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Rare stromatoporoids from the Lower Devonian (Emsian) of Nevada, and their biostratigraphic and paleobiogeographic significance

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Abstract.—Two previously known species of stromatoporoids are reported from Nevada: *Stromatoporella perannulata*, from the Bartine Member of the McColley Canyon Formation (middle Emsian); and *Stictostroma moosense*, from the Oxyoke Canyon Sandstone (uppermost Emsian). A new species, *Syringodictyon nevadense* n. sp., is described from the Coils Creek Member of the McColley Canyon Formation (upper Emsian). *Stromatoporella perannulata* also occurs in Emsian-age strata on Ellesmere Island, arctic Canada, and in strata of Emsian and/or Eifelian age in Ontario, New York, Ohio, and Kentucky. Outside Nevada, *Syringodictyon* is confined to the Emsian of Ellesmere Island, and Emsian/Eifelian of Ontario and New York. *Stictostroma moosense* is known from only the Emsian/Eifelian of Ontario.

It is concluded that the three Nevada specimens are Emsian in age. This implies that in other localities where two of the species, *S. perannulata* and *S. moosense*, occur in strata where the placement of the Emsian-Eifelian boundary is in question, it might be higher than previously thought. The presence of the two species, plus *Syringodictyon*, in both the Old World Realm (Nevada, arctic Canada) and the Eastern Americas Realm (Ontario, New York, Ohio, Kentucky), infers a selective marine connection between the two realms that was not available to other taxa. The breach in the inter-realm barrier most likely occurred as a shallow seaway across the Canadian Shield.

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Introduction

Stromatoporoids are very rare components of the fossil fauna of the middle–upper Emsian (upper Lower Devonian) of Nevada. Three specimens were collected from central Nevada (Fig. 1; Appendix). Three specimens are indeed a small sample size, but considering stromatoporoids' very small populations in the host strata, any amount is significant. All three specimens have both biostratigraphic and paleobiogeographic value.

Although rugose corals are abundant in strata of the study area (Pedder and Murphy, 2004), there are very few stromatoporoids. This situation is most likely due to the fact that stromatoporoids lived in shallower water than most corals (e.g., Walker and Alberstadt, 1975), and/or because corals were better able to resist the effects of fine-grained carbonate or siliciclastic sediments suspended in the water. Two of the stromatoporoid specimens are considered laminar in shape: (1) *Stromatoporella perannulata* Galloway and St. Jean, 1957, does not include any sediments nor other organisms; and (2) *Syringodictyon nevadense* n. sp. grew on an undulating surface, so its shape was probably inherited from that surface. The latter's skeleton includes a sedimentary inclusion, suggesting the bedding surface upon which it grew was not highly consolidated. The specimen of *Stictostroma moosense* (Parks, 1904) encrusted the upper surface of a favositid tabulate coral, inheriting its shape from the coral. Both of these skeletal morphologies are believed to be adaptations to soft substrate (Webby and Kershaw, 2015, p. 432–434, 464–468). Soft sediments accumulate below wavebase, often in deeper water in front of reefs (e.g., Dolphin and Klovan, 1970), or in lagoons in back of reefs or banks (e.g., Laporte, 1967).

Stratigraphy

Lithostratigraphy.—Lithostratigraphic nomenclature adopted in this paper is based on Murphy and Gronberg (1970) for the Roberts Mountains, and Kendall et al. (1983) for the Sulphur Spring Range; the reader is referred to these papers for more detailed stratigraphic information. Lithostratigraphic units from which the stromatoporoids were collected are illustrated in Figure 2. The McColley Canyon Formation is found in both the Roberts Mountains and the southern Sulphur Spring Range. In the latter, there are four members, in ascending order: Kobeh Limestone; Bartine Member; Beacon Peak Member; and Coils Creek Member. The Oxyoke Canyon Sandstone and Sadler Ranch Formation occur above the Coils Creek Member. In the Roberts Mountains, there are only three members in the McColley Canyon Formation—the Beacon Peak Member is absent. Above the Coils Creek Member, there is an unconformity, representing the time when the Oxyoke Canyon Sandstone and Sadler Ranch Formation would have been deposited (Vodrážková et al., 2011).

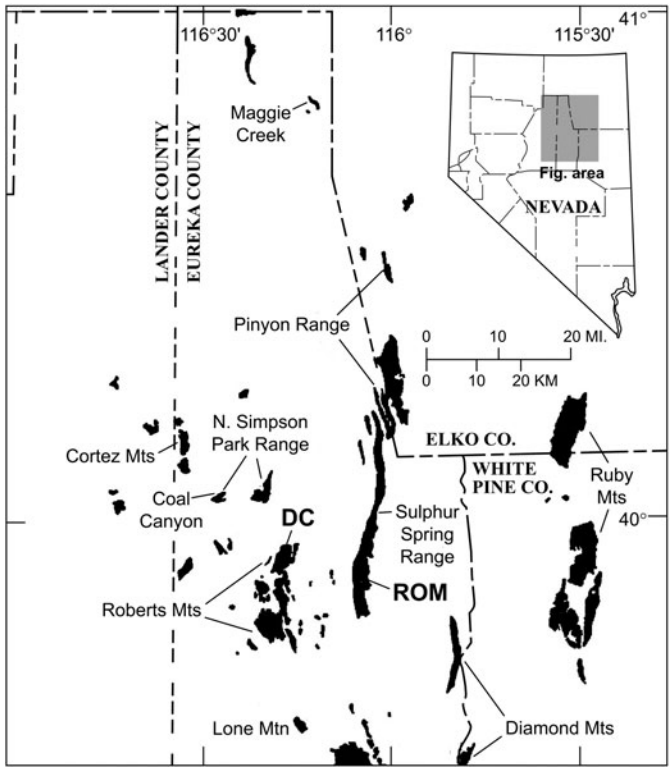

Figure 1. Index map of a portion of central Nevada with county boundaries. Abbreviations: DC = Dry Creek; ROM = Romano Ranch. Modified after Pedder and Murphy (2004, fig. 1).

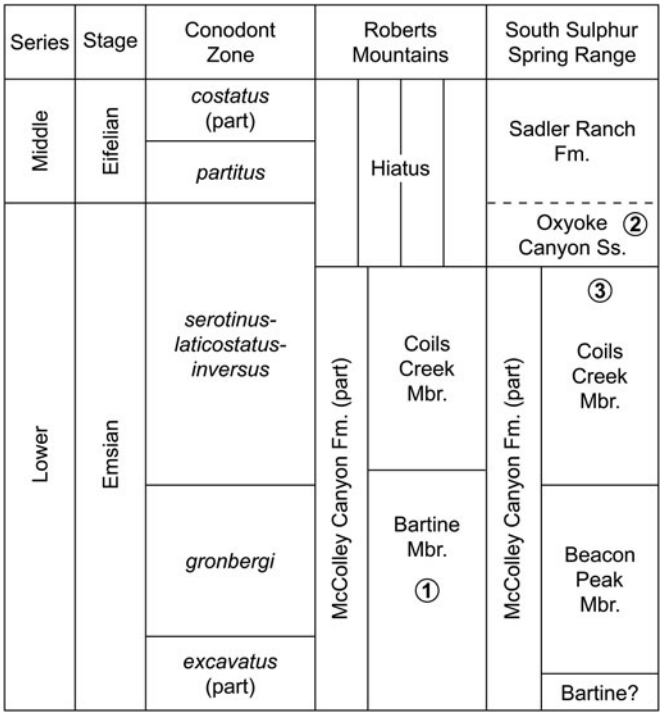

Figure 2. Chronostratigraphy and lithostratigraphy of the study area (after Morrow and Sandberg, 2008). Stromatoporoid occurrences: (**1**) *Stromatoporella perannulata*; (**2**) *Stictostroma moosense*; (**3**) *Syringodictyon nevadense* n. sp.

Chronostratigraphy.—The age of the various strata found in association with the Lower–Middle Devonian (Emsian–Eifelian) is somewhat unsettled (e.g., Pedder and Murphy, 2004; Morrow, 2007; Pedder, 2010). The age of these strata, as depicted in Figure 2, is influenced to some extent by the absence of the *patulus* Zone, which is not found outside the Czech Republic (C.A. Sandberg, personal communication, 2021). At the Romano Ranch localities (Appendix), the *partitus* Zone (Eifelian) sits conformably on the *serotinus* Zone (Emsian).

The McColley Canyon Formation in the Sulphur Spring Range and Roberts Mountains is Pragian to Emsian in age (Fig. 2). *Stromatoporella perannulata* Galloway and St. Jean, 1957, is from the lower Bartine Member. In the southern Sulphur Spring Range, the Coils Creek Member of the McColley Canyon Formation is Emsian in age. *Syringodictyon nevadense* n. sp. is from the Coils Creek Member. The Oxyoke Canyon Sandstone in the Sulphur Spring Range is of Emsian age. *Stictostroma moosense* (Parks) is from the Oxyoke Canyon Sandstone.

Stromatoporoid biostratigraphy.—Sessile benthic organisms such as stromatoporoids rarely are considered potential candidates in biostratigraphic correlation; however, as with most benthic marine organisms, they most likely had planktonic larvae. Some stromatoporoid species occur over large areas, and their potential utility in correlation has been noted by Webby et al. (2015).

In an article that is relevant to the present study, Prosh and Stearn (1993) found that four species of stromatoporoids (*Stromatoporella perannulata* Galloway and St. Jean, 1957; *Stictostroma mamilliferum* Galloway and St. Jean, 1957; *Habrostroma proxilaminatum* [Fagerstrom, 1961]; *Parallelopora campbelli* Galloway and St. Jean, 1957) from the Emsian-age Blue Fiord Formation of Ellesmere Island, arctic Canada, also occur in the Detroit River Group of southwestern Ontario, Canada. They cited Uyeno's (1990) detailed conodont biostratigraphic work to support the Emsian age of the Blue Fiord Formation. Prosh and Stearn (1993, p. 2465) stated, "The Detroit River Group of southwestern Ontario contains a diverse but endemic fauna that has made dating difficult and imprecise. Studies of corals, brachiopods, goniatites, and, more recently, conodonts have generally yielded largely or wholly Middle Devonian ages for the Detroit River Group or its immediate correlatives in New York, Ohio, and Michigan." Prosh and Stearn (1993) concluded that the presence of Emsian-age stromatoporoids in the Detroit River Group of Ontario, as documented by Fagerstrom (1982), along with then-existing conodont data, indicated an Emsian age for the Detroit River Group, not a Middle Devonian (Eifelian) age. They also inferred that this age revision might also apply to the Onondaga Limestone of New York.

Klapper and Oliver (1995) disagreed with Prosh and Stearn (1993), in that they maintained a middle Devonian (Eifelian) age for the Detroit River Group of central-southwestern Ontario, and the correlative Onondaga Limestone of New York and the Niagara Peninsula of Ontario. They stated (p. 1070), "The conodont and goniatite evidence is much stronger than indicated by [Prosh and Stearn] and too strong to be set aside in response to their new data." They also concluded (p. 1072), "The ranges of the stromatoporoid species common to the Blue Fiord and Detroit River have not been adequately tested in zonal biostratigraphy

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…" C.A. Sandberg, accompanied by Klapper, collected and identified conodonts of the lower Eifelian *partitus* Zone from the Detroit River Group of southwestern Ontario (C.A. Sandberg, personal communication, 2018).

In his reply to Klapper and Oliver's (1995) discussion, Prosh (1995) noted that the Detroit River and Onondaga faunas are very endemic. He made no significant changes to his original conclusions, saying that (p. 1076) "The Detroit River Group of Ontario is mostly Lower Devonian. The Edgecliff and Nedrow members of the Onondaga Limestone of New York are also Lower Devonian."

Of the three stromatoporoid species described here from Nevada, *Stromatoporella perannulata* is the most ubiquitous, occurring in the middle Emsian of Nevada, and Emsian of the Blue Fiord Formation of Ellesmere Island (Prosh and Stearn, 1993, 1996). It also occurs in strata of less-certain age in: (1) southwestern Ontario glacial drift (Nicholson, 1873; Parks, 1936); (2) southwestern Ontario, Detroit River Group, including the Formosa Reef Limestone (Fagerstrom, 1982); (3) Niagara Peninsula, Ontario, Onondaga Limestone (St. Jean, 1986); (4) Ohio, Columbus Limestone (Galloway and St. Jean, 1957; Fagerstrom, 1982); and (5) Kentucky, Jeffersonville Limestone (Galloway and St. Jean, 1957).

In the past, *Stictostroma moosense* has been known exclusively from the Kwataboahegan Formation of eastern Ontario, near the Kwataboahegan River, which flows into James Bay (Fagerstrom, 1982). According to Fagerstrom (1982), Sanford et al. (1968) correlated the Kwataboahegan Formation with the Amherstburg Limestone, lower Detroit River Group, of southwestern Ontario. Klapper and Oliver (1995) placed the Amherstburg Limestone spanning, but mostly above, the Emsian-Eifelian boundary. Telford (1989, p. 127) stated, "Strata of the Kwataboahegan Formation are the most fossiliferous of all Devonian units in the Moose River Basin. The fauna is dominated by corals, stromatoporoids and brachiopods …" He (p. 127–128) said that the corals and brachiopods in the Kwataboahegan Formation, "… have many elements in common with the Schoharie-Bois Blanc-Onondaga faunas of the Appalachian Basin and those of the Michigan Basin Detroit River Group." He also noted that conodonts from the lower Kwatboahegan Formation are probably Emsian in age. For New York, Rickard (1975, pl. 3) illustrated the Schoharie and Bois Blanc formations as upper Emsian, and the Onondaga Formation as lower–middle Eifelian. Although Norris (1993, fig. 8.4) depicted the Kwataboahegan Formation as lower Eifelian, he stated (p. 678), "The conodonts from the lower third of the [Kwataboahegan] formation are similar to those from the Edgecliff Member of the Onondaga Limestone of New York dated as late Emsian (Uyeno et al., 1982)." Recent work by Pinet et al. (2013) and Lavoie et al. (2015) placed the Emsian-Eifelian boundary within the Kwataboahegan Formation. In Nevada, *S. moosense* is found in the uppermost Emsian.

Because *Syringodictyon nevadense* n. sp. is known from only the upper Emsian of Nevada, species-level correlation is impossible; however, *Syringodictyon* has limited geographic and stratigraphic ranges. The type species, *S. tuberculatum* (Nicholson, 1873), is known from the Onondaga Limestone of the Niagara Peninsula, Ontario (St. Jean, 1986), and western New York (St. Jean, personal communication, 2010). St. Jean (1986) recognized that a specimen identified as *Labechia* sp. by Stearn (1983) from the Emsian-age Blue Fiord Formation of Ellesmere Island is most likely *Syringodictyon*.

In summary, the controversy regarding the age of the Detroit River Group of southwestern Ontario, and correlative units (Onondaga Limestone of Ontario and New York; Columbus Limestone of Ohio; and Jeffersonville Limestone of Indiana and Kentucky), as described by Prosh and Stearn (1993) and Klapper and Oliver (1995), remains unresolved. My findings, however, support at least a partial Emsian age for a majority of the above-mentioned lithostratigraphic units.

Methods and materials

Measurement.—Procedures used here to measure and count skeletal morphologies are the same as those outlined by Stock (1979, p. 307; 1982, p. 657). Eight to 11 skeletal dimensions were obtained from the three Nevada specimens.

Identification.—Today, identification of stromatoporoids at the genus level is based on qualitative characteristics, such as shape of pillars, nature of laminae (i.e., sheets or colliculi), and nature of the skeletal microstructure. Identification at the species level, on the other hand, is based on quantitative characteristics, such as the number of laminae in a 1 mm distance, thickness of laminae, and diameter of pillars.

Repositories and institutional abbreviations.—ROM, Royal Ontario Museum, Toronto, Ontario, Canada; USNM, U.S. National Museum, Smithsonian Institution, Washington D.C., U.S.A.

Systematic paleontology

Phylum Porifera Grant, 1836
Class Stromatoporoidea Nicholson and Murie, 1878
Order Stromatoporellida Stearn, 1980
Family Stromatoporellidae Lecompte, 1951
Genus *Stromatoporella* Nicholson, 1886

1886 *Stromatoporella* Nicholson, p. 92.
1956 *Stictostromella* Galloway and St. Jean in Fritz and Waines, p. 92.
1956 *Stromatoporella*; Fritz and Waines, p. 126. [Addendum citing a letter from Galloway stating that *Stictostromella* Galloway and St. Jean was *Stromatoporella* instead]
1969 *Pseudostictostroma* Flerova, p. 26.
1971 *Cancellatodictyon* Khalfina and Yavorsky, p. 119.
1971 *Pseudostromatoporella* Kazmierczak, p. 76.
1999 *Stromatoporella*; Stearn et al., p. 39.
2001 *Stromatoporella*; Dong, p. 207.
2011 *Stromatoporella*; Stearn, p. 1.
2015 *Stromatoporella*; Stearn, p. 781.

Type species.—*Stromatopora granulata* Nicholson, 1873, p. 94, pl. 4, figs. 3, 3a.

Diagnosis.—Laminae continuous, thinner than galleries high. Pillars not superposed, of two types: (1) spool-shaped post-pillars;

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and (2) ring-pillars formed by upturns of laminae. Microstructure of laminae ordinicellular, of pillars cellular to fibrous.

Remarks.—*Stromatoporella* is unique among the stromatoporoids in possessing common to abundant ring-pillars. Where ring-pillars are superposed, they are called tube-pillars, as in *Tubuliporella* Khalfina, 1968.

Stromatoporella perannulata Galloway and St. Jean, 1957
Figure 3.1, 3.2

non 1878 *Clathrodictyon cellulosum* Nicholson and Murie, p. 221, pl. 2, figs. 6–10.
1936 *Stromatoporella cellulosa*; Parks, p. 108, pl. 4, figs. 6, 7.
1951 *Stictostroma eriense* Parks; Lecompte, p. 137, pl. 20, figs. 2, 2a, b.
1957 *Stromatoporella perannulata* Galloway and St. Jean, p. 142, pl. 9, figs. 3a, b.
1957 *Stromatoporella eriensis*; Galloway and St. Jean, p. 145, pl. 10, figs. 2a, b.
1968 *Stromatoporella perannulata*; Flügel and Flügel-Kahler, p. 310.
1982 *Stromatoporella perannulata* (?); Fagerstrom, p. 38, pl. 7, figs. 2–4.
1982 *Stromatoporella eriense* (?); Fagerstrom, p. 39, pl. 7, fig. 5.
1985 *Stromatoporella eriense*; Bogoyavlenskaya and Khromych, p. 20.
1985 *Stromatoporella perannulata*; Bogoyavlenskaya and Khromych, p. 43.
1986 *Stromatoporella perannulata*; St. Jean, p. 1043, fig. 5.4–5.6.
1993 *Stromatoporella perannulata*; Prosh and Stearn, figs. 3a, b.
1996 *Stromatoporella perannulata*; Prosh and Stearn, p. 26, pl. 10, figs. 1, 2.
1998 *Stromatoporella perannulata*; Stearn, p. 19, fig. 4.

Holotype.—Specimen ROM 1340 Cn, from Onondaga Formation drift, near Simcoe, Ontario (Parks, 1936, pl. IV, figs 6–8).

Occurrence.—Dry Creek, Roberts Mountains (Appendix), 57–60 m above the base of the Bartine Member of the McColley Canyon Formation (*gronbergi* Zone).

Description.—Specimen laminar fragment 90 mm wide, 54 mm thick. Skeletal dimensions given in Table 1.

Material.—Specimen USNM 706515.

Remarks.—Of the species of *Stromatoporella* described in the literature, the Nevada specimen most closely resembles *S. perannulata* Galloway and St. Jean of Prosh and Stearn (1996) (Table 2) from the lower and middle Emsian of Ellesmere Island. The latter differs from the Nevada specimen only in having more closely spaced post-pillars, as seen in tangential section.

Genus *Stictostroma* Parks, 1936

1936 *Stictostroma* Parks, p. 77.
1999 *Stictostroma*; Stearn et al., p. 42.
2001 *Stictostroma*; Dong, p. 205.
2011 *Stictostroma*; Stearn, p. 7.
2015 *Stictostroma*; Stearn, p. 787.

Type species.—*Stromatopora mammillata* Nicholson, 1873, p. 94, pl. 4, fig. 4.

Diagnosis.—Laminae continuous, thinner than galleries high. Spool-shaped pillars not superposed. Microstructure of laminae ordinicellular, of pillars cellular to fibrous.

Remarks.—*Stictostroma* lacks the ring-pillars of *Stromatoporella* Nicholson, 1886; otherwise these two genera are identical.

Stictostroma moosense (Parks, 1904)
Figure 3.3, 3.4

1904 *Actinostroma moosensis* Parks, p. 183, pl. 2, fig. 3, pl. 3, figs. 3, 4.
1936 *Clathrodictyon moosense*; Parks, p. 34, pl. 8, figs. 5–7.
non 1956 *Clathrodictyon moosense*; Flügel, p. 48, pl. 1, fig. 6.
1957 *Stromatoporella moosensis*; Galloway and St. Jean, p. 256.
1968 *Stromatoporella moosensis*; Flügel and Flügel-Kahler, p. 276.
non 1971 *Pseudostromatoporella moosensis*; Kazmierczak, p. 79, pl. 14, fig. 1a–c.
non 1985 *Pseudostromatoporella moosensis*; Bogoyavlenskaya and Khromych, 1985, p. 39.

Holotype.—Specimen ROM 2619 D, from the Middle Devonian, Kwataboahegan River, James Bay, Ontario (Parks, 1904, pl. III, figs. 3, 4; Parks, 1936, pl. 8, figs. 5–7).

Occurrence.—The Oxyoke Canyon Sandstone (*serotinus* Zone) at Romano Ranch I, southern Sulphur Spring Range (Appendix).

Description.—Specimen encrusted favositid tabulate coral. Fragment 45 mm wide, 8 mm thick. Skeletal dimensions given in Table 3.

Material.—Specimen USNM 706516.

Remarks.—The microstructure of the laminae and pillars of the specimen is compact, a condition not typical of *Stictostroma*, which has ordinicellular laminae and pillars that are cellular to fibrous (Stearn, 2011); however, the microstructure of genera such as *Stictostroma* can be diagenetically altered to compact. Photomicrographs of the specimen were examined by C.W. Stearn, and he strongly agreed that it is a specimen of *Stictostroma* (C.W. Stearn, personal communication, 2011).

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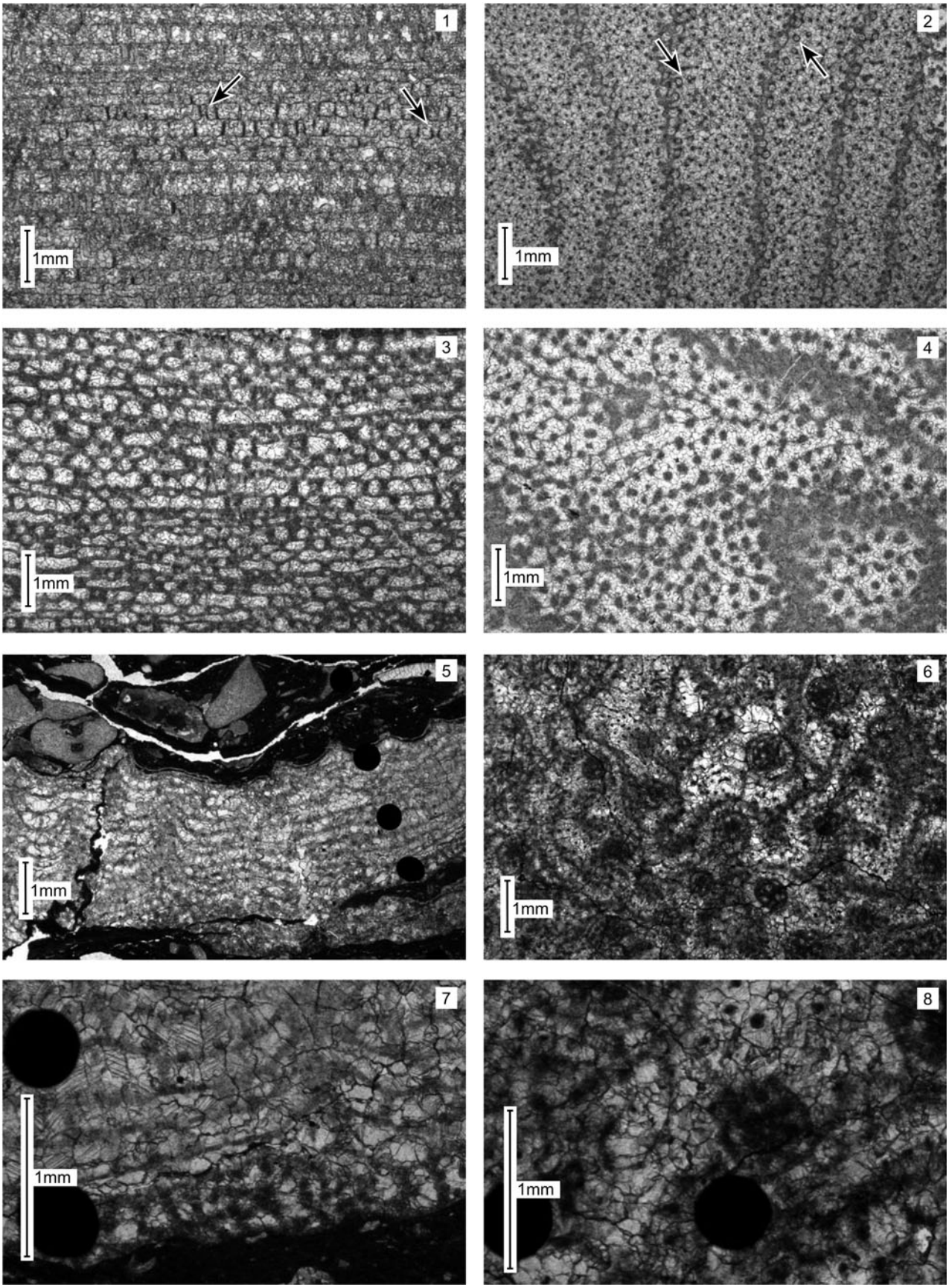

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Figure 3. (**1, 2**) *Stromatoporella perannulata* Galloway and St. Jean, 1957, USNM 706515 (×10); arrows indicate examples of ring-pillars; (**1**) longitudinal section; (**2**) tangential section. (**3, 4**) *Stictostroma moosense* (Parks, 1904), USNM 706516 (×10); (**3**) longitudinal section; (**4**) tangential section. (**5–8**) *Syringodictyon nevadense* n. sp., holotype, USNM 706517; black dots were applied to thin-sections by Pedder; (**5, 6**) (×10); (**5**) longitudinal section; (**6**) tangential section; (**7, 8**) (×40); (**7**) longitudinal section; (**8**) tangential section.

Table 1. Skeletal dimensions (in mm) of specimen USNM 706515 of *Stromatoporella perannulata* Galloway and St. Jean, 1957. r = range; mdn = median (for counts); x = mean (for measurements); s = standard deviation; N = sample size.

Characteristic	r	mdn/x	s	N
Longitudinal Section				
Laminae per mm	3–6	4.5	—	32
Post-pillars per mm	2–6	3.5	—	36
Post-pillar width	0.013–0.075	0.038	0.012	51
Ring-pillar width	0.100–0.213	0.153	0.031	18
Laminar thickness	0.013–0.050	0.021	0.008	36
Gallery height	0.125–0.388	0.221	0.058	36
Tangential Section				
Post-pillar diameter	0.025–0.075	0.046	0.012	40
Post-pillar distance	0.100–0.250	0.190	0.040	26
Ring-pillar diameter	0.100–0.150	0.119	0.016	19
Lumen diameter	0.050–0.100	0.072	0.015	18

Table 2. Comparison of skeletal dimensions (in mm) of specimen USNM 706515 of *Stromatoporella perannulata* with those of Prosh and Stearn (1996). Measurements from Table 1 are reduced to two decimal places to facilitate comparison with Prosh and Stearn. They reported counts per 2 mm—these have been divided by two to obtain the values below. They did not give means for any of these skeletal characteristics.

Characteristic	USNM 706515	Prosh and Stearn
Longitudinal Section		
Laminae per mm	3–6	3.5–5
Post-pillars per mm	2–6	3–4.5
Post-pillar width	0.01–0.08	0.02–0.05
Ring-pillar width	0.10–0.21	—
Laminar thickness	0.01–0.05	0.02–0.04
Gallery height	0.13–0.39	—
Tangential Section		
Post-pillar diameter	0.03–0.08	0.03–0.08
Post-pillar distance	0.10–0.25	0.10–0.12
Ring-pillar diameter	0.10–0.15	—
Lumen diameter	0.05–0.10	0.04–0.12

Table 3. Skeletal dimensions (in mm) of specimen USNM 706516 of *Stictostroma moosense* (Parks, 1904). r = range; mdn = median (for counts); x = mean (for measurements); s = standard deviation; N = sample size.

Characteristic	r	mdn/x	s	N
Longitudinal Section				
Laminae per mm	4–6	5.0	—	24
Pillars per mm	2–4.5	3.0	—	24
Pillar width	0.013–0.263	0.120	0.066	38
Laminar thickness	0.025–0.125	0.069	0.024	32
Gallery height	0.075–0.300	0.186	0.058	32
Tangential Section				
Pillar diameter	0.050–0.275	0.161	0.055	54
Pillar distance	0.138–0.425	0.298	0.060	42
Astrorhizal canal width	0.200–0.388	0.306	0.055	18

The genus identification of *Stictostroma moosense* (Parks) has changed a few times in the past. Parks' (1904) assignment to *Actinostroma* makes no sense because that genus has long pillars and colliculi, rather than short pillars and sheetlike laminae. Parks' (1936) reassignment to *Clathrodictyon* makes some sense, if one takes the compact microstructure at face value. There is less sense in Galloway and St. Jean's (1957) inclusion of the species in *Stromatoporella* because no ring-pillars are present.

Pseudostromatoporella moosensis (Parks) of Kazmierczak (1971) from the Givetian of Poland is not included in synonymy for at least two reasons. Whereas pillars in the Polish specimens that branch upward at the top are capped by straight laminae, those in the Nevada and Ontario specimens are associated with downward deflections in the laminae. The Polish specimens display large gaps in the laminae that are not present in *Stictostroma moosense* (Parks).

Although I was not able to borrow the holotype specimen from the Royal Ontario Museum, I did borrow a longitudinal section of an apparent topotype specimen (ROM 2026D). Measurements from the latter compare well with those of the Nevada specimen (Table 4) in longitudinal section, with the Nevada specimen having somewhat: (1) more widely spaced laminae; (2) higher galleries; and (3) wider astrorhizal canals. A few other species assigned to other genera by their authors also resemble the Nevada specimen of *S. moosense*: (1) *Clathrodictyon amygdaloides* var. *subvesiculosum* Lecompte, 1951, from the Couvinian (Eifelian) of Belgium; (2) *Clathrodictyon abnorme* Yang and Dong, 1979, from the Eifelian of Guangxi, China; (3)

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Table 4. Comparison of skeletal dimensions (in mm) of specimen USNM 706516 of *Stictostroma moosense* (Parks, 1904) with ROM 2026D of *S. moosense*. The mean score is followed by the range in parentheses.

Characteristic	USNM 706516	ROM 2026D
Longitudinal Section		
Laminae per mm	4.9 (4.0–6.0)	5.7 (4.5–7.0)
Pillars per mm	3.0 (2.0–4.5)	3.3 (2.0–4.5)
Pillar width	0.12 (0.01–0.26)	0.13 (0.05–0.19)
Laminar thickness	0.07 (0.03–0.13)	0.07 (0.03–0.15)
Gallery height	0.19 (0.08–0.30)	0.14 (0.09–0.28)
Tangential Section		
Pillar diameter	0.16 (0.05–0.28)	—
Pillar distance	0.30 (0.14–0.43)	—

Simplexodictyon artyschense (Yavorsky in Thanh et al., 1988) from the Pragian of North Vietnam; and (4) *Schistodictyon amygdaloides subvesiculosum* (Lecompte in Avlar and May, 1997) from the lower Eifelian of Germany. These species must be investigated further before synonymy with *S. moosense* can be established.

Genus *Syringodictyon* St. Jean, 1986

1986 *Syringodictyon* St. Jean, p. 1050.
1999 *Syringodictyon*; Stearn et al., p. 42.
2011 *Syringodictyon*; Stearn, p. 9.
2015 *Syringodictyon*; Stearn, p. 789.

Type species.—*Stromatopora tuberculatum* Nicholson, 1873, p. 92, pl. 4, figs. 2, 2a.

Emended diagnosis.—Laminae continuous, thinner than galleries high. Post-pillars not superposed, spool-shaped. Laminae turn up into many small mamelons, superposed into mamelon columns. Skeletal macrostructures form amalgamated structure in mamelon columns. At least some columns contain axial canal. Microstructure of laminae tubular and ordinicellular, of pillars transversely fibrous.

Remarks.—In his original generic diagnosis, St. Jean (1986) stated that pillars are rare—this appears to be the case in only the type species because pillars are common in the Nevada species.

Syringodictyon nevadense new species
Figure 3.5–3.8

Holotype.—Specimen USNM 706517; from the upper Coils Creek Member of the McColley Canyon Formation (*serotinus* Zone) at Romano Ranch IV, southern Sulphur Springs Range, Nevada (Appendix). This specimen consists of only three thin-sections.

Diagnosis.—Mamelon centers 1.43 mm apart. Laminae 5.6 per mm, pillars 4.0 per mm. Pillar width in longitudinal section and diameter in tangential section both 0.05 mm. Laminar thickness 0.04 mm, gallery height 0.17 mm. Pillar distance 0.18 mm.

Occurrence.—The holotype is the only known specimen.

Description.—Specimen laminar fragment 50 mm wide, 9 mm thick. Skeletal dimensions given in Table 5.

Etymology.—After the state of Nevada, in which it occurs.

Remarks.—There are only two known species of *Syringodictyon*, *S. tuberculatum* St. Jean, 1986, and *S. nevadense* n. sp. Examination of Table 6 reveals several strong differences between *S. nevadense* n. sp. and *S. tuberculatum*. The laminae in *S. nevadense* n. sp. are more closely spaced (5–7 per mm) than are those in *S. tuberculatum* (0.8–3.7 per mm), with no overlap in ranges. This characteristic is reflected by differences in gallery height: 0.06–0.28 mm in *S. nevadense* n. sp.; and 0.24–0.32 mm in *S. tuberculatum*. The laminae in *S. tuberculatum* are much thicker (0.04–0.20 mm) than are those of *S. nevadense* n. sp. (0.03–0.05 mm). Pillar diameters in tangential section are also much greater in *S. tuberculatum* (0.07–0.43 mm) than those of *S. nevadense* n. sp. (0.03–0.08 mm). The mamelon centers in *S. nevadense* n. sp. are much farther apart (0.88–2.38 mm) relative to those of *S. tuberculatum* (0.63–0.95 mm). There are so few pillars in *S. tuberculatum* that St. Jean (1986) did not report either the count of pillars per mm, or pillar distance.

St. Jean (1986) thought that a specimen of *Labechia* sp. from the lower Emsian of Ellesmere Island in the Canadian arctic that was described by Stearn (1983) might very well be *Syringodictyon*. Unfortunately Stearn's specimen is poorly preserved, and he illustrated only a longitudinal section. What

Table 5. Skeletal dimensions (in mm) of specimen USNM 706517 of *Syringodictyon nevadense* n. sp. r = range; mdn = median (for counts); x = mean (for measurements); s = standard deviation; N = sample size.

Characteristic	r	mdn/x	s	N
Longitudinal Section				
Laminae per mm	5–7	5.6	—	18
Pillars per mm	1.5–5.5	4.0	—	24
Pillar width	0.025–0.125	0.050	0.022	38
Laminar thickness	0.025–0.050	0.038	0.010	38
Gallery height	0.063–0.275	0.166	0.051	38
Tangential Section				
Pillar diameter	0.025–0.075	0.046	0.011	34
Pillar distance	0.125–0.250	0.177	0.034	34
Vertical canal diameter	0.075–0.400	0.178	0.103	9
Mamelon center distance	0.875–2.375	1.425	0.309	29

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Table 6. Comparison in ranges of skeletal dimensions (in mm) of specimen USNM 706517 of *Syringodictyon nevadense* n. sp. with those of St. Jean (1986) for *Syringodictyon tuberculatum*. Measurements from Table 5 are reduced to two decimal places to facilitate comparison with St. Jean. He reported counts per 4 mm—these have been divided by four to obtain the values below.

Characteristic	USNM 706517	St. Jean
Longitudinal Section		
Laminae per mm	5.0–7.0	0.8–3.7
Pillars per mm	1.5–5.5	—
Pillar width	0.03–0.13	0.02–0.15
Laminar thickness	0.03–0.05	0.04–0.20
Gallery height	0.06–0.28	0.24–0.32
Tangential Section		
Pillar diameter	0.03–0.08	0.07–0.43
Pillar distance	0.13–0.25	—
Vertical canal diameter	0.08–0.40	0.04–0.18
Mamelon center distance	0.88–2.38	0.63–0.95

Stearn thought were pillars of *Labechia*, St. Jean saw as mamelon columns of *Syringodictyon*. Stearn (1983) reported "pillars" [mamelon columns] 0.3 mm in width in longitudinal section, and 0.3–0.5 mm in diameter in tangential section.

Paleobiogeography

Devonian realms.—Stock and Burry-Stock (2020, p. 20–24) summarized in detail the faunal realms of the Devonian Period, and how the geographic distribution of stromatoporoids was affected by these paleogeographic constraints. Traditionally, the Devonian world has been divided into three realms: (1) Eastern Americas Realm (EAR), southeastern North America; (2) Old World Realm (OWR), western and northern North America, northwestern Africa, Europe, Asia, and Australia; and (3) Malvinokaffric realm, southern high latitudes (Stock et al., 2015). Stromatoporoids are absent from the Malvinokaffric Realm, most likely due to its cold climate; however, the EAR and OWR were located in tropical to subtropical regions, which were ideal for stromatoporoids.

Oliver (1977, table 1) determined that for a geological region to be considered a realm, at least 33% of the genera of a particular taxon (e.g., rugose corals, brachiopods, conodonts) must be endemic to that realm. For example, he found that in the EAR of the late Emsian, 92% of the rugose coral genera were endemic, and for the Eifelian, 64% were endemic.

It has been generally accepted that the land barrier separating the EAR from the OWR consisted of the Canadian Shield and the Transcontinental Arch (e.g., Witzke, 1990; Stock in Stock et al., 2015). This barrier existed from the Early Devonian (Lochkovian) through the Middle Devonian (early Givetian), until the barrier became submerged by what is known as the Taghanic Onlap (e.g., Johnson et al., 1985).

There was one exception to Oliver's (1977) definition of the OWR, which he illustrated several times (e.g., Oliver, 1990, fig. 1; 1993, fig. 1). He determined that the Great Basin Province, which included Nevada, switched from the OWR to the EAR during the Pragian–early Emsian. In support of this, he cited Boucot et al. (1968, 1969) and Boucot (1975) as, "… [having] convincingly shown that during the Siegenian [Pragian] and early Emsian time, Great Basin (Nevada) brachiopods were dominantly ENA [EAR] ("Appalachian") types" (Oliver, 1977, p. 105). He also gave an example of the rugose coral *Breviphrentis*, saying, "This genus ranges from the Gedinnian [Lochkovian] to Eifelian in ENA [EAR]. It apparently moved into the Great Basin area during the Siegenian [Pragian], where it persisted to the late Emsian" (Oliver, 1977, p. 105).

The anomalous nature of the Great Basin Province was taken further by Pedder and Murphy (2004), who emphasized its differences from the EAR and OWR. They stated (p. 845), "… the Great Basin Province began with sparse low-diversity faunas in early Pragian time (*nevadensis* conodont zone …), and culminated in distinctiveness in middle Emsian time (*gronbergi* Zone). It ended with the Breviphyllidae and Papiliophyllidae in the late Emsian *serotinus* Zone, and the arrival of OWR Cystiphyllidae, Ptenophyllidae, and Stringophyllidae in the early Eifelian *costatus* Zone." They (p. 847) concluded, "… Rugosa of the Great Basin Province do not fit well into either the OWR or EAR."

Pedder (2010) defined the location of the Emsian-Eifelian boundary in association with the Chotec Event, representing eustatic deepening of the ocean. He stated (p. 3) that, "Never again was rugose coral provincialism to be as high as it had been in Emsian time." The aforementioned fall and subsequent rise in sea level had an effect on stromatoporoid paleobiogeography, described next.

Stromatoporoid paleobiogeography.—All three of the genera and two of the species described in this paper occurred in both the EAR and OWR during the Emsian, a time when the EAR had left Nevada, and the OWR returned. *Stromatoporella perannulata* has been reported in the EAR of Ontario, Ohio, and Kentucky, and in the OWR of Ellesmere Island, arctic Canada. *Stictostroma moosense* is known from the EAR of Ontario. *Syringodictyon nevadense* n. sp. is found only in Nevada, and the previously known occurrence of the genus is in Ontario and New York (EAR), with a possible occurrence on Ellesmere Island (OWR).

Johnson et al. (1985) illustrated sea levels in the Emsian as lower than in any other Devonian age. This lowstand is associated with Sloss' (1963) transition from the Tippecanoe Sequence to the Kaskaskia Sequence. This sea-level fall may have been a consequence of, "paleoclimatically driven glacio-eustasy and thermo-eustasy" (Elrick et al., 2009, p. 179).

Breaching the barrier.—We must ask the question, "How did stromatoporoids manage to breach barriers that were closed to other taxa?" Stock and Burry-Stock (2020, p. 20–22) summarized the ecological characteristics of stromatoporoid-hosting depositional environments: (1) warm water; (2) normal salinity; (3) shallow subtidal depth; (4) medium to high turbulence; (5) firm substrate; and (6) low turbidity. These characteristics do not

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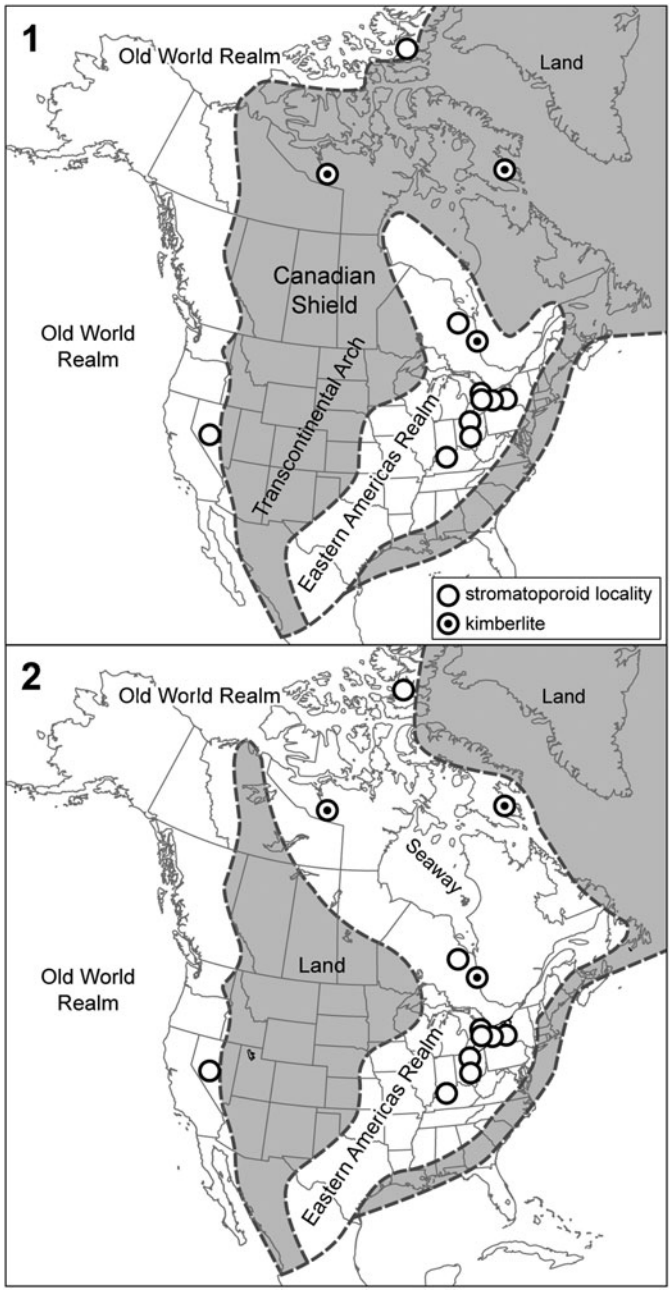

Figure 4. Emsian paleogeography and paleobiogeography of North America. (**1**) Map with location of OWR (Old World Realm), EAR (Eastern Americas Realm), Canadian Shield, and Transcontinental Arch (based on Oliver, 1977). Open circles represent locations of the nine areas from which specimens described in this paper were collected; circles containing dots represent the three kimberlite pipes containing Paleozoic xenoliths. (**2**) Map showing the proposed location of a shallow seaway across the Canadian Shield.

seem like the type of criteria necessary either for biostratigraphic correlation or inter-realm transport, especially the exclusion of deep water, and the nature of the substrate. Stromatoporoids were sessile benthic, whereas typical Paleozoic index fossils were nektonic (conodonts; cephalopods) or planktonic (graptolites). Sessile benthic organisms used frequently in biostratigraphy, such as brachiopods, lived in many different depositional environments over a range of depths. An equalizing factor between benthic and pelagic organisms is that many have planktonic larvae. Thorson (1971, p. 79, 81) stated that ~74% of marine benthic animals today produce planktonic larvae, but these larvae are confined to "relatively shallow waters of the continental shelf." Bergquist (1978, p. 106) noted that many living sponges produce free-swimming larvae that remain in the plankton for 3–48 hours.

There are three types of pathways by which a taxon can cross a barrier: (1) corridor, which is an easily traversed pathway for the majority of organisms at both ends, containing a wide variety of habitats; (2) filter, which contains fewer habitats, restricting those that can inhabit the limited number of habitats; and (3) sweepstakes route, in which two isolated, but similar, habitats are connected for a short period of time. The latter route does not support the entire life history of an organism (e.g., only planktonic larvae can cross the barrier) (Cox and Moore, 2000, p. 37).

Some authors have envisioned straits across the Transcontinental Arch as likely pathways for inter-realm mixing. One example of such a route was proposed by Sandberg (1970), who envisioned a northwest-southeast strait between the Williston Basin (OWR) and the North Kansas Basin (EAR) that existed from the Ordovician through the Mississippian. This strait appeared in subsequent publications (e.g., Sandberg et al., 1989; Johnson et al., 1991) without explanation. More recently, McCormick et al. (2018) described northwest-southeast oriented faults in South Dakota and Minnesota, which occurred at the same time as the Midcontinent Rift in the Mesoproterozoic.

Other authors have turned to the Canadian Shield for evidence of trans-barrier pathways. Using well logs, Thorpe (1989) described the occurrence of the Emsian-age Stooping River Formation in the Hudson Bay Basin, surrounded by Precambrian rocks of the Canadian Shield. He saw this basin as isolated from basins to the west during the Devonian, and noted that it received sediments intermittently at that time (i.e., there are several unconformities in the Devonian sequence). Even more exciting is the discovery of Devonian-age xenoliths composed of normal-marine sedimentary rocks in Jurassic kimberlites in the Canadian Shield of Northwest Territories (Cookenboo et al., 1998), the Ontario-Quebec boundary area (McCracken et al., 2000), and southern Baffin Island, Nunavut (Zhang and Pell, 2014; Fig. 4).

Discussion

It has become clear that stromatoporoids were able to overcome the barrier formed by the Canadian Shield and Transcontinental Arch during the Lochkovian (Stock and Burry-Stock, 2020), and now during the Emsian as well. It is doubtful that stromatoporoids were able to circumnavigate what is now the southwestern end of the Transcontinental Arch, even as planktonic larvae. Adult planktonic and nektonic organisms did not traverse that, or any other, route—if they could, there would be no EAR and OWR. Likewise, neither other benthic organisms nor their larvae did so. Clearly no corridor or sweepstakes route existed; if so, stromatoporoids would have been joined by other organisms, larval or adult, as they breached the barrier. This leaves only one likely option—the stromatoporoids crossed the inter-realm barrier using a highly selective version of a filter, during which several generations existed. Their larvae could travel by currents at least part of the way, as no doubt did the larvae of other of organisms; however, only stromatoporoid adults could inhabit the very shallow conditions present in such a passage (Fig. 4).

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Conclusions

Biostratigraphy.—One of the species described in this paper, *Stromatoporella perannulata* Galloway and St. Jean, 1957, which occurs in Nevada in the *gronbergi* Zone (middle Emsian), is conspecific with stromatoporoids in the Canadian arctic, Ontario, New York, Ohio, and Kentucky. *Stictostroma moosense* (Parks, 1904), which occurs in Nevada is in the *serotinus* Zone (uppermost Emsian), is conspecific with stromatoporoids in Ontario. The third species, *Syringodictyon nevadense* n. sp., which occurs in Nevada is in the *serotinus* Zone (upper Emsian), is only the second species in that genus to be named—the type species occurs in Ontario and New York, and an unnamed species is found in the Emsian of the Canadian arctic. In the case of arctic Canada, strata there containing *S. perannulata* are known to be Emsian in age, but there is some uncertainty regarding the placement of the Emsian-Eifelian boundary for the age of the stromatoporoid-bearing strata in the other areas mentioned above. My findings lend some credence to the assertion of Prosh and Stearn (1993) that many of the strata in question are Emsian in age.

Paleobiogeography.—*Stromatoporella perannulata* and *Stictostroma moosense* occurred at about the same time in both the Eastern Americas Realm and Old World Realm, as did two species of the genus *Syringodictyon*. The coeval occurrences of these taxa indicate a limited connection between two paleobiogeographic realms.

Evidence from xenoliths in kimberlite pipes in the Canadian Shield, and strata beneath Hudson Bay, indicates deposition of normal-marine sediments well onto the modern margins of the Canadian Shield. There was a shallow-water passage across the Canadian Shield in what was previously seen as an impervious cross-continental barrier, which represented a filter—a seaway containing a few habitats, restricting the kinds of organisms to those capable of inhabiting those depositional settings.

Conclusions drawn here are very similar to those of Stock and Burry-Stock (2020, p. 24, fig. 11), who proposed an Early Devonian (Lochkovian) seaway across the Canadian Shield that allowed the stromatoporoid *Habrostroma centrotum* (Girty, 1895) to simultaneously inhabit the Eastern Americas Realm (Virginia, New York, Maine) and the Old World Realm (Bathurst and Ellesmere islands, Canadian arctic) in what is now North America.

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Appendix: collecting localities

Dry Creek.—Gully on eastern side of Dry Creek, ~250 m south of valley entrance, northern Roberts Mountains; 39°57′42″N, 116°17′10″W; UTMG: 561620mE 4422430mN, Cooper Peak 7½ Minute Quadrangle. Locality 1996-27 of Pedder and Murphy (2004).

Romano Ranch I.—Butte above lake terrace, eastern foot of southern Sulphur Spring Range, 700 m northwest of Romano Ranch house; 39°52′34″N, 116°04′04″W; UTMG: 579320mE 4414855mN, Bailey Pass 7½ Minute Quadrangle. Locality 1998-25 of Pedder and Murphy (2004).

Romano Ranch IV.—Piedmont exposure in lake terrane, eastern foot of southern Sulphur Spring Range, 600 m northwest of Romano Ranch house; 39°52′34″N, 116°04′04″W; UTMG: 579440mE 4414740mN, Bailey Pass 7½ Minute Quadrangle. Locality 2000-19 of Pedder and Murphy (2004).

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