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Invited Research Article

Coralliths of tabulate corals from the Devonian of the Holy Cross Mountains (Poland)

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ABSTRACT

Tabulates, an extinct Palaeozoic group of corals, developed diverse colony morphologies during the Silurian to Devonian peak of reef development. Coralliths, or circumrotatory colonies, are passively motile coral colonies constantly overturned by wave action or currents. Such overturning allows tissue growth on all sides of the colony. They are among the most rarely reported growth forms. Recent corallith-forming scleractinian corals mostly inhabit the shallowest reef environments, but coralliths can also develop at greater depths in areas of low topographic relief, unconsolidated substratum, low coral cover and high water movement. Here, we report on Devonian (Givetian *Favosites goldfussi* and Frasnian *Alveolites*? *tenuissimus*) coralla from the Holy Cross Mountains, Poland. Our analysis suggests these colonies are coralliths, although less mature than usually reported. These corals, unlike previously described growth forms of this kind, lived in relatively deep environments: probably the upper mesophotic (Givetian, Miłoszów), or deep reef fore-slope (Frasnian, Jaźwica and Kowala). Microfacies analysis of the Jaźwica site suggests unconsolidated substratum and high hydrodynamic energy. We conclude that these corals lived in deeper environments where bottom currents caused their autorotation. A good modern analogue for such a corallith-forming environment is the Wistari Channel (Southern Great Barrier Reef), where bottom tidal currents at nearly 30 m of depth are strong enough to overturn colonies of *Stylocoeniella* cf. *guentheri* reaching 15 cm in diameter. Our discovery shows that the spectrum of coral growth forms during the Devonian peak of reef development was broader than previously assumed, and that tabulate corals displayed numerous adaptive strategies to various environments.

1. Introduction

Palaeozoic corals during the peak of reef development (Silurian and Devonian) colonized a wide array of environments (e.g., Lecompte, 1958; Racki, 1992). Morphological plasticity and diversified colony morphologies allowed colonization of various environments, and like their modern scleractinian analogues, tabulates had diverse growth forms, including platy, massive and branching. The shapes colonies take are a result of the interplay between the genetic program and environmental factors such as water motion, irradiance and sedimentation ratio (Rogers, 1990; Todd, 2008). Nearly all of the colony morphologies known from Palaeozoic tabulates have corresponding growth forms in recent seas (except for the Early Palaeozoic cateniform coralla, organized in chain-like corallite ranks; see Hill, 1981). Because similar colony morphologies (including growth form and structure) suggest occupancies of similar ecological niches (Porter, 1976), and assuming that form is related to function, functional comparisons between fossil and recent corals are possible (e.g., Plusquellec et al., 1999; Rosen et al., 2002; Zapalski et al., 2021).

Motility in scleractinian corals is very rare, and can be either passive or active; such modes of life reflect adaptations to either high hydrodynamic energy, e.g., *Siderastrea varians*, or to high sedimentation rates

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e.g., *Herpolitha limax* (Kissling, 1973; Lewis, 1989; Hoeksema and Bongaerts, 2016). Active movement in some Palaeozoic coral taxa (e.g., in *Procterodictyum, Palaeacis*) was suggested by Plusquellec et al. (1999). Passive movement, usually through autorotation in high water agitation results in detached, usually strongly rounded colonies referred to as coralliths (Glynn, 1974), and this mode of life, reflected in colony shape, has very high fossilization potential. A separate category is mobility provided by other organisms (both benthic and nectonic, and often in symbiotic interaction with the host coral) that are able to move or overturn coral colonies (Glynn, 1974; Gill and Coates, 1977; Stolarski et al., 2001; Capel et al., 2012).

In modern seas, passively rotated colonies typically occur in very shallow waters (0–5 m) frequently on the windward sides of reefs (Kissling, 1973; Lewis, 1989). In rare cases, such coral colonies can grow in deeper environments (15–20 m), but this requires simultaneous occurrence of the following factors: low seafloor relief, unconsolidated substratum, low coral cover and exposure to swell (Hoeksema et al., 2018). Dullo and Hecht (1990), however, described coralliths from submarine alluvial fans in the Gulf of Aqaba at depths reaching 25 m, on sloping seafloor.

Only twenty-three extant scleractinian taxa (out of the total ~1500) are known to form coralliths (Rodríguez-Martínez and Jordán-Dahlgren, 1999), so even in modern seas this growth form is rare. Coralliths are also formed by representatives of the hydrozoan genus *Millepora* (Richards et al., 2013).

The fossil record of coralliths is, despite good fossilization potential, limited. Most of the described cases are from the Meso- and Cenozoic (see review by Denayer, 2018), and Palaeozoic examples are very scarce. Palaeozoic tabulate corals forming coralliths are limited to a few examples. Kissling (1973) studied autorotatory colonies of *Favosites favosus* from a very shallow-water bioherm from the Silurian of Ohio. Abbott (1975) briefly described Silurian *Favosites* and *Heliolites* that were spherical, thus potentially circumrotatory, and briefly compared it with recent *Siderastrea varians*. Stel (1978) briefly described *F. forbesi* from the oncoidal beds of Hamra-Sundre Beds (Ludfordian, Silurian) of Gotland. Król et al. (2016) described Lower Devonian *Favosites bohemicus* from the Anti-Atlas that grew on unstable slope of a mud mound, and several specimens displayed features of autorotation, being the result of gravitational tilting. An interesting study from the Upper Devonian (Frasnian) of the Namur-Dinant Basin was published by Denayer (2018), who described polytaxic coralliths, many of which included tabulate corals – as either coralliths nuclei, on which other encrusters grew, or as encrusters. The latter included representatives of the ubiquitous Devonian genus *Alveolites*. In this case, the main factors hypothesised to cause circumrotatory growth were short-lasting hydrodynamic events, such as storms. Additionally, Gill and Coates (1977) mentioned coralliths of Carboniferous *Michelinia* sp.

Shallow Palaeozoic reefs were commonly dominated by stromatoporoid sponges, and tabulate corals typically preferred deeper environments (e.g., Lecompte, 1958; Machel and Hunter, 1994). Formation of autorotatory colonies in most cases requires high hydrodynamic energy, therefore the absence of corals in the shallows might explain the scarcity of this growth forms in the fossil record of tabulate corals.

The Holy Cross Mountains are a range of hills in Central Poland (Fig. 1A) where Devonian carbonate rocks crop out. During the Devonian, the Holy Cross Mountains were located on the southern shelf of Laurussia, in southern tropical latitudes (Golonka, 2020). These Middle to Upper Devonian carbonate rocks originated in a topographically diversified carbonate platform, which hosted reefs and bioconstructions (Racki, 1992). Middle to Late Devonian tabulate corals of the Holy Cross Mountains are well known, and have been the topic of research since the 19th century (e.g., Gürich, 1896; Stasińska, 1958; Nowiński, 1992; Zapalski, 2012). However, to date no circumrotatory corals have been described from this reef system. The aim of this paper is to describe and analyse the Givetian and Frasnian monotaxic coralliths (circumrotatory colonies) of tabulate corals belonging to representatives of two common genera – Givetian *Favosites* (Tabulata: Favositida: Favositidae) and Frasnian *Alveolites* (Favositida: Alveolitidae). The material comes from sites located at the northern and southern flanks of the carbonate platform (Fig. 1B), thus in the fore-reef environments (Racki, 1992). Globally, Palaeozoic coralliths were unknown from these kinds of environments. We also describe a modern analogue of these Palaeozoic coralliths that occurs in deeper environments on the Great Barrier Reef.

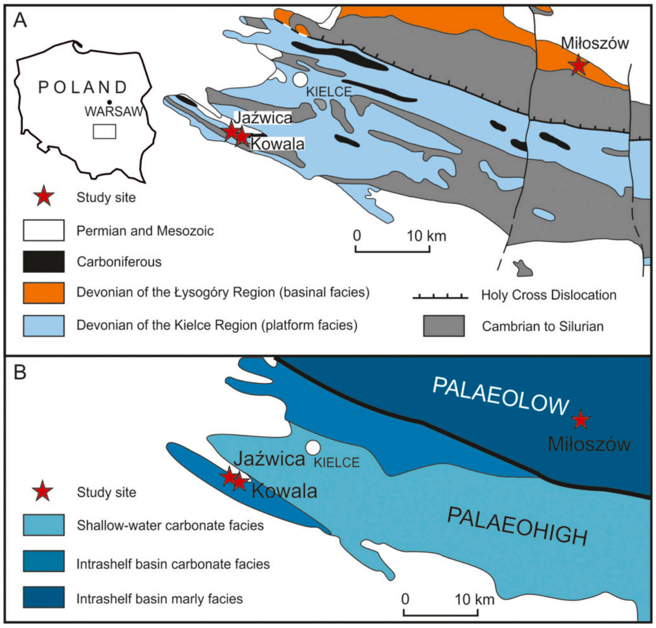

Fig. 1. A. Location of study sites on a simplified geological map of the Palaeozoic inlier of the Holy Cross Mountains, central Poland. Based upon Szulczewski, 1971 and Racki, 1992. B. Location of study sites within the simplified palaeogeographic framework. Based upon Racki, 1992 and Pisarzowska et al., 2006.

2. Geological setting

The Devonian strata of the Holy Cross Mountains were deposited in two, environmentally, and thus facially different basins – the Łysogóry Region (northern), being the deeper part, and the Kielce Region (southern), much shallower, but deepening southwards (Racki, 1992, Szulczewski, 1995a and references therein; Fig. 1B, 2).

The Middle Devonian in the Łysogóry Region is represented by mixed, carbonate-siliciclastic facies. A number of diversified coral communities thrived in this part of basin from Emsian to Givetian (e.g., Stasińska, 1958, 1974; Zapalski, 2005). Some of these communities have been interpreted as mesophotic coral ecosystems (MCEs, Zapalski et al., 2017), especially from the upper Eifelian part of the Skały Beds (Fig. 2). The material for the present study comes from the Miłoszów section, which is situated in the Bodzentyn Syncline of the Łysogóry Region (Fig. 1A). It consists of a series of four natural or artificial outcrops of the upper part of Skały Beds (Pajchlowa, 1957; Halamski, 2005; Halamski and Racki, 2005) in the vicinity of the Miłoszów hamlet near the Nieczulice village. The *Favosites goldfussi* material comes from the locality M-1 sensu Halamski (2009), more precisely from the level M-1-IIa. The fauna of the M-1-IIa level consists of numerous and diversified small brachiopods, rugose and tabulate corals (including platy *Roseoporella* sp. and *Alveolites* sp., branching *Striatopora* sp., and *Aulopora serpens*, encrusting other corals), bryozoans, and representatives of several other groups (A.T. Halamski and A. Baliński, unpublished data). The analysis of the epizoans of rugose corals from M-1-IIa suggests that the fauna lived in the photic zone (Zatoń and Wrzołek, 2020). The age of the M-1-IIa is uncertain; it is undoubtedly Givetian, but a more precise dating is contentious. These beds may belong to the *timorensis* Zone or the lower

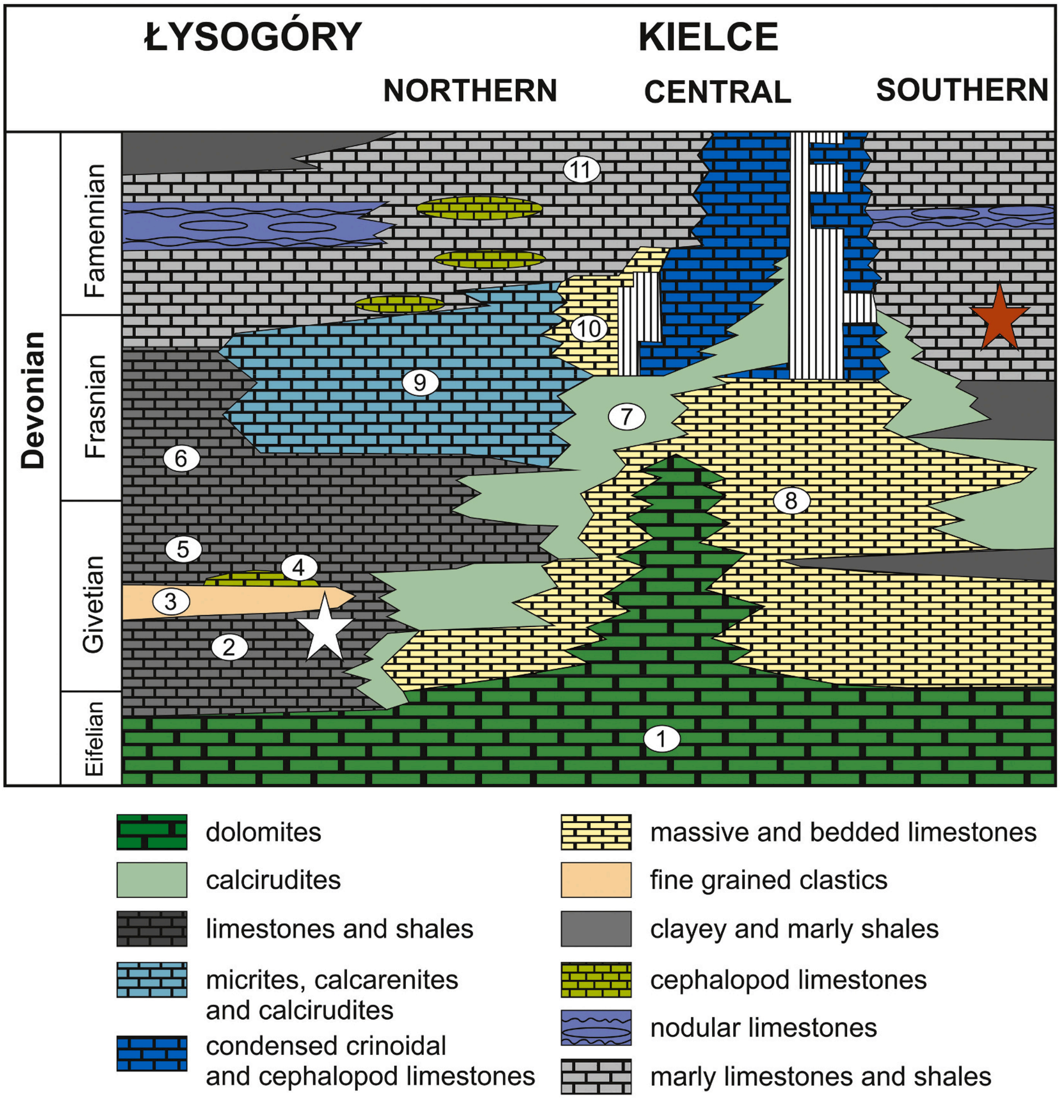

Fig. 2. Simplified chronostratigraphic scheme of the Middle–Late Devonian of the Holy Cross Mountains (after Szulczewski, 1995a), an orange asterisk indicates position of the Jaźwica and Kowala sections, a white asterisk indicates Miłoszów section.
1. Wojciechowice Formation; 2. Skały Beds; 3. Świętomarz Formation; 4. Pokrzywianka Beds; 5. Nieczulice Beds and Śniadka Formation; 6. Szydłówek Beds; 7. Laskowa Góra Beds; 8. Kowala Formation; 9. Kostomłoty Beds; 10. *Manticoceras* limestone; 11. Radlin Beds; 12. Zaręby Beds; 13. Gałęzice Debrite Member of Lechówek Formation; 14. Górno Beds; 15. Gułaczów Member of Lechówek Formation, 16. remaining portion of Lechówek Formation.

part of the *rhenanus/varcus* Zone (thus early to middle Givetian, see Zatoń and Wrzołek, 2020).

The Middle and Upper Devonian of the Kielce Region is represented by carbonates representing platform deposits. Szulczewski (1971) and subsequently Racki (1992) proposed a subdivision of the Givetian-Frasnian carbonate platform into, among others, four major subregions; the central, the shallowest, with fore-reef environments to the north and south, and the southernmost palaeolow. The Late Frasnian carbonate platform of the central subregion is represented by peritidal and lagoonal deposits with frequent emersion surfaces (Szulczewski et al., 1996). Two sites of the southern subregion (representing reef foreslope) of the Kielce Region, namely Kowala and Jaźwica quarries (Fig. 1) yielded *Alveolites*? *tenuissimus.*

Racki (1992) divided the Jaźwica section into fifteen lithological sets, with the oldest dated as middle Givetian, and the youngest as late Frasnian. Tabulate corals from this site were described by Nowiński (1992) and Zapalski (2012). The youngest beds (lithological set R sensu Racki, 1992 or set H2 sensu Racki and Baliński, 1998; Rigby et al., 2001) are marly limestones with silicified benthic fauna, representing basinal facies with occasional tempestite intercalations. They cropped out at Góra Łgawa hill, nowadays consumed by progressive limestone exploitation in the Jaźwica quarry. Besides numerous rugose corals, these beds yielded the material of alveolitids investigated here. *A.*? *tenuissimus* is the only species described from these beds (Zapalski, 2012).

The sections at Kowala (road-cut, railroad-cut and quarry), a village south of Kielce, span the uppermost Middle Devonian to the lowermost Carboniferous interval (Berkowski, 2002; Pisarzowska et al., 2006; De Vleeschouwer et al., 2013; Rakociński et al., 2021). The oldest beds represent coral-stromatoporoid bioherms (lithological sets A–C of Szulczewski, 1971), and the rest of sequence corresponds to a deepening trend (Racki, 1992). The material investigated here comes from the uppermost Frasnian beds of the quarry – lithological set H1 (Frasnian/Famennian boundary runs within the H3 set; Szulczewski, 1995b, Racki, 1996). These beds are composed of marly-micritic and graded detrital limestones, containing slump structures and broken fragments of bioconstructors (Racki, 1996). The upper Frasnian interval at Kowala and Jaźwica corresponds to the IId deepening pulse (Racki and Baliński, 1998).

3. Material and methods

Altogether 16 coralla were analysed. The Givetian material from Miłoszów consists of four nearly complete coralla of *Favosites goldfussi* (Figs. 3A–D, 4A), a species reported previously from nearby sites of similar age by Stasińska (1958). The Frasnian material from Jaźwica consists of ten nearly complete corallaof *Alveolites*? *tenuissimus* (Figs. 3E–J, 4B–H); see Lecompte (1933) and redescription of paralectotypes followed by description of the material from Jaźwica by Zapalski (2012). Two more specimens of this species come from Kowala. As the majority of the material studied comes from Jaźwica, we performed microfacies analysis in order to reveal the sedimentary environment of this site.

Thirty-four thin sections were prepared for the present study. Specimens were observed under a stereoscopic microscope (Zeiss Discovery V20), and photographed using a Canon EOS 70D camera with a 28–80 mm lens. Thin sections were scanned with an Epson Perfection V800 scanner and Epson Perfection V850 Pro scanner; microphotographs were taken using a Nikon Eclipse 50*i* transmitted light microscope with an integrated DS-Fi2 digital camera. Additionally, three lithological slabs moistened with water were used to describe the lithology of the Jaźwica section. The fossil specimens are housed at the University of Silesia, Faculty of Natural Sciences, Sosnowiec, Poland (institutional abbreviation GIUS), and in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (institutional abbreviation ZPAL).

Additionally, for comparison we include a corallith of *Stylocoeniella* cf. *guentheri*, collected at 28 m depth between Heron Island and Wistari Reef (Wistari Channel) on the southern Great Barrier Reef. This specimen is housed at the Museum of Tropical Queensland, Townsville, Australia (specimen G79987).

4. Results

4.1. *Alveolites? tenuissimus*

The colonies of *A.*? *tenuissimus* are small, the largest diameter not exceeding ~40 mm (often smaller), elongated in a single direction and often strongly flattened at one end (surface perpendicular to the longer axis of the colony), somewhat wrinkled on external surfaces (Fig. 3E). One of specimens (Fig. 4H) shows amoeboidal outgrowths, making its surface bumpy. Corallites open on nearly the whole surface of each specimen, except a very small area at the proximal end of each specimen. We interpret this as an attachment scar. The arrangement of corallites, seen in sections perpendicular to the long axis of the colony is vortex-like (Fig. 4B–D, F), with corallites strongly inclined to the corallum surface. In longitudinal section, specimens have a chaotic arrangement of corallites (Fig. 4 E, G, H).

Four specimens (GIUS J 143, 148, 150, 153) show growth-interruption surfaces, visible on cross-sections of the corallum. The surfaces are relatively rare to moderately abundant – from one to two in a corallum, up to seven. These are Type 2 (“surfaces of rejuvenation or recolonization with reorientation of tubules”; Fig. 4D) and Type 3 (“sediment-filled tubules or trapped sediment partings”; Fig. 4C, E) growth interruption surfaces sensu Miller and West (1997). Type 3 surfaces often pass into Type 2, i.e. the sediment is only preserved in parts of the break, not in its entire extent. Additionally there is a single example (GIUS J 143) of a Type 4 growth interruption surface (“encrusted surfaces”, sensu Miller and West, 1997; Fig. 4H), consisting

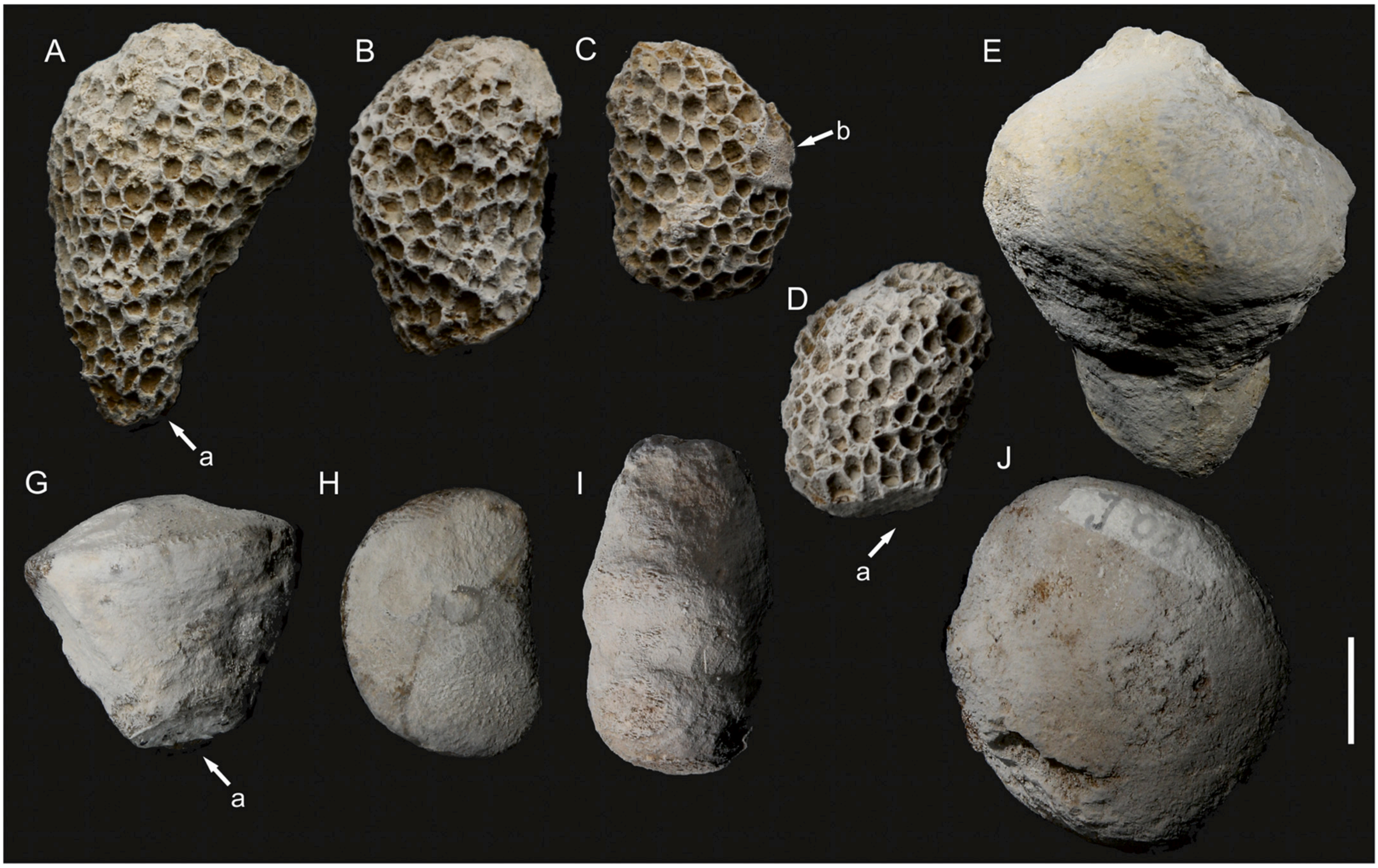

Fig. 3. External views of coralliths from the Devonian of the Holy Cross Mountains. A–D. *Favosites goldfussi*, Givetian, Miłoszów (A. ZPAL V.74/T/01, B. ZPAL V.74/T/02). C–D. Two views of the same specimen (ZPAL V.74/T/03). E. *Alveolites*? *tenuissimus*, upper Frasnian, Kowala (GIUS 388 KK 358A). G–J *A.*? *tenuissimus*, upper Frasnian, Jaźwica. G–H side and top view of slightly conical corallum (GIUS 402 J180). I. GIUS 402 J181; J. GIUS 402 J182 a – attachment scar, b – encrusting bryozoan. Scale bar 10 mm.

Fig. 4. Sections of coralliths from the Devonian of the Holy Cross Mountains. A. *Favosites goldfussi*, Givetian, Miłoszów (ZPAL V.74/T/04). B–H. *A.*? *tenuissimus*, late Frasnian, Jaźwica. B, C. sections perpendicular to long axes of two different colonies (B. GIUS 402 J155, C. GIUS 402 J150). D–E. Perpendicular (D) and longitudinal (E) sections of a colony (GIUS 402 J148). F–G. Perpendicular (F) and longitudinal (G) sections of a colony (GIUS 402 J153). H. Longitudinal section of a colony (GIUS 402 J143), note the amoeboidal outline of the specimen. b – bioclaustration. Arrows show growth interruption surfaces (sensu Miller and West, 1997): gi2 – Type 2; gi3 – Type 3; gi4 – Type 4. Scale bar 10 mm.

of a juvenile stromatoporoid? epibiont, subsequently overgrown by the coral, following the rejuvenation. Other encrusters have not been preserved, however there are empty spaces overgrown by *A.*? *tenuissimus*, which can be interpreted as bioclaustrations (Fig. 4G; specimens GIUS J 148, 153). Borings also occur. No difference between colonies from Kowala and Jaźwica are visible.

4.2. *Favosites goldfussi*

The colonies of *F. goldfussi* are also small, similar in size to those of *A.*? *tenuissimus* (the largest specimen is 38 mm along the long axis), elongated in one direction and generally roundish in sections perpendicular to the longer axis (Fig. 3A–D), somewhat “pear-shaped”. On all specimens, corallites open on all surfaces, except for the minute spots in the proximal parts of colonies that we interpret as attachment scars (Fig. 3A, D). A section longitudinal to the longer axis reveals fan-shaped arrangement of corallites (Fig. 4A), while a cross section shows a radial arrangement of corallites. One specimen is encrusted by a bryozoan (Fig. 3C).

4.3. Microfacies analysis

The investigated upper Frasnian rocks from set R at Jaźwica quarry consist of cherry-red, intraformational conglomerate and grainstone with isolated intraclasts (Fig. 5). The conglomerates are composed of rounded and flattened light-grey intraclasts (Fig. 5A) consisting of micritic limestone with peloids or packstones with numerous tentaculitids, sponge spicules, smooth-shelled and entomozoid ostracods. The boundary between intraclasts and the matrix is generally sharp, but sometimes is gradational (Fig. 5B). The matrix is composed of poorly sorted bioclastic micritic limestones, partly neomorphosed. Fossils in the matrix include numerous brachiopods (atrypides and rhynchonellides, e.g., *Pammegetherhynchus*), numerous trilobite remains, solitary rugose corals, smooth-shelled ostracods, fragmented sponges and corals, mollusc and brachiopod shell debris. In addition, this fossil assemblage includes fragmented ostracods, foraminifers (*Tikhinella* and *Eogenitzina*), ichthyoliths, crinoid ossicles, calcisphaeres and fragments of microconchids (Fig. 6). The brachiopod shells are filled mainly by sediment lithologically identical to the matrix; partly geopetal structures filled with sparry calcite occur. The fossils are unsorted.

The second lithology consists of cherry-red grainstones with isolated intraclasts (Fig. 5C). Fossils include brachiopods (atrypides and rhynchonellides, e.g., *Pammegetherhynchus*), solitary rugose corals, smooth-shelled ostracods, foraminifers (*Tikhinella* and *Nodosaria*). Calcisphaeres are represented, among others, by volvocacean green algae as well as *Parathurammina* and *Radiosphaera* morphotypes, fragments of ostracods, ichthyoliths, mollusc and brachiopod shell debris.

The third lithological type are limestones with micritic matrix, partly neomorphosed. Fossils are represented by sponges and numerous sponge spicules, fragments of smooth-shelled ostracods, foraminifers (*Eogenitzina*), tentaculitids, juvenile ammonoids, mollusc and brachiopod shell debris.

5. Discussion

5.1. Comparison of branching and autorotatory forms

The coralla described here have a peculiar form that could be interpreted in a number of different ways: massive-fixed, massive-autorotatory, broken fragments of branching forms, or fragments of larger, irregular colonies. Typical massive-fixed colonies have attachment surfaces similar in size to the largest diameter of such a colony. Moreover, in alveolitids, corallites are usually inclined both on the upper and lower surfaces of coralla, which is not the case here. In favositids, if colonies are adapted to soft substrata, the attachment scar may be smaller, but the growth axis is tilted or curved. Also the base is often concave, which is reflected by growth rings in later growth stages (Król et al., 2016). None of these features are visible on our material, hence the massive-fixed growth form can readily be ruled out.

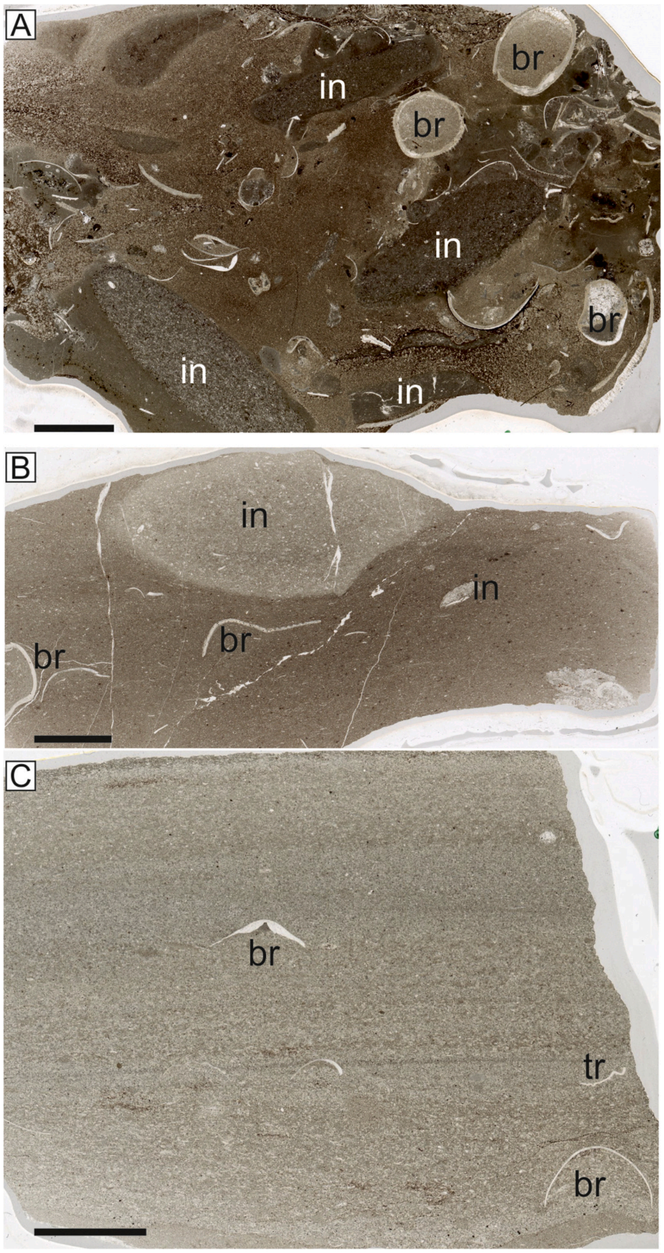

Fig. 5. Examples of thin-section photographs of microfacies at Jaźwica (upper Frasnian, set R = H2). A. Cherry-red intraformational conglomerate with numerous brachiopods (br) with rounded and flattened light-grey intraclasts (in) (GIUS 402 JA). B. Cherry-red intraformational conglomerate with brachiopods (br) and intraclasts (in) (GIUS 402 JB). C. Cherry-red grainstones with fragmented brachiopods (br) and trilobites (tr) (GIUS 402 JC1). Scale bars 10 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The specimens could also be interpreted as broken branching forms. However, they clearly differ from typical branching forms that have cylindrical branches with tapering distal branch tips. In branching forms, in case of breakage, the attachment scar is always on the wider side, and has the size of the branch diameter. Conversely, our specimens are somewhat spindle-shaped or irregular, with a tapering proximal end, and maximum thickness towards the distal part. The fragment that we interpret as an attachment scar represents only a fraction of each colony

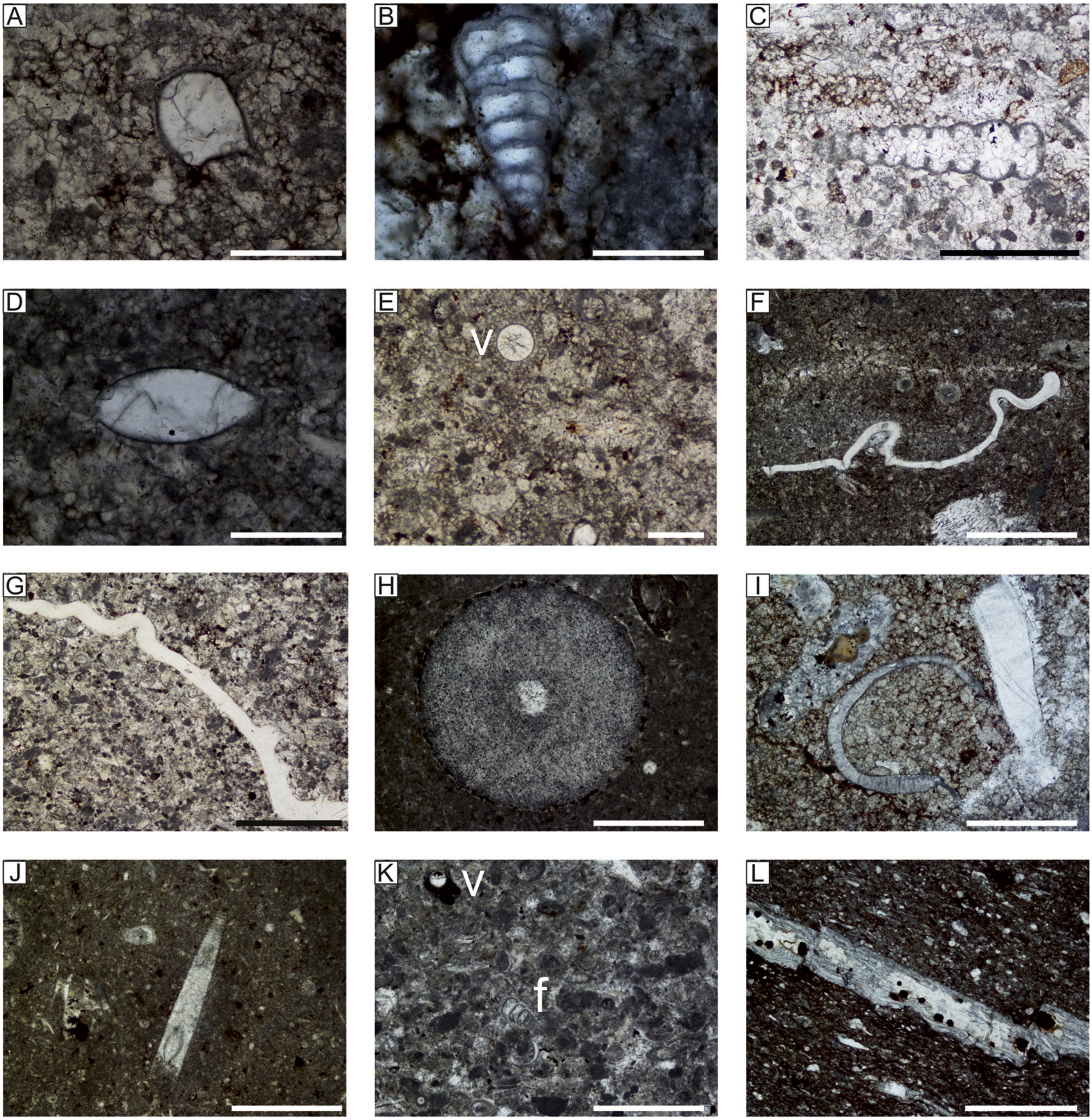

Fig. 6. Thin-section photomicrographs of biotic constituents in investigated sediments at Jaźwica, lithological complex R (sensu Racki, 1992). A. *Parathurammina* calcisphaera (GIUS 402 JC3). B. *Eogenitzina* sp. (GIUS 402 JA). C. ?*Nodosaria* sp. (GIUS 402 JC1). D. Smooth-shelled ostracod (GIUS 402 JC3). E. Volvocaean calcisphaera (v) (GIUS 402 JC1). F. Trilobites (GIUS 402 J173a03). G. Trilobites (GIUS 402 JC1). H. Crinoid (GIUS 402 J173a01). I. Microconchid (GIUS 402 JA). J. Tentaculite (GIUS 402 J149). K. Volvocaean calcisphaera (v) and *Tikhinella* (f) (GIUS 402 J173a02). L. Fragmented brachiopod shell (GIUS 402 JB2). Scale bars 200 μm (A–D), 1 mm (E–L).

smallest diameter. Such a form is unknown in branching tabulates. Branching alveolitids (e.g., *Alveolitella fecunda* or *A. polygona,* see Nowiński, 1992 & Zapalski, 2012) have a typically fan-shaped corallite arrangement in longitudinal branch sections. In the case of our specimens the arrangement of corallites in longitudinal sections is much more chaotic, with calyces opening also towards the proximal side. In both taxa investigated here corallites open on nearly all surfaces, and cross sections reveal either radial or vortex-like corallite arrangement that indicates circumrotatory growth. Alveolitids typically have corallites reaching the corallum surface at an acute angle (e.g., Lecompte, 1939; Hill, 1981), and *A.*? *tenuissimus* display vortex-like arrangement of corallites in the sections perpendicular to the long axis of our specimens. Such arrangement of corallites suggests autorotatory growth. The potential point of attachment is the narrowest point of the colony, which makes its attachment in environments with strong currents unlikely. As Dullo and Hecht (1990), their Fig. 2E) have shown, some coralliths may display unidirectional growth, and this seems to be the case at least in some of our specimens.

While alveolitids in the Holy Cross Mountains are very well recognized (Stasińska, 1953, 1958; Nowiński, 1992; Zapalski, 2012), specimens of such a form are unknown as fragments of massive or irregular coralla. Therefore, the interpretation of our specimens as fragments of larger colonies can be excluded. Also one of the specimens of *A.*? *tenuissimus* (Fig. 4H) displays a "bumpy" surface, typical for coralliths (see e.g., Dullo and Hecht, 1990, their Fig. 2A, E; Fig. 7 herein).

The "pear-shaped" colonies of *F. goldfussi* are strikingly similar to the scleractinian coralliths shown by Lewis (1989), his Fig. 4). This growth form was reported by Lecompte (1939) as "*F. goldfussi* forma *pyriformis*"

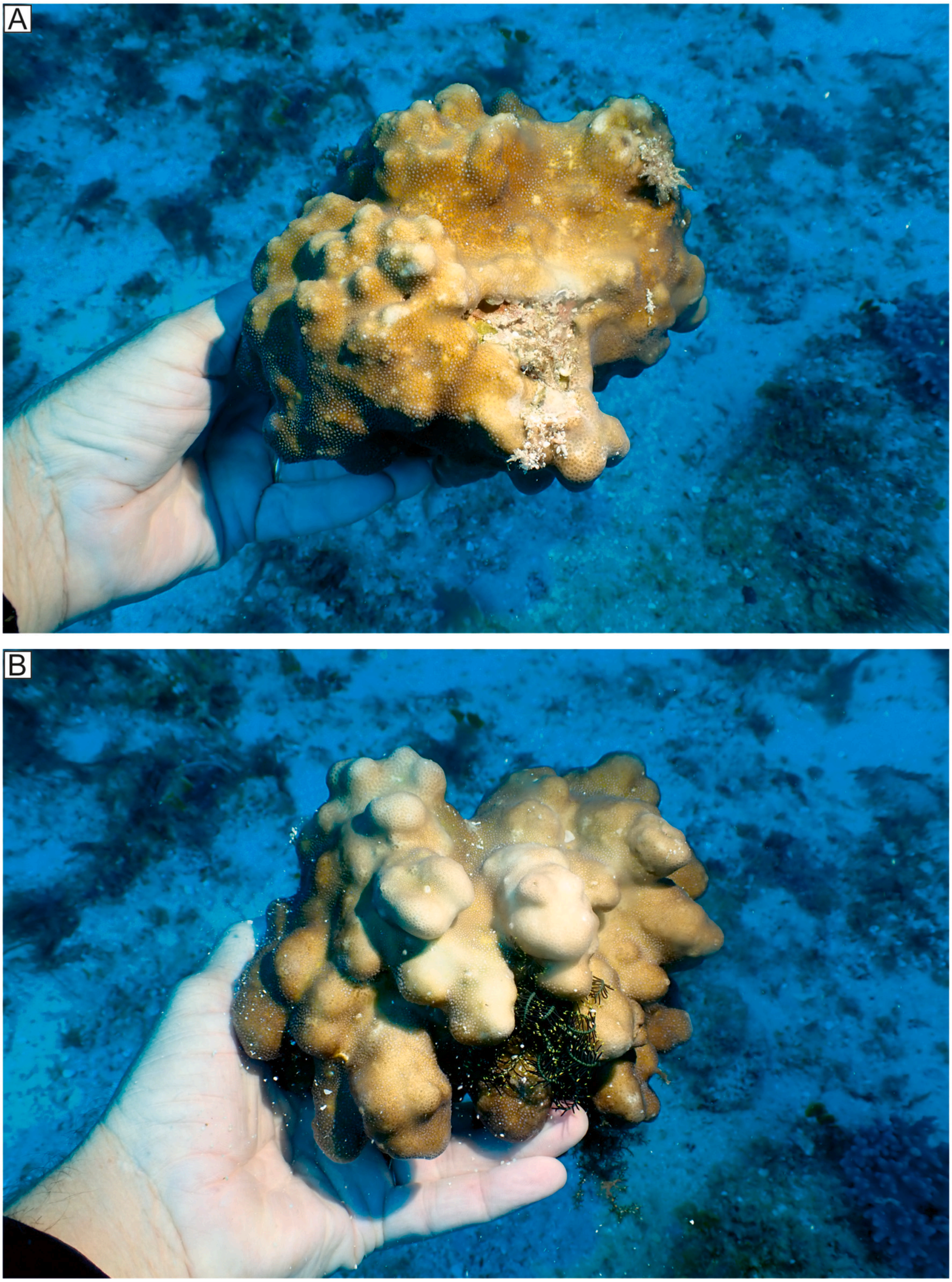

Fig. 7. A, B. Underwater photograph of a corallith of Recent *Stylocoeniella* cf. *guentheri* (MTQ G79987). This specimen was collected at 28 m of depth on the sandy bottom of the Wistari Channel (between Heron Island and Wistari Reef) on the southern Great Barrier Reef in an area of low topographic relief, unconsolidated substratum, low coral cover and high bottom currents.

from the Devonian of Ardennes and by Stasińska (1958) from Miłoszów. The preservation of our material did not allow preparation of more thin sections, but those shown by Lecompte (1939, his pl. 13) are nearly identical with cross sections shown by Kissling (1973) as typical coralliths. Externally, our material is very similar to that of both Lecompte (1939) and Stasińska (1958). It is therefore possible that this species developed such an evolutionary strategy on a broader scale.

The term "corallith" was introduced by Glynn (1974) for "coral colonies subspherical, globular or amoeboidal in growth form (…) that are mobile and subject of periodic transport (…)". Our specimens have all these features of coralliths, with the exception of a fully rounded morphology. We have also ruled out other potential growth forms. While the specimens described here do not represent fully round colonies, the remaining features allow us to interpret them as autorotatory, thus coralliths sensu Glynn, 1974.

Moreover, the material described above, although coming from localities scattered in space and time, is very similar in size and shape. Lewis (1989) described various morphologies of free-living *Siderastrea radians*, and interpreted them as subsequent stages of growth from attached to entirely free-living forms. The colonies described by Lewis (1989) are of very similar size and shape to the Devonian corals described here. In his classification of the typical coralliths, nearly completely round forms represent the final, fifth stage of growth. Our specimens probably represent an earlier stage, close to the 4th stage of growth (Lewis, 1989, see his Fig. 4 for comparison and his Table 1), at which the colony has already detached from the substratum and is showing early signs of circumrotatory growth, while still retaining the attachment scar. While Lewis (1989) regarded only 4th and 5th growth stages as true coralliths, Glynn's (1974) definition seems to be broader, and, as outlined above, we interpret our material as coralliths following the latter definition. An attachment scar is visible in stage 4 coralliths of Lewis (1989), see his Fig. 4), so even mature coralliths can display this structure. We can conclude that this is the first record (in the Palaeozoic) of earlier stages of colony development towards a fully circumrotatory form.

5.2. Sediment rejection in *A.? tenuissimus* and *F. goldfussi*

A.? tenuissimus is a species of alveolitids characterized by minute corallites – below 0.5 mm of the largest diameter (Zapalski, 2012), as compared to about 1 mm, being the usual size in the family. Stafford-Smith and Ormond (1992) revealed that Recent scleractinian taxa with polyps under 2.5 mm in diameter are poor sediment rejectors. Also Hubbard and Pocock (1972) noticed that corals with horizontal calical floors (such as in the case of *A.? tenuissimus*) are rather passive sediment rejectors. The presence of Type 3, sediment-derived growth interruption surfaces (sensu Miller and West, 1997), gradually passing into the "clean" Type 2 surfaces without sediment, in *A.? tenuissimus* specimens, seems to reinforce the hypothesis of this species being a passive sediment rejector (Król et al., 2018; Król et al., 2021). This may reveal why more mature corallith growth forms (sensu Lewis, 1989) are absent – due to poorly dealing with sediment the small colonies might have had higher mortality rates. Partial mortality can be seen in two specimens (Fig. 4C, D); due to concentric growth the colony recovered and damaged tissues were healed. Similar partial mortality was noted on *Siderastrea varians* (Lewis, 1989). The other species, *F. goldfussi*, has larger corallites (up to 2.5 mm in diameter) but is also likely to be a passive sediment rejector, using the criteria established by Stafford-Smith and Ormond (1992). Scleractinian corals that are passive sediment rejectors usually prefer higher hydrodynamic settings, since wave action is their main agent of sediment removal (Stafford-Smith, 1993; Sanders and Baron-Szabo, 2005). If the same held true for tabulate corals, it would either reinforce the hypothesis of bottom currents at larger depths, or that the studied corals were redeposited from a shallower, high-energy environment. As stated below, the presence of cephalopod coquinas (Rakociński and Borcuch, 2016) suggest bottom currents, and thus advocate for the former hypothesis. Tidal bottom currents at depths of over 100 m can exceed 20 m s^{-1} (Matsuyama and Teramoto, 1985), which is ten times stronger than the currents in Wistari Channel on the Southern Great Barrier Reef that were sufficient to produce a corallith of 15 cm in diameter.

5.3. Environmental interpretation

In modern seas, coralliths are a growth form that develops typically in very shallow waters, where frequent wave action allows rotation of such colonies (Kissling, 1973; Glynn, 1974). As outlined in the Introduction, tabulate corals preferred deeper environments (Lecompte, 1958; Embry and Klovan, 1972), so ecological niches for this growth form were more restricted and less frequent in Palaeozoic tabulates than in Mesozoic to Recent scleractinians, as scleractinians occur commonly also in the most shallow environments. In the Palaeozoic, circumrotatory forms of growth have been reported among favositids (Kissling, 1973; Abbott, 1975; Gill and Coates, 1977; Król et al., 2016), heliolitids (Abbott, 1975) and alveolitids (Denayer, 2018). The Lower Silurian favositid material from Ohio (Kissling, 1973) originated from slopes of small bioherms, located at very shallow depths. These specimens of *Favosites favosus* are either round or spindle-shaped, and must have been subject of nearly constant wave agitation. Similarly, the Late Devonian (Frasnian) material described by Denayer (2018) was found in association with oncoids, thus attesting high-energy, shallow environments. Only Król et al. (2016) described *F. bohemicus* from deeper Early Devonian environments, but in this case the features of autorotatory growth were an effect of gravitational tilting.

The environments in both the Łysogóry Region in the Givetian, and in southern Kielce subregion in the Frasnian are considered as relatively deep (Szulczewski, 1977; Racki, 1992). Most contemporary coralliths are found in shallow and very shallow environments (e.g., Glynn, 1974; Lewis, 1989; Rodríguez-Martínez and Jordán-Dahlgren, 1999). Our material does not fit this scheme and is unusual.

Although it is difficult to estimate absolute depth of these three sites, we can infer that all sites, the Givetian at Miłoszów, and Frasnian at Jaźwica and Kowala were located below the fair-weather wave base. Microfacies analysis of the set R of Jaźwica confirms such a conclusion. These sediments were formed in open-marine environments in the lower part of the slope in the relatively quiet water environments, however, close to storm-wave base with the influence of higher energy events such as storms or seismic activity, or occasional bottom currents. A depth below the fair-weather wave base can also be confirmed by the occurrence of flattened and rounded light-grey intraclasts, an ecologically mixed biota and fragmentation of numerous fossils. Such ecologically mixed biota is represented by calcisphaeres representing volvocacean green algae characteristic for back-reef environments (Kaźmierczak, 1976) and sponges, corals, and brachiopods – especially deeper-water rhynchonellides such as *Pammegetherhynchus* (see e.g., Sartenaer et al., 1998) characteristic for open-marine environments. We could interpret mixing of back-reef and deeper water biotas as a result of synsedimentational transport of back-reef biotas to deeper, fore-reef zone. Also the occurrence of sponge-rhynchonellide (Rigby et al., 2001) and polygnathid-palmatolepid biofacies (Rakociński and Borcuch, 2016) is characteristic for deeper, open marine environments. This palaeoenvironmental interpretation is consistent with the conclusions by Rigby et al. (2001) and Rakociński and Borcuch (2016). The latter authors described coquinas formed by small (<10 mm) cephalopod shells from the investigated strata and concluded that they must have accumulated due to bottom currents.

In Miłoszów, the microfacies data are deficient, but platy corals (coenitids and alveolitids) were found, thus suggesting that this environment might have been in the lower part of the photic zone, potentially even mesophotic, as in the nearby Skały site (similar age and same taxa of platy corals; Zapalski et al., 2017).

While most of reported to date Recent coralliths come from very shallow environments, these growth forms occur occasionally in deeper water settings. Dullo and Hecht (1990) described coralliths from the submarine alluvial fans of the Red Sea, Gulf of Aqaba, found at the depths reaching 25 m, and on seafloor sloping as steep as 30–35°. Occurrence of rhodoliths in a somewhat similar environmental setting was demonstrated by Piller and Rasser (1996). They analysed material from northern Red Sea, Gulf of Safaga. Destructional and bioerosional processes led to fragmentation of corals and algae, and accumulation of rhodoliths below the source reef – in discharge channels and between the reef and algae meadows below, on the leeward side of the reef.

Consequently, a possible interpretation of our material is that the colonies representing initial stages of circumrotatory growth were washed out to deeper environments from a shallow-water carbonate platform, where they continued their growth as autorotatory forms. Such a scenario might be correct particularly regarding the Kowala material – these beds contain broken bioconstructing organisms and slump structures (Racki, 1996) that evidence gravitational movements of sediment. Such a scenario might also be possible in regard to the Jaźwica material. Reefal faunas from the shallows of the Central Kielce subregion situated immediately north of these two sites are well known, and tabulate corals were very rare in these environments. Moreover, coralliths are unknown from these shallow-water sites, therefore such an interpretation seems unlikely.

On recent reefs, coralliths occasionally occur in deeper reef areas if conditions are favourable. In particular, Hoeksema et al. (2018) predicted that coralliths can develop at depth in areas of low topographic relief, unconsolidated substratum, low coral cover and high water movement. The channel between Heron Island and Wistari Reef on the Southern Great Barrier Reef (Wistari Channel) has a bottom made up largely of sand, the topography is remarkably flat, coral cover is low and the channel is regularly flushed by tidal currents that reach 7.5 km/h ($\sim$2 m s^{-1}; Jell and Webb, 2012). Such velocities are much higher than minimal required for the coralliths rotation, which is about 0.5 m s^{-1} (Scoffin et al., 1985). A corallith of *Stylocoeniella* cf. *guentheri* (Fig. 7) was found in the channel at 28 m depth. This specimen is significantly larger (15 cm maximum diameter) than the fossil specimens described herein, which demonstrates that even relatively large colonies can be systematically overturned by bottom currents frequently enough to sustain living tissue on all their sides. This environment may therefore be a good modern analogue to those described here, especially for Jaźwica, where local bottom currents are well documented (Rakociński and Borcuch, 2016).

It is also worth mentioning that bioclaustrations are not uncommon in the studied specimens of *A.*? *tenuissimus*, and a case of a *syn-vivo* encrustation has also been noticed on *A.*? *tenuissimus* and one specimen of *F. goldfussi* (Fig. 3C). If these bioclaustrations formed around currently not preserved, possibly non-skeletal epibionts (Król et al., 2018), it would imply that the overturning of the colonies must have been either very slow, or sufficiently irregular to provide the time needed for epibionts to settle. However, uneven overturning could result in developing a non-fully sphaerical form, and very slow overturning would rule out the hypothesis of these colonies developing under high water agitation in shallow environment. As a result, such bioclaustrations and encrustations advocate for rather deeper environment, where constant wave action does not exist.

While the ideal circumrotatory, round colonies of radial structure are typical for very shallow water environments with frequent, regular overturning (Kissling, 1973), our weakly irregular colonies with somewhat unidirectional growth, especially in *F. goldfussi* is what should be expected in environment with less regular overturning currents. Less frequent overturning may result in unidirectional growth in corallites (Dullo and Hecht, 1990).

6. Conclusions

We report the first record of coralliths (circumrotatory coral colonies) in the Devonian (Givetian and Frasnian) of the Holy Cross Mountains, Poland. While these favositid colonies represent developmental stage 4 sensu Lewis (1989) and have a potential attachment scar, they display nearly all other features of passively rotated colonies, and are interpreted as such. Our discovery demonstrates that the spectrum of coral growth forms in the Devonian peak of reef development was broader than assumed heretofore, and that tabulate corals displayed more numerous adaptive strategies to various environments than previously thought. The passively motile colonies were also broadly geographically distributed (north and south shores of the Rheic Ocean).

Most coralliths to date (both fossil and Recent) were described from very shallow environments (a few metres deep). The material we reported comes from relatively deep environments. We have shown that rather than redeposited, these corals lived in deeper environments where bottom currents caused their autorotation. A good modern analogue for such corallith-forming environment is the Wistari Channel where bottom tidal currents at nearly 30 m of depth are strong enough to overturn colonies of *Stylocoeniella* cf. *guentheri* reaching 15 cm in diameter.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Abbott, B.M., 1975. Implications for the fossil record of modern carbonate bank corals. Geol. Soc. Am. Bull. 86, 203–204.
Berkowski, B., 2002. Famennian Rugosa and Heterocorallia from Southern Poland. Palaeontol. Pol. 61, 3–88.
Capel, K.C.C., Segal, B., Bertuol, P., Lindner, A., 2012. Corallith beds at the edge of the tropical South Atlantic. Coral Reefs 31, 75.
De Vleeschouwer, D., Rakociński, M., Racki, G., Bond, D.P., Sobień, K., Claeys, P., 2013. The astronomical rhythm of Late-Devonian climate change (Kowala section, Holy Cross Mountains, Poland). Earth Planet. Sci. Lett. 365, 25–37.
Denayer, J., 2018. From rolling stones to rolling reefs: a Devonian example of highly diverse macroids. Lethaia 51, 564–580.
Dullo, W.-F., Hecht, C., 1990. Corallith growth on submarine alluvial fans. Senckenberg. Marit. 21, 77–86.
Embry, A.F., Klovan, J.E., 1972. Absolute water depth limits of Late Devonian paleoecological zones. Geol. Rundsch. 61, 672–686.
Gill, G.A., Coates, A.G., 1977. Mobility, growth patterns and substrate in some fossil and recent corals. Lethaia 10, 119–134.
Glynn, P.W., 1974. Rolling stones among the Scleractinia: mobile coralliths in the Gulf of Panama. In: Proc 2nd Int Coral Reef Symp, 2, pp. 183–198.
Golonka, J., 2020. Late Devonian paleogeography in the framework of global plate tectonics. Glob. Planet. Chang. 186, 103129.
Gürich, G., 1896. Das Palaeozoicum im Polnischen Mittelgebirge. In: Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu Sankt-Petersburg (2), 32. Kaiserlichen Akademie der Wissenschaften, Sankt Petersburg, pp. 1–539.
Halamski, A.T., 2005. Annotations to the Devonian Correlation Table, R220dm05: Poland; Holy Cross Mts; Łysogóry Region. Senckenb. Lethaea 85, 185–187.
Halamski, A.T., 2009. Middle Devonian brachiopods from the northern part of the Holy Cross Mountains, Poland in relation to selected coeval faunas. Part I: Introduction, Lingulida, Craniida, Strophomenida, Productida, Protorthida, Orthida. Palaeontogr. Abt. A 287, 41–98.
Halamski, A.T., Racki, G., 2005. Supplements 2005. In: K. Weddige (ed.), Devonian Correlation Table. With 24 Table-columns. Senckenb. Lethaea 85, 191–200.
Hill, D., 1981. Tabulata. In: Moore, R.C., Teichert, C. (Eds.), Treatise On Invertebrate Paleontology. Part F, Coelenterata. Supplement 1(2). The Geological Society of America, Boulder, and The University of Kansas, Lawrence, pp. F430–F762.

Hoeksema, B.W., Bongaerts, P., 2016. Mobility and self-righting by a free-living mushroom coral through pulsed inflation. Mar. Biodivers. 46, 521–524.

Hoeksema, B.W., Hassell, D., Meesters, E.H., van Duyl, F.C., 2018. Wave-swept coralliths of Saba Bank, Dutch Caribbean. Mar. Biodivers. 48, 2003–2016.

Hubbard, J.A., Pocock, Y.P., 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol. Rundsch. 61, 598–626.

Jell, J.S., Webb, G.E., 2012. Geology of Heron Island and adjacent reefs, Great Barrier Reef, Australia. Episodes 35, 110–119.

Kaźmierczak, J., 1976. Volvocacean nature of some Palaeozoic non-radiosphaerid calcispheres and parathuraminid 'foraminifera'. Acta Palaeontol. Pol. 21, 245–258.

Kissling, D.L., 1973. Circumrotatory growth form in recent and Silurian corals. In: Boardman, R.S., Cheetham, A.H., Oliver Jr., W.A. (Eds.), Animal Colonies: Development and Function Through Time: Stroudsburg. Dowden, Hutchinson and Ross, pp. 43–58.

Król, J.J., Zapalski, M.K., Jakubowicz, M., Berkowski, B., 2016. Growth strategies of the tabulate coral *Favosites bohemicus* on unstable, soft substrates: an example from the Hamar Laghdad (Lower Devonian, Anti-Atlas, Morocco). Palaeogeogr. Palaeoclimatol. Palaeoecol. 449, 531–540.

Król, J.J., Jakubowicz, M., Zapalski, M.K., Berkowski, B., 2018. Massive tabulates in competition for space: a case study from Aferdou el Mrakib (Middle Devonian, Anti-Atlas, Morocco). Palaeogeogr. Palaeoclimatol. Palaeoecol. 497, 105–116.

Król, J.J., Denayer, J., Wolniewicz, P., Zapalski, M.K., 2021. Heliolitid corals and their competitors: a case study from the Wellin patch reefs, Middle Devonian, Belgium. Lethaia 54, 540–557. https://doi.org/10.1111/let.12421.

Lecompte, M., 1933. Le genre Alveolites Lamarck dans le Dévonien moyen et supérieur de l'Ardenne. In: Mémoires du Musée royal d'Histoire naturelle de Belgique, 55, pp. 1–49.

Lecompte, M., 1939. Les Tabules du Dévonien moyen et supérieur du bord sud du basin de Dinant. In: Mémoires du Musée royal d'Histoire naturelle de Belgique, 90, pp. 1–227.

Lecompte, M., 1958. Les récifs paléozoïques en Belgique. Geol. Rundsch. 47, 384–401.

Lewis, J.B., 1989. Spherical growth in the Caribbean coral Siderastrea radians (Pallas) and its survival in disturbed habitats. Coral Reefs 7, 161–167.

Machel, H.G., Hunter, I.G., 1994. Facies models for Middle to Late Devonian shallow-marine carbonates, with comparisons to modern reefs: a guide for facies analysis. Facies 30, 155–176.

Matsuyama, M., Teramoto, T., 1985. Observations of internal tides in Uchiura Bay. J. Oceanogr. Soc. Japan 41, 39–48.

Miller, K.B., West, R.R., 1997. Growth-interruption surfaces within chaetetid skeletons: Records of physical disturbance and depositional dynamics. Lethaia 29, 289–299.

Nowiński, A., 1992. Tabulate corals from the Givetian and Frasnian of the Holy Cross Mountains and Silesian Upland. Acta Palaeontol. Pol. 37, 183–216.

Pajchlowa, M., 1957. The Devonian in the Grzegorzowice-Skały section. Biul. Inst. Geol. 122, 145–254 (In Polish, with English summary).

Piller, W.E., Rasser, M., 1996. Rhodolith formation induced by reef erosion in the Red Sea, Egypt. Coral Reefs 15, 191–198.

Pisarzowska, A., Sobstel, M., Racki, G., 2006. Conodont-based event stratigraphy of the Early-Middle Frasnian transition on the South Polish carbonate shelf. Acta Palaeontol. Pol. 51, 609–646.

Plusquellec, Y., Webb, G.E., Hoeksema, B.W., 1999. Automobility in Tabulata, Rugosa, and extant scleractinian analogues: stratigraphic and paleogeographic distribution of Paleozoic mobile corals. J. Paleontol. 73, 985–1001.

Porter, J.W., 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. Am. Nat. 110 (975), 731–742.

Racki, G., 1992. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. Acta Palaeontol. Pol. 37 (2–4), 87–182.

Racki, G., 1996. Frasnian-Famennian boundary at Kowala. In: Szulczewski, M., Skompski, S. (Eds.), Sixth European Conodont Symposium, Excursion Guide, pp. 30–33.

Racki, G., Baliński, A., 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian–Famennian biotic crisis. Acta Palaeontol. Pol. 43, 273–304.

Rakociński, M., Borcuch, E., 2016. Concentrations of silicified cephalopods within upper Frasnian carbonate concretions from the Holy Cross Mountains, Poland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 449, 475–483.

Rakociński, M., Marynowski, L., Zatoń, M., Filipiak, P., 2021. The mid-Tournaisian anoxic event (Lower Carboniferous) in the Laurussian shelf basin (Poland): an integrative approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 566, 1–28.

Richards, Z.T., Bryce, M., Bryce, C., 2013. New records of atypical coral reef habitat in the Kimberley, Australia. Journal of Marine Sciences, 363894. https://doi.org/10.1155/2013/363894.

Rigby, J.K., Pisera, A., Wrzołek, T.T., Racki, G., 2001. Upper Devonian sponges from the Holy Cross Mountains, Central Poland. Palaeontology 44, 447–488.

Rodríguez-Martínez, R.E., Jordán-Dahlgren, E., 1999. Epibiotic and free-living Porites *astreoides*. Coral Reefs 18, 159–161.

Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62, 185–202.

Rosen, B.R., Aillud, G.S., Bosellini, F.R., Clack, N.J., Insalaco, E., Valldeperas, F.X., Wilson, M.E.J., 2002. Platy coral assemblages: 200 million years of functional stability in response to the limiting effects of light and turbidity. In: Proceedings of the Ninth International Coral Reefs Symposium, Bali, 1, pp. 255–264.

Sanders, D., Baron-Szabo, R.C., 2005. Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. Palaeogeogr. Palaeoclimatol. Palaeoecol. 216, 139–181.

Sartenaer, P., Racki, G., Szulczewski, M., 1998. The late Frasnian rhynchonellid genus *Pammegetherhgnchus* (Brachiopoda) in Poland, and its relevance to the Kellwasser Crisis. Acta Palaeontol. Pol. 43, 379–394.

Scoffin, T.P., Stoddart, D.R., Tudhope, A.W., Woodroffe, C., 1985. Rhodoliths and coralliths of Muri Lagoon, Rarotonga, Cook Islands. Coral Reefs 4, 71–80.

Stafford-Smith, M.G., 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar. Biol. 115, 229–243.

Stafford-Smith, M.G., Ormond, R.F.G., 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Mar. Freshw. Res. 43, 683–705.

Stasińska, A., 1953. Rodzaj *Alveolites* Lamarck z franu Gór Świętokrzyskich. Acta Geol. Pol. 3, 211–238.

Stasińska, A., 1958. Tabulata, Heliolitida et Chaetetida du Dévonien moyen des monts de Sainte-Croix. Acta Palaeontol. Pol. 3, 161–282.

Stasińska, A., 1974. On some Devonian Auloporida (Tabulata) from Poland. Acta Palaeontol. Pol. 19, 265–280.

Stel, J.H., 1978. Growth and reproduction in the tabulate *Favosites forbesi* from the Silurian of Gotland. Geologiska Föreningen i Stockholm Förhandlingar 100, 181–188.

Stolarski, J., Zibrowius, H., Loser, H., 2001. Antiquity of the scleractinian-sipunculan symbiosis. Acta Palaeontol. Pol. 46, 309–330.

Szulczewski, M., 1971. Upper Devonian conodonts, stratigraphy and facial development in the Holy Cross Mts. Acta Geol. Pol. 21, 1–130.

Szulczewski, M., 1977. Główne regiony facjalne w paleozoiku Gór Świętokrzyskich. Prz. Geol. 25, 428–432 (In Polish, with English summary).

Szulczewski, M., 1995a. Depositional evolution of the Holy Cross Mts. (Poland) in the Devonian and Carboniferous-a review. Geol. Q. 39, 471–488.

Szulczewski, M., 1995b. Devonian succession in the Kowala quarry and railroad cut. In: Dvořák, J., Galle, A., Herbig, H.G., et al. (Eds.), Evolution of the Polish-Moravian carbonate platform in the Late Devonian and Early Carboniferous: Holy Cross Mts., Krakow Upland, Moravian Karst. Guide to Excursion 4B, International Congress on Carboniferous-Permian, pp. 13–16.

Szulczewski, M., Belka, Z., Skompski, S., 1996. The drowning of a carbonate platform: an example from the Devonian-Carboniferous of the southwestern Holy Cross Mountains, Poland. Sediment. Geol. 106, 21–49.

Todd, P.A., 2008. Morphological plasticity in scleractinian corals. Biol. Rev. 83, 315–337.

Zapalski, M.K., 2005. Paleoecology of Auloporida: an example from the Devonian of the Holy Cross Mts., Poland. Geobios 38, 677–683.

Zapalski, M.K., 2012. Tabulate corals from the Givetian and Frasnian of the southern region of the Holy Cross Mountains (Poland). Spec. Pap. Palaeontol. 87, 1–100.

Zapalski, M.K., Wrzołek, T., Skompski, S., Berkowski, B., 2017. Deep in shadows, deep in time: the oldest mesophotic coral ecosystems from the Devonian of the Holy Cross Mountains (Poland). Coral Reefs 36, 847–860.

Zapalski, M.K., Baird, A.H., Bridge, T., Jakubowicz, M., Daniell, J., 2021. Unusual shallow water Devonian coral community from Queensland and its recent analogues from the inshore Great Barrier Reef. Coral Reefs 40, 417–431.

Zatoń, M., Wrzołek, T., 2020. Colonization of rugose corals by diverse epibionts: dominance and syn vivo encrustation in a Middle Devonian (Givetian) soft-bottom habitat of the Holy Cross Mountains, Poland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 556, 109899.