

Dead or alive? Brachiopods and other shells as substrates for endo- and sclerobiont activity in the Early Devonian (Lochkovian) of the Barrandian (Czechia)

MICHAL MERGL



Twelve encrusters and three endobiont trace fossils were distinguished on silicified brachiopod, coral and gastropod shells coming from the Kotýs Limestone (Lochkovian) of the Prague Basin, Bohemia. Encrusters preferred larger and costellate brachiopod shells with prominent convexity of valves. Locations and developments of coral encrustations produced by tabulate *Aulopora* sp., rugose *Syringaxon* sp., and an unnamed rugose coral indicate different strategies in selection of substrate. The auloporid preferred living host, articulated shells or intact valves, the rugose corals were less selective and colonised also dead and broken shells. Unlike encruster associations of middle and upper Devonian age in other areas (France, Poland, USA), in Bohemia, the encruster hosts were chiefly orthids (*Parmorthina* Havlíček, 1975; *Isorthis* Kozłowski, 1929; *Dalejina* Havlíček, 1953; *Resserella* Bancroft, 1928) and atrypids (*Spinatrypa* Stainbrook, 1951). Apart from corals, a microproblematicum *Allonema* Ulrich & Bassler, 1904, two pterobranchs, bryozoans, a hederellid, a craniid, a protorthid brachiopod, and a microconchid were observed on host shells together with small dendritic borings, cylindrical borings of *Trypanites* Mägdefrau, 1932, and a dendritic structure of unclear origin. • Key words: bioerosion, encrusters, Brachiopoda, *Aulopora*, *Allonema*, Lochkovian.

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Michal Mergl, Centre of Biology, Geosciences and Environmental Sciences, Faculty of Education, University of West Bohemia, Klatovská 51, 30619, Plzeň, Czech Republic; mmergl@cbg.zcu.cz

Encrusting epibionts and traces of boring endobionts provide valuable tools for palaeoecological reconstructions, especially in the Palaeozoic ecosystems, which differ from younger ecosystems dominated by groups of the Modern Evolutionary Fauna. Apart from synoptic works (Ager 1963, Boucot 1981, Brett *et al.* 2012), numerous detail studies on brachiopod and epibiont/endobiont interactions appeared (Ager 1961; Richards 1972; Thayer 1974; Hurst 1974; Pitrat & Rogers 1978; Sparks *et al.* 1980; Kesling *et al.* 1980; Watkins 1981; Hoare & Walden 1983; Spjeldnaes 1984; Alexander & Scharpf 1990; Bordeuax & Brett 1990; Brice & Mistiaen 1992; Vinn 2004, 2005; Zapalski 2005; Zhan & Vinn 2007; Daley 2008; Bose *et al.* 2011, Mistiaen *et al.* 2012; Barclay *et al.* 2013; Furlong & McRoberts 2014; Smrecak & Brett 2014). Crucial task of these analyses is recognition whether living host was infested and this was followed by interaction between host and occupant or a dead shell was used as a suitable substrate.

Research focused to various aspects of bioerosion, sclerobiont, epibiont and endobiont life strategies became attractive in last decades (Wisshak & Tapanila 2008). Newly developed visual techniques became exploited.

Scanning electron microscopy (SEM), microscopic-computed tomography (micro-CT) (Schönberg & Shields 2008, Wisshak *et al.* 2017), resin castings (Vinn 2005, Furlong & McRoberts 2014), stacked images for mapping of sclerobionts (Barclay *et al.* 2015) and other methods (Tapanila 2008, Bose *et al.* 2011) became standard in study of recent borers and encrusters and their ancient ancestors. However, employed methods and achievements always depend on quality of the source, which count for preservation of sampled material.

Many publications on the Palaeozoic sclerobionts and endobionts are based on material sampled from claystone, marlstone or other removable materials, or on fossils preserved as internal and external moulds (*e.g.* Hurst 1974, Sparks *et al.* 1980, Głuchowski 2005, Zapalski 2005, Berkowski & Klug 2012, Furlong & McRoberts 2014, Jarochovska *et al.* 2016). Mechanical splitting of solid limestone reliably removes most of sclerobionts. Endobiont borings stay filled by rock and recrystallization of shell substance hides their traces. That is common case of the Silurian and Devonian fossils coming from the Barrandian in the Czech Republic. Here the limestones are exceptionally rich in fossils of marine biota, but

data on endobionts and sclerobionts are curiously rare. Together with encrusting hederellids (Prantl 1938) and microconchids (Horný 1965, Šnajdr 1983), the symbiotic interaction between encrusting bryozoans, favositids, crinoids and hyoliths (Marek & Galle 1976, Galle & Prokop 2000, Galle & Parsley 2005) were reported from the Silurian and Devonian. Turek (1987) described large epibionts on gastropod and cephalopod shells from the Silurian. Dendritic borings in brachiopod shells were observed not long ago in the Silurian (Mergl 2020).

The extensive laboratory dissolving of limestone blocks by acids not only enlarged our knowledge of so far poorly known brachiopods of Lochkovian age (Havlíček 1999; Mergl 2003, 2010) but also recover diverse sclerobionts and traces of endobionts. Therefore, the silicification of these fossils provides a promising window for observation of these groups. The silicification affected brachiopod, corals and mollusc shells and their encrusting sclerobionts, whereas endobiont traces may be observed in translucent silicified shells. Despite certain limits this laboratory technique demonstrates promising approach in study of biotic interactions in the past not only in the Barrandian of Czechia.

Geological setting

The locality investigated in this study is located in the Barrandian, in the northern limb of the Devonian infill of the Prague Basin in the Central Bohemia of Czechia (the Czech Republic) approximately 7 km NE from the Beroun town (Fig. 1A, B).

The Devonian marine sedimentary succession of the Prague Basin consists of carbonate-dominated deposits of the Lochkovian age, and continues to the Givetian. The Lochkovian to Eifelian shallow-water succession is characterised by biodetrital mostly crinoidal limestones. It also comprises reef bioskeletal accumulations of Pragian and, in limited extent, Emsian and Eifelian age, preserved now in the north-western part of the basin. South-eastwardly the more pelagic lithofacies appear. They are represented mostly by dark coloured calcisiltites. The overlying Givetian succession is siliciclastic and marked beginning of the Variscan orogeny (Chlupáč *et al.* 1998, Vacek & Žák 2019).

Shallow-water biodetrital and peri-reefal accumulations of the Lochkovian are located along north-western limb of the Prague Basin. The Kotýs Limestone is grey bioclastic crinoidal well-bedded limestone with common cherts in the middle part of the sequence. Limestone is rich in brachiopods and crinoidal detritus, with fauna referred to the *Coniproetus-Decoroscutellum* trilobite Assemblage (Chlupáč 1983). This SW-NE strip of shallow-water Kotýs Limestone subsides towards the south-east, where the

Radotín Limestone represents the Lochkovian stage. The Radotín Limestone is distinct by rhythmical alternation of dark-grey to black bituminous platy limestones intercalated with black calcareous shales. The fauna contains many planctonic and nectonic organisms including graptolites and dacyroconarid tentaculites. An overview of the Lochkov Formation and the Devonian of the Prague Basin is best given by Chlupáč *et al.* (1998).

Detailed data about locality with studies of silicified fauna were published by Mergl (2003). The locality is situated between Bubovice and Loděnice, in a short survey trench in north side of small abandoned quarry in the Kotýs Limestone (Fig. 1C). Grey platy limestone beds in trench are steeply dipping toward the south (Fig. 1D). Limestone beds contain chert nodules and accumulations of bioskeletal material, mainly the brachiopod shells. The lowest exposed beds yielded highly diversified brachiopod association for which genera *Parmorthina* Havlíček, 1975, *Isorthis* Kozłowski, 1929, *Dalejina* Havlíček, 1953, *Resserella* Bancroft, 1928, *Quadrithyrus* Havlíček, 1957, *Iridistrophia* Havlíček, 1965, strophomenid brachiopods and *Gypidula* Hall, 1867 are distinctive (Fig. 1E). The higher part of exposed sequence abounds in atrypids *Spinatrypa* Stainbrook, 1951 and *Spinatrypina* Rzhonsnitskaya, 1964, associated mostly with *Dalejina* and *Skenidioides* Schuchert & Cooper, 1931. The highest limestone beds exposed in a trench are poor in brachiopods, mainly with smooth-shelled *Lissatrypa* Twenhofel, 1914. Conodonts indicate base of the middle Lochkovian of *omoalpha-carsi* conodont Zone (Slavík 2011, Slavík *et al.* 2012).

Material and methods

All sclerobionts and endobiont traces were observed on or were associated with silicified shells of rhynchonelliform brachiopods, gastropods and corals, which were released from crinoidal limestone by hydrochloric or acetic acids solutions. Quantity and quality of shell preservation vary in great extent and differ from bed to bed. The stratigraphically lowest limestones (Fig. 1E) are rich in silicified brachiopods and corals and quality of preservation is excellent. The middle part of the section (Fig. 1D) yielded taxonomically less diverse but still favourable preserved shells. The higher part of the studied section provided shells having exclusively coarse-grained and often incomplete silicification. In general, a form of silicification follows the massive type (Mergl 2010).

The silicification was clearly selective depending on mineral composition of the shell. Rhynchonelliform brachiopods and other calcitic shells, *e.g.* platycerid gastropods and corals, were completely preserved. Attached sclerobionts exhibit the same favourable mode of preservation. Low-magnesium calcite of echinoderms

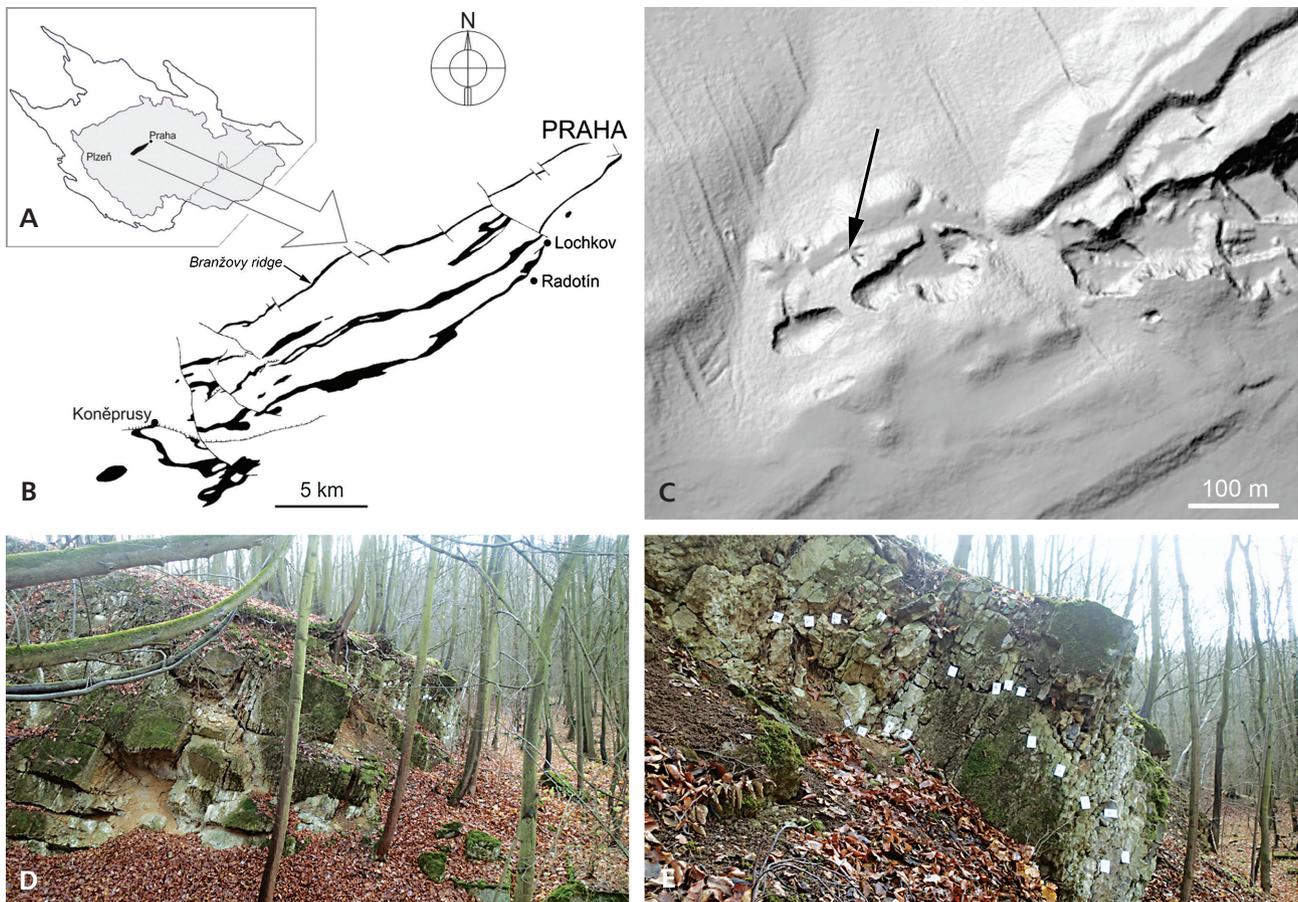


Figure 1. Geographical setting of the Prague Basin (A) and the Lochkov Formation in the Prague Basin with the locality investigated (B), location of quarries and the sampled section in old trench (indicated by arrow) at the Branžovy ridge (C, after <https://ags.cuzk.cz/geoprohlizec/?p=22517>, modified), middle and lower part of the section (D) (year 2015), and the richly fossiliferous outcrop of the lowest exposed limestone beds (E).

shows coarse-grained or imperfect silicification. Bryozoans are rarely replaced by silica. Trilobites and ostracods are not silicified apart from specimens affixed to other silicified objects. Phosphatic and silica internal moulds prove original presence other invertebrate groups (bivalves, bellerophonid gastropods) whose shells were less susceptible to silicic replacement.

These different modes of silicification affected preservation of some sclerobionts and their host. Likely, some host substrates were not silicified. Numerous auloporid colonies and solitary corallites are loose in residues after etching, while other corallites remain firmly attached to silicified host shell. Despite this taphonomic selectivity, the author is convinced that the observed sclerobionts and endobiont traces plausibly illustrate the original distribution pattern of sclero- and endobionts. Quantity of shells in samples, with more than ten thousand brachiopod shells and hundreds of sclerobionts examined, provides representative insight to original life association of the sea floor biota in the Early Devonian.

Illustrations. – Representative specimens were photographed with an OLYMPUS E-410 camera equipped by

Macro 35 mm Zuico Digital objective, and with digital microscope Dino-Lite Edge. All sclerobionts and endobiont traces referred to *Trypanites* were whitened by ammonium chloride before photography; other specimens were photographed without whitening.

Repository. – All specimens are housed in the palaeontological collections of the Centre of Biology, Earth and Environmental Sciences in the Faculty of Education of the University of West Bohemia, Plzeň (PCZCU), the Czech Republic, with the prefix PCZCU.

Terminology

Many terms have been used to categorize organisms inhabiting marine hard substrates (for review see Davis *et al.* 1999; Taylor & Wilson 2002, 2003; Tapanila & Ekdale 2007; Glaub *et al.* 2007; Rakociński 2011). Herein, a term endobiont is used for any organism boring into hard substrate. A term encruster is used for organism growing on other host organism. The terms sclerobiont (with preservable hard part) and epibiont (with unsclerotized

Table 1. Brachiopod species of the locality Branžovy and their main characteristics: Sh/size – maximum of observed shell size in mm; Sh/pro – shell profile (biconx = biconvex; cconvx = concavo-convex; plconx = planoconvex; splanar = subplanar); Orn/rad – type of radial ornamentation; Orn/con – type of concentric ornamentation; Sh/sub – type of shell substance; Occurrence – approximate abundance of species at locality; N/Aul – observed number of *Aulopora* sp. encrustations; N/Syr – observed number of *Syringaxon* sp. encrustations; N/Rug – observed number of calceoloid rugose coral encrustations; grey colour – shell size smaller than 5 mm. Note that shell smaller than 5 mm are without encrustations. Note that abundant shell larger than 10 mm exhibit majority of encrustations.

| Species | Sh/size | Sh/pro | Orn/rad | Orn/con | Sh/sub | Occurrence | N/Aul | N/Syr | N/Rug |
|---|---------|---------|------------|-----------|----------------|---------------|-------|-------|-------|
| <i>Rugoleptaena skalicensis</i> (Havliček, 1967) | >10 | splanar | costellate | fine | pseudopunctate | abundant | 4 | | 6 |
| <i>Mesodouwillina herinkiana</i> Havliček, 1999 | >10 | splanar | costellate | fine | pseudopunctate | rare | 4 | | 8 |
| <i>Procymostrophia costatula</i> (Barrande, 1848) | >10 | splanar | costellate | fine | pseudopunctate | rare | | | |
| <i>Mesoleptostrophia index</i> (Havliček, 1967) | >10 | splanar | costellate | fine | pseudopunctate | rare | | | |
| <i>Barbaestrophia praestans</i> (Barrande, 1879) | >10 | splanar | costellate | fine | pseudopunctate | very rare | | | |
| <i>Plectodonta mimica</i> (Barrande, 1879) | <5 | cconvx | costellate | fine | pseudopunctate | abundant | | | |
| <i>Asymmetrochonetes lanx</i> (Havliček et Racheboeuf 1979) | <5 | cconvx | costellate | fine | pseudopunctate | rare | | | |
| <i>Iridistriophia umbella</i> (Barrande, 1848) | >10 | splanar | costellate | fine | pseudopunctate | rare | 1 | | |
| <i>Skenidioides famulus</i> Havliček, 1977 | <5 | plconx | costate | fine | impunctate | abundant | | | |
| <i>Isorthis svatojanica</i> Havliček, 1977 | >10 | biconx | costate | fine | punctate | abundant | 40 | | 42 |
| <i>Resserella walmsleyi</i> Havliček, 1977 | 5–10 | plconx | costate | fine | punctate | abundant | 1 | | 14 |
| <i>Molongella lineata</i> Havliček, 1975 | 5–10 | plconx | costate | fine | punctate | rare | | | |
| <i>Parmorthina protopragensis</i> Havliček, 1977 | >10 | plconx | costate | moderate | punctate | abundant | 101 | 2 | 18 |
| <i>Dicoelosia praedimera</i> Mergl, 2003 | <5 | plconx | costate | fine | punctate | abundant | | | |
| <i>Dalejina austera</i> Havliček, 1977 | 5–10 | biconx | costate | fine | punctate | very abundant | 6 | 3 | 17 |
| <i>Muriferella pishulinae</i> Mergl, 2003 | <5 | plconx | costate | fine | punctate | rare | | | |
| <i>Anastrophia</i> sp. | 5–10 | biconx | costate | fine | impunctate | very rare | | | |
| <i>Gypidula pelagica</i> (Barrande, 1847) | >20 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Clorinda pseudolingulifera</i> Kozłowski, 1929 | 5–10 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Eoglossinotoechia mystica</i> Havliček, 1961 | 5–10 | biconx | costate | fine | impunctate | very rare | | | |
| <i>Hebetoechia</i> sp. | no data | biconx | costate | fine | impunctate | very rare | | | |
| <i>Plethorhyncha</i> sp. | no data | biconx | costate | fine | impunctate | very rare | | | |
| <i>Kyrtatrypa annulata</i> (Havliček, 1987) | >10 | biconx | costate | moderate | impunctate | very rare | | | |
| <i>Spinatrypa senilis</i> (Havliček, 1987) | >10 | biconx | costate | lamellose | impunctate | very abundant | 31 | 5 | 30 |
| <i>Spinatrypina variabilis</i> Mergl, 2003 | 5–10 | biconx | costate | moderate | impunctate | abundant | 4 | 3 | 2 |
| <i>Atrypina eremita</i> Havliček, 1999 | <5 | plconx | costate | fine | impunctate | abundant | | 1 | |
| <i>Lissatrypa neglecta</i> Havliček, 1984 | 5–10 | biconx | smooth | spinose | impunctate | abundant | 5 | 1 | 3 |
| <i>Glassina gutta</i> Mergl, 2003 | <5 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Merista pruniformis</i> Havliček, 1999 | 5–10 | biconx | smooth | fine | impunctate | rare | | | 1 |
| <i>Merista</i> cf. <i>herculea</i> (Barrande, 1847) | >10 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Nucleospira robusta</i> Kozłowski, 1929 | 5–10 | biconx | smooth | spinose | impunctate | abundant | 2 | | |
| <i>Retzia pyriformis</i> Mergl, 2003 | <5 | biconx | costate | fine | impunctate | very rare | | | |
| <i>Navispira trepida</i> Havliček, 1999 | <5 | plconx | costate | fine | impunctate | very abundant | | | |
| <i>Havlicekia amarantha</i> Havliček, 1980 | >20 | biconx | smooth | fine | impunctate | very rare | 1 | 1 | 2 |
| <i>Myriospirifer</i> sp. | 5–10 | biconx | smooth | fine | impunctate | very rare | | | |
| <i>Ambocoelia bubovica</i> Mergl, 2003 | <5 | plconx | smooth | spinose | impunctate | abundant | | | |
| <i>Tenellodermis microdermis</i> Havliček, 1971 | >10 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Spurispirifer fuscus</i> Havliček, 1971 | >10 | biconx | plicate | fine | impunctate | abundant | | | 2 |
| <i>Howellella angustiplicata</i> (Kozłowski, 1929) | >10 | biconx | plicate | fine | impunctate | rare | | | 1 |
| <i>Quadrithyrus subrobusta</i> Mergl, 2003 | >10 | biconx | smooth | fine | impunctate | rare | | | |
| <i>Cyrtina</i> sp. | 5–10 | plconx | plicate | fine | punctate | very rare | | | |

parts) are used for encrusters that differs by mineralized or unmineralized shell, respectively. Some encrusters surely preferred shells of dead gastropods, brachiopods and corals, but others likely grew on shells of living brachiopods or other invertebrates. Discrimination of these groups may be problematic without direct evidence of encruster-host interaction. Therefore terms epicole and epizoan used by Davis *et al.* (1999) for an organism that attached to hard shell of dead organism and for an organism attached to surface of living host, respectively, are not used.

Complete taxonomic names of examined brachiopod species including authors and years of description are listed in Table 1. To make the text more concise, only generic names are used in text, because all except one species are definitely matched with particular genus.

Brachiopod association

Forty-one rhynchonelliform brachiopods were determined in the material. In estimation, twenty to thirty thousand specimens were examined in all samples that originated from more than 300 kg of limestone. The common size of adult brachiopods range between 5 to 15 mm. *Parmorthina*, *Isorthis*, *Dalejina*, and *Spinatrypa* are the key species among the medium-sized species (Fig. 2). The large shelled taxa are rare (*Havlicekia* Boucot, 1963; *Kyriatrypa* Struve, 1966). Some medium- to small-sized species are extraordinary rare (*Anastrophia* Hall, 1867; *Clorinda* Barrande, 1879; *Cyrina* Davidson, 1859; *Retzia* King, 1850) with only one to five specimens observed, but others are moderately common (*Howellella* Kozłowski,

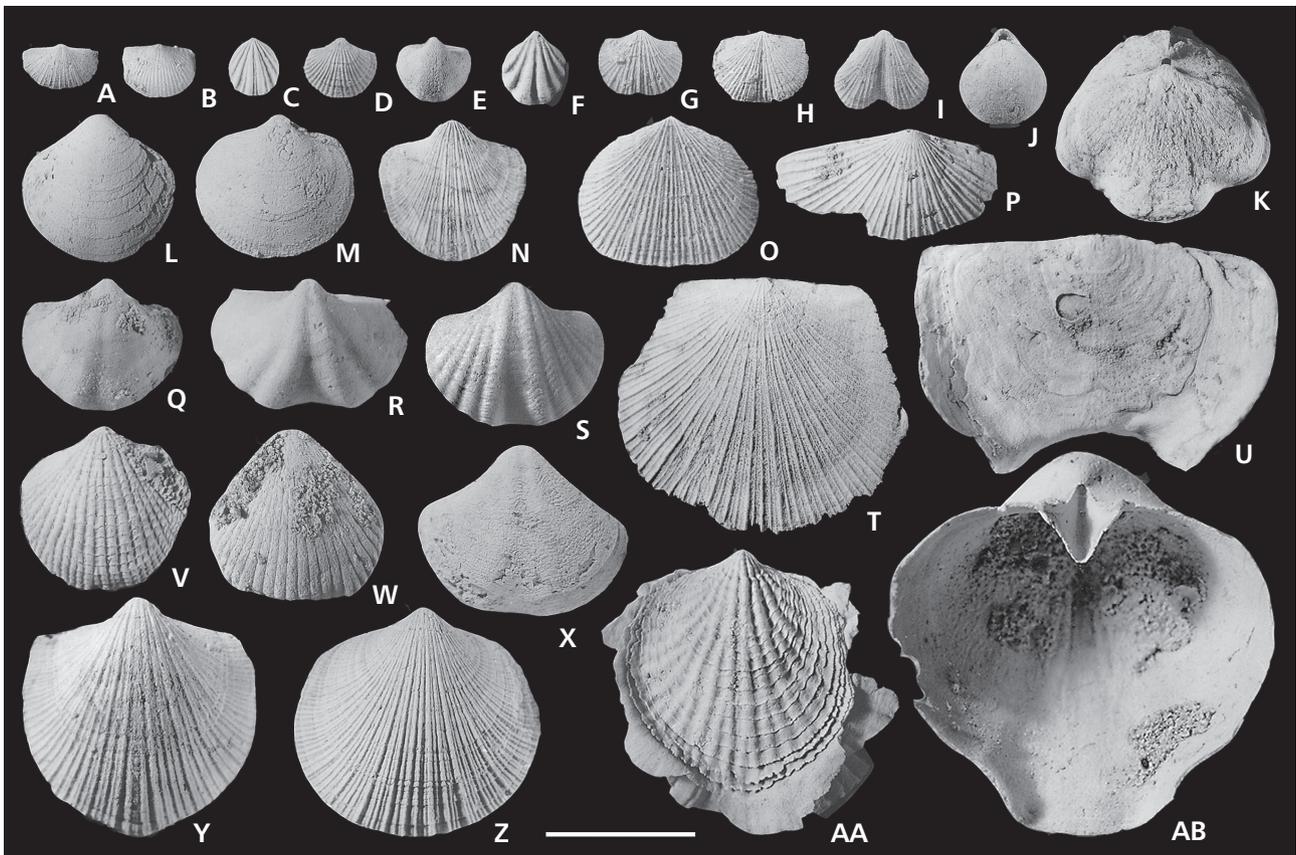


Figure 2. Illustrations of the commoner brachiopods of the Branžovy locality. Scale bar = 2 cm. • A – *Plectodonta mimica* (Barrande, 1879), PCZCU 997. • B – *Asymmetrochonetes lanx* (Havliček & Racheboeuf 1979), PCZCU 1006. • C – *Navispira trepida* Havliček, 1999, PCZCU 1052. • D – *Skenidioides famulus* Havliček, 1977, PCZCU 909. • E – *Ambocoelia bubovica* Mergl, 2003, PCZCU 942. • F – *Atrypina eremita* Havliček, 1999, PCZCU 1032. • G – *Muriferella pishulinae* Mergl, 2003, PCZCU 854. • H – *Molongella lineata* Havliček, 1975, PCZCU 906. • I – *Dicoelosia praedimera* Mergl, 2003, PCZCU 860. • J – *Glassina gutta* Mergl, 2003, PCZCU 1037. • K – *Clorinda pseudolinguifera* Kozłowski, 1929, PCZCU 922. • L – *Lissatrypa neglecta* Havliček, 1984, PCZCU 981. • M – *Nucleospira robusta* Kozłowski, 1929, PCZCU 1012. • N – *Resserella walmsleyi* Havliček, 1977, PCZCU 908. • O – *Dalejina austera* Havliček, 1977, PCZCU 878. • P – *Iridistrophia umbella* (Barrande, 1848), PCZCU 846. • Q – *Tenellodermis microdermis* Havliček, 1971, PCZCU 946. • R – *Spurispirifer fuscus* Havliček, 1971, PCZCU 950. • S – *Howellella angustiplicata* (Kozłowski, 1929), PCZCU 953. • T – *Barbaestrophia praestans* (Barrande, 1879), PCZCU 8414. • U – *Rugoleptaena skalicensis* (Havliček, 1967), PCZCU 822. • V – *Spinatrypina variabilis* Mergl, 2003, PCZCU 1018. • W – *Eoglossinotoechia mystica* Havliček, 1961, PCZCU 916. • X – *Quadrithyris subrobusta* Mergl, 2003, PCZCU 937. • Y – *Parmorthina protopragensis* Havliček, 1977, PCZCU 886. • Z – *Isorthis svatojanica* Havliček, 1977, PCZCU 894. • AA – *Spinatrypa senilis* (Havliček, 1987), PCZCU 970. • AB – *Gypidula pelagica* (Barrande, 1847), PCZCU 924.

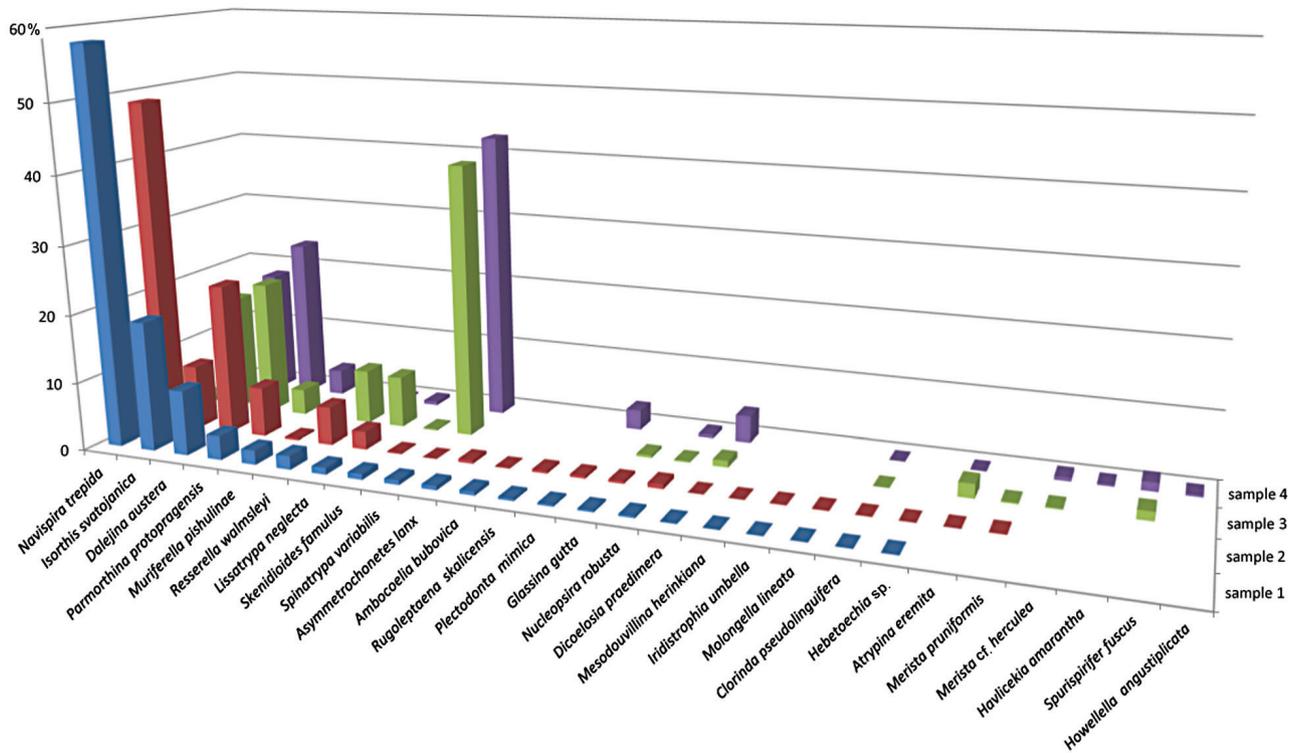


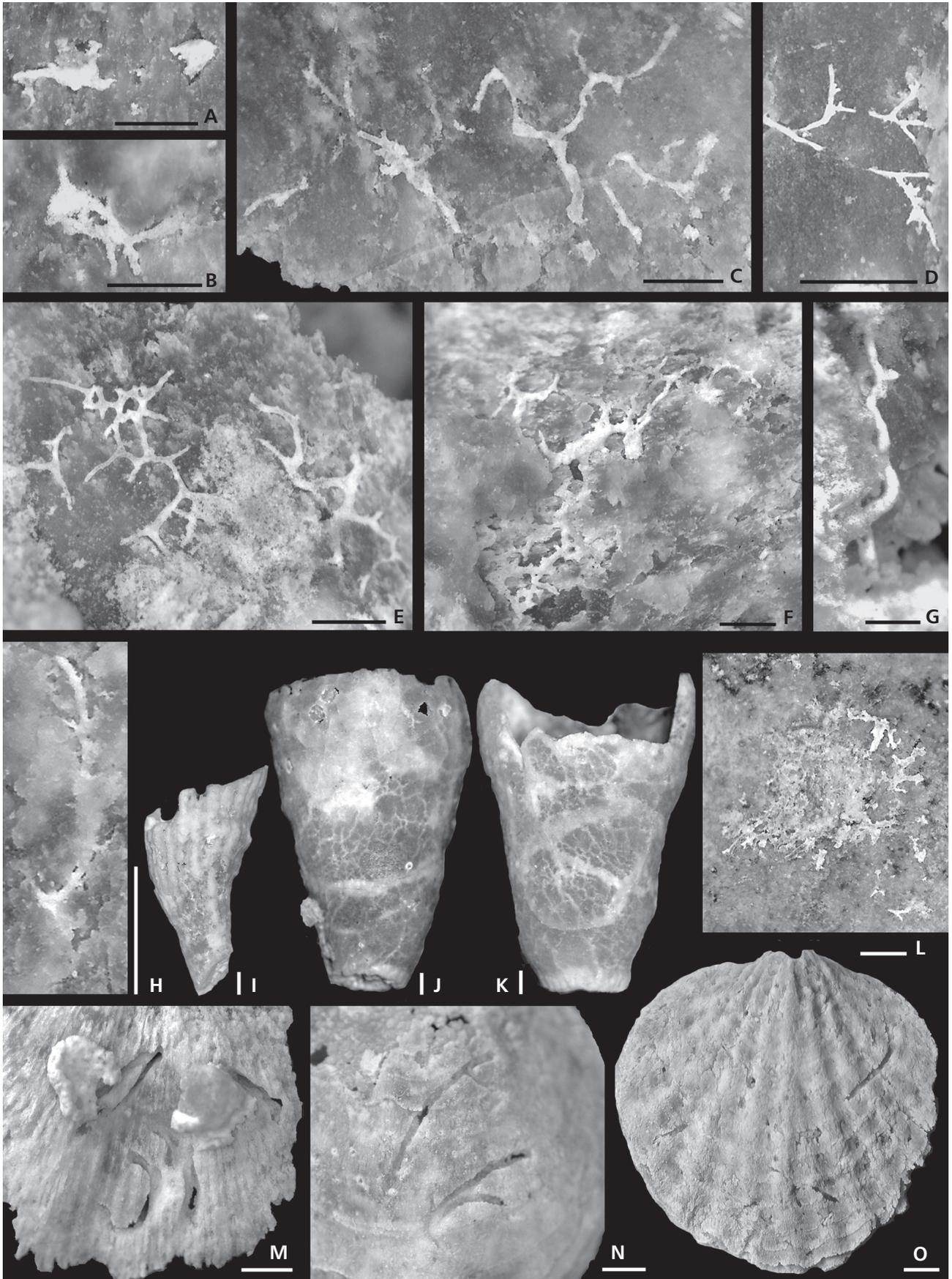
Figure 3. Estimated compositions of four brachiopod samples (in total, 3750 specimens were examined). Samples 1 and 2 came from the lowest limestone beds, samples 3 and 4 came from the middle part of the section.

1946; *Merista* Suess, 1851; *Nucleospira* Hall in Davidson, 1858; *Quadrithyris*; *Tenellodermis* Havlíček, 1971; *Spurispirifer* Havlíček, 1971). The smallest brachiopod species are only 3 to 5 mm wide in adult stage (*Ambocoelia* Hall, 1860; *Asymmetronetes* Smith, 1980; *Atrypina* Hall in Hall & Clarke, 1893; *Dicoelosia* King, 1850; *Glossina* Hall & Clarke, 1893; *Molongella* Savage, 1974; *Muriferella* Johnson & Talent, 1967; *Navispira* Amsden, 1983; *Plectodonta* Kozłowski, 1929; *Skenidioides*), but some of them are the commonest brachiopods in investigated samples. Medium to large-sized thin-shelled strophomenids are diversified but uncommon and show imperfect silicification [*Barbaestrophia* Havlíček, 1965; *Cymostrophia* (*Protocymostrophia*) Harper & Boucot,

1978; *Mesodouvillina* Williams, 1950; *Mesoleptostrophia* Harper & Boucot, 1978; *Rugoleptaena* Havlíček, 1956]. Key morphological characteristics and abundance of all species are in Table 1.

Small-sized species and tiny juvenile shells of larger species are abundant to dominant in all examined samples. Relative abundance of particular species and proportion of small-, medium- and large-sized species differs from bed to bed. Summary of four counted samples is illustrated (Fig. 3). Weak inaccuracy might be due to the mode of preservation; number of the smallest individuals, especially shells of *Navispira* and juvenile shells of *Dalejina*, *Resserella*, and *Isorthis* may be underestimated due to poor preservation of the finest fraction in the counted samples.

Figure 4. Endobiont traces from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžový ridge. • A–K – Dendritic borings of *Clionolithes* isp.; A – small simple boring in exterior of *Dalejina austera* Havlíček, 1977, PCZCU 2422; B – small branching boring in exterior of *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2423; C – several meandering borings in interior of *Dalejina austera* Havlíček, 1977, PCZCU 2424; D – laterally branching borings in interior of *Parmorthisa protopragensis* Havlíček, 1977, PCZCU 2425; E – sparsely branching dendritic borings in interior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2429; F – densely branching boring with uneven diameter of tunnels in exterior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2427; G – weakly expanding tunnel on *Dalejina austera* Havlíček, 1977 located below corallite of overgrowing coral, PCZCU 2428; H, I – shortly branching tunnel in wall of *Syringaxon* sp. corallum, PCZCU 2471; J, K – complex plexus of tunnels visible under translucent silicified external wall of *Syringaxon* sp. corallum. Note white strips of bleached silica alongside cracks of the corallum, PCZCU 2472. • L – ?*Rhopalondendrina* isp. forming discoidal plexus of tunnels on shell of gastropod *Platyceras* sp., PCZCU 2426. • M–O – *Trypanites* sp.; M – Several curved borings in exterior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2431; N – three borings in exterior of *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2430; O – long boring in right posterior part and several shorter oblique borings in anterior part of *Spinatrypa senilis* (Havlíček, 1987) shell, PCZCU 2473. Scale bars = 500 µm (A–H) and 1 mm (I–O).



Results

Dendritic borings

Dendritic borings are fairly frequent in brachiopod shells of studied samples. The canals were filled by white silica substance contrasting with grey and slightly translucent shells. Majority of observed cavities and canals are short, with length about 1 mm, having few shortly extended radiating tunnels (Fig. 4A, B). These small borings may expand to much more complex plexus forming stellate or dendritic systems of evenly sized tunnels (Fig. 4E, F). Secondary tunnels diverge at high angle from the main tunnel in uneven distances. Width of main lateral and distal tunnels is 20 to 40 µm. The distal tunnels ramify into thinner and sharply pointed extensions (Fig. 4D). Proximal tunnels have greater diameter, expanding to 50 µm or even more (maximum 75 µm). Stellate plexus has seven or more radially arranged tunnels (Fig. 4E), but other examined borings are less regular and less branched (Fig. 4C). Tunnels may fuse and form circular to polygonal system (Fig. 4E).

This type of borings was formed in shell wall near shell surface, both external and internal. Borings of the same type was observed in coral *Syringaxon* sp. (Fig. 4J, K), but tunnels form larger and much complex dendritic plexus visible under a translucent surface of silicified corallite. Other corallite shows moderately branching pattern of weakly curved tunnels (Fig. 4H). The dendritic borings are common in brachiopods *Parmorthina*, *Isorthis*, *Dalejina*, *Spinatrypa*, *Lissatrypa*, and rare on other medium to large-sized brachiopods having moderate thick shell walls. Different circumradial plexus of radiating and closely spaced flattened canals was observed in shell of a gastropod *Platyceras* sp. (Fig. 4L). Borings were observed both in external and internal shell surfaces and are concentrated to thicker parts of shell, with clear preference of posterolateral flanks of brachiopod shells. The endobiont boring activity in exterior of live shells cannot be excluded, but borings in shell interior conclusively indicate infestation of dead shells.

Endobiont traces of complex plexus of variable branching radial canals were systematically grouped

into ichnofamily Dendrinidae (Wisshak 2017). However, because observed borings differ from reviewed dendritic and rosette microborings, no formal naming of observed borings is used. Dendritic borings described by Mergl (2020) from the Silurian of the Barrandian differ by other arrangement of tunnels. These are weakly branching forming dense cluster of short tunnels or stellate plexus with tapering tunnels. None of newly described traces on silicified shells show such branching patterns.

Worm borings

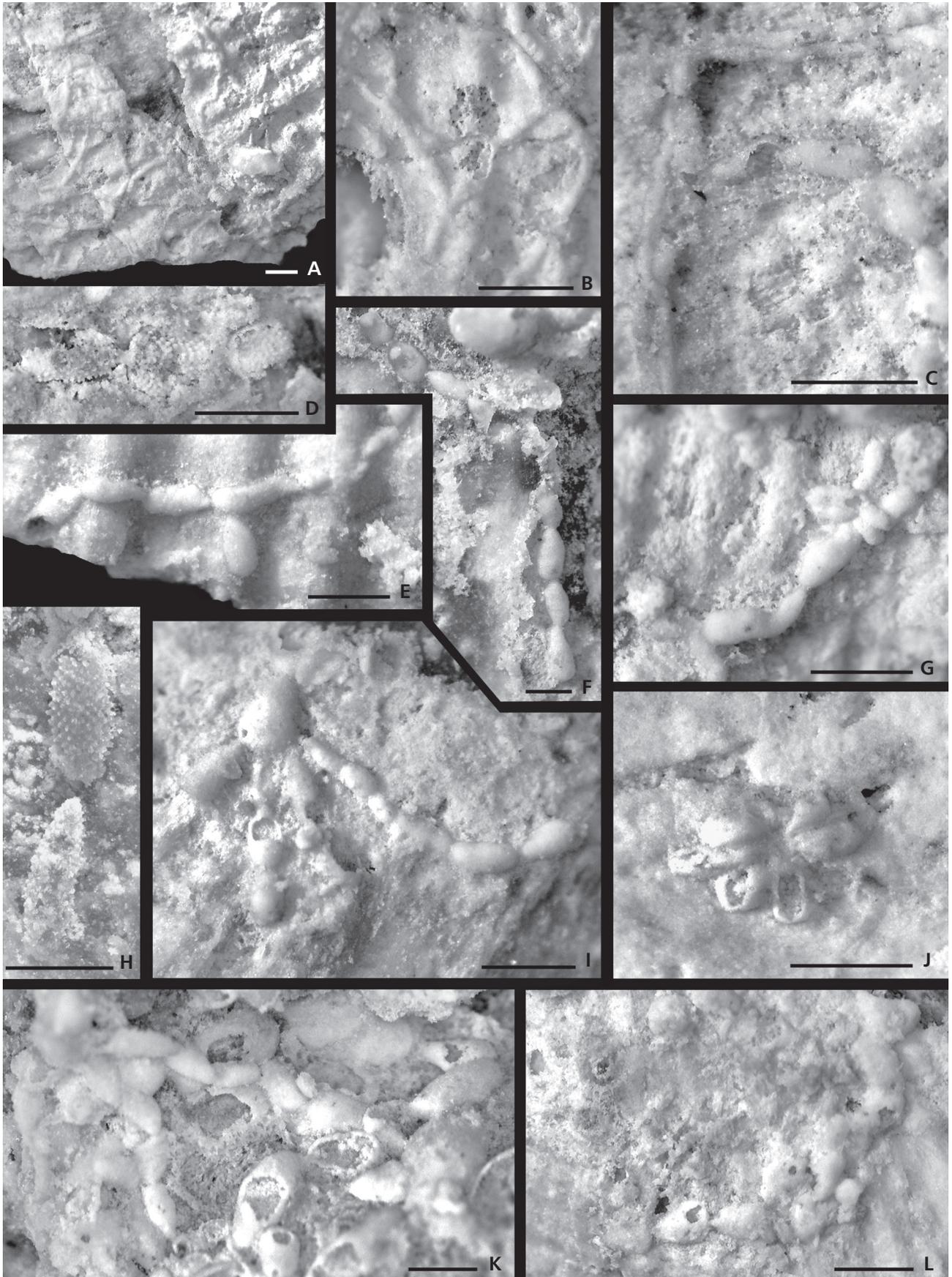
Cylindrical borings subtangential to surface of brachiopod shell are rare. Trace starts by a shallow excavation in shell exterior and shallowly plunges into the wall by bent tube of approximately 200 µm in diameter (Fig. 4M–O). Borings do not penetrate into shell interior. The surface openings are directed toward periphery of host shell. More complex system of several tunnels was observed on convex dorsal valves of *Spinatrypa* (Fig. 4N). Another ventral valve shows one long boring in right flank associated with several shorter borings in anteromedian part of the valve (Fig. 4O). Worms likely infested brachiopods, which were alive, because the borings were observed only at shell exteriors and openings are directed toward anterior margin of shell. Borings were observed only in brachiopods *Spinatrypa* and *Dalejina*.

Traces are referred to *Trypanites* Mägdefrau, 1932 because they lack swollen distal ends characteristic for otherwise similar *Palaeosabella* Clarke, 1921. Traces of this type are known from the Ordovician to the Recent (Cameron 1969; Pickerill 1976; Opalinski & Harland 1980; Hoare & Walden 1983; Vinn 2004, 2005; Furlong & McRoberts 2014; Vinn *et al.* 2021). The agents of traces were probably the commensal worms.

Microproblematica

Chains of vesicles referred to *Allonema moniliforme* (Whiteaves, 1891) were observed in diverse biogenic substrates. The walls of vesicles are silicified, with preserved

Figure 5. Protozoan? sclerobionts from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžovy ridge. • A, B – *?Rhopalonaria* sp., cylindrical branching stolons on shell exterior on exterior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2432. • C – *Allonema moniliforme* (Whiteaves, 1891), chains and adjacent thinner stolons *?Rhopalonaria* sp. on brachiopod shell, PCZCU 2432. • D–L – *Allonema moniliforme* (Whiteaves, 1891); D – chain of broken vesicles showing infillings of pores, PCZCU 2432; E – branching chain of vesicles on shell exterior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2433; F – chain of small vesicles on interior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2434; G – chains of vesicles of different size overgrowing one another on exterior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2435; H – moulds of two vesicles with infillings of pores on interior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2436; I – large pyriform vesicle with four radiating chains of smaller vesicles on exterior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2437; J – stellate group of vesicles similar to *Ascodictyon* sp. on exterior of strophomenid brachiopod, PCZCU 2438; K – clustered chains of unevenly sized vesicles on shell of *Platyceras* sp., PCZCU 2439; L – meandering chain of tightly adjacent pyriform vesicles on exterior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2440. Scale bars = 500 µm.



interval cavity, but different type of preservation sometimes exhibits the natural internal moulds where infillings of pores penetrating the walls of vesicles are discernible (Fig. 5D, H). Vesicles are elongated to rounded, with broad size range (100 to 300 µm width and 125 to 600 µm length). Vesicles are moderate convex in elongate and transverse profiles. Constrictions between separate vesicles are clearly defined in the chains. Chains of vesicles are straight on plane surfaces (Fig. 5E) but others are variably bent on uneven substrates (Fig. 5K). Stellate cluster of seven vesicles similar to *Eliasopora* Bassler, 1952 were observed (Fig. 5J) on one brachiopod shell. This vesicle group due similarity to another examined vesicles is better referred to extremely shaped *Allonema* Ulrich & Bassler, 1904. Another group of *Allonema* consists of central large pyriform-outlined vesicle surrounded by four radiating chains of smaller vesicles (Fig. 5I). These smaller vesicles are morphologically identical with vesicles observed in regular chains. Vesicles of uneven size may be present in the same chain (Fig. 5K, L). Chains may be in near contact (Fig. 5K) or may overgrow one another (Fig. 5G, K).

More slender tubular stolons were observed in one shell of *Parmorthina* together with vesicles of *Allonema* (Fig. 5A–C). They resemble stolons referred by Kiepurá (1965) and Bertling (1995) to *Ropalonaria* Ulrich, 1879. Although their preservation is poor they are distinctly thinner than chains of *Allonema* vesicles.

Encrustation of *Allonema* were observed on shells of *Parmorthina*, *Isorthis*, *Iridistrophia*, an unidentified fragment of strophomenidine brachiopod, corallites of *Syringaxon* sp. and *Aulopora* sp., and shells of gastropod *Platyceras* sp. They are evenly common both in external and internal surfaces of brachiopod shells. Clustered chains are concentrated in shallow depressions, sheltered corners and other protected sites frequently near basal parts of other larger sclerobionts.

Allonema was originally considered a ctenostomate bryozoan (Ulrich & Bassler 1904, Kiepurá 1965) with stratigraphical range from the Silurian to the Pennsylvanian. Modern revisions (Wilson & Taylor 2001, 2014; Jarochovska *et al.* 2016) placed *Allonema* to “pseudo-

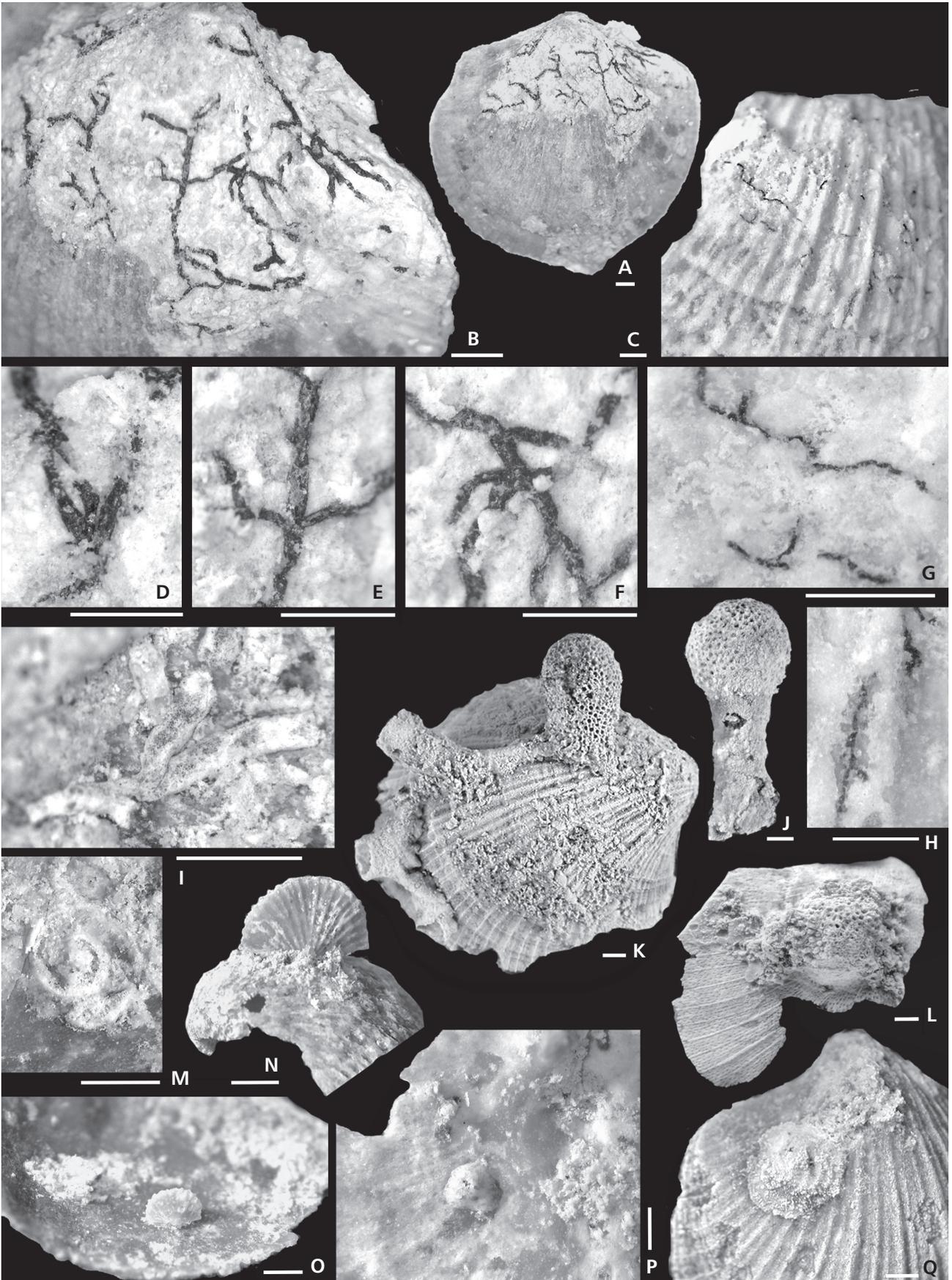
bryozoans”. Many aspects of their ultrastructure indicate affinity to some foraminifers (Dzik 1975, Taylor & Wilson 2003, Jarochovska *et al.* 2016), but Wilson & Taylor (2014) referred *Allonema/Ascodyctyon* continuum to *incertae sedis* (Microproblematica). *Allonema* was mainly reported from off-platform marls and shales (Gluchowski 2005, Jarochovska *et al.* 2016), commonly attached to brachiopod shells (Spjeldnaes 1984, Jarochovska *et al.* 2016). According to Jarochovska *et al.* (2016) at least seven species of *Allonema* have been proposed, but their revision left only three distinct species: *Allonema moniliforme*, *A. aggregatum* (Ulrich & Bassler, 1904) and *A. sp.* Morphology of observed vesicles from the Kotýs Limestone matches characteristics of *A. moniliforme*. The same elongate internal moulds covered by characteristic spines were observed in many residues of acetic-acid etched limestone of Pragian and Emsian ages in other localities of the Barrandian. These moulds demonstrate high abundance of *Allonema* in the Devonian of the Prague Basin.

Microconchids

Two poorly preserved spirorbiform microconchids referred to *Anticalyptraea* sp. were observed on posterolateral part of planar dorsal valve of *Parmorthina* and inside the dead shell of *Isorthis*. Silicification brachiopod shells partly continued into adhered parts of microconchid shells (Fig. 6M). Therefore, only weak traces of spiral coiled walls of 1.4 mm sized microconchid shell are discernible. Other parts of microconchid shell are not preserved and the structure of the tube wall is unknown. Microconchids were attached to coarsely costellate exterior of the valve, with opening directed toward anterior of the brachiopod shell. The second observed microconchid specimen is also spirally coiled but lacks other details.

Microconchids and similarly shaped problematic tubeworms are known from the Ordovician (Vinn *et al.* 2017) and the Silurian (Vinn & Isakar 2007, Vinn & Wilson 2010) to the Middle Jurassic (Vinn & Taylor

Figure 6. Epibionts and sclerobionts from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on north slope of the Branžovy ridge. • A, B, D–F – *Chaunograptus* cf. *novellus* Hall, 1882; A – network on ventral valve of *Parmorthina protopragensis* Havlíček, 1977; B – the same on oblique view; D–F – detail of tubes showing mode of branching, PCZCU 2417. • C, G, H – *Chaunograptus* sp.; C – remains of network on flank of *Parmorthina protopragensis* Havlíček, 1977; G – detail of tubes along concentric ornament of a brachiopod shell; H – tubes intercalated between radial costae of brachiopod shell, PCZCU 2418. • I – *Hederella* sp., a small zoarium on interior of *Lissatrypa neglecta* Havlíček, 1984, PCZCU 2419. • J–K – trepostomate bryozoan; J – small zoarium at aperture of cylindrical auloporid corallite, PCZCU 2464; K – zoarium entirely overgrowing the parent corallite of auloporid colony, PCZCU 2462. • L – mound-shaped, only partially silicified zoarium on exterior of brachiopod *Mesodouvillina herinkiana* Havlíček, 1999, PCZCU 2463. • M – microconchid *Anticalyptraea* sp. on exterior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2420. • N, O – brachiopod *Skenidioides famulus* Havlíček, 1977; N – shell attached near the apex of ventral valve of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2461; O – small shell on interior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2460. • P, Q – craniid brachiopod indet.; P – small shell attached to interior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2459; Q – shell attached to left flank of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2431. Scale bars = 1 mm.



2007, Vinn & Mutvei 2009, Zatoń & Vinn 2011), even from fresh-water environment (Zatoń *et al.* 2012). Some published data showed similar mode of preservation with only general outline patterned (Jarochovska *et al.* 2016, fig. 4c).

In the Prague Basin, the remains of spiral microconchids are known from the Gorstian (Horný 1965, Mergl 1989) to the Eifelian (Šnajdr 1983). The Gorstian species *Anticalyptraea bastli* Horný, 1965 encrusted brachiopods, corals, and shells of molluscs, indicating minimal host preference. From the Ludlow of Gotland, Hurst (1974) pointed high substrate preference of microconchids to brachiopods with angular and prominent ribs. Microconchids are rare in currently studied association, but it is unclear whether this rarity is primary or is affected by selective silicification.

Hederellids

Only one small encrustation that can be referred to *Hederella* sp. was observed on inner concave floor of *Lissatrypa* (Fig. 6I). Zoarium is very small, 2.5 mm long, depressed, with two lateral branches, preserved as the internal mould.

Prantl (1938) described several species of hederelloids, some with remarkable regular branching pattern, from the late Silurian and the Early Devonian of the Prague Basin. Zoaria of these species are attached to exterior of gastropod and cephalopod shells. A poor preservation of the observed specimen prevents any plausible comparison. Hederellids are frequent sclerobionts in the Silurian and Devonian commonly forming extensive encrustations on brachiopods (Prantl 1938; Solle 1952, 1968; Sparks *et al.* 1980; González-Mora *et al.* 2018) and crinoid pluricolumnars (Kiepusa 1973, 2003; Głuchowski 2005). Their latest occurrence was from the Permian strata (Lisitsyn 1998, Taylor & Wilson 2008, González-Mora *et al.* 2018). Affinity of *Hederella* Hall, 1881 to bryozoans is matter of discussion (Taylor & Wilson 2003, 2008).

Brachiopods

Adhered fixo-sessile brachiopods are rare in the material. Two poorly preserved but unequivocal craniid shells were observed on interior and exterior, respectively of *Parmorthina* shells. They are definitely in life position, still adhered by dorsal valve to host surface (Fig. 6P, Q). Both shells are small, with the largest one only 3 mm wide. The smaller individual indicates settlement of the larva on inner surface of vacant shell, but the larger specimen may grow when host was alive. The second epibiont brachiopod species may be protorthid *Skenidioides famulus* Havlíček, 1977. One mature specimen with closed

shell was observed on exterior of convex ventral valve of *Parmorthina* (Fig. 6N). *Skenidioides* is pushed by a large planar interarea to shell surface. The second specimen is an immature individual adhered by interarea to weakly concave interior of *Isorthis*.

Epibiont craniid brachiopods are known from the Ordovician to the Recent. In the Prague Basin, the similarly sized and shaped craniids are present in limestone of Pragian age (Havlíček & Vaněk 1998). Their epifaunal life style with cementation to some hard substrate already occurred in the Ordovician and persisted to the Recent (Emig 1997).

Skenidioides was likely plenipedunculate (Bassett 1984). Attachment of its larva to a larger empty shell is plausible explanation for both observed shells. Morphology of *Skenidioides* with large interarea faced to substrate and large opened delthyrium closely resembles shell shape of a much larger Devonian cyrtinoid *Cyrtina*. That *Cyrtina* life habit might be fixosessile and was conclusively documented by Głuchowski (2005) by specimens directly attached by interarea to hard substrate. However, in the Branžovy locality, the shells of *Cyrtina* sp. are very rare and all were observed unattached to any substrate (Tab. 1).

Bryozoans

Bryozoans are rare sclerobionts in the material. Only 14 small zoaria were observed. All are referred to one species unnamed trepostome species. There is evidence that bryozoans were common and more taxonomically diverse in the original benthic life association. Rare loose fragmentary imperfectly silicified zoaria of cystoporates and cryptostomates were observed in examined samples.

Silicified trepostome zoaria are small, adhered to elevated sites of bioskeletons. They were chiefly observed on tips of vacant corallites of encrusting coral *Aulopora* sp. (Fig. 6J, K) and at the top of highly convex ventral valve of *Parmorthina*. Small dome-shaped zoarium attached directly to host shell was observed on weakly convex shell of strophomenid *Mesodouvillina* Williams, 1950 (Fig. 6L). Very small encrusting zoarium, which definitely began to grow on empty shell of dead brachiopod was observed on the tip of dental plate of strophomenid *Rugoleptaena* Havlíček, 1956. Another valve of *Rugoleptaena* bears small discoid zoarium on left flank of dorsal valve (Mergl 2003, pl. 1, fig. 9). In the latter case, a complete preservation of the host shell and location of zoarium indicate that brachiopod host was likely alive when the zoarium grew. Another small semiglobose zoarium was observed on specimens of *Syringaxon* sp., which encrusts the brachiopod shell. Bryozoan location at the very edge of the calice confirms the larval settlement on corallum without polype.

Trepostomes and other stenolaemates were common epibionts since the Ordovician. They used diverse hard substrates, both biotic (coral, brachiopods, cephalopod shells, conulariid tests, trilobites, echinoderm ossicles) (Röhlich & Chlupáč 1952, Spjeldnaes 1984, Gluchowski 2005, Wyse Jackson *et al.* 2014) and abiotic (*e.g.* phosphatic nodules). Trepostomes from the Kotýs Limestone clearly preferred hard and erect substrates. Whether small size of observed trepostome zoaria represented the colonization pattern or was merely consequence of selective silicification remains unclear.

Pterobranchs

Two remains of putative encrusting pterobranchs have been identified. Preserved networks likely belong to two separate species tentatively referred to the genus *Chaunograptus* Hall, 1882. Both observed networks encrust convex parts of the ventral valves of *Parmorthina* and are not associated by other encrusters. Both are incomplete. Their preservation was facilitated by secondary silica crust to which network of carbonized tubes is partly embedded.

The first network referred to *Chaunograptus* cf. *novellus* Hall, 1882 is confined to apical part of the valve, covering at least one-third of its surface including the ventral edge of the interarea (Fig. 6A, B). Tubes are straight to sinuous, with random orientation. Width of tubes ranges is 150 to 200 μm . New side tubes have the same diameter as the primary tube, diverging in 30–70° angle (Fig. 6D–F). Tubes had overgrown one another, but all are attached to shell surface and any erect tubes of thecae have not been observed. However, this should be the result of preservation.

The smaller and less complete network of tubes covers the left flank of another shell. It is referred to *Chaunograptus* sp. (Fig. 6C). Sparse network is formed by thin, less than 50 μm wide tubes, which partly imitate course of growth lines (Fig. 6G) and radial costellation (Fig. 6H) of the valve.

Similar organic tubes of unclear affinity are known from early Cambrian (see Ramírez-Guerrero & Cameron 2021 for a review and phylogenetic analysis) to Silurian (Hall 1882). *Chaunograptus* was initially (Chapman 1919, Ruedemann 1947) considered a hydroid but later studies (Obut 1964, Maletz & Steiner 2015, Maletz & Beli 2018, Ramírez-Guerrero & Cameron 2021) placed this genus to the Graptolithina. Recent benthic *Rhabdopleura* Allman, 1869 should be the sister clade of the *Chaunograptus* (Ramírez-Guerrero & Cameron 2021). Other authors (St. John & Wilson 1998) considered that similar network of thin irregularly branching strands represent a network of hydrozoan stolons. *Chaunograptus* sp. from the Cin-

cinnatian of Ohio, Indiana and Kentucky commonly encrust hardgrounds, pebbles and strophomenid brachiopods. Similarly shaped coalified networks are known from late Ordovician and Silurian.

The larger colony is by overall shape, mode of branching and tube width undistinguishable from *Chaunograptus novellus* Hall, 1882 of Silurian age. The Bohemian species *Chaunograptus confertus* Bouček, 1957 differs by dense and closely aggregated sack-like thecae and shortly predates the occurrence of described encrusting pterobranchs.

Auloporid tabulate corals

Auloporid corals are the commonest sclerobionts in examined samples from Branžovy locality. Several hundred fragments of their colonies were picked up, overall consisting from one to three corallites. There are likely two different auloporid species distinguishable by different diameter of their corallites.

The gracile form of unnamed auloporid has columnar 1.1 to 1.5 mm wide and up to 8 mm high corallites. The basal encrusting part of corallites is slender having only 0.5 to 1.0 mm width. Particular corallites are more distant in comparison with the second type of auloporid. Gracile auloporid was never observed on hard surfaces. It likely grew on substrates having low ability for preservation, likely of organic composition.

The second auloporid *Aulopora* sp. is more robust, with shorter conical to almost cylindrical corallites of greater diameter, 1.7 to 2.0 mm wide at calix. Height of corallites reach up to 8 mm. Exterior of corallites is wrinkled and finely striated by growth rings (Fig. 7J, K). Fine septal grooves are perceptible on surface of large corallites (Fig. 7K). New corallites originated by lateral budding in a variable angle. Some are in opposite direction to the parent corallite (Fig. 7J) but others continued with moderate deviation in growth direction of the parent corallite (Fig. 7E, F). Corallites are often in at high angle to upright position to surface of host shell (Fig. 7F, I, M, N). All auloporid encrustations attached on brachiopods, gastropods and corals exclusively belong to this robust type. In total, 212 colonies of this type were observed on hard substrates (brachiopods, corals, gastropods, hyoliths). The same corallites are comparatively abundant among loose material and common growth on unpreserved substrate is supposed. One to seven corallites assemble a colony, but in overall two to four corallites are preserved on host shell. Only one colony is present on majority of examined host shells. Two colonies were rarely observed on host shells.

Auloporid colonies were observed in twelve brachiopod species, two species of rugose corals, one hyolith

species, and one gastropod species. Moderately-sized orthid *Parmorthina* is the commonest host, bearing almost 50% of all auloporid encrustations. The auloporid larva clearly preferred large and coarsely ribbed shells and highly convex and elevated surfaces. This is apparent from the fact that most encrustations are on ventral valve of plano-convex *Parmorthina*, ventral valve of ventri-biconvex *Isorthis*, and dorsal valve of dorsi-biconvex *Spinatrypa*. Encrustations on other brachiopod species are rare, apparently for their smaller and smoother shells.

Coralla of host rugose coral *Syringaxon* sp. are rarely encrusted by auloporid colony. Parent corallite of auloporid rests near the calice or on upper sides of host corallum. Some auloporid corallites are clearly overgrown over the edge or grew alongside edge of host calice. This indicates the post-mortem encrustation of *Syringaxon* corallum. Auloporid encrustations are also common on large shells of gastropod *Platyceras* sp. Auloporid colony is located near or at sheltered area on inner side of spirally coiled shell (Fig. 7L, M). One observed auloporid colony penetrates inside the aperture of the gastropod shell indicating occupation of vacant conch.

Parent corallites adhered on brachiopod shells are often located near or at the maximum convexity of host shell (Fig. 7E, J, O). In 55 examined shells of *Parmorthina*, 26 parent corallites are located in anteromedian sector of valve, and 5 and 10 corallites in anterolateral left and right sectors, respectively. Only 14 corallites are situated in posterior half of shell, with majority of corallites clustered along the mid-sector of host shell (Fig. 8A). None corallite was observed on surface of interarea and on deeply concave interior of *Parmorthina* shell. Similar distributional patterns of parent corallites were observed in shells of *Isorthis* (Fig. 8B) and *Spinatrypa*. Only two encrustations with parent corallite near shell apex were observed (Fig. 7E). The convex surfaces of host shell are strictly preferred. Only one colony of two corallites was observed on weakly concave surface of the ventral valve of *Spinatrypa*.

In overall, the growth of colony progressed towards anterior and antero-lateral margins of host shell. Subsequently a growth vector follows the outline of host shell to form ring-shaped chain of corallites (Fig. 7A, C, G, N)

alongside margin of host shell. Very few corallites are directed towards the hinge line of brachiopod shell. Some corallites crossed the host commissure and continued alongside margin of the opposite valve (Fig. 7A–D, H). Other corallites may overhang host commissure without interference with the shell opening (Fig. 7G). Distal parts of high corallites of some well-preserved colonies are gently bent toward the commissure (Fig. 7C, D, H).

Auloporid corals are the commonest encrusters in the Devonian (Grabau 1899, Pitrat & Rogers 1978, Kesling *et al.* 1980, Sparks *et al.* 1980, Brice & Mistiaen 1992, Zapalski 2005, Mistiaen *et al.* 2012). Detail analyses provided by these authors indicate high host specificity, with preference of larger shells, costate shells, and the convex surfaces.

Calceoloid rugose coral

Colonies of unnamed rugose with strongly asymmetrical corallites are abundant on shells and shell fragments. The species form groups of two to seven, in overall three to five closely packed calceoloid corallites of uneven size. Corallites are fixed by the largest flat side to surface of host shell, and tightly copy structure of its surface. They are up to 8 mm long and 7.5 mm wide. Calice is deep with septa unevenly preserved by imperfect silicification, but some 15 septa may be counted on interior of fixed side of corallite. Exterior of corallites are coarsely wrinkled (Fig. 9G). New smaller corallites originated by side budding near the apical end of a parent corallite (Fig. 9E).

In total 146 coralla of the rugose were identified on hard substrates. They were documented in 13 brachiopod host species. Coral definitely preferred convex, rough surfaces and larger bioclasts (Fig. 9D, G). Concave surfaces are rarely encrusted, representing less than 6% of host substrate (n = 8). Costellate ventral valves of orthids *Parmorthina*, *Isorthis*, *Dalejina*, *Resserella* and costate atrypid *Spinatrypa* are the commonest host substrates (Fig. 2). Some corallites are attached to incomplete valves and their fragments, some remarkably small-sized (Fig. 9H). Some of host bioclasts were deeply corroded and bored by endobionts before or during initial growth of

Figure 7. Sclerobiont tabulate corals *Aulopora* sp. on brachiopod, coral and gastropod shells from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžovy ridge. • A, B, E–G – *Isorthis svatojanica* Havlíček, 1977; A, B – colony of three corallites growing over a shell commissure of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2446; E, F – linear chain of corallites on *Isorthis svatojanica* Havlíček, 1977, PCZCU 2449; G – colony growing alongside margin of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2448. • C, D, H, N, O – *Parmorthina protopragensis* Havlíček, 1977; C, D, H – colony growing over a shell commissure of *Parmorthina protopragensis* Havlíček, 1977, with corallites turned above commissure plane, PCZCU 2447; N – colony of four corallites tracing periphery of flat dorsal valve of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2452; O – two corallites at the highest point of convex ventral valve of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2450. • I – corallites attached to proximal part of *Syringaxon* sp. corallum, PCZCU 2465. • J, K – colony of three corallites and attached new corallite at the highest point of auloporid colony on *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2451. • L, M – colony of five corallites attached to shell of gastropod *Platyceras* sp., PCZCU 2453. Scale bars = 2 mm.



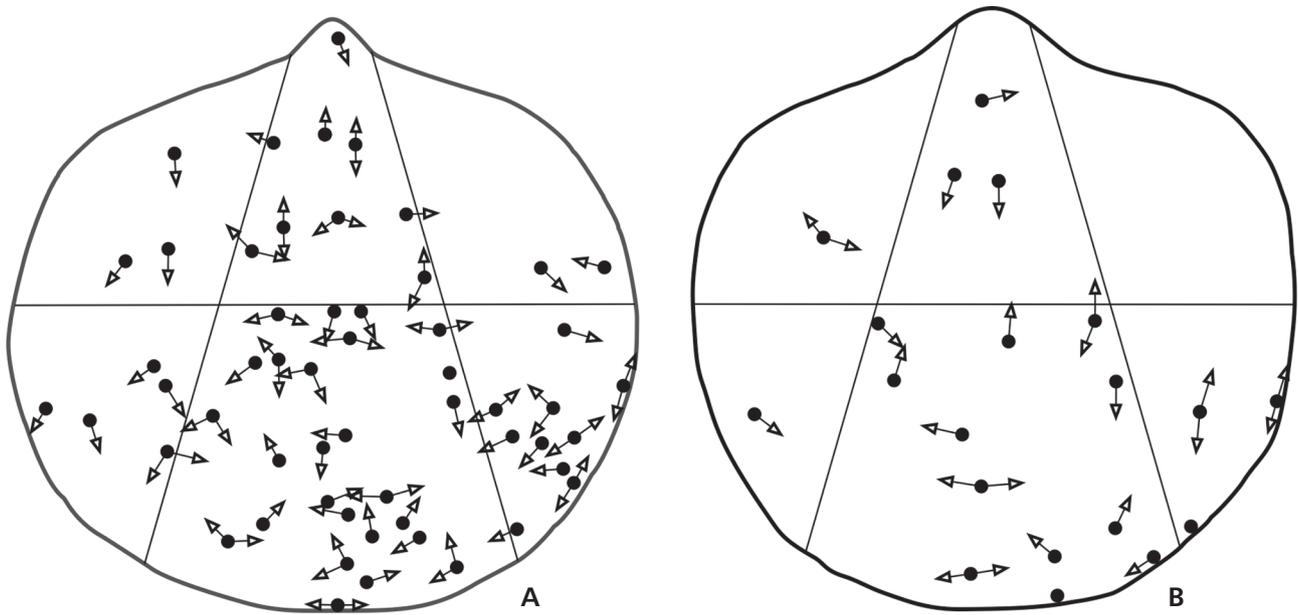


Figure 8. *Parmorthina protopragensis* Havlíček, 1977 (N = 55) (A) and *Isorthis svatojanica* Havlíček, 1977 (N = 20) (B) shell outlines divided into six sectors with numbers of parent corallites indicated. Parent corallites of *Aulopora* sp. are marked by black dot, growth directions of budding daughter corallites are marked by arrows. Note clustering of parent corallites in anterior sectors. Growth directions of daughter corallites are generally toward anterior and anterolateral margins of host shells.

coral. Imprinting of host surface into wall of corallite and preservation of endobiont borings below corallites are common. Some coralla considerably extend beyond the edge of host bioclast and their epitheca with concentric wrinkles preserve the original outline of embedded shell (Fig. 9D, G, H). This adaptation for support on soft sea floor when colony expanded over the larval substrate is known as the snowshoe adaptation (Thayer 1975, Seilacher 1978).

The exceptional encrustation of five corallites was observed on *Havlicekia* (Fig. 9A, B). The parent corallite is situated on edge of the concave surface of shell sulcus. Budding daughter corallites are directed to more elevated flanks of host shell. Small endobiont borings preserved in *Havlicekia* shell have been overgrown by any of corallites. Endobiont borings are also preserved in host sulcus anterior to encrusting corallum. Other encrusters are preserved at the same host shell. The right flank of valve bears apical parts of *Syringaxon* (Fig. 9A). Other corallum of *Syringaxon* sp. is attached on left steep slope of brachiopod interarea (Fig. 9B).

The colonies somewhat resemble initial stages of encrusting tabulate corals *Hyostragulum* Marek & Galle, 1976 and *Pleurodictyum* Goldfuss, 1829. It is suggested that unnamed rugose encrusted wide variety of stable substrates but it was semiselective, with preference of dead and incomplete brachiopod valves. Substrate preference of gastropod shells with similarly shaped

but much larger colony of the taxonomically unrelated *Pleurodictyum americanum* Roemer, 1876 were studied by Brett & Cottrell (1982). Substrate preference of crinoid pluricolumnals is known in tabulate coral *Antholites* (McIntosh 1980). Vinn (2017) summarised symbiosis between Devonian corals and other invertebrates.

Solitary rugose coral

Only one species of solitary rugose coral was observed in the material. It is referred to *Syringaxon* sp. It has a form of simple regularly conoidal, evenly expanding corallum with prominent septal grooves. The calice is very deep, surrounded by thin walls. Corallum was attached by a small prototheca to diverse hard substrate, with very short roots, which copied wrinkles of host surface (Fig. 10D). Development of small attachment scar in most of unbroken coralla indicates uprightness growth positions of live corals. The size of the largest examined corallum is 21 mm with 12 mm calice diameter.

Fifty coralla have been observed on brachiopod shells and ten other were observed in living position on other coralla. Costellate orthoids *Parmorthina*, *Isorthis*, and costate atrypid *Spinatrypa* are the commonest host substrates (Tab. 1) but coralla were observed in more species, even a small shell of *Atrypina*. This sharply contrasts with abundance of hundreds of loose silicified coralla in

examined material. Loose coralla have 1 to 3 mm sized attachment scars, lacking any indicative patterns of the substrate.

Coralla growing on brachiopod shells are located on moderately to weakly convex surfaces, some attached to the highest point of the substrate (Fig. 10E, G). Some coralla have the base attached to edge of shell (Fig. 10K, Q).

That indicates the larval settlement on empty host shell. Other coralla attached near periphery of host shell likely grew on a dead shell. Their relatively large size and growth direction would negatively affect the opening mechanism of living host. However, one observed coral (Fig. 10M, N) definitely occupied living brachiopod and grew simultaneously with them. The host valve of *Spinatrypa*

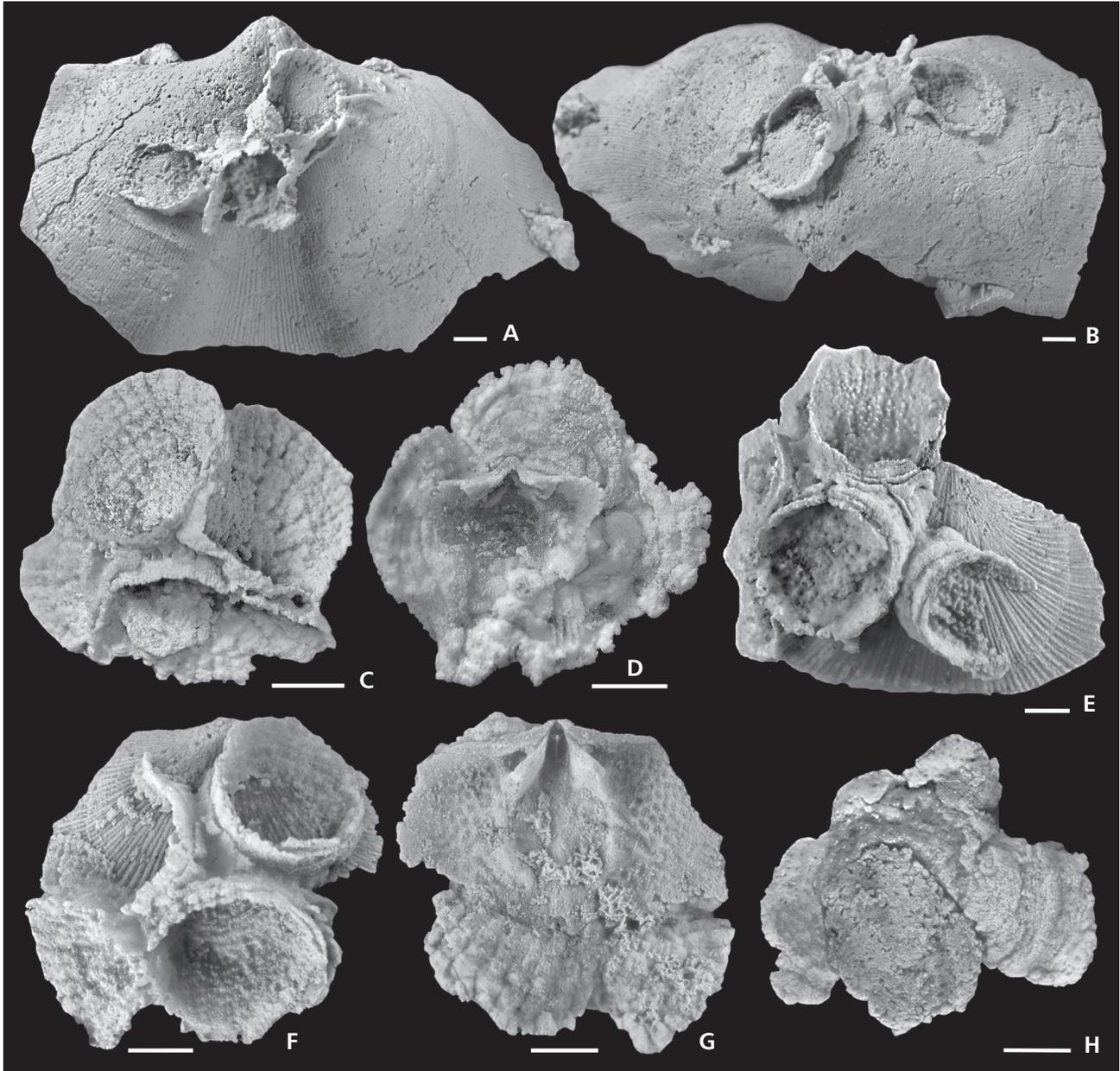
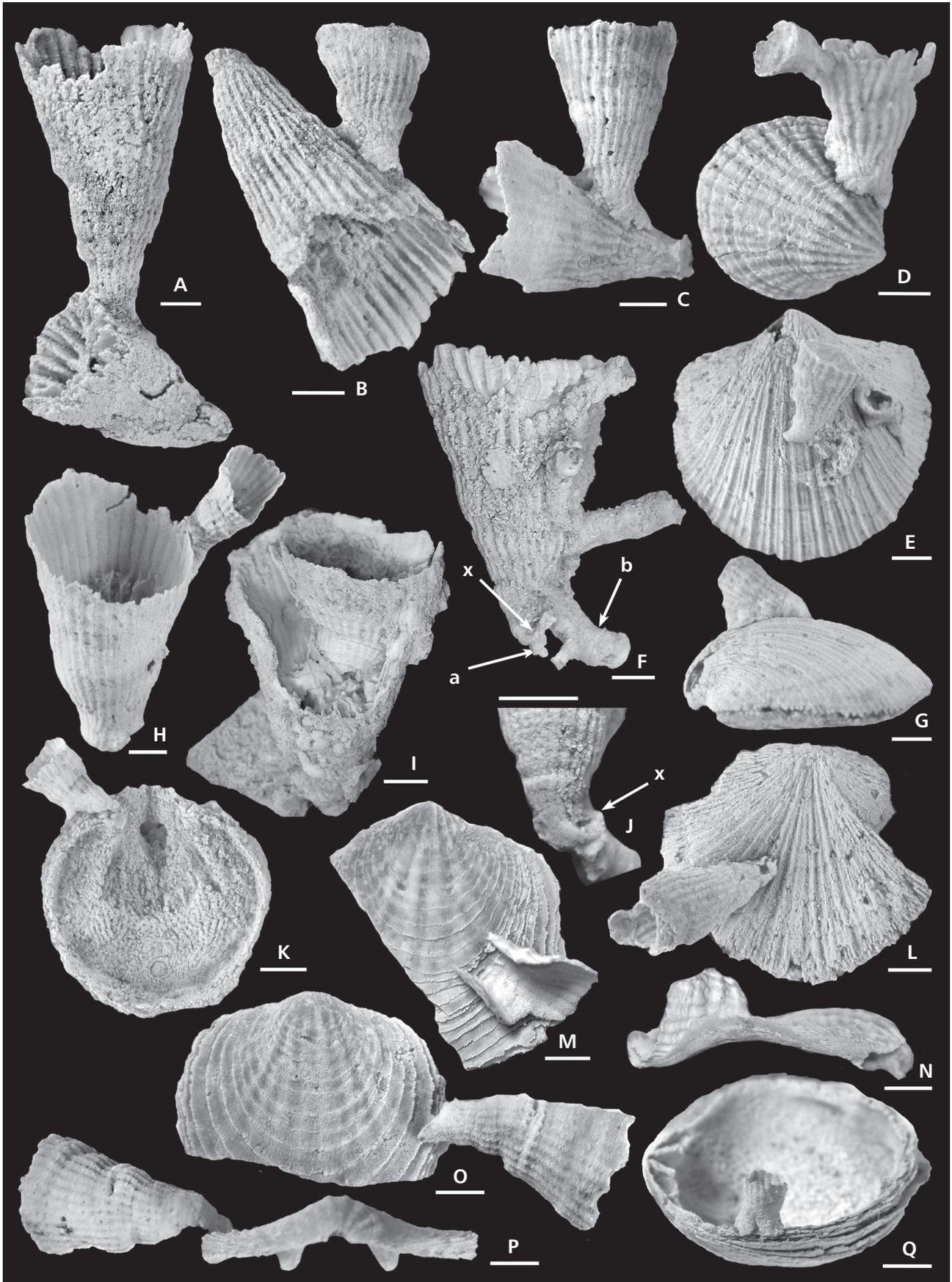


Figure 9. Colonial calceoloid rugose corals on brachiopods from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžovy ridge. • A–H – *Rugosa* gen. et sp. indet.; A, B – three corallites attached at sulcus of *Havlicekia amarantha* Havlíček, 1980; note also three small coralla of rugose *Syringaxon* sp. on flanks of brachiopod shell, PCZCU 2441; C, D – colony of four corallites growing at shell fragment of *Resserella walmsleyi* Havlíček, 1977, and its lower side, PCZCU 2445; E – colony of five corallites attached to exterior of *Isorthis svatojanica* Havlíček, 1977, PCZCU 2443; F, G – colony of four corallites attached to eroded fragment of *Isorthis svatojanica* Havlíček, 1977, note extensively overgrown periphery of fragment, PCZCU 2444; H – lower side of colony of three corallites extensively overgrowing a small brachiopod fragment, PCZCU 2442. Scale bars = 2 mm.



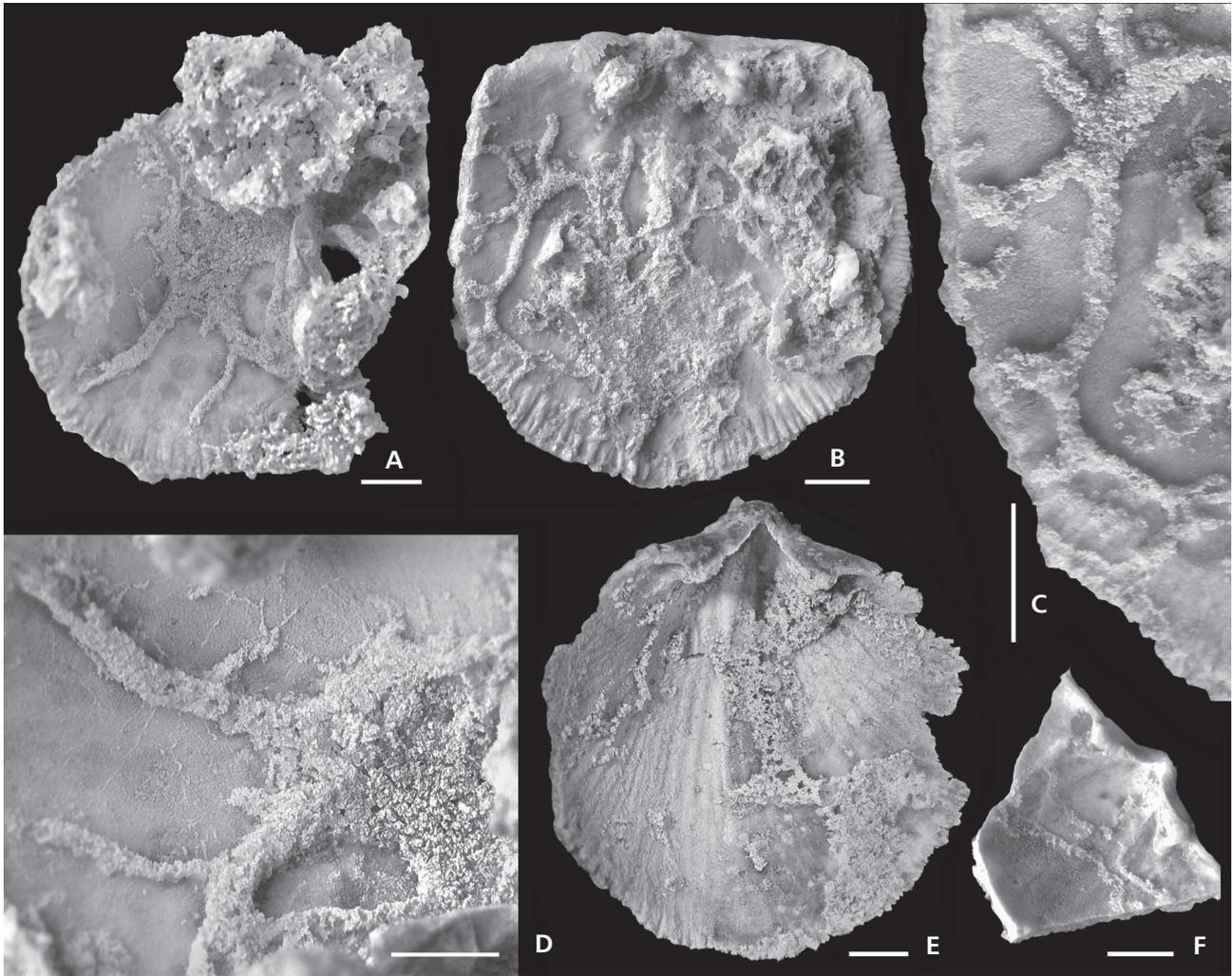


Figure 11. Dendritic structure in brachiopods from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžový ridge; A, D – dendritic structure extending from central body on interior of *Parmorthina protopragensis* Havlíček, 1977 and its detail, note very fine filose structures (middle top) of abiotic origin representing silica infillings of interspaces between calcitic crystals, PCZCU 2474; B, C – dendritic structure with evenly wide tunnels extending from imperfectly preserved central body on interior of *Parmorthina protopragensis* Havlíček, 1977 and its detail, PCZCU 2475; E – broad and weakly branching dendritic structure on interior of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2476; F – broken tunnel attached to shell floor of *Parmorthina protopragensis* Havlíček, 1977 showing evenly thick walls and chamber of tunnel, PCZCU 2477. Scale bars = 2 mm.

is regularly bent alongside the attached corallum. This deformation indicates an influence of living polype to regularity of brachiopod growth. The coral calice was

directed towards the anterior margin of host shell and supposed stinging cells on coral tentacles maintained mantle edge of the brachiopod in a safe distance.

Figure 10. Solitary rugose coral *Syringaxon* sp. (A–Q) on brachiopods and corals from the Kotýs Limestone, Lochkov Formation (Lochkovian); Bubovice, old section near entry to an abandoned quarry on the north slope of the Branžový ridge; A – adult coral resting at other adult coral, PCZCU 2470; B – coral attached under low angle to other coral, PCZCU 2469; C – coral attached perpendicularly to other coral, PCZCU 2467; D – two successive corals on exterior of *Spinatrypina variabilis* Mergl, 2003, PCZCU 2466; E, G – coral at the highest point of shell of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2456; F, J – large corallum of *Syringaxon* sp. with two generations of *Aulopora* sp., a juvenile corallum of the rugose (coral x) encrusting a side of auloporid corallite (a), corallum of adult rugose coral was subsequently encrusted by larger auloporid colony of four corallites (b), PCZCU 2479; H – coral attached to edge of the calix of other coral, PCZCU 2468; I – coral *Syringaxon* sp. growing inside abandoned calyx of the same species; PCZCU 2480; K – coral attached near posterior internal margin of *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2455; L – coral attached to exterior of flat dorsal valve of *Parmorthina protopragensis* Havlíček, 1977, PCZCU 2457; M, N – coral attached to ventral valve of *Spinatrypa senilis* (Havlíček, 1987), note (N) the deflexed surface of brachiopod valve in its side view, PCZCU 2478; O, P – coral attached to shell exterior near periphery of *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2458; Q – small coral attached to shell edge of *Spinatrypa senilis* (Havlíček, 1987), PCZCU 2454. Scale bars = 2 mm.

Coralla growing on other corallum of *Syringaxon* are located near the edge of calice (Fig. 10H) or at various places and at various angles on side of host corallum (Fig. 10A–C). At least some of attached coralla likely grew on dead coral, because there are great difference of growth directions (Fig. 10B) of host and encrusting coralla. One specimen began to grow inside empty calice (Fig. 10I). This definitely demonstrates the occupation of dead coral. Another interesting example indicates a larval settlement of rugose at the edge of aulopodid corallite (Fig. 10J). The same full-grown rugose corallum was subsequently encrusted by the second generation of aulopodid encruster (Fig. 10F).

Encrusting rugose corals definitely growing on living hosts were described on crinoid stems (Głuchowski 2005, Berkowski & Klug 2012, Bohatý *et al.* 2012) where caused stereomic reaction of a crinoid. Encrusting rugose corals or rugose corals as host substrate for sclerobionts were examined just recently by Vinn & Toom (2016) and Zatoń *et al.* (2020). Rugose corals forming symbiotic associations with stromatoporoids are known from the Silurian (Kershaw 1987, Lebold 2000, Vinn & Wilson 2012, Vinn & Motus 2014, Vinn *et al.* 2015), but as known to author, the rugose-brachiopod interaction is insufficiently known in fossils records. However, Merriam (1974) described the Lower Devonian of Nevada the *Syringaxon* Biofacies, which by composition of brachiopods and small amount of other rugose corals and stromatoporoids resembles the association from the Branžovy locality.

Dendritic structures

Well preserved dendritic structures of undoubtedly biogenic origin but of unknown agent were observed in four valves of orthid *Parmorthina*. These structures are formed by ramifying and tapering tunnels radiating from a larger flat central body (Fig. 11A–D). Scrapped (Fig. 11B) central body reveals structure of weakly defined and extended broad tunnels (Fig. 10E). Walls of tunnels were formed by porous silica and are uniformly thick (Fig. 11F). Bottom of tunnel forms a floor of host shell. Dendritic structures are adjacent to concave surface of brachiopod shell, but there are poor indices of tunnels on convex external surface of other host shell.

The structure may be silicified trace fossil resembling the genus *Arachnostega* Bertling, 1992. Tunnels show some degree of similarity to *Arachnostega* described from the Ordovician of Estonia (Vinn *et al.* 2014) but differ by presence of central body, which is not present in traces from Estonia. Therefore, the dendritic structure is not likely a consumption trace fossil. The dendritic shape resembles *Clionolithes* Clarke, 1908, which is generally considered the trace of boring sponge. *Clionolithes* is common boring

ichnofossil on brachiopod shells in the Silurian and the Devonian (Wisshak 2017). *Clionolithes* is known from the Silurian of the Prague Basin (Mergl 2020). Regardless the shape similarity, the observed dendritic structure does not penetrate into brachiopod shell and tunnel floor does not corrode a host surface.

Size, shape and suggested cryptic habitat of the dendritic structure agent resemble any Recent encrusting demosponges. Notable is morphological similarity to exhalant canals of Recent Mediterranean demosponge, e.g. *Clatria* Schmidt, 1862 and *Crambe* Vosmaer, 1880. Recent calcareous sponges with similarly anastomose tubular canals, e.g. genera *Clathrina* Gray, 1867 have walls reinforced by calcareous spicules. One may speculate that siliceous walls of observed dendritic structures originated by silicification of calcitic spicules of calcisponges. However, the walls of tunnels show only fine three-dimensional structure of silica lamellae that imitates interstice between calcite crystals of limestone. Therefore, in present state of art, the origin of the dendritic structure remains unclear.

Discussion

In summary, twelve epibiont taxa have been observed on brachiopods or, rarely, on gastropod shells and corals: two alleged protozoans, a hederellid, a trepostome bryozoan, a microconchid, two brachiopod species, two species of pterobranchs, two species of rugose corals, and one species of tabulate coral. Endobiont boring activity is referred to two ichnotaxa. The substrate selectivity of some of the biota (boring worms, microconchids, hederellids, brachiopods, pterobranchs) cannot be assessed due to their rarity. On the other hand, abundance of aulopodid and rugose corals and microproblematicum *Allonema* allow plausible conclusions about host preferences. From the data available, it is clear that encruster rate depends on more factors.

Substrate size. – Shell size was important control factor of colonisation. The large shell represents more stable host substrate on sea floor. With very few exceptions almost all encrusters were observed on shells longer than 10 mm (Tab. 1). Overwhelming majority of encrusted shells belongs to brachiopods *Parmorthina*, *Isorthis*, *Iridistrophia* and *Spinatrypa* (Fig. 12). The largest brachiopods of the assemblage, a spiriferid *Havlicekia* and an atrypid *Kyrtatrypa* are rare but some examined shells carry traces of encrusters. Large to medium-sized shells of strophomenids, *Gypidula*, *Merista*, and spiriferids *Quadrithyris*, *Howellella*, *Spurispirifer* and *Tenellodermis* were rarely utilized as the host substrate. The long-standing stability of seabed and shell durability necessary for encruster growth could not be achieved by thin, subplanar

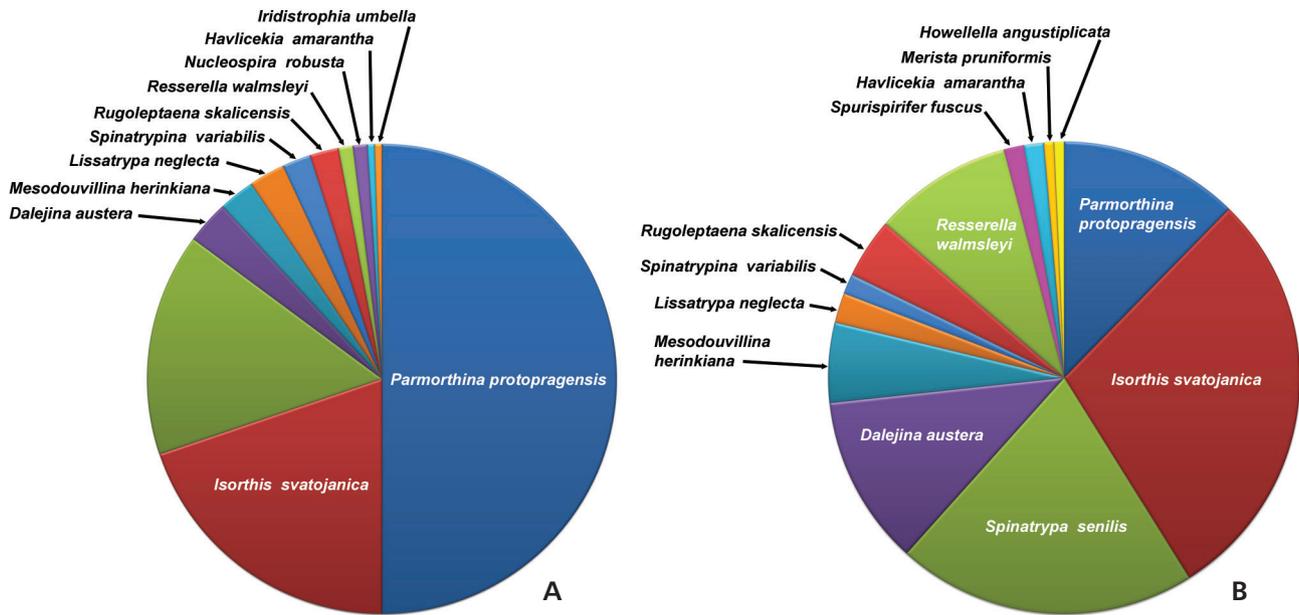


Figure 12. Host species composition of *Aulopora* sp. (N = 200) (A) and of the unnamed calceoloid rugose coral (N = 146) (B).

and relatively light shells of strophomenids and subglobose shells of spiriferids. Shells smaller than 10 mm (*Skenidioides*, *Plectodonta*, *Dicoelosia*, *Muriferella*, *Atrypina*, *Navispira*) and juvenile and small-sized shells of *Parmorthina* and *Isorthis* are not encrusted. These shells were diminutive for encrusters, because did not provide enough space area for their growth and also represented a less stable substrate on sea floor. Shells of costellate orthids *Dalejina* and *Resserella* and atrypid *Spinatrypa* were just near critical 10 mm shell size required by majority of encrusters (Fig. 12). Apart from large and rare *Havlicekia*, there is not any brachiopod having transverse shell outline, which is characteristic for overall large and encrusted spiriferids common in the Middle and the Upper Devonian.

Zapalski (2005) described similar size-related dependence in brachiopods of upper Eifelian and lower Givetian age (Skaly Beds) from Poland. Almost 60% of host species is *Kyrtatrypa*, which, however, represents less than 2% of all brachiopods in Polish sample. The second most encrusted is a spiriferid *Mucrospirifer* (15%), which represent only 4% of Polish brachiopods. Shells shorter than 11 mm are not encrusted (Zapalski 2005, fig. 5). There is obvious coincidence between *Dalejina* in Bohemia and its homeomorphic and taxonomically related *Aulacella* in Poland. The maximum length of *Aulacella* is 15 mm (Biernat 1959). It is the commonest brachiopod in the Poland with 70% dominance in brachiopod assemblage but its shells bear only 3% of encrusters (Zapalski 2005, figs 2, 3).

Dalejina is moderately common in Bohemia, with 9 to 25% abundance among brachiopods. It is rarely used by

auloporids (Fig. 12A) but commonly used by calceoloid corals (Fig. 12B). This difference demonstrates higher demand of the auloporid colony to substrate stability. *Aulopora* sp. was not able to stabilize substrate alone and therefore grew on larger (brachiopod shells over 10 mm size), heavier (coral *Syringaxon* sp.), and fixed (living fixosessile brachiopods) substrates. Calceoloid coral colony was able to achieve stability by expansion over the edge of host substrate and therefore it used also smaller shells (*Dalejina*, *Resserella*) or smaller bioeroded shell fragments of larger brachiopods.

Mistiaen *et al.* (2012), in the analysis of brachiopod encrusters from the Upper Devonian of Boulonnais, France, considered that size of host shell is the main control factor of encrusters. However, the overall size of brachiopods from Boulonnais is considerably larger than those from Bohemia and Poland. Other authors (Pitrat & Rogers 1978, Sparks *et al.* 1980) analysed significantly larger encrusted shells, mostly spiriferids and atrypids of Middle and Upper Devonian age. However, the significance of sole shell size as important selective factor is called into question by Zapalski (2005).

Substrate ornamentation. – Overwhelming majority of auloporid and rugose coral encrustations has been observed on costellate and costate brachiopods, mainly on *Parmorthina*, *Isorthis*, *Iridistrophia* and *Spinatrypa*. Shells with delicate ribbing of comparable size represented by *Rugoleptaena*, *Cymostrophia*, *Mesodouvillina* and *Mesoleptostrophia* and smooth-shelled *Gypidula* and *Merista* lack encrustations at all or bear rare and small bryozoans.

However, costellate ornamentation was not the main factor because some but much smaller brachiopods are also costellate (*Skenidioides*, *Molongella*, *Muriferella*, *Dicoelosia*).

There are differences among equally costellate valves of distinct convexity. Coarsely costate *Parmorthina* provided 83 colonies in convex ventral valve but only 17 colonies in planar and equally costate dorsal valve. Similar ratio (33:7) has been observed in *Isorthis*, where the dorsal valve is less convex than the ventral valve. *Spinatrypa* is dorsi-biconvex and show reverse encrustation, with 8 colonies in ventral valve and 21 colonies in dorsal valve exterior. Lower number of observed encrusters on *Spinatrypa* might be related to weaker ribbing and prominent concentric frills. Frills likely trapped sedimentary particles and protected feeding currents against a scramble competition (Zapalski 2005).

In the Skaly Formation of Poland, the coarse ornamentation was probably the most important control factor. Zapalski (2005) noted that abundant shells distinct by delicate ribs are rarely encrusted. Hurst (1974) observed similar reliance between coarseness of ornamentation and encrusters. Among six examined species from the Ludlow of Gotland, only coarsely ribbed *Ptychopleurella*, *Homoeospira* and *Microsphaeridiorhynchus* were extensively encrusted. Unlike considered Devonian brachiopods, all Gotland species are markedly smaller. This indicates that in some cases the ornamentation might be much important selective factor than the shell size.

Substrate microornamentation. – Low encrustation of *Lissatrypa* may be related to the presence of spines on this species. Another spinose species is *Nucleospira* but this has subglobose and thin-walled shell not attractive for settlement of the larva. Absence or paucity of encrusters on spiriferids *Howellella*, *Quadrithyris*, *Tenellodermis* and *Spurispirifer*, apart from subglobose shape might be related to microspines and short lamellae on exterior of their shells, which might have the same function as thin long spines. Spines and short lamellae evidently trapped and held sediment on the shell, which might have made the shell surface less suitable for settling of epibiont larvae (Bordeaux & Brett 1990).

Substrate profile. – Highly convex surfaces were preferentially encrusted by auloporid corals. Also both colonies of pterobranchs are attached to convex surfaces and some corals of *Syringaxon* were observed on highly convex substrates. The most convex and sufficiently large substrates offered shells of brachiopods *Parmorthina*, *Isorthis*, *Spinatrypa*, *Gypidula*, *Lissatrypa* and *Havlicekia*. Apart from *Gypidula* these genera more or less regularly bear the encrusters. Their absence in *Gypidula* might be related to its smooth shell and also to sporadic occurrence

of this brachiopod. Protocorallites of auloporid colonies are often clustered along line of maximum convexity. In *Parmorthina* and *Isorthis*, ventral valves are more convex than dorsal valves. *Spinatrypa* shows reverse convexity. This difference in convexity corresponds with dissimilar ratio of encrusters in ventral and dorsal valves (see foregoing paragraph). The subplanar and concave surfaces were never used by auloporids but were occasionally utilized by unnamed calceoloid coral. Rugose coral *Syringaxon* efficiently used planar and sufficiently stable surfaces including outer and inner surfaces of disarticulated brachiopod shells (Fig. 10K, L, Q).

Prevalence of encrustation on convex surfaces has been emphasized by more authors. Degree of convexity and absence or presence of fold and sulcus, respectively, are the second most important in encrustation control among the Upper Devonian brachiopods from Boulonnais (Mistiaen *et al.* 2012). The same dependence was observed by Zapalski (2005). Likewise the diverse encrusters on mid- and upper Devonian spiriferid brachiopods favoured elevated and convex surfaces (Pitrat & Rogers 1978, Sparks *et al.* 1980).

Unlike corals, the calcareous sclerobiont *Allonema* likely favoured concave and protected sites. Concave surfaces of shell interior, interspaces between costae and crevices near base of coral were frequently occupied by this taxon. Spjeldnaes (1984) suggested that *Allonema* was able to live below water-sediment interface of the mud substrate and speculated about its ability to tolerate hypoxic conditions. Jarochovska *et al.* (2016) emphasized insufficient knowledge of ecology and biological affinity of this taxon. They noted that its records mainly come from quiet shallow water muddy environment. *Allonema* encrustations occur on brachiopods, trilobites, bryozoans, crinoids, and leperditiid crustaceans (Gluchowski 2005, Jarochovska *et al.* 2016), confirming unspecificity of substrates.

Elevated zone within host substrate. – Periphery of valve and rim of coral calyx were the most elevated hard surfaces accessible for larval settlement. Encruster had competitive benefit from uninterrupted oxygen and food inflow. However, the elevated site was attractive for predation and was susceptible to mechanical abrasion. This disadvantage was surmounted by protective ability of coral polypes. Therefore it is not surprising that auloporid encrustations and solitary corals were observed at rim of calyx of rugose corals and most elevated surfaces of brachiopod shells. Corals *Syringaxon* were observed at edge of brachiopod shells, which were disarticulated already in time of the larval settlement. On a whole, encrustations on extreme edges and rims were comparatively rare.

Elevated tip was common target of bryozoan larvae. Small zoaria were observed almost exclusively at elevated

edges of vacant auloporid corallites and projections of brachiopod internal structures. This indicates a post-mortem encrustation of a host.

Bioeroded surface. – Unlike of other encrusters, the calceoloid rugose coral (Fig. 9) utilized also small and bioeroded surfaces. Rough surface affected by endobiont bioerosion was its favoured substrate. This is in a clear difference to other encrusters in the Branžovy locality. Coralla extended for a great distance over margin the host substrates supporting stability on soft sediment-water interface and document vacant area along the coral. This strategy is well known in the Devonian tabulates (Thayer 1975, Brett & Cottrell 1982).

Shell structure. – Shell structure has likely no importance for observed encrusters because none of examined shells belong to exopunctate brachiopods. The most encrusted shells belong to endopunctate dalmanellidines (*Parmorthina*, *Isorthis*, *Resserella*, *Dalejina*) and to impunctate atrypids. Mistiaen *et al.* (2012) noted that pentamerids and rhynchonellid brachiopods, unlike atrypids, athyridids and spiriferids were never encrusted in the Devonian of Boulonnais. The current results rather confirm their suggestion but pentamerids (*Gypidula*, *Clorinda*, *Anathyris*) and rhynchonellids are comparatively rare at the locality Branžovy. A weak encrustation of athyridids and spiriferids in Branžovy is more linked with their small size and shell morphology providing low hydrodynamic stability on sea floor.

Hosts dead or alive? – Boring endobionts commonly used dead shells. It is evident from bioerosion of inner side of brachiopod valves where the thickest shell parts were the most attractive sites for their activity. The originator of dendritic structures regardless its biological affinity definitely occupied dead shells, but might attack also external surface of living brachiopods. *Allonema* used dead shells but might encrusted also living brachiopods. It preferred sheltered sites, such as cavities, interpaces between costae and concave surfaces. These sites might be shaded when the valve was in hydrodynamically stable convex-up position.

Colonies of *Aulopora* sp. show oriented growth overwhelmingly toward and along anterior and anterolateral margin of host shell, distinct preference of costellate surfaces, and large convex substrates. Auloporid refused concave interior of brachiopod shells and planar surfaces. Distal parts of long corallites are gently bent toward commissure of host shell. Corallites mostly do not obstruct a commissure of the host but large colonies were able to cross host's commissure. This indicates that coral grew at already dead host or the coral was able exceed the protective function of host's mantle. If the latter

was a case, the brachiopod's metabolism was hindered by lost of ability to control food and oxygen inflow. Auloporid colonies also encrusted definitely dead shells of gastropods and corals because their corallites areally replaced sites of host's soft tissues.

Coral *Syringaxon* sp. used brachiopod shells both dead and alive or other dead coral. It is evident from larval settlement into interior of brachiopod valve. However, the coral attached to exterior of *Spinatrypa* caused deformation of brachiopod shell (Fig. 9M, N) and was definitely attached to living host.

Unnamend rugose coral is often attached on broken and corroded shells indicating the different life strategy. Preference of dead shell is evident. Whether the coral used alive brachiopods is unclear, but even large shell of *Havlicekia* must belong to dead specimens due encrustation of posterior shell edge by another encrusters.

Initial stage of bryozoan colony selected the most elevated sites. Top rims of auloporid corallites were completely overgrown by bryozoan colony (Fig. 6K, L). This indicates that bryozoan larva settled to already abandoned corallite because the larva of bryozoan hardly eliminated a protective ability of polype.

Craniid brachiopods definitely occupied dead shells, likely in cryptic concave surface (Fig. 6P). Life in cryptic habitat is common strategy of the Recent craniids (Bassett 1984, Emig 1997, Asgaard 2008).

Conclusions

Described fauna represents an example of diverse endo- and sclerobiont fauna with complex interactions in the Lochkovian of Bohemia. Silification preservation, unusual in Bohemian strata, provides local insight in structure of Lower Devonian benthic faunas of Bohemian type.

No simple equations can be made between encrusting organism and host substrate.

Most attractive substrates for encrusters were hydrodynamically stable brachiopod shells, *i.e.* larger shells with planoconvex profile, costate or costellate shells, and shells fixed by a pedicle. Shells of *Parmorthina*, *Isorthis* and *Spinatrypa* well meet these requirements. *Parmorthina* and *Isorthis* have likely root-like pedicle, were plenipectunculate, and the same is assumed in atrypids. Large but thin-shelled and reclining strophomenids and diminutive smooth-shelled and subglobose brachiopods were not stable enough for thriving encrusters growth. Each coral species exhibits distinct colonisation strategy.

Location, mode of growth and shape of tabulate coral *Aulopora* sp. indicate a control of larval settlement site followed by spation control of subsequent encrustation. Auloporids preferred elevated convex sites of living brachiopod host but also grew on freshly to lately dead shell.

There is possibility that auloporid occupation of shell commissure brought a brachiopod to the death. Auloporids were able to use also other substrate such as rugose coralla, dead corallites of other auloporids and vacant gastropod shells if these host substrates were sufficiently elevated. Auloporids made effort to target the special host and to select special place on host that enabled some sort of “topping”. This targeting brought some advantage to an auloporid colony by the higher intake of food. Colonies attached to living brachiopods were further favoured by inflow current produced by hosts.

Rugose coral *Syringaxon* sp. likely preferred substrate of dead host including coralla of the same species, but accidentally grew on brachiopod that was alive. *Syringaxon* sp. made effort to achieve substrate stable enough without a special relationship to the host.

Unnamed calceoloid rugose coral likely preferred dead shells and shell fragments. It overallly occupied smaller substrates than other corals. It was able to use any stable substrate, which allowed an expansion of the colony.

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