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Symbiosis in Late Devonian-Mississippian corals: a review

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Abstract There are four symbiotic associations involving corals known from the Late Devonian. Corals formed at least six symbiotic associations in the Mississippian, most of which involved crinoids. There was an escalation in the abundance and complexity of coral symbiosis from the Ordovician into the Devonian, and no decline in the Carboniferous. Coral symbiosis after the Kellwasser biotic crises was impoverished and presumably did not recover to Middle Devonian levels in the early Carboniferous. Recovery of symbiotic associations after the Hangenberg Event was due to the re-establishment of associations known from earlier Palaeozoic times and appearance of new symbiotic associations. The lack of various worm bioclaustrations and endobiotic tentaculitoid tubeworms in Carboniferous corals is the main difference from the Ordovician, Silurian, and Devonian coral symbiosis. Late Devonian symbiotic associations involving corals are different from early Carboniferous associations.

Keywords Symbiosis · Tabulate corals · Rugose corals · Crinoids · Bioclaustrations · Mississippian

Introduction

Symbiotic interactions are a critical component of relationships between organisms in the modern oceans. The history of symbiotic interactions of corals helps us to better understand the processes influencing evolution of symbiosis in modern marine ecosystems. Symbiotic interactions played an important role in the Palaeozoic marine faunas, though there are somewhat limited data for the late Palaeozoic (Tapanila 2005). Symbiotic relationships are most easily recognised in the fossil record when one organism has caused changes in the growth of another's skeleton. Often symbionts are embedded within the skeleton of another organism, leaving only small apertures exposed for feeding. These embedment structures are termed bioclaustrations (Palmer and Wilson 1988). Other data of symbiosis involve the attachment of a symbiont to the skeleton of other living organisms when the skeletal structures show that both organisms were alive at the same time (Liddell and Brett 1982).

The decline of corals in the Late Devonian takes place at the Frasnian/Famennian boundary (i.e. Kellwasser Event). Frasnian coral faunas are even richer than those of the Givetian (Scrutton 1997, 1998). The Carboniferous had a rich and diverse coral fauna; both tabulates and rugosans occurred in Carboniferous seas, but tabulates were less common and diverse than in the Silurian and Devonian (Scrutton 1997, 1998). Corals were both primary and secondary reef builders in the Carboniferous and had an important role along with microbes in the development of reef limestones (e.g. Webb 2002; Aretz and Herbig 2003, 2008; Aretz and Chevalier 2007; Coronado and Rodríguez 2014). Symbiosis with the other invertebrates was not common in the Carboniferous corals and only few cases are known (Meyer and Ausich 1983; Donovan and Lewis 1999; Donovan et al. 2005; Coronado et al. 2015; Pickett 2016). There are also many examples of Carboniferous corals being epibionts on other invertebrates and corals being encrusted by other organisms (Rodríguez 2004), but usually this is not regarded as symbiosis.

The aims of this study are as follows: (1) to summarise the symbiotic associations involving corals found in the Upper Devonian and Mississippian strata; and (2) to discuss trends in the stratigraphical distribution of symbiosis in the Palaeozoic.

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Symbiotic associations in the Late Devonian and early Carboniferous

Brachiopod-auloporid association

This symbiotic association has a stratigraphic range from Silurian to Frasnian and it is apparently absent in the Famennian (Taylor and Wilson 2003; Mistiaen et al. 2012). More than forty brachiopod species were encrusted by auloporids in the Frasnian strata of the Boulonnais (Mistiaen et al. 2012). Usually auloporids encrusted their hosts in vivo. Zapalski (2005) described relationship between coral and brachiopod and found that it may have been a scramble competition, because coral used water currents produced by brachiopod's lophophore (Alvarez and Taylor 1987; Brice and Mistiaen 1992). Intercepting food particles by auloporid may have impoverished brachiopod's food supply.

Stromatoporoid-syringoporid association

This association ranges from Ludlow (Mistiaen 1984; Kershaw 1987) to Frasnian (Da Silva et al. 2011). Syringoporids can grow independently or as symbiotic endobionts within stromatoporoids.

Symbiotic syringoporids are always completely embedded within stromatoporoid skeleton, leaving only their apertures free on the growth surface of the host (Kershaw 1987; Vinn 2016). Symbiotic syringoporids could have benefitted from the stable growth substrate provided by stromatoporoids. Calcareous rigid skeletons of syringoporid symbionts may have reinforced skeletons of stromatoporoids (Vinn 2016). Twenty-seven stromatoporoid genera contained syringoporid symbionts in the Devonian (Mistiaen 1984). The *Caunopora*-type of syringoporid-stromatoporoid symbiosis is extremely common in the Middle Devonian, but somewhat less common in the Late Devonian (Mistiaen 1984; May 1999; May 2005).

Rugosan-auloporid association

This association occurs in the Frasnian of Russia (Zatoń et al. 2015). The auloporid coralla are embedded within the host rugose coral skeleton (Zatoń et al. 2015). They are visible on the external surface of the rugosan in the form of protruded coralla (Zatoń et al. 2015). The host rugose corals, both colonial (*Disphyllia russiensis*) and solitary forms (*Mictophyllum heckeri* and *Mictophyllum pseudosociale*), possess auloporid symbionts. There are one to seven embedded auloporid symbionts per a single rugose individual (Zatoń et al. 2015). Location of embedded auloporid corallites along growth axis of host rugosans suggests a continuous interaction between the two corals (Zatoń et al. 2015).

Tabulate-Chaetosalpinx association

The association has a stratigraphic range from Late Ordovician (Tapanila 2004) to late Famennian (Zapalski et al. 2008). *Chaetosalpinx* is a bioclaustration that includes straight to curved cavities that are parallel to the tabulate's axis of growth (Mõtus and Vinn 2009). *Chaetosalpinx* in tabulates is circular to oval in transverse-section and it lacks a wall lining and tabulae (Mõtus and Vinn 2009). *Chaetosalpinx* sp. occurs within the tabulate coral *Yavorskia* sp. (Favositida) in the latest Famennian in the northern France (Zapalski et al. 2008). The relationship in this association was presumably parasitic (Zapalski 2007, 2011). Zapalski (2009) has demonstrated on Emsian–Eifelian material of *Favosites goldfussi* that parasites were absent in the early astogenetical stages, and that during astogeny, both the number of parasites per colony and the number of parasites per polyp increased.

Syringopora-rugosan association

This association is known from the late Tournaisian to early Viséan of New South Wales, Australia. *Symplectophyllum* is frequently associated with the phaceloid tabulate coral *Syringopora* (Pickett 2016) (Fig. 1). Rugosans occur within the coralla of *Syringopora*, and they grew in tandem (Pickett 2016). The settlement of *Symplectophyllum* larvae appears to have been associated with periodic mortality events in *Syringopora* that caused breaks in vertical growth (Pickett 2016). The manner in which *Symplectophyllum* corallites acquired space for growth in the *Syringopora* colony suggests the presence of sweeper tentacles in the rugosan symbiont (Pickett 2016).

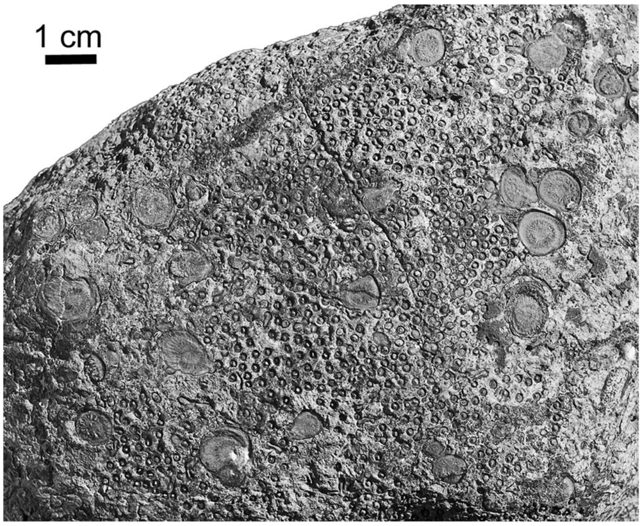

Fig. 1 Syringoporid-rugosan association. *Symplectophyllum* in *Syringopora*, weathered surface, Caroda Formation, Pinaroo, Australia (after Pickett 2016, p. 47, fig. 5)

Rugosan-rugosan association

This association is known from the late Tournaisian to early Viséan of New South Wales, Australia (Pickett 2016). Solitary rugosan *Symplectophyllum* can rarely be associated with branching lithostrotionids such as *Cionodendron* Benson and Smith or *Pickettodendron* Denayer and Webb (Pickett 2016) (Fig. 2). *Symplectophyllum* occurs within the coralla of lithostrotionids and grew in tandem (Pickett 2016). The settlement of *Symplectophyllum* larvae appears to have been associated with periodic mortality events in branching lithostrotionids (Pickett 2016).

Syringopora-alcyonarian association

This association is known from the Viséan of Morocco and Spain (Coronado et al. 2015).

Syringoalcyon is an association between the tabulate coral *Syringopora* and an alcyonarian epibiont that was attached to the syringoporoid (Coronado et al. 2015). Syringoalcyon is composed of vertical tubes of *Syringopora*, with the addition of numerous monocrystalline scales with their apices directed upwards and densely arranged around the external wall of each corallite (Coronado et al. 2015).

Crinoid-favositid association

The favositid-crinoid association had a stratigraphic range from the Silurian to the lower Carboniferous (e.g. Brett and Eckert 1982; Meyer and Ausich 1983). Favositid larva settled on living crinoid stems forming a symbiotic association (Meyer and Ausich 1983). Pluricolumnals are overgrown from all sides, indicating a *syn vivo* interaction between the two organisms (Berkowski and Zapalski 2014). The epizoan influence on the host may have been negative as it caused a loss in flexibility of the crinoid stalk (Berkowski and Zapalski 2014). Favositids profited from the elevated position over the seafloor and nutrient-bearing water currents (Berkowski and Zapalski 2014). Berkowski and Zapalski (2014) supposed that this interaction was close to parasitism.

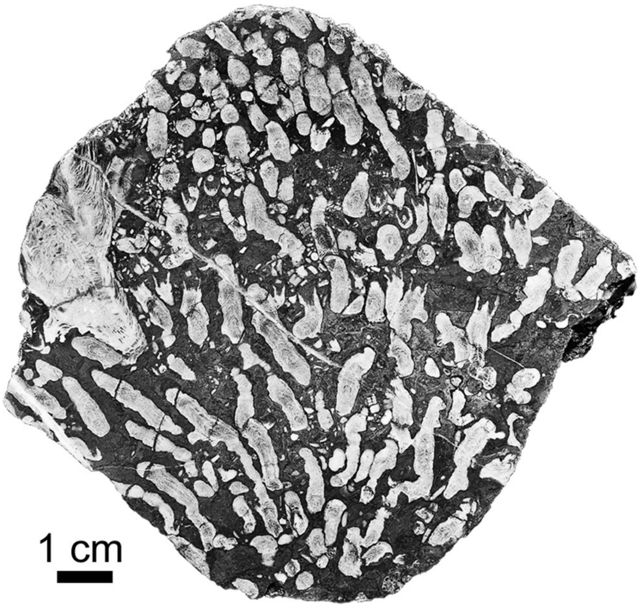

Fig. 2 Rugosan-rugosan association. *Cionodendron* "*arundineum*" with *Symplectophyllum*, vertical section, Caroda Formation, Pinaroo, Australia (after Pickett 2016, p. 45, fig. 3)

Crinoid-*Cladochonus* association

The crinoid-*Cladochonus* symbiotic association occurred during the Mississippian (Lane 1973; Kammer 1985; Donovan and Lewis 1999). *Cladochonus* corallites grew in a ring around an erect column of a living crinoid (Lane 1973; Kammer 1985; Donovan and Lewis 1999) (Fig. 3). *Cladochonus* branched out away from the column, forming a three-dimensional loosely arranged corallite (Lane 1973; Kammer 1985; Donovan and Lewis 1999). *Cladochonus* often caused malformations such as swellings of the crinoid stem, and it was partially embedded by the crinoid skeleton (Lane 1973; Kammer 1985; Donovan and Lewis 1999). The epizoan influence on the host may have been negative as it often caused malformations of the column and a loss in its flexibility. This interaction could be best classified as parasitism.

Crinoid-rugosan association

This association has a stratigraphic range from the Early Devonian (Berkowski and Klug 2012; Bohatý et al. 2012) to the Viséan (Donovan et al. 2005). Donovan et al. (2005) described an unidentified specimen of a solitary rugosan embedded within the calyx of *Amphoracrinus gilbertsoni* from the Viséan of Clitheroe, Lancashire, England (Fig. 4). Evidence for the coral infesting a living crinoid includes its perpendicular orientation to

Fig. 3 Crinoid-*Cladochonus* association. *Platycrinites* sp. with *Cladochonus* sp. from the Brigantian of Hunterstone Bank, Yorkshire, UK (after Donovan and Lewis 1999, p. 322, fig. 1A-B)

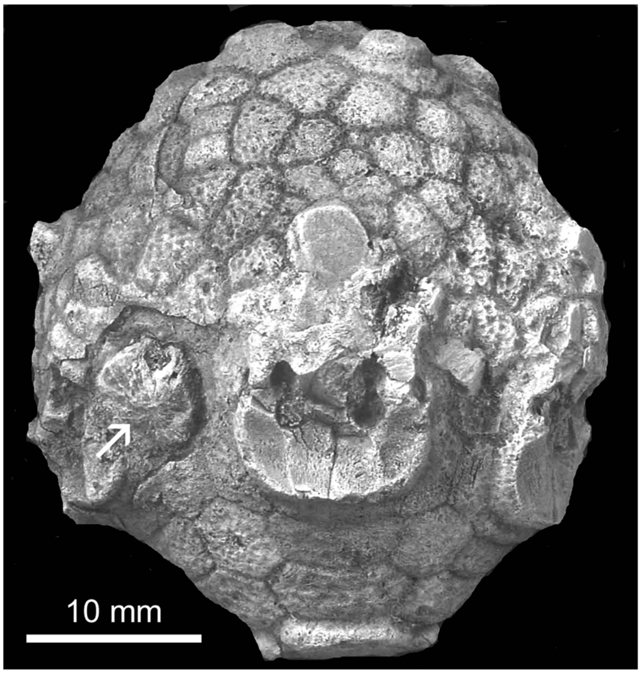

Fig. 4 Crinoid-rugosan association. *Amphoracrinus gilbertsoni* with a solitary rugose coral from the Viséan, Clitheroe, Lancashire, UK (after Donovan et al. 2005, p. 302, fig. 1)

the calyx, its position at the base of a free arm in the AB interray, breakage of the crinoid plates around the coral, and a growth deformity in the AB interray (Donovan et al. 2005). The position of the rugosan indicates that, in life, it was directed into the prevalent water current by the crinoid (Donovan et al. 2005). The rugosan location on the crinoid is at least suggestive that the coral may have actively harvested food with its tentacles from the adoral groove of the crinoid's arm (Donovan et al. 2005). The rugosan was likely both a filter feeder and a parasite on the crinoid (Donovan et al. 2005). In the Middle Devonian, other rugosans infested crinoid stems by sclerenchymal outgrowth that formed a skeletal ring (Bohatý et al. 2012). In the latter case, crinoid axial canals are not penetrated, and rugosans presumably were not parasites of crinoids (Bohatý et al. 2012).

Results

There are four symbiotic associations involving corals known from the Late Devonian. Tabulates participated in all four symbiotic associations, whereas rugosans were only involved in one association. Six symbiotic associations involving corals are known from the Mississippian. Tabulates ($N = 4$) formed a similar small number of symbiotic associations as rugose corals ($N = 3$) in the Mississippian. These corals formed most ($N = 3$) of their symbiotic associations with crinoids. In three associations, Mississippian corals were epibionts and in two associations, they were endobionts. In five associations, Mississippian corals were symbionts and in three associations, they were hosts. The largest number of different taxa was involved in crinoid-coral symbiosis in the Mississippian. Three (i.e. *Syringopora*-rugosan association, rugosan-rugosan association, crinoid-*Cladochonus* association) of six symbiotic associations first appeared in the Carboniferous. Symbiotic associations involving corals are different in the Late Devonian and Mississippian.

Discussion

Coral symbiosis with the other invertebrates was not very common in the Carboniferous. The appearance rate of symbiotic associations involving corals in the Carboniferous ($N = 3$) was lower than in the Silurian ($N = 4$) (Vinn and Wilson 2016) and Ordovician ($N = 6$) (Vinn and Wilson 2015), and much lower than in the Devonian ($N = 8$) (Vinn 2017). This indicates that there was no continuous increase in the number of symbiotic associations involving corals from the Ordovician to the Carboniferous. The number of symbiotic association involving corals was six in the Ordovician (138 coral genera according to Paleobiology Database) (Tapanila 2005; Vinn and Wilson 2015), seven in the Silurian (274 coral genera according to Paleobiology Database) (Tapanila 2005; Vinn and Wilson 2016; Vinn 2017), fifteen in the Devonian (424 coral genera according to Paleobiology Database) (Tapanila 2005; Vinn 2017), and at least six in the Mississippian (167 genera according to Paleobiology Database). The number of symbiotic associations clearly parallels the number of coral genera. Hence, coral diversity is main factor controlling abundance of symbiotic associations.

Across the Late Devonian biotic crisis, also sclerobionts declined in diversity and abundance (Schneider 2013). Most of the major sclerobiont clades were common in the Givetian to Mississippian ecosystems (Schneider 2013). However, most abundant sclerobionts in most Devonian assemblages, microconchids, were replaced by bryozoans in the Mississippian (Schneider 2013). Diversity and abundance of sclerobionts in the Mississippian was lower than in Frasnian–Famennian assemblages (Schneider 2013).

There was a drop in coral diversity in the Late Devonian due to the Kellwasser Event at the Frasnian–Famennian boundary (see Aretz 2010) and a very important faunal turnover at the Devonian-Carboniferous boundary (e.g. Poty 1999). There are almost no survivors among corals, and hence, it seems obvious that there are major differences between the symbiotic associations. A lot of the organisms that participated in the Devonian associations did not survive the two major late Devonian extinctions; e.g. no stromatoporoids in the Carboniferous. This caused further differences between Devonian and Carboniferous symbiotic associations.

Coral symbiosis with crinoids in the Carboniferous was in general similar to the Devonian. Favositid-crinoid and rugosan-crinoid associations occurred also in the Devonian, but Crinoid-*Cladochonus* association which is known from the USA and

England was added in the early Carboniferous. Rugosans and tabulates formed symbiotic associations both in the Devonian (Zatoń et al. 2015) and Carboniferous (Pickett 2016). Coral symbiosis reached its Paleozoic maximum in the Middle Devonian (243 coral genera according to Paleobiology Database 2017) (Tapanila 2005; Vinn 2017), had a remarkable decline in Frasnian (96 coral genera according to Paleobiology Database), and had an absolute minimum in the Famennian (54 genera according to Paleobiology Database 2017) (Figs. 5 and 6). The drop in absolute numbers between the Devonian and Carboniferous is due to the disappearance of the eight Devonian associations with tubeworms sensu lato. Coral symbiosis after the Late Devonian biotic crises related to Frasnian–Famennian mass extinction was impoverished and presumably did not recover to Middle Devonian levels (~12 Ma; 13 symbiotic associations per 243 coral genera) in the Mississippian (~40 Ma; six symbiotic associations per 167 coral genera). One would ask what the consequences are when symbiotic associations disappear. The consequences of disappearance of symbiotic association depend on the type of ecosystem; some ecosystems rely more on symbiosis than the others. If the late Palaeozoic corals lived in an ecosystem which relied on symbiosis, it is possible that termination of symbiotic associations may have contributed to extinction of some taxa relying on symbiosis. However, coral symbiosis with the other invertebrates was rare in the Late Devonian and Mississippian, so it may have been a problem only locally. One would also ask how the recovery went after the Hangenberg Event (D/C Boundary). Recovery of symbiotic associations after Hangenberg Event as the result of increase of coral diversity was partially the re-establishment of association known from earlier Palaeozoic ($N = 3$) and partially appearance of new symbiotic associations ($N = 3$). It would be interesting to know why three associations appear for the first time in the Carboniferous. The appearance of three symbiotic associations involving corals in the early Carboniferous presumably results from the appearance of new symbiosis prone coral taxa or the other invertebrates that tolerated corals. This indicates that taxa involved in symbiosis with corals had enough time of co-evolution with corals for appearance of symbiotic ties. It also indicates that ecosystem had at least a minimal stability for formation of symbiotic associations. However, this is concerning very few taxa and it seems that symbiosis is an exception, which occurs sporadically.

The number of described Mississippian symbiotic associations involving corals ($N = 6$) is more similar to the Ordovician ($N = 6$) and Silurian ($N = 7$) than to the Devonian ($N = 15$). The actual number of symbiotic associations may have been larger in the Carboniferous. There are data that chaetetids, sponges s.l., algae, and soft-bodied organisms also formed symbiotic associations with corals in the Carboniferous (Julien Denayer and Victor Ogar personal comm.). The actual number of symbiotic association in the entire Carboniferous may have been about ten (214 coral genera according to Paleobiology Database). This is more than in the Ordovician and Silurian and less than in the Devonian, but also the diversity of corals was lower in the Carboniferous than in the Devonian (424 genera).

Pre-Carboniferous coral symbiosis is characterised by a large number of coral endobionts and endobiotic corals. Both endobiotic corals in stromatoporoids and numerous bioclaustrations in corals were common from the Ordovician to Middle Devonian (Tapanila 2005; Zapalski 2009). Stromatoporoid-coral associations ended with the extinction of true stromatoporoids in the Late Devonian. Only rugosan endobionts in syringoporids and other rugosans are known from the Carboniferous (Pickett 2016). The lack of various worm bioclaustrations (i.e. *Chaetosalpinx*, *Helicosalpinx*, *Phragmosalpinx*) and endobiotic

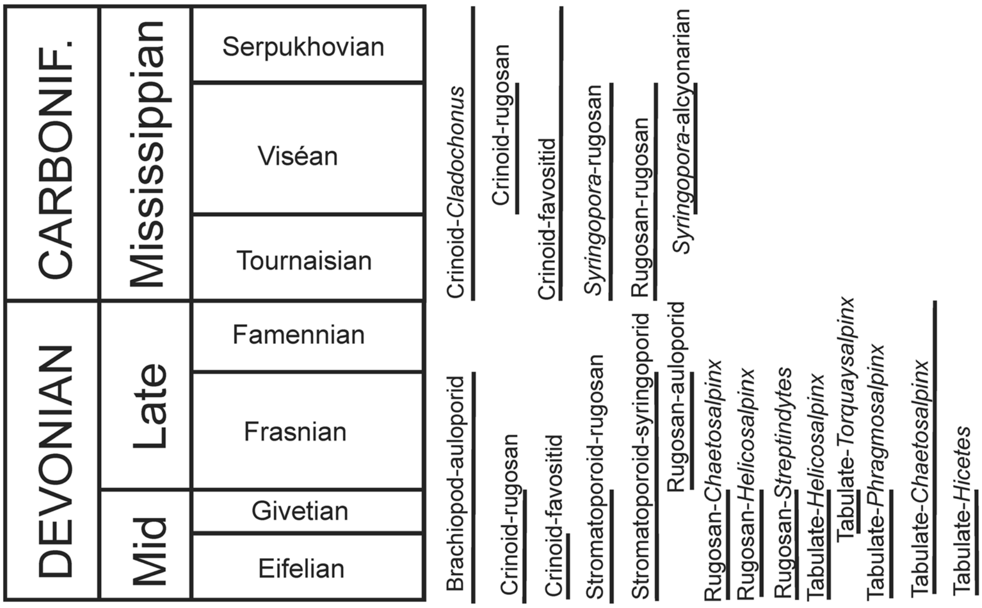

Fig. 5 Stratigraphic distribution of symbiotic associations from Middle Devonian to upper Carboniferous

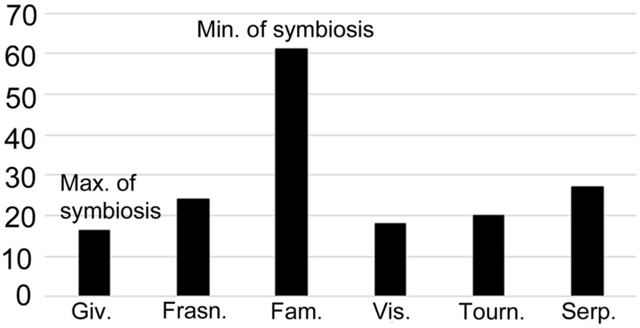

Fig. 6 Graphic showing number of coral genera per a symbiotic association. There are 61 coral genera per a symbiotic association in the Famennian and 16.2 in the Givetian

tentaculitoid tubeworms (i.e. cornulitids, trypanoporids, *Streptindytes*) in Carboniferous corals is the main difference from Ordovician to Devonian coral faunas. The worms responsible for bioclaustrations presumably became extinct in the Late Devonian (Tapanila 2005; Zapalski et al. 2008), but several tentaculitoid tubeworms survived into the Carboniferous, such as cornulitids and *Streptindytes* (Vinn 2010), but did not form symbiotic associations (Vinn 2016). *Streptindytes* occurs in the Devonian rugosans and tabulates. It is known from the Carboniferous chaetetids, but not from corals. One could speculate that corals tolerant of tentaculitoid tubeworms may have become extinct in the Late Devonian.

Conclusions

There are four symbiotic associations involving corals known from the Late Devonian and six associations known from the early Carboniferous. Both tabulates and rugosans formed symbiotic associations with the other invertebrates. There was no continuous increase in the number of symbiotic associations involving corals that appeared from the Ordovician to the Carboniferous. The number of symbiotic associations was mostly controlled by coral diversity. Symbiotic associations of corals are different in the Late Devonian and early Carboniferous. The lack of various worm-shaped bioclaustrations and endobiotic tentaculitoid tubeworms in Carboniferous corals is the main difference from Ordovician to Devonian coral faunas. Coral symbiosis had a remarkable decline in Frasnian and an absolute minimum in the Famennian. Recovery of symbiotic association after Hangenberg Event was partially the re-establishment of earlier Palaeozoic associations and partially appearance of new symbiotic associations.

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