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STENOLAEMATE BRYOZOANS FROM THE LATEST DEVONIAN (UPPERMOST FAMENNIAN) OF WESTERN GERMANY

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(2 figures, 2 plates and 3 tables)

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ABSTRACT. Three bryozoan species are described from the uppermost part of the Velbert Formation ("Strunian", uppermost Famennian), Velbert Anticline (Rhenish Massif, Germany), including two new species: *Stenophragmidium velbertensis* sp. n. and *Nikiforovella gracilis* sp. n., and one species in open nomenclature: *Dyscritella* sp. The bryozoans thrived on a shallow high-energetic clear-water carbonate ramp characterized by the microbiota *Girvanella*, *Paracaligelloides* and *Quasiendothyra*. The discovery of *Nikiforovella* suggests the existence of faunal migrations between Europe and eastern Palaeotethys realms (China, Kazakhstan).

KEYWORDS. Bryozoa, Taxonomy, Devonian, Facies, Palaeobiogeography.

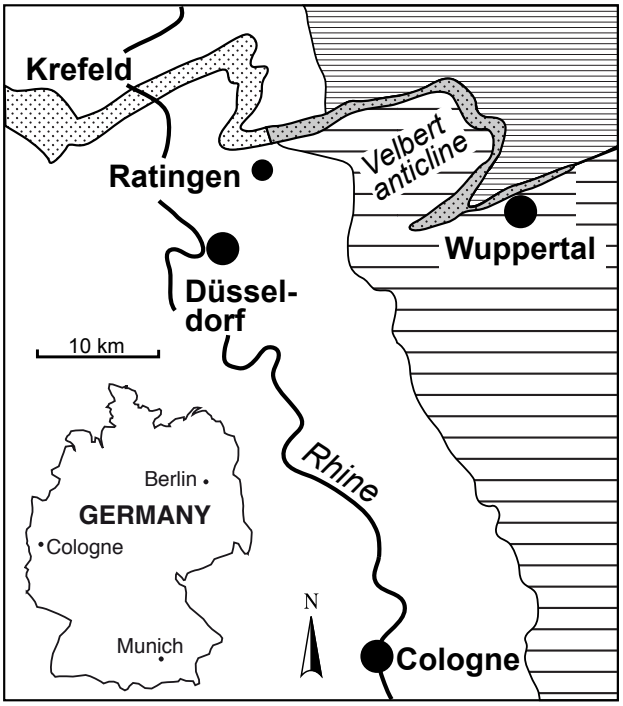

Figure 1. Location of the Velbert Anticline between Ratingen and Wuppertal at the the northwestern margin of the Rhenish Massif. "Strunian" and Lower Carboniferous (Dinantian) strata (stippled) continue in subcrop below Tertiary-Quaternary sediments of the Niederrhein Embayment (white) towards the Ardennes of the Aachen region and eastern Belgium. Upper Carboniferous (narrow horizontal ruling) and pre-Strunian strata (wide horizontal ruling) flank the anticline towards north and south; their subcrop in the Niederrhein Embayment is omitted for clarity (modified from Amler & Herbig, 2006).

1. Introduction

Famennian bryozoans are poorly known in Europe. There are few publications concerning Famennian bryozoan faunas of Europe (Whidborne, 1896, 1898; Nekhoroshev, 1932; Michels, 1986; Weber & Wyse Jackson, 2006). Whidborne (1896, 1898) mentioned four bryozoan species from the Famennian of South England. Weber & Jackson (2006) made an overview of bryozoans recorded from the latest Famennian in Germany using the earlier publications of Nekhoroshev (1932) and Michels (1986). They listed 20 bryozoan species from the "Etroeungt", *i.e.* from the uppermost Devonian. However, most of these species are inadequately described and illustrated, many are in open nomenclature. Their identification is mainly uncertain.

The present paper deals with a description of a bryozoan fauna from the uppermost Velbert Formation ("Strunian", uppermost Famennian, Upper Devonian) of the Velbert Anticline (Rhenish Massif, Germany; Fig. 1). All samples have been derived from the westernmost part of the northwestern flank of the anticline (topographic map 1 : 25.000, sheet 4607 Heiligenhaus, respectively geological map 1 : 25.000, sheet 4607 Kettwig, Wunstorf, 1931). They were collected during a mapping thesis (Richter, 1992) from isolated limestone horizons and meter-sized sections cropping out in the Angerbach valley between the classical localities Cromford and Klein Steinkothen (for a review see Amler *et al*., 1994, see sections in Conil & Paproth, 1968; our Fig. 2). Three bryozoan species were identified here: *Dyscritella* sp., *Stenophragmidium velbertensis* sp. n., and *Nikiforovella gracilis* sp. n. Unidentifiable fragments of trepostome and fenestrate bryozoans also occur in the studied thin sections.

The bryozoan fauna was described using thin sections studied with a transmitted light binocular microscope. Studied material is housed at the Geological Institute of the University Cologne, under collection numbers GIK 2266-2269

2. Geological and stratigraphical setting

The Velbert Anticline is the northwesternmost structure of the Rheinisches Schiefergebirge east of the Rhine River that exposes Late Devonian and Mississippian strata. From the Middle Famennian onward its northwestern flank forms the transition from the shallow Northwest European Laurussian shelf to the Rhenohercynian Culm basin (see review in Amler & Herbig, 2006). During latest Famennian ("Strunian") time a southwest dipping carbonate ramp and adjoining tidal and supratidal flats were reconstructed by Herbig & Mamet (2006). Within ten kilometres along strike from southwest to northeast, a high-energy, clear-water ramp graded into an intermediate and finally a low-energy, muddy ramp. Within a distance of ten kilometres further towards northeast the facies changed into a predominantly sandy-silty succession close to the northern edge of the anticline. The bryozoans described herein have been derived from the southwestern clear-water ramp, whereas the material listed by Michels (1986) is from the sandy-silty succession at the northern edge of the syncline.

The studied material comes from the Velbert Formation in the sense of Paproth *et al*. (1983, p. 213: "Etroeungt-Kalk und Schiefer are part of "Velberter Schichten"), Amler *et al*. (1994) and Amler & Herbig (2006). The badly exposed and strongly tectonized, 500-1000 m thick formation comprises most of the middle and late Famennian. Only in its topmost part, and restricted to the northwestern flank of the syncline, limestone packages become important. The partly sandy, crinoid-rich limestones form a cyclic, mixed carbonate-siliciclastic succession of uppermost Famennian ("Strunian") age ("Etroeungt-Schichten" of Paul, 1939; for biostratigraphic data see Conil & Paproth, 1968; Herbig & Mamet, 2006). The bryozoan-bearing samples have been derived from that uppermost part of the Velbert Formation, but no precise biostratigraphic data are available for the single thin-sections. According to mapping, the sample GIK 2266 with *Dyscritella* sp. is the lowermost sample. *Stenophragmidium velbertensis* sp. n.(GIK 2268) is further up-section and in GIK 2269 still slightly younger (Fig. 2). The position of GIK 2267 with the holotype of *Stenophragmidium velbertensis* sp. n. is difficult to relate to the other samples, but is Strunian without doubt. *Nikiforovella gracilis* sp. n. occurs in all samples.

The "Strunian" is an international widely used chronostratigraphic unit and can be interpreted as a separate Famennian substage, although not yet formalized. The lower boundary is under discussion and should be at the base of the Upper *expansa* conodont zone, which is close to the base of the *Quasiendothyra kobeitusana* foraminifer zone (Streel *et al*., 2006). Earlier, authors proposed a lower boundary at the base of the "Fa2d", respectively at the first appearance of the miospore *Retispora lepidophyta* (Conil & Lys, 1976, 1980). The upper boundary of the substage coincides with the Devonian-Carboniferous boundary. In summary, the "Strunian" corresponds to the uppermost Famennian and comprises sediments deposited during the latest Devonian

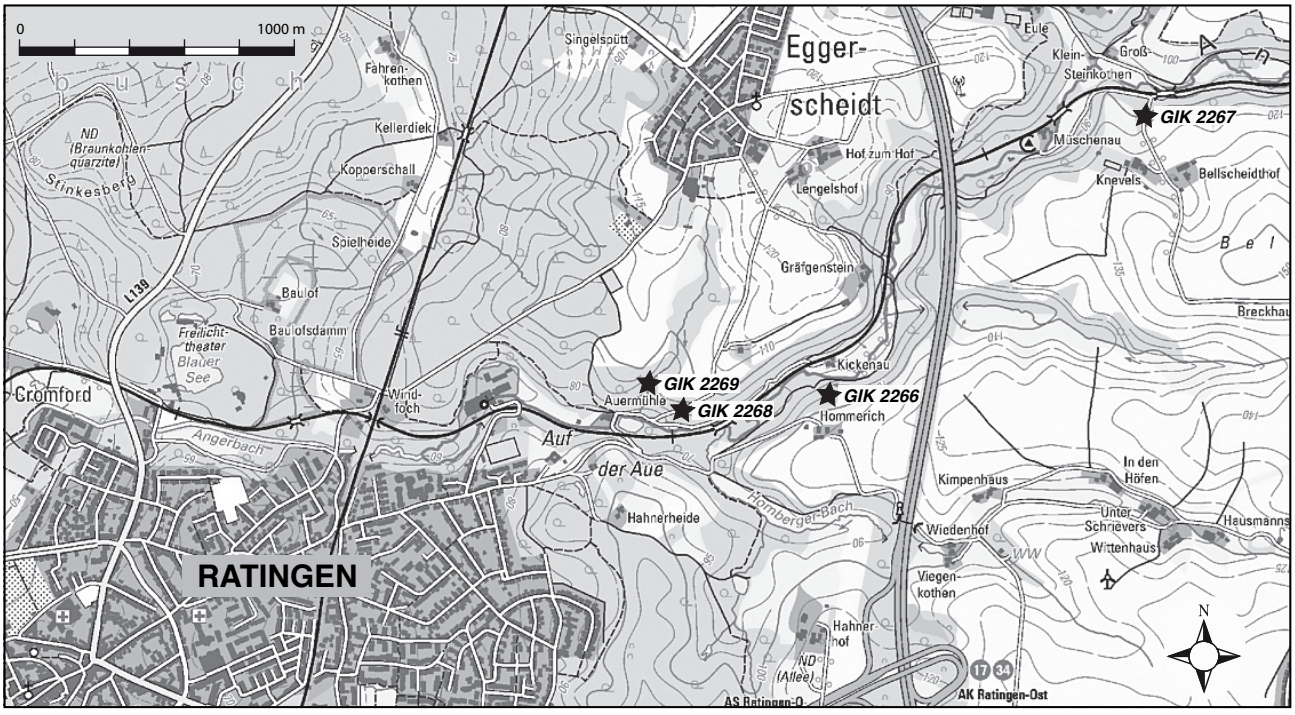

Figure 2. Location of bryozoan-bearing samples in the Angerbach valley east of Ratingen (see Fig. 1 for position of Ratingen). Topographic map from www.tim-online.nrw.de (© Geobasisdaten Land NRW, Bonn).

transgression (TR cycle IIf, Johnson *et al.*, 1885, 1986; see also Conil *et al*., 1986). Correspondingly, the substage is widely recognized along the continental shelves bordering the Palaeotethys (Laurussia, northern Gondwana, Siberia, Chinese cratons).

3. Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Trepostomata Ulrich, 1882
Suborder Amplexoporina Astrova, 1965
Family Dyscritellidae Dunaeva & Morozova, 1967
Genus *Dyscritella* Girty, 1911

Type species: *D. robusta* Girty, 1911, by original designation. Lower Carboniferous; Arkansas (USA).
Diagnosis: Branched and incrusting colonies with abundant acanthostyles and exilazooecia. Autozooecia parallel to longitudinal direction of the colony in endozone; gradually bending outward in exozone. Diaphragms in autozooecia lacking or rare; lacking in exilazooecia. Exilazooecia circular to angular in cross section and separated from the autozooecia and from each other by thick walls. Two sizes of acanthostyles may be present: one set large with few per autozooecia, the other set is small with several around each autozooecium. Autozooecial walls granular, thin in endozones; laminated, rapidly and evenly thickening in exozones (modified after Astrova, 1978).
Comparison: *Dyscritella* Girty, 1911 differs from *Dyscritellina* Morozova in Dunaeva & Morozova, 1967 by rare or absent diaphragms and large acanthostyles of two sizes.
Occurrence: Devonian to Permian; worldwide.

Dyscritella sp. (Pl. 1A-C)

Material: Single colony GIK 2266 (sample Skb of Richter, 1992).
Description: Encrusting colony, 0.28 mm in thickness. Autozooecia growing from thin epitheca, bending sharply in exozone. Autozooecial apertures polygonal with rounded corners. Autozooecial diaphragms absent. Exilazooecia absent. Styles of two sizes. Macroacanthostyles large, 4-5 surrounding each autozooecial aperture; having indistinct cores and laminated sheaths. Microacanthostyles arranged in one row between macroacanthostyles. Autozooecial walls granular, 0.010-0.012 mm thick in endozones; thick, showing indistinct lamination without distinct zooecial boundaries, 0.06-0.07 mm thick in exozones. Maculae not observed.
Comparison: *Dyscritella* sp. is similar to *D. incrustans* Dunaeva, 1964 from the Lower Carboniferous of Ukraine in having thin encrusting colony, but differs in having distinctly differentiated styles (both macro- and microacanthostyles), absence of exilazooecia and in smaller autozooecial apertures (0.09-0.11 mm vs. 0.12-0.15 mm in *D. incrustans*). The available material (one incomplete colony) is not enough to erect a new species.
Occurrence: uppermost Velbert Formation ("Strunian", uppermost Famennian, Upper Devonian); map sheet 4607 Heiligenhaus, 150 m north of the hamlet Hommerich, r 25 62 240 h 56 86 160, northwestern flank of Velbert Anticline (Rhenish Massif), Germany (Fig. 2).

Family Stenoporidae Waagen & Wentzel, 1886
Genus *Stenophragmidium* Bassler, 1952

Type species: *Stenophragma lobatum* Munro, 1912, by original designation. Lower Carboniferous (Viséan); Ravenstonedale, Cumbria, England.
Diagnosis: Encrusting, erect ramose, hollow erect or adnate colonies. Zooecia growing from basal membrane in endozone, being first sub-parallel to the basal membrane, then changing direction of growth and thickening at endozone/exozone boundary to reach the surface of colony at or near 90°. Exozone walls usually clearly laminated, occasionally with moniliform structure. One or more hemiphragms present in autozooecial tube on proximal walls only, varying in shape but appear in longitudinal section most often as barbs, with bulbous tips, or needlelike. Hemiphragm tips mostly point posteriorly. Hemiphragms can extend less than one-third across a chamber to almost its entire width. Complete diaphragms rare. Autozooecial apertures polygonal, or rounded/sub-circular in tangential section, the largest commonly in monticules. Interapertural walls varying greatly in thickness. Acanthostyles usually present, mainly located at interapertural wall junctions. Heterostyles may be present, usually on interapertural walls in large numbers. Exilazooecia may or may not be present and occur in isolation and/or in groups (modified after Cleary & Wyse Jackson, 2007).
Comparison: *Stenophragmidium* Bassler, 1952 differs from *Tabulipora* Young, 1883 by the presence of hemiphragms instead of ring septa.
Occurrence: Lower to Upper Carboniferous; Europe, North America, China, and Russia.

Stenophragmidium velbertensis sp. n. (Pl. 1D-I)

Etymology: The new specific is named after the Velbert Formation where it was found.
Holotype: GIK 2267 (sample WB of Richter, 1992).
Paratypes: GIK 2268 (sample AC 14 of Richter, 1992) – GIK 2269 (Sample Am 11 of Richter, 1992).
Locus typicus: northwestern flank of Velbert Anticline (Rhenish Massif, Germany), map sheet 4607 Heiligenhaus, 250 m SSE of the hamlet Klein Steinkothen, at the southern valley flank, r 25 63 450 h 56 87 220 (Fig. 2).
Stratum typicum: uppermost Velbert Formation ("Strunian", uppermost Famennian, Upper Devonian).
Location and age of paratypes: both from northwestern flank of Velbert Anticline (Rhenish Massif, Germany), map sheet 4607 Heiligenhaus (Fig. 2). GIK 2268 – 250 m east of Auermühle at the southern side of the road, r 25 61 680 h 56 86 120. GIK 2269 – 200 m northeast of

Auermühle at the entrance of the south leading valley, r 25 61 720 h 56 86 230. Both paratypes are from the uppermost Velbert Formation ("Strunian", uppermost Famennian, Upper Devonian).

Diagnosis: Thin encrusting colonies; hemiphragms common, moderately large; acanthostyles large, abundant; heterostyles common; exilazooecia absent.

Description: Encrusting colonies in form of thin lamellar expansions and hollow ramose branches. Encrusting sheets 0.30-0.48 mm thick. Autozooecia growing from thin epitheca, bending sharply in exozone. Autozooecial apertures rounded-polygonal. Diaphragms absent in autozooecia. Hemiphragms common, positioned on the proximal side of the autozooecial chamber, restricting more than half of the autozooecial chamber space. Exilazooecia not observed. Acanthostyles large, 5-6 surrounding each autozooecial aperture; having indistinct cores and laminated sheaths. Heterostyles common, short, protruding from walls in the exozone, positioned perpendicular to the skeletal lamination, arranged irregularly, 0.010-0.015 mm in diameter. Autozooecial walls granular, 0.010-0.015 mm thick in endozones; with weak monilae-shaped thickenings, showing indistinct lamination without distinct zooecial boundaries, 0.015-0.045 mm thick in exozones.

Comparison: *Stenophragmidium velbertensis* sp. n. is similar to *S. megistum* Perry & Gutschick, 1959 from the Amsden Formation (Mississippian – Pennsylvanian) of Montana, USA. The new species has thinner colonies (sheet thickness 0.30-0.48 mm vs. ca. 4.00 mm in *S. megistum*) and less pronounced monilae-shaped thickenings of the autozooecial walls. The new species is also similar to *S. granulosum* Dunaeva, 1964 from the Lower Carboniferous of Ukraine, but differs in having thinner colonies and smaller autozooecia (0.13-0.18 mm vs. 0.18-0.19 mm in *S. granulosum*). *S. paramirandum* Ernst, Schäfer & Rejimer, 2005 from the San Emiliano Formation (Pennsylvanian) of Spain is also similar, but differs in having larger apertures (autozooecial apertures width 0.18 mm vs. 0.16 mm in *S. velbertensis* n. sp. on average).

Order Cryptostomata Vine, 1884
Suborder Rhabdomesina Astrova & Morozova, 1956
Family Nikiforovellidae Gorjunova, 1975
Genus *Nikiforovella* Nekhoroshev, 1948

Type species: *Nikiforovella alternata* Nekhoroshev, 1948, by original designation. Lower Carboniferous; Altai, Russia.

Diagnosis: Branched colonies. Autozooecia diverging at low angles from distinct median axis. Hemisepta absent, diaphragms rare. Autozooecial walls laminated, with dark zooecial boundaries. Metazooecia few between longitudinally successive autozooecial apertures; acanthostyles common to abundant. Longitudinal ridges absent.

Comparison: *Nikiforovella* Nekhoroshev, 1948 is similar to *Streblotrypella* Nikiforova, 1948, but differs from it mainly in shape of autozooecia, which bend at higher angles in exozone, and absence of longitudinal ridges. Moreover, styles can absent in *Streblotrypella*.

Occurrence: Devonian to Permian; worldwide.

Nikiforovella gracilis sp. n. (Pl. 2A-I)

Etymology: The specific name '*gracilis*' refers to thin branches of the new species (derived from Latin 'gracilis' = slender).

Holotype: GIK 2269 (Sample Am 11 of Richter, 1992).

Paratypes: GIK 2266 – GIK 2268 (samples Skb, WB, AC 14 of Richter, 1992).

Locus typicus: northwestern flank of Velbert Anticline (Rhenish Massif, Germany), map sheet 4607 Heiligenhaus, 200 m northeast of Auermühle at the entrance of the south leading valley, r 25 61 720 h 56 86 230 (Fig. 2).

Stratum typicum: uppermost Velbert Formation ("Strunian", uppermost Famennian, Upper Devonian).

Location and age of paratypes: GIK 2266 – see below *Dyscritella* sp.; GIK 2267-2268 – see below *Stenophragmidium velbertensis* sp. n.

Diagnosis: Branched colonies; autozooecia growing from a distinct median axis; autozooecial diaphragms absent; 1-5 metazooecia and 1-3 acanthostyles arranged between longitudinally successive autozooecial apertures.

Description: Branched colonies. Branches 0.75-1.05 mm in diameter, with 0.40-0.63 mm wide endozones and 0.18-0.21 mm wide exozones. Autozooecia growing in spiral pattern from the median axis, abruptly bending in exozone, having triangular cross section in endozone. Autozooecial apertures oval, arranged in regular diagonal rows on branches. Autozooecial diaphragms absent. Autozooecial walls granular, 0.010-0.015 mm thick in endozone; finely laminated, without visible zooecial boundaries, 0.030-0.055 mm thick in exozone. Metazooecia originating at the base of exozone, 1-5 arranged in clusters between longitudinally successive autozooecial apertures. Acanthostyles large, 1-3 arranged between longitudinally successive autozooecial apertures, sometimes positioned in the centre of a metazooecial cluster, having distinct hyaline cores and laminated sheaths.

Comparison: *Nikiforovella gracilis* sp. n. is most similar to *Nikiforovella alternata* Nekhoroshev, 1948 from the Lower Carboniferous of Altai, Russia. The new species has thinner branches (branch diameters 0.75-1.05 mm vs. 1.20-1.50 mm in *N. alternata*), and 1-5 metazooecia and 1-3 acanthostyles vs. 2 metazooecia and 2 acanthostyles between longitudinally successive autozooecial apertures *N. alternata*. *Nikiforovella gracilis* sp. n. is also similar to *N. novella* Ariunchimeg, 1992 (in Ariunchimeg & Morozova, 1992), from the Lower Carboniferous of Mongolia. However, *Nikiforovella gracilis* has fewer metazooecia between autozooecial apertures (1-5 vs. 4-6 in *N. novella*).

4. Discussion

All bryozoan-bearing samples have been derived from a cyclically developed, high-energy clear-water carbonate

ramp, which is characterized by the abundance of the oncoid-, lump- and bafflestone-forming cyanobacterium *Girvanella*, the *incertae sedis* taxon (foraminifer?) *Paracaligelloides* and the foraminifer *Quasiendothyra* (Herbig & Mamet, 2006). In part, the bryozoans were reworked and redeposited on tidal flats and in tidal pools. *Dyscritella* sp., encountered in the oldest sample (GIK 2266), is from such a pool on a siliciclastic flat (facies IV_2, dwarfed palaeoberesellid ponds, Herbig & Mamet, 2006). That quartz-bearing, bioturbated microbioclastic palaeoberesellid-echinoderm wackestone to packstone represents the most restricted facies encountered herein. Reworked *Stenophragmidium velbertensis* sp. n. occurs in the very shallow subtidal and on the adjoining clear-water tidal flat (GIK 2267: microfacies III_3, *Girvanella problematica* bafflestone, Herbig & Mamet, 2006, sample figured on pls. 3/6, 4/1-2, 5/2, 6/4, 6/6). Less reworked to parautochthonous specimens occur on the shallow clear-water ramp in *Girvanella staminea* microfacies which is characterized by abundant *G. staminea* forming encrustations around echinoderms and, after micritisation, peloids, lumps and cortoids (GIK 2269, microfacies II_4, Herbig & Mamet, 2006). The bryozoan species also occurs in *Asphaltinella* bafflestones, which formed laterally in about the same environment. The encrusting and oncoid-forming red alga is associated with echinoderms and *Girvanella* (GIK 2268, microfacies II_5, Herbig & Mamet, 2006, sample figured on pls. 2/6, 6/7). *Nikiforovella gracilis* sp. n. is known from all preceding microfacies.

Similar bryozoan-bearing clear-water facies has been recorded from the subsurface of the Niederrhein embayment (Bless *et al*., 1998) and the Aachen region (Herbig & Weber, 1996, Weber, 1999; for orientation compare our Fig. 1), from southern Belgium and northern France (Avesnois) (Mamet & Preat, 2003; Casier *et al*., 2004), which stresses the greater importance of the studied fauna and should foster the interest in the Strunian bryozoan fauna of the calcareous parts of the "Condroz shelf" along the southeastern margin of Laurussia.

The described fauna contains genera which have a worldwide distribution in the late Palaeozoic. Few species of *Dyscritella* are known from the Devonian of Europe and Siberia, whereas *Stenophragmidium* is recorded for the first time from rocks of Devonian age. Both these genera are mainly known from Carboniferous and Permian strata.

The genus *Nikiforovella* occurs predominantly in the Carboniferous, with few species survived in the Lower Permian. The Devonian records of this genus are known exceptionally from the Famennian: *N.? verellaformis* Lu, 1999 (undivided Famennian, Xinjiang, China), *N. nitida* Troizkaya, 1979 (early Famennian, Kazakhstan), *Nikiforovella* sp. (early Famennian, Altay; Tolokonnikova, 2010), *Nikiforovella* sp. (late Famennian, Mongolia; Ariunchimeg, 2000), *N. bytchokensis* Trizna, 1958 (late Famennian, Eastern Transbaikalia, Kuzbass; Popeko, 2000, Tolokonnikova, pers. comm., 2010), *N. multipitata* Trizna, 1958 (late Famennian, Kuzbass; Tolokonnikova, pers. comm., 2010), *N. alternata* Nekhoroshev, 1948 (late Famennian, Altay; Nekhoroshev, 1956), *N. amazarica* Nekhoroshev, 1960 (late Famennian, Transbaikalia, Russia), and *N. gracilis* sp. n. (late Famennian, western Germany). That suggests faunal migrations between Western Europe, Kazakhstan, China, Altay and Transbaikalia area in Russia along shelves of the Palaeotethys realm in the late Upper Devonian.

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Tables

Table 1. Descriptive statistics for *Dyscritella* sp. Abbreviations: N = number of measurements, X = mean, SD = sample standard deviation, CV = coefficient of variation, MIN = minimal value, MAX = maximal value.

	N	X	SD	CV	MIN	MAX
Aperture Width, mm	15	0.10	0.006	5.97	0.09	0.11
Aperture Spacing, mm	10	0.19	0.014	7.17	0.17	0.22
Macroacanthostyle Diameter, mm	10	0.041	0.006	13.59	0.035	0.050
Microacanthostyle Diameter, mm	20	0.023	0.003	15.29	0.015	0.030

Table 2. Descriptive statistics for *Stenophragmidium velbertensis* sp. n. Abbreviations as for Tab. 1.

	N	X	SD	CV	MIN	MAX
Colony Thickness, mm	5	0.36	0.072	19.77	0.30	0.48
Aperture Width, mm	10	0.16	0.016	9.98	0.13	0.18
Aperture Spacing, mm	10	0.21	0.019	9.14	0.18	0.24
Acanthostyle Diameter, mm	10	0.040	0.006	14.43	0.035	0.050
Wall Thickness in Exozone, mm	10	0.031	0.008	26.12	0.015	0.045

Table 3. Descriptive statistics for *Nikiforovella gracilis* sp. n. Abbreviations as for Tab. 1.

	N	X	SD	CV	MIN	MAX
Branch Width, mm	9	0.89	0.115	12.95	0.75	1.05
Aperture Width, mm	30	0.11	0.014	12.50	0.08	0.14
Aperture Spacing Along Branch, mm	20	0.33	0.025	7.61	0.30	0.40
Aperture Spacing Across Branch, mm	25	0.20	0.021	10.26	0.17	0.24
Acanthostyle Diameter, mm	25	0.050	0.007	13.93	0.030	0.065
Metazooecia Width, mm	25	0.031	0.009	29.26	0.020	0.055
Number of Acanthostyles between Apertures	25	1.8	0.577	32.08	1.0	3.0
Number of Metazooecia between Apertures	25	2.9	0.971	33.72	1.0	5.0
Wall Thickness in Exozone, mm	10	0.043	0.010	23.69	0.030	0.055

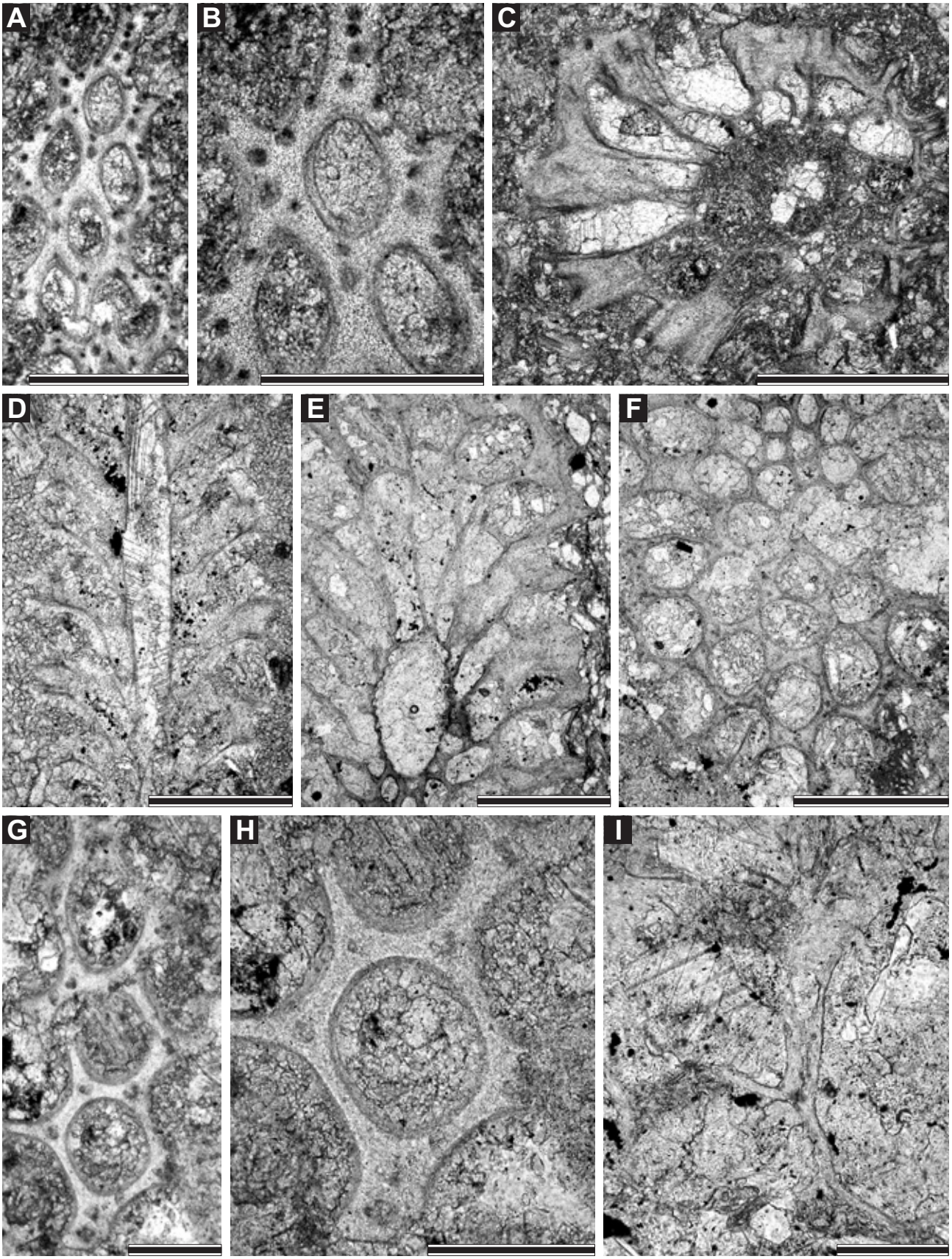

Plate 1. **A-C**, *Dyscritella* sp. (GIK 2266). **A-B**, tangential section, **C**, longitudinal section, scale bars 0.5 mm. **D-I**, *Stenophragmidium velbertensis* sp. n. (holotype GIK 2267). **D**, longitudinal section, scale bar = 0.5 mm (holotype GIK 2267). **E**, oblique section of incrusting colony, scale bar = 0.5 mm (holotype GIK 2267). **F**, tangential section, scale bar = 0.5 mm (holotype GIK 2267). **G-H**, tangential section, scale bars 0.2 mm (paratype GIK 2268). **I**, longitudinal section showing hemiphragms, scale bar 0.1 mm (paratype GIK 2269).

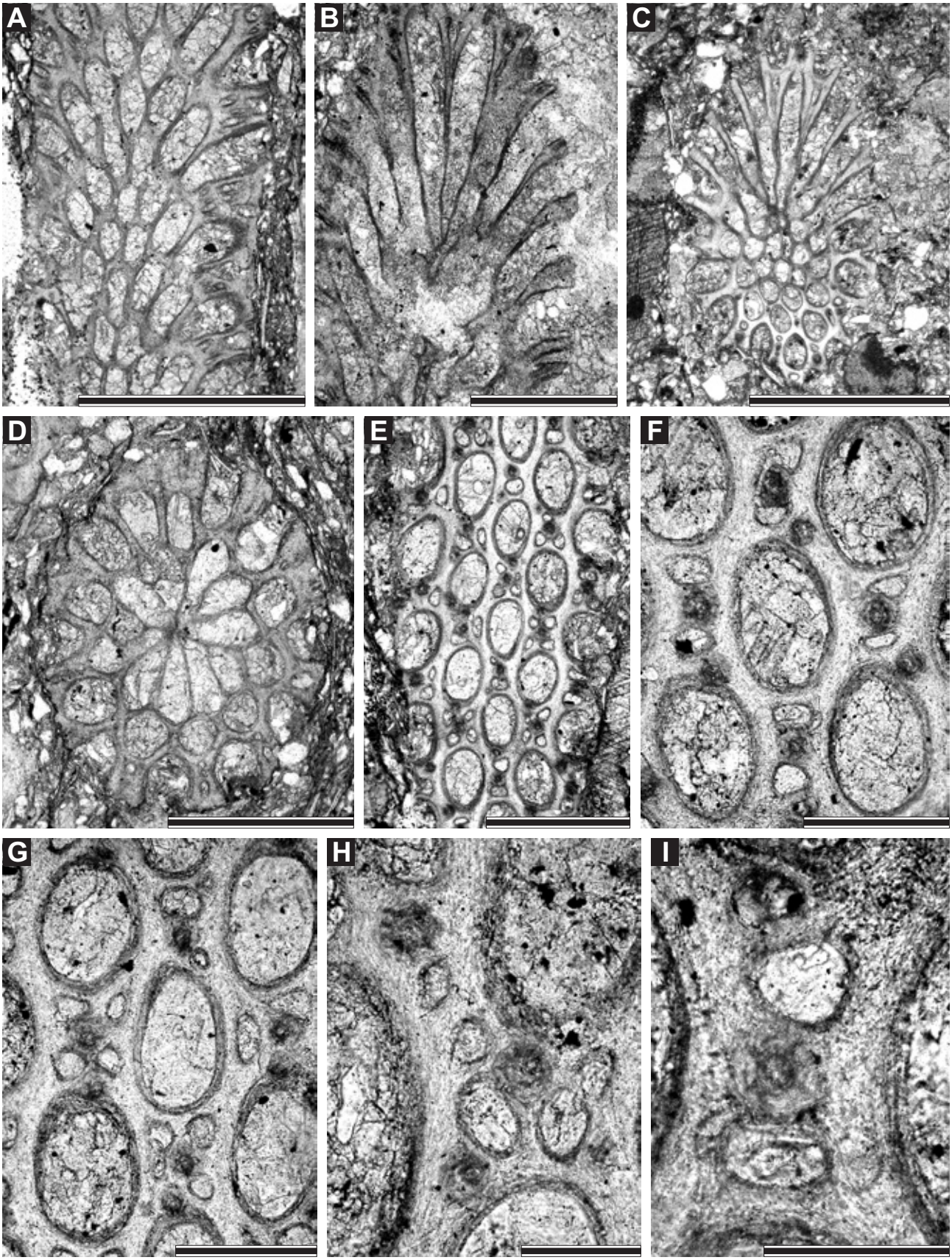

Plate 2. **A-I**, *Nikiforovella gracilis* sp. n. **A**, longitudinal section, scale bar = 1 mm (holotype GIK 2269). **B**, longitudinal section, scale bar = 0.5 mm (paratype GIK 2267). **C**, oblique section of the branch, scale bar = 1 mm (holotype GIK 2269). **D**, transversal section of the branch, scale bar = 0.5 mm (paratype GIK 2267). **E**, tangential section, scale bar = 0.5 mm (holotype GIK 2269). **F-I**, tangential section, showing acanthostyles and metazooecia, scale bars 0.2 mm for **F-G** and 0.1 mm for **H-I** (holotype GIK 2269).