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New records of Pennsylvanian phyllocarid crustaceans (Phyllocarida, Archaeostraca) from the Donets Basin, eastern Ukraine

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Abstract

A small phyllocarid faunule comprising *Dithyrocaris colei* Portlock, 1843, *D.* cf. *granulata* Woodward & Etheridge, 1873 and Phyllocarida indet. is described from black shale beds within coal-bearing deposits of the Mospyne Formation (upper Bashkirian, Lower Pennsylvanian) in the central Donets Basin, eastern Ukraine. All records of Carboniferous phyllocarids from the Donets Basin, including those by previous researchers, are preserved in black shales formed under dysaerobic conditions. In the Carboniferous of the Donets Basin, phyllocarids are found predominantly in the Bashkirian interval. Significantly fewer taxa have been recorded from the Serpukhovian, the Serpukhovian/Bashkirian boundary interval and the Upper Pennsylvanian.

Keywords: Phyllocarida, Carboniferous, Donets Basin, palaeoecology.

1. Introduction

Phyllocarids (Phyllocarida Packard, 1879) constitute a relatively diverse group of crustaceans distributed nearly globally (Rolfe, 1969; Rode & Lieberman, 2002; Briggs et al., 2011; Liu et al., 2023). They first appeared during the late Cambrian and include the extinct order Archaeostraca Claus, 1888 as well as the order Leptostraca Claus, 1880, which is distributed in modern marine basins (Collette & Hagadorn, 2010; Liu et al., 2023).

The Donets Basin in eastern Ukraine is a key region for studying Carboniferous marine and terrestrial biota of the palaeoequatorial belt, particularly crustaceans (e.g., Chernyshev, 1924, 1925, 1927, 1928, 1939, 1941; Bondarchuk, 1929; Batalina, 1933; Tchernyshev, 1935; Prykhod'ko, 1948; Dunaeva, 1950; Birshtein, 1966; Gorak, 1950, 1956, 1958a, 1958b, 1964, 1971, 1977; Schram, 1980; Fohrer et al., 2007; Dernov, 2022c).

The Carboniferous phyllocarid crustaceans of the Donets Basin are not well studied. Riabinin (1921) described *Dithyrocaris granulata* var. *doneziana* Riabinin, 1921 from limestone bed D_1 in the Serpukhovian part of the Kalmius Formation. Later, Krestovnikov (1961) recorded three species of the genus *Dithyrocaris* Scouler, *in* Portlock, 1843 from three stratigraphical levels, namely *D. colei* Portlock, 1843 from the upper Bashkirian succession recovered in borehole No. 816 drilled near the town of Petropavlivka in the western Donets Basin, *D. tricornis* var. *aisenvergi* Krestovnikov, 1961 from Upper Pennsylvanian strata recovered at a depth of 396.0–398.2 m in borehole No. 9 near the village of Oskil in the Kharkiv Oblast, and *Dithyrocaris tenuistriata* M'Coy, 1844 from the Amvrosiyivka Formation (lower Bashkirian) in the core of borehole No. 2295 (depth interval 213.35–214.0 m) in Pokrovs'k Raion, Donetsk Oblast.

Specimens of *Dithyrocaris* sp. (here identified as *Dithyrocaris colei* Portlock, 1843) from the upper Bashkirian Mospyne Formation were figured by Dernov & Udovychenko (2019a, figs. 2.5, 2.9) and Dernov (2023, fig. 3). Poorly preserved specimens, defined as Phyllocarida indet., co-occurring with the probable phyllocarid resting trace fossil *Hankoichnus bandersnatchi* Dernov, 2023, are known from black shales in the lower Bashkirian part of the Dyakove Group in the southern part of the Luhansk Oblast (Dernov, 2023; Dernov & Poletaev, 2024).

The present paper outlines results of a study of a collection of relatively well-preserved phyllocarids assigned to *Dithyrocaris colei*, *D.* cf. *granulata* Woodward & Etheridge, 1873 and Phyllocarida indet. from the upper Bashkirian Mospyne Formation exposed in the southern part of Luhansk Oblast, eastern Ukraine. Arthropods from this formation comprise millipedes (Dernov, 2019a, 2019b, plus still undescribed material), horseshoe crabs (Dernov, 2019a, 2019b), trilobites (Weber, 1933; Mychko & Dernov, 2019), cyclids (Dernov, 2022c), conchostracans (Dernov & Udovychenko, 2021) and insects (Dernov, 2019a, 2019b). The novel data obtained clarify the taxonomic diversity of Pennsylvanian phyllocarids of the Donets Basin.

2. Geological setting

The fossils described in the present paper were collected by the author from three stratigraphical levels in the Mospyne Formation as exposed in the southern part of Luhansk Oblast (Fig. 1) in 2011–2013. A brief description of the phyllocarid-bearing stratigraphical levels is given below.

(1) A black shale bed, 55 m below limestone layer G_1^2 in the middle part of the Mospyne Formation (Fig. 2A, B). The shales (Fig. 2C) contain a rich assemblage of fossils, consisting of cnidarians (*Sphenothallus* sp.; Fig. 3L), brachiopods (*Orbiculoidea* sp.), gastropods, bivalves (species of the genera *Phestia* (Fig. 3F), *Sanguinolites* (Fig. 3G), *Palaeoneilo*, *Nuculopsis*, *Solenomorpha*, *Posidoniella*, *Euchondria* and others), orthocerids, coiled nautiloids, ammonoids (*Anthracoceratites* sp.; Fig. 3I), Neodimorphoceratidae indet. (Fig. 3E), *Brannerоceras* sp., fragments of ammonoid jaw apparatuses (Fig. 3J)), the phyllocarid *Dithyrocaris colei*, allochthonous terrestrial plants (species of the genera *Cyperites*, *Lepidostrobophyllum* (Fig. 3A), *Stigmaria*, *Calamites*, *Cordaites*, *Mariopteris* and *Neuralethopteris*), fishes (Fig. 3K), macroscopic problematics (Fig. 3B, C, H) and trace fossils (*Chondrites*, *Phycosiphon*, *Planolites* (Fig. 3D) and bromalites) (Dernov & Udovychenko, 2019a; Dernov, 2022b; Dernov & Poletaev, 2024).

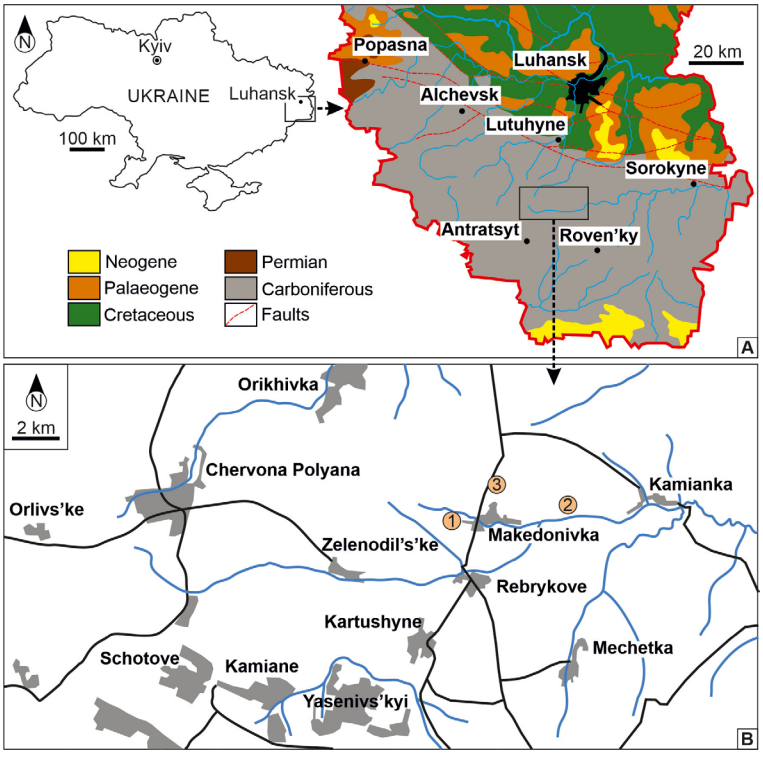

Fig. 1. Geographical location of sites yielding phyllocarids (orange circles).

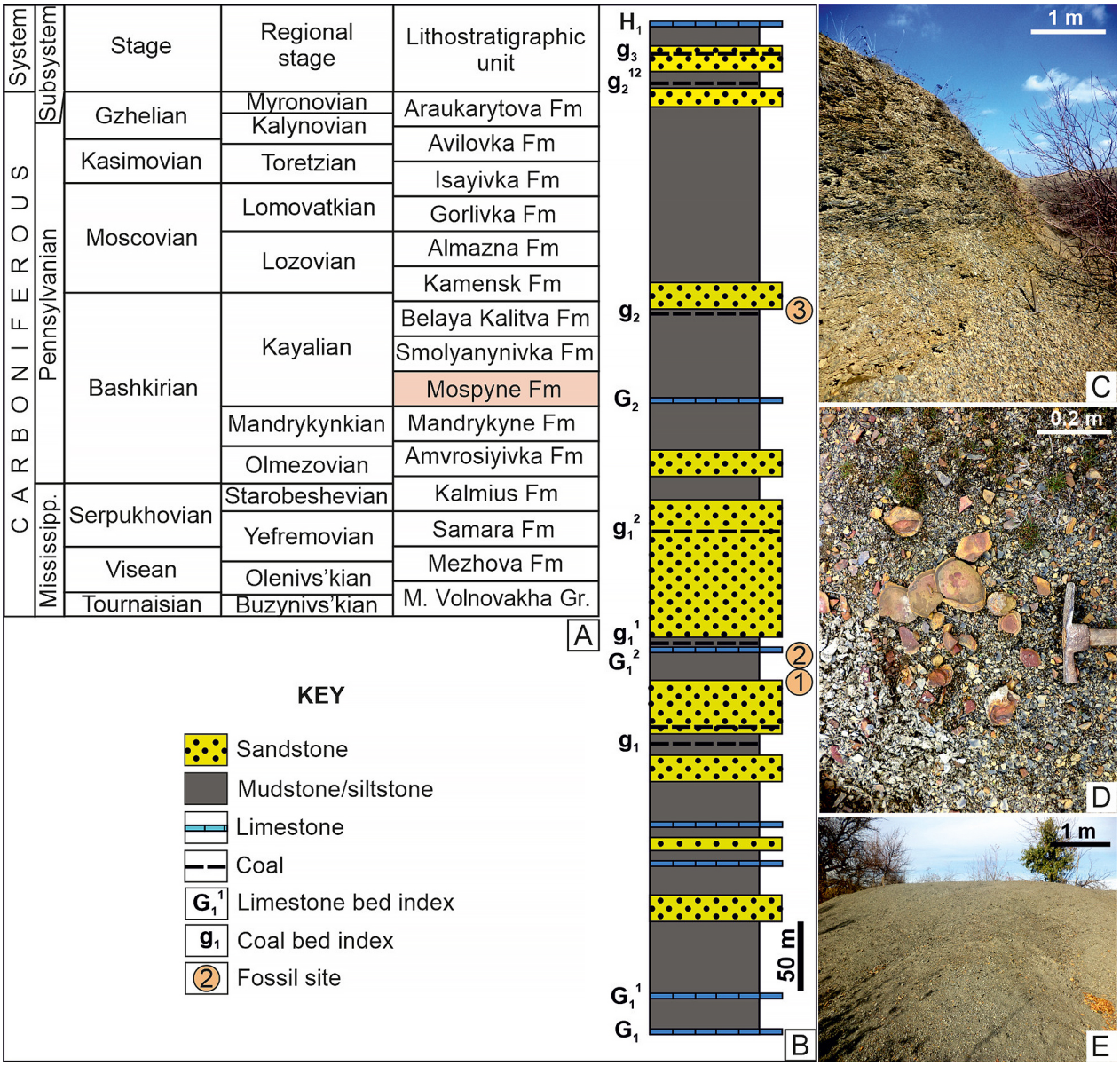

Fig. 2. Stratigraphical position and general view of the phyllocarid-bearing sites. **A** – Carboniferous stratigraphy of the Donets Basin (Mospyne Formation marked in orange); **B** – Section of the Mospyne Formation with stratigraphical position of phyllocarid-bearing levels; **C** – General view of fossil site no. 1; **D** – Phyllocarid-bearing nodules from the black shale bed of fossil site no. 1; **E** – General view of fossil site no. 3. Abbreviations: Fm – Formation, Gr. – Group, M. – Mokra.

The black shales lie on a bed of shallow-marine, calcareous, fine-grained sandstone with diverse fossils (for more details, see Mychko & Dernov, 2019; Dernov, 2022b). The deltaic sandstone bed with remains of diverse non-marine fauna, terrestrial plants and trace fossils (Dernov, 2019a) lies above the phyllocarid-bearing black shales. The phyllocarid remains occur mainly in the lowest part of the black shale bed, which is approximately 0.3 m thick. In this part of the bed, there is an interlayer of siderite nodules (Fig. 2D), from which the bulk of the studied material comes. It should be noted that this interlayer is present in outcrops that are 3–4 km apart.

The shale bed is exposed in several areas at a distance of 3–4 km from each other near the village of Makedonivka (Luhansk Raion, Luhansk Oblast, Ukraine), but the bulk of the material studied was found in a small pit near the western outskirt of this village (co-ordinates: 48°13′58.3″N 39°16′24.8″E). In total, 23 phyllocarid specimens were collected from the black shale bed.

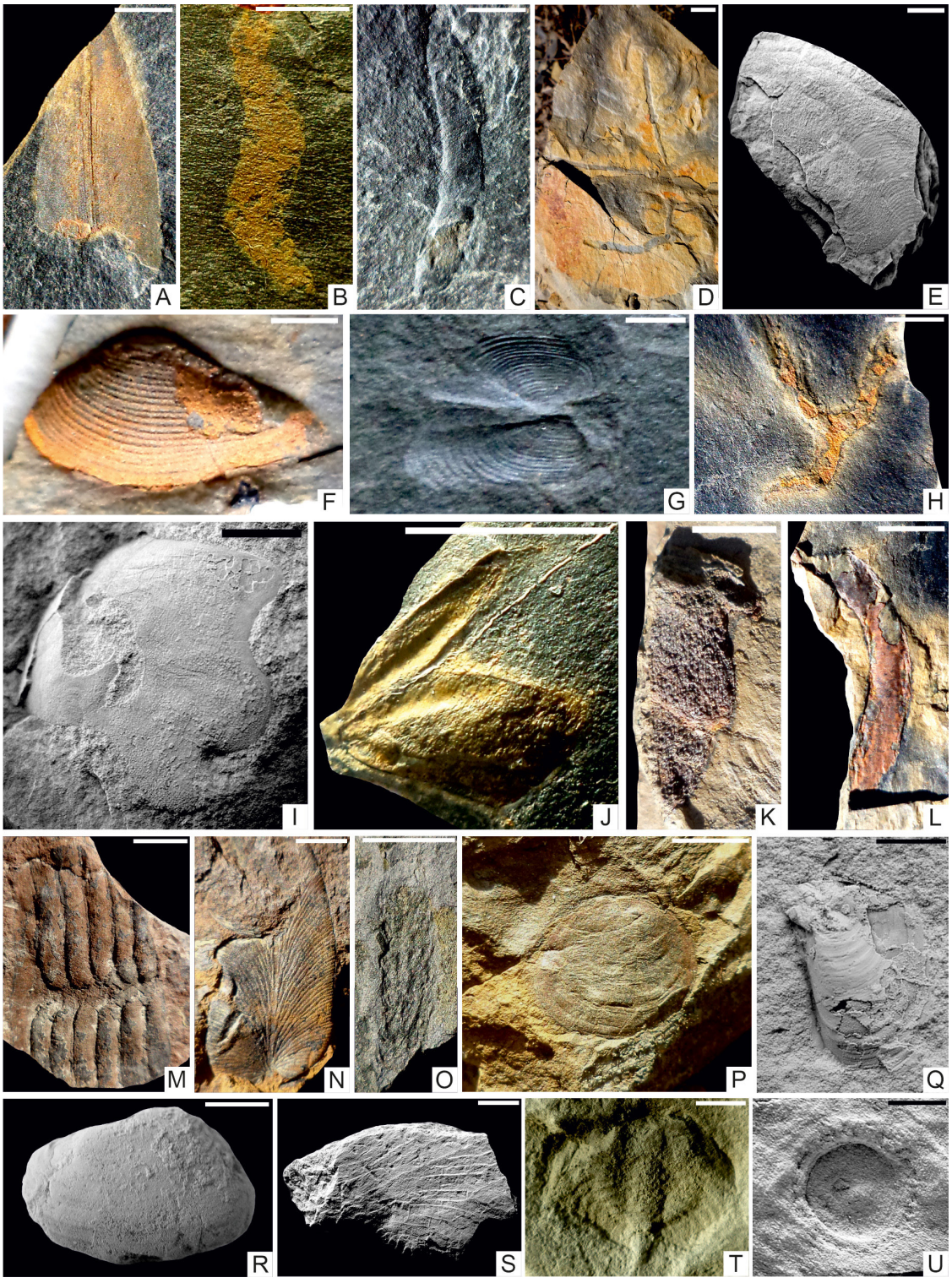

Fig. 3. Fossils co-occurring with phyllocarids at stratigraphical levels no. 1 (**A–L**) and no. 3 (**M–U**). **A** – Plant, *Lepidostrobophyllum* sp.; **B, C** – Soft-body(?) problematica; **D** – Burrows, *Planolites*; **E** – Ammonoid, Neodimorphoceratidae indet.; **F** – Bivalve, *Phestia* sp.; **G** – Bivalve, *Sanguinolites* sp.; **H** – Macroproblematicum, *Tanaisina mavka* Dernov, *in* Dernov & Poletaev, 2024; **I** – Ammonoid, *Anthracoceratites* sp.; **J** – Ammonoid jaw apparatus; **K** – Fragment of an indeterminate bone; **L** – Cnidarian, *Sphenothallus* sp.; **M** – Plant, *Calamites* sp.; **N** – Plant, *Paripteris gigantea* (Sternberg, 1823) Gothan, 1941; **O** – Plant, *Cordaianthus* sp.; **P** – Conchostracan crustacean, *Pseudestheria* sp.; **Q** – Bivalve, *Naiadites* sp.; **R** – Bivalve, *Carbonicola obtusa* (Hind, 1894); **S** – Insect, ?Orthoptera indet.; **T** – Horseshoe crab; **U** – Pseudofossil (gas-escape structure), Astropolithon. Scale bars equal 5 mm.

(2) A black shale bed with siderite nodules, 40 m below limestone layer G_1^2 in the middle part of the Mospyne Formation (see Fig. 2B). The mudstone contains rare brachiopods (lingulids, *Densepustula* sp. and other rare productidines), gastropods, bivalves (species of the genera *Phestia, Sanguinolites, Palaeoneilo, Solenomorpha* and others), orthocerids, coiled nautiloids (*Liroceras* sp., *Metacoceras perelegans* Girty, 1915 and *Peripetoceras* sp.), ammonoids (*Melvilloceras rotaii* (Librovitch, *in* Popov, 1979), *Brannerocera*s sp., *Gastrioceras* sp. and ammonoid jaws), as well as allochthonous terrestrial plants (species of the genera *Calamites, Lepidostrobophyllum, Lepidodendron* and *Cordaites*), the problematicum *Coleolus*, as well as trace fossils (*Chondrites, Cyclopuncta*, faecal pellets and bromalites) (Dernov, 2022b, 2024a, 2024b). A single small fragment of the posterior part of a phyllocarid carapace (specimen GM LNU-45/24, not described; see Fig. 5G) preserved in a siderite nodule was found in this bed.

The shale bed is exposed in the Sukha Ravine, 2.5 km east of the village of Makedonivka (co-ordinates: 48°14′28.4″N 39°20′08.2″E).

(3) A roof shale of coal bed g_2 in the upper half of the Mospyne Formation (see Fig. 2B). Shale debris forming small rock dumps of the former small coal mines 1.5 km north of the village of Makedonivka (co-ordinates: 48°14′54.1″N 39°18′20.6″E; see Fig. 2E). Remains of terrestrial plants, including *Bothrodendron minutifolium* (Boulay, 1876) Zeiller, 1879, *Cyperites bicarinatus* Lindley & Hutton, 1832, *Lepidodendron* sp., *Lepidophloios laricinus* (Sternberg, 1820) Goldenberg, 1857, *Sigillaria elongata* Brongniart, 1828, *Stigmaria ficoides* (Sternberg, 1820) Brongniart, 1822, *Syringodendron* cf. *alternans* Sternberg, 1820, *Calamariophyllum kidstoni* (Zalessky, 1907) Hirmer, 1927, *Calamites* sp. (see Fig. 3M), *Pinnularia cappilacea* Lindley & Hutton, 1834, *Dictyoxylon* sp., *Karinopteris acuta* (Brongniart, 1831) Boersma, 1972, *Pariptеris gigantea* (Sternberg, 1823) Gothan, 1941 (see Fig. 3N), *Trigonocarpus* sp., *Cordaianthus* sp. (see Fig. 3O), *Cordaicarpus cordai* (Geinitz, 1861) Zeiller, 1888, *Cordaites principalis* (Germar, 1848) Geinitz, 1855, as well as the non-marine bivalves *Carbonicola obtusa* (Hind, 1894) (see Fig. 3R), *Curvirimula trapeziforma* (Dewar, 1939) and *Naiadites* sp. (see Fig. 3Q), the conchostracan *Pseudestheria* sp. (see Fig. 3P), horseshoe crabs (see Fig. 3T), a phyllocarid crustacean *Dithyrocaris* cf. *granulata*, a fragmentary impression of the wing base of a large insect (?Orthoptera indet., see Fig. 3S; identification by Joerg W. Schneider, Freiberg), terrestrial plants with biodamage of arthropods and pseudofossils (Astropolithon; see Fig. 3U) have been collected from this locality (Dernov, 2021, 2022a). In the roof shale, a single phyllocarid carapace positive impression was found, preserved in a sandy limonite nodule (specimen IGS NASU-41/01).

The Mospyne Formation comprises a 315- to-730-m-thick sequence of mudstones, siltstones, sandstones, limestones and coals (Aisenverg et al., 1975; Feofilova & Levenstein, 1963; Dunaeva, 1969; Poletaev et al., 2011; Nemyrovska & Yefimenko, 2013). The rocks of the formation are represented by shallow-marine, lagoonal, lacustrine, prodeltaic, deltaic, peat and clastic swamp deposits (Logvinenko, 1953; Feofilova & Levenshtein, 1963; Dernov, 2017, 2019a, 2019b, 2022a, 2022b).

The Mospyne Formation corresponds to the lower part of the Kayalian Regional Stage of the Regional Stratigraphic Scheme of the Dnipro-Donets Downwarp (Poletaev et al., 2011; Nemyrovska & Yefimenko, 2013; see Fig. 2A). The formation contains typical Langsettian (= Westphalian A, early late Bashkirian) terrestrial plants (Novik, 1974; Dernov & Udovychenko, 2019b) and ammonoids of the *Brannerocera*s-*Gastrioceras* Genozone (Popov, 1979; Dernov, 2022b), non-marine bivalves of the upper part of the *lenisulcata* Zone and the lower part of the *communis* Zone (Dernov, 2022a), late Bashkirian conodonts (Nemyrovska, 1999) and other marine and terrestrial biota including miospores, foraminifera, corals, bryozoans, brachiopods, scaphopods, gastropods, horseshoe crabs, millipedes, insects and fishes (Poletaev et al., 2011; Nemyrovska & Yefimenko, 2013).

Bashkirian-aged coal-bearing deposits in the Donets Basin accumulated mainly in a large alluvial-deltaic plain, which was flooded periodically by epicontinental seas (Logvinenko, 1953; Feofilova & Levenshtein, 1963; Ustinovsky, 1993), located along the south-eastern margin of Laurussia. Only the central part of the Donets Basin was characterised by a continuous regime of marine sedimentation during the Bashkirian (Reznikov, 1993; Dernov & Poletaev, 2024). This plain was located in a humid tropical and/or subtropical climate (Novik, 1952, 1974; Logvinenko, 1953; Fissunenko, 2000).

3. Material and methods

A total 25 moderately well- and poorly preserved specimens (GM LNU-45/01 to GM LNU-45/24 and IGS NASU-41/01), comprising articulated carapaces, separated valves, telsons with furcae and other parts of phyllocarid exoskeletons were examined. The material studied is stored in the Geological Museum of the Luhansk Taras Shevchenko National University, Poltava (collection GM LNU-

45) and in the Department of Palaeontology and Stratigraphy of the Palaeozoic Sediments, Institute of Geological Sciences of the NAS of Ukraine, Kyiv (collection IGS NASU-41).

The material was collected both by extracting siderite nodules with phyllocarid remains from the outcrop face (phyllocarid-bearing levels no. 1 and 2) and by searching for these nodules in black shale rock dumps (phyllocarid-bearing levels no. 1 and 3). Remains from the nodules are the best preserved in the collection studied, while in the nodule-bearing shale they are fragmentary. However, this circumstance may be an artefact of collecting, as black shales break up into very small pieces during collection and weathering, while ellipsoidal nodules with phyllocarid remains are often relatively large, reaching a diameter of 15 cm.

Abbreviations used in the "Systematic palaeontology" section below are as follows: L – midline length of carapace, W – maximum width of carapace, L_T – length of telson, L_F – length of furcae.

4. Systematic palaeontology

Phylum Arthropoda Gravenhorst, 1843
Class Malacostraca Latreille, 1806
Subclass Phyllocarida Packard, 1879
Order Archaeostraca Claus, 1888
Suborder Rhinocarina Clarke, *in* Zittel, 1900
Family Rhinocarididae Hall & Clarke, 1888

Genus *Dithyrocaris* Scouler, *in* Portlock, 1843

Type species. *Argus testudineus* Scouler, 1835, by subsequent designation of Bronn & Roemer (1850).

Diagnosis. See Rolfe (1969: p. R321).

Distribution. Devonian–Pennsylvanian of Europe and North America.

Dithyrocaris colei Portlock, 1843

Figs 4A–K, 5A–F; Table 1

1843 *Dithyrocaris Colei* Portlock, p. 314, pl. 12.

1898 *Dithyrocaris Colei*: Jones & Woodward, p. 103, pl. 22, fig. 7; pl. 23, figs 1–4; pl. 24, figs 2, 4; pl. 27, fig. 5.

1961 *Dithyrocaris colei*: Krestovnikov, p. 25, pl. 3, fig. 6; pl. 5, fig. 3.

cf. 1984 *Dithyrocaris* sp.: Brauckmann, p. 105, fig. 1.

cf. 1997 *Dithyrocaris* sp. n. Rolfe et Richardson: Schram et al., p. 165, figs 12.30–12.32.

2019 *Dithyrocaris* sp.: Dernov & Udovychenko, figs. 2.5, 2.9.

2023 *Dithyrocaris* sp.: Dernov, fig. 3.

Table 1. Dimensions (in mm) of *Dithyrocaris colei* Portlock, 1843.

Specimen	L	W	L/W	L_T	L_F
GM LNU-45/04	20.04	22.1	0.91	–	–
GM LNU-45/02	26.5	23.4	1.13	–	–
GM LNU-45/01	35.2	35.4	0.99	–	–
GM LNU-45/05	35.9	37.5	0.96	–	–
GM LNU-45/09	–	–	–	12.6	12.5
GM LNU-45/10	–	–	–	*c.* 7.4	7.3

Material. Twenty-three fragments of poorly to moderately preserved, flattened articulated carapaces, isolated valves, pleomeres and telsons with furcae preserved in siderite nodules and black shale of the phyllocarid-bearing stratigraphical interval no. 1 (specimens GM LNU-45/01 to GM LNU-45/23).

Description. Valves with an approximate length/width ratio of 1.82–2.26 (mean: 2.0), relatively narrowly rounded or slightly concave anteriorly, with a posterior shallow swing; posterior margin inclined posteroventrally (Fig. 4D). Straight, narrow pointed posteroventral spine occurring on mid-posterior margin (Fig. 4E, H). Dorsal contact margin straight. Ventral margins broadly rounded. Narrow border, gradually thickening from posterior to anterior margin, present along ventral valve margin. Maximum width occurring near mid-length. General carapace outline slightly longitudinally ellipsoidal with gradual slight narrowing towards anterior margin and with slight excess of carapace length over width; posterior margin bearing wide, short spine (Fig. 4A, B).

Mesolateral carinae of carapace well developed, arcuate, slightly pointed; extending from cephalic carinae and produced into posteroventral spine (Fig. 4H). Juxtadorsal carinae more weakly developed than mesolateral carinae, pointed, extended and gradually moving away from dorsal hinge line, from posterior margin of nuchal carina almost to posterior margin of carapace valve. Entire carapace surface smooth, although in some areas of carapaces studied (e.g. Fig. 4C) rather coarse wrinkles occur; these may be a taphonomic artefact.

Specimen GM LNU-45/16 has relatively large mandibles (Fig. 5E, F), but due to poor preservation and partial overlap with hard-to-remove siderite, these cannot be described.

Most abdominal segments, except for last one, not preserved. Last (seventh) pleomere (Fig. 5C) partially studied; surface covered with coarse striae extending posteriorly under oblique angle from narrow, dorsal carina. Telson long and slender, with indistinct dorsal carina (Figs 4I–K, 5A). Furcae coarsely striate longitudinally, long and slender,

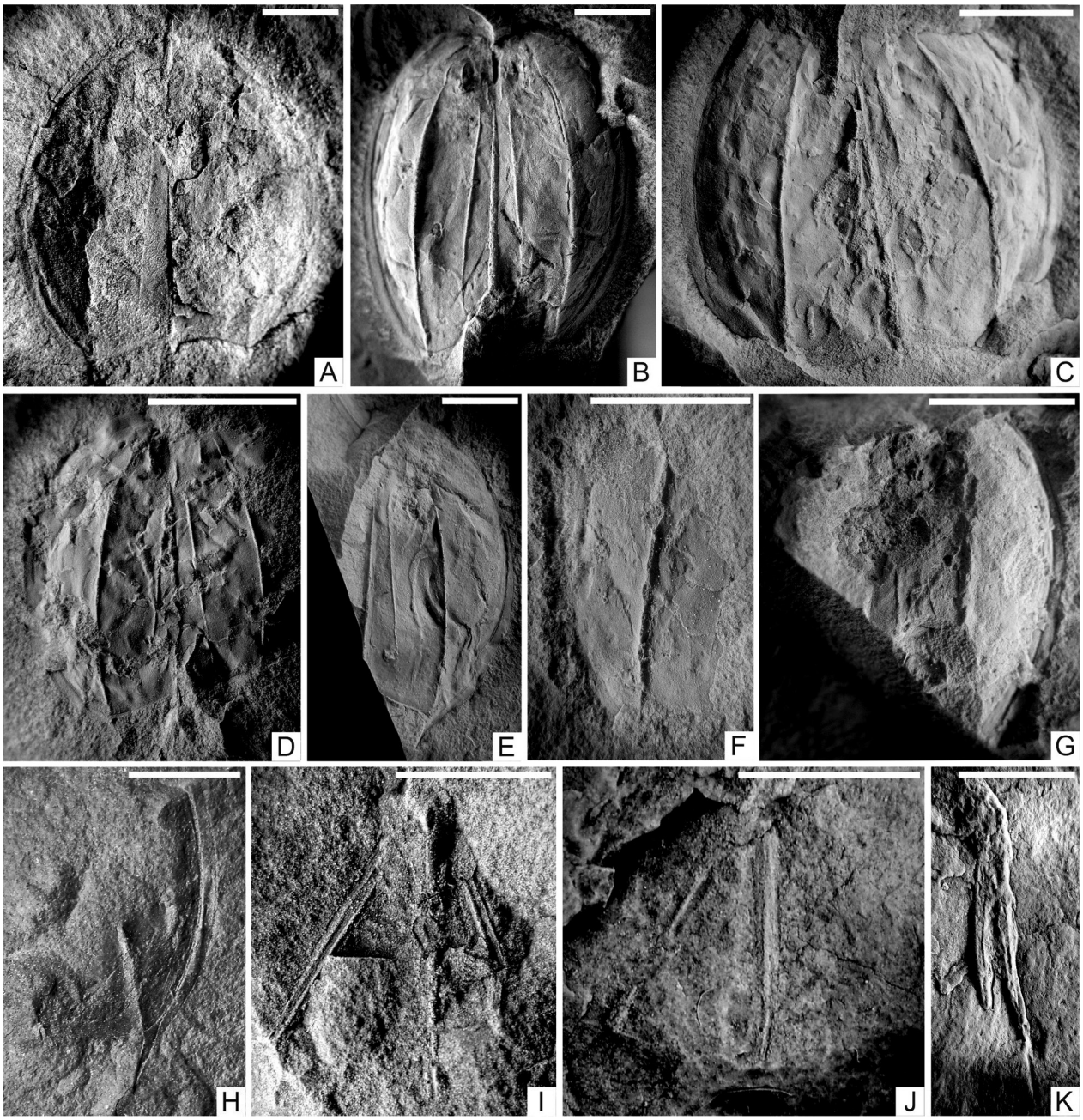

Fig. 4. *Dithyrocaris colei* Portlock, 1843 from the Mospyne Formation of the Donets Basin. **A–D –** Articulated carapaces in dorsal views (**A –** GM LNU-45/01; **B –** GM LNU-45/02; **C –** GM LNU-45/03; **D –** GM LNU-45/04); **E –** Right valve, GM LNU-45/05 in dorsal view; **F –** Fragment of left valve, GM LNU-45/06 in dorsal view; **G –** Articulated carapace in dorsal view (GM LNU-45/07); **H –** Posterior part of right valve, GM LNU-45/08 showing posteroventral spine; **I–K –** Telsons with furcae (**I –** GM LNU-45/09; **J –** GM LNU-45/10; **K –** GM LNU-45/11). Scale bars equal 5 mm.

probably about same length as telson. Telson and furcae not decorated with any setae.

Remarks. The morphology of this species conforms with that of the genus *Dithyrocaris*, with all important morphological features matching the generic diagnosis presented by Rolfe (1969: p. R321). The present specimens are morphologically closely similar to individuals of *Dithyrocaris colei* illustrated by e.g. Jones & Woodward (1898: pl. 22, fig. 7; pl. 23, figs 1–4; pl. 24, figs 2, 4; pl. 27, fig. 5). The sole morphological difference involves the better-developed juxtadorsal carinae in the present material. However, it is likely that this morphological feature falls within the range of intraspecific variation.

Dithyrocaris colei differs from the morphologically similar species, *Dithyrocaris tricornis* (Scouler,

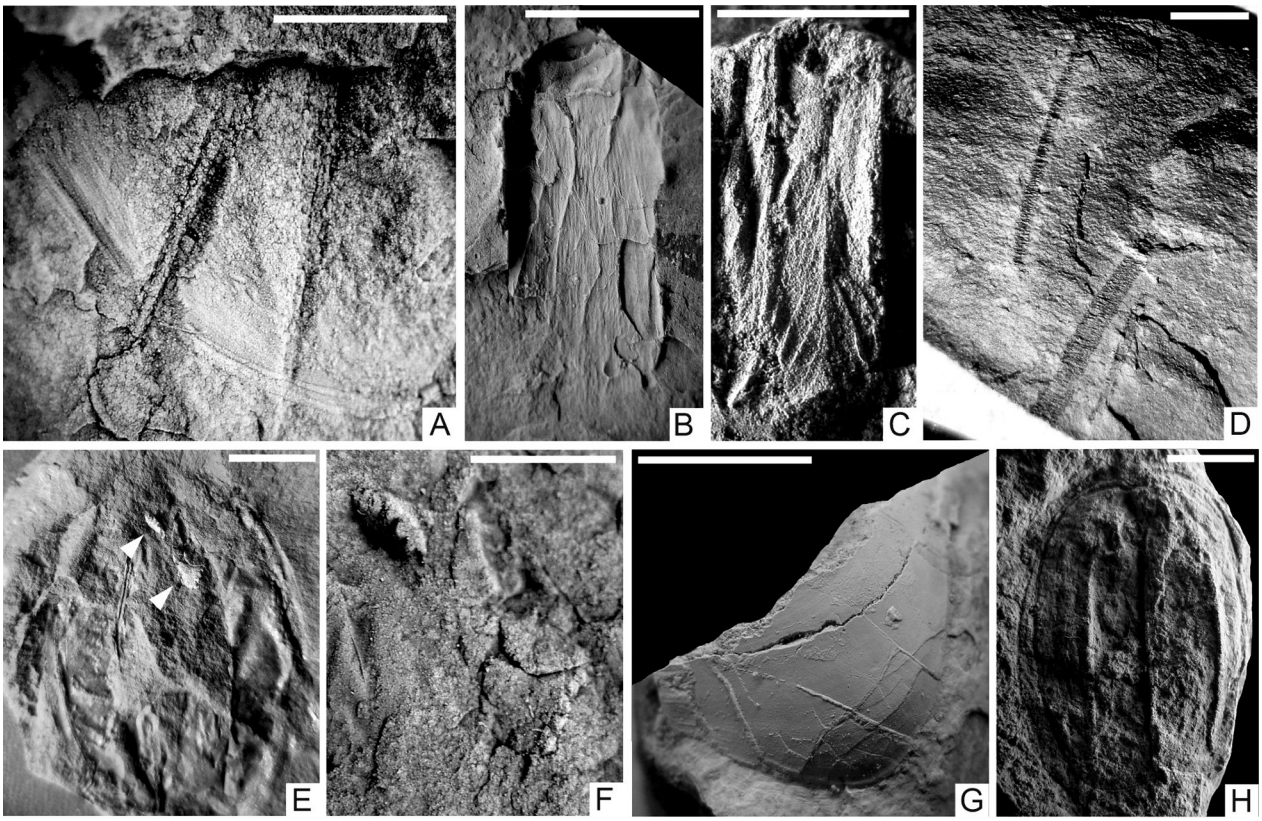

Fig. 5. *Dithyrocaris colei* Portlock, 1843 (**A–F**), Phyllocarida indet. (**G**) and *Dithyrocaris* cf. *granulata* Woodward & Etheridge, 1873 (**H**) from the Mospyne Formation of the Donets Basin. **A** – Telson with furcae, GM LNU-45/12; **B**, **C** – Last abdominal segments (**B** – GM LNU-45/13; **C** – GM LNU-45/14); **D** – Antennal exopod, GM LNU-45/15; **E, F** – Poorly preserved mandibles, GM LNU-45/16 (**E** – indicated by white arrows, **F** – enlarged); **G** – posterior part of right valve in dorsal view (GM LNU-45/24); **H** – Articulated carapace, IGS NASU-41/01 in dorsal view. Scale bars equal 5 mm.

1835), in the absence of tubercles on the surfaces of the mesolateral and juxtadorsal carinae and on the surface of the valve between them. *Dithyrocaris colei* differs from *Dithyrocaris quinni* Copeland, 1967 by a straight dorsal contact line, the presence of juxtadorsal carinae and a smooth dorsal carapace surface. In addition, *Dithyrocaris colei* can be differentiated from *Dithyrocaris rolfei* Schram & Horner, 1978 by the smooth surface of the valves; in *D. rolfei* these are covered with fine, 'hair-like' ornamentation.

It is impossible to compare carapaces of *Dithyrocaris colei* and *Dithyrocaris carbonarius* Meek & Worthen, 1870 from the Pennsylvanian of Illinois (USA), because the latter is described only from a telson with furcae, which in that species are much thicker than those of *Dithyrocaris colei*. The main morphological difference between *Dithyrocaris colei* and *D. testudineus* (Scouler, 1835) (= *Dithyrocaris scouleri* M'Coy, 1844, according to Woodward & Etheridge, 1873, p. 482) is the absence of juxtadorsal carinae in the latter species, in addition to some other, less obvious morphological features. Moreover, *D. testudineus* has a complex carapace ornamentation, while specimens of *Dithyrocaris colei* described here have a smooth carapace surface. The telson and furcae in *Dithyrocaris testudineus* are thicker than in *Dithyrocaris colei*.

There are no significant morphological differences between specimens from the upper Bashkirian of the Donets Basin here referred to *Dithyrocaris colei* and those recorded by Krestovnikov (1961), except for much better-developed juxtadorsal carinae in the present individuals in comparison to the single valve described by Krestovnikov. It should be noted that *Dithyrocaris colei* described by Krestovnikov (1961) came from approximately the same stratigraphical interval (i.e. upper Bashkirian, Mospyne–Belaya Kalitva formations) as the material described here.

Distribution. Serpukhovian of England, Scotland, Ireland and, possibly, France. In the Donets Basin, this species is known from the upper Bashkirian (Krestovnikov, 1961; present study) and probably also in Germany.

Dithyrocaris cf. *granulata* Woodward & Etheridge, 1873

Fig. 5H

Material. A single specimen (IGS NASU-41/01) of a moderately preserved positive impression of a flattened articulated carapace, from the phyllocarid-bearing stratigraphical interval no. 3.

Description. IGS NASU-41/01, an articulated carapace, measuring 20 mm in length and 15 mm in width, with longitudinally ellipsoidal outline and maximum width occurring near mid-length. Valves with approximate length/width ratio of 2.67, relatively narrowly rounded anteriorly, with posterior shallow swing and narrow, straight and pointed posteroventral spine on mid-posterior margin. Dorsal contact margin straight. Ventral margins broadly rounded with narrow border, gradually thickening from 0.5 to 1.5 mm, from posterior to anterior margin. Mesolateral carapace carinae well developed, arcuate, slightly pointed; extending from cephalic carinae and produced into posteroventral spine. Valve surface ornamentation absent or not preserved.

Remarks. Morphologically speaking, IGS NASU-41/01 does not differ significantly from carapaces of *Dithyrocaris granulata* described by Woodward & Etheridge (1874: pl. 5, figs 2, 3) and Jones & Woodward (1898: pl. 18, figs 4–6; pl. 19, figs 5, 6; pl. 20, figs 1–3). However, in view of the fact that the fine carapace ornamentation cannot be seen in the present specimen assignment to *Dithyrocaris granulata* is with a query.

5. Discussion and concluding remarks

In the Carboniferous succession of the Donets Basin, phyllocarids are distributed predominantly in the Bashkirian interval (Fig. 6), where *Dithyrocaris tenuistriata* (see Krestovnikov, 1961), *D. colei* (see Krestovnikov, 1961; present study), *D.* cf. *granulata* (present study) and Phyllocarida indet. (Dernov, 2023; Dernov & Poletaev, 2024; present study) have been recorded. *Ceratiocaris* sp. (undescribed material; see Fig. 6D) has been recorded from the Serpukhovian/Bashkirian boundary interval of the southern Donets Basin.

Only two taxa, *Dithyrocaris granulata doneziana* Riabinin, 1921 and *D. tricornis aisenvergi* Krestovnikov, 1961, are known from beyond the Bashkirian interval, occurring in the Serpukhovian and Upper Pennsylvanian, respectively (Riabinin, 1921; Krestovnikov, 1961). The latter subspecies differs from the nominal species, *D. tricornis* (Scouler, 1835), by its wrinkled ornamentation and the absence of tubercles on the surface of the valves (Krestovnikov, 1961).

In summary, Carboniferous phyllocarids from the Donets Basin are represented by only two genera, *Dithyrocaris* and *Ceratiocaris* M'Coy, 1849. *Dithyrocaris* is a relatively widely distributed genus in Carboniferous strata across Europe (Scouler, 1835; Portlock, 1843; M'Coy, 1844; Armstrong, 1865; Woodward, 1865, 1871; Woodward & Etheridge, 1873, 1874; Etheridge, 1879; Jones & Woodward, 1887–1899; Carpentier, 1913; Riabinin, 1921; Van Straelen, 1933; Currie et al, 1937; Krestovnikov, 1961; Brauckmann, 1984; Schraut, 1999) and North America (Meek & Worthen, 1870; Copeland, 1967; Copeland & Rolfe, 1978; Schram & Horner, 1978; Schram J.M., 1980; Schram et al., 1997) and represented by at least 18 species, many of which were described on the basis of poorly preserved, fragmentary fossils.

An analysis of available palaeontological and lithological data allows us to state that the lower part of the shale bed in the phyllocarid-bearing stratigraphical level no. 2, which yielded *Dithyrocaris colei*, formed in a shelf environment characterised by low depositional rates and a calm hydrodynamic regime. This is confirmed by the lithological composition of the strata, the presence of infaunal organisms (some bivalves and the problematicum *Coleolus*) and cnidarians of the genus *Sphenothallus,* the occurrence of faecal pellet accumulations and more. This part of the inundated area was contaminated with hydrogen sulphide in the sediments and, probably, in the lowermost part of the water column. However, the presence of hydrogen sulphide in the water column is deemed unlikely, because bivalves (e.g. *Phestia*) and other benthic animals would not have existed here. According to this, the black shales described do not differ significantly from other Palaeozoic black shale strata (compare Zangerl & Richardson, 1963; Antia & Wood, 1977; Quinn, 1977; Barron & Ettensohn, 1981; Kammer et al., 1986; Thompson & Newton, 1987; Wignall, 1994; Malinky & Heckel, 1998; Boyer & Droser, 2007, 2009; Nyhuis et al., 2015).

The remaining shales formed under prodeltaic conditions, deposition being marked by delta progradation, which can be clearly seen, for example, in sediment coarsening in the upper part of the shale succession and their overlapping with a thick deltaic sandstone bed.

Biota associated with *Dithyrocaris* cf. *granulata* include terrestrial plants, non-marine horseshoe crabs and bivalves belonging to the genera *Naiadites* and *Curvirimula*, insects and conchostracans, all indicative of freshwater environments. *Naiadites*

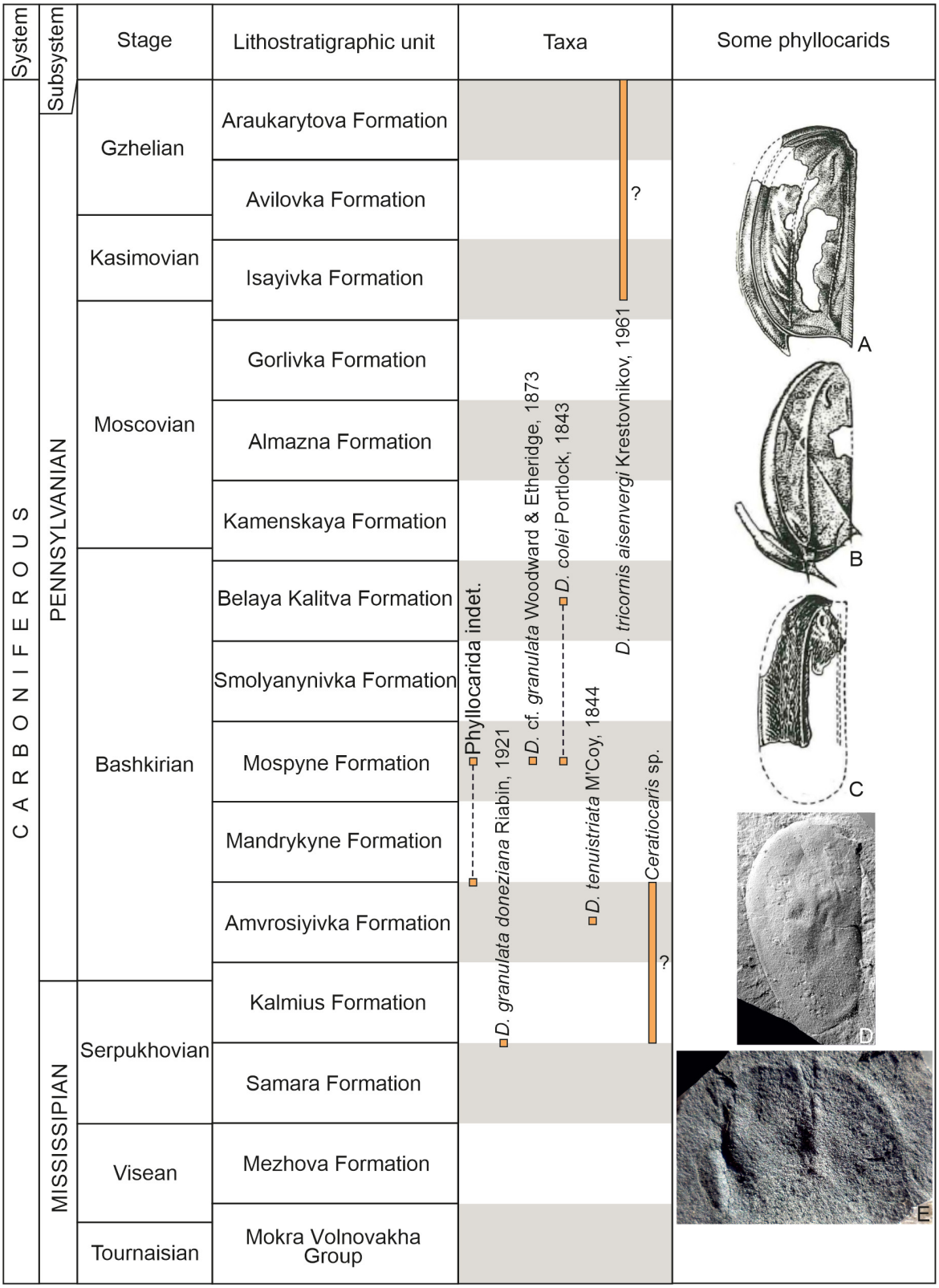

Fig. 6. Stratigraphical distribution of phyllocarid taxa in the Carboniferous succession of the Donets Basin. **A** – *Dithyrocaris tricornis aisenvergi* Krestovnikov, 1961 (after Krestovnikov, 1961: pl. 3, fig. 7); **B** – *Dithyrocaris colei* Portlock, 1843 (after Krestovnikov, 1961: pl. 3, fig. 6); **C** – *Dithyrocaris tenuistriata* M'Coy, 1844 (after Krestovnikov, 1961: pl. 3, fig. 5); **D** – *Ceratiocaris* sp. (undescribed specimen, collections of the Institute of Geological Sciences of the NAS of Ukraine, Kyiv); **E** – Phyllocarida indet. (after Dernov, 2023: fig. 2b). Abbreviation: D. – *Dithyrocaris*.

and *Curvirimula* (Betekhtina, 1974; Anderson et al., 1997) are possible indicators of brackish settings. Lithological features of the fossil-bearing rocks (e.g., black colour, presence of pyrite and limonite concretions) are evidence of dysaerobic palaeoenvironments.

Dithyrocaris cf. *granulata* and other fossils were collected from the dumps of small mines; consequently, they probably originated from different parts of the roof shale of coal seam g_2. As a rule, roof shales of coal beds in the Donets Basin consist of several interlayers differing in depositional conditions (Chernyshev, 1931;Yefimov, 1934; Logvinenko, 1953; Posudiyevsky, 1977; Dernov, 2022a), namely: (1) swamp (in the lower part) and lacustrine (in the upper part) black mudstones and siltstones with frequent plant debris, non-marine bivalves and conchostracans; (2) shallow-marine and brackish black mudstones and siltstones with lingulid brachiopods, marine bivalves and ostracods; (3) offshore marine shales with bivalves, gastropods, ammonoids and other fauna. Apparently, the phyllocarid *Dithyrocaris* cf. *granulata* originated from shallow-marine and brackish shales of interlayer no. 2, as brackish-water fauna predominates in the present collection, while undoubtedly non-marine organisms (e.g. the bivalve *Carbonicola* and horseshoe crabs *Euproops*) are of subordinate importance.

Almost all phyllocarid records from the Carboniferous of the Donets Basin (see Fig. 6) are confined to black shales formed under dysaerobic marine conditions (Krestovnikov, 1961; Dernov & Udovychenko, 2019a; Dernov, 2023; Dernov & Poletaev, 2024). The palaeoenvironmental context of *Dithyrocaris granulata doneziana* Riabinin, 1921 from the Kalmius Formation is slightly unclear. Limestone bed D_1 of the Kalmius Formation (in modern nomenclature, limestone bed D_1^5), which yielded this subspecies, contains a rich marine biota comprising calcareous algae, foraminifera, corals, bryozoans, brachiopods, bivalves, gastropods, cephalopods, crinoids, echinoids, etc., and forms a relatively small bioherm (Aisenverg et al., 1987; Poletaev et al., 1988). It is possible that *Dithyrocaris granulata doneziana* came from the shale bed separating the limestone beds of the D_1 limestone group consisting of five beds, from D_1 to D_1^5 (Poletaev & Vdovenko, 2013). However, it should be noted that relatively large (6–8 mm long) isolated mandibles, not yet studied in detail, have been found in some Bashkirian-aged limestone beds in the Donets Basin.

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