Article

When a Worm Loves a Coral: A Symbiotic Relationship from the Jurassic/Cretaceous Boundary

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Abstract: Reefal limestones of the Štramberk Carbonate Platform are preserved as olistoliths and pebbles in deep-water flysch of the Outer Carpathians (Czech Republic, Poland). They contain the richest coral assemblages of the Jurassic/Cretaceous transition (Tithonian–Berriasian). Symbiotic associations between corals and tube-dwelling macroorganisms were recognized only in the branching scleractinian corals *Calamophylliopsis flabellum* and *Calamophylliopsis* sp. One to seven calcareous tubes were recognized either in coral calyces, embedded in the wall, or attached to it. Two types of tubes were recognized: Type 1: tubes with a diameter of 0.3–0.6 mm and a very thin wall (ca. 0.05 mm), mostly occurring inside corallites, and nearly exclusively in the Štramberk-type limestone of Poland; Type 2: tubes with an outer diameter of 0.8–2.0 mm and a thick wall (ca. 0.1 mm, some even up to 0.2 mm), mostly found in the Štramberk Limestone of the Czech Republic. Growth lamellae were observed in some thick walls. Most tubes are almost straight, some are curved. The tubes were probably produced by serpulids or by embedment of organic-walled sabellid polychaete worms. It is likely the oldest record of a sabellid–coral association. Modification of the coral skeleton in contact with tubes indicates that the worms were associated with live corals. For many modern and fossil worm–coral associations, this symbiotic association is interpreted as mutualistic or commensal.

Keywords: tube-dwelling worms; Polychaeta; Scleractinia; symbiosis; Carpathians

1. Introduction

Coral reefs are among the world's marine ecosystems with the highest biodiversity. Research on coral-associated organisms in terms of their diversity and functioning is urgent [1,2]. Corals themselves form highly diverse habitats for other organisms. Some coral-associated macro- and microorganisms have fossilization potential and are recorded in extinct corals. Even coral-associated microendoliths, as part of the coral microbiome, are reported from fossil material [3].

Worms of various taxa of the phylum Annelida are the most common macroorganisms reported as in vivo associated organisms in modern [4] and fossil corals, both in Paleozoic Rugosa and Tabulata, Mesozoic–Cenozoic scleractinian corals (Refs. [5–7] and references therein), as well as in stromatoporoid sponges, which were the most important reef builders in the Paleozoic (e.g., Ref. [8]). Palaeontological studies of coral-associated polychaetes and other organisms provide insight into the evolution of corals and reef ecosystems.

The title of this paper has been inspired by a conference presentation by Martinell et al. [9] about associations between Pliocene solitary corals and worms. Long groove-shaped bioerosional structures running along the surface of the coral skeleton were left by eunicid polychaetes. This case of symbiosis was interpreted as commensalism [6]. In fact, many

coral–worm associations are interpreted as not detrimental for the host coral, although there are exceptions [10,11].

The association from the uppermost Jurassic–lowermost Cretaceous described here—based on some samples from the Štramberk-type limestones (Poland)—was previously reported in the conference presentation [12], and a published illustration (Figure 1B in [13]). Corals from the Štramberk Limestone (Czech Republic) were subject of many taxonomic papers (most of them published in the 1960s–1970s, see [14,15]). However, the genus *Calamophylliopsis* (together with other genera from the family Dermosmillidae) was not subject of recent publications. Recent studies allowed to collect and study specimens of this coral genus. Limestone of the Štramberk Carbonate Platform contains some of the world's most diversified reef coral assemblages of the Jurassic/Cretaceous transition [16,17]. However, apart from the here described symbiosis and an earlier encrusting symbiosis [18], other symbiotic associations between corals and organisms were not recognized in highly diversified corals from these limestones. The purpose of this paper is (1) to describe in detail the intergrowth between host corals and tubeworms from the Jurassic/Cretaceous transition of the Štramberk Carbonate Platform; (2) to assess the palaeoecology of this tubeworm–coral association; and (3) to compare its fossil record with modern tubeworm–coral associations.

2. Materials and Methods

The biotic association studied here was recognized in the Štramberk Limestone (Czech Republic) and in the Štramberk-type limestone (Poland). These limestones were deposited during the Tithonian (mostly) and Berriasian (Jurassic/Cretaceous transition) on the Štramberk Carbonate Platform. Until the 1960s, the Štramberk Limestone was considered as only of Tithonian age, based on the available biostratigraphic data. The Štramberk Carbonate Platform is a collective term for small, narrow platforms that were attached to intra-basinal ridges in the Carpathian Basin of the Tethys Ocean. It is called a lost carbonate platform, because these limestones occur in the Cretaceous–Paleogene deep-water flysch deposits of the Outer Western Carpathians as olistoliths (megablocks) and pebbles [16]. Olistoliths of the Štramberk Limestone in a large Kotouč Quarry in Štramberk (Moravia, Czech Republic) occur in the Cretaceous flysch of the Silesian Nappe [19–21]. The Štramberk-type limestones (Poland) occur as pebbles and small blocks in many localities in the Cretaceous (locally uppermost Jurassic)–Paleogene flysch [16]. These limestones are represented by various facies of the carbonate platform and its slope. They are mainly known for reef sediments, with the world's most diverse fossil coral assemblages on record (ca. 120 species of 50 genera; especially numerous in Štramberk), in reefs developed at the Jurassic/Cretaceous boundary, which were studied already in the 19th century [13–17]. It is also one of the richest coral communities of Jurassic reefs, which developed mainly in the Oxfordian–Kimmeridgian. Other groups of macrofossils are also common in the Štramberk Limestone [14].

We examined about 15 specimens of *Calamophylliopsis flabellum* (Blainville, 1830) and *Calamophylliopsis* sp. Coral-associated worms were recognized in four coral specimens from the Štramberk Limestone (Czech Outer Carpathians) and in three coral specimens from the Štramberk-type limestones. Samples from the Štramberk Limestone are from huge olitoliths in the Kotouč Quarry in Štramberk [20,21]. Samples from the Štramberk-type limestones (clasts of pebble size from the Cretaceous flysch deposits) are from localities Woźniki, Jastrzębia and Lusina (Polish Outer Carpathians; see localities 7, 10 and 14 in [16]; and Figure 1 based on [22]). Seventeen standard thin sections (4 × 2.7 cm) were studied under petrographic and binocular microscopes. All specimens are stored in the Institute of Geological Sciences, Jagiellonian University in Kraków.

Figure 1. Geological map (simplified after [22]) showing the general location of sampling sites. 1: Štramberk; 2–4: Woźniki, Jastrzębia, Lusina.

3. Results

Some of the branching *Calamophylliopsis* corals (larger corallite diameter: 7–11 mm, smaller corallite diameter: 3–8 mm) contain calcareous tubes. They usually range from one to five, very rarely up to seven, in a single corallite, either inside the inner part of a calyx, embedded in the corallite wall, or attached outside the wall. The tubes are mostly oriented along the growth direction of the corallite. Some of them are slightly curved.

Two types of tube wall were recognized. Type 1: tubes with a diameter of 0.3–0.6 mm and a very thin wall (ca. 0.05 mm), occurring mostly in the inner part of corallites (Figure 2). The walls of these tubes are calcareous, but they lack internal structure in the form of growth lamellae. The tube walls are free of macroscopic remnants of organic matter, which would differ from the calcareous skeleton by their dark colour (i.e., carbonaceous composition). The series of sections through different growth stadia of coral indicate that the tubes are almost straight and not U-shaped. Type 2: tubes with a thick wall (ca. 0.1 mm, some even up to 0.2 mm) with a diameter of 0.8–2 mm (Figure 3). They were recognized more commonly in the wall region. Tubes of Type 1 are much more numerous in a corallite (one coral branch) and were recognized nearly exclusively in the Štramberk-type limestones of Poland. Tubes of Type 2 occur mostly in samples from the Štramberk Limestone of the Czech Republic and are mostly associated with the corallite wall, but may also occur in the inner part of a corallite. In some corallites, there is only one tube of Type 2. The growth lamellae are observed in some thick walls of large tubes. The series of sections through different growth stadia of coral indicate that these tubes are almost straight or somewhat undulating, and with a single entrance. The distances between the tubes are rather large and tubes do not cluster, with the exception of one corallite to which a cluster of four tubes is attached (which modified the growth of the coral wall).
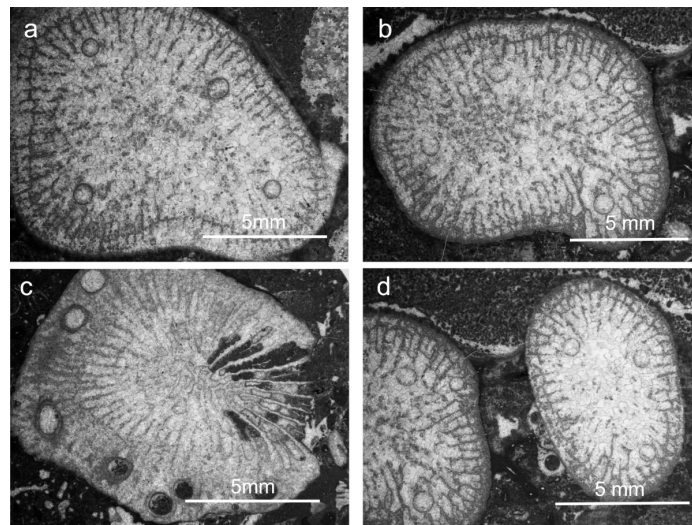
Figure 2. Coral–worm association in the Štramberk-type limestones (Poland). (**a**,**b**) Thin-walled tubes (Type 1) in the coral calyx, transverse section. (**c**) Relatively thin wall of tubes of Type 2 in the peripheral region of the calyx, transverse section. (**d**) Thin-walled tubes in the calyx; serpulid tubes attached to the exterior of the corallite, transverse section. (**a**,**b**,**d**)—*Calamophylliopsis flabellum*, (**c**)—*Calamophylliopsis* sp. (**a**,**b**,**d**)—Woźniki, (**c**)—Lusina.
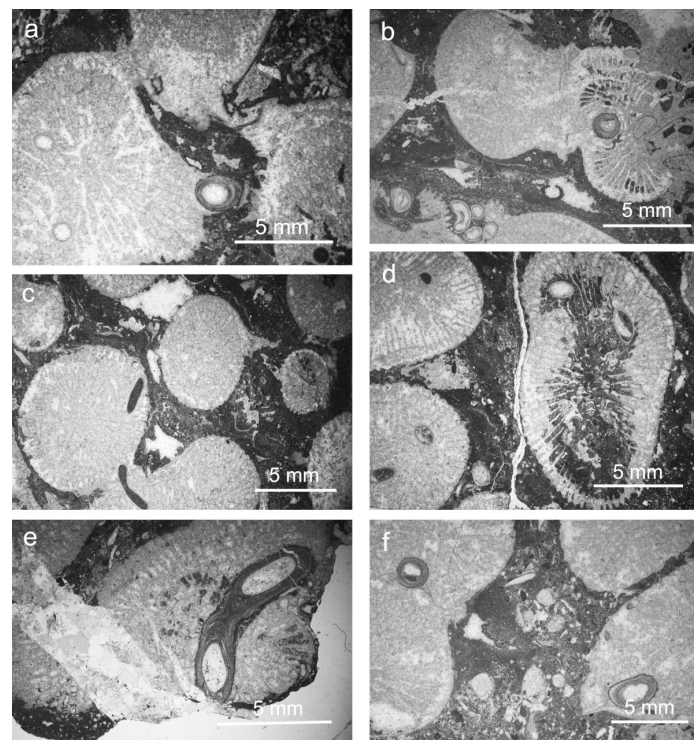

Figure 3. Coral–worm association in the Štramberk Limestone (Czech Republic). (**a**) Thin walled-tubes (Type 1) in the calyx and thick-walled tube (Type 2) at the edge of the corallite, transverse section. Note: wall modification induced by the worm. (**b**) Thick-walled tube in the middle of the calyx and serpulid tubes attached to the coral wall (note skeleton aberrations), transverse section. (**c**) Thin-walled tube in oblique section. (**d**) Thick-walled tubes in the middle of the calyx, transverse section. (**e**) Thick-walled tube with growth lamellae, oblique section. (**f**) Thick-walled tubes in the transverse section. (**a**,**b**,**d**)—*Calamophylliopsis flabellum*, (**c**)—*Calamophylliopsis* sp. (**a**,**b**,**d**,**f**)—*Calamophylliopsis* sp., (**c**)—*Calamophylliopsis flabellum*.

4. Discussion

4.1. Coral

Among corals from the Štramberk Carbonate Platform, symbiotic worms were recognized only in the species *Calamophylliopsis flabellum* and *Calamophylliopsis* sp. (order Scleractinia, family Dermosmiliidae). *Calamophylliopsis flabellum*, showing a phaceloid colony growth form, was common in the Late Jurassic [23]. Other species of the genus *Calamophylliopsis* Alloiteau, 1952 were also common during the Late Jurassic–Early Cretaceous [24]. Phaceloid colonies are branching with a low degree of corallite integration. Coral polyps occur only on the top of coral branches, which were only connected during budding. Phaceloid corals are rare in Cenozoic reefs, but were common during the Jurassic, where they inhabited low-energy reef environments with fine-grained sedimentation [25].

4.2. Nature of Tubes

The walls of thin-walled bioclaustrations are too thin for calcareous tubeworms, such as serpulids. The study of the tube wall under a light microscope did not reveal any dark-coloured remains of supposed organic tubes, although a complete decay of organic material is common in fossils that are millions of years old. The tube walls of calcareous Mesozoic tubeworms of such diameters are usually about 0.1 mm thick or even thicker (O. Vinn personal observations). They likely result from embedment of organic-walled tubeworms, such as sabellids in modern corals [26] or represent a bioclaustration of a soft-bodied worm, though likely a polychaete. The thin walls of bioclaustrations are likely composed of coral skeleton and are analogous to those of *Chaetosalpinx* in Paleozoic corals [7]. Such bioclaustrations formed during the process of embedment of a non-biomineralized endobiont in a living coral. The organic walls of sabellids usually do not fossilize and their absence in the studied corals is not surprising. However, the dimensions of the thin-walled bioclaustrations fit well with the sizes of modern sabellid tubes and make the sabellid affinity of the bioclaustratons very likely [27].

The lamellae of thick-walled tubes (Figure 4) resemble serpulid growth lamellae that are chevron-shaped in the longitudinal section. The morphology and microstructure of thick-walled calcareous tubes indicate that they likely belong to serpulid tubeworms. The dwellings of modern endobiotic serpulids such as *Spirobranchus* spp. in tropical corals [28–31] very much resemble those of thick-walled tubes in *Calamophylliopsis*, studied here. The morphology of thick-walled tubes does not allow the identification at genus level as a large number of serpulid genera contain species with smooth unornamented tubes with circular cross-section [32]. The modification of the coral skeleton observed at the contact with tubes indicates that the worms were associated with live corals. Similar tubes are also produced by coral-dwelling worm snails [33], but it is unclear if these already existed during the Jurassic/Cretaceous boundary since worm snail-like tubes older than the Upper Cretaceous lack preserved protoconchs [34]. Therefore, we do not consider worm snails plausible as possible producers of the tubes in our study.

4.3. Type of the Coral–Worm Association

Activity of polychaete worms has modified the coral morphology, which indicates that it was an in vivo relationship. Thus, it was a symbiosis in a broad sense (living together), an original meaning of this term, accepted by most researchers. Symbiotic relationships can represent parasitism (− +), commensalism (0 +), mutualism (+ +) or amensalism (00) [6]. In a fossil record, it is usually difficult or impossible to determine the exact nature of the association. Some interactions are strongly affected by environmental conditions. Recent studies revealed that an archetypal model of symbiosis (mutualism), namely the association of corals and dinoflagellate algae from the family Symbiodiniaceae (originally attributed to *Symbiodinium*), is a continuum of interactions from mutualism to parasitism [35]. Endosymbionts usually benefit from the feeding currents of host organism, such as many endobiotic symbionts in bryozoans [36]. However, corals do not produce feeding currents and as micropredators, they feed on other organisms than serpulids

and sabellids, which are suspension feeders. Thus, kleptoparasitism can be ruled out for tubeworm–coral associations. In contrast, tubeworms are active suspension feeders and could have provided host corals with a nutrient flow. The question under debate is whether poorly integrated (phaceloid) scleractinian corals were photosymbiotic by their zooxanthellate. Recent corals showing such morphology are rare and asymbiotic. There is, however. evidence that Late Triassic phaceloid corals were zooxanthellate [37]. The host coral also benefitted from increased water circulation to adjacent polyps facilitating coral recovery in zooxanthellate coral colonies. The worms in turn found protection against predators within a coral that protected them with nematocysts. There is a possibility that such tubeworm–coral associations may have been mutualistic. Fossil coral macrosymbioses are classified into intergrowth, encrusting and boring categories [5]. Some tubeworms studied here encrusted coral skeletons in vivo, but most coral–worm relationships as this one recognized here represent an intergrowth symbiosis.
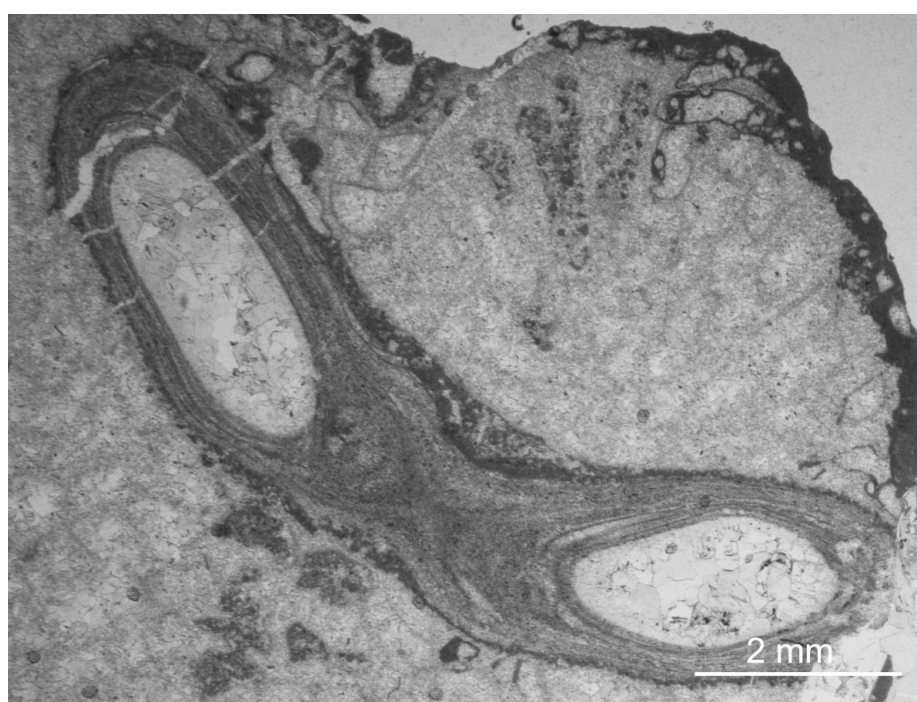

Figure 4. Growth lamellae in the thick-walled worm tube in *Calamophylliopsis* sp.; Štramberk.

4.4. Coral–Worm Symbiosis in a Fossil Record

The symbiotic relationships between corals and worms have a long evolutionary history. Worms colonized rugose and tabulate corals already since the Late Ordovician, in the Paleozoic [7,38–40]. However, the polychaete affinity of some of these worm bioclaustrations is problematic. A symbiotic relation between the solitary rugose corals ?*Yuanophyllum* and ?*Dibunophyllum* and a large soft-bodied worm-like endobiont has been described from the Hezhou Formation (Serpukhovian) of South China. This endobiotic symbiont lived in a U-shaped tube, probably with a horizontally sideways bent base connecting the vertical shafts, which differed from the straight or undulating single-entrance calcareous worm tubes known from the Mesozoic [41]. The earliest confirmed polychaete fossils are associated with Mesozoic corals. In the Lower Cretaceous of Argentina, serpulids have been found to be embedded within a coral skeleton, suggesting an in vivo interaction between the coral and the worm [42]. The symbiotic association between the serpulid *Propomatoceros sulcicarinata* Ware, 1974 and ramose corals of the scleractinians *Stereocaenia triboleti* (Koby, 1896) and *Columastrea antiqua* (Gerth, 1928) has been described from the early Hauterivian of the Neuquén Basin, Argentina [43]. *Propomatoceros sulcicarinata* tubes grew parallel to the coral branches reaching their upper tips and they were bioimmured within

the coral as they grew upwards, similarly to our serpulid–coral association. The symbiotic relationship between *P. sulcicarinata* and two species of corals has been interpreted as a mutualism as both members of the association probably benefitted from each other [43]. It is possible that serpulids in the latter association obtained protection against predators such as fish and crabs [44,45] while being bio-immured by an organism having tentacles with protective nematocysts, whereas the polychaetes, by actively creating water currents for feeding, would have improved water flow around coral surface, thus improving the elimination of waste products and/or the increasing availability of nutrients [44,46,47]. In the Miocene of Poland, the serpulid polychaete *Josephella commensalis* Bałuk & Radwański, 1997, encrusted the calyces of the living *Tarbellastraea reussiana* (Milne Edwards & Haime, 1850) [48], but this association differs from our serpulid–coral association by the lack of full intergrowth of the two partner organisms. *Tarbellastraea* corals participated in two different in vivo associations with serpulids in the Miocene of Central Paratethys of Moravia (T. Kočí personal communication).

4.5. Polychaete Worms Symbiotically Associated with Modern Corals

The larvae of various polychaetes settle on living corals (e.g., [49,50]). After metamorphosis, they either bore into the coral skeleton [51,52] or alternatively will act as fouling organisms [53], which eventually may become embedded by coral tissue [10,11,28,29]. Among polychaetes, serpulids and sabellids are the most famous coral associates. The serpulids *Spirobranchus* spp. and *Floriprotis sabiuraensis* Uchida, 1978 are endobiotic symbionts in various modern corals [30,31,54,55]. The Caribbean feather duster worm *Anamobaea* sp. (Sabellidae) has been found as an associate of 27 stony coral species (Scleractinia spp. and *Millepora* spp.) [26]. *Serpula vermicularis* Linnaeus, 1767 tube aggregations are sometimes intergrown with the deep-sea coral *Madrepora oculata* Linnaeus, 1758 [56] and *Filograna* sp. has been reported from *Desmophyllum pertusum* (Linnaeus, 1758) [57]. Caribbean Christmas tree worms of the genus *Spirobranchus* are considered common host generalists in their associations with anthozoan (Scleractinia) and hydrozoan (*Millepora*) stony corals in depths less than 30 m [31,44,58]. Secondary hosts of *S. giganteus* (Pallas, 1766) (overgrowing the primary hosts) include various octocorals [30], the zoantharian *Palythoa caribaeorum* [31], the ascidian *Trididemnum solidum* (Van Name, 1902) [30] and numerous sponge species [59]. The serpulid *Spiropbranchus giganteus* and sabellid feather duster worm *Anamobaea* sp. both form a secondary association with the Caribbean encrusting octocoral *Erythropodium caribaeorum* (Duchassaing & Michelotti, 1864) [26,30]. An aggregated distribution in serpulids occurs in an undescribed species of *Vermiliopsis* Saint-Joseph, 1894 from corals of the Caribbean scleractinian genus *Stephanocenia* Milne Edwards & Haime, 1848 [4]. The tubes of this serpulid are surrounded by coral tissue and the crowns are regularly distributed on the coral surface [4].

Non-tubicolous polychaetes also form symbiotic associations with modern corals. Such polychaetes may either construct their own refuges on the host's surface or stimulate their hosts to build protective structures around them. Among tubeless polychaetes, the eunicid *Eunice floridana* (Pourtalès, 1867) and the scaleworms *Harmothoe melanicornis* Britaev, 1981, *Malmgreniella dicirra* Hartman, 1967, *Gorgoniapolynoe uschakovi* (Britaev, 1981) and several species of *Gorgonyapolynoe* Pettibone, 1991 live inside tunnels or gall-like cavities formed by coenenchymal walls of gorgonian or hydrocoral hosts [4]. A boring polychaete *Polydora villosa* Radashevsky & Hsieh, 2000 colonizes corals of the scleractinian genera *Montipora* and *Porites* [60]. The lumbrinerid *Lumbrineris flabellicola* Fage, 1936 associated with scleractinian corals lives in membranous transparent tubes attached to the side of the host coral [61,62]. Wright and Woodwick [63] reported blisters formed by the small syllid *Proceraea penetrans* (Wright & Woodwick, 1977) on the hydrocoral *Stylaster californicus* (Verrill, 1866) [4]. This worm penetrates the surface of the host resulting in a hyperplasia of cellular and calcareous material, which produces a characteristic vermiform mound [4].

The relationships between polychaetes and corals can be mutualistic, commensal or parasitic [4]. Modern serpulid–coral associations have the strongest analogy with

the presently described fossil association. The relationships in *Spirobranchus giganteus*–coral associations range from commensalism to mutualism [46]. *Spirobranchus giganteus* protects the host coral from predation [64] and increases water circulation to adjacent polyps facilitating coral recovery in algal dominated coral colonies [46]. Such relationships illustrate the importance of associated species on coral reefs [47]. Symbiotic sabellids of the genus *Anamobaea* Krøyer, 1856 can cause distinct injuries in most host coral species and morphological deformities in a few of them. Since these tubeworms can form high densities, they have the potential to become a pest species on Caribbean coral reefs when environmental conditions become more favourable for them [26].

5. Conclusions

Two types of tubes occur in corals: *Calamophylliopsis flabellum* and *Calamophylliopsis* sp. The thin-walled bioclaustrations are surrounded by skeleton of the host coral and likely lack their own mineral tube wall. Thin-walled bioclaustrations were formed around soft-bodied worms or worms with organic tubes, such as sabellids. The dimensions of the thin-walled bioclaustrations fit well with the sizes of modern sabellid tubes and make the sabellid affinity of the bioclaustrations very likely. These specimens are likely the oldest record of sabellid–scleractinian associations. Thick-walled tubes likely belong to serpulids and are similar to the modern endobiotic serpulids such as *Spirobranchus* species. They have their own biomineral wall as do serpulids. The tubeworms are active suspension feeders and could have provided the host coral with nutrient flow, which could have been important if the Jurassic corals were azooxanthellate. If the corals were zooxanthellate and received most of nutrients from photosymbionts, then they still would have benefitted from the improved elimination of waste products and the prevention of algal settlement. The worms may have found protection against predators within a coral that protected them with nematocysts. Alternatively, the worms could have protected host coral similarly to modern *Spirobranchus*–coral associations. It is likely that such tubeworm–coral associations may have been mutualistic. The coral–worm intergrowth symbiosis described here was recognized only in the Štramberk Limestone and the Štramberk-type limestones, although *Calamophylliopsis* was a common coral genus during the Late Jurassic–Early Cretaceous. This supports linking sedimentary areas of studied limestones from the Czech Republic and Poland into a single palaeogeographic unit of the Štramberk Carbonate Platform.

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