

Coexistence of algae and a graptolite-like problematicum: a case study from the late Silurian of Podolia (Ukraine)

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ABSTRACT:

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This contribution presents the record of an abundant assemblage of well-preserved, thallophytic noncalcified algae and of an epibiotic form that has been recognised as a putative graptolite from the upper Silurian (Ludlow, Gorstian–Ludfordian) of Podolia (western part of Ukraine). The sediments represent a shallow peritidal zone of the shelf. A new genus and species, *Voronocladus dryganti*, belonging to the Dasycladales Pascher, 1931, is established. Most of the specimens representing the algal thallus are overgrown by problematical epibiotic graptolites, described as *Podoliagraptus algaeoides* gen. et sp. nov. This phenomenon is explained as an epiphytic mode of life of the putative graptolite on algae, and is herein compared to recently known coexistences of algae with other organisms. The excellent state of preservation, and the abundance of studied Dasycladales algae and epibiotic problematics indicate that the investigated mudstone layer can be treated as a ‘Konservat Lagerstätte’ *sensu* Seilacher (1970).

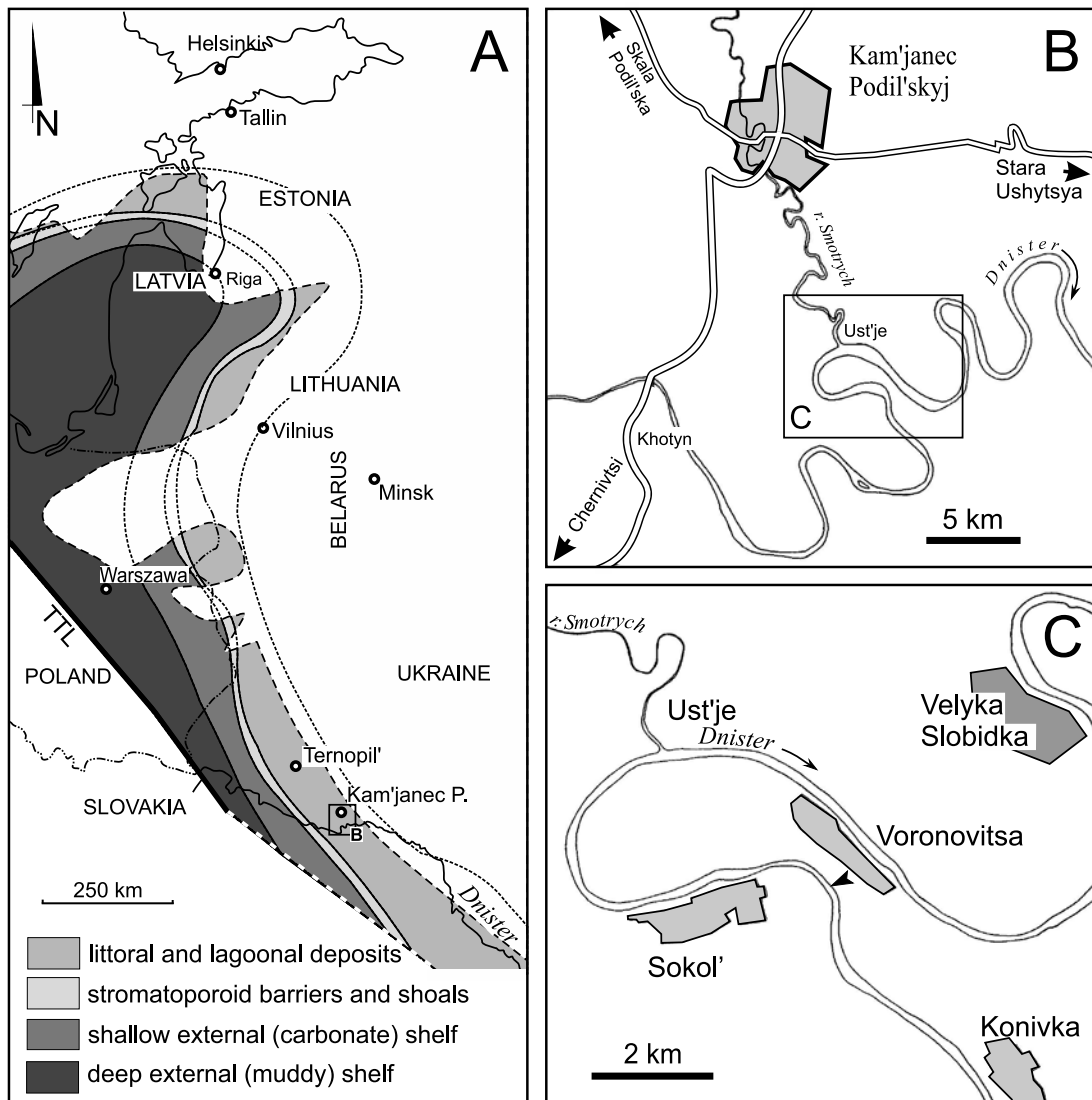
Key words: Dasycladales; Graptolite-like epibionts; Silurian; Ludlow; Ukraine; Peritidal environment.

INTRODUCTION

Calcified members of the Order Dasycladales Pascher, 1931 are well-known in the fossil record. Their calcareous sleeve enhances their fossilisation potential, as well as their palaeoecologic, stratigraphic and rock-forming significance (Berger and Kaever 1992; Vachard 2021). The findings of noncalcified specimens are rare and are mostly linked with the Ordovician and Silurian successions of Laurentia (e.g., LoDuca *et al.* 2013, 2017; LoDuca 2019). In the last twenty years, however, numerous new records have been reported also from the shelves of Baltica (e.g., Kenrick and Vinther 2006; Mastik and Tinn 2015; Tinn *et al.* 2015; Pettersson *et al.* 2020).

A common feature of most of these ‘algal Lager-

stätten’ is the concomitance of thallophytic algae with benthic graptolites (living separately), with at the same time a distinct impoverishment of other fossils (Ruedemann 1925; LoDuca 1990; LoDuca and Brett 1997; LoDuca *et al.* 2003, 2013). There is an apparent similarity between some benthic graptolites and algae that are preserved on rock surfaces, which usually causes some difficulties in their taxonomical recognition. In numerous cases in the past, the remnants of algae have been described as graptolites and *vice versa*. For instance, the genus *Medusaegraptus* Ruedemann, 1925 was described as a graptolite, but after a long debate (Bulman 1955; Bouček 1957) it has been placed among the noncalcified dasycladalean algae (LoDuca 1990). Although the common appearance of noncalcified algae and benthic graptolites is



Text-fig. 1. Location of the study area. A – Distribution of upper Silurian facies along the margin of the East European Craton (after Einasto *et al.* 1986, simplified; TTL stands for the Teisseyre-Tornquist Line); B – location of the study area with regard to Kam'janec Podil'skyj; C – location of section studied (arrowed).

clearly visible and underlined in numerous papers (e.g., LoDuca 1990, 1995; LoDuca *et al.* 2011; Bykova *et al.* 2020), the relationship between these forms is ambiguous.

During investigations carried out at an exposure of the upper Silurian in Voronovitsa village, south of Kam'janec Podil'skij (Podolia, Ukraine) along the Dnister river (Text-fig. 1), a thin layer of marly shales with extremely abundant assemblages of coalified fossils has been found. The main fossils belong to the Order Dasycladales. The algal specimens are frequently overgrown by problematical forms similar to graptolites. The objective of the present paper is

twofold. Firstly, we investigate details of the algal specimens and their taxonomy. Secondly, we try to explain the relationships, likely epiphytic, between the algae and the problematical graptolite-like forms. We also discuss the abundance of specimens, their excellent state of preservation, and the unique composition of the assemblage in the context of treating the mudstone layer as a 'Konservat Lagerstätte' *sensu* Seilacher (1970).

All investigated specimens are housed at the S.J. Thugutt Geological Museum, Faculty of Geology, University of Warsaw, under the collection number MWG ZI/110.

STRATIGRAPHIC AND SEDIMENTARY INTERPRETATION OF THE VORONOVITSA SECTION

In the up to 30 m high banks of the Dnister river and its tributaries, between the Ternava tributary to the east, and Dnestrove village to the west, a carbonate succession of the Silurian (Wenlock–Pridoli), typical of the southern margin of Baltica, is well exposed (Nikiforova and Predtechenskij 1968; Tsegelnyuk *et al.* 1983; Drygant 1984; Koren' *et al.* 1989). The several hundred metres thick Podolian section is characterised by a diverse spectrum of carbonate facies (Einasto *et al.* 1986; Skompski *et al.* 2008). The outer shelf facies are usually developed as nodular, fossiliferous wackestones/packstones or stromatoporoid-crinoid biohermal facies. The shallow-water facies, typical of peritidal or lagoonal environments, are dominated by laminites and dolomicrites with thick intercalations of stromatoporoid-rich beds (Abushik *et al.* 1985). In the entire succession, three large 1st order cyclothems can be distinguished; two of them (older) shallowing upward, and the youngest, with a transition from the Silurian to the Devonian, deepening upward (Predtechenskij *et al.* 1983). 2nd and 3rd order sedimentary cycles can be distinguished within each of these cyclothems.

The investigated part of the Silurian section is located on the right bank of the Dnister, between Konivka and Voronovitsa villages, south of Kam'janec Podil'skij (Text-fig. 1). The described algal-graptolitic assemblage has been found in a very thin (5–10 cm) layer of marly shales (X in Text-fig. 2A), occurring 2 m above the top of a bioherm, which is visible just above river level (Text-fig. 2B). The broader stratigraphic and facies context of the discussed profile was presented in detail in an earlier work by Łuczyński *et al.* (2015), in which the exposed succession was interpreted in terms of sedimentology and stratigraphy. The studied section is indicated there as the Voronovitsa-reef (3), and was illustrated in text-fig. 4 therein.

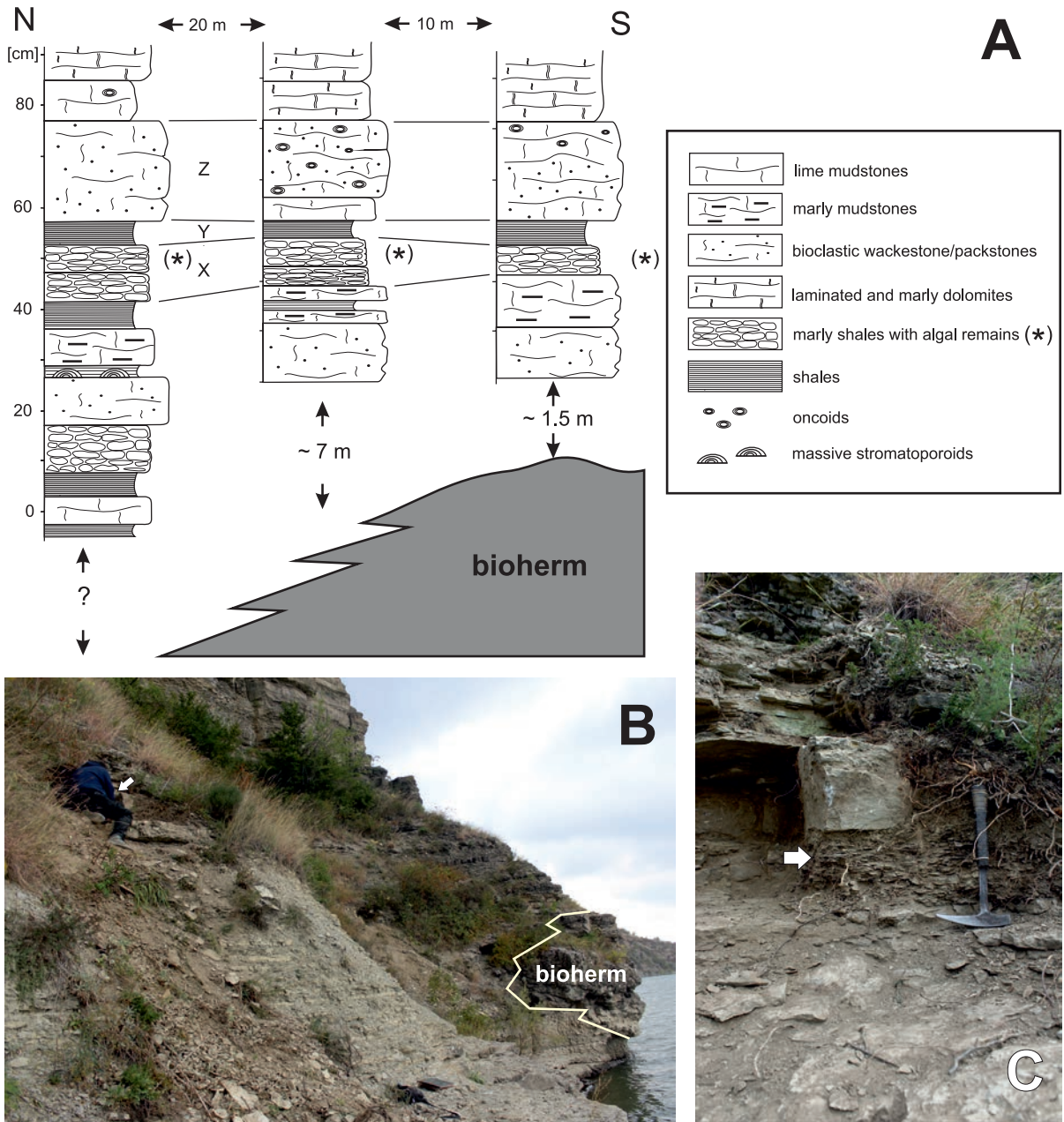
Strict identification of the chronostratigraphic position of the algal bed is impossible due to lack of a precise biostratigraphy. It has been ascribed here to the topmost part of the Goloskov Subformation, just below its boundary with the Shutnovtsy Subformation (subsuite in the original description) of the Konivka Formation (Text-fig. 3). The Goloskov Member (9 to 13 m thick) crops out along the Dnister river between Ustje and Konivka villages, and is developed as clayey nodular limestones and marls with stromatoporoid-coral-algal bioherms, up to 4.5 m thick (Tsegelnyuk *et al.* 1983). The Shutnovtsy Subformation usually contains

characteristic wavy-bedded, fine-grained limestones and two beds of volcanic ash (M0 and M1 according to Tsegelnyuk *et al.* 1983; Huff *et al.* 2000). However, near Konivka, the 11–12 m thick complex is developed as lagoonal dolomites and dolomitic marls.

Based on the fossil assemblage, the Konivka Formation correlates with the middle part of the Hemse Beds on Gotland, and with the Leintwardine Formation of Great Britain (Tsegelnyuk *et al.* 1983; Koren' *et al.* 1989). According to Jarochowska *et al.* (2016), the Konivka Formation equates with the lower part of the Gorstian Stage of the Ludlow, but this opinion is based only on the similarity of the brachiopod fauna of the Goloskov Subformation to that of the Lower Elton Formation of the Midland Platform in England. However, according to Drygant (1984), the investigated Voronovitsa section contains conodonts indicating the *Kockella variabilis*–*Ancoradella ploekensis*–*Polygnathoides siluricus* zones (middle Gorstian–lower Ludfordian), and this interpretation is adopted here.

Against the background of the Silurian environmental succession of Podolia, the transition from the Goloskov to the Shutnovtsy Subformation records a prominent regressive event in the facies record. Its position corresponds to a regressive episode between the 6th and 7th Silurian transgressive peaks, which occurs at the Gorstian–Ludfordian boundary (Johnson 2006). This event may be correlated with the Linde Event (Jeppsson and Aldridge 2000) or with the Kuppen-Snabben unconformity on Gotland (Taromi Sandström *et al.* 2021).

In the investigated layer of marly shales with the algal assemblage, other fossils are rare and dominated by leperditicopid arthropods, *Campylites*-type tubes, bivalves, relatively numerous gastropods, and rare fragments of eurypterids. The layer is best traceable in the vicinity of a bioherm (for precise location see Łuczyński *et al.* 2015; Text-fig. 2A, B herein), and several tens of meters south and north of it. To the north (offshore direction), the layer becomes more marly and grey, and passes into grey bioclastic limestones with trilobites and the brachiopods *Camarotoechia* spp., while gastropods disappear. To the south, the equivalent of the layer is more dolomitic, and the abundance of gastropods, leperditicopids and algae is evidently smaller. The marly shales layer is overlain by a several centimetres thick intercalation of black shales (layer Y in Text-fig. 2A), with rare fossils: leperditicopid arthropods, bivalves and *Campylites*-type tubes. A significant feature of layers X and Y is a 10-fold enrichment of thorium in the clay component (Łuczyński *et al.* 2015), which may indicate that the



Text-fig. 2. Geology of the Voronovitsa section. A – detailed lithology; B – general position of layer with algal assemblage (arrowed) in relation to the bioherm; C – close-up view of layer with algal assemblage (arrowed); X, Y, Z – symbols of layers described in text.

marly-clay interval is composed of residual clays derived from dissected palaeosol covers, exposed on the nearby land areas.

The part of the Voronovitsa section described above is interpreted as representing a shallowing-upward succession, which started with sedimentation in a shallow subtidal zone of the shelf (bioclastic packstones and lime mudstones with stromatoporoids), followed by fast regression, up to final

emersion (black shales). In this context, the layer with the algal assemblage (X in Text-fig. 2A) is characteristic of tidal flat deposition, with an evidently slowed down production of carbonates, due to emersion of a carbonate platform and its chemical weathering. The sedimentation of the black clays (Y in Text-fig. 2A) probably took place in a small embayment of an emerged platform. The existence of such embayments or residual ponds has been proposed in

Series	Stage	Lithostratigraphy		Cyclothems		
		Formation	Subfm.	meso- deep	shallow	macro-
Ludlow	Ludfordian	Malynivtsy Group	Rykhtha	Isakovtsy	[Cyclothem pattern]	[Cyclothem pattern]
				Hrynchuk		
	?		Tsvikleivtsy	Bernovo	[Cyclothem pattern]	[Cyclothem pattern]
				Sokol		
	Constanian		Konivka	Shutnovtsy	[Cyclothem pattern]	[Cyclothem pattern]
				Goloskov		
	Homerian		Bahovytsya	Ust'je	[Cyclothem pattern]	[Cyclothem pattern]
				Muksha		

Text-fig. 3. Simplified stratigraphic scheme of the Podolian Ludlow. Lithostratigraphy and chronostratigraphic correlation after Tsegelnjuk *et al.* (1983), Drygant (1984), Koren' *et al.* (1989) and Racki *et al.* (2012), with changes proposed by Jarochovska *et al.* (2016); cyclothem interpretation after Predtechenskij *et al.* (1983). Stratigraphic position of the studied sections indicated by grey bar.

Subfm. stands for subformation.

our earlier paper devoted to peritidal sedimentation on the Silurian tidal flats of Podolia (see text-fig. 11 in Skompski *et al.* 2008), based on observations carried out in a more or less time equivalent section of the Zubravka Quarry near Kam'janec Podil'skij (Łuczyński *et al.* 2009).

The early transgressive part of the observed succession starts with a member characterised by Łuczyński *et al.* (2015) as the lowermost part of the 'laminated dolomite complex'. In the here discussed localities, it is represented by early diagenetic dolomites and micritic limestones with oncolites (Z in Text-fig. 2A). A microfacies of bioclastic grainstones with conspicuous blocky cementation (shelter porosity) is characteristic of this part of the succession, and is interpreted here as a tempestitic deposit. In some other nearby outcrops, this interval is developed in the form of large scale calcirudites with bioclastic and lithoclastic components, formed by destruction of carbonate laminites or micritic deposits during high-dynamic sedimentary episodes (storms, hurricanes). Łuczyński *et al.* (2015) interpreted this part of the complex as deposited during a 'reflooding window' *sensu* Jorry *et al.* (2010).

SYSTEMATIC PALAEONTOLOGY

Order Dasycladales Pascher, 1931

Family Triploporellaceae Berger and Kaeffer, 1992
emend. LoDuca, 1997

Genus *Voronocladus* gen. nov.

TYPE SPECIES: *Voronocladus dryganti* sp. nov.

DIAGNOSIS: Noncalcified alga with a simple, unbranched, elongate and annulated main axis, which has a 'beaded morphology'. Euspondyl type of laterals, which are arranged in verticils. Laterals undivided, straight, trichophorous, sometimes slightly expanded in the distal end. Each whorl composed of 3–4 rows of laterals. Reproductive structures unknown.

ETYMOLOGY: According to the Voronovitsa village in western Ukraine, where the investigated specimens have been found.

Voronocladus dryganti sp. nov.

(Text-figs 4–9)

HOLOTYPE: Specimen MWG ZI/110/1, Text-fig. 4A, A₁.

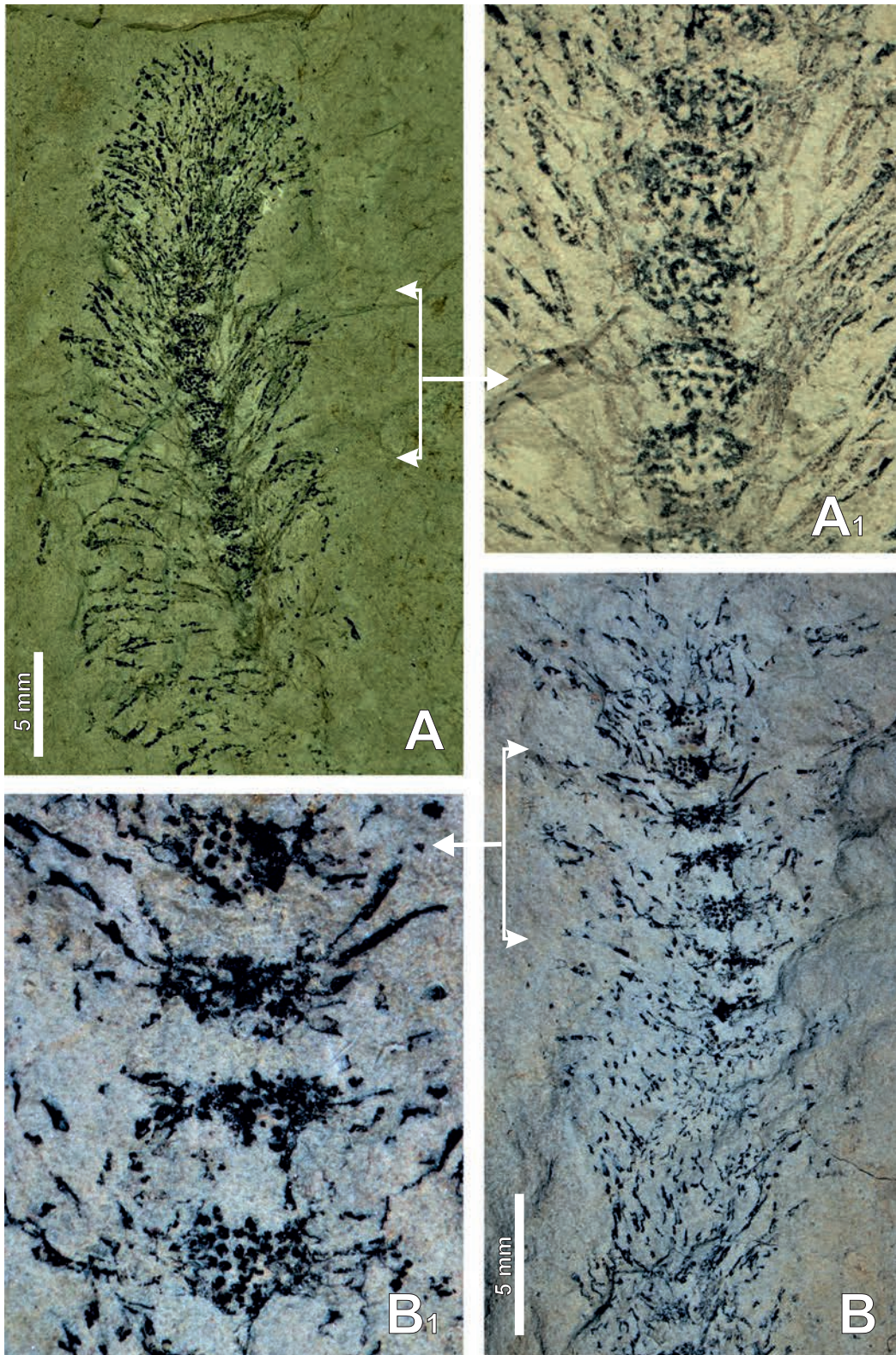
TYPE LOCALITY: East bank of Dnister river, below the Voronovitsa village, south of Kam'janec Podil'skij, Ukraine.

ETYMOLOGY: The species name comes from the name of Professor Danylo Drygant, an Ukrainian researcher of the Podolian Silurian.

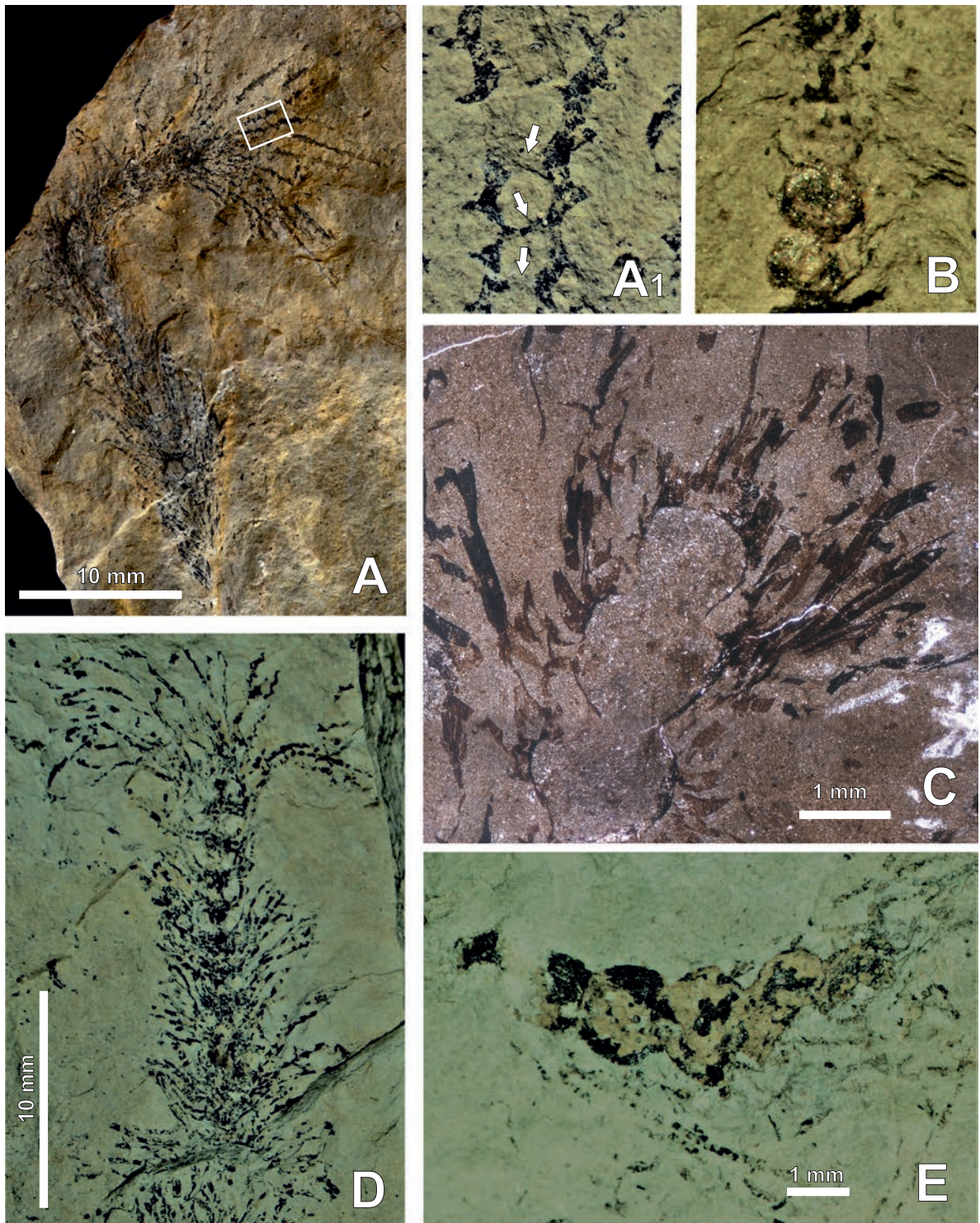
DIAGNOSIS: As for genus.

MATERIAL: 53 rock samples which contain forms classified as algae and 46 samples which contain algae with graptolite-like forms on their surface. The material for the present study includes 99 specimens, but only 20 of them are more or less complete.

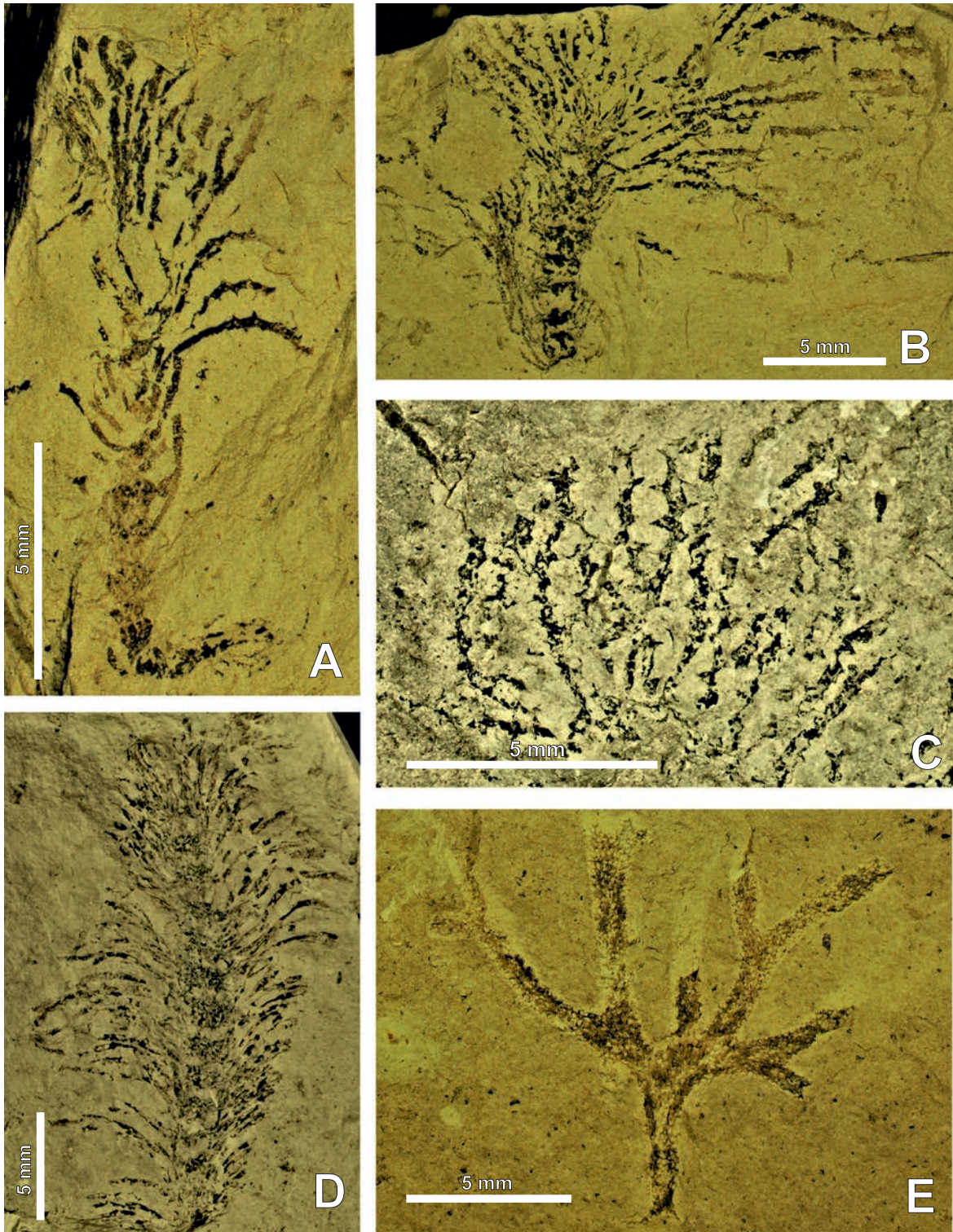
DESCRIPTION: The longest observed thallus is about 40 mm; in these specimens the distance between central points of the whorls is about 1.4–2.0 mm. The main axis is annulated and has a 'beaded morphology'; the diameter of the 'beads' (repetitive globular fragments of the main axis; Text-figs 4, 5, 6, 8B, C, 9B) is about 1.5–2.0 mm. The longest lateral is near 10 mm, with maximal diameter of about 200 μm. Laterals are band-shaped, of grey colour, with smooth edges (Text-figs 8, 9B). They are slightly coalified (Text-fig. 8A₁, C₁), therefore their shape is reconstructed on the base of their imprints in the host rock. Complete thalli are characterised by three sectors from bottom to top (see reconstruction in Text-fig. 7). The lowermost sector A lacks laterals (Text-



Text-fig. 4. *Voronocladus dryganti* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – holotype, MWG ZI/110/1; A₁ – same specimen, enlarged main axis with distinctive ‘beads’ and whorls with black scars after laterals; B – specimen with several well-visible ‘beads’, MWG ZI/110/35; B₁ – same specimen, enlarged part with four ‘beads’.



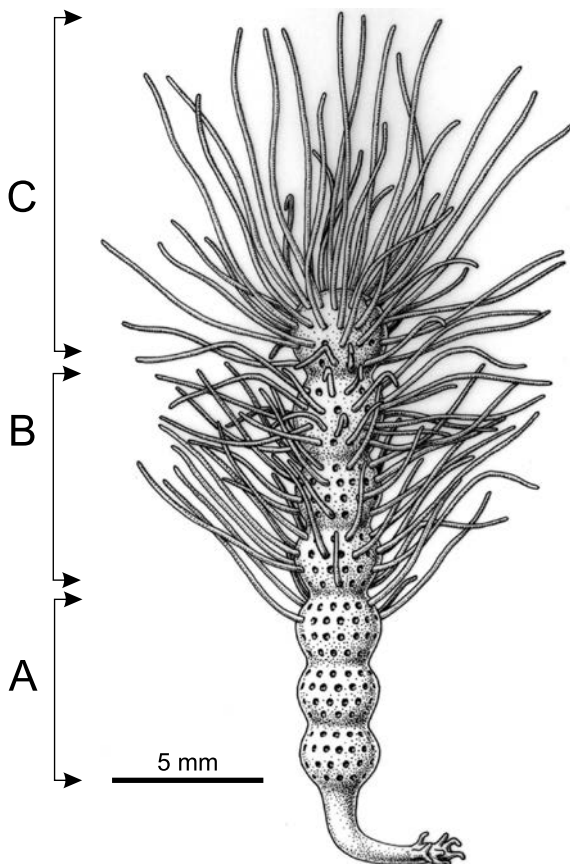
Text-fig. 5. *Voronocladus dryganti* gen. et sp. nov. and the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – algal specimen with branches of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov. (holotype) in the uppermost part of thallus, MWG ZI/110/25; A₁ – same specimen, two possibly connected neighbouring branches of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov. (arrowed); B – fragment of lower part of main axis with two ‘beads’ covered by mineralised coating, MWG ZI/110/402; C – longitudinal cross-section of main axis of alga with 3 ‘beads’ and details of laterals, internal part of main axis infilled by sediment, MWG ZI/110/26; D – bunch of putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov. branches in uppermost part of alga, MWG ZI/110/15; E – fragment of main axis with four ‘beads’ covered by mineralised coating, MWG ZI/110/ 202.



Text-fig. 6. *Voronocladus dryganti* gen. et sp. nov. and the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – algal thalli with rhizoidal part, the distal end is dominated by branches of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov., MWG ZI/110/705; B – algal specimen with well-developed laterals along thallus, MWG ZI/110/509; C – fragment of typical form with two types of branches: algal laterals in the lower part and bunch of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov. branches in the upper part, MWG ZI/110/708. D – fragment of radial form of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov., MWG ZI/110/512; E – rhabdosome of *Inocaulis plumulosus* Hall, 1851, MWG ZI/110/703.

figs 5B, E, 6B, 8B, C), but their former presence and arrangement is indicated by attachment scars that are visible on the main axis surfaces (Text-figs 4, 5D, 8C, C₁); the second sector B is characterised by the presence of a few laterals that are relatively long and mostly arrayed horizontally (Text-fig. 4); the third (uppermost) sector C comprises a dense tuft formed of laterals that are relatively short and are largely directed upwards. This 3-stage gradation is similar to some taxa of recent Dasycladales, e.g., the genus *Cymopolia* Lamouroux, 1816 (compare *Cymopolia van bosseae* Solms-Laubach, 1893 in Berger and Kaefer 1992, figs 3.41–3.43). Sometimes, in the lower part of the main axis, specific mineralisation occurs and the ‘beads’ are covered by yellowish-brown coats (Text-figs 5B, E, 6A, B, 8B, C). The elemental composition of coats is generally similar to that of mudstone matrix, with a domination of Si, Fe (evidently greater in the coats), Al, K, Ca and Mg.

The lowermost part of the thallus, which can be interpreted as a rhizoidal fragment, is visible only in one specimen (Text-fig. 6A). In this case, the rhizoid



Text-fig. 7. Reconstruction of *Voronocladus dryganti* gen. et sp. nov. A, B, C indicate the three basic parts of the thallus (see text for details). Drawing by Bogusław Waksmundzki.

is simple and formed by a right angle inflection of the lowermost axial part of the stem, similarly to other thallophytic algae, as for example *Medusaegraptus* Ruedemann, 1925 (LoDuca 1990, fig. 1; see LoDuca *et al.* 2017) or *Chaetocladus* Whitfield, 1894 (see LoDuca 2019, fig. 5/2).

DISCUSSION: There are several features, which allow us to classify the investigated specimens as algae: their general ‘brush-bottle’ shape of thalli (e.g., Text-figs 4A, 5D, 6D, 8), the presence of a main axis (Text-figs 4, 5D, 6D, 8), its segmentation (annulated, ‘beaded morphology’) (Text-figs 4, 5, 8C, C₁) and lateral branches (laterals) assembled in whorls (Text-figs 4A₁, B₁, 5C, 8, 9B). The vast majority of the algal laterals running along the thalli are thin, parallel sided and of grey colour (Text-fig. 8). There are several specimens with very dense branches totally covering the main axis. The fully algal outline of the topmost part of the main axis, with the rounded shape of the axis termination clearly visible, and with radially arranged laterals (Text-figs 4A, B, 6D, 8A and especially 9A) unequivocally indicate that the studied forms represent noncalcified algae, belonging to the Order Dasycladales.

There are several Silurian thallophytic dasycladalean algae, which are similar to the specimens described here in their general bottle-brush shape of thallus, including *Medusaegraptus*, *Chaetocladus*, *Heterocladus* LoDuca, Klussendorf and Mikulic, 2003 and *Kalania* Tinn, Maastik, Ainsaar and Meidla, 2015 (see also taxonomic description of *Chaetocladus* in LoDuca 1997 and general discussion of Ordovician–Devonian noncalcified Dasycladales in LoDuca *et al.* 2003). However, none of these taxa display the pronounced annulation of the main axis. *Medusaegraptus* has laterals arranged in an aspondyl type. In *Chaetocladus*, the laterals are grouped in verticils (euspondyl type), but the genus shows only minor annulation of the main axis, not the pronounced annulation that is diagnostic of *Voronocladus* gen. nov. *Heterocladus* is characterised by two types of laterals in the same specimen. Particular attention was paid to the similarity of *Voronocladus* gen. nov. to the early Silurian *Kalania*. The rationale for this particular treatment is the proximity of occurrence; *Kalania* has been described from the Kalana Lagerstätte from Estonia, which in the Silurian was located on the same continental shelf as Podolia. *Kalania* is most similar to the forms investigated here, but it is characterised by two orders of laterals grouped in a metaspondyl pattern and a lack of annulation of the main axis. In *Voronocladus* gen. nov. this pattern seems to be eus-

pondyl, as demonstrated by the distribution of scars on the surfaces of the ‘beads’ (see Text-figs 4A₁, B₁, 8C, C₁, 9B).

OCCURRENCE: Known only from the type locality.

?Subclass Graptolithina Bronn, 1849

Genus *Podoliagraptus* gen. nov.

TYPE AND ONLY SPECIES: *Podoliagraptus algaeoides* sp. nov.

DIAGNOSIS: Undivided branches with prominent triangular bristles projecting alternately on both sides, attached in large numbers to the upper and middle parts of the thallus of the alga *Voronocladus dryganti* gen. et sp. nov. and to the rounded objects representing the singular ‘beads’ of the alga. Branches gradually widen distally. Occasionally, the triangular bristles of adjacent branches are possibly connected by spines.

ETYMOLOGY: Named after the Podolia region in Ukraine, where the investigated material has been found.

Podoliagraptus algaeoides sp. nov.

(Text-figs 5A, A₁, D, 6A–C, 10)

HOLOTYPE: Specimen MWG ZI/110/ 25, Text-fig. 5A.

TYPE LOCALITY: East bank of Dnister river, below Voronovitsa village, south of Kam’janec Podil’skij, Ukraine.

ETYMOLOGY: *Alga* from Latin *Algae*; *-oides* from Latin *-ōidēs*, ‘resembling’; according to the epibiotic association with the alga *Voronocladus dryganti* gen. et sp. nov.

DIAGNOSIS: As for the genus.

MATERIAL: 59 rock samples with *Podoliagraptus algaeoides* gen. et sp. nov. and 46 rock samples with the algae *Voronocladus dryganti* gen. et sp. nov. and *Podoliagraptus algaeoides* gen. et sp. nov. branches on their thallus. Specimens are flattened and strongly coalified, which makes it difficult to recognise the details of the internal structure of branches.

DESCRIPTION: The undivided branches of *Podolia-*

graptus algaeoides gen. et sp. nov. are located along the algal thallus (Text-figs 6A, B, 10A₁, B₁), mostly on its upper part, creating some form of ‘brush’ (Text-figs 5A, D, 6A, B). The branches also grow on the rounded objects representing probably singular ‘beads’ of the alga (Text-fig. 10A). The size of the *Podoliagraptus algaeoides* gen. et sp. nov. branches is similar to the size of the algal laterals. However, they are wider in the distal end of the longest branches. The exact way of attachment to alga is not well visible, since the surface of the ‘beads’ is covered by black organic material, in many specimens partly destroyed.

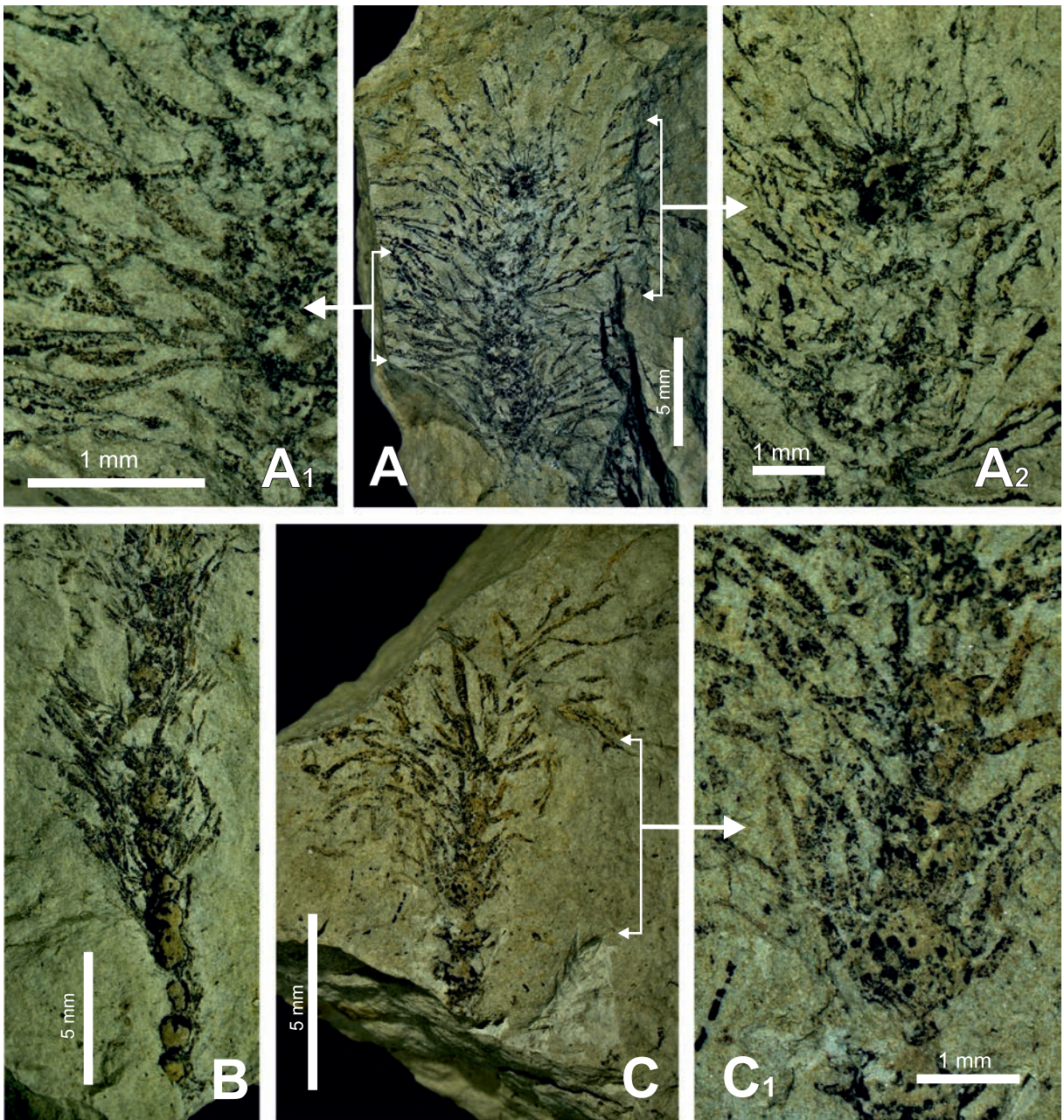
Erect, undivided branches have distinctive triangular bristles located relatively regularly, alternatively on both sides of the branches. In most cases the triangular bristle has equal sides, tilted from the axis of the stipe at an angle between 50° and 80°. The apical angle between the margin of the triangular bristle and its side is between 40° and 70°.

The most typical specimen of *Podoliagraptus algaeoides* gen. et sp. nov. (Text-fig. 5A) is represented by branches located on the most distal ‘bead’ of *Voronocladus dryganti* gen. et sp. nov. About 20 branches of *Podoliagraptus algaeoides* gen. et sp. nov. are visible on the rock surface, other are covered by the rock. The longest branches are in the middle part of the specimen, they reach about 12 mm. The width of the branches is about 150–300 µm proximally and 200–350 µm in the distal part. In the middle part of the specimen, 3 (?) triangular bristles of the adjacent branches are probably connected by triangle tops. Some of the connections are covered by sediment, but the interval between the two connected branches is kept (Text-fig. 5A₁).

In other specimens the width of the branches varies from 150 µm proximally to 450 µm distally. The length of branches is from 2 mm to 10 mm. The triangular bristles are placed regularly at mostly equal intervals, about 500–1000 µm, alternately on both sides of the branches.

Among the investigated material, there are several forms, in which the branches of *Podoliagraptus algaeoides* gen. et sp. nov. radially surround small circular objects (Text-fig. 10A), most probably representing the ‘beads’ of broken thalli of the alga *Voronocladus dryganti* gen. et sp. nov.

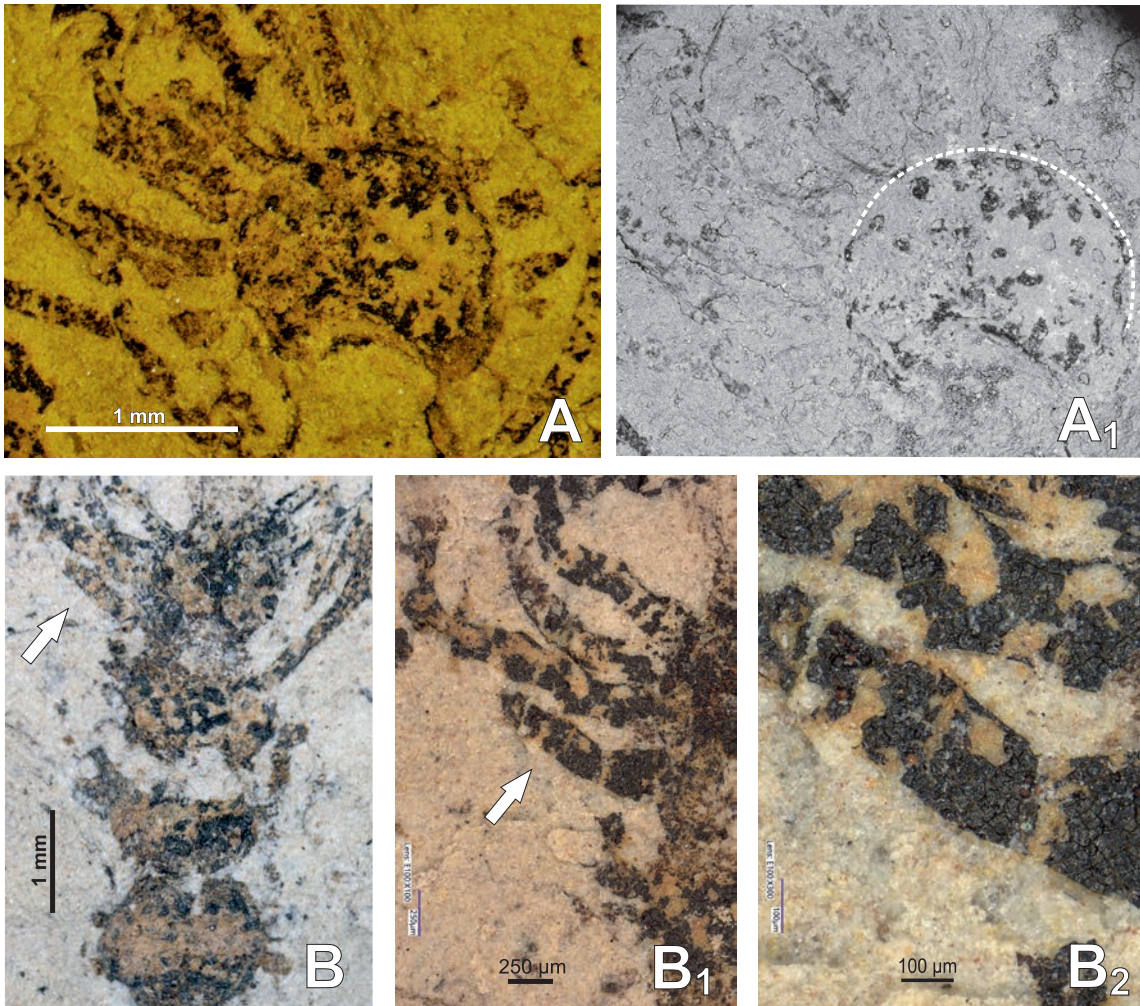
DISCUSSION: As mentioned above, according to the most far-reaching interpretation the specimens of *Podoliagraptus algaeoides* gen. et sp. nov. possess some features similar to the representatives of Graptolithina.



Text-fig. 8. *Voronocladus dryganti* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – complete specimen, MWG ZI/110/ 7; A₁ – same specimen, enlarged lateral part showing typical state of preservation of laterals; A₂ – same specimen, enlarged topmost part; B – complete specimen with lowermost part composed of pronounced coalified or mineralized ‘beads’, middle and upper part of specimen with laterals, MWG ZI/110/100; C – fragment of MWG ZI/110/26; C₁ – same specimen, close-up of distal part.

SEM BSE studies reveal that in some specimens of *Podoliagraptus algaeoides* gen. nov. et sp. nov. the black coalified material is interrupted by parallel spaces without organic matter (Text-figs 10A₁, B₁), located at nearly equal distances of 50–100 µm. Some of the cracks are twice or more times wider,

showing empty places corresponding to a suitable number of the succeeding presumed graptolite fuselli (Text-fig. 10A₁). The cracks can be interpreted as the boundaries between the succeeding fuselli. However, this could be a specific effect of coalification processes of the studied specimens.



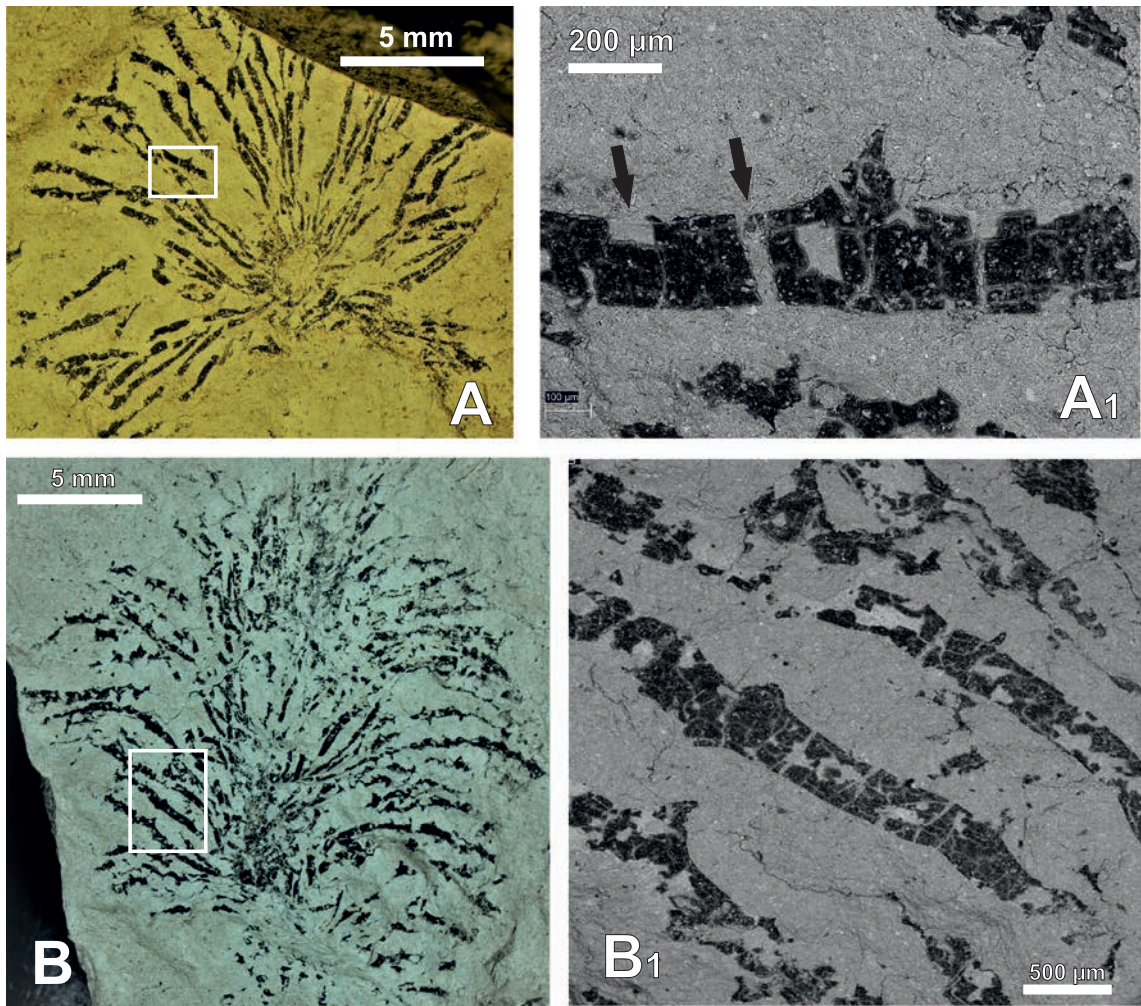
Text-fig. 9. Details of *Voronocladus dryganti* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – topmost part of thallus with rounded, distinct border of ‘bead’, MWG ZI/110/205; A₁ – same specimen, SEM BSE photo, dotted line shows ‘bead’ margin; B – fragment of specimen showing lower part of thallus with well visible ‘beads’, MWG ZI/110/712; B₁ and B₂ – same specimen, enlargements of laterals (arrowed in B and B₁, respectively).

A similar picture of fuselli preservation has been discovered, using SEM BSE, in *Tarnagraptus palma* Sdzuy, 1974, from the Cambrian of Spain (Maletz and Steiner 2015, fig. 2). Until now, SEM BSE studies have shown the presence of fuselli also in some benthic graptolites, e.g., *Sphenoecium* Chapman and Thomas, 1936 and *Dalyia* Walcott, 1919 (Maletz and Steiner 2015), identified before as hydroids or algae. Similarly, *Yuknessia* Walcott, 1919 was reinterpreted from green algae to graptolites thanks of the presence of fuselli visible under SEM BSE (Maletz *et al.* 2005; LoDuca *et al.* 2015, 2017).

Some doubts are also related to the interpretation of the triangular bristles as graptolitic thecae. Their shape and alternating arrangement

show some similarities to the triangular bristles known in some Graptolithina *incertae sedis*, e.g., *Cactograptus* Ruedemann 1908 (figs 99–101, pl. 8/1) from the Silurian (Llandovery) and *Nephelograptus* Ruedemann 1947 (pl. 14/18–28) from the Ordovician. However, the Llandovery dendroids *Dictyonema venustum* Lapworth, 1881 (pl. 7: 1) and *D. delicatum* Lapworth, 1881 (pl. 7: 2) have the same arrangement of the triangle-shaped thecae.

Connections between the triangular bristles of adjacent branches, observed in one specimen of *Podoliagraptus algaeoides* gen. et sp. nov. (Text-fig. 5A, A₁), resemble dissepiments characteristic of some benthic graptolites, such as *Dictyonema* Hall, 1851; *Capillograptus* Bouček, 1957 (Chapman



Text-fig. 10. Branches of the putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov. growing on *Voronocladus dryganti* gen. et sp. nov., Silurian, Voronovitsa village, Podolia, Ukraine. A – putative graptolite branches around the algal ‘bead’, MWG ZI/110/700; A₁ – same specimen, SEM BSE photo of branch with triangular bristle resembling graptolite theca, coalified material of stipe is disintegrated in the form of rectangles (black arrow) similar to possible graptolite fuselli; B – distal end of thalli with only putative graptolite *Podoliagraptus algaeoides* gen. et sp. nov., MWG ZI/110/403; B₁ – same specimen, SEM BSE photo of branches, partly covered by sediment.

et al. 1993) and of some early planktic forms, e.g., *Rhabdinopora* Eichwald, 1855 (Erdtmann 1982; Cooper *et al.* 1998). However, a closer look at the connections in the specimen illustrated in Text-fig. 5A (the only specimen with well visible ‘dissepiments’) shows that most probably it is an accidental feature resulting from the preservation of the specimen.

Overall, we can conclude that there are not enough data to determine *Podoliagraptus algaeoides* gen. et sp. nov. as a graptolite, despite the similarities to graptolites. Therefore, it is preferred here to keep the taxon under ?Subclass Graptolithina Bronn, 1849.

OCCURRENCE: Known only from the type locality.

DISCUSSION

Sedimentary environment

As mentioned in the Introduction, the facies development recorded in the investigated section is similar to that observed in the North American sections with thallophytic algae assemblages; in both cases they are known from the most regressive parts of regressive-transgressive cyclothems. Their characteristic feature is the proximity of biohermal deposits, which has been emphasised in the primary description (Ruedemann 1925) of the Laurentian Gasport Channel section (Niagara Falls Member),

with the ‘*Medusaegraptus epibole*’ of LoDuca (1990). However, in the more recent investigations, LoDuca and Brett (1997) have proven that the sedimentation of argillaceous dolomitic layers with algae is regionally extremely extensive (traceable on a distance of 100 km) and that depositional event postdates the growth of bioherms.

Another feature that shows close similarities between the Ukrainian outcrops described here and the North American ones, is the small thickness of the algal-graptolite bed (not exceeding 10 cm). The most significant difference is that in the Gasport Channel section, the soft-bodied fossils occur in the top parts of graded beds, while in the Voronovitsa section, the tempestitic episode evidently postdates the deposition of algal beds. Despite this difference, the general succession of sedimentary events in both sections is very similar, and with some reservation it can be concluded that in both cases the algal beds are coincident with the critical moments (maximum of regression) of regressive-transgressive cyclothems. According to LoDuca and Brett (1997), the appearance of an algal assemblage, defined as the ‘*Medusaegraptus epibole*’, is concomitant with a similar Konservat-Lagerstätten and synchronised with a shallowing episode on the 6th order sea-level curve, chronostratigraphically correlated with the upper part of the Gorstian. The stratigraphic position of the investigated Ukrainian section is more or less analogous in the sense of the sea level curve (Predtechenskij *et al.* 1983; Łuczyński *et al.* 2015), and similar in the chronostratigraphical sense. However, a more precise correlation is impossible due to the lack of sufficient biostratigraphic data. One can only suspect that the appearance of rich algal assemblages on the Laurentia and Baltica shelves is a simultaneous bio-event, but to demonstrate it would require more detailed stratigraphic studies.

More and more frequent descriptions of thalphytic algae assemblages from the Silurian shelf of Baltica encourage stratigraphic and facies comparisons. Ishchenko (1985) reported the presence of thalphytic coalified algae (genus *Chaetocladus*) in the Ukrainian sections, within the Bagovitsa, Furmanovka and Varnitsa formations, but she did not provide a precise description of the sedimentological features of the algae-yielding layers. In the Estonian Kalana Quarry section, a rich and diversified algal assemblage has been found in the several meters thick complex of organic rich, microlaminated, partly dolomitized limestones. The shallow water nature of these beds is documented by the appearance of layers with desiccation cracks, and in-

tercalations with leperditiid and eurypterid remains, suggesting short-term periods of shallow lagoonal environments (Tinn *et al.* 2009, 2015; Ainsaar *et al.* 2014). In the Swedish sections in Skania, ‘algal-Lagerstätten’ have been found in the inter-biostromal mudstone succession, in a generally lagoonal setting. A rapid burial of fossils during storms has been underlined in this case (Kenrick and Vinther 2006; Pettersson *et al.* 2020).

Assemblage composition characteristics

The studied fossil assemblage fits well into the category of a thalphytic-algal community, in which the dominant components are the noncalcified alga *Voronocladus* gen. nov. and benthic graptolite-like *Podoliagraptus* gen. nov. The present observations and numerous descriptions of similar Silurian communities, where algae and independently living benthic graptolites occurred (Kenrick and Vinther 2006; LoDuca and Tetreault 2017; Pettersson *et al.* 2020), indicate that these two groups of organisms co-occurred in the same environment. Other fossils in the assemblage are represented mostly by *Campylites*-type tubes and gastropods, sometimes several centimetres long. Only one, but a well-preserved specimen (Text-fig. 6E) of the benthic graptolite *Inocaulis plumulosus* Hall, 1851 (Muir *et al.* 2013, fig. 1; LoDuca *et al.* 2017, fig. 3G) was recorded, as well as single specimens of the trilobite *Proetus conspersus* Angelin, 1854.

In accordance with detailed sedimentological observations, and the nature of the facies succession, the layer under study represents a tidal flat environment (Łuczyński *et al.* 2015). The occurrence of noncalcified as well as calcified dasycladacean algae in such a bathymetric interval is to be expected, as shown by observations of both fossil and recent environments. These algae prefer environments with a depth of not more than 10 m, with normal salinity and protected from ground and tidal waves (Flügel 1985, 2020; Berger and Kaever 1992), although single specimens are found even at depths of 100 m.

Habitat of benthic graptolites

Recent benthic graptolite *Rhabdopleura* Allmann, 1869 colonies (Mitchell *et al.* 2013) occur in a wide range of marine environments, from shallow waters up to the depth of several hundred meters (Beli *et al.* 2018). Dilly (1985) found recent *Rhabdopleura* in coral rubble on reefs of the intertidal zone providing the epiphytic style of life. Thus, the environment,

in which the recently living *Rhabdopleura* occurs is comparable to the tidal flat zone suggested here for the *Voronocladus* gen. nov. As mentioned above, numerous studies in Silurian communities indicate that the coexistence of algae and independently living benthic graptolites is relatively common. All this indicates that graptolites could have lived in the described habitat.

Probable way of coexistence of the alga *Voronocladus* gen. nov. and the putative graptolite *Podoliagraptus* gen. nov.

A unique feature of the studied assemblage is the presence of the graptolite-like *Podoliagraptus* gen. nov. growing on the thallus of the alga *Voronocladus* gen. nov. in such an arrangement that it gives the impression of a single organism. This phenomenon is observed for the first time. There is a problem with the explanation of the lifestyle of both organisms. Some solution may come from the comparison with the lifestyle of the recent benthic *Rhabdopleura* (Lester 1988), assuming that the development of Palaeozoic graptolite colonies was similar to their recent counterparts. Both recent *Rhabdopleura* and some extinct graptolites occur in a tidal flat environment as is the case in the studied material. *Rhabdopleura* larvae settle down on a suitable surface on the sea floor, e.g., on brachiopod shells or coral debris, and after metamorphosis the first zooid starts the development of the colony. It can be assumed that the *Voronocladus* gen. nov. alga might have served as a suitable surface for the attachment of the *Podoliagraptus* gen. nov. larvae, and assured a successful growth of their colony.

During the growth of both organisms (*Voronocladus* gen. nov. alga and *Podoliagraptus* gen. nov. putative graptolite), some kind of relationship started to develop. It may be comparable to the most possible epibiotic life style, a widespread phenomenon in recent marine environments, e.g., *Macrocystis* Agardh, 1820, a large benthic brown alga is the basis for diverse epibiotic bryozoans, hydroids and plants (Graham *et al.* 2007). Some hydroid epifauna are observed on the thalli of the benthic alga *Sargassum* Agardh, 1820 in recent marine waters of the Mexican Caribbean (Mendoza-Becerril *et al.* 2020). Epiphytic algal communities are frequent on the aquatic plant *Potamogeton perfoliatus* L. (Sultana *et al.* 2004). Nowadays, there are possibilities to study the growth rates of epibionts and their hosts, and in some cases their interactions are shown to be competitive (Seed 1986) if the epiphytes cover large surfaces of the host organism.

The possible epibiotic graptolite colony, being an active planktivorous organism, could have had better access to food particles present in the higher water horizons of this specific, shallow-water environment. This assumption is supported by the observation of the studied material, in which the graptolite colonies are particularly prolific at the top of the algal forms. It seems to be most probable that the most frequent place of the graptolite larval attachments was the top of the algal thalli as it is seen in the most typical specimen of *Voronocladus* gen. nov. with *Podoliagraptus* gen. nov. branches (Text-fig. 5A).

The graptolite zooid excrements, probably rich in phosphorus and nitrogen, could fertilise the algal basis. On the other hand, the epibiotic graptolites could block the access of algae to sunlight, and thus the benefit of alga in this kind of coexistence is rather doubtful.

In the fossil material the epibionts represent different groups of organisms, e.g., corals, bryozoans, brachiopods, crinoids (Gluchowski 2005; Zatoń *et al.* 2018). Colonies of benthic graptolites are known to grow inside nautilus conchs (Vinn *et al.* 2019). Examples of an epibiotic life style of fossil and recent organisms, mainly of the recent *Rhabdopleura*, show that it is possible to interpret the coexistence of the *Voronocladus* gen. nov. alga and *Podoliagraptus* gen. nov. putative graptolite as epiphytic.

The presented concept of epibiotic cohabitation of *Voronocladus* gen. nov. alga and putative graptolite *Podoliagraptus* gen. nov. is understood here as the most reasonable. However, there are not enough data to assign the phenomenon of alga and putative graptolite coexistence as a kind of symbiosis, parasitism or commensalism (see Zapalski 2007; Taylor 2015).

CONCLUSIONS

Two groups of noncalcified and coalified fossils, representing dasycladalean algae and putative epibiotic graptolites, are the basic components of a rich association in the late Silurian of Podolia, Baltica. The Silurian associations of dasycladalean algae and some graptolites are well-known, especially from the Laurentian part of the Laurussian shelf. In the studied material, the probable graptolites are unexpectedly found growing on algal thalli; they occur with the same frequency as separate specimens of both organisms.

The main distinguishing features of these two forms are the dissimilar shapes of the laterals: smooth, thinner and longer in the case of algae, in

contrast to the thicker, more coalified, black putative graptolite branches with their triangular bristles. The dasycladalean algae are assigned to *Voronocladus dryganti* gen. et sp. nov. whereas the taxonomic position of the problematic graptolite-like form named as *Podoliagraptus algaoides* gen. et sp. nov. is not clear, but its affinity to graptolites seems to be highly probable.

Current observations do not allow for a precise definition of the alga and putative graptolite relationship; whether it is a result of putative graptolite growth strategy or an effect of some accidental growth on algae as a substrate. The overriding suggestion of a symbiotic nature of this relationship is rather dubious, as it is difficult to indicate the benefits that both organisms would obtain. The epibiotic putative graptolite would have been neutral or rather harmful to the algal host in case of its excessive growth. The temporarily proposed model suggests some relationship similar to the functioning epibiotic style of life of various organisms living on modern algae, and their interaction can be considered as a kind of neutralism or commensalism.

The epibiotic organism, in the case of the described forms probably representing a graptolite, growing on the thallus of an alga is a unique phenomenon described herein for the first time from the Silurian.

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REFERENCES

- Abushik, A.F., Berger, A.Ya., Koren, T.N., Modzalevskaya, T.L., Nikiforova, O.I. and Predtechenskij, N.N. 1985. The fourth series of the Silurian System in Podolia. *Lethaia*, **18**, 125–146.
- Agardh, C.A. 1820. Species algarum rite cognitae, cum synonymis, differentiis specificis et descriptionibus succinctis. Volumen primum, pars prima, 168 pp. Berlingiana; Lundae.
- Ainsaar, L., Tinn, O., Männik, P. and Meidla, T. 2014. Stop B1: Kalana quarry. In: Bauert, H., Hints, O., Meidla, T. and Männik, P. (Eds), 4th Annual Meeting of IGCP 591, 174–177, Estonia, University of Tartu; Tartu.
- Allman, G. 1869. *Rhabdopleura normani*, Allman, nov. gen. et sp. *Report of the British Association for the Advancement of Science*, **1868**, 311–312.
- Angelin, N.P. 1854. Palaeontologia Scandinavica, Pars 1. Crustacea formationis transitionis, Fasciculus II, 21–92. Berlin-gianis; Lund.
- Beli, E., Aglieri, G., Strano, F., Maggioni, D., Telford, M.J., Piraino, S. and Cameron, C.B. 2018. The zoogeography of extant rhabdopleurid hemichordates (Pterobranchia: Graptolithina), with a new species from the Mediterranean Sea. *Invertebrate Systematics*, **32** (1), 100–110.
- Berger, S. and Kaever, M.J. 1992. Dasycladales: an illustrated monograph of a fascinating algal order, 246 pp. Thieme; Stuttgart.
- Bouček, B. 1957. The dendroid graptolites of the Silurian of Bohemia. *Rozprawy Ustředního ústavu geologického*, **23**, 1–294.
- Bronn, H.G. 1849. Handbuch der Geschichte der Natur. Dritter Band, Zweite Abtheilung. II. Theil: Organisches Leben (Schluß). Index palaeontologicus oder Ueberblick der bis jetzt bekannten fossilen Organismen, 1106 pp. Schweizerbart; Stuttgart.
- Bulman, O.M.B. 1955. Graptolithina. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology. Part V, 101 pp. The Geological Society of America and The University of Kansas Press; New York and Lawrence.
- Bykova, N., LoDuca, S.T., Ye, Q., Marusin, V., Grazhdankin, D. and Xiao, S. 2020. Seaweeds through time: Morphological and ecological analysis of Proterozoic and early Paleozoic benthic macroalgae. *Precambrian Research*, **350**, 105875.
- Chapman, F. and Thomas, D.E. 1936. The Cambrian hydroids of the Heathcote and Monegeeta districts. *Proceedings of the Royal Society of Victoria*, **48**, 193–212.
- Chapman, A.J., Rickards, R.B. and Grayson, R.F. 1993. The Carboniferous dendroid graptolites of Britain and Ireland. *Proceedings of the Yorkshire Geological Society*, **49** (4), 295–319.
- Cooper, R.A., Maletz, J., Haifeng, W. and Erdtmann, B.D. 1998. Taxonomy and evolution of earliest Ordovician graptoloids. *Norsk Geologisk Tidsskrift*, **78** (1), 3–32.

- Dilly, P.N. and Ryland, J.S. 1985. An intertidal *Rhabdopleura* (Hemichordata, Pterobranchia) from Fiji. *Journal of Zoology*, **205** (4), 611–623.
- Drygant, D.M. 1984. Correlation and conodonts of the Silurian –Lower Devonian deposits of Volyn' and Podolia, 192 pp. Naukova Dumka; Kiev. [In Russian]
- Eichwald, C.E. 1855. Zur Naturgeschichte des Kaspischen Meeres. Nouveaux mémoires de la Société Impériale des Naturalistes, Moscou, **10**, 283–323.
- Einasto, R.Z., Abushik, A.F., Kaljo, D.P., Koren', T.N., Modzalevskaya, T.L. and Nestor, H.Z. 1986. Silurian sedimentation and the fauna of the East Baltic and Podolian marginal basins: a comparison. In: Kaljo, D. and Klaamann, E.J. (Eds), Theory and practice of ecostratigraphy. All-Union conference, Tallinn, October 19–22, 1982, Abstracts, 37–54. Academy of Sciences of the Estonian S.S.R.; Tallinn. [In Russian]
- Erdtmann, B.D. 1982. *Rhabdinopora* and the planktonic dicyonemids. *Graptolite Working Group of the International Palaeontological Association Newsletter*, **3**, 14–16.
- Flügel, E. 1985. Diversity and Environments of Permian and Triassic Dasycladacean Algae. In: Toomey, D.F. and Nitecki, M.H. (Eds), Paleogeology, 344–351. Springer; Berlin, Heidelberg.
- Flügel, E. 2010 (with a contribution by Munnecke, A.). Microfacies of carbonate rocks: analysis, interpretation and application, 984 pp. Springer; Heidelberg, Dordrecht, London, New York.
- Głuchowski, E. 2005. Epibionts on upper Eifelian crinoid columnals from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, **50**, 315–328.
- Graham, M.H., Vasquez, J.A. and Buschmann, A.H. 2007. Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanography and Marine Biology*, **45**, 39–88.
- Hall, J. 1851. New genera of fossil corals from the report by James Hall on the Paleontology of New York. *American Journal of Sciences*, Ser. 2, **11**, 398–401.
- Huff, W.D., Bergström, S. M. and Kolata, D.R. 2000. Silurian K-bentonites of the Dnestr Basin, Podolia, Ukraine. *Journal of the Geological Society*, **157** (2), 493–504.
- Ishchenko, A.A. 1985. Silurian algae of Podolia, 116 pp. Naukova Dumka; Kiev. [In Russian]
- Jarochowska, E., Munnecke, A., Frisch, K., Ray, D.C. and Castagner, A. 2016. Faunal and facies changes through the mid Homerian (late Wenlock, Silurian) positive carbon isotope excursion in Podolia, western Ukraine. *Lethaia*, **49** (2), 170–198.
- Jeppsson, L. and Aldridge, R.J. 2000. Ludlow (late Silurian) oceanic episodes and events. *Journal of the Geological Society*, **157** (6), 1137–1148.
- Johnson, M.E. 2006. Relationship of Silurian sea-level fluctuations to oceanic episodes and events. *GFF*, **128** (2), 115–121.
- Jorry, S.J., Droxler, A.W. and Francis, J.M. 2010. Deepwater carbonate deposition in response to re-flooding of carbonate bank and atoll-tops at glacial terminations. *Quaternary Science Reviews*, **29**, 2010–2026.
- Kenrick, P. and Vinther, J. 2006. *Chaetocladus gracilis* n. sp., a noncalcified Dasycladales from the Upper Silurian of Skåne, Sweden. *Review of Palaeobotany and Palynology*, **142** (3–4), 153–160.
- Koren', T.N., Abushik, A.F., Modzalevskaya, T.L. and Predtechenskij, N.N. 1989. Podolia. In: Holland, C.H. and Bassett, M.G. (Eds), A global standard for the Silurian System. *Natural Museum Wales Geological Service*, **9**, 141–149.
- Lamouroux, J.V.F. 1816. Histoire des polypiers coralligenes flexibles vulgairement nommés Zoophytes, 217–316. F. Poisson; Caen.
- Lapworth, C. 1881. On the *Cladophora* (Hopk.) or dendroid graptolites collected by Professor Keeping in the Llandoverly Rocks of Mid Wales. *Quarterly Journal of the Geological Society of London*, **37**, 171–177.
- Lester, S.M. 1988. Settlement and metamorphosis of *Rhabdopleura normani* (Hemichordata: Pterobranchia). *Acta Zoologica*, **69**, 111–120.
- LoDuca, S.T. 1990. *Medusaegraptus mirabilis* Ruedemann as a noncalcified dasyclad alga. *Journal of Paleontology*, **64**, 469–474.
- LoDuca, S.T. 1995. Thallophtic-alga-dominated biotas from the Silurian Lockport Group of New York and Ontario. *North-eastern Geology and Environmental Sciences*, **17**, 371–382.
- LoDuca, S.T. 1997. The green alga *Chaetocladus* (Dasycladales). *Journal of Paleontology*, **71**, 940–949.
- LoDuca, S.T. 2019. New Ordovician marine macroalgae from North America, with observations on *Buthograptus*, *Calithamnopsis*, and *Chaetocladus*. *Journal of Paleontology*, **93**, 197–214.
- LoDuca, S.T. and Brett, C.E. 1997. The *Medusaegraptus* epibole and lower Ludlovian Konservat-Lagerstätten of eastern North America. In: Brett, C.E. and Baird, G. (Eds), Paleontological events: Stratigraphic, ecological, and evolutionary implications, 369–405. Columbia University Press; New York.
- LoDuca, S.T., Bykova, N., Wu, M., Xiao, S. and Zhao, Y. 2017. Seaweed morphology and ecology during the great animal diversification events of the early Paleozoic: a tale of two floras. *Geobiology*, **15** (4), 588–616.
- LoDuca, S.T., Kluessendorf, J. and Mikulic, D.G. 2003. A new noncalcified dasycladalean alga from the Silurian of Wisconsin. *Journal of Paleontology*, **77**, 1152–1158.
- LoDuca, S.T., Melchin, M.J. and Verbruggen, H. 2011. Complex noncalcified macroalgae from the Silurian of Cornwallis Island, Arctic Canada. *Journal of Palaeontology*, **85**, 11–121.
- LoDuca, S.T., Miller, R.F. and Wilson, R.A. 2013. *Medusaegraptus* (Chlorophyta, Dasycladales) from the Pridolian to middle Lochkovian Indian Point Formation, New Brun-

- wick, Canada. *Atlantic Geology: Journal of the Atlantic Geoscience Society/Atlantic Geology: revue de la Société Géoscientifique de l'Atlantique*, **49**, 118–125.
- LoDuca, S.T. and Tetreault, D.K. 2017. Ontogeny and reproductive functional morphology of the macroalga *Wartonella nodifera* n. gen. n. sp. (Dasycladales, Chlorophyta) from the Silurian Eramosa. *Journal of Paleontology*, **91**, 1–11.
- LoDuca, S.T., Wu, M., Zhao, Y., Xiao, S., Schiffbauer, J. D., Caron, J.-B., and Babcock, L.E. 2015. Reexamination of *Yuknessia* from the Cambrian of China and first report of *Fuxianospira* from North America. *Journal of Paleontology*, **89**, 899–911.
- Łuczynski, P., Kozłowski, W. and Skompski, S. 2009. Sedimentary history of Upper Silurian biostromes of Podolia (Ukraine) based on stromatoporoid morphometry. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **271**, 225–239.
- Łuczynski, P., Kozłowski, W. and Skompski, S. 2015. Regressive-transgressive cyclothem with facies record of the re-flooding window in the Late Silurian carbonate succession (Podolia, Ukraine). *Acta Geologica Polonica*, **65**, 297–318.
- Maletz, J. and Steiner, M. 2015. Graptolite (Hemichordata, Pterobranchia) preservation and identification in the Cambrian Series 3. *Palaeontology*, **58** (6), 1073–1107.
- Maletz, J., Steiner, M. and Fatka, O. 2005. Middle Cambrian pterobranchs and the question: What is a graptolite? *Lethaia*, **38**, 73–85.
- Mastik, V. and Tinn, O. 2015. New dasycladalean algal species from the Kalana Lagerstätte (Silurian, Estonia). *Journal of Paleontology*, **89** (2), 262–268.
- Mendoza-Becerril, M.A., Serviere-Zaragoza, E., Mazariegos-Villarreal, A., Rivera-Perez, C., Calder, D.R., Vázquez-Delfín, E.F., Freile-Peigrín, Y., Agüero, J. and Robledo, D. 2020. Epibiont hydroids on beachcast *Sargassum* in the Mexican Caribbean. *PeerJ*, **8**, e9795.
- Mitchell, C.E., Melchin, M.J., Cameron, C.B. and Maletz, J. 2013. Phylogenetic analysis reveals that *Rhabdopleura* is an extant graptolite. *Lethaia*, **46**, 34–56.
- Muir, L.A., Zhang, Y.D. and Lin, J.P. 2013. New material from the Ordovician of China indicates that *Inocaulis* is a graptolite. *Alcheringa: An Australasian Journal of Palaeontology*, **37**, 565–566.
- Nikiforova, O.I. and Predtechenskij, N.N. 1968. A guide to the geological excursion on Silurian and Lower Devonian deposits of Podolia (Middle Dniestr River). Proceedings of the 3rd international symposium on Silurian–Devonian boundary and Lower and Middle Devonian stratigraphy, 58 pp. Ministry of Geology of the USSR; Leningrad.
- Pascher, A. 1931. Systematische Übersicht über die mit Flagellaten in Zusammenhang stehenden Algenreihen und Versuch einer Einreihung dieser Algenstämme in die Stämme des Pflanzenreiches. *Botanische Centralblatt Beihefte*, **48**, 317–332.
- Pettersson, J., Ahlberg, P., Lindskog, A., Lindgren, J., and Eriksson, M.E. 2020. The fossil alga *Chaetocladus gracilis* revisited: new material from the Silurian of Sweden. *GFF*, **142**, 304–308.
- Predtechenskij, N.N., Koren', T.N., Modzalevskaya, T.L., Nikiforova, O.I., Berger, A.Y. and Abushik, A.F. 1983. Cyclicity of deposition and changes of ecological assemblages of fauna in the Silurian of Podolia. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **194**, 61–74. [In Russian]
- Racki, G., Baliński A., Wrona R., Małkowski, K., Drygant, D. and Szaniawski, H. 2012. Faunal dynamics across the Silurian–Devonian positive isotope excursions ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) in Podolia, Ukraine: Comparative analysis of the Ireviken and Klonk events. *Acta Palaeontologica Polonica*, **57**, 795–832.
- Ruedemann, R. 1908. Graptolites of New York. Part II. *New York State Museum Memoir*, **11**, 1–547.
- Ruedemann, R. 1925. Some Silurian (Ontarian) fossils of New York. *New York State Geological Survey Bulletin*, **25**, 1–81.
- Ruedemann, R. 1947. Graptolites of North America. *Geological Society of America, Memoir*, **19**, 1–651.
- Sdzuy, K. 1974. Mittelkambrische Graptolithen aus NW-Spanien. *Paläontologische Zeitschrift*, **48**, 110–139.
- Seed, R. 1986. Ecological pattern in the epifaunal communities of coastal macroalgae. In: Moore, P.G. and Seed, R. (Eds), *The Ecology of Rocky Coasts*, 22–35. Columbia University Press; New York.
- Seilacher, A. 1970. Begriff und Bedeutung der Fossil-Lagerstätten. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1970** (1), 34–39.
- Skompski, S., Łuczynski, P., Drygant, D. and Kozłowski, W. 2008. High-energy sedimentary events in lagoonal successions of the Upper Silurian of Podolia, Ukraine. *Facies*, **54**, 277–296.
- Solms-Laubach, H. 1893. Über die Algengenera *Cymopolia*, *Neomeris* und *Bornetella*. *Annales du Jardin botanique de Buitenzorg*, **11**, 61–97.
- Sultana, M., Asaeda, T., Manatunge, J. and Ablimit, A. 2004. Colonisation and growth of epiphytic algal communities on *Potamogeton perfoliatus* under two different light regimes. *New Zealand Journal of Marine and Freshwater Research*, **38**, 585–594.
- Taylor, P.D. 2015. Differentiating parasitism and other interactions in fossilized colonial organisms. *Advances in parasitology*, **90**, 329–347.
- Taromi Sandström, O., Dahlqvist, P., Erlström, M., Persson, L., Kershaw, S., and Calner, M. 2021. Stratigraphy of the Gorstian and Ludfordian (upper Silurian) Hemse Group reefs on Gotland, Sweden. *GFF*, **143**, 71–83.
- Tinn, O., Mastik, V., Ainsaar, L. and Meidla, T. 2015. *Kalania pusilla*, an exceptionally preserved noncalcified alga from the lower Silurian (Aeronian, Llandovery) of Estonia. *Palaeoworld*, **24** (1–2), 207–214.

- Tinn, O., Meidla, T., Ainsaar, L., and Pani, T. 2009. Thallophtic algal flora from a new Silurian Lagerstätte. *Estonian Journal of Earth Sciences*, **58**, 38–42.
- Tsegelnyuk, P.D., Gritsenko, V.P., Konstantinenko, L.I., Ishchenko, A.A., Abushik, A.F., Bogoyavlenskaya, O.V., Drygant, D.M., Zaika-Novatsky, V.S., Kadlets, N.M., Kiselev, G.N. and Sytova, V.A. 1983. The Silurian of Podolia. The guide to excursion, 224 pp. Naukova Dumka; Kiev.
- Vachard, D. 2021. Calcareous algae (Rhodophyta and Chlorophyta). In: Alderton, D. and Elias, S.A. (Eds), *Encyclopedia of Geology*, 389–406. Academic Press.
- Vinn, O., Wilson, M.A. and Toom, U. 2019. A crustoid graptolite lithoimmured inside a Middle Ordovician nautiloid conch from northern Estonia. *Annales Societatis Geologorum Poloniae*, **89**, 285–290.
- Walcott, C.D. 1919. Cambrian geology and paleontology IV. Middle Cambrian algae. *Smithsonian Miscellaneous Collections*, **67** (5), 217–260.
- Zapalski, M.K. 2007. Parasitism versus commensalism: the case of tabulate endobionts. *Palaeontology*, **50**, 1375–1380.
- Zatoń, M., Zapalski, M.K., Berkowski, B. and Wrzolek, T. 2018. Cryptic encrusting communities in a Middle Devonian mesophotic paleoenvironment of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **501**, 82–91.

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