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Stromatoporoid-coral/tubeworm intergrowths in the lowermost Silurian Varbola Formation of Estonia: first evidence of competitive interaction

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Tabulate corals, particularly auloporids and syringoporids, are commonly found as intergrowths in host stromatoporoids in Palaeozoic shallow marine limestones. These associations are, in almost all cases, interpreted to be favourable to the intergrown corals but neither favourable nor unfavourable to the host. Here, in order to further investigate their palaeoecological interactions, the growth behaviour of host stromatoporoid and intergrown corals is evaluated in the association of the stromatoporoid *Clathrodictyon boreale* Nestor 1964 and the tabulate Auloporoidea indet. from the lowermost Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry, central Estonia. Also, intergrown tubeworms (*Cornulites* and *Helicosalpinx*) occur in the stromatoporoid and are compared with the coral to address variation of growth interactions. Two types of *syn-vivo* interactions between the organisms are recognized near their physical contacts: (1) upward- or downward-bending laminae of the host stromatoporoid with high skeletal density; and (2) irregular shape of the outer wall of auloporid corals with uneven wall thickness. Auloporid corals and tubeworms probably benefitted from the stable growth substrate provided by *C. boreale*, but spatial competition with the host stromatoporoid, local to the tubes, occurred during their intergrowth, judging from their skeletal deformations. Distorted skeletal structures in the intergrown organisms and host stromatoporoids are not persistently found in Palaeozoic intergrowth examples, indicating variation of growth interactions between each intergrown coral/tubeworm and host stromatoporoid species. This finding implies that stromatoporoid–coral/tubeworm associations were more complex than the previous interpretations and emphasizes that evaluation of skeletal deformations is critical in understanding the nature of palaeoecological interactions. □ *Stromatoporoid–coral/tubeworm intergrowth, competition, palaeoecology, early Silurian, skeletal deformation, symbiosis.*

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Intergrown tabulate corals in stromatoporoids, particularly syringoporids, are commonly found in Siluro–Devonian shallow marine limestones (e.g. Mori 1970; Mistiaen 1984; Kershaw 1987; Young & Noble 1989; Da Silva *et al.* 2011; Zapalski 2012; Stearn 2015). Early stromatoporoid–coral intergrowth associations were reported from the Upper Ordovician strata of the peri-Gondwanan regions including South China (Lin & Webby 1988; Young & Xu 2002; Lee *et al.* 2016) and New South Wales (Webby 1969), involving the clathrodictyid stromatoporoids *Clathrodictyon* and *Ecclimadictyon* and the auloporid coral *Bajgolia*. The early intergrowth interactions seem to be developed initially with the appearance of clathrodictyid-form stromatoporoids, involved with auloporid tabulate corals. Although the early history of this interaction can provide important information for understanding the initial development of stromatoporoid–coral intergrowth associations, the subsequent symbiotic interactions between non-syringoporid (auloporid) tabulate corals and stromatoporoids have received less attention, as most of the studies focused on intergrown syringoporid corals in Siluro–Devonian cases (e.g. Mistiaen 1984; Kershaw 1987; Young & Noble 1989; Da Silva *et al.* 2011). Similar to stromatoporoid–coral intergrowth, the earliest-known stromatoporoid–tubeworm association was reported from Upper Ordovician strata of New South Wales, Australia (Webby & Morris 1976), and became common during the Silurian and Devonian (e.g. Vinn & Wilson 2010; Vinn 2016a, b; Zapalski & Hubert 2011).

The first recognition of intergrown corals is *Syringopora* by Roemer (1844), who regarded them as independent organisms in stromatoporoid skeletons. Phillips (1841) interpreted the intergrowth as a taxon of stromatoporoids, '*Caunopora*', a generic name possessing features of both coral and stromatoporoids. Subsequently, various interpretations of the stromatoporoid–coral relationships have been proposed, including mutualism, commensalism and parasitism (e.g. Carter 1879; Mistiaen 1984; Kershaw 1987; Young & Noble 1989; Taylor 2015). The relationships between intergrown corals and host stromatoporoids have long been controversial due to the absence of clear evidence showing whether either benefitted or was harmed as a result of their association. Many publications suggested commensal relationships (e.g. Mori 1970; Kershaw 1987; Vinn 2016a), although a lack of interaction cannot be proven due to the absence of skeletal changes (Zapalski 2011).

In the present study, we document and interpret the intergrowth association between clathrodictyid stromatoporoid *Clathrodictyon boreale* Nestor 1964 and tabulate coral Auloporoidea indet. from the lowermost Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry, central Estonia. Associated intergrown tubeworms are also compared, thereby presenting a wider range of ecological variation among ancient benthic organisms. With the purpose of assessment and discussion of palaeoecological interactions between *C. boreale*, Auloporoidea indet. and tubeworms, this study attempts to evaluate their skeletal deformations that resulted from the *syn-vivo* interaction. Thus we aim to provide new information regarding the understanding of the biological development of reef community and ecological relationships of these benthic organisms.

Geological background and material

Early–Middle Palaeozoic carbonate strata are well-exposed in Estonia, representing a shallow epicontinental sea. During the early Silurian, Baltica was located in equatorial latitudes and continued its northward drift (Cocks & Torsvik 2005; Torsvik & Cocks 2013, 2017). Five main facies belts (and thus sedimentary environments) are recognized in the Estonian part of the Baltic Basin, ranging from tidal flat/lagoonal, shoal, open shelf, basin slope to basin depression, which represent a wide range of tropical environments (Nestor & Einasto 1977).

The lower Rhuddanian (Juuru in regional stage terminology) strata containing rich shelly faunas crop out widely in the western (Hiiumaa and Saaremaa islands) to the eastern (mainland) parts of Estonia, consisting of two lithostratigraphical units: the Varbola and Tamsalu formations in ascending order (Nestor 1997; Fig. 1). The Reinu Quarry is one of the classic exposures of the Varbola Formation (N59°5'14.28", E24°44'15.65"; Fig. 1), characterized by slightly argillaceous and nodular packstones of eight metres in thickness, containing bioclastic lenses with rich brachiopods, corals and echinoderms (Wright & Toom 2017). Many skeletal elements of these fauna are relatively small, presumably representing a Lilliput fauna. Stromatoporoids are the most common fossils in the Reinu Quarry, and they are up to 50 cm in diameter. 176 stromatoporoid skeletons were collected from the quarry. A specific-level taxonomic study of these specimens will be published in a separate paper. Among these stromatoporoid specimens, only a single stromatoporoid (GIT 666-47) contains intergrown corals (Fig. 1C), and two other symbionts. This host stromatoporoid was prepared with 35 transverse and 11 vertical thin sections for taxonomic identification and analysis of the growth behaviour of the stromatoporoid and its intergrown organisms. All thin sections and remaining fossil material are deposited at the Department of Geology, Tallinn University of Technology. In order to explore variation of growth interactions through Palaeozoic, we compared specimens of intergrowth associations between host stromatoporoids and intergrown corals/tubeworms, deposited in Tallinn University of Technology (GIT) and Nanjing Institute of Geology and Palaeontology (NIGP), from other ages (NIGP 159437 and 176515 for the Katian Stage of the Late Ordovician, GIT 656-47-2 for the Ludlow Epoch of the Silurian, NIGP 13674, 176516-1, 2, 176517 and 176518 for the Givetian Stage of the Middle Devonian).

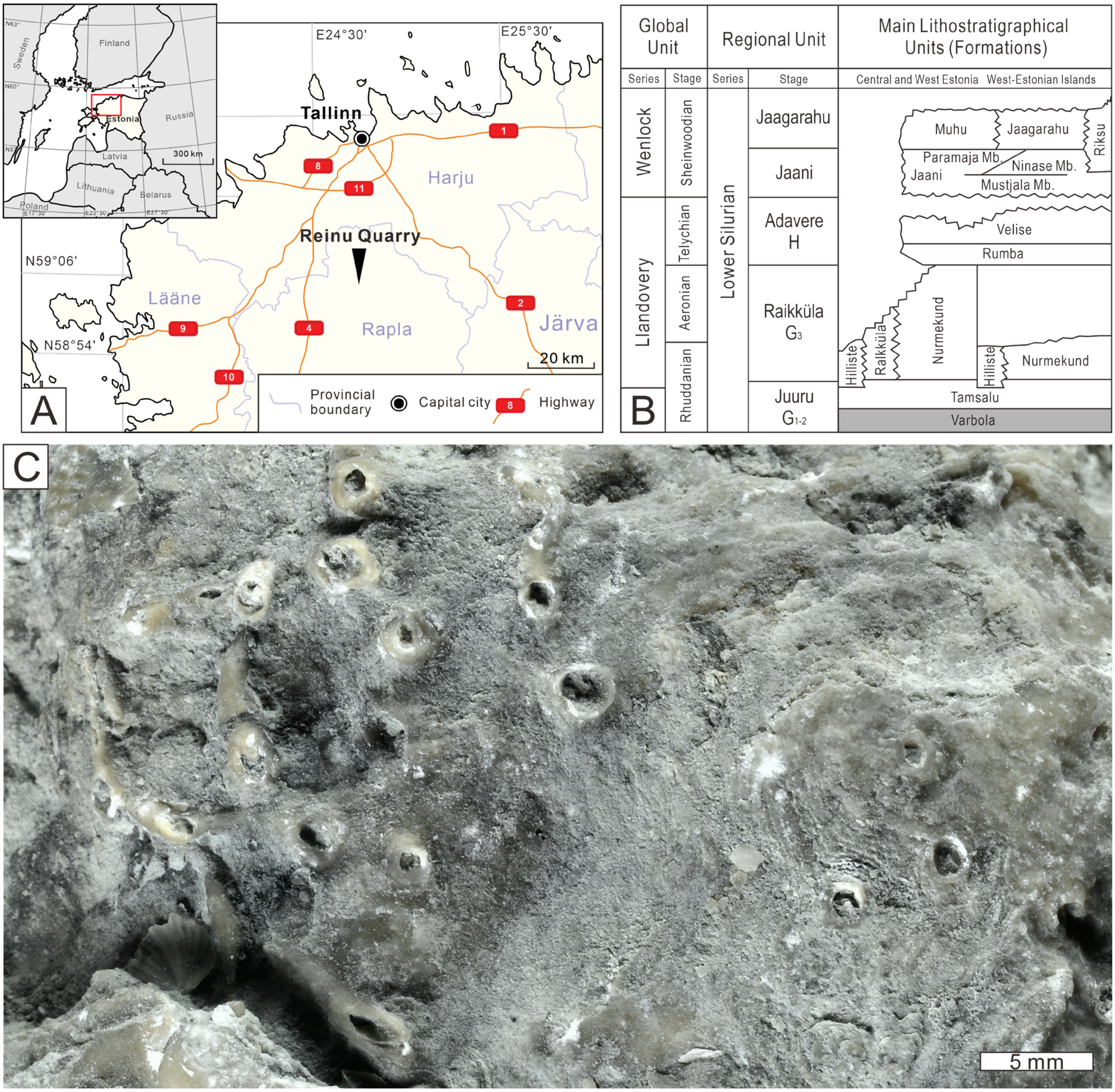

Fig. 1. A, geographical map of the study location at Reinu Quarry, Estonia. B, Silurian lithostratigraphy in Estonia, with the grey-coloured Varbola Formation from which the studied intergrowth specimen was collected (modified after Mõtus & Hints, 2007). C, *Clathrodictyon boreale* Nestor, 1964–auloporid coral Auloporoidea indet. intergrowth associations (GIT 666-47) from the lowermost Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry of Estonia. Note that auloporids are patchily distributed, and partly to entirely enveloped by the host stromatoporoid.

Results

Host stromatoporoid and intergrown auloporid coral

Stromatoporoids are one of the common benthic fossil organisms found in the lower Rhuddanian Varbola Formation. Clathrodictyid stromatoporoids are more diverse than labechiids. Two *Clathrodictyon* species (*C. kudriavzevi* Nestor, 1964 and *C. boreale* Nestor, 1964), three *Ecclimadictyon* species (*E. koigiense* Nestor, 1964, *E. microvesiculosum* Nestor, 1964 and *E. porkuni* Nestor, 1964) and only one species of labechiid (*Pachystylostroma rosensteinae* Nestor, 1964) are known from the formation (Nestor 1964).

In the specimen GIT 666-47, the host stromatoporoid is characterized by its finely crumpled laminae with short pillars (Figs 2, 3), which is consistent with the generic characteristics of *Clathrodictyon* (Nestor 2015). This *Clathrodictyon* species has laminae ranging from 0.11 to 1.10 mm in thickness (species average 0.25 mm; n = 60; standard deviation 0.23) and spacing of 8 to 14 laminae per two millimetres. Pillars are variable, ranging from incomplete rod- to funnel-like pillars, spacing 5 to 10 pillars per two millimetres. Galleries are round and elongated, ranging from 0.19 to 1.10 mm (species average 0.50 mm; n = 60; standard deviation 0.22). These morphological measurements and skeletal features closely resemble the key morphological characteristic features of *C. boreale* Nestor, 1964, and the species is thus herein identified as *C. boreale* Nestor, 1964.

Early Silurian tabulate corals in the Varbola Formation include *Paleofavosites*, *Catenipora*, *Halysites* and *Aulopora* (Klaamann 1959, 1962, 1964, 1966, 1970; Mõtus 1997). Among these tabulate corals, the intergrown corals are auloporids, an intergrowth which has not previously received attention in the lower Silurian of Estonia. A single species of *Aulopora* (*Aulopora* sp.) in the Juuru Regional Stage was listed by Klaamann (1959), but without description and illustration. In more recent papers, the genus is not listed in the Juuru Regional Stage (Klaamann 1966, 1970; Mõtus 1997).

Intergrown corals possess cylindrical to trumpet-like shapes, and commonly encrusted growth interruption surfaces in the host stromatoporoid (Figs 1C, 2, 3A–E). In the initial growth stage, corallites are commonly parallel to the host stromatoporoid laminae. In subsequent growth, the corallites curve slightly upward, and then show perpendicular growth to the stromatoporoid laminae (Figs 1C, 2A, 3A). The corallites (Figs 1C, 2, 3A–E) are cylindrical to subcylindrical, ranging from 0.90 to 2.29 mm in diameter (average 1.63 mm; n = 28; standard deviation 0.38). The corallite wall thickness of the intergrown auloporids is relatively thick and variable, ranging from 0.11 to 1.06 mm (average 0.40 mm; n = 78; standard deviation 0.20). Calices are relatively deep and show funnel-shaped morphology with thin corallite walls (Figs 2E, 3A, B). These skeletal features match representatives of auloporid corals, possessing short coralla with a prostrate growth habit. Owing to its wide range of morphological variation within the host stromatoporoid, the features of the intergrown corals seem to match those of *Aulocystis* representatives (Auloporoidea: Aulocystidae) judging from the following features: 1) budding pattern; 2) proximally prostrate, distally oriented upwards corallites; and 3) septal spines. However, lack of typical *Aulocystis* tabulae does not allow determination with certainty. Scarce tabulae and overall corallum habit may suggest *Remesia* (Auloporoidea: Romingeriidae), but not all diagnostic features are clearly visible in our material. In addition, the skeletal structures of the intergrown coral were possibly modified by the host stromatoporoid growth, therefore it is difficult to compare with other auloporid corals for specific-level taxonomy. It is most appropriate to consider this intergrown auloporid coral in open nomenclature, therefore determining it as Auloporoidea indet. in this study. It is uncertain whether the listed *Aulopora* sp. in Klaamann (1959) might be conspecific with the current specimen or not, due to the absence of specimens; description and further comprehensive taxonomic work on these corals is required.

Other intergrown organisms

Intergrown tubeworms *Cornulites* and *Helicosalpinx* are also found within the skeleton of the stromatoporoid (Fig. 3F, G). Specimens of cornulitid *Cornulites*, characterized by vesicular wall structure, were commonly intergrown with Silurian stromatoporoids (e.g. Vinn & Mõtus 2014; Vinn & Wilson 2010). The cornulitid tube is characterized by its annulated wall with vesicular structure, which is 1.58 mm in diameter and 3.16 mm in height. It resembles *Cornulites stromatoporoides* Vinn & Wilson, 2010 (Fig. 3F). *Helicosalpinx* is characterized by a spiral shaft and lack of tabulae (Tapanila 2004, 2005). The tube diameter of the present specimens is less than 0.5 mm (0.44 to 0.47 mm) and narrower than its coiling radius, which has similar features to *H. concoenatus* Clarke, 1908 (Fig. 3G; Vinn & Mõtus 2014).

Skeletal deformations of host stromatoporoid and intergrown organisms

The intergrowth association between *Clathrodictyon boreale* Nestor, 1964 and Auloporoidea indet. is interpreted to demonstrate *syn-vivo* interactions, judging from skeletal deformations that occurred during their growth (Figs 2, 3A–E). The distorted skeletal elements are represented by: (1) abnormally upward- or downward-bent marginal laminae of *C. boreale* (Fig. 2A, C, E, 3A); and (2) irregularly shaped outer wall of Auloporoidea indet. with uneven wall thickness near the physical contact between the host stromatoporoid and the intergrown corals (Figs 2, 3A–E). The intergrowth association started with the settlement and encrustation of auloporid corals on the growth surface of *C. boreale* (Fig. 2A). The initial growth stages of the auloporid corals are commonly associated with growth interruptions of the stromatoporoid (Fig. 2A). Downward-curved laminae of *C. boreale* occur below the corallite of the auloporid coral (the white arrow in Fig. 2C), indicating that the encrustation of the intergrown coral affected the growth of the

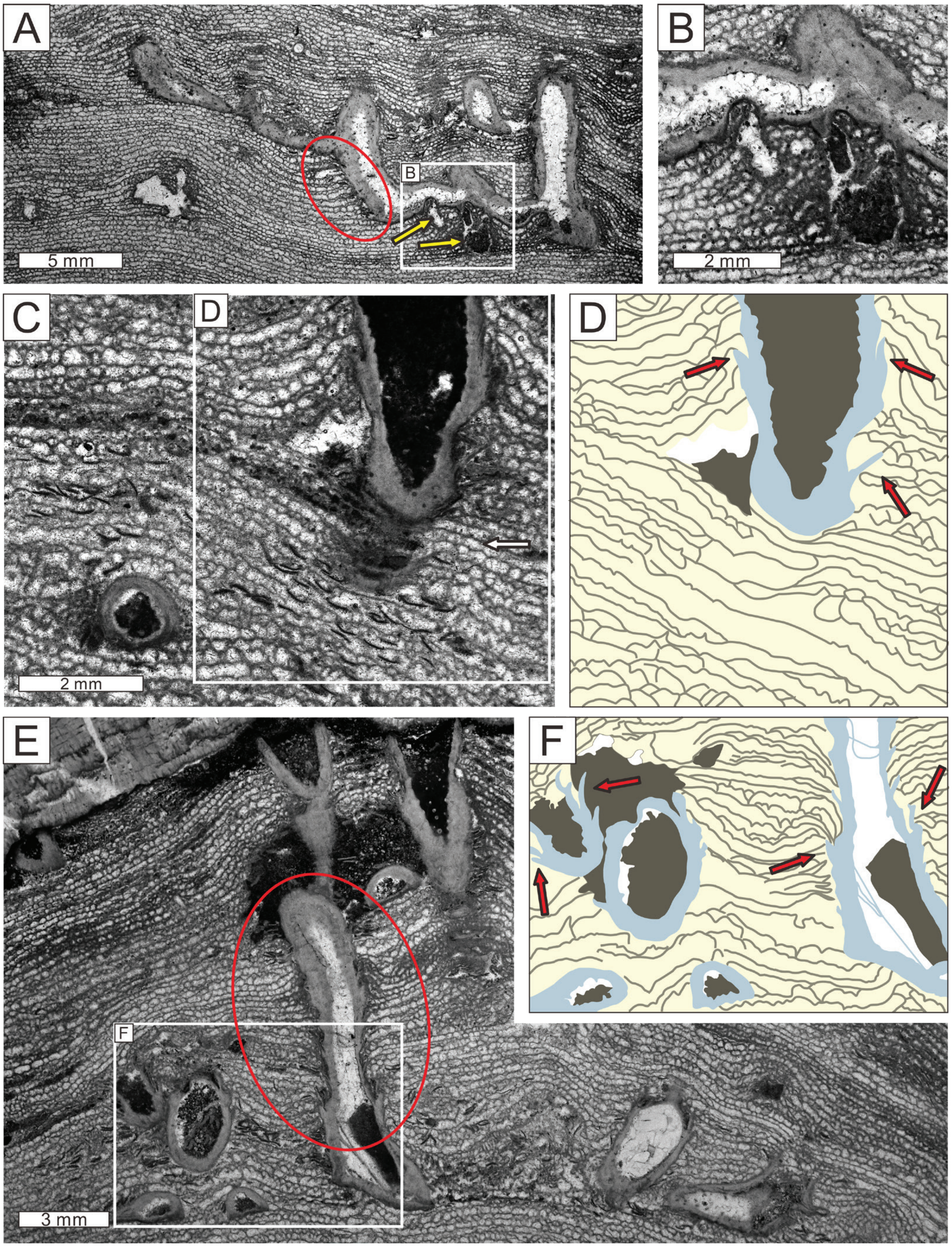

Fig. 2. Thin section photographs of the clathrodictyid stromatoporoid *Clathrodictyon boreale* Nestor, 1964–auloporid coral Auloporoidea indet. intergrowth associations from the lowermost Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry of Estonia. A, longitudinal section showing auloporid coral within the skeleton of *C. boreale*. The red oval highlights an area showing the irregular shaped outer wall of the intergrown auloporid coral and crumpled laminae of the host stromatoporoid during the subsequent upward growth stage of auloporid coral. In the central lower part of the photograph is an irregular shaped cavity related to deflections of stromatoporoid laminae (yellow arrows in the white rectangle) and an enlargement in (B). Both cement filled and sediment-filled cavities (left and right, respectively) may be cross-sections through another (unknown) intergrown organism, lacking a shell and are therefore bioclaustrations. The small circular cavity in the lower-left corner of the photograph may be another bioclaustration, GIT 666-47#1. C, longitudinal section showing downward curved laminae of *C. boreale* below the perpendicularly intergrown auloporid coral (white arrow), GIT 666-47#4. D, schematic drawing of white rectangle in (C), showing irregularly shaped outer wall of auloporid coral with its uneven wall thickness near the physical contacts with the host stromatoporoid (red arrows). E, longitudinal section showing skeletal deformations of the host stromatoporoid *C. boreale* and the intergrown coral Auloporoidea indet., GIT 666-47#3. The red oval indicates the skeletal change from the down- to upward bending marginal laminae of *C. boreale*. F, schematic drawing of white rectangle in (E), showing irregularly shaped outer wall of Auloporoidea indet. with its uneven wall thickness near the physical contacts with the host stromatoporoid (red arrows). Note that in (A, C, E), the growth of auloporid tubes coincided with growth interruption events in the stromatoporoid growth and might be the reason for the initial development of the auloporids, that took advantage of a pause in stromatoporoid growth, but the auloporids were ultimately overgrown by recovery of the stromatoporoid. See also the legend in Figure 3.

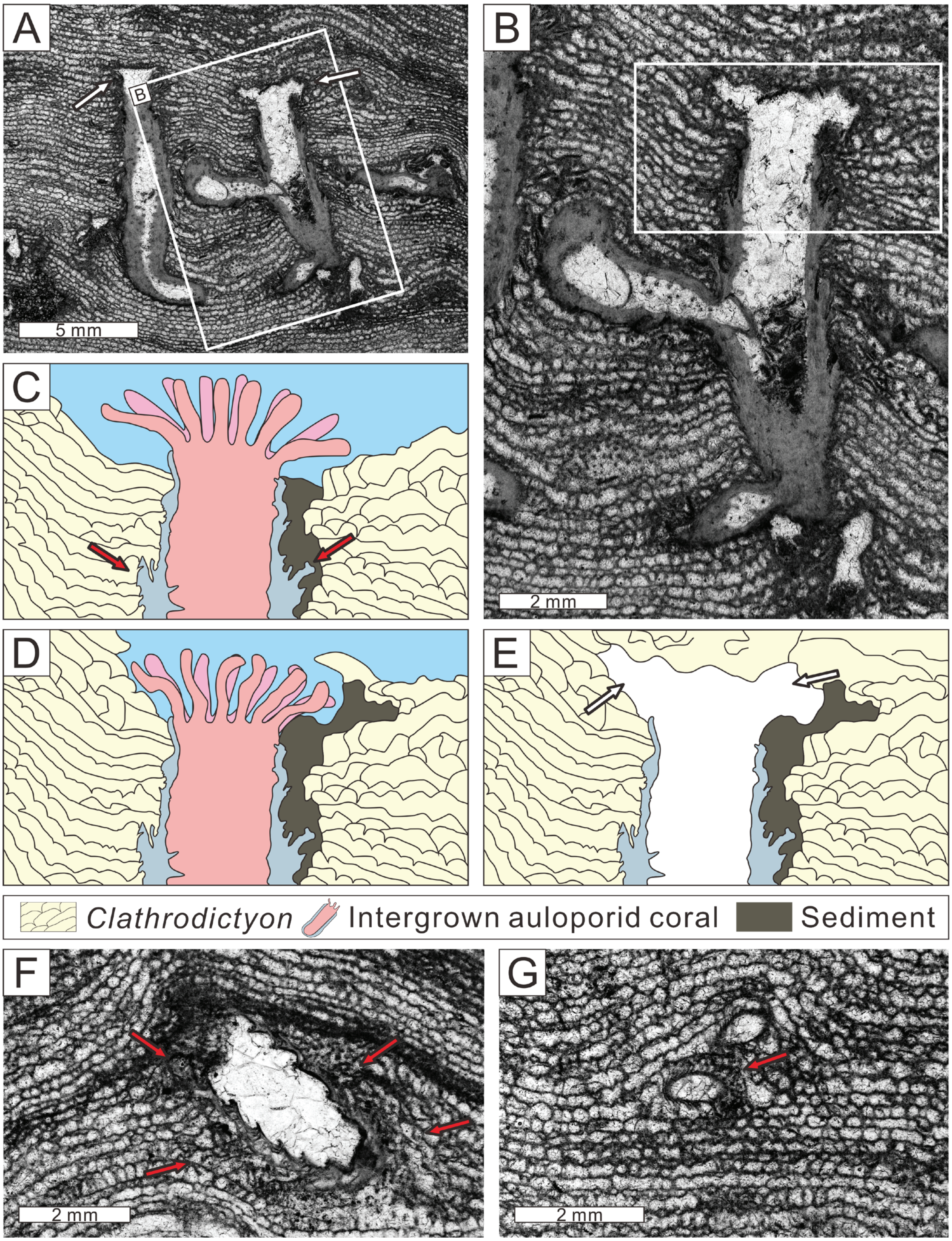

Fig. 3. Thin section photographs of the intergrown auloporid corals and tubeworms within the host stromatoporoid from the lowermost Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry of Estonia. (A–E) shows features and interpretation of the structures preserved. A, longitudinal section showing the skeletal deformations including down- to upward bending laminae of *Clathrodictyon boreale* and irregular-shape outer wall of Auloporoidea indet. with its uneven wall thickness near the physical contacts between them, GIT 666-47#2. Note that T-shape cavities were formed by overgrown *C. boreale* indicated by the white arrows in (A). B, enlarged area, which is indicated by the white rectangle in (A). C–E, schematic drawings to show a possible interpretation of the formation of the T-shape cavities, indicated by the white arrows in (A, E) and the white rectangle in (B). Red arrows in (C) indicate irregularly shaped outer wall of Auloporoidea indet. with its uneven wall thickness near the physical contacts with the host stromatoporoid laminae and micritic sediment. F, longitudinal section of the intergrown tubeworm *Cornulites* within the skeleton of *C. boreale*, surrounded by distorted crumpled laminae of the host stromatoporoid (red arrows), GIT 666-47#4; note the growth interruption event in the stromatoporoid's development, directly above the *Cornulites* shell. G, longitudinal section of the intergrown tubeworm *Helicosalpinx*, GIT 666-47#4. Note that the distorted crumpled laminae of *Clathrodictyon* are locally found on the right side of the *Helicosalpinx* cross-section (red arrow).

host stromatoporoid. Later, the growth direction of auloporid corals changed from parallel to perpendicular together with the growth of the host stromatoporoid (Figs 2A, E, 3A). During the changes in growth direction, auloporid corals have a sharp interfingering contact of the epitheca with the host stromatoporoid, exhibiting irregularly shaped outer walls and uneven wall thickness (Figs 2, 3A–E). On the other hand, the laminae of the host *C. boreale* were up- or downward bent and became more densely distributed near the physical contact with the coral (Figs 2, 3A–E). In some places, the down-curved marginal laminae turned to the up-curved direction (red oval in Fig. 2E, also see Fig. 3B), possibly indicating that the growth rate of the intergrown auloporid corals became relatively faster. During this process, the corallite wall of the intergrown auloporid corals became thinner than that of the earlier growth (Figs 2E, 3A), and the irregular shape of the outer wall is also observed, presumably due to sediment influx (Figs 2E, 3B, and red arrows in Figs 2F, 3C, respectively). Finally, the growth of the intergrown coral was terminated by the overgrown stromatoporoid *C. boreale* (Figs 2E, 3A, B). T-shaped small cavities, formed by irregular growth of the *Clathrodictyon* laminae (mm-scale) are observed (white arrows in Fig. 3A, and enlarged photograph in Fig. 3B). These cavities are possibly due to the delayed growth of the *Clathrodictyon* laminae due to the influence of the intergrown coral (Fig. 3C–E). The alternative scenario is that the calice of the dead coral was occupied by a different unknown organism as a way of surviving in the stromatoporoid, but was only able to do so for a short period before being overgrown by the stromatoporoid. Sediment influx is commonly found to have influenced the growth of the host *C. boreale* and the intergrown auloporid corals (Fig. 2E, F). In some cases, the auloporid coral appears to have survived the sediment influx, while the host stromatoporoid was partially buried by sediment. Afterwards, the intergrown corals became re-incorporated within the recovered skeleton of *C. boreale* (Fig. 2E).

In addition to the interaction with Auloporoidea indet., *Clathrodictyon boreale* also hosted two different tubeworms including *Cornulites* and *Helicosalpinx* (Fig. 3F, G). *Cornulites* is surrounded by crumpled laminae of the host *Clathrodictyon* with high skeletal density (red arrows in Fig. 3F), while distorted *Clathrodictyon* laminae are locally developed in the vicinity of *Helicosalpinx* (red arrow in Fig. 3G).

Discussion

Skeletal irregularities in Palaeozoic corals are recognized commonly in their normal growth. One of the main components of phenotypic variation in Palaeozoic corals can be represented by cyclomorphism (Hill 1981; Nowiński 1991; Scrutton 1998), expressed as growth bands and epithecal sheaths (Hill 1981; Scrutton 1998). Such features are also commonly recognized in skeletons of stromatoporoids (Young & Kershaw 2005; Nestor *et al*., 2010), but are more ambiguous than those of the corals (Young & Kershaw 2005). Variation in growth bands has been interpreted to indicate seasonal changes (Hill 1981; Scrutton 1998; Young & Kershaw 2005; Nestor *et al*. 2010), and commonly associated with: 1) alteration of different skeletal density; 2) growth interruption; and/or 3) sediment inclusions (Young & Kershaw 2005; Nestor *et al*. 2010).

Growth bands in corals are represented by features such as spacing of tabulae, irregularities in the shape of outer walls and uneven wall thicknesses during normal growth in corals (Scrutton, 1998; Young & Kershaw 2005; Liang *et al*. 2013). Such variations therefore raise a question as to whether such features in the intergrown examples described in this study are related to interaction with the host stromatoporoid, or not. This question can be addressed by study of variation in spacing of tabulae in the intergrown coral. If the skeletal irregularities of the outer wall are cyclomorphic in origin, it is postulated that the corallites might accompany low or high-density bands, characterized by spacing of tabulae with regularity (e.g. Liang *et al*. 2013). However, the tabulae in these Ordovician and Silurian intergrown examples are randomly developed, and no regularity of skeletal elements were found. It is therefore reasonable to interpret that the distorted skeletal elements of the intergrown corals are due to their *syn vivo* palaeoecological interactions, rather than cyclomorphism.

The irregularly shaped outer walls of the Ordovician and Silurian intergrown auloporid corals can also be compared with epithecal sheaths. The unusual structure of the intergrown corals possesses an upward-opening sharp outline with uneven thickness (Figs 2, 3), which is far from the general concept of growth ridges in corals. Epithecal sheaths are known to represent transverse growth ridges or wrinkles, exhibiting relatively smoothly wrinkled walls (see fig. 290.4 in Hill, 1981 for a common example of epithecal sheaths). It is thus reasonable to interpret that the upward-opening irregularly shaped outer walls of the intergrown corals resulted from interaction with the host stromatoporoid because this structure of the intergrown corals also commonly occurs with distorted crumpled laminae of the host stromatoporoid.

The earliest-known stromatoporoid-coral association was reported from the Upper Ordovician (middle to upper Katian) Xiazhen Formation of South China (Lee *et al*. 2016). Both free-living and intergrown

Bajgolia specimens appear to lack a definite epithecal sheath (Lee *et al.* 2016). Smooth physical contacts were commonly found in numbers of intergrowth associations between the host clathrodictyid stromatoporoid and the intergrown auloporid *Bajgolia* (Fig. 4A; see also figures and corresponding text in Lee *et al.* 2016). However, some of the intergrown *Bajgolia* unusually possess irregularly shaped outer walls (Fig. 4B). This skeletal distortion in the earlier auloporid coral can be comparable with the current Silurian specimens. Lee *et al.* (2016) recognized two *Bajgolia* species in the Xiazhen Formation (*Bajgolia* spp. A, B), but taxonomic work has not been done yet. It is not possible to evaluate whether the different growth behaviour, represented by different physical contacts with the host clathrodictyid (Fig. 4A, B), is due to interspecific palaeoecological variation or other causes.

Both the earlier Ordovician auloporid *Bajgolia* and Silurian Auloporoidea indet. show similar growth behaviour in relation to local sedimentation (compare Ordovician example, Fig. 4A, B with Silurian example, Fig. 2E). These examples show that growth of the host stromatoporoid was partly interrupted, while the intergrown auloporids survived and were reincorporated with the stromatoporoid recovery (see also Kershaw *et al.* 2018, fig. 24 for additional cases). These different growth behaviours of the host stromatoporoids and the intergrown corals possibly indicate that corals were more advanced in removing sediment from their growth surface, or that partial sediment influx only slightly affected the growth of these small corallites.

In the initial growth stage of free-living auloporids, corallites can be parallel to the substrate, and calices subsequently raised above substrate (Hill 1981). The intergrown auloporid species also shows similar growth patterns, so such features in the intergrown corals are not necessarily related to interaction with the host stromatoporoid. During the initial stage of the encrustation, the outer wall is relatively smooth (the white rectangle in Fig. 2A and the enlarged area for Fig. 2B). The latter growth stage began to develop upward-curved corallites with an irregularly shaped outer wall, facing crumpled laminae of the host stromatoporoid (red oval in Fig. 2A). The smooth outer wall in the initial growth stage of the encrustation presumably indicates that there was no significant interaction between the auloporid and underlying stromatoporoid as the coral encrusted on the growth interruption surface of the stromatoporoid. This arrangement demonstrates a complexity in the interaction between the two organisms, whereby a growth interruption event played a part in the development of the association. Whether the host stromatoporoid caused the upward growth of the intergrown corals or not, is uncertain, but these features are evidence in that these associated organisms interacted during the upward growth of the intergrown auloporid corals.

In the Varbola Formation, evaluation of skeletal deformations in the host stromatoporoid and the intergrown coral demonstrates that the relationships between host stromatoporoids and intergrown corals are too complex to be defined as a single palaeoecological interaction, and spatial competition should be considered a key palaeoecological trait for the nature of intergrowth associations. Intergrown corals might have taken advantage of the host stromatoporoid for elevation of feeding positions to occupy a higher tiering level (Vinn & Mõtus 2014; Lee *et al.* 2016), or for protection from water turbulence (Kershaw 1987; Lee *et al.* 2016). Conventionally, the host stromatoporoid was regarded as receiving negligible influence from the relationship (e.g. Kershaw 1987; Young & Noble 1989). These perspectives can be equivalent to the current Silurian example. It is obvious that the many examples of physical contact between the host stromatoporoid and the intergrown corals were represented by smooth walls (Fig. 4C–E; see figures in Mori 1970; Mistiaen 1984; Kershaw 1987; Young & Noble 1989; Zapalski 2012). In fact, most of the examples in the previous studies show that intergrown syringoporid corals did not develop any skeletal deformations. In contrast, the irregular shape of the outer walls of Ordovician and Silurian auloporids provides direct evidence that the growth of corals was negatively affected by the host stromatoporoid. Such variety of palaeoecological interaction depending on intergrown corals and host stromatoporoids reflects different growth behaviours of the participating organisms.

Intergrown tubeworms might have been parasitic due to occurrence of downward-curved laminae of the stromatoporoid in the vicinity of the tubeworms (Figs 3F, G, 5, 6; see also figures and corresponding text in Zapalski & Hubert 2011). The conceivable scenario of the arrangement is that the tubeworm grew rapidly, or pre-existed, and subsequently the stromatoporoid encrusted the inter-space of the spiral tubeworm, causing up- or downward-curved laminae (Fig. 5A, C, D), and sediment influx also caused such curved laminae near those parts of the host stromatoporoid (Fig. 5B). Skeletal deformation of the host stromatoporoid is particularly obvious near the open aperture of the intergrown tubeworm (white arrow in Fig. 6). In addition to the deformation, a sharply interfingering contact between the two organisms (red arrows in Fig. 6) was developed. Both skeletal features were interpreted to be indicative of antagonistic biotic interactions. However, it is also observed that the stromatoporoid partly infilled the aperture without

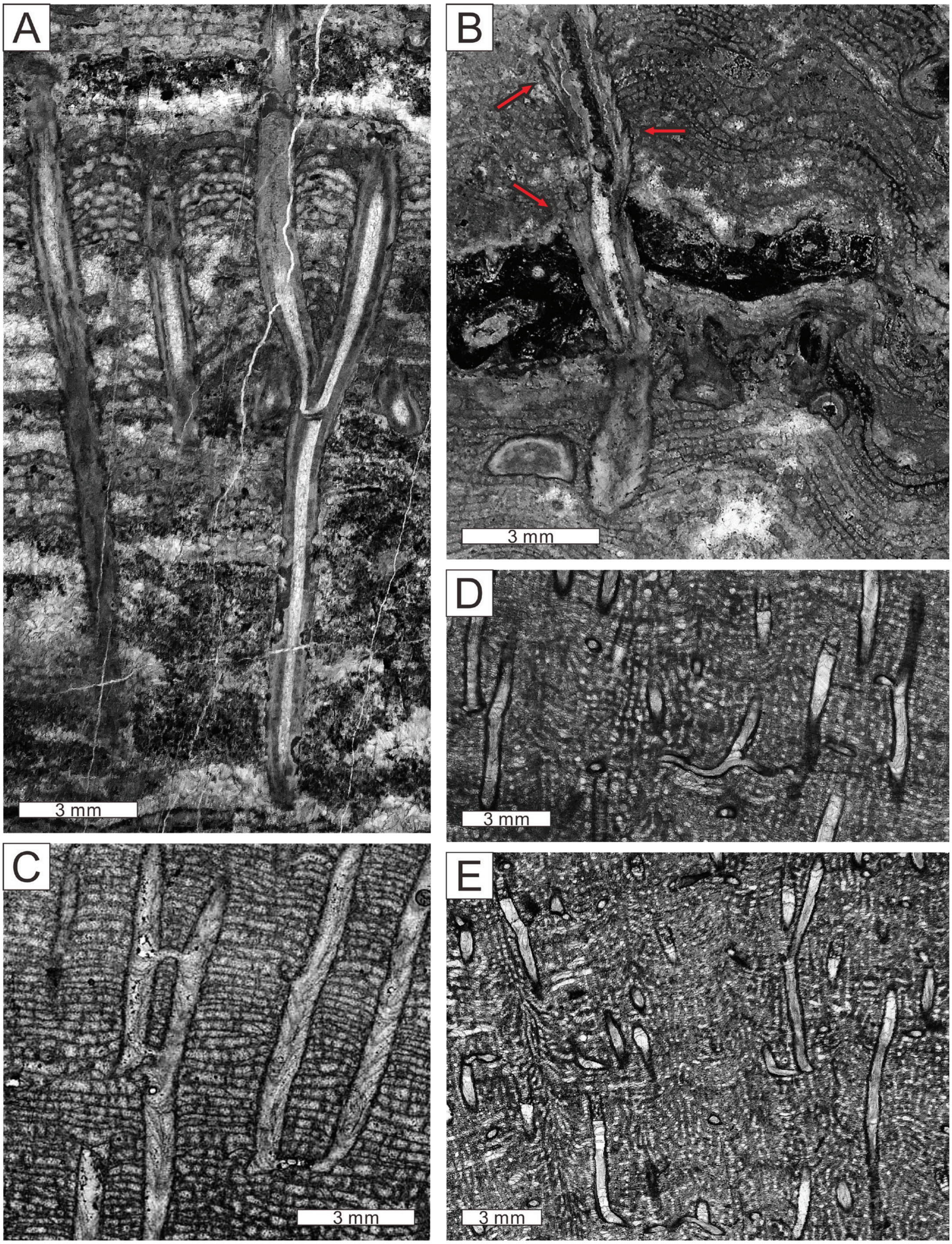

Fig. 4. Representative examples of stromatoporoid–coral intergrowth associations in the Early to Middle Palaeozoic. A, B, *Bajgolia–Clathrodictyon* intergrowth associations from the Upper Ordovician Xiazhen Formation of South China, NIGP 159437 and 176515, respectively. Note that (A) shows smooth physical contact between the intergrown *Bajgolia* sp. and the host *Clathrodictyon* cf. *C. microundulatum* Nestor, 1964, while (B) shows sharp irregularly shaped outer wall of *Bajgolia* sp. (red arrows) within the host *Clathrodictyon plicatum* Webby & Banks, 1976. See Lee *et al.* (2016) for detailed information on various stromatoporoid–coral intergrowth associations in the Xiazhen Formation. C, *Petridiostroma–Syringopora* intergrowth association from the biostrome interval of the upper Silurian Paadla Formation (middle Ludlow) of Estonia, GIT 656-47-2. Note that the intergrown coral *Syringopora affabilis* Klaamann, 1962 and the host stromatoporoid *Petridiostroma convictum* (Yavorsky, 1929) have smooth physical contacts. See Kershaw & Mõtus (2016) for palaeoecological and palaeoenvironmental information on corals and stromatoporoids in the Paadla biostrome at Katri site on Saaremaa Island. D, E, longitudinal sections of *Stromatopora–Syringopora* intergrowth association from the biostrome interval (Jiwozhai Member) of the Middle Devonian Dushan Formation of South China, NIGP 176516-1, 2, respectively. Note that the host stromatoporoid *Stromatopora* has smooth physical contacts with the intergrown *Syringopora*. As in other photographs of this study, there is evidence that the syringoporids used growth interruption surfaces to achieve initial growth on stromatoporoid surfaces.

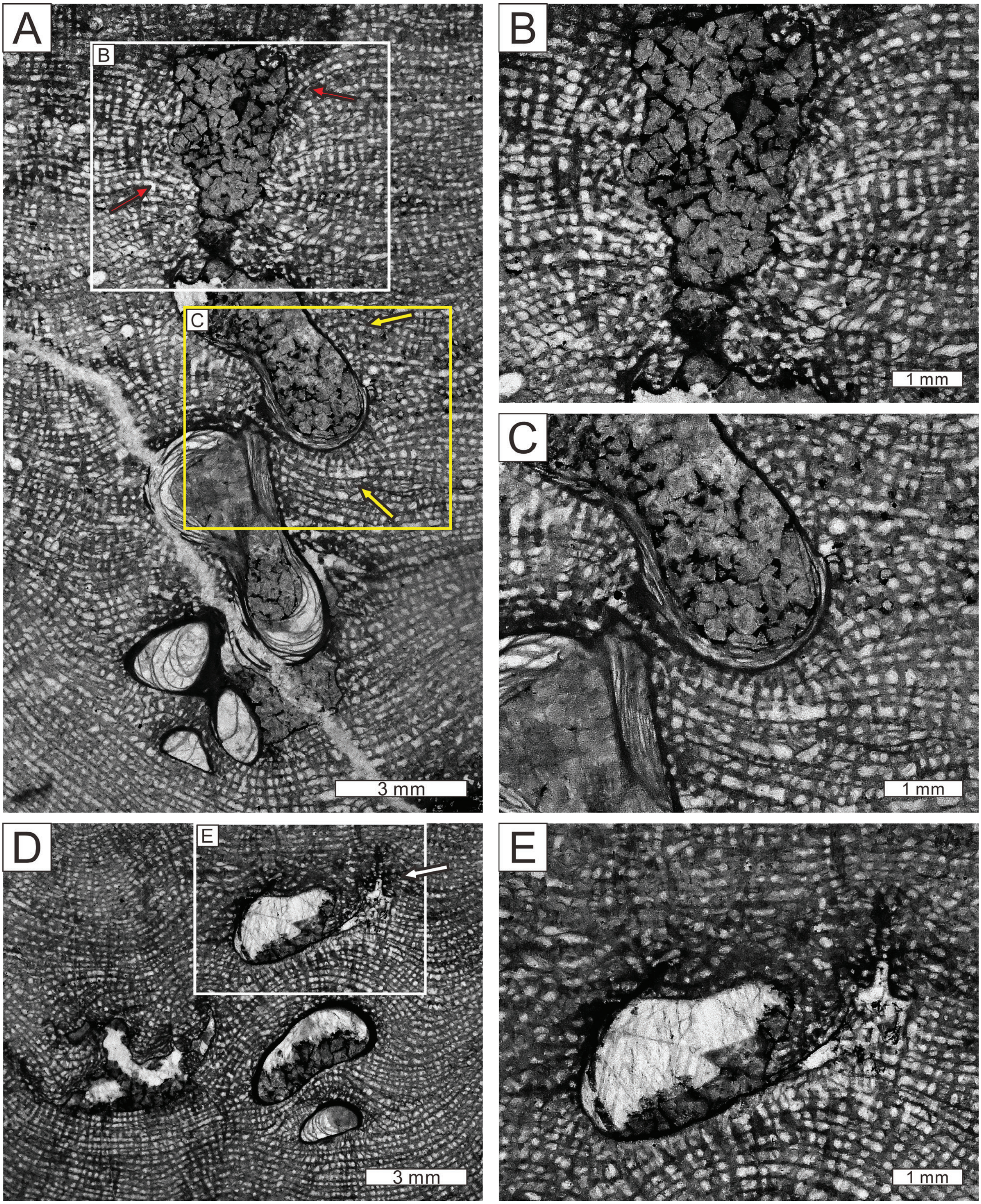

Fig. 5. Examples of stromatoporoid–tubeworm intergrowth association from the biostrome interval (Jiwozhai Member) of the Middle Devonian Dushan Formation of South China. A–D, the intergrown spiral tubeworm *Torquaysalpinx* in the host stromatoporoid *Hermatostroma*, NIGP 176517 (A–C) and NIGP 176518 (D, E). Yellow arrows in (A) indicate the up- or downwardly curved stromatoporoid laminae near the intergrown tubeworm. B, enlarged area of white rectangle in (A), showing sediment influx caused growth interruption in those part of the host stromatoporoid (red arrows in A). C, enlarged area of yellow rectangle in (A), showing the up- or downwardly curved stromatoporoid laminae close to the intergrown tubeworm. D, white arrow indicates normal skeletal phase of the host stromatoporoid, which completely encloses the *Torquaysalpinx*. Note that curved laminae surrounded the intergrown tubeworm. E, enlarged area, which is indicated by white rectangle in (D). Note that skeletal deformation of the host stromatoporoid and intergrown tubeworm did not develop.

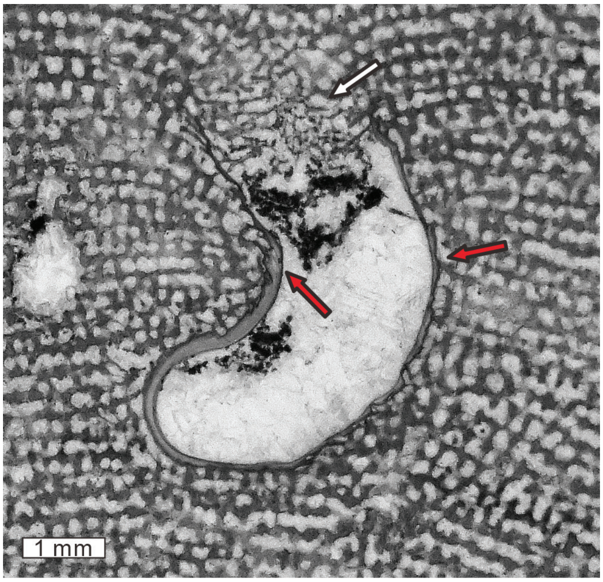

Fig. 6. An example of stromatoporoid–tubeworm intergrowth association from the biostrome interval (Jiwozhai Member) of the Middle Devonian Dushan Formation of South China. Note that skeletal deformation of the host stromatoporoid *Atelodictyon*, represented by distorted skeletal structure (white arrow) and irregularly shaped outer walls of tubeworm *Torquaysalpinx* with the sharp interfingering contact (red arrows), possibly indicate hostile interactions of the host stromatoporoid and the intergrown tubeworm, NIGP 13674.

any skeletal distortion (white arrow in Fig. 5D and enlarged area for Fig. 5E), which may reflect variation of the host stromatoporoid reactions or alternatively just simple growth of stromatoporoid in association with a dead tubeworm. All things considered, it is presumed that these examples demonstrate that the host stromatoporoid and the intergrown tubeworm were hostile to each other judging from their skeletal deformations during their live-live interaction although it is yet difficult to determine their precise palaeoecological relationship. A similar interaction is also known from the intergrowth association between chaetetid sponges (a related group of hypercalcified sponge, possessing tabulae, which has a different skeletal structure from stromatoporoids) and annelid *Spirorbis* (see pl. 3, fig. 8 of Fagerstrom *et al.* 2000), which may or may not be comparable with those host stromatoporoids and intergrown tubeworms. Only a few stromatoporoid-type sponge occurrences are known through the Carboniferous (e.g. Kershaw & Sendino, 2020), none of which record intergrowth relationships with other organisms. Thus chaetetid sponges might have been selected as alternative intergrowth hosts beyond the end-Devonian Hangenberg Crisis.

Overall, unlike the other reported intergrowth associations between corals and stromatoporoids, the current example from the lowermost Rhuddanian Varbola Formation is characterized by occurrence of skeletal deformations of both host *Clathrodictyon boreale* and intergrown Auloporoidea indet. These distorted skeletal elements were secreted during their growth, indicating *syn-vivo* interactions between the host stromatoporoid and the intergrown corals. Our study presents evidence that the palaeoecological interaction between host stromatoporoids and intergrown organisms is more complex than the simple interpretation that the corals only benefitted from the intergrowth. The skeletal deformations were most likely to be results of highly localized spatial competition, representing antagonistic competitive interactions. Difficulty continues in determination of the exact relationship in the context of mutualism, commensalism or parasitism, but spatial competition is identified here that must be considered in further studies. This work demonstrates that evaluation of skeletal deformations should be further explored to develop interpretations of the palaeoecological relationship and interactions between the involved organisms (Jeon *et al.*, 2020) and can be further applied to evaluate the nature and evolution of reef organisms.

Conclusions

The following conclusions can be made.

1) Intergrowth association between the host clathrodictyid stromatoporoid *Clathrodictyon boreale* Nestor, 1964 and the intergrown corals of Auloporoidea indet. is found in the lowest Rhuddanian Varbola Formation (Juuru Regional Stage) at Reinu Quarry of Estonia. This association exhibits two different kinds of skeletal deformation represented by upward- or downward-bending laminae of the host *C. boreale* and irregularly shaped outer wall of the intergrown auloporid corals with uneven wall thickness near their physical contacts. This is the first record of mutual skeletal modifications in stromatoporoid–coral associations.
2) In addition, the intergrown tubeworms, *Cornulites* and *Helicosalpinx*, are also found in the skeleton of *Clathrodictyon boreale*. *Cornulites* is surrounded by distorted laminae of *C. boreale*; crumpled *Clathrodictyon* laminae are locally developed in the vicinity of *Helicosalpinx*.
3) On the basis of skeletal deformations, we interpret the intergrown corals and tubeworms to have not always benefitted from living within the host stromatoporoid and possibly were hostile to each other.

4) The occurrence of skeletal deformations in stromatoporoid–coral intergrowth associations is not persistent, possibly reflecting different growth behaviours of the intergrown coral and host stromatoporoids depending on the involved species.
5) This study provides evidence that the antagonistic interaction between *Clathrodictyon boreale*, Auloporoidea indet. and tubeworms increases our understanding of the intergrowth interaction and growth behaviour of the host stromatoporoid, intergrown corals and tubeworms. The results imply that the intergrowth association between stromatoporoids and other organisms is more complex than simply interpreted as mutualism, commensalism and/or parasitism, and requires detailed evaluation of their skeletal deformations near the physical contacts.

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