

First fossil record of parasitism in Devonian calcareous sponges (stromatoporoids)

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SUMMARY

Introduction. Palaeozoic calcareous sponges (stromatoporoids) are common bio-constructing fossils; they are sometimes found in association with helicoidal structures of unknown biological affinities. The interaction between the tube-forming organisms has usually been classified as commensalism. **Methods.** About 260 stromatoporoid skeletons from the Middle Devonian (Givetian) of the Mont d'Hairs section near Givet (Champagne-Ardenne, France) were thin-sectioned and analysed under transmitted light. **Results.** Approximately 10% of the examined stromatoporoids (mainly belonging to the genera *Actinostroma*, *Stromatopora* and *Stromatoporella*) contain tubes classified as *Torquaysalpinx* sp. The *Torquaysalpinx* organisms penetrated the skeletons of stromatoporoids *in vivo* (as evidenced by skeletal overgrowths); around the infesting organisms, growth bands are bent down. **Conclusion.** Diminished growth rates around the infesting organism demonstrate a negative influence on the host, similar to that seen in the modern demosponge–polychaete association of *Verongia–Haplosyllis*. This is demonstrated by changes in growth bands. As in the above-mentioned association, the endosymbiont might have been feeding directly upon the tissues of the host. The *Torquaysalpinx* organisms were gaining habitat and possibly also food resources—for them this interaction was clearly positive. This long-term association can therefore be classified as parasitism. This is the first evidence for parasitism in Palaeozoic sponges.

Key words: stromatoporoid, calcareous sponge, endobiont, parasitism, Devonian, Givetian, *Torquaysalpinx*, fossil record.

INTRODUCTION

Palaeozoic stromatoporoids are a group of calcareous sponges considered to be either monophyletic (Riding and Kershaw, 1977; Stearn *et al.* 1999) or polyphyletic (Pisera, 2006, and references therein). Like modern sponges (Wulff, 2006), stromatoporoids could host numerous symbiotic organisms (Kershaw, 1980; Tapanila, 2006). Among the stromatoporoid symbionts were organisms of unknown biological affinities, forming tube-like structures that each have a single aperture (e.g. Stel, 1976; Cook, 1999; Tapanila, 2005, 2006). These structures are located inside stromatoporoids' calcareous basal skeletons (referred to as coenosteia), and have various morphological features. They are straight or helicoidal, some possessing their own calcareous walls; internal structures such as tabulae or diaphragms may also occur (Plusquellec, 1968; Tapanila, 2005). Intergrowths between stromatoporoid skeletons and tubes demonstrate *in vivo* relationships (Plusquellec, 1968, p. 168; Tapanila, 2008) and the reliability of such evidence is absolute (Taylor and Wilson, 2003, p. 24). Relationships between stromatoporoids and

these endobionts were most often considered as commensal (Tapanila, 2005), as the symbionts were not observed to influence growth rates or anatomy.

The present paper documents that helicoidal tubes assigned to *Torquaysalpinx* sp., found in the skeletons of the Middle Devonian (Givetian; 392–385 Myr) stromatoporoids from the Mont d'Hairs section near Givet (Ardennes, France), were parasitic. This is the first known evidence of parasitism in Palaeozoic sponges.

MATERIALS AND METHODS

Study site

The analysed material comes from outcrops around the fortifications of Mont d'Hairs in Givet (Champagne-Ardenne, France; Fig. 1). This classic Middle Devonian (Givetian) section exposes rocks from argillaceous limestones of the Hanonet Formation to massive and biostromal limestones of the Mont d'Hairs Formation. Samples included in this study come from the upper part of the section (Mont d'Hairs Fm.), which consists of massive coral limestones, interbedded with siltstones. The microfacies are principally crinoidal mudstones and stromatoporoid-tabulate boundstones (Hubert, 2008, and references therein).

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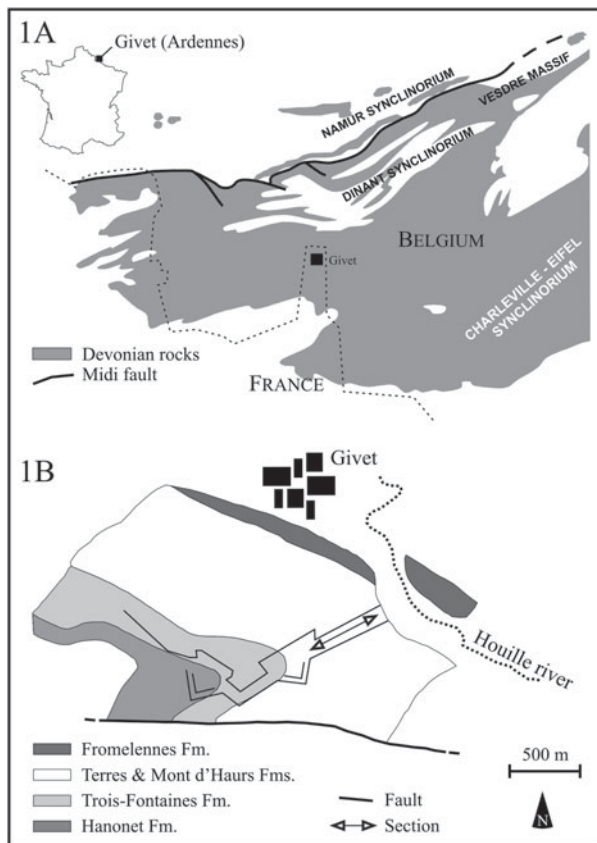


Fig. 1. Location of the Givet area on the map of France and the main geological structures of the Ardennes (A) and detailed location of the studied section in the Fortifications of Mont d'Hairs (B).

Preparation and repository of samples

A collection of 260 coenostea was investigated. The coenostea were analysed in thin sections, a standard method of analysis for bio-constructing organisms. Each thin section was prepared by cutting, grinding and polishing a rock sample. The sample was glued to a glass slide using epoxy adhesive. The portion glued to the glass was cut and polished, until light could pass through the rock slice. Thin sections were observed under a binocular microscope in transmitted light. In total, 29 specimens (37 thin sections) contained fossils of *Torquaysalpinx* sp. The analysed material is housed at the Faculté Libre des Sciences et Technologies in Lille (France), figured specimens have repository numbers GFCL 641 to 644.

The biological affinities of *Torquaysalpinx*

Plusquellec (1968) created the genus *Torquaysalpinx* based on Devonian examples that infested a chaetetid from Torquay (UK). He stated that the microstructure of *Torquaysalpinx* is lamellar, with lamellae obliquely oriented to the tube surface; he concluded that it is different from serpulids. On the other hand he remarked that some serpulids (e.g. *Ditrupea*) show similar diaphragms closing the tube lumen.

Plusquellec (1968) concluded that these Palaeozoic endosymbionts are difficult to assign to any modern group, and suggested their classification as organisms *incertae sedis*.

Tapanila (2005) published an overview of fossil coral and sponge endosymbionts, in which he referred *Torquaysalpinx* to ichnofossils (traces of life activity). *Torquaysalpinx* possess their own calcareous walls and diaphragms closing their lumen. However, the presence of skeletal structures places it among body fossils, contrary to the opinion of Tapanila.

Plusquellec (1968) stated that the microstructures of *Torquaysalpinx* are different from those of serpulids. Recent studies, however, show that serpulids can have extremely diversified wall structures, with 1–4 layers and various microstructures (Vinn *et al.* 2008). The unilamellar structure of *Torquaysalpinx*, with lamellae obliquely oriented to the tube surface, could thus fit among the serpulids. It is necessary to point out that modern-type serpulids appeared in the Late Triassic (Vinn and Mutvei, 2009); between the youngest *Torquaysalpinx* and known serpulids there is a gap of at least 150 Ma. In any case, diagenetic processes can strongly change original microstructures (see discussions by Oekentorp, 2001, 2007; Zapalski, 2010). Microstructural criteria must be therefore treated with caution.

The internal septa and microstructure of *Torquaysalpinx* resemble that of trypanoporids (O. Vinn, personal communication). Trypanoporids have recently been considered as relatives of tentaculitids (Weedon, 1991), which form the separate class Tentaculita (probably allied to lophophorans; Vinn and Isakar, 2007).

Modern *Spirobranchus* polychaetes are usually associated with corals. These polychaetes are, however, an order of magnitude larger in diameter (attaining nearly 10 mm) and length (attaining nearly 100 mm; Nishi and Nishihira, 1996). Moreover, modern polychaetes do not show helicoidal coiling, in contrast with *Torquaysalpinx*.

The absence of *Torquaysalpinx* specimens with diagenetically unaltered microstructure makes any comparisons very speculative. To conclude, it must be stated that biological affinities of *Torquaysalpinx* are unclear and following Plusquellec (1968) this genus must be classified as *incertae sedis*.

RESULTS

Hosting organisms

The stromatoporoids hosting *Torquaysalpinx* organisms belong to 8 genera and 13 species. Most of them are well known in the southern Ardennes and form an important element of the regional biota (Lecompte, 1951, 1952; Hubert *et al.* 2007; Zapalski *et al.* 2007a). These include: *Atelodictyon*

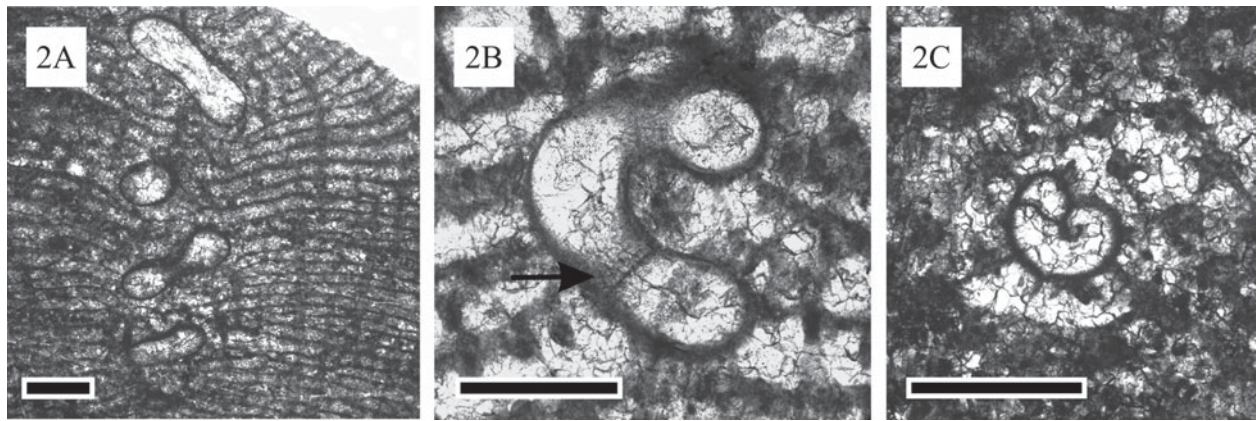


Fig. 2. Stromatoporoids of the genus *Actinostroma* and parasites *Torquaysalpinx* sp. from the Givetian of Mont d'Haurs section (Champagne-Ardenne, France). (A) *Actinostroma crassepilatum* (specimen GFCL 641), longitudinal section. (B) Detail of *Actinostroma sertiforme* (specimen GFCL 642), arrow shows diaphragm in the *Torquaysalpinx* sp., longitudinal section. (C) *Actinostroma crassepilatum* (specimen GFCL 643), tangential section. A, C – Scale bars = 1 mm. B – Scale bar = 500 μ m.

sp., *Actinostroma clathratum*, *A. crassepilatum*, *A. sertiforme*, *A. tabulatum crassum*, *A. verrucosum*, *Densastroma?* sp., *Stromatoporella granulata*, *Stromatoporella?* sp., *Clathrocoilona spissa*, *Trupetostroma?* sp., *Stromatopora huepschii* and *Atopostroma* sp.

Most of these organisms had massive or low domical skeletons, with the exception of *Clathrocoilona*, which formed lamellar coenostea. These skeletons are composed of horizontal elements (laminae *sensu lato*) and vertical (pillars *sensu lato*); more details concerning the morphology of coenostea have been given by Stearn *et al.* (1999).

Infesting organisms

Torquaysalpinx endosymbionts (Figs 2 and 3) are helicoidally curved tubes of various lengths. The tubes possess their own calcareous walls, as well as small, often bent calcareous diaphragms closing the lumen (Fig. 2B, C); these features are diagnostic for the genus (Hill, 1981). Tube diameter increases slightly towards the top of each coenosteum (the mean diameter is 0.332 mm, ranging from 0.22 to 0.58 mm). The longest observed tubes attained 10 mm; the smallest diameter of coiling is about 0.22 mm and the largest are 1.30 mm.

Torquaysalpinx endosymbionts were very rare in the examined material; out of the collection of 260 samples of stromatoporoids, only 29 skeletons contained these symbionts. Besides *Torquaysalpinx* sp. another endosymbiont, *Streptindytes* sp. (see Tapanila, 2005) also occurred in several samples.

The positions of endosymbionts in the host skeleton

The endosymbionts are rare in coenostea, with up to 7 (usually 1–3) found in each. They do not exhibit any particular preference for placement, and are not

concentrated in either peripheries or centres of coenostea. In contrast, tabulate corals occurring in the same beds contain much more abundant *Torquaysalpinx*, with dozens in a single corallum.

Torquaysalpinx tubes are oriented perpendicular to the laminae of the stromatoporoid. The laminae around each tube are bent slightly downward (Figs 2A and 3A–D), and pillars are often less abundant in these areas (Fig. 3D); these changes are evidence of skeletal modification of the host.

The interaction between *Torquaysalpinx* and its hosts

Endosymbionts are common in Palaeozoic bio-constructing colonial organisms – stromatoporoids and corals (Tapanila, 2005). They are far more commonly found in corals, while in stromatoporoids they are infrequent (Tapanila, 2005, 2006) and for this reason analyses of coral endosymbionts have been more frequently published (e.g. Oekentorp, 1969; Stel, 1976; Zapalski *et al.* 2008; Zapalski, 2009). Since the work of Sokolov (1948), the relationship between coral hosts and endosymbionts was considered as commensal (e.g. Plusquellec, 1968; Oekentorp, 1969; Tapanila, 2005). An opposite opinion was expressed by Stel (1976); and Zapalski (2007) has shown that at least some of these organisms were parasitic in corals. The relationship between similar symbionts and stromatoporoids has remained vague until now.

The growth rates of bio-constructing organisms are reflected by changes in vertical spacing of elements; thus changes of spacing reflect changes in growth rate (Insalaco, 1996; Young and Kershaw, 2005; Zapalski *et al.* 2007b). It has been shown that endosymbionts may affect growth rate (Tapanila, 2005, Fig. 1). This statement was, however, not supported by the material. Finding specimens with growth rhythm changed by the endosymbiont would

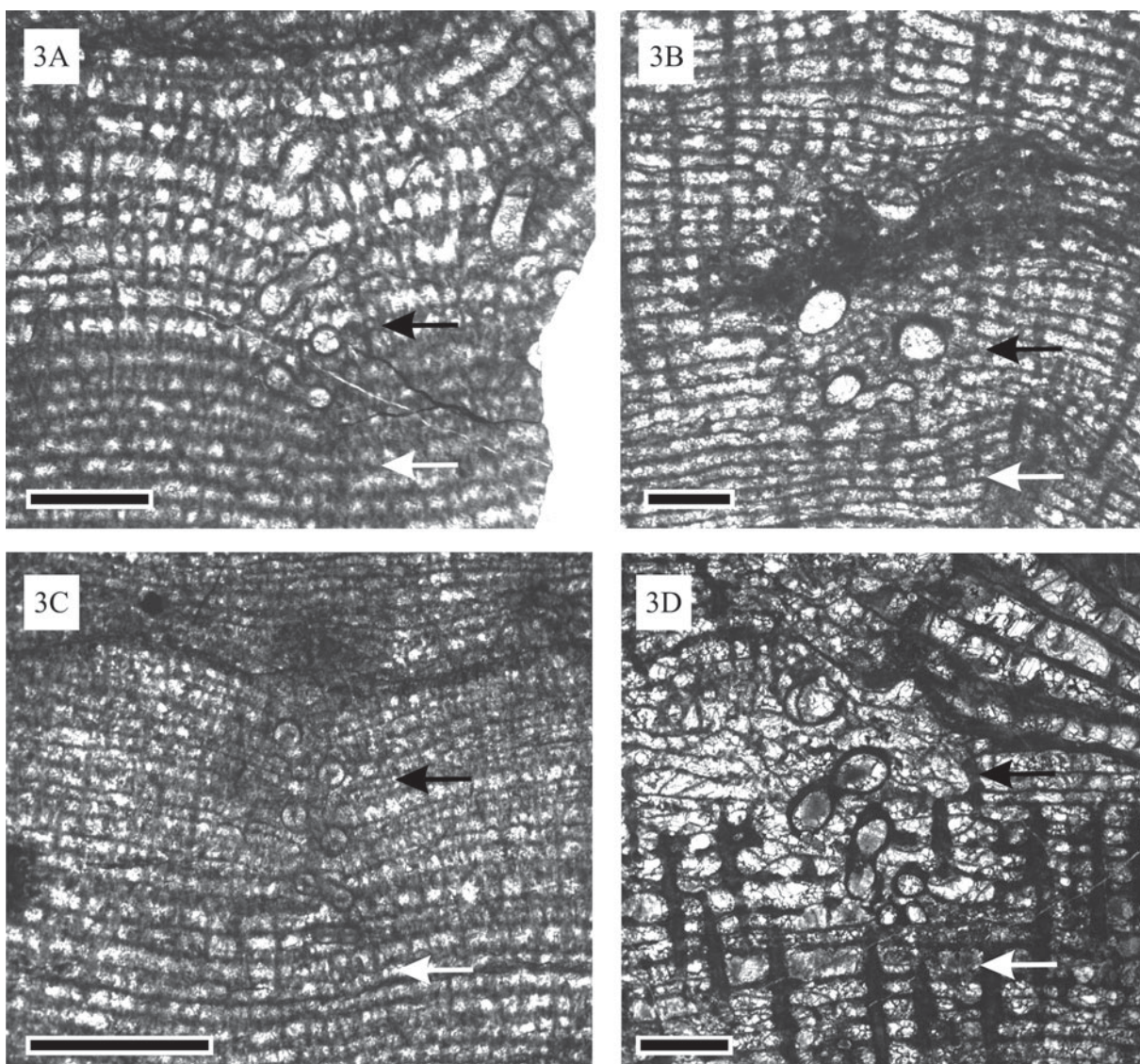


Fig. 3. Stromatoporoids of the genus *Actinostroma* and parasites *Torquaysalpinx* sp. from the Givetian of Mont d'Hairs section (Champagne-Ardenne, France). Changes in the skeletal organization of the host. (A) *Actinostroma verrucosum* (specimen GFCL 644), longitudinal section. Note that laminae around the host are bent down (black arrow and above), while below the parasite the skeletal organization is normal (white arrow and below). (B) *Actinostroma crassepilatum* (specimen GFCL 641), longitudinal section. The white arrow shows a region with normal skeletal organization, the black arrow with modified skeleton. (C) *Actinostroma verrucosum* (specimen GFCL 644), longitudinal section. The white arrow shows a region with normal skeletal organization, the black arrow shows a modified skeleton where laminae are bent down. (D) *Actinostroma crassepilatum* (specimen GFCL 643), longitudinal section. The white arrow shows a region with normal skeletal organization, the black arrow shows a modified skeleton. Note that around the parasite (black arrow) the skeletal elements are much thinner than below (white arrow). Scale bars = 1 mm.

solve the problem of the nature of this symbiosis (Zapalski, 2007).

The fossil record is strongly biased in the terms of palaeoecological relationships. Parasites are rarely identified in the fossil record; this relationship may be identified on the basis of taxonomic position of the infesting organism and/or inferred from host modifications and symbiont placement (e.g. Bassett *et al.* 2004; Poinar and Poinar, 2004; Poinar and Boucot, 2006). Tapanila (2008) proposed tests permitting the recognition of various kinds of symbioses in fossil records. He stated that parasitism could be

recognized on the basis of reduction of the host's growth rate, as this demonstrates a negative influence on the host. Such a reduction of growth rate is clearly visible in some of our material: laminae around the endosymbionts are bent downwards, and pillars are less abundant (Fig. 3). Settling of the endosymbiont and decrease of growth rates around its spiral tube in successive growth stages is schematically shown in Fig. 4. The inhibition of growth observed in the *Torquaysalpinx*-stromatoporoid association resembles that in the modern demosponge *Verongia gigantea* infested by *Haplosyllis* polychaetes. In the

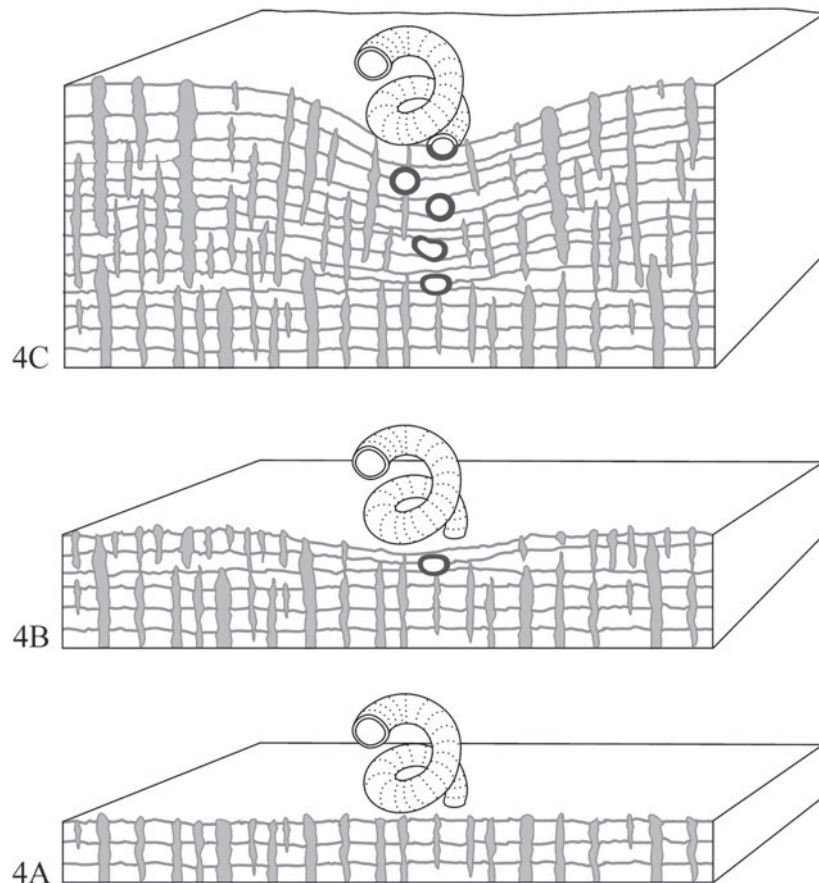


Fig. 4. Scheme showing parasite settling. (A) Initial stage of endosymbiont settling. (B) Endosymbiont settled in the skeleton; note the disturbance of laminae, as in Fig. 3A. (C) Endosymbiont after a certain time; note the disturbance of laminae, as in Fig. 3A and C.

latter association the reduction of host growth rates is significant (Reiswig, 1973).

Stromatoporoids, like corals, show growth banding. In our material the seasonal growth bands are not clearly visible, but Young and Kershaw (2005) have shown that annual growth band thickness may vary from 3 to 8 mm (but there is no unequivocal evidence that stromatoporoid bands are annual, see Young and Kershaw, 2005, p. 645). It can therefore be estimated that the duration of the *Torquaysalpinx*–stromatoporoid association was 1–2 years. Long-term relationship is a feature of parasitism (Combes, 2001). Moreover, modification of normal growth bands by *Torquaysalpinx* can be treated as a phenotypic modification; this is another indicator of parasitism (Dawkins, 1982; Combes, 2001).

Modern *Haplosyllis* infesting *Verongia* can be considered as a model for the relationship between *Torquaysalpinx* and stromatoporoids. In the recent association the polychaete feeds directly upon the host by inserting its chitinized proboscis through canal walls and sucking up the soft sponge tissues (Reiswig, 1973, p. 214). A similar situation might have occurred in the discussed case, although one must keep in mind that there is no direct evidence for a polychaete affinity for *Torquaysalpinx*.

Torquaysalpinx organisms occurring in stromatoporoids meet the criterion of ‘host as habitat’, typical for parasitism (Littlewood and Donovan, 2003). We can state that the infesting organism profited by gaining habitat and the food resource.

Some of the analysed specimens showed clear inhibition of growth of the sponge host around the parasite, but in other specimens this effect was not distinct. The interaction between host and individual may fluctuate during the lives of individuals (Cheney and Côté, 2005) or from individual to individual (a symbiont not harmful for one individual can become pathogenic for another; Casadevall and Pirofski, 2000; Sachs and Wilcox, 2006) – such a situation is very common in modern associations (Drake, 2008; Leung and Poulin, 2008).

A large variety of symbiotic organisms occurs in sponges, in spite of anti-fouling agents secreted by the latter (Krug, 2006). Endosymbionts are rare in stromatoporoids – only about 10% of specimens are affected. The scarcity of these endosymbionts might indicate that such anti-fouling agents were already present during the Palaeozoic (this is, however, speculative). The fitting of ancient parasites to their hosts and *vice versa* might have caused the evolution of the relationship from parasitic to mutualistic.

CONCLUSIONS

Skeletal overgrowths of stromatoporoid sponges and their endosymbionts demonstrate *in vivo* relationships. The decrease of host growth rates indicates the negative influence of *Torquaysalpinx* sp. on its stromatoporoid hosts. *Torquaysalpinx* organisms were gaining habitat and possibly also food resources. This relationship was therefore negative for the host, and positive for the parasite. We can speculate that food transfer between the parasite and its host was similar to that in modern *Verongia* (demosponge) infested by *Haplopyllis* (polychaete). In this association the parasite feeds directly upon the tissues of the host. Moreover, the *Torquaysalpinx*–stromatoporoid association meets the criterion of ‘host as habitat’ typical for parasitism; it was also a long-term relationship. This is the first evidence of parasitism in Palaeozoic sponges.

Torquaysalpinx sp. shows numerous similarities to polychaetes, but is older than the oldest known serpulids by at least 150 Ma. Microstructural features place it close to tentaculitids (Vinn, personal communication), but the lack of specimens with diagenetically unaltered microstructures makes any comparisons deficient. Owing to a lack of evidence for biological affinities, these organisms are classified as *incertae sedis*.

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