A new Middle Devonian cystoporate bryozoan from Germany containing a new symbiont bioclaustration

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An unusual cystoporate bryozoan from the Middle Devonian (Givetian) Ahbach Formation of the Hillersheim Syncline (Eifel, Rhenish Massif, Germany) is described as *Stellatoides muellertchensis* gen. et sp. nov. The lamellar colonies have elongate stellate maculae with depressed centres consisting of vesicular skeleton. All colonies collected contain vertical axial tubular holes, which are embedment structures formed by the bryozoan around a soft-bodied symbiont and lined by bryozoan skeleton. These bioclaustrations are referred to the ichnogenus *Chaetosalpinx*, previously known in Ordovician–Devonian corals and sponges, and are described as *Chaetosalpinx tapanilai* ichnosp. nov. Ecological analogues to *Chaetosalpinx tapanilai* can be found in modern bryozoans in which tubes formed of bryozoan calcite are occupied by spionid polychaetes, or less often tanaidacean crustaceans.

Key words: Bryozoa, taxonomy, bioclaustration, evolution, Devonian, Germany.

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Introduction

The Devonian represents a transitional time in the evolution of bryozoans, with a switchover from early Palaeozoic faunas typically dominated by trepostomes to late Palaeozoic faunas in which fenestrates generally dominate (Cuffey and McKinney 1979; Bigey 1983). These changes were apparently induced by a series of mass extinctions, which led to shifts in the taxonomic composition of bryozoan faunas (Horowitz and Pachut 1993; Horowitz et al. 1996). Despite their abundance and importance, Devonian bryozoan faunas in Europe have been scarcely investigated. The main reason for this is the complicated internal morphology demanding extensive preparation, mainly using oriented thin sections, for study.

During the course of this project, Devonian bryozoan faunas of the European region have been studied. These have proved to be abundant and diverse (e.g., Ernst 2008; Ernst and Königshof 2010). For example, Middle Devonian bryozoan faunas from the Rhenish Massif contain approximately 70 species (Ernst 2008). A component of this fauna is a distinctive cystoporate found in the lower Givetian in the Eifel (Rhenish Massif). Colonies of this bryozoan, here described as a new genus and species, contain abundant tubes preserved as embedment structures by bryozoan skeletal growth around a soft-bodied symbiont. These bioclaustrations are described as a new species of the ichnogenus *Chaetosalpinx*, previously recorded in corals and stromatoporoids (Tapanila 2006). The aim of the present paper is to describe the new bryozoan and its associated ichnofossil, and to discuss the palaeoecology of the symbiosis.

Institutional abbreviations.—SMF, Senckenberg Museum, Frankfurt am Main, Germany.

Geological and palaeontological setting

Middle Devonian carbonate strata of the Eifel are only preserved within the "Eifel Limestone Synclinorium" (Fig. 1), a north-south trending axial depression of the Rhenish Massif (Fig. 1A). Palaeogeographical facies interpretation is difficult because relatively little of this Middle Devonian shelf is preserved. In general, siliciclastic sediments were derived from the northern Old Red Continent, with a retreating coastline toward the north.

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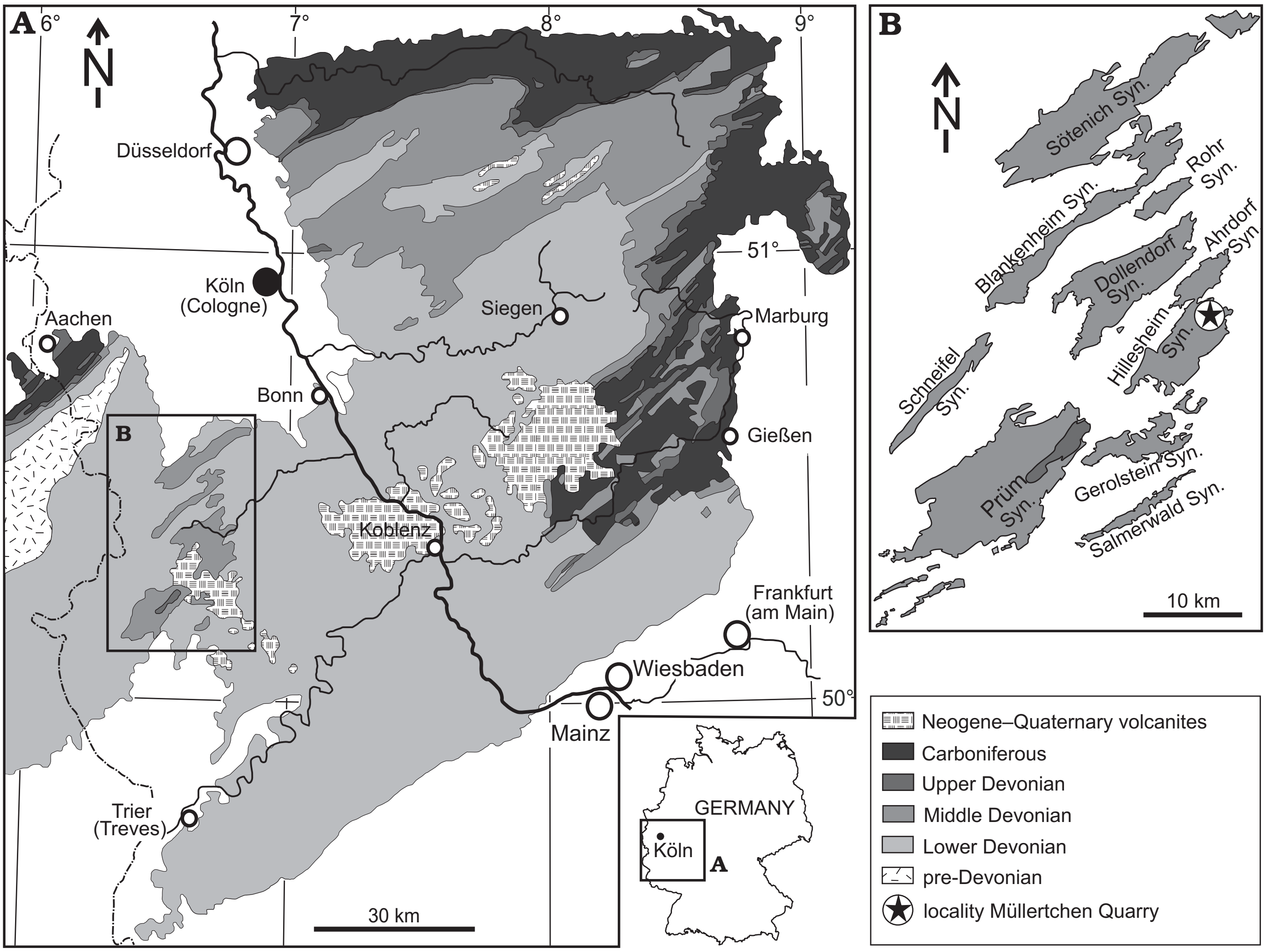
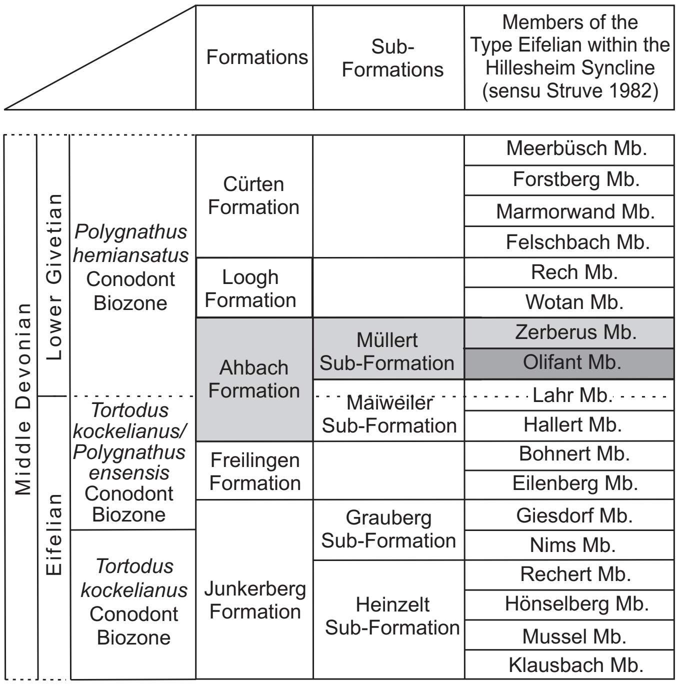


Fig. 1. Map showing location of the abandoned Müllertchen Quarry within the Hillesheim Syncline. Geological overview of the Rhenish Massif (**A**), showing the studied area (taken from Bohatý et al. 2012; modified from Korn 2008 after Walter 1995) and detailed view of the Eifel Synclines (**B**) with the fossil locality 1 (modified after Struve 1996c).

Winter (in Meyer et al. 1977) defined three characteristic facies (Facies Types A–C) of considerable importance for faunal distribution and associations in the Eifel Sea. Facies Type A, distinguished by clastic sediments with low carbonate content, is developed within the northern Eifel Limestone Synclinorium. Facies Type B is developed within the eastern part of the Eifel Limestone Synclinorium and is characterized by pure, commonly biostromal limestone, with minor marly and silty components. This facies is indicative of a shallow-water setting and was located close to a shallow-marine barrier in the NE-Eifel ("Mid-Eifelian High" sensu Winter in Meyer et al. 1977). Facies Type C, outcropping in the south of the Eifel Limestone Synclinorium, is characterized by interbedded limestone and marl deposited under normal marine conditions. Clay content increases in a southerly direction and Facies Type C passes into the clay-rich facies of the Moselle Trough (= "Wissenbach Slate"). Faber (1980: 122) characterized the lower Eifelian environment as a two-phase, shallow-marine carbonate platform, which was temporarily interrupted during regressions. He inferred a relatively undifferentiated open shelf characterized by southwest-northeast trending facies belts in the west.

The basic threefold stratigraphic division can be modified locally due to short transgressive and regressive phases leading to lateral facies displacement or loss of facies identity. In the upper Eifelian, Freilingen Formation (Fig. 2), facies differences become indistinct and Facies Type C is present everywhere. In the Lower Givetian, stromatoporoid/coral-biostromes extended all over the Eifel Sea. Krebs (1974) characterized the whole Eifel as a shelf lagoon, enclosed by a barrier to the south.

Paproth and Struve (1982: fig. 4) proposed another subdivision based on faunal composition. They identified distinct biofacies between the northern, western and southern Eifel; the *Spinocyrtia ostiolata*-biofacies being the most common in the western and the southern parts of the Eifel. The north-Eifel biofacies correlates with Facies Type A, and the *ostiolata*-biofacies with Facies Types B–C.



			Formations	Sub-Formations	Members of the Type Eifelian within the Hillesheim Syncline (sensu Struve 1982)
Middle Devonian	Lower Givetian	*Polygnathus hemiansatus* Conodont Biozone	Cürten Formation		Meerbüsch Mb.
					Forstberg Mb.
					Marmorwand Mb.
					Felschbach Mb.
			Loogh Formation		Rech Mb.
					Wotan Mb.
			Ahbach Formation	Müllert Sub-Formation	Zerberus Mb.
					Olifant Mb.
	Eifelian	*Tortodus kockelianus*/ *Polygnathus ensensis* Conodont Biozone		Maiweiler Sub-Formation	Lahr Mb.
					Hallert Mb.
			Freilingen Formation		Bohnert Mb.
					Eilenberg Mb.
			Junkerberg Formation	Grauberg Sub-Formation	Giesdorf Mb.
		Tortodus kockelianus Conodont Biozone			Nims Mb.
				Heinzelt Sub-Formation	Rechert Mb.
					Hönselberg Mb.
					Mussel Mb.
					Klausbach Mb.

Fig. 2. Lowermost Lower Givetian stratigraphy of the "Type Eifelian Profile" sensu Struve (1982); light grey: biostratigraphic distribution of fistuliporid bryozoan *Stellatoides muellertchensis* gen. et sp. nov.; dark grey: maximum distribution.

The classic fossil localities, as well as all of the fossil sites studied herein, are situated within the fossil-rich deposits of Middle Devonian Facies Type C (*Spinocyrtia ostiolata*-biofacies) in the middle and southern parts of the Eifel. Consequently, the deposits within the Hillesheim Syncline were chosen as the "Type Eifelian", the reference section for all synclines (Struve 1982), although correlation has proven difficult between synclines (Hotz et al. 1955) due to numerous bio- and lithofacies differences, especially within the northern and southernmost Eifel. The erection of regional members reflects the complexity of the depositional realm but results in a puzzling array of, in part, uncorrelated formations, subformations and members (sensu Struve 1961, 1992). Therefore, Struve (1996a, b) tried to correlate the Middle Devonian sequences using brachiopod biostratigraphy to erect valid lithostratigraphical units.

The studied bryozoans come from the abandoned "Müllertchen Quarry" near the village of Ahütte (Rhineland Palatinate, western Germany) within the Hillesheim Syncline (Eifel, Rhenish Massif) (Fig. 1). The quarry is dominated by marly and silty deposits of the Eifelian/Givetian boundary interval: lower Lahr Member of the uppermost upper Eifelian to upper Lahr, and, predominantly Olifant and Zerberus members of the Müllert Subformation (Ahbach Formation, lowermost Lower Givetian) (Fig. 2). Colonies of *Stellatoides muellertchensis* gen. et sp. nov. hosting *Chaetosalpinx tapanilai* ichnosp. nov. were found within beds of the upper Olifant Member ("Wurmweide Set" sensu Struve and Werner 1982), which is characterized by traces of *Chondrites* sp. extending from the overlying lower Zerberus Member. The facies of both the Olifant and Zerberus members indicates a soft-bottom mainly populated by crinoids (e.g., the cladids *Halocrinites sampelayoi* [Almela and Revilla, 1950] and *H. inflatus* [Schultze, 1866], the flexible *Ammonicrinus leunisseni* Bohatý, 2012), brachiopods (e.g., *Xystostrophia umbraculum* Schlotheim, 1820), receptaculids, proetid trilobites, and rugose corals (e.g., *Macgeea bathycalyx bathycalyx* [Frech, 1886] and *Microcyclus clypeatus* [Goldfuss, 1826]). Blackish plant fossils and well-preserved remains of the sponge *Astraeospongium* cf. *meniscum* (Römer, 1848) also occur. These autochthonous fossils are associated with well-preserved cystoporate, trepostome, cryptostome, and fenestrate bryozoans (Ernst 2008).

The terms subformation and member are not synonymised sensu Steininger and Piller (1999) but are used hierarchically (Ulrich Jansen, personal communication 2005; also see Bohatý 2005; Bohatý et al. 2012). Capitalization of the Givetian subdivisions follows Becker (2005, 2007).

Methods

Specimens were cleaned using the ethanol-tenside Rewoquad and micro-sand streaming methods, and initially studied using a binocular microscope. Thin sections of *Stellatoides muellertchensis* gen. et sp. nov. hosting *Chaetosalpinx tapanilai* ichnosp. nov. were made from hand specimens and from colonies embedded in the epoxy resin SpeciFix-40. They were investigated using transmitted light microscopy.

The following morphological characters were measured in thin sections: aperture width, distance between aperture centres, length of lunaria, width of lunaria, thickness of lunaria, diameter of vesicles, spacing of vesicles, and maculae length and width. Statistics are summarized in the tables accompanying the bryozoan species description.

Systematic palaeontology

Phyllum Bryozoa Ehrenberg, 1831

Class Stenolaemata Borg, 1926

Order Cystoporata Astrova, 1964

Suborder Fistuliporina Astrova, 1964

Family Fistuliporidae Ulrich, 1882

Genus *Stellatoides* nov.

Type species: *Stellatoides muellertchensis* gen. et sp. nov., by monotypy; see below.

Etymology: From Latin *stellatus*, star shaped; in reference to the presence of star-shaped maculae.

Diagnosis.—Colony encrusting, lamellar, often with multiple overgrowths. Maculae stellate with depressed centres. Autozooecia cylindrical with thin granular walls and complete diaphragms. Autozooecial apertures rounded. Lunaria

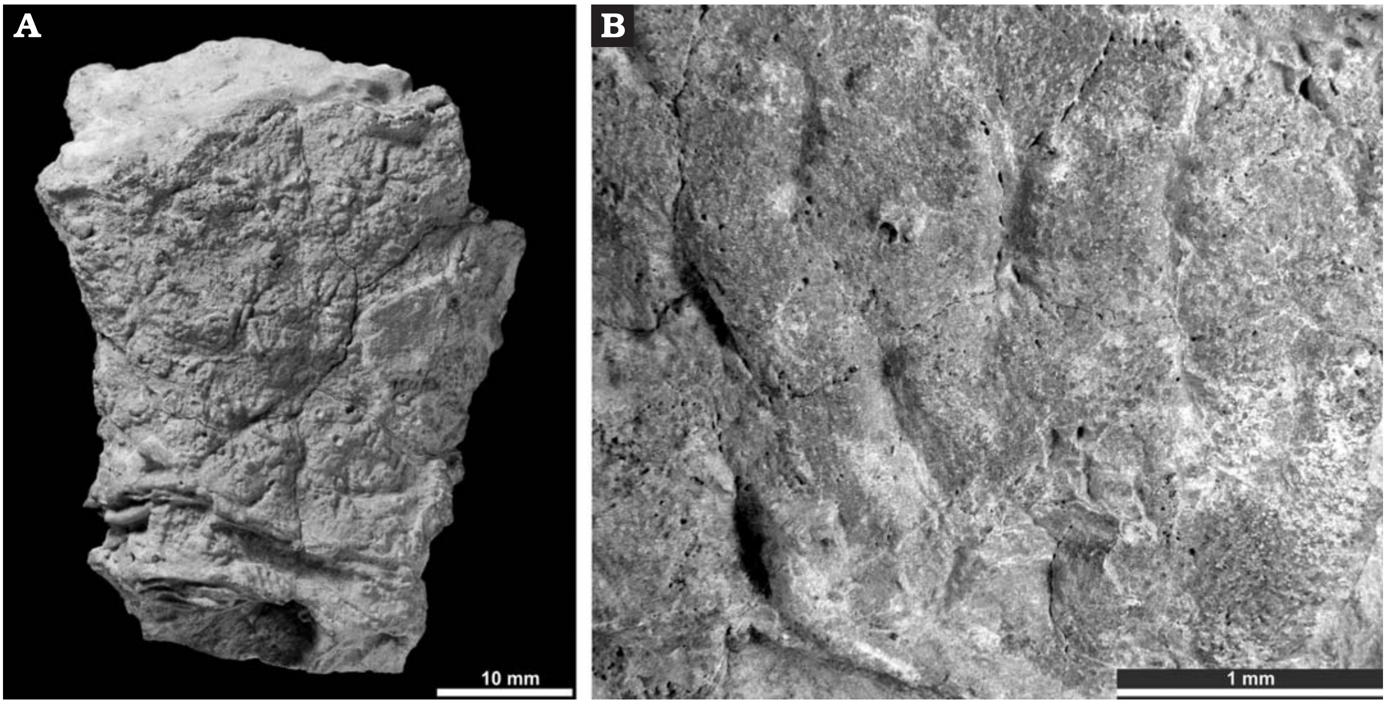


Fig. 3. Fistuliporid bryozoan *Stellatoides muellertchensis* gen. et sp. nov., Middle Devonian (Lower Givetian, Ahbach Formation) of the abandoned "Müllertchen Quarry" (Hillesheim Syncline, Eifel, Rhenish Massif, northwestern Rhineland-Palatinate, Germany). **A**. Paratype SMF 21.115, goblet-shaped colony, side view. **B**. Paratype SMF 21.110, fragment of goblet-shaped colony showing maculae.

triangular. Autozooecia separated by extrazooidal vesicular skeleton. Acanthostyles occurring in roofs of vesicles.

Remarks.—*Stellatoides* gen. nov. differs from other known cystoporate bryozoans in having stellate maculae. *Fistuliporella* Simpson, 1897 resembles *Stellatoides* in the morphology of the autozooecia and vesicular skeleton. However, the new genus possesses long triangular lunaria unlike the semicircular ones found in *Fistuliporella*. *Eridopora* Ulrich, 1882 has long triangular lunaria but differs from *Stellatoides* in having smaller vesicles. Similar elongated maculae with depressed centres are known in *Ceramella* Hall and Simpson, 1887, which belongs to the family Hexagonellidae Crockford, 1947. However, maculae in *Ceramella* are not stellate, and this genus is characterised by a bifoliate colony shape contrasting with the encrusting colonies of *Stellatoides* gen. nov.

Stratigraphic and geographic range.—Lower Givetian (Middle Devonian) of the Rhenish Massif, Germany.

Stellatoides muellertchensis gen. et sp. nov.

Figs. 3–5.

Etymology: Named after the type locality Müllertchen Quarry.

Type material: Holotype: SMF 21.108 (Fig. 4A), 4 thin sections. Paratypes: SMF 21.109-SMF 21.116 (19 thin sections from 4 colonies and 5 unprepared colonies).

Type locality: Üxheim-Ahütte, abandoned Müllertchen Quarry, Hillersheim syncline, Eifel, western Rhenish Massif (geological map sheet 5606 Üxheim; 50°21', 6°46').

Type horizon: Set 2 "Wurmweide", Olifant Member, Müllert Subformation (Ahbach Formation, lowermost Lower Givetian, Middle Devonian; *Polygnathus hemiansatus* Conodont Biozone).

Other material.—Eight cleaned colonies in the private collection of Robert Leunissen (Nideggen-Wollersheim, Germany).

Diagnosis.—As for monotypic genus.

Description.—Colonies lamellar, often with multiple overgrowths (Fig. 4B), freely growing or encrusting ephemeral substrates and producing hollow ramose, goblet-shaped colonies (Fig. 3A). Encrusting sheets 0.5–2.2 mm in thickness, multilayered colonies reaching up to 4.3 mm thick. Maculae

Table 1. Measurements (in mm) of fistuliporid bryozoan *Stellatoides muellertchensis* gen. et sp. nov. (Middle Devonian, Rhenish Massif). Summary descriptive statistics of three colonies. Abbreviations: CV, coefficient of variation; MIN, minimum values; MAX, maximum values; N, number of measurements; SD, sample standard deviation; X, arithmetic mean.

	N	X	SD	CV	MIN	MAX
Aperture width	30	0.16	0.024	15.21	0.11	0.21
Aperture spacing	30	0.46	0.066	14.39	0.35	0.58
Lunarium length	20	0.13	0.030	22.63	0.07	0.20
Lunarium width	20	0.13	0.026	20.65	0.08	0.20
Lunarium thickness	20	0.03	0.009	26.97	0.02	0.05
Diameter of vesicles	30	0.22	0.051	22.83	0.15	0.35
Spacing of vesicles	30	0.15	0.048	31.50	0.07	0.25
Vesicles per aperture	20	6.45	1.050	16.28	5.0	9.0
Maculae length	20	6.6	2.037	30.78	2.8	12.0
Maculae width	20	1.8	0.586	32.66	1.0	2.9
Maculae spacing	20	9.8	1.917	19.46	6.4	13.8

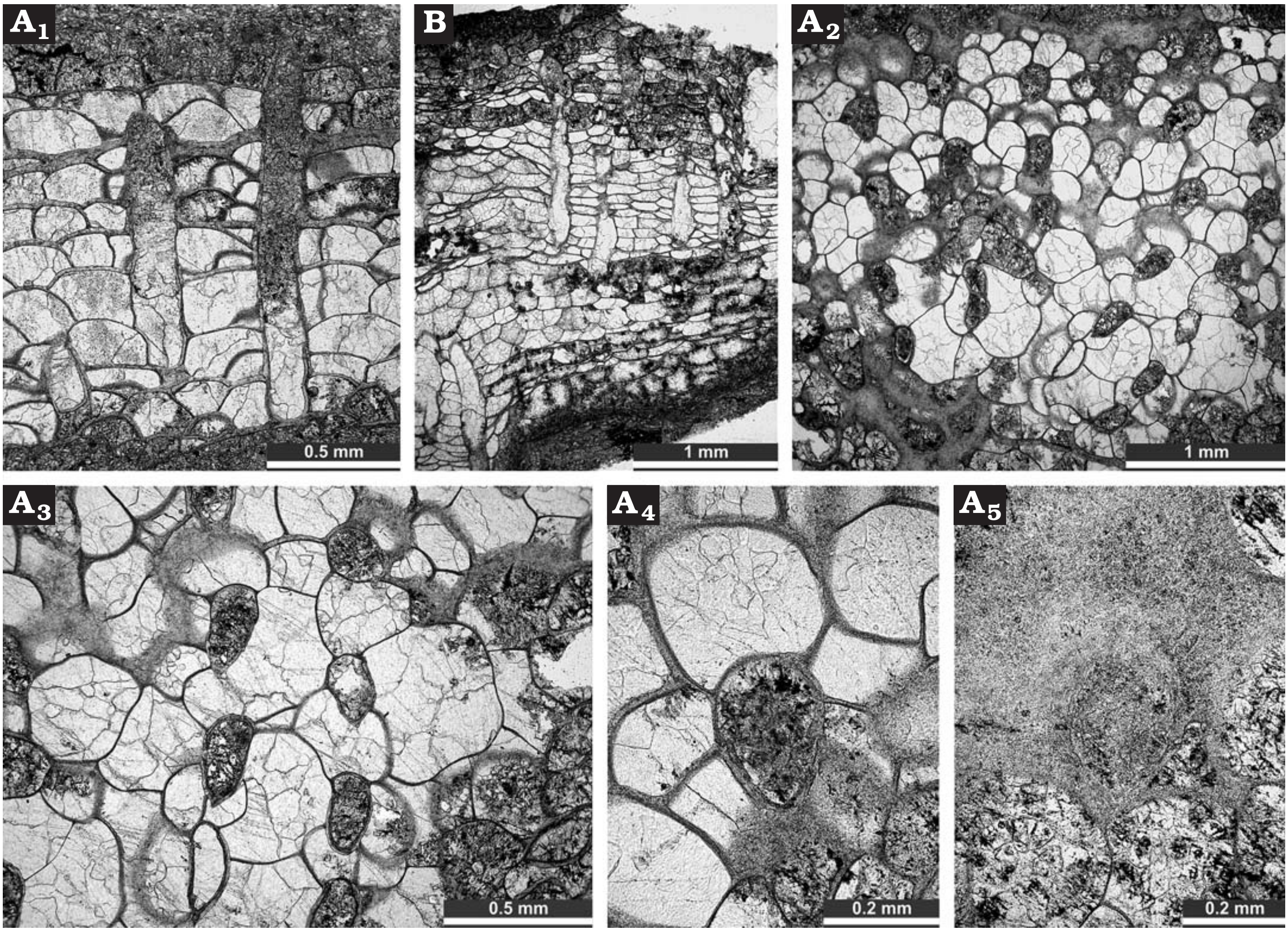


Fig. 4. Fistuliporid bryozoan *Stellatoides muellertchensis* gen. et sp. nov., Middle Devonian (Lower Givetian) of the Rhenish Massif, north-western Rhineland-Palatinate, Germany. **A**. Holotype SMF 21.108, transverse section showing autozooecial chambers and vesicular skeleton (A_1), tangential sections showing autozooecial apertures with lunaria and vesicles (A_2–A_5). **B**. Paratype SMF 21.113, longitudinal section showing multilayered secondary overgrowths.

elongate (Fig. 3B), 2.8–12.0 mm long by 1.0–2.9 mm wide, spaced 6.4–13.8 mm from centre to centre, stellate, with depressed centres comprising vesicular tissue (Fig. 4A_2); shorter and wider at the base of ramose colonies, becoming longer and narrower in distal parts of goblet-shaped colonies.

Autozooecia cylindrical (Fig. 4A_1), growing from thin epitheca, bending sharply towards colony surface at their bases. Apertures circular to oval. Lunaria triangular, consisting of hyaline material, directed towards the nearest macula. Basal diaphragms rare, thin, horizontal or inclined. Vesicles medium to large in size (Fig. 4A_3), separating autozooecia in 1–2 rows, 5–9 surrounding each autozooecial aperture, polygonal in tangential section, box-like to hemispherical, with plane or concave roofs, consisting of granular skeleton. Single acanthostyle occurring at centre of each vesicle roof (Fig. 4A_5), with narrow laminated sheath and distinct hyaline core, 0.020–0.035 mm in diameter. Autozooecial walls granular, 0.010–0.020 mm thick.

Stratigraphic and geographic range.—As for genus.

Systematic ichnology

Ichnogenus *Chaetosalpinx* Sokolov, 1948

Type species: *Chaetosalpinx ferganensis* Sokolov, 1948; Silurian, Uzbekistan (see Zapalski 2007).

Chaetosalpinx tapanilai ichnosp. nov.

Fig. 5.

Etymology: Named for Leif Tapanila (Idaho State University) in recognition of his work on bioclaustrations.

Type material: Holotype: SMF 21.118, specimen shown in Fig. 5C. Paratypes: SMF 21.117, SMF 21.119-SMF 21.125.

Type locality: Üxheim-Ahütte, abandoned Müllertchen Quarry, Hillersheim Syncline, Eifel, western Rhenish Massif (UTM: 50°20’05.16’’N, 6°46’15.19’’E).

Type horizon: Set 2 “Wurmweide”, Olifant Member, Müllert Subformation (Ahbach Formation, lowermost Lower Givetian, Middle Devonian; *Polygnathus hemiansatus* Conodont Biozone).

Diagnosis.—*Chaetosalpinx* bioclaustrated by bryozoans

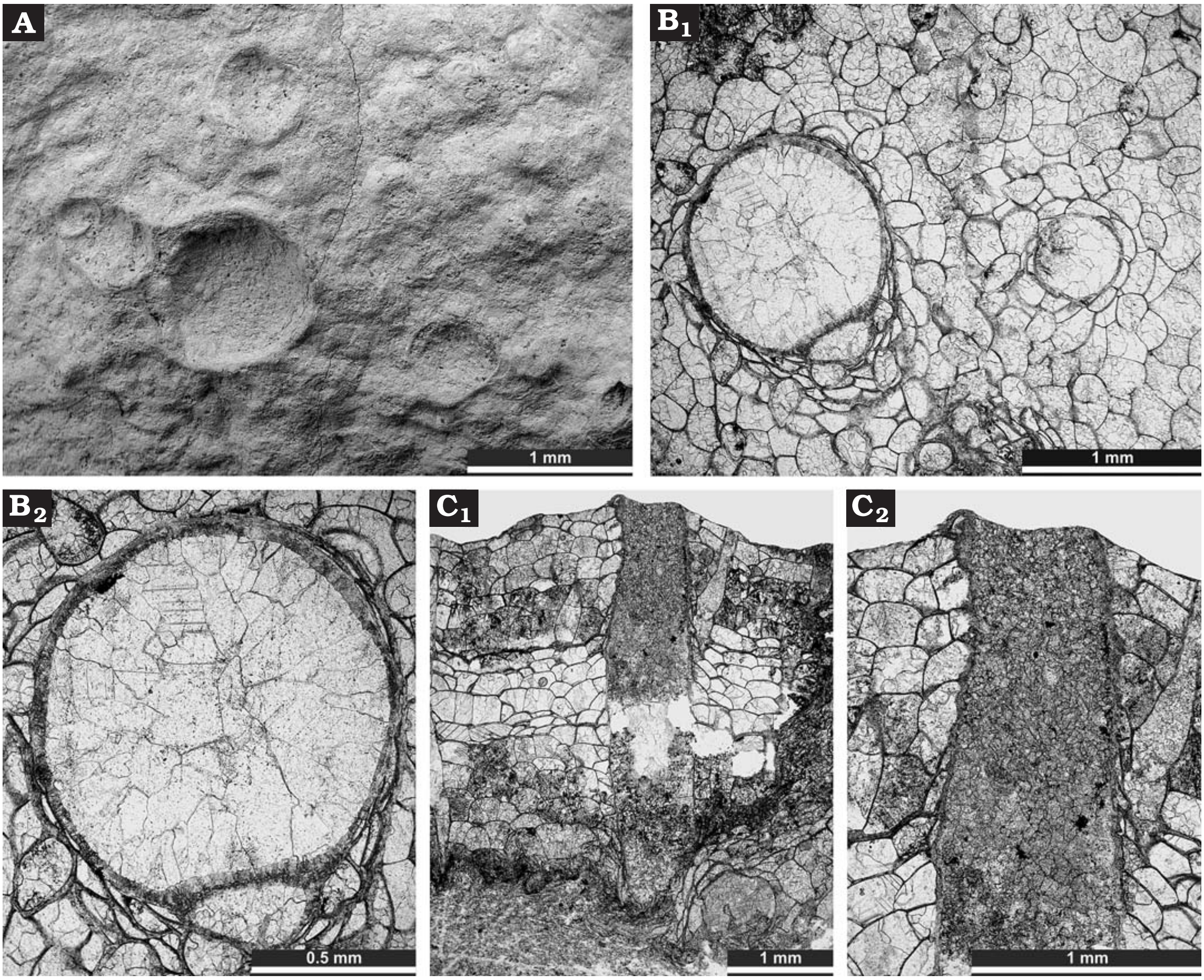


Fig. 5. Cylindrical embedment trace (bioclaustration) *Chaetosalpinx tapanilai* ichnosp. nov., Middle Devonian (Lower Givetian) of the Rhenish Massif, north-western Rhineland-Palatinate, Germany. **A**. Paratype SMF 21.115, colony surface of fistuliporid bryozoan *Stellatoides muellertchensis* gen. et sp. nov. showing tubes of *C. tapanilai*. **B**. Paratype SMF 21.122, tangential section of tubes of *C. tapanilai*. **C**. Holotype SMF 21.118, longitudinal section of a tube.

(*Stellatoides muellertchensis* gen. et sp. nov.), cylindrical, averaging 0.7 mm in diameter, ranging from 0.4–1.3 mm, aperture circular, less commonly elliptical or reniform, edges raised slightly above surface of host bryozoan.

Description.—Cylindrical embedment trace (bioclaustration) found within colonies of cystoporate bryozoan *Stellatoides muellertchensis* gen. et sp. nov. Cylinder up to at least 4 mm long, oriented vertically (i.e., parallel to upward bryozoan growth direction) for most of length; straight, parallel sided, infilled either with calcite cement (Fig. 5B) or fine-grained sediment (Fig. 5C). No internal structures observed. Originating at or very close to the base of bryozoan colony, basal part of cylinder apparently horizontal in some examples. Cylinder bounded by wall formed by bryozoan skeleton (?interior wall calcification), up to 0.06 mm thick but usually about 0.03 mm thick, other bryozoan skeletal walls deflected upwards in vicinity of tube (cf. the downwards deflection of walls around autozooecial tubes); cystose skeleton often concentrically arranged around the tube when viewed in transverse section. Tube diameter ranging from 0.4–1.3 mm, averaging 0.7 mm. Numerous individuals of varying diameters opening on surface of same host bryozoan colony, located in intermacular areas, arranged semiregularly. Apertures circular, less commonly elliptical or reniform, edges raised by up to 0.3 mm above surrounding colony surface (Fig. 5A).

Remarks.—The new species fits within the concept of the ichnogenus *Chaetosalpinx* as applied by Stel (1976), Tapanila (2002, 2005, 2006), and Tapanila and Ekdale (2007) for tubular, vertical embedment traces with margins defined by skeletal walls secreted by biomineralized host organisms. Seven species of *Chaetosalpinx* have been described: the type species *C. ferganensis* Sokolov, 1948, and its subjec-

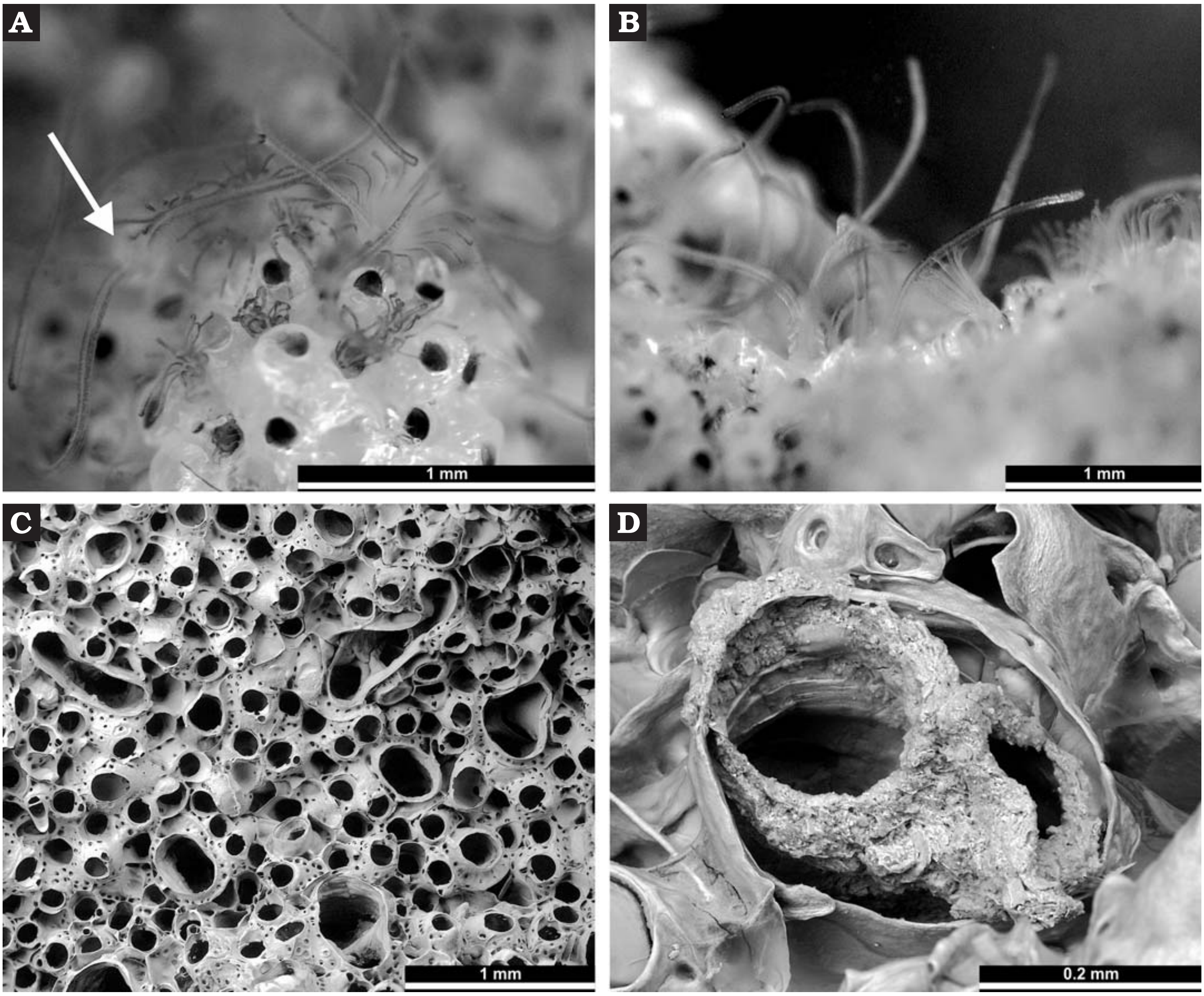


Fig. 6. Spionid polychaete symbionts in the Recent cheilostome bryozoan *Celleporaria brunnea* (Hincks, 1884), Point Loma, San Diego, California. **A**. Living associations showing two long palps emerging from a spionid tube (arrowed), shorter tentacles of the bryozoan and black opercula. **B**. Spionid palps extending above level of bryozoan lophophores. **C**. Scanning electron microscope of bleached colony (NHM 2010.11.30.1) showing numerous spionid worm bioclaustrations varying in shape and size but consistently larger than the bryozoan orifices and new buds. **D**. Scanning electron micrograph of dried, unbleached colony showing mud tube constructed by a spionid worm surrounded by calcareous tube formed by the bioclaustrating bryozoan (NHM 2010.11.30.1).

tive synonyms *C. khatangaensis* Sokolov, 1948, *C. huismani* Stel, 1976 and *C. groningae* Stel, 1976 (see Tapanila 2002, 2005), *C. siberiensis* Sokolov, 1948, *C. rex* Tapanila, 2002, and *C. alamo* Tapanila, 2006. Tubes of *C. siberiensis*, *C. rex*, and *C. alamo* are conical, narrow basally, unlike the parallel-sided *C. tapanilai* ichnosp. nov. The diameter of *C. tapanilai* (0.4–1.3 mm) contrasts with the larger tubes of *C. alamo* (2.5–12.8 mm) and *C. rex* (up to 5 mm), whereas the smaller tubes of *C. ferganensis* range from 0.05–0.4 mm in diameter according to Tapanila (2002). Only *C. siberiensis* has a tube diameter (0.3–0.9 mm according to Stel 1976) overlapping that of *C. tapanilai* in diameter. However, as previously noted this species is conical and furthermore the tubes are described as being sinuous in longitudinal sections whereas those of *C. tapanilai* are straight.

Host symbionts for previously described species of *Chaetosalpinx* include rugose and tabulate corals (Tapanila 2005: table 1) as well as stromatoporoid sponges (Tapanila 2006). This Ordovician (Caradoc)–Devonian (Givetian) ichnogenus has not been described previously in bryozoans. Perhaps the closest similarity among bryozoans is with an un-named bioclaustration described from mid-Cretaceous cyclostomes (Taylor and Voigt 2006). This has a similar diameter to *C. tapanilai* but is distinctly funnel shaped rather than cylindrical. Incipient tubular bioclaustrations are present in some Recent bryozoans growing around symbiotic spionid worms and tanaiid crustaceans (see below).

Discussion

Colony shape.—*Stellatoides muellertchensis* sp. nov. developed encrusting colonies, commonly with multiple secondary overgrowths. This colony shape is broadly distributed among fistuliporine cystoporates (Utgaard 1983: 380). However, many colonies of *S. muellertchensis* are more unusual in being goblet-shaped with extensive encrusting bases and expanded distal edges (Fig. 3A). These colonies are up to 11 cm high and 5.5 cm wide, and some bifurcate. The inner walls are smooth, and it is likely that the colonies grew around ephemeral substrates which decayed after death.

Deposits at the type locality in which *S. muellertchensis* is found are dominantly marls and siltstones. The environment in which these bryozoans lived was a quiet basin of soft substrates. Encrusting bryozoans are generally poor competitors for space and consequently tend to occur more commonly and abundantly on ephemeral rather than more permanent substrates (McKinney and Jackson 1989). Together with another cystoporate bryozoan, *Fistuliphragma gracilis* Ernst, 2008, *S. muellertchensis* is the only encrusting bryozoan species in the assemblage from the Müllertchen Quarry (Ernst 2008). Like *S. muellertchensis*, *F. gracilis* occurs mainly in the form of hollow tubes (cavariiform colonies), which were also probably developed around an ephemeral substrate. Other bryozoans from Müllertchen Quarry are erect and branched (*Cliotrypa*, *Leioclema*, *Intrapora*, *Acanthoclema*, and *Streblotrypella*), or erect and reticulate (diverse fenestrates). Tubes of *Fistuliphragma gracilis* are of consistent size, so it can be inferred that this bryozoan encrusted only a certain type of living substrate. The same assumption can be made for *Stellatoides muellertchensis*. Among 13 studied colonies, only two are freely encrusting, the rest being goblet-shaped. Identification of "soft-bodied" substrates is sometimes possible based on bioimmured textures (e.g., Rohr and Boucot 1989; Taylor 1990) but no bioimmurations are visible in *S. muellertchensis* and *F. gracilis*. In general, bryozoans are capable of using any suitable (stable) substrates that are available (Hageman et al. 2000). However, substrate preferences have been documented for some epibiotic bryozoans (Stebbing 1971, 1972; Barnes 1994, 1995). Various soft-bodied organisms can act as hosts for epibiotic bryozoans, including hydroids, ascidian tunicates, sponges, soft worm tubes, vascular plants and algae (e.g., Hayward 1980; Hageman et al. 2000; Kocak et al. 2002).

Maculae.—Maculae of *Stellatoides muellertchensis* contrast with those of most other bryozoans. They are 2.8–12.0 mm long, 1.0–2.9 mm wide and 0.6–1.0 mm deep, and spaced regularly on the colony surface. The centre of each macula consists of broad, flat vesicles, surrounded by 8–20 rays giving the distinct stellate shape. Maculae edges are elevated so that areas between maculae are depressed (Fig. 3B). In goblet-shaped colonies, maculae are more rounded near the colony base, becoming longer and more narrow near the edge of the goblet. This may be an adaptation to different hydrodynamic conditions at different levels of the water column above the boundary layer. The shape and dimensions of maculae in encrusting colonies could not be observed, but they are at least as deep as those in goblet shaped colonies, as observed in longitudinal thin sections.

The stellate shape of maculae is unique for *S. muellertchensis* in the family Fistuliporidae. However, greater similarities are evident with the maculae of bryozoans from the family Constellariidae, including *Constellaria* Dana, 1846 from the Ordovician of the USA, and *Revalopora* Vinassa de Regny, 1921 from the Ordovician of Estonia. However, the rays in constellariid maculae are commonly formed from bifoliate ridges, whereas rays in *Stellatoide*s are formed by loosely packed autozooecia. Similar constructions can also be observed in colonies of the Devonian genus *Botryllopora* Nicholson, 1874 and the Silurian genus *Inconobotopora* Tang and Cuffey, 1998. These disc-shaped cystoporates have central clusters of vesicles surrounded by ridges with autozooecia arranged in stellate patterns. Stellate maculae also occur in other stenolaemates groups including the trepostomes (Key et al. 2002) in response to the development of colony wide feeding currents (Key et al. 2011).

Bioclaustration.—Colonial animals such as bryozoans, corals and sponges frequently harbour symbionts. The inherent plasticity in colony growth and the fact that colonial animals are able to sustain partial mortality (i.e., death of some but not all zooids) makes them particularly suitable as hosts for smaller symbionts. The discovery of symbiont bioclaustrations in a Devonian bryozoan is therefore not totally unexpected. Indeed, it is perhaps surprising that more such bioclaustrations have not been recorded in fossil bryozoans. Bioclaustrations previously reported in fossil bryozoans include only the ichnogenera *Catellocaula* Palmer and Wilson, 1988, found in Ordovician trepostomes, and *Caupokeras* McKinney, 2009, an inferred hydroid bioclaustration in Devonian fenestrates. In addition, un-named bioclaustrations have been described in Cretaceous cheilostomes (Voigt 1955; Ernst 1985) and cyclostomes (Taylor and Voigt 2006). The discovery and description of *Chaetosalpinx tapanilai* ichnosp. nov. in a Devonian cystoporate bryozoan therefore adds significantly to our knowledge of bryozoan bioclaustrations, as well as providing the first example in a cystoporate bryozoan.

Modern analogues of *C. tapanilai* can be found in some Recent cheilostomes and cyclostomes, although these structures have yet to be fully described. Taylor (1991) reported the occurrence of small tubes within colonies of *Disporella gordoni* Taylor, Schembri, and Cook, 1989, a cyclostome bryozoan often living symbiotically with hermit crabs in New Zealand. The tubes have diameters of 1–6 mm and are distributed randomly with respect to the exhalent water outlets (monticular maculae) found in this cyclostome bryozoan. Some of the tubes are occupied by tanaidacean crustaceans, others by spionid polychaetes. Similar infestation of a cheilostome bryozoan, *Celleporaria brunnea* (Hincks, 1884), was recently observed by one of us (PDT) in southern California (Fig. 6). In this case the tubes were all occupied by spionids and were made of bryozoan skeleton, with a planar spherulitic fabric characteristic of an exterior wall secreted against a cuticle, built around the tubes of agglutinated mud constructed by the spionids themselves. The two feeding tentacles (peristomial palps) of the spionids maintained a sweeping motion above the level of the bryozoan tentacle crowns, occasionally contacting a bryozoan tentacle and sometimes eliciting retraction of the tentacle crown. Some of the tube apertures are elliptical, others dumbbell-shaped accommodating both limbs of the U-shaped mud tube of the spionid (Fig. 6D).

Spionids are suspension feeders and may potentially compete with the host bryozoan for food, occupying space where feeding zooids would otherwise have been located. Unlike symbiotic hydroids, which have been shown to be beneficial to their host bryozoans because of the protection afforded by their nematocysts (e.g., Osman and Haugsness 1981), it unclear how spionids can benefit their hosts. Therefore, the symbiosis is more likely to be parasitic than mutualistic.

Another spionid, *Polydora villosa*, can form bioclaustrations (described as “burrows”) in modern corals belonging to the genera *Montipora* and *Porites* (Liu and Hsieh 2000). These traces are U-shaped, the proximal part being a boring that cuts through the coral skeleton but the distal part developing as a bioclaustration simultaneously with upward growth of the host coral. Like the spionids hosted by bryozoans, the host coral secretes a calcareous lining around the mud tube made by the worm. Similarly, Lewis (1998) has described examples of the spionid *Dipolydora armata* inhabiting colonies of *Millepora complanata*. This hydrozoan coral also secretes tubes around the worms that project above the colony surface. While it would be stretching the available evidence too far to attribute the trace fossil *Chaetosalpinx* unequivocally to the activities of spionid worms, these modern symbioses involving colonial host organisms do provide plausible ecological analogues which help in understanding this Ordovician–Devonian trace fossil.

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