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A stem of an arborescent lycopsid *Sigillaria* with attached rooting organs *Stigmaria* from the Pennsylvanian of the Donets Basin, eastern Ukraine

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abstract

The macroscopic remains of Carboniferous plants in the Donets Basin are represented by a variety of preservation types, including compressions, impressions, casts, as well as permineralised wood of gymnosperms preserved in alluvial and marine sandstones, permineralised organs of peat-forming plants in 'coal balls', etc. In contrast to other Carboniferous basins of the palaeotropical belt of Euramerica, the remains of arborescent lycopsid trunks preserved *in situ* are very rare in the Donets Basin. To date, only two such finds have been documented here, namely: a fragment of the *Subsigillaria* trunk found in the coal-bearing deposits of the Avilovka Formation (Upper Pennsylvanian) and a fragment of the *Sigillaria* trunk with attached rooting organs *Stigmaria* from the Gorlivka Formation (Middle Pennsylvanian). The latter trunk is currently on display at the National Museum of Natural History, National Academy of Sciences of Ukraine. *Stigmaria* represents root organs of several families of tree-like lycopsids, i.e. they are a classic form-genus. The remains of *Stigmaria* are among the most common Carboniferous fossils in the Donets Basin. Tree-like lycopsids, including representatives of the genera *Lepidodendron*, *Sigillaria*, *Lepidophloios*, and *Asolanus*, were among the dominants of wet forests growing within deltaic and alluvial lowlands, where peats were common. The taphonomic features of this trunk fragment indicate that *Syringodendron*, the preservation type of *Sigillaria* axes, may occur not only due to postmortem water transport of axes, but also due to the destructive effects of aggressive environmental agents on the surface layers of the stem, such as wind, moisture, activity of organisms, etc. The relatively large vertical angles of branching of *Stigmaria* rhizomorphs from the base of the trunk indicate their deep penetration into a substrate. This fact contradicts the assumptions of some experts about the subaerial or aerial location of at least some of the *Stigmaria* rhizomorphs. The fragment of *Sigillaria* stem with attached rhizomorphs *Stigmaria* is a valuable find, since the trunks of Pennsylvanian tree-like lycopsids are usually preserved without rooting organs.

Стовбур деревоподібної лікопсиди *Sigillaria* з прикріпленими кореневими органами *Stigmaria* з пенсильванських відкладів Донецького басейну (Схід України)

Віталій Дернов, Галина Анфімова

Резюме. Макроскопічні рештки кам'яновугільних рослин Донецького басейну представлені різними типами збереження: відбитками, зліпками, а також мінералізованою деревиною голонасінних, що збереглася в алювіальних та морських пісковиках, мінералізованими органами рослин-торфоутворювачів у так званих «кол-болах» тощо. На відміну від інших кам'яновугільних басейнів палеотропічного поясу Єврамерики, рештки стовбурів деревоподібних лікопсид, поховані інситно, трапляються на Донбасі дуже рідко. На даний момент, задокументовано всього дві такі знахідки: фрагмент стовбура *Subsigillaria*, знайдений серед відкладів авіловської світи (верхній пенсильваній) та фрагмент стовбура *Sigillaria* з прикріпленими кореневими органами *Stigmaria*, що походить з горлівської світи (середній пенсильваній). Друга знахідка експонується в Національному науково-природничому музеї НАН України. Вивченню цього екземпляру присвячена ця стаття. *Stigmaria* є кореневими органами кількох родин деревоподібних лікопсид, тобто є класичним форм-родом. Рештки стігмарій є одними з найпоширеніших фосилій серед кам'яновугільних відкладів Донецького басейну. Деревоподібні лікопсиди, такі як представники родів *Lepidodendron, Sigillaria, Lepidophloios* та *Asolanus*, були одними з домінантів вологих лісів, що росли в межах понижених ділянок приморських низин, де були поширені торфовища. Тафономічні особливості вивченого фрагмента стовбура свідчать про те, що тип збереження осей сигілярій *Syringodendron* може виникати не лише завдяки посмертному водному переносу осей, а і завдяки руйнівному впливу на поверхневі шари стовбура агресивних агентів навколишнього середовища, таких як вітер, вологість, життєдіяльності організмів тощо. Порівняно великі вертикальні кути відгалуження ризоморфів *Stigmaria* від основи стовбура сигілярії свідчить про їхнє глибоке проникнення в субстрат. Цей факт суперечить припущенням деяких фахівців щодо субаерального чи аерального прижиттєвого розташування ризоморфів *Stigmaria*. Фрагмент стовбура *Sigillaria* з прикріпленими ризоморфами *Stigmaria* є цінною знахідкою, оскільки стовбури пенсильванськх деревовидних лікопсид зазвичай зберігаються без кореневих органів.

Ключові слова: карбон, інситне збереження, *Sigillaria*, *Stigmaria*, Донецький басейн, Україна.

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Introduction

Macroscopic remains of Carboniferous plants in the Donets Basin (eastern Ukraine) are represented by various preservation types, including compressions, impressions, and casts (see Zerov *et al.* [1972] for the bibliography for 1872–1971 and for the last 50 years in Boyarina [2006a, 2006b, 2010]; Dernov and Udovychenko [2019, 2021]), as well as siliceous and calcareous permineralisations preserved in sandstones [Krendovsky 1880; Zalessky 1910a; 1937; Lepekhina 1984; Rößler *et al.* 2023] and in 'coal balls' [Zalessky 1910b; Snigirevskaya 1972 and references therein]. Unfortunately, there is a paucity of data on stems of Carboniferous arborescent lycopsids preserved *in situ* from the Donets Basin [Novik 1939, 1952; Shchogolev 1978, 1991].

Rodygin [1924] reported the presence of rock casts of *Sigillaria* stumps in the roof shale of the k_5 coal bed (Kamensk Formation, lower part of the Moscovian, Middle Pennsylvanian) in the Kraselshchik's mine in the town of Antratsyt (Luhansk Oblast). Local miners called them 'domes' (Ukrainian: 'kupoly') [Rodygin 1924]. These 'domes' are likely analogous to the so-called kettlebottoms, i.e. '…a sediment-filled cast of a tree stump that is exposed underground at or near the contact of the coal bed and overlying roof rock…' [DiMichele *et al.* 1996: 251].

Meffert and Krym [1926] noted that remains of lycopsid trunks preserved *in situ* are much less common in the Donets Basin compared to the coal basins of England, Belgium, and France. These authors propose that the absence of lycopsid trunk is due to the inability of the trunks to withstand the unstable wet substrate. Once the plants died, the trunks were unable to retain their structural

integrity in the aerobic environment, leading to their eventual collapse. This, in conjunction with the possibility of minor erosion, is likely to account for the frequent occurrence of rootlets of *Stigmaria* in the absence of their rhizomorphs in some Pennsylvanian palaeosoils in the Donets Basin.

Shchogolev [1978, 1991] described the stem base of *Subsigillaria* ex gr. *brardii* (Brongniart, 1822) Brongniart, 1828 from the Gzhelian (Upper Pennsylvanian) part of the Avilovka Formation of the eastern Donets Basin. According to Shchogolev [1978], the rock cast of the stem is 60 cm high, 32 cm in diameter, and covered with a 5 to 7-mm-thick coal crust. The base of the trunk is situated within a thin coal seam. The majority of the trunk is preserved in a carbonaceous grey lacustrine or swamp mudstone, while the upper part of the trunk has been intruded upon by 5–7 cm of a yellowish-grey lacustrine mudstone bearing impressions of ferns. The stem cast is composed of this yellowish-grey mudstone, which contains remains of ferns and lycopsid branches belonging to two formal species [Shchogolev 1991]. Shchogolev [1978, 1991] makes an conclusion that the accumulation of the lacustrine and swamp deposits containing this stem fragment occurred very quickly, no longer than a few decades.

Fissunenko and Snigirevskaya [1981] reported that in the Donets Basin, only a few localities of lycopsid trunks buried in the growth position have been found. They do not specify the localities in question, but noted that trunks are known in a number of coal mines in the Seleznevskyi mining and industrial district (the area of the towns of Debaltseve and Adrianopil) and Central mining and industrial district (the area of the towns of Gorlivka and Yenakijeve) among deposits of the early Moscovian-aged Kamensk Formation.

The Carboniferous macroflora of the Donets Basin has been studied for more than 150 years [Zerov *et al*. 1972], yet numerous questions pertaining to taxonomy, ecology, and stratigraphic distribution of plant taxa remain unresolved. In this regard, new data on the ecology of Carboniferous terrestrial plants of the Donets Basin are important, especially in the context of identifying the palaeoenvironments by palaeoecological analysis. This paper presents the results of a re-examination of a specimen of the stem base of an arborescent lycopsid belonging to the genus *Sigillaria* Brongniart, 1822, bearing rhizomorphic root organs of the formal genus *Stigmaria* Sternberg, 1822. This specimen is currently on display at the National Museum of Natural History of the Academy of Sciences of Ukraine, Kyiv. Novik [1939, 1952] provided a brief description and illustration of the trunk, but did not offer a palaeoecological interpretation of her observations. Lycopsid trunks are frequently preserved *in situ* in paralic coal basins in Western Europe and the USA [e.g. DiMichele *et al*. 1996, 2009; Appleton *et al*. 2011; Thomas & Seyfullah 2015; Archer *et al*. 2016]. Often these remains are buried as a result of catastrophic events such as landslides, mudflows, and volcanic ash fall [Calder *et al*. 2006; Wagner & Diez 2007; DiMichele *et al*. 2009; D'Antonio *et al*. 2023]. Consequently, their study is of significant importance from both a taphonomic and a palaeoecological perspective.

A plethora of descriptions of lycopsid trunks preserved in growth position have been published (see review in: Gastaldo 1986; Thomas & Seyfullah 2005), yet there are fewer reports on lycopsid trunks with attached *Stigmaria*. The aim of this study is to re-describe the stem of *Sigillaria* sp. bearing rooting organs *Stigmaria* sp. and to identify its taphonomic and palaeoecological significance.

Material and Methods

This paper is based on the results of the study of the *Sigillaria* sp. trunk rock cast bearing attached rhizomorphs *Stigmaria* sp. (specimen NMNH-967) exhibited in the 'History of geological development of the territory of Ukraine' hall of the National Museum of Natural History, NAS of Ukraine, Kyiv (acronym: NMNH). The specimen was found in the face of the mine No. 19–20 situated in the city of Gorlivka (Donetsk Oblast, Ukraine) at a depth of 176 m, 300 m south of the mine shaft [Novik 1939] (Fig. 1). This trunk was discovered by the Ukrainian palaeobotanist Kateryna Y. Novik (Fig. 2, *a*) in 1935. In 1937, this trunk was mounted for display at the Geological Museum of the Academy of Sciences of the Ukrainian SSR (now NMNH) in preparation for the exhibition at the 17th International Geological Congress [Novik 1939].

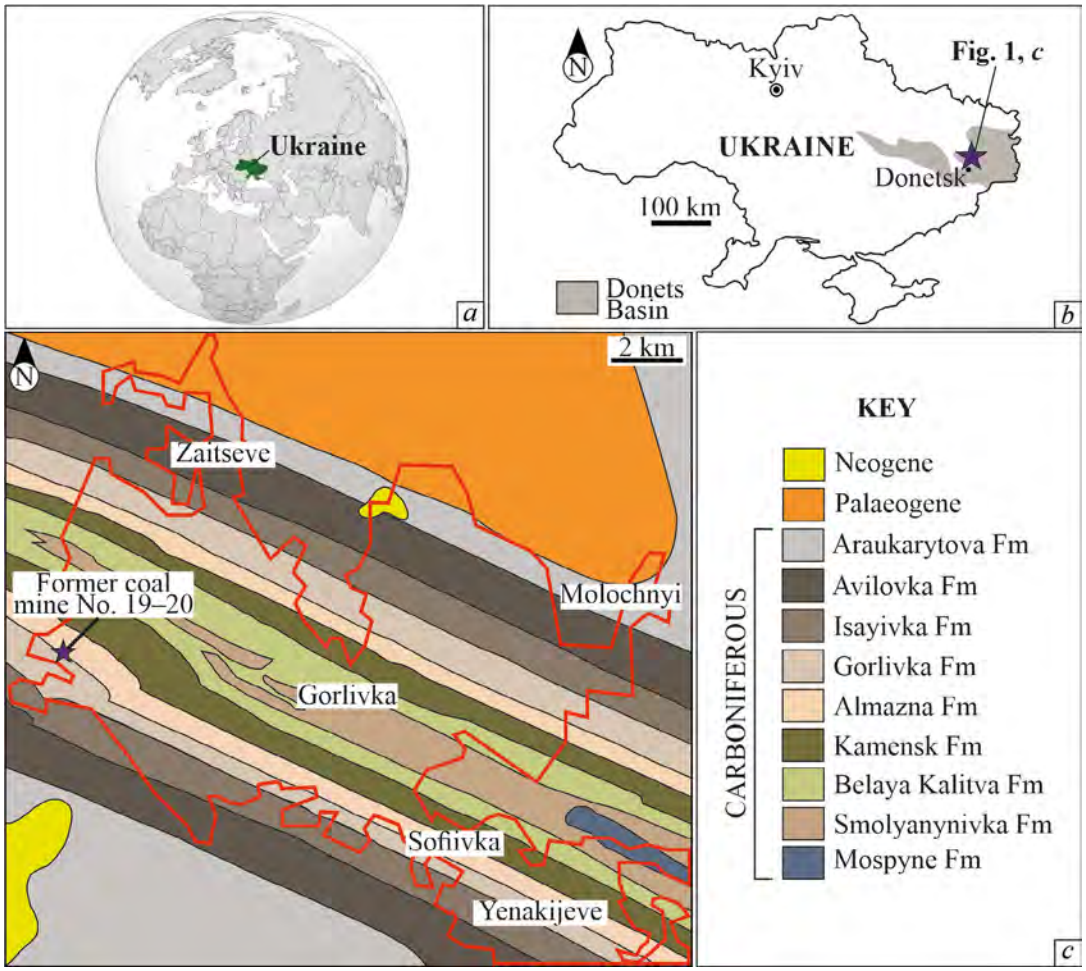

Fig. 1. Geographical location of the coal mine No. 19–20. Geological map in Fig. 1, *c* is modified after Tarasevich [1960].

Рис. 1. Географічне положення вугільної шахти № 19–20. Геологічна карта на рис. 1, *c* взято з Tarasevich [1960].

From the moment the specimen NMNH-967 was mounted until now, it has been an integral part of the museum's exhibition. Initially, it was on display in the Palaeontology Department of the Geological Museum of the Academy of Sciences of the Ukrainian SSR. Since December 1967, after a radical restructurisation of the Geological Museum's exhibition, the specimen has been a central piece of the hall 'History of geological development of the territory of Ukraine' and has been displayed at the end of the hall under the painting 'The Carboniferous forest' (Fig. 2, *b*) by the outstanding Ukrainian painter and graphic artist Ivan S. Yizhakevych (1864–1962). The advantage of such a location of the *Sigillaria* trunk in the exhibition was the logical sequence in the display in accordance with the chronological principle of the exhibition construction. In 1994, artists V. V. Kolochko and M. I. Ostrovsky and scientific consultant Dr Oleksandr K. Shchogolev (researcher at the Institute of Geological Sciences, NAS of Ukraine) created the diorama 'The forest of the Carboniferous Period,' and in connection with this, the *Sigillaria* trunk was moved from the previous location to the front of the hall 'History of geological development of the territory of Ukraine.'

The description and measurements of the specimen NMNH-967 were performed in January 2024. The taphonomic and palaeoecological interpretation of the studied stem fragment is rather complicated, as it was almost entirely removed from the host rock. Consequently, it is not possible to rely on the lithological features of the rock, except for the information documented by Novik [1939].

Fig. 2. Ukrainian palaeobotanist Dr Kateryna Y. Novik (1898–1984) (*a*) and the specimen NMNH-967 in the exhibition of the Geological Museum, Academy of Sciences of the Ukrainian SSR in 1967 (a distant object under the wall, from the personal archive of Vira P. Franchuk) (*b*).

Рис. 2. Українська вчена-палеоботанік доктор геолого-мінералогічних наук Катерина Йосипівна Новик (1898–1984) (*a*) та зразок NMNH-967 в експозиції Геологічного музею Академії наук Української РСР в 1967 (дальній об'єкт під стіною, з особистого архіву В. П. Франчук) (*b*).

Geological setting

The area of the city of Gorlivka belongs to the Central mining and industrial district of the Donets Basin (cities of Gorlivka, Yenakijeve, and Sofiyivka of Donetsk Oblast; see Fig. 1), which is one of the oldest coal mining areas in the Donets Basin [Belokon 1963; Babenko *et al.* 1975]. This area is situated in the western part of the Golovna Anticline [Babenko *et al.* 1975] or Gorlivka branch (Anticline) of the Golovna Anticline of the Donets folded structure [Sokolov & Lutugin 1910; Nikolsky 1958; Babych *et al.* 1969].

The Gorlivka Formation lies on the Almazna Formation and is overlain by the Isayivka Formation (Fig. 3, *a*). It consists of a paralic succession of sandstones, siltstones, mudstones, coals (up to 28 seams), and limestones (20 beds) (Fig. 3, *b*). Beds of fine to coarse-grained sandstones are most developed in the middle and lower parts of the formation. The limestone layer M_1 is a basal bed of the Gorlivka Formation; the upper boundary of this formation is at the base of the N_1 limestone bed. The thickness of this formation varies from 230 m in the north-western part of the Donets Basin to 960 m in the south-eastern part of the basin [Aisenverg *et al.* 1963; Feofilova & Levenshtein 1963; Dunaeva 1969; Kucherenko & Rudometov 1971; Nemyrovska & Yefimenko 2013].

Alluvial rocks (16.9% of the section thickness), as well as rocks of peat and clastic swamps (14.2%), lacustrine (3.9%), lagoonal (47.8%), and shallow marine (17.2%) rocks are present in the section of the Gorlivka Formation [Feofilova & Levenshtein 1963: table 2]. Limestones of the formation are mostly bioclastic with rich stenohaline fauna. Some limestone beds are quite thick (up to 3–5 m). A characteristic feature of the lower part of the formation is an exceptionally fast transition up the section of a number of limestones rich in marine fauna, including corals and foraminifers, into swamp rocks [Feofilova & Levenshtein 1963].

The Gorlivka Formation corresponds to the Sabivkian Horizon of the Regional stratigraphic scheme of the Dnipro–Donets Downwarp [Poletaev *et al.* 2011; Nemyrovska & Yefimenko 2013]. This formation contains conodonts of the *Swadelina dissecta* Zone (stratigraphic interval bounded by the M_1 and M_8 limestone beds) and the lower part of the *Swadelina gurkovaensis* Zone (the M_8–M_{10}^1 limestone beds) [Nemyrovska 2017]. According to conodont studies [Nemyrovska 2017: text-fig. 2],

the Sabivkian Horizon of the Donets Basin corresponds to the Podolskian Regional Stage of the stratotype section of the Moscovian Global Stage.

The Gorlivka Formation also contains typical Asturian (= Westphalian D) terrestrial plants [Zalessky & Chirkova 1938; Novik 1974; Fissunenko 1991, 2000; Boyarina 2016], nonmarine bivalves of the *phillipsi* Zone of Western Europe [Sergeeva 1981, 1984]. Popov [1979] and Dernov [2022c] reported the Westphalian D ammonoid species *Wiedeyoceras cambriense* (Bisat, 1930) and *Politoceras* cf. *politum* (Shumard, 1858) from the lower part of the Gorlivka Formation. *Politoceras politum* is typical for the *Wellerites–Paralegoceras* subzone of the *Wellerites* Zone of the Demoinesian (analogous to the upper part of the Moscovian) of the USA [Miller & Owen 1939; Boardman & Work 2013]. The absolute age of the tonstein from the m_3 coal bed, which lies in the lower part of the Gorlivka Formation, is 310.55 ± 0.10 Mya [Davydov *et al*. 2010].

According to Novik [1939, 1952], the studied trunk fragment was removed from a layer of a phytoturbated siltstone (Unit 2 in Fig. 3, *c*), which lie directly below the m_1 coal bed (= Gryaznyi coal bed in the old nomenclature of coal seams of the Central mining and industrial district; see: [Sokolov & Lutugin 1910; Meffert *et al*. 1926; Sudoplatov & Kurnosov 1965]), wich was mined by the coal mine No. 19–20 (Fig. 3, *d-e*). The m_1 coal seam occurs in the lower part of the Gorlivka Formation (see Fig. 3, *b*). The rock cast of the trunk was located at approximately perpendicularly to the base of the coal bed [Novik 1939].

Novik [1939] reports the discovery of two additional *Sigillaria* trunks with rooting organs belonging to the genus *Stigmaria.* These were found in the siltstone bed directly below the m_1 coal seam at a depth of 250 m in the coal mine No. 19–20. The Carboniferous rocks of the Central mining and industrial district form anticline with very high angles (about 50–65° [Nikolsky 1958; Sudoplatov & Kurnosov 1965: fig. 85; Babych *et al*. 1969] (see Fig. 1, *c*), thus the occurrence of the trunks in the same bed at different depths is not open to doubt.

Description of the specimen NMNH-967

The trunk NMNH-967 is 1.5 m high and has a maximum diameter (at the base) of 0.75 m (Fig. 4, *a-b*). The trunk tapers relatively quickly from the base and at a distance of approximately 0.7 m from the base, near a natural break, its diameter is approximately 0.55 m. The surface of the cast is covered with a thin (2–12 mm) carbonitised periderm. The cast of the trunk consists of carbonaceous mudstone containing fragments of terrestrial plants. Longitudinal ribs 3–6 cm wide have been preserved on some parts of the trunk (Fig. 4, *e*); the width of the same rib may vary slightly. According to Novik [1939], the imprints of these ribs were observed in a shale up to the base of the coal seam, but were not removed from the rock. On the trunk cast, these ribs extend all the way to the base of rooting organs.

Four cylindrical casts of the main rhizomorph axes are radially branching from the base of the trunk at an angle of approximately 40–45° relative to each other (Fig. 4, *c*). Relative to the vertical axis of the trunk, the rhizomorphs are inclined at angles of approximately 25–30°. Two of these main axes are secondary branching by isotomous dichotomies by angles of *c*. 30–35°. The distal ends of the rhizomorph axes are cut off when the trunk is removed from the rock or when the mine face is sinking. The rhizomorphs are about 1 m in maximal lenght, 0.3–0.5 m wide at the base and 0.15–0.20 m at the narrowest part. They are strongly flattened during diagenesis and therefore have an ellipsoidal cross-section. It is not entirely clear whether the rhizomorphs on the side of the trunk facing the wall of the museum hall and almost invisible to the observer were originally absent (which is unlikely, because Novik [1939] reports seven rhizomorhs after branching) or they were not preserved/not removed from the rock.

The surface of the rhizomorphs is covered with a glossy and smooth coal crust of unknown thickness (Fig. 4, *d*). However, in some places, longitudinal rough wrinkles, 10–15 mm wide, have been preserved (Fig. 4, *f*). The rootlets attachment points are not preserved. The trunk is on a pedestal, 0.1 to 0.5 m high.

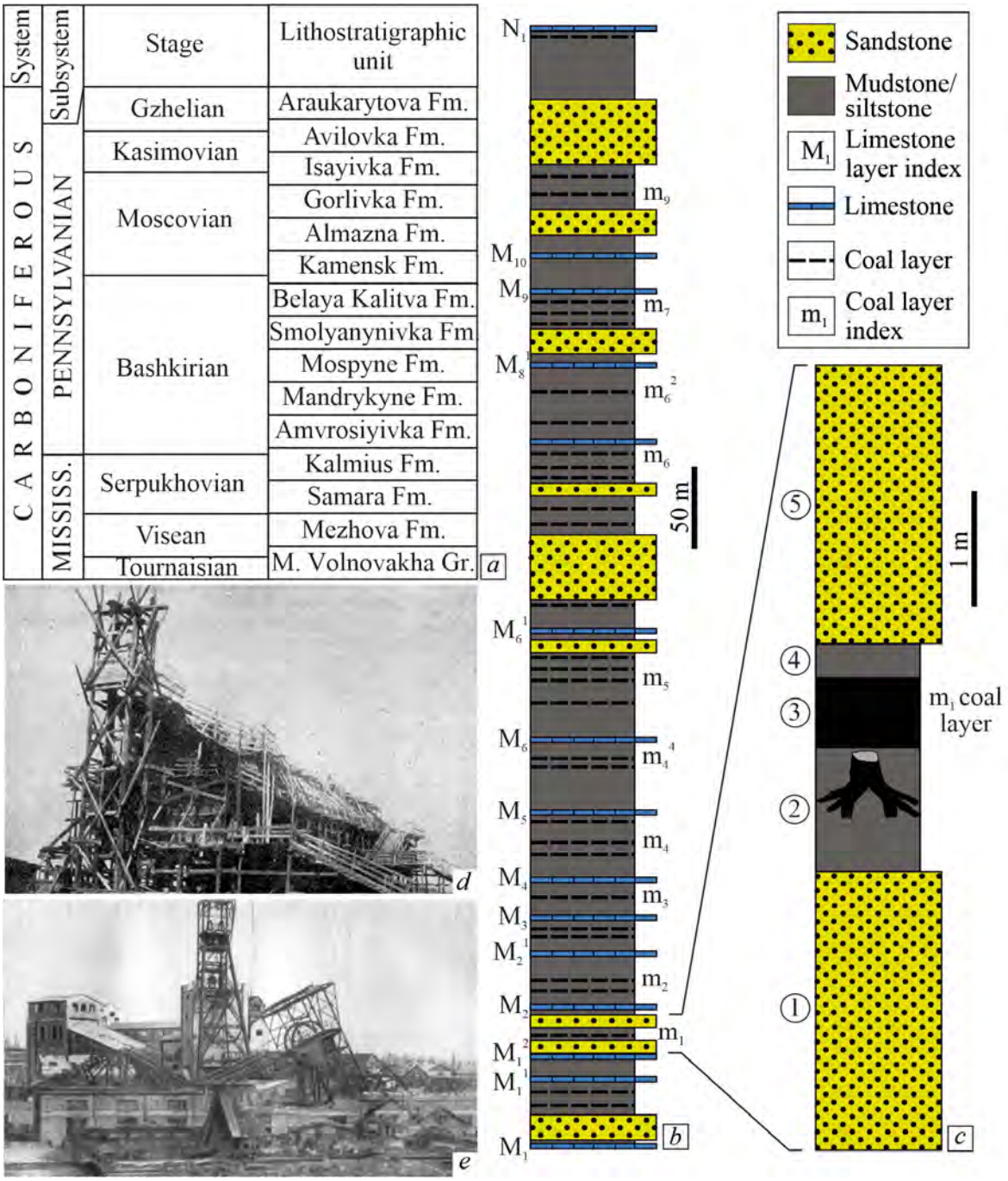

Fig. 3. Stratigraphic position of the locality of *Sigillaria* sp. preserved *in situ* (*a*–*c*) and general view of the coal mine No. 19–20 in 1926 (*d*) and in 1943 (*e*). Abbreviations: Kasimov.—Kasimovian, M. Volnovakha Gr. — Mokra Volnovakha Group, Mississip.—Mississippian, Serpukhov.—Serpukhovian, Tour.—Tournaisian. The images in Fig. 2, *d* and 2, *e* were sourced from the periodical Vsesvit [1929, No. 43–44, November 7, p. 20] and Bakuliov [1956: fig. 10], respectively.

Рис. 3. Стратиграфічне положення місцезнаходження *Sigillaria* sp., що збереглась *in situ* (*a*–*c*) та загальний вигляд вугільної шахти № 19–20 у 1926 р. (*d*) та у 1943 р. (*e*). Скорочення: Kasimov. — касимівський, M. Volnovakha Gr. — мокроволноваська серія, Mississip. — міссісіпій, Serpukhov. — серпуховський, Tour. — турнейський. Фотографії на рис. 2, *d* та 2, *e* взяті з журналу «Всесвіт» [1929, № 43–44, 7 листопада, с. 20] та Bakuliov [1956: рис. 10], відповідно.

Fig. 4. Trunk of *Sigillaria* with attached rooting organs belonging to *Stigmaria* sp. (National Museum of Natural History, NAS of Ukraine, Kyiv; specimen NMNH-967): (*a, b*) general view of the trunk (white arrow shows an area enlarged in Fig. 3, *f*), (*c, d*) rooting organs *Stigmaria* sp., (*e*) longitudinal ribs, (*f*) wrinkles on the surface of *Stigmaria* sp. Scale bars = 0.5 m (*a–e*) and 0.1 m (*f*).

Рис. 4. Стовбур сигілярії з прикріпленими кореневими органами *Stigmaria* sp. (Національний науково-природничий музей НАН України, Київ; екземпляр NMNH-967): (*a, b*) загальний вигляд стовбура (білою стрілкою показано ділянку, збільшену на рис. 3, *f*), (*c, d*) органи вкорінення *Stigmaria* sp., (*e*) поздовжні ребра, (*f*) зморшки на поверхні *Stigmaria* sp. Масштабні відрізки — 0,5 м (*a–e*) та 0,1 м (*f*).

Discussion and concluding remarks

Taxonomic remarks. Novik [1939, 1952] attributed the trunk described above to *Sigillaria* sp. This attribution is generally accepted, as some parts of it have preserved the longitudinal broad ribs (see Fig. 4, *c*) characteristic of this genus [Novik 1952; Ishchenko 1957]. It is important to note that the preservation of this *Sigillaria* stem is very similar to the *Syringodendron*-type preservation, i.e. lycopsid axes that have lost the outer layer of a periderm including the leaf bases [Cleal & Thomas 2018] due to water transportation. However, the trunk is buried *in situ*. This paradox suggests that *Syringodendron*-type preservation of axes occurs not only as a result of transportation, but also subaerial destruction of the trunk surface by aggressive environmental agents, such as precipitation, fluctuations in air temperature, wind, organismal activity, etc., or possible periodic immersion in water.

It should also be noted that the characteristic morphological features of the species *Stigmaria ficoides* Sternberg, 1822, such as the rounded shape of the lateral appendage scars [Crookall 1966; Novik 1968; Jennings 1980; Charlton & Watson 1982], were not preserved in the specimen NMNH-967. So the assignment of the described rooting organs to *Stigmaria ficoides* by Novik [1939, 1952] is premature and cannot be determined more accurately than *Stigmaria* sp.

The form genus *Stigmaria* Sternberg, 1822 is recognised in plants of at least four families (Ulodendraceae, Sigillariaceae, Diaphorodendraceae, and Lepidodendraceae) and may have been the rooting system in other extinct genera, including *Hizemodendron* Bateman & DiMichele, 1992 [Bateman 1994; DiMichele & Bateman 1996; DiMichele *et al*. 2022]. *Stigmaria* is the most common Carboniferous plant fossil in the Donets Basin and one of the most common fossils in general (Fig. 5). This genus is represented in the Carboniferous of the basin by five species: *Stigmaria evenii* Lesquereux, 1866 (upper Bashkirian–upper Moscovian), *S. ficoides* Sternberg, 1822, *S. rugulosa* Gothan, 1922 (both: the upper Bashkirian–lower Moscovian), and *S. stellata* Goeppert, 1841 (Visean–Serpukhovian) [Novik 1952, 1968, 1974; Shchogolev 1991; Fissunenko 2000].

Palaeoecology and taphonomy. As illustrated in Fig. 4, *a*, the main axes of the rhizomorphs branched off the trunk at a rather steep vertical angle. This suggests that the rhizomorphs were situated at a considerable depth within the substrate. This is at odds with the hypothesis put forth by D'Antonio *et al*. [2023] that *Stigmaria* axes were subaerial at the proximal end, as it is difficult to assume that rhizomorphs branching at an angle close to 30° remained subaerial. It is important to note that the studied trunk of *Sigillaria* sp. is positioned vertically, with no tilt towards the observer, as is the case of the specimen exhibited in the Osnabrück Museum (D'Antonio *et al*., 2023). Therefore, there can be no error in our measurements of the angles of the vertical plane.

This assumption is also consistent with the fact that the significantly moist soils on which lycopsids grew were a rather unstable substrate on which it was difficult to establish a foothold. Fissunenko and Snigirevskaya [1981] note that *Stigmaria*, at least from the Carboniferous deposits of the Donets Basin, were predominantly subhorizontal, avoiding the deep horizons of soils contaminated with hydrogen sulphide. It can be added that the probably high water table in the moist soils of the coastal lowland, where peat-forming plant assemblages grew, also limited the depth of penetration of *Stigmaria* into the substrate.

The rocks immediately below the coal seams in the Donets Basin are typically mudstones and siltstones, and rarely sandstones, containing *in situ* remains of rhizomorphs of *Stigmaria* bearing rootlets [Zaritsky 1970; Babenko *et al*. 1975]. These rocks are heavily phytoturbated and usually lack faunal remains. The plant remains, with the exception of *Stigmaria*, are also not typical for these rocks [Zaritskyi 1970]. However, Fissunenko and Snigirevskaya [1981] reported the discovery of marine fauna in palaeosoils below coal seams in the Donets Basin. In the older geological literature on the Carboniferous of the Donets Basin [e.g. Sokolov & Lutugin 1910; Stepanov 1911; Rodygin 1924], these rocks are called 'swamp soils', '*Stigmaria* layers/beds' or simply 'curly rocks' (Ukrainian: 'kutcheryavchyk'). The latter is an old expression used by the first Donets miners to refer to phytoturbated rocks with *Stigmaria* [Meffert & Krym 1926; Feofilova & Levenshtein 1963; Zaritsky 1970].

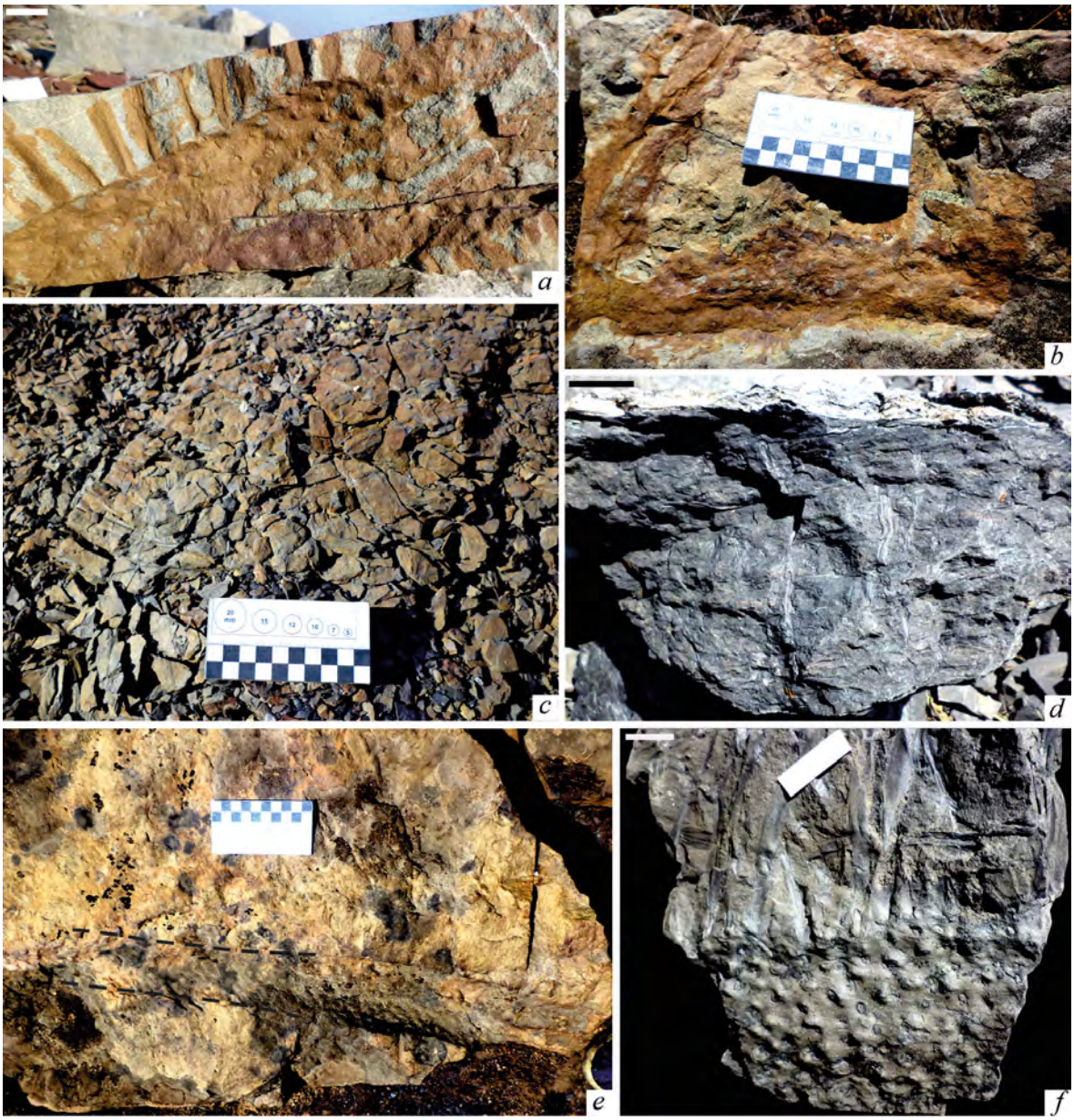

Fig. 5. *Stigmaria* preserved *in situ* from the Pennsylvanian of the Donets Basin: (*a, b, e*) *Stigmaria ficoides* from fluvisols of the Mospyne Formation, upper Bashkirian (Luhansk Raion, Luhansk Oblast), (*c, f*) *Stigmaria ficoides* from histosoils of the Mospyne Formation, (*d*) lateral appendages of *Stigmaria* in a histosoil of the late Bashkirian-aged Smolyanynivka Formation. Scale bars = 10 mm (*a, f*) and 100 mm (*b–e*).

Рис. 6. *Stigmaria*, що збереглися *in situ* з пенсильванію Донецького басейну: (*a, b, e*) *Stigmaria ficoides* з флювісолі моспинської світи (верхня частина башкирського ярусу), Луганський район, Луганська область, (*c, f*) *Stigmaria ficoides* з гістосолі серед відкладів моспинської світи, (*d*) аппендикси *Stigmaria* в гістосолі серед відкладів смолянинівської світи. Масштабні відрізки — 10 мм (*a, f*) та 100 мм (*b–e*).

Arborescent lycopsids were a significant component of peat-forming plant communities growing in river valleys and wetlands of the coastal lowland of the Donets Basin during the Early and Middle Pennsylvanian [Fissunenko 1964, 1967, 1988]. In addition to lycopsids (e.g. species of the genera *Lepidodendron*, *Lepidophloios*, *Asolanus*, *Sigillaria*, etc.) that formed the upper layer, these associations also included tree-sized sphenopsids (e.g. *Calamites*), ferns and pteridosperms that formed the middle and lower layers, respectively [Fissunenko 1964, 1967, 1988]. These wet forests were inhabited

by a diverse fauna, including millipedes belonging to the genus *Arthropleura* [Dernov 2019b], trigonotarbids [Dunlop & Dernov 2023], thelyphonids [Selden *et al*. 2013], and insects [Sharov & Sinitshenkova 1977; Dernov 2019a]. Freshwater lakes formed on the sites of silted peats were inhabited by microconchids [Dernov 2019a], bivalves [Chernyshev 1931; Shul'ga 1948; Sergeeva 1969, 1984; Dernov 2022a and references therein], eurypterids [Chernyshev 1933], concostracans [Chernyshev 1927, 1928; Dunaeva, 1950], horseshoe crabs [Chernyshev 1928; Karlov 1948; Dernov 2019a, b], cyclids [Dernov 2022b], freshwater barnacles [Tchernyshev 1935], and malacostracans [Birshtein 1966; Schram 1980], as well as acanthodians and crossopterigians [Khabakov 1927; Yefimova 1932; Karlov 1968]. It is likely that the water of these lakes was poorly oxygenated because of large amounts of hydrogen sulphide produced by bacterial communities that decomposed large masses of plant debris [Dernov 2019b].

The possibilities of reconstructing the burial conditions of the studied trunk are very limited, since we can rely on a limited data reported by Novik [1939]. The following scenario can be assumed. The sandstone of the Unit 1 is probably of alluvial or deltaic origin, since in the Pennsylvanian deposits of the Donets Basin, thick sandstone beds are of this origin [Logvinenko 1953; Feofilova & Levenshtein 1963]. According to Novik [1939], the siltstone in the lower part of the Unit 2 (see Fig. 3, *c*) is horizontally-bedded and are probably lacustrine in origin. The progressive downward tectonic movement of the Donets Basin territory resulted in a change from freshwater lakes (Unit 2a) to siliciclastic swamps (Unit 2b), and subsequently to peat swamps (Unit 3). Under such conditions, the palaeosoil (Unit 2a) probably formed very rapidly, as Carboniferous arborescent lycopsids, which had little wood, were very quickly destroyed after the plant died. As a result of upward tectonic movements, the coastal lowland began to receive large volumes of clastic material from the surrounding upland, which had sparse vegetation [Fissunenko 1964, 1967, 1988] and was therefore heavily affected by water erosion. The silting of peat swamps resulted in the formation of freshwater lakes (Unit 4), which were probably later replaced by alluvial and/or deltaic facies (Unit 5).

The presence of at least three *Sigillaria* stumps in a limited area [Novik 1939], while they are absent from many other Carboniferous plant fossil sites in the Donets Basin, indicates unique taphonomic conditions of burial of trunks in the palaeosoil bellow the m_1 coal bed. Perhaps these conditions were caused by some catastrophic event (e.g. landslide or mudflow) caused by an earthquake or other phenomenon. Evidences of palaeo-earthquakes in the Donets Basin during Carboniferous are represented by clastic dykes [Balynsky 1972; Luchinkin 1978] and submarine slumpings [Reznikov & Lobanov 1973; Dernov 2013; Dernov & Poletaev 2024]. However, we cannot state this confidently due to the inability to get acquainted with the taphonomic conditions of the locality. The absence of a surface layer of bark on both the trunk and rhizomorphs may indicate its rapid destruction in sediment, or, as we are more likely to believe, in subaerial conditions shortly after the plant's death.

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