

<https://doi.org/10.30836/igs.1025-6814.2023.2.275044>
UDC 550.4 (477); 551.21:551.24

***Tymkivia primitiva* gen. nov. sp. nov., a new type of fossils from the Late Ediacaran (Vendian) Kanylivka Group in Podolia, Ukraine**

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Tymkivia primitiva gen. nov. sp. nov. is described from Late Ediacaran shallow-water marine rocks of the Podolia region of Ukraine. The fossils are casts of the inner surface and imprints on the surface of bacterial mats (“death masks”) of small, sedentary sac-like organisms. Numerous imprints on the surface of mudstone and siltstone slabs testify to the existence of mass settlements of these organisms in the Volyn-Podilsky sedimentary basin in the Late Ediacaran. Morphological details that could be interpreted as a mouth, anus, and internal organs are not found in the fossils. *Tymkivia* was found in association with bacterial mat remains, and the carbonaceous compressions of *Vendotaenia*, *Kanilovia*, and the problematic rod-shaped *Harlaniella*. *Tymkivia* is interpreted as possible remains of benthic plants; it is morphologically similar to some modern green algae. The option of interpretation as a fossil record of the polyp stage of Medusozoa (Cnidaria) cannot be ruled out either. The appearance and disappearance of these organisms are the benchmarks of the stage of sedimentation of the Kanylivka Group.

Keywords: Ediacaran; Vendian; taphonomy; Podolia; green algae.

Citation: Martyshyn A.I. 2023. *Tymkivia primitiva* gen. nov. sp. nov., a new type of fossils from the Late Ediacaran (Vendian) Kanylivka Group in Podolia, Ukraine. *Geologičnij žurnal*, 2 (383): 58–67. <https://doi.org/10.30836/igs.1025-6814.2023.2.275044>

Цитування: Мартишин А.І. *Tymkivia primitiva* gen. nov. sp. nov. – новий вид скам’янілостей з відкладів канилівської серії пізнього едіакарію (венду) Поділля, Україна. *Геологічний журнал*. 2023. № 2 (383). С. 58–67. <https://doi.org/10.30836/igs.1025-6814.2023.2.275044>

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Introduction

Fossils of bag-shaped organisms are quite rare in the Late Ediacaran sedimentary rocks of the Podolia (Podolia) region. An exception is the mass accumulation of possible cnidarian *Nemiana simplex* Palij, 1976, which usually show plastic deformation of their originally spherical bodies. *Vaveliksia velikanovi* Fedonkin, 1983 is characterized by a sac-shaped morphology; it was found in the deposits of the Lomoziv (Lomozov) Member of the Mohyliv (Mogilev) Formation of the Mogilev-Podolsky Group (Velikanov et al., 1983). Information about such records is scarce in publications from other regions with Ediacaran rocks. The bag-like fossil *Vaveliksia vana* Serezhnikova, 2004 is known from the Yorginskya Formation at the coast of the White Sea (Ivantsov et al., 2004). This species was interpreted as the likely ancestor of the Porifera based on the presence of spicule-like elements on the surface of their bodies. *Vaveliksia velikanovi* is known in the deposits of the Mogilev-Podolsky Group in Podolia (Nesterovsky et al., 2018). This discovery made it possible to compare *Tymkivia* gen. nov. and *Vaveliksia* and recognize important differences between them.

Accumulations of small bag-like fossils were discovered in the deposits of the Late Ediacaran Kanilovka Group (Kanilovskaya Series in the Russian-language literature) during fieldwork in 2015. Dozens of similar fossils were collected in outcrops along the Dniester River and its left tributaries in subsequent field seasons. Poor knowledge of the deposits of the Kanilovka Group, atypical morphology, and the small size of most of the fossil remains were the reasons why the material did not attract the attention of previous researchers. The new fossils show a significant range of morphological variation due to taphonomic factors.

Geological situation

The study area is located on the Podilskiy ledge on the southwestern slope of the Ukrainian crystalline shield. This region was a continental slope in the Late Precambrian (Velikanov et al., 1983). At the base of the sediments of the basin, there are crystalline rocks of the Paleoproterozoic: granites, migmatites, and their weathering products. The basement rocks are divided by numerous vertical faults into tectonic blocks with different ampli-

tudes of subsidence and uplift. On the surface of the blocks, which were raised close to the water surface, there were favorable conditions for the development of biotic communities of Ediacaran organisms. A thick layer of clastic rocks accumulated in the basin during the slow subsidence of the continental slope during the Ediacaran and early Cambrian times (Velikanov et al., 1983). Clastic rocks of different facies lie with a slight slope (1–2°) in the southwest direction (Gozhik, 2013).

The Ediacaran sedimentary succession in Podolia was studied in detail during the 1960s and 1970s; a detailed stratigraphic scheme of the deposits has been compiled and stratotype sections have been described (Korenchuk, Ishchenko, 1980; Velikanov et al., 1983). Subdivisions of the stratigraphic scale was based on lithological and paleontological features. Ediacaran rocks are accessible for study in outcrops along the Dniester River (Fig. 1). A part of the Volyn Group (Early Ediacaran), the complete section of the Mogilev-Podolsky and Kanilovka groups (Late Ediacaran), the transitional Okunets Formation and the Khmelnytsky Formation (Early Cambrian) are exposed in surface outcrops (Fig. 2). The Middle Ordovician, Early Silurian, Cretaceous, and Neogene carbonate sequences overlie these deposits. Kanilovka Group rocks overlie the deposits of the Mogilev-Podolsky Group with an unconformity. This sequence cuts off the more ancient levels of the Ediacaran up to



Fig. 1. Regional scheme of the research area. Outcrops of Ediacaran rocks:

1 – Vinozh, 2 – Popelyukhy Ravine, 3 – Bandashivka, 4 – Novodnistrovsk quarry, 5 – Bernashivka, 6 – Mohyliv-Podilskyi, Borshchiv Ravine, 7 – Lypchany, 8 – Tymkiv, 9 – Berezivka, 10 – Gorayivka, 11 – Kytaygorod

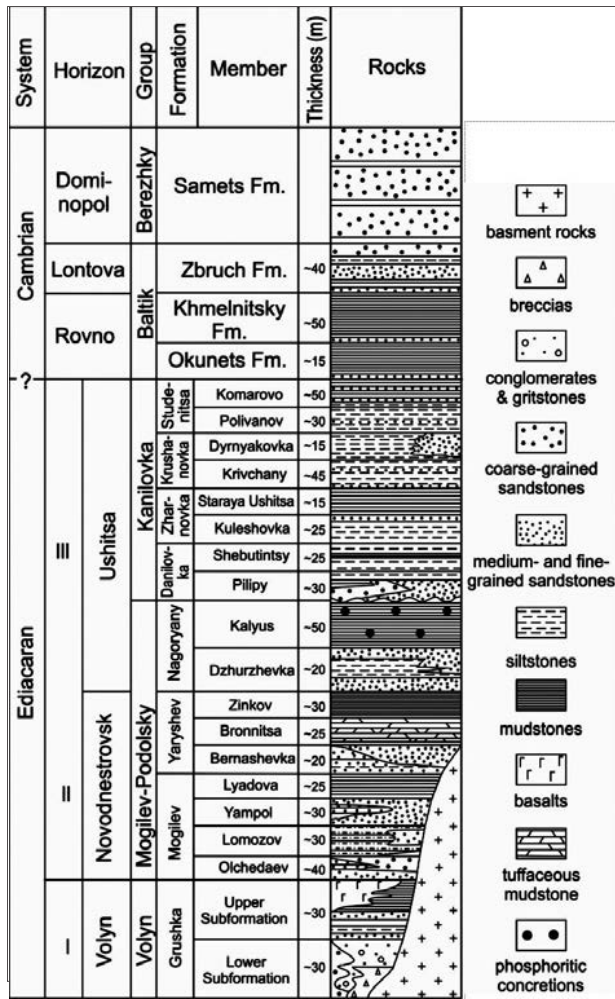


Fig. 2. Stratigraphic scheme of Upper Ediacaran deposits of Podolia

the Volyn Group in the direction from the Dokanilovskiy trough to the Galician geosynclinal trough (Gozhik, 2013). The Kanilovka Group includes four sedimentation rhythms. Each of these rhythms has a basal sandstone part and predominantly mudstone-siltstone interbedding higher in the section (Korenchuk, Ishchenko, 1980). These rhythms served as the basis for the identification of stratigraphic units, which were named the Danilovka, Zhar-novka, Krushanovka, and Studenitsa formations (see Fig. 2). The constituent elements of these rhythms were identified as Members (Velikanov et al., 1983).

Outcrop description

Fossils of *Tymkivia primitiva* gen. nov. sp. nov. were collected from outcrops of the Danilovka and Studenitsa formations near the villages of

Tymkiv, Kytaygorod, Berezivka, Khrebtiviv and Buchaya (Khmelnyskiy region) (see Fig. 1). The fossil site near the village of Tymkiv is located on the western outskirts of the village in an inactive quarry on the right slope of the Ushitsya River. Dark gray bituminous mudstones of the Kalyus Member are exposed in the lower part of the quarry (Fig. 3, A). The weathering crust sustained along the strike is recognized at the upper boundary of these mudstones. This layer of half a meter thickness is a loose claystone. The boundary with the Pilipy Member sandstones, a member of the Kanilovka Group, is sharp. Erosion patterns are imprinted on the lower surface of the sandstone. Bag-like fossils were collected in the basal layer of sandstones of the Pilipy Member and in the overlying layers. Above the basal layer lies a sequence of siltstones and mudstones with separate interbeds and lenses of fine-grained sandstones. The problematic rod-shaped fossil *Harlaniella podolica* Sokolov, 1972, a representative of the Namibian type biota *Rangea schneiderhoehni* Gurich, 1930, a member of the dickinsoniid group *Epibaion axiferus* Ivantsov, 2002, ring-shaped fossils of *Nimbia* cf. *occlusa* Fedonkin, 1980, spherical *Beltanelloides* sp., imprints of thalli of *Arumberia banksii* Glaessner & Walter, 1975, algal phytollems *Vendotaenia antiqua* Gnilovskaya, 1971 and *Kanilovia insolita* Istcenko, 1983, trace fossils of *Didymaulichnus* cf. *miettensis* Young, 1972 form a biotic association with *Tymkivia primitiva* at a locality near the village of Tymkiv (Glaessner, Walter, 1975; Ivantsov, Malakhovskaya, 2002; Nesterovsky et al., 2018).

The outcrop near the village of Kytaygorod has been studied by many researchers (Korenchuk, Ishchenko, 1980; Velikanov et al., 1983 and references therein; Martyshyn, Uchman, 2021). The abandoned quarry is located on the left slope of the Ternava River near the bridge (see Fig. 3, B). The upper part of the Komarovo Member of the Studenitsa Formation is composed of intercalation of mudstones and siltstones. These deposits are overlain by mudstones of the transitional Okunets Formation and a mudstone-siltstone-sandstone succession of the Early Cambrian Khmelnytskyi Formation (see Fig. 2). The ichnofossils *Treptichnus pedum* Seilacher, 1955 and numerous traces of burrowing organisms occur in the section at the boundary between the Okunets and Khmelnytsky formations (Seilacher, 1955; Nesterovsky et al., 2018).

The lower base of the distribution of ichnofossils is a centimeter layer of glauconite, which is the conspicuous horizon in the section. According to the author of this work, this level can be considered the boundary between the Ediacaran and Cambrian systems. Fossils of *Tymkivia* were found in the middle part of the lower ledge of the quarry in the mudstone of the Komarovo Member. Remains of several morphotypes of *Harlaniella*, carbonaceous compression fossils of *Vendotaenia*, *Tyrasotaenia*, and imprints of the problematic *Palaeopascichnus delicatus* Paliy, 1976 have been collected from this outcrop in the Komarovo Member rocks (Paliy, 1976; Nesterovsky et al., 2018). One specimen of the probable ancestor of chordates (Tunicata) *Burykhia* sp. was discovered here at approximately the same level as *Tymkivia* (Martyshyn, Uchman, 2021). The geographic coordinates of the location

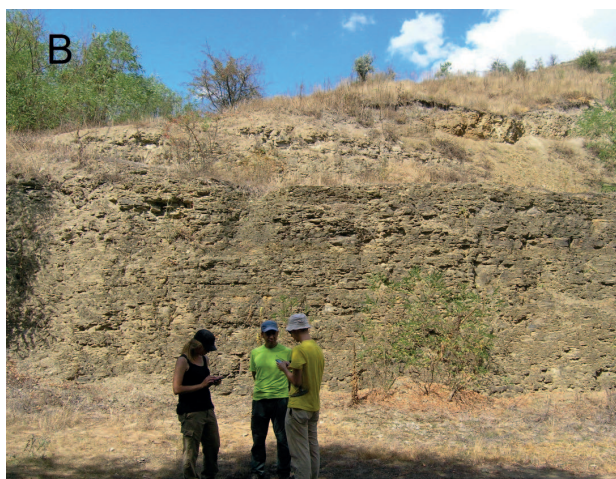


Fig. 3. Outcrops of Late Ediacaran section on which research was conducted:

A – outcrop of the boundary of deposits of Nagoryany and Danilovka formations near Tymkiv village; B – outcrop of the uppermost part of the Late Ediacaran near Kitaygorod village

where the holotype of *Tymkivia primitiva* was found are 48°63'84" N, and 26°78'21" E (see Fig. 3).

The outcrop near the village of Berezivka, Khmelnytsky region, is located at the mouth of the Danylivka River at its confluence with the Dniester River (see Fig. 1). Mass accumulations of *Tymkivia* fossils were found in the basal layers of the Pilipy Member siltstones. Imprints of *Arumberia banksii* and undescribed bilateral trace fossils constitute the biotic association of the basal sequence here. Fossils of *Arumberia* are represented by several morphotypes and are probably the remains of algae (Kumar, Pandey, 2008; McMahon et al., 2022).

Materials

The fossils described here were collected during fieldwork between 2015 and 2022. The author has collected more than 30 fossil slabs in varying degrees of preservation. This work uses seven slabs that illustrate different fossil preservation types. The high densities of aggregations and the wide range of fossil preservation do not allow an accurate count of individuals. The specimens of the described taxon are stored in the collection of the T. Shevchenko Kyiv National University, Monographic Collection No. 26.

Systematic description

FAMILY INCERTAE SEDIS

Genus *Tymkivia* gen. nov.

Etymology. From the village of Tymkiv, Khmelnytskyi region, where the first specimen was found.

Type species: *Tymkivia primitiva* sp. nov.

Diagnosis. Soft-bodied, sac-like organism less than a centimeter in size. The imprint of the organism's body is elongated-oval, wider at the upper end and narrower towards the lower end. The lower end is conical or conically rounded, the upper end is spherical. The organism's length exceeds the maximum width by 2.5–3 times.

Species composition: The genus is monotypic.

Comparison. The new genus is partially similar to the rather rare *Vaveliksia* Fedonkin, 1983, but differs by several times smaller size and morphology of the attachment structure (the attachment is a conical “anchor” in *Tymkivia* in contrast to a voluminous disk in *Vaveliksia*).

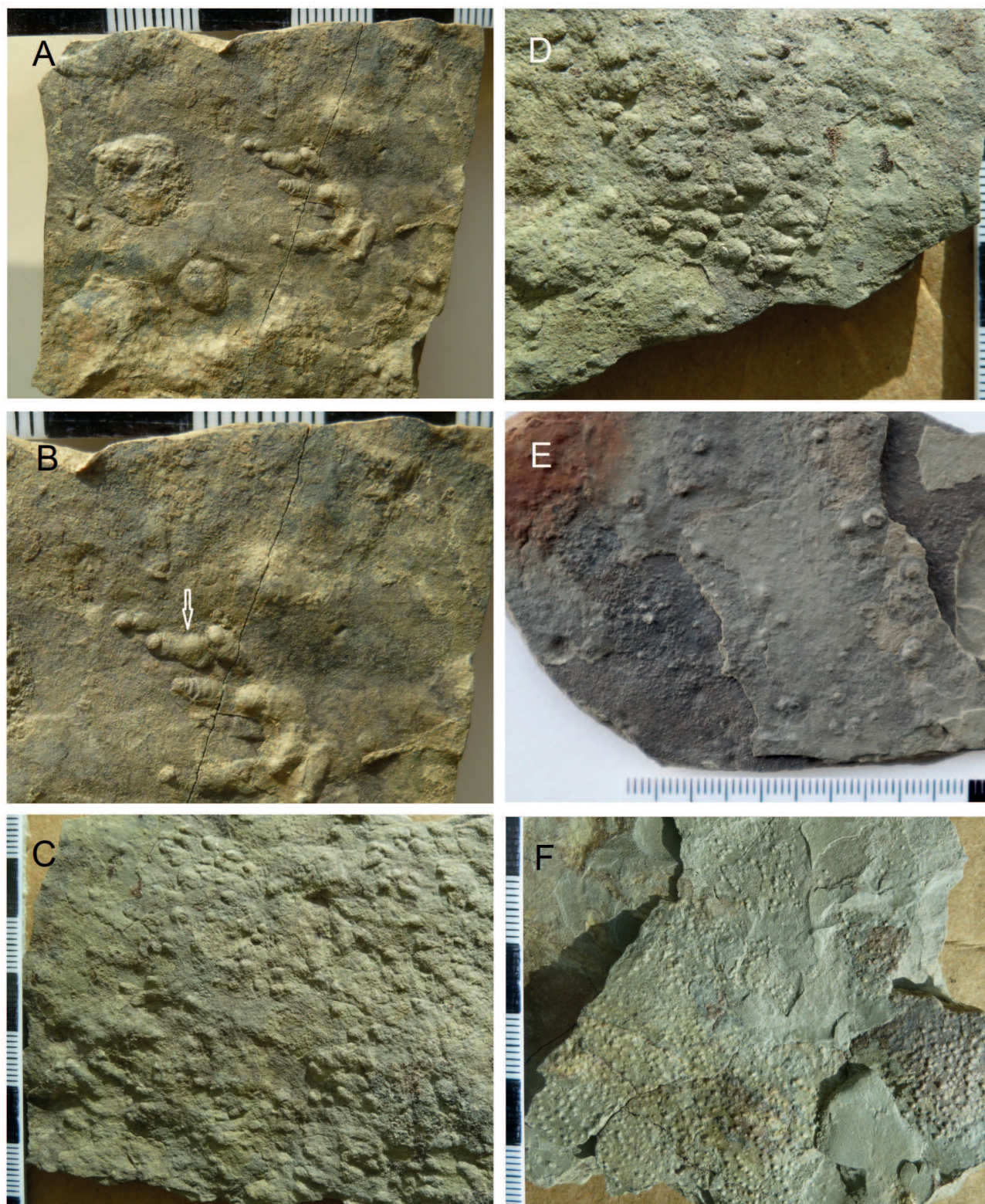


Fig. 4. Fossils of *Tymkivia primitiva*:

A – specimen IG KNU No. 17p195. Holotype of *Tymkivia primitiva*. Positive hyporelief. Kytaygorod outcrop. Komarovo Member; B – fragment of specimen IG KNU No. 17p195. Holotype of *Tymkivia primitiva* (white arrow). Positive hyporelief; C – specimen IG KNU No. 17p261. Three-dimensional casts of bodies *T. primitiva* in an inclined and lying position. Positive hyporelief. Tymkiv outcrop. Pilipy Member; D – fragment of specimen IG KNU No. 17p261; E – specimen IG KNU No. 17p257. Impressions of attachment anchors on the lower surface of layer 1 (right) and imprints of the upper end of the *Tymkivia* bodies on the lower surface of layer 2 (left). Positive hyporelief. Kytaygorod outcrop. Komarovo Member; F – specimen IG KNU No. 17p262. Mass accumulation of *Tymkivia* on two layers of mudstone. Positive hyporelief. Tymkiv outcrop. Pilipy Member

Organisms of a new species are usually found in mass aggregations or groups, while *Vaveliksia* is rather rare single specimens or small group settlements.

***Tymkivia primitiva* sp. nov.**

Etymology. From the Latin *primitiva* (primitive), because the impressions and casts of the bodies of the organism have a simple form and are devoid of signs of internal or external organs.

Holotype. IG KNU No. 17p195 (Fig. 4, A, B); from the left slope of the Ternava River valley near the village of Kytaygorod, Khmelnytskyi region; Late Ediacaran Komarovo Member (Studenitsa Formation, Kanilovka Group).

Holotype dimensions: Length of the sac-like body 5 mm, width 2 mm. The diameter of the attachment cone is about 1 mm, it protrudes above the rock level by less than 1 mm. The convex cast of the sac-shaped body protrudes above the lower surface of the rock by about 0.2 mm.

Description. The holotype (Fig. 4, B) is an elongated oval bag-shaped cast on the lower surface of a thin layer of mudstone. One end is wider and more rounded (taken here as the upper one), and the opposite end is more elongated with a conically rounded end. The edges of the imprint are clear, and the surface is smooth and complicated by minor deformations, probably of a post-mortem nature.

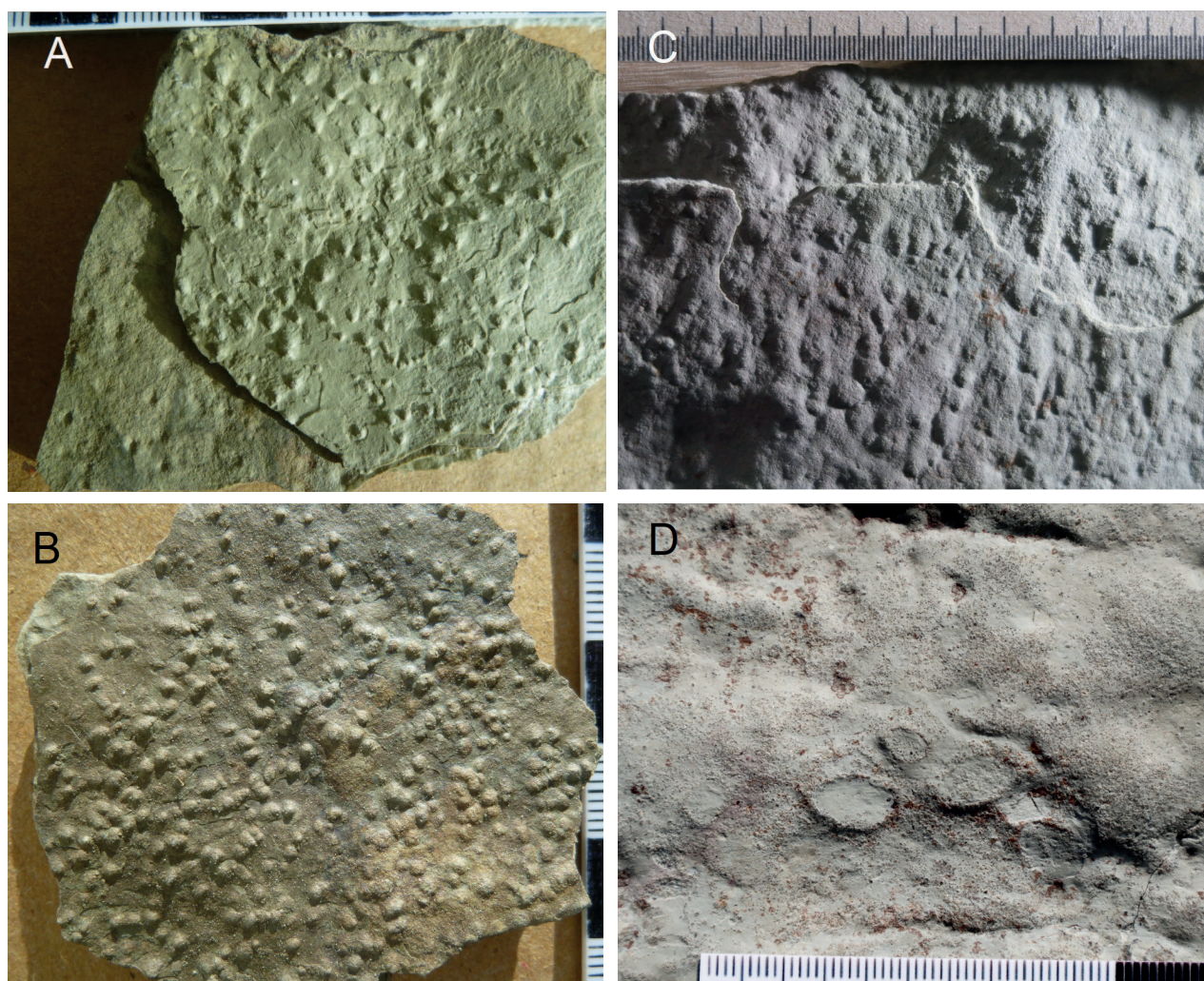


Fig. 5. Taphonomic variants of *Tymkivia* fossils:

A – specimen IG KNU No. 17p263. Impressions of attachment anchors on the lower surface of layer 1 (right) and imprints of the upper end of the *Tymkivia* bodies on the lower surface of layer 2 (left). Positive hyporelief. Tymkiv outcrop. Pilipy Member; B – specimen IG KNU No. 17p264. Mass accumulation of *Tymkivia*. Positive hyporelief. Tymkiv outcrop. Pilipy Member; C – specimen IG KNU No. 17p266. Body prints of *T. primitiva* on the bottom of a sandstone slab. Positive hyporelief. Berezivka outcrop. Pilipy Member; D – specimen IG KNU No. 17p266. Impressions of a transverse section of *T. primitiva* bodies filled with clay on the upper surface of a sandstone layer. Berezivka outcrop. Pilipy Member

Next to the holotype are seven other *Tymkivia* prints with approximate size and morphology.

Taphonomy and preservation. The most common form of preservation shows that only anchor attachments are preserved in the form of conical or round-conical relief protrusions at the bottom of mudstone beds (Fig. 4, F; Fig. 5, A, B). Attachment anchors with body imprints are much rarer (Fig. 4, A–D; Fig. 5, C). Sometimes there is such a variant of volumetric preservation: conical anchors in the lower plane of the layer (Fig. 5, C) and a ring or oval ridge on the upper surface on the opposite side (Fig. 5, D). The rock layer thickness in such cases is 5–10 mm, and the wall width of the annular ridge is in the range of 0.5–1 mm. Such fossils show a cross-section of the body of organisms (Fig. 6). The inner part of such three-dimensional casts is often filled with finely dispersed clay mass (Fig. 5, D). These fossils often show a unidirectional recumbent or reclining posture of organisms during burial; they recorded the direction of the mudflow front, leading to rapid burial (Fig. 4, C, D; Fig. 5, C).

Specimens IG KNU No. 17p261 (Fig. 4, C), IG KNU No. 17p266 (Fig. 4, D), and IG KNU No. 17p263 (Fig. 5, A) show a cast of a body buried in an inclined position. The lower conical end protrudes at an acute angle to the plate surface (positive hyporelief). The rest of the body and the upper end is inside the rock layer. Concave imprints at the bottom of the upper layer show the spherical shape of the upper end of *Tymkivia*'s body. (see Fig 4, E; Fig. 5, A). The length of the visible

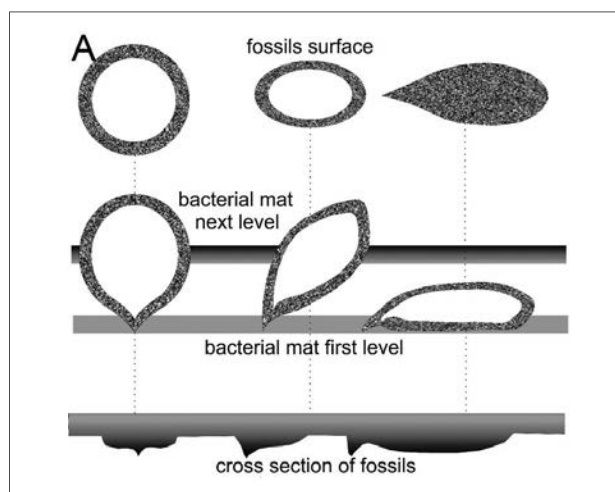


Fig. 6. Reconstruction of the formation processes of various taphonomic variants of *T. primitiva*

part is 3.5 mm, the width is 3 mm; the anchoring width is about 0.5 mm. Pointed and oval-conical fastening anchors cover the bottom of the slab. More than 20 *Tymkivia* fossil slabs are not presented in this work because they are similar to those described here.

Comparison. *Tymkivia primitiva* differs from *Vaveliksia velikanovi* Fedonkin in a much smaller size (*Tymkivia* has a maximum body length of up to 15 mm, a width of 5 mm vs *Vaveliksia* has a maximum body length of up to 80 mm, a width of 20 mm) (Velikanov et al., 1983). *Tymkivia*'s absence of an attachment disc.

Prevalence. Ukraine, Podillia, Khmelnytskyi region, Late Ediacaran, Kanilovka Group.

Material. The holotype and IG KNU No. 17p257–17p260, Kytaygorod village, Komarovo Member (Studenitsa Formation, Kanilovka Group, Late Ediacaran); specimens No. 17p261–17p265, Tymkiv village; specimens No. 17p266–17p268, Berezivka village; specimens No. 17p269, 17p270, Khrebtiviv village, Pilipy Member (Studenitsa Formation, Kanilovka Group, Late Ediacaran). All outcrops are located in the Khmelnytskyi region.

Discussion

Tymkivia primitiva shows a close similarity with bacterial mats that served as a support platform for fixation on the seabed (Fig. 4, E, F; Fig. 5, A–C). The fossils are “death masks”, meaning that they are imprints of the inner surface of bodies and imprints on the surface of bacterial films (Fig. 4, A–F; Fig. 5, A–D). This type of preservation of soft-bodied organisms is caused by a rather rapid pyritization process of organic surfaces during burial (Gehling, 1999). Such a taphonomic process was widespread in the Late Precambrian due to the formation of a biochemical membrane of a bacterial mat at the boundary between the anoxic sediment zone and the oxygenated water column (Gibson et al., 2018). An analysis of the morphology of taphonomic variants of *T. primitiva* suggests that this fossil belongs to benthic algae (Fig. 7, A, B). The grounds for such a hypothesis are as follows: a) the absence of a mouth, anus, and internal organs on the prints; b) in all likelihood, the organisms received nutrients by their diffusion through the surface; c) the close connection of extinct creatures with bacterial mats is obvious.

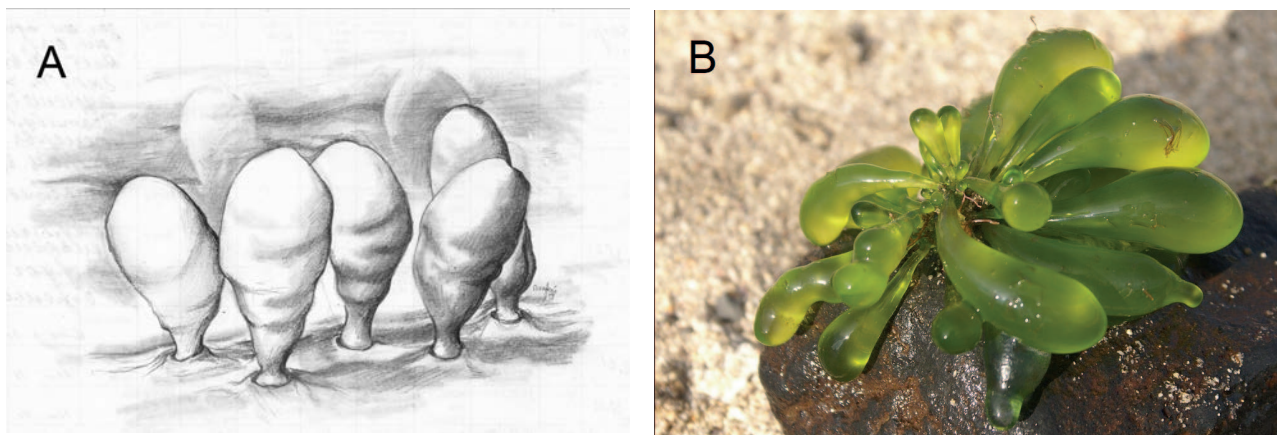


Fig. 7. Reconstruction of *Tymkivia* and modern algae:

A – reconstruction of *Tymkivia primitiva* (author Andrii Martyshyn, art editor Serhiy Solodkyi); B – settlement of modern green algae *Boergesenia forbesii* (Wikipedia.org)

Recently, it has been widely believed that the basis of the diet of Ediacaran organisms was a suspension of semi-decomposed organic matter (Sperling et al., 2011; Rahman et al., 2015). This type of diet is consistent with the putative fossil interpretation. We have found a characteristic pattern between the size parameters of *Tymkivia* and the dispersion of rocks. The sizes of imprints of the organisms in accumulations in mudstones are usually smaller than in sandstones.

Numerous carbonaceous compression fossils of the oldest benthic macroalga *Longfengshania* have been found in the Tonian deposits of China and Canada (Du, 1982; Hofman, 1985; Jing et al., 2022). Modern green algae *Boergesenia*, *Valonia*, and *Derbesia* are similar to *Tymkivia* morphologically and probably in their ecology (Fig. 7, A, B). The difference lies in the method of attachment to the substrate: modern plants are attached to solid areas of the bottom with the help of rhizoids. These modern algae are also characterized by the formation of mass settlements. Other interpretations cannot be unambiguously ruled out. For example, a fossil may be a Medusozoa (Cnidaria) polyp stage. Such a possibility exists in connection with the discovery by the author in the deposits of the Late Ediacaran in Podolia of a large number of fossils of probable Medusozoa (unpublished data).

Conclusions

Tymkivia primitiva gen. nov. sp. nov. was a widespread organism in the Volyn-Podilsky sedimentation basin. The appearance and disappearance of these organisms are the benchmarks of the stage of sedimentation of the Kanylivka Formation. *Tymkivia primitiva* shows a set of morphological parameters and preservation patterns that allow them to be interpreted as a benthic plant fossil, possibly belonging to green algae because of morphological similarity with modern representatives. The appearance of these organisms at the end of the Ediacaran period indicates the formation of a biotic association of the Phanerozoic type on the eve of the “Cambrian explosion”.

Acknowledgments

The author would like to express their gratitude to S.S. Solodkyi, who devoted participant in field expeditions and also performed the artistic editing of the reconstruction of *Tymkivia* and helped to reconstruct the scheme of taphonomic processes. The author is also grateful to the editor-in-chief of the magazine O.B. Klimchuk, who gave valuable advice and helped transform the manuscript into a meaningful text. I express my deep gratitude to all anonymous reviewers and editors for their effective help and assistance in working on the text of the article.

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Received 07.03.2023

Received in revised form 02.05.2023

Accepted 22.05.2023

Tymkivia primitiva gen. nov. sp. nov. – новий вид скам'янілостей з відкладів канилівської серії пізнього едіакарію (венду) Поділля, Україна

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У південно-західній частині України вздовж долини р. Дністер та його лівих приток відслонюється на поверхні потужна товща відкладів едіакарію (венду). Стратиграфія та літологія цих відкладів вивчені досить детально, але інформація про скам'янілі рештки все ще дуже обмежена. Найнижчий рівень вивченості має осадова товща канилівської серії. Скам'янілі рештки організмів *Tymkivia primitiva* gen. nov. sp. nov. зібрані з мілководних

морських теригенних відкладів верхнього діакарію (венду) Поділля. Фосилії є зліпками внутрішньої поверхні та відбитками на поверхні бактеріальних матів («посмертними масками») малорозмірних седентарних організмів мішководної форми. Скам'янілості демонструють тісний зв'язок вимерлих організмів з бактеріальними матами, які виконували функцію опорної платформи на поверхні мулистого осаду. Скупчення численних відбитків на нижній площині шарів аргілітів та алевролітів свідчать про існування масових поселень організмів *Tymkivia* у Волино-Подільському седиментаційному басейні у пізньовендський час. Широкий діапазон морфологічних варіантів скам'янілостей відображає тафономічні процеси захоронення м'якотілих організмів. На скам'янілостях не виявлено морфологічних деталей, які можна було б інтерпретувати як оральний і анальний отвори та внутрішні органи. Скупчення *Tymkivia* знаходяться в асоціації з рештками бактеріальних матів, обвугленими рештками водоростей *Vendotaenia*, *Kanilovia* та проблематичними стрижневидними скам'янілостями *Harlaniella*. Сукупність морфологічних ознак скам'янілих решток дозволяє припустити приналежність *Tymkivia* до бентосних водоростей завдяки морфологічній схожості з деякими сучасними зеленими водоростями. Не можна також виключати варіант інтерпретації *Tymkivia* як скам'янілостей стадії поліпів *Medusozoa* (*Cnidaria*). Поява та зникнення цих скам'янілостей у розрізі відкладів є реперами канилівського етапу осадконакопичення.

Ключові слова: едіакарій; венд; тафономія; Поділля; зелені водорості.