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Late Bashkirian (Early Pennsylvanian) horseshoe crabs (Chelicerata: Xiphosura) from the Mospyne Formation, Donets Basin, Ukraine

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Abstract

The Bashkirian xiphosurid assemblage of the Donets Basin comprises only three genera: *Euproops*, *Prestwichianella*, and *Belinurus*. With the exception of *Euproops danae*, all recorded species appear to be endemic to the basin. A small xiphosurid assemblage consisting of *Belinurus* sp., ?*Euproops* sp., and indeterminate xiphosurid remains is described from non-marine deposits of the Mospyne Formation (upper Bashkirian, Lower Pennsylvanian) in the central Donets Basin, eastern Ukraine. Together with *Belinurus iswarinensis* (Chernyshev, 1927), previously reported from the Bashkirian Mandrykyne and Mospyne formations, these specimens represent the oldest known Carboniferous xiphosurids from the Donets Basin.

Keywords: Xiphosura, *Belinurus*, *Euproops*, late Bashkirian, palaeoecology

1. Introduction

Extant horseshoe crabs (Xiphosura Latreille, 1802) comprise four species: *Limulus polyphemus* (Linnaeus, 1758), *Carcinoscorpius rotundicaudata* (Latreille, 1802), *Tachypleus gigas* (Müller, 1785), and *T. tridentatus* (Leach, 1819), distributed along the Atlantic coast of eastern North America and throughout southern and southeastern Asia (Lamsdell, 2019, 2020). During the Pennsylvanian, regarded as the evolutionary heyday of the group, xiphosurids were characteristic components of non-marine faunal assemblages (Selden et al., 2019; Bicknell & Pates, 2020). Their fossils are relatively common in Bashkirian to Kasimovian coal-bearing strata throughout Euramerica (e.g., Bölsche, 1885; Packard, 1886; Dix & Pringle, 1929, 1930; Pruvost, 1930; Eller, 1938; Stainier, 1938; Schwarzbach, 1962; Ambrose & Romano, 1972; Siegfried, 1972; Anderson, 1994; Schultka, 1994; Filipiak & Krawczyński, 1996; Anderson et al., 1999; Tashman et al., 2019; Lustri et al., 2020; Bicknell et al., 2019, 2021, and references therein).

In Ukraine, Pennsylvanian coal-bearing successions occur in three principal regions: the Lviv Palaeozoic Trough, the Dnipro-Donets Depression, and the Donets Basin (Shulga et al., 2007; Nemyrovska & Yefimenko, 2013; Poletaev & Vdovenko, 2013). To date, however, xiphosurids have been recorded only from the Donets Basin in eastern Ukraine (Chernyshev, 1927, 1928; Karlov, 1948; Shpinev, 2018; Dernov, 2019a, b). Their stratigraphic distribu-

tion is restricted to a relatively narrow stratigraphic interval extending from the lower Bashkirian (*Bilinguites-Cancelloceras* ammonoid genus zone) to the upper Moscovian (*Pseudoparalegoceras-Wellerites* ammonoid genus zone). This interval corresponds to the most coal-rich part of the Carboniferous succession in the basin (Logvinenko, 1953).

Chernyshev (1927, 1928) provided the first formal descriptions of Carboniferous xiphosurids from the Donets Basin, although a xiphosurid specimen had been earlier noted by Zalessky (1907). In the first paper, Chernyshev (1927) documented previously established species *Prestwichia danae* (Meek & Worthen, 1865) and described four new taxa: *Prestwichianella zalesskii*, *Bellinurus iswarinensis*, *B. metschetnensis*, and *B. stepanowi*, all from the Pennsylvanian strata of the basin. Subsequently, Chernyshev (1928) briefly described and illustrated new specimens of *Prestwichia danae*, *Bellinurus iswarinensis*, and *B. stepanowi*. Because the generic name *Prestwichia* Woodward, 1867 is preoccupied, it was replaced by *Prestwichianella* Cockerell, 1905 (Shpinev, 2018).

Karlov (1948) later described a further species, *Prestwichianella tschernyshewi*, but its taxonomic validity remains uncertain. Shpinev (2018) partly revised the taxa established by Chernyshev and examined additional material from the Donets Basin. Shpinev (2018) and Bicknell & Pates (2020) illustrated several specimens of the type series of the species described by Chernyshev (1927). Nevertheless, the species of *Belinurus* erected by Chernyshev (1927) require comprehensive revision to clarify their generic assignments (Lamsdell, 2022).

The present study formally documents new xiphosurid material from the upper Bashkirian Mospyne Formation of the Donets Basin. These fossils represent some of the oldest horseshoe crabs known from the Carboniferous succession of the basin. Previously, Chernyshev (1928) briefly described and figured *Bellinurus iswarinensis* from the roof shale of the g_3 coal in the Mospyne Formation. This formation has yielded a diverse arthropod fauna, including trilobites (Weber, 1933; Mychko & Dernov, 2019), arthropleurid myriapods (Dernov, 2019a, 2025b), conchostracans (Dernov & Udovychenko, 2021), cyclids (Dernov, 2022c), phyllocarids (Dernov, 2025a), and insects (Dernov, 2019a, 2019b, 2025b). Xiphosurid remains from the Mospyne Formation have also been briefly mentioned by the present author in earlier studies (Dernov, 2019a, 2019b, 2025a).

The aims of this study are twofold: (1) to document the systematic diversity of horseshoe crabs from the early late Bashkirian of the Donets Basin, and (2) to discuss their palaeoenvironment, habitat preferences, and taphonomic conditions.

2. Materials and methods

Twelve poorly to moderately preserved impressions and compressions of xiphosurid exoskeletal fragments were examined. Owing to the generally poor preservation of the material, the systematic placement of a substantial proportion of the material remains uncertain.

The material described herein was collected by the author from three stratigraphic horizons within the Mospyne Formation (Zuyivkian Horizon, lower part of the Kayalian regional stage, upper Bashkirian, Lower Pennsylvanian; Fig. 1A) in southern Luhansk Oblast, Ukraine. These horizons comprise: (1) a 0.7 m thick interval of greyish-yellow shale interbedded within a deltaic sandstone succession, approximately 43 m below the G_1^2 limestone; (2) the roof shale of the g_1^2 coal seam; and (3) the roof shale of the g_2 coal seam (Fig. 1B).

The fossil-bearing horizons are exposed at three localities in the vicinity of the village of Makedonivka, Luhansk Raion, Luhansk Oblast (Fig. 2): (1) sandstone quarries approximately 1 km west of the village (48°14'12.0"N, 39°15'19.4"E); (2) spoil heaps of an abandoned small coal mine near the northern

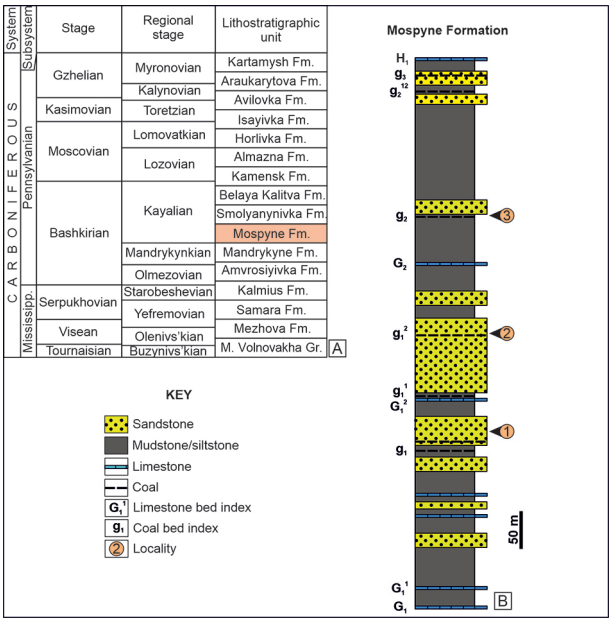

Fig. 1. A – Stratigraphic position of the Mospyne Formation within the Carboniferous succession of the Donets Basin. **B** – Stratigraphic position of the xiphosurid-bearing horizons within the Mospyne Formation. Abbreviations: Fm, Formation; Gr, Group; M., Mokra.

outskirts of the village, where the g_1^2 coal seam was formerly exploited (48°14'36"N, 39°17'58"E); and (3) spoil heaps of small-scale coal mines approximately 1.5 km north of the village, where the g_2 coal seam was mined (48°14'54.1"N, 39°18'20.6"E).

Five impressions and compressions of prosomal and thoracetronic remains assigned to ?*Euproops* sp. and Xiphosurida indet. (specimens NMNHU G-10659/01-05) were recovered from Horizon 1 (Fig. 3A). These are preserved within small weathered siderite concretions embedded in shale associated with the deltaic sandstone succession.

Horizon 2 (Fig. 3B, C) yielded three impressions and compressions of thoracetronic fragments referred to *Belinurus* sp. and Xiphosurida indet. (GMLNU-56/06-08). These specimens occur in black carbonaceous shale and in siderite and limonite concretions derived from several beds within the roof-shale succession above the g_1^2 coal seam. The best-preserved specimen (GMLNU-56/06) was collected from greyish-yellow siltstone exposed immediately above the entrance to the abandoned mine.

Three specimens consisting of the prosomal and thoracetronic remains assigned to ?*Euproops* sp. and Xiphosurida indet. (GMLNU-56/09-11) were collected from Horizon 3 (Fig. 3D). They are preserved in siderite and limonite concretions enclosed within the roof shale of the g_2 coal seam.

Most specimens are preserved either within siderite and limonite concretions or as impressions on shale bedding planes. The concretions are strongly weathered as a result of prolonged exposure on spoil heaps or shallow burial in the bedrock. The original preservation of the xiphosurid remains was probably considerably better, but weathering of the concretions substantially reduced the quality of preservation. In some cases (e.g. Fig. 6F), weathering of the concretion core produced hollow cavities containing detached internal moulds of the exoskeleton that move freely within the concretion. Such heavily weathered concretions are known locally as "rattles" (*kolotushky* in Ukrainian; Logvinenko, 1953). Most xiphosurid remains occur as flattened exoskeletal fragments preserved parallel to the bedding plane, although several specimens

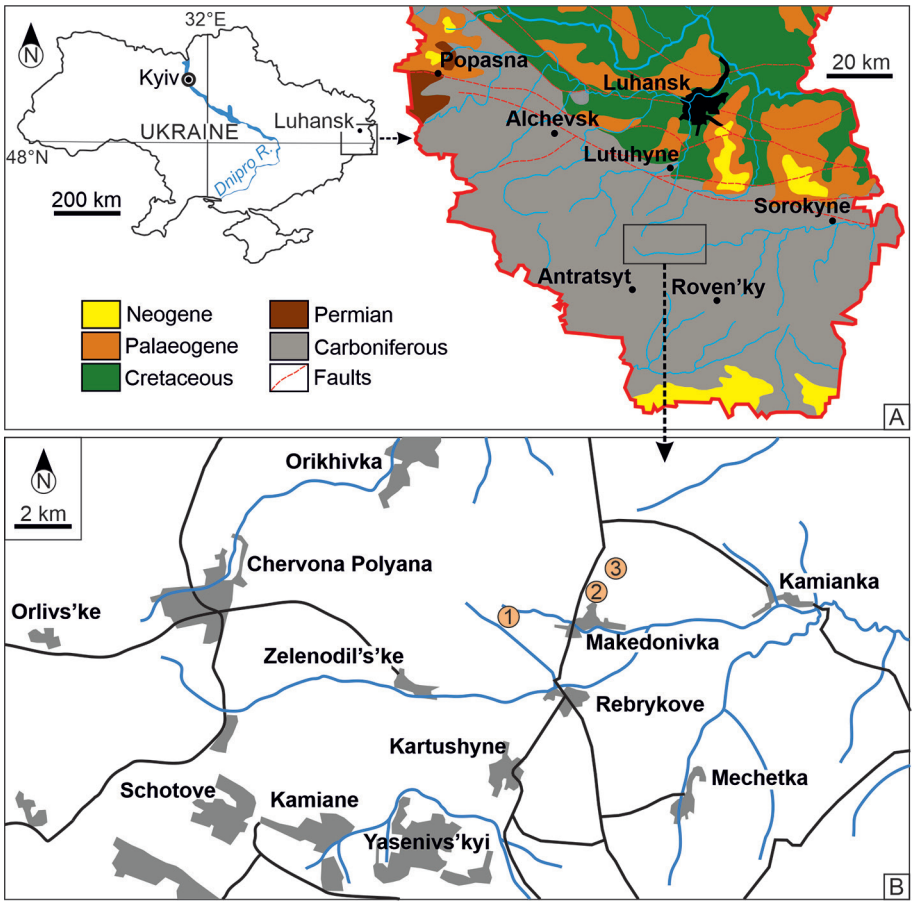

Fig. 2. Localities yielding horseshoe crabs. **A** – Geological map of the southern part of Luhansk Oblast (modified after Dernov, 2025a). **B** – Detailed map of the area outlined in Fig. 2A.

Fig. 3. General views of the xiphosurid-bearing localities (A–D) and biota associated with horseshoe crabs from fossiliferous Horizon 1 (E–M). **A** – Siltstone exposure at fossil site No. 1; **B** – Spoil heap of an abandoned coal mine at fossil site No. 2; **C** – Slope above the entrance to an abandoned coal mine at fossil site No. 2; **D** – Spoil heap of an abandoned coal mine at fossil site No. 3; **E–J** – Non-marine bivalves from fossiliferous Horizon 1: **E** – *Carbonicola rectilinearis* Trueman & Weir, 1948 (IGS NASU-11/03); **F** – *Carbonicola limax* Wright, 1934 (IGS NASU-11/15); **G–J** – Shells showing injuries sustained during life (G, H) and blister pearl-like structures (I, J) (G – IGS NASU-11/09; H – IGS NASU-11/14; I – IGS NASU-11/17; J – IGS NASU-11/16); **K** – Poorly preserved prosoma of a horseshoe crab from the sandstone of fossiliferous Horizon 1 (GMLNU-56/01); **L** – Poorly preserved pygocephalomorph crustacean from fossiliferous Horizon 1 (field photograph); **M** – Evidence of a possible fungal–plant interaction on a lycopsid leaf (field photograph). Scale bars = 5 mm.

(e.g. Fig. 6D, G) appear to have been preserved in an enrolled posture.

One uncatalogued specimen illustrated in Fig. 3K is preserved in sandstone and was probably transported prior to burial, as indicated by its poor preservation and its association with fragments of arthropleurid exoskeletons and plant stems (Dernov, 2019a). In contrast, the remaining specimens are interpreted as autochthonous or parautochthonous because neither the xiphosurid remains nor the associated faunal elements exhibit evidence of transport.

Although the studied material originates from only three stratigraphic horizons, it represents the outcome of many years of field collecting. Non-marine deposits within the Mospyne Formation, particularly the lacustrine roof shales of the coal seams that have yielded most Carboniferous xiphosurids from the Donets Basin (Chernyshev, 1927, 1928; Karlov, 1948; Shpinev, 2018), are uncommon in this formation. By contrast, the overlying Smolyanynivka Formation, deposited during the late Bashkirian regression (Ustinovsky, 1993), contains considerably more extensive non-marine facies and preserves a much richer non-marine biota (Logvinenko, 1953).

The studied xiphosurid specimens are housed in the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (NMNHU G-10659), and the Geological Museum of the Taras Shevchenko National University of Luhansk, Poltava (GMLNU-56). Collections of associated fossils are deposited in the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (NMNHU-G 8640), the Department of Stratigraphy and Palaeontology of the Palaeozoic Sediments, Institute of Geological Sciences, National Academy of Sciences of Ukraine, Kyiv (IGS NASU-11, IGS NASU-15, IGS NASU-41, and two uncatalogued specimens), and the Geological Museum of Taras Shevchenko National University of Luhansk, Poltava (GMLNU-9 and GMLNU-19).

Morphological terminology and measurement protocols follow Filipiak & Krawczyński (1996). The systematic framework adopted for the family Belinuridae von Zittel in von Zittel & Eastman, 1913, including the spelling of the type genus, follows Lamsdell (2020) and Lamsdell & Clapham (2021).

3. Geological setting

The Donets Basin forms the southeastern segment of the northwest-southeast-trending Pripyat-Dnipro-Donets intracratonic rift system, which extends from the Baltic region to the Caspian Sea across Belarus, Ukraine, and Russia. The rift is situated between the Voronezh Massif to the north and the Ukrainian Shield to the south and occupies the southwestern margin of the East European Platform (Izart et al., 1996; Eros et al., 2012; Sachsenhofer et al., 2012; Van Hinsbergen et al., 2015).

The Mospyne Formation is a 315–730 m thick cyclic succession composed of mudstones, siltstones, sandstones, limestones, and coal seams (Aisenverg et al., 1963, 1975; Feofilova & Levenstein, 1963; Dunaeva, 1969; Poletaev et al., 2011; Nemyrovska & Yefimenko, 2013). In the study area, the lower part of the formation (below the g_1 coal seam) is replaced by a shale-dominated succession that is notably poor in fossils. This interval is most likely assignable to the Dyakove Group (upper Visean–upper Bashkirian), a predominatly argillaceous unit recognized throught the southern Donets Basin (Reznikov, 1993; Dernov, 2022b; Dernov & Poletaev, 2024).

The Bashkirian coal-bearing succession accumulated predominantly on an extensive alluvial-deltaic plain along the southeastern margin of Laurussia. Deposition took place under alternating continental and marginal-marine conditions, with repeated incursions from the epicontinental sea producing the characteristic cyclothemic succession of the basin (Logvinenko, 1953; Feofilova & Levenshtein, 1963; Ustinovsky, 1993). During the Bashkirian, marine sedimentation was concentrated mainly in the central part of the Donets Basin, whereas marginal areas, including the study area, remained dominated by continental depositional environments (Reznikov, 1993; Dernov & Poletaev, 2024).

4. Associated biota

Macroscopic plant remains assigned to genera *Cyperites*, *Lepidodendron*, *Stigmaria*, *Asterophyllites*, *Eusphenopteris*, *Karinopteris*, and *Cordaites*, as well as non-marine bivalves *Carbonicola rectilinearis* Trueman & Weir, 1948 (Fig. 3E) and *C. limax* Wright, 1934 (Fig. 3F), and a poorly preserved impression of a pygocephalomorph crustacean caparace (Fig. 3L), co-occur with xiphosurids in fossiliferous Horizon 1. Some shells of *Carbonicola* exhibit injuries sustained during life (Fig. 3G–J) (Dernov, 2022d). Lycopsid leaves are commonly preserved in 3D form owing to carbonate mineralisation and occasionally show evidence of fungal colonisation (Fig. 3M).

Xiphosurid resting traces (Cubichnia) assigned to the ichnogenera *Arborichnus*, *Selenichnites*, and *Crescentichnus*, occur at several stratigraphic lev-

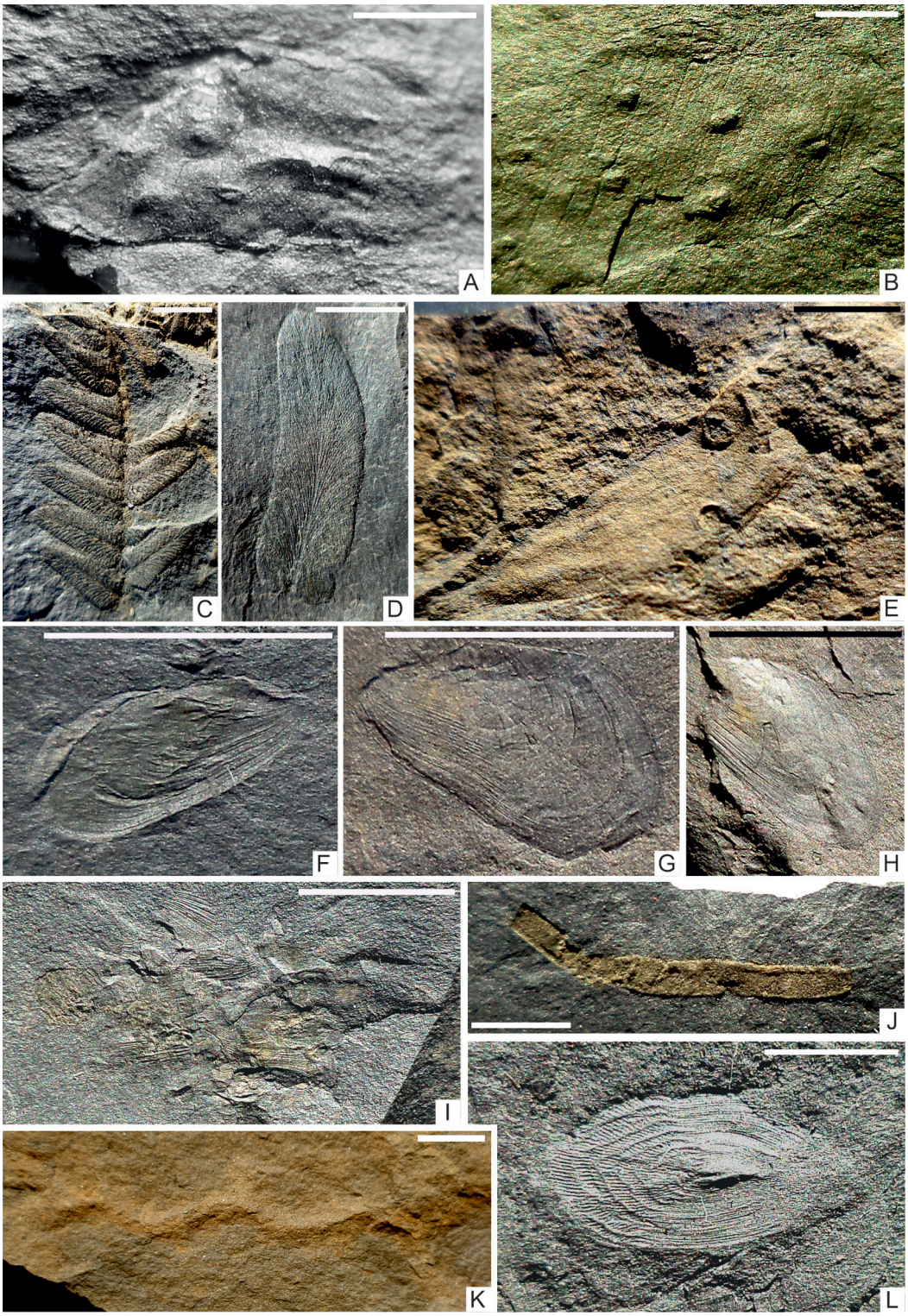

Fig. 4. Biota associated with horseshoe crabs from fossiliferous Horizon 2. **A, B** – ?Paratergites of the myriapod *Arthropleura* sp. (A – NMNHU-G 8640/01; B – GMLNU-19/01); **C** – Pteridosperm *Neuralethopteris schlehanii* (Stur) Cremer (uncatalogued); **D** – Pteridosperm *Paripteris gigantea* (Sternberg) Gothan (uncatalogued); **E** – Galls on a plant stem (uncatalogued); **F, G** – Bivalves *Curvirimula trapeziforma* (Dewar, 1939) (F – IGS NASU-11/32; G – IGS NASU-11/34); **H** – Bivalve *Curvirimula tesselata* (Jones, 1891) (IGS NASU-11/43); **I** – Gastric residue composed of fragmented fish scales (uncatalogued); **J** – Limonitised coprolite (uncatalogued); **K** – Trace fossil *Cochlichnus anguineus* Hitchcock, 1858 (GMLNU-9/02); **L** – Fish scale belonging to *Rhizodopsis sauroides* (Williamson, 1849) (uncatalogued). Scale bars = 5 mm.

els within the Mospyne Formation, including the sandstone associated with fossiliferous Horizon 1 and the sandstone overlying fossiliferous Horizon 2 (Dernov, 2019a, 2023b). All these trace fossils originate from deltaic and prodeltaic deposits, suggesting that their producers were likely marine xiphosurids.

The width of *Crescentichnus* resting traces from the sandstone associated with fossiliferous Horizon 1 indicates that the prosoma of some trace-making xiphosurids measured approximately 15 cm across (Dernov, 2019a). If so, the producers of these traces this would rank among the largest Carboniferous xiphosurids known. At present, the largest known Carboniferous horseshoe crab is *Xaniopyramis linseyi* Siveter & Selden, 1987, from the Serpukhovian of England, with a prosomal width of approximately 14 cm (Siveter & Selden, 1987). *Crescentichnus* is associated with arthropleurid exoskeleton fragments, plant stem remains, and pebbles (Dernov, 2019a). A poorly preserved compression of the prosoma of an unidentified xiphosurid was also discovered at this level (Fig. 3K).

The roof shale of the g_1^2 coal seam (fossiliferous Horizon 2) yields a diverse fossil assemblage comprising the non-marine bivalves *Curvirimula trapeziforma* (Dewar, 1939) (Fig. 4F, G) and *C. tesselata* (Jones, 1891) (Fig. 4H); the myriapod *Arthropleura* sp. (Fig. 4A, B); scales of crossopterygian fishes including *Rhizodopsis sauroides* (Williamson, 1849) (Fig. 4L) and *Rhabdoderma elegans* (Newberry, 1856); a bradyodont tooth referred to *Helodus* sp.; and fragmentary fish skeletal remains. Also present are macroproblematica, trace fossils including burrows ?*Palaeophycus* isp., locomotion traces such as *Cochlichnus anguineus* Hitchcock, 1858 (Fig. 4K) and *Diplichnites* isp., bromalites (Fig. 4I, J), and evidence of plant-arthropod interactions, including galling, endophytic oviposition, and margin feeding (Fig. 4E) (Dernov, 2019b, 2021, 2022a, 2023a, 2025b).

The best-preserved specimen (Fig. 3A), assigned to *Belinurus* sp., was recovered directly from the outcrop face, in contrast to all other specimens, which were collected from the spoil heap. Associated with this specimen were impressions of the terrestrial plants *Calamites* and *Karinopteris*, bivalves, and trace fossils ?*Palaeophycus* isp. and *Cochlichnus anguineus* (Dernov, 2019b; 2023a).

A diverse assemblage of terrestrial plants was also collected from fossiliferous Horizon 2, including the genera *Asolanus, Bothrodendron, Cyperites, Halonia, Lepidodendron, Lepidophloios, Lepidostrobophyllum, Syringodendron, Stigmaria, Asterophyllites, Calamites, Pinnularia, Sphenophyllum, Corynept-*

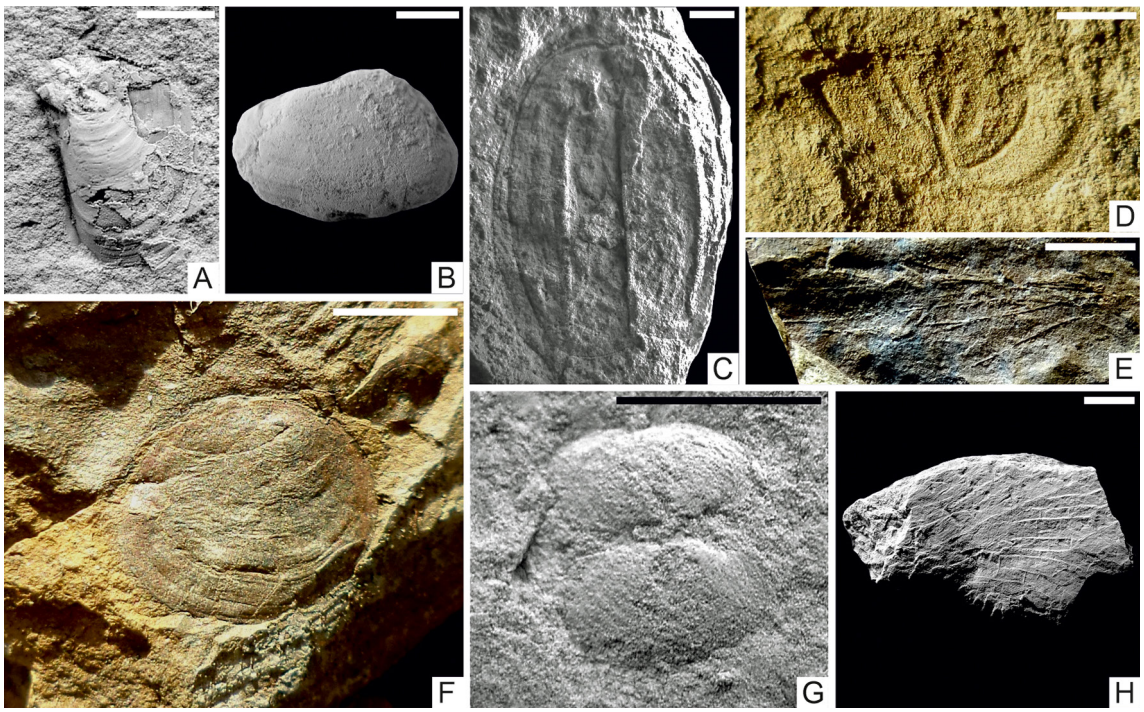

Fig. 5. Biota associated with horseshoe crabs from fossiliferous Horizon 3. **A –** Bivalve *Naiadites* sp. (IGS NASU-11/45); **B –** Bivalve *Carbonicola obtusa* (Hind, 1894) (IGS NASU-11/21); **C –** Phyllocarid crustacean *Dithyrocaris* cf. *granulata* Woodward & Etheridge, 1873 (IGS NASU-41/01); **D –** Cyclidan crustacean *Brittaniclus* cf. *scotti* (Woodward, 1893) (IGS NASU-15/02); **E, H –** Insect wings (uncatalogued); **F –** Conchostracan *Pseudestheria* sp. (uncatalogued); **G –** Indeterminate conchostracan crustacean (uncatalogued). Scale bars = 5 mm.

eris, Dictyoxylon, Eusphenopteris, Neuralethopteris (Fig. 4C), and *Paripteris* (Fig. 4D) (Dernov & Udovychenko, 2019).

An assemblage of terrestrial plant remains has been recovered from the roof shale of the g_2 coal seam (fossiliferous Horizon 3), including *Bothrodendron*, *Cyperites*, *Lepidodendron*, *Lepidophloios*, *Sigillaria*, *Stigmaria*, *Syringodendron*, *Calamites*, *Pinnularia*, *Dictyoxylon*, *Karinopteris*, *Paripteris*, *Trigonocarpus*, *Cordaianthus*, *Cordaicarpus*, and *Cordaites* (Dernov, 2025a). In addition to plants, the site has yielded a variety of non-marine invertebrates, including microconchids; the bivalves *Carbonicola obtusa* (Hind, 1894) (Fig. 5B), *Curvirimula trapeziforma* (Dewar, 1939), and *Naiadites* sp. (Fig. 5A); the conchostracans *Pseudestheria* sp. (Fig. 5F); and the phyllocarid crustacean *Dithyrocaris* cf. *granulata* Woodward & Etheridge, 1873 (Fig. 5C). Other notable finds include a fragmentary impression of a wing base of a large insect (Fig. 5H), plant remains showing arthropod-induced damages, and pseudofossils assigned to Astropolithon (Dernov, 2021, 2022a, 2025a). The cyclid crustacean *Brittaniclus* cf. *scotti* (Woodward, 1893), previously reported from the base of the g_2 coal seam (Dernov, 2022c) (Fig. 5D), may in fact have originated from the roof shale of this coal seam. It was found in association with an assemblage dominated by terrestrial plants, as well as myriapods, conchostracans (Fig. 6G), and insects (Fig. 6E).

5. Age of the xiphosurid fauna

The Mospyne Formation contains numerous biostratigraphic indicators that constrain its age to the early late Bashkirian (equivalent to the Langsettian or Westphalian A of the West European stratigraphic scale). These include characteristic terrestrial plant assemblages containing stratigraphically significant species *Sigillaria elegans* Brongniart, *Lyginopteris hoeninghausi* Potonié, *Neuralethopteris rectinervis* (Kidston) Laveine, *N. schlehanii* (Stur) Cremer, and *Karinopteris acuta* (Brongniart) Boersma (Novik, 1974; Fissunenko, 1991; Boyarina, 2016; Dernov & Udovychenko, 2019); ammonoids of the *Brannerоceras-Gastrioceras* Genus Zone (Popov, 1979; Dernov, 2022b); and non-marine bivalves belonging to *Curvirimula trapeziforma* (Dewar, 1939), *C. tesselata* (Jones, 1891), *Carbonicola rectilinearis* Trueman & Weir, 1948, *C. limax* Wright, 1934, which indicate the upper part of the *lenisulcata* Zone and the lower part of the *communis* Zone (Dernov, 2022a).

Conodonts identified from these strata include '*Streptognathodus*' *expansus* Igo & Koike, 1964, '*S.*' *suberectus* Dunn, 1966, *Idiognathoides sinuatus* Harris & Hollingsworth, 1933, *I. corrugatus* Harris & Hollingsworth, 1933, *I. sulcatus* Higgins & Bouckaert, 1968, and *Idiognathodus sinuosus* Ellison & Graves, 1941, all of which indicate the '*Streptognathodus*' *expansus* Zone (Kozitskaya et al., 1978; Nemyrovska, 1999, 2017). This zone is correlated with the Langsettian *Idiognathoides sulcatus parvus* Zone of England, the *Idiognathodus klapperi* Zone of the upper Morrowan (Pennsylvanian) of the United States, and the lower part of the *Declinognathodus marginodosus* Zone in the historical stratotype of the Bashkirian Stage in Bashkiria, Russia (Nemyrovska, 1999).

6. Systematic palaeontology

The best-preserved specimens of horseshoe crabs, assigned to *Belinurus* sp. and ?*Euproops* sp., are described below. The more poorly preserved fossils are only illustrated (Fig. 6F–I).

Order Xiphosurida Latreille, 1802
Suborder Belinurina von Zittel in von Zittel & Eastman, 1913
Family Belinuridae von Zittel in von Zittel & Eastman, 1913

Genus *Belinurus* Bronn, 1839

Type species. *Limulus trilobitoides* Buckland, 1837; by subsequent designation.

Included species. *Belinurus carwayensis* Dix & Pringle, 1929; *B. concinnus* Dix & Pringle, 1929; *B. grandaevus* Jones & Woodward, 1899; *B. kiltorkensis* Baily, 1869; *B. morgani* Dix & Pringle, 1930; *B. pustulosus* Dix & Pringle, 1929; *B. silesiacus* (Roemer, 1883); *B. sustai* (Prantl & Přibyl, 1956); *B. trechmanni* Woodward, 1918 (Lamsdell & Clapham, 2021).

Diagnosis. Belinurid with axis of first thoracetron tergite medially inflated; thoracetron ovoid to semicircular in outline; thoracetron fixed tergopleural spines elongate, needle-like (after Lamsdell & Clapham, 2021, p. 1354).

Remarks. The correct authorship and spelling of *Belinurus* was recently clarified by Lamsdell & Clapham (2021), who demonstrated that *Belinurus* Bronn, 1839 was the correct spelling and attribution as opposed to *Bellinurus* Pictet, 1846.

Belinurus sp.

Fig. 6A

Material. One specimen (GMLNU-56/06) from fossiliferous Horizon 2 (fossil site No. 2).

Description. Specimen GMLNU-56/06 is preserved as a compression of the dorsal surface of the thoracetron and the proximal part of the telson within a siderite nodule. The thoracetron measures 9.5 mm in length and 15 mm in width at its broadest point (width/length ratio = 1.58). It is ovoid to weakly subtriangular in outline and consists of eight segments, each 0.6–1.0 mm wide. The thoracetronic axis is 4.2 mm wide anteriorly, where it reaches its maximum width, and tapers gradually posteriorly. The axial segments and the microtergite are not preserved. The lateral ends of the thoracetronic segments bear poorly preserved, narrow spines that are gently recurved posteriorly. The best-preserved spine, on the fourth segment of the right side, is 3 mm long. A roll-shaped callosity extends along the posterior margin of each segment from the pleural region to the base of the corresponding spine. The thoracetronic flange is narrow, approximately 0.5 mm wide, and maintains a nearly constant width throughout. Only the proximal part of the telson is preserved; it is approximately 12 mm long and 1 mm wide at the base and bears a distinct median ridge.

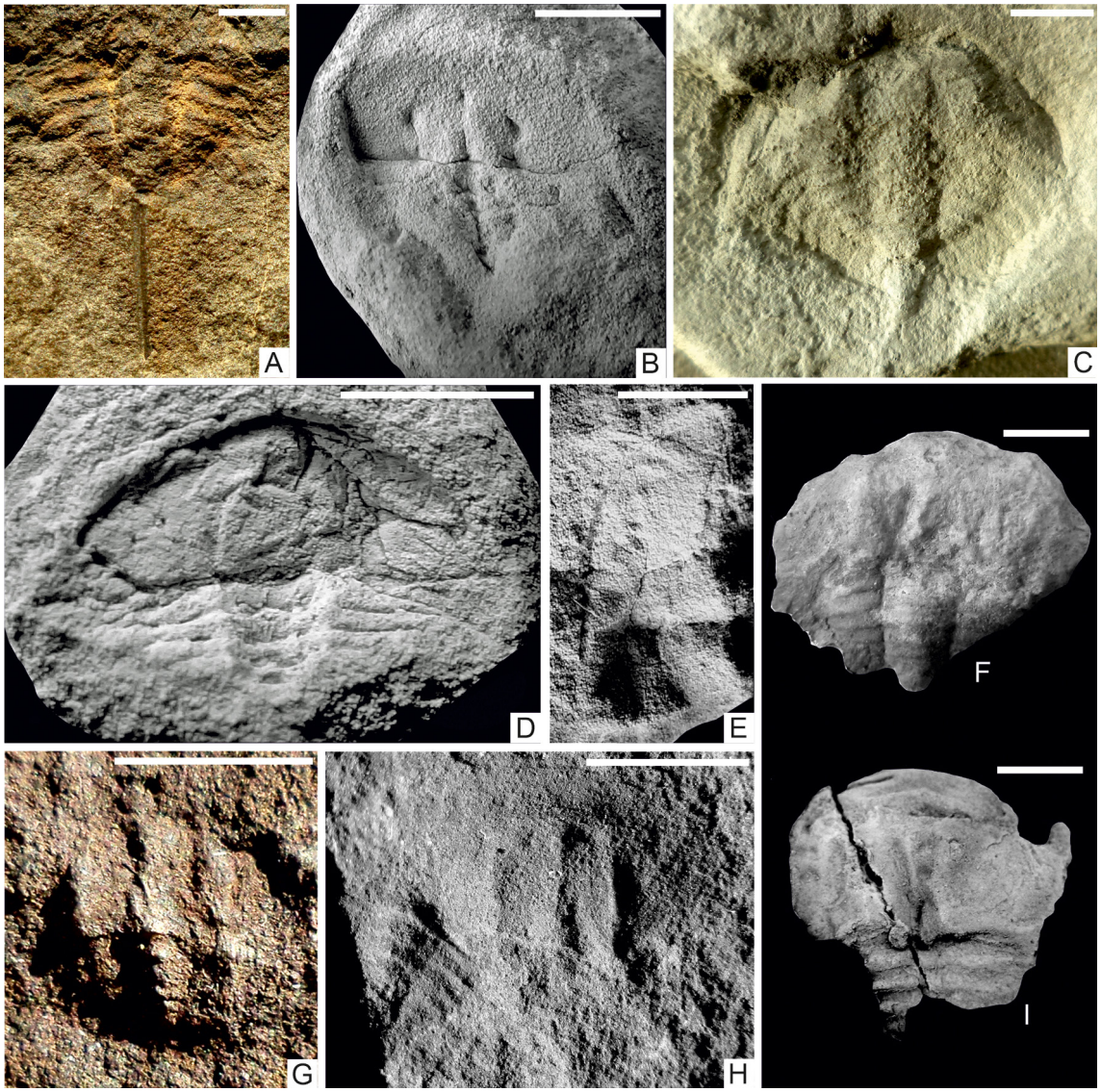

Fig. 6. Xiphosurids from the Mospyne Formation. **A** – *Belinurus* sp. (compression of the thoracetron in dorsal view, GMLNU-56/06); **B–E** – ?*Euproops* sp. (**B** – impression of the prosoma and thoracetron in dorsal view, NMNHU G-10659/01; **C** – compression of the thoracetron with part of the prosoma, in dorsal view, GMLNU-56/09; **D** – enrolled exoskeleton, NMNHU G-10659/04; **E** – impression of a genal spine, NMNHU G-10659/03); **F–I** – Xiphosurida indet. (**F, G** – enrolled exoskeletons, GMLNU-56/11 and GMLNU-56/08; **H** – impression of the prosoma in dorsal view, NMNHU G-10659/02; **I** – compression of the prosoma with a partially preserved thoracetron, in dorsal view, GMLNU-56/10). Scale bars = 5 mm.

Remarks. The specimen described above is referred to *Belinurus* on the basis of its ovoid thoracetron bearing elongate, needle-like fixed tergopleural spines. It differs from *Belinurus iswarinensis*, specimens of which have been reported from several localities, including the Mospyne Formation (Chernyshev, 1927, 1928), in possessing (1) a weakly subtriangular thoracetron rather than the semicircular outline characteristic of *B. iswarinensis* and (2) considerably more slender spines at the lateral margins of the thoracetronic segments. On the basis of the overall thoracetronic outline and the presence of long, slender pleural spines, the specimen described here most closely resembles *Belinurus metschetnensis* (cf. the specimen illustrated in Shpinev, 2018, fig. 3B, and Bicknell & Pates, 2020, fig. 15D). However, the poor preservation of the present specimen precludes a detailed morphological comparison with other representatives of the genus *Belinurus*.

Genus *Euproops* Meek, 1867

Type species. *Bellinurus danae* Meek & Worthen, 1865; by original designation.

Included species. Type species only.

Diagnosis. Belinurid characterised by ophthalmic ridges that curve axially posterior to the lateral eyes; a cardiac lobe bordered by dorsal furrows; elongate ophthalmic spines arising from the posterior ends of the ophthalmic ridges and extending over the thoracetron; proximally expanded fixed tergopleural spines forming an opisthosomal flange; and a conical opisthosomal boss (after Lamsdell, 2020, p. 14).

?*Euproops* sp.

Fig. 6B–E

Material. Four specimens (NMNHU G-10659/01, NMNHU G-10659/03, NMNHU G-10659/04, and GMLNU-56/09) from fossiliferous horizons 1 and 3 (fossil sites Nos. 1 and 3).

Description. Specimen NMNHU G-10659/01 (Fig. 6B) is the best-preserved specimen referred to ?*Euproops* sp. It consists of a weathered, fragmentary impression of the prosoma and thoracetron preserved within a siderite nodule. The prosoma is semicircular in outline, measuring approximately 11 mm in width and 3.8 mm in length. A single, slender genal spine is preserved; it is 2.5 mm long, 0.7 mm wide at the base, and oriented subparallel to the longitudinal axis of the exoskeleton. The cardiac lobe is small, subtriangular, and tapers anteriorly. The paired ophthalmic ridges curve axially posterior to the small lateral compound eyes. The median ocelli are situated anteriorly at the point where the ophthalmic ridges converge. The thoracetron measures 6.5 mm in length and 8.5 mm in maximum width (width/length ratio = 1.31). It is fully fused and has a semicircular to weakly subtriangular outline. The pleural segments and the axial structures of the thoracetron are not preserved. The thoracetronic axis is narrow (approximately 1.5 mm wide), but its outline cannot be determined.

Specimen GMLNU-56/09 (Fig. 6C) is preserved as an impression of the dorsal surface of the thoracetron together with the posterior part of the prosoma within a siderite nodule. The prosoma is very poorly preserved, and its morphology cannot be determined. The thoracetron measures approximately 8 mm in length and 13 mm in maximum width (width/length ratio *c.* 1.63), and has a subtriangular to nearly semicircular outline. It appears to consist of seven segments, each 0.5–0.9 mm long. The thoracetronic axis is cylindrical and approximately 4.0 mm wide at its widest point. The axial segments and microtergite are poorly preserved. The lateral and posterior margins of the thoracetron bear a poorly preserved flange with narrow spines that curve slightly posteriorly and are approximately 2.0–2.5 mm long. A ridge-like callosity extends along the posterior margin of each segment from the pleural region to the base of the corresponding spine. Only the proximal part of the telson is preserved, with a basal width of approximately 2 mm.

Remarks. An additional specimen (Fig. 6D), representing an enrolled horseshoe crab, probably also belongs to ?*Euproops* sp. However, owing to its poor state of preservation, this assignment remains tentative. Specimen NMNHU G-10659/03 (Fig. 6E) consists of an impression of the lateral part of the prosoma bearing a slender, elongate genal spine.

The poor preservation of the available material precludes confident assignment to *Euproops*, as it does not permit determination of the number of opisthosomal segments, assessment of the morphology of the fixed tergopleural spines, or confirmation of the presence of ophthalmic spines. Nevertheless, the specimens are tentatively referred to ?*Euproops* on the basis of several morphological features, including the course of the ophthalmic ridges, the relatively slender genal spines oriented nearly parallel to the longitudinal axis of the exoskeleton, the semicircular prosoma, the small subtriangular cardiac lobe, and the position of the median ocelli.

7. Discussion

Palaeoenvironments. According to the available lithological and palaeontological evidence, fossiliferous Horizon 1 was deposited in a shallow, low-energy lagoon with reduced salinity or in a freshwater lake (Dernov, 2022a). The bivalves from fossiliferous Horizon 2 are interpreted to have inhabited shallow, freshwater or brackish lakes situated on a coastal alluvial plain. These water bodies were characterised by low biodiversity, slow sedimentation rates, dysaerobic bottom-water conditions, and a continuous supply of nutrients from the surrounding wetlands (Dernov, 2022a, 2025b).

Bivalves of the genus *Curvirimula* probably adopted a pseudoplanktonic mode of life, attaching themselves to floating substrates such as fragments of wood or to benthic organisms, including macroscopic algae (Warth, 1967; Wignall & Sims, 1990). This life habit enabled them to remain above the oxygen-depleted bottom waters. However, the pseudoplanktonic habit was probably facultative, and under more favourable environmental conditions these bivalves may also have adopted a benthic mode of life (Dernov, 2022a). *Curvirimula* is well known from brackish-water depositional environments (Betekhtina, 1974; Eagar, 1981; Anderson et al., 1997).

The margins of these lakes were occupied by dense but taxonomically monotonous hydrophilic vegetation, dominated by monospecific stands of the arborescent sphenopsid *Calamites* (Fissunenko, 1987).

The fossils from fossiliferous horizons 2 and 3 were collected from mine spoil heaps and most probably originated from different parts of the roof shales of the g_1^2 and g_2 coal seams. In the Donets Basin, the roof shales of coal seams typically comprise several palaeoenvironmental zones (facies) representing different depositional settings (Chernyshev, 1931; Yefimov, 1934; Logvinenko, 1953; Posudiyevsky, 1977; Dernov, 2022a): (1) swamp (lower part) to lacustrine (upper part) facies, represented by black mudstones and siltstones containing abundant plant debris, non-marine bivalves, and conchostracans; (2) brackish to shallow-marine facies, represented by black mudstones and siltstones with lingulide brachiopods, marine bivalves, and ostracods; and (3) offshore marine facies, represented by shales containing marine bivalves, gastropods, ammonoids, and other typical marine fauna. The horseshoe crabs described here most probably originated from the lacustrine subdivision of facies zone 1 (Dernov, 2025a).

These lakes developed on an alluvial–deltaic swampy plain (Zhemchuzhnikov et al., 1960; Feofilova & Levenshtein, 1963; Zaritskiy, 1970; Dernov, 2022a, 2025a). Their occurrence directly above the coal seams indicates that they formed following the burial of peat mires by clastic sediments and the consequent cessation of peat accumulation. The lake-bottom muds were probably enriched in hydrogen sulphide as a result of sulphate-reducing bacterial activity, stimulated by the abundant organic detritus, chiefly fragments of terrestrial plants transported into the lakes from the surrounding highly productive wetlands (Dernov, 2022a, 2025a). Hydrogen sulphide probably accumulated periodically within the water column or may even have persistently contaminated its lowermost part (Dernov, 2022a, 2025a).

General characteristics of the xiphosurid faunule. No xiphosurids have previously been described or illustrated from the study area, namely the central Donets Basin. However, Shpinev (2018: pl. 10, fig. 6; text-fig. 6) figured and described a juvenile specimen of *Belinurus* sp. from an abandoned coal quarry located approximately 3.3 km south of the village of Zakhidne, Luhansk Raion, Luhansk Oblast, about 23 km northwest of the village of Makedonivka. The specimen was collected from the upper Bashkirian Smolyanivka Formation, probably from shale beds associated with the h_{10} coal seam near the top of the formation. Biostratigraphically, these strata belong to the terminal *Branneroceras–Gastrioceras* Genus Zone or the lowermost *Diaboloceras–Axinolobus* Genus Zone (Popov, 1979; Dernov, 2022b, e).

The juvenile specimen figured by Shpinev closely resembles the *Belinurus* sp. described herein in possessing long, slender pleural spines. However, it differs in several respects. Its thoracetron is semicircular in outline, whereas that of *Belinurus* sp. described herein is weakly subtriangular, and its prosoma is proportionally much broader than the thoracetron.

The horseshoe crabs described herein, together with *Belinurus iswarinensis* described by Chernyshev (1927, 1928) from the roof shale of the f_1 coal in the lower Bashkirian Mandrykyne Formation and from the roof shale of the g_3 coal in the Mospyne Formation, currently represent the oldest known Carboniferous xiphosurids from the Donets Basin. In total, the following xiphosurid species have been reported from the Bashkirian of the Donets Basin: *Euproops danae*, ?*Euproops* sp., *Prestwichianella tschernyshewi*, *Belinurus iswarinensis*, *B. metschetnensis*, and *B.* sp. (Chernyshev, 1927, 1928; Karlov, 1948; Shpinev, 2018; this study).

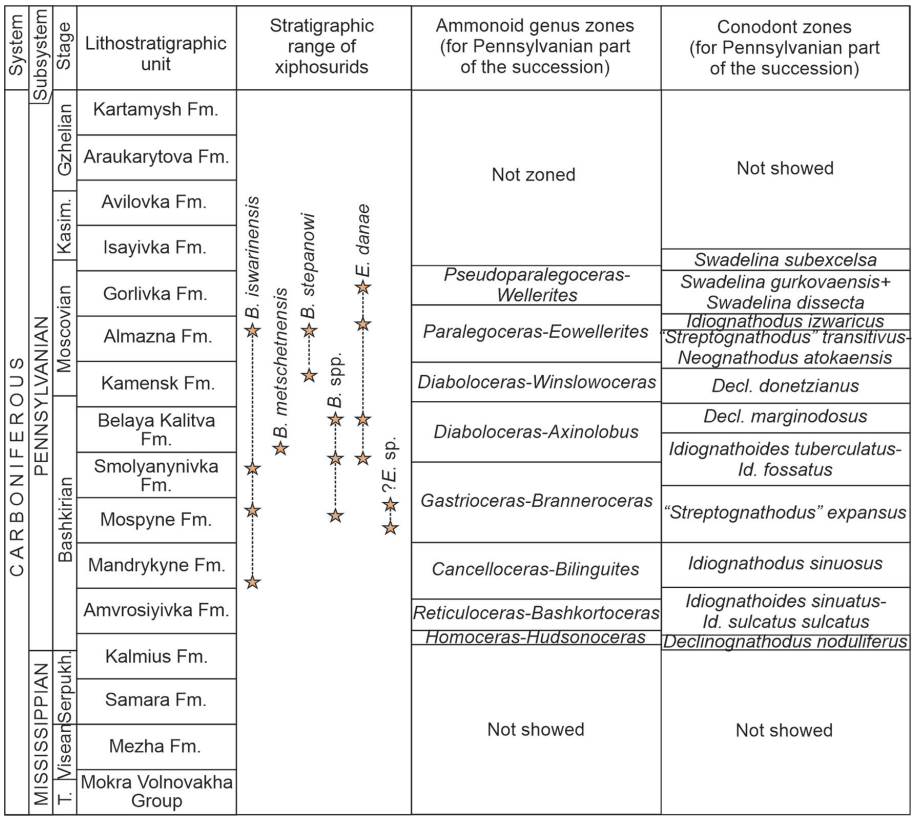

Fig. 7. Stratigraphic distribution of horseshoe crab taxa within the Carboniferous succession of the Donets Basin (after Chernyshev, 1927, 1928, 1939; Shpinev, 2018; and this study). Abbreviations: B., *Belinurus*; D., *Declinognathodus*; E., *Euproops*. Ammonoid zonation after Popov (1979) and Dernov (2022e); conodont zonation after Nemyrovska (2017). Note: The precise stratigraphic position of the locality yielding the type series of *Prestwichianella tschernyshewi* Karlov, 1948, is unknown.

At present, the Bashkirian xiphosurid assemblage of the Donets Basin comprises only three genera: *Euproops*, *Prestwichianella*, and *Belinurus* (Fig. 7). Almost all recorded species appear to be endemic to the basin, with the exception of *Euproops danae*, which is widely distributed in Pennsylvanian deposits throughout Euramerica (e.g. Meek, 1867; Fisher, 1977, 1979; Brauckmann, 1982; Anderson, 1994; Mikulic, 1998; Babcock & Merriam, 2000; Haug et al., 2012; Lucas et al., 2014; Tashman et al., 2019; Bicknell et al., 2021, and references therein).

The generally poor preservation of xiphosurids in the Mospyne Formation limits detailed comparisons with other palaeoequatorial xiphosurid faunas of Euramerica. In contrast, other arthropod groups from the Mospyne Formation, including phyllocarids and cyclids identified to species level (Dernov, 2022c, 2025a), exhibit much broader palaeobiogeographical distributions and are also known from Westphalian (upper Bashkirian–Moscovian) strata of the United Kingdom.

7. Conclusions

The xiphosurid fauna of the Mospyne Formation provides new insights into the diversity, distribution, and palaeoecology of Carboniferous horseshoe crabs in the Donets Basin. New material recovered from three fossiliferous horizons documents the presence of at least two belinurid taxa, referred to *Belinurus* sp. and ?*Euproops* sp., among the oldest known Carboniferous xiphosurids from the basin.

The specimens were recovered from deposits formed in low-energy continental to marginal environments, including freshwater and brackish lakes developed on an alluvial–deltaic swampy plain. The associated faunal and floral assemblages, together with sedimentological evidence, indicate that these horseshoe crabs inhabited shallow water bodies characterised by abundant organic input and periodically dysaerobic bottom waters. These environmental conditions are consistent with the ecological preferences inferred for Pennsylvanian belinurids elsewhere in Euramerica.

Biostratigraphic evidence derived from terrestrial plants, ammonoids, non-marine bivalves,

and conodonts constrains the age of the xiphosurid-bearing strata to the early late Bashkirian (equivakebt of the Langsettianof the Western European chronostratigraphic scheme). The occurrence of *Belinurus* and ?*Euproops* in these deposits extends the documented record of Carboniferous horseshoe crabs in eastern Euramerica.

The Bashkirian xiphosurid assemblage of the Donets Basin currently comprises three genera—*Belinurus*, *Euproops*, and *Prestwichianella*—with most species apparently endemic to the basin. Although the available material is generally too poorly preserved to permit detailed taxonomic and palaeobiogeographical comparisons, the new discoveries demonstrate that horseshoe crabs were a regular component of Bashkirian non-marine and marginal-water ecosystems in the Donets Basin and provide an important contribution to our understanding of the early evolutionary and palaeobiogeographical history of Carboniferous xiphosurids.

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