



HORSESHOE CRAB TRACE FOSSILS *ARBORICHNUS ROMANO ET MELÉNZ*, 1985 FROM THE BASHKIRIAN (CARBONIFEROUS) OF THE DONETS BASIN, UKRAINE

VITALY DERNOV

Institute of Geological Sciences of the National Academy of Sciences of Ukraine, 55-b Oles Honchar Str., 01054, Kyiv, Ukraine;
e-mail: vitalydernov@gmail.com.

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Abstract: This paper describes resting traces of horseshoe crabs *Arborichnus repetitus* ROMANO et MELÉNZ, 1985 from marine deposits of the Dyakove Group (Viséan–Bashkirian) and the Bashkirian coal-bearing rocks of the Mandrykyne and Mospyne formations in the Donets Basin, eastern Ukraine. The presence of *Arborichnus repetitus* indicates the widespread distribution of horseshoe crabs in the coastal paleobiocenoses of the Dyakove Paleobasin, located in the central part of the Donets Basin. The horseshoe crab resting traces *Arborichnus repetitus* from the Bashkirian strata of the Donets Basin are typical of deltaic and prodeltaic rocks, usually represented by sandstones and siltstones. Horseshoe crabs are the most likely trace-makers of *Arborichnus* ROMANO et MELÉNZ, 1985, but some other arthropods, e.g., aglaspids, could also have produced these trace fossils. The discovery of the presumably horseshoe crab thoracetrone on the same sandstone bedding plane as the traces *Arborichnus* indirectly confirms that xiphosurans were the trace-makers of these ichnofossils.

Key words: trace fossils, horseshoe crabs, cubichnia, *Arborichnus*, Carboniferous, Donets Basin.

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Introduction

Trace fossils attributed to arthropod producers are relatively common in the Pennsylvanian marine and nonmarine deposits of the Donets Basin (eastern Ukraine) and include a variety of wood borings, burrows, trackways, oviposition, coprolites, etc. (Snigirevskaya 1989, Schneider et al. 1992, Dernov 2019a, b, 2021a, b, 2022a). Among these ichnofossils, traces of locomotion and resting of horseshoe crabs, which, unfortunately, are almost unstudied, are of great diversity (Dernov 2019a, b).

Horseshoe crabs (Chelicerata HEYMONS, 1901: Xiphosura HEYMONS, 1901) are arthropods, originating in the Early Ordovician and reaching peak diversity in the Pennsylvanian (Bicknell and Pates 2020). They survived the K-T extinction event, and four species of these arthropods, *Limulus polyphemus* (L., 1758), *Carcinoscorpius rotundicaudata* (LATREILLE, 1802), *Tachypleus gigas* (MÜLLER, 1785) and *T. tridentatus* (LEACH, 1819), currently live in basins along the Atlantic coast of North America and some regions of East and Southeast Asia (Lamsdell 2019).

Horseshoe crab body fossils are rare, whereas their trace fossils, e.g., *Arborichnus* ROMANO et MELÉNZ, 1985, *Crescentichnus* ROMANO et WHYTE, 2015, *Kouphichnium* NOPCSA, 1923, *Limulicubichnus* MILLER, 1982, and *Selenichnites* ROMANO et WHYTE, 1987 (Hardy 1970, Miller

1982, Romano and Meléndez 1985, Romano and Whyte 1987, 2015, Gibb et al. 2011) are relatively common in the fossil record and play an important role in understanding palaeoecology and the living environments of xiphosurans. Most of the ichnogenera listed above, except *Kouphichnium* NOPCSA, 1923, are resting traces (cubichnia), i.e., various depressions on the surface of unconsolidated seafloor silt or other soft mineral substrate, resulting from the resting or hiding of various vertebrate and invertebrate animals (Mikuláš and Dronov 2006, Seilacher 2007, Gand et al. 2008). Currently, a large number of ichnogenera associated with arthropod resting traces have been identified (Tab. 1). The most numerous among them is *Rusophycus* HALL, 1852 (Cambrian–Triassic), which includes about 30 ichnospecies (O’Brien et al. 2009). The producers of these traces are assumed to be mainly trilobites, rarely other arthropods (Pollard et al. 2008).

Here, I describe the horseshoe crab resting traces *Arborichnus repetitus* ROMANO et MELÉNZ, 1985 from the flyschoid deposits of the Dyakove Group (Viséan–Bashkirian) and the coal-bearing rocks of the Mandrykyne (lower Bashkirian) and Mospyne (upper Bashkirian) formations in the Donets Basin, eastern Ukraine. The deposits of the Dyakove Group have not been studied in depth, and the palaeontological features of this stratigraphic

Table 1. Non-trilobite arthropod resting traces (as of March 2023)

Ichnospecies	Age	Potential tracemaker(s)
<i>Alph hartselleanus</i> RINDSBERG, 1994	Mississippian	Crustacea
<i>Arborichnus repetitus</i> ROMANO et MELÉNZ, 1985	Carboniferous	Xiphosurida
<i>Aglaspidichnus sanctacrucensis</i> RADWANSKI et RONIEWICZ, 1967	Late Cambrian	Aglaspidida
<i>Alacranichnus braddyi</i> LUCAS et al., 2013	Cisuralian	Chelicerata: Scorpionida
<i>Chagrinichnites brooksi</i> FELDMANN et al., 1978	Late Devonian	Crustacea: Eocarida
<i>Chelicericatichnus lockleyi</i> DALMAN et LUCAS, 2015	Early Jurassic	Solifugae-like arachnid
<i>Crescentichnus antarcticus</i> WEBER et BRADDY, 2004	Early Ordovician	Xiphosurida, Eurypterida, Aglaspidida Crustacea, Euthycarcinida, Trilobita
<i>Crescentichnus langridgei</i> TREWIN et McNAMARA, 1995	Late Silurian	
<i>Faciemichnus belosis</i> MINTER et BRADDY, 2009	Cisuralian	?Xiphosurida
<i>Gluckstadella cooperi</i> SAVAGE, 1971	Carboniferous	Crustacea: Peracarida
<i>Gluckstadtella elongata</i> LIMA et al., 2015	Pennsylvanian	Crustacea: Peracarida
<i>Hankoichnus bandersnatchi</i> DERNOV, 2023	Pennsylvanian	Crustacea: Phyllocarida
<i>Hedriumichnus apacheensis</i> BRADDY et BRIGGS, 2002	Cisuralian	Insecta: Ephemeroptera or Plecoptera
<i>Herradurichnus scagliai</i> BORRELLO, 1966	Cambrian–Late Cretaceous*	Xiphosurida, Trilobita
<i>Herradurichnus tesiltus</i> (GIBB et al., 2011)	Middle Cambrian	Xiphosurida, Eurypterida, Aglaspidida, Crustacea, Euthycarcinida, Trilobita
<i>Kingella natalensis</i> SAVAGE, 1971	Carboniferous	Crustacea: Syncarida or Peracarida
<i>Limulicubichnus serratus</i> MILLER, 1982	Pennsylvanian	Xiphosurida: Limulidae
<i>Pollichianum cubiculum</i> HEIDTKE, 1990	Cisuralian	Crustacea: Astacidea
<i>Quadrispinichnus parvia</i> BRADDY et BRIGGS, 2002	Cisuralian	Crustacea
<i>Pseudobilobites jefferiesi</i> KENNEDY, 1967	Late Cretaceous	Crustacea
<i>Raaschichnus gundersoni</i> HESSELBO, 1988	Late Cambrian	Aglaspidida
<i>Rotterodichnium longinum</i> WALTER, 1983	Cisuralian	Insecta: Protodonata, Odonata or Megasecoptera
<i>Rotterodichnium major</i> BRADDY et BRIGGS, 2002	Cisuralian	Insecta: Protodonata, Odonata or Megasecoptera
<i>Rusophycus carbonarius</i> DAWSON, 1864	Cisuralian	Crustacea: Notostraca
<i>Rusophycus furcosus</i> GAND, 1994	Cisuralian	Crustacea: Notostraca
<i>Rusophycus versans</i> SCHLIRF et al., 2001	Pennsylvanian	<i>Camptophyllia</i> GILL, 1924
<i>Selenichnites cordiformis</i> FISCHER, 1978	Ordovician	Xiphosurida
<i>Selenichnites eotassicus</i> NAUGOLNYKH, 2022	Early Triassic	Xiphosurida
<i>Selenichnites hundalensis</i> ROMANO et WHYTE, 1987	Middle Jurassic	Xiphosurida
<i>Selenichnites rossendaleensis</i> HARDY, 1970	Mississippian	Xiphosurida
<i>Solusichnium southamensis</i> O'BRIEN et al., 2009	Early Jurassic	Crustacea: Decapoda
<i>Svalbardichnus trilobus</i> WISSHAK et al., 2004	Devonian	Crustacea: Phyllocarida
<i>Tonganoxichnus buildexensis</i> MÁNGANO et al., 1997	Pennsylvanian	Insecta: Monura
<i>Tripartichnus triassicus</i> VALLON et RÖPER, 2006	Early Triassic	Euthycarinida
<i>Tripartichnus imbergi</i> VALLON et RÖPER, 2006	Jurassic	Crustacea: Palinuridae

* Analysis of the morphology of the «dinosaur» tracks *Gumatagichnus unguliformis* GABUNIA et al., 1988 from Gumatag Tracksite in Uzbekistan (Kurbatov and Gabunia 1987, Gabunia et al. 1988, Nessov 1995) and their position in the layer and their relationship to each other suggests that they are morphologically identical to the ichnospecies *Herradurichnus scagliai* (BORRELLO, 1966). *Gumatagichnus unguliformis* GABUNIA et al., 1988 is also significantly similar to the arthropod resting traces *Crescentichnus* ROMANO et WHYTE, 2015. Thus, *Gumatagichnus unguliformis* GABUNIA et al., 1988 is probably a junior synonym of *Herradurichnus scagliai* BORRELLO, 1966 and some ichnospecies of the ichnogenus *Crescentichnus* ROMANO et WHYTE, 2015.

unit are limited: very rare and poorly preserved remains of terrestrial plants, as well as rugose corals, brachiopods, bivalves, cephalopods, crinoids, a single dragonfly impression, and allochthonous remains of an acanthodian fishes are known from the Dyakove Group (Dernov 2016). The same-aged Late Mississippian and Early Pennsylvanian

coal-bearing sediments in the Donets Basin contain a variety of fossils, but the trace fossils from these strata are poorly understood.

The finds of *Arborichnus repetitus* trace fossils has considerable palaeogeographic and stratigraphic significance. The results of the study are also important

for reconstruction of the depositional environments in the Donets Basin during the Bashkirian.

Geological settings

The study area is located in the southern part of Luhansk Region, eastern Ukraine (Text-fig. 1a, b); this territory belongs to the central part of the Donets Basin. The studied material was found in the coal-bearing rocks of the Mandrykyne and Mospyne formations and the marine rocks of the Dyakove Group, which laterally replaced the Mandrykyne and Mospyne formations (Text-fig. 1c).

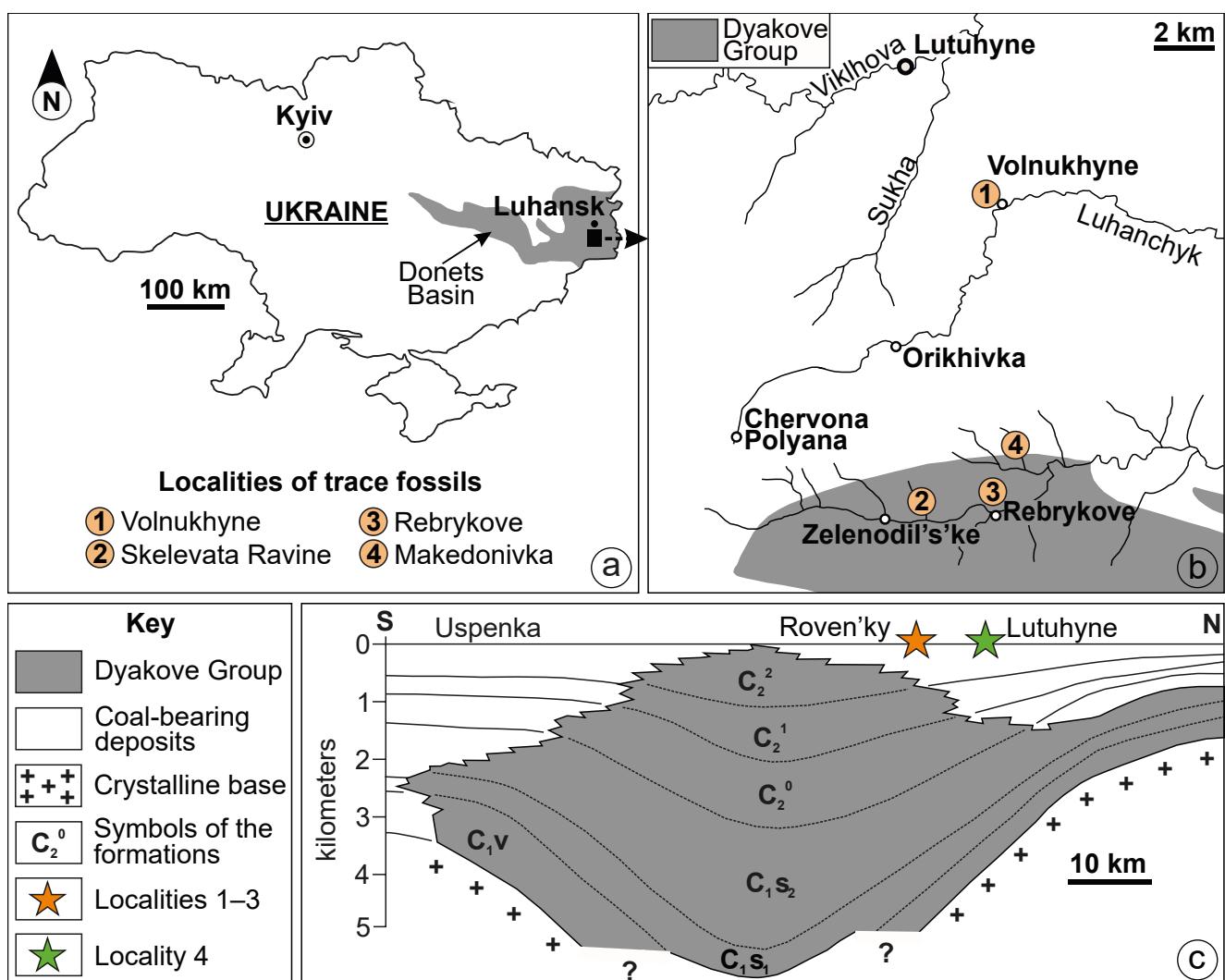
The flyschoid sequence of the Dyakove Group, exposed in the central part of the Donets Basin, consist of a non-rhythmic and fine-rhythmic sequence of mudstones and siltstones (80–90 % of the section) with rare sandstone beds (Fissunenko and Reznikov 1985, Reznikov 1993). The lower limit of the Dyakove Group corresponds to the base of the Viséan (Fissunenko and Reznikov 1985) or even Devonian-Carboniferous boundary interval (Reznikov 1993); the

upper boundary varies laterally from the upper Viséan to the upper Bashkirian (Reznikov 1993) (Text-fig. 1c).

The Mandrykyne Formation (called also C_2^1 or F) is represented by a paralic sedimentary sequence of sandstones, siltstones, mudstones and limestones with very rare coal beds. The thickness of this formation varies from 265 m in the NW part of the Donets Basin to 650 m in the SE part of the Donets Basin (Aisenverg et al. 1963, 1975, Dunayeva 1969, Nemyrovska and Yefimenko 2013). This formation corresponds to the Blagodatnian Horizon (upper part of the Mandrykyne Regional Stage) of the Regional stratigraphic scheme of the Dnipro-Donets Downwarp (Poletaev et al. 2011, Nemyrovska and Yefimenko 2013).

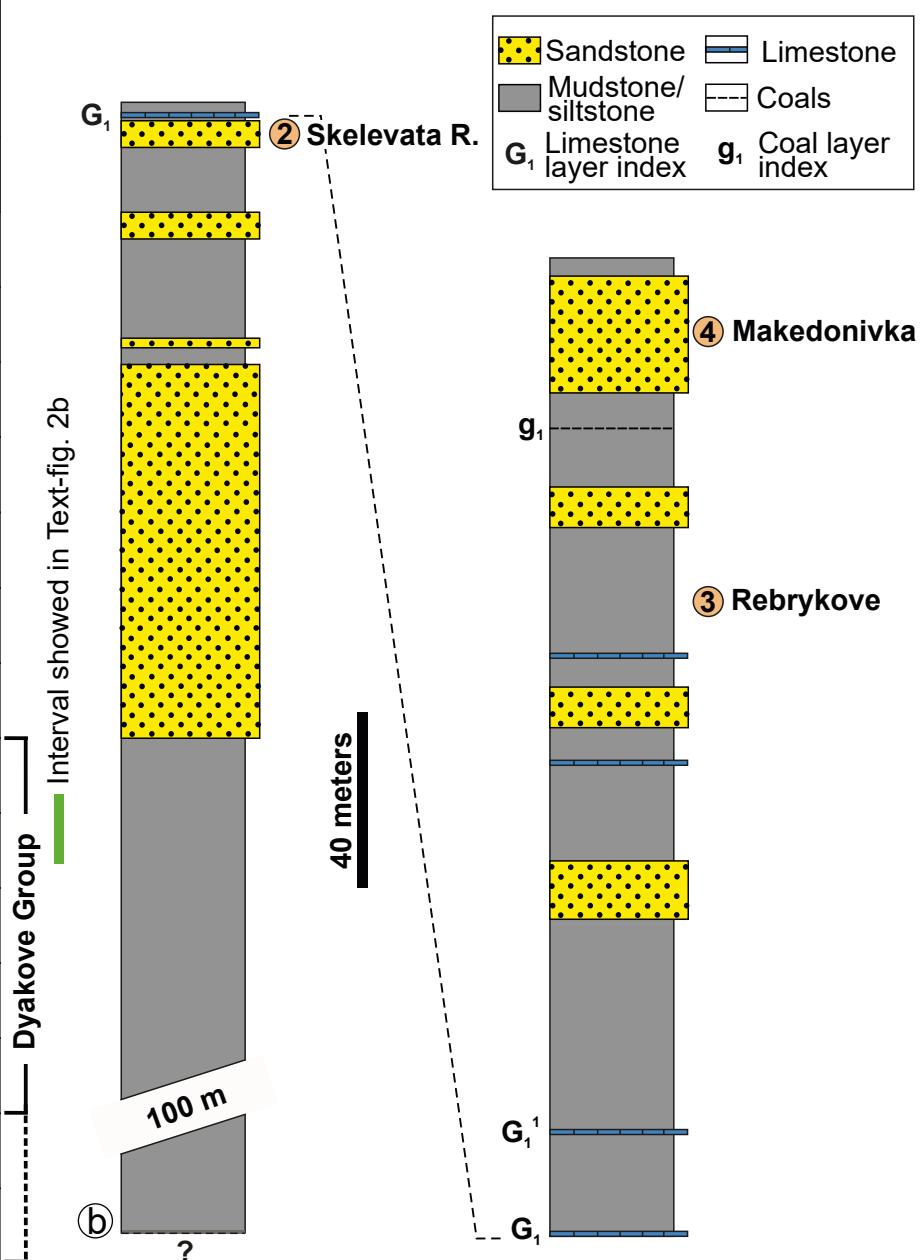
Rocks of the Mandrykyne Formation contain remains of terrestrial plants (Novik 1974 and references there) and ammonoids (Popov 1979) typical for the Namurian C of Western Europe, as well as early Bashkirian conodonts (Nemyrovska 1999), and other marine and terrestrial biota: miospores, foraminifers, corals, chaetetids, bryozoans, brachiopods, gastropods, etc.

The Mospyne Formation (C_2^2 or G) consists of a paralic sedimentary succession of sandstones, siltstones, mudstones,



Text-fig. 1. Geographic location and geological settings of the studied fossil sites. a, b: geographic location of the localities of *Arborichnus repetitus*, c: geological profile showing lateral replacing of the Bashkirian coal-bearing succession by flyschoid rocks of the Dyakove Group in the central Donets Basin (modified from Poletaev et al. 1991: fig. 6).

System		Lithostratigraphic units		Stage
	Subsystem	Kasim.	Gzhel.	
CARBONIFEROUS	PENNSYLVANIAN	Araukarytova Fm. (C ₃ ³ or P)		
		Avilovka Fm. (C ₃ ² or O)		
		Isayivka Fm. (C ₂₋₃ ³ or N)		
		Gorlivka Fm. (C ₂ ⁷ or M)		
		Almazna Fm. (C ₂ ⁶ or L)		
		Kamenskaya Fm. (C ₂ ⁵ or K)		
		Belya Kalitva Fm. (C ₂ ⁴ or I)		
		Smolyanynivka Fm. (C ₂ ³ or H)		
		Mospyne Fm. (C ₂ ² or G)		
		Mandrykyne Fm. (C ₂ ¹ or F)		
		Amvrosiyivka Fm. (C ₂ ⁰ or E)		
		Kalmius Fm. (C ₁₋₂ ⁴ or D)		
		Samara Fm. (C ₁ ³ or C)		
		Mezheva Fm. (C ₁ ² or B)		
MISSISSIPPIAN	Bashkirian	Mokra Volnovakha Group (C ₁ ¹ or A)		
		T. Visean	Serpukh.	



Text-fig. 2. Stratigraphic position of the studied localities. a: Carboniferous stratigraphy of the Donets Basin, b: stratigraphic position of the localities of *Arborichnus repetitus* in the Dyakove Group of the central Donets Basin. Abbreviations: Fm. – Formation, Gzhel. – Gzhelian, Kasim. – Kasimovian, Serpukh. – Serpukhovian, T. – Tournaisian.

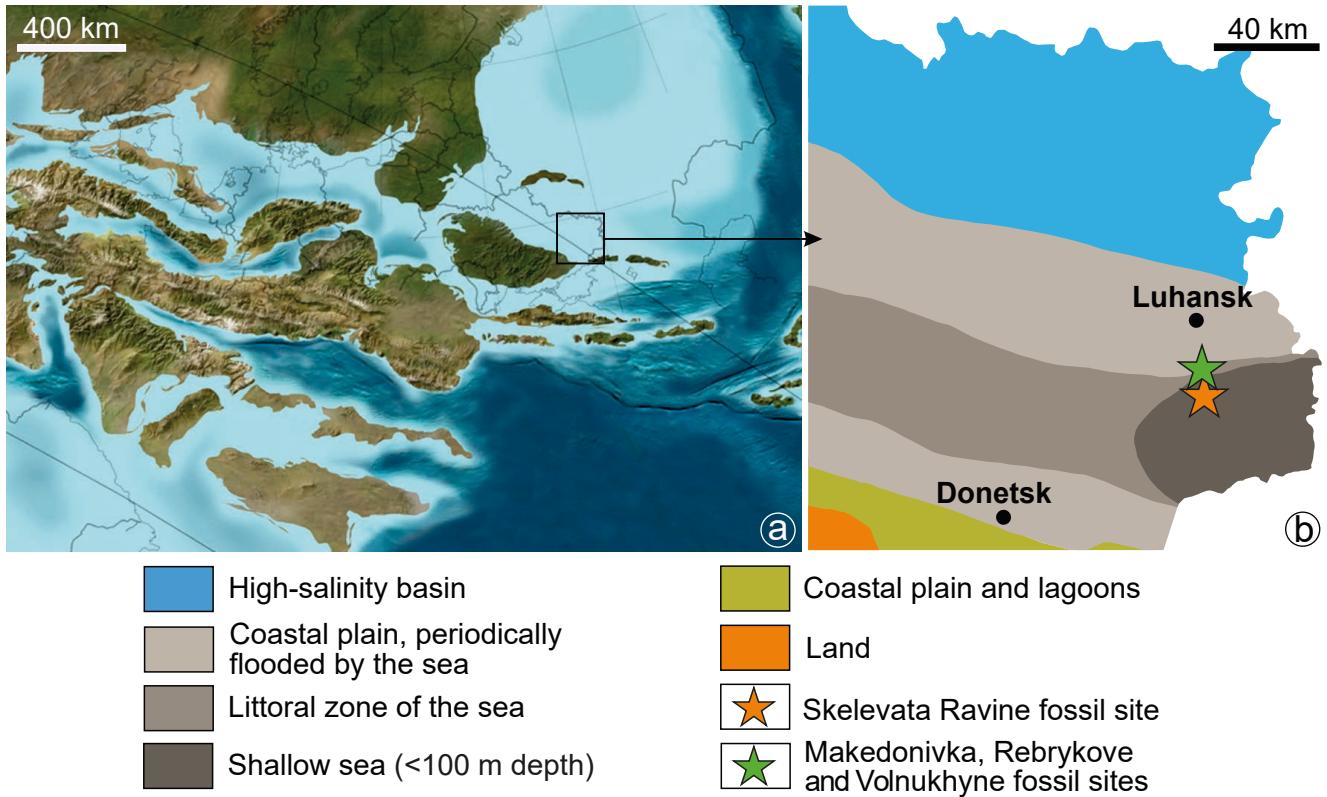
coals and limestones. The thickness of this formation varies from 315 m in the NW part of the Donets Basin to 730 m in the SE part of the Donets Basin (Aisenverg et al. 1963, 1975, Dunayeva 1969, Nemyrovska and Yefimenko 2013). The Mospyne Formation corresponds to the lower part of the Zuyivkian Horizon (lower half of the Kayalian Regional Stage) of the Regional stratigraphic scheme of the Dniipro-Donets Downwarp (Poletaev et al. 2011, Nemyrovska and Yefimenko 2013). The lower part of the Mospyne Formation (below the g₁ coal layer) in the study area (Luhansk and Roven'ky districts) is replaced by the flyschoid rocks of the Dyakove Group, which are very poor in fossils.

Rocks of the Mospyne Formation contain remains of typical Langsettian terrestrial plants (Novik 1974, Dernov

and Udovychenko 2019, etc.) and ammonoids (Popov 1979, Dernov 2022c), non-marine bivalves of the upper part of the *lenisulcata* Zone and lower part of the *communis* Zone (Dernov 2022b), late Bashkirian conodonts (Nemyrovska 1999), and other marine and terrestrial biota, e.g., miospores, foraminifers, corals, bryozoans, brachiopods, scaphopods, gastropods, trilobites, horseshoe crabs, millipedes, insects, and fishes.

The studied material comes from four localities, which are briefly described below.

(1) **Volnukhyne**: Ukraine, Luhansk Region, Luhansk District, left bank of the Luhanchyk River, 0.5 km SW of the outskirts of the village of Volnukhyne (N 48° 20' 0.8", E 39° 16' 19.8"). The trace fossils-bearing rock is a grey marine siltstone (Text-fig. 2c) which lies between the F₁² and the



Text-fig. 3. Pennsylvanian paleogeography of eastern Ukraine. **a:** paleogeographic map of Europe in the Pennsylvanian (<https://deep timemaps.com>), **b:** paleogeographic map of the Donets Basin in the Bashkirian Age (modified from Ustinovsky 1993: fig. 33).

F_1^3 limestone layers in the lower part of the Mandrykyne Formation (early Bashkirian; Text-fig. 3a). The remains of the marine bivalves and allochthonous terrestrial plants, e.g., *Calamites* sp. and *Paripteris gigantea* (STERNB. 1823) GOTHAN, 1941, as well as one specimen of *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 were found here.

(2) **Skelevata Ravine:** Luhansk Region, Roven'ky District, Skelevata Ravine, 2 km E of the village of Zelenodil's'ke ($N\ 48^{\circ}\ 13'\ 2.7''$, $E\ 39^{\circ}\ 14'\ 40.5''$), where a part of the Dyakove Group section is exposed, corresponding to the upper part of the Mandrykyne Formation (Text-fig. 3a, b). The rare marine bivalve steinkerns and trace fossils *Arborichnus* ROMANO et MELÉNDEZ, 1985, *Aulichnites* FENTON et FENTON, 1937, *Diplichnites* DAWSON, 1873, *Gordia* EMMONS, 1844, *Planolites* NICHOLSON, 1873, *Protovirgularia* McCoy, 1850, and *Skolithos* HALDEMAN, 1840 were identified from fine-grained sandstones in this fossil site. The trace fossil *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 (specimen GMLNU-5/4438) was also found 1 km SW of the Skelevata Ravine in a limonitized siltstone corresponding to the lower part of the Mandrykyne Formation.

(3) **Rebrykove:** Luhansk Region, Roven'ky District, ravine 1.2 km NE of the village of Rebrykove ($N\ 48^{\circ}\ 13'\ 21.5''$, $E\ 39^{\circ}\ 17'\ 33.3''$). A turbidite sequence of interbedded siltstones and fine-grained sandstones (Text-fig. 2a) is exposed in the ravine containing rare isolated steinkerns of small marine bivalves, corresponding to the middle part of the Mospyne Formation (late Bashkirian) (Text-fig. 3b). One specimen of *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 was also found in sandstone 10 m above this turbidite

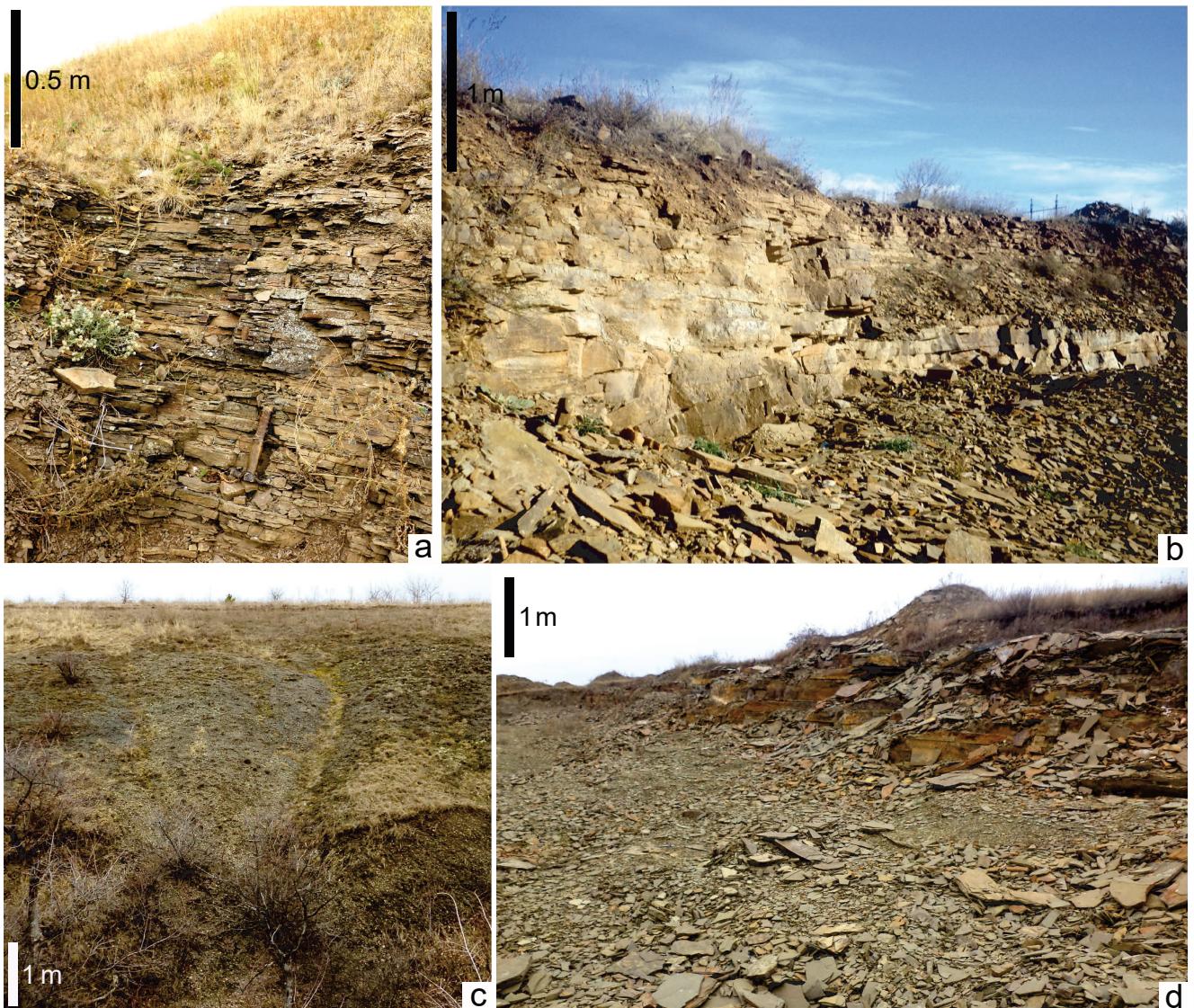
sequence, exposed in a small old quarry 0.4 km E of the ravine mentioned above.

(4) **Makedonivka:** Luhansk Region, Luhansk District, quarries near the NE outskirts of the village of Makedonivka ($N\ 48^{\circ}\ 14'\ 20.5''$, $E\ 39^{\circ}\ 18'\ 23.3''$). The trace fossil bearing rock is a sandstone bed 60 m below the G_1^2 limestone layer in the middle part of the Mospyne Formation (Text-fig. 2b, d). This sandstone contains rare plant debris, shell impressions of marine bivalves and numerous diverse trace fossils.

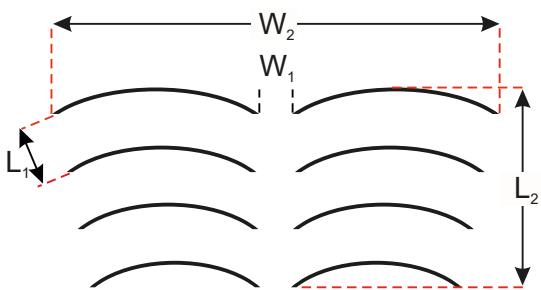
The Bashkirian coal-bearing deposits in the Donets Basin were accumulated mainly in a large alluvial-deltaic plain, which was flooded periodically by the warm epicontinental seas (Logvinenko 1953, Feofilova and Levenshtein 1963, Ustinovsky 1993). Only the central part of the Donets Basin was characterized by a continuous regime of marine sedimentation during the Bashkirian (Reznikov 1993) (Text-fig. 4).

Material and methods

In this study I examined about 30 mostly well-preserved specimens. Some traces could not be removed from the outcrop, so they were photographed and measured. The collection of trace fossils *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 (GMLNU-5), collected by the author between 2009 and 2013, is stored in the Geological Museum of the Taras Shevchenko National University of Luhansk (Poltava, Ukraine). The scheme used for recording dimensions of the trace fossils *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 is shown in Text-fig. 5.



Text-fig. 4. Some studied fossil sites. a: locality Rebrykove, b, d: locality Makedonivka, c: locality Volnukhyne.



Text-fig. 5. Scheme of dimensions of *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985. W_1 – maximum distance between two rows of ridges or grooves, W_2 – maximum trace width, L_1 – distance between ridges or grooves of the same row, L_2 – maximum trace length.

Systematic ichnology

Ichnogenus *Arborichnus* ROMANO et MELÉNDEZ, 1985

Type ichnospecies. *Arborichnus repetita* ROMANO et MELÉNDEZ, 1985; original designation by monotypy.

Diagnosis. Sets of paired, symmetrical scratch marks. At the anterior end of the set, the scratches are short

and directed inward and backward; the posterior scratches are aligned at approximately right angles to the mid-line of the set (after Romano and Meléndez 1985: 321).

Included ichnospecies. Only the type ichnospecies is known to date.

Occurrences. Carboniferous of Spain, Canada, the USA, and Ukraine; Carboniferous or Permian of Uruguay.

Arborichnus repetitus ROMANO et MELÉNDEZ, 1985

Text-figs 6–9, 10a, c, d

- 1938 Series of scratches; Caster, pl. 9, figs 2–4, pl. 10, fig. 2.
- 1985 *Arborichnus repetita*; Romano and Meléndez, p. 321, text-fig. 1, pl. 1, pl. 2, fig. 3.
- 1990 Arthropod resting trace (n. gen.); Rindsberg and Box, fig. VI-41A.
- 1994 Set of striae; Rindsberg, pl. 19, figs A–D.
- 2005 *Arborichnus repetita*; Lucas and Lerner, p. 150, fig. 2F.
- 2005 *Arborichnus repetita*; Buta et al., pls 103–106.
- 2013 *Arborichnus repetita*; Kopaska-Merkel and Buta, p. 183, fig. 3.
- 2013 *Arborichnus*; Buta et al., p. 50, figs 19E, 20A.
- 2016 *Arborichnus repetita*; Buta and Kopaska-Merkel, fig. 16.11.

Table 2. Dimensions of *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 (in mm)

Specimen	W ₁	W ₂	L ₁	L ₂	W ₂ /L ₂	Locality
GMLNU-5/3521	7.7	41.0	10.0	38.4	1.06	Skelevata Ravine
GMLNU-5/4440a	1.9	15.6	3.7	8.5	1.83	Makedonivka
GMLNU-5/5853	7.0	26.0	5.0	18.0	1.44	Skelevata Ravine
GMLNU-5/7584	6.4	40.2	7.0	20.7	1.94	Volnukhyne

2019 *Arborichnus repetita*; King et al., p. 18, fig. 19.

2022 *Arborichnus repetita*; Verde et al., p. 10, fig. 6c, f.

Holotype. Specimen Z1016 in the Natural History Museum (London); figured by Romano and Meléndez (1985) in fig. 1 (2a).

Type locality and stratigraphic horizon. The area of the town of Guardo in Palencia, Spain; upper part of the Westphalian D (Middle Pennsylvanian).

Diagnosis. As for ichnogenus.

Material. About 30 well-preserved trace fossils.

Figured specimens. GMLNU-5/3521, GMLNU-5/3530, GMLNU-5/3538, GMLNU-5/4440, GMLNU-5/4442, GMLNU-5/4443, GMLNU-5/4444, GMLNU-5/5853, GMLNU-5/5853a, GMLNU-5/5853b, GMLNU-5/5853c, GMLNU-5/7584, GMLNU-5/7645, GMLNU-5/7646, GMLNU-5/7647, GMLNU-5/7653a and several field photos of the trace fossils in situ.

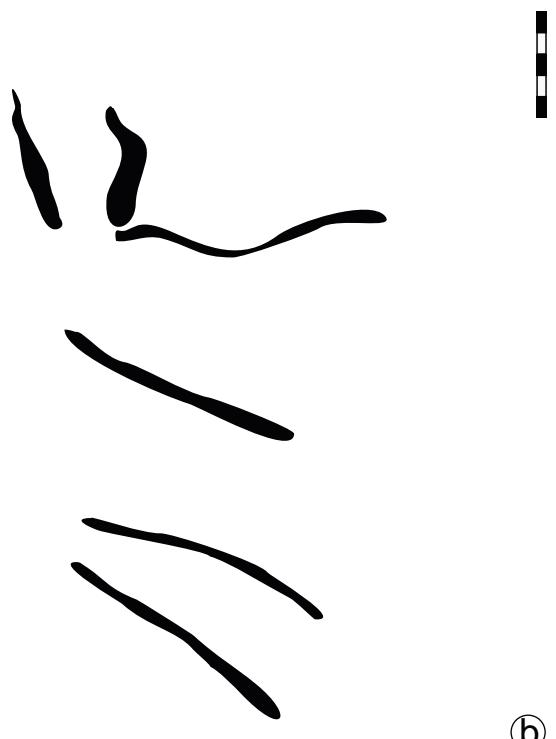
Description. The trace fossils are represented by sets of short, bilaterally symmetrical systems of limb scratch marks on unconsolidated sediment on the lower surface of sandstone and siltstone layers (convex hyporelief) and on

the upper surface of sandstone and siltstone layers (concave epirelief). The width of the traces is about 1.0–2.0 times their length (Tab. 2). *Arborichnus repetitus* consist of four pairs of slightly curved or straight, thin (0.2–0.8 mm) ridges (convex hyporelief) or grooves (concave epirelief). They usually become thinner toward the periphery of the trace.

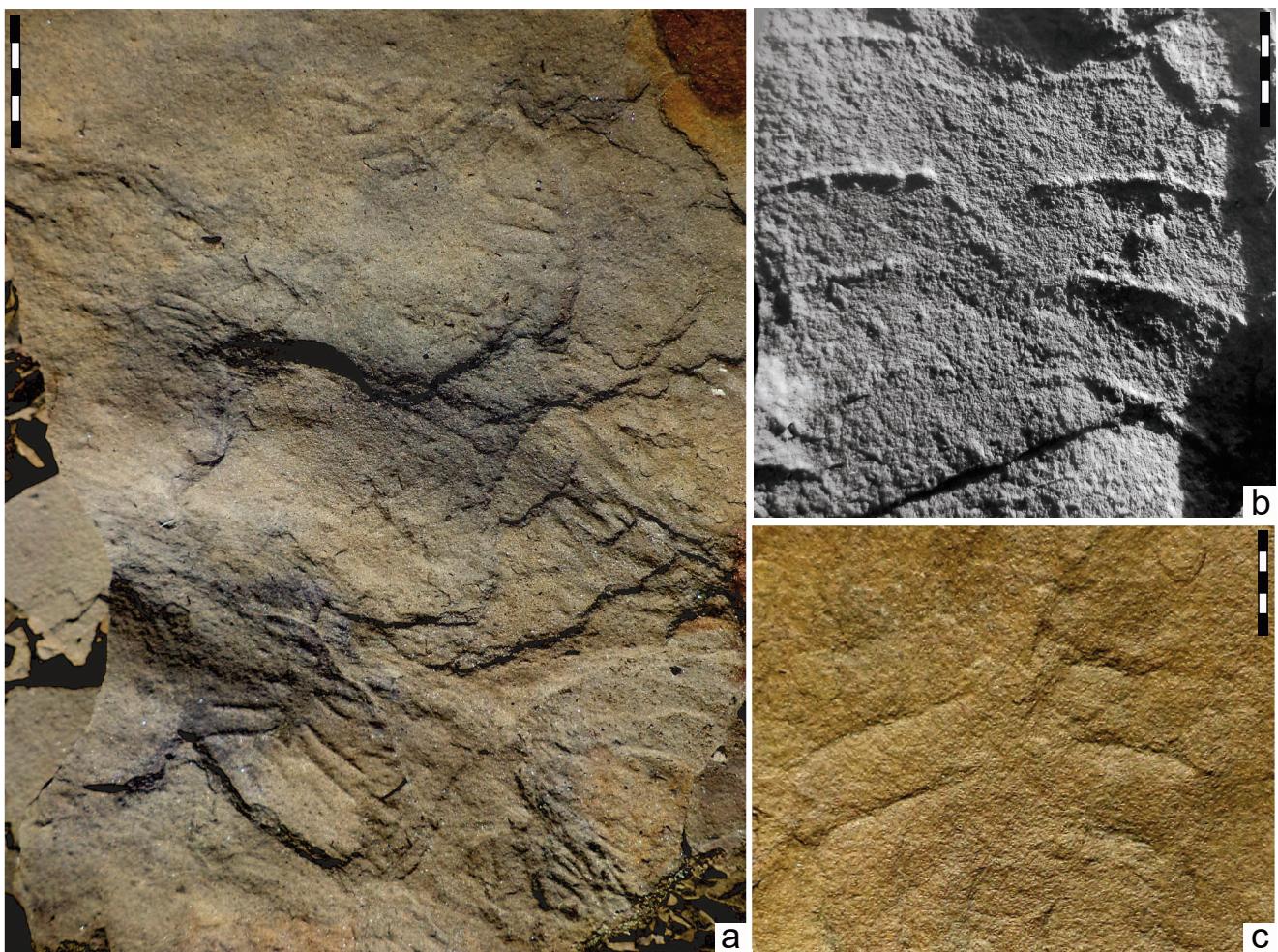
The ridges/grooves are arranged in two rows with four in each. The distance between the rows is 1.8–8.0 mm; the distance between the ridges/grooves in the same row is 3–10 mm. The length of the ridges/grooves is 12–30 mm. The general dimensions of the trace fossil are as follows: length 8–40 mm, width 15–41 mm (see Tab. 2 for details). The ridges diverge at angles of 80–110° from the midline of the trace fossils.

One specimen (GMLNU-5/3583; Text-fig. 6) has two additional short ridges approximately perpendicular to the other ridges in the anterior part (i.e., the part that presumably contains the prosoma of the horseshoe crab). They converge towards the anterior margin of the fossil trace in a V-shape. Its width is approximately the same as that of the other ridges in this trace, and its length is 10 mm. It is possible that these are chelicerae marks.

Clusters of *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 were found on several sandstone slabs. Text-figure 7a



Text-fig. 6. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 from the Bashkirian strata of the Donets Basin: specimen GMLNU-5/3538 (Skelevata Ravine); the white arrow shows the presumably chelicerae marks. Scale bars = 10 mm.



Text-fig. 7. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 from the Bashkirian strata of the Donets Basin. a: field photo (Skelevata Ravine), b: GMLNU-5/7584 (Volnukhyne), c: GMLNU-5/5853 (Skelevata Ravine). Scale bars = 10 mm (b, c) and 20 mm (a).

shows a fragment of the axis of an arborescent lycophyte *Lepidodendron* STERNB., 1820 with numerous traces of arthropod burrows (probably *Arborichnus* ROMANO et MELÉNDEZ, 1985). The horseshoe crabs probably used the axis fragment of the arborescent lycophyte as a shelter. The *Arborichnus* cluster is shown in Text-fig. 7d, and traces of horseshoe crabs burrowing in the sediment in search of food, similar to ichnogenus *Radulichnus* VOIGT, 1977 are shown in Text-fig. 7c.

Discussion. The limb scratch marks of some specimens of *Arborichnus repetitus* are straight, others are slightly curved; there is variation between individuals in the distance between scratch marks in a single row. This fact should not come as a surprise as these trace fossils were formed in different depositional environments or belong to individuals at different stages of ontogeny and, undoubtedly, belong to different taxa of horseshoe crabs, and possibly not only to horseshoe crabs.

Arborichnus ROMANO et MELÉNDEZ, 1985 is sometimes difficult to distinguish from the ichnogenera *Monomorphichnus* CRIMES, 1970 and *Rusophycus* HALL, 1852; e.g., ?*Rusophycus* isp. from the Cambrian of the Czech Republic figured by Mikuláš (1995: pl. II, fig. 1) is very similar to *Arborichnus* ROMANO et MELÉNDEZ, 1985. In

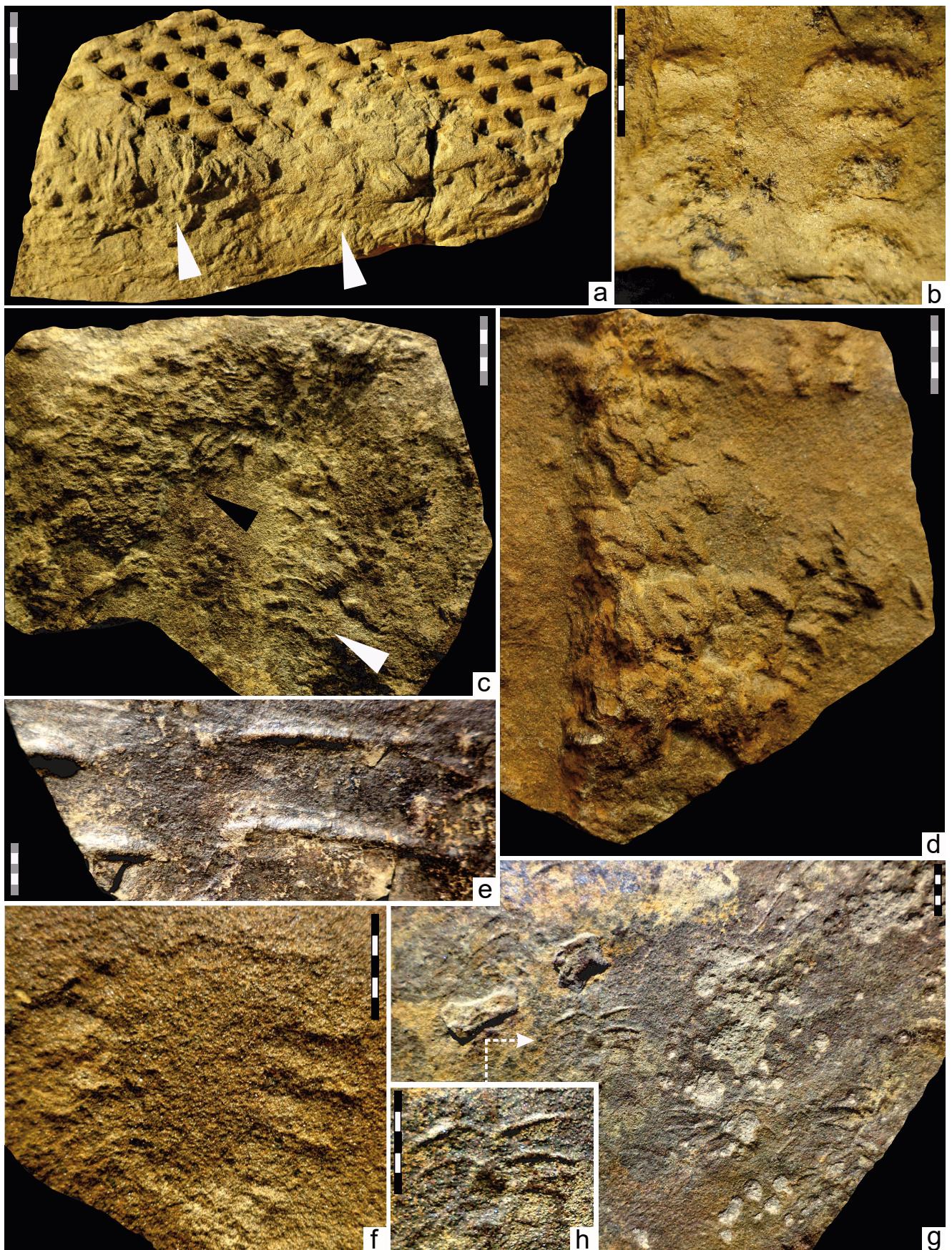
addition, the trace fossil ?*Rusophycus* HALL, 1852 from the sandstone bed in the lower part of the Mospyne Formation, morphologically similar to *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 is figured in Text-fig. 10b. It should be noted that arthropod swimming traces cf. *Monomorphichnus biserialis* MIKULÁŠ, 1995 were found together with *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 on the same surface of the sandstone slab from the Makedonivka fossil site.

Locality. See section “Geological settings”.

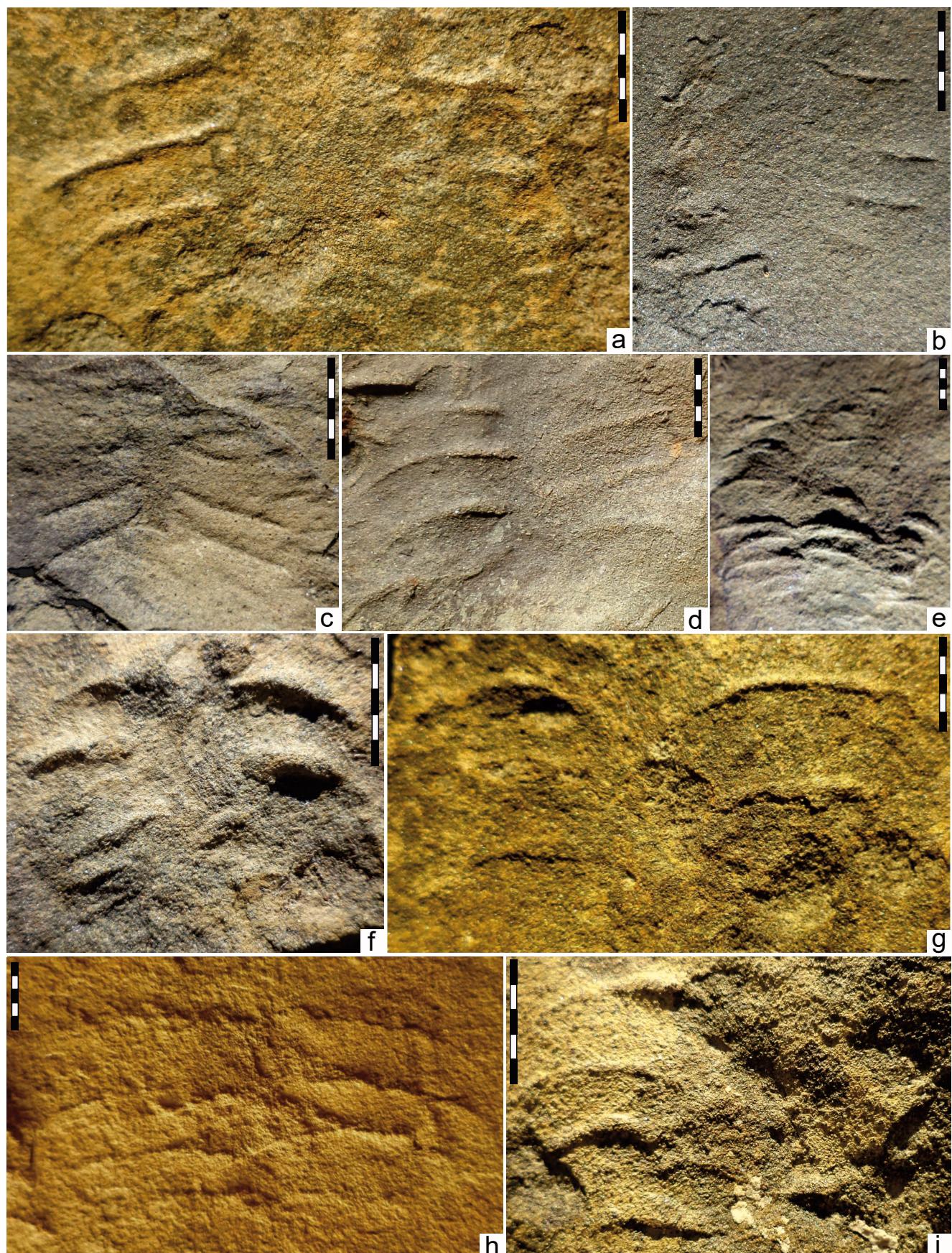
Occurrence. Carboniferous of Canada, the USA, Spain, and Ukraine; Carboniferous or Permian of Uruguay.

Discussion

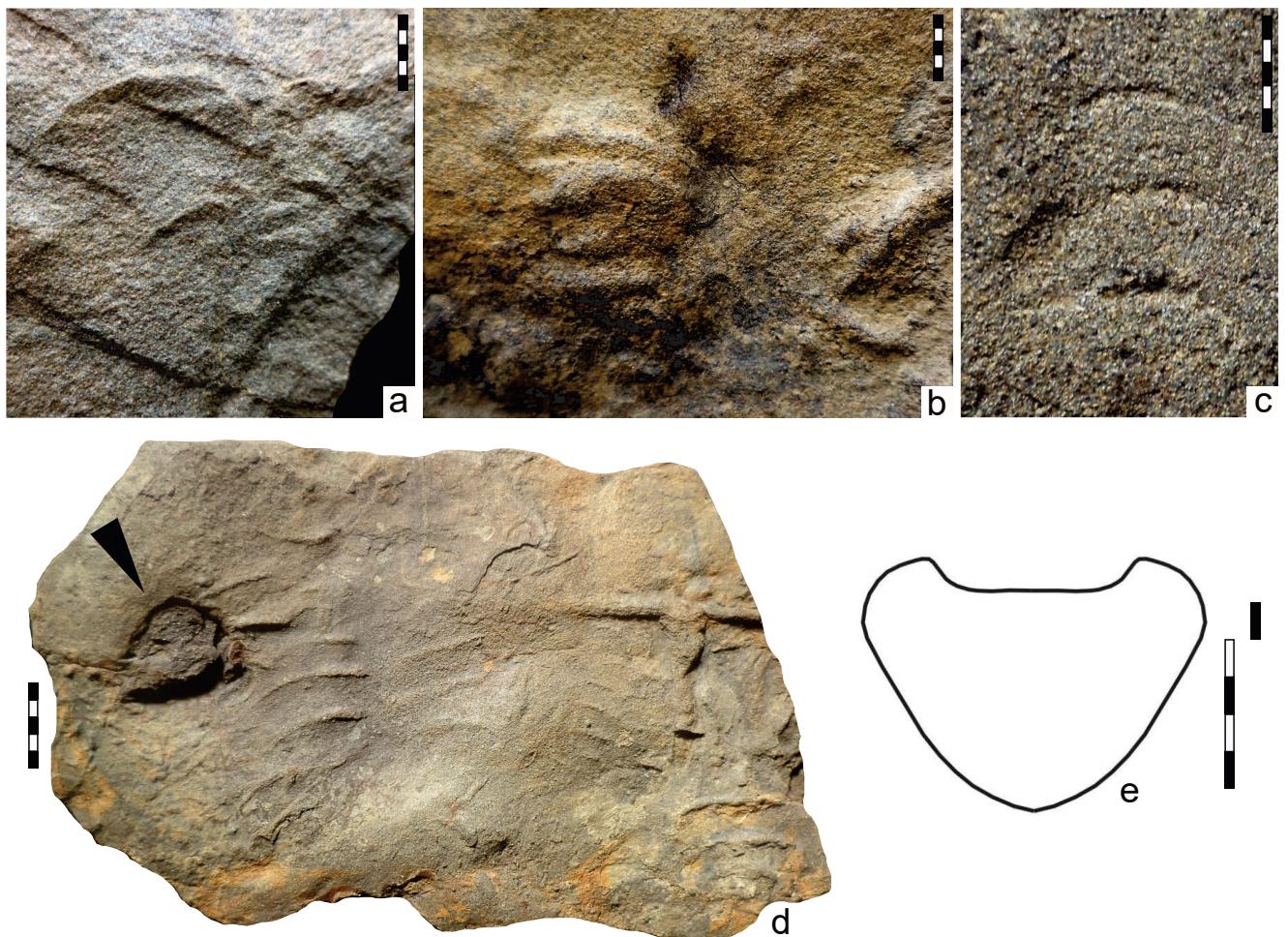
Horseshoe crabs are thought to be producers of the trace fossils *Arborichnus* ROMANO et MELÉNDEZ, 1985 (Buta et al. 2005, King et al. 2019, etc.). One of the sandstone slabs studied (specimen GMLNU-5/3521: Text-fig. 10d, e) shows several trace fossils, *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 and *Palaeophycus* HALL, 1847 and a body fossil very similar to the limuloid horseshoe crab thoracetron. In some other sites, *Arborichnus* ROMANO et



Text-fig. 8. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 and some other trace fossils from the Bashkirian of the Donets Basin. a: fragment of the axis of *Lepidodendron* with numerous burrows of arthropods around it (probably *Arborichnus*), GMLNU-5/4444 (Makedonivka), b: *Arborichnus repetitus*, field photo (Makedonivka), c: presumably horseshoe crab burrows similar to *Radulichnus* VOIGT, 1977 (shown by the black arrow) and *Arborichnus repetitus* (shown by the white arrow), GMLNU-5/4443 (Makedonivka), d: cluster of the trace fossils *Arborichnus repetitus*, GMLNU-5/4442 (Makedonivka), e: *Arborichnus repetitus*, GMLNU-5/7645 (unknown locality), f: *Arborichnus repetitus*, GMLNU-5/3530 (Skelevata Ravine), g: several trace fossils *Arborichnus repetitus* on sandstone slab surface, GMLNU-5/4440 (Makedonivka), h: enlarged trace fossils *Arborichnus repetitus* from Text-fig. 7g. Scale bars = 10 mm (b-h) and 20 mm (a).



Text-fig. 9. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 from the Bashkirian of the Donets Basin. a: GMLNU-5/7646 (Makedonivka), b: field photo (Skelevata Ravine), c: enlarged part of the sandstone bedding plane shown in Text-fig. 6a (Skelevata Ravine), d: GMLNU-5/3521 (Skelevata Ravine), e: field photo (Makedonivka), f: field photo (Makedonivka), g: GMLNU-5/7647 (Makedonivka), h: GMLNU-5/7653a (Rebrykove), i: field photo (Makedonivka). Scale bars = 10 mm.



Text-fig. 10. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 from the Bashkirian of the Donets Basin (a, c), ?*Rusophycus* sp. (b) and presumably horseshoe crab body fossil (d, e). a: *Arborichnus repetitus*, GMLNU-5/5853a (Skelevata Ravine), b: ?*Rusophycus* sp. similar to *Arborichnus repetitus*, GMLNU-5/5853b (near Makedonivka, Mospyne Fm.), c: ?*Arborichnus repetitus*, GMLNU-5/5853c (Rebrykove), d: a sandstone slab with *Arborichnus repetitus* and *Palaeophycus* HALL; the arrow indicates a presumed thoracetrace of the horseshoe crab, GMLNU-5/3521 (Skelevata Ravine), e: interpretive sketch of the possible horseshoe crab thoracetrace. Scale bars = 10 mm (a-c, e) and 20 mm (d).

MELÉNDEZ, 1985 have also been found together with remains of xiphosurids, e.g., in the Blue Beach, Nova Scotia, Canada (Mansky and Lucas 2013). Also, chelicerae impressions on the specimen described above (Text-fig. 6) indicate that *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 belongs to the trace fossils of aquatic chelicerates.

Nevertheless, the presence of *Arborichnus* ROMANO et MELÉNDEZ, 1985 in relatively geologically old deposits in which remains of xiphosurids and eurypterids are absent (e.g., Cambrian strata of India; see Chaubey et al. 2018) indicates that *Arborichnus* ROMANO et MELÉNDEZ, 1985 apparently can also be produced by some other arthropods, e.g., Aglaspida WALCOTT, 1911.

Buta et al. (2013) and Buta and Kopaska-Merkel (2016) suggested that *Arborichnus* was most likely produced by decapod crustaceans. This is obviously incorrect because decapods are not known from the Cambrian where the oldest trace fossils *Arborichnus* ROMANO et MELÉNDEZ, 1985 were found (Chaubey et al. 2018).

The ichnogenus *Arborichnus* ROMANO et MELÉNDEZ, 1985 is known from the Carboniferous of Spain (Romano and Meléndez 1985), the United States (Buta et al. 2005,

Lucas and Lerner 2005, Buta et al. 2013, Kopaska-Merkel and Buta 2013, Mansky and Lucas 2013, King et al. 2019), eastern Ukraine (this paper) and the Carboniferous or Permian of Uruguay (Verde et al. 2022).

Some of the finds described by previous authors are provisionally attributed to the ichnogenus *Arborichnus* ROMANO et MELÉNDEZ, 1985. For example, ?*Arborichnus* isp. described from the Upper Pennsylvanian of Kansas (United States) by Leibach et al. (2021: fig. 2), in my opinion, should be attributed to the ichnogenus *Monomorphichnus* CRIMES, 1970. The trace fossil *Arborichnus* isp. from the Cisuralian strata of New Mexico (USA), described by Lucas et al. (2005: fig. 3A) is quite different from the discussed ichnogenus and, apparently, is not related to it. ?*Arborichnus* isp. which is morphologically very similar to *A. repetitus* ROMANO et MELÉNDEZ, 1985, as already mentioned above, is known from the Cambrian strata of India (Chaubey et al. 2018: fig. 8e). It is not clear what animal produced this trace fossil as the first xiphosurans are known from the Ordovician (Bicknell and Pates 2020).

At the Skelevata fossil site, locomotion traces of giant terrestrial arthropods *Arthropleura* JORDAN in Jordan and von

Meyer, 1854 (*Diplichnites cuithensis* BRIGGS et al., 1979) along with *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 were found. The trace fossils *Aulichnites* FENTON et FENTON, 1937, *Protovirgularia* MCCOY, 1859, *Gordia* EMMONS, 1844, *Planolites* NICHOLSON, 1873, *Psammichnites* TORREL, 1870, and *Skolithos* HALDEMAN, 1840 were also found at this fossil site, the rocks were interpreted as deltaic and prodeltaic deposits. *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985, *Cochlichnus* HITCHCOCK, 1858, *Monomorphichnus* CRIMES, 1970, *Psammichnites* TORREL, 1870, *Selenichnites* ROMANO et WHYTE, 1987 and *Treptichnus* MILLER, 1889 are often found in prodeltaic rocks at the Makedonivka fossil site, on the same bedding plane and in close proximity to each other.

The trace fossils *Arborichnus* ROMANO et MELÉNDEZ, 1985 were found in estuarine rocks of the Pottsville Formation (Middle Pennsylvanian) in Alabama (USA) together with *Cochlichnus* HITCHCOCK, 1858, *Gordia* EMMONS, 1844, *Helminthopsis* HEER, 1877, *Kouphichnium* NOPCSA, 1923, *Planolites* NICHOLSON, 1873, *Treptichnus* MILLER, 1889, *Undichna* ANDERSON, 1976 and tetrapod tracks (Buta et al. 2005, Lucas and Lerner 2005). *Arborichnus* ROMANO et MELÉNDEZ, 1985 has also been found together with *Cruziana* d'ORBIGNY, 1842, *Diplichnites* DAWSON, 1873, *Diplopodichnus* BRADY, 1947, *Gordia* EMMONS, 1844, *Kouphichnium* NOPCSA, 1923, *Limulocubichnus* MILLER, 1982, *Palaeophycus* HALL, 1847, *Paleohelcura* GILMOR, 1926, *Planolites* NICHOLSON, 1873, *Protichnites* OWEN, 1852, *Rusophycus* HALL, 1852, *Skolithos* HALDEMAN, 1840, *Taenidium* HEER, 1877 and tetrapod tracks in the Tournaisian strata of Nova Scotia, Canada (Mansky and Lucas 2013).

In the deltaic deposits of the Westphalian D of Spain, trace fossils *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 were found with *Kouphichnium* NOPCSA, 1923, *Monomorphichnus* CRIMES, 1970, *Petalichnus* MILLER, 1880, *Psammichnites* TORREL, 1870, and *Scolicia* de QUATREFAGES, 1849 (Romano and Meléndez 1985).

In the Late Paleozoic deposits of Uruguay, *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 occurs together with *Crescentichnus* ROMANO et WHYTE, 1987, *Cruziana* d'ORBIGNY, 1842, *Diplichnites* DAWSON, 1873, *Gluckstadtella* SAVAGE, 1971, *Helminthoidichnites* FITCH, 1850, *Maculichnna* ANDERSON, 1975, *Rusophycus* HALL, 1852, *Treptichnus* MILLER, 1889 and *Umfolozia* SAVAGE, 1971 (Verde et al. 2022).

Carboniferous xiphosurans from the Donets Basin were described and/or figured in the publications of Zalessky (1907), Chernyshev (1927, 1928), Karlov (1948), Shpinev (2018), and Dernov (2019a, b). Unfortunately, these publications present the results of studies of exclusively non-marine horseshoe crabs, mainly representatives of the genus *Euproops* MEEK, 1867; there have been no finds of marine xiphosurans in the Carboniferous of the Donets Basin.

Conclusions

The horseshoe crab resting traces *Arborichnus repetitus* ROMANO et MELÉNDEZ, 1985 were described from the Bashkirian marine strata of the Donets Basin. These findings indicate a wide distribution of horseshoe crabs in the shallow marine paleobiocenoses of the Dyakove

Paleobasin in the central part of the Donets Basin, as well as in the coastal marine environments of the northern Donets Basin. Horseshoe crabs are the most probable producers of trace fossils *Arborichnus* ROMANO et MELÉNDEZ, 1985 but some other arthropods, e.g., aglaspidids, are also potential producers of these trace fossils. The new data extends the geographic distribution of the ichnogenus *Arborichnus* ROMANO et MELÉNDEZ, 1985 and improves the palaeontological characteristics of the Bashkirian strata in the Donets Basin.

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References

- Aisenverg, D. E., Belenko, N. G., Dedov, V. S., Levenshtein, M. L., Makarov, I. A., Nesterenko, L. P., Poletaev, V. I., Popov, V. S., Sokolova, G. U., Fissunenko, O. P., Shchegolev, A. K. (1975): Stratigraphicheskaya ekskursiya [Stratigraphic excursion]. – In: Aisenverg, D. E., Lagutina, V. V., Levenshtein, M. L., Popov, V. S. (eds), Field excursion guidebook for the Donets Basin. Nauka, Moscow, pp. 201–245. (in Russian)
- Aisenverg, D. E., Brazhnikova, N. E., Novik, K. O., Rotai, A. P., Shulga, P. L. (1963): Stratigraphiya kamennou-gol'nykh otlozheniy Donetskogo Basseyna [Carboniferous stratigraphy of the Donets Basin]. – Izdatel'stvo Akademii Nauk Ukrainskoy SSR, Kyiv, 182 pp. (in Russian)
- Anderson, A. M. (1975): Turbidites and arthropod trackways in the Dwyka glacial deposits (Early Permian) of Southern Africa. – Transactions of the Geological Society of South Africa, 78: 265–273.
- Anderson, A. M. (1976): Fish trails from the Early Permian of South Africa. – Palaeontology, 19: 397–409.
- Bicknell, R. D. C., Pates, S. (2020): Pictorial atlas of fossil and extant horseshoe crabs, with focus on Xiphosurida. – Frontiers in Earth Science, 8(98): 1–60. <https://doi.org/10.3389/feart.2020.00098>
- Borrello, A. (1966): Trazas y cuerpos problemáticos de la Formación La Tinta, sierras Septentrionales de la provincia de Buenos Aires [Traces and problematic bodies of the La Tinta Formation, Northern Sierras of the province of Buenos Aires]. – Publicación especial de la Comisión de Investigaciones Científicas de la provincia de Buenos Aires, 5: 1–42. (in Spanish)
- Brady, L. F. (1947): Invertebrate tracks from the Coconino Sandstone of northern Arizona. – Journal of Paleontology, 21: 466–472.

- Braddy, S., Briggs, D. E. G. (2002): New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. – *Journal of Paleontology*, 76(3): 546–557. [https://doi.org/10.1666/0022-3360\(2002\)076<0546:nlpnat>2.0.co;2](https://doi.org/10.1666/0022-3360(2002)076<0546:nlpnat>2.0.co;2)
- Briggs, D. E. G., Rolfe, W. D. I., Brannan, J. (1979): A giant myriapod trail from the Namurian of Arran, Scotland. – *Palaeontology*, 22: 273–291.
- Buta, R. J., Kopaska-Merkel, D. C. (2016): Footprints in stone, fossil traces of coal-age tetrapods. – University of Alabama Press, Tuscaloosa, 352 pp.
- Buta, R. J., Kopaska-Merkel, D. C., Rindsberg, A. K., Martin, A. J. (2005): Atlas of Union Chapel mine invertebrate trackways and other traces. – In: Buta, R. J., Rindsberg, A. K., Kopaska-Merkel, D. C. (eds), *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*. Alabama Paleontological Society Monograph, 1: 277–337. <https://doi.org/10.1130/abs/2023se-385602>
- Buta, R. J., Pashin, J. C., Minter, N. J., Kopaska-Merkel, D. C. (2013): Ichnology and stratigraphy of the Crescent Valley mine: evidence for a Carboniferous megatracksite in Walker County, Alabama. – In: Lucas, S. G., DiMichele, W. A., Barrick, J. E., Schneider J. W., Spielmann, J. A. (eds), *The Carboniferous-Permian Transition*. New Mexico Museum of Natural History and Science Bulletin, 60: 42–56.
- Caster, K. E. (1938): A restudy of the tracks of *Paramphibius*. – *Journal of Paleontology*, 12(1): 3–60.
- Chaubey, R. S., Singh, B. P., Mikuláš, R., Bhargava, O. N., Subhay, N. K., Prasad, S. K. (2018): Integrated ichnological and sedimentological analysis of the Cambrian Kunzam La (Parahio) Formation, Shian Section, Pin Valley, Spiti, Northwest Himalaya. – *Stratigraphy and Geological Correlation*, 26(7): 721–733. <https://doi.org/10.1134/S0869593818070079>
- Chernyshev, B. I. (1927): Zametka o predstaviteleyakh Xiphosura iz Donetskogo basseyna [Note on the representatives of Xiphosura from the Donets Basin]. – *Izvestiya Geologicheskogo komiteta*, 46(7-10): 645–655. (in Russian)
- Chernyshev, B. I. (1928): Yeshche raz Phyllopoda i Xiphosura Donetskogo basseyna [More on the Phyllopoda and Xiphosura of the Donets Basin]. – *Izvestiya Geologicheskogo komiteta*, 47(5): 519–531. (in Russian)
- Crimes, T. P. (1970). Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales. *Geological Journal*, 7(1): 47–68. <https://doi.org/10.1002/gj.3350070104>
- Dalman, S. G., Lucas, S. G. (2015): Lower Jurassic arthropod resting trace from the Hartford Basin of Massachusetts, USA. – *Ichnos*, 22(3-4): 177–182. <https://doi.org/10.1080/10420940.2015.1059337>
- Dawson, J. W. (1864): On the fossils of the genus *Rusophycus*. – *Canadian Naturalist and Geologist*, 1: 363–367.
- Dawson, J. W. (1873): Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks. – *American Journal of Science*, 105: 16–24. <https://doi.org/10.2475/ajs.s3-5.25.16>
- Dernov, V. S. (2016): Novi dani shchodo paleontolohichnoyi kharakterystyky vidkladiv dyakivs'koyi seriyi (baskys'kyy yarus) Donbasu [New data on the paleontology of the Dyakove Group (Bashkirian) of the Donets Basin]. – *Visnyk Natsional'noho naukovo-pryrodnychoho muzeyu NAN Ukrayny*, 14: 35–46. (in Ukrainian with English summary)
- Dernov, V. S. (2019a): K izucheniyu nemorskoy fauny mospinskoj svity (sredniy karbon, Donbass) [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. (2019b): Taphonomy and paleoecology of fauna and flora from deltaic sandstones of the Mospinka Formation (Middle Carboniferous) of Donets Basin. – *GEO&BIO*, 18: 37–63. <https://doi.org/10.15407/gb1805>
- Dernov, V. (2021a): 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. (2021b): Biopovrezhdeniya rasteniy iz bashkirskikh otlozheniy Donetskogo basseyna (Vostochnaya Ukraina) [Plant biodamage from the Bashkirian of the Donets Coal Basin, eastern Ukraine]. – *Lethaea Rossica*, 23: 32–44. (in Russian with English summary)
- Dernov, V. (2022a): Bioposhkodzhennya vykopnykh roslyn z vidkladiv bilokalytvens'koyi svity (verkhnya chasty-na bashkyrs'koho yarusu, karbon) Donets'koho baseynu, Ukrayina [Fossil plant biodamage from the Belaya Kalitva Formation (upper Bashkirian, Carboniferous) of the Donets Basin, Ukraine]. – *Ukrainian Botanical Journal*, 79(5): 314–328. (in Ukrainian with English summary) <https://doi.org/10.15407/ukrbotj79.05.314>
- Dernov, V. S. (2022b): Nemors'ki peletsypody mospyns'koyi svity (verkhniy bashkyr) Donets'koho baseynu: sistematichnyy sklad, paleoekoloziya ta stratygrafichne znachennya [Non-marine bivalves from the Mospyne Formation (upper Bashkirian) of the Donets Basin: taxonomy, paleoecology, and stratigraphic significance]. – *Geologichnij zhurnal*, 380(3): 34–56. (in Ukrainian with English summary) <https://doi.org/10.30836/igs.1025-6814.2022.3.255491>
- Dernov, V. (2022c): 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): *Hankoichnus* ichnogen. nov., a new arthropod (?) trace fossil from the Carboniferous of the Donets Basin (Ukraine). – *Geologičnij žurnal*, 382: 53–58. <https://doi.org/10.30836/igs.1025-6814.2023.1.265486>
- Dernov, V. S., Udovichenko, N. I. (2019): K paleobotanicheskoy kharakteristike mospinskoy svity (sredniy karbon, Donbass) [On the paleobotanical characteristic of the Mospino Formation]. – *Visnyk of V. N. Karazin Kharkiv National University, Geology, Geography, Ecology*, 51: 67–82. (in Russian with English summary) <https://doi.org/10.26565/2410-7360-2019-51-05>

- Dunayeva, N. M. (1969): Vidkrytyi Donbas [Open Donets Basin]. – In: Bondarchuk, V. G. (Eds), Stratigraphya Ukrayins'koyi RSR. Tom 5. Karbon [Stratigraphy of the Ukrainian SSR. Volume V. Carboniferous]. Kyiv, Naukova Dumka, pp. 21–48. (in Ukrainian)
- Emmons, E. (1844): The Taconic System: based on observations in New York, Massachusetts, Maine, Vermont and Rhode Island. – Caroll and Cook, Albany, 66 pp.
- Feldmann, R. M., Osgood, R. G., Szmuc, E. J., Meinke, D. W. (1978): *Chagrinichnites brooksi*, a new trace fossil of arthropod origin. – Journal of Paleontology, 52(2): 287–294.
- Fenton, C. L., Fenton, M. A. (1937): *Archaeonassa*: Cambrian snail trails and burrows. – The American Midland Naturalist, 18: 454–456.
<https://doi.org/10.2307/2420587>
- Feofilova, A. P., Levenshtein, M. L. (1963): Osobennosti osadko- i uglenakopleniya v rannem i srednem karbone Donetskogo Basseyna [Features of the sedimentation and coal accumulation in the Early and Middle Carboniferous of the Donets Basin]. – Izdatel'stvo Akademii Nauk SSSR, Moscow, 175 pp. (in Russian)
- Fischer, W. A. (1978): The habitat of the early vertebrates: trace and body fossil evidence from the Harding Formation (Middle Ordovician), Colorado. – Mountain Geology, 15: 1–26.
- Fissunenko, O. P., Reznikov, A. I. (1985): O novom metode stratigrafi flishoidnykh tolshch karbona Donbassa [On the new method in stratigraphy of flyshoid sequence of the Donets Basin]. – In: Vyalov, O. S. (ed.), Fossil organisms and stratigraphy of the sedimentary rock succession of Ukraine. Naukova Dumka, Kyiv, pp. 34–38. (in Russian)
- Fitch, A. (1850): A historical, topographical and agricultural survey of the County of Washington. Part 2-5. – Transactions of the New York Agricultural Society, 9: 753–944.
- Gabunia, L. K., Kurbatov, V. V., Sennikov, A. G. (1988): O kopytoobraznykh sledakh iz melovykh otlozheniy Yugo-Zapadnogo Gissara [Hoof-like footprints in the Cretaceous of southwest Gissar]. – Reports of the Academy of Sciences of the Georgian SSR, Biological Series, 14(3): 189–197. (in Russian)
- Gand, G. (1994): Ichnocoenoses à *Isopodichnus furcosus* nov. ichnosp. dans le Permien du Bassin de Lodève (Massif Central, France). – Geobios, 27(1): 73–86.
[https://doi.org/10.1016/S0016-6995\(06\)80214-7](https://doi.org/10.1016/S0016-6995(06)80214-7)
- Gand, G., Garric, J., Schneider, J., Walter, H., Lapeyrie, J., Martin, C., Thiery, A. (2008): Notostraca trackways in Permian playa environments of the Lodève basin (France). – Journal of Iberian Geology, 34(1): 73–108.
- Gibb, S. G., Chatterton, D. E., Pemberton, S. G. (2011): Prod traces (*Selenichnites*) from the Middle Cambrian of Morocco, with hypotheses on the ethology of the trace-maker(s). – Ichnos, 18(3): 156–165.
<https://doi.org/10.1080/10420940.2011.601373>
- Gill, E. L. (1924): Fossil arthropods from the Tyne Coal-field. – Geological Magazine, 1: 455–471.
<https://doi.org/10.1017/s0016756800086829>
- Gilmore, C. W. (1926): Fossil footprints from the Grand Canyon. – Smithsonian Miscellaneous Collection, 77: 1–41.
<https://doi.org/10.1126/science.63.1638.xvi.s>
- Gothan, W. (1941): Paläobotanische Mitteilungen 5–7. – Paläontologische Zeitschrift, 22: 424–438.
<https://doi.org/10.1007/bf03042701>
- Hall, J. (1847): Palaeontology of New York. Volume 1. – C. Van Benthuyzen, Albany, 338 pp.
- Hall, J. (1852): Natural History of New York. Palaeontology. Volume 2. – C. Van Benthuyzen, Albany, 362 pp.
- Haldeman, S. S. (1840): Supplement to Number One of «A monograph of the Limniades, or freshwater univalve shells of North America» containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in in *Paludina* and *Ancylosa*. – J. Dobson, Philadelphia, 3 pp.
<https://doi.org/10.5962/bhl.title.11226>
- Hardy, P. G. (1970): Xiphosurid trails from the Upper Carboniferous of northern England. – Palaeontology, 13(2): 188–190.
- Heer, O. (1877): Florafossilis Helvetiae. Die vorweltliche flora der Schweiz. – J. Wurster and Co., Zurich, 182 pp.
- Heidtke, U. (1990): *Pollichianum cubicnum* nov. ichnogen. et ichnospec. und *Pollichianum repichnum* nov. ichnospec., zwei neue Invertebratenichnia aus dem saar-pfälzischen Rotliegend (Unter-Perm, SW-Deutschland). – Pollichnia, 77: 133–139.
<https://doi.org/10.1127/njgpm/2003/2003/363>
- Hesselbo, S. P. (1988): Trace fossils of Cambrian aglaspid arthropods. – Lethaia, 21(2): 139–146.
<https://doi.org/10.1111/j.1502-3931.1988.tb02064.x>
- Heymons, R. (1901): Die Entwicklungsgeschichte der Scolopender. – Stuttgart, E. Nägele, 1–244 pp., Taf. I–VIII.
<https://doi.org/10.5962/bhl.title.1587>
- Hitchcock, E. (1858): Ichnology of New England: a report on the sandstone of the Connecticut Valley, especially its footmarks. – W. White, Boston, 220 pp.
- Jordan, F. W. H., von Meyer, H. (1854): Über die Crustaceen der Steinkohlenformation von Saarbrücken. – Palaeontographica, 4: 1–15.
- Karlov, M. M. (1948): *Prestwichianella tschernyschewi* sp. nov. – novyy predstavnyk Xiphosura z produktyvnoyi tovshchi donets'koho karbonu [*Prestwichianella tschernyschewi* sp. nov., a new xiphosuran from the Carboniferous coal-bearing rocks of the Donets Basin]. – Zbirnyk prats' z paleontolohiyi ta stratyhrafiyi, 1(2): 41–47. (in Ukrainian)
- Kennedy, W. J. (1967): Burrows and surface traces from the Lower Chalk of southern England. – Bulletin of the British Museum (Natural History), Geology, 15: 125–167.
- King, O. A., Stinson, M. R., Lucas, S. G. (2019): The ichnogenus *Kouphichnium* and related Xiphosuran traces from the Steven C. Minkin Paleozoic footprint site (Union Chapel Mine), Alabama, USA: ichnotaxonomic and paleoenvironmental implications. – Ichnos, 26(4): 266–302.
<https://doi.org/10.1080/10420940.2018.1561447>
- Kopaska-Merkel, D. C., Buta, R. J. (2013): Field trip guidebook to the Steven C. Minkin Paleozoic footprint site, Walker County, Alabama. – In: Lucas, S. G., DiMichele, W. A., Barrick, J. E., Schneider J. W., Spielmann, J. A. (eds), The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science Bulletin, 60: 178–198.
- Kurbatov, V. V., Gabunia, L. K. (1987): Mestonakhozhdennye sledov kopytokhodyachikh «Gumatag» [Gumatag,

- a locality of hoof-like tracks]. – In: Djalilov, M. R., Novikov, V. P. (eds), Trace fossils on the territory of Central Asia (excursion guide of the All-Union workshop). Donish, Dushanbe, pp. 27–30. (in Russian)
- Lamsdell, J. C. (2019): Evolutionary history of the dynamic horseshoe crab. – In: Sitters, H. P., Clark, J. A., Smith, P. A., Niles, L. J. (eds), Conservation and research on shorebirds and horseshoe crabs in Delaware Bay 1997–2018. International Wader Studies, 21: 1–14.
- Latreille, P. A. (1802): *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes*. Ouvrage Faisant suite à l'*Histoire Naturelle Générale et Particulière*, Composée par LeClerc de Buffon, et Rédigée par C. S. Sonnini, Membre de Plusieurs Sociétés Savantes. – Dufart, Paris, 468 pp.
<https://doi.org/10.5962/bhl.title.60678>
- Leach, W. (1819): Entomostracés. – In: Levrault, F. (Ed.), *Dictionnaires des Sciences Naturelles*, 14. Strasbourg, pp. 524–543.
- Leibach, W. W., Rose, N., Bader, K., Mohr, L. J., Super, K., Kimmig, J. (2021): Horseshoe crab trace fossils and associated ichnofauna of the Pony Creek Shale Lagerstätte, Upper Pennsylvanian, Kansas, USA. – *Ichnos* 28(1): 34–45.
<https://doi.org/10.1080/10420940.2020.1811268>
- Lima, J. H. D., Netto, R. G., Corrêa, C. G., Corrêa Lavina, E. L. (2015): Ichnology of deglaciation deposits from the Upper Carboniferous Rio do Sul Formation (Itararé Group, Paraná Basin) at central-east Santa Catarina State (southern Brazil). – *Journal of South American Earth Sciences*, 6: 137–148.
<https://doi.org/10.1016/j.jsames.2015.07.008>
- Linnaeus, C. (1758): *Systema Naturae*, Vol. 1., 10th ed. – Laurentius Salvius, Holmiae, 824 pp.
<https://doi.org/10.5962/bhl.title.542>
- Logvinenko, N. V. (1953): *Litologiya i paleogeografiya produktivnoy tolshi donetskogo karbona* [Lithology and paleogeography of the Carboniferous coal-bearing strata of the Donets Basin]. – Izdatel'stvo Kharkiv'skogo Universitetu, Kharkiv, 436 pp. (in Russian)
- Lucas, S. G., Lerner, A. J. (2005): Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama: a preliminary assessment. – In: Buta, R. J., Rindsberg, A. K., Kopaska-Merkel, D. C. (eds), Pennsylvanian Footprints in the Black Warrior Basin of Alabama. Alabama Paleontological Society Monograph, 1: 147–152.
https://doi.org/10.31390/gradschool_disstheses.1257
- Lucas, S. G., Lerner, A. J., Voigt, S. (2013): Scorpionid resting trace from the lower Permian of Southern New Mexico, USA. – *Ichnos*, 20(4): 195–201.
<https://doi.org/10.1080/10420940.2013.845096>
- Lucas, S. G., Minter, N. J., Spielmann, J. A., Hunt, A. P., Braddy, S. J., Zeigler, K. E. (2005): Early Permian ichnofossil assemblage from the Fra Cristobal Mountains, Southern New Mexico. – *New Mexico Museum of Natural History and Science Bulletin*, 31: 140–150.
- Mansky, C. F., Lucas, S. G. (2013): Romer's Gap revisited: continental assemblages and ichno-assemblages from the basal Carboniferous of Blue Beach, Nova Scotia, Canada. – In: Lucas, S. G., DiMichele, W. A., Barrick, J. E., Schneider, J. W., Spielmann, J. A. (eds), *The Carboniferous-Permian Transition*. New Mexico Museum of Natural History and Science Bulletin, 60: 244–273.
- Mángano, M. G., Buatois, L. A., Maples, C. G., Lanier, W. P. (1997): *Tonganoxichnus* a new insect trace from the Upper Carboniferous of eastern Kansas. – *Lethaia*, 30(2): 113–125.
<https://doi.org/10.1111/j.1502-3931.1997.tb00451.x>
- McCoy, F. (1850): On some genera and species of Silurian Radiata in the collection of the University of Cambridge. – *Annals and Magazine of Natural History*, Series 2, 6: 270–290.
- Meek, F. B. (1867): Note on a new genus of fossil Crustacea. – *American Journal of Science and Arts*, 2: 394–395.
- Mikuláš, R. (1995): Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic). – *Journal of the Czech Geological Society*, 40(4): 37–54.
- Mikuláš, R., Dronov, A. (2006): Palaeoichnology – introduction to the study of trace fossils. – Institute of Geology, Academy of Sciences of Czech Republic, Prague, 122 pp.
<https://doi.org/10.1134/s0031030108050122>
- Miller, M. F. (1982): *Limulicubichnus*: a new ichnogenus of limulid resting traces. – *Journal of Paleontology*, 56(2): 229–233.
- Miller, S. A. (1880): Silurian ichnolites, with definitions of new genera and species. – *Cincinnati Society of Natural History Journal*, 2: 217–222.
- Miller, S. A. (1889): North American geology and paleontology for the use of amateurs, students and scientists. – Western Methodist Book Concern, Cincinnati, 664 pp.
<https://doi.org/10.5962/bhl.title.133644>
- Minter, N. J., Braddy, S. J. (2009): Ichnology of an Early Permian intertidal flat: the Robledo Mountains Formation of southern New Mexico, USA. – *Special Papers in Palaeontology*, 82: 1–107.
- Müller, O. (1785): *Entemostraca, seu, Insecta testacea quae in aquis Daniae et Norvegiae reperit, descriptis et iconibus illustravit*. – F.W. Thiele, Hauniae, 135 p.
- Naugolnykh, S. V. (2022): *Selenichnites eotriassicus* ichnosp. n., possible limulid traces from the Lower Triassic of the Volga River Basin, Russia. – *Arthropoda Selecta*, 31(4): 449–456.
<https://doi:10.15298/arthsel.31.4.05>
- Nemyrovska, T. I. (1999): Bashkirian conodonts of the Donets Basin, Ukraine. – *Scripta Geologica*, 119: 1–116.
- Nemyrovska, T. I., Yefimenko, V. I. (2013): Seredniy karbon (Nyzhniy Pensyl'vaniy) [Middle Carboniferous (Lower Pennsylvanian)]. – In: Gozhik, P. F. (ed.), *Stratyhrafija verkh'oho proterozoyu ta fanerozoyu Ukrayiny. T. 1. Stratigraphiya verkh'oho proterozoyu, paleozoyu ta mezozoyu Ukrayiny*. LAT&K, Kyiv, pp. 283–303. (in Ukrainian)
- Nessov, L. A. (1995): *Dinozavry Severnoy Evrazii: novyye dannyye o sostave kompleksov, ekologii i paleobiogeografi* [Dinosaurs of Northern Eurasia: new data on the assemblage composition, ecology and paleobiogeography]. – St. Petersburg, 156 pp. (in Russian)
- Nicholson, H. A. (1873): Contributions to the study of the errant annelids of the older Palaeozoic rocks. – *Royal Society of London Proceedings*, 21: 288–290.
<https://doi.org/10.1098/rspl.1872.0061>

- Nopsca, F. (1923): Die Familien der Reptilien. – Fortschritte der Geologie und Paläontologie, 2: 1–210.
<https://doi.org/10.1126/science.58.1512.517.b>
- Novik, E. O. (1974): Zakonomernosti razvitiya kamennou-gol'noy flory yuga Evropeyskoy chasti SSSR [Regularities of development of the Carboniferous flora of the south part of the European part of the USSR]. – Naukova Dumka, Kyiv, 140 pp. (in Russian)
- O'Brien, L. J., Braddy, S. J., Radley, J. D. (2009): A new arthropod resting trace and associated suite of trace fossils from the Lower Jurassic of Warwickshire, England. – *Palaeontology*, 52(5): 1099–1112.
<https://doi.org/10.1111/j.1475-4983.2009.00901.x>
- d'Orbigny, A. (1842): Voyage dans l'Amérique méridionale (le Brésil, la République oriental de l'Uruguay, la République Argentine, la Patagonie, République du Chili, la République de Bolivie, la République du Pérou) exécuté pendant les années 1826, 1827, 1829, 1330, 1831, 1832, et 1833, pt. 4 (Paléontologie). – Pitois-Levrault (Paris), Levrault (Strasbourg), 188 pp.
<https://doi.org/10.5962/bhl.title.8353>
- Owen, R. (1852): Description of the impressions and footprints of the *Protichnites* from the Potsdam Sandstone of Canada. – *Quarterly Journal of the Geological Society*, 8: 214–225.
<https://doi.org/10.1144/GSL.JGS.1852.008.01-02.26>
- Pollard, J., Selden, P., Watts, S. (2008): Trace fossils of the arthropod Camptophyllia from the Westphalian (Carboniferous) rocks of Lancashire, UK and their palaeoenvironmental context. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 270: 399–406.
<https://doi.org/10.1016/j.palaeo.2008.01.032>
- Poletaev, V. I., Vakarchuk, V. G., Vinnichenko, L. G., Kononenko, L. P., Lukin, A. Y., Reznikov, A. I. (1991): Raschleneniye i korrelyatsiya raznofatsial'nykh tolshch nizhnego i nizov srednego karbona Dneprovsko-Donetskogo avlakogena [Subdivisions and correlation of different facies sequences of the Lower and lower Middle Carboniferous of the Dnipro-Donets Aulacogen]. – Institute of Geological Sciences, Kyiv, 52 pp. (in Russian)
- Poletaev, V. I., Vdovenko, M. V., Shchogolev, O. K., Boyarina, N. I., Makarov, I. A. (2011): Stratotypy regional'nykh stratigraphichnykh pidrozdiliv karbonu ta nyzhnyoyi permi Dono-Dniprovs'kogo progrunu [Stratotypes of the Carboniferous and Lower Permian regional stratigraphic units of the Dnipro-Donets Downwarp]. – Logos, Kyiv, 236 pp. (in Ukrainian)
- Popov, A. V. (1979): Kamennougol'nye ammonoidei Donbassa i ikh stratigraficheskoe znachenie [Carboniferous ammonoids of the Donets Basin and their stratigraphic significance]. – Trudy VSEGEI, n. s., 220: 1–119. (in Russian)
- de Quatrefages, M. A. (1849): Note sur la *Scolicia prisca* (A. De Q.) annélide fossile de la craie. – *Annales des Sciences Naturelles, Zoologie*, 12: 265–266.
- Radwanski, A., Roniewicz, P. (1967): Trace fossils *Aglaspidichnus sanctacrucensis* n. gen., n. sp., a probable resting place of an Aglaspid (Xiphosura). – *Acta Palaeontologica Polonica*, 12(4): 545–552.
- Reznikov, A. I. (1993): D'yakovskaya seriya i yeye polozheniye v stratigraficheskoy skheme karbona Donbassa [D'yakove Group and its position in the Carboniferous sedimentary succession of the Donets Basin]. – *Geological Journal (Academy of Sciences of Ukrainian SSR)*, 1: 52–57. (in Russian)
- Rindsberg, A. K. (1994): Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. – *Bulletin of Geological Survey of Alabama*, 158: 1–108.
<https://doi.org/10.1017/s2475262200008078>
- Rindsberg, A. K., Box, P. O. (1990): Freshwater to marine trace fossils of the Mary Lee coal zone and overlying strata (Westphalian A) Pottsville Formation of Northern Alabama. – In: Gastaldo, R. A., Demko, T. M., Liu, Y. (eds), Carboniferous coastal paleoenvironments and paleocommunities of the Mary Lee coal zone, Marion and Walker Counties, Alabama. A Guide for field trip VI, Tuscallosa, pp. 82–96.
[https://doi.org/10.1016/0166-5162\(92\)90003-f](https://doi.org/10.1016/0166-5162(92)90003-f)
- Romano, M., Meléndez, B. (1985): An arthropod (merostome) ichnocoenosis from the Carboniferous of northwest Spain. – *Compte Rendu Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère*, 5: 317–325.
- Romano, M., Whyte, M. A. (1987): A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire; its occurrence, taxonomy and interpretation. – *Proceedings of the Yorkshire Geological Society*, 46: 85–95.
<https://doi.org/10.1144/pygs.46.2.85>
- Romano, M., Whyte, M. A. (2015): A review of the trace fossil *Selenichnites*. – *Proceedings of the Yorkshire Geological Society*, 60: 275–288.
<https://doi.org/10.1144/pygs2015-357>
- Savage, N. M. (1971): A varvite ichnocoenosis from the Dwyka Series of Natal. – *Lethaia*, 4: 217–233.
<https://doi.org/10.1111/j.1502-3931.1971.tb01290.x>
- Schlirf, M., Uchman, A., Kummel, M. (2001): Upper Triassic (Keuper) non-marine trace fossils from the Hassberge area of Franconia, south-eastern Germany. – *Paläontologische Zeitschrift*, 75: 71–96.
<https://doi.org/10.1007/BF03022599>
- Schneider, J., Schamaev, M. I., Walter, H. (1992): Paläobiogeographie und Stratigraphie von Tetrapoden- und Arthropoden-Fährten aus dem paralischen Oberkarbon und Perm (Gzhel/Assel) des Donez Bassins. – *Freiberger Forschungshefte*, C445: 104–121.
- Seilacher, A. (2007): Trace fossils analysis. – Springer-Verlag, Berlin, 226 pp.
- Snigirevskaya, N. S. (1989): *Physostoma elegans* (Lyginopteridales) v ugol'nykh pochkakh Donetskogo basseyna [*Physostoma elegans* (Lyginopteridales) in coal balls of the Donets Basin]. – *Botanical Journal*, 10: 1442–1450. (in Russian)
- Shipnev, E. S. (2018): New data on Carboniferous xiphosurans (Xiphosura, Chelicera) of the Donets Coal Basin. – *Paleontological Journal*, 52(3): 271–283.
<https://doi.org/10.1134/s0031030118030127>
- Sternberg, K. M. (1820): Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Bd 1. H. 1. – Verlag von F. Fleischer, Leipzig, 24 pp.
<https://doi.org/10.5962/bhl.title.154066>
- Sternberg, K. M. (1823): Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Bd 1. H. 3. – Ernst Brenck's Wittwe, Regensburg, 39 pp.

- Torrell, P. (1870): Petrifacta Suecana Formnationis Cambriæ. – Gleerup, 14 pp.
- Trewin, N. H., McNamara, K. J. (1995): Arthropods invade the land: Trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. – Transactions of the Royal Society of Edinburgh: Earth Sciences, 85(3): 177–210.
<https://doi.org/10.1017/S026359330000359X>
- Ustinovsky, Yu. B. (1993): Kayal's'kyi etap (pozdniy bashkir) [Kayalian Stage (late Bashkirian)]. – In: Tsegelnyuk, P. D. (ed.), Geologicheskaya istoriya territorii Ukrayny. IGS NASU, Kyiv, pp. 147–154. (in Russian)
- Vallon, L. H., Röper, M. (2006): *Tripartichnus* n. igen. – a new trace fossil from the Buntsandstein (Lower Triassic) and from the Solnhofen Lithographic Limestones (Upper Jurassic), Germany. – Paläontologische Zeitschrift, 80: 156–166.
<https://doi.org/10.1007/BF02988974>
- Verde, M., Netto, R., Azurica, D., Lavina, E. L., Di Pasquo, M. (2022): Revisiting the supposed oldest bilaterian trace fossils from Uruguay: Late Paleozoic, not Ediacaran. – Palaeogeography, Palaeoclimatology, Palaeoecology, 602: 1–21.
<https://doi.org/10.1016/j.palaeo.2022.111158>
- Voigt, E. (1977): On grazing traces produced by the radula of fossil and recent gastropods and chitons. – In: Crimes, T. P., Harper, J. C. (eds), Trace fossils 2. Geological Journal, Special Issue 9, pp. 335–346.
- Walcott, C. D. (1911): Cambrian geology and paleontology II. Middle Cambrian Merostomata. – Smithsonian Miscellaneous Collections, 57: 17–40.
<https://doi.org/10.1017/s0016756800115006>
- Walter, H. (1983): Zur Taxonomie, Ökologie und Biostratigraphie der Ichnia limnisch-terrestrischer Arthropoden des mitteleuropäischen Jungpaläozoikums. – Freiberger Forschungsheft, C382: 146–193.
- Weber, B., Braddy, S. J. (2004): A marginal marine ichnofauna from the Blaiklock Glacier Group (?Lower Ordovician) of the Shackleton Range, Antarctica. – Transactions of the Royal Society of Edinburgh: Earth Sciences, 94(1): 1–20.
<https://doi.org/10.1017/S026359330000050X>
- Wissak, M., Volohonsky, E., Seilacher, A., Freiwald, A. (2004): A trace fossil assemblage from the fluvial Old Red deposits (Wood Bay Formation; Lower to Middle Devonian) of NW Spitsbergen, Svalbard. – Lethaia, 37(2): 149–163.
<https://doi.org/10.1080/00241160410005763>
- Zalessky, M. D. (1907): Materialy po kamennougol'noy flore Donetskogo basseyna [Data on the Carboniferous flora of the Donets Basin]. – Izvestiya Geologicheskogo komiteta, 26(8-10): 28–98. (in Russian)