



Heliolitid corals and their competitors: a case study from the Wellin patch reefs, Middle Devonian, Belgium

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Wellin patch reefs are small Upper Eifelian build-ups within the fine-grained argillaceous limestone of the Hanonet Formation. Whereas the reefs themselves are not well exposed, their fossil assemblage is accessible in the hills near the town of Wellin, approximately 40 km SE of Dinant in Belgium. It is especially rich in massive stromatoporoids, heliolitids and other tabulate corals. They exhibit predominantly domical and bulbous morphologies. This paper focuses primarily on the palaeoautoecology of the heliolitid corals and their relationships with other organisms. Cases of mutual overgrowth between heliolitids, other corals and stromatoporoids suggest a high degree of competition for space on the reefs, possibly related to the scarcity of hard substrates. Coral and stromatoporoid growth forms, as well as the prevalence of micritic matrix, point to a relatively low energy environment. However, abundant growth interruption surfaces, sediment intercalations and rejuvenations of corals suggest episodically increased hydrodynamic regime and sediment supply. It is inferred that the patch reefs developed in a relatively shallow environment, where the reefal assemblage was regularly affected by storms. Heliolitids exhibited high sediment tolerance and relied on passive sediment removal for survival. They also could regenerate effectively and commonly overgrew their epibionts, after the colony's growth was hampered by the sediment. This is recorded in extremely abundant growth interruption surfaces, which allow the analysis of the impact of sediment influxes on the heliolitid corals. □ *Coral-stromatoporoid reefs, Eifelian, palaeoecology, survival strategy, Tabulata.*

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The high sea level and favourable climate in the Middle Devonian resulted in the global proliferation of reefal ecosystems. Tabulate corals and stromatoporoids were the main reef constructors of that time (Wood 1998; Copper 2002; Edinger *et al.* 2002; Copper & Scotese 2003; Hubert *et al.* 2007; Zapalski *et al.* 2007, 2017a; Joachimski *et al.* 2009). Unfortunately, these reefal structures are often difficult to analyse due to pervasive dolomitization, erosion or remaining preserved sub-surface (Wood 1998; Kiessling *et al.* 1999; Jakubowicz *et al.* 2019). Palaeoecological studies on fossil reefs were intensively performed during the 1930–70s interval (e.g. Lecompte 1937, 1958, 1960, 1970; Tsien 1971, 1980) before being overcome by studies focusing on taxonomy of corals and stromatoporoids in the last 30 years or so.

In a relatively small area, southern Belgium includes a wide range of Devonian reefs from very large Eifelian bioherms (Denayer 2019) to Frasnian coral biostromes (Poty & Chevalier 2007) and from Famennian shallow-water stromatoporoid biostromes (Aretz & Chevalier 2007) to deeper water Frasnian

red mud-mound-like bioherms (Tsien 1977, 1979; Boulvain 1993). Type and development of reefs were seemingly dictated by eustatic fluctuations, as well as regional and global tectonics and local settings, resulting in differentiated facies, thickness and depositional gaps (Lecompte 1958, 1960; Kasimi & Préat 1996; Aretz 2002). The Upper Eifelian Wellin patch reefs are relatively small build-ups that seemingly developed on top of palaeohighs produced by the bioherms of the Tienne Sainte-Anne Member of the underlying Jemelle Formation (Denayer 2019).

Heliolitids are here understood as the group of tabulate corals with massive, plocoid coralla and septal elements in hexameric or possibly dodecameric symmetry (Chatterton *et al.* 2008) – that is not including the cateniform representatives of Halysitina. They were described at different taxonomic ranks by various researchers – for example as the family Heliolitidae (Dixon 1974; Noble & Young 1984), the suborder Heliolitina (Hill 1981; Scrutton 1997), the order Heliolitida (Oliver 1996; Ospanova 2012), the superorder (Bondarenko 1992) or the sub-class Heliolitoidea

(Sokolov 1962; Mironova 1974). They are commonly classified as tabulate corals (Dixon 1974; Hill 1981; Noble & Young 1984; Scrutton 1997; Chatterton *et al.* 2008), but some authors considered them a group separate from the Tabulata (Sokolov 1962; Oliver 1996; Dixon 2010; Ospanova 2010). Heliolitids are fairly common in Middle Devonian reefal facies of Europe and N Africa (Goldfuss 1826; Kettnerova 1933; Lecompte 1936; Flügel 1956; Stasińska 1958; Iven 1980; Hladil 1988; Nowiński 1992; Fernández-Martínez 1998; Król *et al.* 2018a; Jakubowicz *et al.* 2019). Their taxonomic diversity, however, was globally reduced – to only five known genera in the Middle Devonian, as compared to 13 in the Early Devonian, 24 in the Late Silurian or 33 in the Ordovician (after Hill 1981). This decline in diversity was followed by the disappearance of heliolitids from the fossil record during the Givetian.

Though many researchers put tremendous emphasis on the taxonomical problems of heliolitids, relatively few have focused on their remarkable ecological features, such as adaptability, relationships with other organisms and similarities to some Recent corals (Richards & Dyson-Cobb 1976; Noble & Lee 1990; Young & Scrutton 1991; Król *et al.* 2018a). The purpose of this study is to: (1) analyse the relationships between heliolitids and other associated fauna, especially stromatoporoids and alveoline tabulate corals of similar growth forms, occurring in the Wellin patch reefs; and (2) ascertain the main factors controlling the development of the reefal assemblage as well as reconstruct the sedimentary environment.

Geological setting

Belgium is part of the Rhenohercynian Fold Belt, extending across Europe from south Portugal through southern England, northern France, Belgium and Germany, into Poland. During the Devonian, the Namur-Dinant Basin was situated on the southeastern margin of Laurussia in the Rheno-Hercynian Ocean at a latitude close to 25°S (Stampfli *et al.* 2013). The Namur-Dinant Basin recorded proximal facies in its northern part whereas its southern part acted as a shallow basin with more distal facies. The Eifelian recorded the development of many types of reefs which are structurally located in peculiar palaeogeographical position, notably due to the interplay of tectonic blocks within the Namur-Dinant Basin.

The Wellin locality is situated at the eastern margin of the Lesse Block which possibly had a higher accommodation rate than the neighbouring blocks during the late part of the Eifelian, resulting in the

accumulation of the >250 m thick Chavées Member of the Jemelle Formation, dominantly shaly, with frequent carbonate levels (Godefroid 1968; Dumoulin & Blockmans 2008) and the most remarkable development of a very large bioherm of the Tienne Sainte-Anne Member (Denayer 2019). The bioherm is overlain by the argillaceous, often dark-coloured biolastic wackestone-packstone of the Hanonet Fm, except where the Tienne Saint-Anne Mbr is present and probably acted as a local high in the sea floor, where more hydrodynamically active facies developed (Jamart & Denayer 2020). These facies are typically crinoidal and bioclastic rudstone and floatstone, with a locally very abundant and diverse fauna. Denayer (2019) considers the unit to be the Wellin Member of the Hanonet Formation.

A complete description of the member can be found in Coen-Aubert *et al.* (1991) and Bultynck & Dejonghe (2001). In the type section along the Fond des Vaux creek (Coen-Aubert *et al.* 1991; Denayer 2019), the member can be divided as follows: a lower unit (60 m thick) of well-bedded coarse-grained crinoidal limestone rich in tabulate corals and stromatoporoids; a median unit (20 m thick) of massive light-grey limestone with large bulbous stromatoporoids and abundant corals; an upper unit (45 m thick) of bedded coarse grained limestone including two reefal beds or lenses, locally extremely rich in tabulate corals. The present study focuses on the fauna sampled from this third unit. The member has a limited extension of <2 km and passes laterally and upwards to the regular facies of the Hanonet Fm. Approximatively 500 m west of the type section, the Wellin Member is accessible in the furrows of ploughed fields where the weathering of the limestone allows a very good sampling of the fossil fauna. This place was nicknamed the '*Heliolites* Field' as large numbers of *Heliolites* colonies can be collected there. A detailed mapping of these numerous isolated spot outcrops in the 'La Marlière' hill, c. 500 m N of the Wellin village allowed to place the '*Heliolites* Field' in the upper part of the Wellin Member (Fig. 1). If *Heliolites* are largely dominant, together with stromatoporoid in the '*Heliolites* Field', they are less common to rare in surrounding areas where darker facies are observed. Conversely, solitary rugose corals, including very large (>10 cm in diameter) *Mesophyllum* spp., are much more abundant away from the *Heliolites* core.

The Hanonet Fm straddles the Eifelian-Givetian boundary and covers the whole *ensensis* conodont Zone and the lower part of the Givetian *hemiansatus* Zone. In the Fond des Vaux section, Bultynck & Godefroid (1974) reported *Ozarkodina bidentata* in the upper unit of the member, a species only known

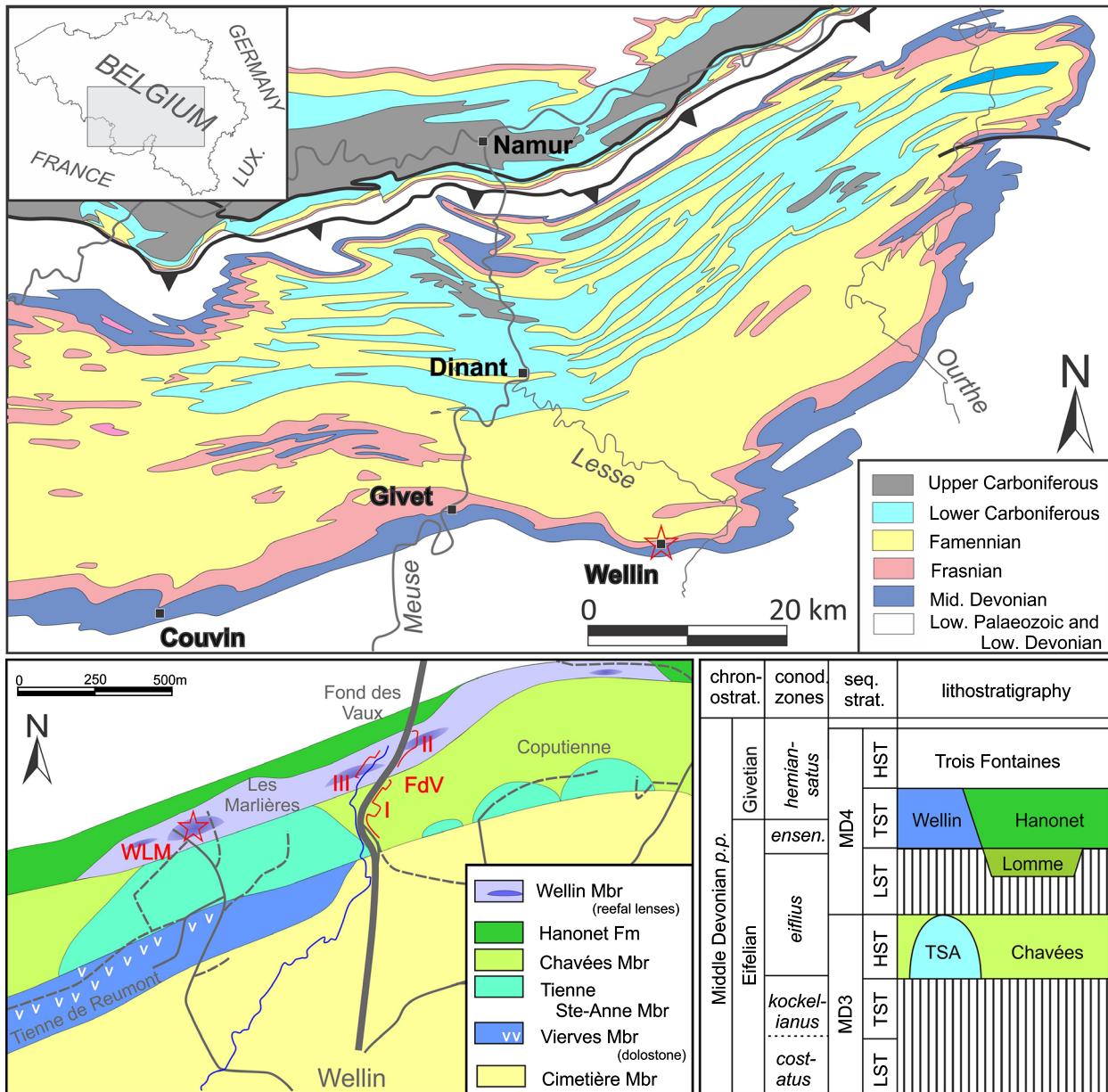


Fig. 1. Geological maps of the Dinant Synclinorium (after de Bethune 1954) and of the studied area (after Denayer 2019, modified), with a synthesized stratigraphical column of Upper Eifelian–Lower Givetian. The red star indicates the studied locality. FdV is the abbreviation of Fond des Vaux section, and WLM refers to the name of the hill (Wellin, Les Marlières), where the ‘*Heliolites* Field’ is located.

in the *ensensis* Zone in Belgium, the Wellin Mbr is therefore equivalent to the lower part of the Hanonet Fm as previously suggested by Maillieux (1938). Hence, a late Eifelian age can be confidently attributed to the ‘*Heliolites* Field’ assemblage.

Materials and methods

A total of 111 rock samples, including 83 heliolitid coralla, were collected in the ‘*Heliolites* Field’. The specimens were cut longitudinally, polished and

lacquered, to be scanned using a high-resolution scanner for detailed observation. Additionally, 43 thin sections were prepared for more precise measurements and observations of fauna and microfaecies. Studied specimens are housed at the Institute of Geology of Adam Mickiewicz University in Poznań (samples K1932-K19114) and at the University of Liège (samples PAULg. WLM/23-WLM/52).

Taxonomical identification of heliolitids has been performed on the basis of morphometric measurements: corallite diameter, corallite wall thickness, number of tabulae per 5 mm, diameter of

coenenchymal tubuli – all measured 20 times per corallum, where possible. These particular measurement techniques were taken partly from Young & Noble (1990) and partly from Dixon (1999). The tabulae spacing and wall thickness proved relevant in distinguishing between the heliolitid species, contrary to the observations of Dixon (1999), which is the reason why these measurements were included. The corallite diameters were measured instead of tabularium diameters (cf. Young & Noble 1990), as it is a more broadly used value for different groups of compound corals and therefore allows for more inter-species comparisons. Measurements were taken digitally on the scanned material, with 0.01 mm accuracy. Basic statistical parameters for these measurements were calculated: mean, standard deviation (s) and the coefficient of variation (c_v). These parameters provide a basic understanding of intracolonial variability of morphological features and are commonly used in taxonomy of tabulate corals (e.g. Young & Elias 1995; Zapalski 2012).

Palaeoecological analysis of heliolitids and the associated biota has been performed on the basis of growth patterns, taphonomical signatures and the analysis of the surrounding microfacies, in thin sections and polished slabs. The terminology for coral growth forms is used in this paper as defined by Stearn (1982): domical (domal) – upwardly convex corallum with a broad base; bulbous – upwardly convex corallum, narrowing towards the base; branching – dendroid or stick-like coralla; and tabular – a corallum with horizontal or undulated upper surface. Specimens not fitting the criteria of Stearn (1982) for any growth form category are referred to as irregular. The classification of growth interruption surface types is taken from Miller & West (1997) and summarized in Table 1. The descriptions of features such as individual growth interruption surfaces and inter-species interactions recorded in the fossil material are not quantified. This is due to factors such as preservation bias and sampling bias resulting from the poor state of the outcrop (most of it remaining underground). For extended discussion on sampling bias in palaeoecological studies, see, for example, Forcino & Stafford (2020).

Results

Facies

Studied material comes from the reefal lenses occurring in the upper part of the Wellin Member. The dominant facies is a brownish-dark grey coral-stromatoporoid boundstone with a packstone-wackestone to poorly

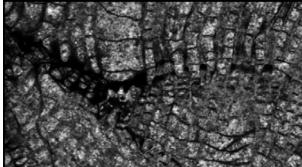
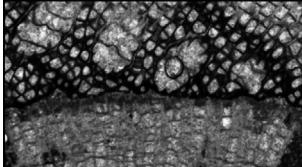
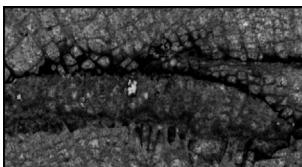
washed grainstone matrix (Fig. 2A–D). The fossil assemblage is predominantly comprised of stromatoporoids (Fig. 3), heliolitids (Figs 4–6) and other tabulate corals (in comparable proportions) (Fig. 2A–E), with solitary and subordinately also colonial rugose corals (Figs 2B, E, 4B–D, 5A), as well as thin-layered indeterminate chaetetids (Figs 2F, 3D, 5A, 6A). The micrite-dominated microfacies surrounding the corals and the stromatoporoids consists of crinoid plates and columnals, bryozoans, trilobite and brachiopod fragments, calcareous algae and other small, poorly preserved bioclasts (Fig. 2D). The skeletons of reefal organisms are adjacent (Fig. 2A, B), with some of them in direct contact (Fig. 2C, E), also often forming multi-layered encrustations on each other (Fig. 2F). They commonly point to different bottom-up directions, most probably because they are overturned or toppled (Fig. 6G, H). Some bioclasts are fragmented or slightly rounded; however, most of them do not bear any apparent signs of transport, suggesting at least partially parautochthonous character of the assemblage. Cavities are not rare between organisms but they are commonly filled up with late diagenetic blocky calcite, commonly dolomitic or ferroan-dolomitic, at the origin of the usual yellowish weathering observed in the hand samples. The biohermal boundstone is embedded in bioclastic crinoidal limestones.

Stromatoporoids

Stromatoporoids are very abundant and relatively diverse, with seven genera belonging to three orders occurring in the samples. Laminar and low-domical growth forms predominate. Stromatoporoids mostly settled on other organisms, post-mortem or *syn-vivo* (Figs 2C, E, 3D, 4A–E, 6G). Most commonly, they encrusted heliolitid and alveolitid tabulates. Two groups of stromatoporoids are recognized in the sampled material on the basis of the presence or absence of syringoporid tabulate symbionts. The abundance of specimens in both groups is comparable (55% non-symbiotic, 45% symbiotic in the studied 35 stromatoporoid samples).

Non-symbiotic stromatoporoids include *Actinostroma* (Figs 2E, 3B), *Clathrocoilona* (Figs 2C, F, 4B, C, 4E), *Stictostroma* (Fig. 2F) and *Taleastroma* (Figs 2F, 3D). They are small, with most of them (70%) not exceeding 1 cm in height and exhibiting laminar shapes (*Clathrocoilona*), while others show domical growth forms and grew up to 5 cm in height. Growth interruption surfaces occur in ca. 37% specimens – which is likely an underestimate due to their small sizes. They are often accompanied by sediment intercalations. Non-enveloping style of latilaminate

Table 1. Types 1-4 of growth interruption surfaces, as defined by Miller & West (1997), with the proportional abundance in the studied material and examples.

Types of growth interruption surfaces (Miller & West 1997)	Visual representation in the studied material	Abundance of growth interruptions in organisms: + rare, ++ common and +++ very abundant		
		Heliolitids	Stromatoporids	Alveolitines
1. Breaks in growth with apparent continuity of tubules across the surface		+++	++	++
2. Surfaces of rejuvenation or recolonization with reorientation of tubules		++	+	+
3. Sediment-filled tubules or trapped sediment partings		+++	++	++
4. Encrusted surfaces		++	+	++

growth dominates. Skeletons with smooth and ragged external surfaces are equally represented within the sample. Roughly 10% of specimens contain rejuvenations and bioclastrations. Borings are rare in this group (for more detailed data on stromatoporoid growth patterns see Table 2).

Symbiotic syringoporid tabulates are immured in most specimens of *Talestroma* (Fig. 4A, B, D) and in all studied specimens of *Clathrodictyon*, *Stromatopora* (Fig. 3C) and *Salairella* (Fig. 3A). Due to their low-domical and domical growth form they attain larger dimensions than non-symbiotic stromatoporoids – commonly up to 5 cm or more in height. In the field, they can often be mistaken for heliolitid coralla at the macroscopic level. Smooth and ragged skeletal margins are equally represented in the specimens under study; latilaminar style of growth differs from enveloping to non-enveloping. In roughly 60% of the symbiotic specimens, growth interruption surfaces are present, often with sediment intercalations;

77% of specimens in this group were also encrusted. Features such as rejuvenation, boring and bioclastication are relatively rare (Table 2).

Heliolitid corals

Heliolitids are some of the most abundant corals of the Wellin Member, at least in the sampled '*Heliolites* Field'. Their coralla are mostly relatively small (rarely >20 cm in diameter). They are represented by the species *Heliolites porosus* Goldfuss 1826 (80 coralla; Fig. 4) and *Heliolites cf. vesiculosus* Penecke 1887 (3 coralla; Fig. 5). *H. porosus* is characterized by plocoid coralla with round corallites ('autopores'), 1.1–1.4 mm in diameter, separated by a coenenchyme of prismatic tubules ('siphonopores'). The siphonopores can be rounded or angular in transverse section, often both in the same corallum. Corallites consist of 12 septa. Corallite wall thickness most commonly falls between 0.05 and 0.08 mm. Corallite spacing

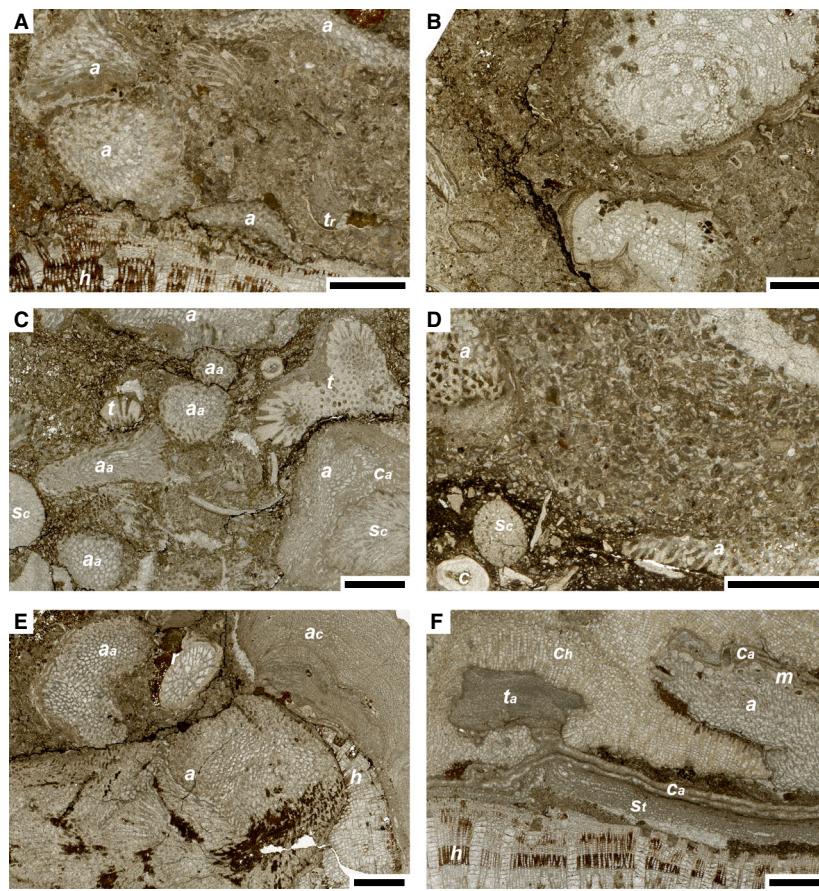


Fig. 2. Microfacies of the Wellin patch reefs. A, K1940, *Heliolites porosus* (h), *Alveolites* sp. (a) and trilobite remains (tr). B, K1940, a solitary rugosan with a? Bryozoan encrustation and *H. porosus* with multi-layered encrustations of stromatoporoids, alveolitids and auto-porids. C, K1977, *Alveolites* sp. (a), *Alveolitella* cf. *fecunda* (aa), *Scoliopora* sp. (sc), *Thamnopora* cf. *irregularis* (t), *Clathrocoilona* sp. (ca). D, K1995, *Cladochonus*? sp. (c), *Scoliopora*? sp. (sc), *Alveolites*? sp. (a). Abundant, poorly preserved, small bio- and lithoclasts are embedded in a matrix grading from packstone (lower parts of the image) to poorly washed grainstone (in the centre); E, K1972, *Alveolites* cf. *parvus* (a), *A. cf. fecunda* (aa), *H. porosus* (h), a solitary rugosan (r) – *Tremophyllum*? sp. and *Actinostroma* sp. (ac); F, K1968, multi-layered encrustations on *H. porosus* (h): *Stictostroma* sp. (st), *Clathrocoilona* sp. (ca), *Taleastroma* sp. (ta), *Alveolites* sp. (a), *Mastopora* sp. (m) and a chaetetid (ch). Scale bars are 5 mm.

and tabulae spacing is varied. Tabulae are usually flat. For detailed measurements and statistical parameters, see Table 3.

Heliolites cf. *vesiculosus* differs from *H. porosus* in having larger corallite diameters, thicker corallite walls and denser, more uniform tabulae spacing. Corallites consist of 12 septa and are 1.20–1.65 mm in diameters. There are 16–18 corallites per 1 cm². Their walls are usually between 0.07 and 0.10 mm thick. Tabulae spacing is commonly 15–20 tabulae per 5 mm. Tabulae are often concave or oblique. Siphonopores are rounded to polygonal, usually 0.25–0.35 mm in diameters. For detailed measurements and statistical parameters, see Table 3.

Heliolites porosus and *H. cf. vesiculosus* typically have domical (64% of specimens) and bulbous (29% of specimens) growth forms (Fig. 6) that were often altered in later stages of growth, due to external factors such as overturning (Fig. 6G, H). As a result, some of them exhibit more flattened (tabular) or

irregular morphologies. Approximately 4% of the studied heliolitid coralla were too fragmentary to determine the coral's growth form. Corallum bases are commonly missing, but where preserved, in most cases they are convex (Fig. 6B, F) or shaped to fit the surface of another organism which served as the substrate for the heliolitid (Figs 4B, C, 6A). However, specimens with concave bases also occur (Fig. 6E).

A very common and distinct feature of the studied heliolitid coralla is the prevalence of growth interruption surfaces, represented by dark lines or zones in longitudinal sections (Figs 4–6). All studied specimens but one, small, juvenile corallum, consist of multiple growth interruptions – in some cases over 30 in a single colony (Fig. 6B). Usually, the number of the growth interruption surfaces correlates with the size of the corallum. These are predominantly Type 1 growth interruption surfaces *sensu* Miller & West (1997) (for the types of growth interruption surfaces, see Table 1), where vertical skeletal elements

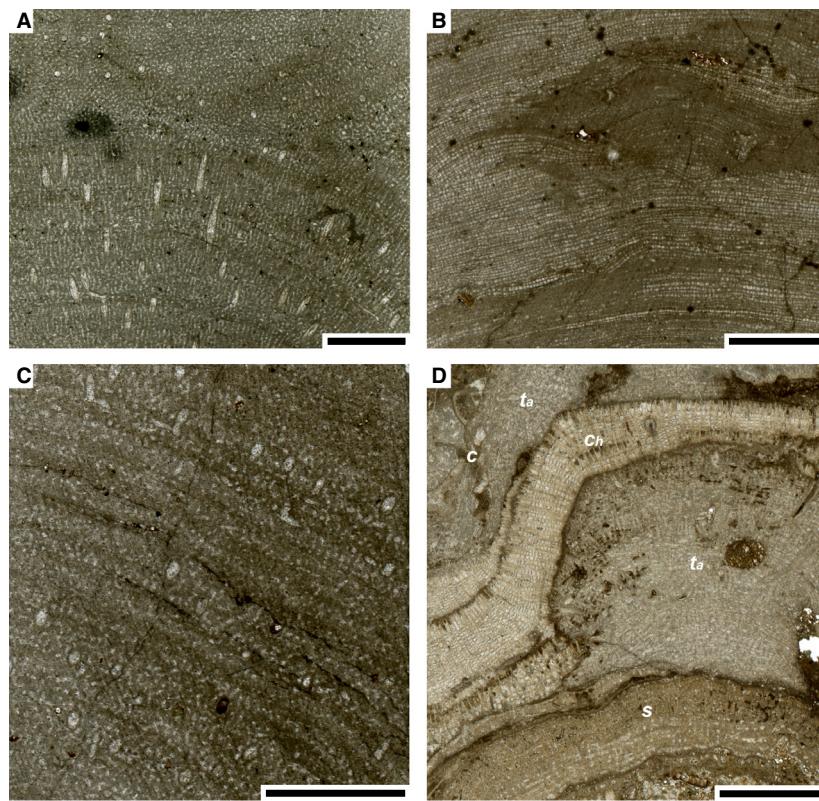


Fig. 3. Stromatoporoids of the Wellin patch reefs. A, K1987, *Salairella* sp. with syringoporid symbionts, longitudinal section in lower part of the photograph, tangential section in upper part. B, K19113b, *Actinostroma* sp., longitudinal section. C, K1979, *Stromatopora* sp. with syringoporid symbionts, longitudinal section. D, K1945, an indeterminate stromatoporoid (s, possibly *Actinostroma?* sp.), *Taleastroma?* sp. (ta) and a chaetetid (ch), forming multi-layered encrustations which envelop a colony of *Cladochonus?* sp. (c). Scale bars are 5 mm.

continue across the break (e.g. Figs 4B, F, 5B, 6B). Other types of growth interruptions (2, 3 and 4, according to the same classification) also occur, with discontinuities of skeletal elements (Fig. 6G, H), sediment (Figs 4F, 6F), or encrustations present (Figs 4C, 6B, C, 6G). Type 1 growth interruptions in some cases also form zones, instead of surfaces (Figs 4B, 6F, G). In such cases, the skeletal elements like tabulae are sometimes condensed (Fig. 4B). However, these zones lack the rhythmic character of seasonal bands, and both their presence and the condensation of skeletal elements accompanying the dark colour, appear to be inconsistent within a corallum and across the population. Where growth interruptions can be traced to the marginal parts of the corallum, it is very common for them to change type, typically from Type 3 (with sediment preserved in the break) in the outer parts, to Type 1 and Type 2 clean surfaces towards the central parts (Fig. 4A, F).

In 59% of the studied specimens, the growth interruptions were also followed by a rejuvenation of the colony. This was often accompanied by a radical change in the direction of growth which is usually a sign of the colony being overturned or toppled

(Fig. 6F–H). It is also noteworthy that in some heliolitid specimens, remains of other organisms are preserved, seemingly thrown with the sediment on top of the coral colony and later overgrown. This can include, for example, small brachiopod shells or pachyoporid tabulate branches (Fig. 4E, F).

Encrustations on heliolitids are very common. They were formed predominantly by stromatoporoids and subordinately by alveolitines and chaetetids, but in some cases solitary rugose corals also settled on them (Fig. 4B, D). These corals however are relatively small and do not seem to reach their adult size. In case of over 40% of the studied specimens, the encrustation occurred *syn-vivo*, as evidenced by the apparent continued growth of the heliolitid after the epibiont had settled on its surface (Figs 4A–C, 6B, G). The appearance of epibionts seems to always coincide with the growth interruption surfaces in the heliolitids and in some cases with the overturning of the colony as well.

Studied heliolitids show capability to overgrow some of their epibionts, including all recorded cases of infestation by stromatoporoids without syringoporid symbionts. Attempts of overgrowing rugosan,

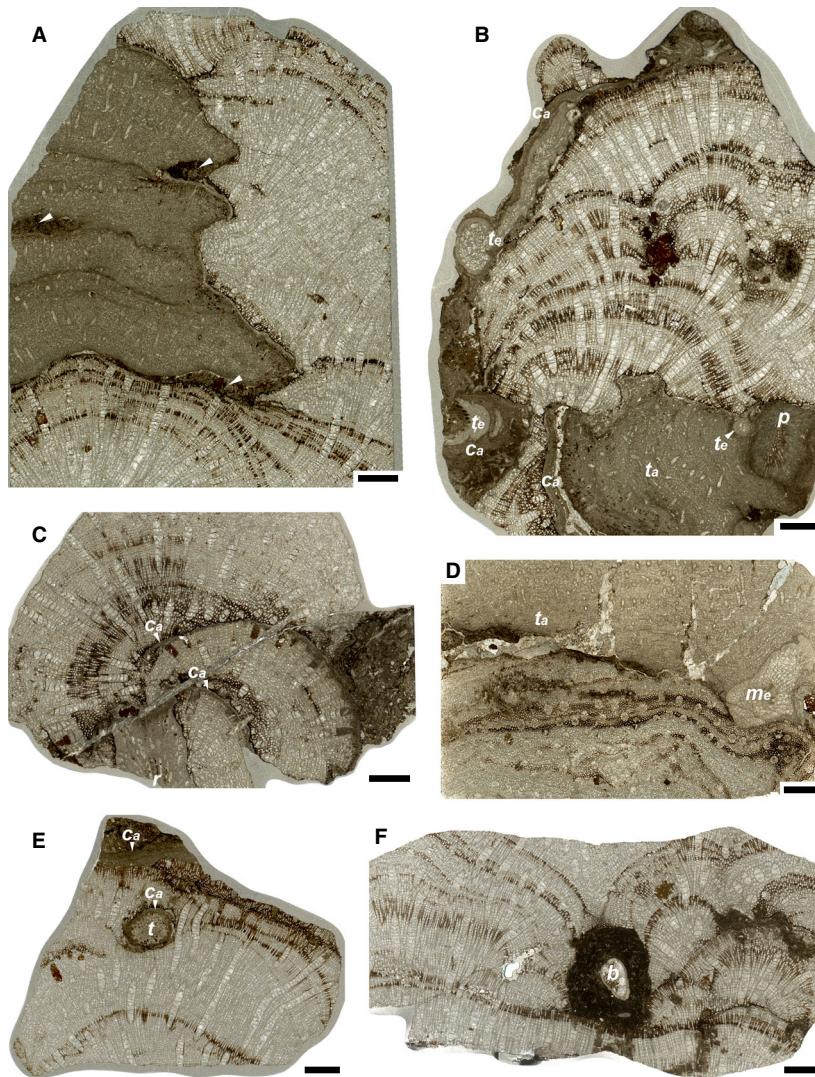


Fig. 4. *Heliolites porosus*. A, K1934, a record of overgrowth competition between a *H. porosus* colony and a symbiotic stromatoporoid *Taleastroma* sp. Sediment inclusions associated with the growth interruption surfaces are indicated with arrows. B, K1980, a sequence of encrustations and overgrowth starting with a *Platyaxum* sp. (p) colony, followed by a *Temnophyllum*? sp. (te), a symbiotic *Taleastroma* sp. (ta), a *Clathrocoilona* sp. (ca), *H. porosus*, and subsequently *Clathrocoilona* sp., *Temnophyllum*? sp. and *H. porosus* again. The *H. porosus* colony was overturned 90 degrees and rejuvenated – the remainder of the initial colony is visible in the bottom left corner. C, K1944, *H. -porosus* settled on the remains of solitary rugosan (r). The growth interruption surfaces consist of thin layers of *Clathrocoilona* sp. (ca), subsequently overgrown by the heliolitid. D, K1983, *Mesophyllum*? sp. (me) and a symbiotic *Taleastroma* sp. (ta) settled on *H. porosus*. E, K1967, a branch of *Thamnopora* cf. *irregularis* (t) encrusted by *Clathrocoilona* sp. (ca), deposited post-mortem onto the surface of a *H. -porosus* colony, during a growth interruption. F, K1989, a brachiopod (b) deposited with sediment onto the surface of a *H. porosus* colony, during a growth interruption. Scale bars are 5 mm.

alveolitid and symbiotic stromatoporoid epibionts had mixed results, but in some cases, the heliolitid could succeed. Nearly 20% of the studied heliolitids settled on other organisms themselves, but predominantly *post-mortem* (Figs 4B, C, 6A). Additionally, 12% of them consist of bioclaustrations, often subsequently overgrown by the coral (Figs 5A, 6F, H). Approximately 13% of specimens also bear signs of bioerosion by unidentified organisms (Fig. 5A). For the summary of data on the heliolitid growth patterns, see Table 2.

Non-heliolitid tabulate corals

Alveolitine tabulates are also abundant. They are represented by such taxa as *Alveolites* sp. (Figs 2A, C, F, 6A), *Alveolites* cf. *parvus* (Fig. 2E), *Alveolitella* cf. *fecunda* (Fig. 2C, E), *Coenites* sp. and *Platyaxum* sp. (Fig. 4B). Their growth forms are usually irregular or domical, and in the case of *A. cf. fecunda*, branching. They are mostly small, but some specimens attain up to 15 cm in diameter. They commonly contain growth interruption surfaces, in some cases with

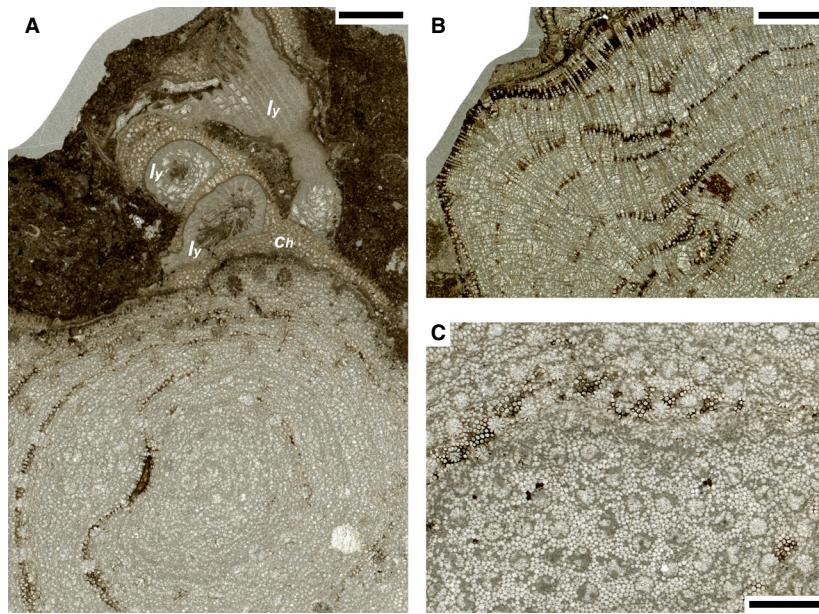


Fig. 5. *Heliolites* cf. *vesiculosus*. A, WLM/45, *H. cf. vesiculosus* encrusted *syn-vivo* by a cheatetid (*ch*), with rugosan *Lyrielsma* sp. epibionts (*ly*). B, WLM/45, *H. cf. vesiculosus*, longitudinal view. C, WLM/47, *H. cf. vesiculosus*, transverse view. Scale bars are 5 mm.

sediment intercalations. Rejuvenations and cases of alveolitines settling on or overgrowing other organisms (e.g. their stromatoporoid epibionts) are relatively common, as they were observed in about one third of the studied specimens (Fig. 2C, E, F). This includes *syn-vivo* interactions, evidenced by mutual attempts of overgrowth (Fig. 2F).

Other tabulates include favositids (*Favosites goldfussi*), pachyoporids (*Thamnopora* cf. *irregularis* (Fig. 2C), *Striatopora* sp.), syringoporids (the above-mentioned symbiotic *Syringopora* sp. and rare, non-symbiotic *Syringocystis* sp.) and auloporids – *Aulopora* sp. (Fig. 2B), *Aulocystis* sp., *Aulostegites* sp., *Mastopora* sp. (Fig. 2F). Auloporid-like hydrozoan (?) *Cladochonus* sp. also occurs (Figs 2D, 3D).

Rugose corals

The rugose fauna are mostly solitary forms. The colonial *Cyathophyllum multicarinatum* is abundant in the Wellin Member, forming large domes up to 80 cm in diameter and 25 cm high with corallites diverging quickly from the base of the colonies. Internal banding is common and regular, suggesting a seasonal origin. Their outer surface is commonly burrowed by *Entobia*-like shallow borings of uncertain affinity. Surprisingly, no fasciculate colonies occur in the ‘*Heliolites* Field’ with the exception of small, isolated corallites attributed to the colonial genus *Lyrielsma* that possibly corresponds to an aborted protocorallite. The sub-colonial coral *Cyathopaeidium paucitabulatum* occurs is

fine-grained facies. The solitary rugose corals *Acanthophyllum* spp., *Stringophyllum* spp., *Glossophyllum* spp. and small cystimorphs are the most common.

Discussion

Palaeoenvironmental interpretation

Despite the lack of fully exposed outcrops of the Wellin patch reefs, the analysis of microfacies and abundant fossil material enable the reconstruction of some parameters of the environment in which they developed. The analyses of massive corals and stromatoporoids growth patterns and interactions between reefal organisms recorded in the fossil material can facilitate the assessment of such aspects of the palaeoenvironment as sedimentary regime, hydrodynamics, bathymetry, or bottom conditions (Gibson & Broadhead 1989; Young & Scrutton 1991; Baarli *et al.* 1992; Seilacher & Thomas 2012; Król *et al.* 2016, 2018a; Jakubowicz *et al.* 2019).

The skeletons that are adjacent but mostly not in contact, embedded in a micrite-dominated matrix, suggest that the reefs were matrix-supported and a skeletal reef framework was not present. These characteristics classify them as close cluster reefs *sensu* Riding (2002). Those are often prone to being affected by storms (Riding 2002), which seems to be the case for the Wellin patch reefs – hence the partially paraautochthonous assemblage with overturned and toppled corals and stromatoporoids. Aside from

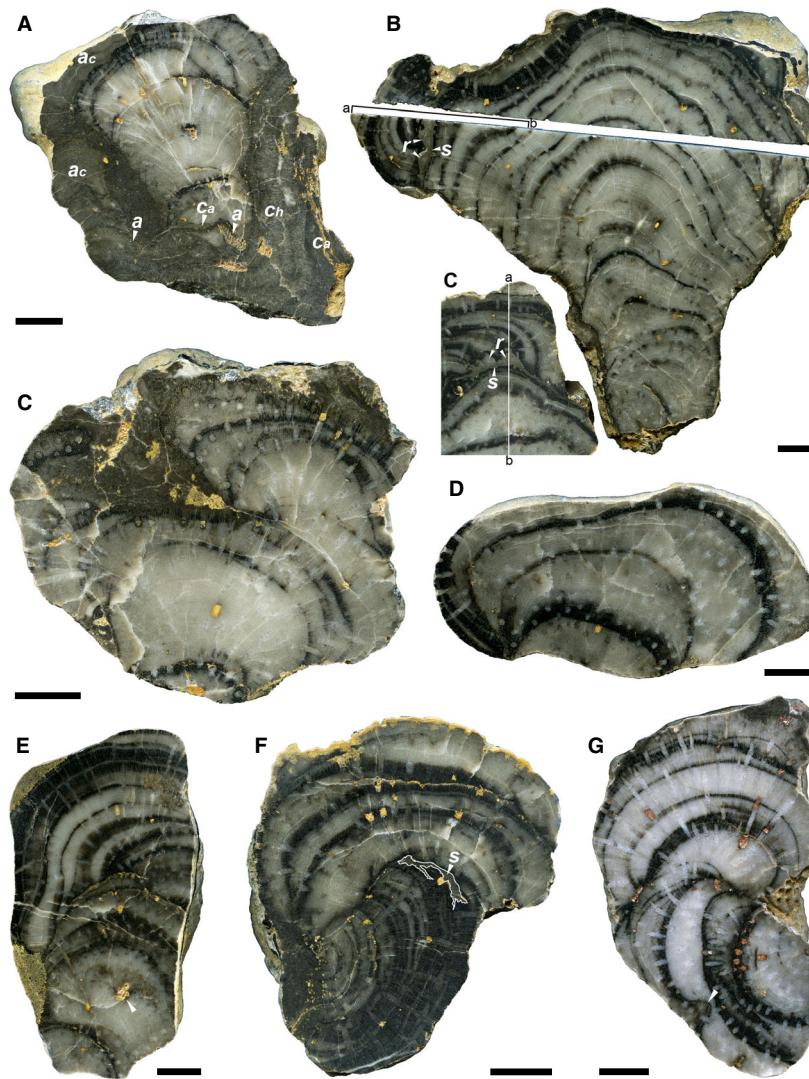


Fig. 6. Heliolitid growth forms. A, K1998, a bulbous *Heliolites porosus* settled on *Clathrocoilona* sp. (*ca*) and *Alveolites* sp. (*a*), encrusted by *Actinostroma* sp. (*ac*) and a cheetetid (*ch*). B, C, K1951, bulbous *H. porosus* with small stromatoporoid (*s*) and solitary rugosan (*r*) epibionts. B, longitudinal view, a-b bracket indicates the part of the transverse section shown in C. C, transverse view. D, K1991, a domical *H. porosus* with multiple rejuvenations following growth interruptions. E, WLM/44, a low-domical *H. porosus*. F, K1974, *H. porosus* rejuvenated after a sediment-induced growth interruptions. The arrow indicates a bioclastration. G, WLM/28, a domical *H. porosus* rotated and rejuvenated. The white outline indicates a stromatoporoid (*s*) epibiont. H, WLM/46, a domical *H. porosus* rotated and rejuvenated. The arrow indicates a bioclastration. Scale bars are 1 cm.

episodically increased water agitation however, the prevalence of micritic matrix suggests a generally low to moderate water energy setting. Close cluster reefs commonly develop in protected or deeper environments (Riding 2002). They correspond roughly to the *annularis* reef type/zone as distinguished in the Recent Caribbean reefs (Geister 1977, 1980, 1983; Riding 2002) – dominated by massive, domical corals, commonly settled on soft bottoms, at depths providing less water agitation, but still well above the storm wave base.

The abundance of massive heliolitids and stromatoporoids also seems to reinforce the hypothesis of the Wellin patch reefs developing in somewhat

deeper conditions. Sedimentological and palaeontological studies of a similar cluster reef assemblage from the Maider basin in the Givetian of Morocco also ruled out the very shallow, high-energy interpretation (Król et al. 2018a; Jakubowicz et al. 2019). It is important to emphasize however that tabulate corals did not prefer the extremely shallow, high-energy environments, where many modern scleractinian reefs develop. That was because tabulate-dominated communities did not form reefal frameworks providing the necessary wave-resistance in such conditions (Lecompte 1958; Philcox 1971; Embry & Klovan 1972; Scrutton 1998, 1999). In the Devonian, that kind of habitat was usually occupied by

Table 2. Growth patterns of heliolitids and stromatoporoids in the studied material.

	Heliolitids	Stromatoporoids (non-symbiotic)	Stromatoporoids (symbiotic)
Size*	Up to 20 cm (diameter)	Up to 5 cm (height)	5 cm and above (height)
Growth forms**	Domical (63.9%) Bulbous (28.8%) Irregular/flattened (3.6%)	Tabular (68.4%) Domical (31.6%)	Tabular to low-domical (100%)
Growth interruption surfaces	98.8%	36.8%	58.8%
Rejuvenations	59.0%	9.5%	5.6%
Settling on other organisms	19.3%	84.2%	70.6%
Encrusted	42.2%	0%	76.5%
Bioclastrations	12.0%	9.5%	11.1%
Borings	13.3%	4.8%	5.6%
Taxonomic composition	<i>Heliolites porosus</i> <i>Heliolites cf. vesiculosus</i>	<i>Actinostroma</i> <i>Clathrocoilona</i> <i>Stictostroma</i> <i>Taleastroma</i>	<i>Clathrodictyon</i> <i>Salairella</i> <i>Stromatopora</i> <i>Taleastroma</i>

* Since stromatoporoids in the studied material are commonly found as encrustations on and enveloped by corals, their size given here is height. The size of heliolitids, which were mostly found as whole coralla, is given here as diameter.

** Growth form was not determined in case of incomplete, poorly preserved specimens.

stromatoporoids, rather than corals, which in the terms of classic reef zonation, more commonly occupied fore-reef type habitats instead (Machel & Hunter 1994). Therefore, what could be considered deep by modern scleractinian reef standards (i.e. *annularis* zone) should be actually considered a relatively shallow habitat for tabulate corals, which could also thrive in significantly deeper environments (Brachert *et al.* 1992; Król *et al.* 2016, 2018b; Berkowski *et al.* 2019).

Table 3. Biometric measurements of heliolitid corals and basic statistical parameters.

Measurement/parameter	<i>Heliolites porosus</i>	<i>Heliolites vesiculosus</i>	cf.
Specimens (N)	80	3	
Corallite diameter (N)	973	60	
Corallite diameter (range)	1.10–1.40 mm	1.20–1.65 mm	
Corallite diameter (mean)	1.30 mm	1.47 mm	
Corallite diameter (s)	0.092 mm	0.093 mm	
Corallite diameter (c_v)	0.071	0.063	
Wall thickness (N)	220	60	
Wall thickness (range)	0.02–0.15 mm	0.03–0.13 mm	
Wall thickness (mean)	0.068 mm	0.077 mm	
Wall thickness (s)	0.020 mm	0.025	
Wall thickness (c_v)	0.294	0.319	
Siphonopore diameter (N)	240	60	
Siphonopore diameter (range)	0.20–0.51 mm	0.22–0.40 mm	
Siphonopore diameter (mean)	0.33 mm	0.31 mm	
Siphonopore diameter (s)	0.051 mm	0.041 mm	
Siphonopore diameter (c_v)	0.153	0.133	
Corallite spacing (per cm^2)	12–25	16–18	
Tabulae spacing (per 5 mm)	5–20	15–20	

Abbreviations: c_v , coefficient of variation; N, the number of specimens/measurements taken; s, standard deviation.

The matrix-supported patch reefs stand in contrast to the Fond des Vaux section, which is approximately contemporary to them. Its fossil assemblage is similar, but more diverse (with increased diversity and abundance of branching tabulate and rugose corals), and the reefal organisms there are more closely packed, embedded in a packstone-grainstone matrix (Coen-Aubert *et al.* 1991; Denayer 2019). This suggests that Fond des Vaux was possibly a filled frame reef developed under relatively high-water agitation (Riding 2002). Considering the close proximity between them, most likely Fond des Vaux reef developed at a shallower depth, than the Wellin patch reefs studied in this paper. Unfortunately, the Fond des Vaux section is mostly not accessible at present due to the filling of the part of the quarry where it crops out. For this reason, the comparison here is made on the basis of literature and archival material.

The abundance of *syn-vivo* encrustation and mutual overgrowths of corals and stromatoporoids suggests an intense competition for space on the Wellin patch reefs. This was likely stimulated by two factors. Firstly, judging by the prevalence of micritic matrix without any signs of early cementation, the reefs developed on a soft bottom. This limited the available hard substrate for settlement. However, heliolitids and other massive tabulates could thrive in soft bottom conditions (Gibson & Broadhead 1989; Young & Scrutton 1991; Seilacher & Thomas 2012; Król *et al.* 2016, 2018a). Secondly, the patch reefs were developed on the palaeohighs resulting from the Tienne Sainte-Anne Mbr (Jemelle Formation), and tabulate and rugose corals often settled on such underwater elevations (Berkowski 2008; Król *et al.* 2016, 2018a). They could provide the organisms with better access to nutrients and light, but in turn those

advantageous positions provided them with limited space, which resulted in the organisms competing for it. The exposure to light is mentioned here under the assumption that some of the Palaeozoic corals could hypothetically be photosymbiotic, particularly heliolitids (Król *et al.* 2018a), albeit that is still a matter of discussion (e.g. Coates & Jackson 1987; Scrutton 1998; Wood 1998; Copper 2002; Copper & Scotese 2003; Zapalski 2014; Jakubowicz *et al.* 2015; Zapalski *et al.* 2017a, 2017b; Zapalski & Berkowski 2019).

The studied coral-stromatoporoid assemblage holds many similarities to the Aferdou el Mrakib reef from the Givetian of Anti-Atlas in Morocco. It is characterized by similar bathymetry (below fair weather, but within storm wave zone), the prevalence of massive heliolitids and stromatoporoids, the intense competition for space due to the scarcity of hard substrates, and a periodically increased hydrodynamic setting (Kaufmann 1998; Król *et al.* 2018a; Jakubowicz *et al.* 2019). The influence of storms on that reef also resulted in overturned and toppled massive corals and stromatoporoids, but in case of Aferdou el Mrakib, they were significantly larger – up to over 1 m in diameter, compared to the diameters of the corals from Wellin, rarely exceeding 20 cm. On both reefs *H. porosus* was the most abundant coral species (Kaufmann 1998; Król *et al.* 2018a; Jakubowicz *et al.* 2019). Since the size of the corallum is related to the lifespan of the colony, it can be assumed that *H. porosus* colonies from Wellin did not live as long as the specimens from Aferdou el Mrakib, despite relatively similar life environments. One possible cause of that could be a significantly higher frequency of large storms, capable of dislodging massive coral colonies from the Wellin patch reefs. Positioned at c.25°S, on the southern margin of Laurussia, the patch reefs likely developed within the zone affected by tropical hurricanes (Witzke 1990; Stampfli *et al.* 2013; Vierek 2013; van Hengstum *et al.* 2016). This stands in contrast with the Aferdou el Mrakib reef, which estimated position was at 40–45°S (Jakubowicz *et al.* 2019 and the references therein), likely outside of the reach of most tropical hurricanes.

Assessment of the sedimentation rate using coral and stromatoporoid skeletal growth patterns is based mainly on the gross morphology of the coralla, as different coral growth forms are adapted to surviving under different sedimentary regimes (e.g. Young & Scrutton 1991; Bosellini & Stemann 1996; Sanders & Baron-Szabo 2005; Król *et al.* 2018b). The abundance of growth interruption surfaces, which in cross-section outline the morphology of the colony at different stages of development, facilitates this further (Miller & West 1997; Król *et al.* 2018a). If preserved,

the shape of the base of the corallum can also be a useful proxy (Philcox 1971; Gibson & Broadhead 1989; Król *et al.* 2016), especially for colonies which grew directly on the sea bottom – and not on other organisms, as it is the case for many specimens from Wellin, particularly alveolitines. The predominantly convex bases and abundant bulbous growth forms of the studied heliolitids, along with the absence of tabular morphologies, are typical for massive tabulate assemblages developing under relatively high sedimentation rate (Philcox 1971; Gibson & Broadhead 1989; Young & Scrutton 1991). The very high abundance of Type 1 growth interruption surfaces (a break followed by a continuation of growth, without sediment; after Miller & West 1997) in heliolitids, in some cases in the form of wider zones (in vertical section) suggest that the increased sedimentation rate was not constant, but possibly featured periodic pulses of sediment influx. This is further confirmed by the dominance of domical growth forms (64% of heliolitid specimens), which are not favourable in conditions of constant, high sedimentation rate. In some specimens, the seemingly cyclic growth interruptions (Fig. 4B) could result from quasi-regular events, for instance seasonal storms causing sediment pulses. However, it needs to be emphasized that actual seasonal cyclic density banding, which is often considered a proxy of photosymbiosis in corals (Scrutton & Powell 1980; Young & Kershaw 2005; Stanley & Helmle 2010; Stanley & Lipps 2011), does not occur in the studied heliolitids. The growth interruptions are in no case truly cyclic; they are commonly irregularly spaced, discontinuous and consist of sediment intercalations or epibionts. They are also often followed by rejuvenations.

Inter species interactions

Frequent *syn-vivo* interactions between different species inhabiting the Wellin patch reefs can be divided into two types: hostile and mutualistic. The hostile interactions are related to the competition for space between corals and stromatoporoids, which are evidenced by reciprocal overgrowths between them. In case of this type of interaction in the Wellin patch reef assemblage, heliolitid corals seem to be the most frequent host for the initial settling of coral and stromatoporoid epibionts. The settling of epibionts always coincided with growth interruptions, and these occur in heliolitid coralla much more often than in other organisms in the assemblage. In modern corals sediment covering soft tissue, which is the likely cause of the growth interruptions discussed here, often causes damage to the soft tissue and barring of the skeleton (Wesseling *et al.* 1999). The

presence of bare skeleton would greatly increase the chances of successful settlement by epibiont larvae, as it provides hard substrate. Heliolitids being apparently prone to growth interruptions could be the reason why other organisms preferred them as hosts (Król *et al.* 2018a).

While other corals also settled on heliolitids, stromatoporoid epibionts are definitely the most abundant. Considering the link between their settling and the occurrence of growth interruption periods, it seems to be a matter of recruitment. Possibly the stromatoporoids were capable of faster recruitment when provided with hard substrate in the form of bare coral skeleton. Another likely controlling factor on the infestation by corals would be their sexual reproduction cycles, limiting the time window of when the coral larvae capable of settling on the heliolitid were actually available. The time of releasing larvae would likely have to overlap with the period of bared skeleton in heliolitids in order to facilitate infestation. On the other hand, reproduction of hypercalcified sponges, which include stromatoporoids, is poorly understood even in case of living taxa (Vacelet *et al.* 2010). However, some marine sponges are capable of gemmulation, and the gemmulae often perform a role of dormant structures in periods of unfavourable conditions (Hammel *et al.* 2009). They are produced in large numbers in the sponge body while the sponge itself decays. The gemmulae are usually used to repopulate their parent sponge, but they can also disperse (Hammel *et al.* 2009 and references therein). Sedimentary stressors could possibly constitute such unfavourable conditions for the stromatoporoids. If they were capable of gemmulation, it could lead to producing and dispersing gemmulae following the sediment influxes and growth interruptions – in a similar time window as heliolitid skeleton baring. This would explain increased abundance of stromatoporoids as epibionts, compared to corals.

Whereas the infestations of corals and stromatoporoids seem to be dependent on the presence of growth interruption and possibly skeleton baring of the host, the same cannot be said about overgrowth. Particularly tabulate corals proved to be very effective in overgrowing living stromatoporoids and other corals. The effectiveness of the overgrowth is here attributed to the rate of skeletal growth, as in some cases the organisms ‘raced’, trying to envelop each other in their own skeleton (Fig. 4A). Similarly to the findings of Król *et al.* (2018a), *H. porosus* from Wellin proved to be the most efficient in overgrowing its own epibionts. This includes rare bioclaustrations (Tapanila 2008), formed presumably by non-skeletal epibionts, which were also overgrown by the

coral (cf. Król *et al.* 2018a). Solitary Rugosa and alveolinine corals also settled on heliolitids and stromatoporoids *syn-vivo*. Where rugosans infested other organisms, they could not be overgrown by the massive tabulates and stromatoporoids (aside from very small, likely juvenile specimens, e.g. Fig. 6B, C), possibly suggesting a higher rate of their vertical growth. Alveolinines were effective in overgrowing some epibionts (cf. Denayer 2018), particularly stromatoporoids, but the growth rate of heliolitids was apparently higher, as the alveolid corals could not compete with them in overgrowth.

Mutualistic interspecies interactions within the studied assemblage refer to the symbiotic association of stromatoporoids and syringoporid tabulate corals ('caunopore tubes'), which is a common occurrence in Palaeozoic (Mistiaen 1984; Kershaw 1987). In case of Wellin specimens however, a few things require explanation. Firstly, free-living syringoporid corals were rarely encountered in the assemblage, while the ones that lived in symbiosis with stromatoporoids occur commonly. Free-living and symbiotic syringoporids are here attributed to different taxa, so it is possible that the symbiosis was obligate for the latter (Young & Noble 1989). Most likely, the conditions of episodically increased hydrodynamics and competition for space were not favourable for the delicate, fasciculate syringoporids. Secondly, symbiotic and non-symbiotic stromatoporoids from Wellin predominantly belong to different taxa, which could suggest some host selectivity by the syringoporids, a phenomenon reported also by Kershaw (1987). Lastly, stromatoporoids containing syringoporid corals usually attained larger sizes and were more effectively competing in overgrowth with other organisms, especially heliolitids (Fig. 4A). Meanwhile non-symbiotic stromatoporoids also commonly infested living tabulate corals during growth interruptions, but were usually overgrown easily after the coral colony regenerated (Figs 4C, 6G). This conforms to the findings of Król *et al.* (2018a) from the Aferdou el Mrakib reef, where heliolitid corals were very effective in overgrowing stromatoporoids, and stromatoporoid-syringoporid symbiosis was not observed. Overgrowth competition seems to largely rely on the rate of skeletal growth and apparently stromatoporoids with syringoporid endobionts could attain faster rate of vertical growth. Commensalism, although often described from the fossil record can be ruled out, as this interaction is very difficult to evidence in Recent associations and require utmost rigour in designing and conducting of an experiment (Mathis & Bronstein 2020), impossible to achieve in analysing fossil associations (Zapalski 2011). For this reason, the stromatoporoid-syringoporid association

present in the Wellin locality is here considered mutualistic (cf. Tapanila 2008): the stromatoporoids gained the ability for more effective overgrowth, and possibly also some defensive capabilities provided by the coral's tentacles; in turn, the syringoporid corals supposedly used the bodies of their hosts for protection from increased water energy during storms and mechanical damage to their fragile skeletons.

Palaeoecology of heliolitid corals

The growth form analysis, crucial for the palaeoecological study of heliolitids, is at least partially related to the issue of phenotypical plasticity of corals. The morphology of the coral skeleton can be affected by intrinsic (genetic) and extrinsic (environmental) factors. It is important to mention however, that both in case of Recent and extinct corals, the extent to which the coral skeleton development is controlled intrinsically and extrinsically varies from species to species (Young & Scrutton 1991; Muko *et al.* 2000; Meroz *et al.* 2002; Sanders & Baron-Szabo 2005; Todd 2008; Martí-Puig *et al.* 2014; Sadler *et al.* 2015). Young & Scrutton (1991) found that a Silurian heliolitid *Stelioporella parvistella* exhibited high morphological plasticity in response to sedimentary stress. However, a representative of the genus *Heliolites* living in the same environments as *S. parvistella*, *H. interstinctus*, had a significantly more genetically constrained range of growth forms – limited to tabular, domical and low-bulbous (Young & Scrutton 1991). This seems to conform with the observations of Middle Devonian *H. porosus*, which exhibits similar morphologies, even in sedimentary conditions where they could be sub-optimal compared to, for example, a branching growth form that *S. parvistella* could develop (Young & Scrutton 1991; Król *et al.* 2018a). It seems that *H. porosus* and *H. cf. vesiculosus* could not develop a growth form-related response to the sedimentary stress on the Wellin patch reefs, beyond the bulbous morphologies formed as an effect of 'catching up' to the accumulating sediment (Philcox 1971; Gibson & Broadhead 1989). This might suggest that these species, similarly to the Silurian *H. interstinctus* studied by Young & Scrutton (1991), had their growth forms more genetically constrained. Considering the age difference and different species concerned, it is also possible that this was a feature of the genus *Heliolites* as a whole.

Similarly to *H. porosus* from Aferdou el Mrakib, *H. porosus* and *H. cf. vesiculosus* specimens from Wellin seem to exhibit signs of high sediment tolerance (Król *et al.* 2018a). Sediment tolerance is the capability of the coral to survive under the sediment cover, usually relying on passive means of sediment

removal (i.e. by wave action) during the period of burial (Hubbard & Pocock 1972; Sanders & Baron-Szabo 2005). It is typically observed in small-polyped Recent corals, such as representatives of the genera *Porites* and *Heliopora* (Wesseling *et al.* 1999; Sanders & Baron-Szabo 2005; Król *et al.* 2018a). This is in contrast to corals with larger polyps (corallite diameters exceeding 2.5 mm), which often use various means of active sediment rejection, such as water uptake and release, tentacle movement, ciliary currents, or mucus secretion (Stafford-Smith & Ormond 1992; Stafford-Smith 1993; Sanders & Baron-Szabo 2005). It is here assumed that most likely the growth interruption surfaces in heliolitids from Wellin mark the periods of sediment covering the living tissue of the coral, at least partially. Type 3 growth interruption surfaces consisting of sediment (Miller & West 1997) suggest that sedimentary stress was indeed the cause of their formation. In turn, Type 1 growth interruption surfaces were formed in places, where the sediment was successfully removed by wave action before the death of the coral tissue. Where traced from the outside of the corallum towards the centre, many of the growth interruption surfaces change from Type 3 to Type 1. This seems to support the hypothesis of passive sediment removal, as the sediment cover could be more easily removed by waves from the top parts of a domical or bulbous heliolitid colony, whereas the sedimentary grains were more likely to remain in place on its flanks. However, it needs to be mentioned that in modern corals, the position of the damaged tissue is very relevant for recovery, regardless of sediment removal mechanisms. Meesters *et al.* (1992) found that lesions positioned in such a way that living coral tissue surrounds it on all sides (e.g. on top of a domical colony) can heal more effectively. This could also explain the abundance of Type 1 growth interruption surfaces usually in the central parts of the corallum.

The abundance of the Wellin heliolitids suggests that they were quite successful in surviving under the sedimentary stress, but at the same time they consist of more growth interruption surfaces than other corals and stromatoporoids. This is very similar to the case of Givetian *H. porosus* from Aferdou el Mrakib (Król *et al.* 2018a). In both cases, the heliolitids were very abundant in the reefal assemblage, yet consisted of more growth interruptions than the associated sessile organisms, which would suggest that they suffered from sedimentary stress more often, or more easily. However, the abundance of Type 1 surfaces suggests that despite this, they could very effectively recover from a growth interruption and continue its growth. The capability for quick recovery could explain how massive heliolitids, most likely incapable

of skeletal plasticity, active sediment rejection and easily affected by sediment influxes, were relatively successful in the Wellin reefal assemblage. This reinforces the observation from the Givetian Aferdou el Mrakib reef, that *H. porosus* was a resilient species capable of surviving under sedimentary stress (Król *et al.* 2018a). Furthermore, it also seems to apply to *H. cf. vesiculosus*, although as it was less abundant, decisive conclusions about the palaeoecology of this species are hampered by the limited material.

The capabilities for recovery after growth interruptions and to overgrow other organisms are difficult to directly explain, when analysing fossil material with no preserved soft tissue. However, they both seem to be related to the secretion of the skeleton by heliolitids, particularly relatively fast skeletal growth. Their coralla composed of septate corallites ('autopores') separated by coenenchymal tubules ('siphonopores') are here understood as plocoid. It is worth emphasizing that heliolitids were some of the few groups of Palaeozoic corals featuring this mode of colony organization. Plocoid corals are considered to have relatively high degree of colony integration – significantly higher than cerioid or phaceloid corals, more common in the Palaeozoic. But additionally, highly integrated colonies of small-polyped corals, attaining large sizes, are typical for modern photosymbiotic corals (Coates & Jackson 1987; Barbeitos *et al.* 2010). Heliolitid skeletons had thin-walled coralla, advantageous for rapid vertical growth, which would be greatly facilitated in case of the presence of algal symbionts. And whereas the specimens from Wellin are predominantly relatively small, *H. porosus* colonies commonly attained very large sizes – which is also typical for corals aided in calcification by algae (Coates & Jackson 1987; Król *et al.* 2018a).

Hence, it is not possible to prove that heliolitids possessed algal symbionts, it seems that their high degree of colony integration and organization was crucial anyway. Król *et al.* (2018a) drew parallels between *H. porosus* and a modern alcyonarian hermatypic coral of very similar plocoid structure, *Heliopora coerulea* (Colgan 1984). It exhibits very similar sediment tolerance and recovery capabilities as *Heliolites* from Wellin and Aferdou el Mrakib (Wesseling *et al.* 1999; Król *et al.* 2018a). Fast-growing *H. coerulea* can thrive under sedimentary stress and can recover from complete burial within several weeks (Wesseling *et al.* 1999). Although the precise reasons for these similar capabilities in unrelated coral species of very similar skeletal structure, yet separated by 260 millions of years, are unclear, high degree of colony integration and thin-walled,

fast-growing skeleton, are probably favourable factors for their adaptations through homeomorphy.

Conclusions

Patch reefs of Wellin developed in relatively shallow waters (well above the storm wave base), on the palaeohighs formed by bioherms within the underlying Jemelle Formation. They were covered with soft sediment and regularly witnessed episodically increased hydrodynamics and sediment input, most likely due to storm events – as evidenced by the abundant overturned corals and growth interruptions.

The reefs were largely dominated by massive stromatoporoids and corals – mainly heliolitids and alveolitids, with relatively abundant solitary rugosa and pachyoporid tabulates. The assemblages also included subordinate favositids, chaetetids and colonial rugose corals (*Cyathophyllum*). Their abundance on the spatially restricted palaeohighs covered with soft sediment resulted in relatively high living tissue coverage.

There was an intense competition for space and hard substrates among the reefal organisms. Overgrowth was the most common survival strategy. Stromatoporoids relied on the quicker recruitment and in case of some taxa, on syringoporid symbionts, which seemingly boosted their growth rate, providing a kind of internal framework. Heliolitids relied on their relatively fast growth rate, facilitated by the porous skeleton, and the ability to quickly recover after growth interruptions. Alveolitids successfully competed in overgrowth with non-symbiotic stromatoporoids, but their growth rate did not allow them to overgrow heliolitids.

The massive organisms relied on passive sediment removal during increased sediment influxes. These influxes however, caused growth interruptions, which the heliolitids suffered more often than other organisms. Heliolitid colonies were likely more susceptible to the sediment cover, but also showed good recovery capabilities. These features could result from the more highly integrated colony organization of heliolitids. It allowed them to survive on the reef despite the lack of skeletal plasticity capabilities, likely caused by a more constraining genetic control on the growth forms of the genus *Heliolites*.

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References

- Aretz, M. 2002: Habitatanalyse und Riffbildungspotential kolo-nialer rugoser Korallen im Unterkarbon (Mississippium) von Westeuropa. *Kölner Forum für Geologie und Paläontologie* 10, 1–155.
- Aretz, M. & Chevalier, E. 2007: After the collapse of stromatoporid-coral reefs – the Famennian and Dinantian reefs of Belgium: much more than Waulsortian mounds. *Geological Society Special Publication* 275, 163–188.
- Baarli, B.G., Johnson, M.E. & Keilen, H.B. 1992: Size and shape distribution of level-bottom tabulate corals and stromatoporoids (Silurian). *Lethaia* 25, 269–282.
- Barbeitos, M.S., Romano, S.L. & Lasker, H.R. 2010: Repeated loss of coloniality and symbiosis in scleractinian corals. *Proceedings of the National Academy of Sciences of the United States of America* 107, 11877–11882.
- Berkowski, B. 2008: Emsian deep-water Rugosa assemblages of Hamar Laghdad (Devonian, Anti-Atlas, Morocco). *Palaeoontographica A*284, 17–68.
- Berkowski, B., Jakubowicz, M., Belka, Z., Król, J.J. & Zapalski, M.K. 2019: Recurring cryptic ecosystems in Lower to Middle Devonian carbonareous mounds of Hamar Laghdad (Anti-Atlas, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology* 523, 1–17.
- Bethune, P.D. 1954: *Carte géologique de Belgique (échelle 1/500.000)*. Atlas de Belgique, planche 8. Académie royale de Belgique, Bruxelles.
- Bondarenko, O.B. 1992: Sistema geliolitoidei. *Moskovskoe obshchestvo ispytatelej prirody*, 205 pp.
- Bosellini, F.R. & Stemmann, T.A. 1996: Autecological significance of growth form in the scleractinian *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). *Bollettino della Società Paleontologica Italiana* 3, 31–43.
- Boulvain, F. 1993: Sédimentologie et diagenèse des monticules mictitiques 'F2j' du Frasnien de l'Ardenne. *Professional Paper-Service Géologique de Belgique* 260, 1–427.
- Brachert, T.C., Buggisch, W., Flügel, E., Hüssner, H.M., Joachimski, M.M., Tourneur, F.J. & Walliser, O.H. 1992: Controls of mud mound formation: the Early Devonian Kess-Kess carbonates of the Hamar Laghdad, Anti-Atlas, Morocco. *Geologische Rundschau* 81, 15–44.
- Bultynck, P. & Dejonghe, L. 2001: Devonian lithostratigraphic units (Belgium). In Bultynck, P. & Dejonghe, L. (eds): Guide to a Revised Lithostratigraphic Scale of Belgium. *Geologica Belgica* 4, 39–68.
- Bultynck, P. & Godefroid, J. 1974: Excursion G. In Bouckaert, J. & Streel, M. (eds): *International Symposium on Belgian Micropalaeontological limits from Emsian to Viséan, September 1st to 10th, Namur, Guidebooks*. Service géologique de Belgique, Bruxelles, 1–44.
- Chatterton, B.D.E., Copper, P., Dixon, O.A. & Gibb, S. 2008: Spicles in silurian tabulate corals from Canada, and implications for their affinities. *Palaeontology* 51, 173–198.
- Coates, A.G. & Jackson, J.B.C. 1987: Clonal growth, algal symbiosis, and reef formation by corals. *Paleobiology* 13, 363–378.
- Coen-Aubert, M., Mamet, B., Preat, A. & Tourneur, F. 1991: Sédimentologie, Paléocéologie et Paléontologie des calcaires crinoïdiens au voisinage de la limite Couvinién-Givetien à Wellin (Bord Sud du Synclinorium de Dinant, Belgique). *Mémoires pour servir à l'Explication des Cartes Géologiques et Minieries de la Belgique* 31, 1–61.
- Colgan, M.W. 1984: The Cretaceous Coral *Heliopora* (Octocorallia, Coenothealia) – a Common Indo-Pacific Reef Builder. In Eldredge, N. & Stanley, S.M. (eds): *Living Fossils*. Springer-Verlag, New York, 266–271.
- Copper, P. 2002: Reef development at the Frasnian/Famennian mass extinction boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 181, 27–65.
- Copper, P. & Scotese, C.R. 2003: Megareefs in Mid-Devonian supergreenhouse climates. *Geological Society of America Special Papers* 370, 209–230.
- Denayer, J. 2018: From rolling stones to rolling reefs: a Devonian example of highly diverse macrooids. *Lethaia* 51, 564–580.
- Denayer, J. 2019: Revised stratigraphy of the Eifelian (Middle Devonian) of southern Belgium: sequence stratigraphy, global events, reef development and basin structuration. *Geologica Belgica* 22, 149–173.
- Dixon, O.A. 1974: Late Ordovician Propora (Coelenterata: Heliolitidae) from Anticosti Island, Quebec, Canada. *Journal of Paleontology* 48, 568–585.
- Dixon, O.A. 1999: Upper Silurian heliolitine corals, Canadian Arctic: taxonomic method, keys to identification, and biogeographic relationships. *Journal of Paleontology* 73, 1002–1014.
- Dixon, O.A. 2010: Fossilized polyp remains in Silurian Heliolites (Anthozoa, Tabulata) from Nunavut, Arctic Canada. *Lethaia* 43, 60–72.
- Dumoulin, V. & Blockmans, S. 2008: Le passage latéral entre les formations de Couvin et de Jemelle (Eifelian) au bord sud du Synclinorium de Dinant (Belgique): Introduction du Membre du Vieux Moulin – Formation de Jemelle. *Geologica Belgica* 11, 25–33.
- Edinger, E.N., Copper, P., Risk, M.J. & Atmojo, W. 2002: Oceanography and reefs of recent and Paleozoic tropical epeiric seas. *Facies* 47, 127–150.
- Embry, A.F.I. & Klovan, J.E. 1972: Absolute water depth limits of Late Devonian paleoecological zones. *Geologische Rundschau* 61, 672–686.
- Fernández-Martínez, E.M. 1998: Heliolitidae (Cnidaria, Tabulata) del Devónico de la Cordillera Cantábrica (NW de España). *Trabajos de Geología* 21, 97–110.
- Flügel, H. 1956: Revision der ostalpinen Heliolitina. *Mitteilungen des Museums für Bergbau, Geologie und Technik am Landesmuseum Joanneum*, Graz 17, 102.
- Forcino, F.L. & Stafford, E.S. 2020: The influence of collection method on paleoecological datasets: in-place versus surface-collected fossil samples in the Pennsylvanian Finis Shale, Texas, USA. *PLoS One* 15, e0228944.
- Geister, J. 1977: The influence of wave exposure on the ecological zonation of caribbean coral reefs. In *Proceedings of Third International Coral Reef Symposium Vol. 2: Geology*. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, 23–29.
- Geister, J. 1980: Calm-water reefs and rough-water reefs of the Caribbean Pleistocene. *Acta Palaeontologica Polonica* 25, 541–556.
- Geister, J. 1983: Holozäne westindische Korallenriffe: Geomorphologie, Ökologie und Fazies. *Facies* 9, 173–283.
- Gibson, M.A. & Broadhead, T.W. 1989: Species-specific growth responses of favositid corals to soft-bottom substrates. *Lethaia* 22, 287–299.
- Godefroid, J. 1968: Contribution à l'étude du Couvinién entre Wellin et Jemelle (bord sud du bassin de Dinant). *Mémoire de l'Académie royale de Belgique, Classe des Sciences* 13, 1–79.
- Goldfuss, A. 1826: *Petrefacta Germaniae: Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder*. Verlag des lithographischen Instituts von Arzn & Company, Düsseldorf.
- Hammel, J.U., Herzen, J., Beckmann, F. & Nickel, M. 2009: Sponge budding is a spatiotemporal morphological patterning process: insights from synchrotron radiation-based x-ray microtomography into the asexual reproduction of *Tethya wilhelma*. *Frontiers in Zoology* 6, 1–14.
- van Hengstum, P.J., Donnelly, J.P., Fall, P.L., Toomey, M.R., Albury, A.A. & Kakuk, B. 2016: The intertropical convergence zone modulates intense hurricane strikes on the western North Atlantic margin. *Scientific Reports* 6, 21728.
- Hill, D. 1981: Part F – Coelenterata – Suplement 1 – Rugosa and Tabulata. In Teichert, C., Ashlock, V., Keim, J.D., McCormick,

- L. & Williams, R.B. (eds): *Treatise on Invertebrate Paleontology*. The Geological Society of America, Boulder and the University of Kansas, Lawrence, F380–F762.
- Hladil, J. 1988: Structure and microfacies of Middle and Upper Devonian carbonate buildups in Moravia, Czechoslovakia. In *Devonian of the World: Proceedings of the 2nd International Symposium on the Devonian System — Memoir 14, Volume II: Sedimentation*, 607–618.
- Hubbard, J.A.E.B. & Pocock, Y.P. 1972: Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geologische Rundschau* 61, 598–626.
- Hubert, B.L.M., Zapalski, M.K., Nicollin, J.-P., Mistiaen, B. & Brice, D. 2007: Selected benthic faunas from the Devonian of the Ardennes: an estimation of palaeobiodiversity. *Acta Geologica Polonica* 57, 223–244.
- Iven, C. 1980: Alveolitiden und Heliolitiden aus dem Mittel- und Oberdevon des Bergischen Landes (Rheinisches Schiefergebirge). *Palaeontographica A*167, 121–179.
- Jakubowicz, M., Berkowski, B., López Correa, M., Jarochowska, E., Joachimski, M. & Belka, Z. 2015: Stable isotope signatures of middle Palaeozoic ahermatypic rugose corals – deciphering secondary alteration, vital fractionation effects, and palaeoecological implications. *PLoS One* 10, e0136289.
- Jakubowicz, M., Krol, J., Zapalski, M.K., Wrzolek, T., Wolniewicz, P. & Berkowski, B. 2019: At the southern limits of the Devonian reef zone: palaeoecology of the Aferdou el Mrakib reef (Givetian, eastern Anti-Atlas, Morocco). *Geological Journal* 54, 10–38.
- Jamart, V. & Denayer, J. 2020: The Kačák event (late Eifelian, Middle Devonian) on the Belgian shelf and its effects on rugose coral palaeobiodiversity. *Bulletin of Geosciences* 95, 279–311.
- Joachimski, M.M., Breisig, S., Buggisch, W., Talent, J.A., Mawson, R., Gereke, M., Morrow, J.R., Day, J. & Weddige, K. 2009: Devonian climate and reef evolution: insights from oxygen isotopes in apatite. *Earth and Planetary Science Letters* 284, 599–609.
- Kasimi, R. & Preat, A. 1996: Eifelian-Givetian siliciclastic carbonate ramp systems. 2 – cyclostratigraphy and palaeostructuration. *Bulletin des Centres de Recherches Exploration-Production Elf Aquitaine* 20, 61–90.
- Kaufmann, B. 1998: Middle Devonian reef and mud mounds on a carbonate ramp; Mader Basin (eastern Anti-Atlas, Morocco). In Wright, V.P. & Burchette, T.P. (eds): *Carbonate Ramps*. Geological Society, London, 417–435.
- Kershaw, S. 1987: Stromatoporoid-coral intergrowths in a Silurian biostrome. *Lethaia* 20, 371–380.
- Kettnerová, M. 1933: The *Heliolites* of the Devonian of Bohemia. *Zvláštní Otisk z Vestniku Státního Geologického Ustavu Česko-slovanské Republiky* 9, 1–8.
- Kiessling, W., Flügel, E. & Golonka, J. 1999: Paleoreef maps: Evaluation of a comprehensive database on Phanerozoic reefs. *AAPG Bulletin* 83, 1552–1587.
- Król, J.J., Jakubowicz, M., Zapalski, M.K. & Berkowski, B. 2018a: Massive tabulates in competition for space: a case study from Aferdou el Mrakib (Middle Devonian, Anti-Atlas, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology* 497, 105–116.
- 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). *Palaeogeography, Palaeoclimatology, Palaeoecology* 449, 531–540.
- Król, J.J., Zapalski, M.K. & Berkowski, B. 2018b: Emsian tabulate corals of Hamar Laghdad (Morocco): taxonomy and ecological interpretation. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 290, 75–102.
- Lecompte, M. 1936: Revision des tabulés Dévoniens décrits par Goldfuss. *Mémoires de l'Institut Royal de Sciences Naturelles de Belgique* 75, 1–112.
- Lecompte, M. 1937: Contribution à la connaissance des récifs du Dévonien de l'Ardenne. *Bulletin du Musée royal d'histoire naturelle de Belgique* 13, 1–14.
- Lecompte, M. 1958: Les récifs paleozoïques en Belgique. *Geologische Rundschau* 47, 384–401.
- Lecompte, M. 1960: Compte rendu de la session extraordinaire de la Société géologique de Belgique et de la Société belge de Géologie, de Paléontologie et d'Hydrologie du 25 au 28 septembre 1959. *Annales de la Société géologique de Belgique* 83, 1–134.
- Lecompte, M. 1970: Die Riffe im Devon der Ardennen und ihre Bildungsbedingungen. *Geologica Palaeontologica* 4, 25–71.
- 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.
- Maillieux, E. 1938: Le Couvinien de l'Ardenne et ses faunes. *Mémoires du Musée royal des Sciences naturelles de Belgique* 83, 57.
- Marti-Puig, P., Forsman, Z.H., Havercort-Yeh, R.D., Knapp, I.S.S., Maragos, J.E. & Toonen, R.J. 2014: Extreme phenotypic polymorphism in the coral genus *Pocillopora*; micro-morphology corresponds to mitochondrial groups, while colony morphology does not. *Bulletin of Marine Science* 90, 211–231.
- Mathis, K.A. & Bronstein, J.L. 2020: Our current understanding of commensalism. *Annual Review of Ecology, Evolution and Systematics* 51, 167–189.
- Meesters, E.H., Bos, A. & Gast, G.J. 1992: Effects of sedimentation and lesion position on coral tissue regeneration. In *Proceedings of the 7th International Coral Reef Symposium, Guam*, volume 2, 681–688.
- Meroz, E., Brickner, I., Loya, Y., Peretzman-Shemer, A. & Ilan, M. 2002: The effect of gravity on coral morphology. *Proceedings of the Royal Society B: Biological Sciences* 269, 717–720.
- Miller, K.B. & West, R.R. 1997: Growth-interruption surfaces within chaetetid skeletons: records of physical disturbance and depositional dynamics. *Lethaia* 29, 289–299.
- Mironova, N.V. 1974: Early Devonian Tabulata of Gornij Altai and Salair. In Kim, A.I. (ed.): *Zapadno-Sibirskoe knizhnoe izdatel'stvo*, 164 pp. Stroizdat, Novosibirsk.
- Mistiaen, B. 1984: Disparition des Stromatopores paleozoïques ou survie du groupe; hypothèse et discussion. *Bulletin de la Société Géologique de France* 7, 1245–1250.
- Muko, S., Kawasaki, K., Sakai, K., Takasu, F. & Shigesada, N. 2000: Morphological plasticity in the coral *Porites sillimaniani* and its adaptive significance. *Bulletin of Marine Science* 66, 225–239.
- Noble, J.P.A. & Lee, D.-J. 1990: Ontogenies and astogenies and their significance in some favositid and heliolitid corals. *Journal of Paleontology* 64, 515–523.
- Noble, J.P.A. & Young, G.A. 1984: The Llandovery-Wenlock heliolitid corals from New Brunswick, Canada. *Journal of Paleontology* 58, 867–884.
- Nowiński, A. 1992: Tabulate corals from the Givetian and Frasnian of the Holy Cross Mountains and Silesian Upland. *Acta Palaeontologica Polonica* 37, 183–216.
- Oliver, W.A. Jr 1996: Origins and relationships of Paleozoic coral groups and the origin of the Scleractinia. *The Paleontological Society Papers* 1, 107–134.
- Ospanova, N.K. 2010: Remarks on the classification system of the Heliolitida. *Palaeoworld* 19, 268–277.
- Ospanova, N.K. 2012: Taxonomical problems of the Heliolitida. *Geologica Belgica* 15, 215–219.
- Penecke, K.A. 1887: Ueber die Fauna und das Alter einiger paläozoischer Korallrifte der Ostalpen. *Zeitschrift der Deutschen Geologischen Gesellschaft Band 39 Heft 2*, 267–276.
- Philcox, M.E. 1971: Growth forms and role of colonial coelenterates in reefs of the Gower Formation (Silurian), Iowa. *Journal of Paleontology* 45, 338–346.
- Poty, E. & Chevalier, E. 2007: Late Frasnian phillipsastreid biostromes in Belgium. *Geological Society, London, Special Publications* 275, 143–161.
- Richards, R.P. & Dyson-Cobb, M. 1976: A *Lingula-Heliolites* association from the Silurian of Gotland, Sweden. *Journal of Paleontology* 50, 858–864.

- Riding, R. 2002: Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. *Earth-Science Reviews* 58, 163–231.
- Sadler, J., Webb, G.E. & Nothdurft, L.D. 2015: Structure and palaeoenvironmental implications of inter-branch coenositeum-rich skeleton in corymbose *Acropora* species. *Coral Reefs* 34, 201–213.
- Sanders, D. & Baron-Szabo, R.C. 2005: Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeography, Palaeoclimatology, Palaeoecology* 216, 139–181.
- Scrutton, C.T. 1997: The Palaeozoic corals, I: origins and relationships. *Proceedings of the Yorkshire Geological Society* 51, 177–208.
- Scrutton, C.T. 1998: The Palaeozoic corals, II: structure, variation and palaeoecology. *Proceedings of the Yorkshire Geological Society* 52, 1–57.
- Scrutton, C.T. 1999: Palaeozoic corals: their evolution and palaeoecology. *Geology Today* 15, 184–193.
- Scrutton, C.T. & Powell, J.H. 1980: Periodic development of dimorphism in some favositid corals. *Acta Palaeontologica Polonica* 25, 477–491.
- Seilacher, A. & Thomas, R.D.K. 2012: Self-organization and emergent individuality of favositid corals adapted to live on soft substrates. *Lethaia* 45, 2–13.
- Sokolov, B.S. 1962: Subclass Tabulata. Subclass Heliolitoidea. In Orlov, J.A. (ed.), *Foundations of Paleontology. Sponges, Archaeocyatha, Coelenterates, Vermes*. Izdatel'stvo Akademii nauk, Moscow, 192–285.
- Stafford-Smith, M.G. 1993: Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology* 115, 229–243.
- Stafford-Smith, M.G. & Ormond, R.F.G. 1992: Sediment-rejection mechanisms of 42 species of Australian Scleractinian corals. *Australian Journal of Marine and Freshwater Research* 43, 683–705.
- Stampfli, G.M., Hochard, C., Vérard, C., Wilhem, C. & von Rauher, J. 2013: The formation of Pangea. *Tectonophysics* 593, 1–19.
- Stanley, G.D. Jr & Helmle, K.P. 2010: Middle Triassic coral growth bands and their implication for photosymbiosis. *Palaios* 25, 754–763.
- Stanley, G.D. Jr & Lipps, J.H. 2011: Photosymbiosis: the driving force for reef success and failure. *Paleontological Society Papers* 17, 33–60.
- Stasińska, A. 1958: Tabulata, Heliolitida et Chaetetida du dévonien moyen des Monts de Sainte-Croix. *Acta Palaeontologica Polonica* 3, 161–282.
- Stearn, C.W. 1982: The shapes of Paleozoic and modern reef-builders: a critical review. *Paleobiology* 8, 228–241.
- Tapanila, L. 2008: Direct evidence of ancient symbiosis using trace fossils. In Kelley, P.H. & Bambach, R.K. (eds): *From Evolution to Geobiology: Research Questions Driving Paleontology at the Start of a New Century*, Paleontological Society Short Course, October 4, 2008. *The Paleontological Society Papers* 14, 19–35.
- Todd, P.A. 2008: Morphological plasticity in scleractinian corals. *Biological Reviews* 83, 315–337.
- Tsien, H.H. 1971: The middle and upper Devonian Reef-complexes of Belgium. *Petroleum Geology of Taiwan* 8, 119–173.
- Tsien, H.H. 1977: Morphology et developments of Devonian reefs and reef-complexes in Belgium. In *Proceedings of the 3rd International Coral Reef Symposium, Miami, Florida*, 191–200.
- Tsien, H.H. 1979: Paleoecology of algal-bearing facies in the Devonian (Couvian to Frasnian) reef complexes of Belgium. *Palaeogeography, Palaeoclimatology, Palaeoecology* 27, 103–127.
- Tsien, H.H. 1980: Les régimes récifaux dévoniens en Ardenne. *Bulletin de la Société belge de Géologie* 89, 71–102.
- Vacelet, J., Willenz, P. & Hartman, W.D. 2010: Living hypercalcified sponges. *Treatise Online Part E, Revised 1*, 1–16.
- Vierek, A. 2013: The palaeogeographical background of Late Devonian storm events in the western part of the Holy Cross Mountains (Poland). *Geologos* 19, 257–272.
- Wesseling, I., Uychiaoco, A.J., Alino, P.M., Aurin, T. & Vermaat, J.E. 1999: Damage and recovery of four Philippine corals from short-term sediment burial. *Marine Ecology Progress Series* 176, 11–15.
- Witzke, B.J. 1990: Palaeoclimatic constraints for palaeozoic Palaeolatitudes of Laurentia and Euramerica. *Geological Society, London, Memoirs* 12, 57–73.
- Wood, R. 1998: The ecological evolution of reefs. *Annual Review of Ecology and Systematics* 29, 179–206.
- Young, G.A. & Elias, R.J. 1995: Latest Ordovician to Earliest Silurian Colonial Corals of the East-Central United States. *Bulletins of American Paleontology* 108(347), 1–153.
- Young, G.A. & Kershaw, S. 2005: Classification and controls of internal banding in Palaeozoic stromatoporoids and colonial corals. *Palaeontology* 48, 623–651.
- Young, G.A. & Noble, J.P.A. 1989: Variation and growth in a syringoporid symbiont species in stromatoporoids from the Silurian of eastern Canada. In Jell, P.A. & Pickett, J.W. (eds): *Fossil Cnidaria 5, Proceedings of the Fifth International Symposium on Fossil Cnidaria Including Archaeocyatha and Spongiomorphs Held in Brisbane, Queensland, Australia, 25–29 July, 1988. Association of Australasian Palaeontologists, Memoir* (8), 91–98.
- Young, G.A. & Noble, J.P.A. 1990: Silurian Proporidae and Plasmoporidae (Anthozoa, Tabulata) from the Chaleurs Bay Region, Canada. *Journal of Paleontology* 64, 184–199.
- Young, G.A. & Scrutton, C.T. 1991: Growth form in Silurian heliolitid corals: the influence of genetics and environment. *Paleobiology* 17, 369–387.
- Zapalski, M.K. 2011: Is absence of proof a proof of absence? Comments on commensalism. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302, 484–488.
- Zapalski, M.K. 2012: Tabulate coral from the Givetian and Frasnian of the southern region of the Holy Cross Mountains (Poland). *Special Papers in Palaeontology* 87, 1–100.
- Zapalski, M.K. 2014: Evidence of photosymbiosis in Palaeozoic tabulate corals. *Proceedings of the Royal Society B* 281, 20132663.
- Zapalski, M.K. & Berkowski, B. 2019: The Silurian mesophotic coral ecosystems: 430 million years of photosymbiosis. *Coral Reefs* 38, 137–147.
- Zapalski, M.K., Hubert, B.L.M., Nicollin, J.-P., Mistiaen, B. & Brice, D. 2007: The palaeobiodiversity of stromatoporoids, tabulates and brachiopods in the Devonian of the Ardennes – changes through time. *Bulletin de la Société Géologique de France* 178, 383–390.
- Zapalski, M.K., Nowicki, J., Jakubowicz, M. & Berkowski, B. 2017a: Tabulate corals across the Frasnian/Famennian boundary: architectural turnover and its possible relation to ancient photosymbiosis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487, 416–429.
- Zapalski, M.K., Wrzolek, T., Skompski, S. & Berkowski, B. 2017b: 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.