	1.76	3.28
distance between branch centres, mm	20	1.65	0.195	11.80	1.35	1.93
zooecial chamber width, mm	20	0.14	0.013	9.11	0.13	0.17
apertures per fenestrule length	17	7.8	1.074	13.73	6.0	9.0

Remarks — *Polypora remota* Condra, 1902, is similar to *P. gracilis* Prout, 1860, from the Mississippian of North America, but differs by having slightly wider stems (0.76 mm vs. 0.58 mm in *P. gracilis*), larger distances between aperture centres (1.65 mm vs. 1.33 mm) and smaller autozooecial chambers (maximum autozooecial chamber width 0.14 mm vs. 0.21 mm).

Stratigraphic and geographic range — Pennsylvanian; North America. Pennsylvanian; Carnic Alps, Italy. Spain, Picos de Europa Formation, Moscovian, Pennsylvanian; La Hermida; Playa de la Huelga, Calizas del Cuera, Upper Moscovian (Podolsky horizon), Pennsylvanian. Localities 1a and 4 herein.

Genus Paucipora Termier & Termier, 1971

Type species — Polypora hemiseptata Schulga-Nesterenko, 1951, by original designation; Pennsylvanian (Moscovian), Russian Platform.

Paucipora sp.

Pl. 25, figs. 1-7.

1999 Polypora sp. B; González & Suárez Andréz, pp. 605, 606, pl. 2, figs. 7-9.

Material - Single colony, RGM 211 495 (thin section).

Description — Reticulate colony. Branches commonly bifurcating, 0.54-0.90 mm wide, joined by dissepiments. Autozooecia arranged in 3-4 rows on branches. Autozooecial apertures rounded, 5-6 per fenestrule length. Autozooecia rhombic to hexagonal in mid tangential section. Both superior and inferior hemisepta present, long. Fenestrules oval to rectangular in shape, 1.72 mm long and 0.36-0.54 mm wide. Outer laminated skeleton moderately developed, containing abundant microstylets. Nodes irregularly spaced between apertures; weak keels developed on obverse colony surface; microacanthostyles spaced irregularly on reverse colony surface.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	15	0.71	0.130	18.19	0.54	0.90
dissepiment width, mm	6	0.42	0.100	24.18	0.32	0.60
fenestrule width, mm	5	0.45	0.065	14.59	0.36	0.54
autozooecial aperture width, mm	20	0.11	0.007	6.37	0.095	0.12
aperture spacing along branch, mm	20	0.33	0.032	9.76	0.26	0.37
aperture spacing across branch, mm	20	0.23	0.015	6.48	0.19	0.25
distance between branch centres, mm	15	1.02	0.142	13.91	0.87	1.35
node width, mm	20	0.060	0.013	20.98	0.035	0.090
node spacing, mm	6	0.27	0.061	22.71	0.20	0.37
zooecial chamber width, mm	12	0.140	0.007	4.84	0.125	0.145
branch thickness, mm	10	0.79	0.045	5.68	0.72	0.87

Remarks — The present material is too fragmentary for a comprehensive comparison. *Paucipora krasnopolsky* (Stuckenberg, 1895) from the Gzhelian of northern Urals is generally similar, differing in having slightly shorter fenestrules (0.875-1.125 mm vs. 1.72 mm in the present material) and 4-5 apertures per fenestrule length instead of 5-6 in the present material.

Stratigraphic and geographic range — Locality 5a.

Genus Thamniscus King, 1849

Type species — *Thamniscus perplexus* Ernst *in* Lisitsyn & Ernst, 2004; *pro Thamniscus dubius* King, 1849, *non Keratophytes dubius* Schlotheim, 1820, subsequently designated by Ernst (*in* Lisitsyn & Ernst, 2004); Middle Permian (Zechstein), Germany.

Remarks — The real specific composition of the genus *Thamniscus* is unknown because many species have been included in it only on the basis of external characters. The species "*Thamniscus*" octonarus Ulrich, 1890, described below, does not belong to *Thamniscus sensu stricto*, because it lacks cyclozooecia which are characteristic of *Thamniscus*. It is placed in *Thamniscus* with reservation, because it shows some similarities and its real generic assignment is unknown. Also, the material is unsuitable for creating a new genus.

"Thamniscus" octonarus Ulrich, 1890 Pl. 26, figs. 1-4.

cf. 1890 Thamniscus octonarus Ulrich, p. 611, pl. 61, figs. 7, 7a, 7b.

Material — Three colonies, RGM 211 523b, 211 529c, 211 536d.

Description — Branched, freely dichotomizing colonies. Branches 0.50-0.65 mm wide. Autozooecia arranged in 3-5 rows. Large nodes irregularly spaced on obverse colony surface. Autozooecial apertures circular, often bearing ovicells in the form of hemispherical chambers, 0.09-0.12 mm in diameter.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	8	0.57	0.051	8.90	0.50	0.65
autozooecial aperture width, mm	20	0.065	0.011	16.90	0.050	0.085
aperture spacing along branch, mm	20	0.34	0.047	13.82	0.25	0.43
aperture spacing across branch, mm	20	0.23	0.024	10.31	0.20	0.28
ovicell diameter, mm	12	0.13	0.027	20.06	0.09	0.19
node width, mm	10	0.07	0.010	13.32	0.05	0.09

Remarks — The present material is identical with the species described as *Thanniscus octonarus* Ulrich, 1890, from the Pennsylvanian of Kansas. However, the internal structure of both bryozoans is unknown, so that their closer comparison and assignment among known taxa are not possible. Furthermore, the species *T. pinnatus* Condra, 1902, from the Coal Measures of Nebraska has the same type of ovicells, but a pinnate colony shape and thicker branches (1-2 mm vs. 0.50-0.65 mm in the present material). It should be noted that species of *Acanthocladia, Penniretepora, Synocladia* and *Kalvariella* from the Zechstein (Upper Permian) of Europe also reveal the same ovicell type as "*T.*" *octonarus* Ulrich, 1890 (Southwood, 1985; Ernst, 2001).

Stratigraphic and geographic range – Pennsylvanian? of Kansas, U.S.A.. Locality 6 herein.

Fenestellida sp. indet. 1-1 Pl. 27, figs. 1-3.

Material - Five colonies, RGM 211 513d, 211 523c, , 211 526e, 211 530c, d.

Description — Branched colonies. Branches freely dichotomizing, 0.43-0.83 mm wide. Autozooecia arranged in 4-6 alternating rows. Autozooecial apertures circular to oval. Large nodes irregularly spaced on the colony surface. Smaller nodes (microacanthostyles?) on the colony surface and in the peristomes of autozooecial apertures. Heterozooecia (cyclozooecia?) irregularly spaced between autozooecia on the obverse colony surface. Fine ribs covering the colony surface.

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	Ν	X	SD	CV	MIN	MAX
branch width, mm	7	0.67	0.129	19.31	0.43	0.83
autozooecial aperture width, mm	30	0.095	0.013	13.38	0.07	0.12
aperture spacing along branch, mm	30	0.49	0.093	18.86	0.38	0.66
aperture spacing across branch, mm	30	0.26	0.023	8.54	0.21	0.31
node width, mm	6	0.12	0.017	13.95	0.10	0.14
node spacing, mm	3	0.61	0.042	6.79	0.58	0.66
cyclozooecia diameter, mm	20	0.061	0.008	13.71	0.046	0.075

Measurements –

Remarks – Fenestellida sp. indet. 1-1 is superficially similar to Thamniscus perplexus

Ernst *in* Lisitsyn & Ernst, 2004, from the Upper Permian (Zechstein) of Europe. The two species share such characters as a branched colony shape, nodes and, apparently, the same type of heterozooecia. However, the internal morphology of the Spanish material is unknown.

Stratigraphic and geographic range — Localites 1a and 6.

Fenestellida sp. indet. 1-2

Pl. 27, figs. 4, 5; Pl. 28, fig. 1.

Material – Single colony, RGM 211 534c.

Description — Colony consisting of straight branches. Dichotomy not observed. Branch 0.80-0.82 mm wide. Very short, rudimentary secondary branches arranged in quincunx. Autozooecia arranged in two rows, apertures circular. Single heterozooecium (cyclozooecium?) situated between two neighbouring autozooecia longitudinally. Heterozooecial apertures 0.06-0.07 mm in diameter. Nodes absent.

Measurements –

	Ν	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	5	0.097	0.004	3.95	0.093	0.100
aperture spacing along branch, mm	10	0.31	0.019	6.27	0.28	0.34
aperture spacing across branch, mm	10	0.26	0.021	7.82	0.24	0.30

Remarks — The internal morphology of this species is not known. The species *Acanthocladia fruticosa* Ulrich, 1890 (pl. 65, figs. 2, 2a-c), from the Pennsylvanian of Illinois, shows a similar arrangement of heterozooecia, but has distinct main stems with rows of autozooecia and secondary stems with 2-3 rows of autozooecia.

Stratigraphic and geographic range — Locality 6.

Fenestellida sp. indet. 2 Pl. 28, figs. 2-4.

Material - Single colony, RGM 211 500a.

Description — Branched pinnate colonies. Main branch 1.06-1.20 mm wide; secondary branches 0.53-0.58 mm wide. Autozooecia arranged in two irregular rows. Autozooecial apertures circular, surrounded by 13-16 peristomal nodes. Heterozooecia absent. Prominent nodes on the obverse side, arranged in one row between rows of autozooecial apertures. Keels absent. Colony surface covered with fine ribs.

	Ν	X	SD	CV	MIN	MAX
main branch width, mm	2	1.13	0.099	8.76	1.06	1.20
lateral branch width, mm	4	0.55	0.024	4.32	0.53	0.58
lateral branch spacing, mm	3	1.38	0.104	7.52	1.30	1.50
autozooecial aperture width, mm	10	0.13	0.012	9.14	0.12	0.15
aperture spacing along branch, mm	10	0.48	0.042	8.81	0.42	0.53
aperture spacing across branch, mm	10	0.45	0.046	10.10	0.37	0.53
node width, mm	6	0.14	0.017	11.95	0.12	0.17
node spacing, mm	5	0.71	0.051	7.11	0.65	0.78

Remarks — The internal morphology of this species is not known. The arrangement of autozooecia is similar in various *"Penniretepora"* species, but no externally similar species are known.

Stratigraphic and geographic range — Locality 6.

Fenestellida sp. indet. 3

Pl. 28, figs. 5, 6; Pl. 29, fig. 1.

Material — Nine colonies, RGM 211 500c, 211 501f, 211 531a, b, c, 211 532c, 211 533d, 211 535b, c.

Description — Branched colonies. Branches freely dichotomizing, irregularly joined by thin dissepiments, 0.66-1.35 mm wide. Autozooecia arranged in 5-7 alternating rows. Autozooecial apertures circular to oval, often having long peristomes. Heterozooecia absent. Prominent nodes on the reverse side, arranged in one row, 0.25-0.40 mm in diameter.

Measurements -

	Ν	Х	SD	CV	MIN	MAX
branch width, mm	13	1.04	0.214	20.54	0.66	1.35
autozooecial aperture width, mm	30	0.10	0.015	14.92	0.08	0.13
aperture spacing along branch, mm	35	0.57	0.088	15.44	0.42	0.75
aperture spacing across branch, mm	35	0.32	0.066	20.48	0.22	0.47

Remarks — The internal morphology of this species is not known, but externally it is similar to various species described under the name "*Thamniscus*" from the Palaeozoic worldwide.

Stratigraphic and geographic range – Locality 6.

Fenestellida sp. indet. 4

Pl. 29, figs. 2,3.

Material - Single colony, RGM 211 511e.

Description — Colony consisting of straight branches. Dichotomy not observed. Branches 0.94-1.12 mm wide. Very short, rudimental secondary branches arranged in quincunx. Autozooecia arranged in two rows. Autozooecial apertures circular. Heterozooecia, nodes and keels absent.

Measurements —						
	Ν	X	SD	CV	MIN	MAX
branch width, mm	3	1.04	0.092	8.81	0.94	1.12
lateral branch spacing, mm	5	1.25	0.149	11.89	1.06	1.47
autozooecial aperture width, mm	10	0.11	0.016	15.06	0.09	0.12
aperture spacing along branch, mm	10	0.53	0.051	9.62	0.47	0.62
aperture spacing across branch, mm	10	0.43	0.033	7.77	0.38	0.47

Remarks — The internal morphology of this species is not known. The arrangement of autozooecia in general resembles "*Penniretepora*" species, but no closely similar species are known.

Stratigraphic and geographic range – Locality 6.

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Suborder Phylloporinina Lavrentjeva, 1979 Family Chasmatoporidae Schulga-Nesterenko, 1955 Genus Bashkirella Nikiforova, 1939

Type species — Bashkirella ornata Nikiforova, 1939, by original designation; Lower Permian (Sakmarian), Bashkiria (Russia).

Bashkirella minor sp. nov.

Pl. 29, figs. 4, 5; Pl. 30, figs. 1-4.

Derivation of the name — The name refers to the small size of this species (from Latin *minor*, the smaller).

Type material — Holotype, SMF 2694; paratypes, SMF 2693, RGM 211 526b.

Type locality — Section Villafeliz (Ernst *et al.*, 2005), northern Spain.

Type horizon — The uppermost part of the Valdeteja Formation or the lower part of the San Emiliano Formation (both Marsdenian–Langsettian, upper Bashkirian to lower-most Vereisky) (Locality 2).

Material – Six colonies, RGM 211 519c, 211 523e, 211 527b.

Diagnosis — Narrow branches producing reticulate colony by fusion (anastomosis); 2-3 rows of autozooecia on branches; diaphragms and hemisepta absent.

Description — Reticulate colonies, produced by fusion of branches. Autozooecia long, growing from a medial axis, opening in 2-3 alternating rows on the obverse branch

surface. Autozooecial apertures oval. Paurostyles abundant, arranged in 2-3 rows between autozooecial apertures. Diaphragms and hemisepta absent.

	Ν	X	SD	CV	MIN	MAX
branch width, mm	10	0.49	0.077	15.56	0.40	0.63
autozooecial aperture width, mm	10	0.12	0.015	12.81	0.10	0.14
aperture spacing along branch, mm	10	0.49	0.052	10.79	0.40	0.57
aperture spacing across branch, mm	10	0.26	0.030	11.75	0.21	0.30

Remarks — The new species differs from all known species of *Bashkirella* by its small dimensions. Bashkirella bifurcata (Gorjunova, 1966) from the Middle Devonian of the Caucasus is similar, but the autozooecia are arranged in 4-5 rows on the branch in B. bifurcata vs. 2-3 rows in B. minor sp. nov.

Stratigraphic and geographic range — Localities 1a, 2, 3 and 6.

Family Chainodictyonidae Schulga-Nesterenko, 1955 Genus Rhombocladia Rogers, 1900

Type species – Rhombocladia delicata Rogers, 1900, by original designation. Lower part of the Pennsylvanian (Upper Coal Measures), Kansas, U.S.A..

Rhombocladia delicata Rogers, 1900

Pl. 30, figs. 5, 6.

1900 Rhombocladia delicata Rogers, p. 12, pl. 1, fig. 1a-d. pars 1906 Rhombocladia delicata Rogers; Johnsen, p. 58, pl. 11, fig. 30a [? non 30b]. pars 1929 Rhombocladia delicata Rogers; Moore, p. 149, pl.17, figs. 26-28, 30,31 [non 29, 32]. 1963 Rhombocladia delicata Rogers form A; Ceretti, p. 327, pl. 6, fig. 10. 1964 Rhombocladia delicata Rogers; Ceretti, pp. 184, 185, pl. 33, fig. 2a, b, 4a, b. 2003 Rhombocladia delicata Rogers; Ernst, pp. 63, 64, pl. 5, figs. 4-7; text-fig. 3.

Material - Two colonies, RGM 211 502b, 211 510b.

Description - Branches 1.68 mm wide. Oval apertures arranged diagonally in five to eight rows. Microacanthostyles arranged in two to three rows between apertures, up to 0.02 mm in diameter. Single macroacanthostyle between two neighbour apertures in the longitudinal row, 0.04-0.07 mm in diameter. Heterozooecia absent.

Measurements — Ν X SD CV MIN MAX 10 autozooecial aperture width, mm 0.14 0.016 11.71 0.11 0.17 aperture spacing along branch, mm 0.47 0.035 7.56 0.43 0.53 10 aperture spacing across branch, mm 10 0.26 0.028 0.21 0.30 10.60 macroacanthostyle diameter, mm 8 0.06 0.009 14.70 0.04 0.07

Monsuromonts _

Remarks — *Rhombocladia delicata* Rogers, 1900, is similar to *R. dichotoma* (M'Coy, 1844) in the presence of different types of styles (microacanthostyles and larger acanthostyles), but the latter species differs in having long superior hemisepta.

Stratigraphic and geographic range — Kron Alpe (Monte Corona), Carnic Alps (Austria); Pennsylvanian, Corona Formation (Lower Gzhelian). Auernig, Carnic Alps (Udine, Italy); Auernig Formation (Lower Gzhelian). Pennsylvanian; Kansas, U.S.A. Locality 6 herein.

Rhombocladia carnica Ceretti, 1964 Pl. 31, figs. 1-5.

1964 Rhombocladia carnica Ceretti, pp. 186, 187, pl. 33, fig. 3a, b.

Material — Five colonies, SMF 2695-2699.

Description — Branches 0.63-0.96 mm (0.77 mm on average) wide and 0.20-0.40 mm thick in their middle part, hemielliptical in cross-section. Oval apertures arranged diagonally in three to five rows. Autozooecial chambers long, bending gently to the colony surface, becoming rhombic in deeper tangential section, appearing rhombic to hexagonal in cross-section. Superior hemisepta short, curved proximally. Diaphragms rare. Single macroacanthostyle between two neighbouring apertures in a longitudinal row, 0.025-0.040 mm in diameter. Microacanthostyles arranged uniserially between apertures, up to 0.02 mm in diameter. Walls 0.01 mm thick in the endozone, 0.07-0.10 mm thick in the exozone.

Measurements -

	Ν	X	SD	CV	MIN	MAX
branch width, mm	4	0.77	0.152	19.87	0.63	0.96
autozooecial aperture width, mm	6	0.12	0.005	4.19	0.12	0.13

Remarks — *Rhombocladia carnica* Ceretti, 1964, differs from other species of *Rhombocladia* by having narrower branches with 3-5 rows of autozooecia. It is morphologically similar to *R. delicata* in the presence of macroacanthostyles and microacanthostyles as well as hemisepta, but differs in the arrangement of autozooecia in 3-5 rows instead of the 5-8 of *R. delicata* and also in having smaller apertures (average width 0.12 mm vs. 0.14 mm).

Stratigraphic and geographic range — Auernig, Carnic Alps (Udine, Italy); Auernig Formation (Lower Gzhelian). Locality 2 herein.

Palaeobiogeography

Bryozoa have a high potential for applications in palaeobiogeography and biostratigraphy in the Palaeozoic (Ross, 1981; Ross & Ross, 1985, 1987, 1996; Bancroft, 1987). The bryozoan faunas from the Pennsylvanian of the Cantabrian Mountains show com-

Table 1.	Distribution	of bry	vozoans in	the inve	stigated	localities

a ·		-			-	6
Species	1	2	3	4	5	6
Fistulipora multivesiculata Morozova, 1955						x
Fistulipora micidolamina McKinney, 1972		x				x
Fistulipora cf. elegans Schulga-Nesterenko, 1955						x
Eridopora sp. 1				x		x
Eridopora sp. 2						x
Fistuliporid sp. indet.						x
Prismopora digitata Crockford, 1957						x
Cystocladia hispanica Ernst & Minwegen, 2006						x
Ramiporidra minuta (Schulga-Nesterenko, 1933)		x				
Sulcoretepora lophodes Condra, 1902	x					x
Leioclema? sp.						x
Crustopora? sp.						x
Stenophragmidium paramirandum Ernst, Schäfer & Reijmer, 2005						x
Tabulipora cf. demissa Trizna, 1961						x
Trepostomata sp. indet. 1		x				x
Trepostomata sp. indet. 2		x				
Pseudorhabdomeson bispinatum (Schulga-Nesterenko, 1955)		x				
Asconora sp					x	
Strehlotrung (Strehlotrung) neculiaris sp. nov	x					x
Streblotryng (Streblasconorg) cf. densa (Morozova, 1955)						x
Streblatruma (Streblasconora) sp. 1						x
Streblatrung (Streblascoporg) sp. 2						×
Clausetrung monticola (Fichwald, 1860)	v	v		v		~ ~
Rhowhonorg lenidodendroides Mook 1872	x	~		~		×
Rhomboporu teptuouenurbiues Nieck, 1672						~
Rhombopora corticata Moore, 1929						X
NibiGeneralle en	X	X	X			X
$\frac{Nikiforobellu \text{ sp.}}{1 - \frac{1}{2}}$	x	x				
Laxifenestella? filistriata (Ufrich, 1890)		x				x
Spinofenestella subspeciosa (Schulga-Nesterenko, 1955)					x	x
Fabifenestella praevirgosa (Schulga-Nesterenko, 1951)		x				x
Fabifenestella? plummerae Moore, 1929						x
Ptiloporella irregularis Nikiforova, 1939						x
Cervella sp.						x
"Fenestella" modesta Ulrich, 1890						x
Septopora robusta Ulrich, 1890					x	
Penniretepora sp. 1		x				x
Penniretepora sp. 2						x
Penniretepora sp. 3						x
Penniretepora sp. 4						x
Penniretepora sp. 5	x					
Penniretepora cf. beresovensis Morozova, 1955						x
Penniretepora cf. nodocarinata Richards, 1959						x
Polypora remota Condra, 1902	x			x		
Paucipora sp.					x	
"Thamniscus octonarus" Ulrich, 1890						x
Fenestellida sp. indet. 1-1	x					x
Fenestellida sp. indet. 1-2						x
Fenestellida sp. indet. 2						x
Fenestellida sp. indet. 3						x
Fenestellida sp. indet. 4						x
Bashkirella minor sp. nov.		x	x			x
Rhombocladia delicata Rogers, 1900						x
Rhombocladia carnica Ceretti, 1964		x				
	1		1	1	1	1



plex palaeobiogeographic connections. We have identified 54 bryozoan species from six localities (Table 1). These faunas show the most striking similarity to the Pennsylvanian of North America, supporting the Iberian-Midcontinent Seaway suggested by Vai in 2003 (see Fig. 3). Nine species are known from different localities in U.S.A.: *Fistulipora micidolamina* McKinney, 1972; *Sulcoretepora lophodes* (Condra, 1902); *Rhombopora corticata* Moore, 1929; *Rhombopora lepidodendroides* Meek, 1872; *"Fenestella" modesta* Ulrich, 1890; *Fabifenestella? plummerae* Moore, 1929; *Polypora remota* Condra, 1902; *Septopora robusta* Urlich, 1890; and *Rhombocladia delicata* Rogers, 1900. Two species are assumed to be similar with North American species, *Rhombopora* cf. *tenuimuralis* Ulrich, 1890, and *Laxifenestella? filistriata* (Ulrich, 1890).

Six species are known from the Upper Carboniferous of the Russian Platform: *Fistulipora multivesiculata* Morozova, 1955; *Ramiporidra minuta* (Schulga-Nesterenko, 1933); *Pseudorhabdomeson bispinatum* (Schulga-Nesterenko, 1955); *Clausotrypa monticola* (Eichwald, 1860); *Fabifenestella praevirgosa* (Schulga-Nesterenko, 1951); and *Ptiloporella irregularis* (Nikiforova, 1938). *Streblotrypa* (*Streblascopora*) cf. *densa* (Morozova, 1955) is compared with *S.* (*Streblascopora*) *densa* (Morozova, 1955) from the Upper Carboniferous of Ukraine. *Clausotrypa monticola* (Eichwald, 1860), *Rhombocladia delicata* Rogers, 1900, and *R. carnica* Ceretti, 1964, are also known from the Pennsylvanian of the Carnic Alps of Austria and Italy (Cetretti, 1964; Ernst, 2003). *Ramiporidra minuta* (Schulga-Nesterenko, 1933) and *Clausotrypa monticola* (Eichwald, 1860) are known from the Pennsylvanian of Spitsbergen (Nakrem, 1994).

In general, our results coincide with those on other groups, like poriferans and cor-

als. Garcia-Bellido & Rodrigez (2005) maintained high palaeobiogeographical correlations of the Late Carboniferous poriferan and coral faunas from the Iberian Peninsula to contemporary faunas of the American Midcontinent. They suggested, therefore, the presence of the Iberian-Midcontinent Seaway supporting the palaeogeographical reconstruction of Pangaea by Vai (2003) (Fig. 3). Beside this connection, a strong similarity to the Russian Platform is also evident. Relatively few species are shared with the Carnic Alps, although these territories seem to be closely situated during the Pennsylvanian. It can be explained by existence of barriers (depth, currents) between the two areas or, perhaps, by the fact that the bryozoans studied from the Carnic Alps are generally younger than the material from Spain described in this paper. It should be noted that there are close connections between the Carnic Alps and the Cantabrian Mountains (both considered to belong to the western Palaeotethys) during the upper Pennsylvanian when, for example, the fusulinids (e.g., Villa *et al.*, 2002, 2003; Villa & Wahlman, 2007a), algae (Mamet & Villa, 2004) and brachiopods (Winkler Prins, 1983; Martínez Chacón *et al.*, 2007) are concerned.

It is a pity that the bryozoans from the late Bashkirian or early Moscovian reef mounds of the Hare Fiord Formation of Ellesmere Island apparently have not yet been described, since the brachiopods of this formation (see Carter & Poletaev, 1998) are closely comparable to those from similar Bashkirian/Moscovian limestones (e.g., the Valdeteja Formation) of the Cantabrian Mountains (e.g., Winkler Prins, 2007; Martínez Chacón & Bahamonde, 2008). Since these two faunas are more closely related than either of them with the faunas from the Urals, it seems likely that the connection was through a branch of the Iberian-Midcontinent Seaway rather than through the Urals Seaway (Fig. 3), as has been suggested (e.g., Martínez Chacón & Winkler Prins, 2007). It would have been interesting to know whether bryozoan data could support this.

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Figs. 1, 2. *Fistulipora multivesiculata* Morozova, 1955, RGM 211 499a. (1) Massive colony. (2) Colony surface with apertures.

Figs. 3-5. *Fistulipora micidolamina* McKinney, 1972.Fig. 3. RGM 211 508a, colony surface.Fig. 4. RGM 211 517b, apertures with lunaria.Fig. 5. Locality 2, SMF 2641, longitudinal thin section.

Figs. 6, 7. *Fistulipora* cf. *elegans* Schulga-Nesterenko, 1955.Fig. 6. RGM 211 516c, massive colony.Fig. 7. RGM 211 505a, colony surface with apertures and lunaria.

Fig. 8. Eridopora sp. 1, RGM 211 521a, encrusting colony.

All specimens from Locality 6 unless stated otherwise.



Figs. 1-3. *Eridopora* sp. 1.Fig. 1. RGM 211 511a, colony surface with apertures.Figs. 2, 3. RGM 211 497f, Locality 4. (2) Tangential thin section. (3) Longitudinal thin section.

Fig. 4. Eridopora sp. 2, RGM 211 517a, colony surface with apertures and lunaria.

Figs. 5, 6. Fistuliporid sp. indet., RGM 211 505b, colony surface with apertures and hemiphragms (arrows).

Figs. 7, 8. Prismopora digittata Crockford, 1957, RGM 211 533a.

All specimens from Locality 6 unless stated otherwise.



Figs. 1-3. *Prismopora digittata* Crockford, 1957.Fig. 1. RGM 211 498a, fragment of the colony with lobes.Fig. 2. RGM 211 501b, colony surface with apertures and lunaria.Fig. 3. RGM 211 503a, fragment of the lobe showing autozooecia and vesicular skeleton.

Figs. 4-6. *Cystocladia hispanica* Ernst & Minwegen, 2006. Fig. 4. RGM 211 520a. Figs. 5, 6. RGM 211 511c.

All specimens from Locality 6.

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Figs. 1-6. *Ramiporidra minuta* (Schulga-Nesterenko, 1933), Locality 2.
Fig. 1. SMF 2645, main branch with secondary branches.
Fig. 2. SMF 2644, longitudinal section of the branch.
Fig. 3. SMF 2646, longitudinal section of the branch.
Figs. 4, 5. SMF 2643, cross sections of the branch.
Fig. 6. SMF 2644, tangential section of the branch.

Figs. 7-9. Sulcoretepora lophodes (Condra, 1902).

Figs. 7, 8. Locality 1b, RGM 211 528a. (7) Fragment of the colony. (8) Colony surface.

Fig. 9. Locality 6, RGM 211 501a, colony surface.



Figs. 1-3. Sulcoretepora lophodes (Condra, 1902).

Figs. 1, 2. RGM 211 533b, cross section, showing autozooecia with hemisepta (arrow), mesotheca and vesicular skeleton.

Fig. 3. RGM 211 534a, view of autozooecia with hemisepta (arrows).

Figs. 4, 5. Leioclema? sp., RGM 211 521b, encrusting colony.

Fig. 6. Crustopora? sp., RGM 211 518a, fragment of a branched colony.

All specimens from Locality 6.



Figs. 1, 2. *Crustopora*? sp., RGM 211 532a. (1) Colony surface with a macula. (2) Colony surface showing apertures, heterozooecia and acanthostyles.

Figs. 3-5. Stenophragmidium paramirandum Ernst, Schäfer & Reijmer, 2005.

Fig. 3. RGM 211 522a, encrusting colony.

Fig. 4. RGM 211 522a, colony surface showing apertures and hemiphragms.

Fig. 5. RGM 211 519a, colony surface with acanthostyles.

Figs. 6, 7. Tabulipora cf. demissa Trizna, 1961.

Fig. 6. RGM 211 505c, colony surface with apertures, ring septa, acanthostyles and microacanthostyles. Fig. 7. RGM 211 513a, colony fragment with ring septa.

All specimens from Locality 6.


Fig 1. Tabulipora cf. demissa Trizna, 1961, RGM 211 505c, colony surface with ring septa and acanthostyles.

Figs. 2-6. Trepostomata sp. indet. 1. Figs 4-6 from Locality 2.

Figs. 2, 3. RGM 211 514a. (2) Spherical massive colony. (3) Fragment of the colony surface with autozooecial apertures, exilazooecia and acanthostyles.

Figs. 4, 5. SMF 2648. (4) Tangential thin section, showing autozooecial apertures, acanthostyles and exilazooecia. (5) Longitudinal section through an encrusting colony.

Fig. 6. SMF 2649, longitudinal section of an autozooecium showing spoon-like hemiphragm (arrow).

All specimens from Locality 6 unless stated otherwise.



Figs. 1, 2. Trepostomata sp. indet., SMF 2649. (1) Longitudinal section of an autozooecium showing spoon-like hemiphragms (arrow). (2) Close-up of a spoon-like hemiphragm.

Figs. 3-6. Trepostomata sp. indet. 2.

Fig. 3. SMF 2654, longitudinal section of an encrusting colony.

Figs. 4, 5. SMF 2653, tangential sections showing autozooecial apertures, acanthostyles, exilazooecia and stylets.

Fig. 6. SMF 2658, tangential thin section.

Figs. 7, 8. *Pseudorhabdomeson bispinatum* (Schulga-Nesterenko, 1955), SMF 2660, tangential thin section showing autozooecial apertures, macroacanthostyles and microacanthostyles.

All specimens from Locality 2.



Figs. 1, 2. Pseudorhabdomeson bispinatum (Schulga-Nesterenko, 1955), Locality 2.

Fig. 1. SMF 2665, branch cross section.

Fig. 2. SMF 2660, branch longitudinal section.

Figs. 3, 4. Ascopora sp., Locality 5a, RGM 211 495, oblique sections of branch.



Figs. 1, 2. *Ascopora* sp., Locality 5a, RGM 211 495. (1) Longitudinal section of branch showing hemisepta. (2) Oblique section of branch showing autozooecial apertures, macroacanthostyles and microacanthostyles.

Figs. 3-7. Streblotrypa (Streblotrypa) peculiaris sp. nov.

Figs. 3-5. Locality 6.

Fig. 3. Holotype, RGM 211 513b.

Fig. 4. RGM 211 529a, colony branch.

Fig. 5. RGM 211 534b, internal view of a broken branch.

Figs. 6, 7. Locality 2.

Fig. 6. Paratype SMF 2671, longitudinal section of branch.

Fig. 7. SMF 2667, tangential section of branch, showing autozooecial aperture and metazooecia.



Fig. 1. *Streblotrypa* (*Streblotrypa*) *peculiaris* sp. nov., Locality 2, paratype SMF 2669, cross section of the branch.

Figs. 2-4. Streblotrypa (Streblascopora) cf. densa (Morozova, 1955).

Fig. 2. RGM 211 516d, internal view of a broken branch.

Fig. 3. RGM 211 536a, basal part of a branched colony.

Fig. 4. RGM 211 516d, colony surface showing autozooecial apertures and metazooecia.

Figs. 5, 6. Streblotrypa (Streblascopora) sp. 1, RGM 211 524c.

Figs. 7, 8. *Streblotrypa* (*Streblascopora*) sp. 2, RGM 211 520d. (7) Fragment of the branched colony. (8) Colony surface showing autozooecial apertures and metazooecia.

All specimens from Locality 6 unless stated otherwise.



Figs. 1-3. *Clausotrypa monticola* (Eichwald, 1860). Fig. 1. RGM 211 516a fragment of the branched colony. Figs. 2, 3. Locality 4, RGM 211 497, oblique sections of branches.

Figs. 4-6. *Rhombopora lepidodendroides* Meek, 1872, Locality 1b, RGM 211 528b. (4) Fragment of the branched colony. (5) Colony surface showing autozooecial apertures and acanthostyles. (6) Internal view of a broken branch.

Figs. 7, 8. *Rhombopora corticata* Moore, 1929, RGM 211 515a. (7) Fragment of the branched colony. (8) Colony surface showing autozooecial apertures and acanthostyles.

Fig. 9. Rhombopora cf. tenuirama Ulrich, 1890, RGM 211 513c, fragment of the branched colony.

All specimens from Locality 6 unless stated otherwise.



Figs. 1-4. Rhombopora cf. tenuirama Ulrich, 1890

Fig. 1. Locality 6, RGM 211 513c, details of the colony surface: autozooecial apertures, macroacanthostyles and microacanthostyles.

Fig. 2. SMF 2674, cross section of branch.

Fig. 3. SMF 2681, longitudinal section of branch.

Fig. 4. SMF 2682, oblique section of branch.

Fig. 5. Nikiforovella sp., SMF 2683, tangential section.

All specimens from Locality 2 unless stated otherwise.



Figs. 1-4. Nikiforovella sp.

- Figs. 1-3. SMF 2684. (1, 2) Longitudinal sections of branches. (3) Cross section of branch.
- Fig. 4. Locality 1a, RGM 211 526a, colony surface with autozooecial apertures and paurostyles.

Fig. 5. Laxifenestella? filistriata (Ulrich, 1890), SMF 2686, deep tangential thin section.

All specimens from Locality 2 unless stated otherwise.



Figs. 1-6. Laxifenestella? filistriata (Ulrich, 1890).

Fig. 1. RGM 211 509a, fragment of colony.

Figs. 2, 3. RGM 211 506a. (2) Fragment with an ovicell. (3) Detail of ovicell .

Fig. 4. RGM 211 524a, fragment of branch with two ovicells.

Fig. 5. RGM 211 529b, ovicell on branch.

Fig. 6. Locality 2, SMF 2687, shallow tangential section showing autozooecial apertures and chambers, hemisepta and keel.

All specimens from Locality 6 unless stated otherwise.



Figs. 1, 2. *Laxifenestella? filistriata* (Ulrich, 1890), Locality 2, deep tangential thin section showing autozooecial chambers and hemisepta (arrows). (1) SMF 2687. (2) SMF 2686.

Figs. 3-9. Spinofenestella subspeciosa (Schulga-Nesterenko, 1955).

Figs. 3, 4. Locality 6.

Fig. 3. RGM 211 536b, fragment of the colony showing obverse side.

Fig. 4. RGM 211 532b, reverse side of the colony with nodes.

Figs. 5-9. Locality 5c, RGM 211 494. (5) Thin section showing reverse side. (6) Deep tangential section. (7) Cross section. (8, 9) Thin section showing reverse side with nodes.



Figs. 1-5. *Fabifenestella praevirgosa* Schulga-Nesterenko, 1951. Figs. 1,2. RGM 211 520b, obverse colony surface. Figs. 3-5. Locality 2, SMF 2688, tangential thin sections.

Figs. 6-8. Fabifenestella? plummerae Moore, 1929.

Fig. 6. RGM 211 514b, obverse colony surface.

Figs. 7, 8. RGM 211 515b, obverse colony surface with ovicells (arrowed).

All specimens from Locality 6 unless stated otherwise.



Figs. 1, 2. Fabifenestella? plummerae Moore, 1929, RGM 211515b, obverse colony surface with ovicells.

Figs. 3-6. Cervella sp.

Fig. 3. RGM 211 520c, obverse colony surface with apertures.

Fig. 4. RGM 211 530a, obverse colony surface with "dendroid" nodes on the keel (arrows).

Fig. 5. RGM 211 520c, oblique view of dendroid nodes and apertures with nodes.

Fig. 6. RGM 211 515c, reverse side of the colony with nodes.

Figs. 7, 8. "Fenestella" modesta Ulrich, 1890, RGM 211 514c, obverse colony surface.

All specimens from Locality 6.



Figs. 1-4. *Ptiloporella irregularis* Nikiforova, 1938, Locality 6. Figs. 1, 4. RGM 211 519b. Figs. 2, 3. RGM 211 507a, obverse colony surface.

Figs. 5-9. *Septopora* sp., Locality 5b, RGM 211 496. (5, 7) Shallow tangential section showing autozooecial apertures, nodes and cyclozooecia (arrows). (6, 8) Deep tangential section showing autozooecial chambers. (9) Deep tangential section showing cyclozooecia.



Figs. 1-4. *Penniretepora* sp. 1.
Figs. 1, 2. RGM 211 516b, colony fragments .
Figs. 3, 4. Locality 2, SMF 2689. (3) Shallow tangential section showing apertures. (4) Deep tangential section showing autozooecial apertures with long hemisepta (arrowed).

Figs. 5, 6. *Penniretepora* sp. 2, RGM 211 524b, colony fragments showing autozooecial apertures, keel and nodes.

All specimens from Locality 6 unless stated otherwise.



- Figs. 1, 2. Penniretepora sp. 3, RGM 211 522, colony fragments.
- Figs. 3, 4. Penniretepora cf. beresovensis Morozova, 1955, RGM 211 509b, colony fragments.

All specimens from Locality 6.



Figs. 1, 2. Penniretepora sp. 4, Locality 6, RGM 211 511d, colony fragments showing long nodes.

Figs. 3, 4. Penniretepora sp. 5, Locality 1a, RGM 211 525a, colony fragments.



Figs. 1, 2. Penniretepora cf. nodocarinata Richards, 1959, Locality 6.

Fig. 1. RGM 211 510a.

Fig. 2. RGM 211 533c, fragments showing autozooecial apertures, keel and nodes.

Figs. 3-5. Polypora remota Condra, 1902

Figs. 3, 4. Locality 1a, RGM 211 525b. (3) Fragment showing autozooecial apertures. (4) Fragment showing the obverse side of the colony.

Fig. 5. Locality 4, RGM 211 497, tangential section of branch showing autozooecial apertures, chambers and reverse side of the colony.



Figs. 1-5. *Polypora remota* Condra, 1902. Locality 4, RGM 211 497. (1) Shallow tangential section of the branch showing autozooecial apertures. (2) Deep tangential section of the branch showing autozooecial chambers. (3) Tangential section of reverse side of branch with microacanthostyles. (4, 5) Transverse sections of the branch.


Figs. 1-7. *Paucipora* sp., RGM 211 495, Locality 5a. (1) Tangential section showing autozooecial chambers and part of a fenestrule. (2) Oblique section of branch. (3) Deep tangential section of the branch showing autozooecia. (4) Shallow tangential section of branch showing autozooecial apertures and nodes. (5) Oblique section of the branch showing hemisepta. (6) Transverse cross section of the branch. (7) Oblique longitudinal section of branch showing autozooecial chambers with hemisepta (arrows).



Figs. 1-4. "Thamniscus" octonarus Ulrich, 1890, Locality 6.
Fig. 1. RGM 211 529c, colony fragment .
Fig. 2. RGM 211 523b, colony fragment.
Figs. 3, 4. RGM 211 523b, obverse colony surface with ovicells (arrows).



Figs. 1-3. Fenestellida sp. indet. 1-1.Fig. 1. RGM 211 513d, colony fragment.Figs. 2, 3. RGM 211 523c. (2) Colony fragment. (3) Colony surface showing autozooecial apertures, nodes and cyclozooecia (arrows).

Figs. 4, 5. Fenestellida sp. indet. 1-2, RGM 211 534c. (4) Colony fragment. (5) Colony obverse surface showing autozooecial apertures and cyclozooecia (arrows).

All specimens from Locality 6.

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Fig. 1. Fenestellida sp. indet. 1-2; 3 km southeast of Sotres, below Pico Grajal, Asturias; strata probably attributable to the Las Llacerias Formation, Kasimovian. RGM 211 534c, colony obverse surface showing autozooecial apertures and a cyclozooecium (arrow).

Figs. 2-4. Fenestellida sp. indet., RGM 211 500a. (2) Colony fragment. (3) Colony surface showing autozooecial apertures, nodes and striation. (4) Detail of an autozooecial aperture.

Figs. 5, 6. Fenestellida sp. indet. 3, Fig. 5. RGM 211 531a, obverse side of the colony. Fig. 6. RGM 211 531b, reverse side of the colony.

All specimens from Locality 6.

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Fig. 1. Fenestellida sp. indet. 3, RGM 211 531a, obverse side of the colony showing autozooecial apertures.

Figs. 2, 3. Fenestellida sp. indet. 4, RGM 211 511e. (2) Colony fragment. (3) Obverse side of the colony showing autozooecial apertures.

Figs. 4, 5. *Bashkirella minor* sp. nov., Locality 1a, paratype RGM 211 526b. (4) Colony fragment. (5) Obverse side of colony showing autozooecial apertures.

All specimens from Locality 6 unless stated otherwise.



Figs. 1-4. Bashkirella minor sp. nov., Locality 2.

Fig. 1. Paratype SMF 2693, transverse section of branch.

Figs. 2, 3. Holotype SMF 2694. (2) Oblique tangential section of branch showing autozooecial apertures and chambers. (3) Tangential section of the branch showing autozooecial chambers and paurostyles. Fig. 4. Paratype SMF 2693, transverse section of branch showing laminated wall and paurostyles.

Figs. 5, 6. *Rhombocladia delicata* Rogers, 1900, Locality 6. Fig. 5. RGM 211 510b.

Fig. 6. RGM 211 502b, obverse side of colony.



Figs. 1-5. Rhombocladia carnica Ceretti, 1963, Locality 2.

Fig. 1. SMF 2696, transverse section of branch.

Fig. 2. SMF 2699, shallow tangential section of branch showing autozooecial apertures.

Figs. 3, 5. SMF 2698, longitudinal section of branch showing autozooecial chambers with hemiseptum (arrow).

Fig. 4. SMF 2699, shallow tangential section of branch showing autozooecial apertures and macroacanthostyles.

