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REPORT

Deep in shadows, deep in time: the oldest mesophotic coral ecosystems from the Devonian of the Holy Cross Mountains (Poland)

Mikołaj K. Zapalski[1] · Tomasz Wrzołek[2] · Stanisław Skompski[1] · Błażej Berkowski[3]

Abstract Recent mesophotic coral ecosystems (MCE) occur at depths between 30 and 150 m and are characterized by dominance of platy corals. Such morphology is an effect of specific adaptation to efficient light harvesting. Here, we describe and analyze platy coral assemblages from two Middle Devonian localities in the Holy Cross Mountains (Poland) that during this time were located on the southern shelf of Laurussia at tropical latitudes. The Eifelian argillaceous sediments of Skały are dominated by platy and encrusting tabulate corals (*Roseoporella*, *Platyaxum* and *Alveolites*). Coeval faunas from the shallow-water parts of the Holy Cross Mountains basin display bulbous and branching morphology, thus indicating a Paleozoic coral zonation similar to that known in the Recent. Hence, the Skały site seems to be the oldest known MCE (ca. 390 Ma). A Givetian biostrome from Laskowa Quarry is a second example dominated by platy corals, with abundant branching forms; this site can be recognized as another Devonian MCE. Frondescent *Platyaxum*, common at both sites, had a growth habit similar to that of Recent *Leptoseris*, *Mycedium* or *Pavona*. Platy morphology is photoadaptive and may evidence photosymbiosis in tabulate (*Alveolites*, *Roseoporella*, *Platyaxum*) and rugose

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corals (*Phillipsastrea*). Furthermore, it may serve as a tool for recognition of the lower euphotic zone in the fossil record.

Keywords Platy corals · Devonian · Photosymbiosis · Mesophotic · Tabulate corals

Introduction

Recent coral reefs are formed principally by photosymbiotic corals. Symbiosis with photosynthetic algae (zooxanthellae) significantly enhances calcification, and as a result, photosymbiotic corals are able to build large bioconstructions. Large and highly biodiverse reefs occur in very shallow, tropical zones. Photosymbiotic corals, however, occur much deeper than the 30 m broadly recognized as the lower depth limit of reefs (e.g., Fricke and Meischner 1985; Bridge et al. 2011). Below 30 m, where light attenuation is stronger, zooxanthellate corals can still form reefs and many zooxanthellate species are known below the depth limit of 100 m (e.g., Dinesen 1980; Pochon et al. 2015). The deepest zooxanthellates occur even below 150 m, as in the case of *Leptoseris papyracea* (e.g., Lesser et al. 2009; Slattery et al. 2011). Reefs at 30–150 m developing in the shadows with substantial contribution from zooxanthellates are referred to as mesophotic reefs or mesophotic coral ecosystems (MCEs, Baker et al. 2016). Although still poorly known, it seems that MCEs are more widespread than their shallow-water counterparts (Bare et al. 2010; Slattery et al. 2011).

Life in an environment with depleted light requires special adaptations. Because of light scarcity, corals in the deeper water must develop morphologies promoting light harvesting. One such adaptation is the morphology of the

corallum. The best adaptations to depleted light are shown by platy corals (e.g., Kühlmann 1983; Kahng et al. 2010). Such corals can grow with as little as 4% of the surface light energy, while bulbous colonies require at least 20%, and branching 60% of the surface light energy (Hallock 2005). A species can display bulbous or massive morphology in shallow waters, but in deeper water the same species becomes flattened, as in the case of the Caribbean *Montastraea cavernosa* (Baker et al. 2016). Under a low light regime corals tend to grow toward the expanding surface rather than by expanding volume (Anthony and Hoegh-Guldberg 2003), and production of a platy skeleton is energetically more efficient (Kahng et al. 2010). In general, shade-dwelling corals have flat morphologies and small sizes of coralla, mostly 20–60 cm (Dinesen 1983). MCEs are dominated by platy or encrusting corals, and such a morphology is broadly considered as photoadaptive growth (e.g., Graus and Macintyre 1976, 1982; Rosen et al. 2002; Anthony and Hoegh-Guldberg 2003; Kahng et al. 2010, 2012, 2014).

Platy morphologies in scleractinians were possibly widespread in Meso- and Cainozoic reefs (Rosen et al. 2002), and are indicative of photosymbiosis in fossil record (e.g., Insalaco 1996; Rosen et al. 2002; Santodomingo et al. 2015). Platy corals were recorded as early as in the Late Triassic (ca. 230 Ma; Martindale et al. 2012) which suggests that such an adaptation is ancient as well as efficient. Scleractinian corals, however, massively appeared in the Triassic (ca. 245 Ma); large Paleozoic "reefs" were built with contribution from rugose and tabulate corals that became extinct by the end of Permian (ca. 250 Ma).

Tabulate corals were important bioconstructors of these Paleozoic "reefs" in the past (e.g., Wood 1999; Hubert et al. 2007; Zapalski et al. 2007) and are considered photosymbiotic on the basis of morphological criteria, such as colony integration, corallite size and overall morphological similarities to Recent photosymbiotic scleractinians (e.g., Coates and Jackson 1987; Stanley and Lipps 2011), or stable isotopes of carbon and oxygen of the coral skeleton, combined with growth rates and morphology (Zapalski 2014). Yet, there are some views questioning either photosymbiosis of tabulates (Scrutton 1998) or the use of isotopes in Paleozoic corals as a tool for recognition of photosymbiosis (Jakubowicz et al. 2015). Occurrence of platy colonies in a Paleozoic community may therefore be an unequivocal argument in favor of photosymbiosis. On the other hand, if mesophotic communities are widespread in the Recent, and have been recorded in the Meso- and Cainozoic, then they should also have occurred in the Paleozoic. Finding a Paleozoic community of platy corals would provide evidence of the presence of MCEs before the rise of scleractinian reefs.

The aim of this paper is to analyze two Middle Devonian tabulate coral communities from the Holy Cross Mountains (Central Poland), to analyze their paleoecology and possible evidence for photosymbiosis.

Materials and methods

This research is based principally on field observations carried out in 2016 at two fossiliferous sites: Skały and Laskowa Quarry (also erroneously called Laskowa Góra Quarry; Fig. 1). Dimensions of the coral colonies were measured in Laskowa Quarry in situ; at Skały, the lower coral-bearing unit is no longer exposed; therefore, all measurements were made on material collected as rubble. Often the sections of corals observed in the Laskowa Quarry walls do not cut colonies at their widest places, so their width is systematically underestimated. This is probably not the case for height, as extracted colonies appear mostly uniformly flat (with very few exceptions). Following Rosen et al. (2002), we use the term "platy corals" for those that have width-to-height ratio (W/H) exceeding 4:1.

Selected samples were cut, and polished slabs were observed; selected specimens were used to make thin sections for microfacies analysis. Samples of corals were also taken for determination in thin section. Altogether, over a thousand specimens of tabulates, rugosans and other fossils have been analyzed. Because smaller and more fragile colonies are represented by broken fragments, and larger ones are often preserved whole, only approximate ratios between various types of colonies are given. Part of the collection is housed at the University of Silesia, Sosnowiec, and the remaining material at the University of Warsaw, Faculty of Geology.

The field photographs were taken using a Canon EOS 70D body and various lenses. The 10–18 mm lens used in the field may produce some distortion at the edges of photographs. Microphotographs were taken using a Zeiss Discovery V20 stereoscopic microscope and the Canon EOS 70D body with transmitted light, and using 24–85 mm and 100 mm macro lenses. Most specimens for the photographs were coated with ammonium chloride. The contrast and sharpness of photographs were adjusted in Corel Photo Paint software. The terms colony and corallum are used interchangeably throughout the text.

Devonian in the Holy Cross Mountains

The Holy Cross Mountains (Central Poland) were located on the tropical southern shelf of Laurussia during the Devonian. The Devonian here is developed in two distinct
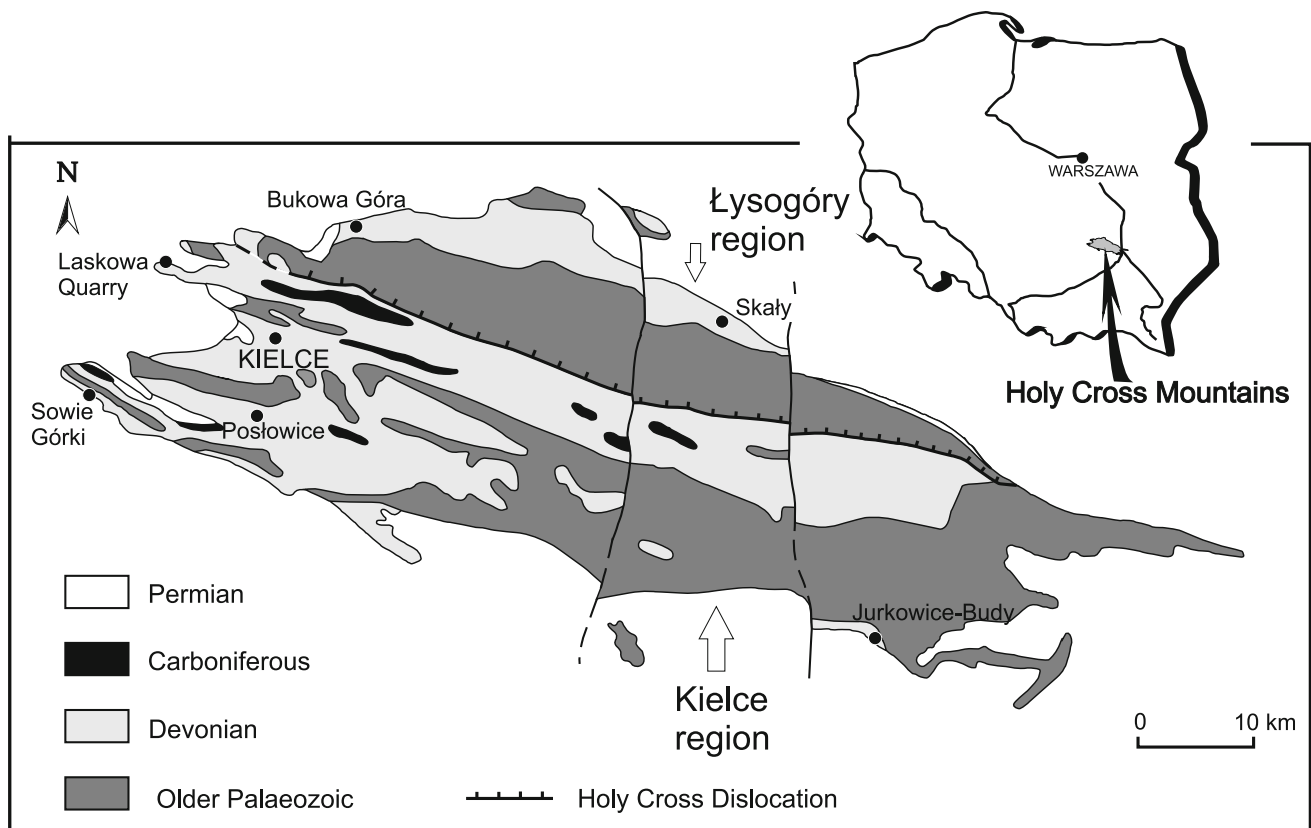
Fig. 1 Location of the quarries at Laskowa and Skały on a simplified geological map of the Paleozoic inlier of the Holy Cross Mountains, Poland

paleogeographic units: the Łysogóry paleolow (northern) and Kielce paleohigh (southern), with the Kostomłoty Transitional Zone between these (e.g., Szulczewski 1977; Racki 1992). Bioconstructions in which tabulate corals play a significant role occur in both regions, but those occurring in the Kielce region were formed in relatively shallow water, and those in two other zones represent deeper environments (Racki 1992).

Skały

The outcrops of Skały Beds (50°53′44.69″N 21°9′33.75″E) near Skały village (Fig. 1) are part of the Grzegorzowice-Skały section (Łysogóry region). These outcrops have yielded numerous faunas (tabulates: Stasińska 1958; Zapalski 2005; rugosans: Różkowska 1954, 1956, 1965; Fedorowski 1965; for other faunas see Halamski and Zapalski 2006).

At this location, the dolomitic/limestone Kowala Formation represents shallow environments (Skompski and Szulczewski 1994) and is overlain by the Skały Beds, composed of marly and clayey shales interbedded with marls and limestones (lithological sets XIII to XXVIII of Pajchlowa 1957) that represent deeper, intrashelf environments (Kłossowski 1985; Racki and Narkiewicz 2000).

The outcrop analyzed first displays fossiliferous brachiopod shales (set XIV), which are overlain by marly limestones (set XV). The limestone layers are represented by wackestones/packstones with abundant corals, crinoids and bryozoan debris. The gastropods, rare large-eyed phacopids, tentaculoids, single problematical alga *Globochaete* and a single receptaculitid make up the supplementary material. A second small outcrop of set XVIII is located some 100 m northeast from the previous one. Crinoidal limestones cropping out here yielded scarce tabulates accompanied by bryozoans and small gastropods. The age of these complexes has been determined as upper Eifelian to lower Givetian *kockelianus* to *timorensis* conodont zones (Malec and Turnau 1997; Narkiewicz and Narkiewicz 2010).

Laskowa Quarry

Laskowa Quarry is an active quarry (50°55′45.2″N 20°32′49.5″E), located a few kilometers northwest of Kielce (Kostomłoty Transitional Zone). The lower part of the section is composed of thickly bedded dolomites of the Kowala Formation, sporadically containing remains of corals in growth position, amphiporids and stringocephalids. The dolomites are overlain by limestones of the

coenitid biostrome (Set A sensu Racki et al. 1985; Laskowa Góra Beds sensu Racki and Bultynck 1993), which is a significant subject of this study. This biostrome is exposed in the northeast corner of the quarry on the two upper levels. The lateral extent of the biostrome is ~200 m. Its age is dated as Late Givetian *hermanni-cristatus* through *disparilis* conodont zones (Racki 1985; Narkiewicz and Narkiewicz 2010). The Laskowa Beds are overlain by gray to black shales and marly shales of Szydłówek Beds with cephalopods and stylolinids that indicate pelagic sedimentation.

Results

Coral beds at Skały

The Eifelian coral-bearing beds at Skały yielded broken fragments of tabulates: frondescent and encrusting coenitids and platy and mushroom-shaped alveolitids (Fig. 2), a single platy favositid and a single massive heliolitid (full list of taxa in Table 1). *Roseoporella* representatives in Skały form mostly encrusting coralla, 2–4 mm thick and over 10–15 cm across. Multiple layers of *Roseoporella* very often form small domes, 5–7 cm high and 10–15 cm in diameter. These domes sometimes overgrow other corals, such as the one shown in Fig. 2, starting with mushroom-shaped *A.* cf. *taenioformis*. W/H ratio in *Roseoporella* frequently exceeds 10:1. *Platyaxum* representatives are found as broken fronds, mostly 2–4 mm in thickness and up to 3–4 cm in length (the largest fragment is over 11 cm across). *Alveolites, Favosites* and *Heliolites* form an accessory part of this community and have flat coralla, with a W/H ratio approximately 3:1–6:1. Upper

surfaces of coralla are very often encrusted by auloporids, bryozoans and microconchids, but under the overhanging colonies microconchids and bryozoans also frequently occur, forming a peculiar cryptic association. In general, in these environments platy and encrusting tabulates dominate, and massive colonies are very rare. Rugose corals are represented by various small, solitary taxa. Among them the most common are perfectly preserved solitary undissepimented taxa like the operculate *Calceola* and button shaped like *Microcyclus* (see Stolarski 1993; Jakubowicz et al. 2015). There are also typical solitary, undissepimented small horn-shaped taxa (*Cyathaxonia* fauna) described by Fedorowski (1965) and, less commonly, larger dissepimented taxa (full list in Table 1). The corallites of the rugose solitary corals from Skały often reveal the phenomenon of rejuvenescence due to instability of the soft argillaceous bottom. Such bottom conditions are also corroborated by the presence of the genus *Microcyclus*, which is regarded as displaying automobility on the soft sediment. No colonial rugosan taxa are so far known from this locality. Most specimens were collected from rubble.

Coral beds at Laskowa

The biostrome (Fig. 3a–c) is strongly heterogenous, both lithologically and faunistically. Coral bafflestones dominate, intercalated with marly levels and crinoidal limestones. Microfacies of the matrix of biostromal layers are represented by packstones or wackestones, with dominance of tabulate debris and crinoidal grains (Fig. 3d). Occasional ostracods are the only supplementary material. Fossils in the biostromal unit are somewhat silicified (Racki et al. 1985) and contain numerous tabulate and
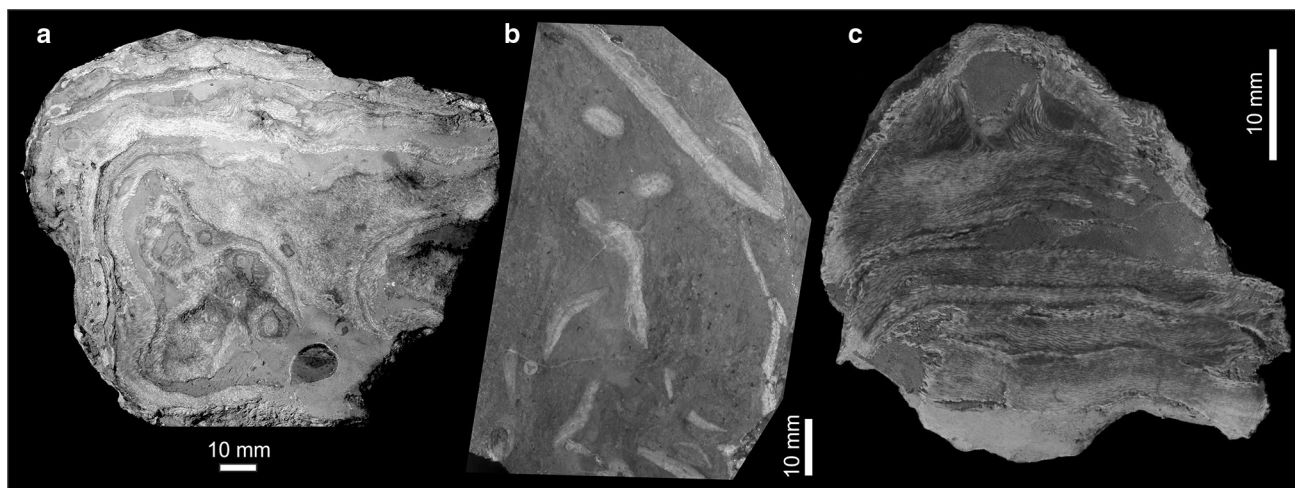

Fig. 2 Polished slabs from Skały, Late Eifelian. **a** Mushroom-shaped *Alveolites* cf. *taenioformis*, encrusted by *Roseoporella*. Complex XV. **b** Fronds of *Platyaxum escharoides*. Complex XVIII. **c** Multilayered coralla of *Roseoporella* sp. with overgrown solitary rugose coral in *upper* part. Complex XV

Table 1 List of tabulate and rugose corals from the coral beds in Skały, based on Fedorowski (1965) and this study

| Tabulate corals	Comments	Rugose corals	Comments
Platyaxum escharoides	Frondescent	*Calceola sandalina*	Operculate
P. clathratum minus	Frondescent	*Microcyclus praecox*	Button shaped
Roseoporella sp.	Encrusting	*Metriophyllum skalense*	Small, horn shaped
Alveolites cf. *taenioformis*	Platy/mushroom	*Metrionaxon schlueteri*	Small, horn shaped
A. cf. *fornicatus*	Platy/mushroom	*M. accipiter*	Small, horn shaped
Favosites sp.	Platy (rare)	*Syringaxon bohemica*	Small, horn shaped
Heliolites cf. *porosus*	Massive (rare)	*Stewartophyllum polonicum*	Small, horn shaped
		Amplexocarinia tortuosa	Medium sized, horn shaped
		Blothrophyllum skalense	Large, dissepimented
		Macgea sp.	Medium sized, dissepimented
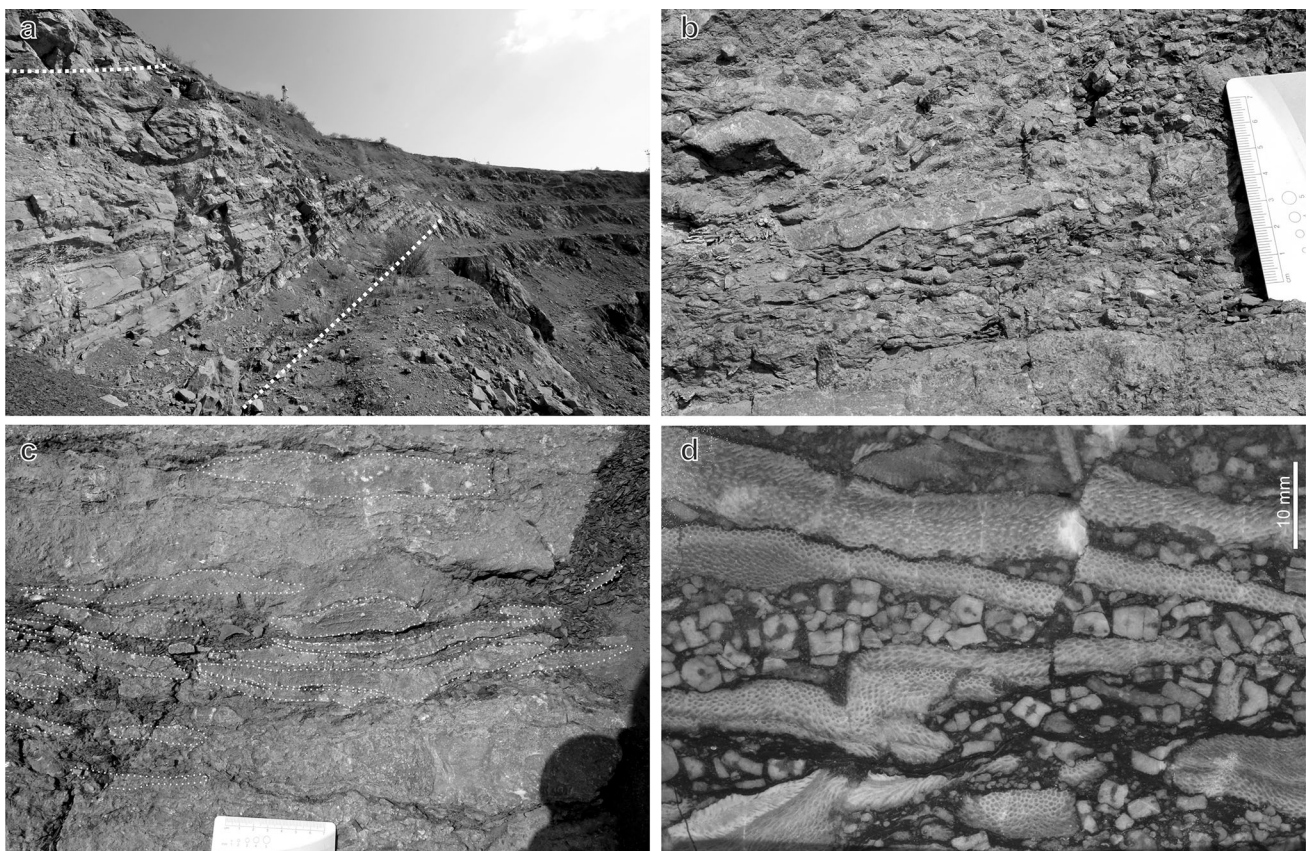
Fig. 3 Platy coral biostrome in Laskowa Quarry, Late Givetian. **a** Approximate position in the quarry (*dashed lines*), NE corner, lower level. **b** Fragment of biostrome with dominant branching corals. **c** Fragment of biostrome with platy coral dominance. **d** Polished slab of platy coral assemblage with crinoids

rugose corals, brachiopods, and less frequent chaetetid sponges, stromatoporoids, and bryozoans; also abundant are crinoid remains, and occasional crowns of *Cupressocrinites* can be found (Racki et al. 1985; Morozova et al. 2002; Wrzołek 2002, 2005; Zapalski 2012). Stromatoporoids, although very useful in paleoenvironmental analyses, are exceptionally rare here; only two small, broken fragments of coenostea were found in the rubble.

Tabulate corals are abundant and are represented by platy coenitids and alveolitids, frondescent coenitids (Figs. 3, 4 and 5) and branching coenitids and pachyporids (full list of taxa in Table 2). Among rugose corals, colonial
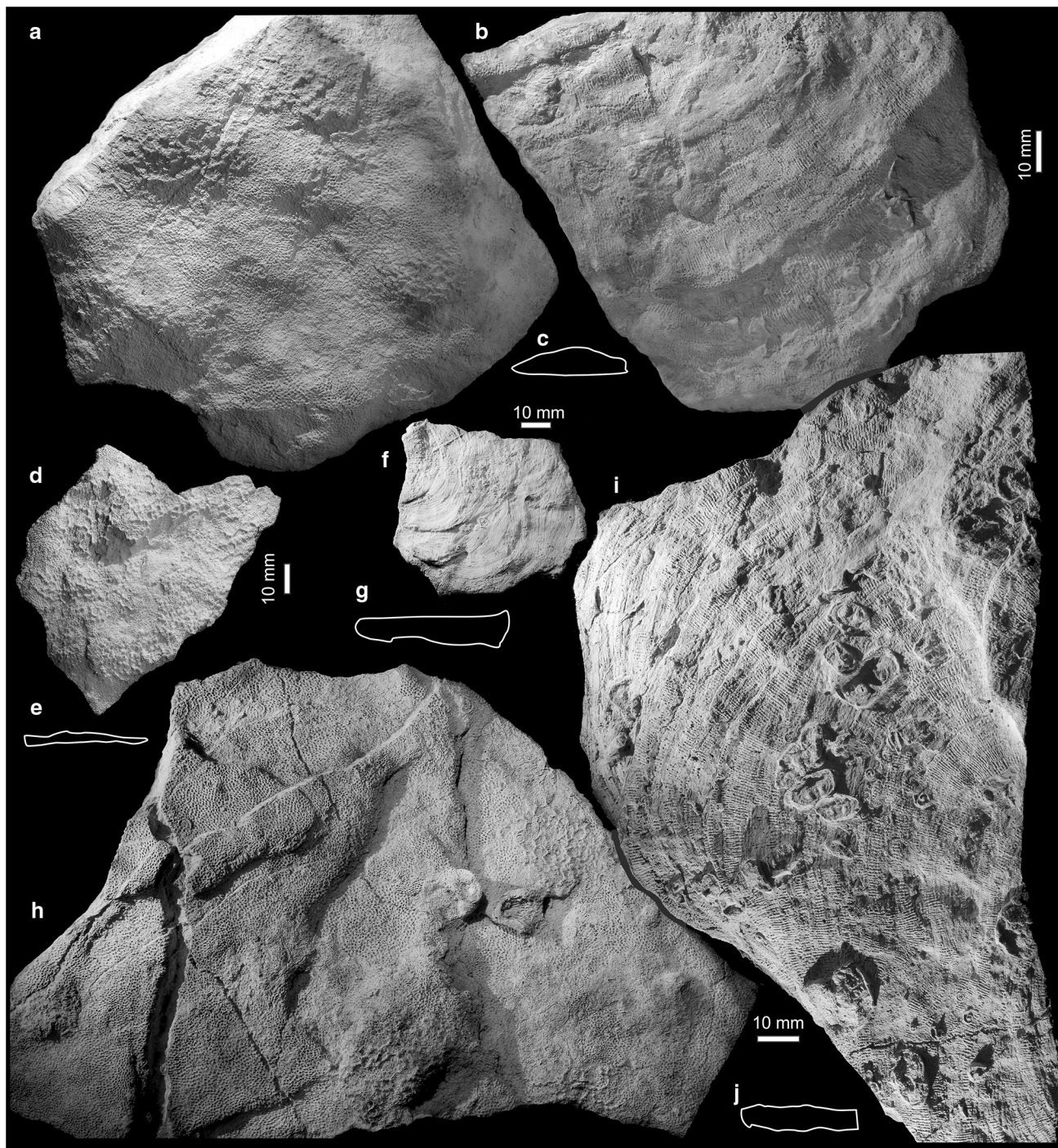
Fig. 4 Platy coral assemblage from Laskowa, Givetian. *White outlines* show profiles of colonies (not to scale). *Alveolites* sp.: **a** upper surface of a colony, **b** lower surface of a colony, **c** outline. *Platyaxum* sp.: **d** upper surface of a colony, **e** outline, *Platyaxum* sp.: **f** upper surface of a colony, **g** outline. Fragment of mushroom-shaped *Alveolites* cf. *taenioformis*: **h** lower surface of a colony with numerous specimens of the brachiopod *Davidsonia*, **i** upper surface of a colony, **j** outline

Phillipsastrea jachowiczi and numerous solitary taxa have been recognized (Table 2; see also Wrzołek and Wach 1993; Wrzołek 2002, 2005).

Platy tabulates (coenitids and alveolitids) are usually 10–20 cm wide, rarely exceeding 40 cm in corallum diameter, and their thickness rarely exceeds 2.0–2.5 cm. The W/H ratio varies: mostly 4–10:1, but we have observed colonies over 35 cm wide and 1.5 cm high, thus with W/H ratio of ca 23:1. In the lower quarry level, branching colonies of *Striatopora* and *Thamnopora* may dominate
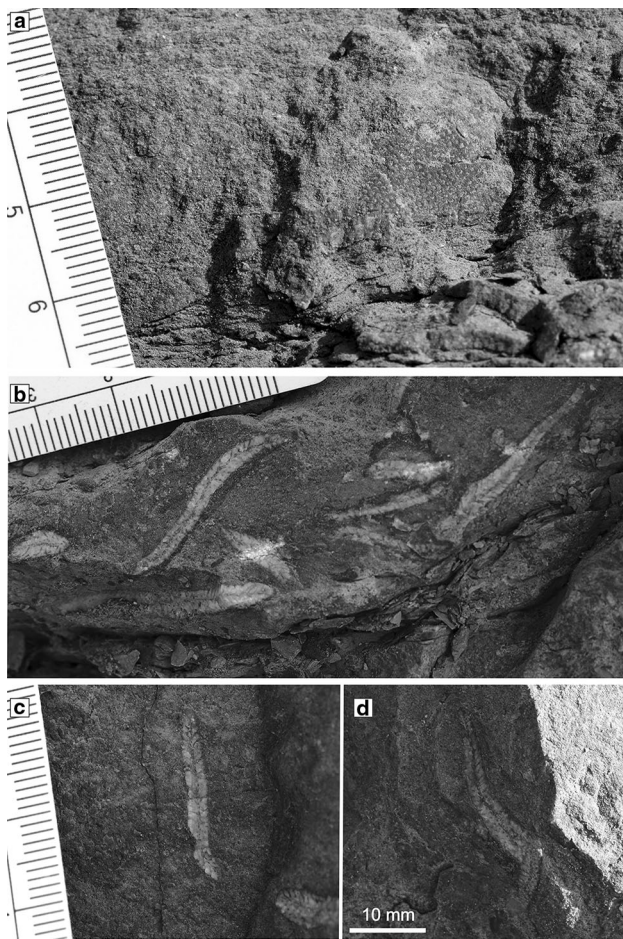
Fig. 5 *Platyaxum*, Laskowa Quarry, Givetian, specimens in situ. Lower photo edges are parallel to the bedding planes. **a** Face of a frond. **b–d** Cross sections of fronds

over platy ones. Only few massive alveolitid coralla have been encountered throughout the biostrome and these display W/H ratios close to 2:1 or 1:1.

Frondescent *Platyaxum* occur throughout the whole biostrome, but large concentrations of broken fronds, lying flat, parallel to the bedding planes, occur at the sides of the bed in the lower part of the biostromal complex, in its lateral part and they occur somewhat more frequently within more marly beds. In several places, we observed fronds either perpendicular or at an angle to the bedding planes, which seem to represent life position (Fig. 5). Brachiopods in some levels are disarticulated (gypidulids), while atrypids are often preserved as bivalved specimens. Chaetetid sponges form colonies in the shape of inverted cones or mushrooms, with cryptic habitats in overhanging parts. Similar overhangs occur in *Roseoporella* and *Alveolites*. The brachiopod *Davidsonia* and microconchids are common in these cryptic habitats. Other frequent encrusters are auloporid tabulates (*Aulopora* spp. and *Mastopora* sp.); they often occur on the upper surfaces of sponges and corals. A detailed investigation of the distribution of epibiontic faunas will be the subject of a separate study.

Locally, some fossils display traces of overturning such as spiral cylindrical tetracorals (Racki et al. 1985: Pl. 12, Fig. 2) or a platy *Phillipsastrea* displaying crinoid holdfasts on its corroded basal surface (Racki et al. 1985: Pl. 12, Fig. 4).

Above the coenitid biostrome, a small bioherm with platy alveolitids has been recorded (Racki et al. 1985), but in 2016 this biostrome was untraceable. In the basal parts of the Szydłówek Beds, within intercalations of red detrital limestones, abundant fragments of dendroid phillipsastreids (*Thamnophyllum*) and less common large solitary *Siphonophrentis georgii* occur (Wrzołek 2002).

Discussion

Photosymbiosis in platy corals

Numerous studies have shown that platy morphology of coralla is photoadaptive (e.g., Graus and Macintyre 1976; Muko et al. 2000; Kahng et al. 2010) and such a morphology has already been used to establish photosymbiosis in fossil scleractinians (Rosen et al. 2002; Martindale et al. 2012; Novak et al. 2013). This kind of morphology does not occur in azooxanthellate scleractinians (Fricke and Meischner 1985); representatives of the genera *Astrangia* and *Cladangia* (Rhizangiidae) can form encrusting coralla (N Santodomingo, pers. comm.), but they are facultatively photosymbiotic. Thus, it can be concluded that platy morphology indicates photosymbiosis in the genera *Alveolites*, *Roseoporella* and *Phillipsastrea*.

Recent azooxanthellates display low levels of colony integration, while moderate colony integration occurs rarely. Moderate colony integration in *Alveolites* and *Roseoporella* therefore suggests photosymbiosis. Moreover, corallites in all *Roseoporella* and most *Alveolites* are less than 1 mm in diameter. Azooxanthellate *Madracis asperula* is the colonial coral with the smallest corallites among azooxanthellates (S. Cairns, pers. comm.), with corallites not smaller than 1.3 mm (Cairns 2000). On the other hand, corallites smaller than 1 mm in diameter are common in Recent zooxanthellates such as *Porites monticulosa* (0.5–0.7 mm), *P. rus* (0.5–0.7 mm) and *Montipora stellata* ($\sim$0.7 mm) (Veron 2000). Thus, corallite diameter also implies photosymbiosis in the corals discussed here.

Platyaxum formed frondescent, platy coralla. Its colonies, although not lying flat on the sea floor, and with very thin fronds, were nevertheless adapted for capturing light. The colony morphology of *Platyaxum* strongly resembles that of typical mesophotic corals such as *Leptoseris*

Table 2 List of tabulate and solitary rugose taxa from the coral beds in Laskowa, based on this study and Wrzołek and Wach (1993), Wrzołek (2002, 2005)

Tabulate corals	Comments	Rugose corals	Comments
Platyaxum escharoides	Frondescent	*Cystiphylloides secundum*	Large, dissepimented
P. clathratum minus	Frondescent	*?Zonophyllum* sp.	Large, dissepimented
Roseoporella spp.	Encrusting	*Spinophyllum* sp.	Large, dissepimented
R. heuvelmansi	Encrusting	*S.* cf. *longiseptatum*	Large, dissepimented
Coenites ex gr. *laminosa*	Branching	*Amplexocarinia tortuosa*	Medium sized, horn shaped
Alveolites cf. *taenioformis*	Platy/mushroom/massive	*Syringaxon bohemica*	Small, horn shaped
A. cf. *obtortiformis*	Platy/mushroom/massive	*Syringaxon* sp.	Small, horn shaped
Alveolitella polygona	Branching	*Guerichiphyllum skalense*	Small, horn shaped, dissepimented
A. fecunda	Branching	*Macgeea* sp.	Medium sized, dissepimented
Striatopora sciuricauda	Branching	*Acanthophyllum* sp.	Large, dissepimented
Thamnopora micropora	Branching	*Grypophyllum* sp.	Large, dissepimented
Th. cervicornis	Branching	*Siphonophrentis georgii*	Large, with long septa and tabulae
		S. laskowae	Large, with long septa and tabulae
		Stringophyllum acanthicum	Large, dissepimented
		S. buechelense	Large, dissepimented
		S. primordiale	Large, dissepimented
		S. schwelmense	Large, dissepimented
		Stringophyllum sp.	Large, dissepimented
		Heliophyllum sp.	Large, dissepimented

(Dinesen 1980, 1983). Such frondescent coralla may sometimes occur in shallower waters as well, yet their distribution is restricted by wave action as they are quite fragile. *Platyaxum* has very small corallites (usually ∼0.5 mm) and moderate colony integration. These features also suggest its photosymbiotic condition.

It must be kept in mind that these comparisons are made between quite distinct groups of corals that probably differed in their physiology. Light capture, however, is a purely physical process, and relevant adaptations are most probably not related to the systematic position of the groups of corals investigated. Such analogies can even be relevant across kingdoms (Anthony and Hoegh-Guldberg 2003). Models inferred from Recent scleractinians probably also work for other calcifying, photosynthetic organisms. The possible differences between tabulates and scleractinians may be in light reflection of different kinds of skeletal mineralogy (aragonitic in scleractinians vs. calcitic in tabulates) and the amount of organic matrix in the skeleton and pigments in coral tissues. However, these differences are minor and do not obscure the general interpretations presented here. It is unclear whether Paleozoic photosymbionts were dinoflagellates or other photosymbiotic microorganisms; therefore, any discussion of particular physiological adaptations for light harvesting at greater depths in the Paleozoic must remain speculative, especially because recent studies suggest that the origin of dinoflagellates might be post-Paleozoic (Janouškovec et al.

2016). Similarly, the composition of photosynthetic pigments in symbionts remains unknown.

About 50% of colonies of *Phillipsastrea jachowiczi* from Laskowa have a W/H ratio of 4:1 or higher, and most specimens have flat upper surfaces. The colonies of *Phillipsastrea* from Laskowa were possibly adapted both to low light and to a periodically, but not constantly increasing sedimentation rate. They were possibly able to escape burial by regulating the ratio of lateral expansion to vertical growth. It is also possible that they cleared their upper surfaces with streaming mucus.

Although phillipsastreids possess rather large corallites (more than 10 mm in diameter), they had high colonial integration (astreoid to thamnasterioid), with weak intercorallite walls. Large polyps are characteristic of azooxanthellates, but also commonly occur in zooxanthellates, whereas high colony integration is typical for zooxanthellate corals (Coates and Jackson 1987). It can be concluded that platy morphology, as a photoadaptive growth form, unequivocally indicates photosymbiosis in the groups of corals discussed here.

Growth form of coenitids and alveolitids in the Laskowa Quarry

Coenitid tabulates are one of the most understudied groups of tabulates. Recently, Zapalski (2012) revised coenitid genera, but did not discuss the ecology of these corals.

Three coenitid genera occur in the Laskowa Quarry, namely *Coenites, Platyaxum* and *Roseoporella,* and two at Skały (*Platyaxum* and *Roseoporella*). *Coenites* forms branching, bushy colonies. The growth form of the two remaining genera has not previously been discussed. Alveolitids in the Laskowa biostrome are either platy or mushroom shaped, with numerous overhanging fragments that formed cryptic environments.

Platyaxum

These corals form frondescent coralla, with fronds rarely exceeding several centimeters in length. Corallites open on both sides of the corallum, which suggests that these colonies did not lie flat on the bottom but were erect. Most specimens represent broken fronds lying parallel to the bedding plane. Such broken fronds occur in more marly levels; thus, they may have been broken during compaction of the sediment. In several places (Fig. 5), fronds occur at an angle, or even perpendicular to the bedding planes. This may indicate *syn vivo* burial and thus the orientation of the fronds. Moreover, we found two specimens (one from Laskowa, the other from Skały) which probably represent initial growth stages of the corallum (Fig. 6a, b). These specimens are in the form of an inverted, broad cone that starts from a small point that seems to be a point of attachment; subsequently, the corallum widens, forming a small cup. The abundance of broken fragments and the multilayered structure of one of the specimens suggest that these colonies were much more complex, composed of multiple fronds. In Recent scleractinians, a similar morphology occurs in *Pavona cactus, Pachyseris speciosa* or *Mycedium steeni*, although in the two former species the corallites are unifacial; only the latter has bifacial fronds. This is also a very common growth habit in mesophotic *Leptoseris*. It is, however, difficult to state whether the fronds in colonies were oriented at 60–70°, as seen on several rock samples, or if the angle was variable, reaching as much as 90° (Fig. 5). The broken fronds of *Platyaxum escharoides* are usually small, and palmate, making these colonies somewhat similar to *Leptoseris papyracea*. The preserved edges of the fronds suggest deep incisions into the fronds (Fig. 6c). The largest fragments of *P. escharoides* rarely exceed 3–4 cm, and this suggests that colonies were probably smaller than 10 cm. On the other hand, *P. clathratum minor* seems to have been larger, as the largest fragment exceeds 11 cm across (and 3–4 mm in thickness) and it is certainly not complete, so this species probably formed larger colonies. Reconstructions based on our material are shown in Fig. 6d–g.

Hydrodynamics are also an important factor affecting growth in deeper waters, especially for more fragile organisms that can be broken in environments with wave action (Kahng et al. 2010). Thin, platy *Platyaxum* were fragile and, like more delicate Recent corals, could survive and grow only in environments of low energy and low sedimentation rates (James and Bourque 1992).

Roseoporella and Alveolites

Two species of *Roseoporella* are known from Laskowa. They are strongly flattened, usually several millimeters in thickness (sporadically reaching 1.5–2.0 cm in thickness), mostly encrusting and often exceeding 10 cm in maximum corallum diameter. The genus *Roseoporella* is characterized by unifacial coralla, with corallites at the proximal parts of colonies parallel or subparallel to the lower surface of the corallum. The presence of numerous *Davidsonia* specimens on the undersides of some coralla (Fig. 4i) of both *Roseoporella* and *Alveolites* suggests that some of these corals were raised over the substratum. Others, were either encrusting of were probably lying on the sea floor.

Alveolites had a similar growth habitat, forming platy coralla reaching around 40–50 cm in diameter; however, a few non-platy coralla (irregular or domal) have also been observed in situ. Some *Alveolites* representatives were probably mushroom-shaped, with numerous overhanging portions. These overhangs may have reached significant size, more than 20 cm wide and 3 cm thick in some colonies (Fig. 4h–j).

The ecology of platy coral assemblages

Studies on Recent corals show that one of the main factors controlling the morphology of colonies is depth, related to light availability. Branching corals very often dominate in the shallowest environments, massive corals in deeper settings, and platy corals in the deepest environments, and this distribution depends on light availability (Hallock and Schlager 1986; Hallock 2005). Shallow-water corals may differ from site to site, but at depths below 20–30 m platy corals dominate (e.g., Kahng et al. 2010; Baker et al. 2016), sometimes with significant contribution from branching forms (Bare et al. 2010). In the Florida Reef Tract, in clear waters (euphotic zone 50 m deep) platy corals start to dominate below 20 m, and this depth is reduced significantly to ca 10 m in murky waters with a euphotic zone only 20 m deep (Hallock 2005). A similar situation has been observed in the Red Sea (Safaga Bay, Egypt), where branching and massive corals occur in shallow waters, and a platy coral assemblage appears below 25 m depth (Riegl and Piller 1997).

Tabulates from Skały fit well within the lower euphotic zone, which agrees with the placement of Late Eifelian sedimentation in Skały within the deep intrashelf zone. The Kowala Formation, especially the cyclically deposited part
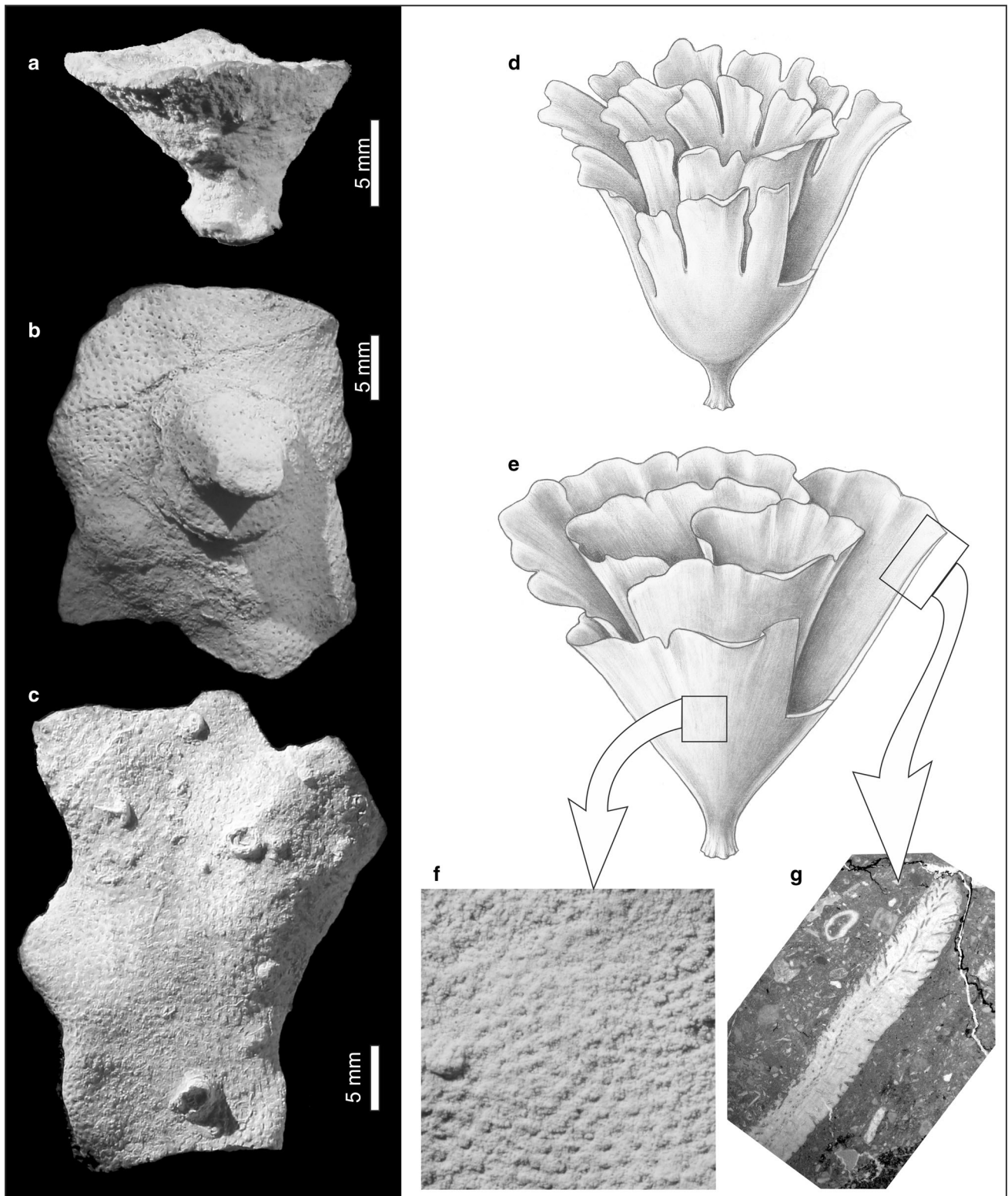
Fig. 6 *Platyaxum* reconstruction. **a** *P. clathratum minor,* proximal part of a corallum, side view. **b** *P. escharoides,* proximal part of a corallum, bottom view. **c** *P. escharoides*, frond, side view. **d** *P. escharoides* reconstruction. **e** *P. clathratum minor* reconstruction **f** Surface of a frond. **g** Cross section of a frond. **a**, **c**, **g** Skały, Eifelian; **b**, **f** Laskowa Quarry, Givetian. **a**, **c** A. Boczarowski collection. Drawings by B. Waksmundzki

underlying the Skały Beds, represents a very shallow, even tidal environment (Skompski and Szulczewski 1994). Successive transgressive pulses (Id–IIa sensu Johnson et al. 1985) in the Middle Devonian caused deepening and drowning of the carbonate platform in the Holy Cross Mountains (Racki 1992; Narkiewicz and Narkiewicz 2010), which also confirms deeper environments within the Skały Beds. If Devonian tabulates (and their photosymbionts) had an ecology similar to that of scleractinians, then shallow-water environments should be dominated by non-platy corals, mostly massive and branching.

Three coral-bearing localities in the Holy Cross Mountains provide the opportunity to test such a hypothesis. Shallow reefal environments of similar age are known from the Bukowa Góra (late Emsian), Sowie Górki and Jurkowice Budy sections (early and middle Givetian). Tabulate corals from the shallow marine Bukowa Góra Shale Formation (locality Bukowa Góra) are massive and bulbous (our observations). In addition, faunas from Sowie Górki and Jurkowice Budy are dominated by bulbous and massive, irregular coralla (Nowiński 1992; Zapalski 2012). Platy corals are absent in all these localities. This indicates that coral zonation based on colony shape in the Eifelian-Givetian basin of the Holy Cross Mountains was similar to that of Recent scleractinians (e.g., Goreau and Goreau 1973; Kühlmann 1983; Fig. 1 in Hallock 2005: Fig. 1).

It is difficult to evaluate absolute depths of the Skały MCE. The attenuation of solar radiation depends on the optical quality of water, latitude and sediment influx or plankton abundance. Clayey sedimentation in some parts of the Skały Beds may suggest murky waters, thus not very deep environments, but within an intrashelf basin. It can be therefore concluded that the environment of Skały was that of a seafloor near the lower limit of the euphotic zone in turbid waters, but its precise bathymetry remains unknown.

The Laskowa biostrome has been poorly recognized so far, and its bathymetry has never been discussed. It possibly lies between the shallow water typical of the Wojciechowice and Kowala Formations and the pelagic environment of the Szydłówek Beds. In this community, platy and frondescent tabulate corals dominate. Branching pachyporids are locally abundant. On the other hand, platy colonies rarely seem to be overturned. Sponges, such as chaetetids and stromatoporoids are significantly subordinate. In marly levels, corals are less abundant, but frondescent *Platyaxum* and platy *Roseoporella* occur here, with rare branching *Coenites*. The Laskowa biostrome can be recognized as a reefal structure in the lower euphotic zone due to strong dominance of platy corals, thus another MCE. A locality at Jurkowice Budy (the same age as Laskowa; Racki 1992) or at Posłowice (somewhat younger) yielded numerous small, bulbous and columnar corals, such as

Caliapora or *Alveolitella* (Nowiński 1992; Zapalski 2012), and it represents shallow, well-lit environments.

Tabulate corals at Laskowa are most frequently 10–20 cm in size, rarely exceeding 40 cm. Such a size distribution is also very characteristic in MCEs. A recent study on mesophotic reefs from Curaçao shows that corals exceeding 50 cm in diameter are very rare, and small *Madracis* colonies, mostly up to 15 cm across, dominate in the 80–90 m zone (Bongaerts et al. 2015), and similar observations are known from the Great Barrier Reef (Dinesen 1983). Thus, the size of colonies also supports the interpretation of the Laskowa biostrome as an MCE. It must be stressed that tabulates exceeding 50 cm are rare in the Devonian, but such colonies are known from the Givetian of Anti-Atlas (Tessitore et al. 2013).

The extant mesophotic reef community of Tutuila (American Samoa) has been investigated in detail by Bare et al. (2010). Plate-like corals dominate the mesophotic communities at 40–70 m, and they may even constitute as much as 64% of coral cover of the whole community. Encrusting corals also commonly occur in such deeper environments, with two maxima of abundance: at 30–40 and at 70–90 m depth. Massive corals play an important role in the shallow parts of mesophotic environments, and they effectively disappear below 80 m (Bare et al. 2010). Thus, sporadic occurrences of massive colonies at both Skały and Laskowa also fit well with these observations. Branching corals occur within the whole range of the mesophotic zone, yet their largest contribution is below 80 m (Bare et al. 2010). Such a distribution is similar to the assemblage of Laskowa, with abundance of platy *Roseoporella* and *Alveolites,* frondescent *Platyaxum*, a significant contribution from branching forms such as *Striatopora, Thamnopora* and *Coenites,* and sporadically occurring massive alveolitids. As in modern MCEs, the coral assemblage at Laskowa is dominated by platy forms, but others, such as branching corals also occur abundantly. Branching corals, as in modern environments, could have been either photo- or aposymbiotic.

The corals from Laskowa are preserved with fine details of external morphology. Branching coralla occur as finely preserved, large fragments, or even complete, bushy colonies with branches 3–8 mm in thickness. This suggests that the coral assemblage is autochthonous. This also is a premise for the placement of the biostrome below the fair-weather wave base. On the other hand, in certain beds frondescent and branching coralla are numerous and broken, but again, with fine external details preserved. Some rare platy coralla are possibly overturned. Brachiopods occur in thin, marly intercalations, and are sometimes disarticulated. This may suggest either very short transport or episodes of deeper wave action, thus placing the
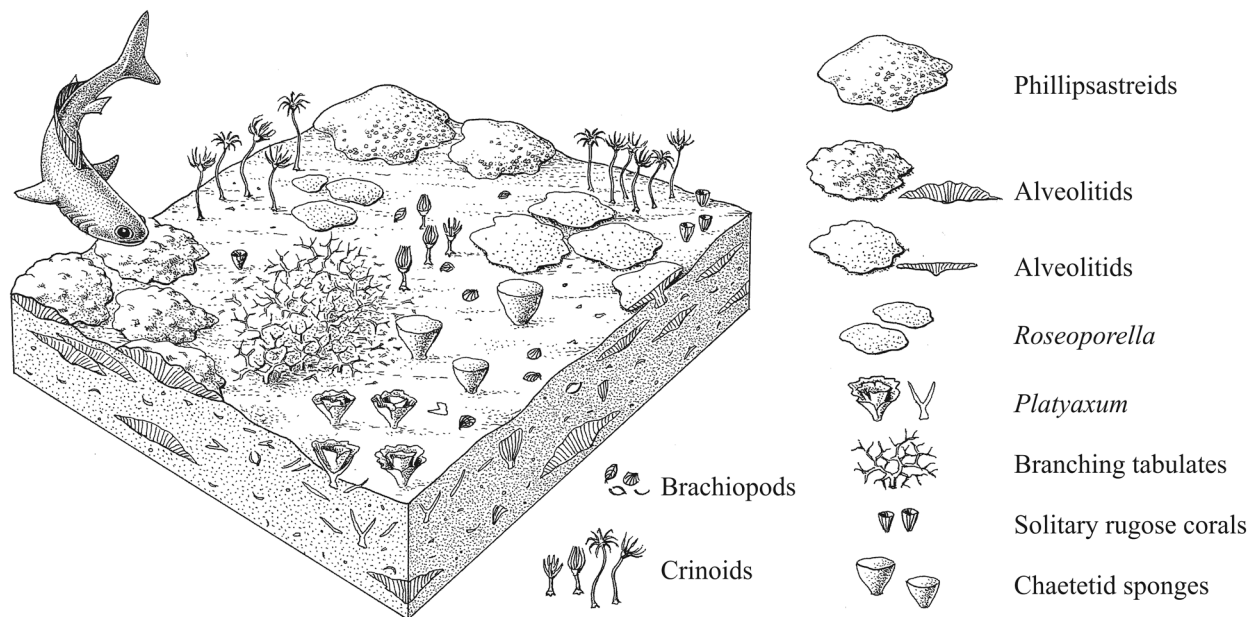
Fig. 7 Reconstruction of Laskowa MCE. Drawing by B. Waksmundzki

biostrome between the fair-weather wave base and the storm wave base. The peripheral growth of platy corals with corallites facing upwards was probably a useful strategy in a situation of very low or nonexistent sediment influx (Scrutton 1998), thus such a morphology also suggests low sedimentation rates. A reconstruction of the Laskowa MCE is shown in Fig. 7.

Other possible Paleozoic MCEs

Although mesophotic communities have never been recognized in the Paleozoic, platy tabulates and rugose corals occur in wide range of localities. Poty and Chevalier (2007) described phillipsastreid biostromes from the Frasnian of Belgium. Numerous platy *Frechastrea-Alveolites* associations occur in the Aisemont Formation, and these were formed below the fair-weather wave base. Flat corals were sporadically overturned during strong wave action. Phillipsastreids and alveolitids often occupy 80–90% of the volume of these biostromes, thus strongly dominating other elements of the fauna (Poty and Chevalier 2007). This can be possibly recognized as a large MCE (at least several km long). Platy corals in the Paleozoic are also known from the Silurian of Gotland (Stumm 1967) and the Devonian of North America (Stumm 1964), and this may provide evidence of their photosymbiosis, but conclusions about a mesophotic environment in these cases need more detailed studies.

In summary, platy morphology in the tabulate genera *Roseoporella, Platyaxum* and *Alveolites* and in the rugosan *Phillipsastrea*, as in modern scleractinians, is an effect of photoadaptive growth at the lower limits of the euphotic

zone and thus provides evidence of photosymbiosis in these genera. The distribution of corals along the depth gradient during the Devonian (and possibly also whole Paleozoic) was similar to that of the Recent, with massive and branching forms in the shallowest environments, and platy forms in the lower euphotic zone. Thus, the presence of platy corals may help in identification of mesophotic environments in the fossil record. Two ancient communities, a Late Eifelian one at Skały and another of middle Givetian age at Laskowa, were dominated by platy corals. They can therefore be described as MCEs. We can also speculate that biostromes described by Poty and Chevalier (2007) from the Frasnian of Ardennes are possibly also MCEs. A tabulate coral common at both sites, *Platyaxum*, had a frondescent growth habit, resembling that of Recent *Pavona cactus, Pachyseris speciosa, Mycedium steeni* or *Leptoseris.* The Skały and Laskowa communities are the oldest (ca. 390 Ma) MCEs recognized so far, and much older than those previously recognized from the Triassic (Martindale et al. 2012). This shows that the strategy of harvesting light using "solar panels" appeared not long after the onset of photosymbiosis in tabulates (possibly mid-Silurian; Zapalski 2014), and this kind of ecological niche is much older than previously thought.

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