GEO&BIO

2023 • vol. 25, pp 109–120
https://doi.org/10.53452/gb2508

The first record of the trace fossils *Cochlichnus* from the Pennsylvanian continental and marine deposits in the Donets Basin, Ukraine

Vitaly Dernov

Institute of Geological Sciences, NAS of Ukraine (Kyiv, Ukraine)

article info

key words

trace fossils, *Cochlichnus anguineus*, late Bashkirian, Pennsylvanian, Donets Basin, Ukraine.

correspondence to

Vitaly Dernov; Institute of Geological Sciences, NAS of Ukraine; 55-b Oles Honchar Street, Kyiv, 01054 Ukraine;
Email: vitalydernov@gmail.com;
orcid: 0000-0002-5873-394X

article history

Submitted: 21.07.2023. Revised: 20.10.2023. Accepted: 30.12.2023

cite as

Dernov, V. 2023. The first record of the trace fossils *Cochlichnus* from the Pennsylvanian continental and marine deposits in the Donets Basin, Ukraine. *GEO&BIO*, **25**: 109–120.

abstract

Sinusoidal trace fossils *Cochlichnus anguineus* are described for the first time from marine and continental siltstones and sandstones of the Mospyne and Smolyanynivka formations (late Bashkirian, Early Pennsylvanian) in Luhansk Oblast, eastern Ukraine (central Donets Basin). Previously, in Ukraine, *Cochlichnus anguineus* was recorded in the early Bashkirian Buzhanka Formation of the Lviv Paleozoic Trough. *Cochlichnus* isp. is known from the Ediacaran of western Ukraine. The studied ichnofossils come from four localities representing sedimentary sequences of shallow marine, lagoonal, and lacustrine terrigenous rocks. The ichnogenus *Cochlichnus* Hitchcock, 1858 is known from the Precambrian to Holocene and were generally distributed in non-marine environments in the Carboniferous, although it has been recorded in a wide range of environments, from lacustrine (Mermia Ichnofacies) to marine (Cruziana Ichnofacies). In the Pennsylvanian deposits of eastern Ukraine, these trace fossils are predominantly found in lacustrine black shales, but also in lagoonal siltstones and shallow marine sandstones and siltstones. *Cochlichnus* has been interpreted as traces of grazing, feeding, and locomotion, and it is suggested that traces, depending on the environmental conditions and potential producers, may be combinations of all these ethological categories. Potential producers of *Cochlichnus* include worms *sensu lato*, as well as nematodes, annelids, insect larvae, or cyclostomates. In modern freshwater basins, traces morphologically similar to *Cochlichnus* are produced by nematodes and dipteran larvae. It seems that nematodes and/or annelids are the most likely producers of the studied *Cochlichnus*, since representatives of Diptera are not known in the Carboniferous. In the Donets Basin, *Cochlichnus anguineus* usually co-occurs with the trace fossils *Lockeia*, *Planolites*, and *Palaeophycus*. Sometimes these ichnofossils are found on the layer surfaces bearing microbially induced sedimentary structures together with *Taphrhelminthopsis* and *Aulichnites*.

Перша знахідка іхнофосилій *Cochlichnus* у пенсильванських континентальних та морських відкладах Донецького басейну, Україна

Віталій Дернов

Інститут геологічних наук НАН України (Київ, Україна)

Резюме. Синусоїдальні іхнофосилії *Cochlichnus anguineus* Hitchcock, 1858 вперше описані з верхньобашкирських (нижній пенсильваній) морських та континентальних відкладів моспинської та смолянинівської світ Луганської області (центральний Донбас). На території України іхнофосилії *Cochlichnus anguineus* були відомі раніше з відкладів бужанської світи (нижня частина башкирського ярусу) Львівського палеозойського прогину; *Cochlichnus* isp. відомий з едіакарію Заходу України. Вивчені іхнофосилії походять з чотирьох місцезнаходжень, що представляють осадові послідовності мілководно-морських, лагунних та озерних теригенних порід. Сліди *Cochlichnus* відомі починаючи з докембрію і по сучасність. В карбоні вони були поширені в основному в неморських фаціях, хоча загалом їх зафіксовано в широкому діапазоні фаціальних обстановок: від озерних (мермієва іхнофація) до морських (крузіанова іхнофація). У пенсильванських відкладах Сходу України ці іхнофосилії трапляються переважно в озерних чорних сланцях, а також в лагунних алевролітах і мілководних морських пісковиках і алевролітах. Іхнорід *Cochlichnus* інтерпретується як сліди пастьби, харчування та пересування, і припускається, що вони, в залежності від умов навколишнього середовища та потенційних продуцентів, можуть бути комбінаціями всіх цих етологічних категорій іхнофосилій. Потенційними продуцентами *Cochlichnus* можуть бути черви *sensu lato*, а також нематоди, анеліди, личинки комах або круглороті. У сучасних прісноводних басейнах сліди, схожі або навіть ідентичні *Cochlichnus*, продукуються нематодами та личинками комах ряду Diptera. Схоже, що нематоди та/або анеліди є найвірогіднішими продуцентами вивчених іхнофосилій *Cochlichnus*, оскільки представники Diptera не відомі в карбоні. В Донецькому басейні *Cochlichnus anguineus* зазвичай трапляються разом з іхнофосиліями *Lockeia, Planolites* та *Palaeophycus*. Іноді вони, а також іхнофосилії *Taphrhelminthopsis* і *Aulichnites* присутні на поверхнях нашарування, які несуть мікробіальні осадові структури.

Ключові слова: Іхнофосилії, *Cochlichnus anguineus*, верхня частина башкирського ярусу, пенсильваній, Донецький басейн, Україна

Адреса для зв'язку: В. С. Дернов; Інститут геологічних наук НАН України; вул. Олеся Гончара, 55-б, Київ, 01054 Україна; email: vitalydernov@gmail.com; orcid: 0000-0002-5873-394X

Introduction

Cochlichnus Hitchcock, 1858 is a trace fossil in the form of a sinusoidal wave preserved on lower and upper bedding surfaces mainly of sandstones and siltstones [Hitchcock 1858; Gluszek 1995; Metz 1995, 1996; Buatois *et al*. 1996; etc.]. These trace fossils occur in marine and continental deposits from the Ediacaran to Holocene and are described in many works [e.g. Hitchcock 1858; Gluszek 1995; Buatois *et al*. 1996, 1997; Keighley & Pickerill 1997; etc.]. However, the producers of these ichnofossils are not reliably known, although traces identical to them have also been found in recent non-marine sediments [Chamberlain 1975; Ratcliffe & Fagerstrom 1980; Metz 1987].

In Ukraine, *Cochlichnus anguineus* Hitchcock, 1858 was recorded in the early Bashkirian Buzhanka Formation of the Lviv Paleozoic Trough [Shul'ga *et al*. 2007: fig. 30; author's interpretation]. In addition, *Cochlichnus* isp. is known from the Ediacaran of Podillia (western Ukraine) [Paliy 1978; Gureev 1986; Ivantsov *et al*. 2015]. *Cochlichnus* isp. figured by Ivantsov *et al.* [2015: pl. 7, fig. 3] is very similar to *Cochlichnus anguineus* from the Pennsylvanian strata of Indiana, USA [Archer & Maples 1984: fig. 3*c*] and Early Devonian rocks of Algeria [Bendella *et al.*, 2022: fig. 4*G*].

Here, I describe the first record of *Cochlichnus anguineus* in the continental and marine deposits of the late Bashkirian Mospyne and Smolyanynivka formations exposed in the southern part of Luhansk Oblast, Ukraine. The studied material indicates a wide distribution of these trace fossils in the Pennsylvanian rocks of eastern Ukraine and brings us closer to uncover their producers.

Geological setting and Material

Material. In this study, I investigated 13 sandstone and siltstone slabs with *c*. 30 well-preserved *Cochlichnus anguineus* (specimens GMLNU-9/01 to GMLNU-9/13) and several field photos of these trace fossils *in situ*. The studied collection (GMLNU-9) is stored in the Geological Museum of Luhansk Taras Shevchenko National University (Poltava, Ukraine).

Fossil sites. The studied material was collected at four fossil sites of the Mospyne and Smolyanynivka formations (Fig. 1) in the central part of the Donets Basin:

(1) Makedonivka-1: Ukraine, Luhansk Oblast, Luhansk Raion, quarries near the village of Makedonivka (coordinates: 48°14'20.5"N 39°18'23.3"E). These quarries exposed a thick fine-grained sandstone bed, which lie 60 m below the G_1^2 limestone layer of the Mospyne Formation (Fig. 2*c*). The sandstone contains rare plant debris, impressions of marine bivalves and diverse trace fossils, including *Arborichnus*, *Circulichnis*, *Laevicyclus*, *Lockeia*, *Psammichnites*, *Treptichnus*, etc. [Dernov, 2023].

(2) Makedonivka-2: Luhansk Oblast, Luhansk Raion, the ravine slope and old coal mine dumps near the northern outskirts of the village of Makedonivka (coordinates: 48°14'36"N 39°17'58"E). This fossil site represents the 10-m-thick shale-dominated succession that lie above the g_1^2 coal layer, Mospyne Formation (Figs 2*a, b*).

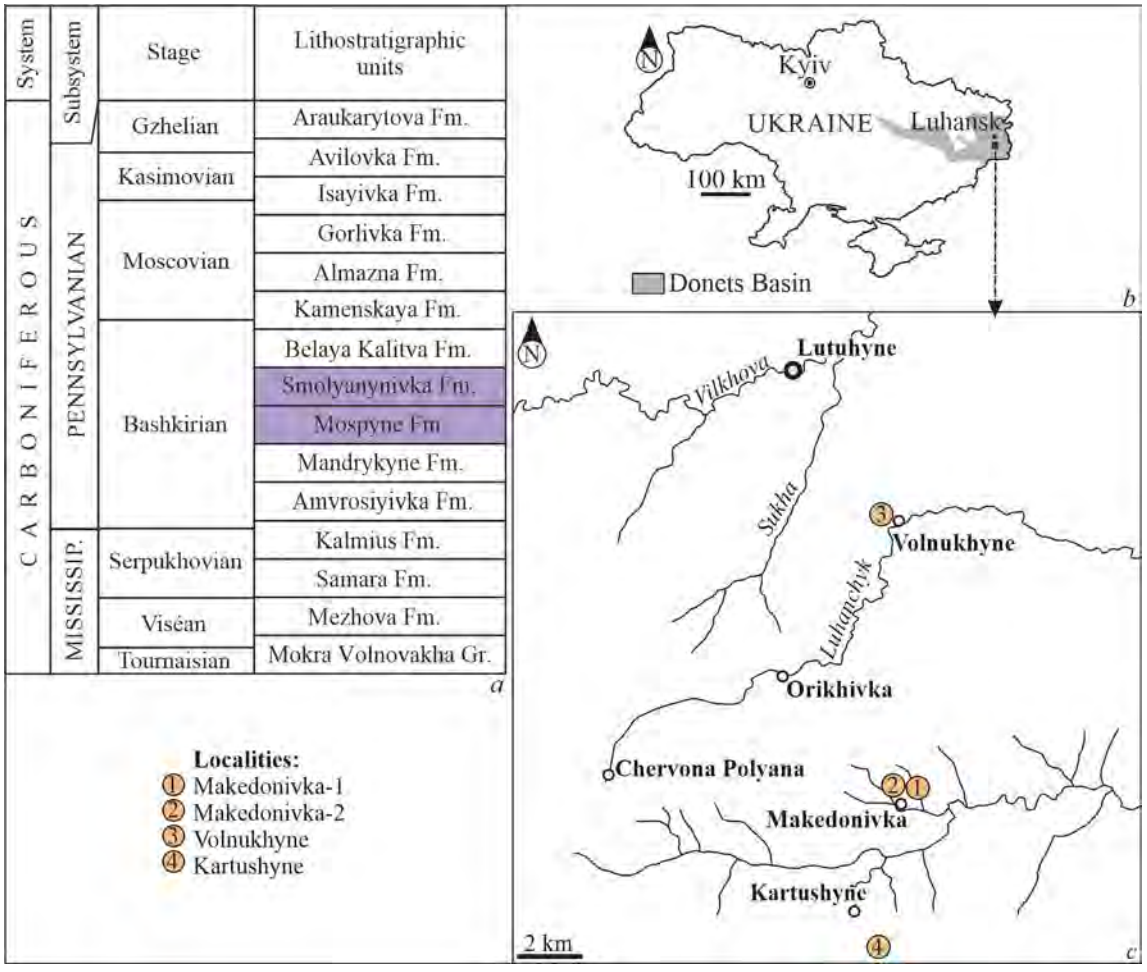

Fig. 1. Stratigraphic position (*a*) and geographical location (*b, c*) of the *Cochlichnus*-bearing fossil sites.
Рис. 1. Стратиграфічне положення (*a*) та географічне розташування (*b, c*) вивчених місцезнаходжень.

The roof shale of the g_1^2 coal bed contains remains of the non-marine bivalves *Curvirimula trapeziforma* (Dewar, 1939) and *C. tesselata* (Jones, 1891) [Dernov 2022a], horseshoe crabs [Dernov 2019], crossopterygian scales *Rhizodopsis sauroides* (Williamson, 1849) and *Rhabdoderma elegans* (Newberry, 1856) [Dernov 2019], coprolites, and evidence of plant-arthropod interactions (endophytic oviposition, leaf margin feedings, etc.) [Dernov 2021].

A rich terrestrial plant assemblage consisting of the genera *Asolanus, Bothrodendron, Cyperites, Lepidodendron, Lepidophloios, Lepidostrobophyllum, Syringodendron, Stigmaria, Asterophyllites, Calamites, Pinnularia, Sphenophyllum, Corynepteris, Alethopteris, Dictyoxylon, Eusphenopteris, Karinopteris, Mariopteris, Lyginopteris, Neuralethopteris, Paripteris, Trigonocarpus, Cordaicarpus, Cordaites*, and *Samaropsis* was studied from this locality by Dernov and Udovychenko [2019].

The siltstone with *Cochlichnus anguineus* is grey and greyish-yellow, fine-grained, micaceous, horizontally bedded with plant debris and rare steinkerns of non-marine bivalves. *Cochlichnus anguineus* is concentrated mainly in a 3 to 4-cm-thin interlayer of limonitised brown siltstone with small plant debris and the trace fossils ?*Palaeophycus* isp. and *Diplichnites* isp. A thin interlayer of ellipsoidal siderite nodules with rare remains of horseshoe crabs [Dernov 2019: fig. 3.8] and pteridosperms *Karinopteris* lies in the lower part of the siltstone layer, just above limonitised siltstones with *Cochlichnus anguineus*.

(3) Volnukhyne: Luhansk Oblast, Luhansk Raion, a quarry near the village of Volnukhyne (coordinates: 48°21'28"N, 39°16'53"E). This quarry exposed lacustrine and lagoonal siltstones that lie above the g_3 coal layer of the Mospyne Formation (Fig. 2*d*).

A single slab of the fine-grained grey lacustrine or lagoonal siltstone with several *Cochlichnus anguineus* was found on the talus along with trace fossils *Planolites*, microbially induced sedimentary structures, and gas-escape structures (Fig. 2*e*). At this fossil site, in the roof shale of the g_3 coal layer, a rich assemblage of terrestrial plants, including the genera *Asolanus*, *Bothrodendron*, *Cyperites*, *Lepidodendron*, *Lepidophloios*, *Lepidostrobophyllum*, *Asterophyllites*, *Calamites*, *Calamostachys*, *Sphenophyllum, Alethopteris, Cardioneura*, *Cyclopteris*, *Karinopteris*, *Lyginopteris, Mariopteris*, *Neuropteris*, *Palmatopteris*, *Artisia*, *Cordaites,* and *Samaropsis* was recorded [Dernov & Udovychenko 2019]. Plant debris often bears attached microconchids, as well as galls, endophytic oviposition, etc. [Dernov & Udovychenko 2019; Dernov 2021].

(4) Kartushyne: Luhansk Oblast, Roven'ky Raion, heap spoils of the coal mine 1.2 km south of the village of Kartushyne (coordinates: 48°09'53.7"N, 39°15'33.1"E); upper part of the Smolyanynivka Formation, roof shale of an unidentified coal layer in the interval between the h_7 and h_{11} coal beds.

The mine dumps are composed mainly of slabs of black and dark grey lacustrine siltstones with remains of terrestrial plants (*Bothrodendron, Cyperites, Lepidodendron, Lepidophloios, Lepidostrobophyllum*, *Sigillaria, Stigmaria, Annularia, Asterophyllites, Calamites, Radicites, Sphenophyllum, Asterotheca, Renaultia*, *Eusphenopteris, Neuropteris, Paripteris, Odontopteris, Alethopteris, Mariopteris, Cyclopteris*, *Cordaianthus, Cordaites*, *Samaropsis*, etc.), microconchids, non-marine bivalves *Carbonicola acuta* (Sowerby, 1812), ?millipedes, insects, horseshoe crabs, scales of the crossopterygians *Rhizodopsis sauroides* and *Megalichthys* sp., fish egg capsule *Palaeoxyris* sp. and the trace fossils *Cochlichnus anguineus*, ?*Skolithos*, *Palaeophycus*, and *Diplichnite*s.

Regional stratigraphy. The Mospyne Formation (C_2^2 or G) consists of a paralic succession of sandstones, siltstones, mudstones, coals, and limestones [Aizenverg *et al.* 1963, 1975; Dunaeva 1969; Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013]. The thickness of this formation varies from 315 m in the NW part of the Donets Basin to 730 m in the SE part of the Donets Basin [Aizenverg *et al.* 1963; Dunaeva 1969; Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013]. The Mospyne Formation corresponds to the lower part of the Zuyivkian Horizon (lower half of the Kayalian Regional Stage) of the Regional stratigraphic scheme of the Dnipro–Donets Downwarp [Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013].

Fig. 2. Geological setting of the studied fossil sites: (*a*) general view of the fossil site Makedonivka-2; (*b*) siltstone layer with *Cochlichnus anguineus* (Makedonivka-2), scale bar = 100 mm; (*c*) general view of the fossil site Makedonivka-1; (*d*) siltstone layer with *Cochlichnus anguineus* (Volnukhyne); (*e*) gas-escape structure in the siltstone with *Cochlichnus anguineus* (Volnukhyne).

Рис. 2. Геологічні особливості вивчених місцезнаходжень: (*a*) загальний вигляд місцезнаходження Македонівка-2; (*b*) алевроліти з *Cochlichnus anguineus* (Македонівка-2), масштабна лінійка = 100 мм; (*c*) загальний вигляд місцезнаходження Македонівка-1; (*d*) алевроліти з *Cochlichnus anguineus* (Волнухине); (*e*) знаки виділення газу із нелітифікованого осаду в алевролітах з *Cochlichnus anguineus* (Волнухине).

The Smolyanynivka Formation (C_2^3 or H) consists of a paralic succession of sandstones, siltstones, mudstones, coals, and limestones [Aizenverg *et al.* 1963, 1975; Dunaeva 1969; Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013]. This formation is characterised by thick (40–60 m) beds of coarse-grained alluvial sandstones [Aizenverg *et al.* 1963]. The thickness of this formation varies from 330 m in the NW part of the Donets Basin to 670 m in the SE part of the Donets Basin [Aizenverg *et al.* 1963; Dunaeva 1969; Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013]. The Smolyanynivka Formation corresponds to the upper part of the Zuyivkian Horizon (stratigraphic interval between the H_1 and the H_4 limestone layers) and almost completely to the Makiyivkian Horizon (interval between the H_4 and the I_1 limestone layers) [Poletaev *et al.* 2011].

Age. Mospyne and Smolyanynivka formations contain remains of typical Langsettian terrestrial plants [Novik 1974; Dernov & Udovychenko 2019; etc.] and ammonoids [Popov 1979; Dernov 2022b], non-marine bivalves of the upper part of the *lenisulcata* Zone and lower part of the *communis* Zone (Mospyne Formation) [Dernov 2022a] and upper part of the *communis* Zone and *lower modiolaris* Subzone (Smolyanynivka Formation) [Sergeeva 1981], as well as late Bashkirian conodonts [Nemyrovska, 1999], and other marine and terrestrial biota, such as miospores, foraminifers, corals, bryozoans, brachiopods, scaphopods, gastropods, horseshoe crabs, millipedes, insects, and fishes.

Palaeogeography. The Bashkirian coal-bearing deposits in the Donets Basin were accumulated mainly in a large alluvial-deltaic plain, which was flooded periodically by the warm epicontinental seas [Logvinenko 1953; Feofilova & Levenshtein 1963; Ustinovsky 1993]. Only the central part of the Donets Basin was characterised by a continuous regime of marine sedimentation in the early late Bashkirian (Fig. 3).

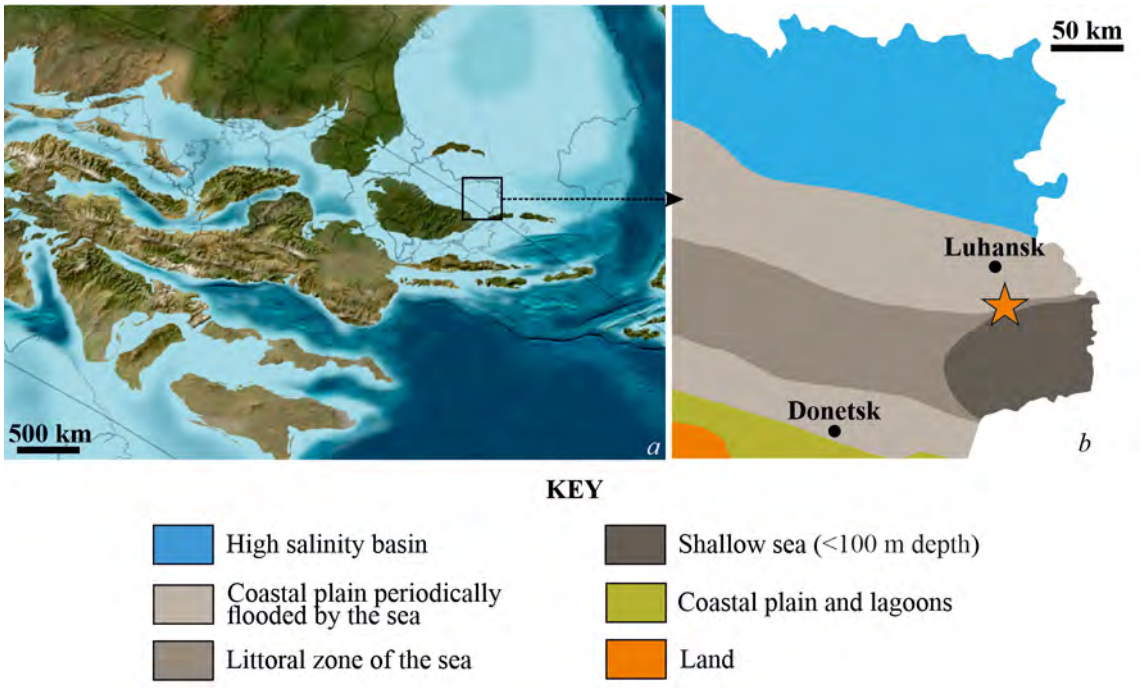

Fig. 3. Bashkirian palaeogeography of eastern Ukraine: (*a*) palaeogeographic map of Europe in the Pennsylvanian (https://deeptimemaps.com); (*b*) palaeogeographic map of the Donets Basin in the Bashkirian (modified from Ischenko *et al.*[1993: fig. 33]).

Рис. 3. Палеогеографія Сходу України в башкирський час: (*a*) палеогеографічна карта Європи в пенсильванії (https://deeptimemaps.com); (*b*) палеогеографічна карта Донбасу в башкирський час (взято з [Ischenko *et al.*, 1993: fig. 33]).

Systematic ichnology

Ichnogenus ***Cochlichnus*** Hitchcock, 1858

Type ichnospecies. *Cochlichnus anguineus* Hitchcock, 1858; original designation, by monotypy.

Other included ichnospecies. *C. annulatus* Orlowski, 1989; *C. antarticus* Tasch, 1968.

Diagnosis. Regular, sinusoidal, horizontal trails and burrows resembling a compressed and stretched corkscrew. The overall width of an individual trace may change progressively [after Häntzschel 1975; Keighley & Pickerill 1997; Uchman 1998].

Remarks. *Cochlichnus* differs from *Belorhaphe* Fuchs, 1895 by smooth rounded rather than angular curves of the trace. *Cochlichnus* differs from *Helminthopsis* Heer, 1877 by regular curves of the sinusoid, while the outlines of *Helminthopsis* resemble river meanders rather than sinusoidal wave [Buatois *et al*. 1997].

Stratigraphic range. From the Ediacaran to the present.

Cochlichnus anguineus Hitchcock, 1858

Figs 4 and 5

See Stanley & Pickerill [1998: p. 9], Schlirf [2000: p. 176] and Uchman *et al*. [2004: p. 135] for synonymy.

Diagnosis. Regular, sinusoidal, smooth, horizontal trails and burrows resembling a compressed and stretched corkscrew. The overall width of an individual trace may change progressively [after Häntzschel 1975; Keighley & Pickerill 1997; Uchman 1998].

Material. Thirteen sandstone and siltstone slabs preserving *c*. 30 trace fossils and several field photos of the trace fossils *in situ* (specimens GMLNU-9/01 to GMLNU-9/13).

Description. Horizontal, cylindrical, thin, sinusoidal trails and burrows with a smooth surface preserved as a convex hyporelief on the lower bedding surface and concave epirelief on the upper surface of the fine-grained sandstone and siltstone layers. The traces are straight, less often weakly arched (Fig. 4*d*) or sharply curved at an angle of about 45° (Fig. 4*a*), not branching, and usually occur singly; if several traces co-occur, they may intersect (Figs 4*d* and 5*d*). The diameter of the trails/burrows mainly ranges between 1.2 and 1.5 mm; much less frequently, the width of the trails is 5.0 mm (Fig. 5*c*). The length of the most complete trace fossil is 150 mm (Fig. 4*a*). The wavelength of the sinuous meanders ranges between 8.0 and 12.0 mm, and the amplitude between 3.0 and 5.5 mm. The cross section of the positive ridges is rounded or ellipsoidal, sometimes slightly flattened from above.

Remarks. *Cochlichnus anguineus* differs from other ichnospecies of the ichnogenus *Cochlichnus* in the absence of annulation and lateral markings [Buatois *et al.* 1996, 1997]. *Cochlichnus kochi* (Ludwig, 1869), which is widely distributed in the Westphalian strata of England [Elliott 1985], is a junior synonym of *Cochlichnus anguineus* [Gluszek 1995]. Stanley & Pickerill [1998] consider *Cochlichnus antarcticus* to be a junior synonym of *C. anguineus*; ichnospecies *C. kochi*, *C. serpens* Webby, 1970, *C. lagartensis* Muniz, 1980, *C. duomaensis* Yang et al., 1983 and *C. sousensis* Muniz, 1985 are all junior synonyms of *C. anguineus* [Fillion & Pickerill 1990; Buatois & Mangano 1993; Stanley & Pickerill 1998].

In 1994, a new name *Cymataulus* Rindsberg, 1994 was proposed for sinusoidal traces inside rather than on the surfaces of layers [Rindsberg 1994]. However, this idea has not found support among researchers, because in many cases it is difficult and sometimes impossible to establish whether *Cochlichnus* burrows inside the sediment or traces on its surface [Pickerill & Narbonne 1995]. Thus, *Cymataulus* is considered a junior synonym of *Cochlichnus* [Buatois *et al.* 1996, 1997; Keighley & Pickerill 1997].

Localities. See 'Geological setting and Material' section.

Occurrences. Ediacaran–Holocene.

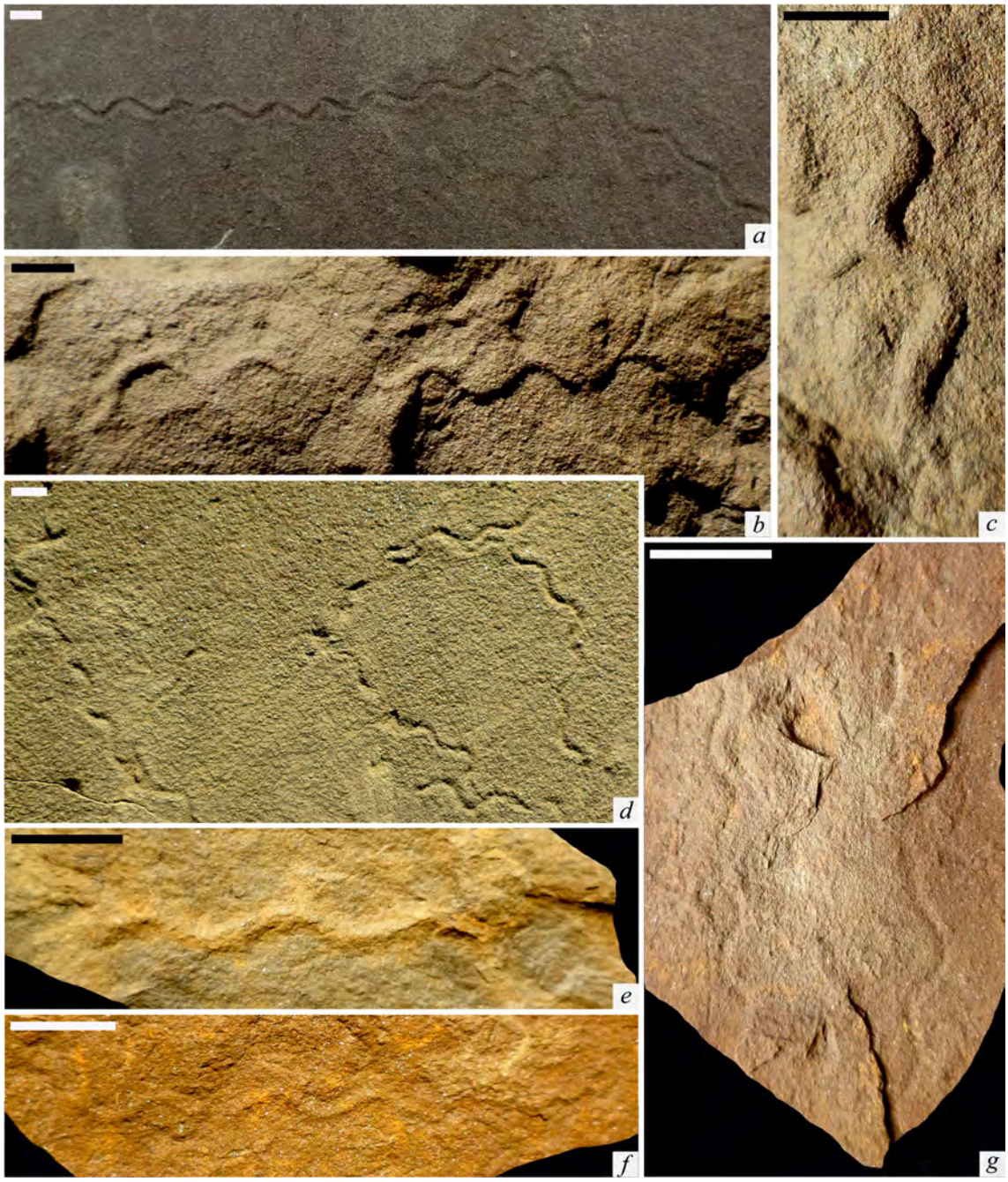

Fig. 4. *Cochlichnus anguineus* Hitchcock, 1858 from the Mospyne Formation: (*a–d*) Makedonivka-1 fossil site (*a*—GMLNU-9/01, *b*—GMLNU-9/05, *c*—GMLNU-9/03, *d*—field photo of the trace fossil *in situ*); (*e–g*) Makedonivka-2 fossil site (*e*—GMLNU-9/02, *f*—GMLNU-9/04, *g*—GMLNU-9/06). Scale bars = 10 mm.

Рис. 4. *Cochlichnus anguineus* Hitchcock, 1858 з моспинської світи: (*a–d*) місцезнаходження Македонівка-1 (*a* — GMLNU-9/01, *b* — GMLNU-9/05, *c* — GMLNU-9/03, *d* — польове фото іхнофосилій *in situ*); (*e–g*) місцезнаходження Македонівка-2 (*e* — GMLNU-9/02, *f* — GMLNU-9/04, *g* — GMLNU-9/06). Масштабні відрізки = 10 мм.

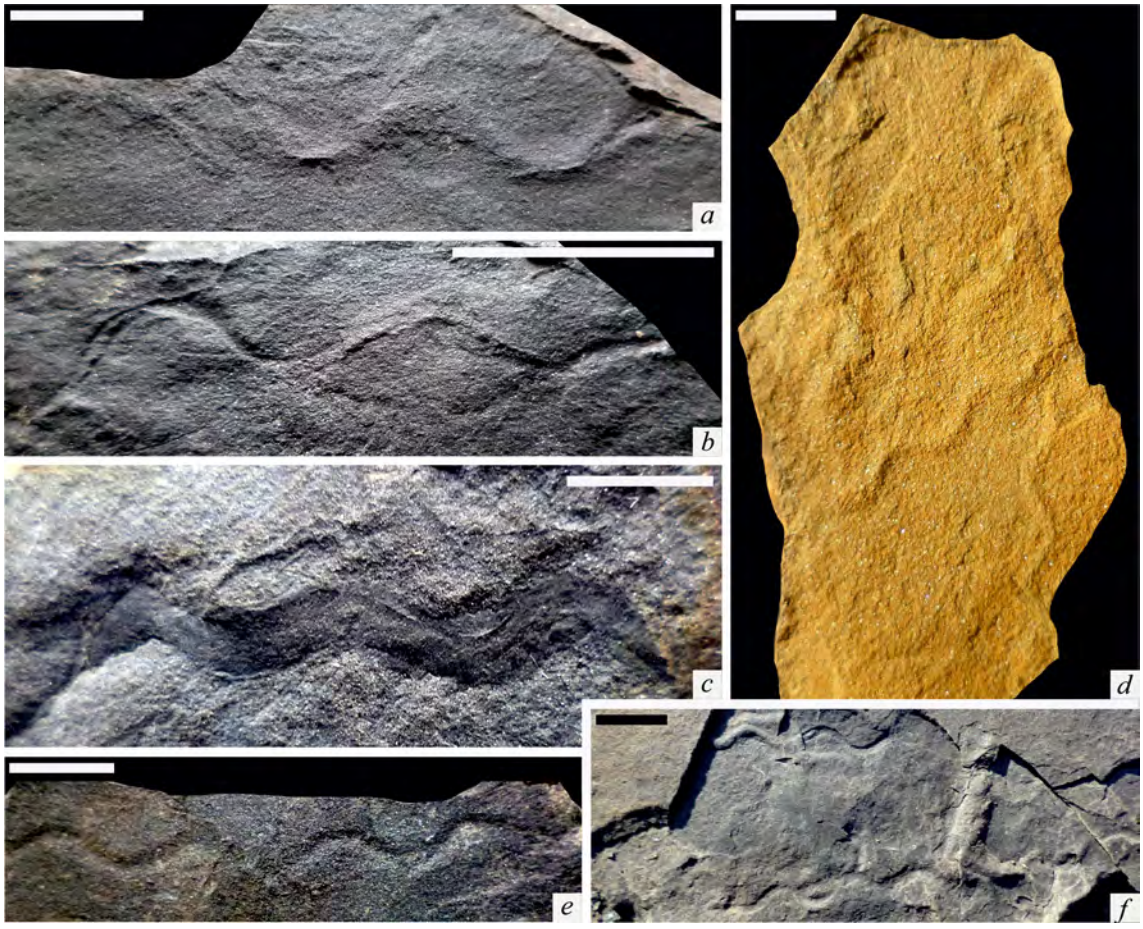

Fig. 5. *Cochlichnus anguineus* Hitchcock, 1858 from the Mospyne and Smolyanynivka formations: (*a–c, e*) Kartushyne fossil site (*a*—GMLNU-9/09, *b*—GMLNU-9/07, *c*—GMLNU-9/10, *e*—GMLNU-9/12); (*d*) Makedonivka-2 fossil site (GMLNU-9/11); (*f*) Volnukhyne (GMLNU-9/08). Scale bars = 10 mm.

Рис. 5. *Cochlichnus anguineus* Hitchcock, 1858 з моспинської та смолянинівської світ: (*a–c, e*) Картушине (*a* — GMLNU-9/09, *b* — GMLNU-9/07, *c* — GMLNU-9/10, *e* — GMLNU-9/12); (*d*) Македонівка-2 (GMLNU-9/11); (*f*) Волнухине (GMLNU-9/08). Масштабні відрізки = 10 мм.

Discussion and concluding remarks

In the Donets Basin, *Cochlichnus anguineus* usually co-occurs with *Lockeia* (Makedonivka-1), *Planolites* (Volnukhyne), and *Palaeophycus* (Makedonivka-2). Sometimes these trace fossils are found on the bedding surfaces bearing microbially induced sedimentary structures (Fig. 4*a*) together with *Taphrhelminthopsis* and *Aulichnites* (Makedonivka-1).

Cochlichnus is known from the entire Phanerozoic [Buatois *et al.* 1996; Lucas *et al.* 2004] and was generally distributed in non-marine environments in the Carboniferous, although it has been recorded in a wide range of environments, from lacustrine (Mermia Ichnofacies) to marine (Cruziana Ichnofacies) [Buatois *et al.* 1997; Lucas & Lerner 2005; Uchman *et al.* 2008, 2009; Smith *et al.* 2011).

Cochlichnus has been interpreted as traces of grazing, feeding, and locomotion and it is suggested that traces, depending on the environmental conditions and potential producers, may be combinations of all these trace fossil ethological categories [Buatois *et al.* 1997]. Potential producers of *Cochlichnus* include worms *sensu lato* [Webby 1970; Hakes 1976], nematodes [Moussa 1970; Chamberlain 1975; Metz 1998], annelids [Hitchcock 1858], cyclostomates [Gluszek 1995] or insect larvae [Toula

1908; Uchman *et al*. 2004]. In modern freshwater basins, traces morphologically similar to *Cochlichnus* are produced by nematodes [Chamberlain 1975], larvae of Ceratopogonidae [Metz 1987], Therevidae [Michealis 1972] and *Chironomus motilator* [Tarr 1935]. It seems that nematodes and/or annelids are the most likely producers of *Cochlichnus*, since representatives of Diptera are not known from the Carboniferous.

Acknowledgements

I would like to thank the anonymous reviewers whose comments and suggestions improved the quality of the final version of the manuscript. The research was carried out within the framework of the scientific theme 'Late Precambrian and Phanerozoic biota of Ukraine: biodiversity, revision of systematic composition and phylogeny of leading groups' (No. 0122U001609).

References

Aizenverg, D. E., N. G. Belenko, V. S. Dedov, M. L. Levenshtein, I. A. Makarov, [et al.]. 1975. Stratigraphic excursion. In: *Aizenverg, D. E., V. V. Lagutina, M. L. Levenshtein, V. S. Popov (eds). Field excursion guidebook for the Donets Basin*. Moscow, 201–245. [In Russian]

Aizenverg, D. E., N. E. Brazhnikova, K. O. Novik, A. P. Rotai, P. L. Shulga. 1963. *Carboniferous stratigraphy of the Donets Basin.* Publishing House of the Academy of Sciences of the Ukrainian SSR, Kyiv, 1–182 [In Russian]

Archer, A. W., C. G. Maples. 1984. Trace fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of Southwestern Indiana. *Journal of Paleontology*, **58** (2): 448–466.

Bendella, M., M. Benyoucef, R. Mikuláš, I. Bouchemla, B. Ferré. 2022. Storm-dominated shallow marine trace fossils of the Lower Devonian Teferguenite Formation (Saoura valley, Algeria). *Italian Journal of Geosciences*, **141** (3): 400–425. https://doi.org/10.3301/IJG.2022.23

Buatois, L. A., G. Jalfin, F. G. Acenolaza. 1997. Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina: ichnologic signatures of substrate consolidation and colonization sequences. *Journal of Paleontology*, **71** (2): 324–337. https://doi.org/10.1017/S0022336000039238

Buatois, L. A., M. G. Mángano, X. Wu, G. Zhang. 1996. Trace fossils from Jurassic lacustrine turbidites of the Anyao Formation (central China) and their environmental and evolutionary significance. *Ichnos*, **4** (4): 287–303. https://doi.org/10.1080/10420949609380137

Buatois, L. A., M. G. Mángano. 2003. La icnofauna de la Formación Puncoviscana en el noroeste argentino: la colonizacin de fondos oceánicos y reconstrucción de paleoambientes y paleoecosistemas de la transición precámbrica-cámbrica. *Ameghiniana*, **40** (1): 103–117.

Chamberlain, C. K. 1975. Recent Lebensspurren in nonmarine aquatic environments. *In: Frey R. W. (ed.). The study of trace fossils*. Springer-Verlag, New York, 431–458. https://doi.org/10.1007/978-3-642-65923-2_19

Dernov, V. 2019. On the study of the non-marine fauna of the Mospino Formation (Middle Carboniferous, Donets Basin). *Tectonics and Stratigraphy*, **46**: 105–115. [In Russian] https://doi.org/10.30836/igs.0375-7773.2019.208882

Dernov, V. 2021. The earliest insect endophytic oviposition (Early Pennsylvanian, eastern Ukraine). *Visnyk of Taras Shevchenko National University of Kyiv. Geology,* **95** (4), 16–24. https://doi.org/10.17721/1728-2713.95.02

Dernov, V. 2022a. Nonmarine bivalves from the Mospyne Formation (upper Bashkirian) of the Donets Basin: taxonomy, paleoecology, and stratigraphic significance. *Geologichnij zhurnal*, **380** (3): 34–56. [In Ukrainian] https://doi.org/10.30836/igs.1025-6814.2022.3.255491

Dernov, V. 2022b. Late Bashkirian ammonoids from the Mospyne Formation of the Donets Basin, Ukraine. *Fossil Imprint*, **78** (2), 489–512. https://doi.org/10.37520/fi.2022.021

Dernov, V. 2023. Horseshoe crab trace fossils *Arborichnus* Romano et Meléndez, 1985 from the Bashkirian (Carboniferous) of the Donets Basin, Ukraine. *Fossil Imprint*, **79**, 9–25. https://doi.org/10.37520/fi.2023.002

Dernov, V. S., N. I. Udovychenko. 2019. On the paleobotanical characteristics of the Mospino Formation. *Visnyk of V.N. Karazin Kharkiv National University, Geology, Geography, Ecology*, **51**: 67–82. [In Russian] https://doi.org/10.26565/2410-7360-2019-51-05

Dewar, W. 1939. *Anthraconauta (Anthracomya) minima* (Auctorum) and its associates in the Lancashire coalfield. *Bulletin of Geological Survey of Great Britain*, **1**: 47–66.

Dunaeva, N. M. 1969. Open Donets Basin. *In: Bondarchuk, V. G. (ed.). Stratigraphy of the Ukrainian SSR. Vol. V. Carboniferous.* Naukova Dumka, Kyiv, 21–48. [In Ukrainian]

Elliott, R. E. 1985. An interpretation of the trace fossil *Cochlichnus kochi* (Ludwig) from the East Pennine Coalfield of Britain. *Proceedings of the Yorkshire Geological Society*, **45**: 183–187. https://doi.org/10.1144/pygs.45.3.183

Feofilova, A. P., M. L. Levenshtein. 1963. *Features of the sedimentation and coal accumulation in the Early and Middle Carboniferous of the Donets Basin.* Publishing House of the Academy of Sciences of the USSR, Moscow, 1–175. [In Russian]

Fillion, D., R. K. Pickerill. 1990. Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada. *Palaeontographica Canadiana*, **7**: 1–119.
Fuchs, T. 1895. Studien über Fucoiden und Hieroglyphen. *Denkschriftender Kaiserlichen Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse*, **62**: 369–448.
Gluszek, A. 1995. Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geologica Polonica*, **108**: 171–202.
Gureev, Yu. A. 1986. On the prospects for palaeoichnological analysis in stratigraphy. *Tectonics and Stratigraphy*, **27**: 42–47. [In Russian]
Hakes, W. G. 1976. Trace fossils and depositional environments of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *University of Kansas Paleontological Contributions*, **63**: 1–43.
Häntzschel, W. 1975. Trace fossils and Problematica. *In: Teichert, C. (ed.). Treatise on Invertebrate Paleontology. Part W. Miscellanea. Suppl. 1*. Geological Society of America and University of Kansas Press, Lawrence, W3–W269.
Heer, O. 1876–1877. Flora fossilis Helvetiae. Die vorweltliche Hora der Schweiz. Verlag J. Wurster & Co., Zürich, 1–182. (Parts 1, 2 (1876):1–90; Parts 3, 4 (1877): 91–182).
Hitchcock, E. 1858. *Ichnology of New England; a report on the sandstone of the Connecticut Valley, especially its footmarks.* W. White, Boston, 1–220.
Ischenko, A. A., T. I. Nemirovskaya, A. A. Skovorodnikova, O. P. Fissunenko. 1993. The Olmezivkian-Mandrykinkian Stage. *In: Tsegelnyuk, D. P. (ed.). Geological history of Ukraine. Paleozoic*. Naukova Dumka, Kyiv, 136–141 [In Russian]
Ivantsov, A. Yu., V. P. Gritsenko, V. M. Paliy, V. A. Velikanov, L. I. Konstantinenko, [et al.]. 2015. *Upper Vendian macrofossils of Eastern Europe. Middle Dniester area and Volhynia.* PIN RAS, Moscow, 1–144. [In Russian]
Keighley, D. G., R. K. Pickerill. 1997. Systematic ichnology of the Mabou and Cumberland groups (Carboniferous) of western Cape Breton Island, Eastern Canada 1: Burrows, pits, trails and coprolites. *Atlantic Geology*, **33:** 181–215.
Logvinenko, N. V. 1953. *Lithology and paleogeography of the Carboniferous coal-bearing sediments of the Donets Basin.* Kharkiv University, Kharkiv, 1–436. [In Russian]
Lucas, S. G., M. Bruner, P. Shipman. 2004. Middle Pennsylvanian ichnofauna from eastern Oklahoma, USA. *Ichnos*, **11** (1–2): 45–55. https://doi.org/10.1080/10420940490442322
Lucas, S. G., A. J. Lerner. 2005. Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama: a preliminary assessment. *Pennsylvanian Footprints in the Black Warrior Basin of Alabama. Alabama Paleontological Society Monograph*, **1**: 147–152.
Ludwig, R. 1869. Fossile Pflanzenreste aus den palälithischen Formationen der Umgebung von Dillenburg, Biedenkopf und Friedberg und aus dem Saalfeldischen. *Palaontographica*, **17**: 105–128.
Metz, R. 1987. Sinusoidal trail formed by recent biting midge (Family Ceratopoginidae): trace fossil implications. *Journal of Paleontology*, **61** (2): 312–314. https://doi.org/10.1017/S0022336000028481
Metz, R. 1995. Ichnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southeastern Pennsylvania. *Ichnos*, **4** (1): 43–51. https://doi.org/10.1080/10420949509380113
Metz, R. 1996. Newark Basin ichnology: the Late Triassic Perkasie Member of the Passiac Formation, Sanatoga, Pennsylvania. *Northeastern Geology and Environmental Sciences*, **18**: 118–129.
Metz, R. 1998. Nematode trails from the Late Triassic of Pennsylvania. *Ichnos*, **5** (4): 303–308. https://doi.org/10.1080/10420949809386428
Michealis, P. 1972. *Belorhaphe kochi* (Ludwig 1869), eine Wurmspur im europischen Karbon. *Geologisches Jahrbuch,* **71**: 299–330.
Moussa, M. T. 1970. Nematode fossil trails from the Green River Formation (Eocene) in the Uinta Basin, Utah. *Journal of Paleontology*, **44** (2): 304–307.
Muniz, G. C. B. 1980. *Cochlichnus lagartensis* ichnosp. nov., ichnofóssil da Formação Lagarto, Grupo Estância, no. Estado de Sergipe. *Academia Brasileira de Ciencias,* **5**: 3101–3103.
Muniz, G. C. B. 1985. *Cochlichnus sousensis*, icnospecie da formacao Sousa, Grupo Rio do Peixe, no. Estado da Parafba. *Coletanea de trabalhos paleontologicas. Trabalhos apresentados VIII congresso Brasileiro de paleontologia, 1983. Ministerio das minas e energia, departmento nacional da producao mineral*, 239–241.
Nemyrovska, T. I. 1999. Bashkirian conodonts of the Donets Basin, Ukraine. *Scripta Geologica*, **119**: 1–116.
Nemyrovska, T. I., V. I. Yefimenko. 2013. Middle Carboniferous (Lower Pennsylvanian). In: Gozhik, P. F. (ed.). *Stratigraphy of the Upper Proterozoic and Phanerozoic of Ukraine. Vol. 1. Stratigraphy of the Upper Proterozoic, Paleozoic and Mesozoic.* LAT&K, Kyiv, 283–303. [In Ukrainian]
Newberry, J. S. 1856. Description of several new genera and species of fossil fishes, from the Carboniferous strata of Ohio. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**, 96–100.
Novik, E. O. 1974. *Regularities of development of the Carboniferous flora of the south part of the European part of the USSR.* Naukova Dumka, Kyiv, 1–140. [In Russian]
Orlowski, S. 1989. Trace fossils in the Lower Cambrian sequence in Swietokryskie Mountains, Central Poland. *Acta Paleontologica Polonica*, **34** (3): 211–231.
Paliy, V. M. 1978. Late Precambrian and Cambrian trace fossils from Ukraine. *In: Vyalov, O. S. (ed.). Trace fossils of ancient organisms and problems of paleogeographic reconstruction.* Apatity, 26–34. [In Russian]

Pickerill, R. K., G. M. Narbonne. 1995. Composite and compound ichnotaxa: a case example from the Ordovician of Quebec, eastern Canada. *Ichnos*, **4** (1): 53–69. https://doi.org/10.1080/10420949509380114
Poletaev, V. I., M. V. Vdovenko, O. K. Shchogolev, N. I. Boyarina, I. A. Makarov. 2011. Stratotypes of the Carboniferous and Lower Permian regional stratigraphic units of the Dnipro-Donets Downwarp. Logos, Kyiv, 1–236. [In Ukrainian]
Popov, A. V. 1979. Carboniferous ammonoids of the Donets Basin and their stratigraphic significance. Nedra, Leningrad, 1–119. [In Russian]
Ratcliffe, B. C., J. A. Fagerstrom. 1980. Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. *Journal of Paleontology*, **54** (3): 614–630.
Rindsberg, A. K. 1994. Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. *Geological Survey of Alabama Bulletin*, **158**: 1–107.
Schlirf, M. 2000. Upper Jurassic trace fossils from the Boulonnais (northern France). *Geologica et Palaeontologica*, **34**: 145–213.
Sergeeva, M. T. 1981. Bashkirian (Middle Carboniferous) bivalves of the Donets Basin and their stratigraphic significance. *Tectonics and stratigraphy*, **21:** 53–61. [In Russian]
Shul'ga, V. F., A. Zdanovski, L. B. Zaytseva, A. V. Ivanova, A. V. Ivanina, [et al.]. 2007. Correlation of Carboniferous coal-bearing formations of the Lviv-Volhynian and Lublin basins. Varta, Kyiv, 1–427. [In Russian]
Smith, C. J., D. L. Fillmore, E. L. Simpson, S. G. Lucas. 2011. Invertebrate trace fossils from deposits of the Pennsylvanian-age Llewellyn Formation, eastern Pennsylvania, USA. *In: Sullivan, R. M., S. G. Lucas, J. A. Spielmann (eds). Fossil Record 3. New Mexico Museum of Natural History and Science*, **53**: 152–156.
Sowerby, J. 1812. *The mineral conchology of Great Britain; or, Coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth. Vol. 1.* Printed by Benjamin Meredith, London, 1–236.
Stanley, D. C. A., R. K. Pickerill. 1998. Systematic ichnology of the Late Ordovician Georgian Bay Formation of Southern Ontario, eastern Canada. *Royal Ontario Museum publications in life sciences*, **162**: 1–56.
Tarr, W. A. 1935. Concretions in the Champlain Formation of the Connecticut River Valley. *Bulletin of Geological Society of America*, **46** (10): 1493–1534. https://doi.org/10.1130/GSAB-46-1493
Tasch, P. 1968. A Permian trace fossil the Antarctic Ohio Range. *Kansas Academy of Science Transactions*, **71** (1): 33–37. https://doi.org/10.2307/3627396
Toula, F. 1908. Kriechspuren von *Pisidium amnicum* Müller. Beobachtungen auf einer Donauschlickbarre bei Kahlenbergerdorf-Wien. *Verhandlungen der kaiserlichekųniglichen geologischen Bundesanstalt*, **11**: 239–244.
Uchman, A. 1998. Taxonomy and ethology of flysch trace fossils: revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae*, **68**: 105–218.
Uchman, A., A. Gaigalas, V. Kazakauskas. 2008. Trace fossils from the Upper Pleistocene glaciolacustrine laminated sediments of Lithuania. *Geologija*, **50** (3): 212–226. https://doi.org/10.2478/v10056-008-0047-9
Uchman, A., A. Gaigalas, V. Kazakauskas. 2009. Trace fossils from Late Pleistocene varved lacustrine sediments in eastern Lithuania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **272** (3–4): 199–211. https://doi.org/10.1016/j.palaeo.2008.08.003
Uchman, A., M. Pika-Biolzi, P. A. Hochuli. 2004. Oligocene trace fossils from temporary flood plain ponds: an example from the freshwater molasses of Switzerland. *Ecologae Geologicae Helvetia*, **97** (1): 133–148. https://doi.org/10.1007/s00015-004-1111-z
Ustinovsky, Yu. B. 1993. Kayalian Stage (late Bashkirian). *In:* Tsegelnyuk, P. D. (ed.). *Geological history of the territory of Ukraine*. Naukova Dumka, Kyiv, 147–154. [In Russian]
Webby, B. D. 1970. Late Precambrian trace fossils from New South Wales. *Lethaia*, **3** (1): 79–109. https://doi.org/10.1111/j.1502-3931.1970.tb01265.x
Williamson, W. C. 1849. On the microscopic structure of the scales and dermal teeth of some ganoid and placoid fish. *Philosophical Transactions of the Royal Society of London*, **139**: 435–475. https://doi.org/10.1098/rstl.1849.0023
Yang, S., Z. Song, D. Liang. 1983. Late Carboniferous-Early Permian flysch trace fossils from Ali, Xizang (Tibet), China. *Journal of Wuhan College of Geology*, **1**: 93–103. [In Chinese]