

First record of a receptaculitid algae (Receptaculitaceae) in Ukraine

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article info

key words

Upper Ordovician, Receptaculites, living conditions, Dasycladales, calcareous algae, Podillia

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article history

Submitted: 07.05.2024. Revised: 31.10.2025. Accepted: 27.02.2026

cite as

Grytsenko, V., Rudenko, K., Kovalenko, O. (2026). First record of a receptaculitid algae (Receptaculitaceae) in Ukraine. *GEO&BIO*, 28, 17–26. [English, with Ukrainian summary]

abstract

Most exposures of the Upper Ordovician Subich Formation of western Ukraine are submerged beneath the Dniester Hydroelectric Power Station reservoir, complicating field studies. Nevertheless, several outcrops remain above the water level and provide valuable information on the biota of Late Ordovician ecosystems. Fossils of corals, crinoids, stromatoporoids, bryozoans, brachiopods, cephalopods, bivalves, gastropods, and other faunistic groups have been reported from the Subich Formation; however, no information regarding calcareous algae of the order Dasycladales from these deposits was previously available. We studied a sample of gray clayey-detrital limestone containing remains of an unknown organism, collected by Leonid Ivanovych Konstantynenko from the Subich Formation of the Molodove Horizon on the left bank of Studenytsia Bay of the Dniester Reservoir. Although the fossil was initially interpreted as a coral, detailed analysis revealed a thin (~5 mm) plate composed of rhomboidal cross-section elements (prisms) arranged in a spiral pattern resembling a sunflower inflorescence. These morphological features correspond to the species *Receptaculites occidentalis*, a member of a problematic group of fossil organisms found in deposits from the Ordovician to the Permian across multiple continents. Historically, these organisms were considered problematic, and their systematic position remains debated. While similar specimens were previously interpreted as corals, a specific type of sponge, or bryozoans, modern studies of their microstructure have clarified their classification as calcareous algae of the order Dasycladales. We report *Receptaculites occidentalis* from the Ordovician of Ukraine for the first time. This study provides a detailed description of the fossil, includes photographs, and presents a comparison with receptaculitid specimens from the National Museum of Natural History Museum of the NAS of Ukraine, collected from Silurian deposits of the Barrandian region (Czech Republic). These findings enhance our understanding of the palaeontological diversity of the Subich Formation and provide insights into the palaeogeography and environmental characteristics of Late Ordovician marine basins.

Перша знахідка рецептакулітиди (*Receptaculitaceae*) в Україні

Володимир Гриценко, Ксенія Руденко, Олексій Коваленко

Резюме. Виходи порід ордовіцької послідовності Заходу України переважно покриті водою водосховища Дністровської гідроелектростанції, що ускладнює їхнє дослідження, однак деякі з них залишилися над рівнем води і є цінним джерелом інформації про екосистеми пізнього ордовіку. Із верхньордовіцьких відкладів субіцької світи відомі рештки коралів, кріноїдей, строматопорідей, моховаток, брахіопод, молюсків (головоногих, двостулкових та черевоногих) та інших систематичних груп організмів, однак жодних відомостей про викопні рештки вапнистих водоростей порядку *Dasycladales* із цих відкладів раніше не було відомо. Нами було досліджено зразок сірого глинисто-детритового вапняку з рештками невідомого організму, який знайшов Леонід Іванович Константиненко у вапняках субіцької світи молодовського горизонту на лівому березі Студеницької затоки водосховища Дністровської ГЕС. Попри первинну інтерпретацію фосилії як корала, детальне дослідження знахідки показало наявність тонкої (близько 5 мм) пластинки, котра складена ромбовидними в перетині елементами (призмами), які утворюють спіральну структуру подібну до суцвіття соняшника. Такі деталі морфології відповідають виду *Receptaculites occidentalis* — представнику проблематичної групи викопних організмів під назвою рецептакулітиди, представників якої фіксують у відкладах від ордовіку до пермі на багатьох континентах. Ці організми довгий час вважалися проблематикою і навіть зараз їхнє систематичне положення є предметом дискусій. Попри попередні інтерпретації подібних зразків як коралів, губок чи моховаток, нові дослідження мікроструктури дозволили уточнити їхнє систематичне положення та класифікувати їх як вапнисті водорості порядку *Dasycladales*. Ми вперше наводимо *Receptaculites occidentalis* для відкладів ордовіку України. У статті представлено опис фосилії, її зображення, показані результати порівняння знахідки зі зразками рецептакулітид із фондів Національного науково-природничого музею НАН України, які походять із силурійських відкладів Баррандієна (Чехія). Ці дані розширюють наші знання про палеонтологічну різноманітність субіцької світи, дозволяють уточнити особливості та палеогеографії морських басейнів пізнього ордовіку.

Ключові слова: *Receptaculites*, вапнисті водорості, *Dasycladales*, верхній ордовик, Поділля.

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Introduction

In memory of Leonid Konstantynenko (1943–2014)

The Ordovician succession of western Ukraine comprises several lithostratigraphic units, namely the Vyzhivka Group (= regional series), which is subdivided into the Leetse, Smidyn, and Pischka formations in Volyn, and the Molodove Horizon in Podillia, consisting of two formations: the Horaivka Formation (Middle Ordovician) and the Subich Formation (Upper Ordovician) (Anfimova & Grytsenko, 2023). The Horaivka and Subich formations commonly yield diverse marine fossils (Konstantinenko, 2011, 2013).

Most exposures of this sequence are now submerged beneath the Dniester Hydropower Station reservoir (Fig. 1), which complicates field investigations. However, several outcrops remain above the water level and provide valuable information about the Late Ordovician ecosystems. These outcrops were thoroughly studied by Dr. Leonid Konstantynenko prior to the filling of the reservoir. The grey carbonate strata traditionally represent shallow-marine deposits exposed along the banks of the Dniester River. The limestones of the Subich Formation contain abundant fossils, and newly exposed outcrops that appeared after the construction of the Dniester Hydropower Station have yielded particularly interesting finds. Fossils discovered here include corals, stromatoporoids, bryozoans, brachiopods, mollusks (cephalopods, bivalves, gastropods), crinoids, and other marine organisms (Anfimova & Grytsenko, 2023).

The preservation of these fossils depends strongly on burial conditions, as well as on diagenetic processes such as recrystallization and mineralization. Detailed analysis using thin-section microscopy has revealed a remarkably intricate internal structure.



Fig. 1. Geographical location of the outcrop with *Receptaculites occidentalis* Salter, 1859.

Рис. 1. Географічне положення відслонення, з якого походить *Receptaculites occidentalis* Salter, 1859.

We examined a sample of grey clayey-detrital limestone containing the remains of an unknown organism, collected by Leonid Ivanovych Konstantynenko from the Subich Formation of the Molodove Horizon, exposed on the left bank of the Studenytsia Bay of the Dniester Hydroelectric Power Station reservoir. Although the fossil remains were initially interpreted as a coral, detailed study revealed a thin (~5 mm) plate composed of rhomboidal cross-section prisms arranged in a spiral pattern resembling a sunflower inflorescence. These morphological characteristics correspond to the species *Receptaculites occidentalis* Salter, 1859, a member of a problematic group of fossil organisms found in deposits ranging from the Ordovician to the Permian on many continents.

The genus *Receptaculites*, known for more than 200 years, has long posed taxonomic difficulties. Receptaculitids (or Receptaculitaceae, according to recent studies) have at various times been interpreted as foraminiferans, 'sunflower corals', echinoderms, or sponges. However, recent research supports their classification as calcareous algae. Until now, no remains of calcareous algae had been reported from the Upper Ordovician deposits of Podillia.

The objectives of this study are: (1) to describe *Receptaculites occidentalis* Salter, 1859, representing the first record of a receptaculitid in Ukraine, and (2) to draw conclusions regarding the palaeoenvironmental conditions of its occurrence.

Geological setting

The sedimentary succession on the western slope of the Ukrainian Shield is highly diversified, comprising strata of various systems — Ediacaran, Cambrian, Ordovician, Silurian, and Devonian — that form the monoclinial cover of the Neoproterozoic and Palaeozoic portion of the Podillian Plate

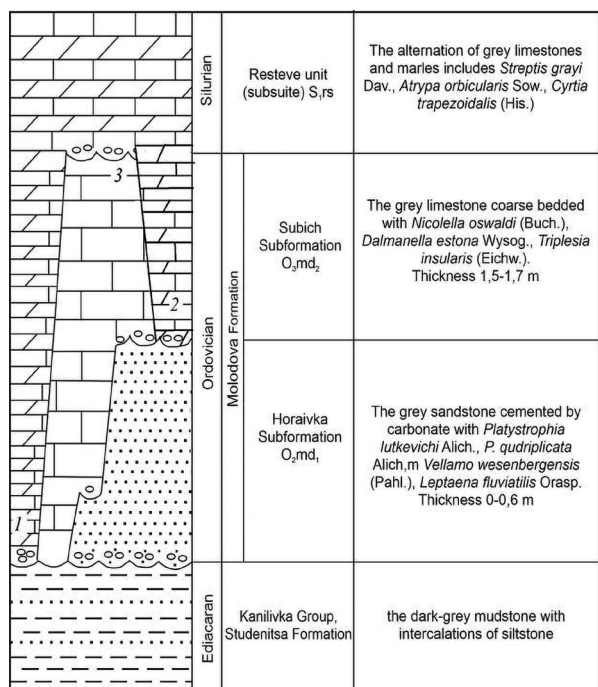


Fig. 2. The generalization of the Ordovician sections near the estuary of the Studenysia River in the Dniester Hydropower Plant (Station) reservoir.

Рис. 2. Генералізований розріз (ордовик у середній частині) в естуарії Студеницької затоки водосховища Дністровської ГЕС.

(Tsegelnyuk, 1972). This monoclinial structure is overlain by Cretaceous, Neogene, and Quaternary deposits. The specimen of *Receptaculites occidentalis* (NMNHU-G 8647/1) originates from the Upper Ordovician Subich Formation (Fig. 2) (Konstantynenko, 2011, 2013; Anfimova & Grytsenko, 2023). The formation consists of grey limestones containing a diverse assemblage of marine fossils (Anfimova & Grytsenko, 2023).

Materials and methods

Dr. Leonid Konstantynenko collected the specimen of *Receptaculites occidentalis* in 2009. The specimen is thin, broken, and subsequently glued, with a thickness of approximately 2–5 mm, and is preserved on the surface of a grey limestone bed. The sample was first meticulously washed using a powdered solution in a portable ultrasonic cleaner, and then carefully brushed. It was subsequently photographed under oblique lighting to highlight its low-relief features. The specimen exhibits well-preserved rhomboidal cells, arranged in a spiral pattern reminiscent of sunflower seeds. Comparison with published illustrations and descriptions allowed us to interpret the fossil as representing the remains of green algae.

Systematic palaeontology

Regnum Plantae, Phylum Chlorophyta, Class Ulvophyceae, Order Receptaculitales

Family Receptaculitaceae, Genus *Receptaculites* DeFrance, 1827

Type species: *Receptaculites neptuni* DeFrance, 1827; Devonian of Europe.

Diagnosis. The bodies have oval, round or disk shapes. The sizes are different. The external cover is constructed from little diamond-shaped scales (squamula) from 3 up to 5 mm, which are located by spiral rows, like Sunflower seeds. The radials have cylindrical shapes thickened at the ends.

Species included: *Receptaculites abhorrens*, *R. arcticus*, *R. australis*, *R. biconstrictus*, *R. bronni*, *R. bursiformis*, *R. calceferus*, *R. camacho*, *R. carbonarius*, *R. chardinii*, *R. cornucopiae*, *R. crassiparies*, *R. damesii*, *R. elegantulus*, *R. ellipticus*, *R. elongates*, *R. forniculosus*, *R. fungosus*, *R. globularis*, *R. maeandriiformis*, *R. monticulatus*, *R. neptuni*, *R. occidentalis*, *R. orbis*, *R. poelmii*, *R. radiates*, *R. rhombifer*, *R. sacculus*, *R. scyphioides*, *R. tessellatus* and others. Nevertheless, the list requires a thorough revision.

Receptaculites occidentalis Salter, 1859

Figs 3, 7

Material. Specimen NMNHU-G 8647/1 from the outcrop on the left bank of the Dniester Hydropower Station Reservoir; Upper Ordovician, Molodove Horizon, Subich Formation.

Description. The sample has the shape of a disk with an uneven surface, measuring approximately 10 × 8 cm in diameter and up to 5 mm or more in thickness. The colony consists of diamond-shaped

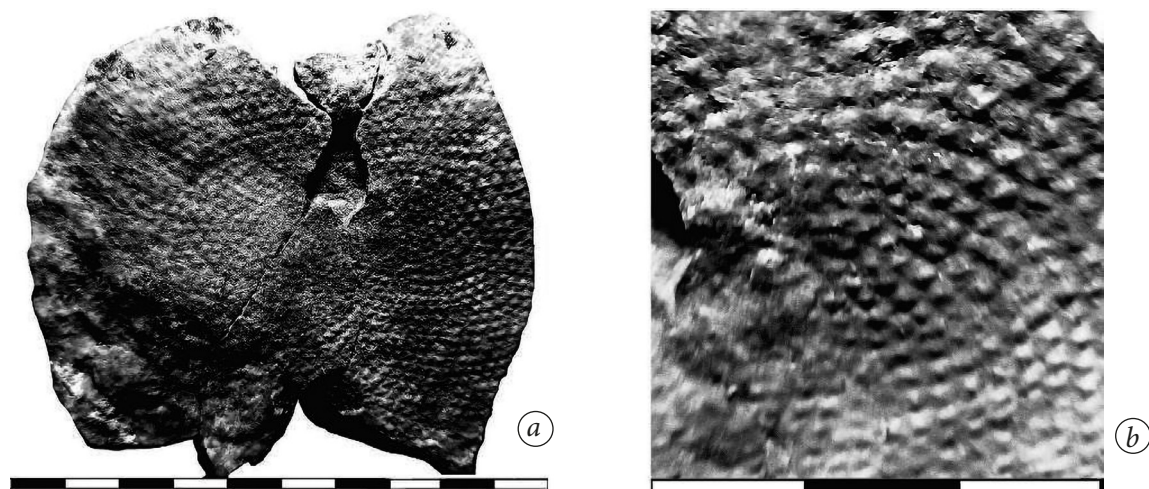


Fig. 3. *Receptaculites occidentalis* Salter, 1859: (a) view of colony; (b) detail view. Scale bar unit equals 10 mm.
Рис. 3. *Receptaculites occidentalis* Salter, 1859: (a) вигляд колонії; (b) збільшені деталі будови. Масштабний штрих – 10 мм.



Fig. 4. *Ischadites koenigi* Murchison, 1839 (NMNHU-G 582/698) from the Silurian of Loděnice, Barrandien, Czech Republic. Scale bar unit equals 10 mm.

Рис. 4. *Ischadites koenigi* Murchison, 1839 (NMNHU-G 582/698) із силуру Льоденіце, Баррандієн, Чехія. Поділki масштабної лінійки – 10 мм.

elements (plates or squamulae) measuring 2.3×3.3 mm, which are supported by cylindrical elements with extensions at both the top and bottom (Fig. 3). The lower surface of the specimen is missing; however, previous studies provide images of the cross-sectional structure of similar fossils. We assume that our specimen exhibits a comparable structure, although its preservation is imperfect due to the absence of the lower part.

Remarks. Comparison with *Ischadites koenigi* Murchison, 1839, from the Silurian of Loděnice, Barrandien, Czech Republic (specimen NMNHU-G No. 582/698), shows differences from *R. occidentalis*, including smaller size and six grains per single unit (Fig. 4). It also differs from other species in the size and morphology of the thalomes.

Stratigraphic range. Ordovician to Devonian (?Permian).

Discussion

Originally, receptaculitids were referred to as “sunflower corals,” but they are no longer considered corals (Finney *et al.*, 1994). Although receptaculitids resemble the head of a sunflower, with a double-cross spiral pattern of rhomboid-shaped plates on the surface (prisms in the interior), they are marine fossils (Byrnes, 1968) and are commonly found in ancient shallow-water sedimentary rocks of Illinois, the U. S. Midwest, and Canada (Salter, 1859; Ross *et al.*, 1982). Their first occurrences date to the Lower Ordovician, and the last known occurrences, prior to their extinction in the Upper Permian, coincide with periods of mass extinction (~250 Ma). The systematic position of receptaculitids has been debated for over a century. Salter (1859) initially placed them among the Foraminifera. Eichwald (1860) interpreted the hollow casts of vertical spicular rays as polyp cells, classifying them

as “sunflower corals”. Billings (1865) assigned them to sponges. Roemer (1861) and authorities such as Rupert Jones provisionally retained them among foraminiferans, while Dames (1868) allied them with the Orbitolitidae. Gümbel (1876) included them in the same order but assigned them to Dactyloporidae, whereas von Zittel (1924) rejected their inclusion in Foraminifera, leaving them as incertae sedis. Modern research suggests that Receptaculitaceae (Receptaculitidae) likely represent dasycladacean-like algae that flourished in warm, shallow seas, probably confined to within $\sim 15^\circ$ of the palaeo-equator (Byrnes, 1968).

Ischadites lindstroemi Hinde, 1884, from the Ordovician Daylesford Formation of central western New South Wales, Australia, occurs as a distinctive banded unit throughout the formation (Hinde, 1884). This species likely inhabited offshore and marginal shallow-water calcareous mud environments. Fully extracted silicified specimens, as well as thin sections prepared from twelve individuals, reveal their internal structure (Semeniuk & Byrnes, 1971). In particular, long cylindrical “spindles” in the center of the meroms terminate in rhombic plates at the surface, forming spiral patterns characteristic of receptaculitids.

Nitecki (1972a, 1972b) reported the presence of “gametangia” in the Silurian receptaculitid *Ischadites hemisphericus* (Hall, 1861) from North America, supporting the algal affinity of Receptaculitaceae. The gametangia are preserved in the floors of lateral heads, and their position has been compared to other receptaculitids. Interpretations of primitiveness in various Dasycladales are now questioned. Well-preserved receptaculitids from the Middle Ordovician Grapevine Mountains, Eastern California, USA, have been studied by Foster (1973). These highly variable specimens were considered intra-population variants of a single species, with variation attributed to microenvironmental differences and growth stages. They were assigned to *Ischadites mammillaris* (Walcott, 1884). This species differs from other *Ischadites* and *Receptaculites* in: (1) numerous smaller outer plates; (2) Interlocking rays between elements; and (3) curved and bifurcated inner shafts.

Although historically compared to sponges and dasycladacean algae, recent interpretations suggesting the closed extremity as a growing end are considered incorrect. Foster (1973) concluded that *Ischadites mammillaris*, along with similar receptaculitids, should retain a tentative alignment with Porifera. Spiral growth patterns, observed in receptaculitids, reflect a basic spatial-filling principle in nature, rather than a feature unique to this group. Similar constraints are observed in bryozoans, which grow in radial peripheral rows, producing comparable final patterns (Gould & Katz, 1975).

Receptaculitids from the Elk River Reef, Tennessee, USA, occupied a palaeolatitude within ~ 10 – 15° of the Ordovician equator (Alberstadt & Walker, 1976). Much controversy surrounding receptaculitids stems from difficulties reconstructing their growth mode, which result from ambiguous comparative morphological analyses and challenges in interpreting interspecific variation (Fisher & Nitecki, 1982). Consequently, they were ecologically unlike any calcareous green algae and cannot reliably serve as palaeoequatorial indicators, although merom arrangements suggest plant affinities (Beadle, 1988).

Cyclocrinids, an extinct tribe of dasycladacean algae, were anatomically similar to living dasyclads, even at early growth stages. Their siphonous cellular organization with extracellular aragonitic calcification restricted them to low-energy, warm tropical waters, often within reefal limestones, making them useful palaeoequatorial indicators (Alberstadt & Walker, 1976).

The decline of these algae during the Late Ordovician to Early Silurian may reflect simultaneous cooling and glaciation. Receptaculitids, however, are entirely unrelated organisms. Their meroms possess distinctive features not homologous to the lateral branches of cyclocrinids or dasyclads. Their extensive calcification produced sturdy thalli, allowing them to thrive in reefs and high-latitude cold-water environments. Thus, receptaculitids were ecologically distinct from calcareous green algae and remain a problematic group, despite the plant-like arrangement of their meroms. If the interpretation of specimen NMNHU-G 8647/1 as algae is correct, it allows us to infer that sedimentation occurred within the euphotic zone, i.e., under shallow-water shelf conditions. A second line of evidence

supporting this interpretation is the diversity of associated fossils. Thus, our reconstruction of the palaeoenvironmental conditions during the deposition of the grey limestones of the Subich Formation is consistent with previous studies (Anfimova & Grytsenko, 2023).

According to von Zittel (1924), the structure of *Receptaculites* comprises the following elements: a rounded or pear-shaped body with a central cavity, surrounded by a double limestone wall formed by numerous identically constructed plates arranged in spiral rows on the body's surface. Each plate, typically rhombic or hexagonal, is supported by a column (or spicule) extending radially beneath the plate. Each column bears four processes directly under the outer plate. The column extends toward the central cavity, with adjacent columns expanding and contacting each other to form an inner wall. Its processes are arranged crosswise, roughly in the same plane beneath the outer plate: two lie along the meridional plane, while the other two are perpendicular. The process directed toward the lower pole grows to join the outer plate, whereas the process directed toward the upper pole inclines slightly obliquely toward the central cavity and does not connect to the outer plate. Both the column and its processes contain axial channels (Figs 5, 6).

The lower pole of the body is surrounded by a crown of eight by four plates, while the upper pole bears a variable, generally larger number of plates (von Zittel, 1924: 84).

A detailed description of the structure of *Receptaculites* is possible due to the complexity of the material. When the specimen is well-preserved and collection integrity is not compromised, preparations can be made that reveal the fine structure (microstructure) in detail (Fig. 7). Preservation varies with

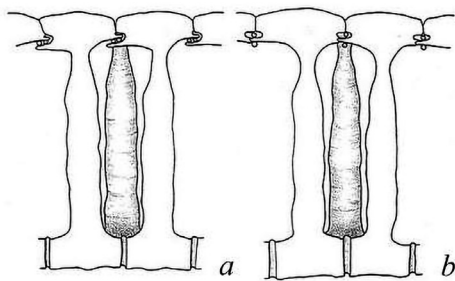


Fig. 5. Morphology of meroms of *Fisherites reticulatus*: (a) Cutaway view showing a meridional cross section (apical lacuna to left; nuclear pole to right) through meroms of one orthostichy, and the shaft (shaded) of one merom immediately to the east; (b) similar cutaway view of meroms of one circlet (and shaded shaft of a merom to the north or south) (Finney *et al.*, 1994: Fig. 7).

Рис. 5. Морфологія меромів *Fisherites reticulatus*: (a) вигляд у розрізі, що показує меридіональний поперечний розріз (апикальна лакуна ліворуч; ядерний полюс праворуч) через мером одного ортостихія та стовбур (заштрихований) та один мером безпосередньо на схід; (b) подібний розріз меромів одного кола (і заштрихований стрижень мерому на півночі чи півдні) (Finney *et al.*, 1994: Рис. 7).

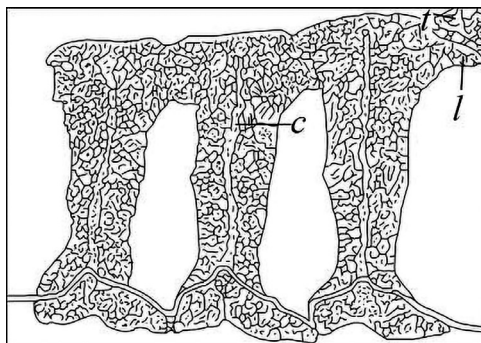


Fig. 6. *Receptaculites neptuni* Deifr.: *t*—outer plates, *l* — tangential processes, *c* — a column with an axial channel. Middle Devonian, Eifel (after Rauff, 1877).

Рис. 6. *Receptaculites neptuni* Deifr.: *t* — зовнішні пластинки, *l* — тангенціальні відростки, *c* — стовпчик з осьовим каналом. Середній девон, ейфельський ярус (за: Rauff, 1877).

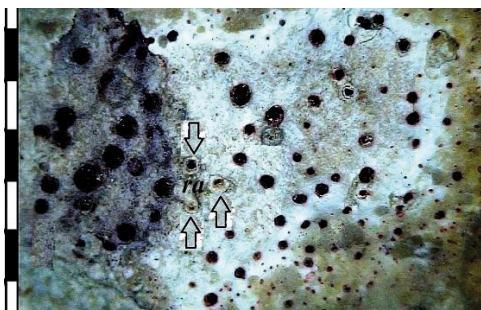


Fig. 7. *Receptaculites occidentalis* Salter, 1859 (NMNHU-G 8647/1): detail view of polished thallus surface showing black dots of carbonaceous organic tissue, white spot probably — modern lichen colony, *ra* — radial arm section or connecting neck. Scale bar unit equals 10 mm.

Рис. 7. *Receptaculites occidentalis* Salter, 1859 (NMNHU-G 8647/1): вигляд полірованої поверхні таллуса; чорні точки вуглефікована органічна речовина; біла пляма — новоутворення лишайника, *ra* — перетини радіальних рук або зв'язуючих горловин. Поділki масштабу — 10 мм.

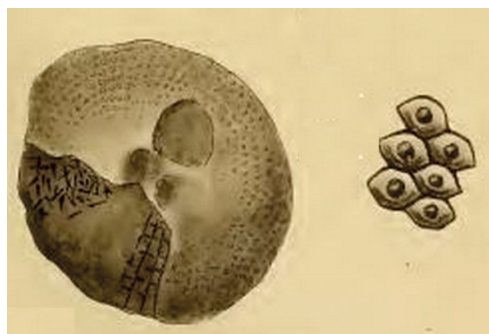


Fig. 8. *Spaerospongia podolica* Siemiradzki, 1906 (after Siemiradzki, 1906: pl. 7, fig. 35). Not to scale.

Рис. 8. *Spaerospongia podolica* Siemiradzki, 1906 (за Siemiradzki, 1906: табл. 7, фір. 35). Не в масштабі.

burial depth, and in some cases, the carbonate skeletons have been replaced by silica or even iron oxides (Hinde, 1884). Hinde's observations were based on examples of *R. neptuni* from Devonian strata in Belgium and Silesia. He considered the original form of these bodies to be open cup-shaped, as they are commonly found, rather than conical with a small central aperture, as suggested by Billings (1865). By making sections through specimens, Gümbel (1876) was able to examine their internal structure more thoroughly and expand upon the descriptions provided by Billings. Typically, the skeleton consists of three distinct layers: a thin, coaly surface layer; an upper calcitic layer; and an underlying layer of the same substance (Hinde, 1884: 801).

In the process of preparing the publication, we were sent an old publication with an image and description of a receptaculitid *Spaerospongia podolica* Siemiradzki, 1906 (Fig. 8) from the Lochkovian deposits (Borshchiv Fm.) of Ternopil Oblast (Siemiradzki, 1906: 278). He described this fossil as follows: "The only very well-preserved specimen available to us reveals the characteristic features of the genus *Spaerospongia*. The only difference is that the entire test is not cup-shaped like the Devonian *S. tessellata* Phill., but rather flat, plate-shaped, which, incidentally, is irrelevant for this group. The round, plate-shaped shell is slightly depressed in the center. From the center, the hexagonal plates are arranged in a quincunx pattern so that, depending on the lighting, they appear arranged in concentric circles, sometimes in radial rows winding to the right, sometimes to the left. Each plate bears a flat, rounded rim that occupies almost the entire surface of the plate" (Siemiradzki, 1906: 278).

Fossils occur in different preservation states, which can be categorized as follows (Hinde, 1884: 805): skeleton entirely removed, leaving only impressions or hollow casts; skeleton preserved as crystalline calcite; skeleton composed of iron oxides or pyrite; skeleton composed of silica. Merrill Foster concluded that *Ischadites mammillaris* and other similar receptaculitids should retain their tentative alignment with the Porifera (Foster, 1973). A comprehensive list of literature on receptaculitid algae can be found in the work by Nitecki *et al.* (1987).

Conclusions

Dasycladacean-like algae flourished in warm, shallow seas, and their decline during the Late Ordovician and Early Silurian likely reflects simultaneous cooling and glaciation. If Receptaculitids were cosmopolitan algae, their presence indicates shallow-water conditions with sufficient light. They also participated in the construction of bioherms. Individual finds require additional fieldwork and the preparation of further thin sections for detailed microstructural study. The typical forms of this family have been confirmed as calcareous algae (Finney *et al.*, 1994). If *Receptaculites* is correctly placed among calcareous algae within the Plantae, there is no need to rename it as *Fisherites*, because plant nomenclature is independent of zoological nomenclature (ICZN, 1999; Turland *et al.*, 2018).

Each new find contributes to a deeper understanding of palaeontological diversity, the conditions of ancient sea basins, and palaeogeographic connections. The current confusion in the systematics of receptaculitids underscores the need for further comprehensive studies of both fossil and extant algae. *Receptaculites occidentalis* is reported from the Ordovician deposits of Ukraine for the first time. This find expands knowledge of the region's palaeontological diversity. Morphological analyses clarified the systematic position of the specimen, which had previously been misinterpreted as a coral or other organismal group.

The discovered fossil indicates the presence of complex Upper Ordovician ecosystems in shallow marine environments and can serve as an indicator of palaeoecological conditions. Future research will further illuminate the evolution of marine organisms and the palaeogeography of Ordovician marine basins. Analysis of literature sources has expanded our knowledge of the chronological distribution of Receptaculitids in Palaeozoic sediments in Ukraine. We now know that on the western slope of the Volyn–Podillia Plate, finds of these problematic plants are known from the Late Ordovician to the Early Devonian.

It is important that the Siemiradskyi find has hexagonal plates, while most receptaculitids are quadrangular. In further research, we will pay more attention to this circumstance.

Acknowledgements

We would like to thank Drs Petro Tsegelnyuk, late Leonid Konstantynenko and Vladyslav Poletaev who for many years have helped us during fieldwork. We are sincerely grateful to reviewers and to the editorial board representatives and Dr. Igor Zagorodniuk for valuable comments on manuscript context to polish our article.

Declarations

Funding. National Museum of Natural History (NMNH) of the National Academy of Sciences of Ukraine funded this study (No. 0122U000429 “Scientific bases conservation of geological diversity of Ukraine in context of sustainability”, which is performed in the Department of Geology NMNH NAS of Ukraine).

Conflict of interests. The authors have no conflicts of interest to declare.

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