Coleolus carbonarius Demanet, 1938 (incertae sedis) from the late Bashkirian (Carboniferous) of the Donets Basin, Ukraine

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abstract

Problematic fossils Coleolus carbonarius Demanet, 1938 were described from seven localities of the Mospyne Formation (late Bashkirian, Carboniferous) of the central Donets Basin. Many authors attributed these conoidal fossils to various groups of animals, including worms, conulariids, pteropods, hyoliths, tentaculitids, gastropods, scaphopods, and other molluscs without specifying the class, as well as phyllocarids. Representatives of the genus Coleolus cannot belong to the scaphopods because the apex of their tube is closed. The aperture of the tube in living *Coleolus* is directed upwards, while in scaphopods it is directed downwards. The belonging of Coleolus to pteropods was challenged by previous authors. The assignment of Coleolus to Coniconchia is also incorrect, because the shells of Coniconchia have chambers, which are absent in Coleolidae. The ecological and some morphological characteristics of *Coleolus* indicate their proximity to sedentary polychaete annelids (Sedentaria) or phoronids (Phoronida). Almost all Coleolus remains come from sediments that formed in a shallow marine environment with a low sedimentation rate and contamination of the bottom silt and, possibly, the bottom layer of the water column with hydrogen sulphide. Coleolus carbonarius, according to all of the obtained data, was a semi-infaunal animal. The apical end of the tube was deeply immersed into the semi-liquid clayey silt. Only a small part of the tube protruded above the surface. The characteristic transverse ornament of the tube surface, possibly, increased the contact area of the unstable semi-liquid clayey silt and the tube and further stabilized the vertical position of the animal in the bottom sediment. The sedentary lifestyle of *Coleolus* apparently suggests that these animals fed on planktonic organisms and organic detritus suspended in the water column. This type of feeding is possible only in the presence of a developed hunting apparatus. The morphology of the tubes of Coleolus carbonarius Demanet, 1938 is described in the article, including the structure of their apical end and aperture. Traces of damage caused during the lifetime of animals on the apical part of their tube are also studied.

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Coleolus carbonarius Demanet, 1938 (incertae sedis) з пізнього башкиру (карбон) Донецького басейну

Віталій Дернов

Резюме. Із семи місцезнаходжень серед відкладів моспинської світи (пізній башкир, карбон) Центрального Донбасу описано проблематичні фосилії Coleolus carbonarius Demanet, 1938. Погляди щодо систематичного положення цих вузькоконічних фосилій різняться. Їх відносили до червів, конулярій, птеропод, хіолітів, коніконхій, гастропод, скафопод, молюсків без уточнення класу та філокарид. Представники роду Coleolus не можуть належати до скафопод, оскільки апікальний кінець їхньої житлової трубки закритий. До того ж, прижиттєве положення трубок Coleolus, порівняно зі скафоподами, протилежне - апертура трубки звернена вгору, тоді як у скафопод вона направлена вниз-в товщу осаду. Зарахування колеолусів до птеропод визнано як помилкове попередніми авторами. Віднесення колеолусів до коніконхій, на нашу думку, також помилкове, оскільки черепашки останніх мають камери, чого немає у колеолід. Екологічні та деякі морфологічні особливості колеолусів, на нашу думку, можуть свідчити про їх близькість до седентарних поліхет (Sedentaria) або форонід (Phoronida). Майже всі вивчені рештки колеолусів походять з відкладів, що утворилися у спокійних мілководно-морських умовах за низьких темпів седиментації та зараження мулів та, можливо, придонного шару водної товщі сірководнем. Представники описаного виду, зважаючи на всі отримані дані, були напівінфаунними тваринами. Апікальним кінцем житлової трубки вони глибоко занурювалися у напіврідкий глинистий мул. Над поверхнею дна височіла лише зовсім невелика частина трубки. Поперечна скульптура поверхні житлової трубки, мабуть, збільшувала площу контакту нестабільного напіврідкого глинистого мулу та житлової трубки і додатково стабілізувала вертикальне положення тварини в товщі донного осаду. Нерухомий спосіб життя колеолусів, мабуть, свідчить на користь того, що ці тварини харчувалися планктонними організмами та органічним детритом, зваженим у товщі води. Такий тип живлення можливий лише за наявності розвинутого ловчого апарату. Описано морфологію житлових трубок Coleolus carbonarius Demanet, 1938, в тому числі будова їх апікального кінця та апертури. Досліджено сліди прижиттєвих травм на апікальній частині житлових трубок колеолусів.

Ключові слова: карбон, пізній башкир, Coleolus, Донецький басейн, Україна.

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Introduction

The problematic *Coleolus* Hall, 1879 is well represented in the Early and Middle Pennsylvanian sediments of the Donets Basin, Ukraine. Representatives of this genus also occur in the Carboniferous of Ireland [Brandon 1972], England [Moseley 1953], Scotland [Craig 1954], Belgium [Demanet 1938; 1941; 1943; Demanet & van Straelen 1938], the Czech Republic [Przybylok & Zelewski 2012], and Poland [Bojkowski 1967; Korejwo 1969; 1974; Zakowa 1974; 1982; 1989]. However, most reports on the presence of *Coleolus* in the Carboniferous are not supported by descriptions or illustrations of fossils.

The systematic position of these animals is unknown, although they have been studied for about a century and a half. Apparently, the genus *Coleolus* Hall, 1879 is an artificial taxon. It includes morphologically similar conical calcareous fossils that probably belong to different classes or phyla of animals.

I have a small collection of *Coleolus* remains from marine sediments of different lithology; this material characterises previously unknown details of the morphology of the aperture and apical part of the *Coleolus* tubes. This work is devoted to clarifying the morphology, paleoecology, and systematic position of *Coleolus carbonarius* Demanet, 1938.

There is little information on *Coleolus* and morphologically similar calcareous conical worm tubes (?) from the Carboniferous of the Donets Basin. Shimansky [1974] described the 'scaphopod' *Quasidentalium opiparium* Shimansky, 1974 from the I_1 limestone layer of the Belaya Kalitva Formation, upper Bashkirian. Later, after revision of the original material, Yochelson [1999] placed the genus *Quasidentalium* Shimansky, 1974 in the family Coleolidae Fischer, 1962 ('worms').

Material and Methods

The studied collection, consisting of 83 specimens of tube fragments (collection GMLNU-3), comes from several localities of the Mospyne Formation (late Bashkirian) of the Donets Basin (Fig. 1 b–c).

The Mospyne Formation (C_2^2 or G) consists of a sequence of sandstones, siltstones, mudstones, coals (10–12 layers), and limestones (8 layers) (Fig. 2 *a*) [Nemirovska & Yefimenko 2013]. The thickness of the formation laterally varies from 315 to 730 m. The studied material is represented by fragments and imprints of *Coleolus* tubes, which were collected in seven localities of the Mospyne Formation. A brief description of the studied localities is given below.

(1) Ukraine, Luhansk Oblast, Luhansk Raion, ravine 1.5 km NW of Makedonivka (48.239888, 39.268959): brownish-grey, fine-grained, feldspar-quartz, calcareous, strongly bioturbed sandstone 55 m below the G_1^2 limestone layer (Fig. 2 e).

Remains of bryozoans, brachiopods (Alphachoristites kschemyshensis (Semichatova), Alph. cf. pseudobisulcatus (Rotai), Alph. cf. medovensis (Rotai), Brachythyrina ex. gr. proba (Rotai), Br. sp., Echinaria sp., Parajuresania sp., Linoproductus sp., etc.; identified by the author and Vladyslav Poletaev, IGS NASU), scaphopods, gastropods, bivalves (Phestia, Sanguinolites, Anthraconeilo, etc.), cephalopods (Gzheloceras pulcher (Crick), Pseudogzheloceras falcatum (Sowerby in Prestwich), Metacoceras mcchesneyi Murphy, Planetoceras yefimenkoi Dernov, Paradomatoceras applanatum Delépine, Peripetoceras cf. globatoides Shimansky, Ephippioceras sp., Megaglossoceras sp., Melvilloceras rotaii (Librovitch in Popov), Gastrioceras kutejnikovense Popov, etc.; [Dernov 2021a] and unpublished data of the author), crinoids, trilobites (Carniphillipsia) kumpani (Weber); identified by Eduard Mychko, PIN RAS), fishes (Listracanthus, Lagarodus, etc.) and trace fossils (Zoophycos, Planolites, fish coprolites) have been collected from this stratigraphic horizon.

(2) Luhansk Oblast, Luhansk Raion, ravine in the NW outskirts of Makedonivka (48.237219, 39.291406): mudstone 40 m below the G_1^2 limestone layer (Fig. 2 c).

The mudstone is dark grey with ellipsoidal siderite nodules and thin interlayers of fine-grained siltstones in the upper part of the layer. This mudstone contains remains of brachiopods (*Parajuresania* sp. and other productids), gastropods, bivalves (*Phestia, Sanguinolites, Anthraconeilo, Solenomorpha*, etc.), cephalopods (*Melvilloceras rotaii* (Librovitch in Popov), etc.) [Dernov 2021b]), terrestrial plants (*Calamites, Lepidostrobophyllum*, and *Cordaites*), and trace fossils *Chondrites* and bromalites. Cephalopod conchs bearing bioerosion traces *Cyclopuncta* [Dernov 2021c].

- (3) Luhansk Oblast, Luhansk Raion, Sukha Ravine 4 km W of Kamianka (48.239570, 39.337004): siltstones directly overlying mudstones of locality no. 2. The siltstones are yellowish-grey, yellowish-brown and fine-grained, with remains of rugose corals, bivalves (*Phestia*), gastropods, and cephalopods.
- (4) The same ravine (48.239570, 39.337004): sandstone directly underlying the G_1^2 limestone layer. The sandstone is brownish-grey, fine-grained, and horizontally bedded. The remains of the fauna are rare and represented by shells of brachiopods, bivalves, and orthocerids; often trace fossils *Planolites* and *Chondrites* are found.
- (5) The same ravine (48.250447, 39.331057): mudstone under the siderite layer that laterally replaces the G_4 limestone layer (Fig. 2 d). The mudstone is dark grey with siderite nodules and remains of bivalves (*Sanguinolites*, *Anthraconeilo*, and *Solenomorpha*), gastropods and cephalopods (*Metacoceras*).
- (6) Luhansk Oblast, Luhansk Raion, left bank of the Luganchyk River 0.6 km W of Volnukhyne (48.348086, 39.275627): grey, fine-grained, and horizontally bedded siltstone in the upper part of the Mospyne Formation.
- (7) Luhansk Oblast, Luhansk Raion, sandstone quarry in Volnukhyne (48.357697, 39.281083): mudstone under the g_3 coal layer (Fig. 2 b). The mudstone is dark grey, carbonaceous, with siderite nodules, and remains of bivalves, gastropods, and cephalopods. A rich terrestrial flora has been studied from the roof shale of the g_3 coal seam [Dernov & Udovychenko 2019].

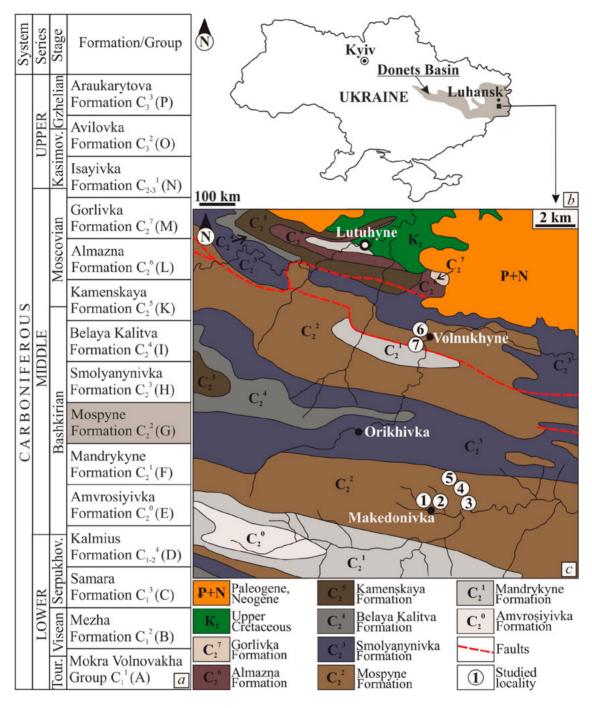


Fig. 1. Stratigraphic position of the Mospyne Formation (*a*) and the geographic location of the study area (*b*, *c*). Abbreviations: Tour.—Tournaisian, Serpukhov.—Serpukhovian, Kasimov.—Kasimovian.

Рис. 1. Стратиграфічне положення моспинської світи (a) та географічне положення району досліджень (b, c). Скорочення: Tour. — турнейський, Serpukhov. — серпуховський, Kasimov. — касимовський.

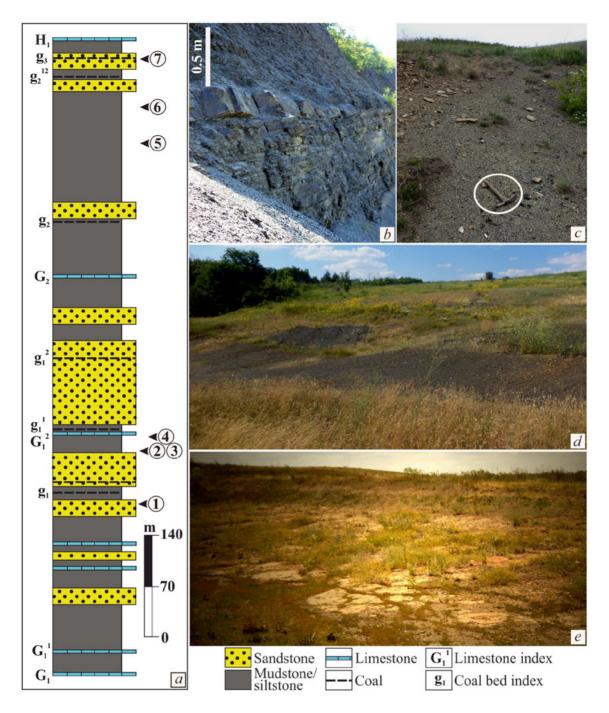


Fig. 2. The position of the studied localities in the section of the Mospyne Formation (a) and the general view of some outcrops: (b) locality no. 7; (c) locality no. 2; (d) locality no. 5; (e) locality no. 1.

Рис. 2. Положення вивчених місцезнаходжень в розрізі моспинської світи (a) та загальний вигляд деяких відслонень: (b) місцезнаходження № 7; (c) місцезнаходження № 2; (d) місцезнаходження № 5; (e) місцезнаходження № 1.

The abbreviations used in the species description are as follows: L — length of tubes (incomplete); h_{max} — maximum width (width of the adoral part of the deformed tube); α — apical angle (approximate); d — maximum diameter of non-deformed tubes. The open end of the tube is called adoral, the closed (narrow) end is called apical.

Ecology and Taphonomy

Almost all of the *Coleolus* remains come from dark grey mudstones formed in shallow marine environments with low sedimentation rates (so-called 'black shale'). The lithological features of the mudstone and biota suggest the contamination of silt and, possibly, the lower water layer of the basin with hydrogen sulphide. Several specimens come from shallow marine calcareous siltstone; single specimens were found in shallow marine calcareous fine-grained sandstone (Fig. 3 d, f, g); in this case, the fossils are probably allochthonous or suballochthonous.

The substance of the tubes from the mudstones is completely dissolved, more rarely replaced by limonite (=oxidized pyrite); in calcareous sandstones and siltstones they are calcitic. The remains of the tubes are always deformed in mudstone and siltstone, but the finest details of the tube surface ornament are preserved. The remains are usually not deformed in the siderite nodules in the mudstone, but the ornament of the tube surface is not preserved on them, and the substance itself is always replaced by limonite. The study of the deformations of the rounded in cross section *Coleolus* tubes from these nodules is important for determining the intensity of the reduction in volume of the rocks during diagenesis.

Limonite replaces not only the substance of the tubes from the mudstone, but also the sediment inside them (Fig 3 *a*, *i*). The formation of pyrite is probably related to the decomposition of the *Colelus* body and the activity of widespread anaerobic microbial communities in the bottom sediments (Fig. 3 *h*).

Sometimes the fossils are preserved as clusters consisting of two or four tube fragments (Fig. 3 b, e). Fragments of bivalve and gastropod conchs are also often found in these clusters (Fig. 3 b). Occasionally, these clusters consist of detritus of shells and tubes oriented by the near-bottom current (Fig. 3 e). The remains of the tubes are usually positioned parallel to the bedding plane; rarely remains are at a slight angle to the bedding plane (the apex is directed downward). In this case, the remains are in a position close to that in lifetime (Fig. 3 e, e). Bivalves, gastropods, cephalopods, and occasionally rugose corals, brachiopods, bryozoans, and crinoids are the common associate biota of *Coleolus*.

A layer of tempestite (fine-grained calcareous sandstones with many fragments of *Coleolus* tubes as well as bivalves, gastropods, cephalopods, plant detritus, and rare pebbles) is in the upper part of the mudstone layer of the locality no. 2. The cluster of *Coleolus* tube fragments in this tempestite is explained by their washing out of clay sediment, which, being lighter than sand, was removed from this part of the seabed by the current and storm waves.

Since Coleolidae Fisher, 1962 occur in sediments of various types (from sandstones to black shales), they were classified as pelagic animals by Donald Fischer [1962]. According to all the data obtained, *Coleolus carbonarius* Demanet, 1938 was a semi-infaunal animal, which led a sedentary lifestyle. They were deeply submerged in the semi-liquid clay bottom silt with the apex of the tube. Only a very small part of the tube protruded above the surface of the sea floor (Fig. 4 *a*).

The characteristic transverse ornament of the tube surface apparently increased the contact area between the unstable, semi-liquid clayey silt and the tube and further stabilized the vertical position of the animal in the thickness of the bottom sediment.

The polychaetes (?) *Ladatheca cylindrica* (Grabau, 1900) from the Cambrian of Newfoundland [Landing 1993] led a similar lifestyle. The calcareous tubes of these worms were located vertically in the silt and the tube apex is tip down.

The apex of the tube of one of the specimens (Fig. 4 b) is curved and deviates at an angle of about 20° from the symmetry axis of the tube. The formation of this bend cannot be explained by the deformation of the fossil during the compaction of the sediment. The injured part of the tube lacks transverse sculpture (the outer surface of the wall is smooth) and has faint irregularities. The apical part of the other specimen (Fig. 4 c-d) is twice bent, while other parts of the tube buried in siderite nodule were not deformed during diagenesis, which suggests that the change in the morphology of the apical part of the tube is caused by trauma.

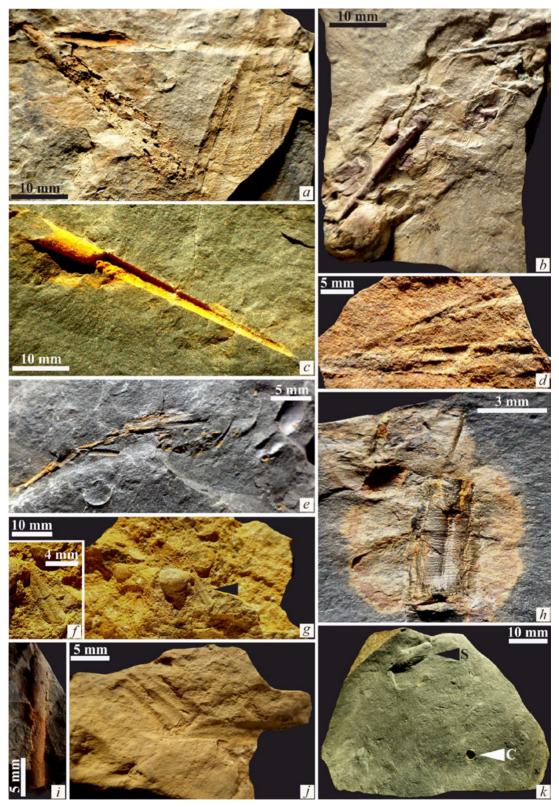


Fig. 3. Taphonomy of *Coleolus*: (*a*) partially limonitized fragments of *Coleolus* tubes together with a fragment of the body chamber of an orthocerid (?) bearing bioerosions trace fossils *Cyclopuncta* (locality no. 2; GMLNU–3/7551); (*b*) cluster of shell detritus and fragments of *Coleolus* tubes (locality no. 2; GMLNU–3/7520); (*c*) limonitized tube of *Coleolus* on a transverse cleavage of a siderite concretion in a position similar to that

in lifetime (locality no. 2; GMLNU-3/5211); (*d*) remains of tubes in fine-grained sandstone (locality no. 4; GMLNU-3/7543); (*e*) small fragments of *Coleolus* tubes regularly oriented by the bottom current (locality no. 2; GMLNU-3/4346); (*f*-*g*) fragment of *Coleolus* tube among gastropod and bivalve shells (locality no. 1; GMLNU-3/1514); (*h*) fragment of *Coleolus* tube with a sulphate reduction halo around it (locality no. 5; GMLNU-3/7559); (*i*) steinkern of the non-deformed tube *Coleolus* (locality no. 2; field photo); (*j*) imprints of tube fragments in the siltstones (locality no. 3; field photo); (*k*) shale slab with remains of bivalve *Sanguinolites* (S) and problematic *Coleolus* (C), preserved in a position similar to that in lifetime (locality no. 2; field photo).

Рис. 3. Тафономічні особливості решток *Coleolus*: (*a*) частково лимонітизовані фрагменти житлових трубок *Coleolus* разом із фрагментом житлової камери ортоцериди (?), що несе сліди біоерозії *Cyclopuncta* (місцезнаходження № 2; GMLNU–3/7551); (*b*) скупчення черепашкового детриту та фрагментів житлових трубок *Coleolus* (місцезнаходження № 2; GMLNU–3/7520); (*c*) лимонітизована житлова трубка на поперечному зламі сидеритової конкреції в положенні, близькому до прижиттєвого (місцезнаходження № 2; GMLNU–3/5211); (*d*) рештки житлових трубок у тонкозернистих пісковиках (місцезнаходження № 4; GMLNU–3/7543); (*e*) дрібні фрагменти трубок *Coleolus*, які закономірно орієнтовані придонною течією (місцезнаходження № 2; GMLNU–3/4346); (*f*–*g*) фрагмент житлової трубки *Coleolus* серед черепашок гастропод та пелеципод (місцезнаходження № 1; GMLNU–3/1514); (*h*) фрагмент житлової трубки *Coleolus* з ореолом сульфатредукції навколо (місцезнаходження № 5; GMLNU–3/7559); (*i*) внутрішнє ядро недеформованої житлової трубки *Coleolus* (місцезнаходження № 2; польове фото); (*j*) відбитки фрагментів житлових трубок в алевролітах місцезнаходження № 2; польове фото); (*k*) плитка глинистого сланцю з місцезнаходження № 2 з рештками пелециподи *Sanguinolites* (S) та житловою трубкою *Coleolus* (С), похованих в положенні, близькому до прижиттєвого (польове фото).

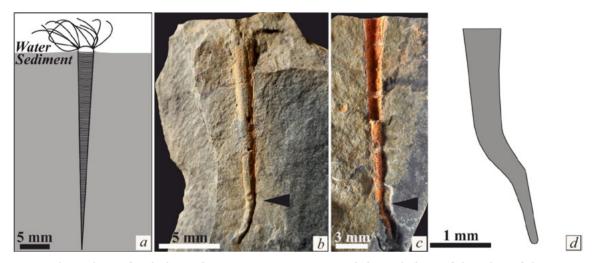


Fig. 4. Paleoecology of *Coleolus carbonarius* Demanet, 1938 and the pathology of the tubes of this species: (a) reconstruction of *Coleolus* in life position; (b-d) pathology of the tubes of *Coleolus carbonarius* Demanet, 1938 (b, c — lateral view, d — sketch of apical part of tube on Fig. 4 c).

Рис. 4. Палеоекологія *Coleolus carbonarius* Demanet, 1938 та патології житлових трубок цього виду: (a) реконструкція *Coleolus carbonarius* Demanet, 1938 у прижиттєвому положенні; (b-d) патології житлових трубок *Coleolus carbonarius* Demanet, 1938 (b, c — житлова трубка збоку, d — замальовка апікальної частини житлової трубки, зображеної на Рис. 4 c).

Fischer [1962] in a diagnosis of the family Coleolidae reported that the tubes of some Coleolidae are slightly curved. Despite the fact that the tubes of some species of the genus *Coleolus* (e.g. ?C. iowaensis James, 1890) are slightly curved, the specimens described above certainly bear traces of injury, since the rest of the studied tubes of this species are straight. The origin of the injuries is not entirely clear. We suggest the mechanical origin of these injuries with subsequent partial regeneration of the tube and the soft body of the animal.

The growth rate of the tube after its fixation in the bottom silt could be close in value to the sedimentation rate, which was quite low for mudstones, from which most of the studied material comes.

The sedentary lifestyle of *Coleolus* probably suggests that these animals fed on planktonic organisms and organic detritus suspended in the water. This type of feeding is only possible with a developed hunting apparatus and also confirmed by the presence of a relatively narrow aperture (the

morphological description of *Coleolus carbonarius* Demanet, 1938 see below), which did not allow the animal to protrude far from the tube.

The confinement of *Coleolus* remains mainly to mudstones suggests that these animals required an environment with low sedimentation rate. Sandstones were formed in a more active environment with higher sedimentation rates, due to which animals could not be securely fixed in the sediment and withstand the high sedimentation rate. Thus, these circumstances are probably the main reasons for the almost complete absence of *Coleolus* remains in psammites.

Systematic position of the genus Coleolus

The genus *Coleolus* Hall, 1879 in its original description and in some subsequent works was attributed to the pteropods [Hall 1879; 1888; Walcott 1885; Miller 1889]. It was later assigned to worms [Fischer 1962; Yochelson & Hlavin 1985; Yochelson 1999], phyllocarids [Reed 1908], coniconchs [Syssoiev 1958; Bouček 1964; Zakowa 1969; 1974], conulariids [Demanet 1938], gastropods [Demanet 1941], scaphopods [Grabau & Shimer 1909; Craig 1953], hyoliths [Skovsted 2006], and molluscs without specifying the class [Syssoiev 1962; Downie *et al.* 1967].

Donald Fischer [1962] identified problematic calcareous conical fossils to the family Coleolidae Fischer, 1962. He included seven genera to this family known from the Cambrian to the Carboniferous. He cautiously suggested that this family could be the ancestor of scaphopods, which is dubious. This genus is currently considered a taxon of unclear systematic position [Yochelson & Hlavin 1985; Yochelson 2002].

Representatives of the genus *Coleolus* cannot belong to the scaphopods because the apex of their tube is closed. In addition, the lifetime position of *Coleolus* tubes, in comparison with scaphopods, is opposite (the aperture of the tube is directed upwards, while in scaphopods it is directed towards the layer of the sediment [Yochelson 2002]). The assignment of *Coleolus* to pteropods has long been recognised as erroneous [Sysoev 1958; Fischer 1962]. The assignment of *Coleolus* to Coniconchia is also wrong, since the shells of the latter have chambers, which the *Coleolus* do not have.

Yochelson [2002; Yochelson & Hlavin 1985] attributes *Coleolus* to 'worms,' although he does not provide conclusive evidence other than the calcareous composition of the tubes. Ecological and some morphological features of *Coleolus* may indicate their proximity to sessile polychaete annelids (Sedentaria) or phoronids (Phoronida). It should be noted that some representatives of the genus *Coleolus*, such as *C. namurcensis* Demanet, 1938 resemble fossils classified as hyolith. Some fossils (e.g. '*Hyolithes*' roermeri Koenen, 1879) are attributed by some authors to hyoliths, while others attribute them to coleolids [Malinky & Mapes 1983; Malinkey *et al.* 1986; Brauckmann *et al.* 1997]. Nevertheless, we suggest that the genus *Coleolus* is polyphyletic.

Systematic Palaeontology Phylum, Class and Order uncertain Family Coleolidae Fisher, 1962 Genus *Coleolus* Hall, 1879

Coleolus: Hall 1879, p. 188; Miller 1889, p. 389; Demanet 1938, p. 134; Syssoiev 1958, p. 189; Fischer 1962, p. W134; Yochelson & Hlavin 1985, p. 1299; Yochelson & Goodison 1999, p. 635; Yochelson 2002, p. 298; Malinky & Skovsted 2004, p. 570.

Type species. *Coleoprion tenuicinctum* Hall, 1876 (Early Devonian, New York State, USA); designated by Hall [1879].

Emended diagnosis. Calcareous, elongated, conical, straight or weakly curved tube with a small apical angle. The outer surface of the tube is smooth, reticulate or covered by circular ribs transverse to the axis of symmetry. The cross-section of the tube is rounded.

Discussion. *Coleolus* Hall, 1879 differs from *Coleoloides* Walcott, 1890 in the transverse ornamentation of the tube surface, which in *Coleoloides* is longitudinal. The genus *Coleolus* Hall, 1879 is quite similar to the genus *Coleolella* Missarzhevsky, 1969. Circular fossils, which may be apertural cap or attachment discs [Missarzhevsky, 1969] are often found together with the remains of *Coleolella*. Such fossils are not known from the Carboniferous of the Donets Basin.

The described genus differs from the fossils *Sphenothallus* Hall, 1847 (Cnidaria), which also occurred in the Carboniferous black shales of the Donets Basin and in the early Carboniferous of the Dnipro–Donets Downwarp, primarily by the calcareous composition of tubes; the tubes of *Sphenothallus* are phosphatic [Vinn & Mironenko 2021]. The tubes of *Sphenothallus* Hall, 1847 are often strongly curved, much more strongly than those of some *Coleolus*. Representatives of the genus *Sphenothallus* led a sedentary, but not infaunal life. Their tubes were attached various substrates, from brachiopod shells to hard ground surfaces [Vinn & Kirsimäe 2015].

Included species. *C. trigonus* Syssoiev, 1962 (Cambrian), ?*C. iowaensis* James, 1890 (Late Ordovician), *C. aciculum* Hall, 1879 (Early Devonian), *C. crenatocinctum* Hall, 1879 (Early Devonian), *C. tenuicinctum* (Hall, 1876) (Early Devonian), ?*C. antiquus* (Goldfuss, 1841) (Middle Devonian), *C. curvatus* Kindle, 1912 (Late Devonian), *C. carbonarius* Demanet, 1938 (Carboniferous), *C. namurcensis* Demanet, 1938 (Carboniferous), *C. reticulatus* Demanet, 1938 (Carboniferous), *C. polonicus* (Weigner, 1938) (Carboniferous). *C. missouriensis* Howell, 1952 is also conventionally included into this genus [Yochelson 1999]. There is now a clear need to revise the genus and re-examine the original type species [Yochelson 2002].

Numerous references to *Coleolus* sp. are known from the Carboniferous of various regions (see [Moseley 1952; Betekhtina 1966; Musiał & Tabor 1982], etc.). It is impossible to verify the correctness of this definition, as the finding is not described. Apparently, the remains of 'worms' from the Devonian of Burma [Feldmann *et al.* 1984] also belong to the genus *Coleolus*.

Remarks. Although the genus diagnosis given by Fisher [1962] indicates the presence of transverse ornamentation on the tube surface, there are Carboniferous representatives of this genus bearing reticulate ornamentation of the tube (*C. reticulatus*) or lacking any ornamentation (*C. namurcensis*).

Occurrence. Early Cambrian to Carboniferous; United States, Greenland, Europe, Siberia, and Australia.

Coleolus carbonarius Demanet, 1938

Fig. 5; Table 1

1930 Hyolithus sturi: Delépine (pars), p. 80, pl. V, fig. 8, non fig. 7.

1938 Coleolus carbonarius flenuensis: Demanet, van Straelen, p. 162, pl. CXXIV, figs 1-4.

1941 Coleolus carbonarius: Demanet, p. 270, pl. XVI, figs 24-25.

1943 Coleolus carbonarius flenuensis: Demanet, p. 116, pl. IV, figs 29-30.

1974 Coleolus carbonarius: Korejwo, pl. 14, figs 5-6.

Material. About 80 tube fragments.

Diagnosis. Calcareous, elongated, conical, straight tube with a small apical angle. The outer surface of the tube is covered with circular ribs transverse to the axis of symmetry. The cross-section of the tube is rounded.

Description. The remains are narrowly-conical, empty, straight tubes. Most of them are crushed, only a few specimens from siderite nodules are just slightly deformed. The apical angle of the tubes is from 4 to 8°. It was probably about 4–5° during the animal's life, since in non-deformed and slightly compressed specimens the apical angle is $4-7^{\circ}$ (see Table 1). Almost all specimens have a well-defined longitudinal furrow, which, however, extends only to the upper (adoral) half of the tube because of the lateral deformations of the fossils (Fig. 5 d). This may be due to dense post mortem filling of the apical part of the tube with sediment. The inner surface of the tube is smooth.



Fig. 5. Remains of *Coleolus carbonarius* Demanet, 1938: (*a*) GMLNU-3/7544; (*b*) GMLNU-3/7525; (*c*) GMLNU-3/1882; (*d*) GMLNU-3/7540; (*e*) GMLNU-3/7552; (*f*) GMLNU-3/5770; (*g*) GMLNU-3/7515; (*h*) GMLNU-3/7528; (*i*) GMLNU-3/2492; (*j*) GMLNU-3/4314; (*k*) GMLNU-3/3095; (*l*) GMLNU-3/7521; (*m*) GMLNU-3/7554; (*n*) GMLNU-3/917; (*o*) GMLNU-3/7524; (*p*) GMNU-3/4331; (*q*) GMLNU-3/4286; (*r*) GMLNU-3/7556; (*s*) GMLNU-3/7521a; (*t*) GMLNU-3/5765a; (*u*) GMLNU-3/7568. Lateral view in *a-m*,

p, and u; Lateral view of the tubes aperture in n, o, q, and s; r — cross section of almost undeformed tube in a siderite nodule; t — tube imprint with indeterminate structures (shown with an arrow; locality 3). Scale bar: 5 mm in a–m, p, q, s–u and 2 mm in n, o, r.

Рис. 5. Рештки житлових трубок *Coleolus carbonarius* Demanet, 1938: (*a*) GMLNU–3/7544; (*b*) GMLNU–3/7525; (*c*) GMLNU–3/1882; (*d*) GMLNU–3/7540; (*e*) GMLNU–3/7552; (*f*) GMLNU–3/5770; (*g*) GMLNU–3/7515; (*h*) GMLNU–3/7528; (*i*) GMLNU–3/2492; (*j*) GMLNU–3/4314; (*k*) GMLNU–3/3095; (*l*) GMLNU–3/7521; (*m*) GMLNU–3/7554; (*n*) GMLNU–3/917; (*o*) GMLNU–3/7524; (*p*) GMLNU–3/4331; (*q*) GMLNU–3/4286; (*r*) GMLNU–3/7556; (*s*) GMLNU–3/7521a; (*t*) GMLNU–3/5765a; (*u*) GMLNU–3/7568. a-m, p, u — вид збоку; r, o, q, s — вид апертури житлових трубок збоку; r — замальовка поперечного перерізу майже не деформованої трубки у сидеритовій конкреції; t — відбиток житлової трубки з нез ясованою структурою (показана стрілкою; місцезнаходження № 3).Масштабний відрізок — 5 мм (a-m, p, q, s-u) та 2 мм (n, o, r).

 Table 1. Dimensions of the tubes of Coleolus carbonarius Demanet, 1938

 Таблиця 1. Розміри житлових трубок Coleolus carbonarius Demanet, 1938

Specimens	L	h_{max}	α	D	Localities
GMLNU-3/1882	38.0	3.0	5°	_	8
GMLNU-3/2492	23.0	2.5	4°	_	2
GMLNU-3/4314	40.0	5.0	10°	_	2
GMLNU-3/4315	21.0	_	5°	1.9	2
GMLNU-3/4331	19.0	3.0	6°	_	2
GMLNU-3/5211	27.0	_	4°	2.4	2
GMLNU-3/5774	18.0	2.9	6°	_	2
GMLNU-3/5776	35.0	5.0	8°	_	2
GMLNU-3/7515	45.0	4.5	7°	_	6
GMLNU-3/7522	44.0	5.0	4.5°	_	2
GMLNU-3/7525	18.0	2.8	7°	_	2
GMLNU-3/7526	9.0	1.0	4^{o}	_	2
GMLNU-3/7528	27.0	3.0	5°	_	2
GMLNU-3/7538	14.0	2.1	7°	_	2
GMLNU-3/7540	24.0	5.0	8°	_	2
GMLNU-3/7543	37.0	5.5	10°	_	4
GMLNU-3/7544	37.0	4.5	7°	_	2
GMLNU-3/7546	16.0	2.0	4^{o}	_	2
GMLNU-3/7547	45.0	4.0	6°	_	2
GMLNU-3/7548	34.0	4.0	7°	_	2
GMLNU-3/7552	16.0	1.9	6°	_	2
GMLNU-3/7554	42.0	5.0	9°	_	3
GMLNU-3/7555	45.0	4.0	5°	_	2
GMLNU-3/7560	43.0	5.0	7°	_	3
GMLNU-3/7564	15.0	_	7°	3.0	2
GMLNU-3/7566	33.0	4.0	6°	_	2

The apex of the tubes is closed. The walls of the tubes are 0.10 to 0.33 mm thick and are replaced by calcite (fossils from calcareous sandstones and siltstones) or pyrite (fossils from mudstones), but most often dissolved. Thus, the lifetime composition of tubes is not reliably known. Based on the specimens from calcareous siltstones and sandstones, they were probably calcareous. The substance of the tubes from mudstones formed in dysaerobic environment, as mentioned above, is replaced by pyrite due to the activity of anaerobic sulphate-generating bacterial assemblages. These sediments do not contain fossils (e.g. bivalves, gastropods, and cephalopods) that retained the original calcareous matter of the shells.

The thickness of tube walls is greater in specimens from calcareous siltstones than in specimens found in calcareous-free mudstones. This is probably due to the greater water activity of the environment during the accumulation of sandstones and siltstones compared to mudstones, which the animal resisted by increasing the thickness of the tube wall.

The aperture margin of the tube consist of two semi-circular projection (Fig. 5 n, o, q) with a smooth surface, which, converging, probably formed a narrow apertural hole. This hole had a shape close to the outlines of the infinity symbol. The aperture morphology of the type species of the genus

(Coleolus tenuicinctum (Hall, 1876)) is much simpler: it is rather wide and does not carry any additional structures [Fischer 1962: fig. 2 b].

The surface of the tubes is covered with thin circular transverse ribs with a thickness of 0.05-0.15 mm. The frequency of ribs is 4–6 per 1 mm of the tube length. Different ribs and spaces between these ribs in the same specimen have different thickness. The space between ribs has approximately the same width as the ribs thickness.

Dimensions can usually be determined only approximately, since most of the material is fragmented or deformed. Only individual specimens can be measured accurately (see: Table 1). The calculated total length of the largest tubes (GMLNU-3/7544 and GMLNU-3/7555) is 50-57 mm. The maximum (apertural) diameter of undeformed tubes is about 4.0-4.5 mm.

Discussion. The described species differs from C. reticulatus Demanet, 1938 in a different transverse tube surface ornamentation (in *C. reticulatus* it is reticulate). Another Carboniferous species — C. namurcensis Demanet, 1938 — has no surface ornamentation at all.

Localities. Ukraine, Luhansk Oblast, Luhansk Raion: Mospyne Formation (for details, see the Material and Methods section).

Stratigraphic and geographic distribution. Late Viséan and Serpukhovian of Poland [Bojkowski 1967; Zakowa 1982], Namurian and Westphalian of Belgium [Demanet & van Straelen 1938; Demanet 1941; 1943], late Bashkirian of Ukraine (this paper). Coleolus carbonarius was found in the Early Carboniferous of Scotland [Craig 1954]. Unfortunately, these fossils are not described or figured.

Conclusions

The remains of Coleolus carbonarius Demanet, 1938 described from the Early Pennsylvanian sediments of the Donets Basin. The new materials allowed us to study previously unknown details of morphology of these organisms, such as the morphology of the aperture and the apex of the tube. It was established that Coleolus carbonarius was a semi-infaunal animal, possibly close to Sedentaria. Coleolus carbonarius inhabited predominantly marine water environments with low sedimentation rates.

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