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VERSITA

The oldest species of ?*Yavorskia* (Tabulata) from the Upper Famennian of the Holy Cross Mountains (Poland)

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ABSTRACT:

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A single perfectly preserved colony of a tabulate coral assigned tentatively to the genus *Yavorskia* Fomitchev, 1931, collected from Upper Famennian beds *(Palmatolepis expansa* conodont Zone) in a trench located north of the Kowala Quarry (Holy Cross Mts., central Poland) is here described as a new species, ?*Y. paszkowskii* sp. nov. It differs from other representatives of the genus in the lack of dissepimental structures and in smaller corallite diameters, and may therefore represent the ancestral taxon of this typically early Carboniferous genus. *Yavorskia* tabulates were apparently migrating eastwards along the southern margin of Laurussia and farther east and north towards Siberia, as they appear in the Famennian in Europe and in the early Carboniferous in the Altaides. Such a conclusion is consistent with previous observations on Early–Middle Devonian pleurodictyform tabulate distribution.

Key words: Corals; Tabulata; Famennian; Holy Cross Mts.; Migrations.

INTRODUCTION

Corals, like many other groups inhabiting shelf environments by the end of the Devonian, were markedly affected by the Late Devonian extinction events at the Frasnian/Famennian boundary and at the end of the Famennian (Sorauf and Pedder, 1986; Poty 1986, 1999; Scrutton, 1988; Sorauf, 1989; Oliver and Pedder, 1994; Berkowski 2001, 2002; Zapalski *et al.* 2007; Hubert *et al*. 2007). These events led to a significant reconstitution of the coral communities and were mainly responsible for the large differences between pre-Famennian and Carboniferous corals. Of the two major groups of Palaeozoic corals, i.e. the Rugosa and Tabulata, the latter, exclusively colonial, lost 80 to 92% of their genera by the end of the late Famennian extinction event (Scrutton 1988, 1997; McGhee 1996). The process of recovery (the so-called Strunian radiation of Poty 1986, 1999 and Berkowski 1996, 1997, 2001, 2002) took place by the end of the Famennian in relatively shallower environments and was manifested mostly by a rapid increase in the diversity of solitary dissepimented rugosan taxa (Poty 1999; Berkowski 2002). Famennian corals include a few earlier taxa and a few which extend into the Carboniferous; however, many of the taxa present are restricted to this stage. On the other hand, Famennian colonial taxa, both rugosan and tabulate, are extremely rare in the fossil record (Scrutton 1988, 1997; Berkowski 2001, 2002; Hubert *et al.* 2007; Zapalski *et al*. 2007). The data on Famennian tabulates are especially scarce and very few tabulate taxa were involved

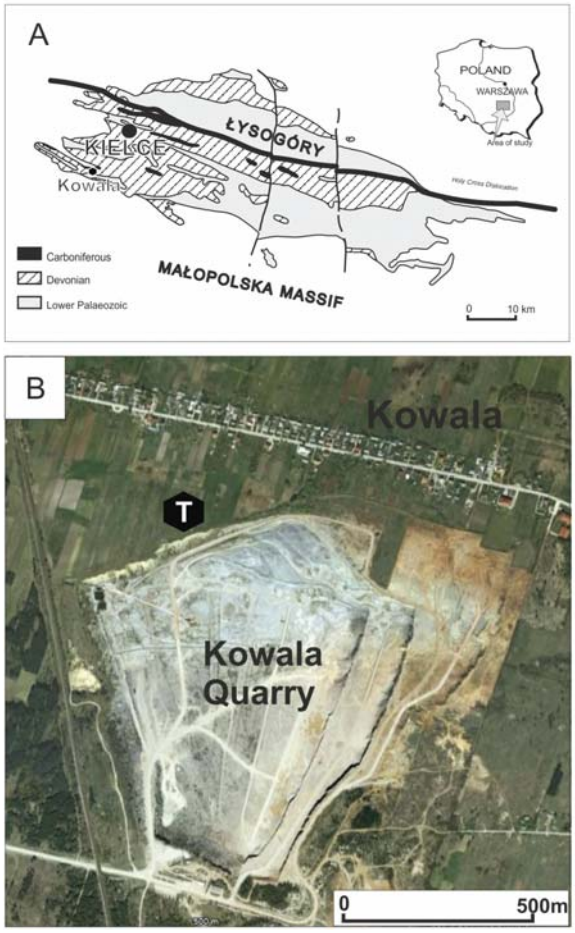
in the Famennian recovery. In most places where tabulates occur, the diversity at generic and specific level is usually extremely low (in Ardennes: 42 species in the Frasnian *vs.* 4 in the Famennian; Hubert *et al.* 2007; Zapalski *et al*. 2007).

Here we present a new species tentatively assigned to the genus *Yavorskia* from the Famennian of the Holy Cross Mountains which, according to the present data seems to be the oldest representative of this massive, favositid tabulate genus.

GEOLOGICAL SETTING

The studied corallum was collected by Dr. Mariusz Paszkowski (Institute of Geological Sciences, Polish Academy of Sciences, Cracow) from the upper Famennian strata exposed in the trench (now buried) that was prepared for the XIII International Congress on the Carboniferous–Permian held in Cracow in 1995. Several trenches were located north of the Kowala (formerly Wola) quarry in fields south of the village of Kowala, about 10 km SW from the city of Kielce (Text-fig. 1A, B). The study area is situated in the southern (or Kielce) Region of the Holy Cross Mountains within the Małopolska Massif (Text-fig. 1A). The beds exposed in the Kowala quarry range in age from Frasnian (Late Devonian) to earliest Tournaisian (Early Carboniferous). Szulczewski (1995) and Berkowski (2002) subdivided the succession into twelve informal lithological sets A–L, described by Szulczewski (1971, 1995) and Berkowski (1990, 1991). The Frasnian part of the section yielded abundant tabulate corals (Nowiński 1992; Zapalski 2012; Zapalski *et al.* 2012), but up to now tabulate corals have never been described from the Famennian part. Malec (1995), Dzik (1997, 2006), Olempska (1997), and Marynowski and Filipiak (2007) provided supplementary data on the uppermost part of the succession, formerly known only from trenches, but since 1999 also exposed in the quarry as quarrying activity progressed.

The corallum was found in the distinctly bedded pelitic and partly nodular olive-green marly limestone (lower part of the lithological set L of Berkowski 1990, 1991, 2002 and Szulczewski 1995). The upper part of this set corresponds to the lithological set ("complex") A *sensu* Malec 1995 and Marynowski and Filipiak 2007, which is assigned to the Early *Palmatolepis expansa* to *Siphonodella praesulcata* conodont zones (Malec 1995; Olempska 1997). The Famennian part of the succession yielded abundant cephalopods (Czarnocki 1989; Dzik 2006) and a much rarer benthic fauna (e.g., rugose corals: Różkowska



Text-fig. 1. Simplified geological map of the Palaeozoic of the Holy Cross Mountains (after Szulczewski 1971 with village of Kowala indicated. B. Satellite aerial view of Kowala and the Kowala quarry (from Google Maps: http://maps.google.com). The locality of the trench is indicated as "T" in hexagon, north of the quarry

1969; Berkowski 2002; brachiopods: Halamski and Baliński 2009; and trilobites: Berkowski 1991; Radwański *et al*. 2009).

MATERIAL AND METHODS

Three large thin sections have been prepared from the single available corallum. Basic biometrical studies were carried out (corallite diameters, wall thicknesses, pore diameters and spacing of tabulae). The coefficient of variation (*V*) is a unitless measure of dispersion and allows comparisons of values having different ranges (e.g., Simpson *et al*. 1960; Young and Elias 1995). It was calculated for each biometrical character in order to investigate intracolonial variation, similarly as in previous studies on tabulate corals (see Zapalski 2012 for a detailed discussion on methods):

V = standard deviation/mean

The specimen is housed at the Institute of Geology of the Adam Mickiewicz University, Poznań, Poland, under the repository number UAM/Tb-B/1/1.

SYSTEMATIC PALAEONTOLOGY

Order: Favositida Dana, 1846
Family: Cleistoporidae Easton, 1944
Genus: *Yavorskia* Fomitchev, 1931

TYPE SPECIES: *Yavorskia barsaensis* Fomitchev, 1931

?*Yavorskia paszkowskii* sp. nov.
(Text-figs 2, 3)

HOLOTYPE: UAM/Tb-B/1/1, three thin sections, and remaining half of the corallum.

DERIVATION OF THE NAME: In honour of Dr. Mariusz Paszkowski (Institute of Geological Sciences, Polish Academy of Sciences, Cracow), who collected the specimen.

TYPE LOCALITY: Trenches (now buried) situated north of the northern wall of the Kowala Quarry, Kowala village, Holy Cross Mountains, Poland.

TYPE STRATUM: Lithostratigraphic complex L (*sensu* Szulczewski 1995; Berkowski 2002), *Palmatolepis expansa* conodont Zone, Famennian, Late Devonian.

DIAGNOSIS: Corallum discoidal. Corallites polygonal, measuring (mean) 5.7 × 6.4 mm. Walls very thin, uneven, spongy, with median line visible; double wall thickness 0.41 ± 0.11 mm. Connecting pores numerous, 0.19 ± 0.05 mm in diameter, often surrounded by septal spines. Septal spines variously shaped, irregularly distributed. Tabulae complete or incomplete, numerous.

MATERIAL: One perfectly preserved, complete colony (holotype). One longitudinal thin section (across the whole colony) and two transverse thin sections.

DESCRIPTION: Corallum discoidal, flattened, measuring about 100 × 100 mm in diameter and 35 mm in thickness (Text-fig. 2). Calyces shallow, polygonal, 6- to 8- sided (Text-figs 2B, 3A), most often with flat bottoms, rarely with slightly convex axial parts of corallites; in a few corallites with a button-like structure in the centre (tabulae strongly convex in the central part). Edges of calyces crenulated, with wall junctions slightly raised over the adjoining walls. Corallites long, polygonal and slightly elongated in cross section. Tabulae slightly convex, most often complete (Text-fig. 2A), frequently suspended on septal spines (Text-fig. 3B). In certain horizontal zones tabulae incomplete, strongly convex, often forming a vesicle on complete tabulate, forming very faint cyclomorphic bands. Walls thin, strongly uneven, with skinny, spongy stereoplasma. Median line nearly black, clearly visible in most places. Septal spines abundant, irregular, usually short. They may end sharply or bluntly, in some cases bifurcating (Text-fig. 3C). They are distributed irregularly. Connecting pores numerous, irregularly distributed, often surrounded by small septal spines, frequently bifunnel shaped or irregularly developed lumen (Text-fig. 3D). Biometrical data are given in Table 1.

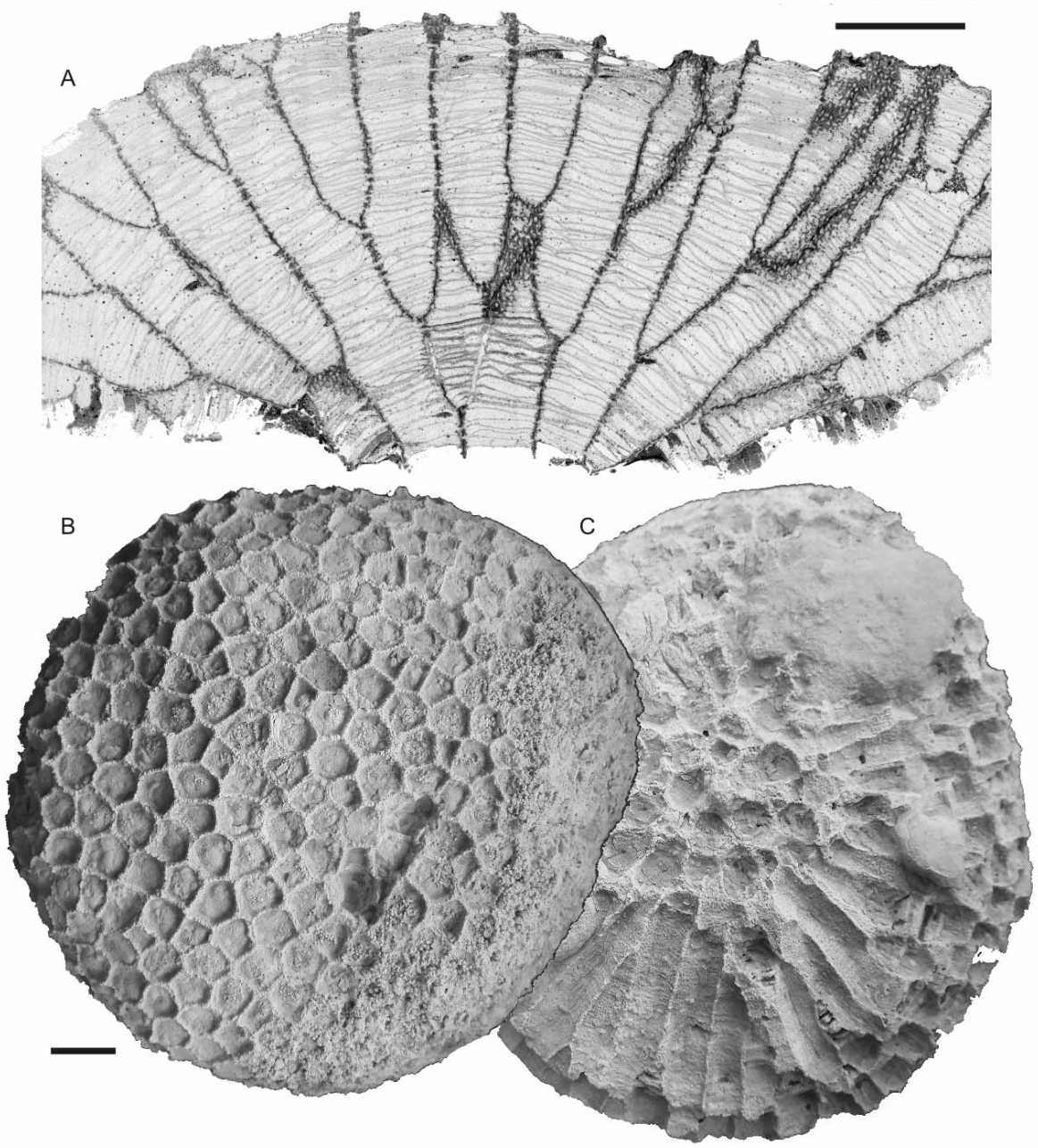
Intracolonial variation: The corallite diameters are rather constant, like those of some heliolitids (*V*~0.1; Mõtus 2006), rather than those of *Alveolites* (Favositida, Alveolitina) or *Avicenia* (Heliolitida); in these genera the *V* values for the corallum diameter are usually between 0.1 and 0.2 (Zapalski 2012; Zapalski and Nowiński 2011). In contrast, the changes in tabulae

	Maximum corallite diameter	Minimum corallite diameter	Double wall thickness	Pore diameter	Tabulae spacing
mean [mm]	6.43	5.69	0.41	0.19	0.51
standard dev. [mm]	0.63	0.50	0.11	0.05	0.30
N	12	12	34	24	57
minimum value [mm]	5.0	4.9	0.25	0.13	0.13
maximum value[mm]	7.0	6.3	0.73	0.30	1.13
V	0.10	0.09	0.27	0.26	0.59

Table 1. Intracolonial variation of the holotype of ?*Yavorskia paszkowskii* sp. nov.

spacing are very large and the *V* value close to 0.6 resembles alveolitids from the Ardennes and the Frasnian part of the Kowala section (Zapalski 2012). The double wall thickness variation is similar, while pore diameters are more constant as compared to alveolitids (Zapalski 2012). The intracolonial variation in other species of *Yavorskia* has never been studied, hence comparison with closely related taxa is not possible.

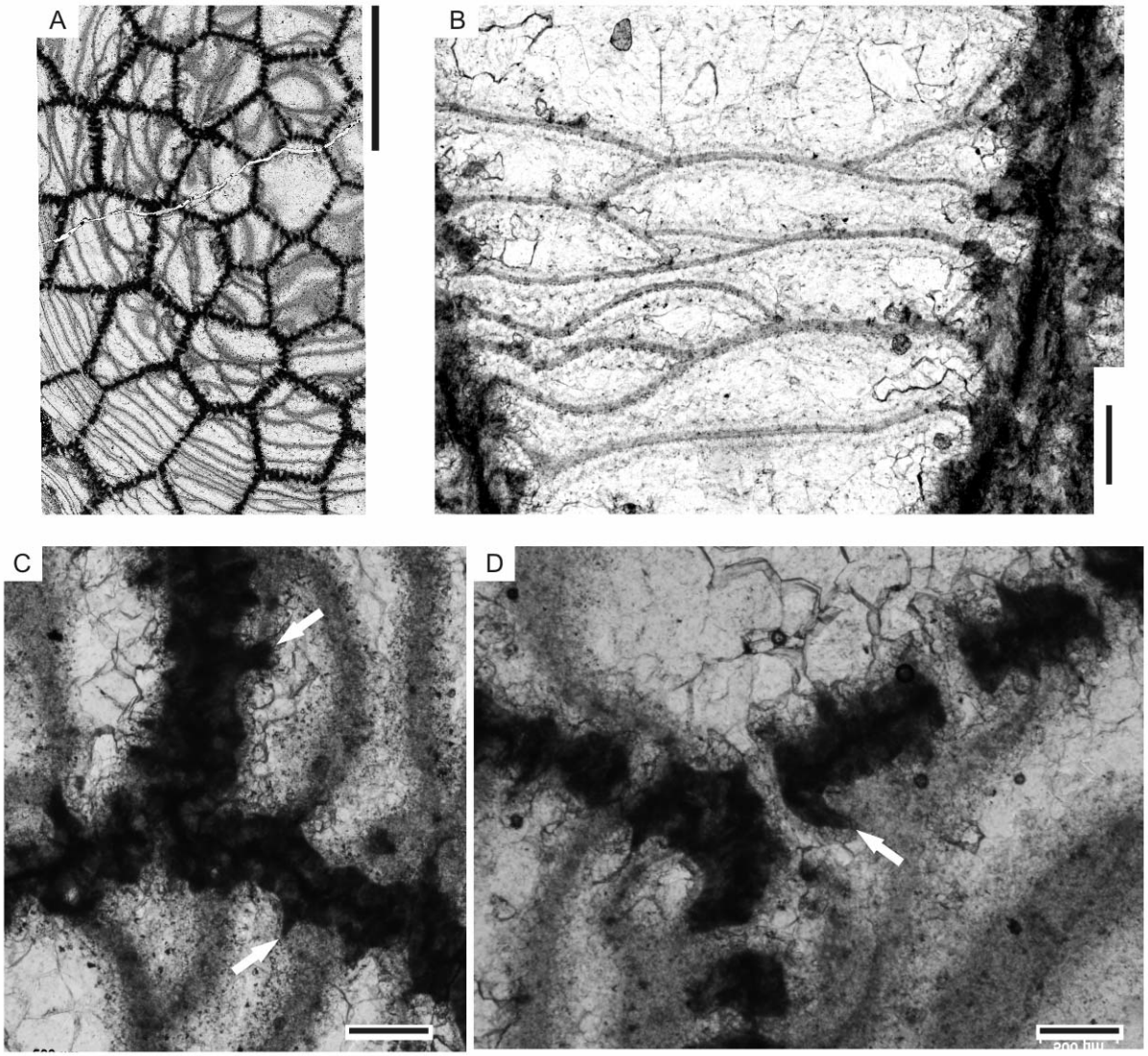
COMPARISON WITH OTHER SPECIES: The specimen investigated here can be tentatively assigned to genus *Yavorskia* on the basis of the cerioidal structure of the corallum, the spongy wall structure, and the numerous tabulae. However, the new species lacks tabellae (dissepimental tissue) near the walls. The genus *Yavorskia* consists of four or five species:
Yavorskia barsaensis Fomitchev, 1931 (Lower Carboniferous of the Kuznetsk Basin, Russia),



Text-fig 2. *Yavorskia paszkowskii* sp. nov., holotype; specimen UAM/Tb-B/1/1. Famennian, lower part of the lithological set L, most probably *P. expansa* conodont Zone, Kowala, Holy Cross Mountains, Poland. A – Longitudinal section through corallum. Note spongy structure of the wall on tangential section through the wall in the right part of the picture. B – Upper surface of the corallum, C – lower surface of the corallum. Scale bar 10 mm, the same for B and C

Yavorskia borealis Gorsky, 1938a (Tournaisian of Novaya Zemlya, Russia),
Yavorskia sp. *sensu* Zapalski *et al.* 2008 (upper Famennian of Étroeungt, France),
?*Yavorskia paszkowskii* sp. nov. (upper Famennian of the Holy Cross Mountains),
and possibly also "*Yavorskia borealis* var. *minor* Gorsky, 1938b" (lower Tournaisian of Novaya Zemlya). Since the original descriptions of Fomitchev (1931) and Gorsky (1938a), the Russian species have never been redescribed and therefore biometrical comparisons are difficult. These authors did not state whether the values they give are mean values or the most often occurring values; finally, they did not give the precise ranges of the values.

The new species differs from most of other species of the genus *Yavorskia* in the absence of dissepimental tissue (tabellae) adhering to the wall. Besides the lack of dissepimental tissue, the new species differs from the type species, *Yavorskia barsaensis* Fomitchev, 1931 in smaller corallite diameters (mean 10 mm in *Y. barsaensis*; Fomitchev, 1931 compared to 5.7–6.4 mm in the new species). Another species, *Yavorskia borealis* Gorsky, 1938a has much larger corallite diameters (up to 12 mm) and thinner walls with poorly developed spongy structures (however, Gorsky, 1938a did not provide biometric data on the wall thickness). The drawing of *Y. borealis* (Gorsky 1938a, text-fig. 1) shows that, besides the presence of tabellae, the tabulae are more convex, with



Text-fig 3. *Yavorskia paszkowskii* sp. nov., holotype; specimen UAM/Tb-B/1/1. Famennian, lower part of the lithological set L, most probably *P. expansa* conodont Zone, Kowala, Holy Cross Mountains, Poland. A – Cross section through the corallum. Note the absence of dissepimental structures adhering to the wall. Scale bar 10 mm. B – Longitudinal section through a corallite, showing incomplete tabulae. C – Cross section through a wall junction. Arrows show two distinct types of septal spines. D – Cross section through wall. Arrow shows septal spine placed next to the connecting pore. Connecting pores are variable in shape. Scale bar for B–D 500 μm

Species/feature	Corallite diameter	Dissepimental tissue (tabellae)	Age
?*Yavorskia paszkowskii* sp. nov.	5–7 mm	absent	Famennian
Y. barsaensis	10 mm	present	L. Carboniferous
Y. borealis	up to 12 mm	present	Tournasian
"Y. borealis var. *minor"*	6–7 mm	present	Tournasian
Y. sp.	10 mm	present	Famennian

Table 2. Comparison of biometry, diagnostic features and age of different *Yavorskia* species

a complicated border visible in cross sections. The specimen described by Gorsky as "*Yavorskia borealis* var. *minor*" (Gorsky 1938b), has corallites similar in size to those of ?*Yavorskia paszkowskii* sp. nov., but differs in that dissepimental tissue is present. The new species differs from *Yavorskia* sp. from the Strunian of Étroeungt (Zapalski *et al.* 2008) in smaller corallite diameters (in *Yavorskia* sp. the corallite diameters are close to 10 mm). Comparison is given in the table below (Table 2).

DISCUSSION

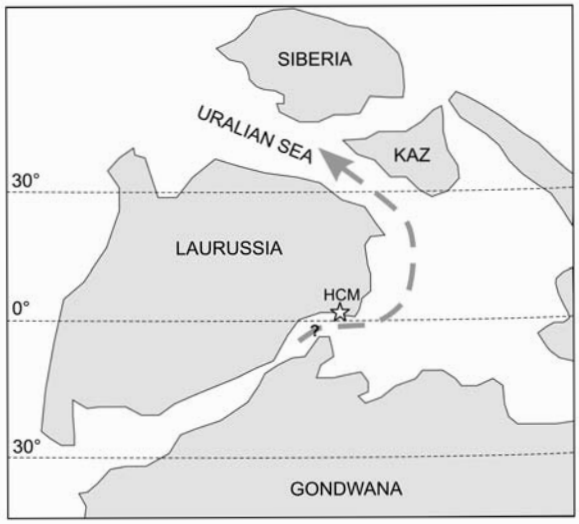
The new species differs from all other *Yavorskia* species in the absence of dissepimental tissue (tabellae). According to Hill (1981), the presence of this feature is diagnostic of the genus. The investigated specimen may therefore belong to a new genus, but a single specimen does not enable evaluation of the taxonomic value of dissepimental tissue in this group of tabulates. The new species is also similar to *Cleistopora,* from which it differs in the absence of reticulate tissue in the corallites.

Most representatives of *Yavorskia* described so far have been found in the Lower Carboniferous (Gorsky 1938a, b; Fomichev, 1931); however, this genus is also typical of the "Strunian" facies in its type locality (Étroeungt in the Ardennes; Hubert *et al.* 2007; Zapalski *et al.* 2007). Late Devonian *Yavorskia* are known from the west Ardennes, Belgium/France but these specimens were not described (see Zapalski *et al.* 2008).

?*Yavorskia paszkowskii* sp. nov. was found in marly limestones representing deeper environments than those typical of late Famennian "Strunian" faunas (Poty 1999; Berkowski 2002). These beds contain small solitary rugose corals (*Friedbergia, Nalivkinella*), bryozoans, brachiopods, clymeniids and goniatites (Berkowski 2002, p. 8). This environment was deep water, probably below the photic zone (Halamski and Baliński 2009).

The "Strunian" facies in the western Ardennes is coeval (*P. expansa–S. praesulcata* conodont Zones, Thorez *et al.* 2006; Streel *et al*. 2006) with the lithological set L of Kowala (the new species comes from the lower part of this complex, thus most probably from the *P. expansa* Zone). However, the Étroeungt limestone is thick and the stratigraphical horizon of the *Yavorskia* was not recorded. It appears that there may be an evolutionary trend in representatives of this genus from a simple morphology (lack of dissepimenta) to more complex (abundant dissepimenta, see Hill 1981), and from smaller to larger corallite diameters, as evidenced by the corallites of the Carboniferous species, which are all larger than those of ?*Y. paszkowskii* sp. nov. However, it must be kept in mind that it is not clear whether the specimens of *Yavorskia* from the Étroeungt Limestone are younger than the new species from Kowala. Moreover, for precise description of evolutionary trends within this group a revision of the Russian species would be necessary.

Representatives of *Yavorskia* appear in the Famennian on the southern margin of Laurussia, while in



Text-fig 4. Possible pathways of *Yavorskia* tabulates migrations plotted on the Early Carboniferous palaeogeography (after Scotese and McKerrow 1990, simplified). Asterisk marks the Holy Cross Mountains (HCM), where ?*Yavorskia paszkowskii* sp. nov. was found. *Yavorskia* tabulates appear on the southern margin of Laurussia in the Famennian, and in Novaya Zemlya and Kuzbas in the Early Carboniferous, so these faunas probably migrated east and later northwards. The east-west migrations on the S margin of Laurussia are not revealed (question mark). KAZ – Kazakhstania

the early Carboniferous they appear east of the Uralian Sea (in the present-day Kuzbas in the Altaides). It can therefore be presumed that the routes of larval dispersal were situated along the southern margin of Laurussia on an E-W axis, and later across the Uralian Sea towards Siberia and Kazakhstania (Text-fig. 4). Such a conclusion is consistent with observations on the late Famennian cerioid rugosan genus *Pseudoendophyllum* (Berkowski 2001, 2002) and the slightly older (Early–Middle Devonian) pleurodictyiform tabulates (Plusquellec 2007). Due to the imprecise stratigraphic positioning of the Étroeungt Limestone specimens (Zapalski *et al*. 2008) it is not possible to state whether the migrations were eastwards and westwards from the present-day Holy Cross Mountains, as was probably the case with the pleurodictyform tabulates (Plusquellec 2007), or from the Ardennes westwards.

CONCLUSIONS

The new species, ?*Yavorskia paszkowskii* sp. nov., occurs in the upper Famennian of the Holy Cross Mountains. It is probably the oldest known *Yavorskia*, differing from other species of this genus in the lack of dissepimental tissue and in smaller corallite diameters. Due to the lack of dissepimental tissue the new species may be regarded as ancestral to Carboniferous members of the genus. The presence of *Yavorskia* in the Famennian of Europe and in the Lower Carboniferous of Novaya Zemlya and Kuzbas suggests that the migration routes of these corals were from the southern margin of Laurussia towards the Uralian Sea.

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