

Symbiosis in corals and stromatoporoids from the Silurian of Baltica

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ABSTRACT

The large collection of thin sections of stromatoporoids and corals from the Silurian of Ukraine, Moldova, Belarus, and Komi Republic (Russian Federation) revealed several incidences of skeletal intergrowth between stromatoporoids/corals and the other invertebrates. The stromatoporoids formed symbiotic associations with soft-bodied worms (*Helicosalpinx* and *Chaetosalpinx*), calcareous tentaculitoid tubeworms (microconchids, *Cornulites*, *Conchicolites*), and rugosans. Tabulate corals formed symbiotic associations with cornulitids. The studied stromatoporoid based associations are dominated by bioclastrations of worms without mineral skeletons. Most likely non-mineralized invertebrates benefitted more from endobiotic life mode than invertebrates with mineralized skeletons as the latter already had protection on their own against predators. There was almost no difference in the number of symbiont taxa per host stromatoporoid species indicating that all studied stromatoporoids were rather similar in their tolerance towards different endobionts.

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INTRODUCTION

There is little doubt that symbiosis has been an important driving force of biological evolution. The relationships between animal diversification and parasitism have been recently studied by De Baets et al. (2021b). However, many fundamental aspects of the evolution of symbiotic relationships have remained poorly understood, especially as compared to the evolutionary history of predation (Huntley and Kowalewski, 2007). Trace fossils often play a pivotal role in the study of parasite-host interactions in deep time (Huntley and De Baets, 2015). The study of symbiotic relationships in fossil animals involves various difficulties (De Baets et al., 2021a,b). It is mostly impossible to distinguish mutualism from commensalism or parasitism (Taylor, 2015; Robin, 2021). Epibionts often use skeletons of dead organisms as a hard substrate for their attachment. However, in the latter case, there is no evidence of intergrowth between two organisms. The intergrowth of two organisms provides us with the best evidence of symbiosis in the fossil record (Tapanila, 2008). We found multiple cases of intergrowth when reviewing our collection of Silurian stromatoporoids and tabulates. The majority of intergrown organisms in our collection are stromatoporoids as hosts but in some cases, it also involves tabulate corals. Frequently symbiotic invertebrates are embedded within the skeleton of a host organism, leaving only small apertures exposed for feeding and such embedment structures are called bioclastrations (Palmer and Wilson, 1988). Ancient symbiotic relations are especially important for the study of coevolution. Symbiosis is here viewed as any type of close and long-term biological interaction between two different animals, whether it is parasitic, commensalistic, or mutualistic (Martin and Schwab, 2013).

The Silurian of Baltica has a rich record of symbiosis (Vinn and Wilson, 2016). There are records of possible polychaetes (Mõtus and Vinn, 2009; Vinn and Mõtus, 2014b), rugosans (Nestor, 1966; Kershaw, 1987; Vinn and Mõtus, 2014a), syringoporids (Nestor, 1966; Kershaw, 1987), and cornulitids (Vinn and Wilson, 2010a, b) in tabulate corals and stromatoporoids from the Silurian of Baltica.

The aims of this study are as follows: (1) to summarize the symbiotic associations found in the Silurian of Ukraine, Moldova, Belarus, and Komi Republic (all regions belonging to Baltica); (2) to discuss symbiosis in Silurian stromatoporoids; and (3) to discuss symbiosis in Silurian tabulates.

HISTORY OF GEOLOGICAL STUDIES

The study of the Silurian from Podillya commenced at the beginning of the nineteenth century by Staszic, Eichwald, and Malevsky. Their findings and observations are discussed in the monography of Kozłowsky (1929). The first stratigraphic schemes of the Upper Silurian and Lower Devonian deposits were created by Stur (1872). Alth (1874) established “the Skala beds” and described the fossils from the outcrops which he analysed. Venyukov (1899) identified and described new corals, brachiopods, bivalves, and other fossil species and established three coral horizons in the lower part of the Silurian which outcropped on the left bank of the Dniester River. A lot of details to the Silurian and Lower Devonian sequence from Podillya were added by Kozłowsky (1929) and Văscăuțanu (1931). Kozłowsky investigated the left bank of the Dniester River, specifically the upper course of the Zbruch River, while Văscăuțanu studied the right bank of the Dniester River. Kozłowsky identified the Skalian, Borschovian, and Chortkopian Regional Stages in the upper part of the sequence.

One of the first stratigraphic schemes that generalized previous discoveries was established by Lungershausen and Nikifiriova (1942). They identified seven horizons: Kitaigorod, Mouksha, and Ustia belonging to the Llandovery epoch; Malynivtsy – Wenlock epoch; Skala – lower Ludlow and Aimestri, Borschov – upper Ludlow; Chortkov – Přidoli epoch. Nikiforova continued to study the brachiopods from the Silurian of Podillya after the Second World War (Nikiforova, 1954). The famous Russian geologist Sokolov published a monograph related to tabulate corals from this region (Sokolov, 1955). Dikenstein (1957) divided the Kitaigorod horizon into the Restevo and Grushevtsy beds and the Skalian horizon into the Isakivtsy, Prigorodok, Rashkiv, and Volkivtsy beds. Boucot and Pankivsky (1962) considered that the boundary between the Silurian and the Devonian is at the base of the Skalian horizon, which they considered to belong to the Devonian system. Sytova (1966) divided the Malinivtsy horizon into the Konivka, Sokil, and Grinchuk beds. Drygant (1967, 1968) identified exclusive species of conodonts which allowed the marking of the exact boundary between the Silurian and Devonian in the Podillyan sequence. The same results were obtained by Tsegelnjuk (1968), Koren (1968), and others.

Drygant and Tsegelnjuk (1968) proved that the previously considered sterile Llandovery deposits from the Silurian of Podillya are fossilifer-

ous by finding conodonts and graptolites in the outcrops located near the Kitaigorod village. Corals were studied by Bondarenko (1982), Grytsenko (1977a, b, 1987). The ecostratigraphical approach toward the Silurian sequence and fossils was used by Grytsenko et al. (1999).

The materials were gathered from hundreds of drilled boreholes, outcrops, and a significant number of fossils from collections were reconsidered for analysis by a group of researchers from Kyiv, Lviv (Ukraine), St. Petersburg, Moscow, and Yekaterinburg (Russia). They summarized previously published data as well as new information regarding the Silurian system and released the guide for geological excursions of the International Subcommittee on Silurian Stratigraphy of the International Union of Geological Sciences (Tsegel'nyuk et al., 1983). The guide contained an improved stratigraphic scheme. All fossil findings were linked to the new detailed scheme. The authors presented a new approach toward correlating the available scheme with the international stratigraphical scheme based on the geological development of the basin, which is attached to the western ridge of Baltica. The sedimentary cover of the basin did not suffer any significant metamorphic changes and tectonic activities. The different degrees of cyclic movements are reflected in the lithological features and allowed to demarcate the local geological groups: Bolotine (Llandovery), Jaruga (Wenlock), Malynivtsy (Ludlow), Skala (Přidoli) and stages: Wenlock, Ludlow, Ulichian (after Ludlow and before Přidoli), and Skalian. Also, a new Graptolitic zonal subdivision was proposed. Additionally, the guide contained 65 tables with the distribution of all studied fossils: brachiopods, trilobites, Tabulata and rugosan corals, Heliolitida, Stromatoporata, conodonts, Chitinozoa, algae, cephalopods, ostracodes, and graptolites.

The International Subcommittee on Silurian Stratigraphy (ISSS) decided to choose the stratotype in Czechia. Among other applicants, the Silurian from Podillya was chosen to be the parastratotype for the boundary between the Silurian and Devonian. Nevertheless, the Silurian section has some advantages. Firstly, the entire sequence is without any significant interruptions, metamorphic changes, or tectonic activities and is rich in different kinds of fossils. Several outstanding outcrops and thousands of drilled boreholes showed the cyclic development of the Silurian Sea basin from the Llandovery to the Gedinnian (Tsegel'nyuk et al., 1983). The final version of the

Silurian scheme of Ukraine was published in the last work of Konstantinenko and Tsegel'nyuk (2013).

GEOLOGICAL SETTING

The Silurian deposits are located along the southwestern and western margins of Baltica and have different areas of extent which depend on the local tectonic structure (Figure 1).

The Silurian from the eastern part of the Moldova-Podillya basin (southwestern Baltica) has minimal facies variations and is mostly consistent throughout the entire region (Bukatchuk et al., 1988). It is divided into the lower (Llandovery and Wenlock) and upper (Ludlow and Přidoli) sequences. The Llandovery sediments are represented by marine limestones in the lower part and by claystones in the upper part of the sequence (Tsegel'nyuk and Bukatchuk, 1974). The Wenlock deposits begin with marine limestones, which are covered by lagoonal limestones and dolostones (Tsegel'nyuk, 1980a). The Ludlow and Přidoli sediments are defined by various limestones and dolostones, which were deposited in lagoonal, inner to outer shelf, and shallow-water depositional environments (Tsegel'nyuk, 1980a, b).

The western part of the Moldova-Podillya basin is less complete than the eastern part of the platform (Pătruț, 1981). It is divided into two sectors, the Bătrânești – Todireni – Iași sector and the Rădăuți sector (Iordan, 1975; Pătruț, 1981). Both of them start with a thin sequence of Llandovery siliciclastic sediments, followed by a thick sequence represented by predominantly calcareous Wenlock – Lower Ludlow deposits. In the Bătrânești – Todireni – Iași sector the limestones from the lower part of the upper sequence are covered by calcareous claystones with ostracods. However, in the Rădăuți sector, these layers are interposed by a thick sequence of Ludlovian graptolitic claystones. Pătruț (1981) considers that the graptolitic claystones are older than the Lower Ludlow upper limestones with brachiopods from the Bătrânești – Todireni – Iași sector, nonetheless they could also represent a lateral facies variation of these limestones or, at least, of their terminal part.

The Volyn basin has a structure similar to a fragmented plate due to the presence of several faults. The territory corresponding to modern-day Belarus is defined by the deep Podlasie-Brest Depression. The Peribaltic basin developed in shallow water conditions and the sedimentary sequence is defined by the presence of several hiatuses, which is especially visible in the out-

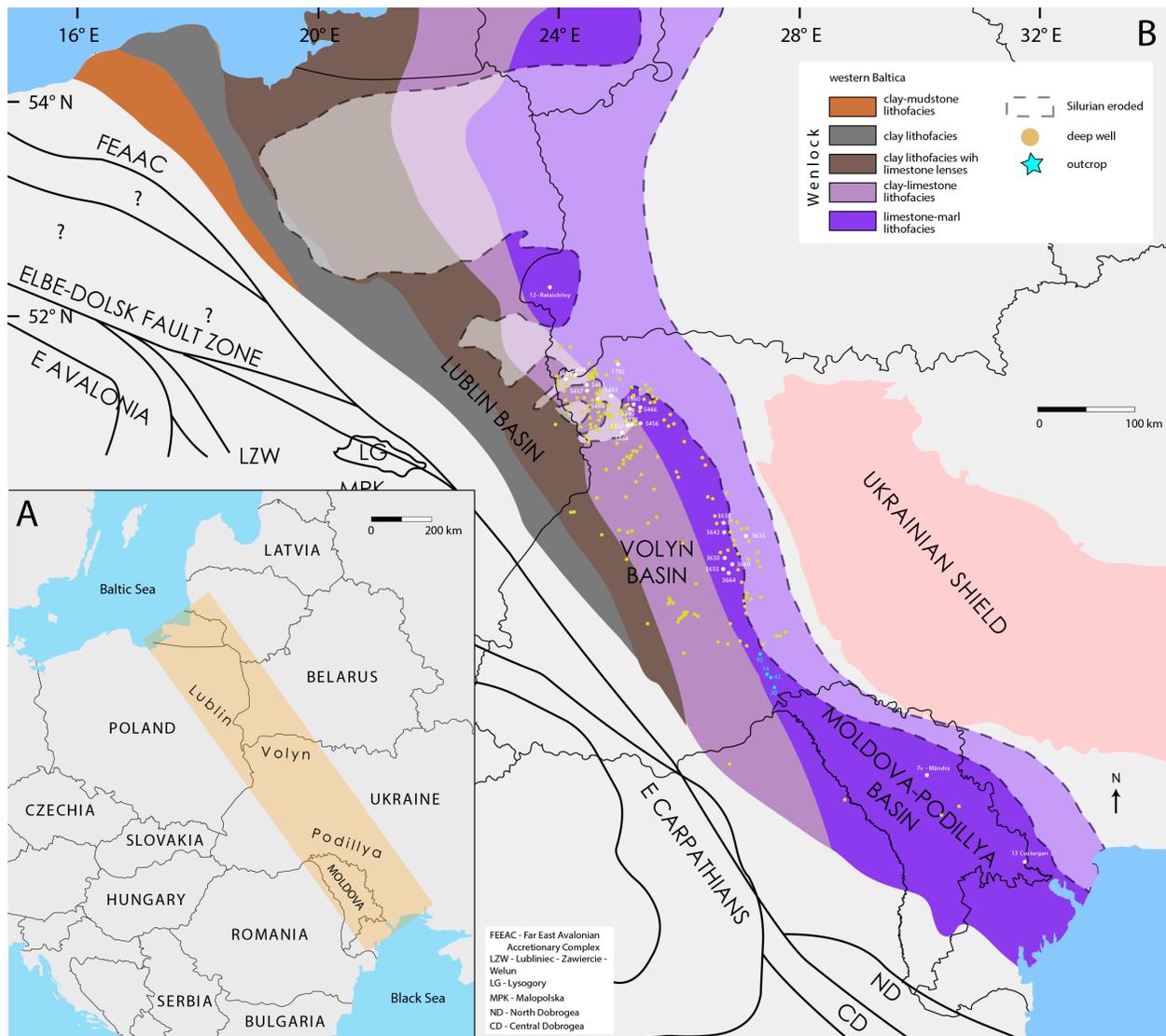


FIGURE 1. A. Map illustrating the position of the Republic of Moldova, western Ukraine and western Belarus. Inset highlights the study area. B. Wenlock lithofacies belts in the southwestern and western parts of Baltica (data for the western part from Modlinski et al., 2010; data for the southwestern part from Bukatchuk et al., 1988).

north of Russia (Timan-Pechora basin) is located in a depression (Figure 2). In this region, outcrops are rare and can be found in the incised valleys of some major rivers (e.g., Kozhym River). The most recent stratigraphical scheme of the Silurian deposits is very complicated and reflects the complex features of Baltica. Facies regions that are described in the scheme have different lithological compositions which depend on the depositional depth as well as the lithological characteristics. The slope of the Silurian Sea basin shows that there is a gradual facies change of the deposits, starting with a lagoon, to a nearshore environment, to a shallow-water facies with corals (Venjukov, 1899; Grytsenko, 1977a, b; Grytsenko, 2007) and

finally transitioning to a deep water one with graptolites.

Stromatoporoids appeared in the sequences of Baltica later than in North America, North China, or Australia where the earliest indubitable stromatoporoids have been already recorded from the Darrivilian strata. It has been explained by the location of the Baltica paleocontinent in the southern temperate climate zone until the Katian time when it finally migrated into the equatorial belt (Nestor, 1997). In the Llandovery, clathrodictyids were diverse and abundant, and *Clathrodictyon* and *Ecclimadictyon* became dominating genera. They could constitute more than 80% of stromatoporoid specimens. Labechiids (*Pachystylos-*

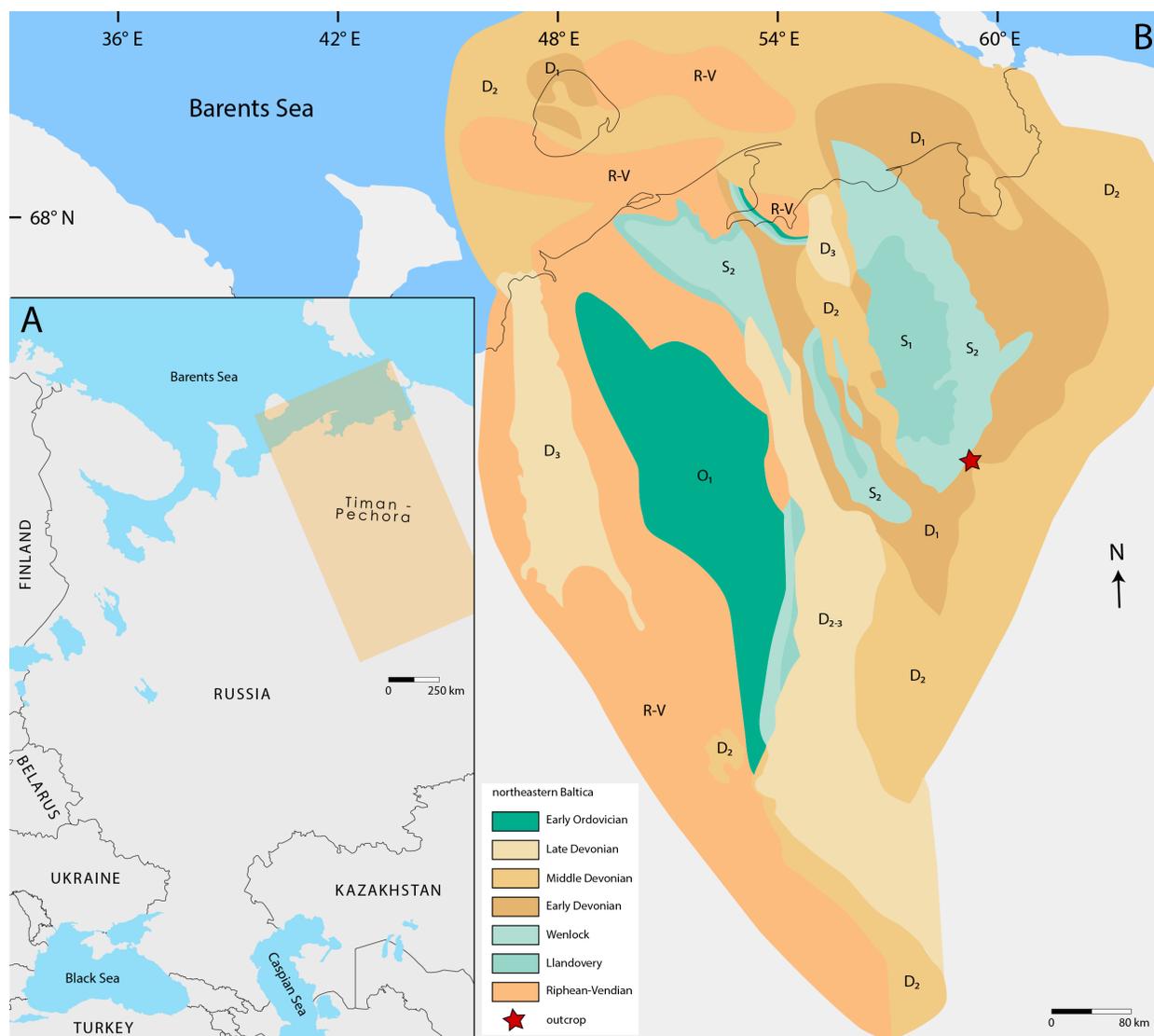


FIGURE 2. A. Map illustrating the position of the Timan-Pechora basin. Inset highlights the study area. B. Precarboniferous geological map of the Timan-Pechora basin, northeastern Baltica (modified from Nikonov, 2000).

troma, *Forlinia*, *Rosenella*, and *Labechia*) were also abundant but slightly less frequent than clathrodictyids. During the Wenlock, the abundance of stromatoporoids increased and their diversification continued (Nestor, 1997). During the Ludlow, the diversity of the stromatoporoid fauna reached its peak in Baltica. In different taxonomical branches new taxa appeared, e.g., *Lophiostroma* among labechiids, *Plexodictyon* among clathrodictyids, *Pseudolabechia* in Actinostromatida, *Syringostromella* among stromatoporoids, and *Parallelostroma* - the first representative of the Order Syringostromatida in the sequences of Baltica (Nestor, 1997). Baltic stromatoporoids were highly facies-dependent organisms with a relatively

narrow ecological niche (Nestor, 1997). The most abundant and diverse stromatoporoid association occurred in the high-energy shoal facies belt, represented in the fossil record by coral-stromatoporoid boundstones, skeletal and coquinite grain- and rudstones (Nestor, 1997). Stromatoporoids were also rather numerous in the moderate- to low-energy open-shelf facies belt where biomicritic deposits were accumulated (Nestor, 1997).

The earliest Silurian was a time of rapid diversification of *Mesofavosites* and *Paleofavosites* (Môtus, 1997). In the middle of Llandovery, *Multisolenia*, and *Parastriapora* appeared and favositids became the dominant group of tabulates in the

Silurian of Baltica (Mötus, 1997). The Wenlock was characterized by major changes in the tabulate fauna. *Syringolites*, *Thecia*, and *Mastopora* appeared whereas *Mesofavosites* and *Catenipora* disappeared in the early Wenlock. During the middle Wenlock, the diversity of tabulates increased again (Mötus, 1997). In the Ludlow, tabulates had a low generic diversity in Baltica and *Favosites* was the most important component of the tabulate fauna (Mötus, 1997). A few representatives of *Thecia*, *Romingerella*, *Laceripora*, and *Syringopora* have also been found from the Ludlow (Mötus, 1997).

MATERIAL AND METHODS

The collection (8000 thin sections, including about 100 with examples of symbiosis containing approximately 30% stromatoporoid and 70% coral specimens) was collected for more than 50 years by the scientists of the National Natural History Museum NAS of Ukraine. The fieldwork started with the investigation of a couple of boreholes drilled in Podillya in 1966. Later on, similar fieldwork took place every year in Ukraine (Podillya) (Appendix 1). In addition, a few field trips visited Moldova, Belarus, Estonia and Komi Republic. Most of the samples were collected from outcrops and boreholes drilled during geological prospecting in western Ukraine, Belarus, and Moldova (Figures 3 and 4). All studied thin sections were prepared in the laboratories in Ukraine, Moldova, and Belarus. The endobionts in thin sections were discovered using a light microscope MBS-9 LOMO. All endobionts were photographed using a digital camera (USB digital microscope, made in China and SONY DSC-H7).

DESCRIPTIONS OF FOSSILS AND SYMBIOTIC ASSOCIATIONS

Stromatoporoid Based Associations

Silurian stromatoporoids from Baltica host a rich fauna of endobionts. In the studied collection, 22 stromatoporoids contain *Helicosalpinx* bioclaustrations, 18 stromatoporoids revealed *Chaetosalpinx* bioclaustrations, 13 stromatoporoids contain syringoporiids intergrown with stromatoporoid, six stromatoporoids contain embedded *Palaeoconchus* microconchids, six stromatoporoids host the cornulitids *Cornulites* and *Conchicolites*, two stromatoporoids contain intergrown rugosans.

Helicosalpinx concoenatus (Figure 5A, D; Figure 6B) occurs in *Densastroma* sp., *Clathrodictyon mukshiensis*, *Clathrodictyon* sp., *Vikingia* sp., *Plex-*

odictyon sp., *Plectostroma podolicum*, and *Perplexostroma savaliensis*. Tubes of *H. concoenatus* lack their own wall; they are helical and oriented more or less perpendicular to the host stromatoporoid's growth lamellae (Figures 5A, D, Figure 6B).

Chaetosalpinx bioclaustrations (Figure 6B) occur in *Clathrodictyon* sp., *Clathrodictyon microstriatellum*, *Vikingia* sp., *Densastroma* sp., *Perplexostroma savaliensis*, and *Parallelostroma pulchra*. Tubes of *Chaetosalpinx* are straight to irregularly curved (Figure 6B). They lack their own wall and are oriented more or less perpendicular to the growth lamellae of host stromatoporoid (Figure 6B).

Syringoporiid endobionts (Figure 6C, D) occur in *Parallelostroma communis*, *Parallelostromapora pulchra*, *Parallelostroma* sp., and *Clathrodictyon* sp. Syringoporiids are oriented perpendicular to the lamellae of host stromatoporoid (Figure 6C, D).

Microconchid *Palaeoconchus* sp. (Figure 5E, F) occurs in *Parallelostroma* sp., *Clathrodictyon mukshiense*, *Clathrodictyon planum*, and *Plectostroma podolicum*. Tubes of *Palaeoconchus* are planispiral and oriented more or less parallel to the growth lamellae of host stromatoporoid (Figure 5E, F).

Cornulites is intergrown with *Stromatopora* sp. and *Conchicolites* sp. occurs in *Clathrodictyon microstriatellum* and *Pseudolabechia* sp. Tubes of cornulitids are crossing growth lamellae of host stromatoporoid at various angles (Figure 6A, E).

Clathrodictyon planum, *Plexodictyon* sp. and *Stromatopora* sp. host single species of endobionts. *Clathrodictyon microstriatellum*, *Clathrodictyon mukshiensis*, *Densastroma* sp., *Parallelostroma* sp., *Parallelostroma communis*, *Parallelostromapora pulchra*, *Perplexostroma savaliensis*, *Plectostroma podolicum*, and *Vikingia* sp. host two species of endobionts. *Clathrodictyon* sp. hosts three species of endobionts.

Tabulate Based Associations

Studied tabulates host only cornulitids (Figure 5B). *Cornulites* sp. is intergrown with *Heliolites* sp. and *Mesosolenia* sp. Cornulitids are oriented at various angles regarding the growth lamellae of host tabulates. There are no obvious changes in the morphology of host corals near the cornulitid endobionts (Figure 5B). It should be noted that in the northeastern part of Baltica, the role of tabulate corals (primarily favositids) as hosts of endobionts increases significantly in the Lochkovian and possibly in the uppermost Přidolian. Numerous favositid

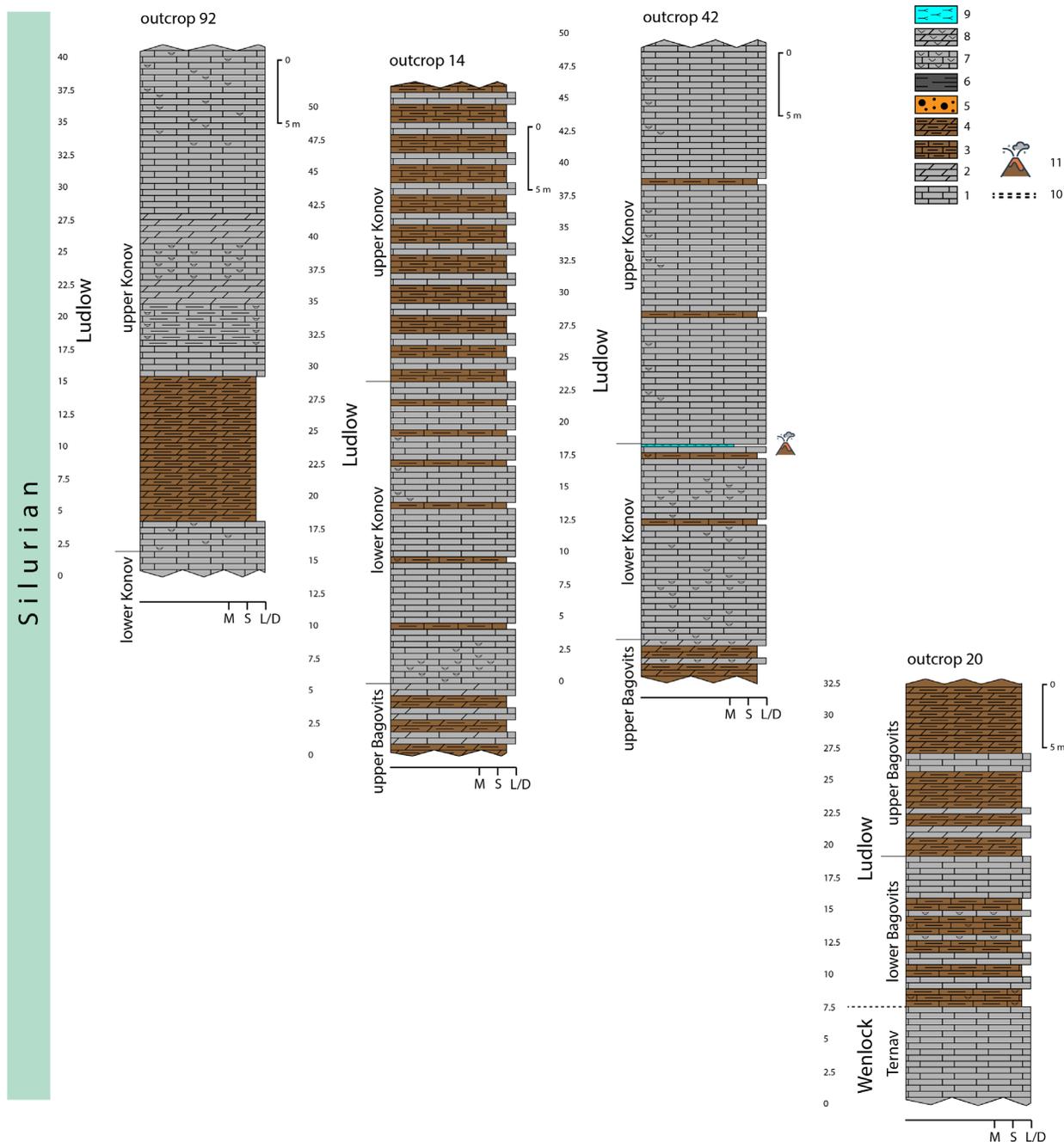


FIGURE 3. Lithostratigraphic columns of the analysed outcrops (92, 14, 42, 20) from the upper course of the Dniester River valley (Moldova-Podillya Basin). 1–limestones; 2–dolomites; 3–marls; 4–argillaceous dolomites; 5–sandstones; 6–mudstones; 7–limestones with anhydrite/gypsum intercalations; 8–dolomites with anhydrite/gypsum intercalations; 9–bentonites; 10–unconformity; 11–volcanic event.

specimens hosting endobionts (*Phragmosalpinx australiensis*) occur in the Lochkovian Ovinparma Formation in the western slope of North Urals and Tchernychev Uplift. At the same stratigraphic level, similar endobionts are also often found in Favositids from other Arctic regions: Vaigach Island, Novaya Zemlya, Taimyr (Zaika, 2007).

DISCUSSION

Endobionts

The studied stromatoporoid based associations are dominated by bioclastrations of worms without mineral skeleton, *Helicosalpinx concoenatus* being the most abundant. Among skeletonized

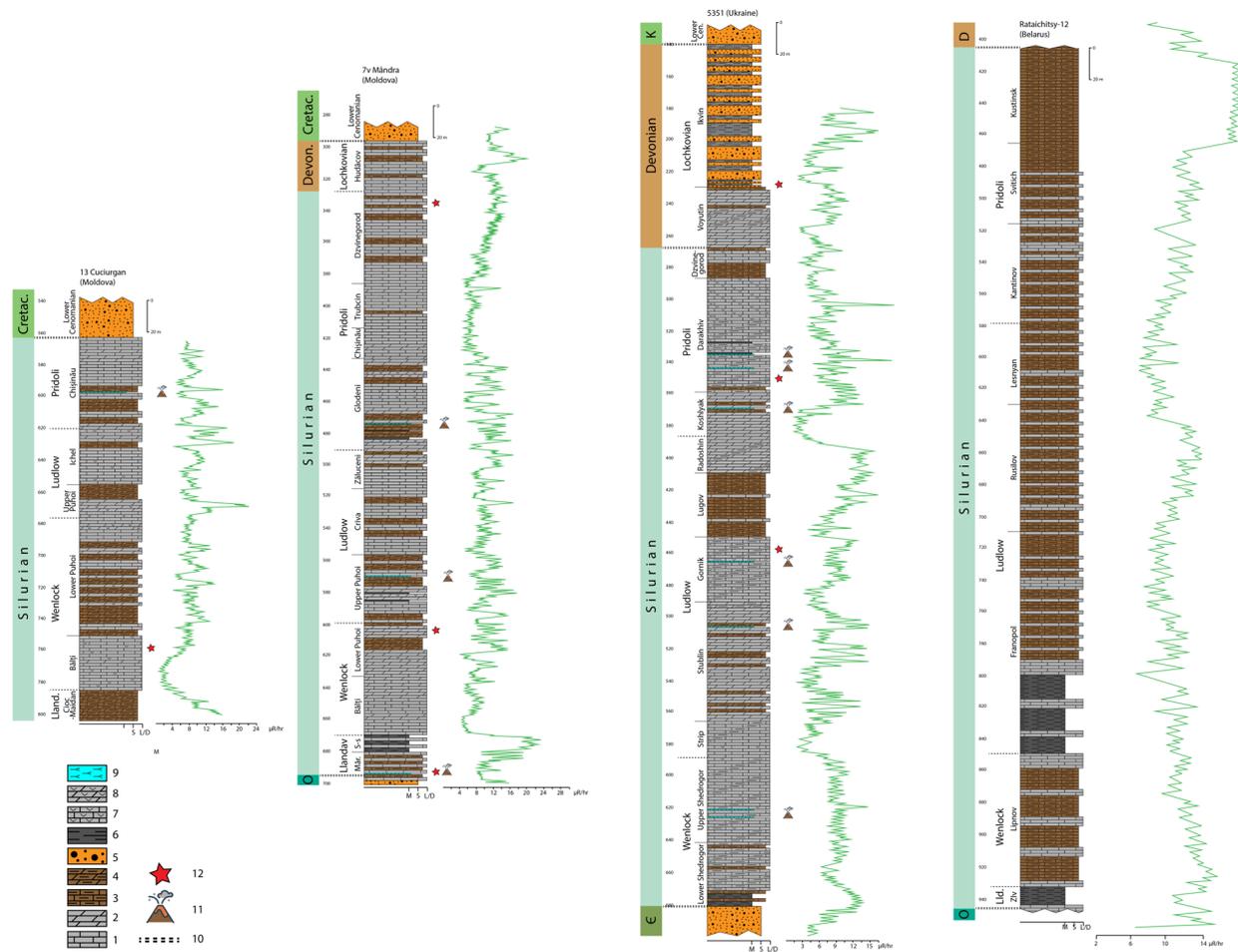


FIGURE 4. Lithostratigraphic columns accompanied by gamma-ray logs for the studied wells from the southwestern and western parts of Baltica (Moldova, Ukraine and Belarus). Legend is explained within Figure 3.

endobionts syringoporiids were most abundant making up more than half of all skeletonized endobionts in stromatoporiids. Syringoporiids are also one of the major groups of endobiont in stromatoporiids from the Ludlow of Estonia and Gotland (both Baltica) (Kershaw, 1987; Kershaw and Mõtus, 2016), and they indicate a similar situation in our sections. Tentaculitoid tubeworms (i.e., microconchids and cornulitids) are more common in the studied Silurian stromatoporiids than rugosans. A strikingly small number of endobiotic rugosans in the studied thin sections likely represents a sampling bias as such associations are very diverse and numerous in the Silurian of Estonia and Gotland (Baltica) (Kershaw, 1987; Vinn and Wilson, 2016). Among tentaculitoid tubeworms, cornulitids are known to form symbiotic associations with stromatoporiids in the Sheinwoodian of Estonia (Vinn and Wilson, 2010a) but embedded microconchids have not been previ-

ously reported from stromatoporiids. It remains unresolved whether microconchid-stromatoporiid associations represent intergrowth of two organisms or an overgrowth. Based on the similarity with endobiotic microconchids in the bryozoans from the Pfidoli of Saaremaa, Estonia it is possible to hypothesize that some microconchids may have had endobiotic life mode within stromatoporiids in the Silurian of Baltica. Alternatively, microconchids encrusted some dead spots on the living stromatoporiid and were thereafter overgrown and killed by the host. Abundant worm bioclastrations in stromatoporiids are known from the Ludlow of Saaremaa, Estonia but our data suggest that worm bioclastrations may have been even more common in the stromatoporiids from the Silurian of Baltica. Worm bioclastration without mineral skeleton forms a major part of endobiont fauna in the Silurian tabulates (Tapanila, 2005; Mõtus and Vinn, 2009), and it is likely that they also formed a major

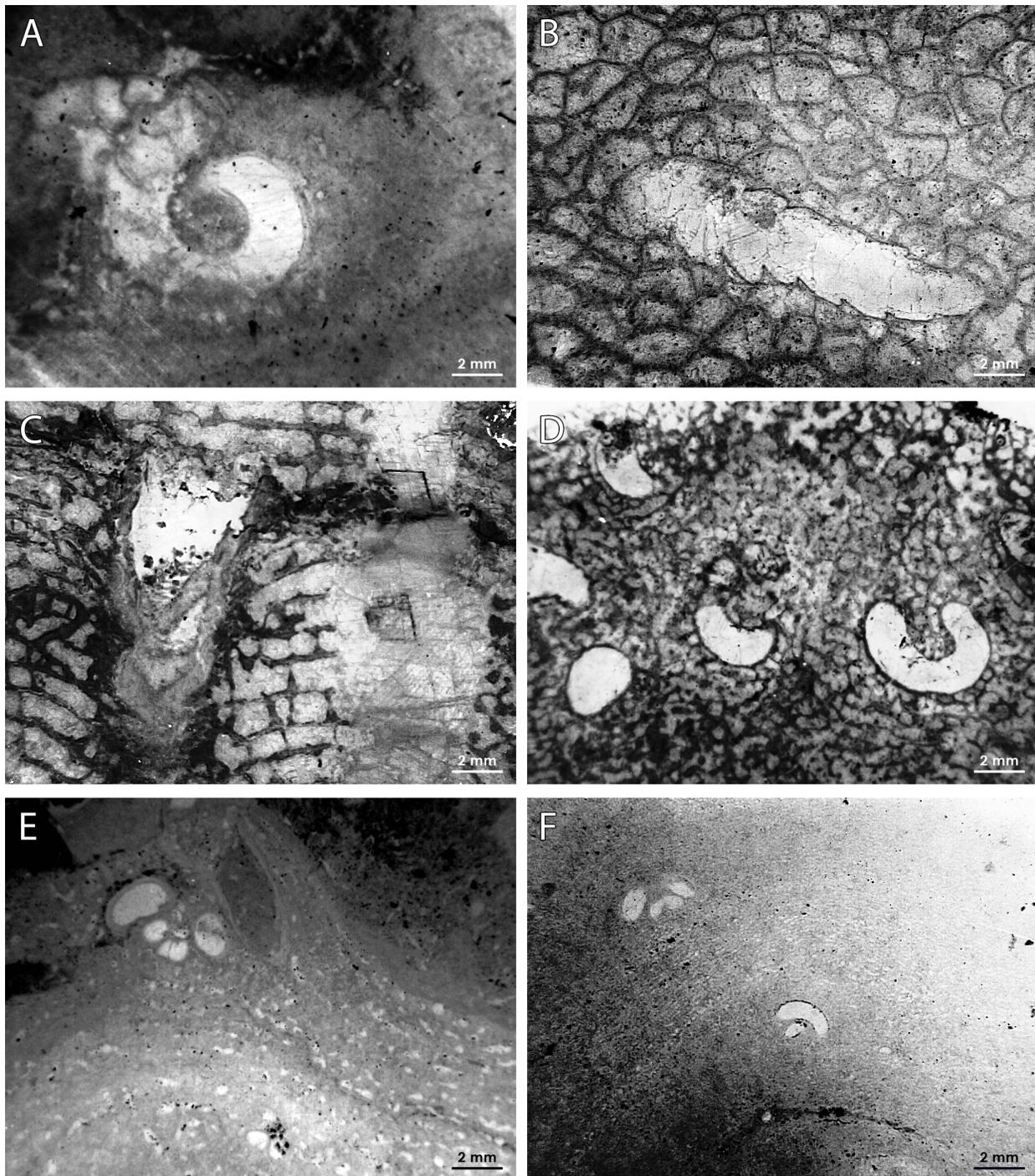


FIGURE 5. A. Coll. No. 2602/92-155, *Helicosalpinx concoenatus* inside a stromatoporoid, the sample was collected from the core of borehole 5483, depth 249 m. B. *Cornulites* sp. in *Mesosolenia* sp., coll. No. 2602/8762b, the sample was collected from the core of borehole 5414, depth 561,5 m. C. Rugosan within *Clathrodictyon planum*, coll. No. 2602/6957a, the sample was taken from outcrop No.117-156, Kozhym River (Komi Republic), Gerd'yu Formation (Přidolian). D. *Helicosalpinx concoenatus* Clarke, 1908 inside a stromatoporoid, coll. No. 2602/6943d, the sample was taken from outcrop No236-156, Kozhym River (Komi Republic), Gerd'yu Formation (Přidolian). E. Microconchid *Palaeoconchus* sp. inside *Parallelostroma* sp., coll. No. 2602/92-121d, the sample was taken from the core of borehole 5478, depth 214 m. F. Microconchid *Palaeoconchus* sp. inside a stromatoporoid, coll. No. 2602/805a, the sample was taken from the core of borehole Scherbin -11, depth 434 m (Podlasie-Brest Depression).

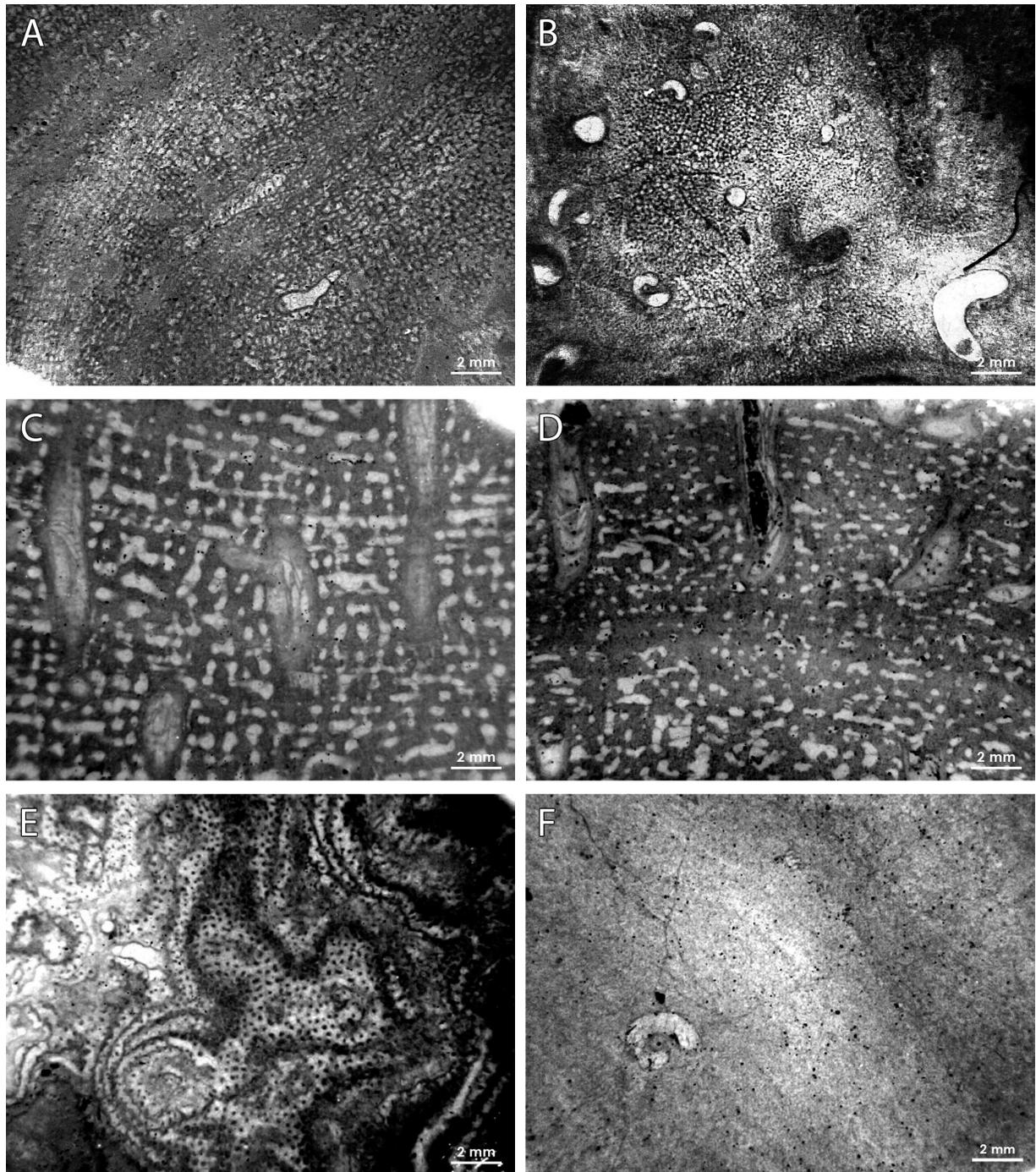


FIGURE 6. A. *Conchicolites* sp. inside *Pseudolabechia* sp., coll. No. 2602/6794, the sample was taken from the core of borehole 3660, depth 61,4 m. B. *Helicosalpinx concoenatus* and *Chaetosalpinx* sp. in *Clathrodictyon* sp., coll. No. 2602/6347b, the sample was taken from the core of borehole 3650, depth 234,8 m, Silurian, Ludlow, Ternava Formation, Sursha Unit, Podillya, Ukraine. C. Syringopora in *Parallelostroma communis* (longitudinal section), coll. No. 2602/1425, the sample was taken from outcrop No 42, Silurian, Ludlow, Konivka Formation, Goloskiv Unit (Cyclite 3R), Podillya, Ukraine. D. *Syringopora* sp. inside *Parallelostroma communis* Bog., coll. No. 2602/92-49e, the sample was taken from outcrop No153, Silurian, Ludlow, Konivka Formation, Goloskiv Unit, Cyclite 1R (Ustia Village, Smotrich River, Podillya, Ukraine). E. *Conchicolites* sp. inside *Clathrodictyon microstriatellum* (Riab.), coll. No. 2602/92-244d, the sample was taken from the core of borehole 7v-Mândra (Mândra, Republic of Moldova), depth 694 m. F. *Helicosalpinx concoenatus* Clarke, 1908 inside *Densastroma* sp., coll. No. 2602/92-230, the sample was taken from core of borehole 5463, depth 347 m (northern Podillya).

part of endobiont fauna of the Silurian stromatoporoids. One could ask why non-mineralized worms dominated both tabulate and stromatoporoid based symbiotic associations. The most likely answer is that non-mineralized invertebrates benefited more from endobiotic life mode than invertebrates with mineralized skeletons as the latter already had protection on their own against the predators. Another likely answer is that, among the Silurian faunas, some worms lacking a mineralized skeleton developed adaptive strategies that led to symbiotic intergrowth, possibly by means of the ability to settle on a living substrate that was not suitable for other potential epibionts. Examples of specialized, host-specific symbiotic taxa occur among recent faunas with well-documented cases such as the hydroid family Zancleidae, with species that are known to be symbionts of corals and bryozoans. Spirally coiled and non-spiral worm bioclaustrations are about equally common in the studied stromatoporoid collection indicating that both of these morphologies were equally successful within a stromatoporoid host. Endobiotic cornulitid occur in the early Silurian tabulates from Canada (Dixon, 2010). However, such an association has not been previously described from the Silurian of Baltica (Vinn and Wilson, 2016). Thus, it is possible that cornulitid-tabulate symbiosis may have had wider geographical or even global distribution in the Silurian. The majority of the studied stromatoporoid thin sections and all tabulate thin sections contain just single species of endobionts. Only *Helicosalpinx* and *Chaetosalpinx* occur together in the same thin section. This occurrence may indicate that stromatoporoids and tabulates were seldom infested by several species of endobionts but stromatoporoid infested by multiple endobiont species were common in the Ludlow of Saaremaa and Gotland. Moreover, thin sections do cover only a small section of the host, and thus it is more likely that most endobionts specimens simply avoided close vicinity of the specimens of another endobiont species. Such distance between endobionts could be due to feeding competition as most of the studied endobionts were suspension feeders with the exception of micropredatory rugosans. Endobionts selectively infested host stromatoporoids. Some endobionts such as *Helicosalpinx* and *Chaetosalpinx* mostly occur in the same taxa of stromatoporoids whereas syringoporiids infested a completely different set of stromatoporoid taxa. The similarity in host taxa of worm bioclaustration could indicate that *Helicosal-*

pinx and *Chaetosalpinx* were ecologically similar. On the other hand, syringoporiids and worms responsible for *Helicosalpinx* and *Chaetosalpinx* bioclaustrations likely had different ecologies. This is not surprising as worms were likely suspension feeders and syringoporiids as all corals were micropredators.

Hosts

The number of stromatoporoids with endobionts exceeds several times the number of endobionts in tabulates which at least partially can be explained by a collecting bias. However, Vinn and Wilson (2016) suggested that stromatoporoids were the most common hosts to various endobionts in the Silurian of Baltica and our data here support this view. Baltic tabulates usually contain worm bioclaustrations (i.e., *Chaetosalpinx*) in large numbers (Mõtus and Vinn, 2009; Klaamann, 1958), and the lack of such specimens in the studied collection likely represents a collecting bias. All studied Silurian stromatoporoids and tabulate species hosted only a small number of endobiont taxa. There was only little or no difference at all in the number of symbiont taxa per host stromatoporoid species. This demonstrates that all of the studied stromatoporoids were rather similar in their tolerance toward different endobionts. It also indicates that all host stromatoporoids created a specific enough environment for their symbionts that could possibly fit only with the requirements of a few endobiont taxa.

CONCLUSIONS

The data from the studied collection confirm that stromatoporoids were the most common hosts to various endobionts in the Silurian of Baltica. Bioclaustrations of non-mineralized worms likely formed a major part of the endobiont fauna of the Silurian stromatoporoids and in this respect, stromatoporoids were similar to the Silurian tabulates. Microconchids formed symbiotic associations with the stromatoporoids in the Silurian of Baltica. The cornulitid-tabulate symbiosis may have had wide geographic or even global distribution in the Silurian. Most endobiont specimens avoided close vicinity of the specimens of another endobiont species due to feeding competition. Endobionts infested selectively the host stromatoporoids and all of the studied Silurian stromatoporoids and tabulate species hosted only a small number of endobiont taxa.

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APPENDIX 1.

Lithological description of some boreholes and outcrops:

Outcrop Khoudykvitsy 170 - (Lower Devonian)

Northwestern outskirts of the Khoudykvitsy Village, left bank of the Dniester River (on the slope)

Lower Devonian, Gedinnian Stage, Borschiv Horizon, Khoudykvitsy Formation (D_1khd):

0 – 1,45 m – dark-grey platy grained limestone

1,45 – 4,30 m – alternation plates of dark-grey limestone and dark-grey argillite

4,30 – 7,10 m – dark-grey argillites with rare plates of dark-grey limestone (in the interval are rhabdosomes of *Monograptus uniformis*) – first Devonian graptolite zone, which indicates the boundary S/D (Gedinnian stage)

7,10 – 9,10 m – dark-grey argillites with interbeds of grey nodular limestone (correlation 1:1)

9,10 – 9,66 m – grey platy limestone (“brickwork”)

9,66 – 10,46 m – dark-grey argillite with interbeds of grey nodular limestone (correlation 2:1)

10,46 – 10,86 m – grey nodular limestone with thin interbeds of argillite

10,86 – 12,86 m – dark-grey argillite with thin interbeds of grey nodular limestone (correlation 4:1)

12,86 – 14,16 m – dark-grey argillites with rare thin interbeds of grey nodular limestone

14,16 – 15,16 m – dark-grey argillite with thin interbeds of grey nodular limestone (correlation 4:1)

15,16 – 16,06 m – dark-grey argillite

16,06 – 16,46 m – dark-grey argillite with interbeds of grey nodular limestone (correlation 1:1)

16,46 – 17,06 – dark-grey argillite

Lower Devonian, Gedinnian Stage, Borschiv Horizon, Mytkiv Formation (D_1mt):

17,06 – 22,76 m – dark-grey argillite with rare nodular interbeds (3 one) of limestone

22,76 – 27,76 m – dark-grey argillite with rare nodules of limestone

22,76 – 29,66 m – green-grey clays with interbeds of dark-grey argillite and nodules of limestone

29,66 - 30,26 m – grey, platy limestone

30,26 – 30,96 m – dark-grey argillite

30,96 – 32,96 m – brown-grey clay

32,96 – 37,96 m – dark-grey argillite with rare interbeds of limestone

37,96 – 39,96 m – light-grey argillite (weathered)

above lie *Cretaceous deposits*

Outcrop Dzvenigorod 97 = 63 from (Tsegelnjuk, Grytsenko et al. 1983p. 130, fig. 18)

Upper part of the Dzvenigorod Formation - dark-grey limestone (S_{3zv})

Outcrop Dzvenigorod 96 (= 47 from Green book, p. 130, fig. 18)

Upper part of the Troubchin Suite black limestone (S_{3tr})

Outcrop Dzvenigorod 3 (= 47 Quarry near Gzvenigorod Village)

Borehole – Lokachi - 14

Borschov horizon, Zhedin Series, Lower Devonian (D_{1br})

1284-1445 m – Skalian Series (S_{3sk})

1445-1545 m – Malynivtsy Series – mostly grey-green grain limestone (S_{2ml})

1545-1610 m – Bahovitsa Series – brown platy limestone and grey and green dolostone and dolomitic marls (S_{2bg})

1610 – 1645 (downhole wells) m – Yarouga Series – mostly grey grain (nodular) limestone (S_{1yr})

Borehole – Lisichyntsy - 3645

58 m and above – *Upper Cretaceous* – glauconitic sands

Přydolian Series S₃

Dzvenyhorod Formation (S_{3zv})

58 – 64 m – light brownish-grey limestone with interbeds of clays (61,6 m – *Thamnopora* sp., *Parallelostroma* sp.; 59 m, 59,2 m – *Parallelostroma* sp.)

Trubchin Formation (S_{3tr})

64 – 68,5 m – brown marls with grey detritic limestone chest (67,5 m – *Favosites pseudoforbes*)

68,5 – 73 m – grey large-nodular limestone with green and brown marls interbeds (69,5 m – *Squameofavosites* sp.; 69,7 m – *Mesofavosites* sp., *Thamnopora* sp., *Favosites* sp.; 70 m – *Favosites* sp.; 71,2 – 72,7 – *Aulopora serpens*, *Tuvaelites hemisphaericus*)

73 – 76 m – green-grey marls with small nodules of grey limestone (in the upper and lower part with corals (75,5 m – *Pseudoplasmopora*, *Cystiphyllum siluriensis*, *Holacanthia sociale*, *Sterexylodes* sp.)

76 – 84 m – brown limestone with very abundant shell detritus and coelenterates with green and black marls interbeds (in the upper and lower parts some corals: 80,9 m – *Spongophylloides nikiforovae*, *Paralellostroma* sp.; 81 m - *Favosites* sp.; 83,7 m *Syringopora* sp.)

84 – 86,5 m – grey chests of limestone easily separated from black-brownish marls

86,5 – 88 m – dark-grey detritic limestone (nodules of limestone more than marls)

Varnitsa Formation – 88-101 m (S₃vr)

88 – 89 m – green-grey solid dolostone

89 – 89,8 m – grey grain-detritic-clayey limestone with greenish-grey marls offside chest

89,8 – 101 m – grey grain-detritic-clayey limestone with dark-grey marls offside nodules (in the depth 94,5 m – *Multisolenia* sp., 97 m – *Holmophyllym holmi*, *Syringopora* sp.)

Koshliaky Formation – 101-148 m (S₃ksh)

101-104,3 m – light-grey limestone thin bedded alternated with thin interbeds of marls.

104,3 – 107,5 m – dark-grey and grey dolostone alternated with plates of “knotty” limestone

107,5 – 111 m – dark-grey and grey solid and horizontally bedded dolostone

111 – 112 m – dark-grey limestone alternated to dolostone (secondary dolostone)

112 – 114 m – grey and dark-grey horizontal and wavy bedded dolostone and domerite

114 – 116 m – grey and dark-grey limestone, in the base – finely grain with interbeds of marls, in upper 30 cm – solid platy

116 - 121,5 m – grey thin bedded dolostone and domerite, in upper 0,5 m – “sizzling” one

121,5 – 123 m – grey weakly brownish solid limestone: in the base – marl, in the middle part – finely grain wavy tiled, cavernous secondary dolostone – in the upper part

123 – 126,5 m – light-grey unclear “sizzling” dolostone

126,5 - 129,8 m – light-grey “sizzling” somewhere cavernous dolostone

129,8 – 140 m – green and grey striped solid dolostone

140 – 142 m – green-grey solid domerite (striped in the upper part)

142 – 142,5 m – light-grey thin bedded dolostone

142,5 - 144,3 m – dirty-grey dolostone

144,2 – 148,2 m – grey dolostone with tree interbeds of clayey-coaly interbeds

Radoshin Formation – 148-167 m (S₃rd)

148,2 - 160 m – brown-grey solid dolostone (cavernous one in the intervals: 149,7 – 150 m, 157,5 – 160 m;)

160 – 163 m – grey dolostone alternated with green domerite

163 – 163,6 m – brown grained dolostone with 2 cm interbed of brown clay in middle part of interval

163,6 – 167 m – green-grey domerite

S₂ Ludlow Series, Ludford Stage

Isakivtsy Formation – 167-197,5 m (S₂is)

167 – 171,5 m – brown cavernous dolostone

171,5 - 180,8 m – grey porous-cavernous secondary dolostone with green thin domerite interbeds in the upper part of the interval – breccias of domerite

180,8 - 197,5 m – grey wavy thin platy dolostone

Velytsa Formation – 197,5-222 m (S₂vl)

197,5 - 206 m – grey solid unclear grain dolostone (on the depth 201 m – ash-grey metabentonite)

206 - 207,5 m – dark-grey cavernous dolostones

207,5 - 216 m – thin interbedding of green and light-grey dolostones and domerites

216 - 222 m – dark-grey brownish and greenish marls (many various corals, on depth 210 m green thin interbed of *metabentonite*; 216-217 m - *Favosites* sp., *Stromatopora* sp. inderem., *Syringopora* sp., *Tuvaelites* sp., rugosan – *Acmophyllum* sp.; 218-220 m - *Favosites* sp., *Stromatopora* sp., *Weissermellia* sp., *Tryplasma* sp., *Tuvaelites* sp.).

Tsviklivtsy Formation – 222-267,5 m (S₂ts)

222 - 234,3 m – brown-grey solid unclear grain limestones (226 m, 231 m - *Favosites* sp.)

234,3 - 267,5 m - dark-grey finely-grain limestones in dark-grey greenish marls. (In the upper part of the unit - 234,3m; 244 m – many corals; 237 m, 237,6 m, 243 m, 244,2 m, 246 m – *Parastriatopora mutabilis* Kl.; *Stromatopora*; 244 m *Syringopora* sp.; 265 m – *Favosites* sp.).

Konivka Formation – 267,5-288,2 m (S₂kn)

267,5 - 281,5 m – thin bedded and thin striped dark-grey domerite alternated with light-grey one

281,5 - 288,2 m – dark- brown limestone with thin interbeds dark-grey marls (283 m – *Favosites* sp., *Syringopora* sp., rugosan and bryozoan; 285 m - *Favosites* sp., 286 m – *Phaulactis cyathophylloides*.; 288 m – *Codonophyllum* sp.)

Horstian Stage, Bahovitsa Suite, Upper subformation – 288,2-328 m (S₂bg)

288,2 - 296,5 m – dark-grey dolostone alternated with green-grey domerite

296,5 - 297,5 m – brown cavernous (secondary) dolostone

297,5 - 328 m – dark-grey dolostone alternated with green-grey domerite

Bahovitsa Formation, Lower subformation – 328-331 m

328 - 331 m – dark-brown grained limestone (329 m - *Heliolites* sp.)

S₁ Wenlock Series

Homerian Stage, Ternava Formation – 331-385 m (S₁tn)

331 - 385 m – dark-grey limestone separated by dark-grey interbeds of clay

Sheinwoodian Stage – Fourmanivka Formation – 385-397,4 m (S₁fr)

Demshin subformation – 385-392,7 m (S₁dm)

385 - 392,7 m – dark-grey detritic marl interbedding with thin beds and concretions of grey solid limestones

Restevo subformation – 392,7-397 m (S₁rs)

392,7 – 397,4 m – green-grey detritic marl

Souboch Formation (O₃)

397,4 – 398,5 m – brown-grey limestone – *Thecia* sp.

Horaivka Formation (O₂)

398,5 – 400 m – green-grey sandstone