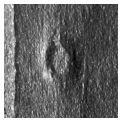
Evidence of arthropod-plant interactions from the Smolyanynivka Formation (upper Bashkirian, Lower Pennsylvanian) of the Donets Basin, Ukraine

Vitaly Dernov



Eleven damage types of terrestrial plants are described from the upper Bashkirian Smolyanynivka Formation of the Donets Basin (Frunze Mine locality in the southern part of Luhansk Oblast, eastern Ukraine). Of these eleven damage types, seven are margin feeding (DTs 12–15, 26, 142, ?143), one represents surface feeding (DT97), one oviposition (DT72), and two galling (DTs 122, 145). The diversity of arthropod-plant interaction evidence from the Smolyanynivka Formation is roughly comparable to that recorded from the adjacent Lower Pennsylvanian formations of the Donets Basin. The most likely producers of the studied arthropod-plant interaction evidence are insects, myriapods, and oribatid mites. • Key words: plant biodamages, insects, myriapods, mites, Carboniferous, feeding, galling, oviposition.

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The Carboniferous Period was a crucial interval in the evolution of modern types of arthropod-plant interactions (Donovan & Lucas 2021). A significant expansion of food webs in terrestrial palaeoecosystems is recorded during the Visean, Middle Mississippian (Schachat *et al*. 2014). This corresponds to the so-called Second phase of terrestrial arthropod colonization, which began in the Late Devonian and continued until the late Permian (Labandeira 2006, Xu *et al*. 2018), coinciding with the emergence and diversification of gymnosperms (Labandeira 2006, Schachat *et al.* 2014, Xu *et al.* 2018, Santos *et al*. 2022). During this phase, nearly all known types of interactions between animals and terrestrial plants appear (Schachat *et al*. 2014). However, the diversification of arthropod-plant interactions was delayed until the mid-Carboniferous (Mississippian–Pennsylvanian boundary) and, for some interaction types, until the Middle Pennsylvanian (Xu *et al*. 2018).

In the Lower and Middle Pennsylvanian strata, the evidence of terrestrial arthropod-plant interactions increases substantially (Schachat *et al*. 2014, Dernov 2022a). For instance, in Kasimovian deposits of the Illinois Basin, USA, plant damage caused by arthropods is predominantly recorded on pteridosperms, but also on ferns, and to a lesser extent on sphenopsids and cordaitaleans (Schachat *et al.* 2014). Plant damages by terrestrial arthropods, primarily insects and oribatid mites, includes margin feeding on pinnulae, piercing-and-sucking on shoots, galls on rachises, borings in stems, and feeding on seeds and spores occur in these deposits (Schachat *et al*. 2014).

The Pennsylvanian coal-bearing succession of the Donets Basin in eastern Ukraine is particularly rich in terrestrial plant remains from wet lowland environments (*e.g.* Novik 1974, Fissunenko 1987, Dernov & Anfimova 2024). Some of these fossils show evidence of arthropod-plant interactions, including margin feedings, galls, oviposition, and other modifications, most of which were likely produced by insects. From the upper Bashkirian (Lower Pennsylvanian) strata of the basin, the earliest known insect endophytic oviposition has been reported (Dernov 2021b), alongside additional records of arthropod-plant interactions (Vasilenko 2015; Dernov 2021a, 2022a; Rößler *et al*. 2023) or incidental illustrations and mentions (Novik 1968, Snigirevskaya 1989, Boyarina 2007, Shevchuk *et al*. 2024) were recorded in the lower Bashkirian, Moscovian, and Gzhelian deposits. Nevertheless, the diversity of such interactions in the Pennsylvanian strata of the Donets Basin appears considerably higher, as demonstrated by the available material.

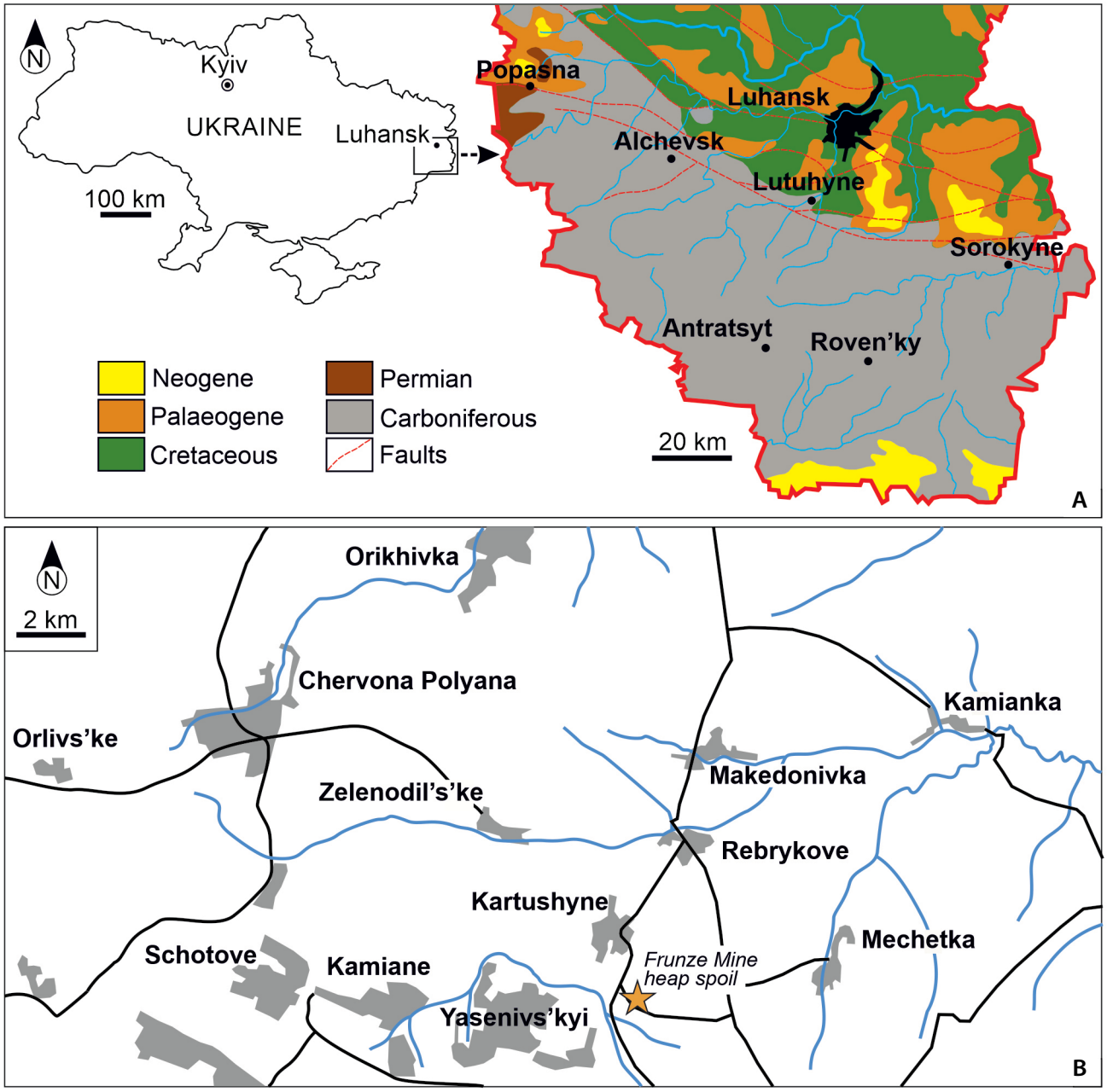


Figure 1. Geographical location of the spoil heap of the Frunze Mine.

Comparable evidence has also been reported from other Carboniferous coal-bearing and red-bed successions within the palaeoequatorial belt of Euramerica (Van Amerom 1966; Cichan & Taylor 1982; Scott & Taylor 1983; Chaloner *et al*. 1991; Labandeira & Phillips 1996a, b; Labandeira *et al*. 1997; Béthoux *et al.* 2004; LoBue, 2010; Jarzembowski 2012; Laaß & Hoff 2015; Štamberg *et al*. 2016; Correia *et al*. 2020; Laaß *et al*. 2020, 2023; Donovan & Lucas 2021; Donovan *et al.* 2022; Santos *et al*. 2022, 2025; Knecht *et al*. 2023, 2024; Rastel 2024; Vallois *et al*. 2024; Molina-Solís *et al.* 2026; and references therein).

In this paper, arthropod-induced damage on plants from the Smolyanynivka Formation (upper Bashkirian, Lower Pennsylvanian) of the Donets Basin are described. The objectives of this study are twofold: (1) to formally document evidence of arthropod-plant interactions from a newly discovered late Bashkirian locality, and (2) to provide a palaeoecological interpretation of these interactions. These data contribute to the Early Pennsylvanian record of arthropod-plant interactions from the palaeoequatorial belt of Euramerica.

Material and methods

This study examines a small collection consisting of 30 specimens of plant impressions and compressions exhibiting evidence of arthropod-plant interactions. The material was collected by the author and Mykola Udovychenko between 2009 and 2013.

The specimens originate from the spoil heap of the Frunze Mine, situated 1.2 km south of the village of Kartushyne (Rovenky Raion, Luhansk Oblast, Ukraine; coordinates: 48° 09 ′ 53.7″ N, 39° 15′ 33.1″ E) (Fig. 1).

The mine exploited the h_7, h_{10}, and h_{11} coal seams, which occur in the upper part of the Smolyanynivka Formation (Fig. 2). Plant fossils are primarily derived from the roof shales of these coal seams. However, in the heap spoil, the rocks are mixed, making it impossible to determine the exact seam from which the fossils originated.

The Smolyanynivka Formation (C_2^3 or H) consists of sandstones, siltstones, mudstones, coals, and limestones. It is characterized by thick (40–60 m) beds of coarse-grained alluvial sandstones (*e.g.* the Babakovskyi sandstone bed). This formation contains the highest coal content among Bashkirian deposits of the basin. Its thickness varies from 250 m in the north-western part of the Donets Basin to 1400 m in the south-eastern part of the basin (Aisenverg *et al*. 1963, 1975; Feofilova & Levenstein 1963; Dunaeva 1969; Poletaev *et al*. 2011; Nemyrovska & Yefimenko 2013).

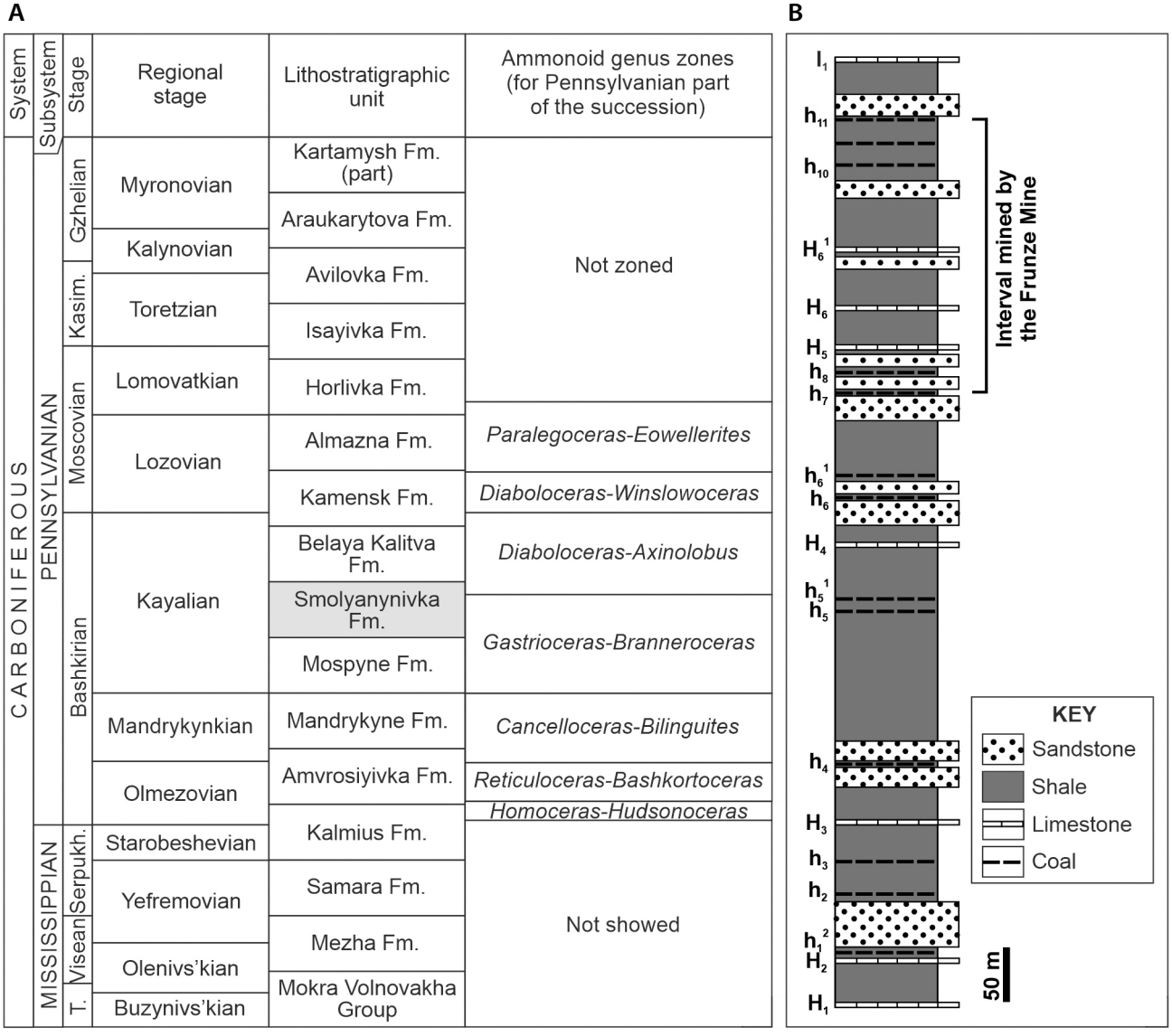


Figure 2. Stratigraphic position of the Smolyanynivka Formation (A) and lithological column of the formation in the study area (B). Abbreviations: Fm. – Formation; H_1 – limestone bed index; h_1 – coal bed index; Kasim. – Kasimovian; Serpukh. – Serpukhovian; T. – Tournaisian. Ammonoid zonation in Fig. 2A after Popov (1979). The lithological column in Fig. 2B after Dernov (2022d).

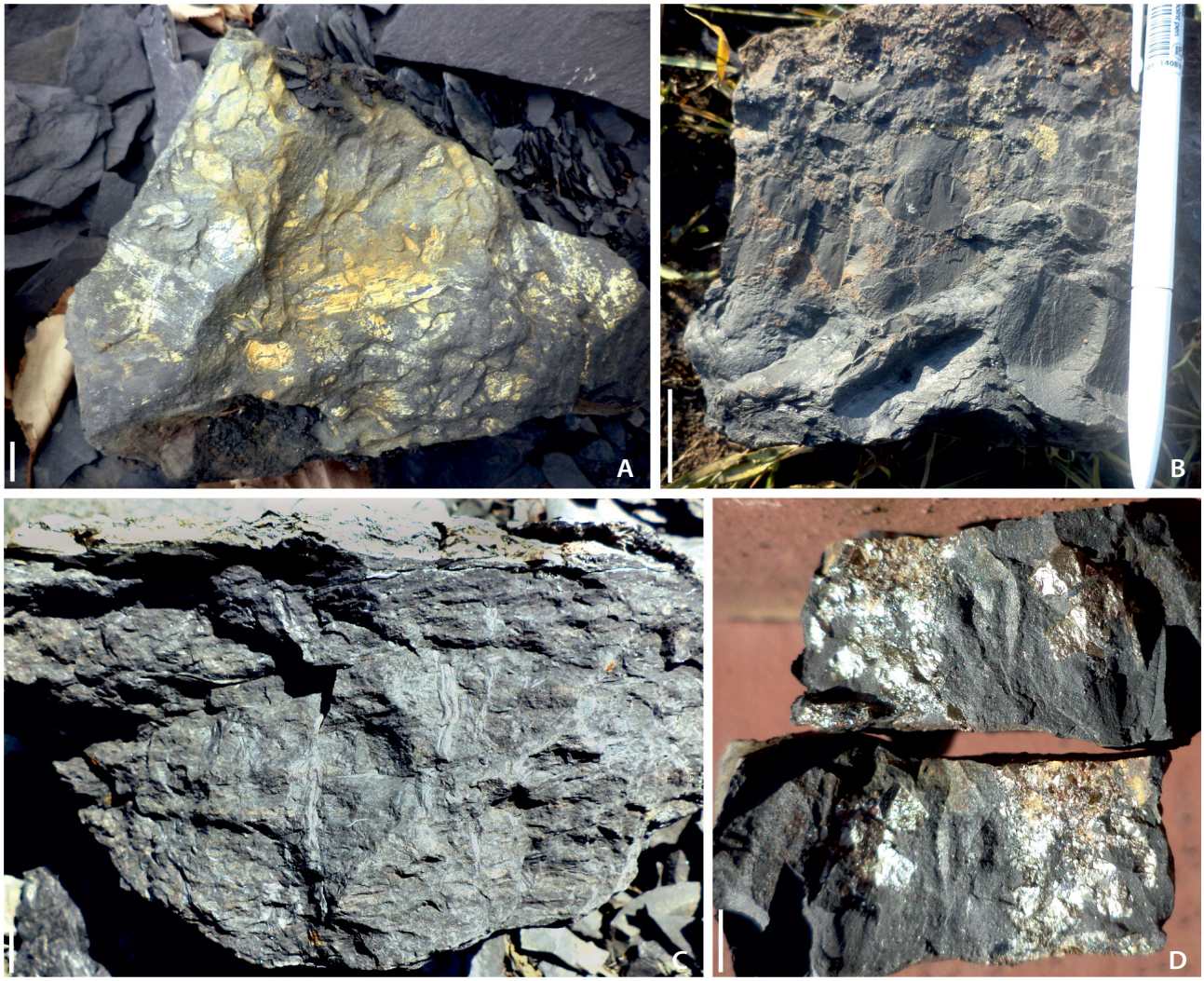
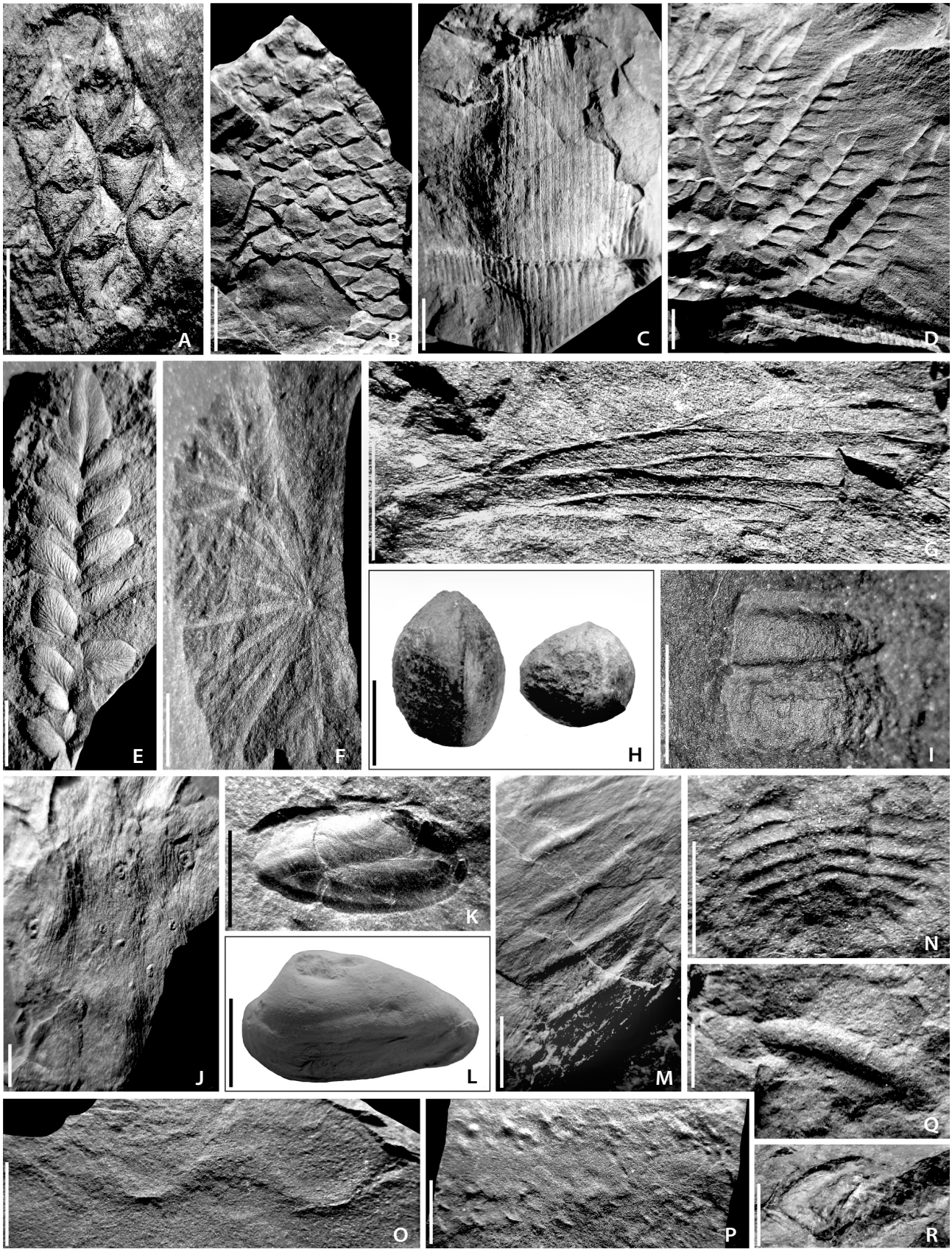


Figure 3. Fossiliferous rocks. • A – lacustrine carbonaceous shale with pyritized plant debris. • B – alluvial conglomerate. • C – vertical rootlets of *Stigmaria* preserved *in situ* in histosol. • D – carbonate concretions with small pyrite crystals. Scale bars equal 10 mm.

The heap spoil consists predominantly of blocks of black and dark-grey carbonaceous shale (Fig. 3A) and coarse-grained grey quartz-feldspar sandstone containing pebble accumulations, including re-deposited limonite concretions (Fig. 3B). Large fragments of decorticated lycopsid axes are also present within this sandstone. Phytoturbated, micaceous, carbonaceous, grey to dark-grey siltstone containing rooting structures of arborescent lycopsids (*Stigmaria ficoides* Sternberg), are fairly common (Fig. 3C). This siltstone is fossil soils, probably histosols (Feofilova 1975, Dernov & Anfimova 2024). Small (up to 2–3 cm), irregularly shaped and ellipsoidal sulphide nodules are frequently observed. Flattened carbonaceous, carbonate concretions, up to 15 cm in size

Figure 4. Some fossils from the heap spoil of the Frunze Mine. • A – *Lepidodendron obovatum* Sternberg (GM LNU 66/09). • B – *Lepidophloios laricinus* (Sternberg) Sternberg (GM LNU 66/18). • C – *Calamites cistii* Brongniart (GM LNU 66/10). • D, E – *Neuropteris heterophylla* (Brongniart) Kidston (GM LNU 66/12). • F – *Annularia radiata* (Brongniart) Sternberg (GM LNU 66/21). • G – insect wing fragment (GM LNU 66/23). • H – *Trigonocarpus parkinsonii* Brongniart (GM LNU 66/26). • I – ?myriapod (NMNHU-G 8640/03). • J – microconchids attached to the plant stem (GM LNU 66/83). • K – nonmarine bivalve *Carbonicola* sp. (GM LNU 66/48). • L – nonmarine bivalve *Carbonicola acuta* (Sowerby, 1813) with a probable shell injury acquired during the organism's lifetime in the apical region (IGS NASU-17/01). • M – fish egg capsule *Palaeoxyris* sp. (GM LNU 66/62). • N – horseshoe crab (GM LNU 66/59). • O – locomotion trace *Cochlichnus anguineus* (Hitchcock, 1858) (GM LNU 66/99). • P – horseshoe crab trackway *Kouphichnium* isp. (GM LNU 66/44). • Q – burrow *Palaeophycus tubularis* Hall, 1847 (GM LNU 66/53). • R – fish scale *Megalichthys* sp. (GM LNU 66/68). Scale bars = 10 mm (A–H, K–Q) and 2 mm (I, J, R).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and containing pyrite crystals, were also recorded within the spoil heap (Fig. 3D).

Shale contains moderately to well-preserved plant remains, including representatives of the genera *Bothrodendron*, *Cyperites*, *Lepidodendron*, *Lepidophloios*, *Lepidostrobophyllum*, *Sigillaria*, *Stigmaria*, *Annularia*, *Asterophyllites*, *Calamites*, *Sphenophyllum*, *Asterotheca*, *Renaultia*, *Eusphenopteris*, *Neuropteris*, *Paripteris*, *Odontopteris*, *Alethopteris*, *Mariopteris*, *Cyclopteris*, *Cordaianthus*, *Cordaites*, *Samaropsis*, among others (Fig. 4A–F, H).

In addition to plant remains, rock slabs at the spoil heap has yielded microconchids (Fig. 4J), non-marine bivalves *Carbonicola* (Fig. 4K, L), probable myriapods (Fig. 4I), horseshoe crabs (Fig. 4N), insects (Fig. 4G), fish scales belonging to *Rhizodopsis sauroides* (Williamson, 1849) and *Megalichthys* sp. (Fig. 4R), a xenacanthid egg capsule *Palaeoxyris* sp. (Fig. 4M), as well as burrows and locomotion traces *Cochlichnus anguineus* (Hitchcock, 1858), *Kouphichnium* isp., and *Palaeophycus tubularis* Hall, 1847 (Fig. 4O–Q) (Dernov 2023 and author's unpublished data).

The carbonaceous shales represent lacustrine deposits formed through the silting of coastal peatlands where peat accumulation took place (Logvinenko 1953, Feofilova & Levenshtein 1963). In contrast, the coarse-grained sandstones correspond to alluvial (channel) facies (Botvinkina 1954, Feofilova & Levenshtein 1963).

The studied collections (GM LNU 66; plant fossils and some associated animal remains) are housed in the Geological Museum of Taras Shevchenko Luhansk National University, Poltava, in the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (NMNHU-G 8640; myriapod and insect specimens from the Mospyne and Smolyanynivka formations), and in the Department of Palaeontology and Stratigraphy of the Palaeozoic sediments, Institute of Geological Sciences, National Academy of Sciences of Ukraine, Kyiv (specimen IGS NASU-17/01).

This study applies the classification of arthropod-plant interaction evidence proposed by Labandeira *et al*. (2007) and supplemented by subsequent publications (*e.g*. MacCracken & Labandeira 2020, Dos Santos *et al*. 2024). This classification includes hole feeding, margin feeding, skeletonization, surface feeding, piercing-and-sucking, oviposition, leaf mining, galling, and seed predation functional groups (Labandeira 1998, 2006; Labandeira *et al*. 2007). Some categories of this classification have analogues among ichnotaxa described in accordance with the rules of biological nomenclature. For example, the ichnospecies *Phagophytichnus ekowskii* Van Amerom, 1966 is morphologically indistinguishable from DT12 (*i.e.* Damage Type 12 *sensu* Labandeira *et al.* 2007) and *Cuniculonomus simplex* (Müller, 1982) is probable analogue of DT97 *sensu* Labandeira *et al.* (2007). Many types of oviposition have also been described as ichnotaxa (*e.g.* Vasilenko 2005, Sarzetti *et al.* 2009, Gnaedinger *et al*. 2014, Laaß *et al*. 2023). For example, oviposition DT72 and DT100 from the upper Bashkirian strata of the Donets Basin (Dernov 2021b; this study) correspond to the ichnospecies *Paleoovoidus megaovoidius* Gnaedinger, Adami-Rodrigues & Gallego, 2014, based on their shape, size, spatial arrangement, and the identity of the host plant organ.

At the same time, plant tissue pathologies (galls) are not trace fossils (Bertling *et al*. 2022), and therefore the rules of the International Code of Zoological Nomenclature (Ride *et al.* 1999) do not apply to them.

Plant damage resulting from abiotic and taphonomic processes exhibits a number of characteristic features that allow it to be distinguished from traces of arthropod-plant interactions, although at first glance they may appear similar (Fig. 5). These features include: (1) the complete absence of reaction (callus) tissue; (2) smooth, "fresh", or mechanically torn margins; (3) destruction of tissues without any evidence of regeneration; (4) chaotic shape and random orientation of damage; (5) lack of repetition (isolated, non-systematic damage and its random spatial distribution); (6) absence of any consistent relationship between the damage and the anatomical structure of the plant organ; (7) damages occurring along structurally weak zones of the tissue; (8) tissue deformation related to transport or mechanical stress during burial (Labandeira 1998, 2006; Labandeira *et al*. 2007; Xu *et a*l. 2018; Bertling *et al*. 2022; Laaß *et al*. 2023).

To distinguish evidence of feeding on living plants (herbivory) from evidence of feeding on dead plant material (detritivory), the criteria proposed by Labandeira (2006) were applied, namely: (1) the presence of callus or other types of reaction tissue formed in response to plant injury (indicating that the plant was alive at the time of damage and capable of responding to it); (2) the presence of microstructural features such as necrotic patches, vein-parallel striping, and characteristic excisions bearing evidence of chewing activity; (3) stereotyped feeding patterns corresponding to typical feeding modes of extant phytophagous arthropods; and (4) specificity of damage patterns targeting particular plant tissues.

These criteria were taken into account during the interpretation of arthropod-plant interaction evidence.

Biostratigraphy and age

The Smolyanynivka Formation corresponds to the upper part of the Zuyivkian Horizon (stratigraphic interval between the H_1 and H_4 limestones) and entirely to the

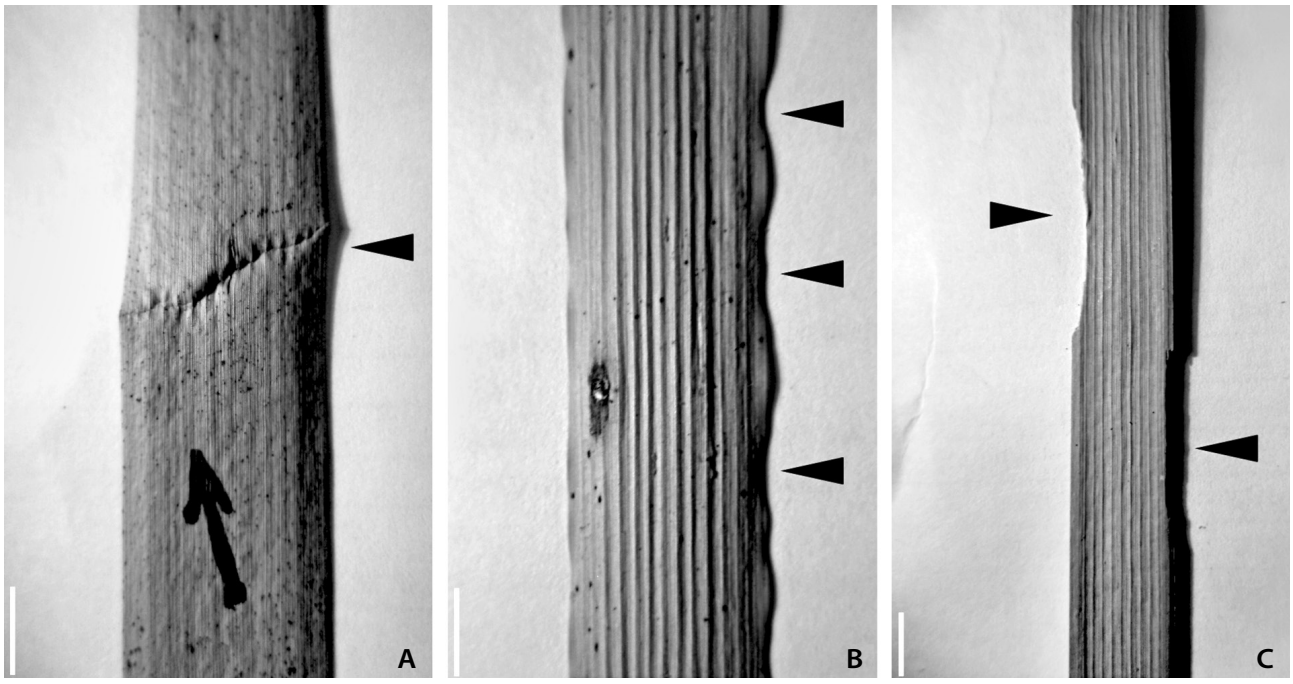


Figure 5. Abiotic damage to leaves of modern reed that is morphologically similar to fossil evidence of arthropod-plant interactions. • A – a transverse groove formed as a result of bending of the leaf under the weight of dew or raindrops. • B – oviposition (left) and a wavy leaf margin (arrowed), probably formed as a result of drying of the leaf. • C – notches along the margins of a dry leaf produced by abrasion of stiff, dry leaves under the action of wind. Scale bars = 5 mm.

Makiivkian Horizon (interval between the H_4 and I_1 limestones) of the Kayalian Regional Stage (Poletaev *et al.* 2011). It contains typical Langsettian (= Westphalian A, early late Bashkirian) terrestrial plants (Novik 1974, Fissunenko 1975). According to Boyarina (2016), the formation is assigned to the *Laveineopteris loshii* Subzone of the *Lyginopteris hoeninghausii* Zone *sensu* Wagner & Álvarez-Vázques (2010) within the upper Langsettian.

Ammonoids such as *Gastrioceras listeri* (Sowerby, 1814) and *G. lupinum* Popov, 1979 from the formation indicate correlation with the *Brannerоceras–Gastrioceras* genus zone and probably with the lowermost part of the *Diaboloceras–Axinolobus* genus zone (Popov 1979). In addition, non-marine bivalves recovered from the formation correspond to the upper part of the *communis* Zone and the lower *modiolaris* Subzone of the Langsettian (Sergeeva 1981, Dernov 2022b).

Evidence of arthropod-plant interaction

Margin feeding

The consumption of the leaf edge and apex characterizes the margin feeding (Pinheiro *et al*. 2024, Dos Santos *et al*. 2024). Margin feeding is considered to be caused by arthropods possessing mandibulate mouthparts and employing a chewing mode of feeding (Dos Santos *et al*. 2024). Margin feeding is among the oldest functional feeding groups (Schachat *et al.* 2014): the earliest known examples are recorded on the liverwort *Metzgeriothallus sharonae* Hernick, Landing & Bartowski from the Middle Devonian of New York State, USA (Schachat *et al*. 2014), and on the pteridosperm *Triphyllopteris austrina* (Etheridge Jr.) Morris from the Serpukhovian of Australia (Iannuzzi & Labandeira 2008). In the Pennsylvanian of Euramerica, margin feeding occurs most commonly on the pinnules of pteridosperms (Schachat *et al*. 2014), a pattern also evident in the present assemblage.

Seven Damage Types (DTs) *sensu* Labandeira *et al*. (2007), belonging to the margin feeding, have been identified in the Smolyanynivka Formation.

Damage Type 12 (Fig. 6C, D) consists of arc-shaped excisions, 2.5–3.0 mm deep and up to 8 mm wide, with smooth margins, located along the lateral edges of pinnules of the pteridosperm *Neuropteris heterophylla* (Brongniart) Kidston. The excisions cross the secondary veins but do not extend to the main vein.

Damage Type 13 (Fig. 6B, G) comprises semicircular excisions, 4.0–4.5 mm wide and 1–2 mm deep, situated at the apical portion of *N. heterophylla* pinnules. These are aligned with the secondary venation, with margins either straight (Fig. 6B) or slightly projecting outward (Fig. 6G) and with a very thin reaction tissue rim.

Damage Type 14 (Fig. 6E) is semi-elliptical excisions, 6.0 mm wide and 2.5 mm deep, on the lateral margins at the base of *N. heterophylla* pinnules. The excisions nearly reach the main vein, and their margins are entire.

Damage Type 15 (Fig. 6I) is a long, narrow excision (30 mm long and 3 mm maximum wide) along the lateral margin of *Cyclopteris* sp., which widens distally into a four-rayed rosette. The excision is oriented parallel to the venation.

Damage Type 26 (Fig. 6H) consists of narrow, wedge-shaped zones of interveinal tissue removal, 2 mm wide and 7–9 mm deep, extending to the base of the main vein of a *Neuropteris* sp. pinnule.

Damage Type 142 (Fig. 6A) is an almost perfectly semi-circular excision, 6.5 mm wide and 4.0 mm deep, on the lateral margin of a pinnule of *Odontopteris robusta* Zalessky. The excision cuts across the secondary veins, with entire margins bordered by a reaction rim approximately 0.8 mm wide.

The specimen illustrated in Fig. 6F, showing a series of shallow but broad marginal excisions, most likely represents margin feeding DT143, although its poor preservation precludes definitive assignment.

Surface feeding

Surface feeding is characterized by partial consumption of the leaf blade thickness (Dos Santos *et al*. 2024).

Damage Type 97 (Fig. 7F) occurs on a pinnule of *Odontopteris robusta*. The damage is a narrow, arch-shaped, slightly curved window feeding trace, measuring 5 mm in length and 2.5 mm in width, positioned at the pinnule margin. Its edges are nearly parallel and aligned with the secondary veins. The surface within the feeding trace is almost smooth and slightly elevated relative to the edges.

Oviposition

Oviposition refers to the process by which female insects use a specialized organ, the ovipositor, to deposit eggs on the surface (exophytic oviposition) of living or dead plants, or within plant tissues (endophytic oviposition) (Gnaedinger *et al*. 2014, Xu *et al*. 2018). Among extant insects, endophytic oviposition is practiced by representatives of Odonata, Orthoptera, Hemiptera, Coleoptera, Lepidoptera, and Hymenoptera (Vasilenko & Rasnitsyn 2007, Laaß & Hoff 2015). Eggs laid within plant tissues are protected from predators as well as from fluctuations in temperature and humidity (Corbet 1963, Laaß & Hoff 2015).

Damage Type 72 (Figs 6J; 7A, B) comprises endophytic oviposition scars on pteridosperm rachises. In specimen GM LNU 66/19 (Fig. 6J), the scars are ellipsoidal, nearly fusiform, and surrounded by raised reaction tissue rims approximately 0.3 mm wide. The scars are slightly inclined relative to the axis surface, as one edge of each scar is more elevated than the other. Scar length ranges from 3–5 mm, width from 2–3 mm. Although the overall arrangement is unclear due to preservation, the long axes of the scars are almost parallel to each other and to the pteridosperm axis.

In specimens GM LNU 66/14 and GM LNU 66/15 (Fig. 7A, B), DT72 appears as ellipsoidal lesions 4–5 mm long and 2.5 mm wide. They occur in small groups arranged parallel to the rachises. The lesion surfaces are micro-tuberculate, and in some cases (Fig. 7B, top photo), fine concentric folds are present.

Galling

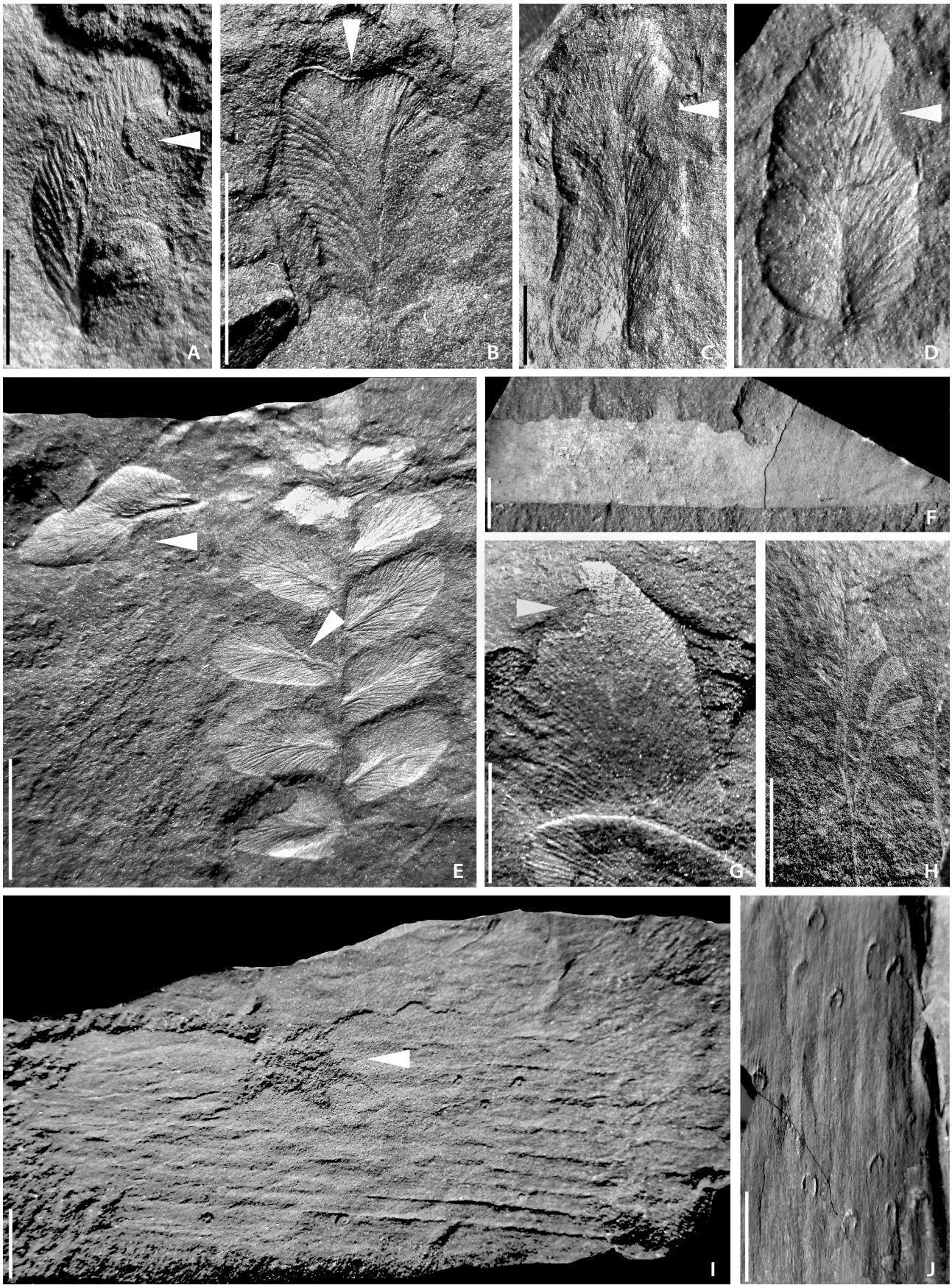
Galling represents pathological modifications of plant tissues induced by the activity of insects, mites, nematodes, fungi, bacteria, or viruses (Labandeira & Phillips 1996b, Xu *et al*. 2018).

Damage Type 122 (Fig. 7E) consists of ellipsoidal to nearly round, smooth galls, 5–6 mm long and 4 mm wide, on the leaf of *Cordaites* sp. The leaf veins remain unmodified within the gall.

Damage Type 145 (Fig. 7C, D, G, H) comprises round to slightly ellipsoidal, flattened galls with diameters of 3–4 mm. Each gall is bordered by a thin (0.5 mm), low (0.3 mm) rim encircling the flattened central region. These galls occur on shoots of indeterminate plants, usually singly; however, in specimen GM LNU 66/20 (Fig. 7H), a series of three galls is transversely aligned along the shoot axis.

In addition to the above types, the collection includes an indeterminate galling type (Fig. 7I) on the axis of an unidentified plant. This damage appears as a slightly swollen area bounded by a transverse, W-shaped, narrow groove.

Figure 6. Evidence of plant-arthropod interactions from the Smolyanynivka Formation. • A – margin feeding DT142 on *Odontopteris robusta* (GM LNU 66/07). • B, G – margin feeding DT13 on *Neuropteris heterophylla* (B – GM LNU 66/06, G – GM LNU 66/05). • C, D – margin feeding DT12 on *Neuropteris heterophylla* (C – GM LNU 66/04, D – GM LNU 66/08). • E – margin feeding DT14 on *Neuropteris heterophylla* (GM LNU 66/03). • F – margin feeding ?DT143 on an unidentified plant (GM LNU 66/02). • H – margin feeding DT26 on *Neuropteris* sp. (GM LNU 66/11). • I – margin feeding DT15 on *Cyclopteris* sp. (GM LNU 66/13). • J – oviposition DT72 on the pteridosperm axis (GM LNU 66/19). Scale bars = 10 mm.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Plant taphonomy and palaeoecology

The studied plant remains represent a typical roof-shale taphoflora, preserved in the rocks overlying coal seams and recording the final stages of peat accumulation in a so-called coal swamp (Gastaldo *et al*. 1995, Cleal 2017). Plant remains with damages likely belong to the hypoautochthonous (or subautochthonous) type of burial classification of Pennsylvanian plants from the Donets Basin, as proposed by Fissunenko (1973). This type includes burials consisting of plant remains that were only slightly transported and buried near their original growth location (Fissunenko 1973). Such burial types are characteristic of deposits from coastal lakes, which are quantitatively dominated by pteridosperms, arborescent ferns, and sphenopsids, as well as of deposits from silting-up swamps, where remains of arborescent lycopsids, sphenopsids, and ferns prevail (Fissunenko 1973).

The carbonaceous black and dark-gray shales bearing studied here plant remains formed in shallow freshwater lakes located on an alluvial-deltaic swampy lowland (Zhemchuzhnikov *et al*. 1960; Feofilova & Levenshtein 1963; Zaritskiy 1970; Dernov 2022b, 2025). The position of these rocks above the coal seams indicates that such lakes developed due to the conservation of peatlands by mineral sediments and the cessation of peat accumulation. The muds of these lakes were likely contaminated with hydrogen sulphide due to the activity of sulphate-reducing bacteria, whose development was triggered by large amounts of organic detritus, mainly fragments of terrestrial plants entering the water body from the adjacent highly biologically productive terrestrial ecosystems (Dernov 2022b, 2025). Periodically, hydrogen sulphide levels likely rose directly into the water column, or even continuously contaminated the bottom part of the water column (Dernov 2022b, 2025).

These lakes were inhabited by a variety of animals, including microconchids (Fig. 4J), non-marine bivalves (Tchernyshev 1931; Shulga 1948; Sergeeva 1958, 1960, 1969, 1981, 1984; Dernov 2022b), horseshoe crabs and eurypterids (Tchernyshev 1927, 1928, 1933; Karlov 1948; Shpinev 2014, 2018; Dernov 2019a, b), crustaceans (Tchernyshev 1927, 1928, 1935; Birshtein 1966; Schram 1980; Dernov 2022c), acanthodians, crossopterigians, and cartilaginous fishes (Khabakov 1927, 1949; Yefimova 1932; Karlov 1968; Dernov & Poletaev 2024).

The shoreline of these lakes was covered by dense, but systematically uniform hygrophilous vegetation, represented by monotaxonomic associations of arborescent sphenopsids (Fissunenko 1973, 1987). However, the sediments of the lakes also likely received plant fragments predominantly from hygrophilous communities, mainly consisting of arborescent lycopsids, which were widespread in the humid coastal lowlands and river floodplains (Fissunenko 1973, 1987; Fissunenko & Snigirevskaya 1981).

Diversity of Damage Types (DTs)

A total of 11 DTs has been identified from the Smolyanynivka Formation (Tab. 1). In the underlying Mospyne Formation, 14 DTs were previously described by the author (Dernov 2021a, b), including: hole feeding DTs 02 and 03; margin feeding DTs 12 and 81; surface feeding DT75; galling DTs 117, 122, and 127; piercing-and-sucking DT46; oviposition DTs 76, 100, 101, 175; and wood boring DT243.

In the overlying Belaya Kalitva Formation, 13 DTs have been recorded, comprising: hole feeding DTs 03, 78, and 103; margin feeding DTs 12, 13, 14, 15, and 81; surface feeding DT75; galling DT146; piercing-and-sucking DT46; and oviposition DTs 102 and 108 (Dernov 2022a).

The diversity of arthropod-plant interaction evidence from the Smolyanynivka Formation is roughly comparable to that recorded from the Mospyne Formation (Dernov 2021a, b) and the Belaya Kalitva Formation (Dernov 2022a). Feeding traces dominate, particularly margin feeding, primarily observed on the pteridosperms *Neuropteris heterophylla* and *Odontopteris robusta*, which are the most abundant taxa in the flora collected from the spoil heap of the Frunze Mine. This conclusion supports the hypothesis that insects preferred broad-leaved pteridosperms as host plants resulting in an expansion of herbivory from the Pennsylvanian to early Permian (*e.g.* Beck & Labandeira 1998, Labandeira 2006, Labandeira & Allen 2007, Donovan & Lucas 2021, Laaß *et al.* 2023). However, in the plant assemblage from the Frunze Mine site, narrow-leaved pteridosperms

Table 1. Summary of the studied arthropod-plant interactions

Functional group	Damage type	Host plants
Margin feeding	DT12	*Neuropteris heterophylla*
	DT13	*Neuropteris heterophylla*
	DT14	*Neuropteris heterophylla*
	DT15	*Cyclopteris* sp.
	DT26	*Neuropteris* sp.
	DT142	*Odontopteris robusta*
	?DT143	?
Surface feeding	DT97	*Odontopteris robusta*
Oviposition	DT72	Pteridosperm
Galling	DT122	?
	DT145	*Cordaites* sp.

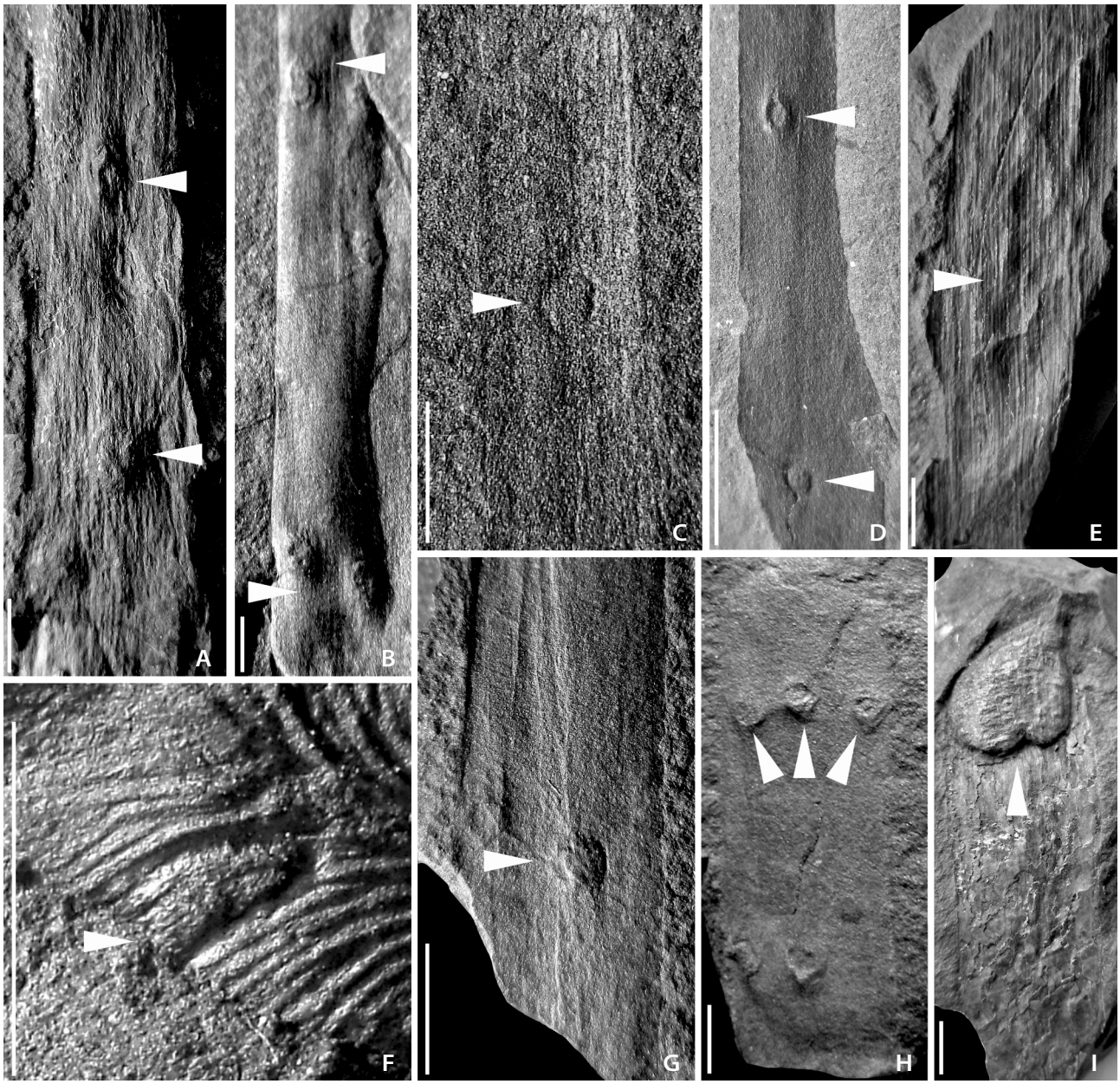

Figure 7. Evidence of plant-arthropod interactions from the Smolyanynivka Formation. • A, B – oviposition DT72 on the pteridosperm axis (A – GM LNU 66/14, B – GM LNU 66/15). • C, D, G, H – galling DT145 on indeterminate plants (C – GM LNU 66/01, D – GM LNU 66/16, G – GM LNU 66/17, H – GM LNU 66/20). • E – galling DT122 on *Cordaites* sp. (GM LNU 66/22). • F – surface feeding DT97 on *Odontopteris robusta* (GM LNU 66/24). • I – indeterminate damage type (GM LNU 66/25). Scale bars equal 10 mm.

(*Alethopteris*) and pteridosperms with strongly dissected fronds (*Eusphenopteris* and *Mariopteris*) are much less frequent than the genera *Neuropteris* and *Odontopteris*. In addition, marginal feeding traces on the dissected margins of *Eusphenopteris* and *Mariopteris* pinnules are more difficult to recognize and may therefore have been overlooked.

In the Smolyanynivka Formation, no piercing-and-sucking damages were observed, in contrast to the adjacent formations. Additionally, seed predations are absent in the Carboniferous of the Donets Basin, likely reflecting collection bias and the incompleteness of the available assemblages rather than a true absence.

Although the formal diversity of arthropod-plant interaction evidence among these three formations is similar, ranging from 11 to 14 DTs, actual diversity is difficult to assess due to differences in collection intensity. The Mospyne Formation material originates from multiple stratigraphic levels and, despite the relative scarcity of plant remains, extensive collecting over many years has

resulted in the most comprehensive assemblage of the three formations. By contrast, material from the Belaya Kalitva Formation comes from a single stratigraphic level (see Dernov & Udovychenko 2021 for more details on the fossil site), yet its diversity of evidence is broadly comparable to that of the Mospyne Formation.

Palaeocological implication

Plant feeding can be divided into two main categories: detritivory, which involves eating dead plant material, and herbivory, which involves consuming living plant tissue (Kellogg & Taylor 2004, Xu *et al*. 2018). In the fossil record, herbivory is more frequently observed and can be identified by signs such as necrotic tissue, callus formation, or other abnormal tissue responses resulting from damage sustained while the plant organ was still alive (Meyer & Marequelle 1983, Labandeira 1998; see Material and methods section). However, the above-described evidence of surface and margin feeding show no evidence of plant tissue reaction, except for some specimens (*e.g.* Fig. 6A), and therefore the feeding traces described here are probably indicative of detritivory.

Currently, the oldest known endophytic insect oviposition (eggs deposited within plant tissues) comes from the Mospyne Formation of the Donets Basin (Dernov 2019b, 2021a). The DT72 oviposition described above is slightly younger, and still younger oviposition evidence has been recorded from the Belaya Kalitva Formation (Vasilenko 2015, Dernov 2022a). Nevertheless, these remain among the oldest known examples worldwide. However, the earliest ovipositors are documented in insects that lived during the Mississippian–Pennsylvanian transition (Labandeira 2006). These include representatives of the Odonatoptera, Palaeodictyopteroidea, Dictyoptera, Archaeorthoptera, Hemipteroidea, and certain holometabolan lineages (Béthoux *et al*. 2004, Labandeira 2006, Laaß & Hoff 2015, Laaß *et al.* 2023).

The oviposition from the Smolyanynivka Formation represent a typical morphotype characteristic of the Late Palaeozoic to Middle Jurassic and characterized by large endophytic egg cavities, whereby the ovipositional scars may often considerably vary both in size and in shape (Laaß & Hoff 2015). In most cases, no clear distinctive pattern of the scars can be observed (Laaß & Hoff 2015). However, the oviposition from the Mospyne Formation (Dernov 2021a, fig. 4b, d) are arranged in an arcuate pattern (see Laaß & Hoff 2015, fig. 1). The rim of reaction tissue around oviposition scars (Fig. 6J) indicate that the pteridosperm rachis was probably still alive when the insect spawned.

In the fossil record, 80% of galls are found on leaves (Labandeira 2002), but galls in the Carboniferous occur almost exclusively on trunks (Labandeira 2021). The galls from the upper Bashkirian strata of the Donets Basin (Dernov 2021a, 2022a; this study) were found predominantly on shoots.

The most likely producers of the arthropod-plant interaction evidence described here are insects, myriapods, and mites. Margin and surface feedings are considered to be caused by arthropods possessing mandibulate mouthparts and employing a chewing mode of feeding (Dos Santos *et al*. 2024). Among Carboniferous insects, this group includes Orthoptera and "Eoblattida" (Dos Santos *et al*. 2024). Myriapods may also have been producers of margin feeding traces on dead leaves (Ponomarenko 2006).

The producers of the oviposition were insects belonging to the Odonatoptera, Palaeodictyopteroidea, Dictyoptera, Archaeorthoptera, Hemipteroidea, and Orthoptera (Grimaldi & Engel 2005, Labandeira 2006, Schachat *et al*. 2014, Romero-Lebrón *et al.* 2022, Laaß *et al*. 2023, Dos Santos *et al.* 2024).

The Carboniferous entomofauna of the Donets Basin remains poorly studied. At present, only sporadic insect remains are known from various intervals of the Pennsylvanian sequence. The oldest of these include a body impression of an undescribed "dragonfly" from black shale in the upper part of the Dyakove Group (age-equivalent to the Mospyne Formation, upper Bashkirian) (Dernov 2016, Dernov & Poletaev 2024), as well as wing impressions of Orthoptera? indet. (Fig. 8B), Palaeodictyopteroidea indet. (Fig. 8E), and other currently undetermined insects (Fig. 8C, D) from the Mospyne Formation.

Within the Belaya Kalitva Formation in the eastern Donets Basin (Kamensk-Shakhtinsky area, Russia), a rich locality of terrestrial arthropod remains has been documented, including the oldest known spider, trigonotarbids, and insects (Selden *et al.* 2014, Shpinev 2018). In the Kasimovian strata of Alchevsk Raion, Luhansk Oblast (Ukraine), the Lomovatka (= Kartanash) locality has yielded insects such as *Spilaptera tanaica* Sharov & Sinitshenkova, 1977, *Lomovatka udovichenkoi* Aristov, 2015, and several other undetermined taxa (Sharov & Sinitshenkova 1977, Udovychenko & Bratishko 2013, Shpinev 2014, Aristov 2015, Pavlenko 2017). From the Smolyanynivka Formation, only a single, fragmentary insect wing impression is currently known (Fig. 4G).

Body remains of myriapods have been documented from the Mospyne and Smolyanynivka formations of the Donets Basin (Figs 4I, 8A). Fossils attributed to the genus *Arthropleura* Jordan *in* Jordan & von Meyer, 1854 also occur in the Mospyne Formation (Dernov 2019a, 2025) and may include juvenile specimens. The diet of

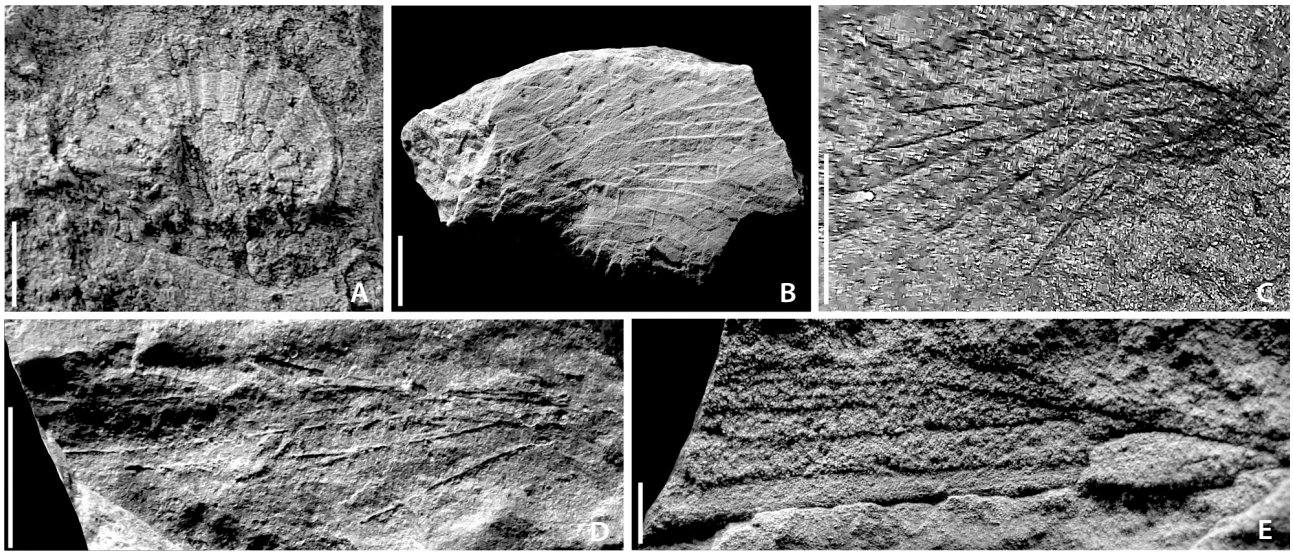

Figure 8. Some late Bashkirian terrestrial arthropods from the Donets Basin. • A – myriapod (NMNHU-G 8640/02). • B – Orthoptera? indet. (uncatalogued). • C, D – undetermined insects (uncatalogued). • E – Palaeodictyopteroidea indet. (uncatalogued). Scale bars = 5 mm (A, B, D, E) and 2 mm (C).

arthropleurids remains uncertain; however, they have been hypothesized to have been detritivores (Lamsdell 2024) or herbivores (Shear & Kukalova-Peck 1990, Eskov 2008, Schneider & Werneburg 2010). Myriapod locomotion traces *Diplichnites* and *Diplopodichnus* are relatively common in Pennsylvanian deposits of the Donets Basin (*e.g*. Dernov, 2019a). This ichnological evidence suggests a widespread distribution of myriapods within humid, coastal alluvial-deltaic lowlands vegetated by arborescent sphenopsids, lycopsids, pteridosperms, and ferns.

Oribatid mite coprolites have also been recorded in the Pennsylvanian sequence of the Donets Basin. In addition to the previously documented mineralized plant tissues preserved in coal balls (Snigirevskaya 1989), coprolites have been found in permineralized wood within the Gzhelian Araukarytova Formation (Rößler *et al*. 2023).

Conclusion

(1) From the upper Bashkirian Smolyanynivka Formation of the Donets Basin (Frunze Mine locality), eleven damage types of terrestrial plants (mainly pteridosperm genera *Neuropteris*, *Odontopteris*, and *Cyclopteris*) are described. Of these eleven damage types, seven are margin feeding (DTs 12–15, 26, 142, ?143), one represents surface feeding (DT97), one oviposition (DT72), and two galling (DTs 122, 145).

(2) The plant remains with damages originate from the roof shales of coal seams. These rocks accumulated at freshwater lakes located on an alluvial-deltaic coastal lowland.

(3) The diversity of arthropod-plant interaction evidence from the Smolyanynivka Formation is roughly comparable to that recorded from the adjacent Lower Pennsylvanian formations of the Donets Basin.

(4) The most likely producers of the studied arthropod-plant interaction evidence are insects, myriapods, and mites.

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