

EPISKELETOBIONTS OF LARGE RUGOSE CORALS FROM THE MIDDLE DEVONIAN MESOPHOTIC PALAEOENVIRONMENT RECORDED IN THE POKRZYWIANKA BEDS (HOLY CROSS MOUNTAINS, POLAND)

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Abstract: Organisms encrusting corals from a coral horizon encountered in a trench in the Middle Devonian (Givetian) Pokrzywianka Beds of the classic Grzegorzowice-Skały section in the Holy Cross Mountains, Poland, are described and analyzed in the context of their palaeoecological and palaeoenvironmental background. These episkeletobionts form rather a low-diversity community, dominated by microconchid tubeworms, crinoids, and tabulate corals. The last group, however, is especially diverse at the family level, represented by auloporids, alveolitids, coenitids and favositids. These episkeletobionts are considered to have developed in a low-light, lower mesophotic palaeoenvironment, as evidenced by the presence of platy, alveolite tabulate coral in the deposits studied. This microconchid-crinoid-tabulate-coral community differs from other Givetian communities from the Holy Cross Mountains (Laskowa and Miłoszów), which also are considered to have developed in low-light habitats. The differences in taxonomic composition of episkeletobionts between these three localities most probably resulted from specific local conditions, related to bathymetry (light levels, nutrient levels), the specific nature of the hosts/substrates occupied, and also differences in larval dispersal patterns. This, in turn, shows that various encrusting communities may have inhabited seemingly similar, marine habitats within a given time interval and neighbouring areas, which may have serious implications for large-scale comparisons of biodiversity within a given palaeoenvironment.

Key words: Epibionts, hard substrates, Palaeozoic, palaeoecology.

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INTRODUCTION

The term *episkeletobiont* was introduced by Taylor and Wilson (2002; see also Taylor and Wilson, 2003) in order to encompass the organisms (animals or plants) encrusting any organic, hard substrate (dead or alive). Although the widely used term *epibiont* is restricted by marine biologists to organisms attached to the surfaces of living hosts (Wahl, 1989), it was often used and is still used by palaeontologists in a more general meaning, regardless of whether the

host was dead or alive during colonization (see Walker and Miller, 1992; Taylor and Wilson, 2003).

Regardless of the terminology used, a wide variety of metazoan encrusting organisms fossilize very well and thus provide a valuable source of information on many palaeobiological aspects since the Cambrian (Taylor and Wilson, 2003; Zhang *et al.*, 2010, 2020; Topper *et al.*, 2014; Vinn, 2017; Zamora *et al.*, 2017). However, the evident abundance

and diversity of such encrusting communities increased during the Ordovician, called a ‘golden age’ for epibionts by Taylor and Wilson (2003), and the Silurian, when diverse groups of both solitary and colonial, skeletal hosts appeared and spread globally. During the Devonian, the episkeletobiont communities are best known on shell-bearing hosts, especially brachiopods (e.g., Hoare and Steller, 1967; Kesling *et al.*, 1980; Alvarez and Taylor, 1987; Bordeaux and Brett, 1990; Zapalski, 2005; Mistiaen *et al.*, 2012; Zatoń *et al.*, 2017). Interestingly, other common Devonian benthic fauna, i.e., rugose corals, are much less recognized with respect to their episkeletobiont inhabitants, which were reported merely by a handful of sources published to date (Liddell and Brett, 1981; Baird and Brett, 1983; Rakowicz, 2010; Balon, 2015; Zatoń *et al.*, 2015; Zatoń and Wrzolek, 2020).

Recently, Zatoń and Wrzolek (2020) investigated a rich collection of encrusted rugose corals from the Givetian siliciclastic deposits in the Miłoszów settlement of Nieczulice village, which is geologically situated in the northern, Łysogóry region of the Holy Cross Mountains, Poland (Fig. 1). In the present paper, the authors focused on the rugose corals from carbonate deposits of the nearby Skały village, where a classic section of the Middle Devonian Pokrzywianka Beds (belonging to the Silurian to Middle Devonian Grzegorzowice-Skały section; Pajchłowa, 1957) occurs. The main aim of the present study is to characterize the episkeletobiont communities inhabiting the rugose corals coming from a low-light, mesophotic ecosystem, their relationships to each other and to the hosts, and to compare them with other, well elaborated Middle Devonian episkeletobiont communities in the context of the palaeoenvironments inhabited.

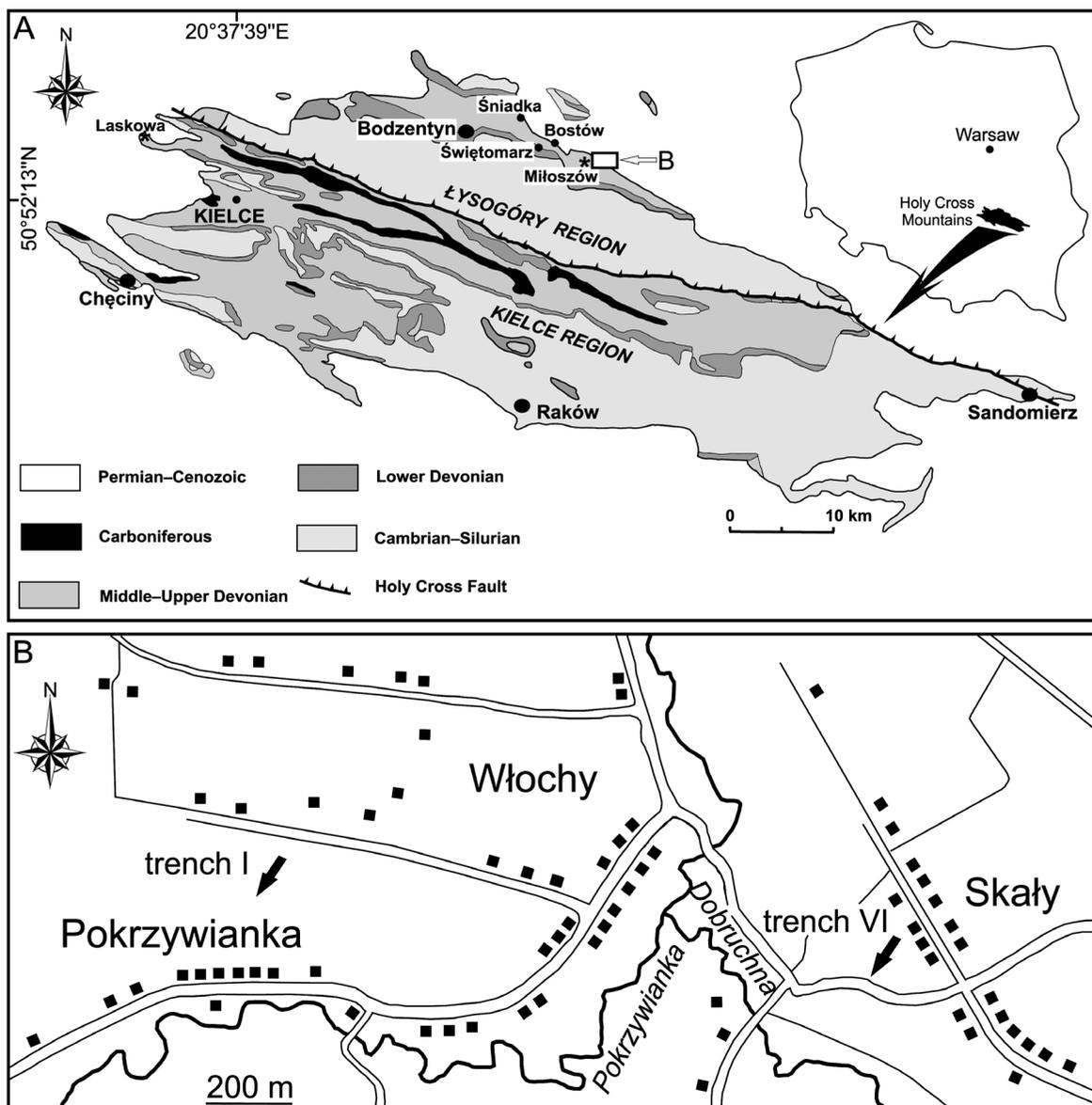


Fig. 1. Location of study area. **A.** Geological sketch map of the Holy Cross Mountains (slightly modified after Malec, 2012), with the Pokrzywianka Beds studied at Skały and at Pokrzywianka indicated (rectangle), and comparative sites at Miłoszów and Laskowa (asterisks). **B.** Sketch map showing location of the trenches cutting the Pokrzywianka Beds: trench I at Pokrzywianka, where the lithological section was made, and trench VI at Skały, where the rugose corals for the present study were collected.

GEOLOGICAL SETTING

General outline

The study area is located in the middle part of the Łysogóry block (also known as the Łysogóry region) which forms the northern part of the Holy Cross Mountains (Central Poland; Fig. 1A). The area investigated is situated in the southern limb of the Bodzentyn syncline (Czarnocki, 1950a; Filonowicz, 1968, 1969; Mizerski, 1995), which, like its northern limb, is made up of Lower Devonian terrigenous deposits, and its axial part is composed of lithologically differentiated, but mainly carbonate complexes of the Middle and Upper Devonian, attaining ca. 2,000 m in thickness (Szczepanik *et al.*, 2002; Narkiewicz, 2011). The lowest part of the Middle Devonian (lowest Eifelian) consists of limestones of the Dąbrowa Member, representing the uppermost part of the Grzegorzowice Formation (Malec 2005). At a higher level, the Middle Devonian sequence, mainly consists of lower to upper Eifelian dolostones of the Wojciechowie Beds, representing carbonate platform deposits (Pajchłowa, 1957; Kłossowski, 1985; Skompski and Szulczewski, 1994; Malec and Turnau, 1997; Narkiewicz and Narkiewicz, 2010). The overlying, upper Eifelian–upper Givetian (Skały Beds, Świętomarz Beds, Pokrzywianka Beds, Nieczulice Beds) and Upper Devonian deposits (Frasnian Kostomłoty Beds and Famennian marly complex) originated in an open-marine palaeoenvironment, ranging from shallow- to deep-shelf settings (Czarnocki, 1950a; Pajchłowa, 1957; Kościelniakowska, 1967; Szulczewski, 1995; Malec, 1996; Narkiewicz *et al.*, 2011).

The Pokrzywianka Beds, which are the focus of the present study, consist of a middle Givetian succession, 9–10 m thick, representing the largest organic buildup in the entire Devonian section of the Łysogóry region. The buildup consists of reefal limestones, the framework of which is mainly formed by stromatoporoids and corals (Czarnocki, 1950a; Różkowska, 1956; Pajchłowa, 1957; Stasińska, 1958; Filonowicz, 1968; Szulczewski, 1995; Halamski, 2005; Malec, 2008). The deposits of the Pokrzywianka Beds crop out solely in the eastern part of the Bodzentyn syncline, between the villages of Skały and Pokrzywianka (Fig. 1B), where they do not form a single horizon, but rather a few larger (up to 1 km in length) lenses (Czarnocki, 1956), bounded at the base by the Świętomarz Beds (sandstones, mudstones) and by the Nieczulice Beds (shales) at the top (Czarnocki, 1950a). In the area situated further to the west (ca. 4 km from Pokrzywianka), these deposits were recognized as far away as at Bostów Village (in the drill-core Bostów 7), where they occur in the form of 1-m-thick, residual limestones and marls with brachiopods and corals (Czarnocki, 1950b; Malec, 2007). West of Bostów, the Pokrzywianka Beds wedge out and the Świętomarz Beds directly make contact with the Nieczulice Beds at the top. Such a situation occurs in the Świętomarz-Śniadka section situated ca. 7 km westwards from Pokrzywianka (Filonowicz, 1968; Kłossowski, 1985; Malec, 2012).

Limestones with a coral fauna, occurring above the Świętomarz Beds in the Skały section, were described for the first time by Sobolev (1904, 1909), who considered them as a local age and facies equivalent of the Upper

Devonian Kadzielnia Limestone, described earlier in the Kielce region of the Holy Cross Mountains. Czarnocki (1950a) assigned these limestones to the lower Frasnian Pokrzywianka Beds. Later, the limestones were dated as late Givetian (Różkowska, 1956; Pajchłowa, 1957; Stasińska, 1958; Biernat, 1964; Filonowicz, 1968) or correlated with the Frasnian Kadzielnia Limestone in the Kielce region of the Holy Cross Mountains (Orłowski and Radwański, 1986). For detailed results of conodont- and spore-based age determinations, see below.

Litho-palaeontological characteristics and age of the Pokrzywianka Beds

In the stratotype section at Pokrzywianka (Fig. 1B), the Pokrzywianka Beds occur as a 9-m-thick complex, comprising biostromal limestones with a subordinate contribution of marls and marly shales at the top (Fig. 2). The lower boundary of the Pokrzywianka Beds was arbitrarily defined by the appearance of organodetritic, bedded limestones without terrigenous material (Malec, 2008). The base of the Pokrzywianka Beds consists of 0.5-m-thick, dark-grey, bioclastic packstones with brachiopods, ostracods, calcispheres and charophyte gyrogonites. Above, a ca. 0.7-m-thick biostrome made up of massive stromatoporoids occurs. It is overlain by ca. 4.8-m-thick, dark-grey, brachiopod-crinoid wackstones and packstones, with massive and branching tabulates and rare laminar stromatoporoids, and large solitary tetracorals in the upper part. The top of the Pokrzywianka Beds (ca. 3 m) is composed of organodetritic packstones and grainstones with massive and branching tabulates, intercalated with grey marls and marly shales with common micro- and macrofaunas. Upper part of the Pokrzywianka Beds is at the top of the marly shales with a rich benthic fauna. Higher above, these deposits directly contact with grey-green shales representing the lower part of the Nieczulice Beds.

Deposits of the Pokrzywianka Beds contain a rich fauna (Fig. 2), in which corals and stromatoporoids occur nearly throughout the entire unit. In the lower part of the Pokrzywianka Beds, the limestones are almost exclusively made up of massive stromatoporoids referable to *Hermatostroma* with a sporadic contribution of the fasciculate tabulates *Syringopora*. Higher up in the section, rare laminar stromatoporoids and a diversified assemblage of tabulates, such as different species of *Alveolites*, *Crassialveolites*, *Heliolites*, as well as *Syringopora*, *Platyxum*, *Coenites* and *Thamnopora*, occur. In the middle part of the Pokrzywianka Beds, within a stratigraphically narrow interval (1.8 m), solitary tetracorals (see below) occur. In the same part of the section, the chaetetid sponge *Chaetetes* occurs, as well. In the marly intercalations in the top part of the Pokrzywianka Beds, rich assemblages of micro- and macrofauna, represented by brachiopods, trilobites, crinoid ossicles, echinoid spines, gastropods, sponge spicules, bryozoans, ostracods, tentaculitids and foraminifers also have been noted (Fig. 2).

No biostratigraphically diagnostic fossils have been documented in the Pokrzywianka Beds. In the ostracod assemblages of the topmost part of the beds, the species

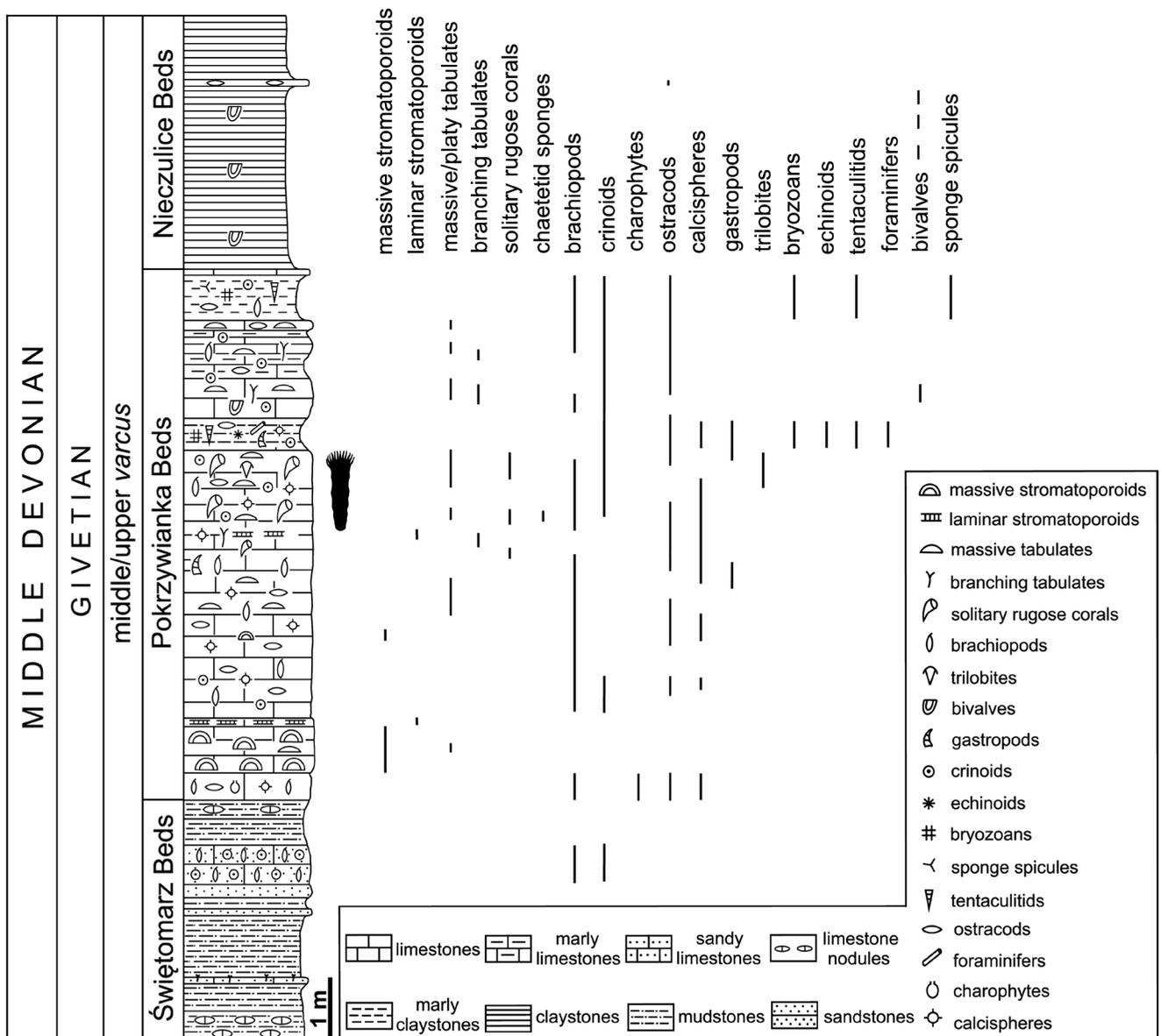


Fig. 2. Lithostratigraphic section of the Givetian deposits in trench I at Pokrzywianka, Holy Cross Mountains, showing the ranges of occurring fossil groups. The black silhouette points to the rugose coral interval sampled.

are characteristic for the Givetian in general (Malec and Turnau, 1997). A Givetian age may also be supported by the presence of a tabulate '*Coenites*' *laminosa*, as coenitids did not survive the late Givetian crisis (Hill, 1981; Zapalski, 2012). On the other hand, the age of the Pokrzywianka Beds may be established indirectly from dating the underlying Świętomarz Beds and the overlying Nieczulice Beds. On the basis of miospores, it has been established that sedimentation of the siliciclastic deposits of the Świętomarz Beds took place in the palynological Ex2 Zone, which corresponds to the middle to upper *varcus* conodont Subzone (Turnau and Racki, 1999). The lower part of the Nieczulice Beds was palynologically dated as the Ex3 Zone, which corresponds to the middle/upper *varcus* subzonal interval (Turnau and Racki, 1999). The miospore assemblages in the upper part of the Nieczulice Beds in the Skąły section date these deposits in the lower part of the *optivus-krestovnikovii* Zone, while conodonts point to the *hermanni* Zone (Malec and Turnau,

1997). Thus, the age of the Pokrzywianka Beds may be considered as the middle-late *varcus* Subzone. In the light of the data mentioned above, the correlation of the Pokrzywianka Beds with the Kadzielnia Limestone of the southern Kielce region (Orłowski and Radwański, 1986) must be refuted, as the latter deposits are dated as early Frasnian (Szulczewski, 1971; Narkiewicz *et al.*, 1990; Racki, 1993).

Depositional environment of the Pokrzywianka Beds

The deposits of the Pokrzywianka Beds originated during a progressive reduction in supply of terrigenous material to the basin and the development of the organic buildup devoid of siliciclastics indicates its total cessation. This process was connected with a rather rapid sea-level rise, enabling the stromatoporoid and coral fauna to develop in relatively clean waters, as evidenced by the presence of stromatoporoids, which in turbid waters would have been commonly

clogged (e.g., Łuczyński, 2020). The emergence of the organic buildup on the siliciclastic deposits of the Świętomarz Beds, with a contribution of calcareous nodules and sandy limestones with brachiopods, crinoids and branching tabulates in their upper part, make the deposits similar to patch reefs developed elsewhere on the prodelta areas of delta systems (Wilson, 2005; Saller *et al.*, 2010; Morsilli *et al.*, 2012; Rösler *et al.*, 2015; Santodomingo *et al.*, 2015). The sedimentation of carbonate deposits of the Pokrzywianka Beds proceeded gradually, with a large contribution of terrigenous deposits in their basal part. The main part of the carbonate deposits of the Pokrzywianka Beds, however, shows that the sequence originated in an already drowned prodelta, without a supply of terrigenous sediment (Malec, 2012).

The massive stromatoporoids, building the basal part of the Pokrzywianka Beds in the Pokrzywianka section, may indicate a shallow water environment, probably no more than 20 m in depth (Nose *et al.*, 2006; Macnell and Jones, 2016; Jakubowicz *et al.*, 2019) during sedimentation of this part of the section, but without detailed investigation of their external morphology and arrangement of latilaminae, their palaeoenvironmental interpretation may be uncertain (Łuczyński, 2003). These organisms inhabited shallow-marine environments, characterized by considerably agitated but clean waters and probably a high light level (Kershaw, 2012, see also discussion in Łuczyński, 2020). Assemblages occurring in the upper part of the Pokrzywianka Beds are represented by laminar stromatoporoids, solitary rugose corals as well as branching and platy tabulate corals (Kubiszyn, 2018), and indicate a progressive drowning of the organic buildup. The presence of wackstones and packstones with common organic detritus in that part of the section indicates that sedimentation proceeded on the slope of the organic buildup. The common occurrence of platy *Alveolites* and *Crassialveolites* tabulates, with a subordinate contribution of branching tabulates in the upper part of the Pokrzywianka Beds, indicates mesophotic environments, which, depending on the optical quality of water, may occur at depths of up to 150 m in modern tropical and subtropical areas (e.g., Kahng *et al.*, 2010; Baker *et al.*, 2016; Muir and Pichon, 2019; Pyle and Copus, 2019). Zapalski *et al.* (2017) identified a nearby site at Skąły (late Eifelian; lithological sets XIV to XVIII after Pajchłowa, 1957, lower part of the Skąły Beds) as a typical Mesophotic Coral Ecosystem, thus indicating lower parts of the euphotic zone. Assuming that the pattern of colony-type zonation is similar in modern and Palaeozoic reefs (see discussion by Zapalski *et al.*, 2017), one can infer that the lower part of the Pokrzywianka Beds reflects an upper mesophotic environment and their upper part, with the predominance of platy tabulates, indicates a lower mesophotic environment. Shallow-water coral communities, although rare, usually have a significant contribution from massive tabulates (Król *et al.*, 2021; Zapalski *et al.*, 2021), and such forms are absent in the upper parts of the Pokrzywianka Beds.

The Holy Cross Mountains area was located within the equatorial zone during the Givetian (Golonka, 2000; Belka and Narkiewicz, 2008). Thus, by analogy to the modern coral fauna in the tropical mesophotic ecosystem, e.g., that of American Samoa (e.g., Bare *et al.*, 2010), the occurrence

of platy and branching tabulate corals indicates that during sedimentation of the upper part of the Pokrzywianka Beds, the lower limit of the mesophotic zone could have even been below 100 m of water depth. While such an analogy is only an estimate, as mesophotic communities are indeed variable (Pyle and Copus, 2019), it seems appropriate to assume such an order of magnitude in depth. Such a depth estimate may be supported by the claystones with a pelagic fauna in the Nieczulice Beds, resting directly upon the Pokrzywianka Beds.

In the Skąły section, located 2 km east of Pokrzywianka (Fig. 1B), however, sedimentation of the lower part of carbonate deposits of the Pokrzywianka Beds lasted longer in a relatively shallower environment. This is supported by the presence of massive stromatoporoids within the 5-m-thick, basal part of the section (trench VI – J. Malec, unpublished data).

Sedimentation of biostromal limestones of the Pokrzywianka Beds in the eastern part of the Bodzentyn syncline most probably occurred in the proximal part of a prodelta (e.g., Saller *et al.*, 2010; Morsilli *et al.*, 2012). This is supported by the large contribution of sandy slump structures within the mudstone and sandstone deposits occurring in the underlying Świętomarz Beds. These deposits wedge out toward the west of the Łysogóry region, according to the direction of progradation of the prodelta deposits of the Świętomarz Beds (Malec, 2012). The lateral expansion of the Pokrzywianka limestones was controlled by the ecological demands of the coral-stromatoporoid fauna. The deepening of the basin toward the west of the Bodzentyn syncline prevented the development of these organisms in the area west of Bostów (Malec, 2007). Sedimentation of the relatively deep-water clay deposits of the Nieczulice Beds above the Pokrzywianka Beds, terminated the development of the organic buildup close to the middle/upper *varcus* Subzone boundary (Turnau and Racki, 1999).

The appearance of the biostromal deposits of the Pokrzywianka Beds in the eastern part of the Łysogóry region during the Givetian coincided with an initial phase of transgression, related with eustatic sea-level rise during the middle *varcus* chrone. That event corresponds to the T-R cycle IIa of Johnson *et al.* (1985), recorded in the Middle Devonian section of the Łysogóry region (Malec and Turnau, 1997; Racki, 1997; Malec, 1999; Racki and Narkiewicz, 2000; Racki and Turnau, 2000; Narkiewicz *et al.*, 2011). Rapid eustatic sea-level rise, occurring during sedimentation of the pelagic claystones of the Nieczulice Beds, should be correlated with a eustatic, transgressive pulse starting with the Taghanic event (Walliser, 1996). The maximum transgression occurred during the late Frasnian (Morrow and Sandberg, 2008). This event was responsible for the demise of coral and stromatoporoid faunas in the Łysogóry basin, as well as in the Kostomłoty subbasin in the western part of the Kielce region (Czarnocki, 1950a; Racki *et al.*, 1985; Malec, 2007).

MATERIAL AND METHODS

The section was measured in trench I at Pokrzywianka, while the coral specimens used in the present study were

collected from the Pokrzywianka Beds (= set XXVII *sensu* Pajchłowa, 1957) section, exposed in trench VI at Skały (Figs 1B, 2). For the sake of clarity, it is noteworthy that the Pokrzywianka Beds occurring in trench VI at Skały were described as outcrop 129 by Pajchłowa (1957), outcrop 6 by Malec and Turnau (1997, fig. 2) and outcrop SK-7 by Halamski (2009). At Pokrzywianka (trench I), the section encompassing the Świętomarz and Pokrzywianka Beds was labelled trench 2 by Malec (2012, fig. 8; outcrop P-1 *sensu* Halamski, 2009).

For the present study, 29 rugose corals were selected. First, the corals were examined under the Nikon SMZ 1000 binocular microscope and all the episkeletobionts observed were identified at the lowest possible taxonomic (usually generic) level and counted in order to decipher their diversity and abundance. Here, as with the solitary encrusters, each colony also was treated as one individual. The corals also were searched for *syn vivo* (during the host's life) relationships in the form of embedded epibionts within the skeleton of the coral host. Any cases of potential competitive interactions (assuming that the encrusted epibiont was alive during the interaction) for space between encrusters (overgrowth and fouling) also were noted on the corallite exteriors and, in the case of overgrowths, an overgrowth ability index (ratio of winners to all encounters for a given epibiont, see Alvarez and Taylor, 1987) was calculated in order to show which epibiont might have been the most efficient in the competition with other encrusters for space. Calculations and data presentations in the form of graphs were done using the Microsoft Excel and PAST software (Hammer *et al.*, 2001).

After inspection for epibionts, the corals were sectioned for the purpose of taxonomic identification and to check on whether some previous interactions between epibionts preserved within the thick encrustation envelope developed around the corallites, did not occur after the death of the overgrown/fouled organisms. Over one hundred thin sections and a few acetate peels of transverse, longitudinal, as well as off-axis, longitudinal sections, were made. Before being photographed, the majority of specimens were coated with ammonium chloride. Only the smallest encrusters were photographed in an uncoated state, using camera Imaging Source DFK NME 33UX265 and NIS-Elements D imaging software.

The coral fossils are housed at the Polish Geological Institute-Polish Research Institute in Kielce, Poland, designated as OS-D/1. The thin sections of rugose corals studied are housed at the Institute of Earth Sciences, University of Silesia, Sosnowiec, under the collection number as GIUS 4-3738.

RESULTS

Host corals

The samples studied are dominated by the large, straight, only slightly curved, solitary siphonophrentid coral *Enallophrentis polonica* (Sobolev, 1904; Fig. 3A–B). The specimens are invariably present as the fragments of larger corallites (diameters from 40 to 50 mm). Possibly, owing to their great length, excavation of a trench typically yielded only small fragments. Their original length could have attained 0.5 m or more. Part of the material does not show any fracturing and presents the original, circular,

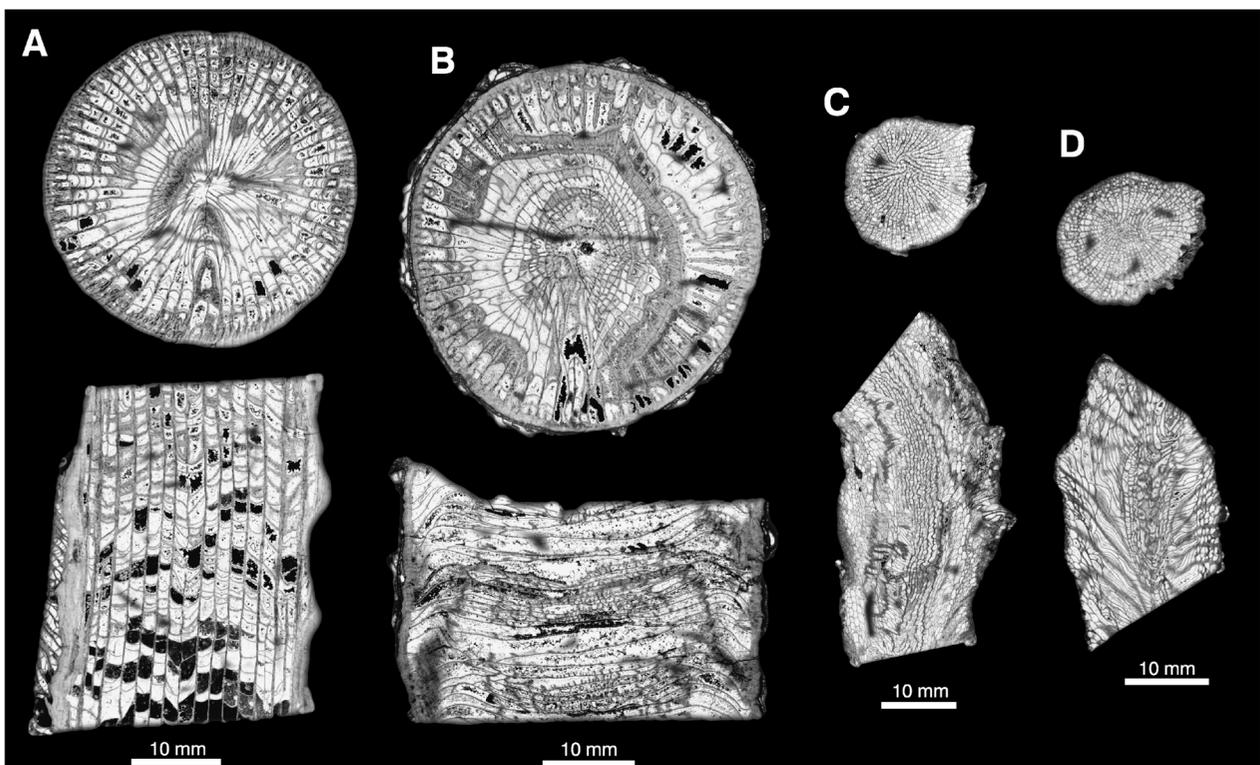


Fig. 3. Thin sections of rugose corals from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI. **A–B.** *Enallophrentis polonica* (Sobolev, 1904) in transverse and longitudinal sections; A – GIUS 3738 JM 32B; B – GIUS 3738 JM 39H. **C.** *Acanthophyllum* sp. in transverse and longitudinal sections, GIUS 3738 JM 38B. **D.** *Stringophyllum* sp. in transverse and longitudinal sections, GIUS 3738 JM 39A.

transverse sections, but some specimens are partially, or completely crushed.

The smaller, solitary corals are less numerous, possibly owing to sampling bias. They are represented by so far undetermined species of the ptenophyllid genus *Acanthophyllum* (Fig. 3C) and the stringophyllid, *Stringophyllum* (Fig. 3D). These are much smaller specimens, generally with a cylindrical, or slightly curved appearance, with diameters from 23 to 30 mm. Of note are some specimens indicating *post-mortem* corrosion: with the part resting on bottom preserved intact, and the upper part corroded and, in some cases, encrusted by epibionts.

It must be noted that the taxonomic composition of the specimens studied here is different from that previously collected by one of us (TW) from the Pokrzywianka Beds at Skały and at Nieczulice: among over a hundred sectioned specimens in this “old collection”, the rugose corals were represented by cystiphyllids (three specimens), *Enallophrentis polonica* (11 specimens, see Wrzolek, 2002), *Acanthophyllum* (18 specimens), *Stringophyllum* (22 specimens, including some *S. acanthicum* and *S. schwelmense*), *Neospongophylloides* sp. (12 specimens), *Phillipsastrea sobolewi* (11 specimens, see Wrzolek, 2005), and other, as yet unidentified rugosans (eight specimens). It seems that the sample from trench VI studied here represents a peculiar horizon, and a special environment within interval represented by the Pokrzywianka Beds.

Episkeletobiont assemblage

The episkeletobionts, colonizing the rugose corals, are represented by both solitary (foraminifers, microconchids, *Anticalyptrea*, brachiopods, crinoids, rugose corals) and colonial organisms (tabulate corals, stromatoporoids, bryozoans and hederelloids). The host corals were colonized

by a minimum of 1 and a maximum of 23 epibionts, with an average of 10 encrusters. The diversity of epibionts ranges from 1 to 8 (average 4) taxa present on a single coral host (see Appendix 1).

The most abundant, solitary epibionts are microconchids (Figs 5A, 8B, C). These tiny, spirorbiform tentaculitoids here mostly are represented by the abraded tubes of planispirally-coiled specimens. However, those sufficiently well-preserved show the presence of two forms: 1) smaller, more evolute and ribbed tubes and 2) larger, more involute, smooth tubes with faint, perpendicular ridges. The first one is similar to the species *Palaeoconchus sanctacrucensis* Zatoń & Krawczyński, 2011, known from the upper Eifelian of Skały (Zatoń and Krawczyński, 2011a). The second, larger form, here represented by only three specimens, may represent an undescribed species. On a single coral host, as few as one to as many as 16 microconchid specimens (on average 5 specimens) were found. Microconchids have been noted on 93% corals (Tab. 1) which make them the commonest encrusting group in the assemblage. The next abundant solitary group is crinoids (Fig. 4), preserved solely as holdfasts attached to the rugose epithecae (Fig. 5D, E). From one to as many as seven holdfasts may occur on a single coral. Crinoids are present on half of the coral hosts (Tab. 1).

Two holdfasts are attached to abraded coral thecae. The rest of the holdfasts are attached either to intact coral thecae or to other, colonial, sheet-like epibionts. Foraminifers and brachiopods have a similar level of abundance, being rather minor components in the assemblage (Fig. 4; Tab. 1). Foraminifers, present on only six corals, are represented by the ‘vermiform’ *Tolypamma* (Fig. 5B), similar to those occurring on the Givetian corals at Miłoszów in the Holy Cross Mountains (Zatoń and Wrzolek, 2020). Brachiopods occur as small-sized attachment valves on five coral hosts. Tentaculitoids of the genus *Anticalyptrea* are very rare on

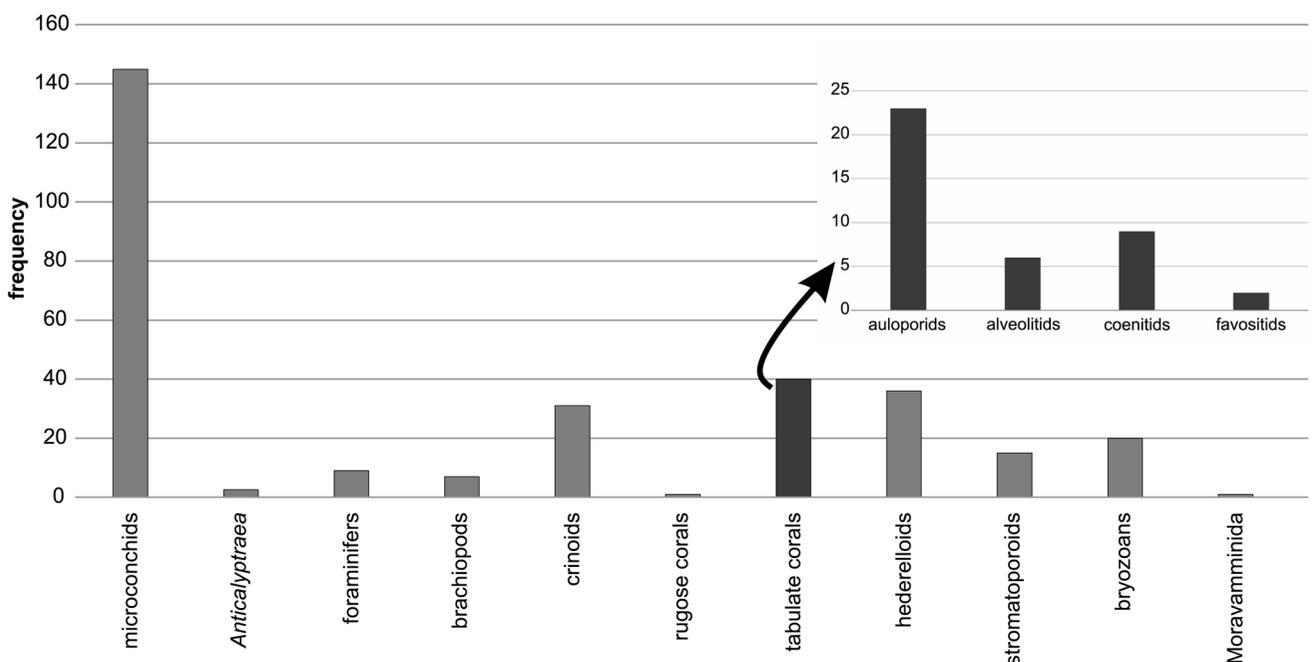


Fig. 4. Diagrams showing frequency of particular episkeletobiont groups and tabulate coral families overgrowing the rugose corals from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI.

Table 1

Composition of episkeletobionts from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI, and their contribution to occupation of the rugose coral hosts.

Episkeletobiont taxon	No. of coral hosts occupied
Foraminifera – <i>Tolypammina</i> sp.	6 (20%)
Stromatoporoidea	14 (48%)
Rugosa	1 (3%)
Tabulata	
Auloporida	
– <i>Aulopora</i> sp.	16 (55%)
– <i>Mastopora</i> sp.	
Alveolitida	
– <i>Alveolites</i> sp.	6 (20%)
Coenitida	
– <i>Roseoporella</i> sp.	9 (31%)
Favositida	
– <i>Favosites</i> sp.	2 (7%)
– <i>Parafavosites</i> sp.	
Microconchida	
– <i>Palaeoconchus</i> sp. 1 (smooth)	27 (93%)
– <i>Palaeoconchus</i> sp. 2 (ribbed)	
Anticalyptrea	2 (7%)
Hederelloidea	21 (72%)
Brachiopoda	4 (14%)
Crinoidea	16 (55%)
Bryozoa	
Cystoporida	
– <i>Fistulipora</i> sp.	10 (34%)
Fenestrata	
– Fenestrata gen. et sp. indet.	1 (3%)
Problematica	
Moravaminida	1 (3%)

the corals studied, as only three individuals were found encrusting two coral hosts (Fig. 4; Tab. 1). These encrusters have a somewhat microconchid-like external appearance in the juvenile stage (Fig. 5A) but are distinguished from the latter by the tube-penetrated pseudopunctae, oriented in an opposite (inward) direction (Vinn and Isakar, 2007). Rugose corals as epibionts are even more rare here, as only one specimen was found encrusting a larger host.

Colonial epibionts, although numerically less abundant than solitary microconchids, can be the predominant encrusters in terms of substrate occupation. The most diverse and numerous of all colonial epibionts are tabulate corals (Fig. 4; Tab. 1). According to their numerical abundance, they are represented by auloporids (*Aulopora*, *Mastopora*, Figs 5C, 6A), coenitids (*Roseoporella*, Figs 6D, 8A, B), alveolitids (*Alveolites*, Fig. 6C) and favositids (*Favosites*, *Pachyfavosites*, Fig. 6B). Alveolitids and coenitids, although less numerous with respect to the number of hosts occupied than auloporids, owing to their sheet-like morphology, can encrust nearly the entire corallite surface of a host

(Fig. 8A, B). The tabulate corals are followed by hederelloids, enigmatic metazoans (Wilson and Taylor, 2001; Taylor and Wilson, 2008) previously assigned to cyclostome bryozoans (e.g., Kiepusa, 1973). Their runner-like colonies (Figs 5F, 8B), represented as one to six colonies on a single rugose coral, encrust more than half of the coral hosts. Bryozoans are rather rare here, represented mainly by the bases of arborescent forms, one of which belonged to a fenestrate type (Fig. 7A), while the others are unidentified (Fig. 8B). The sheet-like colonies belong to the cystoporate *Fistulipora* (Fig. 7B). More common with respect to the number of corals occupied, are sheet stromatoporoids, which in some cases encrust nearly the entire coral surface, together with all epibionts encountered (Fig. 8C, D). One problematic encruster, which may be a representative of Moravaminida (Fig. 7C), an *incertae sedis* taxon similar in characteristics to both algae and foraminifers (Falahatgar *et al.*, 2018), was also observed. A single, transverse section through a corallite of *Enallophrentis polonica* also shows the presence of the encrusting calcimicrobe *Girvanella* (Fig. 7E).

Traces of endolithic organisms (endoskeletobionts) are much rarer and consist of probable *Clionolithes* (Fig. 8A, B), which is considered to be a trace left by sponges (Wisshak, 2017).

Overgrowth and fouling interactions

Overgrowth and fouling are two types of competitive interaction for space between encrusters. Fouling results from the settlement of the larva on the surface of another, previously established individual. Overgrowth occurs, when one or both encrusters sharing the same substrate encroach, come into contact during their growth and overgrow the encounter. When both encrusters start to overgrow each other, then there is reciprocal overgrowth. Unlike fouling and overgrowth, reciprocal overgrowth shows unequivocal *syn vivo* (during life) interaction between encrusters (e.g., Taylor and Wilson, 2003; Taylor, 2016). However, as cases of reciprocal overgrowth are usually very much limited in a given fossil assemblage, they do not indicate any competitive superiority for space (Zatoń *et al.*, 2011). Thus, cases of overgrowth and fouling both may (with some limitation) shed light on competitive dominance within a given fossil encrusting assemblage. Of course, the ideal situation is when it is known that the overgrown or fouled organism was alive during the interaction. In the fossil record, however, except for the situation of reciprocal overgrowth mentioned above, usually this is not known unless some skeletal response of the overgrown organism is visible (Tapanila, 2008). However, even without such evidence, one can assume that the interactions took place, especially when there are no signs of *post-mortem* encrustation in the form of e.g., 1) the presence of the abraded skeleton of the encrusted organism, or 2) the presence of a thin, micritic coating or sediment between the overgrown and overgrowing organisms attesting to the fact that some time passed before the interaction took place. As evidenced from thin sections, in the assemblage studied, there are cases, in which already abraded skeletons were overgrown, indicating *post-mortem*

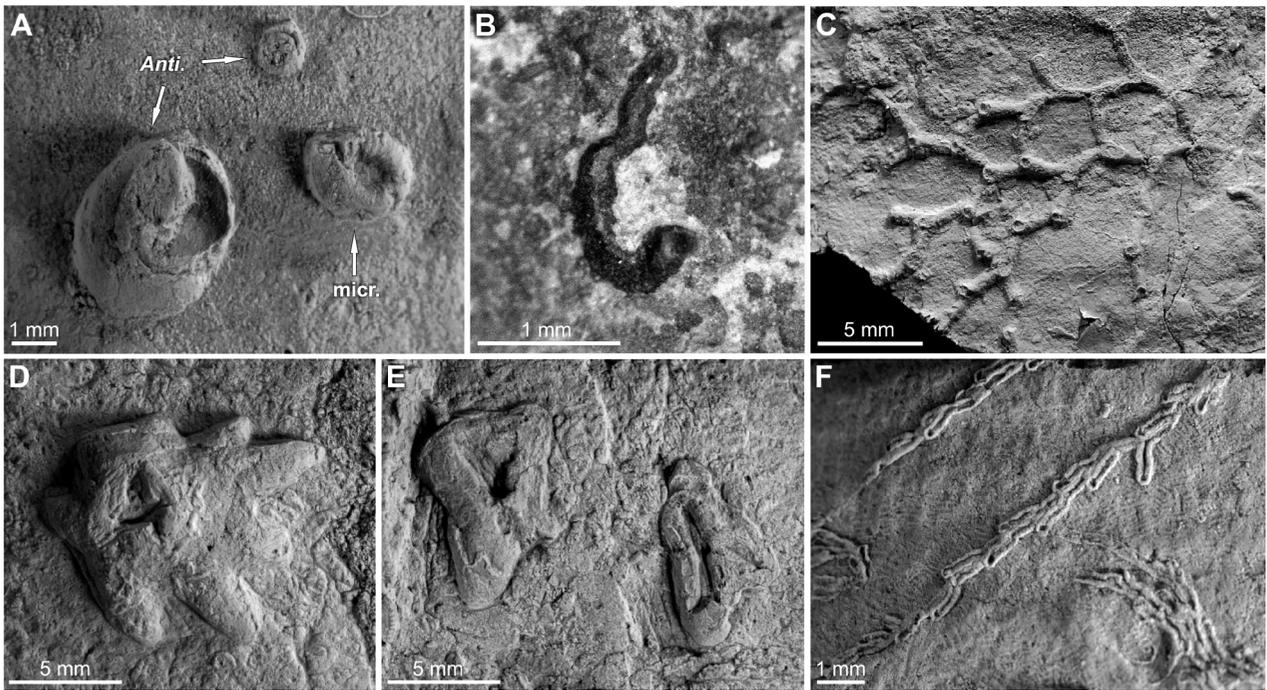


Fig. 5. Episkeletobionts on rugose coral from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI. **A.** Microconchid *Palaeoconchus* (micr.) and tentaculitoid *Anticalyptrea* (Anti.) encrusting *Enallophrentis polonica* (Sobolev, 1904). **B.** Foraminifer *Tolypammina* encrusting *Acanthophyllum* sp. **C.** Tabulate corals *Aulopora* sp. encrusting *Enallophrentis polonica* (Sobolev, 1904). **D, E.** Crinoid holdfasts encrusting a sheet-like stromatoporoid covering *Enallophrentis polonica* (Sobolev, 1904). **F.** Hederelloids encrusting *Enallophrentis polonica* (Sobolev, 1904).

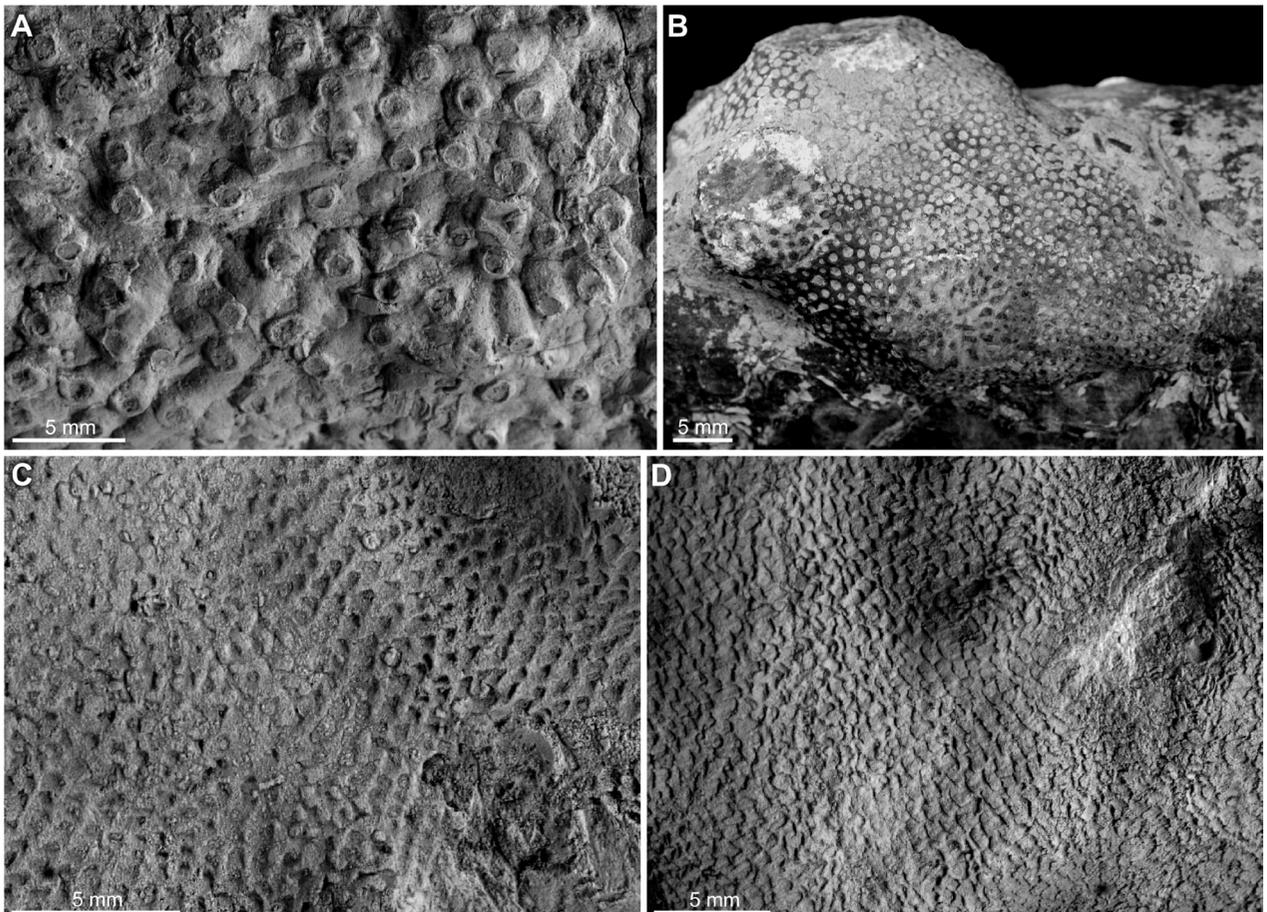


Fig. 6. Tabulate corals encrusting rugose corals *Enallophrentis polonica* (Sobolev, 1904) from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI. **A.** Auloporidae tabulate coral *Mastopora* sp. **B.** Favositid tabulate coral *Pachyfavosites* sp. **C.** Alveolitid tabulate coral *Alveolites* sp. **D.** Coenitid tabulate coral *Roseoporella* sp.

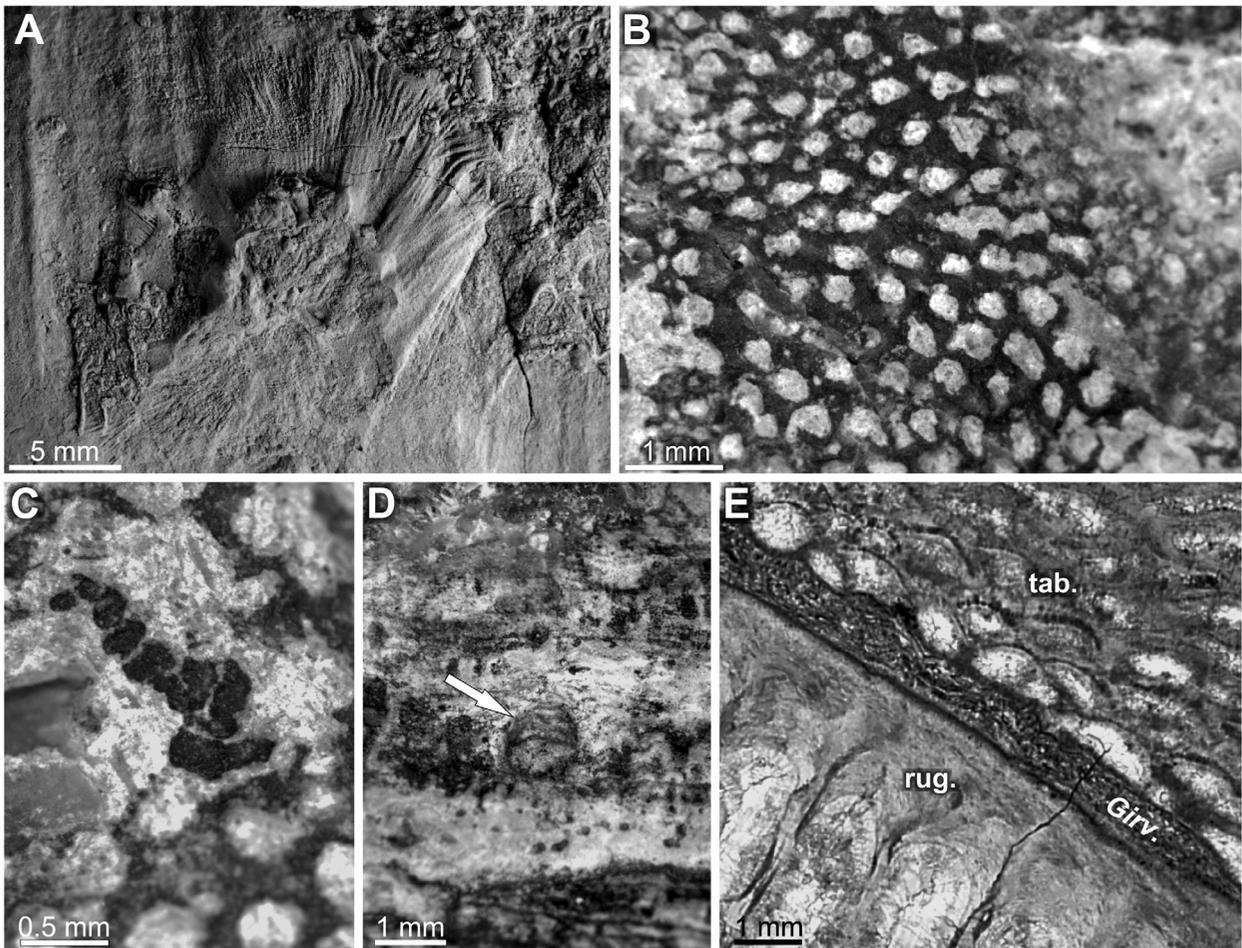


Fig. 7. Episkeletobionts on rugose corals from the Pokrzywianka Beds at Skąły, Holy Cross Mountains, trench VI. **A.** Attachment base of a fenestrate bryozoan. **B.** Cystoporidae bryozoan *Fistulipora* sp. **C.** Problematic microfossil of the group Moravamminida attached to a cystoporidae bryozoan *Fistulipora* sp. **D.** Bioclaustated tube (arrowed) of undetermined organism (?hederelloid). **E.** Colonies of calcimicrobes *Girvanella* (*Girv.*), encrusting the epitheca of the rugose coral *Enallophrentis polonica* (*rug.*) and being encrusted by tabulate corals (*tab.*).

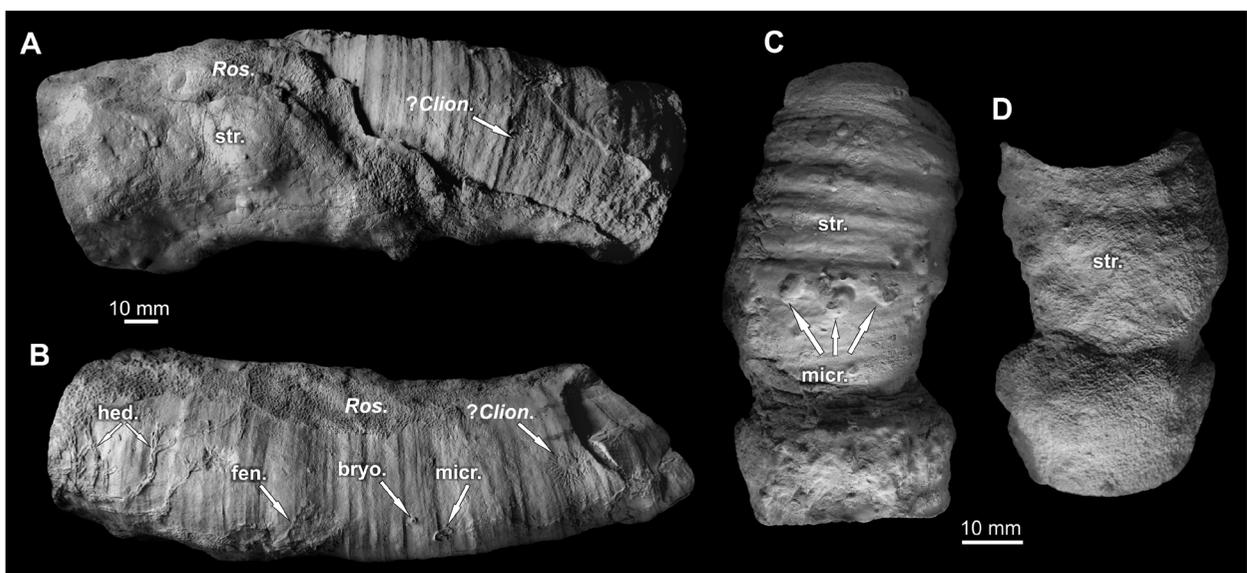


Fig. 8. Episkeletobionts on rugose corals from the Pokrzywianka Beds at Skąły, Holy Cross Mountains, trench VI. **A, B.** *Enallophrentis polonica* (Sobolev, 1904) showing encrustation of a tabulate coral *Roseoporella* sp. (*Ros.*) by a sheet-like stromatoporoid (*str.*) (A), as well as encrustation by hederelloids (*hed.*), fenestrate bryozoans (*fen.*), indeterminate bryozoan base (*bryo.*) and a microconchid (*micr.*) (B). Dendritic, possibly the boring *Clionolithes* also occur (?*Clion.*). **C, D.** Sheet-like stromatoporoid (*str.*) encrusting the entire rugose coral *Acanthophyllum* sp. along with microconchid tubeworms (*micr.*).

overgrowth. However, such cases are recorded inside the thick encrustation envelope, occurring around the corallite (Fig. 9), thus indicating that the overgrowths may have happened either during the life and after death of some of the overgrown/fouled organisms. Therefore, the data presented below is general, biased toward the cases noted on the corallite exteriors and thus must be taken with some reservation.

In the assemblage studied, the fouling encrusters consist of solitary organisms, among which microconchids predominate (34 cases) in different encounters (Tab. 2). They are followed by crinoids (13 cases), while the rest of the epibionts (foraminifers, brachiopods and arborescent bryozoans) belong to a minority.

In the case of overgrowths, the predominant organisms are sheet stromatoporoids (44 cases), which usually encrust large surfaces and overgrow many epibionts encountered. They are followed in abundance by such tabulates as *Aulopora*, *Mastopora* and *Alveolites*, and then by hederelloids, sheet cystoporid bryozoans, and *Roseoporella* and *Pachyfavosites* tabulates. Among these cases, the least

often overgrown (but not fouled) encrusters are sheet stromatoporoids (12 cases), and the most often overgrown are *Roseoporella* tabulates (10 cases; Tab. 3). Reciprocal overgrowths, showing the interaction during the lives of both epibionts are very rare in the assemblage, as only three such cases were noted, all between tabulate corals (*Aulopora* and *Mastopora*) and other encrusters (cystoporid bryozoan, hederelloid and stromatoporoid).

DISCUSSION

Diversity of encrusters compared to other Devonian coral-hosted communities

Taking the epibiont groups above the family level into account, the encrusting assemblage, present on the rugose corals in the Givetian Pokrzywianka Beds, consists of 11 taxa. The rather high value of the Simpson Index of Diversity ($1-D = 0.732$) and the low value of Dominance ($D = 0.268$) noted for the corals, indicate a higher than moderate diversity of

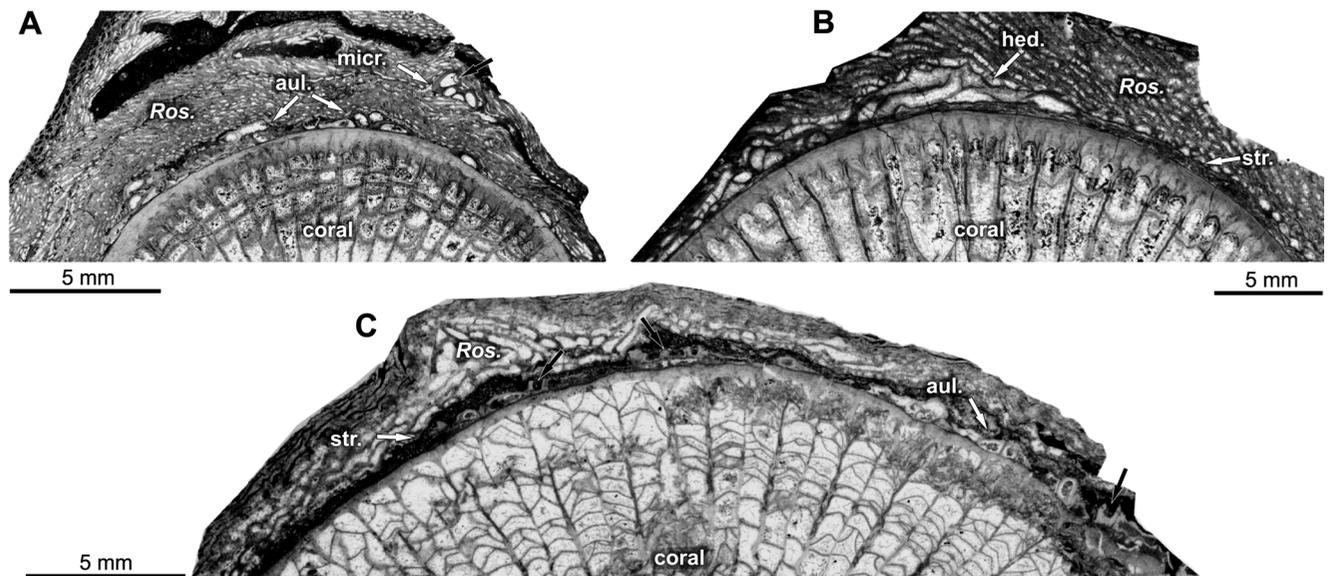


Fig. 9. Transverse thin sections of the rugose corals, showing exteriors covered by a succession of various encrusters. **A.** Encrustation developed around *Enallophrentis polonica* (Sobolev, 1904). Black arrow points to partly eroded tube of a microconchid (micr.), which was *post-mortem* encrusted by a coenitid tabulate coral *Roseoporella* (Ros.). Auloporid tabulates (aul.) directly encrusted the rugose coral. **B.** *Enallophrentis polonica* (Sobolev, 1904) directly encrusted by a stromatoporoid (str.), followed by a hederelloid colony (hed.) and a coenitid tabulate coral *Roseoporella* (Ros.). **C.** *Acanthophyllum* sp. directly encrusted by auloporid tabulates (aul.), of which some corallites later were abraded (black arrows) and *post-mortem* encrusted by stromatoporoids (str.) and coenitid tabulates *Roseoporella* (Ros.).

Table 2

Fouling and fouled encrusters from the Pokrzywianka Beds at Skąły, Holy Cross Mountains, trench VI.

Fouling taxa	No. on top	Fouled taxa
microconchids	34	stromatoporoids, <i>Alveolites</i> , <i>Roseoporella</i>
crinoids	13	stromatoporoids, <i>Alveolites</i> , <i>Roseoporella</i> , <i>Aulopora</i> , <i>Mastopora</i>
foraminifers	5	stromatoporoids, <i>Alveolites</i>
brachiopods	3	stromatoporoids, <i>Roseoporella</i>
bases of arborescent bryozoans	3	<i>Roseoporella</i>

Table 3

Encrusters from the Pokrzywianka Beds at Skały, Holy Cross Mountains, trench VI, involved in overgrowth actions.

Taxa	No. of cases	No. on top
stromatoporoids	56	44
<i>Aulopora</i>	16	10
<i>Mastopora</i>	12	8
<i>Alveolites</i>	10	6
hederelloids	12	6
cystoporate bryzoans	6	4
<i>Roseoporella</i>	13	3
<i>Pachyfavosites</i>	3	2

Explanations: No. of cases refers to the number of all overgrowth actions, in which a particular group of encrusters is involved. No. on top refers to those cases, in which a particular group of encrusters overgrows another one.

epibionts and the distinct domination of single taxa, here evidently by microconchid tubeworms. The values of the Shannon ($H' = 1.714$) and Evenness (0.505) indexes indicate rather dissimilar proportions of individuals within the epibiont groups colonizing the corals, which is also evident in other coral-hosted assemblages (Zatoń *et al.*, 2018; Zatoń and Wrzolek, 2020). Such quantitative data, however, have value when compared to other coral-hosted assemblages of a similar age, insofar as episkeletobiont assemblages are evidently different on different hosts. For example, a characteristic epizoan brachiopod *Deliella*, not infrequent in the Skały Beds, occurs solely on other brachiopods (Halamski, 2004; Halamski and Zapalski, 2006). Data on the diversity of the Middle Devonian encrusting assemblages, hosted by rugose corals, however, are quite rare. In fact, only a few thorough studies concerning the palaeoecology of such communities exist (Tab. 4). Two such studies come from the Holy Cross Mountains, where Balon (2015) examined the epibionts on rugose corals from the Givetian of the Laskowa Quarry, located in the Kielce Region of the Holy Cross Mountains (see Racki *et al.*, 1985; Zatoń *et al.*, 2018), and the second one from the Givetian assemblage of the Miłoszów site, located in the Łysogóry Region of the Holy Cross Mountains, studied recently by Zatoń and Wrzolek (2020). Outside the Polish segment of Laurussia, a thorough study of the encrusters colonizing Givetian corals comes from the Hamilton Group in New York, USA (Baird and Brett, 1983). Additionally, Zatoń *et al.* (2015) also studied encrusted rugose corals but of late Frasnian in age, from the Central Devonian Field, Russia.

Although the encrusting communities from the Givetian of the Pokrzywianka Beds share many common epibiont groups with other coral-hosted assemblages, some striking differences exist. For example, the slightly older (lower/middle Givetian) encrusting communities, inhabiting rugose corals at the neighbouring locality at Miłoszów in the Holy Cross Mountains, similarly are characterized by

abundant microconchids and common auloporid tabulates and hederelloids. The community from the Pokrzywianka Beds studied is distinctly impoverished in bryozoans and totally lacks ascodictyids, the two groups that evidently dominate the Miłoszów community. However, it contains, albeit very rare, tentaculitoids *Anticalyptraea*, which are absent at Miłoszów, but were already recorded in the Middle Devonian of the Holy Cross Mountains by Dzik (1983). Especially striking is the total absence of the enigmatic ascodictyids on corals in the Pokrzywianka Beds. Ascodictyids are a characteristic encrusting component on various hard substrates in the Devonian (e.g., Kiepora, 1965; Baird and Brett, 1983; Bordeaux and Brett, 1990; Zatoń and Krawczyński, 2011b; Schneider, 2013; Olempska and Rakowicz, 2014). Although ascodictyids are the most abundant epibiont group encrusting small Eifelian crinoid columnals in the Skały section (Głuchowski, 2005), Olempska and Rakowicz (2014) considered them as an infrequent component of the encrusters present on the Emsian and Eifelian corals and other shelly substrates in the Grzegorzowice-Skały section in the same area. Interestingly, Kiepora (1965) noted that in the Grzegorzowice-Skały section, ascodictyids are rare on rugose corals and bryozoans and may be very common on brachiopods and crinoids. Thus, their common presence on the Miłoszów corals and small crinoid columnals/pluricolumnals, and absence from large corals in the Pokrzywianka Beds indicate that the occurrence pattern of such a common group as ascodictyids may be complex and most likely dependent on extrinsic factors. It is also possible that some ascodictyids originally were present on the corals studied but have been overgrown by other sheet-like encrusters. However, even large, unoccupied surfaces on many corals also are devoid of any specimens, which may indicate the absence of ascodictyids in the Pokrzywianka biostrome habitat. Webb and Schneider (2013) also did not find any ascodictyids on Givetian brachiopod shells in Iowa, USA, explaining their absence by the general lack of these encrusters in the environment at the time of deposition.

In comparison to the Miłoszów corals, those in the Pokrzywianka Beds possess much more diversified, encrusting tabulate corals, represented by four families and six genera, and more abundant crinoid holdfasts. However, such different encrusting communities, represented by 1) the lower-diversity, microconchid-tabulate coral-crinoid community of the Pokrzywianka Beds, developed on a carbonate substrate, and 2) the high-diversity, microconchid-bryozoan-ascodictyid community of the Miłoszów locality (Skały Beds), occurring on siliciclastic substrates (Zatoń and Wrzolek, 2020), may have developed under similar bathymetric regimes. Like the assemblages in the Pokrzywianka Beds, those at Miłoszów also could have lived within the mesophotic habitat of the generally euphotic palaeoenvironment. Indeed, as in the case of the lower mesophotic community of the Pokrzywianka Beds, that at Miłoszów also inhabited palaeoenvironments, characterized by at least low-light conditions, as evidenced by the presence of the microproblematicum *Rothpletzella* (Zatoń and Wrzolek, 2020), for which recently an algal affinity has been proposed (Zatoń and Jarochowska, 2020). Moreover, in the Miłoszów mudstones, *Semitextularia* regarded as

Table 4

Comparison of Middle Devonian (Givetian) rugose-coral-hosted episkeletobiont assemblages at different localities in Laurussia.

Taxa	Hamilton Group, New York, USA (Baird and Brett, 1983)	Laskowa Quarry, Kielce Region, Holy Cross Mountains, Poland (Balon, 2015)	Miłoszów, Łysogóry Region, Holy Cross Mountains, Poland (Zatoń and Wrzolek, 2020)	Pokrzywianka Beds at Skały, Łysogóry Re- gion, Holy Cross Moun- tains, Poland (this paper)
Foraminifera	?	-	++	+
stromatoporoids	-	-	+	++
microconchids	+++	++	+++	+++
cornulitids	++	+	+	-
<i>Anticalyptraea</i> (= <i>Autodetus</i>)	++	-	-	+
brachiopods	+	+++	+	+
rugose corals	+	+	+	+
tabulate corals (auloporids)	+	++	++	++
tabulate corals (favositids)	+	-	+	+
tabulate corals (alveolitids)	-	-	-	+
tabulate corals (coenitids)	-	-	-	+
bryozoans (trepostomates)	+	?	++?	?
bryozoans (cystoporates)	+	?	+	+
bryozoans (fenestrates)	++	-	?	+
hederelloids	+	-	+++	++
ascodictyids	++	-	+++	-
crinoids	++	-	+	++
algae/calcimicrobes	?	-	+ (<i>Rothpletzella</i>)	+ (<i>Girvanella</i>)
problematica	+	-	-	+ (Moravamminida)

a photosynthetically active foraminifer (Dubicka *et al.*, 2021) was also found (Z. Dubicka, pers. info., June 2021), confirming their origins within the euphotic zone.

The upper Givetian community from the Laskowa Quarry (*Coenites*-biostromes in the Fossiliferous Limestones and Marls unit of set A of Racki *et al.*, 1985) is very impoverished with respect to many epibiont groups, in comparison to both Miłoszów (Skały Beds) and Pokrzywianka Beds as well as to other assemblages (Tab. 4). There, the rugose corals were colonized by a low-diversity community, clearly predominated by *Davidsonia* brachiopods, followed by microconchids and auloporid tabulates (Balon, 2015). Interestingly, a similar suite of epibionts, with predominating *Davidsonia* brachiopods and microconchids, has been noted on large alveolitids and chaetetid sponges at the same quarry (Zatoń *et al.*, 2018). The low-diversity epibiont community of the Laskowa Quarry is hypothesized to have thrived in specific, mesophotic and nutrient-poor conditions (Zapalski *et al.*,

2017; Zatoń *et al.*, 2018). Interestingly, if the coral-rich mudstones at Miłoszów also developed in a similarly low-light habitat, as mentioned above, then the assemblages at Miłoszów, the Laskowa Quarry and the Pokrzywianka Beds would represent completely different epibiont communities, inhabiting sites that differed from each other in specific palaeoenvironmental conditions, related to bathymetry, such as light levels, nutrient levels, and also specificity of the hosts/substrates occupied.

A coral-hosted assemblage, described in mudstone facies of the Givetian Hamilton Group of New York (Baird and Brett, 1983), is somewhat similar to the Miłoszów community. There, microconchids are also abundant and such colonial groups as auloporids, ascodictyids, hederelloids and bryozoans are present, as well (Tab. 4). The community from the Hamilton Group, however, possesses common *Anticalyptraea*, a tentaculitoid epibiont, which is also present (albeit as a very low amount) on corals in the

Pokrzywianka Beds. *Anticalyptrea* is a common constituent of the Silurian hard-substrate communities of Europe and North America (Horný, 1965; Vinn and Isakar, 2007). With the exception of common occurrences in North America, the Devonian *Anticalyptrea* is rather rarely reported (Dzik, 1983; Mergl, 2021) and the example from the Pokrzywianka Beds presented here seems to be the first illustrated one from the Holy Cross Mountains. It is likely, that it may be more common in the Devonian outside of North America, but the external similarity of juvenile individuals of *Anticalyptrea* to microconchid tubeworms could have hampered its correct identification.

The lack of certain algae may indicate that, unlike the Miłoszów assemblage possessing *Rothpletzella*, the Hamilton Group community could have developed in even deeper, low-light to aphotic palaeoenvironment. However, the latter conclusion must be taken with caution, as such delicate algal fossils simply may have not been preserved. Also different in composition is the rugose-coral-hosted biostrome in the upper Frasnian of the Central Devonian Field, in Russia. There, apart from the dominant auloporids, which contributed to biostrome formation, the most abundant are foraminifers, followed by rare epibiontic rugose corals and even rarer productid brachiopods, microconchids and cornulitids. This assemblage also was interpreted as representing an oligotrophic, nutrient-poor palaeoenvironment (Zatoń *et al.*, 2015). However, any evidence of mesophotic conditions for that Frasnian biostrome is lacking.

All the data and comparisons provided above indicate that, at least in the Devonian, each encrusting community, even inhabiting the same type of substrate (here, rugose corals) and occurring in deposits of similar age, location and even occupied habitat zone, may differ significantly with respect to diversity and abundance of particular groups. Evidently, not only substrate type but also extrinsic palaeoenvironmental conditions have exerted an influence on the local species pool and thus the composition of the whole community. Another factor is the recruitment pattern of an encruster's larvae, which certainly differs from one species to another, and are, additionally, the subject of passive, hydrodynamical drag. As a result, recruitment may be random, which results in diverse assemblages (e.g., Goldson *et al.*, 2001; Marshall and Keough, 2003). This is well marked by the Miłoszów and Pokrzywianka assemblages, which, apart from being located close to each other and even within similar mesophotic environments, represented completely different suites of facies and even different compositions of the coral hosts (see Zatoń and Wrzolek, 2020). Thus, it is crucial to look at the whole spectrum of the encrusting communities of a given age and provenance, before any broad-scale conclusions are drawn concerning, for example, the succession of communities through time or their regional/over-regional differences. In such communities, rare groups, such as *Anticalyptrea*, may play an important role in distinguishing particular communities, potentially developing in specific, local/regional palaeoenvironmental conditions.

Biotic interaction

Host coral – epibiont interactions

Encrustation of coral hosts during their life (*syn vivo*) by epibionts here is evidenced primarily by the presence of organisms embedded (bioclaustrated) within the corallite. Bioclaustration is the best evidence for the *syn vivo* relationship, since it shows directly the reaction of the host's skeletal tissue to the presence of infesting organisms, both epi- and endobionts. Apart from occurring in corals, such phenomena have been found commonly in different fossil groups, such as serpulids (e.g., Scrutton, 1975; Słowiński *et al.*, 2020), bryozoans (e.g., Palmer and Wilson, 1988; McKinney, 2009; Vinn *et al.*, 2014a), brachiopods (e.g., Biernat, 1961; Baliński and Sun, 2010; Vinn *et al.*, 2014b) and bivalves (e.g., Rogers *et al.*, 2018).

Although in the Miłoszów corals, bioclaustrations were quite common (found within 24% of larger corals, see Zatoń and Wrzolek, 2020), such phenomena are rare in the corals investigated, being present in only two solitary corals. As only apertures protruding from the corallite (Fig. 7D) are visible, it is difficult to say which encrusters were bioclaustrated.

Some sheet-like epibionts, such as stromatoporoids and tabulate corals, may encrust the rugose corals around the growth axis (e.g., Fig. 8C, D). The lack of distinct signs of the rolling of the corals on the sea bottom at least may indicate that the encrustation proceeded, when the corals thrived in an upright position. However, whether the corals were colonized *syn vivo* is a matter for discussion. Certainly, some of the corallites were encrusted *post-mortem* in a horizontal position, as evidenced by the presence of some epibionts (e.g., auloporids and crinoid holdfasts), cemented to the abraded thecae, as well as from variously oriented holdfasts on a single corallite. Also, the presence of sediment between the two successive colonies of tabulate corals, noted in at least one corallite, may indicate that it was lying on the seabed in a horizontal position and was encrusted in two steps, separated by a sediment flux.

Thus, although many of the corals could have been colonized during life, only very few of them show unequivocal evidence of *syn vivo* colonization.

Potential interactions between epibionts

Potential interactions between particular epibionts, encrusting the coral hosts, are common and consist of the fouling of colonial encrusters by primarily solitary organisms (Tab. 2) and the overgrowth of both solitary and colonial encrusters by other, colonial epibionts (Tab. 3). However, as already mentioned above, such interactions occurred either during the life or after the death of the colonized organisms, as evidenced by sectioned specimens (Fig. 9). So, the discussion provided below concerns only the cases noted on the exteriors of the corallites and thus provide only general and to some extent biased data.

On the corals studied, the most competitive encrusters are certainly sheet-like stromatoporoids and reptant colonies of auloporids and hederelloids (Tab. 3). Especially stromatoporoids were very effective in substrate occupation as they encrusted the rugose corals and all of the epibionts

encountered, especially solitary ones. Microconchids, although a dominant group of epibionts, neither dominated the substrate area owing to their tiny size and spiral growth, nor exerted any serious, negative influence on the other epibionts. Such small colonizers only would have caused some local disturbances in the fouled part of the overgrown animal (e.g., smothering soft parts of a few individuals in a colonial animal), but fouling itself is often non-lethal (e.g., Taylor, 2016). In the assemblage studied, such dominating solitary epibionts as microconchids were as much overgrown by some of the sheet-like encrusters as they were on top of the fouled colonies. For example, although in 34 cases microconchids were on the top of stromatoporoids and tabulate corals, they were also 33 times overgrown by stromatoporoids, clearly implying which encrusting group dominated the substrate and is most effective in its occupancy.

As was already mentioned above, those overgrowths, which might indicate the interactions during life of both epibionts (reciprocal overgrowths), are rare and limited to three cases. In all of them, colonial epibionts, such as tabulate corals, bryozoans, stromatoporoids and hederelloids, were involved. The other evidence of *syn vivo* interactions between epibionts in the assemblage studied involves the embedding of *Mastopora* by sheet-like stromatoporoid. Here, the apertures of the epibionts being embedded protrude from the overgrowing encruster, indicating their success in 'escape' from being entirely overgrown.

CONCLUSIONS

Episkeletobionts, colonizing solitary rugose corals from the Givetian Pokrzywianka Beds at Skały, in the Holy Cross Mountains, Poland, are dominated by microconchid tube-worms, crinoids and tabulate corals. The last group, however, is the most diverse at the family level, represented by auloporids, alveolitids, coenitids and favositids. On the basis of palaeontological evidence, especially the presence of platy, alveolite, tabulate corals in the deposits studied, the episkeletobiont community is considered to have developed in a low-light, mesophotic palaeoenvironment. With respect to the taxonomic composition and relative abundance of various groups, this encrusting community differs from other Givetian communities in the Holy Cross Mountains, which also were considered to have thrived in low-light habitats (Laskowa and Miłoszów). The rugose-coral-hosted community from the Pokrzywianka Beds seems also to be devoid of ascodictyids, a group of encrusters, which was very common in some other Devonian hard-substrate assemblages. The differences in taxonomic composition of episkeletobionts between different localities, even those representing generally similar low-light habitats, may have resulted from specific, local conditions, related to bathymetry (light levels, nutrient levels), the specific nature of the hosts/substrates occupied, and also differences in larval dispersal patterns. Such differences emphasize how various encrusting communities may have inhabited seemingly similar, marine habitats within a given time-interval and in neighbouring areas. It also highlights the fact that any broad comparisons of the encrusting assemblages within

a given timespan and palaeogeographic entity must be carried out with caution and not on the basis of a single site only, as such an approach might lead to erroneous results and an inadequate picture of the biodiversity within a particular palaeoenvironment.

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Data on episkeletobionts encrusting rugose corals from the Pokrzywianka Beds of Skaly, Holy Cross Mountains, trench VI.

sample	coral host	microconchids	<i>Anticadyptraea</i>	foramifera	brachiopods	crinoids	rugose corals	aluloporphids	alveolitids	coenitids	favositids	hederellids	stromatoporphoids	bryozoans	Moravamminida	abundance	richness
s 32/2	<i>Enallophrentis polonica</i>	16			1	3					1	1	1			23	6
s 32/3	<i>Enallophrentis polonica</i>	2				1		2	1	1						7	5
s 32/4	<i>Enallophrentis polonica?</i>	4		1		1		1		1	1	3	2			14	8
s 33/1	<i>Enallophrentis polonica</i>	1		1		2				1		2	1			8	6
s 33/2	<i>Enallophrentis polonica</i>	8				1				1						10	3
s 33/3	<i>Enallophrentis polonica?</i>	7			1			1				2		2	1	14	6
s 34/1	<i>Enallophrentis polonica</i>	11										1		1		13	3
s 34/2	<i>Enallophrentis polonica</i>	3								1		3	1	1		9	5
s 35/1	<i>Enallophrentis polonica</i>	4						3		1		1	1			10	5
s 35/2	<i>Enallophrentis polonica</i>	6		1	3			1		1		1	1	4		18	8
s 36/1-2	<i>Enallophrentis polonica</i>	4				7		1		1		2	1	4		20	7
s 37/1	<i>Enallophrentis polonica</i>	3										6				9	2
s 37/2	<i>Enallophrentis polonica</i>	3														3	1
s 38/1	<i>Acanthophyllum</i> sp.	12		2				1	1				1			17	5
s 38/2	<i>Acanthophyllum</i> sp.					1		1				1		1		4	4
s 38/4	<i>Enallophrentis polonica</i>	12	1			1		1								15	4
s 38/5	<i>Enallophrentis polonica</i>	7		3		1		1	1			1				14	6
s 38/6	<i>Enallophrentis polonica</i>	2				3		2				1	1	2		11	6
s 40/1	<i>Stringophyllum</i> sp.	6				1						3				10	3
s 40/2	<i>Acanthophyllum</i> sp.	2				1			1			1		1		6	5
s 39/1	<i>Stringophyllum</i> sp.	1				1	1					2				5	4
s 39/3	<i>Acanthophyllum</i> sp.	4		1						1		1				7	4
s 39/4	<i>Stringophyllum</i> sp.	2				5		1				1				9	4
s 39/5	<i>Enallophrentis polonica</i>	5				1		1						1		8	4
s 39/8	<i>Enallophrentis polonica</i>												1			1	1
s 39/9	<i>Acanthophyllum</i> sp.	1						1	1				1			4	4
s 39/10	<i>Enallophrentis polonica</i>	7				1		3				1	1			13	5
s 39/11	<i>Enallophrentis polonica</i>	1						2				1	1			6	4
s 39/12	<i>Enallophrentis polonica</i>	11	2		2				1			1	1	3		21	7