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NEW RECORDS OF PENNSYLVANIAN TRACE AND BODY FOSSILS FROM THE NORTHERN CAUCASUS BASIN

НОВІ ЗНАХІДКИ ПЕНСИЛЬВАНСЬКИХ ІХНОФОСИЛІЙ ТА ТІЛЕСНИХ ФОСИЛІЙ У ПІВНІЧНОКАВКАЗЬКОМУ БАСЕЙНІ

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New findings of trace fossils and body fossils assigned to arthropods and/or worms are documented from the Tolstiy Bugor and Maliy Urup formations (upper Bashkirian–Moscovian) of the limnic Northern Caucasian Basin. Among the trace fossils, cf. *Pilichnus* isp. and *Cochlichnus anguineus* Hitchcock, 1858 have been identified. The first ichnotaxon was found on the surfaces of compressions of plant leaf organs. These ichnofossils are likely evidence of detritivory. Possible producers of these traces include arthropods, gastropods, and annelid worms. Considering the continental origin of the deposits, the list can be narrowed down to arthropods and annelids, since terrestrial gastropods are not known from the Carboniferous deposits of the Northern Caucasus and adjacent regions. These fossils likely illustrate the so-called third taphonomic pathway of plants (leaf fossils with co-existing pre-depositional plant–animal interaction and post-depositional plant–animal interaction traces) and the fourth taphonomic pathway of plants (leaf fossils with consumptive post-depositional plant–animal interaction traces [of detritivory] only). *Cochlichnus* represents traces of grazing, feeding, and/or locomotion. Depending on environmental conditions and the nature of potential producers, such traces may reflect a combination of these ethological categories. Possible producers of *Cochlichnus* include worms, cyclostomates, or insect larvae. In addition, a likely carbonised fragment of an arthropod exoskeleton and an impression of the body of a myriapod or worm have been discovered.

Keywords: Pennsylvanian, Northern Caucasus, trace fossils, arthropods, continental deposits.

Ключові слова: пенсильваній, Північний Кавказ, іхнофосилії, артроподи, континентальні відклади.

З товстобугорської та малоурупської світ (верхня частина башкирського ярусу–московський ярус) лімнічного Північнокавказького басейну задокументовано нові знахідки іхнофосилій та тілесних фосилій, віднесених до артропод та/або червів. Серед іхнофосилій визначено cf. *Pilichnus* isp. і *Cochlichnus anguineus* Hitchcock, 1858. Перший іхнотаксон знайдено на поверхнях контрвідбитків листових органів рослин. Ці іхнофосилії, ймовірно, є свідченнями детритофагії. Можливими продуцентами цих слідів можуть бути членистоногі, гастроподи та кільчасті черви. З огляду на континентальне походження відкладів, перелік можна звужити до членистоногих і кільчастих червів, оскільки наземні червононогі молюски не відомі з кам'яновугільних відкладів Північного Кавказу та суміжних регіонів. Ці викопні сліди, ймовірно, ілюструють так званий третій тафономічний шлях рослин (рештки листя зі слідами впливу тварин, що утворилися як до, так і після відкладення осадов) і четвертий тафономічний шлях рослин (рештки листя лише зі слідами впливу тварин, пов'язаного з детритофагією, що утворилися після накопичення осадов). *Cochlichnus* є слідами випасання, живлення та/або пересування.

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Залежно від умов середовища і природи можливих продуцентів, такі сліди можуть відображати поєднання цих етологічних категорій. Потенційними продуцентами *Cochlichnus* є черви, круглороті або личинки комах. Крім того, виявлено ймовірний вуглефікований фрагмент екзоскелета артроподи та відбиток тіла багатоніжки або черва.

INTRODUCTION

The Bashkirian and Moscovian biostratigraphy of the limnic Northern Caucasus Basin is based mainly on plant macrofossils (Zalesky, 1916, 1934; Novopokrovsky, 1939; Novopokrovsky and Teslinov, 1946; Anisimova, 1972, 1973a, 1973b, 1974, 1979a, 1979b; Novik, 1974), as these deposits are exceptionally poor in faunal remains. To date, there are only three reports of animal fossils from the Carboniferous of the basin. Lebedev (1919) listed some Pennsylvanian brachiopod species from limestones, sandstones, and shales exposed in the Kamennaya, Anthratsytovaya, and Nikitina valleys near the villages of Nikitino and Kordon Chernorech'ye (Malaya Laba River basin, Karachay-Cherkessia).

Teslinov (1951) briefly described and illustrated the conchostracans *Leaia tricarinata minima* Pruvost, 1914 from the carbonaceous shales of the Tolstiy Bugor Formation (according to Anisimova, 1979b) recovered at the Bogoslovskoye Coalfield. These conchostracans confirm the Bashkirian to Moscovian age for the coal-bearing strata, based on the terrestrial plant studies (Zalesky 1916; Anisimova, 1974, 1979b; Novik, 1974).

Hampe and Ivanov (2007) described xenacanthid teeth belonging to *Triodus teberdaensis* Hampe & Ivanov, 2007, from the Tolstiy Bugor Formation. They also report that ostracods, bivalves, foraminifers, palaeoniscoid scales, and a rhizodontid scale co-occur with *Triodus teberdaensis*.

In 2025, while reviewing the collection of Bashkirian–Moscovian plants of the Northern Caucasus in the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (NMNHU-G), the first author (VSD) discovered several non-plant fossils that complement the palaeontological characteristics of the Carboniferous deposits of the region.

The aims of this study are: (1) to document the first occurrences of trace fossils and new findings of body fossils in the Carboniferous of the Northern Caucasus Basin, and (2) to provide a palaeoecological interpretation of these occurrences.

MATERIAL AND METHODS

In this paper, nine specimens (NMNHU-G 1966/85a, NMNHU-G 1966/110, NMNHU-G 1966/171, NMNHU-G 1966/172a, NMNHU-G 1966/206, NMNHU-G 1966/217, NMNHU-G 1966/258, NMNHU-G 1966/267, and NMNHU-G 1966/272) of trace fossils and body fossils from the upper Bashkirian–Moscovian Tolstyi Bugor and Maliy Urup formations (Fig. 1A) are examined. This material originates from the Malolabinskoye, Tolstobugorskoye, and Bogoslovskoye coalfields, Gremuchaya Valley on the right bank of the Marukha River, as well as Dzyuvya Mountain (Bambak Ridge) in the Northern Caucasus (Fig. 1B).

These specimens are a part of the collection of Pennsylvanian plants of the Northern Caucasus, which was collected mainly by Dr. Olga I. Anisimova, a member of the former Department of Palaeobotany, Institute of Geological Sciences (Kyiv) and supplemented by collections of Caucasian geologists. The collection NMNHU-G 1966, which consists of about 3000 specimens, was studied by Anisimova (1972, 1973a, 1973b, 1974, 1979a, 1979b). This collection is housed in the Department of Geology of the National Museum of Natural History, National Academy of Sciences of Ukraine (Kyiv).

GEOLOGICAL SETTING

Outcrops of the Carboniferous deposits in the Northern Caucasus occur as a 220 km long belt extending from the Belaya River in the west to the Baksan River in the east (Anisimova, 1974, 1979b; Novik, 1974; Pogrebnov, 1975). These strata include a Tournaisian marine sequence (comprising shales interbedded with limestones), which overlies a 650–1900 m thick continental molasse of early Bashkirian to Late Pennsylvanian age (Pogrebnov, 1956, Anisimova, 1974, 1979b; Novik, 1974; Yegorov et al., 1975). This molasse consists predominantly of grey-coloured alluvial, lacustrine, and swamp sandstones, siltstones, and mudstones, with a basal conglomerate or breccia, as well as coals and volcanic rocks (Pogrebnov, 1956, Anisimova, 1974, 1979b; Novik, 1974; Yegorov et al., 1975). In the upper part of the Upper Pennsylvanian succession, red-bed deposits are also present (Pogrebnov, 1956; Reznikov, 1956; Novik, 1974; Yegorov et al., 1975).

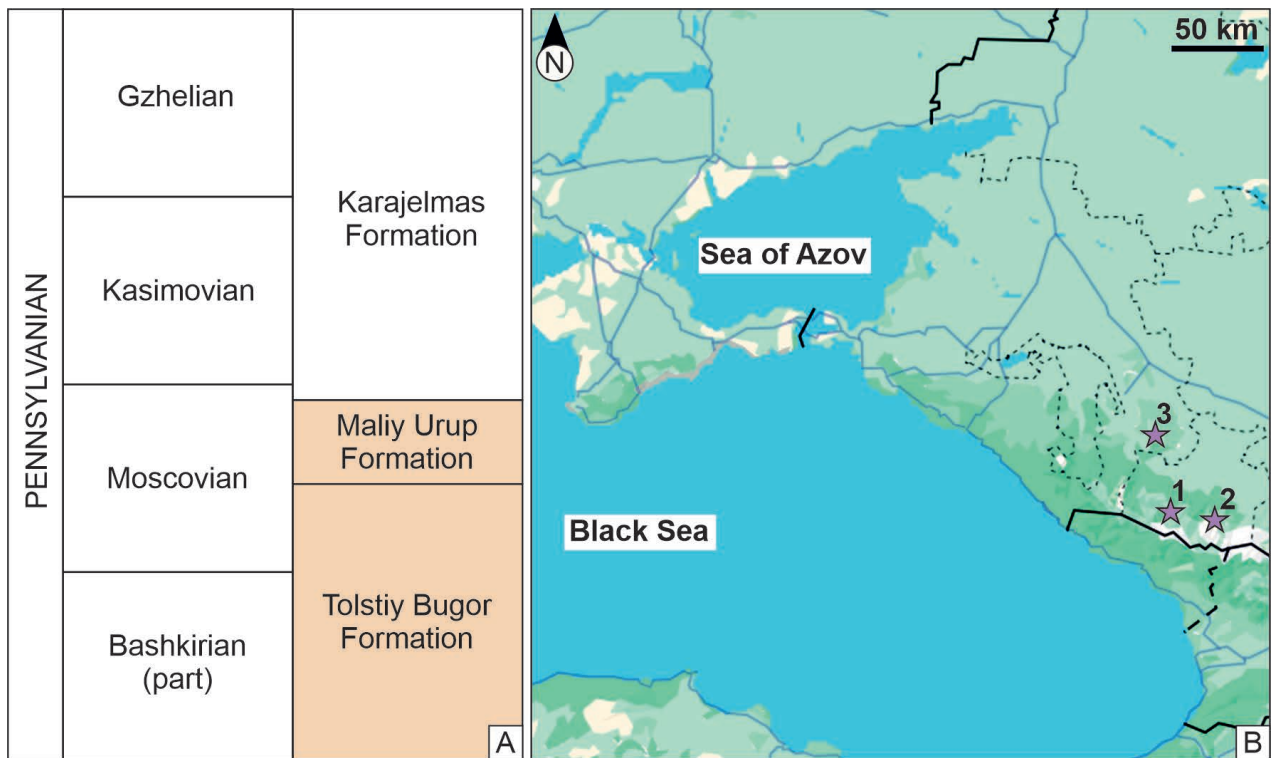


Fig. 1. Pennsylvanian stratigraphy of the Northern Caucasus Basin (A) and a geographical map of the northeastern part of the Black Sea region showing geographical location of the sections with studied fossils (B). Stratigraphic scheme modified after Novik (1974: Scheme 1); interval with studied fossils marked by orange. Locality numbers: 1 – Malolabinskoye Coalfield, 2 – Gremuchaya Valley, Tolstobugorskoye and Bogoslovskoye Coalfield, 3 – Dzyuvya Mountain (Bambak Ridge).

Рис. 1. Стратиграфія пенсильванських відкладів Північнокавказького басейну (А) та мапа північно-східної частини Чорноморського регіону, що ілюструє географічне положення розрізів, з яких походить вивчений матеріал (Б).

Стратиграфічна схема згідно з роботою (Новик, 1974: Схема 1); стратиграфічний інтервал, з якого походить вивчений матеріал позначено помаранчевим кольором. Номери місцезнаходжень: 1 – Малолабінське родовище, 2 – Балка Гремуча, Товстобугорське та Богословське родовища, 3 – гора Дзювья (хребет Бамбак).

The Tolstiy Bugor Formation (or C_2^{tl} Formation) is a sequence of continental sandstones, siltstones, and mudstones with interbeds of coal and tuffs; a conglomerate bed occurs at the base. The formation thickness ranges from 250 to 550 meters (Anisimova, 1974, 1979b; Novik, 1974). Macroscopic plant remains suggest a late Bashkirian–early Moscovian age for the formation (Anisimova, 1974, 1979b; Novik, 1974).

The Maliy Urup Formation (or C_2^{ml} Formation) is a 200 m thick succession of continental mudstones, siltstones, siliceous shales, sandstones, and conglomerates (Anisimova, 1974, 1979b; Novik, 1974; Yegorov et al., 1975). Macroscopic plants suggest a late Moscovian age for this formation (Anisimova, 1974, 1979b; Novik, 1974).

RESULTS

As a result of examining the collection NMNHU-G 1966, the authors identified trace fossils cf. *Pilichnus* isp., *Cochlichnus anguineus* Hitchcock, 1858, as well as body fossils attributed to arthropods.

Trace fossils. Several siltstone slabs contain plant compressions under which burrows, very similar to the ichnogenus *Pilichnus* Uchman, 1999, are preserved (Fig. 2). The burrows are horizontal, very thin (0.5–2.5 mm), cylindrical, long, straight or only slightly sinuous, sometimes dichotomously branching at angles of 45–90° (Fig. 2F). They lack wall lining, and the burrow filling does not differ lithologically from the surrounding matrix. The burrows are clearly visible on the surfaces of plant compressions but are almost invisible in the surrounding rock, although in many places they can be seen gradually disappearing beyond the outer edge of the plant compression.

The continuation of burrows into the ambient rock matrix is suggestive of their post-depositional emplacement. The burrows are probably evidence of detritivory. The possible tracemakers include arthropods (Zimmerman et al., 1979; Momot, 1995; Farmer & Dubugnon, 2008; Chakraborty et al., 2023), gastropods (Mensink & Henry, 2011; Williamson & Cameron, 1976), and annelid worms (Kirchberger et al., 2015). Given the continental origin of the plant-bearing deposits, the list can be narrowed down to arthropods and annelids, since terrestrial gastropods are not known from the Carboniferous of the Northern Caucasus and adjacent regions.

These fossils likely illustrate the so-called Third taphonomic pathway of plants (leaf fossils with co-existing pre-depositional plant–animal interaction and post-depositional plant–animal interaction traces – e.g., Fig. 2C) and the Fourth taphonomic pathway of plants (leaf fossils with consumptive post-depositional plant–animal interaction traces [of detritivory] only – e.g., Fig. 2A, B), as proposed by Chakraborty et al. (2023) for Late Palaeozoic plants of India.

Described ichnofossils are tentatively identified as cf. *Pilichnus* isp. *Pilichnus* is an indicator of anoxic marine conditions (Uchman, 1999; Leszczyński, 2003), which provides additional evidence suggesting that the described ichnofossils represent a form close to *Pilichnus* rather than *Pilichnus* itself, since the rocks are of continental origin.

Cochlichnus anguineus Hitchcock, 1858 (Fig. 3A) was found on a siltstone slab (specimen NMNHU-G 1966/217) from the Maliy Urup Formation of the Malolabinskoye Coalfield. *Cochlichnus anguineus* is a horizontal, cylindrical, thin, unbranched, sinusoidal trail with a smooth surface, preserved as a convex hyporelief on the lower bedding plane of a siltstone bed. The width of the trail is 0.9–1.5 mm; its length is 75 mm. The wavelength of the sinuous meanders ranges from 7 to 10 mm, and the amplitude from 4.0 to 4.5 mm.

Cochlichnus is a trace of grazing, feeding, and/or locomotion (see review in Dernov, 2023). Depending on environmental conditions and the identity of potential producers, such traces may represent a combination of these ethological categories (Buatois et al., 1997). Possible 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 Recent freshwater environments, morphologically similar traces are produced by nematodes (Chamberlain, 1975), larvae of Ceratopogonidae (Metz, 1987), Therevidae (Michaelis, 1972), and *Chironomus motilator* (Tarr, 1935). However, since remains of Diptera are not known from the Carboniferous, nematodes and/or annelids are considered the most probable producers of *Cochlichnus* (Dernov, 2023).

Body fossils. A probable carbonised arthropod exoskeleton fragment (Fig. 3B) was found on the surface of a large siltstone slab (specimen NMNHU-G 1966/110) together with numerous limonitised pteridosperm pinnules, a fern foliage, pteridosperm rachis, and calamitalean axes. This material comes from the Maliy Urup Formation of an outcrop on the right slope of the Gremuchaya Valley on the right bank of the Marukha River.

This fossil is interpreted as a fragment of an arthropod exoskeleton based on its unusual morphology and preservation characteristics. All associated plant remains are preserved as limonitic crusts, in contrast to the distinct preservation of the (?) exoskeletal fragment.

A compression of an elongated structure (Fig. 3C) is preserved with a fern foliage in the carbonaceous shale of the Maliy Urup Formation (specimen NMNHU-G 1966/85a). These deposits are exposed in the Gremuchaya Valley on the right bank of the Marukha River. The fossil is elbow-shaped and curved, preserved at a slight angle relative to the bedding plane, as indicated by varying preservation patterns on different surfaces of the shale. Its thickness ranges from 3 mm in the upper portion to 1.2 mm in the lower portion, and its total length is approximately 25 mm. In the upper half of the fossil, faint transverse segmentation is visible, which transitions into a very thin transverse wrinkle in its widest part.

The interpretation of this fossil uncertain. It may represent remains of an annelid worm or a myriapod. However, it could also be a locomotion trace or flattened burrow, as no evidence of millipede limbs or definitive features indicative of worm anatomy has been observed.

The presence of myriapods and insects in the Pennsylvanian palaeobiocoenoses of the Northern Caucasus is supported by the occurrence of marginal feeding traces on the pinnules of pteridosperms in the collection NMNHU-G 1966 (unpublished data of the first author; see Fig. 2C, arrowed).

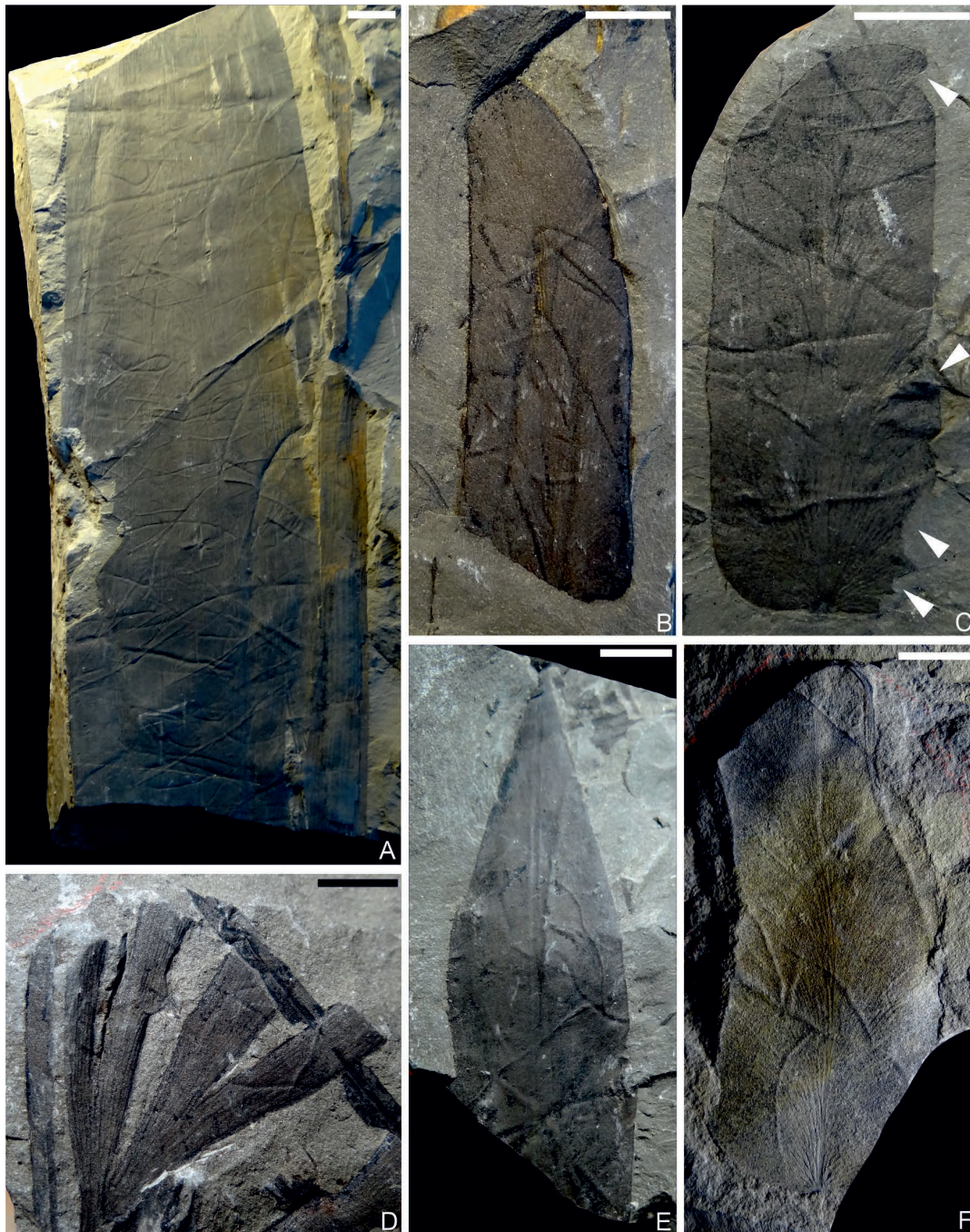


Fig. 2. Trace fossils cf. *Pilichnus* isp. from the Pennsylvanian of Northern Caucasus: A – on *Cordaites* sp. (NMNHU-G 1966/258), Tolstobugorskoye Coalfield, Tolsty Bugor Formation; B, F – on *Linopteris neuropteroides* (NMNHU-G 1966/267 and NMNHU-G 1966/171), Bogoslovskoye and Tolstobugorskoye Coalfield, Tolsty Bugor Formation; C – on *Linopteris subbrongniarti* bearing margin feedings of arthropods (white arrows) (NMNHU-G 1966/272), Tolstobugorskoye Coalfield, Tolsty Bugor Formation; D – on *Caucasia ginkgophylloides* (NMNHU-G 1966/172a), Bambak Ridge, Dzyuvya Mountain, Maliy Urup Formation; E – on *Lepidostrobophyllum majus* (NMNHU-G 1966/206), Tolstobugorskoye Coalfield, Tolsty Bugor Formation. Scale bars equal 10 mm.

Рис. 2. Іхнофосилії cf. *Pilichnus* isp. з пенсильванію Північного Кавказу: А – на *Cordaites* sp. (NMNHU-G 1966/258), Товстобугорське родовище, товстобугорська світа; В, F – на *Linopteris neuropteroides* (NMNHU-G 1966/267 та NMNHU-G 1966/171), Богословське та Товстобугорське родовища, товстобугорська світа; С – на *Linopteris subbrongniarti*, що має сліди крайових об'їдань артроподами (білі стрілки) (NMNHU-G 1966/272), Товстобугорське родовище, товстобугорська світа; D – на *Caucasia ginkgophylloides* (NMNHU-G 1966/172a), хребет Бамбак, гора Дзювя, малоурупська світа; E – на *Lepidostrobophyllum majus* (NMNHU-G 1966/206), Товстобугорське родовище, товстобугорська світа. Масштабні лінійки дорівнюють 10 мм.

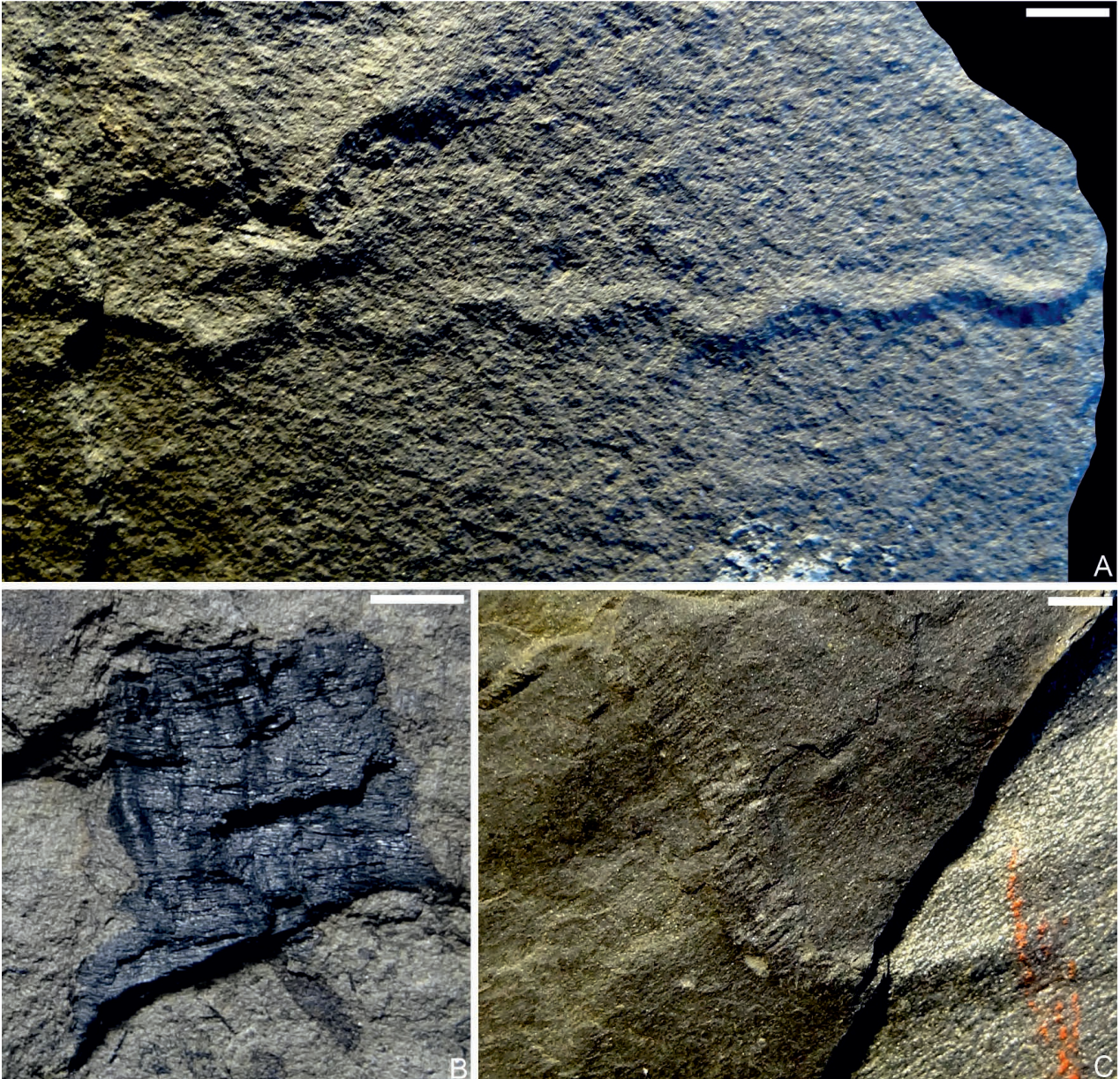


Fig. 3. Fossils from the Pennsylvanian deposits of Northern Caucasus: A – trace fossil *Cochlichnus anguineus* Hitchcock, 1858 (NMNHU-G 1966/217); B – probable carbonised arthropod exoskeleton fragment (NMNHU-G 1966/110); C – worm or myriapod body compression (NMNHU-G 1966/85a). Scale bars equal 2 mm (B, C) and 5 mm (A).

Рис. 3. Фосилії з пенсильванських відкладів Північного Кавказу: А – іхронофосилія *Cochlichnus anguineus* Hitchcock, 1858 (NMNHU-G 1966/217); В – імовірний вуглефікований фрагмент екзоскелета артроподи (NMNHU-G 1966/110); С – відбиток тіла черв'яка або багатоніжки (NMNHU-G 1966/85а). Масштабні відрізки дорівнюють 2 мм (В, С) та 5 мм (А).

DISCUSSION AND CONCLUDING REMARKS

The data on marine fauna within the Carboniferous sequence of the Northern Caucasus (Lebedev, 1919; Hampe and Ivanov, 2007) require re-evaluation, as other researchers did not report the presence of marine fauna in the region

and even denied the existence of marine-origin deposits altogether (Novik, 1974). However, Dernov (2024) reported the occurrence of a low diversity Pennsylvanian marine fauna in the Ukrainian Carpathians, another Carboniferous limnic basin of Eastern Europe. Therefore, the possibility of

short-term incursions of epicontinental seas into intermontane depressions of the Northern Caucasus basin appears plausible, but it requires further investigation.

Cochlichnus anguineus occurs in both marine and non-marine facies (e.g., Dernov, 2023). In Bashkirian deposits of the Donets Basin (eastern Ukraine), it is found in lacustrine and lagoonal mudstones and siltstones, as well as in fluvial sandstones (Dernov, 2023). The presence of possible arthropod remains, along with numerous evidence of terrestrial arthropod-plant interactions, such as margin feeding, galls, and wood borings (unpublished data of the first author), from the Pennsylvanian deposits of the Northern Caucasus, suggests that various arthropods, including myriapods, oribatid mites, and insects, were present

in these palaeoecosystems. However, their body fossils have not yet been discovered in the region.

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