

A revision of Silurian corals (Anthozoa: Heliolitoidea) from the collection of the National Museum of Natural History, NAS of Ukraine (Kyiv)

Volodymyr Grytsenko, Kseniia Rudenko

National Museum of Natural History, NAS of Ukraine

article info

key words

Heliolitoidea diversity, Silurian, reference section, Podillia, museum collections.

correspondence to

Volodymyr Grytsenko; National Museum of Natural History, NAS of Ukraine, 15 Bohdan Khmelnytsky Street, Kyiv, 01054 Ukraine;
Email: favosites@ukr.net;
orcid: 0000-0003-2904-4851

article history

Submitted: 12.04.2023. Revised: 25.12.2023. Accepted: 30.12.2023

cite as

Grytsenko, V., K. Rudenko. 2023. A revision of Silurian corals (Anthozoa: Heliolitoidea) from the collection of the National Museum of Natural History, NAS of Ukraine (Kyiv). *GEO&BIO*, 25: 75–108. (In English)

abstract

The collection of Silurian heliolitoid corals revised in this study has been assembled by the first author (V.G.) for four decades. The material was collected predominantly from Silurian outcrops and borehole cores in the Middle Dnister area. Some of the specimens were found in Belarus and Moldova during field works and field trips. The scientific works were part of the projects elaborated by a collective of scientists from the Institute of Geological Sciences, NAS of Ukraine and Taras Shevchenko National University of Kyiv. The working group consisted of geologists who graduated from the university in 1965 to 1970. Professors M. M. Klushnikov and O. L. Einor were our advisors. P. D. Tsegelnjuk was the oldest and the leader of the group. The collecting of specimens started in 1966 and now is ready to summarise the results. In the last fifty years, a large collection of fossil cnidarians from Silurian deposits has been assembled in the course of long-term geological field expeditions organised to study outcrops, cores of boreholes, and collect fossils. More than fifty outcrops and one hundred boreholes were studied in the territory of the Podillian region and the west slope of the Ukrainian Shield from Volyn to Snake Island. The collection comprises nearly ten thousand samples and 6000 thin sections of cnidarians. The total number of the studied samples belonging to Heliolitoidea is 139, of which 19 came from 9 outcrops and 120 from cores of 37 boreholes. The described samples represent 3 orders, 1 superfamily, 8 families, 2 subfamilies, 16 genera, 20 species (11 new), and 1 new subspecies. The authors consider that all the remains belong to fossil cnidarians. Fossil cnidarians are especially important from a facial point of view. The remains primarily indicate normal sea conditions in warm subtropical and tropical zones. In some cases, the identification of fossil cnidarians is easy, but usually we need to use the oriented thin sections. In the paper, only a small part of the collection is described following the system of Heliolitoidea developed by Olga Bondarenko. A studied collection is deposited in the Geological Department of the National Museum of Natural History, NAS of Ukraine under the number GD-1986.

Ревізія силурійських коралів (Anthozoa: Heliolitoidea) із колекції Національного науково-природничого музею НАН України

Володимир Гриценко, Ксенія Руденко

Резюме. Колекція силурійських коралів геліолітоїдей, переглянута в цьому дослідженні, збиралася першим автором (В.Г.) протягом чотирьох десятиліть. Матеріал зібраний переважно з силурійських відслонень і кернів свердловин Середнього Подністрів'я. Частина екземплярів знайдена в Білорусі та Молдові під час польових робіт і екскурсій. Наукові роботи були частиною проектів, які розроблялися колективом науковців Інституту геологічних наук НАН України та Київського національного університету імені Тараса Шевченка. До робочої групи залучалися геологи, які закінчили університет у 1965–1970 рр. Нашими консультантами були професори М. М. Ключніков та О. Л. Ейнор. Найстаршим і керівником групи був П. Д. Цегельнюк. Збір екземплярів розпочато в 1966 році і зараз ми готові до підбиття підсумків. За останні п'ятдесят років велика колекція викопних кнідарій із силурійських відкладів була зібрана в ході тривалих польових геологічних експедицій, організованих для вивчення відслонень, кернів свердловин і збору скам'янілостей. На території Поділля та західного схилу Українського щита від Волині до острова Зміїного досліджено понад півсотні виходів на поверхню і сотні свердловин. Колекція налічує близько десяти тисяч зразків і 6000 прозорих шліфів кнідарій. Загальна кількість досліджених зразків Heliolitoidea становить 139, з них 19 походять з 9 відслонень і 120 з кернів 37 свердловин. Описані зразки представляють 3 ряди, 1 надродину, 8 родин, 2 підродини, 16 родів, 20 видів (11 нових), 1 новий підвид (*Propora podolica*, *Cystihalysites komarova*, *Helioplasma carinata*, *Yanetella dryganti*, *Agallelites leonidi*, *Agallelites petri*, *Bogimbailites bondarenko*, *Pseudoplasmopora spinifera*, *Pseudoplasmopora minima*, *Podolites irregularis*, *Saaremolites inversus podolica*). Автори вважають, що всі рештки належать викопним кнідаріям. Викопні кнідарії особливо важливі з точки зору фацій. Їхні залишки в першу чергу свідчать про нормальні умови моря в теплих субтропічних і тропічних зонах. У деяких випадках ідентифікувати викопні кнідарії легко, але зазвичай нам потрібно використовувати орієнтовані тонкі прозорі шліфи. У статті лише невелика частина колекції описана за системою Heliolitoidea, розробленою Ольгою Бондаренко. Досліджувана колекція зберігається в геологічному відділі Національного природознавчого музею НАН України під номером ГД-1986.

Ключові слова: геліолітоїдеї, різноманітність, опорний розріз силуру Поділля, музейні колекції.

Адреса для зв'язку: В. Гриценко; Національний науково-природничий музей НАН України; вул. Богдана Хмельницького 15, Київ, 01054 Україна; Email: favosites@ukr.net; orcid: 0000-0003-2904-4851

Introduction

One of the best sequences of Silurian (from Wenlockian to Pridolian without visible interruptions) deposits are outcropped and discovered by boreholes in the western part of Ukraine. An international stratigraphical symposium was dedicated to the evaluation of this series of exposures [Tsegelnjuk *et al.* 1983]. As result, the representatives of the Subcommittee on Silurian Stratigraphy of the International Union of Geological Sciences has improved the international stratigraphic chart and now returned to the consideration of another not yet solved problem. The Silurian session found in the program within the Subcommittee Sessions under the title 'SC13: New stratigraphic insights into the Silurian story.' The current plan for presentations devoted to GSSP candidate sections is based on new updates and data, and will discuss the recently approved category of Standard Auxilliary Boundary Stratotypes. The limitation boundary between Ludlovian and Pridolian stratotypes we consider one of the most important issue.

A recent study of lipid biomarkers of Silurian to Early Devonian reef carbonates with assessing the marine communities and carbon cycling that sustained shallow-marine ecosystems proved that the Podillian pericontinental shelf was characterised by tropical conditions. The biomarkers were extracted from core samples of boreholes of Kotuzhiny-25 [Marshall *et al.* 2022].

The other new idea about the development of biostromes in the Silurian shelf as result of tsunamis was presented by Polish researchers [Łuczyński *et al.* 2016].

The main goal of the paper is to carry out a revision of part of a large collection of Cnidaria stored in the Geological Department of the National Museum of Natural History, NAS of Ukraine in order to describe the taxonomic diversity of the fossils, to shed light on the specifics of the Podillian sea basin in the Silurian, and to draw stratigraphical and facial conclusions. The new results will be used to improve the Silurian stratigraphical chart.

History of study

The investigations of Silurian fossils in Ukraine are linked to the name of the famous Ukrainian scientist Pavel Venyukov from the second half of the 19th century [Venyukov 1899]. In the 1960s, a team of a few Russian researchers from Saint Petersburg and Moscow visited Ukraine and conducted fieldwork in the Podillian Silurian section [Nikiforova *et al.* 1972].

Ukrainian team leader Petro Tsegelnjuk started research on the Silurian and Devonian reference section connected with the construction of the Dnister Hydropower Station and planned to flood the Dnister Valley. The team elaborated a project to save the significant section by choosing new stratigraphical units (neostatotypes) for those that were going to be flooded. In the frame of the project, lithological and palaeontological samples were collected from all units of the sequence, including the Ediacaran System. Another reason for the work was practical help for geologists and palaeontologists who conducted geological prospecting in this zone. The scientists collected colossal amounts of samples of different fossils. There are corals (including Rugosa, Tabulatoidea, and Heliolitoidea), Stromatoporoids, Brachiopoda, Graptolitoidea, Trilobita, Ostracoda, molluscs (including cephalopods, bivalves, and gastropods), Bryozoa, crinoids, Conodontoida, Algae, and Chitinozoa [Tsegelnjuk *et al.* 1983]. Each researcher of the team was interested in two or more fossil groups (mostly two or three one).

The study of corals and stromatoporoid remains has been the interest of the first author (V.G.) for many years. My young colleague joined this research currently. A beginning of our collection started in 1966, when the first author was a student and participated in a fieldwork in Podillia in the so-called 'Dnister expedition' of the Geological Department of Kyiv University. For the last 55 years, a large collection of fossil cnidarians was assembled from Silurian deposits. The Silurian sequence in the west of Ukraine is represented by different varieties of limestones, which includes a rich diversity of corals. The whole collection includes Heliolitoidea but we decided to separate the superorder from other Cnidaria. Therefore, it is part of the biggest collection and this paper deals with remains of Heliolitoidea only.

The Lower Paleozoic succession of the western slope of the Ukrainian Shield includes mainly marine deposits. It is a continuation of the more extensive Paleobaltic marine basin [Motus & Gritsenko 2007; Vinn *et al.* 2022]. The differences are that the Podillian shelf is narrower and has fewer interruptions than the Baltic succession [Grytsenko 1983]. Some levels of the Podillian shelf include rich remains of Cnidaria. There is an important conclusion of Venyukov about three coral horizons in the Podillian Silurian succession [Venyukov 1899]. Then the fieldworks conducted by Boris Sokolov, Olga Nikiforova, Vera Sytova, Yuriy Tesakov, and others. They published their achievements in studying different Podillian fossil corals and brachiopods of Silurian and Devonian age [Ivanovsky 1984].

The specialists who studied fossil corals and stromatoporoids connected with each other in 1963 during the First All-Soviet Union Symposium on corals and reefs at Novosibirsk. After that, on academician Boris Sokolov's initiative, a few All-Soviet Union symposiums were organised. The second one in 1967 in Tallinn with 127 participants attending. In 1971, the first international symposium was conducted in Novosibirsk again with more than one hundred participants who represented many countries: Canada, USA, United Kingdom, France, Germanies, Bulgaria, Poland, Sweden, Japan, Australia, and some republics of the former USSR (Estonia, Kazakhstan, Tajikistan, Russia, and Ukraine). The following international symposiums were held in different countries once in four years. The coral symposiums and workshops were organised under the initiative and support of the International Fossil Coral and Reef Society (IFCRS). As a rule, symposiums of the IFCRS in different

countries were accompanied by field excursions on the region's distribution of cnidarians of different geological ages. Sometimes the participants of the field excursions could see outcropped fossil reefs. The Society edits newsletters and scientific publications with materials of each symposium, where every researcher has an opportunity to put and get essential information on investigations of the items.

The participants of the corals and sponges symposiums took part in meetings and field trips. There were conducted in the following order: 1st in Novosibirsk, USSR, 1971; 2nd in Paris, France, 1975; 3rd in Warsaw, Poland, 1979; 4th in Washington, USA, 1983; 5th in Brisbane, Australia, 1988; 6th in Munster, Germany, 1991; 7th in Madrid, Spain, 1995; 8th in Sendai, Japan, 1999; 9th in 2003, Graz, Austria; 10th in St. Petersburg, Russia, 2007; 11th in Liege, Belgium, 2011; 12th in Muscat, Oman, 2015; 13th in Modena, Italy, 2019; 14th announced in Warsaw, Poland, 2023.

Now palaeontologists and geologists have an opportunity to discuss with colleagues any problems they have in studying corals, sponges, and reefs and see examples of fossil reefs of different ages. The participants of symposiums on coral and sponges took part in the meetings and field trips. The meetings of the specialists in cnidarians are useful for the scientists because they are able to get information on new investigation, which could be important for the deeper understanding of the fossil record.

The fifth All-Union Symposium was held in Dushanbe in 1983. As a result, the 'Fanerozoic Reefs and Corals of the USSR' (Proceedings of the fifth All-Union symposium on corals and reefs) was published issued [Phanerozoic... 1986]. A report was presented on ridges of bioherms divided facial zones on a Silurian shelf in Podillia. It is useful for reconstructing past depositional environments [Gritsenko *et al.* 1997].

A detailed middle Silurian to Early Devonian biomarker stratigraphic record was obtained from thermally well-preserved strata, sampled from > 400 m long/depth drill-core of borehole No 25 from Ternopil Oblast of Ukraine, located in the Podillian peri-continental basin. These lipid biomarker records provide valuable insights into the temporal changes in microbial ecology and ocean chemistry for this ancient, tropical shallow-marine reefal carbonate platform [Marshall *et al.* 2023].

Many genera and species of Heliolitoidea are described in the chronicles of fossil corals with no obvious analogues, for example [Bondarenko 1992]. Systematic palaeontologists discover new features, which could link fossil and modern corals [Copper & Plusquellec 1993; Chatterton *et al.* 2008]. For instance, pseudomorphs of Ordovician polyps, which have six-ray symmetry as modern Scleractinia, were found in Canada [Copper 1985]. That anatomic characteristic allows suggesting a closer affinity between Heliolitoidea and Scleractinia.

The long history of studying fossil corals and their microstructure in the last decades is only one way to infer new information for a deeper understanding of the evolution of this group of fossil animals. The history of coral studies are described in more detail in [Ivanovsky 1984].

Geological setting

The Silurian sequence is located on west slope of the Ukrainian Shield represented mostly by carbonate rocks (limestone, dolostone, domarite, and marl) with a total thickness of more than 400 m. The limestone formation forms monocline structure with nearly 20 interbeds of bentonites, which are evidence of volcanic processes in the nearby Paleocarpatians (?) and could help to correlate the section inside the region. During the Middle and Upper Silurian, the sedimentary area was situated in the almost flat part of a large carbonate ramp on the margin of the Paleo-European shelf [Łuczyński, Skompski, and Kozłowski 2016; Tsegelnjuk *et al.* 1983].

Materials and Methods

The collection is stored in the Geological Department of the National Museum of Natural History, NAS of Ukraine under number GD-1986. The collection includes many fragments of rocks from Silurian sequences: cores of boreholes, samples from outcrops with fossils, and more than 6000 thin sections.

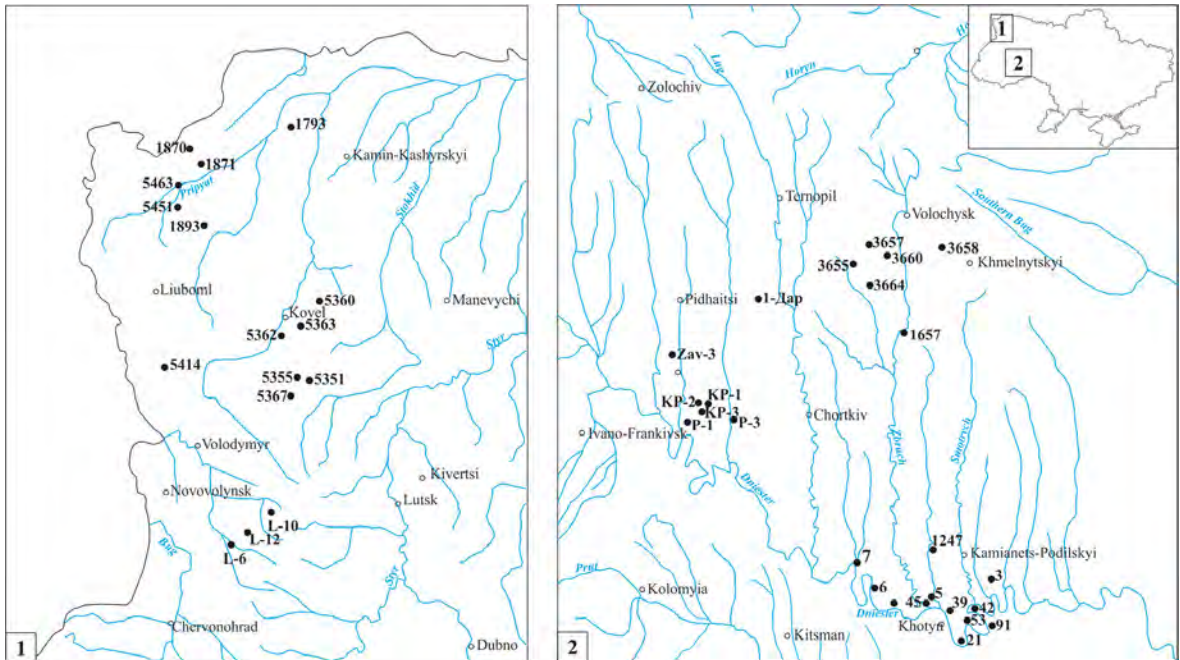


Fig. 1. The location of important boreholes: (1) Volyn; (2) Podillia (boreholes and outcrops in the Middle Dnister area).

Рис. 1. Розташування важливих свердловин: (1) Волинь; (2) Поділля (свердловини та відслонення в районі Середнього Придністер'я).

The samples represent all Silurian sequences of the western slope of the Ukrainian Shield including exposed Podillian sections and adjacent territories from Volyn to Snake Island. In Fig. 1, we show the geographical location of only part of studied outcrops and boreholes.

There are no problems in finding in the sequence and identifying the remains of corals because they differ from the rock in the outcrops and borehole cores by structure and colour. The coral and stromatoporoids remains could sometimes be identified just in the outcrop or in the borehole core wall if we apply low concentration hydrochloric acid (HCl), emphasising the coral skeleton structures. Nevertheless, as usual, the identification of corals needs specially oriented thin sections in two directions: longitudinal and transverse. In some cases, the identification requires more (serial) thin sections. Such (serial) approach is especially need for the study of *Heliolitoidea*.

Weathering and erosion reveal different surfaces of beds and sometimes show fossil remains that are preserved on or in beds of rocks. Often we have to cut sedimentary rocks using geological hammer and different (thin or strong) chisels to search for fossils inside the sequence of sedimentary rock (represented predominantly by limestones). It is perfect if parts of the animal's remains are visible on the weathered walls of the outcrop or on the polished walls of the borehole cores. Then researcher sends the sample for further operations in the laboratory, where a worker makes thin transparent sections of the needed directions and thickness to study the inner structure of the fossil corals.

If, as we expect, the fossil represents new species, serial grinding should be made. It allows seeing and measuring elements of the structure directly (diameters of corallites and intermedial tubes, distance between corallites and tabules inside it, and so on). The study and identification of *Heliolitoidea* usually require using thin sections and microscope. The authors applied a Digital Microscope, PC and traditional programs (Paint and Microsoft Office Manager, and Corel Draw).

We could make a preliminary identification by studying the weathered surface or by emphasising structure by a weak solution of hydrochloric acid (3–5 %). Sometimes, the relevant plans were studied by cutting the specimens with a diamond disc saw. Occasionally, such cut allowed us to make genus or even species definitions.

For descriptions, we follow the approach designed by Olga Bondarenko in the System of Heliolitoidea [Bondarenko 1992] applying to the Podillian diversity of Heliolitoidea and adopted in English.

The geographical location of the studied outcrops and boreholes in the territory of the western slope of the Ukrainian Shield and the outcropped Podillian region is shown in a map (Fig. 1). In this article, we consider only representatives of the superorder Heliolitoidea recovered from the outcrops (Fig. 1, 2) and from cores of boreholes (Fig. 1, 1). The total number of the studied samples of species that represent Heliolitoidea is 19 from 9 outcrops and 120 from cores of 37 boreholes (shown are only the most cited locations).

The materials have different states of preservation—some specimens are in excellent condition, but some pieces suffered the influence of secondary processes (re-crystallisation, dolomitisation, and even replacement by quartz).

The samples represent the entire Silurian sequence of the western slope of the Ukrainian Shield, including outcropped Podillian locations and closed territory from Volyn to Zmiyiny (Snake) Island. Geological setting was described in the other articles, for example in [Grytsenko 2007; Tsegelnjuk, Grytsenko, Konstantinenko, Ischenko *et al.* 1983; Gozhyk 2013].

Systematic Palaeontology

The main skeletal structures are shown in Fig. 2. The reference information is presented in small font.

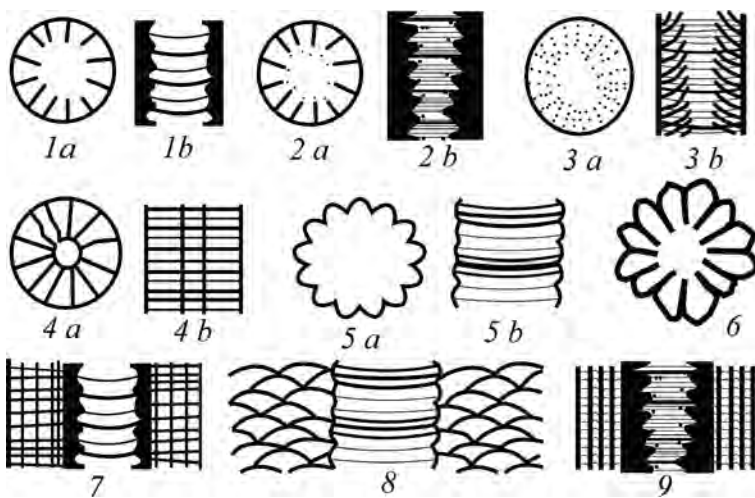


Fig. 2. The main skeletal elements of the structure of Heliolitoidea (sections *a*—transverse, *b*—longitudinal): (1) plate septa; (2) plate septa with spike ending; (3) spike septa; (4) axial tube; (5) wavy walls; (6) star-like section of corallites. Structure of coenenchyma: (7) siphonolites with more or less horizontal diaphragms; (8) cystolites, (9) parasiphonolites (coenenchymal tubes with vesicle diaphragms).

Рис. 2. Головні скелетні елементи будови скелетів *Heliolitoidea* (*a* — у поперечних, *b* — повздожніх перетинах): (1) пластинчасті септи; (2) пластинчасті септи з голчастими закінченнями; (3) голчасті септи; (4) осьові трубки; (5) хвилясті стінки; (6) зіркоподібний перетин коралітів. Структура хененхіми: (7) сифоноліти з більш-менш горизонтальними діафрагмами; (8) цистоліти (пухириста тканина); (9) парасифоноліти (ценехімальні трубки з пухиристими діафрагмами).

лясті стінки; (6) зіркоподібний перетин коралітів. Структура хененхіми: (7) сифоноліти з більш-менш горизонтальними діафрагмами; (8) цистоліти (пухириста тканина); (9) парасифоноліти (ценехімальні трубки з пухиристими діафрагмами).

Superorder Heliolitoidea Frech, 1897

Description. The colonies are different from incrusting, plate-disk and bolder-like to branching ones. The corallites are located separately or close to each other. If corallites are located close to each other, they can form chains. The separately located corallites form equal spreading, chains or disordered positions. The shapes of corallites are prismatic or cylindrical. The cross-sections are polygonal or star-like. The septa are different: spiky, thin plates, squamula-like, and bacula-trabecular. Sometimes the septa are absent. The number of septa rows is 12, rarely 6 or vary from 13 to 32. The septa can be equal to each other. Rarely one or two opposite ones are longer than others, with a possible alternation by length—6 long and 6 or more short ones. The tabula in corallites are completed or interrupted, horizontal (flat) or curved in different ways (concave or convex) and rarely bubble-like. The axial developments are either absent or present: columella, thorn, plate, membranes, prismatic tubes, trabecular, and bacula, cylindrical tube, funnel-shaped tabula, and others. The caps are simple or

trapezium-like, sometimes conical, and others. The symmetry is radial or bilateral. The coenenchima is composed of different types of heterolite structures: protolites, siphonolites, cystolites, and parasiphonolites. The diaphragms are complete and interrupted, curved, and bubble-like. The symmetry of heterolites is absent, rarely bilateral or radial-starry.

The structures of vertical skeletal elements are homogeny, grained, fibrotic, clinofibrotic, trabeculoid, pseudobucular, trabecular, bacular, and stroboid. The trabecula and bacula are oriented vertically and obliquely upward. The trabecula and fibres can develop bundles, panicles, and braids.

In the growing process, corallites appear by waiting for heteromorphy components; the increase in the number of heteromorphic components happens by dividing themselves and by autothomy of corallites. The colonies can be tri-, tetra-, and pentamorphic. The cyclomorphic changing is manifested or rarely absent.

Composition: Coccoseridida Bondarenko, 1992. ($O_2C_2?$)- $O_2C_3-S_1W_2$; Proporida Bondarenko, 1958. O_3-S ; Khangailitida Bondarenko, 1992. ($O_2C_3?$)- O_2/O_3-D_1 ; Heliolitida Frech, 1987. $O_3a-D_2-(D_3?)$.

Remarks. Heliolitoidea differ from Tabulatoidea and Chaetetoidea by the presence of heteromorphic components, through the combination of which they develop tri-, tetra-, and pentamorphic colonies. Besides, most of the Heliolitoidea have a strictly fixed number of septa (12).

Stratigraphical range. $O_2-D_2-(D_3?)$

Geographical distribution. Cosmopolitan.

Order **Proporida** Bondarenko, 1958

Diagnosis. Polyparies have different shapes, including cylindrical, incrusting, and branching. The vertical skeletal elements consist of bundles of trabecula, bacula and fibra, which develop during astogenesis or only in the axial part of the cylindrical polypary. Trabecula, bacula and fibra look like 'broom' or 'bouquet'. Corallites spread separately or closely with different contact with each other. The cross-section differs from roundly polygonal to star-like. The number of septa is 12, sometimes 18–20 in the dark zones in the phase of metagenic expansion. The heteromorphic components are represented by prosiphonolites, cystolites and parasiphonolites. The colonies have tri- and tetramorphic structure.

Composition. Proporidae Sokolov, 1949 and Plasmoporidae Wentzel, 1895.

Remarks. The order Proporida differs from the orders Khangailitida, Heliolitida, and Coccoseridida in that trabecula, bacula and fibrae develop bundles that look like 'broom' or 'bouquet' and thus the edges of walls and septa have dishevelled appearance.

Stratigraphical range. O_3-S_2 [Bondarenko 1992].

Geographical distribution. Cosmopolitan.

Family **Proporidae** Sokolov, 1949

Diagnosis. The corallites are located closely with different contact with each other or separately. The cross-sections differ from roundly polygonal and folded to starry. The spinae and plate septales (septarium) consist of bundles of trabecula, bacula and fibrae. The heteromorphic components are represented by prosiphonolites, cystolites and rarely parasiphonolites. The aureoles, diadems, and crowns are absent. O. Bondarenko considered the colonies belonging to the trimorphic type [Bondarenko 1992].

Composition. Proporinae Sokolov, 1949, Ambiguaporinae Bondarenko, 1992.

Remarks. The family differs from the family Plasmoporidae by the absence of aureoles, diadems, and crowns.

Stratigraphical range. O_3-S_2 .

Geographical distribution. Cosmopolitan.

Subfamily **Proporinae** Sokolov, 1949

Diagnosis. The heteromorphic components are represented by prosiphonolites, cystolites and rarely parasiphonolites. The colonies have one of the listed form of heteromorphic components or components that alterate during astogenesis [Bondarenko 1992].

Composition. *Propora* Milne-Edwards et Haime, 1849, *Acdalopora* Bondarenko, 1958, *Proporella* Leleshus, 1973, *Confertites* Bondarenko, 1992, *Wormsipora* Sokolov, 1955, *Camtonites* Lindstrom, 1899, *Kolongites* Voulykh, 1983, and we propose to include the genus *Cystihalites* Chernyshov, 1941.

Stratigraphical range. O₃–S₂.

Geographical distribution. Cosmopolitic.

Genus *Propora* Milne-Edwards et Haime, 1849

Type species—*Porites tubulata* Lonsdale, 1849, pl. XVI, Figs. 3, 3a-e; lectotype—Great Britain, London, Institute of Geological Science, collection of the Geological Society (GS) No. 6555, Woolhope Limestone, England and Wales.

Diagnosis. The corallites are located on different distances; cross-sections are starry and round. The walls of corallites are independent and waved longitudinally. The bundles of spiky trabecula, bacula and fibrae are oriented obliquely upwards. The short septal plates are developed by the fusion of spines in the dark zones. The tabula are different. The heteromorphic components are presented by cystolites of different forms and covered by individual spikes, and brushes of spikes. The cystolites could be pierced by short robs, which developed fused spikes. The cystolites are located irregularly.

Composition. More than 100 species described that require revision.

Stratigraphical range. S₁

Geographical distribution. Cosmopolitic.

Propora tubulata (Lonsdale, 1839). (Fig. 3, m–n)

Neotype chosen by Hill, 1981, Fig. 426, 2, 32. GS No. 54451, Woolhope Limestone, England, 30 feet upper of beds with *Petalocrinus*, S_{1w} [Bondarenko 1992, pl. 13, Fig. 1].

Diagnosis. The polyparies have a lens-like shape. The vertical skeletal elements consist of bundles of trabecula, which develop on vesicles of different shape and size. Corallites spread separately at a distance of nearly 1 mm from each other. The cross-section differs from round, round-polygonal to starry. The diameter of corallites is near 1.2 mm. The number of septa is 12. In the dark zones, vesicles are smaller. The heteromorphic components are represented by vesicles (cystolites) covered by short

Fig 3. The structure of the described species: (a, b) *Yanetella dryganti* Grytsenko & Rudenko sp. nov., Middle Silurian, Malynivtsy Series (S_{2ld}), Rykhta Formation, Grinchuk Subformation, borehole KP-2, depth 1187 m: a—No. 4364, transverse section; b—No. 4366, longitudinal section; (c, d) *Podolites irregularis* Grytsenko & Rudenko sp. nov., Middle Silurian (S_{2ld}), Malynivtsy Series, Rykhta Formation, Grinchuk Subformation: c—No. 347, transverse section, outcrop No. 20/11R; d—No. 1051, transverse section, outcrop No. 39/12R; (e–g) *Helioplasma carinata* Grytsenko & Rudenko sp. nov., Middle Silurian (S_{2ld}), Malynivtsy Series, Rykhta Formation, Grinchuk Subformation, outcrop No. 39/12R: e—No. 5247e, transverse section, dark zone (12 siphonolites around corallites, thick walls, bubble diaphragms; and light zone thin walls); f—No. 5247a, mostly dark zone (wavy wall of corallites, different size of siphonolites with bubble diaphragms), transverse section; g—No. 5247b, transverse section; (h, i) *Syringoheliolites contrarius* Bond., Middle Silurian (S_{2ld}), Malynivtsy Series, Rhykhta Formation: borehole No. 5463, depth 240 m: h—No. 9975, transverse section; i—No. 9974, transverse section; (j) *Derivatolites cf. parvistellus* (Roemer, 1861), Middle Silurian (S_{2ld}), Malynivtsy Series, Stubla Formation, borehole No. 1793, depth 223.7 m; No. 7164c, transverse section; (k) *Saaremolites inversus podolica* Grytsenko & Rudenko ssp. nov. No.1197, longitudinal thin section, Middle Silurian, (S_{2ld}), Malynivtsy Series, Rykhta Formation, Grinchuk Subsuite, outcrop No. 18; (l) *Bogimbailites bondarenkoe* Grytsenko & Rudenko sp. nov., Upper Silurian (S_{3pf}), Skala (Rukshin) Series, Varnitsa Formation, borehole No. 6, depth 157.4 m: No. 4050, transverse section (curved elongated siphonolites); (m, n) *Propora tubulata* (Lonsdale, 1849), Lower Silurian (S_{1w}), Yaruga Series, Ternava Formation, borehole No. 5360, depth 323 m: m—No. 5316a, longitudinal section; n—No. 5317b, transverse section; (o) *Propora parvituba* (Rominger), Lower Silurian (S_{1w}), Yaruga Series, Ternava Formation, outcrop 62–4, No. 62a–4–5, transverse section; (p–s) *Pachyhelioplasma podolica* Bondarenko, Upper Silurian (S_{3pf}), Skala Series, Dzvenigorod Formation, borehole No. P–1, depth 1099–1102 m: p—thin section No. 1317Aa, transverse section; r—No. 1317Ab, longitudinal section; s—No. 1317 Ag, longitudinal section (Scale bar in all figures 1 mm).

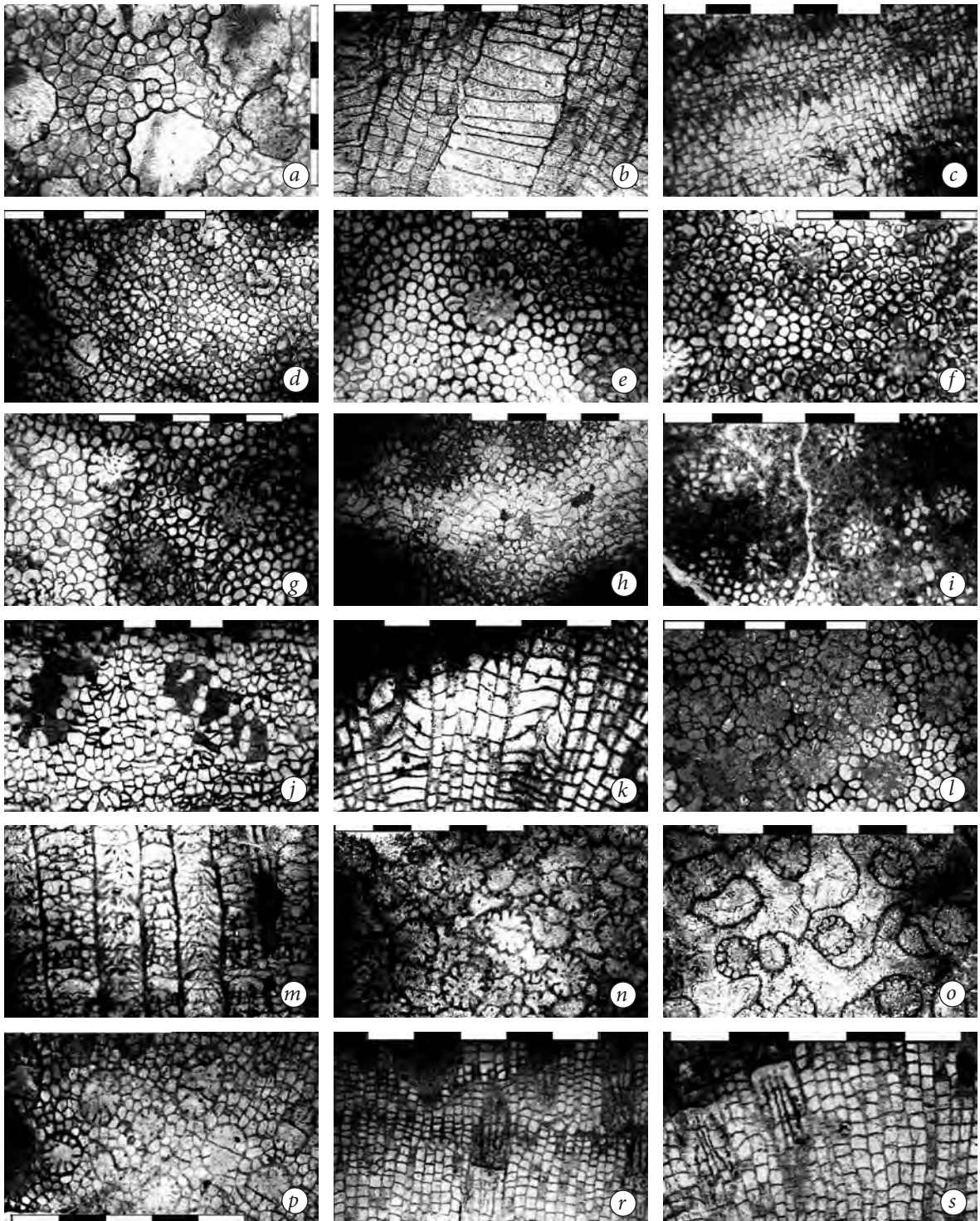
Рис. 3. Будова описаних видів (номери свердловин, шліфів та стратиграфічне положення зазначене в підписах англійською, поділки масштабу — 1 мм, довжина лінійки 5 мм).

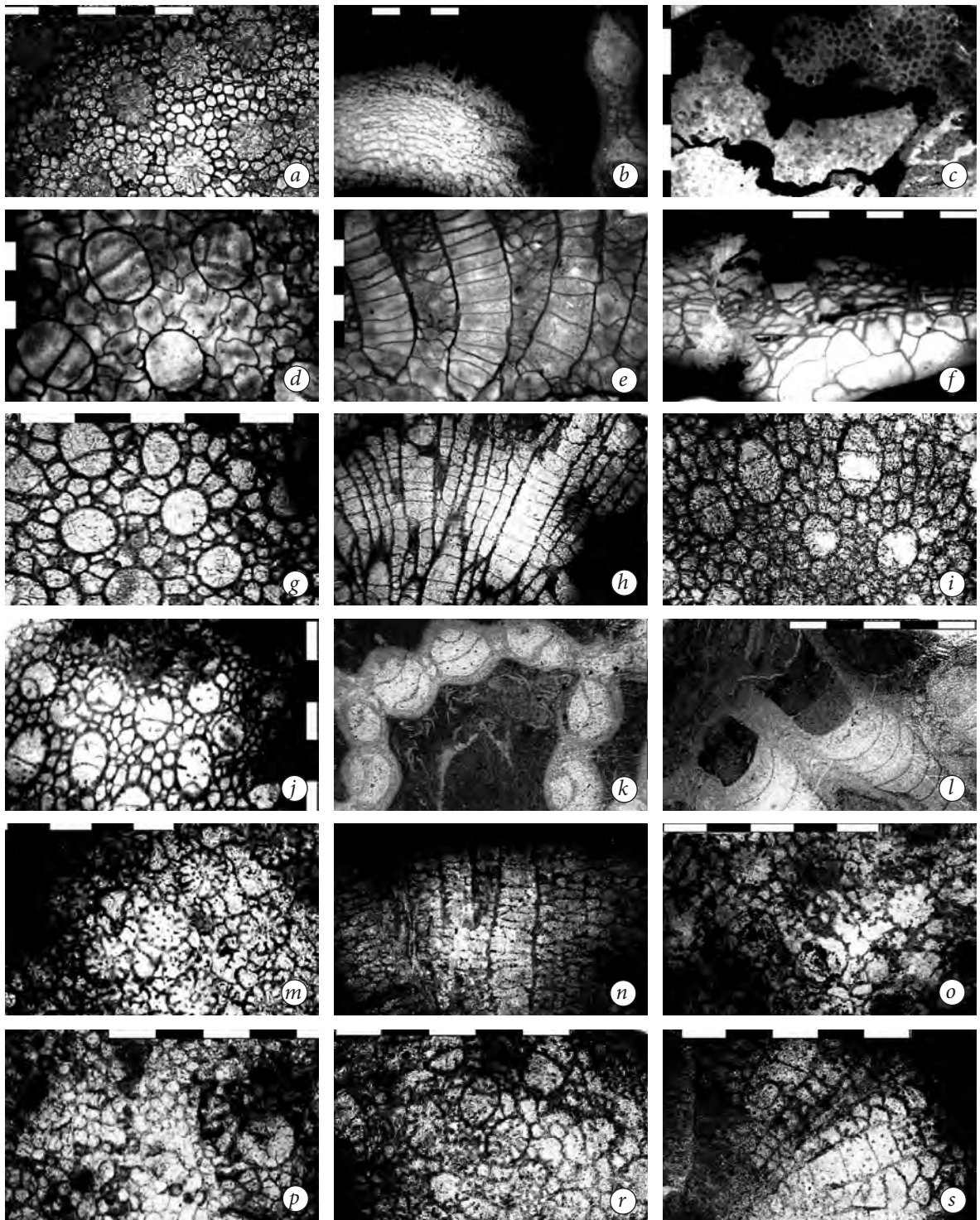
(0.2–0.4 mm) vertically oriented trabecula. The spikes in corallites are thin and long (curved upward and occupy all inner space of corallites).

Remarks. The genus *Propora*, according to Bondarenko [1992], includes nearly 130 species that need revision; of them only ten species could be valid [Bondarenko 1992].

Stratigraphical range. S₁w.

Geographical distribution. Cosmopolitan.





Propora podolica Grytsenko & Rudenko sp. nov. (Fig. 5, g)

Holotype stored in the Geological Department of the National Museum of Natural History, NAS of Ukraine, coll. GD No. 1986/6612, borehole No. 3669, depth 217 m, Podillia, Lower Silurian, Yaruga Series, Ternava Formation, S₁w.

Diagnosis. The polyparies have flat lens-like shape. The vertical skeletal elements are represented only by walls of corallite without visible trabecula, they are staked by lamellar tissue. The vesicles are

← **Fig. 4.** The structure of the described species: (a) *Bogimbailites bondarenko* Grytsenko & Rudenko sp. nov., Upper Silurian (S₃př), Skala (Rukshin) Series, Varnitsa Formation, borehole No. 6, depth 157.4 m; No. 4050a, transverse section (irregular elongated siphonolites); (b, c) *Stelliporella intricata* Lindström, Middle Silurian (S₂ld), Malynivtsy Series, Konivka Formation, borehole No. 5414, depth 518.5 m; b—No. 9235a, longitudinal section; c—No. 9235b, transverse section; (d–g) *Chekhovichia implexus* Grytsenko. Upper Silurian (S₃př), Darakhov Formation: d—No. 9245, transverse section, borehole No. 5676, depth 333.5 m; e—No. 9246, longitudinal section, borehole No. 5676, depth 333.5 m; g—borehole No. P–1, depth 1185 m, No. 459Ab, tangential section (big irregular vesicles); (f–i) *Pseudoplasmopora karaespensis* Kovalevskiy, Upper Silurian (S₃př), Varnitsa Formation: f—KP–1–936, 4008a, transverse section; h—Dar–1, depth 576–579 m, No. 4317, longitudinal section; i—Dar–1, 576–579 m, No. 4316a, transverse section; (j) *Pseudoplasmopora spinifera* Grytsenko & Rudenko sp. nov., S₃př, Darakhiv Formation, borehole 5351, depth 338 m, No. 9583c, transverse section; (k, l) *Cystihalysites komarovae* Grytsenko & Rudenko sp. nov. Middle Silurian (S₂ld), Malynivtsy Series, Rhykhta Formation: k—borehole 5, depth 147.5 m, No. 4504b, transverse section; l—borehole L–10, depth 1475 m, No. 3934, longitudinal section; (m–o) *Plasmopora petalliformis* M.-Edw. & H., Lower Silurian (S₁w), Yaruga Series, Ternava Formation: m—borehole No. 1793, depth 373 m, No. 7204, transverse section; n—borehole No. 5360, depth 323 m, No. 7318, transverse section; o—borehole No. 1793, depth 373 m, No. 7205—longitudinal section; (p) *Agallelites petri* Grytsenko & Rudenko sp. nov., Middle Silurian (S₂ld), Malynivtsy Series, Tsviklivtsy Formation (S₂kn₂), borehole 3655, depth 351.8 m, No. 5819c, longitudinal thin section; (r, s) *Plasmopora* sp. S₁w, Yaruga Series, Ternava Formation, borehole No. 5463, depth 348 m; r—No. 9142b, transverse section; s—longitudinal section. (Scale bar in all figures 1 mm).

Рис. 4. Будова описаних видів (номери свердловин, шліфів та стратиграфічне положення зазначене в підписах англійською, поділki масштабу — 1 мм, довжина лінійки 5 мм).

big, twice as big as the diameter of corallites. The blisters in cross-section resemble fish scales (Fig. 5, g). The corallites are located from each other separately in a distance of nearly 1 mm and more. The cross-sections vary from close to round. The diameter of corallites is nearly 1.0 mm. The septa are not distinct. Zonality is absent. The heteromorphic components are represented by vesicles (cystolites) without any sculpture. The spikes are absent too. The tabula spread rarely.

Remarks. The species is close to *Propora magna* Sokolov, 1962 from the Lower Llandovery, Porkuni Beds, Estonia; but the corallites have smaller diameter and have no visible folding.

Stratigraphical range. Silurian, Wenlockian, Yaruga Group, Ternava Formation (Formation in the sense of the Stratigraphic Codex of Ukraine).

Geographical distribution. Podillia, Ukraine.

***Propora* cf. *raricellata* Sokolov 1962 (Fig. 5, e)**

Diagnosis. The polypary has a hemispherical shape. The vertical skeletal elements are represented only by walls of corallites without visible trabecula, consist of lamellar tissue. The vesicles are big, much bigger than the diameter of corallites. The blisters in cross-section resemble fish scales (Fig. 5, e). The corallites are spread from each other separately on a distance of nearly 1.5 mm. The cross-sections vary from close to round. The diameter of corallites is nearly 0.6 mm. The septa are not distinct. Zonality is not clear. The heteromorphic components are represented by vesicles (cystolites) without any sculpture. The spikes are absent too. The tabula are spread rarely.

Remarks. The species is close to *Propora raricellata* Sokolov, 1962 from the Lower Silurian, Wenlock Stage, Yaani Beds, Estonia; but the corallites have smaller diameter and have no visible folding. In Fig. 3, o we include *Propora parvituba* (Rominger) without description for comparison.

Stratigraphical range. Lower Silurian, Wenlockian (S₁w), Yaruga Group, Kytaihorod Horizon, Ternava Formation.

Geographical distribution. Ukraine, Podillia, Ternopil Oblast.

Genus *Cystihalysites* Tchernychev, 1941

Cystihalysites: Chernyshov, 1941: 70; Sutton, 1964: 456–457; Stasinska, 1967: 58–59.

Halysites (pars): Fischer-Benson, 1871: 16; Amsden, 1949: 94–95; Buchler, 1955: 65–66.

Type species—*Cystihalysites mirabilis*, Chernyshov, 1941: 70, pl. 2, Figs. 5–7, pl. 3, Figs. 1–6; Silurian, East Verkhoyan Mountains, Khandyga River.

Diagnosis. The polyparies develop chains of long dimorphic corallites that fuse into curved plates. The colonies have an appearance of chains like in *Halysites*. The corallites have an elliptic cross-section. ‘Intermediate rectangular corallite’ with one to three rows of domed vesicles inside connect each neighbouring tube. On the convex side of vesicles, spikes are located occasionally similar to trabecula in *Propora*. The walls of corallites have no pores. The tabulae inside corallites can have short trabecula. Septa are short and rear. Reproduction occurs by division [Chernyshov 1941: 70].

Composition: Type species from the Silurian of Verkhoyansk region; *C. liber* Sok. et Tes.—Wenlock of Siberia; *C. dragunovi* Sokolov & Tesakov—S₁ln of Siberia; *C. amplitabulata* (Lambe), *C. blakewayensis* Sutton—S₁w of England; erratic boulders of Poland; *C. komarovae* Grytsebko & Rudenko sp. nov.—S₂ld of Podillia (Bagovitsa and Konivka Formations).

Remarks. Chernyshov first supposed the similarity between *Cystihalysites* and *Propora*. We propose to include the genus into the family Proporidae because of the appearance of vesicles like real coenenchima in *Propora*. Tesakov [1965] found *Favosites* with chaine corallites, so this phenomenon occurs among Tabulatoidea corals too.

Stratigraphical range. Silurian.

Geographical distribution. Cosmopolitan.

Cystihalysites komarovae Grytsenko & Rudenko sp. nov. (Fig. 4, k, l)

Holotype—Palaeontological Museum of Taras Shevchenko National University of Kyiv, No. 2441, Podillia, Upper Silurian, Bagovitsa and Rhykhta Formations, S₂ld.

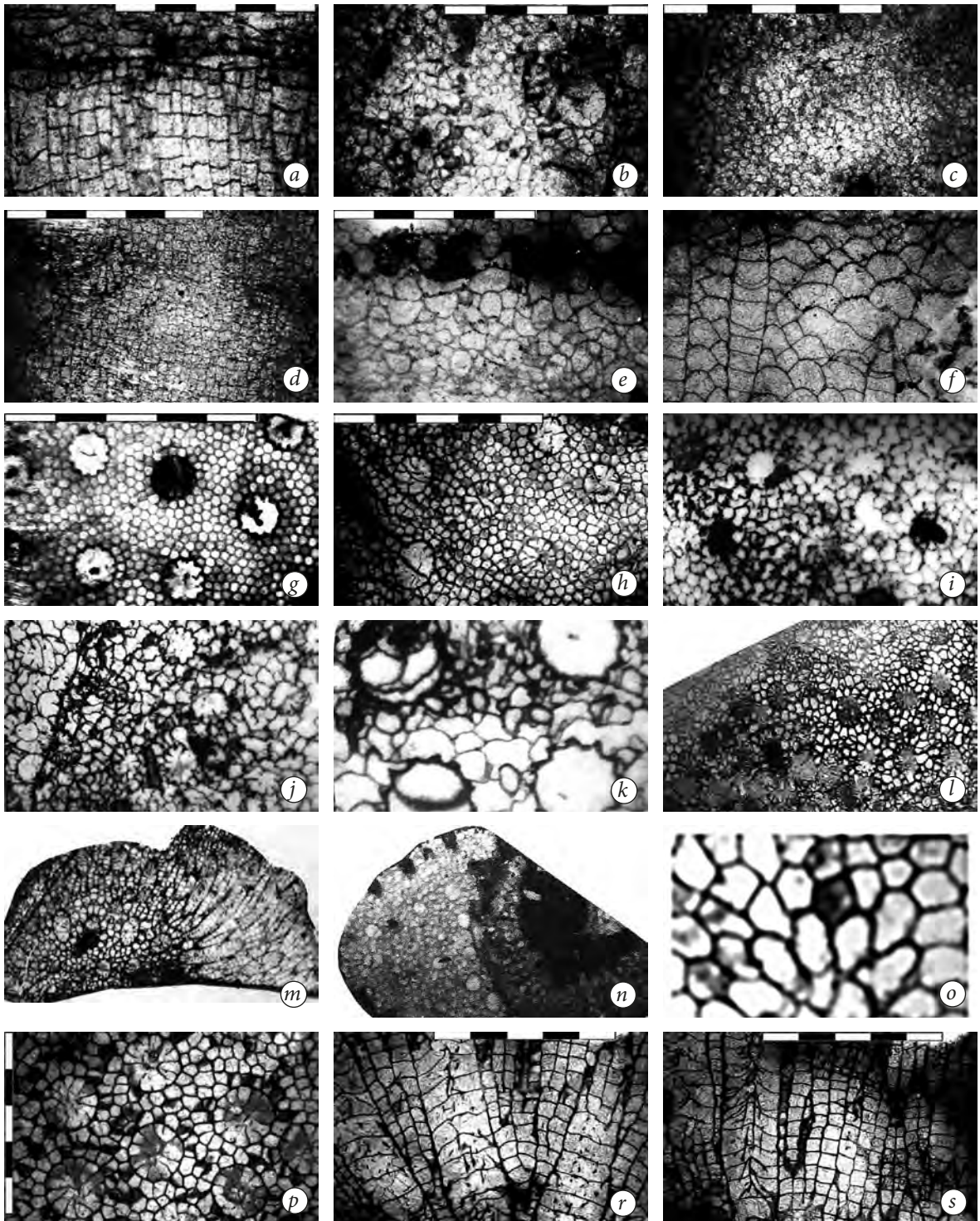
Etymology. The species name is given in memory of Olga Komarova, docent in the Geological Department of Taras Shevchenko National University of Kyiv.

Description. The chains of corallites are long and rarely branching. The height of corallites is 20 mm to 40 mm. The lacunas are rarely developed. The corallite’s cross-section is almost elliptic or rounded; the sizes are 1.2–1.3 x 1.5–1.6 mm up to 1.6 x 2.1 mm, usually the size is 1.5 x 1.6 mm. The vesicles in the intermedium tubes are located in one to three rows. The epitheca is thick, to 0.2 mm. The thin ribs could be visible on the wall of corallites responsible for 12 interseptal intervals in the inner part. The base of septa is located in the wall, but some could be visible by short spikes. The corallites are divided by the coenenchima zone near 0.2–0.5 mm. The domed vesicles have a size of 0.2–0.5 mm (equal length and height). The number of mesured vesicles is 23–25 in 5 mm. The longitudinal

Fig. 5. The structure of the described species: (a–b) *Agalletes petri* Grytsenko & Rudenko sp. nov., Middle Silurian (S₂ld), Malynivtsy Series, Tsviklivtsy Formation, borehole No. 3655, depth 351.8 m: a—No. 5821, longitudinal section; b—No. 5819, transverse section; (c–d) *Stelliporella lamellata* Wenzel, Lower Silurian (S₁w), Yaruga Series, Ternava Formation, Kytaihorod Horizon, borehole No. 3658, depth 66,8; c—No. 6779, longitudinal section, d—No. 6480, transverse section; (e) *Propora raricellata* Sokolov, Lower Silurian (S₁w), Yaruga Series, Ternava Formation, Kytaihorod Horizon, borehole Koropets–3, depth 1230.6 m, No. 6611, transverse section; (f) *Propora podolica* Grytsenko & Rudenko sp. nov., Lower Silurian, Yaruga Series, Ternava Formation (S₁w), borehole No. 3660, depth 217 m, No. 6612, longitudinal section; (g) *Saaremolites inversus podolica* Grytsenko & Rudenko ssp. nov., Middle Silurian (S₂ld), Rykhta Formation, Grinchuk Subformation, outcrop No. 18, No. 1199, transverse section; (h) *Podolites irregularis* Grytsenko & Rudenko sp. nov., Upper Ludlow, Grinchuk Subformation (S₂ld), outcrop 20–11R, No. 347, transverse section; (i–j) *Plasmopora petaliformis* M.-Edw. & H.; Podillia, Kytaihorod Village, Ternava River; Wenlock (S₁w), Ternava Formation: i—transverse section; j—transverse section; (k) *Chekhovichia implexus* Grytsenko, Upper Silurian (S₃pr), Darakhiv Formation, borehole Zavadvivka–3, depth 1290–1292, No. 1309, transverse section (x7); (l, m) *Pseudoplasmapora spinifera* Grytsenko & Rudenko sp. nov., Upper Silurian (S₃pr), Zadariv Formation, Volyn Oblast, borehole Lokachi–6, interval 1703–1706.6 m; l—No. 578, transverse section, m—No. 778, longitudinal/transverse section; (n) *Pseudoplasmapora minima* Grytsenko & Rudenko sp. nov. Upper Silurian, Zadariv Formation, Volyn Oblast, borehole Lokachi–6, interval 1703–1706.6 m; No. 1268, transverse section; (o1, o2) *Stelliporella lamellata* Wentzel, 1894. Lower Silurian, Yaruga Series, Ternava Formation (S₁w), borehole KP–3, depth 1230.6 m, No. 1474, transverse section; (p–s) *Dnestrites transites* Bondarenko, 1978, Upper Silurian, Pridolian Series (S₃pr), Dzvenigorod Formation; outcrop 45 (Dzvenyhorod): p—5005, transverse section, r—5010a, longitudinal section, s—5010 b, longitudinal section. (Scale bar in all figures 1 mm).

Рис. 5. Будова описаних видів (номери свердловин, шліфів та стратиграфічне положення зазначене в підписах англійською, поділки масштабу — 1 мм, довжина лінійки 5 мм).

ribbing is visible on the weathered surface of corallites. The tabula in the corallites are weakly concave and 7–14 are located in 5 mm. The spike is very thin and located on/in the inner wall. The waiting occurs in the coenenchimal intermedium from increasing (magnification up to 1.5 mm). The bud divides big vesicles into two smaller ones. The zonality of structure is emphasised by the appearance of smaller vesicles.



Remarks. The new species differ from other Proporidae by the habitus of chains, which are rarely branching and have no developed lacuna; it differs from *C. blakewaynsis* Sutton by shorter distance among tabulae and by the absence of trabecula in the chenechima.

Stratigraphical range. S₂. Bagovitsa, Konivka and Rykhta Formations.

Geographical distribution. One specimen from the Bagovitsa Formation near Velyka Slobidka, twelve specimens from a quarry near the village of Pudlivtsy, the species is abundant in the outcrops of the Rykhta Formation near the upper part of almost all sections and GD No. 1986/3934, 3937, 3940 (borehole L10, depth 1475 m); GD No. 1986/4504 (borehole 5, depth 147.5 m); GD No. 1986/9537 (borehole 5405, depth 268.2 m) and others.

Order **Khangailitida** Bondarenko, 1992

Diagnosis. The colonies have a different shape of branching and incrusting. The vertical skeletal elements have homogenic, grained, fibrosus or clinofibrosus structure on the whole colony or in the light zones and axial parts of the branches. The structure in the dark zones changes to trabecular, bacular and fibrosus, trabeculoid, stroboid, and pseudotrabecular. The corallites are located separately or closely in contact with each other differently. The corallite cross-sections vary from polygonal to starry. The number of septa is 12 and rarely 6 or 16–20; sometimes the septa are absent or it is singular. The heteromorphic elements are represented by prosiphonolites, cystolites and parasiphonolites. The colonies are tri- and tetramorphic.

Composition. Superfamilies Khangailitidacea Bondarenko, 1992; Sibiriolitacea Lin, 1977; Yanetelacea Volulykh, 1980; and Fuynolitacea Bondarenko, 1992.

Remarks. Khangailitida differs from Heliolitida by heteromorphic components, which are represented by prosiphonolites, cystolites, and parasiphonolites instead of siphonolites; by changing of the skeleton tissue to trabecular, bacular, trabeculoid, stroboid, and pseudobacular structures in some superfamilies in the dark zones and in the end of astogenes. The order differs from Proporida by the structure of the tissue of vertical skeletal elements, which are represented by homogenic, grained, fibrosus and pseudobacular kinds on all body or only in light zones and in the axial parts of branches of the colonies. The order differs from Proporida by having the fibra ungrouped in tousled bunches and brooms, but upgrowing parallel each other. From Coccoseridida the order differs by combination of the fibrosus structure of the skeleton tissue with bacular, trabecular, trabeculoid, and stroboid, which develop together in one colony. In Khangailitidacea, fibrosus tissue develop in the light zones and the axial zones of colony branches, whereas bacular and other types—in the dark zones and periferical parts of branches. In Coccoseridida, bacular, trabecular, and stroboid skeleton tissue develop on all bodies of the colony.

Stratigraphical range. O_{2c}–O₂/O₃–S–D₂eif.

Superfamily **Khangailitidacea** Bondarenko, 1992

Diagnosis. The colonies have a different shape to bolder-like with different growths, besides branchings and incrustating. Coronas, aureols and tiares can surround the corallites. The vertical skeleton elements are constructed by homogenic, grained, fibrosus or clinofibrosus structures in the whole colony.

Composition. Families Khangailitidae Bondarenko, 1992; Ducdoniidae Ospanova, 1989; Protoheliolitidae Kiaer, 1899; Hemiplasmoporidae Bondarenko, 1992; Avicenidae Ospanova, 1986 [Bondarenko 1992].

Remarks. Khangailitidacea differs from Yanetelacea and Sibiriolitacea by the structure of vertical skeletal elements that are constructed by monogenic, grained, fibrosus or clinofibrosus structures in the whole colony. Fuynolitacea have incrustrated shape of colonies [Bondarenko 1992].

Stratigraphical range. (O_{2c3}?)–O₂/O₃–S–D₂eif.

Family **Khangailitidae** Bondarenko, 1992

Diagnosis. The colonies have a different shape to bolder-like with different growths, besides branching and incrustating. The corallites are located separately on different distances from each other; they are located in close contact with each other having common walls; or connecting in some points without development-free lacunas; or closely contact each other with development free-lacunas. The

corallites have polygonal and rounded cross-sections. The structure of the walls and septal developments are equal. The septal spikes are oriented oblique upward and rarely horizontally. The heteromorphic elements are represented by prosiphonolites, cystolites and parasiphonolites. The coronas, aureoles, and tiaras are absent. The structures of vertical skeleton elements are homogenic, grained, and fibrosus. The colonies are considered to be of different types, from tri- to pentamorphic.

Composition. Genera *Khangailites* Bondarenko et Minzhin, 1980; *Mcleodia* Flower et Duncan, 1975; *Kimilites* Sladkovskaia, 1987; *Spumaeolites* Zhizhina, 1967; *Linhuangites* Bondarenko, 1992; *Kreanopora* Ozaki, in Shimizu, Ozaki, Obata, 1934; *Thaumatolites* Yanet in Sokolov, 1955; *Qilianipora* Yu, 1962; *Helioplasma* Kettnerova, 1933. Conditionally: *Kiaerolites* Bondarenko, 1977 [Bondarenko 1992].

Remarks. The family Khangailitidae differs from Protoheliolitidae by the homogenous structure of skeletal tissues (walls and septa) and also by septa orientation (oblique upward or horizontally); from Hemiplasmoporidae by the absence of coronas, aureoles and tiaras; and from Aviceniidae by the absence of thickened walls of heteromorphic components which leads to rounded inner space.

Stratigraphical range. (O₂C₃?)–O₂/O₃–O₃a–D₂eif.

Geographical distribution. Cosmopolitan.

Family Hemiplasmoporidae Bondarenko, 1992

Diagnosis. The corallites are located separately and at different distances. The corallites in the cross-sections are rounded, weakly faceted, wavy, and folded. The structure of walls and septal developments are equal. The septa are represented by spikes, tubercles, squamula-like spikes, squamula, spiky, and squamula-like hemiplates, and brushes of spikes; sometimes the septa are absent. The heteromorphic components are represented by cystolites and parasiphonolites, which can alternate in the astogenesis and cyclomorphosis. The corallites are surrounded by coronas, aureoles, and tiaras. The structures of vertical skeletal elements are fibrosus and clinofibrosus. The colonies are considered to belong to tetra- and pentamorphic types.

Composition. The family includes the genera *Hemiplasmopora* Ospanova, 1979 b; *Losevipora* Ospanova, 1979 a; *Helioplasmolites* Chekhovich, 1955; *Lacerilites* Bondarenko, 1992; *Squameolites* Bondarenko, 1963 b; *Pachyhelioplasma* Kim, 1966; *Bondarenkolites* Kim, 1984.

Remarks. The family differs from Protoheliolitidae, Khangailitidae, and Aviceniidae by developing coronas, aureoles, and tiaras. Besides, in the Hemiplasmoporidae areas with cerioid texture and prosiphonolites are absent, which are characteristic of Protoheliolitidae and some Khangailitidae.

Stratigraphical range. S–D₁eif₁.

Geographical distribution. Cosmopolitan.

Genus *Pachyhelioplasma* Kim, 1966

Holotype. *Pachyhelioplasma kettnerovae* Kim, 1966, pl. 34, Fig. 2, Paleontological-Stratigraphical party, Uzbekistan, Tashkent, No. 435/1; assemblage with *Favosites regularisimus*. D₁eif₁; Middle Asia, Zeravshan Ridge [Bondarenko 1992, pl. 27, Fig.1].

Diagnosis. The corallites have rounded or weakly faceted cross-sections. The walls are straight or weakly curved. The septa are represented by 12 lense-like plates, which often end in spikes. The tabulae are full and cross each other, horizontal or concave. The heteromorphic components are represented by parasiphonolites, filled by bubbles, which often develop braids. The walls of parasiphonolites are thickened, especially in the corners. The corallites are surrounded by aureoles and tiaras. The structures of vertical skeleton elements are clinofibrosus. The colonies are considered to belong to the tetramorphic type.

Composition. *Pachyhelioplasma kettnerovae* Kim, 1966 [Kim et al. 1978; Kim 1984]; *Pachyhelioplasma antiquum* Bondarenko, 1975, Kazakhstan, Ainasu Horizon, S₃př; *Pachyhelioplasma podolicum* [Bondarenko, 1985], Ukraine, Podillia, Skala Horizon. [Bondarenko 1982b, 1985a]; *Pachyhelioplasma rzonnickajae* Kim, 1966, Middle Asia, Zeravshan Ridge; Manak and Shutsk Horizons; *Pachyhelioplasma sp.*, Kazakhstan, North Near-Balkhash Region, Ainasu Horizon.

Remarks. *Pachyhelioplasma* differs from other genera of the family by thickening of the vertical skeletal elements and especially walls of tubuli (parasiphonolites) at the beginning from dark zones (at the beginning of the phylogenesis), and then in both zones (following phylogenesis).

Stratigraphical range. S₃př–D₂eif₁.

Geographical distribution. Middle Asia, Kazakhstan, and western Ukraine [Bondarenko 1992].

***Pachyhelioplasma podolica* Bondarenko, 1985 (Fig. 3, p-s)**

The holotype is described in the paper by Bondarenko [1985].

Diagnosis. The polyparies have different size and shape; most colonies have ligiform structure with outgrowths. The diameter of cross-sections of corallites is nearly 1 mm. The corallites are curved in accordance to the forms of polyparies. The 12 septa are long reaching half the size of the corallites radiuses (Fig. 3, p). The septa often end in spikes. The walls of corallites are thickened, especially in the dark zones. The diaphragms are oblique and rare; their number in light zones is 7 on 2 mm of high parasiphonolites. The parasiphonolites have polygonal cross-sections. The thickness of dark zones is less than 1 mm (Fig. 3, r).

Remarks. Diversity manifested in the different construction of the dark and light zones. Firstly, dark zones are near twice as thick as the light zones. Secondly, the structure in the light zones often can be reduced, especially of the septa, which is well visible in Fig. 3, r-s. The finds were extracted from detritic limestones with tabulata and rugosan corals, stromatoporans, brachiopods and other fossil fauna [Tsegelnjuk et al. 1983].

Stratigraphical range. S₃př, Dzvenihorod Formation.

Geographical distribution. Outcrops No. 45 near Dzvenihorod Village; boreholes No. 1P, depth 1099–1102 m. Location shown in Fig. 1.

Genus *Helioplasma* Ketnerova, 1933

Type species—*Helioplasma kolihai* Ketnerova, 1933, text-Fig. 1–2; Lectotype (Galle, 1969), pl. I, Fig. 1; pl. II, Fig. 4; pl. III, Fig. 1–4; coll. Ketnerova No. K 15 (National Museum, Prague, Czech Republic); Upper Koneprussian limestone, D₁lh; Bohemia, Barrandien, Golden Hill (Zlatý Kun') Golden Horse quarry near Koneprus [Bondarenko 1992, pl. 22, Fig. 2, text-Fig. 21].

Helioplasma: Ketnerova, 1933: 181–182; Sokolov, 1955: 80, 1962: 278; Bondarenko, 1963b, 1966: 193; Galle, 1969:169–170; 1973: 33; Flugel, 1970: 126; Dubatolov, Ivanovsky, 1977: 44.

Bogimbailites (?): Bondarenko, 1966: 192.

Description. The corallites are located in the colony in different ways: separately or contacting each other. The corallites cross-sections are starry. The septa have sawtoothed look (or rows of septal needles). The septa are represented by plates with spiky edges, but sometimes solitary spikes are visible. The tabulae are complete (or occasionally interrupted), usually oriented upward in light zones and slightly downward in dark zones. The heteromorphic elements are represented by parasiphonolites in two variants: polygonal in cross-section with horizontal diaphragms and elongated in cross-section with bubble-like diaphragms. The bubble-like developments can be different in horizontal and vertical directions. Occasionally, it is located in the early astogenetic zone, in the base of the colony, and dark zones. Coenenchima ususally consist of thin tubes like in *Heliolites*, and tubes with blisters. Sometimes the walls of coenenchima tubes are interrupted and diaphragms become veseculate tissue, which fill the place that was released.

Composition: *Helioplasma kolihai* Ketnerova, 1933, D₁, Czech Republic; *H. aliena* Galle, 1973, Bohemia, Barrandien, Limestone with Acanthopyge, D₂eif; *H. domestica* Bondarenko, 1966 and *H. indotata* Bondarenko, 1966, Anasui Horizon, Kazakhstan; *H. propinqua* [Bondarenko 1966], Superanasui Horizon, Kazakhstan; *H. dnestriensis* [Bondarenko 1981], Ukraine, Podillia, Dzvenyhorod Formation, S₃př; [Bondarenko 1981, 1982, 1986, 1987; Bondarenko, Sladkovskaia 1983]; *H. domesticum* Bond., 1966, Kazakhstan, southern outskirts of Karaganda basin, Ainasu and Kokbaital horizons, D₁gd [Bondarenko 1992]; *H. aliena* Galle, 1973, Middle Devonian, in Barrandien; *H. bondarenkoi* Grytsenko & Rudenko sp. nov., Upper Silurian, Přidoly, Rashkiv Formation of Podillia, S₃př.

Remarks. The genus *Helioplasma* Ketnerova differs from representatives of the genus *Heliolites* Dana by the structure of coenenchima; from the genera *Plasmopora* Milne-Edwards & Haime, *Pseudoplasmopora* Bondarenko, and *Squameolites* Bondarenko by the absence of aureole that surrounds the corallites; from *Helioplasmolites* Chekhovich by the absence of intensive reduction of the wall of coenenchimal tubes; from *Bogimbailites* Bondarenko by the absence of elongated and curved in transverse sections coenenchimal structures. The researchers before had not seen or paid attention to blisters in the coenenchimal tubes, because among the corals described under name *Heliolites* could be representatives of the genus *Heliolasma*.

***Helioplasma carinata* Grytsenko & Rudenko sp. nov. (Fig. 3, e–g)**

Holotype: GD No. 1986/5247, outcrop No. 39/12R, Rykhta Formation, Grinchouk Subformation, transverse section: Fig. 3, e—dark zone (12 siphonolites around corallites, thick walls, bubble diaphragms; and light zone with thin walls); Fig. 3, f—GD No. 1986/5247a, mostly dark zone (walls of corallites are wavy; siphonolites have different size and crossed by bubble diaphragms (Fig. 3, g—thin section GD No. 1986/5247b).

Etymology. The species name is derived from Latin ‘carinae’ (plural)—longitudinal or transverse developing on lateral surfaces of septa.

Description. The colonies have medium sizes. The corallites are located in the colony separately at distances of 4–6 rows of parasiphonolites, and surrounded by corona-like rings of parasiphonolites, which are much bigger than other ones. The corallites cross-sections are starry and wavy in the light and dark zones, respectively. The shapes of cross-sections are different and can be representatives of different species, but the thin sections were made from one colony. The cross-sections of parasiphonolites in the ring of aureole are of nearly 0.5 mm, while others tubuli are smaller (0.2–0.3 mm). The tabulae are thin and deformed. The diaphragms are flat in the light zones and blister-like in the dark zones. The walls of coenenchimal tubes (parasiphonolites) are mostly not reduced, but reduced somewhere in the dark zones. The seasonal variability is reflected in the zonal structure of polipary. The septal apparatus and blister-like structure are more developed in the dark zones. In Fig. 3, g, the upper left corallite less folded and having less developed septa, but visible development of carina. The corallites located on left lower angle have almost starry look (in the light zone). Two other corallites on the same picture in the right lower corner (dark zone)—there corallites are filled by septal spikes and surrounded parasiphonolites have bubble-like diaphragms, which are visible in the picture as little rings. In Fig. 3, e–g, most space in the pictures is represented by dark zones beside the right lower part of Fig. 3, e where only coenenchima without corallites can be seen. Other spaces in both picture show thickening of walls of parasiphonolites and many small vesicles inside ones.

The specimen was found in association with remains of many corals, including solitary Rugosa, Tabulata, and Stromatoporata, Bryozoa, and Crinoidea detritus. It is detritic facial zone. The upper part of the Grinchouk Subformation is rich in fossil corals; besides the described here species there are *Favosites* sp., *Syringoheliolites contrarius* Bond., *Rhizophyllum gothlandicus* Roemer and many others which are found in the detritic nodular marly limestones.

Remarks. The described species differs from *H. kolihai* Ketnerova by smaller diameter and rarer location of corallites, and other metric features; from *H. aliena* Galle by longer septa, lesser level of blisters appearance in the tubes; from others species of *Helioplasma* described by Bondarenko [1966] by longer septa and other features. The closest species is *Bogimbailites sytovae* Bondarenko, but it differs by having a bigger size (2.0–2.2 mm), more close location of corallites, more developed thickness of skeletal elements in the dark zones and appearance of squamulae among septa.

Stratigraphical range. S₂ld, Rykhta Formation, Grinchouk Subformation.

Geographical distribution. Malynivtsy Village, Podillia, Ukraine.

Superfamily Yanetellacea Voulykh, 1980

Diagnosis. The polyaries have various forms to conifers with outgrowths except branchy and incrusting. The structures of the vertical skeletal elements in one colony are changing in the cyclo-morphosis from homogeneous grain and fibrotic to trabecular, bacular, and trabecular-like.

Composition. Inoporidae Ospanova, 1979; Yanetellidae Voulykh, 1980; Ellisitidae Dixon, Bolton, Copper, 1986.

Remarks. Yanetellacea differ from Fuynolitacea by the absence of incrustated forms of polyparies; from Siberiolitacea it differs by the absence of branchy and cylindrical colonies. A sudden change of vertical skeletal elements in the cyclomorphosis is characteristic for the Yanetellacea. The structure has homogeneous grain and fibrotic types in the light zones; and its changing into trabecular, bacular, and trabecular-like in dark ones. The same sequence observed in the astogenic changes.

Stratigraphical range. O₂c₁–S₃př.

Geographical distribution. Canada, Ural, Tajikistan, Ukraine (Podillia).

Family **Inaporidae** Ospanova, 1979

Diagnosis. The walls of the corallites are independent closed or dependent interrupting. The walls could be surrounded by chains of vesicles. The numbers of septae are 6 or 12, which represented by trabecular-like structure. The septa could be spiky or plate. The tabulae are flat, interrupted or vesicles. The herteromorphic components represented by different cystolites or parasiphonolites (rarely). The structures of vertical skeleton elements represented by homogeneous grain, and fibrotic to trabecular, bacular, and trabecular-like in the one colony.

Composition. *Concavites* Bondarenko et Minzhin, 1981; *Oskaria* Ospanova, 1983, *Innapora* Leleshus, 1974; *Chekhovichia* Boweld, 2015; *Dilites* Bondarenko et Minzhin, 1981.

Remarks. The Inaporidae differs from the Yanetellidae and the Ellisitidae by presence chains and colonies of vesicles around corallites, which in septal zones filled by fibers and thin trabeculas, and developed rods of trabecular-like structure. The *Chekhovichia* refers conditionally to Inaporidae because it has only chains of vesicles but rods of trabecular-like structure not yet observed. The *Dilites* has colonies of vesicles, but type of filling is unclear.

Stratigraphical range. O₂c₃–S₃př.

Geographical distribution. Kazakhstan, Middle Asia, Kuznetsk Basin, Mountain Altaj, Tuva, Mongolia, China, Australia, and (?) Norway.

Genus **Chekhovichia** Boweld, 2015 (n. subst. pro *Rotalites* Leleshus, 1970, non Lamarck, 1801)

Type species, by original designation: *Propora nuratensis* Chekhovich in Kovalevsky & al., 1960 (p. 217 pl. 43, Figs. 1–2.)

Diagnosis: see Leleshus, 1970: 97, emended by Bondarenko, 1992: 94. The shape of little polyparies are incorrect near-spherical, hemispherical, and nodular. The characteristic feature is the look of the corallites, like a gear with 12 cloves. The walls are unequal with longitudinal folds. The thickness of the corallites walls is more than the thickness of wall tubes and dissepiments in the coenenchima. The septal spines are rare or absent. The tabulae mostly have horizontal position, flat or slightly concave; they can be vesiculate in the near periphaeral zone. The coenenchima consist of vesicles (cystolites).

Composition: *Chekhovichia nuratensis* (Chekhovich) and *Chekhovichia asiaticus* (Chernova) found in the Ludlow Tian-Shan, and *Chekhovichia implexus* Grytsenko found in Pridoly Podillia and Belarus.

Remarks. The species differ from other genera of the family Proporidae by the following: festone cross-sections from *Propora* M. Edwards et Haime; by solid walls from *Innapora* Leleshus, 1974; more clear solid walls and more simple tabulae from *Thaumatolites* Yanet in Sokolov, 1955.

Stratigraphical range. S₂₋₃.

Geographical distribution. Middle Asia, Ukraine (Podillia) and Belarus.

Chekhovichia implexus Grytsenko, 2014 (Fig. 4, d-g; Fig. 5, k; pl. 1)

Holotype NMNH GD No. 1986, thin sections 459, borehole P-1 (Pidhaitsy), depth 1185 m, Ternopil Oblast; borehole L-6 (Locachi), interval 1703–1706.6 m, Volyn Oblast—Upper Silurian, Pridoly Stage (S₃př), Varnitsa Formation.

Description. The polyparies mostly have middle sizes, incorrect nodular, near-spherical, and/or hemispherical shapes. The polipary sizes are 30–40 mm (height), 50–150 mm (cross-sections), and possibly more. The corallites are comparably big, limited by thin or middle-thick walls waved in cross-sections. They are located comparably rare. The coenenchima consists of vesicles. The tabulae spread in different zones of corallites with different distances (in dark zones—closer, somewhere

vesiculate, in light ones—freer, slightly concave). The septal elements are absent or not distinct (the waved walls play the role of the septa). Twelve extrathecal ribs develop in the dark zones. The sizes of structural elements are summarised in Table 1. The age changes are very distinct. The neanic stage of the astogenic development differs by smaller size of corallites compared with the efebic stage (Fig. 4, *d-f*; Fig. 5, *k*, thin section No. 1986/1307). The vesiculate tissues on the neonic stage consist of very few blisters (vesicles). Protocoralite has a thick wall. Seasonal changes shown by periodic increase and decrease in the size of blisters and in changing by the degree of waviness of corallites walls (in dark and light zones).

Remarks. The new species differs from *R. nuratensis* (Chekhovich) by smaller cross-section of corallites, which are located rarer. *Ch. implexus* Grytsenko & Rudenko sp. nov. differs from the type species by the absence of second order corrugating. From the close species, *Ch. asiaticus* (Chernova) it differs by smaller size of corallites and less thick walls.

Twelve specimens were found and 20 oriented thin sections were made. The species was found in clayey-detritic limestones with remains of Bryozoa, branching Tabulata, solitary Rugosa, and lense-like colonies of Heliolitida in moderately shallow water facial zone.

Note. Usually, for tabulate corals, zonality is visible in the thin sections as alternation of dark and light zones. The intensiveness of thick skeletal tissue development depends on the reproductive activity of corals. The slow growth rate is connected with seasonal changes [Preobrazhenskiy 1967, Bondarenko 1978]. In part of polyparies capsules were found—possibly planulas, i.e. fossil larvae [Grytsenko 1978].

Stratigraphical range. Upper Silurian, Přidolian Stage, Varnitsa and Darakhiv¹ Formations.

Geographical distribution. Middle Asia, Ukraine (Podillia), Belarus.

Table 1. The measurements of skeletal elements of *Chekhovichia implexus* (mm)

Таблиця 1. Виміри розмірів елементів скелету *Chekhovichia implexus* (в мм)

Measurements	No. of thin sections		
	1305–1307	2284–2288	840
Diameter of corallites	1.3–1.6	1.2–1.4	1.3–1.5
Distance between corallites	0.7–1.8	0.4–1.7	0.7–1.7
Density of corallites per 1 cm ²	10–11	10–13	—
Wall thickness	0.05–0.10	0.05–0.10	0.05–0.10
Number of tabulae per 5 mm	10	12	9–13

Family Yanetellidae Voulykh, 1980

Composition: *Acdalina* Leleshus & Ospanova, 1979, O_{3a2}; *Yanetella* Voulykh, 1980, S_{3př}.

Stratigraphical range. O_{3a2}, S_{3př}.

Geographical distribution: Middle Asia, Urals, Ukraine (Podillia).

Genus *Yanetella* Voulykh, 1980

Type species—*Propora uralica* Yanet, 1977, pl. II, Fig. 2.

Holotype. UTGM No. 1017/305, 306, the upper part of the Kolonga Formation, S_{3př}; Eastern slope of Middle Ural Mountains (pl. 34, Fig. 3; pl. 36, Fig. 3).

Description. The corallites are located separately. In the light zones, the cross-sections of corallites are irregularly curved and round; the walls are thin, from independent (usually) to dependent (rarely); the role of septa is played by folds of walls; the tabulae are complete, horizontal, interrupted and bubble-like, sometimes separated on axial and peripheral areas; heteromorphic components are represented by cystolites, usually conical, covered by spikes on the top; the structure of vertical skeletal elements is fibrotic. In the dark zones, the cross-sections of corallites are regularly waved and folded; the walls of corallites are thick and independent; the septae are represented by twelve coarse ribbed developments; the tabulae are interrupted by flate-bubble-like elements; heteromorphic components are represented by spiky crust on the top of cystolites; the structure of vertical skeletal elements are trabecular, trabeculoid and bacular.

¹ The Darakhiv Suite is distributed in the eastern slope of the Lviv Paleozoic Depression [Gozhyk 2013].

Composition. The type species from the upper part of Colonga and lower part of Petropavlovka Formation; *Yanetella dryganti* Grytsenko & Rudenko sp. nov.

Stratigraphical range. S₂ld–S₃př.

Geographical distribution. Urals, Ukraine (Podillia).

Yanetella dryganti Grytsenko & Rudenko sp. nov. (Fig. 3, a, b)

Holotype. NMNH GD No. 1986/4364, 4366, Malynivtsy Group, Rykhtha Formation, Grinchuk Subformation; Podillia borehole KP–2, depth 1187 m: No. 4364—transverse section; No. 4366—longitudinal section.

Etymology. The species name given in honour of Danylo Drygant (Ukrainian palaeontologist, specialist in conodonts).

Description. The corallites (d = 2.0–2.5 mm) are located separately and have rings with 20–24 cystolites around and 2–3 rows of cystolites among each other. In the light zones, the cross-sections of corallites are irregularly curved and round; the walls are thin, longitudinally waved, independent (usually); the role of septa is played by folds of walls; the tabulae are complete, horizontal; interrupted and bubble-like, sometimes separated on axial and peripheral areas; heteromorphic components are represented by vertical columns of cystolites, which usually have different cross-sections; the structure of vertical skeletal elements is not clear. In the dark zones, the cross-sections of corallites are regularly waved and folded; the walls of corallites are thick and independent; the role of septa is played by twelve coarse ribbed developments; the tabulae are complete, horizontally flat, weakly convex; heteromorphic components are represented by vertical columns of cystolites, which usually have different cross-sections; the structure of vertical skeletal elements is not clear. Number of tabulae is 10 per 5 mm.

Stratigraphical range. S₂ld (Rykhtha Formation).

Geographical distribution. Ukraine (Podillia).

Family **Plasmoporidae** Bondarenko, 1963

Diagnosis. Polyparies are different in shape—chemisphaerical, lens-like, and cylindrical, excluding incrusting ones. Corallites are located separately. The structure of walls and septa are equal. The septa are represented by simple needles, squamoidal needles with thickened bases, plates or can be absent. The siphonolites, usually, are polygonal in cross-section. The corallites are surrounded by coronas, aureoles and diadems (tiaras). The colonies are of tetramorphic type [Bondarenko 1992].

Remarks. For comparison, we give other approaches for the family Plasmoporidae Wentzel, 1895, which has the following diagnosis: corallites are located separately; they have wavy, folded, and starry cross-sections. The coronas, aureoles and diademas are characteristic for the family. They could be present in the entire colony or only in the dark zones.

Composition. *Plasmopora* Milne-Edwards et Haime, 1849; *Pseudoplasmopora* Bondarenko, 1963; *Sideriolites* Bondarenko, 1992; *Amphilites* Bondarenko, 1975.

Remarks. The family differs from Heliolitidae and Stelliporellidae by the development of coronas, aureoles, and diadems around corallites.

Genus **Plasmopora** Milne-Edwards et Haime, 1849

Plasmopora: Milne-Edwards et Haime, 1849: 262; 1850: lix; 1851: 74; Počta, 1902: 300; Kiaer, 1903: 275; Lindstroem, 1899: 181; Shimer and Shrock, 1944: 103; Sokolov, 1950: 140; 1955: 82; 1962: 279; Lecompte, 1952: 535; Stumm, 1962: 4–5; Bondarenko 1963: 49–50.

Type species—*Porites petalliformis* Lonsdale, 1839; Wenlockian of England.

Holotype. *Porites petalliformis* Lonsdale, 1839: 687, pl. 16, Fig. 4, 4a is probably stored in the Geological Society of London. There is another mention of storage in the Museum of Practical Geology in the Geological Survey of UK [Dubatolov, Ivanovsky 1977].

Composition: *Plasmopora petalliformis* (Lonsdale) from the Wenlockian of England, Ternava Formation of Podillia, Silurian of North America; *P. scita* Milne-Edwards et Haime from Upper Llandoveryan–Wenlockian of England and Sweden (Gotland Island), Upper Llandoveryan of Norway; Lower Ludlovian of England,

Ternava Formation of Podillia; *P. exselsa* Počta, from Lower Ludlovian of Bohemia and *P. nakamurai* Ozaki, found in basal conglomerate of Mesozoic in Korea.

Remarks. *Lamionoplasma* Bondarenko, 1963 is the closest genus, but it differs by the development of septal plates dissecting corallites close to the axis.

Stratigraphical range. S₁₋₂.

Geographical distribution. England, Sweden, Czech Republic (Bohemia), Ukraine (Podillia), North America, Europe, Korea.

***Plasmopora petalliformis* Milne-Edwards & Haime, 1849 (Fig. 5, *i-j*)**

Porites petalliformis Lonsdale, 1839: 687, tabl. 16, Fig. 4, 4a;

Plasmopora petalliformis Milne-Edwards et Haime, 1849: 262; 1850: LIX; 1856: 253, pl. LIX, Fig. 1a, 1c; Lindstroem, 1899: 77, pl. VI, Figs. 1–12;

Palaeopora petalliformis: MacCoy, 1851: 17.

Diagnosis. The polyparies are free, and the shape is close to hemispherical, the flat basal side is covered with concentric epitheca. The septae are rudimentary. The tabulae have a horizontal position. The walls are thin. The ridges of calices are not distinct. The corallites are connected by vertical-radial plates among which are other horizontal plates [Milne-Edwards et Haime, 1849: 262; Dubatolov & Ivanovsky 1977: 69].

Description. The polyparies are of small and middle sizes; hemispherical and lens-like shapes. Its diameter is nearly 30 mm, and its height is about 20 mm. The maximum size is 300 x 200 mm. The basal epitheca is preserved (not destroyed). The corallites have cylindrical shapes surrounded by star-like aureole. The diameter of the corallites is 1.3–1.8 mm, but mostly about 1.5–1.6 mm. The distance among corallites is 1–2 mm. There are 8–10 units of corallites per 1 cm². The corallites are surrounded by 12 extrathecal plates. The walls of corallites are thin, 0.05–0.10 mm. The thickness of extrathecal plates and vesicles (blisters) is not more than 0.05 mm.

The tabulae have a concave shape and are separated from one another by 0.2 to 0.8 mm. The vesicular tissue consists of vertical rows of blisters. The size of separate vesiculae in the central part of the colony is nearly 0.5 mm, but in the peripheral part — dissimulations are more in size and without regular orientation. The needles are usually distinct and form 20 rows in which every needle is bent at an angle of 30–45°. We have 6 specimens from 3 boreholes, and 8 thin sections were made.

Remarks. The described specimens do not differ in detail from the species in the collection of Lindstroem [1899]. The species differ from other ones by: less distance among corallites in *P. calyculata* Ldm; less development of trabecula (needles) in *P. foroense* Ldm; less distance among corallites and absence of separated trabecula—from *P. scita* Milne-Edwards et Haime.

Stratigraphical range. S_{1w}, Ternava Formation.

Geographical distribution. England, Sweden, Ukraine (Podillia).

Order Heliolitida Fresh, 1897

Diagnosis. The colonies have different habitus, including incrusting and branching. The vertical skeleton elements have homogenous, granular, and fibrous structures in all colonies. The corallites are located separately or in close contact to each other. Their cross-section differs from rounded-polygonal to starry. The number of septa is equal to 12, rarely more. Among the septa could be present two orders (i.e. alternation of long and shorter one). The siphonolites are developed. O. B. Bondarenko included the following families in the order: Pseudoplasmoporellidae Bondarenko, 1963; Heliolitidae Lindström, 1873; Stelliporellidae Bondarenko, 1971 [Bondarenko 1992].

Remarks. The order differs from orders Coccoseridida and Proporida by features of the skeletal tissue of vertical elements—septae, wall of corallites, and heteromorphic elements. The order Heliolitida has a lesser diversity of skeletal tissue than Khangailitida, but the corresponding homogenous, granular, and fibrous tissue is similar. The difference is that Heliolitida have only siphonolites but absent stages of prosiphonolites, cystolites and parasiphonolites. The siphonolites have different cross-sections. The axial structures are mostly absent.

Stratigraphical range. S–D.

Geographical distribution. Cosmopolitan.

Family **Heliolitidae** Lindstroem, 1873

Diagnosis. The colonies have different habitus except incrusting. The corallites are located separately. The structure of corallites walls and septa are equal in most cases. The septa are represented by spikes, squamulae, and plates; or could be absent.

Composition: *Heliolites* Dana, 1846, *Paolites* Bondarenko, 1992, *Vishkilites* Bondarenko, 1983, *Incendites* Serezhnikova, 1992, *Heliolitella* Lin in Li *et al.*, 1975, *Agallelites* Bondarenko, 1992, *Okopites* Bondarenko, 1978, *Dnestrites* Bondarenko, 1978, *Paraheliolites* Thanh, 1966, *Bogimbailites* Bondarenko, 1966, *Pachycanalicula* Wentzel, 1985.

Remarks. The family Heliolitidae differs from Pseudoplasmodiidae by the absence of coronas, aureoles and tiaras; from Stelliporellidae—by the absence of different axial complexes in the central part of corallites.

Stratigraphical range. S–D.

Geographical distribution. Cosmopolitan.

Genus **Agallelites** Bondarenko, 1992

Type species—*Heliolites irregularis* Wentzel, 1895 pro *Heliolites interstinctus irregularis* Wentzel, 1895, neotype chosen by Galle, 1973, pl. IV, Figs. 3–4 Prague Geological Academy No. 317; Bohemia, outcrop 'V Kozle'; upper part of Liten' formation, S₁w [Bondarenko 1992, pl. 41, Fig. 2].

Diagnosis. The polyparies are disk-like or nodular. The cross-sections of corallites are rounded. Tabularial walls are straight, slender curved, and thicker than walls of siphonolites. The septa lack both light and dark zones. Tabulae are mainly oriented horizontally. The units of coenenchima (siphonolites) differ in shape and size (from regular polygonal to elongated, and meandric). The diaphragms have a horizontal orientation.

Remarks. Genus *Agallelites* differs from other genera of the family by thick and smooth walls of corallites without septa in the corallites.

Stratigraphical range. S–D.

Geographical distribution. Cosmopolitan.

Agallelites leonidi Grytsenko & Rudenko sp. nov. (Fig. 6, *a-c*)

Holotype. NMNH Collection GD No. 1986/9996, 9997a, 9997b. Borehole 5414, depth 579 m, Rhykhta Formation (S₂ld).

Etymology. The species name is given to honour our colleague Leonid Konstantinenko.

Diagnosis. Corallum small, cross-sections 0.9–1.1 mm, lacks any septal developments. Tabulae have a concave shape and their density is nearly 10 per 2 mm. The distance among corallites corresponds to 4–5 rows of siphonolites. Zonality is emphasised by dark tabulae and by closer distance among diaphragms in polygonal siphonolites.

Remarks. The species differs from others species of the genus by much smaller corallites and relatively bigger distance among them.

Stratigraphical range. Silurian, Rhykhta Formation, Podillia, boreholes: 5463, depth 248; 5414, depth 579 m; 5351, depth 441 m; 3655, depth 351.9 m.

Geographical distribution. Ukraine (northern Podillia).

Agallelites petri Grytsenko & Rudenko sp. nov. (Fig. 5, *a, b*)

Holotype. NMNH Collection GD No. 1986, thin sections 5819–5823. Borehole 3655, depth 351.8 m, Tsviklivtsy Formation.

Etymology. The species name is given to honour Petro Tsegelnjuk, our colleague and chief of the team.

Diagnosis. Corallum of medium size, the cross-section is 1.3–1.4 mm, lacks any septal developments. Tabulae has concave shape and a density of 5 per 5 mm. The distances among corallites corresponds to two rows of siphonolites, which often have an irregular shape. The walls of corallites are twice as thick as the walls of siphonolites.

Remarks. The species differs from other species of the genus by the medium size of corallites and relatively closer distance among them.

Stratigraphical range. Silurian, Tsviklivtsy Formation and its analogues, (S₂ld₂), boreholes: 3655, depth 351.8 m; cross-sections 5819–5823; 1871, depth 221.7 m (14 m lower M–5) and others finds.

Geographical distribution. Ukraine (northern Podillia).

Genus *Okopites* Bondarenko, 1978

Type species—*Okopites okopiensis* Bondarenko, 1978, CGM No. 116365/1, Rashkiv Formation, layer 133, S₃př, Podillia, the left bank of the Dnister River, near the village of Okopy [Bondarenko 1992, pl. 2, Fig. 1, text-Fig. 34.1, 35.1].

Diagnosis. The corallites are located separately. The cross-sections of corallites vary from wrong-way to starry-folded in adult stage of colony development. The septa are represented by spikes, which are steeply oriented upward and sometimes united into fragments of short plates. The complete tabula changes from flat to arc-curved. The siphonolites are different in shape and size; the cross-sections are different in shape (from elongated-curved to weakly elongated and polygonal). The diaphragms are complete and have flat to weakly curved form; a few are interrupted.

Composition. Bondarenko [1992] listed a number species and subspecies from Eurasia.

Remarks. The species differs from *Dnestrites* by the septal apparatus, which is represented by upward oriented spikes. *Okopites* has no septal plates and axial structures. *Paraheliolites* has spikes oriented obliquely upward or has no spikes; siphonolites are the same in shape and size.

Stratigraphical range. S₂ld–D₁lh.

Geographical distribution. Ukraine (Podillia), Central Kazakhstan, Urals, Middle Asia (?), China, Australia.

Genus *Dnestrites* Bondarenko, 1978

Type species—*Dnestrites transites* Bondarenko, 1978, pl. II, Fig.3, text-Fig. 3; the upper part of Troubchin Formation, bed 184, S₃př; Podillia, left bank of the Dnister River, a ravine between the villages Dzvenyhorod and Dniestrove [Bondarenko 1992: pl. 42, Fig. 2, text-Figs (34. 2, 3; 35. 2)].

Diagnosis. The corallites are located separately. The cross-sections of corallites are weakly waved at the beginning of the development of colonies, folded, and starry on other parts. The septae are represented by thin plates with spikes on the edges. The plates are united in the axial zone. The axial structures developed in dark zones. The tabulae are different in the light and dark zones.

Stratigraphical range. Troubchin and Dzvenyhorod Formations; Xibiehe Formation.

Geographical distribution. Ukraine (Podillia). China (Inner Mongolia).

Dnestrites transites Bondarenko, 1978 (Fig. 5, p–s)

Description. The corallites are located separately but close to each other (1–2 rows of siphonolites/cystolites among neighbouring corallites). The cystolites are more characteristic for dark zones. The cross-sections of corallites are 1.6–1.8 mm. The walls are weakly waved at the beginning of colonies development, folded, and starry on other parts. The septa are represented by thin curved plates with spikes on the edges. The plates are united in the axial zone (Fig. 5, s). The complexly built axial structures are developed in dark zones. They are constructed by septal plates and convex tabula. The axial complex is oriented upward like spruce branches (Fig. 5, s). The tabulae are different in light and dark zones, flat and convex, accordingly (Fig. 5, r–s). We made 5 thin sections from 2 specimens collected in an outcrop on the left bank of Dnister River near the village of Dzvenyhorod.

Remarks. Bondarenko [1978] described another species *D. expectatus* Bondarenko, 1978, which we consider to belong to the type species as its features are within the limits of variability of the type species.

Stratigraphical range. Upper Silurian, Přidoly (S₃př), Dzvenigorod Formation.

Geographical distribution. Ukraine (Podillia).

Genus *Paraheliolites* Tong-Gzuy Than, 1966

Type species—*Heliolites* (*Paraheliolites*) *minutus* Tong-Gzuy Than, 1966 a, pl. 29, Fig. 2; BX No 311/25, Miale Horizon, D₁pr; North Vietnam, Baktkhai Province [Bondarenko 1992: pl. 40, Fig. 2].

Diagnosis. The corallites are located separately. The cross-sections of corallites are rounded, or weakly folded. The walls have no longitudinal curves or are weakly folded. The septa are spiky and oriented oblique upward or can be absent. The tabulae are completely oriented horizontally, or concave and can have solitary separated spikes. The siphonolites have a prismatic shape with equal polygonal or rare elongated cross-sections. The thin walls of siphonolites are thickened in the dark zones and thus the inner space have a rounded-polygonal look. The complete diaphragms are oriented horizontally, are weakly concave or convex.

Composition. *Heliolites* (*Paraheliolites*) *minutus* Tong-Gzuy Than, 1966; *Paraheliolites balkhashensis* Kov., 1975, Kazakhstan, Akkan and Kokbaital Horizons, S₂ld–D₁lh; *P. barrandei* sensu Tong-Gzuy Than, 1988, non *P. bohemicus* (Wentzel, 1895); Bohemia, Barrandien, the upper part of Liten Formation, S₁w; *P. pachycanaliculoides* Barskaya, 1963, Altay Mountains, S₂ld₁; Podillia Troubchin and Dzvenyhorod Formations (S₂ld₃?)–S₃pr̄ [Bondarenko 1982b, 1983a]; *P. scaliensis* Bondarenko, 1985a; Podillia, Troubchin and Dzvenyhorod Formations (S₂ld₃?)–S₃pr̄; and many others from Eurasia and Australia.

Remarks. The genus *Paraheliolites* was separated basen on the development of septal spikes or their absence, which differs it from the genus *Heliolites* that has plate septa (Tong-Gzuy Than, 1966). From the very beginning, Tkhan considered that genus as a subgenus within *Heliolites* [Bondarenko 1992].

Stratigraphical range. S₁w–D₁lh.

Geographical distribution. Cosmopolitan.

Paraheliolites scaliensis Bondarenko, 1985 (Fig. 6, d–f)

Diagnosis. The curving corallites are located separately. The cross-sections of corallites are rounded, or weakly folded. The diameter is 1.2–1.4 mm. The corallites are separated from each other by 1–2 rows of siphonolites. The walls have no longitudinal curves or are weakly folded. The septa are spiky and oriented oblique upward or can be absent. The tabulae are completely oriented horizontally or concave and with solitary separated spikes. The siphonolites have a prismatic shape with equal polygonal or rare elongated cross-sections. The thin walls of siphonolites are thickened in the

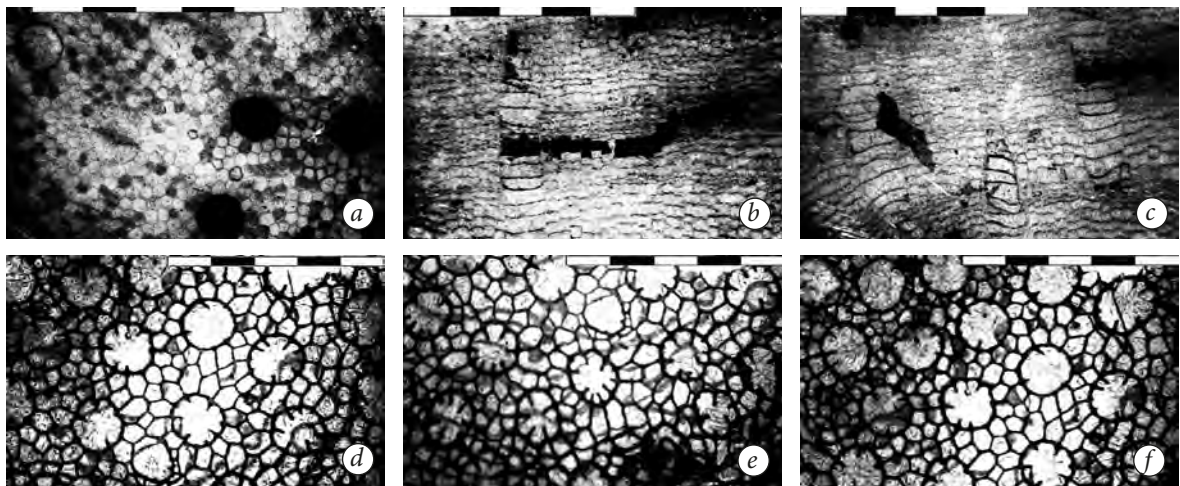


Fig. 6. The structure of the described species: (a–c) *Agallelites leonidi* Grytsenko & Rudenko sp. nov., Malynivtsy Series, Rhykhta Formation (S₂kn₃), borehole No. 5414, depth 579 m; a—No. 9996b, transverse section; b—No. 9997a, longitudinal section; c—No. 9997b, longitudinal section; (d–f) *Paraheliolites scaliensis* Bondarenko, 1985. Pridolian Series (S₃pr̄), Dzvenigorod Formation, outcrop 45 (Dnistrove); transverse sections: No. 5017, No. 5017a, and No. 5017b. (Scale bar in all figures 1 mm).

Рис. 6. Будова описаних видів (номери свердловин, шліфів та стратиграфічне положення зазначене в підписах англійською, поділки масштабу — 1 мм, довжина лінійки 5 мм).

dark zones and thus the inner space have a rounded-polygonal look. The complete diaphragms are oriented horizontally, are weakly concave or convex.

Remarks. The species differs from *P. pachycanaliculoides* Barskaya by larger diameter of the corallites and less developed spiky septa.

Stratigraphical range. Trubchin and Dzvenigorod Formations (S₃př).

Geographical distribution. Ukraine (Podillia).

Genus *Bogimbailites* Bondarenko, 1966

Heliolites: Weissermel, 1938

Type species—*Bogimbailites sytovae* Bondarenko, 1966: 191, pl. XXXII, Figs 1, 4. Lower Devonian, Gedinian, Isen' Formation, Superanasui Horizon, Zone *Bogimbailites sytovae*. Southern ridge of Karaganda Basin, Upper Burnak River, 5 km north-east of the ruins of Bogimbai.

Diagnosis. Polyparies are nodule-like. The corallite walls are waved, septal formations are represented by needles, which are broader (like squamulae) near the base. The walls of coenenchimal tubes are reduced. As a result, it looks like a meander or has a sponge-like appearance in cross-section. The diaphragms are horizontal in the light zones and reduced flat-blistered in the dark zone. The tabulae are complete or interrupted, horizontal flat or curved on different sides. The genus *Bogimbailites* occupies an intermediate position between *Helioplasmolites* Chekhovich and *Helioplasma* Ketnerova. It differs from both by periodic development of blisters in diaphragms and features of walls reduced in siphonolites.

Remarks. O. B. Bondarenko presented information about the holotype: 'Upper Silurian, Ludlow Stage, Isen' Formation; Lower Devonian, Gedinian, Superainasu Horizon, Zone *Bogimbailites*' [Bondarenko 1966: 191]. It is incorrect, and could be explained by a discussion about the age 'Superainasuisky' Horizon, which, as shown by researchers of the Silurian and Devonian of Kazakhstan, corresponded to early selected Kokbaital Horizon, which, in turn, correlates with the Borschov Horizon in Podillia, the lower part of Lokhovian of the International Stratigraphical Chart [Bondarenko *et al.* 1975: 21–26].

Composition: *Bogimbailites sytovae* Bondarenko, 1966, Gedinian of Kazakhstan. *Heliolites* sp. nov. described by W. Weissermel on the opinion of O. B. Bondarenko [Weissermel 1938; Bondarenko 1966], and the new species *B. bondarenkoi* Grytsenko & Rudenko sp. nov. from Rushkiv Horizon, Varnitsa Formation.

Stratigraphical range. S₃př–D₁lh.

Geographical distribution. Kazakhstan, Ukraine (Podillia).

Bogimbailites bondarenkoi Grytsenko & Rudenko sp. nov. (Fig. 5, *l*; Fig. 6, *a*; Table 2)

Holotype. NMNH Collection GD No. 1986, thin section 4050, 4050a; Upper Silurian, Pridolian, Varnitsa Formation, Ternopil Oblast, borehole 6, depth 157.4 m.

Etymology. The species name is given to honour Olga Bondarenko, a famous palaeontologist and specialist in the study of Heliolitoidea.

Diagnosis. The corallites sections are wavy and folded; their diameter is 1.5–1.6 mm. The corallites are surrounded by a ring of large siphonolites with bubble-like diaphragms. The walls of corallites and siphonolites are thickened in the dark zones. The septal formations are represented by 12 rows of needles, which are broader near the base like squamula. The walls of coenenchimal tubes are somewhere reduced. As a result, in cross-section it looks like an elongated slightly curved tube. The diaphragms are oriented horizontally and obliquely in the light zones and little convex-blistered in the dark zone. The tabula is complete or interrupted horizontal flat or curved on different sides. The spikes fulfill the inner part of corallites in the dark zones.

Remarks. *Bogimbailites bondarenkoe* differs from *Heliolites* Dana by more complete coenenchima construction, including having meanders or sponge-like structure of coenenchima. The blister-like diaphragms and waved walls of siphonolites allow distinguishing representatives of the genus *Bogimbailites* from *Heliolites*,

which have direct walls and mostly flat diaphragms. One specimen was found in the core of borehole No. 6. We made four thin sections. The rock is represented by clayey-detritic limestone of marine moderately shallow water (detritic) facial zone. The specimen was accompanied with remains of Bryozoa, Brachipoda, and solitary Rugosa.

Table 2. The measurements of skeletal elements of *Bogimbailites bondarenkoe* No.1316–1319
Таблиця 2. Виміри розмірів елементів скелету *Bogimbailites bondarenkoe* № 1316–1319

Corallites (Tubuli)		Coenenchimal tubes (Siphonolites)	
Diameter of corallites (mm)	0.9–1.0	Diameter of tubes	0.2–0.5
Distance between corallites (mm)	0.2–1.0	Number of rows among corallites	1–3
Wall thickness (mm)	0.05	Wall thickness (mm)	0.025
Number of tabulae per 5 mm	14	Number of diaphragms per 5 mm	19
Number per 1 cm ²	40		

Family **Pseudoplasmodoridae** Bondarenko, 1963

Diagnosis. The colonies have different shape except incrusting. The corallites are located separately. The corallites are surrounded by coronas, aureoles or tiaras. The structure of wall and septa are equal. The septa are represented by simple spikes, squamula-like spikes, which are thickened near walls, thin plates, or can be absent. The siphonolites have a polygonal shape as usual. The colonies have tetramorphic construction.

Composition. *Pseudoplasmodora* Bondarenko, 1963; *Sideriolites* Bondarenko, 1992; *Amphilites* Bondarenko, 1975. Conditionally: *Navoites* Leleshus & Ospanova, 1979a; *Paeckelmannopora* Weissermel, 1939.

Remarks. The family differs from *Heliolitidae* and *Stelliporellida* by the absence of coronas, aureoles, and tiaras, which surround corallites.

Stratigraphical range. (O₂c₂₋₃?)–O₃a–D₁lh.

Geographical distribution. Cosmopolitan.

Genus **Pseudoplasmodora** Bondarenko, 1963

Type species—*Pseudoplasmodora conspecta* Bondarenko, 1963, p. 47, pl. I. IV, Fig. 1, text-Fig. 1. CGM No. 8732/1, Upper Silurian, Ludlow, Isen' Formation, Ainasu Horizon (later the deposits were corresponded to the Lower Devonian [Bondarenko *et al.* 1975]). Southern part of Karaganda Basin, within 3 km south of Akbastau settlement.

Plasmodora: Milne-Edwards et Haime, 1851: 226 (pars); Jones et Hill, 1949: 206 (pars); Ragnell, 1941: 50 (pars).

Heliolites: Chapman, 1914: 311 (pars); Kovalevsky, 1965: 112–133 (125–126 pars).

Pseudoplasmodora: Bondarenko, 1963: 47; 1966: 157, 158.

Diagnosis. The shapes of the polipary are different: from lens-like to conical. The septal elements are represented by needles; sometimes they are absent. The tabulae are horizontal and curved. The corallites are surrounded by aureoles from 12 tubes through all colonies. The tubes have horizontal diaphragms and sometimes cross one another [Bondarenko 1966: 156].

Composition. Sixteen species and two new species described herein.

Remarks. The genus differs from *Heliolites* Dana by the presence of an aureole of 12 tubes surrounding corallites; from *Squamolites* it differs by the absence of septal squamulae.

Stratigraphical range. S₁w–D₁lh.

Geographical distribution. Europe (England and Podillia), North America, Asia (Kazakhstan, Kuznezk Basin, Tarbagatay, Tian Shan, India), and Australia.

Pseudoplasmodora spinifera Grytsenko & Rudenko sp. nov. (Fig. 5, *l–m*)

Holotype. NMNH Collection No. 1986, Upper Silurian Zadariv Formation², Volyn Oblast, Locachi-6 borehole, interval 1703–1706.6 m.

² Zadariv Formation is distributed in the Deep part of the Lviv Paleozoic Depression [Gozhyk 2013].

Etymology. The name is derived from the Latin ‘spinifer’—having spikes (needles).

Description. The tiny *Pseudoplasmodora* has thin corallites with long needles. The polyparies are little, nodule-like or fungous. The diameter of corallites is 0.6–0.9 mm, densely located (48–50 per 1 cm²). It is surrounded by 12-tubes aureole. Among the corallites are 1–2, sometimes 3 siphonolites. The tubes have penta- or hexagonal sections. The walls of corallites and tubes of siphonolites have the same thickness and are almost direct. The zoning (dark and light) is not very clear. The thickness of skeletal elements is nearly 0.05 mm in the light zone and 0.1 mm in the dark zone. The tabulae are often oriented horizontally, direct or slightly concave. The number of tabulae can be 26 per 5 mm. The diaphragms in siphonolites are slightly convex. The edges are directed to the bottom in the places connected to corallites. The frequencies of diaphragms in siphonolites are such to one in the corallites, but their levels do not match. The needles develop in two orders and on the entire lengths of corallites by rows. The long needles reach the centre of corallites. The bases of needles in the dark zone are connected and form septa-like structures. The variability is manifested very weakly. The seasonal zonation is indistinct in the structure. We made six thin transparent sections from two specimens.

Remarks. The preservation is good, although in some places the silicification of skeletons is noticeable. The specimens are distributed in clayey-detritic limestones from middle shallow water facial zone together with remains of Stromatoporida, Favositidae, Rugosa, Bryozoa, and Brachiopoda. The described species differs from other species by having more developed needles. The species differs from *P. bella* (Kovalevsky) by larger corallites and smaller distance among them; from *P. conspecta* Bondarenko by having walls twice as thick, smaller distance among corallites and rarely located diaphragm in the siphonolites. Differences from other species are more significant.

Stratigraphical range. Upper Silurian Zadariv Formation.

Geographical distribution. Ukraine, Volyn Oblast, Locachi–6 borehole.

***Pseudoplasmodora minima* Grytsenko & Rudenko sp. nov. (Fig. 5, n)**

Holotype. NMNH Collection No. 1986/1268, 1269; Upper Silurian, Pridolian Stage, Zadariv Formation, Volyn Oblast, borehole Locachi–6, interval 1703–1706.6 m.

Etymology. The name means ‘very small’ in Latin.

Description. The little *Pseudoplasmodora* polyparies include very thin and closely located corallites. The needles are very thin and short. The little hemispherical polypary is attached to a corallite of *Rhamulophyllum* sp. Its size is 6 x 7 cm. The basal surface is flat concave (the cast of rugosan coral). Corallites are located radially. There are nearly 80 corallites per 1 cm². The diameter of corallites is 0.5 mm, and the distance between them is 0.2–0.4 mm or 3–4 siphonolites. Twelve siphonolites form an aureole, which surrounds every corallite. The size of siphonolites in aureole is 0.15–0.20 x 0.25 mm. It is more or less isometrical in other places, and have a size of nearly 0.2 mm. The walls of corallites have little thickness outside in the places of contact with siphonolites. The trabecular structure of the walls is visible by microscope. The tabula is slightly convex, located with an interval of 0.2–0.5 mm. Diaphragms in the siphonolites are convex and blister-like, somewhere spike-shaped. The ridge of siphonolites in the aureole is tilted towards the corallites. The measured interval between diaphragms is 0.10–0.15 mm. The needles are underdeveloped. The variability is recognised by alternating dark and light zones, where blisters or simply thin plates represent diaphragms, accordingly. The thickness of skeletal elements is almost the same in both types of zones.

Remarks. *P. bella* (Kovalevsky) which redescribed by Bondarenko [Bondarenko 1966] is most close to described species here, but differs on less distance of corallite location, more interval tabulas in corallites and diaphragms in siphonolites. In addition, new species have blister-like diaphragms and poor distincted needles. The difference from others species is more visible. Only one sample found in excellent preservation, and two thin sections (No1268, No1269) made. The rock is clayey-detritic limestone. The sample found with remains of solitary Rugosan, Bryozoan and Crinoidea detritus. It is detritic facial zone.

Stratigraphical range and geographical distribution indicated before.

Family **Stelliporellidae** Bongarenko, 1971

Description. The corallia have different shape from massive or incrusting upto cylindrical and branching. The tabularia separated by coenenchyme (sometimes contacting each other). Each corallite has 12 equal plates (somewhere with spinose ending). The cross-section of corallites is rounded or starry. The plate of septae are connected and, as a result, develop different axial structures: prismatic tubes, cylinders or membranes; sometimes connected by neighbours from two to five. In rare cases, one septum reaches the centre, thickening and developing an axial column, lens-like in cross-section. Tabula is complete but sometimes incomplete, horizontal, concave or convex. The coenenchimal tubes are polygonal, elongate, curved or meandric in cross-sections; the thickening of the wall makes a rounded inner space. The diaphragms are completely horizontal and domed; sometimes interrupted in the dark zones. The number of siphonolites in rings near the corallites can be from 12 to 27. The coronae and/or aureoles are absent, but sometimes tiaras can be developed [Bondarenko 1992].

Remarks. Bondarenko included to the family the following genera: *Parastelliporella* Lin et Chow, 1977; *Cosmiolites* Lindstrom, 1899; *Stelliporella*, Wentzel, 1894; *Derivatolites* Bondarenko, 1971; *Podolites* Bondarenko, 1971; *Saaremolites* Sokolov, 1955; *Syringoheliolites* Bondarenko, 1971; *Pachystelliporella* Lin in Jia et al., 1977; *Tarbagataillites* Bondarenko, 1975, and *Marialites* Bondarenko, 1992 [Bondarenko 1992].

Stelliporella lamellata Wentzel, 1894. (Fig. 5, *o-1*, *o-2*)

Diagnosis. The colonies have a plate-disc shape. The corallites have a starry cross-section. The plate septa reach the axial zone, where they develop special tubes of different sizes, but a few form a special 'pocket' from the wall of corallites to the axial zone. The bases of septa are thickened. The diameter of corallites is nearly 1.0–1.1 mm. Few specimens were recovered found from different boreholes. We made 20 thin sections.

Stratigraphical range. Lower Silurian, Kytaihorod Horizon.

Geographical distribution. Ukraine, Ternopil Oblast, Koropets–3 borehole, depth 1230.6 m.

Stelliporella intricata Lindstroem, 1899 (Fig. 4, *b-c*)

Diagnosis. The colonies have branched shape. Mainly distributed in reef facies, where they were found in clear limestones of Konivka Formation bioherms and some boreholes. The branches are relatively thin and short. The diameter is up to 1.5–2.0 cm. The corallites have a starry look. Two septa run around the free axial zone surrounding the corallite centre and developing a 'special pocket'. The other septa are connected to them. The corallites have a diameter of nearly 1 mm. Coenenchimal tubes have polygonal cross-section and are more or less equal each. The diaphragms can be relatively weakly curved on both sides (up and down); the number of diaphragms is 5 per 2 mm.

Remarks. In the collection, we have only few specimens of the species. We made three thin sections: borehole No. 7, depth 324 m, thin section No. 4029, Shutnivtsy Subformation of Konivka Formation; borehole No. 5414, depth 618.5 m, thin section No. 9235. The additional material we received from Belarus.

Stratigraphical range. Upper Silurian, Malynivtsy Series, Konivka Formation (S₂ld).

Geographical distribution. Ukraine, Volyn Oblast, borehole No. 5414, depth 518.5 m, No. 9235a—longitudinal section, No. 9235—transverse section.

Genus ***Podolites*** Bondarenko, 1971

Type species—*Podolites diseptatus* Bondarenko, 1971; pl. 38, Fig. 4, 2; holotype, Paleontological Institute No. 4239/4, Kitaigorod horizon, Ternava Formation, Sursha Subformation, S₁w [Bondarenko 1992, pl. 37, fig. 2].

Diagnosis. The polyparies have a nodular shape. The transverse section of corallites is close to ring. The walls of corallites are straight, somewhere slightly curved. The neighbouring two or three plates are connected, more rarely four or five, and develop membranes. Tabulae are complete and horizontal. Siphonolites has polygonal shape. Diaphragms are complete and have horizontal position. The rings surrounding corallites consist of 14–16 siphonolites.

Composition. Type species and *P. irregularis* described herein.

Remarks. The genus *Podolites* differs from *Direvatolites* by connecting not only septal plates of opposite sectors but also neighbour plates by two and three, somewhere four and even five simultaneously. The species differs from *Pachystelliporella* by the thin walls of siphonolites.

Podolites irregularis Grytsenko & Rudenko sp. nov. (Fig. 3, *c–d*; Fig. 5, *h*)

Holotype. NMNH Collection No. 1986, thin sections No. 347, No. 1051; Upper Ludlow, Grinchuk Subformation (S₂ld).

Etymology. The species name means ‘irregular’ in Latin.

Diagnosis. Colonies have lens-like shapes. The corallites have rounded form. Their diameter is 1.2–1.3 mm. They are separated from each other by 3–4 rows of siphonolites. The septa are developed in different lengths and are less regular. They are often reduced—it is uncharacteristic for the type species. The septa join in an irregular way: the long thin septa formed connected groups two each as wedge and two each as parallel almost achieved or crossing axial zones. The septa can be wavy curved and form symmetry close to bilateral. Corallites have a typical appearance as in the species described by Olga Bondarenko [1971]. In the early stage of development, corallites can be wavy (Fig. 5, *h*, right, bottom). The species in our collection also differs by other positions in the sequence, i.e. Grinchuk Subformation instead Sursha Subformation in the type species.

Stratigraphical range. Grinchuk Subformation (S₂ld).

Geographical distribution. Ukraine, Podillia.

Genus *Saaremolites* Sokolov, 1955

Type species—*Saaremolites inversus* Sokolov, 1955; pl. 75, Fig. 1–2; holotype VNIGNI No. 599/127, Jagarakhu Horizon, S₁w₂, Estonia, Saarema Island [Bondarenko, 1992, pl. 47, Fig. 1].

Diagnosis. The polyparies have nodular and hemispherical shapes. The transverse section of corallites is folded and starry. The walls of corallites are longitudinally folded. The septa are spiky. The columns are located in the central part (axial) of corallites. It is short and spiky in the light zone. The columns are long and complicated by short spikes in the dark zones. Tabulae are sharply domed, somewhere arcuate in the zone of axial column. The siphonolites has polygonal shape in transverse sections. The diaphragms are complete and have horizontale position. The corallites are surrounded by a ring of 17–22 siphonolites.

Composition. Type species; *Saaremolites kurzemensis* Klaamann, 1984, Latvia, borehole Venspils, Paadla horizon S₂ld₁; *Saaremolites inversus podolica* Grytsenko & Rudenko ssp. nov., Ukraine, Rykhta Formation, Grinchuk Subformation, outcrop No. 18, thin section No. 1197–1199.

Remarks. The genus *Saaremolites* differs from other genera of the family by having spiky septa. In addition, they differ from *Derivatolites*, *Podolites* and *Stelliporella* by presenting an axial column, from *Syringohelolites*—by the absens of the axial tube, which is developed as a result of sequential splicing of septa.

Stratigraphical range. S₁w₂–S₂ld.

Geographical distribution. Estonia, Latvia, and first finding in Podillia, perhaps Sweden (Gothland Island).

Saaremolites inversus podolica Grytsenko & Rudenko ssp. nov. (Fig. 3, *k*, Fig. 5, *g*)

Type specimen—Rykhta Formation, Grinchuk Subformation, outcrop No. 18, thin section No. 1197–1199.

Etymology. The name of subspecies is derived from the name of the region, Podillia.

Diagnosis. The colonies have bolder-like and hemisphaerical shapes. The corallites are located separately. Their cross-sections round or weekly folded, with a diameter of 0.9–1.0 mm. The septal characteristics differ in the light and dark zones. In the light zones, septae are reduced and only short squamula-like developments can be seen. A simple lens-like on transverse section columella developed in the dark zones; septa are longer in these zones. The tabula near the columella are steeply raised (Fig. 5, *g*). The siphonolites have polygonal cross-section. The siphonolites near corallites form rings from 19 to 21 tubes.

Remarks. The subspecies differs from typical *S. inversus* Sokolov by having more reduced septa and more upper stratigraphical position, S₂ld instead of S₁w.
Stratigraphical range. Grinchuk Subformation (S₂ld).
Geographical distribution. Ukraine, Podillia.

Genus *Syringoheliolites* Bondarenko, 1971

Type species—*Syringoheliolites contrarius* Bondarenko, 1971; pl. 38, Fig. 5, text-Fig. 2; holotype PIN No. 4239/5; Malynivtsy local series, the upper part of Grinchuk Subformation; western Ukraine, Podillia [Bondarenko, 1992, text-Fig. 37.3].

Diagnosis. The colonies have different shape from bolder-like to hemispherical and flat disk. The cross-section of corallites is starry or folded. The walls of corallites are weakly folded in the vertical direction. The septal plates are fused near the axial spaces developing cylindrical tubes, which open into segments between two septa.

Syringoheliolites contrarius Bondarenko, 1971 (Fig. 3, *h, i*)

Diagnosis. The colonies have flat-disc shape and different sizes (diameter up to 20–30 cm). The corallites are starry in cross-sections. The diameter varies from 0.9–1.1 mm. The long septa joining developed an axial tube with interruption between two septa. The axial tubes are filled by a few more little tubes (e.g. table A, Fig. 3, *h*, near the right of the central part). The coenenchima is constructed by little equal polygonal siphonolites. The horizontal elements developed in corallites (tabula) and in siphonolites (diaphragms) are almost flat.

Remarks. The species is primarily characteristic for the upper part of the Rhykhta Formation in outcrops and many boreholes, including borehole No. 5463, depth 240 m; thin sections No. 9974, No. 9975 and many others.

Discussion

The remains of fossil cnidarians are mostly connected with deposits of shallow water zones of an ancient sea. Their distribution depends on various factors: palaeoclimate cycles and reflected sea level fluctuations, the characteristic of the sea bottom, level of salinity, food resources, and so on. That conclusion is based on modus vivendi of modern corals, which is characteristic for fossils too.

Cnidarian remains play one of the leading roles in sequence-stratigraphy as indicators of the depth and main features of past sea basins, which researchers reconstruct according to the facial nature of the deposits.

Usually, in Heliolitoidea (and Tabulata) corals zonality is visible in the thin sections as alternation of dark (narrower) and light (broader) zones. The intensiveness of the development of thick skeletal tissue was depended on higher reproductive activity of corals and slower growth rate (dark zone) connected with seasonal changes [Preobrazhensky 1967; Bondarenko 1978]. In part of the polyparies capsules were found—possibly planulas, i.e. fossil larvae [Grytsenko 1978].

The upper level of the system—Phylum Coelenterata Frey & Leuckart, 1847, Subphylum Cnidaria Hatschek, 1888—we adopted following the basic authoritative international source ‘Treatise on Invertebrate Paleontology’ [Treatise 1956: Part F]³.

Heliolitoidea is one of complicated and difficult-to-study superorder of fossils. Almost every researcher represents the system according to own understanding. B. S. Sokolov brought such system: Class Anthozoa, subclass Heliolitoidea, order Protaraeida, order Heliolitida (families: Heliolitidae Lindström, 1873; Plasmoporidae Wentzel, 1895; Cyrtophyllidae Sokolov, 1950; Proporidae Sokolov, 1950; Proheliolitidae Kiär, 1899).

Dorothy Hill and Edwin C. Stumm represented other System in order Tabulata Milne-Edwards et Haime, 1859 they included families: Chaetetidae Milne-Edwards et Haime, 1850; Stringophyllidae Počta, 1902; Favositidae Dana, 1846, and Heliolitidae Lindsrtöm, 1876. In the family the authors

³ This volume was reprinted in 1967.

included Subfamilies: Coccoseridinae Kiär, 1899; Palaeoporitinae Kiär, 1899; Plasmoporinae Wentzel, 1895; Heliolitinae Lindsröm, 1876. The family Heliolitidae Lindsröm, 1876 on the opinion [Hill & Stumm 1956] included 17 genera.

The new 'System Heliolitoidea' created by Olga Bondarenko by using a new tool for painting and a series of oriented thin sections received of real changes of astogenic development on different stages (i.e. neanic, ephabic, gerontic stages, and alternation of dark and light zones). The new approach applied to the study of Heliolitoidea allowed Olga Bondarenko to increase the number of features and show that the periodical changing of features (cyclomorphosis) is not only species-specific but also genus-specific. Therefore, all this led to a conclusion of the necessity to take into account not only one feature but to consider others as well to receive the correct volume of the genera. As a result, the author revised the diagnosis of genera and accordingly, were viewed and given a diagnosis of supragermic categories. In Olga Bondarenko's monograph a new system of Heliolitida, based on other taxonomic criteria, was given, including 4 orders (one new), 7 superfamilies (two new), 25 families (six new), 4 subfamilies (one new), 4 tribes (one new), 122 genera (20 new and 30 were erected earlier), and nearly 1000 species [Bondarenko 1992].

We hope the question about conditions in the Silurian sea basin on the west slope of the East European platform is solved by evidence of some litological basements. Firstly, the sequence consists of limestones, which indicate warm seawater. Secondly, the list of fossils firmly points to sea conditions with normal salinity [Tsegelnjuk *et al.* 1983]. Earlier, based on geological data we considered that the Silurian sea shelf was divided into five sea facial zones with normal and turbulent conditions [Grytsenko *et al.* 1999]. Recently, evidence of tropical conditions within the limits of the Podillian pericontinental shelf was obtained through the application of a new research method—biomarkers were used from core samples of boreholes Kotuzhiny–25 [Marshall *et al.* 2022].

We suggest that gypsum interbeds in the shoal lagoon deposits show warmer times in the Silurian period. The sea level change was reconstructed (Fig. 7) using a detailed study of the Podillian Silurian section [Grytsenko 2007].

The facial spread of sedimentation depends on organic build-up (Fig. 8), which is developed by skeletons of Cnidaria and Algae. The calcereous algae and cnidarian remains constructed strong structures (bioherms), which influenced the current and facial distribution of sediments.

We recently with our colleagues from the University of Riverside (California) provided a study of assessing marine communities and carbon cycles that sustained shallow-marine ecosystems on the Silurian, reef-rimmed carbonate platform [Marshall *et al.* 2022].

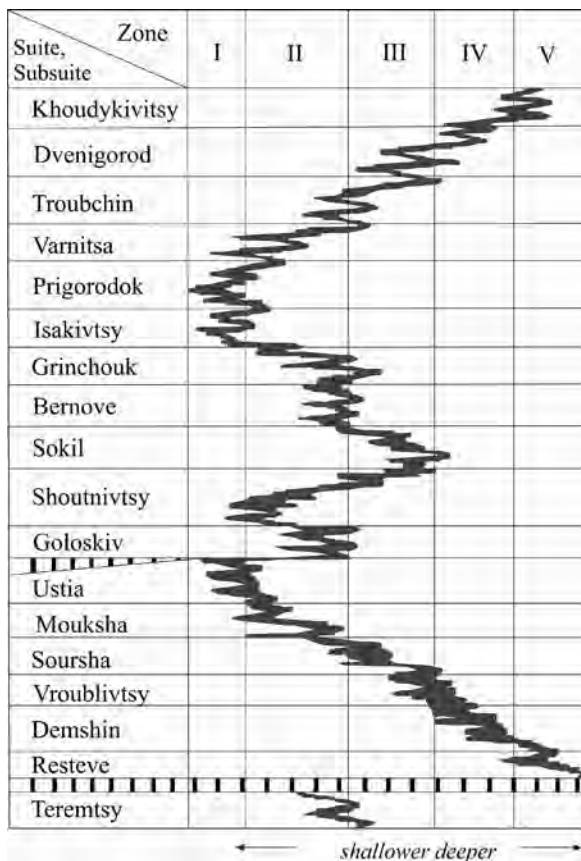


Fig. 7. Sea level changes in the Silurian (transgressions and regression based on outcrop data) or the dynamics of facies in the case of the Podolian reference section [Grytsenko 2007].

Рис. 7. Динаміка рівня моря на протязі силурійського періоду (трансгресії та регресії за даними вивчення відслонень силуру в долині Дністра) або зміна фаціальних обстановок на прикладі опорного розрізу силуру Поділля [Grytsenko 2007].

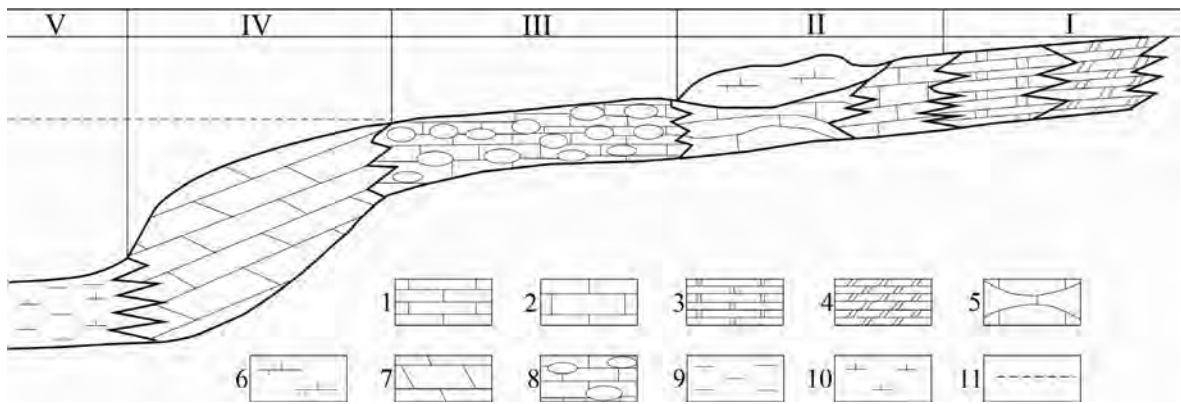


Fig. 8. The facial model of the Podillian Silurian Sea. Zones I–V: I—lagoon; II—bar; III—shallow shelf; IV—deep shelf; V—deep sea. Rocks 1–10: 1—thin bedded limestones; 2—detrital limestones; 3—thin bedded dolomites; 4—dolomitic-marls (domarit); 5—nodular detrital limestones; 6—massive limestones of bioherms; 7—marls; 8—nodular argillaceous-detrital limestones; 9—argillites, 10—calcareous argillites, 11—wave base.

Рис. 8. Фаціальна модель Подільського морського басейну. Зони I–V: I — лагуна; II — бар; III — мілководний шельф; IV — глибоководний шельф; V — глибоке море. Породи 1–10: 1 — тонкошаруваті вапняки; 2 — детритові вапняки; 3 — тонкошаруваті доломіти; 4 — доломітові мергелі (домерити); 5 — грудкуваті детритові вапняки; 6 — масивні вапняки біогермів; 7 — мергелі; 8 — грудкуваті аргіліти-детритові вапняки; 9 — аргіліти; 10 — вапнисті аргіліти; 11 — базис хвиль.

Conclusions

The revision of our collection of Heliolitoidea shows a significant diversity of these corals and requires more deep study based on the ranks of variability.

Heliolitoidea are characteristic of shallow water facies with more or less active turbulence. They are often found in bioherms on almost all stratigraphical levels of the Silurian sequence in the deposits of the west slope of the Ukrainian Shield in the limits of Podillia.

Heliolitoidea are represented by different morphological varieties from globous to flat and chain-like. The skeletal structure is very complicated. They are colonial animals in which corallites are surrounded by siphonites and other components of the coenecium. Septal elements vary from almost absent to extending to the centre of corallites. The walls of corallites can be circular and wavy in cross-section. Sometimes corallites have axial tubes—aulos (genus *Syringoheliolites* Bondarenko and other genera).

Heliolitoidea were distributed globally in the early Paleozoic warm water seas (palaeotropical and palaeosubtropical climate zones from Canada to Australia). Some of them took part in the construction of bioherms that spread along the shoreline on shelf zone like chains of build-ups and could separate the continental slope from lagoons.

The specific look of well-preserved specimens sometimes allowed us to make preliminary identifications to species level. In the other cases, there is a need to make thin transparent sections, which show the coral's inner structure. The identification of fossils is largely complicated by their complex structure, changing features of the skeletons during ontogeny, and 'homologous series in hereditary variability'⁴ in different genera.

Finally, Heliolitoidea are used to correlate geological sections of different regions and in a broader global context.

Acknowledgements

We dedicate this paper to the memory of our colleagues and friends from 1972 Olga Bondarenko and Viktor Pushkin, who studied Lower Paleozoic Heliolitoidea and bryozoans, respectively. We are

⁴ The law of homologous series in hereditary variability [Vavilov 1987].

also grateful to an old friend and colleague, Petro Tsegelnjuk, who led several expeditions to Podillia since the first author was a student and after graduation from the Kyiv University. We express our deepest thanks to friends Galina Furmanchuk and Vasil Sidor for organising and supporting a number of field trips along the Dnister River for sampling after a long interruption. The authors are very grateful to the reviewers for polishing the manuscript and helpful advice and remarks. We are sincerely grateful to I. Zagorodniuk, Z. Barkaszi, V. Dernov and V. Raevsky for helpful advice in the process of preparation and editing of the manuscript. A special thanks to Academician I. Emelianov and O. Chervonenko, leaders of our museum, for constantly supporting and funding field and in-house work to study the fossil corals.

This study was supported by Taras Shevchenko National University of Kyiv, National Academy of Science of Ukraine, the Geological Survey, other national organizations, institutions, as well as the Geological Department of National Museum of Natural History, NAS of Ukraine. The study is also part of the research project ‘Geological diversity’ (No. 0122U000429) carried out in the Geological Department of NMNH NAS of Ukraine.

References

- Bondarenko, O. B. 1963. The revision of genus *Plasmopora*. *Paleontological journal*, **1**: 42–52. [In Russian]
- Bondarenko, O. B. 1966. Heliolitoidea of Isen’ska Formation. *Stratigraphy and Fauna Silurian and Lower Devonian deposits of Nurinsky sinclinary*. MGU, Moscow, 145–197. [In Russian]
- Bondarenko, O. B. 1971. Vertical spreading Heliolitoidea in Podillia and age of compatible deposits. *Vesnyk MGU, geol.*, **2**: 42–48. [In Russian]
- Bondarenko, O. B. 1978. Polymorphism of Paleozoic tabulatamorph corals. *Paleontological journal*, **2**: 23–35. [In Russian]
- Bondarenko, O. B. 1992. *The System of Heliolitids*. Moscow Society of Naturalists, Moskva, 1–209. [In Russian]
- Boweld, B. A. 2015. Chekhovichia, a new generic replacement name for *Rotalites Leleshus* 1970 (Anthozoa: Heliolitoidea) non Lamarck 1801 (Protista: Foraminifera). *Zootaxa. Correspondence* 4034 (2): 399–400. <https://doi.org/10.11646/zootaxa.4034.2.11>
- Chatterton, B., P. Copper, O. Dixon, S. Gibb. 2008. Spicules in Silurian tabulate corals from Canada, and implications for their affinities. *Palaeontology*, **51**: 173–198. <https://doi.org/10.1111/j.1475-4983.2007.00733.x>
- Copper, P. 1985. Fossilized polyps in 430-Myr-old Favosites corals. *Nature*, **3** (16): 142–144. <https://doi.org/10.1038/316142a0>
- Copper, P., Y. Plusquellec. 1993. Ultrastructure of the walls, tabulae and ‘polyps’ in Early Silurian Favosites from Anticosti Island, Canada. *Cour. Forsh. Senckenberg*, **1** (64): 301–308.
- Dubatolov, V. N., A. B. Ivanovsky. 1977. The index of Genera of Tabulata. *Transactions of Institute of Geology and Geophisic of Sibirian branch of AS USSR*, **336**: 1–156. [In Russian]
- Galle, A. 1973. Family Heliolitidae from the Bohemian Paleozoic. *Sbornik geol. Ved. R.P.*, Praha, **15**: 5–48.
- Grytsenko, V. P. 1980. Calcarous capsulae of planulae of Silurian Heliolitoidea: *The coralls and reefs of the Phanerozoic of USSR*. Nauka, Moscow, 67–68. [In Russian]
- Grytsenko, V. 2007. Distribution of Corals on the Silurian Podolian Shelf. *Fossil Coral and Sponges Öster. Akad. Wiss., Schriftenr. Edwiss. Komm. (Wien)*, **17**: 185–198.
- Grytsenko, Volodymyr. 2014. New species of *Rotalites* (Corals) from Silurian Pridolian series of Volyn’ and Podillia (Ukraine). *Paleontological Review*, **46**: 133–141. [In Russian]
- Grytsenko, V., A. Istchenko, L. Konstantinenko, and P. Tsegelnjuk. 1999. Animal and plant communities of Podolia. In: *Paleocommunities: A case study from the Silurian and Lower Devonian*. Ed. by A. Boucot & J. A. B. Lawson. Cambridge University Press, New York, 462–487.
- The Phanerozoic reef and corals of the USSR. 1986. *Proceedings of the V AllUnion symposium on coralls and reefs, Dushanbe, 1983*. Nauka, Moscow, 1–232. [In Russian]
- Hill, Dorothy, Edwin C. Stoom. 1967. Tabulata: F444–F477. In: Moor Raymond C., 1956 (1967). *Treatise on Invertebrate Paleontology. Part F. Coelenterata*. Geological society of America and University of Kansas Press, I–XX, F1–498.
- Ivanovsky, A. B. 1984. *History of Study Paleozoical Coralls and Stromatoporoidea (1975–1982)*. Nauka, Moscow, 1–200. [In Russian]
- Kaljo, D., V. Grytsenko, T. Martma, M.-A. Motus. 2007. Three global carbon isotope shifts in the Silurian of Podolia (Ukraine): stratigraphical implications. *Estonian Journal of Earth Sciences*, **56** (4): 205–220. <https://doi.org/10.3176/earth.2007.02>
- Kovalevsky, O. P. 1965. Tabulata and Heliolitoidea Karaespinsky horizon. In: *Stratigraphy of Lower Paleozoic and Silurian deposits of Central Kazakhstan*. Nedra, Leningrad, 112–133. [In Russian]
- Leleshus, V. L. 1970. The new Late Silurian Heliolitoidea of the Southern Tian-Shan. *News of AS of Tajikistan SSR*, **54** (4): 94–101. [In Russian]

- Lindstroem, G. 1899. Remarks on the Heliolitidae. *Kgl. Svenska Vet. handl.*, **1**: 3–140.
- Łuczyński Piotr, Stanisław Skompski and Wojciech Kozłowski. 2016. Recent studies on the Silurian of the western part of Ukraine. *Acta Geologica Polonica*, **66** (3): 281–297. <http://doi.org/10.1515/agp-2016-0014>
- Marshall, N., G. D. Love, V. Grytsenko, A. Bekker. 2023. Lipid biomarker records for Silurian to Early Devonian reef carbonates: Assessing the marine communities and carbon cycling that sustained shallow-marine ecosystems. *Organic geochemistry*, **175**: 104528. <http://dx.doi.org/10.1016/j.orggeochem.2022.104528>
- Moor, R. C. 1956. *Treatise on invertebrate Paleontology*. Part F. Coelenterata, 1–XX, F1–498.
- Motus, M.-A., V. Grytsenko. 2007. Morphological variation of the tabulate coral *Paleofavosites cf. collatatus* Klamann, 1961 from the Silurian of the Bagovichka River localities, Podolia (Ukraine). *Estonian Journal of Earth Sciences*, **56** (3): 143–156. <https://doi.org/10.3176/earth.2007.17>
- Preobrazhensky, B. V. 1967. The value of zonal evidence in the skeleton of Tabulatamorphic corals. *Paleontological journal*, **3**: 3–8. [In Russian]
- Gozhyk, P. F. (ed.). 2013. Stratigraphy of Upper Proterozoic, Paleozoic and Mesozoic of Ukraine. *Institute of Geological Sciences NAS of Ukraine*, Kyiv, 1–637. [In Ukrainian]
- Sokolov, B. S. 1949. Tabulata and Heliolitida. *Atlas of leading forms of fossil fauna of the USSR. Silurian system. Volume 2*. Publ. House of Geological literature, Moskva, 75–102. [In Russian]
- Sokolov, B. S. 1962. *Basics of palaeontology. Spongy, Archaeocyata, Coelenterata, and Vermes*. Ed. Academy of Science of USSR, 1–485. [In Russian]
- Sokolov, B. S. 1955. *Palaeozoic Tabulata of the European part of USSR*. Transaction of VSRGPI. New Seria, **85**: 1–527. [In Russian]
- Tesakov, Y. I. 1965. Chain Favositida. *Transactions of I Symposium on corals and reefs*. Nauka, Moscow, **1**: 14–20, tables I–IV. [In Russian]
- Tsegelnjuk, P. D., V. P. Grytsenko, L. I. Konstantinenko, A. A. Ischenko *et al.* 1983. The Silurian of Podolia. *The Guide to excursion*. Naukova dumka, Kyiv, 1–224. [In Russian & English]
- Vavilov, N. I. 1987. *The Law of Homological Rows in Hereditary Variability*. Nauka, Leningrad, 1–256. [In Russian]
- Venyukov, P. N. 1899. The Fauna of Silurian deposits of Podolian gubernia. *Materials for Geology of Russia*. Saint-Peterbourg, 1–266. [In Russian]
- Vulykh, P. Y. 1980. Morphogenesis Yanetella gen. nov. new family of Heliolitoidea. *Paleontological Journal*, **4**: 39–44. [In Russian]