The “lower Middle Devonian” part of a coral zonation proposed for the region in 1974 comprised in ascending order D2 and D3 subzones and a “barren” E zone. In terms of the conodont zonation currently employed in Nevada, the D2 subzone is Emsian *grounbergi* and *inversus* zones. The original stratigraphic definition of the D3 subzone places it in the upper Emsian *serotinus* Zone on Lone Mountain, whereas the coral index defining the zone has been collected subsequently only from Eifelian upper *costatus* Zone beds. The original stratigraphic definition of the “barren” E zone places it in a lower part of the *costatus* Zone, above an inferred depositional break. Thus, as defined on Lone Mountain, the D3 subzone is slightly younger than the E zone. These zones are not barren. Revised taxonomy and age determinations of previously described species, coupled with new data from the southern Sulphur Spring and northern Antelope ranges, have revealed four successive coral assemblages ranging from *serotinus* to *costatus* Zone age. Differences between the second and third of these assemblages are particularly significant, and may be considered to represent a local manifestation of the Choteč Event. A detailed review of the genus *Synaptophyllum* shows it to be an Emsian endemic in the Maghrebo-European Realm, not an early Eifelian endemic in the Eastern Americas Realm. New taxa comprise a family, one genus and two species. *Romanophyllum paulyi* gen. et sp. nov., which possibly represents one of the last vestiges of the Pragian-Emsian Great Basin coral province, is assigned to the Romanophyllidae fam. n. *Xystriphyllum trojani* sp. nov. is described as an example of one of earliest ptenophyllid species to return to the Great Basin after the absence of the family from the region since late Lochkovian time. • Key words: Nevada, Devonian, corals, biozones, Choteč Event.


Alan E.H. Pedder, Geological Survey of Canada, Emeritus, 8859 Park Pacific Terrace, Sydney, British Columbia, Canada V8L 4S1; apedder@telus.net

C.W. Merriam devoted much of his working life to studies of the Middle Palaeozoic of the Great Basin, and in 1974 published a rugose coral biozonation for the Lower and Middle Devonian of the region. Seven Lower to middle Middle Devonian zones, informally designated A–G, were recognised. Following Subcommission on Devonian Stratigraphy (SDS) decisions and various conodont studies, the A–G coral zones are presently understood to range from Pragian to lower Givetian. Merriam’s (1974, p. 21) short description of the Lower Middle Devonian E zone was based on its outcrop on Lone Mountain, where crinoidal carbonates of the zone are dolomitised, all but destroying their coral content. Although Merriam reported the presence of *Disphyllum*? and fragments having “characteristics of *Cyathophyllum*” in the zone, he also referred to it as the “barren zone”.

In a review of Merriam’s Silurian and Devonian zonations, Johnson & Oliver (1977) repeated the earlier Devonian E zone identifications and correlated the zone with Johnson’s (1977) Faunal Interval 15 and the *costatus* conodont zone, but noted that there was no described coral to define the zone. The present paper establishes that the E zone was not barren. It will also show that the change from Lower to Middle Devonian coral faunas, which was concurrent with the demise of the Pragian-Emsian Nevada coral province (Pedder & Murphy 2004), involved three steps, and that the middle of these corresponds closely to the Choteč Event of central Europe.

Special attention is given to the taxonomy, occurrences and apparent migrations of the long misunderstood and misidentified genus *Synaptophyllum*. Together with the return of the Ptenophyllidae to central Nevada, *Synaptophyllum* plays an important role in defining the three-step evolution of the “barren” E zone.
Coral bearing lithologic units employed or mentioned in this work are: 1) Bartine Member; 2) Coils Creek Member; 3) Sadler Ranch Formation, undivided; 4) crinoidal unit of the Sadler Ranch Formation; 5) lower member of the Denay Formation.

The Bartine Member of the McColley Canyon Formation is used exactly as it was proposed by Murphy & Gronberg (1977, p. 131). On Lone Mountain, it corresponds approximately to the upper 60 to 70 m of Merriam’s Unit 2 of the Nevada Formation. As proposed, the member comprised two units, both 98 feet (29.9 m) thick. The entire lower unit is referred to the *inversus* conodont zone (Klapper & D.B. Johnson in Klapper 1977, p. 42) and to Nevada Faunal Interval (FI) 13 (Johnson 1977, p. 22). No rugose coral is known from the lower unit on Lone Mountain. However, to the north in the Roberts Mountains, and to the south in Fish Creek Range, *Breviphenis invaginata* (Stumm) is moderately common in some *inversus* Zone beds in the lower part of the member. Pedder & Murphy (2004, p. 838) considered the “Bartine tongue”, recognised by Kendall et al. (1983) in southern Sulphur Spring Range, to be a more argillaceous, less resistant facies of the Coils Creek Member. In the northern Antelope Range TA sections, Johnson et al. (1986) and Johnson et al. (1996) assigned about 32 m of section, between the disconformable base of a sandstone bed (tongue of Oxyoke Canyon Sandstone?) and the base of the Denay Formation, to the Coils Creek Member. This interval, which is given a thickness of 40 m in Morrow (2007, fig. 51), and which represents the entire Devonian T-R cycle Ic of Johnson et al. (1986), is currently referred to the Sadler Ranch Formation (Morrow 2007, p. 51).

The Sadler Ranch Formation was proposed by Kendall et al. (1983, p. 2200) for predominantly crinoidal dolostones exposed on the eastern flank of Sulphur Spring Range. As mapped by Kendall, it overlies a “tongue of Bartine Limestone member” and is overlain by the more widespread Sentinel Mountain Dolomite. Although the base of the formation may be as old as *inversus* Zone, most of the formation ranges from *serotinus* to *costatus* Zone. Johnson et al. (1996, p. 12) believed the Sadler Ranch/Sentinal Mountain contact to be coincident with the base of Devonian T-R cycle Id, and that no part of the Sadler Ranch Formation is as young as the lower Denay Limestone. An outcrop of variably crinoidal dolomite (ROM III section), which includes the type stratum of *Synaptophyllum romanense*, overlies a tongue of Oxyoke Canyon Sandstone and is separated by two high angle faults of small displacement from the Coils Creek Member (ROM I & IV sections), is referred to the Sadler Ranch Formation.

Crinoidal packstones such as those illustrated from Lone Mountain (Johnson et al. 1968, text-fig. 4; Fig. 2 herein) and from northern Antelope Range (Fig. 3 herein) are widely distributed in the *patulus* (undivided) and...
costatus zones of central Nevada. Units in which crinoidal packstones of this age are especially characteristic, have been assigned to: 1) crinoidal member, middle Nevada Formation (Merriam 1940); 2) crinoidal unit or member, Telegraph Canyon Formation (Johnson et al. 1968, Murphy & Gronberg 1970); 3) unit 3, Nevada Formation (Merriam 1974); 4) Denay Limestone (Johnson et al. 1980); 5) crinoidal member Union Mountain Formation (Klapper & Johnson 1975, Kendall et al. 1983); 6) Coils Creek Limestone (Johnson et al. 1986); 7) upper Sadler Ranch Formation (Morrow 2007). In this paper, units of this kind on Lone Mountain and northern Antelope Range are referred to as crinoidal units of the Sadler Ranch Formation.

The Denay Formation was proposed by Johnson (1966, p. 154) for about 275 m (Murphy 1977, fig. 2) Middle Devonian strata, lying between the McColley Canyon and Devils Gate formations, on the eastern side of Willow Creek, northern Roberts Mountains. Debris flows with Xystriphylhum trojani sp. nov. and other allochthonous corals, occurring near the base of the formation in northern Antelope Range, are assigned to the lower member of the formation. The lower member has not been formally named, but has been recognised in the type section (Murphy, 1977) as well as in the northern Antelope Range (Johnson et al. 1980, 1988).

Sub costatus Zone depositional breaks

The postulated disconformity between what are presently known as the Coils Creek Member and overlying Denay Formation on the eastern side of Willow Creek, Roberts Mountains, was first outlined by Johnson (1962, pp. 543, 544). The same break was recognised in northern Sulphur Spring Range between the Sevy Dolomite and Union Mountain Sandstone. The initial estimate of the magnitude of the disconformity, reported by Johnson (1966, p. 153) as the interval between the pinyonensis and circula zones (FI 13–FI 15), was reduced when Murphy (1977, p. 191) noted that about 200 feet (61 m) of strata separate these zones, and that the uppermost beds below the break yield an Elythyna assemblage (lower FI 14). The apparent absence of patulus and partitus Zone conodonts is generally accepted as evidence of the same disconformity on Lone Mountain.

This is not, however, the situation in northern Antelope Range where beds above and below the base of the Denay Formation are costatus Zone age, and a questionable serotinus Zone break has been recognised lower in the succession (C.A. Sandberg in Morrow 2007, fig. 51). Winnowing and redeposition of crinoidal ossicles in the partitus and lower costatus zones of northern Antelope Range must have resulted in very minor sedimentary breaks, but did not seriously affect preservation of the corals of these zones.

In contrast to the Roberts Mountains, there is no certain record of serotinus Zone benthos in northern Antelope Range.

Emsian-Eifelian GSSP

The Emsian-Eifelian Global Stratotype Section and Point (GSSP) is located at the lowest observed occurrence of Polygnathus partitus in the Wetteldorf trench section in the Eifel Hills, Germany (Ziegler & Klapper 1985, p. 105; Ziegler 2000). Although this level has not been detected with certainty in any coral-bearing shelf sequence, operational estimates of the stratigraphic extent of the conodont zones – serotinus (upper Emsian), lower undivided patulus (uppermost Emsian), upper undivided partitus (= partitus Subzone, lowermost Eifelian) and costatus (lower Eifelian) – are possible in Nevada.

Choteč Event

The appearance of Pinacites jugleri and other goniatites “a few layers” above the boundary between the Třeboť and overlying Choteč limestones in the Prague basin has been designated the jugleri Event (Walliser 1985, p. 403), and the boundary between the limestones themselves has been termed the Basal Choteč Event (Chlupáč & Kukal 1986, p. 173). The incoming of Polygnathus partitus, which as far as can be determined is the base of the Middle Devonian, is 2.54 m below the top of the Třebotov Limestone in the Prastav quarry at Praha-Holyně (Klapper et al. 1978, fig. 1). The upper two of these three levels are commonly combined as the Choteč Event, and together are seen as a eustatic deepening event beginning at, or very close to the start of the Middle Devonian (base of partitus Subzone).

Disturbances to coral bearing biotopes during the Choteč Event brought considerable changes to rugosan faunas, and although the event was not a time of major extinction, it did result in an overall loss of rugosan genera. Never again was rugose coral provincialism to be as high as it had been in Emsian time.

Coral biostratigraphy of the serotinus Zone

The youngest unequivocal Lower Devonian coral assemblage in Nevada is the Breviphrentis magna assemblage in the serotinus Zone of the upper Coils Creek Member and lower Sadler Ranch Formation. A typical example from the Coils Creek Member of southern Sulphur Spring Range (sample 1998-25, Pedder & Murphy 2004) includes Polygnathus serotinus, lies above occurrences of Polygnathus inversus lower in the member, and below an occurrence of
The only species definitely assigned to the D₃ subzone by Merriam (1974) was identified as *Mesophyllum* (Arco-
phyllum) *kirki* (Stumm), originally named *Mesophylloides kirki* by Stumm (1937, p. 441). Pedder & McLean (1982, p. 75) regarded Stumm’s species to be a *nomen dubium* and referred to Merriam’s material as *Mesophyllum kirki* (Stumm, 1937) *sensu* Merriam, 1974. Using Merriam’s measurements of his Lone Mountain reference section, Pedder & McLean, and Johnson & Oliver (1977, p. 1466) reasoned that Merriam’s *D₃* *Mesophyllum* specimens came from the serotinus Zone in the Coils Creek Member. However, Merriam’s specimens attributed to *M. kirki* came from more than 1 km northwest of the Lone Mountain reference section. In 1997, M.A. Murphy and the present author examined the Bartine and Coils Creek members on northwestern Lone Mountain (M-P I section) but were unable to recollect Merriam’s *M. kirki* species. After many years of collecting in central Nevada, additional material comparable to *M. kirki* (Stumm) *sensu* Merriam has only been found as partly or wholly decorticated redeposited specimens in upper costatus Zone beds of northern Antelope Range. *Breviphrentis magna* is now considered the most appropriate coral index for the serotinus conodont zone and all but the lowest stata originally assigned to the D₃ coral subzone.

Two other corals that Merriam (1974) thought may have come from his D₃ subzone were identified as *Dendrostella romanensis* sp. nov. and *Hexagonaria* (*Pinyonastraea*) *kirki* (Stumm). The first is *Synaptophyllum romanense* from the undivided patulus Zone; the second (Merriam 1974, pl. 23, fig. 7 only) appears to be an unprepared specimen of an undescribed species of *Pinyonastraea*, known to the present author from the upper gronbergi Zone of the Bartine Member (D₂ subzone of Merriam).

**Coral biostratigraphy of the undivided patulus Zone**

Merriam (1974, p. 45) discovered the *in situ* occurrence of *Synaptophyllum romanense* in the ROM III section, but mentioned none of the other species occurring with it. He assigned it to either his D₂ or D₃ subzone and noted that it lies about 150 feet (46 m) stratigraphically above a large fauna including *Breviphrentis* sp. cf. *invaginata*. After careful examination of the section, it is clear that this fauna is the *Breviphrentis magna* assemblage of the author’s 1998-25 collection, mentioned above. M.A. Murphy’s measurement of the ROM I–III sections indicates that the two assemblages are separated by faults of small displacement and at least 49 m of strata.

The belief advocated here that the bed belongs to the *patulus* (undivided) Zone is based on its stratigraphic
position and coral fauna. The corals are quite distinct from those of the *serotinus* Zone, but include *Synaptophyllum romanense*, which occurs in the *partitus* Subzone and lower *costatus* Zone in northern Antelope Range. The single conodont species identified in the bed is *Pandorinella expansa*. Other conodont data assembled by M.A. Murphy from the ROM III section are: 1) *Polygnathus bultyncki* occurs immediately below the bed; 2) *Polygnathus bultyncki* and *P. cooperi* occur immediately above the bed; 3) *Pandorinella expansa*, which is not known to be younger than early *costatus* Zone, occurs as high as 13.2 m above the bed. The conodont data are consistent with a *patulus* Zone determination, but are not diagnostic of it.

Compared to the older *Breviphrentis magna* assemblage, the *Synaptophyllum romanense* assemblage is most notable for hosting the arrival in Nevada of the genus *Synaptophyllum*, and for its lack of breviphyllid corals, which dominate older upper Emsian faunas of the Great Basin (Pedder 2002). *Romanophyllum paulyi* gen. et sp. nov. and a large species of *Nardophyllum* are the only corals of the *Synaptophyllum romanense* assemblage that may have phylogenetic links to older Nevada species.

**Coral biostratigraphy of the *partitus* and lower *costatus* zones**

The lowest part of the crinoidal unit of the Sadler Ranch Formation (previously Coils Creek limestone) in northern Antelope Range (TA V section) is referred to the *partitus* Zone, while higher parts of the same unit belong to the lower *costatus* Zone (Klapper in Johnson et al. 1986). Many of the corals and presumably most of the crinoidal ossicles in the middle and upper parts of the same crinoidal unit are allochthonous, as shown in Fig. 3, and likely include individuals from the *partitus* Zone. Nevertheless, the rugosan fauna is almost entirely different from the *Synaptophyllum romanense* assemblage in the Romano Ranch area. Specimens of *Synaptophyllum romanense* from northern Antelope Range, on average are larger, have more septa and are not accompanied by species of *Romanophyllum*, *Nardophyllum* or other undescribed genera accompanying the species in the Romano Ranch area. The most emphatic difference, however, is the presence of genera unknown in older Nevada faunas, including *Pseudomicroplasma*, *Mesophyllum*, *Thryptophyllum*, and especially the ptenophyllid genera *Dohmophyllum*, *Taumyrophyllum* (well
preserved – not just the coral illustrated in Fig. 2) and Xystriphyllum.

Coral biostratigraphy of the upper costatus and possibly lowermost australis zones

Allochthonous brachiopods of the Pentamerella wintereri assemblage occur in upper costatus Zone debris flows in the basal 21 m of the Denay Formation in northern Antelope Range (Johnson et al. 1980, Johnson 1990). W.A. Oliver examined fragmentary silicified corals from the same beds, but among the Rugosa was only able to unques­tionably identify three genera – Microplasma, Cystiphyllum and Metrionaxon (tables 2, 3 in Johnson et al. 1980). Although the Metrionaxon may have been autochthonous, the Microplasma and Cystiphyllum were likely alloch­thonous specimens of Pseudomicroplasma?, and Zonophyllum which are moderately common genera in these beds. Besides Pseudomicroplasma? and Zonophyllum, the author’s collections include Mesophyllum sp. cf. M. kirki (Stumm) sensu Merriam, 1974, Taimyrophyllum sp., Xystriphyllum trojani sp. nov. and the earliest Nevada examples of the quintessentially Eifelian and pre-Taghanic Givetian genus Sociophyllum.

The lowest level of the costatus/australis zonal boundary in northern Antelope Range has been set below the first occurrence of Tortodus kockelianus australis, at the entry of Polygnathus parawebbi, 19.9 m above base of the Denay Formation (Klapper in Johnson et al. 1980, p. 92, table 16, collection 153). Two further rugosan genera occur close to this stratigraphic level in the same area. These are Exilifrons strict sense (revised since Pedder 1977) and Utaratusia. Their positions relative to the precise costatus/australis boundary have yet to be determined.

Brachiopods of the “barren” E zone

Three lower Fl 14 brachiopod communities, named Leptocoelina (diverse), Elythyna and Alaliforme, have been demonstr­ated by Johnson (several papers, especially 1990). These were apparently so affected by the offshore shift in biotopes during the latest regressive stage of the T-R cycle Ic that very few brachiopods are known in central Nevada, and none has been described, from the entire T-R cycle Ic. Referring to this, Johnson (1990, p. 912) wrote that all three lower Fl 14 communities “are succeeded upsection by beds barren of benthic invertebrates”. This was an oversight, because Johnson et al. (1980, p. 79) had previously published the discovery of rare unsilicified brachiopods in the upper serotinus Zone and patulas Zone, which represent much of the middle and upper Fl 14 in northern Antelope Range, and referred them collectively to the Warrenella fauna. The only brachiopods recovered by the author from beds of this age in central Nevada are fragments of atrypids and spiriferids from the Synaptophyllum romanense bed of patulas Zone age, in southern Sulphur Spring Range.

The first documented Eifelian brachiopod faunas to succeed the dearth of the phylum in central Nevada during the T-R cycle Ic of Johnson et al. (1996) are from Pentamerella wintereri bearing communities. These have been studied from at least six localities (Johnson et al. 1980, 1981; Johnson 1990). They are costatus Zone age (Klapper 1977 and elsewhere) and, on conodont-based correlations, are a zone above the partitus Subzone ptenophyllid corals of central Nevada. This indicates that the arrival in central Nevada of brachiopods of an Old World provincial affinity was later than the termination of the Pragian-Emsian Great Basin coral province (Pedder & Murphy 2004), which oc­curred in two steps in patulas-partitus Subzones time.

Trans-rheic and other migrations

Regardless of whether the Rheic ocean floor persisted until late Palaeozoic time (Scotese & McAlister 1990, Scotese 1997, Golonka 2002), or was replaced by Middle Devonian time by other narrow ocean floor (Franke 1999, Azor et al. 2008), there is mounting palaeontological evidence from several benthic groups of Devonian migrations between the Maghrebo-European Realm (Plusquellec et al. 1997; Plusquellec 2007, p. 115) and the Eastern Americas Realm.

A detailed review of Synaptophyllum reveals an apparent Emsian origin for the genus in the Maghrebo-European Realm, followed by rapid latest Emsian-early Eifelian migrations of the genus to the EAR, to Nevada where it was one of the pioneer replacements of the Pragian-Emsian Great Basin coral province, and on to the Alxa (Alashan) massif. Further migration took the genus to the South China plate in later Eifelian time. Palaeobiogeographical significance of other Synaptophyllum occurrences in present day Asia cannot be assessed for lack of accurate age determinations and knowledge of plate tectonic setting. Nevertheless, it is interesting to recall that possible occurrences of the genus in East Junggar and Beishan, China, are from the same area as the Balkhash-Mongolia-Okhotsk province, which includes several Emsian EAR brachiopod genera (Hou & Boucot 1990).

None of the few latest Emsian-earliest Eifelian ptenophyllid Rugosa recorded from the Maghrebo-European Realm is likely to have been ancestral to any of the early Eifelian Ptenophyllidae of the Great Basin. And since there is no ptenophyllid of this age span in the EAR, the route taken by Dohmophyllum, Taimyrophyllum and Xystriphyllum to reach the Great Basin must have been dif­ferent from the one travelled earlier by Synaptophyllum to
arrive in the same area. Origins of the early Eifelian Nevada ptyophyllids and the cystimorph genera that accompany them will remain hidden at least until the fauna is described, but present speculation is that they may lie with elements of the latest Emsian Mount Podge fauna (Zhen 1995) preserved on the northeastern Australian craton.

**Systematic palaeontology**

Abbreviations used in this and subsequent parts of the work are: dc for corallite diameter; FI for Faunal Interval; GSC for Geological Survey of Canada; USNM for United States National Museum.

Family Stauriidae Milne Edwards & Haime, 1850

Genus *Synaptophyllum* Simpson, 1900

1900 *Synaptophyllum* n.; Simpson, p. 212 in part (includes Acinophyllum McLaren, 1959).
1900 *Placophyllum* n.; Simpson, p. 216.
1959 *Synaptophyllum* Simpson, 1900. – McLaren, p. 16.
1976 *Synaptophyllum* Simpson. – Oliver, p. 46.
1995 *Synaptophyllum* Simpson, 1900. – Lin et al., p. 174.

Type species. – *Diphyphyllum arundinaceum* Billings, 1859, p. 134. Species revised by McLaren (1959, p. 18, pl. 7, pl. 8, figs 1a–5b, text-figs 2–6) and Oliver (1976, p. 47, pls 2–4, pl. 7, figs 7–11). The strata of the lectotype (chosen by McLaren 1959, p. 19) and fragmentary paralectotypes were originally given as Corniferous limestone. In current terms, all are believed to be from the Edgecliff Member of the Onondaga Limestone. The type locality is three miles (4.8 km) west of Cayuga, southwestern Ontario. Paralectotypes are from Wainfleet township, Welland County, and Walpole township, Haldimand County, in the same general region of southern Ontario. When McLaren (1959, caption pl. 7) recorded the type stratum as the Bois Blanc Formation, he was following Best (1953), who, in applying much of the Michigan stratigraphic nomenclature in southwestern Ontario, employed the term Bois Blanc in a much wider sense than it is currently used in the province (Uyeno et al. 1982).

Type species of *Placophyllum*. – *P. tabulatum* Simpson, 1900, p. 216, text-fig. 41. Species discussed briefly by Lang et al. (1940, p. 100) and Stumm (1949, p. 30), and more fully by McLaren (1959, p. 17) and Oliver (1976, p. 49). Two of three now extant original sections were figured by McLaren (1959, pl. 10, figs 1, 2) as syntypes. Oliver (1976, pl. 5, figs 1–3) illustrated all three sections as the holotype. The type occurrence is in the Onondaga Limestone, Walpole township, Haldimand County, southwestern Ontario, and is almost certainly in the Edgecliff Member.


*Synaptophyllum minus* (Wang Zhiping in Kong & Huang, 1978, p. 49, pl. 15, fig. 7a–c), from the Longdongshui Member of the Houershan Formation, southern Guizhou, China, was first described as a species of *Heterophrentis* Billings (1875?, p. 235). However, it is a fasciculate coral with typical *Synaptophyllum* corallites, which in no way resemble the solitary trochoïd lectotype (Oliver 1993, pl. 1, figs 1, 2; pl. 2, fig. 2) of the type species of *Heterophrentis*.

*Synaptophyllum (?) angustitabulatum* (Altevogt, 1968, p. 758, pl. 1, figs 1a–2a) is based on fragmentary cylindrical corallites having the internal morphology of *Synaptophyllum*. Three of the five types, including the holotype, show intracalicular budding, suggesting that the morphology of a complete corallum would also be consistent with an assignment to *Synaptophyllum*. The types come from Radig’s (1962, p. 256) Basiskalke between Aguion and Sibares, on the Cantabrian coast of Spain. Radig’s Basiskalke (basal Couvin limestone of Altevogt) was specifically included in the Moniello Formation in the formal definition of the formation (Arbizu et al. 1979, p. 105).

Diagnosis. – See Oliver (1976, p. 46) and Hill (1981, p. F143), but note that in both *Synaptophyllum kladion* Oliver and *S. romanense* (Merriam) tabulae are locally depressed.

Discussion. – Simpson erected *Synaptophyllum* for species which had been assigned to *Eridophyllum* Milne Edwards & Haime (1850, p. lxxi), but in his view should not be included in that genus because of differences in radiciform processes (those of *Eridophyllum* do not penetrate the interior of adjacent corallites). Simpson was aware that *Diphyphyllum* Lonsdale (1845, p. 624), which Billings (1859) had used for some of these corals, is an unrelated Carboniferous genus. Confusion first arose because, although Simpson made *Diphyphyllum arundinaceum* the type species of *Synaptophyllum*, his description of the interior of the new genus, which mentioned the presence of dissepiments and septal carinae, was based entirely on species currently assigned to *Acinophyllum* McLaren (1959, p. 22). The problem stemming from Simpson’s misleading description of
Synaptophyllum was aggravated when Lang & Smith (1935, p. 561, figs 19, 20), unable to discover the whereabouts of Billings’s original material, mistakenly illustrated sections of an Upper Devonian coral from western Canada as a typical example of Synaptophyllum arundinaceum. The stylized figures of the western Canadian coral show a pipe of horseshoe dissepiments and phillipsastreid-like trabeculae, and were the basis for the widely held belief (Schouppé 1949, p. 124; Stumm 1949, p. 32; Wang Hongzhen 1950, p. 219; Różkowska 1953, p. 16; Hill 1956, p. F280; Soshkina in Soshkina et al. 1962, p. 308) that these were two of the diagnostic features of Synaptophyllum. McLaren’s 1959 work published the discovery of at least some of Billings’ specimens of Synaptophyllum arundinaceum, and demonstrated the characteristic tabular morphology of the species, as well as the absence of dissepiments and carinae from it, and is the foundation of the correct understanding of the genus.

Occurrences. – The earliest known are occurrences of Synaptophyllum multiseptatum in the upper La Vid Group in the southern part of the Cantabrian zone of northwestern Spain, and occurrences of several species (Soto in Arbizu et al. 1979, p. 109), including S. multiseptatum, in the Middle Moniello Formation, in the northern part of the zone. All are likely to be serotinus Zone age (Keller & Grötsch 1990, fig. 9; García-López & Sanz-López 2002).

The earliest occurrences of Synaptophyllum in the Eastern Americas Realm (EAR) are those of S. arundinaceum, S. kladion and S. tabulatum in the Edgecliff Member of the Onondaga Limestone in New York State and the Niagara Peninsula of Ontario. S. arundinaceum is also present at a comparable (Oliver 1976), or questionable slightly higher (Ver Straeten 2007, fig. 8) level in the uppermost Bellepoint Member of the Columbus Limestone of Ohio. Other possible early EAR occurrences of the genus are in the Formosa reef limestones of the Amherstburg Formation, about 200 km northwest of the Niagara Peninsula occurrences of Synaptophyllum. These include the poorly preserved fragmentary corallites tentatively identified as Placophyllum and Depasophyllum by Fagerstrom (1961, pl. 4, figs 12–15). Klapper & Oliver (1995, fig. 1) favoured a partitus Subzone and possibly uppermost patulus Subzone age for the Edgecliff Member of the Onodaga Limestone, whereas Prosch (1995) argued for an entirely late Emsian (serotinus Zone) age for the member. All the early EAR Synaptophyllum material is from Icriodus conodont biofacies and, as cautioned by Kirchgasser et al. (1985, p. 236), on inference only is assigned to the original undivided patulus Zone. Synaptophyllum kladion, known from one or two specimens from the upper part of the Edgecliff Member in Ontario and a few others from the costatus Zone in the Moorehouse Member of Niagara Peninsula and western New York, is the youngest certain EAR species of Synaptophyllum. An upper Eifelian specimen identified as Placophyllum? sp., from the Dundee Limestone near the northern end of the southern Michigan Peninsula, has been illustrated in an unprepared condition (Ehlers & Kesling 1970, pl. 9, fig. 10), and should only questionably be referred to Synaptophyllum.

See under Synaptophyllum romanense (Merriam), for occurrences of the genus in Nevada.

A lower Eifelian coral from the lower Yikewusu Formation (in, or slightly above beds with costatus Zone conodonts) in the Zhusilenghaierhan area of the Alxa massive, western Inner Mongolia, was identified as Synaptophyllum kladion Oliver by Li Minglu (1987, p. 70, pl. 1, fig. 2a, b). Li described the coral as fasciculate and illustrated a short corallite with a diameter of 18 mm, 31 major septa and sharply peripherally downturned tabulae. However, the types of S. kladion have a maximum dc of 6.9 mm, a maximum of 20 major septa, and irregular tabulae, including some that are flat, undulating or even depressed. Although the Alxa massif coral is not S. kladion, the determination is consistent with current concepts of the genus Synaptophyllum. Synaptophyllum sp. has also been reported from what may be higher beds of the Yikewusu Formation near Wotuashan, in the same Zhusilenghaierhan region (Wang Xunlian & Wang Hongzhen 1987, p. 312, table 2; Wang Xunlian 1987, p. 94). The fauna which includes this undescribed species of Synaptophyllum? comprises the Grypophyllum denecmanni-Acanthophyllum difficile Assemblage. Wang Xunlian & Wang Hongzhen identified several Givetian corals in this assemblage, and were unequivocal concerning its Givetian age. But, other authors have taken the occurrence of a Kayseria lens- and possible Reticulariopsis-bearing brachiopod fauna in the top unit of the Yikewusu Formation (Zhang Yan 1985; Talent et al. 2001, p. 104, fig. 6) as evidence of an Eifelian age for the entire formation.

The only published occurrence of Synaptophyllum on the South China plate is that of S. minus in Guizhou Province. The species is part of the Utarattuia-Sociophyllum Assemblage Zone of the Longdongsu Formation (or Member of the Houershan Formation), which has been correlated with the middle to upper Eifelian (australis and kockelianus zones) Hume Formation of northwestern Canada (Liao 2003, pp. 419, 423).
Possibly the youngest, and the youngest named species of Synaptophyllum is *S. dangchangense* Liao & Li from the Middle Devonian Xihanshui Group in the northern Qinling fold belt, China. Although not precisely dated, other Rugosa of the Xihanshui Group are Givetian.

Wang Zhiping (1985, p. 68) listed *Synaptophyllum* in a combined list of “Yingtang age” (= Eifelian) genera from the Beitaishan Formation in East Junggar and the Que’ershuan Group of the Beishan Mountains area in northwestern Gansu Province, China.

*Synaptophyllum romanense* (Merriam, 1974) comb. nov.

Figures 4A–F, 5A, B, D–N

1974 *Dendrostella romanensis* n.; Merriam, p. 45, pl. 18, figs 1–4.


**Type.** – Holotype, USNM 159318. Type stratum and locality given as Nevada Formation, unit 2, Devonian coral zone D, probably coral zone D2, but “may be in coral zone D1”, at USGS locality M1031, northwest of Romano Ranch, Sulphur Spring Range, Nevada. This is the same as localities 1990-31, 1996-5, 1998-27 and 1999-11 of Appendix 2. No additional material was mentioned by Merriam.


**Description.** – Corallum fasciculate, phaceloid to dendroid. Spacing and curvature of corallites variable; axes of adjacent corallites generally less than 20 mm apart. Maximum height of corallum >150 mm; maximum width of corallum >200 mm. Diameter of adult corallites 6.5–8.2 mm. Offsets generated by nonparricidal lateral budding (Fig. 4B), and apparently also by parricidal, intracalicular (axial) budding (Fig. 5A). Exterior surfaces unexposed in available material; fine septal furrows and interseptal furrows, mentioned in the original description of the species, not discernible in transverse sections. Calice cylindrical, with sharp distal rim, vertical wall and variable base. Depth of calice >8 mm.

Width of corallite wall 0.18–0.5 mm. Wall embeds unexpanded septal bases. Septal arrangement imperfectly radial. Although width of spaces between septa is inconsistent in some corallites, there is no fossula or obvious cardinal-counter plane. Septa in two orders, both variable within a single corallum. Shortest of the major septa extend less than one-third of the distance to the axis. Longest major septa are as long as the radius of the lumen, but normally curve away from the axis. Minor septa locally entirely suppressed. Where present, their length is typically much shorter than that of the major septa; few minor septa exceed 0.3 mm in length. In the holotype and six of seven other specimens from the type stratum and locality, the adult dc is 6.6–8 mm and the number of major septa per adult corallite is consistently 20. In the seventh topotype (USNM 539801), the maximum dc is 8.2 mm and the number of major septa per corallite 23.

No dissepiment present in any of 36 longitudinal sections studied. Tabulae broad, mostly complete. Tabular morphology especially variable, even within corallites of a single corallum (Fig. 4A). Tabulae commonly flat to slightly concave over a wide periaxial area, and sharply downturned around periphery of corallite. Other tabulae may be more or less flat, or only gently concave or convex; a few may form distinctly depressed tabularial surfaces. Spacing of tabulae in periaxial region, 7–19, mostly 9 or 10 tabulae over a vertical distance of 10 mm.

**Discussion.** – *Dendrostella* Glinski (1957, p. 87) is distinguished from *Synaptophyllum* by its characteristic septal bases. This diagnostic feature is not evident in the silhouette illustrations of the genus given in both the Kansas (Hill 1981, fig. 71.1b) and Beijing (Lin et al. 1995, fig. 337) treatises, but is shown well in Glinski’s (1957) figure 14. As comparison of Fig. 5B with Oliver’s (1976, pl. 4) figure 5 shows, the fine structure of the walls in *Synaptophyllum romanense* and *Synaptophyllum arundinaceum* are identical, and different from that of *Dendrostella* (Fig. 5C herein).

The description given above is based on the holotype and seven topotypes. Younger *paritus*-lower *costatus* specimens from northern Antelope Range are from a higher energy facies, and as a result, many are fragmentary. They are larger (dc commonly 8–8.5 mm; maximum 9.4 mm), and have more septa (commonly 22 × 2; maximum 25 × 2).

**Figure 5.** *Synaptophyllum romanense* (Merriam) from Sadler Ranch Formation (A, B, D–N), and *Dendrostella* sp. from Blue Fiord Formation, Arctic Canada (C). – A – USNM 539803, toptype, × 3. – B – USNM 539801, toptype, × 10. – C – GSC 133059 from GSC Locality 26441, × 9. – D, F, H – USNM 539813 from 1996-32, × 3. – E, J – USNM 539811 from 1994-8, × 3. – G, L – USNM 539812 from 1996-32, × 3. – I, M – USNM 539814 from 1996-33, × 3. Bottom left transverse section (M) is from same corallite as longitudinal section (I); top left section (I) is oblique section of *Pseudomicroplasma* sp. – K – USNM 539815 from 1996-33, × 3. – N – USNM 539807 from 1994-8, × 3.
Also, their minor septa are, on the whole, longer, and their tabulae less variable (more typical of the genus *Synaptophyllum*).

Of the two or three species of *Synaptophyllum* named before *S. romanense* was established, *S. arundinaceum* most resembles the Nevada species. The mean dc and mean number of major septa are slightly larger in *S. romanense*. The principal difference, however, is in the tabularium. In *S. romanense* the major septa are infrequently and only locally amplexoid, and the tabulae are much less consistently typical of the genus.

**Occurrence.** – Uppermost Emsian or lowermost Eifelian, undivided *patulus* Zone, Sadler Ranch Formation, southern Sulphur Spring Range. Lower Eifelian, *partitus* Subzone and lower *costatus* Zone, Sadler Ranch Formation, northern Antelope Range.

Family Romanophyllidae nov.

**Type genus.** – *Romanophyllum* nov., a cryptogenic genus.

**Diagnosis.** – As for *Romanophyllum*, the only genus named to the family.

**Remarks.** – At maturity, corals of this family have transverse sections resembling those of the Kyphophyllidae Wedekind (as broadly interpreted by McLean & Pedder 1987 and Sorauf 1998), whereas the longitudinal sections show the combined tabularial-dissepimentarial surfaces, and therefore also the calice, to be similar to cystimorph septal cones.

**Genus Romanophyllum** nov.

**Type species.** – *Romanophyllum paulyi* sp. nov.

**Other species.** – None named. One possible, older and unnamed species form the Emsian Bartine Member of Nevada.

**Diagnosis.** – Solitary rugose coral. Peripheral wall septothecate without periodic calcinial extensions, or other external indications of rejuvenescences. Cardinal septum and bilateral arrangement of septa prominent in early stages. Septa variously bent but not carinate, complete in early stages, and in all but the earliest stages, withdrawn from axis. Major septa commonly based on wide, steeply inclined preseipiments in late stages. Sclerenchymal investment of septa and the steeply inclined dissepimentarial-tabularial surfaces thick in early to middle stages.

**Etymology.** – Romano Ranch and Greek *phyllon* meaning leaf, in Latin form.

**Discussion.** – Transverse sections of adult specimens of *Romanophyllum* resemble those of kyphophyllid corals, such as *Tabulophyllum* Fenton & Fenton, 1924, which has been well illustrated by Sorauf (1998, pls 6–20) and fully discussed by McLean (2007, p. 17), but the deep inversely conical tabularial surfaces of *Romanophyllum* distinguish the genera in longitudinal section. There is some resemblance between *Romanophyllum* and the solitary kakisaphyllinid coral *Dialeptophyllum* Pedder (1990, p. 64). However, the tabularium in *Dialeptophyllum* is not conical, or as depressed. Furthermore, the prominent cardinal cardinal septum, strong bilateral septal symmetry and thick sclerenchyme of the early stages of *Romanophyllum* are not present in *Dialeptophyllum*

A single specimen (USNM 539830) from the upper Bartine Member on Lone Mountain is questionably identified and illustrated (Fig. 8F, H, J) as a species of *Romanophyllum*. Its much fractured tabularium and missing proximal region prevent firm identification. One of the other two corals (USNM 510051) illustrated in Fig. 8 was previously (Pedder 2002, p. 145) considered to be an atypical species of *Breviphyllum* with a depressed tabularium. Since then, another specimen (USNM 53983; Fig. 8A, E, G) of the same Bartine Member species has been prepared. The species cannot be identified certainly with any known Nevada coral genus. The phylogeny of *Romanophyllum* is unknown, but if the problematic phylogeny of *Romanophyllum* is with the Breviphylidae, it might be through atypical breviphylloid corals such as these.

both boss and platform. Maximum diameter and length estimated >41 mm and 80 mm. Evidence of rejuvenescence confined to a few specimens with a flattened tabula overlying a preceding calice, and in one specimen, overlain by thickened rejuvenated septa (Fig. 7R). Periphery septotheca, mostly thin in late stages, although prominent septal bases locally may produce a more robust wall (Fig. 6L).

Brephic stages not preserved. In an early neanic stage (dc 5 mm, Fig. 7N) there are about 22 mostly contiguous septa, and the septal arrangement is bilateral about a relatively large cardinal septum and discernible counter septum. A transverse section of a slightly later neanic stage (dc 6.5 mm, Fig. 7K) shows a similar number of septa and some narrow interseptal loculi. A specimen with elliptical transverse outline (average dc about 12.5 mm, Fig. 6D, H) has shortened cardinal and counter septa, 29 other major septa, a few short minor septa and pronounced cardinal bilateral symmetry. Another late neanic section (dc 13 mm, Fig. 7G) of a damaged specimen shows heavy sclerenchymal coating of the adaxial parts of the major septa and continued strong cardinal bilateral symmetry. There are 30 major septa in addition to the cardinal septum and almost as many minor septa. The lower transverse section of the holotype (dc 16 mm, Fig. 6E) is partly decorticated. There are estimated to be 36 major septa, much coated with sclerenchyme, which almost totally engulfs the minor septa. None of the septa is withdrawn from the periphery; symmetry in this late neanic stage remains essentially bilateral. The neanic stage may continue to dc 21 mm. In an example of this (Fig. 7J), there are 37 × 2 septa, with short minor septa visible in most interseptal loculi.

Peripheral septal withdrawal, reduction of sclerenchyme and near radial septal symmetry with weak cardinal fossula characterise ephich stages. The smallest example in the type series having any of these features (dc 19 mm, Fig. 7A) has three major septa based on one presepmient and a single major septum based on an adjacent presepmient. In late ephich stages, most septa are withdrawn from the septotheca. Septa exhibit small-scale bends in transverse section, but are not carinate, and there is a narrow periaxial region free of septa. Septal counts are 35 × 2 (dc 29, Fig. 6G), 38 × 2 (dc 28 mm, Fig. 7A), 41 × 2 (dc 35 mm, Fig. 7E), and in holotype, 43 × 2 (dc 41 mm, Fig. 6F).

Dissepiments elongate, typically in no more than two rows in brephic stages. In ephich stages, marginarium comprises large presepmients and dissepiments in as many as eight rows. Dissepimentarium and tabularium not clearly distinguished in brephic stages. In neanic stages, tabularium distinguished as the cylindrical periaxial space not penetrated by major septa. Tabulae periaxially depressed and irregularly spaced.

Etymology. – Patronym for G.B. Pauly who helped collect the type series.

Occurrence. – Presently known only from the type stratum and locality.

Remarks. – The small cylindrical corallite illustrated in Fig. 6C, which has a thin nonseptate wall, large presepmients and short septa, does not fit the ontogenetically framed description given for the species. Except for its small size and cylindrical shape, the unillustrated longitudinal section is typical of the species. The corallite (USNM 539827) is tentatively interpreted as a failed intracalicular bud of *Romanophyllum paulyi*, and not evidence of a second species in the genus.

Family Ptenophyllidae Wedekind, 1923

Remarks. – Originally proposed (Wedekind, 1923, p. 33) as a subfamily of the Cyathophyllidae. Promoted to family rank by Wedekind (1924, p. 35).

**Genus Xystriphyllum Hill, 1939**

?1938 *Kozlowiophyllum* n.; Rukhin, p. 34.
1938 *Entelophyllum (Entelophylloides)* subgen. n.; Rukhin, p. 23.
1939 *Xystriphyllum* n.; Hill, p. 62 in part (includes *Entelophylloides*).
1970 *Xystriphyllum* Hill. – Oliver & Galle, p. 57.
1995 *Xystriphyllum* Hill, 1939. – Lin et al., p. 281.

Type species. – *Cyathophyllum dunstani* Etheridge, 1911, p. 3, pl. A, figs 1, 2. Lower Palaeozoic limestone; Clermont, Queensland. The type stratum is in the Douglas Creek Limestone of current terminology. From conodonts in the limestone (Philip & Pedder, 1968, p. 1037 – their *P. linguiformis foveolata is Polygnathus perbonus*) and brachiopods in the overlying silstone (Brock & Talent 1993), the type occurrence is Emsian, *groenbergi perbonus* to *versus* Zone age. The exact type locality is not known, but...
is one of several isolated exposures of the Douglas Creek Limestone around Douglas Creek Homestead, 8–10 km south-southwest of Clermont. A full description of the type species, including choice of lectotype, was given by Hill (1939, p. 63). The lectotype has been illustrated by Hill (1939, pl. 5, fig. 6a, b; 1981, fig. 154, e) and by Jell & Hill (1970, pl. 4, fig. 1a, b), and Strusz (1966, pl. 91, fig. 2a, b) has provided good illustrations of a paralectotype. Jell & Hill’s (1970, p. 101) remarks concerning the type species are especially useful for discriminating Xystriphyllum from Australophyllum Stumm, 1949.

**Type species of Kozlowiaphyllum.** – *K. pentagonum* Rukhin, 1938, p. 34, 99, pl. 3, figs 9, 10. “Upper part of the Upper Silurian”; right bank of Yasachnaya River below mouth of River Torynakh, upper Kolyma River basin, northeastern Russia. The level of the type stratum given by Rukhin is probably wrong. It is more likely to be in the Lochkovian-Eifelian succession, which, on Yasachnaya River, rests unconformably on Ordovician-lower Silurian beds, and includes fossiliferous Eifelian limestone (Gagiev 1997, column 8, fig. 3, p. 80). The type material is lost (Ivanovskiy 1976, p. 94).

**Type species of Hinganophyllum.** – *H. polygonalis* Guo, 1990, p. 30, 36, 3, fig. 1a, b, pl. 4, fig. 1. Wunur Formation; Weinaha River, Toudaoguqiao district, about 150 km south of Hailar City, Ewenkizu Autonomous County, Inner Mongolia, China. Guo believed the type horizon to be early Middle Devonian, but the coral fauna of the Wunur Formation is more consistent with the Emsian age given to the formation by Wang Cheng-yuan (2001, p. 446).

**Remarks.** – There is little doubt that the type species of Rukhin’s available genus *Kozlowiaphyllum*, which is not a nomen oblitum, is congeneric with *Xystriphyllum trojani* sp. nov. Rukhin’s and Soshkina’s (in Soshkina et al. 1962, p. 335) descriptions of *Kozlowiaphyllum pentagonum* suggest it has a typical ptenophyllid tabularium. However, illustration of a longitudinal section and other knowledge of *K. pentagonum* are desirable before *Kozlowiaphyllum* is substituted for *Xystriphyllum*.

**Xystriphyllum trojani** sp. nov.

Figures 3A, B, 9A–E

**Type series.** – Holotype, USNM 539832 from 1996-34. One approximately topotypic paratype, USNM 539833 from 1996-36. Type occurrence is in a debris flow, 4.6–4.9 m above base of the Denay Limestone, lower Eifelian, costatus Zone; TA Va section, northern Antelope Range.

**Diagnosis.** – Species of *Xystriphyllum* with mean adult dc 13–19 mm, and narrow subcylindrical tabularia with adult diameters 2.5–4.4 mm. Septa thin and mostly complete, numbering 16 × 2 – 26 × 2 per adult corallite. Dissepiments small, abundant, in as many as 16 rows.

**Description.** – Corallum cerioid, large with many commonly five-sided prismatic corallites. Mean adult dc 13–18 mm in holotype, 15–19 mm in the slightly better preserved paratype. Increase marginarial, nonparricidal. Offsets generated one at a time, normally in a corner of the parent corallite.

Septothecae from adjacent corallites combine to form wall between corallites. Septal bases prominent, wedge-shaped and trabeculate. Contiguous septal bases forming an intercorallite wall may be back-to-back, or offset causing the wall to be somewhat sinuous. Thinnest parts of intercorallite wall, where septal bases are back-to-back, 0.15–0.5 mm thick. In dispesimentarium, septa undifferentiated, finely trabeculate, thin, slightly crenulate but noncarinate, and radially arranged. Most septa are continuous. A few are briefly ruptured close to their base, especially in corners of large irregular prismatic corallites, where offsets are likely to develop. Minor septa terminate just inside the tabularium; major septa extend to the periaxial area where they are very slightly thickened, weakly flanged, and variably twisted. The fine trabecule are long, parallel, straight and inwardly inclined 40–45° to horizontal in the marginarium. Septal counts in immature corallites (dc 6–9.5 mm) 16 × 2 – 21 × 2, and in mature corallites (dc 14–19 mm) 23 × 2 – 26 × 2.

Dissepiments small, abundant, moderately inflated and inwardly inclined at 40–45° to horizontal throughout most of the dispesimentarium. Inclination of innermost dissepiments increases adaxially, so that transition from dispesimentarium to tabularium is abrupt in the normal ptenophyllid manner. Eight to sixteen rows of dissepiments present in typical adult corallites. Tabularium subcylindrical, narrow relative to corallite width, with adult diameters 2.5–3.5 mm in holotype, and as much as 4.4 mm in some paratype corallites. Tabularial surfaces variably depressed. Tabulæe incomplete, closely spaced, 30–40 occur over a vertical distance of 10 mm.

**Etymology.** – Patronyn for W.R. Trojan, in recognition of his important work in the northern Antelope Range.

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**Figure 8.** Breviphrentid gen. undetermined, Bartine Member, Lone Mountain (A, E, G) and northern Roberts Mountains (B–D, I), and *Romanophyllum?* sp. Bartine Member, Lone Mountain (F, H, J). • A, E, G – USNM 539831 from 1997-51, × 2. • B–D – USNM 510051 from 1997-7, × 2. • I – USNM 510051 from 1997-7, part of transverse section, × 7. • F, H, J – USNM 539830 from 1990-18, × 1.9.
Figure 9. *Xystriphyllum trojani* sp. nov., debris flow near base of Denay Limestone, × 2.5. • A, B – paratype, USNM 539833 from 1996-36. • C–E – holotype, USNM 539332 from 1996-34.
Discussion. – The new species belongs to a group of large ceroid ptenophyllid corals, comprising species originally named Kołowiaphyllum pentagonum Rukhin, 1938, Xystriphyllum magnum Hill, 1942 (p. 147, pl. 3, fig. 2a, b), Stenophyllum uralicum Soshkina, 1949 (p. 129, pl. 52, fig. 1a, b, pl. 53, fig. 5a, b), Australophyllum indigense Cherepnina, 1986 (in Ivaniya & Cherepnina, p. 86, pl. 9, fig. 21b, pl. 10, fig. 21a) and Hinganophyllum polygonalis Guo, 1990. The group also includes an unnamed lower Eifelian species from Devon Island, Arctic Canada. These species differ from smaller, more typical species of Xystriphyllum by having a wide dispersion of coral stems with small diameter, in an irregularly narrow pubescent zone. Their septa are thin and locally discontinuous near the periphery. Hinganophyllum polygonalis and Xystriphyllum trojani differ from the other corals of the group in a prominent septal base in a septothecate wall. Xystriphyllum trojani differs from Hinganophyllum polygonalis by its small size (dc in Guo’s species as high as 35 mm) and by its adaxial septal ends, which are only slightly inflated and not as strongly flanged and rhopaloid as those of Hinganophyllum polygonalis are.

Conclusions

The Devonian coral based E zone has been considered impoverished, even barren of corals or brachiopods for three reasons: 1) knowledge of Devonian corals in Nevada has largely been based on successions in the Roberts Mountains and Lone Mountain on an inferred disconformity appears to exclude much of the zone; 2) dolomitisation has severely affected the biota of the upper part of the zone in the “re-ars to exclude much of the zone; 2) dolomitisation has severely affected the biota of the upper part of the zone in the “re-

The turnover from the second to third of these assemblages in partitus to lower costatus Zone time is profound. It marks the end of the Pragian-Emsian Great Basin coral province and appears to correspond to the Choteč Event of the Bohemian massif.

Identifications of Synaptophyllum and discoveries of ptenophyllid genera Dohmophyllum, Taimyrophyllum and Xystriphyllum in patalus and lower costatus zones are important in defining the three-step change from Lower to Middle Devonian coral faunas in the Great Basin.

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Appendix 1 – Rejected identifications of Synaptophyllum

McLaren’s (1959) and Oliver’s (1976) exclusions from the gen- us are not repeated here.

Excluded species. – Macgeea (Synaptophyllum) heritschi Schouppé 1949 (p. 180, pl. 12, fig. 66) is a nomen nudum. The caption to figure 66 states that the illustrated, but unrecognisable coral is from the Grazer Palaeozoikum. Flügel & Hubmann (1994, p. 22) added that it is from the Barrandekalk at Schindel- graben. This suggests that it is uppermost Emsian or Eifelian.

Rózkowska (1953, p. 16) emended Lang & Smith’s concept of Synaptophyllum (see discussion) by restricting it to species with large lateral (radiciform) processes. Thus, the early Frasnian spe- cies from the Holy Cross Mountains, Poland, named Synapto- phyllum soshkiniae by her (1953, p. 16, text-fig. 6, pl. 2, figs 1–4) has prominent lateral processes as well as a pipe of horseshoe dissepiments and phillipsastreid trabeculae. It is, in McLean’s view (2005, p. 30), another species of Thamnophyllum.

The originally unprepared holotype of Synaptophyllum gra- baui Fagerstrom (1961, p. 13, pl. 3, figs 11–14) is from the upper Emsian or lower Eifelian Amherstburg Formation on Detroit River, dividing Michigan from Ontario. Although after thin sec- toring it remains unrecognisable, it is not a specimen of Syna- tophyllum (Pedder & Oliver 1982, p. 9, pl. 14, figs 10, 11). Fagerström’s illustrated specimens assigned to the species are stauromatidid corals, now referred to Fasciculum trigemma (Da- vis 1887, caption pl. 130, figs 1, 2), from reef facies of the Amherst- burg Formation in Bruce County, Ontario.

Synaptophyllum occidentale Sorauf (1972, p. 435, pl. 3, figs 5, 6; pl. 4, fig. 1) is based on a specimen from Limestone Hill in Pend Oreille County, northeastern Washington State. At the time of publication it was thought to have come from a sequence yield- ing Middle Devonian corals. Subsequently, Greenman et al. (1977) demonstrated faults and at least one major erosional break in the succession, and by means of conodonts established a Frasn- ian age for the topmost part (unit E) of it. The present author has collected twice on Limestone Hill, and has been shown photograph- s of corals from the area by the late G.O. Raasch (pers. comm., circa 1985). Rugosa from unit E include Micropyllum semidilatum Smith, Frechastraeos? sp., Pachyphyllum sp., Penen- cchiella metalinae Sorauf, Phillipisastrea nevalensis (Stumm) and Thamnophyllum colemannense (Warren). Synaptophyllum occi- dentale has not been recollected from its type area, but should al- most certainly be added to the fauna of unit E. McLean & Pedder (1987, p. 158) gave reasons for believing it to be a small, middle Frasian species of Smithiphylum with very few dissepiments and presepiments. The species is evidently rare on Limestone Hill, but is common in the western Canada sedimentary basin.

Synaptophyllum(?) oliveri Rodríguez García, 1978 (p. 344, pl. 3, figs 1–5), from a Pragian (S. Rodríguez, pers.comm., 2009) reef debris bed in the Sierra del Pedroso, southern Central Iberian zone, Spain, lacks the typical tabularial morphology of Synaptophyllum, and its minor septa are either absent, or appear only as peripheral spines.

Rejected transfers to Synaptophyllum. – Several early to mid- twentieth century publications reported the presence of Syna- tophyllum in Silurian beds of eastern North America. The species referred to Synaptophyllum in these works are either those origi- nally named Lithothrostone harmodites Milne Edwards & Haima (1851, p. 440, pl. 15, fig. 1, la), apparently introduced as a replace- ment for Lithodendron irregularae Castelnau (1843, p. 49, pl. 23, fig. 1; not Phillips 1836, p. 202, pl. 2, figs 14, 15), or Syrin-gorons(?) multicaulis Hall (1852, p. 119, pl. 33, fig. 3a–g).

The interior morphology of the lectotype (designed holotype by Easton, 1957, p. 620) of “Lithothrostone” harmodites is un- known, but the exterior of the only known specimen certainly
belonging to the species was redescribed and re-illustrated by Easton (1957, p. 620, pl. 71, fig. 4). Although Easton was aware that the label attached to the lectotype reads “Carboniferous of Indiana”, he believed the coral to be a Silurian “species of Synaptophyllum very close, if not conspecific with S. multicaule (Billings)”. In the absence of full knowledge of the interior morphology, the species is indeterminate. Nevertheless, since Easton was unequivocal that its septa are carinate, the species is not Synaptophyllum as the genus is currently diagnosed.

Ivanovskiy (1965, p. 83; 1978, p. 101) and most earlier workers interpreted Syringopora (?) multicaulis Hall as having dissepiments, and referred it to either Diphophyllum or Entelophyllum. However, Hall’s types (Oliver 1963, p. G-5, pl. 4, figs 1–7) lack both dissepiments and carinae, and are best regarded as a late, and in respect to their strongly elevated tabularium, somewhat atypical species of *Palaeophyllum* Billings (1858, p. 168; Hill 1981, p. F138). Oliver did not discuss the type stratigraphic occurrences of *Palaeophyllum multicaule*, given by Hall as “lower part of the Niagara limestone” at Lockport and Barre, western New York State, but Laub (1983, p. 28) indicated that they are likely in the upper Homeric (LoDuca & Brett 1991) Gasport Formation. Bolton (1966, pl. 12, figs 1, 3) has illustrated the species from the undivided Lockport Formation at Thorold, southwestern Ontario.

Following Lang & Smith’s (1935) interpretation of the type species of *Synaptophyllum* as what today would be considered a phillipsastreid coral, Schouppé (1949, pp. 171, 172) employed *Synaptophyllum* as a subgenus of *Macarea* Webster, 1889. Although used for fasciculate species, the only clearly specified criterion for recognition of *Synaptophyllum* as a subgenus by Schouppé was the presence of peripheral septal carination. Species transferred to *Macarea* (S.) by Schouppé were *Peneckella naliivkini* Soshkina (1939, p. 24, pl. 8, figs 68, 69) and *P. spiraalis* Soshkina (1939, p. 28, pl. 10, figs 79, 80). Both are Frasnian species from the Urals, illustrated by line drawings which do not show trabecular structure. *P. naliivkini* appears to have uninterupted peneckielloid dissepiments and may be *Peneckella* strict sense, whereas *P. spiraalis* appears to have a pipe of horseshoe dissepiments, indicating that it is likely to be a species of *Thamnophyllum* Penecke, 1894 (see also McLean 2005, pp. 31, 41).

*Depasophyllum gansuense* Ouyang (in Cao et al., 1983, p. 135, pl. 29, figs 3a, b) is another species that has probably been erroneously transferred to *Synaptophyllum*. It was described from the southern side of the western Qinling fold belt, Gansu Province, in what later became the Gorizdronia profunda-*Synaptophyllum gansuense* Assemblage Zone (Cao 1987, p. 56; Cao & Ouyang 1987, p. 192). Corals comprising the assemblage come from 220.7–422 m above the base of the Doushishan Formation. *Paleomotelepis glabra lepta* and other conodonts, occurring with the corals, indicate a Late Devonian Famennian age (Li Jensing 1987, p. 80). This inadequately known coral resembles *Synaptophyllum* more than *Depasophyllum*, but most likely will prove to be another small species of *Smithiphyllum* with rare dissepiments. In China, *Smithiphyllum* is one of the rare coral genera to have survived (Liao 2002, fig. 1; 2004, p. 259), or to have reappeared as a lazarus genus (Poty 1999, fig. 3) after the Frasnian-Famennian extinction event.

Other revised identifications of *Synaptophyllum*. – A curiosity of both Lang’s and Smith’s precise systematics was their use of brachyphyllous and *Peneckiella* (Lang & Smith 1935, Lang 1938) or square brackets (Lang 1938, Smith 1945) for genomorphs. Justification for this unconventional procedure was most fully argued in Lang (1938), especially pages 156–159, where genomorphs are defined as small groups of species having morphological characters, which were developed independently in one or several other lineages (see also Smith 1945, p. 7). Names for the genomorphs were taken from subjectively suppressed genera, such as *Disphylum* (*Synaptophyllum*) in Lang (1938, p. 158) or *Disphylum* (*Synaptophyllum*) in Smith (1945, pp. 22–24). These *Synaptophyllum*-named genomorphs were mistakenly used for species of *Disphylum* de Fromentel, 1861, possessing horseshoe dissepiments and sepal carinae. There is no indication that Lang or Smith ever regarded their genomorphs as subgenera. Thus, strictly, the Upper Devonian species *Disphylum* (*Synaptophyllum*) *densum* and D. (S.) *canselli* erected by Smith (1945, p. 22, 23) are currently unacceptable species of *Disphylum*, not subgenus *Synaptophyllum*. The former species has been removed to a previously named species of *Peneckella* Soshkina (1939, p. 23) by McLean (2005, p. 42); the latter conforms to the diagnosis of *Pantophyllum* (Lakhov 1982, p. 21).

Many collections from the area of Eaglesnest Pass, Jasper Park, western Canada have been examined. None contains *Synaptophyllum*. Warren & Stelck’s (1950, p. 68; 1956, pl. 20, fig. 9) identification and exterior illustration of a late Frasnian coral from this area as *Synaptophyllum* n. sp. was made before McLean’s (1959) revision of the genus was available. Warren & Stelck’s specimen is a species of *Disphylum* de Fromentel, 1861.

With the help of the late C. H. Crickmay (pers. comm., 1961) and J. Craig (pers. comm., 1973) it has been possible to assess two of Crickmay’s (1957, p. 4) listings of *Synaptophyllum* from the Upper Devonian “Grumbler Formation” on Hay River, District of Mackenzie, Canada. The reference to *Synaptophyllum* sp., occurring with *Hexagonaria reticulata* above Alexandra Falls, was based on a specimen of *Peneckella floydensis* (Belanski, 1928, p. 176, pl. 12, fig. 1) sense of McLean (2005, p. 42), from the Upper Member of the Frasnian Twin Falls Formation. The reference to *Synaptophyllum* sp. n., in “12 feet of grey, fragmental and coralline limestone”, was based on material of *Smithiphyllum imbaliferum* McLean & Pedder (1987, p. 156, pl. 6, figs 1–5, 10, 11) from near the top of the Upper Member of the Twin Falls Formation.

The identification of *Synaptophyllum* sp. in the Blue Fiord Formation on Bathurst Island by D. J. McLean (in Thorsteinsson & Glenister 1963, p. 593) was based on probable lower Eifelian (costatus Zone) fragments of *Dendrostella* Glinski, 1957. One of these is illustrated in Fig. 5C.

Corals listed by Liberty & Bolton (1971, p. 134) as *Synaptophyllum arundinaceum* (Billings) and *S. simcoense* (Billings) from bioherm facies (Formosa reef facies) of the Detroit River Group are assumed to be species of *Acinophyllum*. The identifications were taken from Best’s unpublished 1953 thesis, and were based on Simpson’s (1900), Shimer & Shrock’s (1944, p. 95) and other’s flawed concept of *Synaptophyllum*.

An unprepared coral from the Columbus Limestone at Bellepoint, Delaware County, Ohio, has been illustrated by Babcock (1996, fig. 7–4.5) as *Synaptophyllum simcoense* (Billings). Although strictly unidentifiable, further study may show it to be a specimen of *Synaptophyllum arundinaceum* (Billings 1859), which is known from the Bellepoint Member of Ohio. It is less likely to be *Acinophyllum simcoense* (Billings 1859).
The Emsian specimen identified as *Synaptophyllum* sp. (Uli-
tina 2003, p. 229, pl. R6, fig. 1a, b), from the sub-inversus Zone part of the Chulun Suite of Gobi Altay, Mongolia, is an uniden-
tifiable corallite, about 22 mm in diameter. The transverse sec-
tion reveals no minor septum, while the upside down longitudi-
nal section appears to show two moderately large dissepiments.

Appendix 2 – Stratigraphic and locality data

Nevada Universal Transverse Mercator Grid references (UTMG) taken from 1986–90 editions of the cited 7.5 minute series topo-
graphic quadrangle maps; all references Zone 11. Unless other-
wise stated, collections were made and identified by the aut-
Thomson (1980, fig. 2). Several species described by

The report of an Emsian *Synaptophyllum* biostrome in the Moulin de Garel section, Montagne Noire (Schröder & Soto
2003, pp. 547, 548), was based on preliminary field identificati-
s of *Breviphyllum* species, as species of *Synaptophyllum* (F. Soto, pers. comm., 2009). These are the species described by
Pedder (in Pedder & Feist, 1998, p. 981) from the same Moulin de
Garel biostrome (R. Feist, pers. comm. 2009).


1996-31. Crinoidal unit, Sadler Ranch Formation, 1–2 m below top of unit exposure; lower costatus Zone. About 100 m north of same TA Va section as 1996-31 (= 100–103 feet level). UTMG 566270 m E 4344900 m N. *Pseudomicroplasma*? sp., *Synaptophyllum romanense* (Merriam).

1996-34. Denay Limestone, debris flow, 4.6–4.9 m above ex-
posed base of lower member; *Pentamerella* diverse community in upper costatus Zone of FI 15 (Johnson et al., 1980, tables 2, 15). Same TA Va Section as 1996-31 (= 121–122 feet level). *Mesop-
hyllum* sp., *Sociophyllum* sp., *Xystriphyllum trojani* sp. nov.

1996-36. Loose specimen free of matrix, collected by M.A. Mur-
phy from debris flow near base of lower member of Denay Limes-
tone; presumed lower costatus Zone. Between sections TA II and
Va, northern Antelope Range (Johnson et al. 1980, fig. 2). Approx-
imate UTMG 566290 m E 4344760 m N, West of Bellevue Peak
Quadrange. *Xystriphyllum trojani* sp. nov.

1997-7. Barte Member, loose specimen collected 45.9 m above base, and 71.6 m below top of member; probably from *gron-
bergi* Zone. MDC II section, gully on right (east) side of Dry Creek, northern Roberts Mountains. UTMG 561620 m E 4422430 m N, Cooper Peak Quadrange. Breviphyllid gen. undetermined (previ-
ously identified as *Breviphyllum* sp. A.).

1997-51. Barte Member, talus collected near middle of mem-
ber; presumed *gronbergi* Zone. About 540 m north-northwest of type Barte Member exposure, Lone Mountain. UTMG 562955 m E 4383450 m N, Barte Ranch Quadrange. *Zonophyllum ro-
bertsense* (Stumm), breviphyllid gen. undetermined.


GSC Locality 26441. Blue Fiord Formation, Eielian (probably costatus Zone). Walker River below mouth of Tarmigan Creek, 4 km inland from coast, Driftwood Bay area, eastern Bathurst Is-
land. Approximate co-ordinates 75° 58´20˝ N Lat.; 97° 48´00˝