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ORIGINAL PAPER

Bryozoan fauna from the Ferques Formation (Upper Devonian, Frasnian) of France

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Abstract

Bryozoan material from the Ferques Formation (Upper Devonian, Frasnian), Boulonnais, France contains two cystoporates *Cystiramus* cf. *kondomensis* Morozova, 1959 and *Canutrypa francqana* Bassler, 1952, a new trepostome species *Dyoidophragma bigeyae* n. sp., as well as two fenestrates *Hemitrypa* sp. and *Anastomopora inflata* (Bigey, 1988b). The diagnosis of the genus *Dyoidophragma* Duncan, 1939 is revised. The species composition reveals palaeobiogeographic relations to the Middle and Upper Devonian of Belgium, Germany and Poland, as well as possible relation to the Upper Devonian of Kuznetsk Basin in Russia.

Keywords Bryozoans · Taxonomy · Frasnian · France · Palaeobiogeography

Introduction

During the Palaeozoic Era bryozoans were involved in different ecosystems contributing significantly to the global biodiversity (e.g. Taylor and Larwood 1990; Taylor and Allison, 1998; Horowitz and Pachut 2000; Ernst 2020). Because of their stable calcitic skeletons (e.g. Smith et al. 2006), bryozoans show remarkable preservation potential, and their remnants are widely distributed in marine sediments worldwide.

Bryozoan faunas are diverse and abundant in Upper Devonian deposits worldwide (e.g. Cuffey and McKinney 1979; Bigey 1988a; Horowitz and Pachut 1993; Ernst 2013). The Devonian Period is characterised by the global expansion of reefs (Copper 1989, 2002), induced due to a "greenhouse" interval with high sea levels. During the Devonian, the organic life experienced a series of variously scaled extinction events (e.g. Walliser 1996). Bryozoans were heavily affected by the end-Givetian Taghanic bioevent, but did not experienced heavy losses during the Frasne/Famennian bioevent (also called the Kellwasser event), unlike most marine groups (e.g. Bigey 1988a; Horowitz et al. 1996; Morozova et al. 2002). In contrast, bryozoan faunas showed even signs of recovery during the early Famennian (Ernst 2013).

In the European region, Frasnian bryozoan faunas are known from France (Bigey 1979, 1980, 1988b, 1991), Belgium (Desilly 1961), and Poland (Morozova et al. 2002, 2006). However, the record of bryozoans from this time interval remains scarce and patchy. The present paper aims to describe five bryozoan species from the Ferques Formation (Upper Devonian, Frasnian) of Ferques, deposited in the collection of the Geowissenschaftliches Zentrum of the University of Göttingen, Germany. Taxonomy and morphological characters of these bryozoans as well as biogeographical implications are discussed.

Studied material and geological settings

Middle and Upper Devonian deposits of the Ferques inlier area (Boulonnais, northern France; Fig. 1) show an alternation of clastic sediments (Caffiers, Beaulieu,

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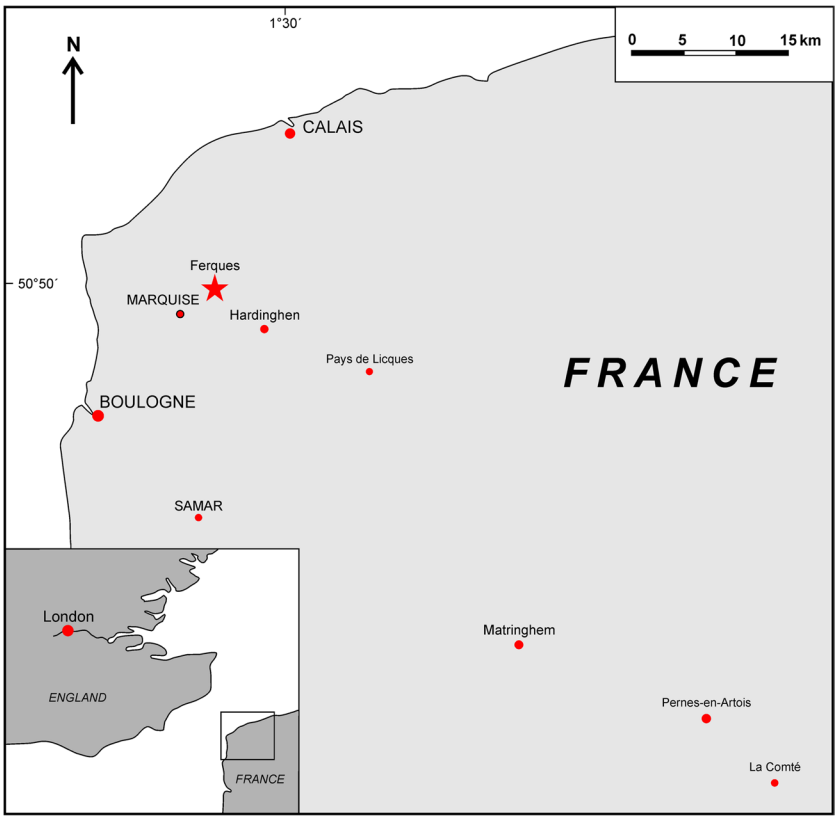


Fig. 1 Position of the La Parisienne quarry at Ferques (asterisk; simplified after Wallace 1969)

Hydrequent and Sainte Godeleine formations) and carbonate rocks which include bioherms and biostromes (Blacourt and Ferques formations) (Robinson 1920; Brice et al. 1979). These deposits were accumulated in nearshore to open marine environments of the western part of the Condroz Shelf, southwest of the London-Brabant High (Brice 1988). Geology and palaeontology of this region has been intensively studied (e.g. Wallace 1969; Brice 1988; Brice et al. 1981, 2002; Mistiaen et al. 2002, 2016), also including some work on bryozoans (Bigey 1980, 1987, 1988b, 1991).

The Frasnian stage at Ferques is represented by the Beaulieu, Ferques, and Hydrequent formations (Fig. 2; Brice 2003). The lithology changes progressively from siliciclastic-carbonate rocks of basal and middle Frasnian to shales (in the low-energy environment) and the sandstones of the Hydrequent Formation at the top of the stage. The overlying Sainte-Godeleine Formation (lower Famennian) comprises 50-m thick fine-grained sandstones.

Methods

The studied material has been loaned at the Geowissenschaftliches Zentrum of the University of Göttingen, Germany. These samples were labelled "Ferques-Formation, Upper Devonian, Frasnian, Ferques, Boulonnais" (GZG.IN.0.010.518), and "Ferques-Kalk, Ferques-Formation, Upper Devonian, Frasnian, quarry les Parisennes; southwestern part, Boulonnais" (GZG.IN.0.010.530, GZG.IN.0.010.567, GZG.IN.0.010.568, GZG.IN.0.010.569, and GZG.IN.0.010.571). The samples represented fragments of grey fossil-rich, slightly argillaceous limestone.

From the studied samples 28 standard thin sections were made (24x48 mm). Bryozoan morphology has been studied using a binocular microscope. Morphologic character terminology is partly adopted from Boardman (1960), Anstey and Perry (1970) for trepostomes, from Hageman (1991a, b) and Snyder (1991) for fenestrates. The following morphologic characters were measured and used for statistics in the studied material: Branch width, branch thickness, exo- (endo-) zone width, axial ratio (ratio of endozone width to the branch width), autozooecial aperture width, aperture spacing, acanthostyle diameter, exilazooecia width, wall thickness in exozone, hemiphragm spacing, vesicle diameter (spacing), number of vesicles per aperture, dissepiment width, fenestrule width (length), distance between branch (dissepiment) centres, number of apertures per fenestrule length, maximal chamber width. For branched bryozoans, the Bryozoan Skeletal Index (BSI) has been calculated, using the formula ((Exozone Width x Exozonal Wall Width)/Aperture Width) x 100 (Wyse Jackson et al. 2020). The spacing of structures is measured as a distance between their centres. Statistics

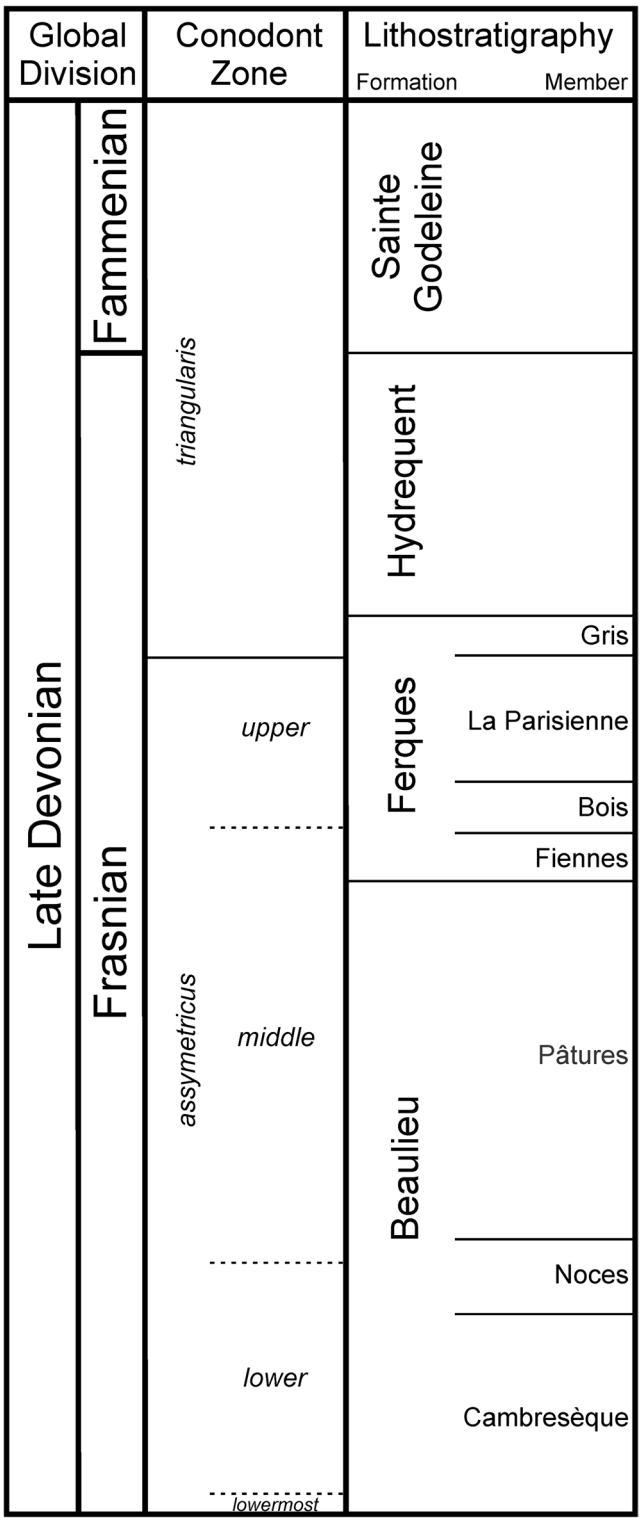


Fig. 2 Stratigraphy of the Frasnian and lower Famennian sediments at Ferques (simplified after Brice 2003)

were summarised using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Superorder Palaeostomata Ma et al. 2014
Order Cystoporata Astrova, 1964
Suborder Fistuliporina Astrova, 1964
Family Fistuliporidae Ulrich, 1882
Genus *Cystiramus* Morozova, 1959

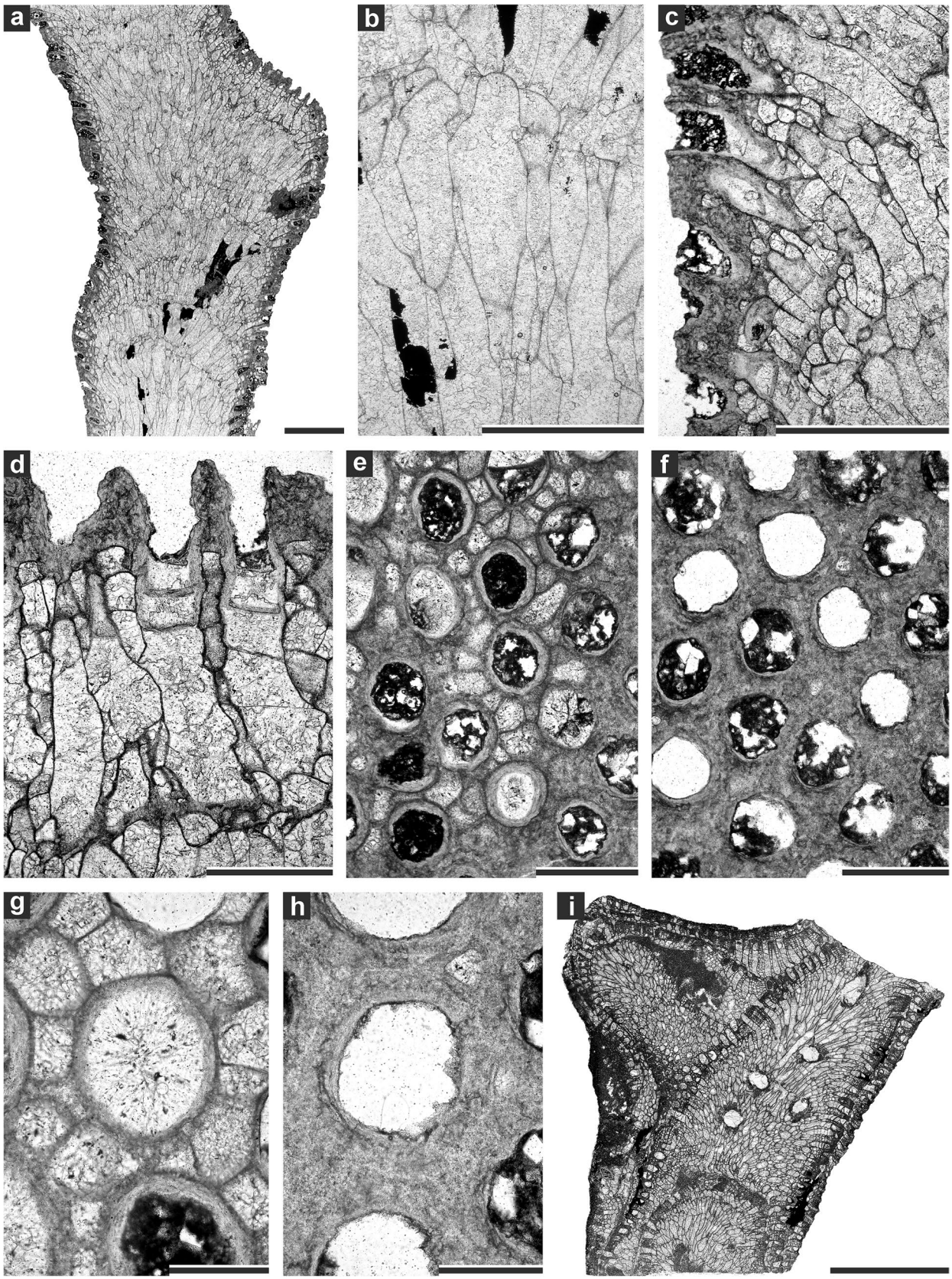
Type species: *Cystiramus kondomensis* Morozova, 1959. Upper Devonian (Frasnian); Kuznetsk Basin, Russia.

Diagnosis: Branched colonies; secondary overgrowths common. Autozooecia short in endozones, rounded-polygonal in transverse section; isolated by vesicular skeleton in exozones. Autozooecial apertures rounded to oval, usually arranged in regularly alternating longitudinal rows; maculae absent or poorly developed. Autozooecial diaphragms present in exozones. Lunaria in exozones, consisting of granular material, usually poorly developed. Vesicles in exozones, subquadrate blisters thickened to stereom through most of exozone. Autozooecial walls thin, granular in endozones; rapidly thickened in inner exozones (diagnosis modified after Utgaard 1983).
Remarks: *Cystiramus* Morozova, 1959 differs from the similar genus *Fistuliramus* Astrova, 1960 in the absence of vesicular skeleton in endozones and maculae as well as in poorly developed lunaria. Autozooecia in *Fistuliramus* are long and subcircular in transverse section of endozones, whereas autozooecia in *Cystiramus* are short in endozones and rounded-polygonal in transverse section. *Cystiramus* is similar to *Fistulophragmoides* Gorjunova *in* Gorjunova and Weis, 2003 in having short autozooecia, but *Fistulophragmoides* differs from *Cystiramus* in having large irregular vesicles in endozones.
Occurrence: Devonian – Mississippian (Carboniferous); Europe, Russia (Altai), China.

Cystiramus cf. *kondomensis* Morozova, 1959
(Figs. 3a–h and Table 1)

1959 *Cystiramus kondomensis* Morozova, p. 80–81, text-fig. 1.
1961 *Cystiramus kondomensis* Morozova, 1959 – Morozova, p. 46–47, pl. 2, fig. 4, pl. 5, fig. 1.

Material: Single colony, four thin sections GZG. IN.0.010.518a–d.
Description: Branched colony with oval shape of transverse section, consisting of successive layers. Short diameter 3.75 mm, long diameter 5.60 mm, exozone 0.50–0.63 mm wide. Autozooecia long in endozones, having polygonal shape in transverse section. Autozooecial apertures oval; lunaria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◂ **Fig. 3** **a–h** *Cystiramus* cf. *kondomensis* Morozova, 1959. **a** longitudinal section of the colony, GZG.IN.0.010.518d. **b** longitudinal section of the endozone, GZG.IN.0.010.518d. **c–d** longitudinal section of the exozone, GZG.IN.0.010.518d. **e–h** tangential section showing autozooecial apertures and vesicles, GZG.IN.0.010.518b. i *Canutrypa francqana* Bassler, 1952, longitudinal section of the colony, with borings in the endozone, GZG.IN.0.010.568f. Scale bars: 5 mm (**i**), 2 mm (**a**), 1 mm (**b, c**), 0.5 mm (**d, e, f**), 0.2 mm (**g, h**)

obscure. Autozooecial diaphragms present in exozones. Vesicles in exozones, subquadrate flattened blisters, polygonal in deep tangential section, completely isolating autozooecia, 8–14 surrounding each autozooecial aperture. Autozooecial walls granular, 0.003–0.005 mm thick in endozones; laminated, showing indistinct zooecial boundaries, 0.09–0.14 mm thick in exozones. Maculae consisting of vesicles, slightly elevated, 0.75–1.50 mm in diameter.

Remarks: The present material is most similar to *C. kondomensis* Morozova, 1959 from the Upper Devonian (Frasnian) of Kuznetsk Basin, Russia. Minor difference is observed in the number and size of vesicles. Figures in Morozova (1961, pl. 5, fig. 1) reveal 6–11 vesicles per autozooecial aperture, whereas the present material possesses 8–14 vesicles per aperture. Vesicle width in the present material is 0.05–0.14 mm vs. 0.10–0.13 mm given by Morozova (1961, p. 47). Moreover, Morozova mentioned absence of maculae, which are present in the sample from Ferques.

Cystiramus cf. *kondomensis* Morozova, 1959 differs from *C. multifarius* Volkova, 1974 from the Upper Devonian (Frasnian) of Altai, Russia, in having only one row of vesicles between autozooecial apertures instead of 3–4 rows in the latter species.

Occurrence: Ferques Formation, Upper Devonian (Frasnian); Ferques, Boulonnais, France.

Genus *Canutrypa* Bassler, 1952

Canutrypa Bassler 1952, p. 382; Desilly 1961, p. 2–3; Utgaard 1983, p. 383; Bigey 1988b, p. 301–302; 1991, p. 27; Ernst 2008, p. 332; Ernst et al. 2012, p. 2–3.
Fistuliporid Bigey 1980, pl. 56, figs 1, 5; 1991, p. 27.
Fistulipora Yang 1954, p. 210; Yang and Lu 1962, p. 11–12.

Type species: *Canutrypa francqana* Bassler, 1952. Upper Devonian, Frasnian; Ferques, France.

Diagnosis: Branched and encrusting colonies. Secondary overgrowths common. Autozooecia long, tubular, curving gently to the colony surface, having circular to oval apertures. Autozooecial diaphragms few to common, thin, straight or inclined. Lunaria poorly defined. One or rarely two hemicylindrical cystlike structures with axes perpendicular to autozooecial axis in many autozooecia in exozone, with a wall consisting of prismatic calcite crystals. Vesicles wide at the base of exozone, becoming narrow at the colony surface. Colony surface covered with a thick layer of granular skeleton (diagnosis modified after Utgaard 1983).

Remarks: *Canutrypa* Bassler, 1952 differs from other cystoporates in the presence of cystlike structures.

Occurrence: Two species of *Canutrypa* Bassler, 1952 were reported: *Canutrypa francqana* Bassler, 1952, from the Middle Devonian (Eifelian–Givetian) of Germany and Poland (Morozova et al. 2002); Upper Devonian (Frasnian) of France (Bassler 1952; Bigey 1980, 1985, 1988b, 1991), Belgium (Desilly 1961) and Poland (Morozova et al. 2002); and *C. hemispheroidea* (Yang, 1954) from the Wutsun Shale, Middle Devonian of Kwangsi, and Devonian of Qilianshan, both China, from the Hajigak Formation (Upper Devonian, Frasnian) of Hajigak, central Afghanistan, and Shishtu Formation (Upper Devonian, Frasnian) of Iran.

Canutrypa francqana Bassler, 1952
(Figs. 3i, 4a–d and Table 2)

1952 *Canutrypa francqana* Bassler, p. 382, figs 3–4.
1953 *Canutrypa francqana* Bassler, 1952 – Bassler, p. G 99, fig. 63 (3a–b).
1961 *Canutrypa francqana* Bassler, 1952 – Dessilly, p. 8–9, pl. 1, figs 1–6, pl. 2, figs 1–5.
1980 *Canutrypa francqana*? Bassler, 1952 – Bigey, pl. 56, fig. 6.
1980 Fistuliporid – Bigey, pl. 56, figs 1, 5.
1983 *Canutrypa francqana* Bassler, 1952 – Utgaard, p. 383, figs 175 (1a–e).
1985 *Canutrypa francqana* Bassler, 1952 – Bigey, p. 27, fig. 4H.
1988b *Canutrypa francqana* Bassler, 1952 – Bigey, p. 302, pl. 37, figs 13–16.
1991 *Canutrypa francqana* Bassler, 1952 – Bigey, p. 27, pl. 1, figs 1–8.
2002 *Canutrypa francqana* Bassler, 1952 – Morozova et. al., p. 332–334, figs 3C–F.
2008 *Canutrypa francqana* Bassler, 1952 – Ernst, p. 309, figs 12A–G, 13A–D.

Material: Single colony GZG.IN.0.010.568a–f.

Description: Ramose colony consisting of series of encrusting sheets with secondary overgrowths; separate sheets, 0.4–1.1 mm thick. Epitheca 0.008–0.010 mm thick. Autozooecia long, tubular, growing from a thin epitheca, curving gently to the colony surface, having circular to oval apertures. Autozooecial diaphragms few to common, thin, straight or inclined. Lunaria indistinct. Vesicles polygonal in cross section, wide at the base of exozone, becoming narrow at colony surface, sealed by granular skeleton at colony surface, 9–12 surrounding each autozooecial aperture. Colony surface covered with thick layer of granular skeleton. Maculae flat, consisting of vesicular skeleton. One hemicylindrical

Table 1 Summary of descriptive statistics for *Cystiramus* cf. *kondomensis* Morozova, 1959 (single colony measured). 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
autozooecial aperture width, mm	20	0.25	0.032	12.78	0.18	0.29
autozooecial aperture spacing, mm	20	0.37	0.042	11.46	0.30	0.45
vesicle width, mm	20	0.10	0.026	27.12	0.05	0.14
vesicles per aperture	16	10.2	2.007	19.70	8.0	14.0
vesicle spacing, mm	20	0.13	0.028	22.40	0.07	0.18

cystlike structure in many autozooecia in exozone, positioned directly on distal autozooecial walls. Cyst wall consisting of prismatic calcite crystals, 0.010–0.015 mm thick. Autozooecial walls granular, 0.003–0.005 mm thick in endozones; laminated, showing indistinct zooecial boundaries, 0.025–0.035 mm thick in exozones.

Remarks: *Canutrypa francqana* Bassler, 1952 differs from *C. hemispheroidea* (Yang, 1954) from the Wutsun Shale, Middle Devonian of Kwangsi, China, in having smaller autozooecial apertures (average aperture width 0.26 mm vs. 0.33 mm in *C. hemispheroidea*) and in having less abundant vesicles (averagely 10.1 vesicles per aperture vs. 13.4 in *C. hemispheroidea*). Measurements for *C. hemispheroidea* (Yang, 1954) are from Ernst et al. (2012).

Occurrence: Ferques Formation, Upper Devonian (Frasnian); southwestern part of the quarry les Parisennes, Boulonnais, France. Junkerberg Formation, Grauberg Subformation, lowermost *Latistriatus* Member, Eifelian, Middle Devonian; Railway cut west of Blankenheim, Blankenheim syncline, Eifel (western Rhenish Massif; locality 1). Honsel and Werdohl Formations (Givetian, Middle Devonian); Lüdenscheid, eastern Rhenish Massif. Uppermost Givetian – lowermost Famennian, Middle to Upper Devonian; Poland.

Order Trepostomata Ulrich, 1882
Suborder Amplexoporidae Astrova, 1965
Family Stenoporidae Waagen and Wenzel, 1886
Genus *Dyoidophragma* Duncan, 1939
[= *Pseudocampylus* Troitzkaya, 1960]

1939 *Dyoidophragma* Duncan, p. 240.
1960 *Dyoidophragma* Duncan, 1939 – Boardman, p. 41.
1960 *Pseudocampylus* Troitzkaya, p. 258.
1968 *Pseudocampylus* Troitzkaya, 1960 – Troitzkaya, p. 112.
1997 *Pseudocampylus* Troitzkaya, 1960 – Xia, p. 107.

Type species: *D. typicale* Duncan, 1939, p. 241, Gravel Point stage, Traverse group (M. Devonian), abandoned quarry, about ¾ mile west of Charlevoix city line, Michigan, USA.

Diagnosis (revised): Colonies encrusting or dendroid, maculae indicated by macrozooecia, some with clusters of large styles (Fig. 5a), others with central cluster of exilazooecia surrounded by macrozooecia. In endozones: in encrusting colonies, budding interzooidal, endozones restricted to recumbent buds, autozooecia rhombic in arrangement. In dendroid colonies, endozones non-uniform, axial autozooecia large, irregularly polygonal in cross section. Some large axial autozooecia split intrazooidaly into more than one peripheral autozooecium. Peripheral autozooecia reduced in size, polygonal in cross section, irregularly rhombic in pattern, no diaphragms, wall thickening to exozone gradual. In exozones: autozooecial surface angles high in dendroid colonies. Autozooecial boundaries polygonal, broadly merged. Autozooecia irregularly rhombic in arrangement on colony surfaces, walls regular in thickness, no cingulum. Diaphragms in autozooecia lacking to rare and thin, unilateral, some secondary from ends of hemiphragms. Hemiphragms on proximal walls only, generally evenly spaced in ontogenetic sequences, some hemiphragms irregularly spaced (Fig. 5b). Exilazooecia rare to common, some with one or two diaphragms widely and irregularly spaced. Between maculae styles few and small in dendroid species, in encrusting species common, centred or off-centred from autozooecial boundaries.

Remarks: *Pseudocampylus* Troitzkaya, 1960, has a dendroid type species comparable generically to encrusting *Dyoidophragma* species. Some confusion arose when Astrova (1978, p. 136) made *Pseudocampylus* a junior subjective synonym of *Tabuliporella* Nikiforova, 1933, and illustrated *Tabuliporella* with the type species of *Pseudocampylus* (pl. 33, fig. 1). *Tabuliporella* differs from both *Pseudocampylus* and *Dyoidophragma* by having hemiphragms alternating in ontogenetic sequence from both proximal and distal walls of autozooecia producing a different shaped living chamber for polypides.

Occurrence: Middle Devonian (Givetian); USA (Michigan, New York). Upper Devonian (Famennian); Kazakhstan, China. Upper Devonian (Frasnian); France.

Dyoidophragma bigeyae n. sp.
(Figs. 4e–f, 6a–h and Table 3)

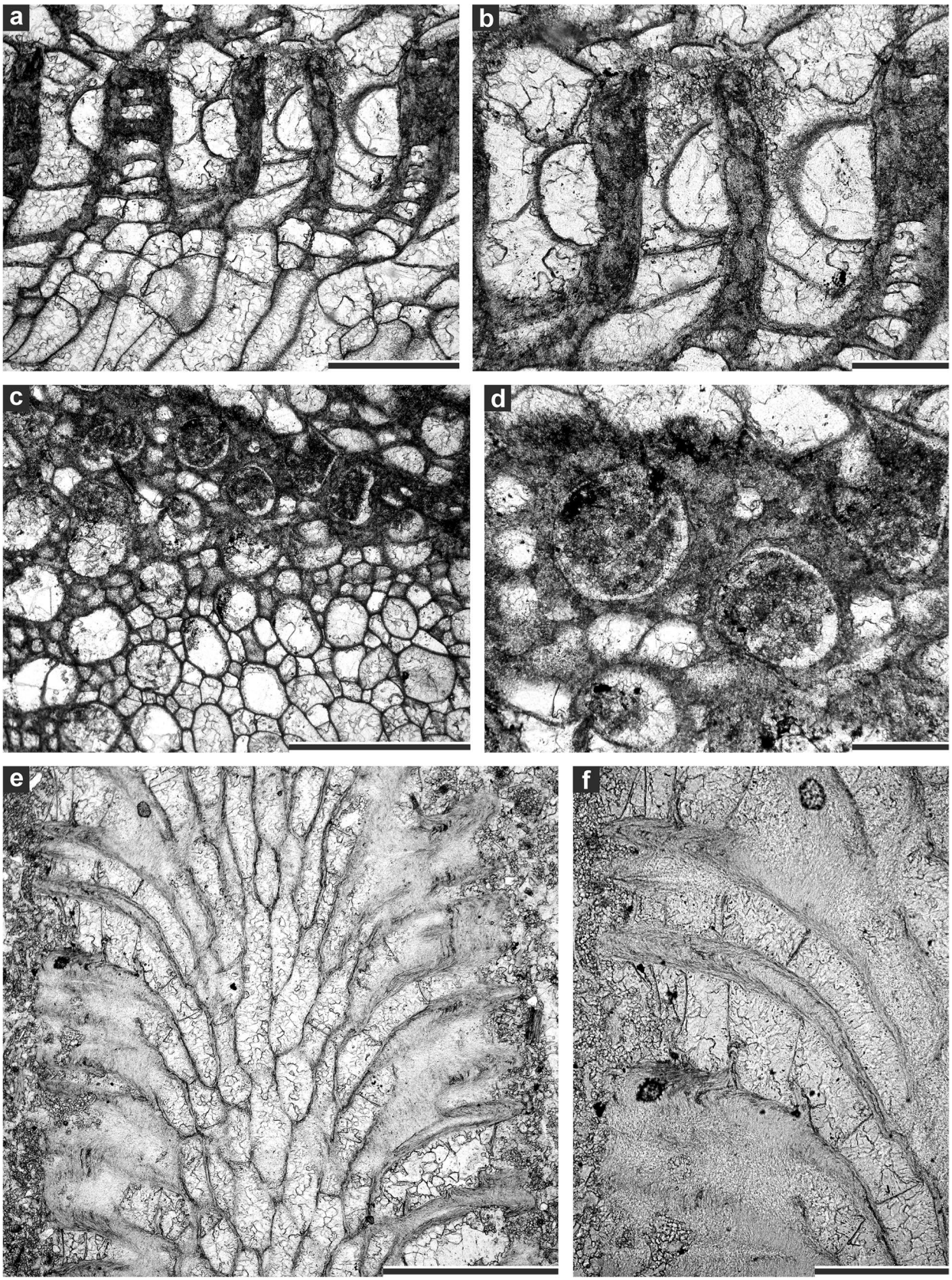
1988b *Rhombopora* cf. *hemiseptata* Morozova, 1961 – Bigey, 314, pl. 39, fig. 6–9.

Etymology: The species is named in honour of Françoise P. Bigey, who contributed greatly to study of Devonian bryozoans.
Holotype: GZG.IN.0.010.567e.
Paratypes: GZG.IN.0.010.530a–i, GZG.IN.0.010.567a–d, f–i.
Type locality: Southwestern part of the quarry les Parisennes, Boulonnais, France.
Type horizon: Ferques Formation, Upper Devonian (Frasnian).
Diagnosis: Branched colonies with distinct exozones; encrusting overgrowths rare; autozooecia tubular-prismatic, with rounded-polygonal apertures; basal diaphragms common to abundant, restricted to exozone; abundant hemiphragms on proximal walls in exozones; autozooecial walls granular in endozone; laminated, merged in exozones; exilazooecia common to abundant; acanthostyles abundant; maculae absent; macrozooecia present.
Description: Branched colonies, 1.0–1.9 mm in diameter, with 0.2–0.6 mm wide exozones and 0.4–0.6 mm wide endozones. Axial ratio is 0.33–0.53. BSI is 26.7. Exozones distinctly separated from endozones. Encrusting overgrowths rare, 0.25–0.28 mm in thickness. Autozooecia tubular-prismatic, growing parallel to branch axes in endozone, bending abruptly in exozones. Autozooecial apertures rounded-polygonal. Basal diaphragms thin, common to abundant, some attached to the ends of hemiphragms (e.g. Fig. 4f), restricted to exozone, straight or slightly curved distally. Hemiphragms abundant in exozones, positioned on proximal wall, moderately thin, short to moderately long, straight to weakly curved proximally. Autozooecial walls granular, 0.015–0.020 mm thick in endozone; laminated, merged, 0.03–0.10 mm thick in exozones. Exilazooecia common to abundant, small, polygonal, originating in basal exozone. Acanthostyles abundant, having distinct cores and laminated sheaths, originating in basal exozone. Maculae absent. Macrozooecia present, 0.13–0.17 mm in width.
Remarks: The species described by Bigey (1988b, p. 314) as *Rhombopora* cf. *hemiseptata* Morozova, 1961 from the Upper Devonian of France is herein assigned to the trepostome genus *Dyoidophragma* and also represents a new species. The species *Rhombopora hemiseptata* Morozova, 1961 was originally described from the Upper Devonian (Frasnian) of Russia. It was later placed in the cryptostome genus *Bigeyella* Morozova and Weiss *in* Morozova et al., 2006 (Morozova et al. 2006, p. 536). This assignment appears questionable because the type species *Bigeyella sparsa* does not have real hemisepta (holotype PIN 4873/119). In contrast, *Rhombopora hemiseptata* has multiple hemiphragms positioned on the proximal walls of autozooecia. Moreover, this species possesses spherules in the autozooecial walls of exozone and rare acanthostyles. The taxonomic position of *Rhombopora hemiseptata* remains dubious. Superficially, it has similarities with the trepostome genus *Eifelipora* Ernst, 2008. Study of the type material of *Rhombopora hemiseptata* is needed.
Dyoidophragma bigeyae n. sp. differs from *D. virgata* (Troitzkaya, 1960) from the Upper Devonian (Famennian) of Kazakhstan in having thinner branches (branch diameter 1.0–1.9 mm vs. 1.85–4.72 mm in *D. virgata*) as well as in less abundant exilazooecia. *Dyoidophragma bigeyae* n. sp. differs from *D. tarbagataica* (Troitzkaya, 1960) from the Upper Devonian (Famennian) of Kazakhstan in having smaller autozooecial apertures (aperture width 0.07–0.11 mm vs. 0.12–0.16 mm in *D. tarbagataica*).

Order Fenestrata Elias and Condra, 1957
Suborder Fenestellina Astrova and Morozova, 1956
Family Fenestellidae King, 1849
Genus *Hemitrypa* Phillips, 1841

Type species: *Hemitrypa oculata* Phillips, 1841. Devonian; Barton, South Devon, England.

Diagnosis: Reticulate colonies, conical or fan-shaped, planar or longitudinally pleated, frontal surface exterior if conical. Branches intermediate in width, linear to moderately sinuous, closely or intermediately spaced, dichotomously divided. Two rows of autozooecia per branch, increasing to four rows proximal of branch bifurcations in some species; low straight to sinuous central keel on obverse side of branch with high nodes, composed of core of granular skeleton and sheath of laminar skeleton. Laminar wall extensions of keel nodes fused together forming a fine meshwork of polygonal openings, each opening centred over a zooecial aperture in the branch below. Axial wall between autozooecial rows zigzag in tangential sections; zooecia not strongly inflated laterally, commonly quadrangular or pentagonal in tangential section deep within endozone, less commonly elongate triangular or semicircular, pentagonal to bean-shaped in shallower endozone; maximum diameter of zooecia corresponds with either length or height; transverse walls at intermediate or high angle to reverse wall; superior hemisepta absent or weakly developed, other interior structures absent. Small- to large-diameter distal tube typically short, opening frontally or slightly inclined laterally and perhaps distally; apertural peristome present or absent; terminal diaphragms planar where present, with central boss in some species. Heterozooecia are isolated zooecia with enlarged endozonal chambers (?gynozooecia) present in proximal parts of colonies, or spherically inflated distal tubes with diameters greater than branch width (? brood chambers). Zooecial walls of granular material that may be absent on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◂**Fig. 4** **a–d** *Canutrypa francqana* Bassler, 1952, GZG.IN.0.010.568f. **a–b** longitudinal section of the exozone showing autozooecia with cyst-like structures and vesicles. **c–d** tangential section showing autozooecial apertures and vesicles. **e–f** *Dyoidophragma bigeyae* n. sp., branch longitudinal section, holotype GZG.IN.0.010.567e. Scale bars: 1 mm (**c, e**), 0.5 mm (**a**), 0.2 mm (**b, d, f**)

obverse side near apertures; laminar extrazooecial skeleton traversed by small to moderate microstyles (modified after F. K. McKinney, pers. comm. 2007).

Remarks: *Hemitrypa* Phillips, 1841 is similar to *Pseudounitrypa* Nekhoroshev, 1926, but differs from it in the composition of the superstructure. The superstructure of *Hemitrypa* is produced by laminar wall extensions of keel nodes forming a meshwork of polygonal openings which are centred over zooecial apertures in the branch below, whereas openings in *Pseudounitrypa* are centred over the branches and terminate laterally over the centres of the fenestrules where the superstructural elements from adjacent branches meet and fuse.

Occurrence: Lower Devonian – Pennsylvanian (Carboniferous); worldwide.

Hemitrypa sp.
(Figs. 7a–i and Table 4)

Material: Single colony, tangential thin section GZG.IN.0.010.569a.

Exterior description: Reticulate colonies with straight branches joined by dissepiments. Autozooecia arranged in two alternating rows on branches, having circular apertures with low peristomes, 2–3 spaced per length of a fenestrule. Peristomes smooth. Fenestrules oval to rectangular, varying in size. Openings in the superstructure irregularly shaped, rounded to petaloid, corresponding to positions of apertures, 0.13–0.18 mm in diameter. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments. Outer lamellar skeleton well developed. Reverse colony surface containing large, irregularly sized nodes, 0.03–0.10 mm in diameter. Apparent gynozooecia produced by two fused autozooecia at places of branch bifurcation occurring, 0.21–0.28 mm in width (Fig. 7g–i). Mutual wall of fused zooecial chambers in gynozooecia partly dissolved.

Interior description: Autozooecia pentagonal in mid tangential section; low and elongated, with short vestibule in longitudinal section. Axial wall between autozooecial rows zigzag in tangential sections; aperture positioned at distal end of chamber. Hemisepta absent.

Remarks: The present material is similar to *Hemitrypa bayanaulensis* Troitzkaya, 1968 from the Upper Devonian (Frasnian) of Kazakhstan. It differs in having longer fenestrules (0.36–0.51 mm vs. 0.33–0.37 mm in *H. bayanaulensis*). The present species differs from *Hemitrypa devonica* Nekhoroshev, 1926 from the Middle to Upper Devonian (Givetian–Frasnian) of Kazakhstan and Russia (Altai) in having longer fenestrules (0.36–0.51 mm vs. 0.37–0.42 mm in *H. devonica*), wider dissepiments (0.22–0.35 mm vs. 0.12–0.18 mm in *H. devonica*) as well as in larger opening of the superstructure (0.13–0.16 mm vs. 0.08–0.12 mm in *H. devonica*).

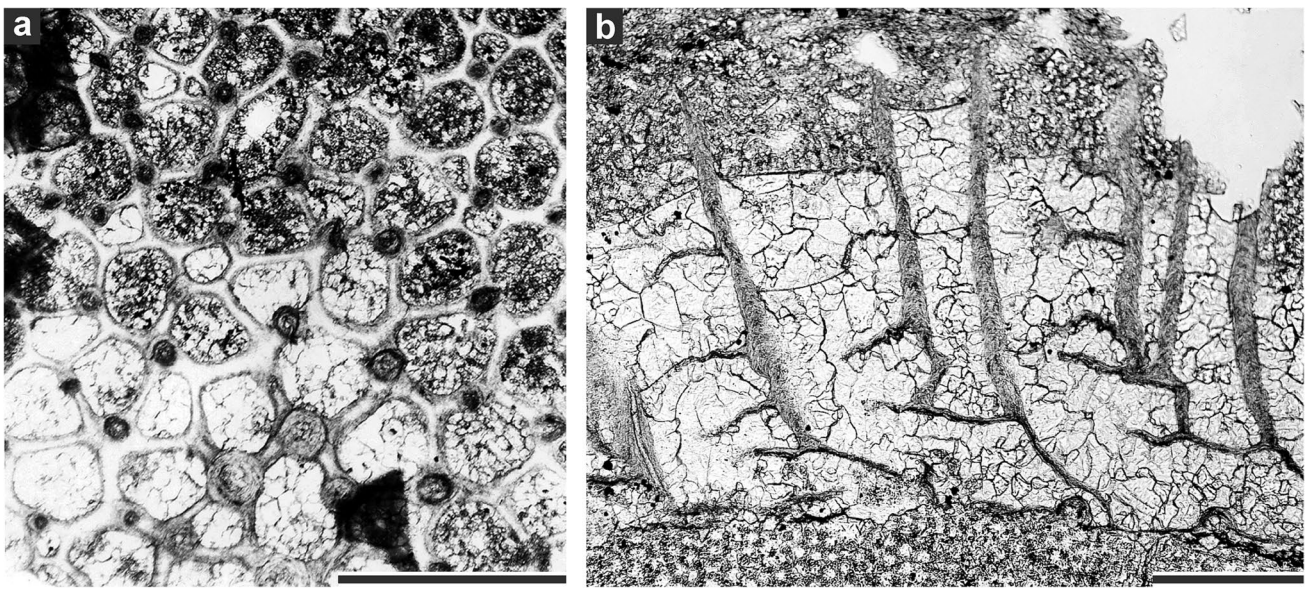


Fig. 5 **a** *Dyoidophragma typicale* Duncan, 1939, tangential section with enlarged styles and macrozooecia in maculum, holotype Univ. Michigan 19854. **b** *Dyoidophragma polymorphum* Boardman, 1960, longitudinal section showing hemiphragms on proximal walls of autozooecia, shorter exilazooecia with thin widely spaced diaphragms, paratype USNM 133860. Scale bars: 0.5 mm (**a**), 0.2 mm (**b**)

Table 2 Summary of descriptive statistics for *Canutrypa francqana* Bassler, 1952 (single colony measured). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
autozooecial aperture width, mm	20	0.26	0.033	12.90	0.19	0.34
autozooecial aperture spacing, mm	20	0.36	0.030	8.28	0.30	0.42
vesicle width, mm	20	0.09	0.020	21.57	0.06	0.14
vesicles per aperture	10	10.1	1.197	11.85	9.0	12.0
vesicle spacing, mm	20	0.07	0.016	21.87	0.05	0.10

Occurrence: Ferques Formation, Upper Devonian (Frasnian); southwestern part of the quarry les Parisennes, Boulonnais, France.

Family Reteporininae Dunaeva and Morozova, 1975
Genus *Anastomopora* Simpson, 1897
[= *Reteporidra* Nickles and Bassler, 1900]

Type species: *Fenestella cinctuta* Hall, 1884. Middle Devonian (Erian); Canada and USA.
Diagnosis: Fan-shaped colonies, some with heavy extrazooidal calcification covering proximal portion of colony; branches broad, strongly sinuous, bifurcating, branch spacing and anastomoses at intermediate distance; keels and superstructure absent; autozooecia arranged in 2–8 rows on branches, large-end intermediate-sized, elongate perpendicular to curved obverse surface, chambers nearly circular oval in tangential section deep in endozone, elongate oval in shallower endozone; transverse wall at high angle to reverse wall; hemisepta and diaphragms absent; elevated peristome present in well preserved specimens. Tubes connecting the endozonal zooecial chambers with the obverse surface present, few or abundant, varying in size. Autozooecial walls of thick granular material may be lined by laminar skeleton in both the distal tube and the inflated chamber; reverse wall flat or minimally curved transversely, longitudinal ridges on reverse side minimally developed; extrazooidal skeleton finely laminated, traversed by closely spaced small microstyles, a gently sloped median keel commonly present on reverse surface, locally forming cystose structures bridging fenestrules where broad expanse of extrazooidal skeleton is deposited as continuous sheet over multiple branches (modified after F. K. McKinney, pers. comm. 2007).
Remarks: *Anastomopora* Simpson, 1897 differs from the similar genus *Reteporina* d'Orbigny, 1849 in having more than 2 rows of autozooecia on branches. Both genera possess exozonal tubes, which number and size are variable in different species.
Occurrence: Lower – Upper Devonian; North America, Europe, Asia.

Anastomopora inflata (Bigey, 1988b)
(Figs. 8a–f and Table 5)

1988b *Reteporidra inflata* Bigey – 312, pl. 39, figs. 3–5.
2007 *Reteporidra inflata* Bigey, 1988b – Ernst and Schroeder, p. 224, figs. 10B–E.
2015 *Anastomopora inflata* (Bigey, 1988b) – Ernst, Tolokonnikova, and Denayer, p. 14, pl. 5, figs. 4–8.

Material: GZG.IN.0.010.567i, GZG.IN.0.010.571a, GZG.IN.0.010.530c, g, i.
Exterior description: Reticulate colonies of unknown shape, composed of undulating, relatively wide branches and joined by long and narrow dissepiments. Branches oval to trapezoid in transverse section. Fenestrules circular to oval. Autozooecia arranged in 3 to 4 rows, after the bifurcation usually in 2 rows on the branches on the branches. Autozooecial apertures circular with high peristome, 3–4 spaced per length of a fenestrule.

Table 3 Summary of descriptive statistics for *Dyoidophragma bigeyae* n. sp. (ten colonies measured). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
branch width, mm	10	1.3	0.379	29.42	1.0	1.9
exozone width, mm	10	0.4	0.157	41.27	0.2	0.6
endozone width, mm	10	0.5	0.077	14.67	0.4	0.6
axial ratio	10	0.43	0.072	16.87	0.33	0.53
autozooecial aperture width, mm	30	0.09	0.011	12.18	0.07	0.11
autozooecial aperture spacing, mm	30	0.18	0.024	13.31	0.14	0.23
acanthostyle diameter, mm	30	0.032	0.005	14.93	0.025	0.040
exilazooecia width, mm	30	0.035	0.014	39.01	0.015	0.075
hemiphragm spacing, mm	20	0.09	0.017	18.45	0.06	0.12
exozonal wall thickness, mm	20	0.06	0.021	38.71	0.03	0.10

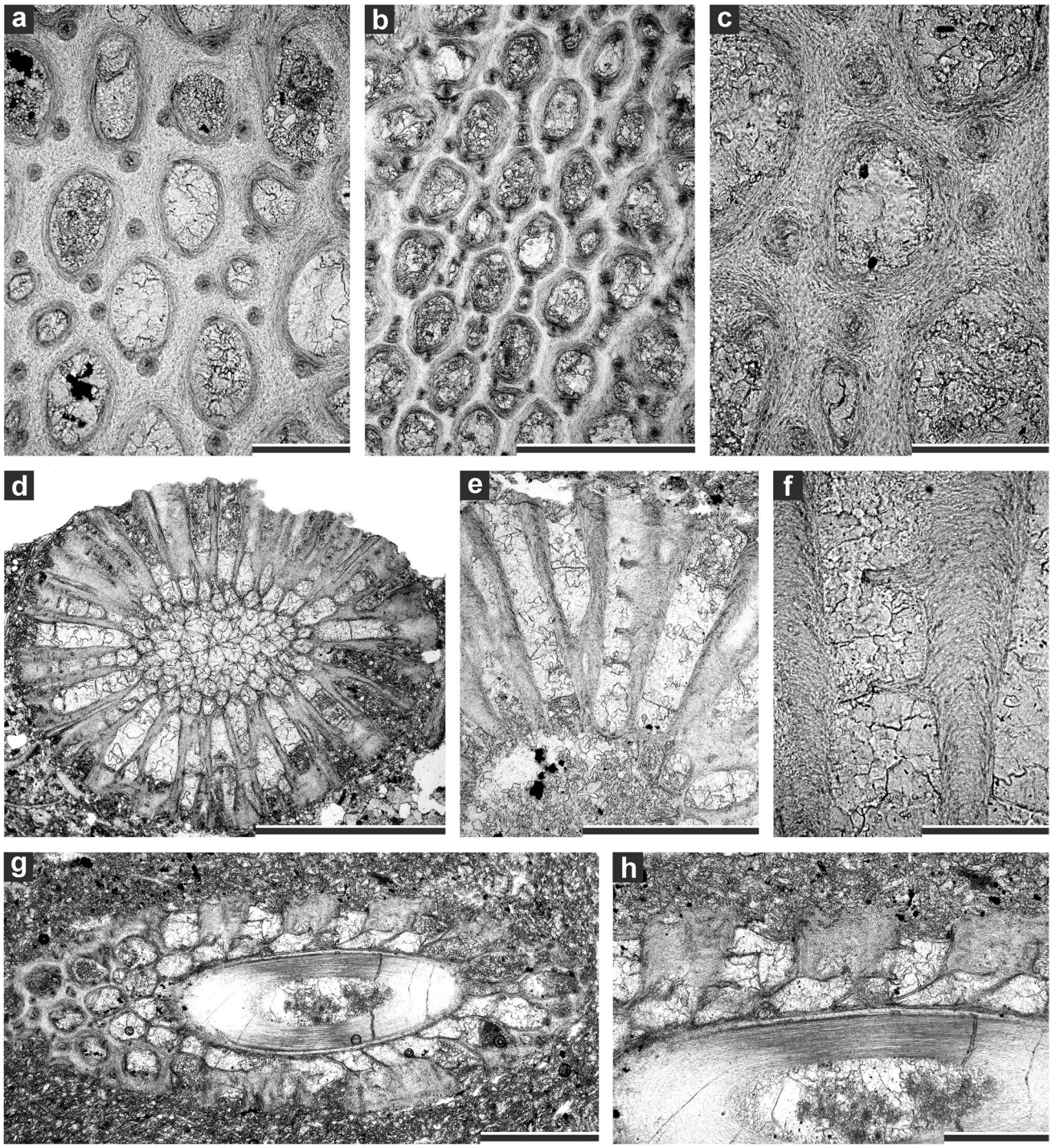
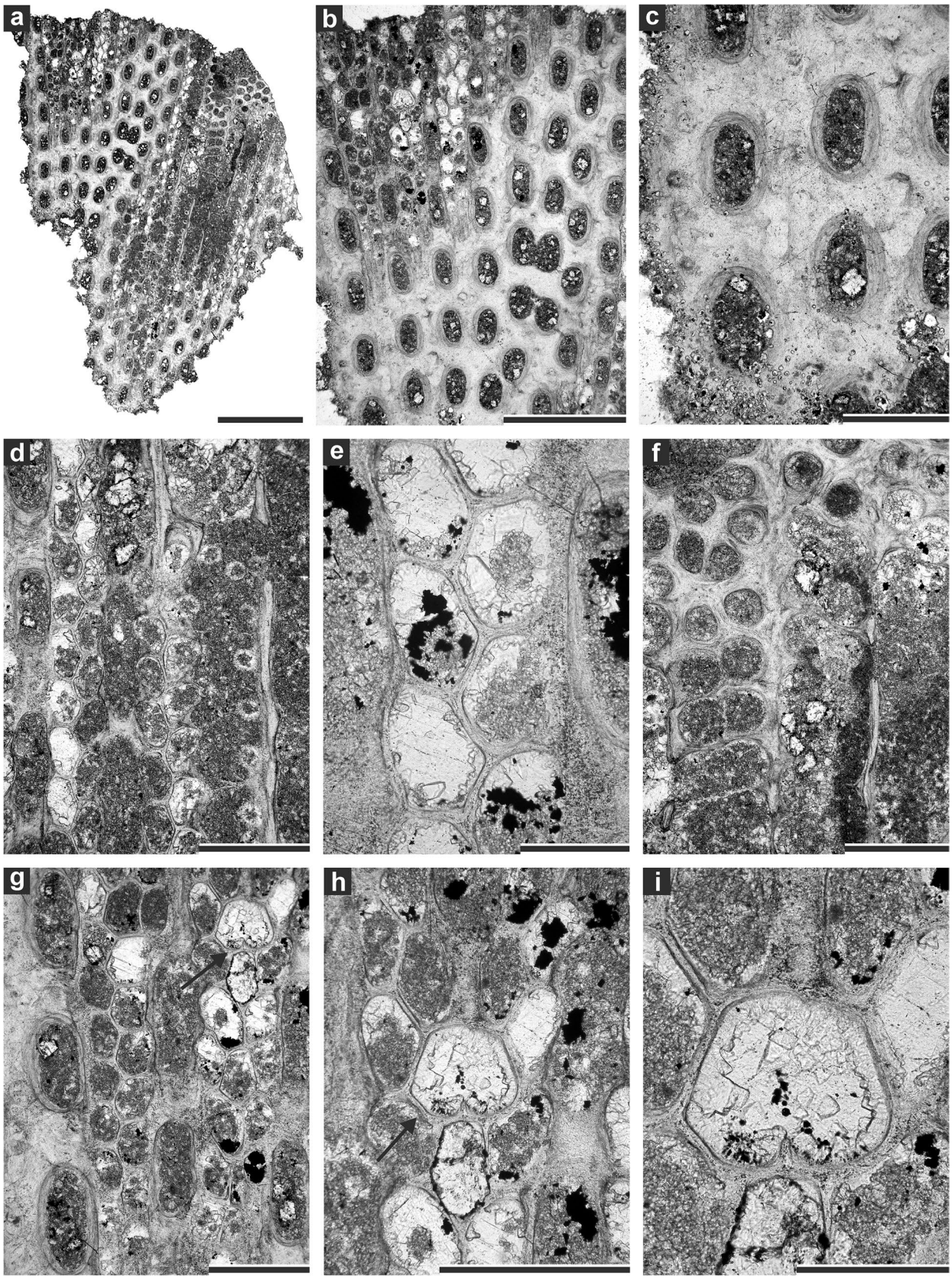


Fig. 6 **a–h** *Dyoidophragma bigeyae* n. sp. **a** tangential section showing autozooecial apertures, mesozooecia and acanthostyles, holotype GZG.IN.0.010.567e. **b–c** tangential section, paratype GZG.IN.0.010.530b. **d** branch transverse section, paratype GZG.IN.0.010.567a. **e–f** branch transverse section showing autozooecia with hemiphragms and diaphragms, paratype GZG.IN.0.010.530i. **g–h** longitudinal section of an encrusting colony on a brachiopod spine with hemiphragms, paratype GZG.IN.0.010.530h. Scale bars: 1 mm (**d, f**), 0.5 mm (**b, e, g**), 0.2 mm (**a, h**), 0.1 mm (**c**)

Microstyles on the reverse surface common, irregularly and densely spaced, originating from inner granular skeleton, 0.005–0.008 mm in diameter.

Interior description: Autozooecial chambers relatively short, deep, displaying rhombic to hexagonal shape and pentagonal (semi-hexagonal) in mid tangential section;


a
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◂**Fig. 7** **a–i** *Hemitrypa* sp., GZG.IN.0.010.569a. **a** thin section of a colony fragment. **b–c** thin section showing reverse side of the colony with nodes. **d** tangential section showing autozooecial apertures and chambers. **e** mid-tangential section showing autozooecial chambers. **f** tangential section showing protective structure. **g–i** mid-tangential section showing apparent gynozooecia in the place of dichotomy (arrows). Scale bars: 2 mm (**a**), 0.5 mm (**b, c, d, f, g, h**), 0.2 mm (**e, i**)

elongate parallel to branch length; aperture positioned at distal to distoabaxial end of chamber; with moderately long vestibule. Hemisepta absent. Tubes connecting endozonal zooecial chambers with the obverse surface present, 5–7 spaced between adjacent apertures, 0.010–0.018 mm in diameter. Heterozooecia are apparent brood chambers represented by enlarged zooecia, rounded to oval in mid tangential section, situated on branches near dissepiments, 0.17–0.20 mm wide. Inner granular skeleton variable in thickness, usually well developed, continuous in nodes and microstyles. Extrazooidal skeleton finely laminated, well developed on reverse side.

Remarks: *Anastomopora inflata* (Bigey, 1988b) is similar to *A. stellata* (Krasnopeeva, 1935) from the Upper Devonian (Frasnian) of Altai. It differs in having larger fenestrules (fenestrule width 0.19–0.34 mm vs. 0.23–0.29 mm in *A. stellata*; fenestrule length 0.47–0.80 mm vs. 0.61–0.72 mm in *A. stellata*). Moreover, the latter species possesses stellate apertures which were not observed in *A. inflata*. *Anastomopora inflata* (Bigey, 1988b) differs from *A.* cf. *quebecensis* Fritz, 1938 from the Upper Devonian (Frasnian) of Iran (Ernst et al. 2012) in having narrower branches (average branch width 0.42 vs. 0.67 mm in *A.* cf. *quebecensis*), smaller fenestrules (average fenestrule width 0.27 mm vs. 0.52 mm in *A.* cf. *quebecensis*; fenestrule length 0.63 mm vs. 0.80 mm in *A.* cf. *quebecensis*), as well as in more autozooecial apertures per fenestrule length (3–4 vs. 4–7 in *A.* cf. *quebecensis*).

Occurrence: Ferques Formation, Upper Devonian (Frasnian); southwestern part of the quarry les Parisennes, Boulonnais, France. Middle Devonian (Givetian); Germany.

Discussion

Bryozoans are still insufficiently known in the Palaeozoic sediments of Europe, despite the long duration of their research history. The likely reason is their complex morphology and preparation requirements, which necessarily demands preparation of thin sections (e.g. Ernst 2020). Bryozoans from the Devonian of Ferques were sporadically studied, whereas the most important work was undertaken by Françoise P. Bigey in the last century (Bigey 1980, 1987, 1988b, 1991). In her main publication on Ferques bryozoans 15 species were described from Givetian and Frasnian sediments, of which 11 were new (Bigey 1988b). The present study shows, however, that our knowledge about bryozoans from the Ferques Formation is still insufficient. Further research on this fauna is required.

In the present paper, bryozoan material from the Ferques Formation (Upper Devonian, Frasnian) of the quarry les Parisennes, deposited at the Geowissenschaftliches Zentrum of the University of Göttingen, Germany, has been described. It contained two cystoporates *Cystiramus* cf. *kondomensis* Morozova, 1959 and *Canutrypa francqana* Bassler, 1952, a new trepostome species *Dyoidophragma bigeyae* n. sp., as well as two fenestrates *Hemitrypa* sp. and *Anastomopora inflata* (Bigey, 1988b). The identified fauna shows close palaeobiogeographic relations to the Middle to Upper Devonian of the European region. The species *Canutrypa francqana* Bassler, 1952 is well known from the Frasnian sediments of Belgium (Desilly 1961), from the Eifelian to Givetian of Germany (Ernst 2008), and from the uppermost Givetian to the lowermost Famennian of Poland (Morozova et al. 2002). The species *Anastomopora inflata* (Bigey, 1988b) is also known from the Frasnian of Belgium (Ernst et al. 2015) and from the Givetian of Germany (Ernst and Schroeder 2007). The species *Cystiramus kondomensis* Morozova, 1959 with which our material is compared was originally established from the Frasnian of the Kuznetsk Basin in Russia.

The studied material contains abundant colonies of the species which was assigned by Bigey (1988b) as

Table 4 Summary of descriptive statistics for *Hemitrypa* sp. (single colony measured). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
branch width, mm	5	0.30	0.035	11.72	0.26	0.34
dissepiment width, mm	15	0.29	0.041	13.96	0.22	0.35
fenestrule width, mm	15	0.18	0.022	12.49	0.14	0.21
fenestrule length, mm	15	0.41	0.044	10.63	0.36	0.51
distance between branch centres, mm	10	0.43	0.055	12.93	0.38	0.52
distance between dissepiment centres, mm	10	0.72	0.029	4.05	0.65	0.75
autozooecial aperture width, mm	8	0.08	0.008	10.27	0.07	0.09
autozooecial aperture spacing along branch, mm	8	0.26	0.023	8.83	0.22	0.3
apertures per fenestrule length	10	2.6	0.516	19.86	2.0	3.0
maximum chamber width, mm	10	0.13	0.009	7.25	0.12	0.15
superstructure opening diameter, mm	10	0.16	0.016	10.20	0.13	0.18

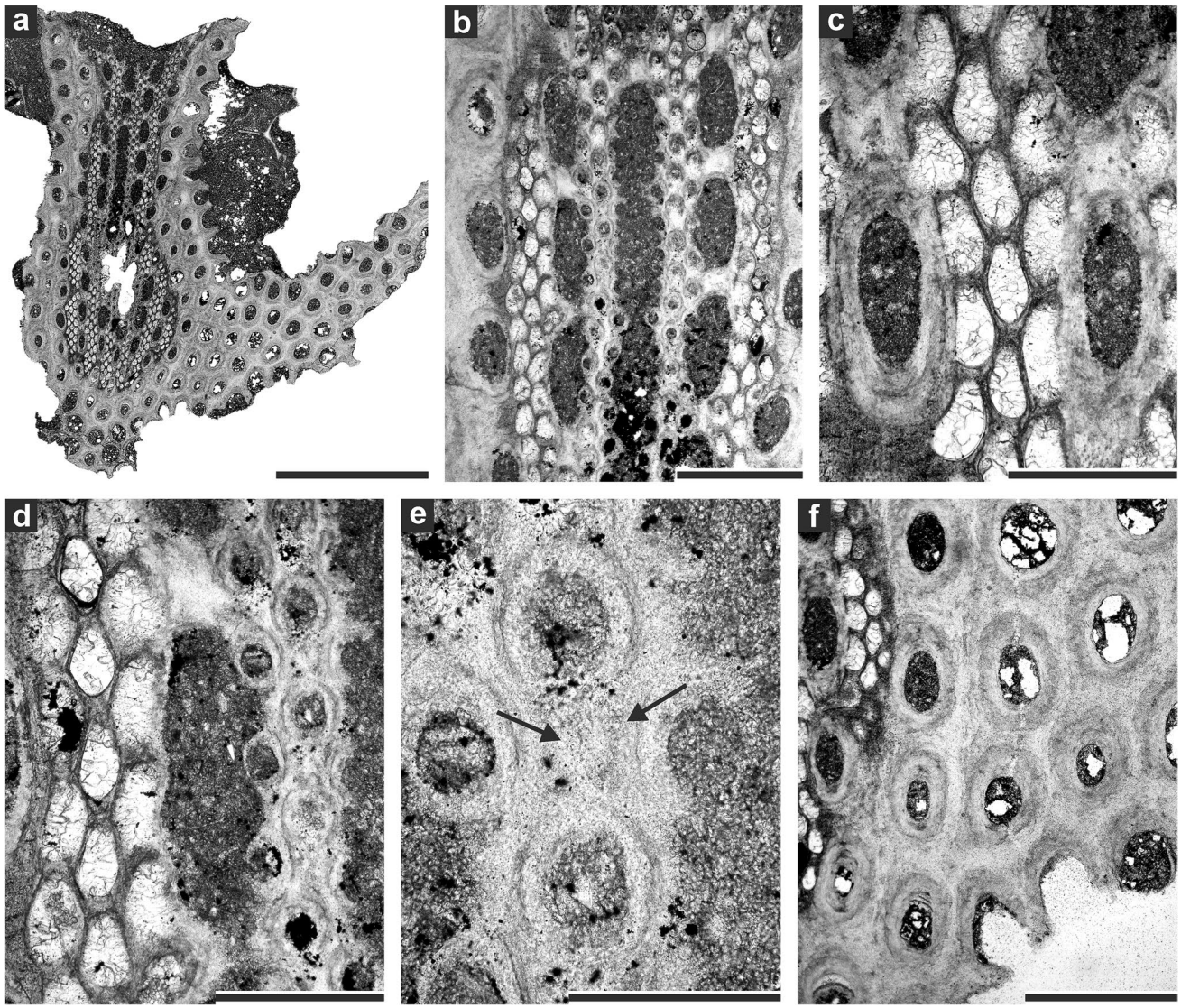

Fig. 8 **a–f** *Anastomopora inflata* (Bigey, 1988b), GZG.IN.0.010.571a. **a** thin section of a colony fragment. **b** tangential section showing autozooecial apertures and chambers. **c** mid-tangential section showing autozooecial chambers. **d** tangential section showing autozooecial apertures and chambers. **e** tangential section showing autozooecial apertures and endozonal tubes (arrows). **f** thin section showing reverse side of the colony. Scale bars: 5 mm (**a**), 1 mm (**b, f**), 0.5 mm (**c, d**), 0.2 (**e**)

Table 5 Summary of descriptive statistics for *Anastomopora inflata* (Bigey, 1988b) (single colony measured). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
branch width, mm	15	0.42	0.038	8.92	0.36	0.48
dissepiment width, mm	15	0.41	0.059	14.16	0.35	0.55
fenestrule width, mm	15	0.27	0.040	14.93	0.19	0.34
fenestrule length, mm	15	0.63	0.102	16.22	0.47	0.80
distance between branch centres, mm	15	0.67	0.073	10.79	0.58	0.82
distance between dissepiment centres, mm	15	1.01	0.085	8.44	0.85	1.15
autozooecial aperture width, mm	25	0.076	0.005	6.70	0.070	0.080
autozooecial aperture spacing along branch, mm	25	0.26	0.022	8.48	0.24	0.32
aperture spacing diagonally, mm	25	0.21	0.017	8.38	0.18	0.24
apertures per fenestrule length	20	3.9	0.366	9.52	3.0	4.0
maximum chamber width, mm	25	0.13	0.010	7.70	0.11	0.14

Rhombopora cf. *hemiseptata* Morozova, 1961. However, our study revealed that this bryozoan belongs to the trepostome genus *Dyoidophragma* Duncan, 1939. Therefore, we assigned it as a new species *Dyoidophragma bigeyae* n. sp. The diagnosis of the genus *Dyoidophragma* Duncan, 1939 is revised here, whereas the genus *Pseudocampylus* Troitzkaya, 1960 is determined to be a junior synonym.

The studied fauna shows an interesting generic composition. The genera *Anastomopora* and *Hemitrypa* exhibit a relatively wide distribution during the Devonian, and are known not only from Europe but also from Asia and North America. The Frasnian species of *Anastomopora* are known from Altai (Krasnopeeva 1935) and Canada (Fritz 1938), whereas those of *Hemitrypa* are known from the Frasnian of Altai (Krasnopeeva 1935) and Kazakhstan (Troitzkaya 1968). The genus *Dyoidophragma* was previously reported from the Middle Devonian of North America and the Upper Devonian of Kazakhstan and China (Duncan 1939; Troitzkaya 1960, 1968; Xia 1997). The genus *Canutrypa* contains only two species from the Middle to Upper Devonian of Europe, China, Iran, and Afghanistan (e.g. Bigey 1988a, b; Ernst et al. 2012). The genus *Cystiramus* shows similarly restricted distribution. One species is known from the Lower Devonian of Spain (Ernst and May 2012), whereas ten species were recorded from the Middle to Upper Devonian of China and Asiatic part of Russia (Morozova 1959; Yang and Hu 1965; Volkova 1974; Yang and Xia 1976; Lu 1999). Three species of *Cystiramus* are known from the Mississippian of China (Lu 1983).

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Data availability The studied specimens (thin sections and rock material) are deposited at the Geological Centre Göttingen, Germany.

Declarations

Conflict of interest The authors declare that they have no conflict of interests.

References

Anstey, R. L., & Perry, T. G. (1970). Biometric procedures in taxonomic studies of Paleozoic bryozoans. *Journal of Paleontology, 44*, 383–398.

Astrova, G. G. (1960). Silurian fistuliporids from the northern regions of the RSFSR. *Trudy Akademii Nauk SSSR Komi Filial, Syktyvkar, Institut Geologii, 1*, 352–376. [in Russian]

Astrova, G. G. (1964). New Order of Paleozoic Bryozoa. *Paleontologicheskij zhurnal*, *1*, 22–31. [in Russian]

Astrova, G. G. (1965). Morphology, history of development and system of the Ordovician and Silurian Bryozoa. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, *106*, 1–432. [in Russian]

Astrova, G. G. (1978). The history of development, system, and phylogeny of the Bryozoa: Order Trepostomata. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, *169*, 1–240. [in Russian]

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

Bassler, R. S. (1952). Taxonomic notes on genera of fossil and Recent Bryozoa. *Journal of the Washington Academy of Sciences*, *42*, 381–385.

Bassler, R. S. (1953). *Bryozoa Volume. Part G*. In R. C. Moore (Ed.), *Treatise on Invertebrate Paleontology* (pp.1–253). Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Bigey, F. P. (1979). Microstructure of the main types of Devonian Bryozoa from the Ferques area, Boulonnais, northern France. In G. P. Larwood, & M. B. Abbott (Eds.). *Advances in Bryozoology* (pp. 153–177). London: Academic Press.

Bigey, F. P. (1980). Bryozoaires et environnement récifal dans le Dévonien français. *Acta Palaeontologica Polonica*, 25, 645–654.

Bigey, F. P. (1985). Biogeography of Devonian Bryozoa. In C. Nielsen, & G. P. Larwood (Eds.), *Bryozoa: Ordovician to Recent* (pp. 9–23). Fredensborg: Olsen & Olsen.

Bigey, F. (1987). Paleoecological aspects of Devonian Bryozoan assemblages in Brittany and Boulonnais, France. In J. R. P. Ross (Ed.), *Bryozoa present and past* (pp. 25–32). Bellingham: Western Washington University.

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

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

Bigey, F. P. (1991). Peculiar structures different from typical skeleton material in Devonian Bryozoa: possible relations to the polypide life cycle. In F. P. Bigey, & J.-L. d'Hondt (Eds.), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, *Mémoire HS*, *1*, 25–38.

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

Boardman, R. S. (1960). Trepostomatous Bryozoa of the Hamilton Group of New York State. *U.S. Geological Survey, professional paper*, *340*, 1–87. https://doi.org/10.3133/pp340

Brice, D. (1988). Le Dévonien de Ferques. Bas-Boulonnais (N. France). *Biostratigraphie du Paléozoique , 7*, 1–520.

Brice, D. (2003). Brachiopod assemblages in the Devonian of Ferques (Boulonnais, France). Relations to palaeoenvironments and global eustatic curves. *Bulletin of Geosciences, 78*(4), 405–417.

Brice, D., Colbeaux, J. P., Mistiaen, B., & Rohart, J.-Cl. (1979). Les formations dévoniennes de Ferques (Bas-Boulonnais – France). *Annales de la Société Géologique du Nord, 98*, 307–324.

Brice, D., Coen, M., Loboziak, S., & Streel, M. (1981). Précisions biostratigraphiques relatives au Dévonien supérieur de Ferques (Bas-Boulonnais). *Annales de la Société Géologique du Nord, 100*, 159–166.

Brice, D., Mistiaen, B., & Rohart, J.-Cl. (2002). Progrès dans la connaissance des flores et faunes dévoniennes du Boulonnais (1971–2001). *Annales de la Société Géologique du Nord, 9*(2ème série)2, 75–84.

Copper, P. (1989). Enigmas in Phanerozoic reef development. In P. A. Jell, & J. W. Picket (Eds.), *Fossil Cnidaria. Memoirs of the Association of Australian Palaeontologists, 8*, 371–385.

Copper, P. (2002). Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages. In W. Kiessling, E. Flügel, & J. Golonka (Eds.), *Phanerozoic reef patterns. SEPM Special Publication 72*, 181–238.

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

Desilly, E. (1961). Les bryozoaires dévoniens de la Belgique. Le genre *Canutrypa* Bassler. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, *37*(9), 1–12.

Dunaeva, N. N., & Morozova, I. P. (1975). Revision of the Suborder Fenestelloidea. In S. Pouyet (Ed.), *Bryozoa 1974* (pp. 225–233). Université Claude Bernard, Lyon.

Duncan, H. (1939). Trepostomatous Bryozoa from the Traverse Group of Michigan. *University of Michigan Paleontology Contributions*, *5*(10), 171–270.

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

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

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

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

Ernst, A. (2020). 2. Fossil record and evolution of Bryozoa. In T. Schwaha (Ed.), *Phylum Bryozoa* (pp. 11–55). Berlin: De Gruyter. https://doi.org/10.1515/9783110586312-002

Ernst, A. & May, A. (2012). Bryozoan fauna from the Lower Devonian (Middle Lochkovian) of Sierra de Guadarrama, Spain. *Journal of Paleontology*, *86*(1), 60–80. http://www.psjournals.org/doi/abs/https://doi.org/10.1666/10-155.1

Ernst, A., & Schroeder, S. (2007). Devonian bryozoans of Rhenish Massif. *Neues Jahrbuch für Geologie und Paläontologie*, *246*(2). 205–233.

Ernst, A., Tolokonnikova, Z., & Yarahmadzahi, H. (2012). Upper Devonian (Frasnian) Bryozoa from the Shishtu 1 Formation of Niaz area (northeast Iran). *Revue de Paléobiologie*, *31*(1), 1–14.

Ernst, A., Tolokonnikova, Z., & Denayer, J. (2015). Upper Frasnian (Upper Devonian) bryozoans in proximal facies of southern Belgium. *Rivista Italiana di Paleontologia e Stratigrafia, 121*(1), 3–20. https://doi.org/10.13130/2039-4942/6517

Fritz, M. A. (1938). Devonian Bryozoa of Gaspé. *Bulletins of American Paleontology*, *24*(80), 87–100.

Gorjunova, R. V., & Weis, O. B. (2003). Novye devonskie mshanki Mongoloii [New Devonian bryozoans from Mongolia]. *Paleontologicheskii Zhurnal*, *2003*(3), 49–52. [in Russian]

Hageman, S. J. (1991a). Discrete morphotaxa from a Mississippian fenestrate faunule: Presence and implications. In F. P. Bigey, & J.-L. d'Hondt (Eds.), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, *Mémoire HS*, *1*, 147–150.

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

Hall, J. (1884). Descriptions of the bryozoans of the Hamilton Group. *Report of the State Geologist for the year 1883, Albany*, 5–61.

Horowitz, A. S., & Pachut, J. F. (1993). Specific, generic and familial diversity of Devonian Bryozoa. *Journal of Paleontology, 67*(1), 42–52.

Horowitz, A. S., & Pachut, J. F. (2000). The fossil record of bryozoan species diversity. In A. Herrera Cubilla, & J. B. C. Jackson (Eds.), *Proceedings of the 11th International Bryozoology Association Conference* (pp. 245–248). Panama City: Smithsonian Tropical Research Institute.

Horowitz, A. S., Pachut, J. F., & Anstey R. L. (1996). Devonian bryozoan diversity, extinctions and originations. *Journal of Paleontology, 70*(3), 373–380.

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

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

Lu, L. (1983). Phylum Bryozoa. In *Paleontological Atlas of northwest China. Shaanxi-Gansu-Ningxia Volume. Part 2. Upper Paleozoic* (pp. 221–244). Beijing: Geological Publishing House. [in Chinese]

Lu, L. (1999). Famennian-Tournaisian bryozoans of the Aergati Mountain, NW Xinjiang. In *Palaeozoic fossils of northern Xinjiang, China* (pp. 37–47, 142–186). Nanjing: Nanjing Institute of Geology and Palaeontology, Academia Sinica. [in Chinese]

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

Mistiaen, B., Brice, D., & Rohart, J.-C. (2002): Trente années de recherche sur le Dévonien de Ferques (Boulonnais): Données acquises en lithoet biostratigraphie. *Annales de la Société Géologique du Nord,* 9(2ème série)2, 5–12.

Mistiaen, B., Brice, D., Blieck, A., Averbuch, O., Cjarlet, J.-M., Cocks, L. M., Colbeaux, J. P., Debuyser, M., Demarque, D., De Wever, P., Groessens, G., Hubert, B. L. M., Loones, C., Mansy, J. L., Martini, G., Meilliez, F., & Vidier, D. (2016). Le Boulonnais (Pas-de-Calais): un patrimoine géologique remarquable, avec une attention particulière au Dévonien. *Annales de la Société Géologique du Nord,* 23(2ème série), 31–39.

Morozova, I. P. (1959). New genus of the Family Fistuliporidae in Devonian in Kuznetz Basin. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, *2*, 79–81. [in Russian]

Morozova, I. P. (1961). Devonian Bryozoa of the Minusinsk and Kuznetsk Basins. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR, 86*, 1–207. [in Russian]

Morozova, I. P., Weis, O. B., & Racki, G. (2002). Emergence and extinction of the Givetian to Frasnian bryozoan faunas in the Kostomłoty facies zone, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, *47*, 307–317.

Morozova I. P., Weiss O. B., & Racki, G. (2006). New Devonian and Carboniferous bryozoans of the Holy Cross Mountains (Central

Poland). *Paleontological Journal, 40*, 529–540. https://doi.org/10.1134/S0031030106050078

Nekhoroshev, V. P. (1926). Middle Devonian bryozoans of northwest Mongolia with a description of the microscopic method for the determination of fenestellids. *Trudy Geologicheskogo muzeya AN SSSR*, *1*, 1–28. [in Russian]

Nickles, J. M., & Bassler, R. S. (1900). A synopsis of American fossil Bryozoa, including bibliography and synonymy. *U.S. Geological Survey Bulletin*, *173*, 1–663.

Nikiforova, A. I. (1933). Carboniferous deposits of the Middle Asia; contributions to the knowledge of the Lower Carboniferous bryozoans of Turkestan. *Trudy VGRO*, *207*, 1–77. [in Russian]

Orbigny, A.D. d'. (1849). *Prodrome de paléontologie stratigraphique universelle des animaux mollusques rayonnés, faisant suite ou cours élémentaire de paléontologie et géologie stratigraphique. Volume 1*. Paris: Victor Masson.

Phillips, J. (1841). *Figures and descriptions of the Paleozoic fossils of Cornwall, Devon and West Sommerset*. London: Longman, Brown, Green & Longmans.

Robinson, J. W. D. (1920). The Devonian of Ferques, (Lower Boulonnais). *Quarterly Journal of the Geological Society*, 76, 228–237. https://www.lyellcollection.org/doi/https://doi.org/10.1144/gsl.jgs.1920.076.01-04.07

Simpson, G. B. (1897). A handbook of the genera of the North American Paleozoic Bryozoa. *14th Annual Report of the State Geologist (of New York) for the year 1894*, 407–608.

Smith, A. M., Key, M. M. Jr, & Gordon, D. P. (2006). Skeletal mineralogy of bryozoans: Taxonomic and temporal patterns. *Earth-Science Reviews, 78*(3–4), 287–306. https://doi.org/10.1016/j.earscirev.2006.06.001

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

Taylor, P. D., & Allison, P. A. (1998). Bryozoan carbonates through time and space. *Geology, 26*, 459–462.

Taylor, P. D., & Larwood, G. P. (1990). Major evolutionary radiations in the Bryozoa. In P. D. Taylor, & G. P. Larwood (Eds.), *Major Evolutionary Radiations. Systematic Association Special Volume 42*, 209–233.

Troitzkaya, T. D. (1960). Novyi famenskii predstavitel heterotriypid iz Tarabagataya [New representative of Heterotrypidae from the Tarbagatai]. In B. P. Markowskii (Ed.), *Novye vidy drevnikh rastenii I zhivotnykh [New species of fossil plants and animals]*, (volume 1, pp. 258–260). VSEGEI. [in Russian]

Troitzkaya, T. D. (1968). *Devonian Bryozoa of Kazakhstan.* Nedra, Moscow. [in Russian]

Ulrich, E. O. (1882). American Palaeozoic Bryozoa. *Journal of the Cincinnati Society of Natural History*, *5*, 121–175.

Utgaard, J. (1983). Paleobiology and taxonomy of the Order Cystoporata. In R. A. Robison (Ed.), *Treatise on Invertebrate Paleontology,* Part G (1): *Bryozoa (revised,* pp. G327–G439*)*. Lawrence: Geological Society of America and University of Kansas Press.

Volkova, K. N. (1974). Devonian Bryozoa from the south-east Altai. *Trudy instituta Geologii i Geofiziki, sibirskoe Otdelenie,* 199, 6–176. [in Russian]

Waagen, W., & Wentzel, J. (1886). Salt–range Fossils. *Productus*–Limestone Fossils: Coelenterata. *Memoirs of the Geological Survey of India, Paleontologica Indica*, *Series 13*(1), 835–924.

Wallace, P. (1969). The sedimentology and palaeoecology of the Devonian of the Ferques inlier, northern France. *Quarterly Journal of the Geological Society, 125*, 83–121.

Walliser, O. H. (1996). Global events in the Devonian and Carboniferous. In O. H. Walliser (Ed.), *Global Events and Events Stratigraphy in the Phanerozoic* (pp. 225–250). Berlin: Springer.

Wyse Jackson, P.N., Key, M.M., Jr., & Reid, C.M. (2020). Bryozoan Skeletal Index (BSI): a measure of the degree of calcification in stenolaemate bryozoans. In P. N. Wyse Jackson, & K. Zágoršek, K. (Eds.), *Bryozoan Studies 2019* (pp. 193–206). Prague: Czech Geological Society.

Xia, F. (1997). Marine microfaunas (bryozoan, conodonts, and microvertebrate remains) from the Frasnian-Famennian interval in northwestern Junggar Basin of Xinjiang in China. *Beiträge zur Paläontologie*, *22*, 91–207.

Yang, J. (1954). The early Middle Devonian bryozoans from Wutsun Shale, Kwangsi. *Acta Paleontologica Sinica*, *2*, 207–226.

Yang, J., & Hu, Z. (1965). Bryozoa of the Tungkangling Formation of Xiangzhou, Kwangsi. *Memoirs of the Institute of Paleontology, Nanking*, *4*, 1–50. [in Chinese]

Yang, J., & Lu, L. (1962). Palaeozoic Bryozoa of Qilianshan. *Geology of Qilianshan*, *4*(5), 1–114. [in Chinese]

Yang, K., & Xia, F. (1976). Devonian bryozoans from Dushan and Wangyou near Huishui, Guizhoa Province. *Acta Geologica Sinica*, *1976* (1), 57–73. [in Chinese]