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A new record of the myriapod genus *Arthropleura* Jordan in Jordan et von Meyer, 1854 from the Pennsylvanian of Ukraine

V.S. Dernov[1, 2]

[1]Institute of Geological Sciences of the NAS of Ukraine, Kyiv, Ukraine; [2]National Museum of Natural History of the NAS of Ukraine, Kyiv, Ukraine

Нова знахідка багатоніжок роду *Arthropleura* Jordan in Jordan et von Meyer, 1854 у пенсильванії України

В.С. Дернов[1, 2]

[1]Інститут геологічних наук НАН України, Київ, Україна; [2]Національний науково-природничий музей НАН України, Київ, Україна

E-mail:vitalydernov@gmail.com,
https://orcid.org/0000-0002-5873-394X

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New finds of remains of probably juvenile giant terrestrial myriapods belonging to the genus *Arthropleura* Jordan in Jordan et von Meyer, 1854, defined under open nomenclature only to the genus level (*A.* sp.), are described from continental (probably lacustrine) rocks of the Mospyne Formation (late Bashkirian, Early Pennsylvanian) of the southern Luhansk Region, eastern Ukraine. The specimens of *A.* sp. differ from most arthropleurid fossils described and figured by previous researchers by their much smaller size, much fewer tubercles on the surface of the probable paratergites, and the absence of a significant size gradation of the tubercles. The new findings support the assumption of some researchers that juvenile and adult individuals of the genus *Arthropleura* may have chosen different habitats for their existence.

Keywords: Arthropoda, *Arthropleura*, Myriapoda, Pennsylvanian, Donets Basin, Ukraine.

Ключові слова: членистоногі, багатоніжки, *Arthropleura,* пенсильваній, Донецький басейн, Україна.

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Introduction

Giant myriapods of the genus *Arthropleura* Jordan in Jordan et von Meyer, 1854, with some individuals reaching a length of about 2.5 m (Hahn et al., 1986; Schneider, Werneburg, 1998, 2010; Pillola, Zoboli, 2021), are among the largest terrestrial invertebrates in the Earth history. This genus ranged from the late Visean (Mississippian) to the Sakmarian (Cisuralian, Permian) of the palaeoequatorial belt of Euramerica (Schneider et al., 2010; Chaney et al., 2013; Davies et al., 2021).

In the fossil record, these arthropods are represented mainly by isolated fragments of the exoskeleton (see review in (Davies et al., 2021)), as well as giant trackways named *Diplichnites cuithensis* Briggs, Rolfe et Brannan, 1979 and its junior synonym *D. minimus* Walter et Gaitzsch, 1988 (Ferguson, 1966; Ryan, 1986; Marks, 1998; Lucas et al., 2005; etc). Trackways assigned to *Diplichnites cuithensis* with widths of 18–50 cm and *D. minimus* with widths of 5–8 cm have been reported from the Visean to the Cisuralian of the USA, Canada, Scotland, France, Germany, Ukraine, and Kazakhstan (for more details see (Moreau et al., 2021: Table 2) and (Davies et al., 2021: Table 1)).

At present, only three more or less complete adult specimens of *Arthropleura* are known, two of which come from the Pennsylvanian of Germany (Guthörl, 1934, 1935; Hahn et al., 1986; Schneider, Barthel, 1997; Schneider et al., 2010) and one specimen was described by Davies et al. (2021) from the Serpukhovian of England. There are several reports of complete exoskeletons of apparently juvenile individuals of *Arthropleura* (Calman, 1915; Almond, 1985; Briggs, Almond, 1994; Schneider et al., 2010; Lhéritier et al., 2024).

Previously, the present author (Dernov, 2019a) figured body remains of *Arthropleura* sp. and locomotion traces assigned to *Diplichnites cuithensis* from two deltaic sandstone beds in the middle part of the Mospyne Formation (late Bashkirian, Early Pennsylvanian) exposed near the village of Makedonivka in Luhansk Region, eastern Ukraine. The body remains of *Arthropleura* sp. are very fragmentary here and occur together with pebbles and plant debris as clusters of numerous exoskeleton fragments on the sandstone bedding plane. The new finds of arthropleurid remains from the Mospyne Formation exposed in the south part of Luhansk Region are described on this paper. These finds come from a new

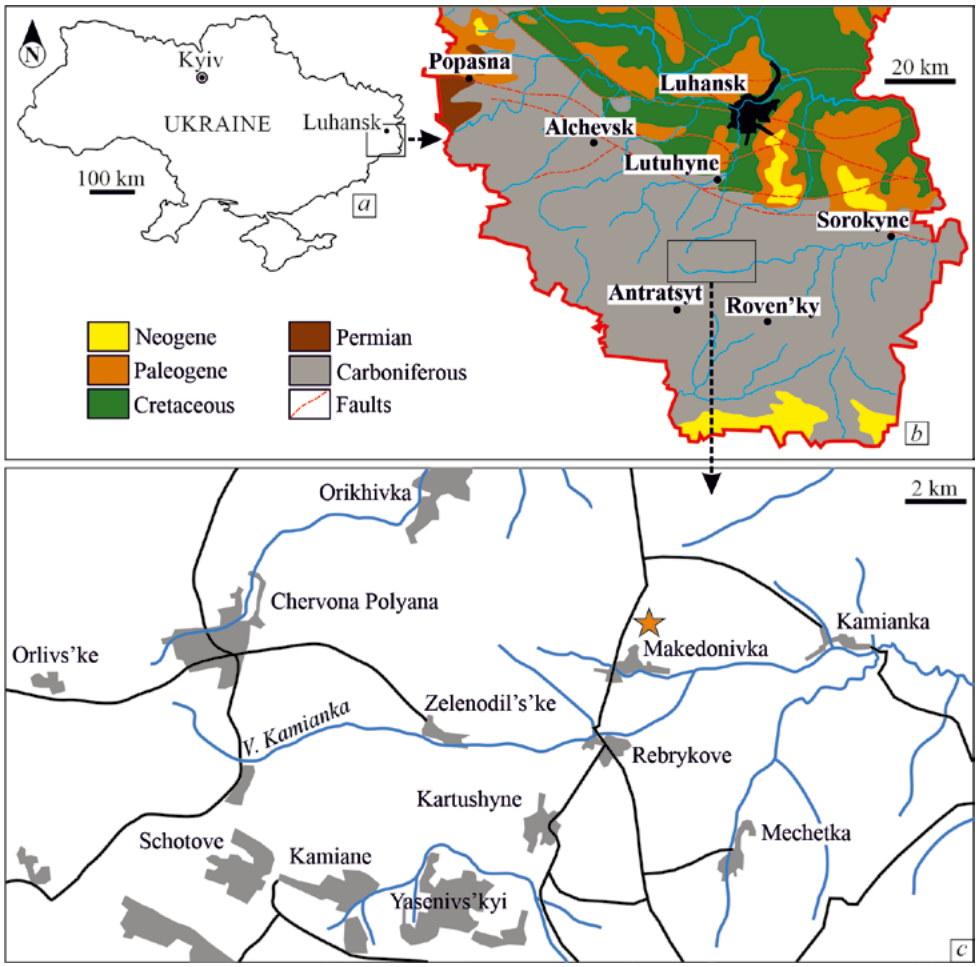

Fig. 1. Geographical location of the arthropleurid-bearing locality (orange asterisk)

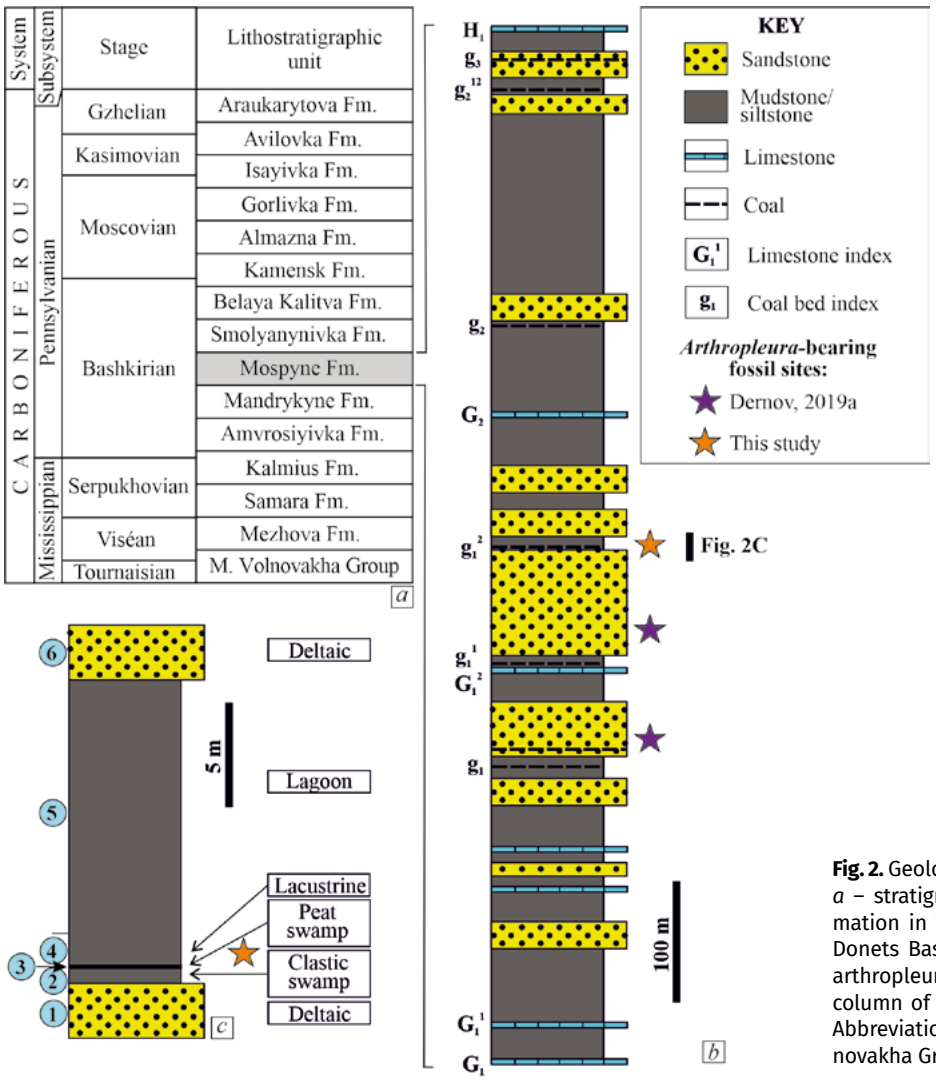

Fig. 2. Geological setting of the studied fossil site: *a* – stratigraphic position of the Mospyne Formation in the Carboniferous succession of the Donets Basin, *b* – stratigraphic position of the arthropleurid-bearing fossil sites, *c* – lithological column of the arthropleurid-bearing fossil site. Abbreviation: M. Volnovakha Group – Mokra Volnovakha Group

stratigraphic level and facies than the previously described fossils (Dernov, 2019a). Various groups of non-marine arthropods have been previously studied from the Carboniferous of the Donets Basin, *i.e.*, arthropleurids (Dernov, 2019a), eurypterids (Chernyshev, 1933; Shpinev, 2014), horseshoe crabs (Chernyshev, 1927, 1928; Karlov, 1948; Shpinev, 2018; Dernov, 2019a, 2019b), trigonotarbids (Dunlop, Dernov, 2023), thelyphonids (Selden et al., 2013), conchostracans (Chernyshev, 1927, 1928; Dunaeva, 1950), cyclids (Dernov, 2022c), freshwater barnacles (Tchernyshev, 1935), pygocephalomorphs (Birshtein, 1966; Schram, 1980), and insects (Sharov, Sinitshenkova, 1977; Aristov, 2015; Dernov, 2019a; Aristov, Rasnitsyn, 2022). Unfortunately, many of these groups need to be revised, because much time has passed since their original study and the taxonomy of arthropods has undergone significant changes since. Arthropleurids are an excellent tool for palaeogeographic and palaeobiogeographic reconstructions, since these arthropods predominantly inhabited wetland forests of the palaeoequatorial belt.

Geological setting

Locality. The studied body fossils of *Arthropleura* sp. were collected from dumps of a small, very old (*c.* 100–120 years old) coal mine near the village of Makedonivka (Ukraine, Luhansk Region; coordinates: 48°14'36"N 39°17'58"E) (Fig. 1). The fossil-bearing rock is a roof shale of the g_1^2 coal bed in the middle part of the Mospyne Formation (Fig. 2, *b*).

Numerous animal fossils such as the non-marine bivalves *Curvirimula trapeziforma* (Dewar, 1939) (Fig. 3, *d, e*) and *C. tessellata* (Jones, 1891) (Fig. 3, *f*), a juvenile horseshoe crab, problematic remains, fish scales assigned to *Rhizodopsis sauroides* (Williams, 1849) (Fig. 3, *i*) and *Rhabdoderma elegans* (Newberry, 1856), a bradyodont tooth assigned to *Helodus* sp., and undetermined fish remains (Fig. 3, *g*) have been collected from this stratigraphic level (Dernov, 2019b, 2022a).

A rich terrestrial plant assemblage consisting of *Asolanus camptotaenia* Wood, 1860,

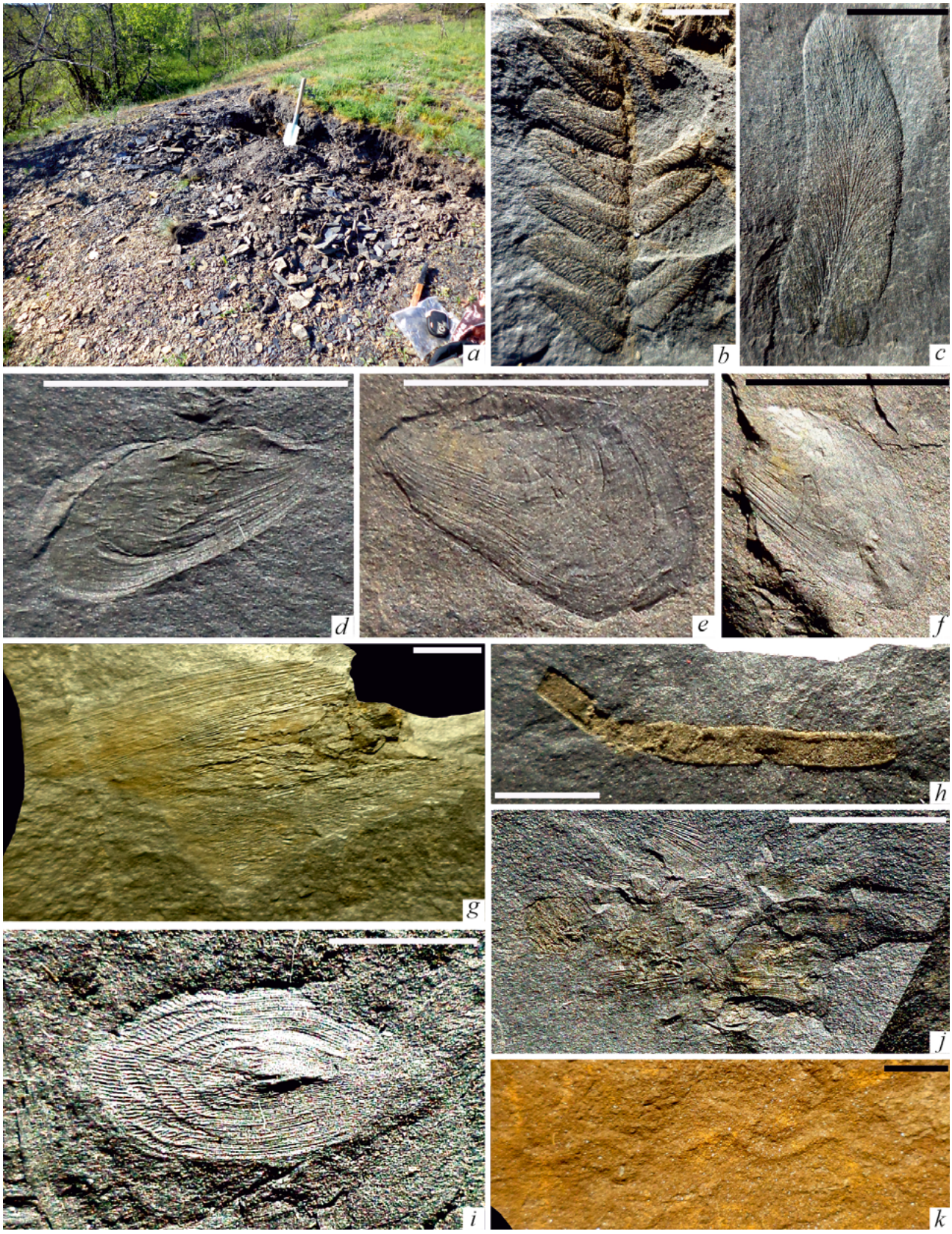

Fig. 3. Geological and palaeontological features of the *Arthropleura*-bearing shale above the g_1^2 coal bed: *a* – general view of the studied fossil site, *b* – pteridosperm *Neuralethopteris schlehanii* (Stur, 1877) Cremer, 1893, *c* – pteridosperm *Paripteris gigantea* (Sternberg, 1823) Gothan, 1941, *d*, *e* – bivalves *Curvirimula trapeziforma* (Dewar, 1939), *f* – bivalve *Curvirimula tessellata* (Jones, 1891), *g* – impression of the fish fin, *h* – limonitized coprolite, *i* – fish scale *Rhizodopsis sauroides* (Williams, 1849), *j* – ?bromalite, *k* – trace fossil *Cochlichnus anguineus* Hitchcock, 1858. Scale bars = 5 mm

Bothrodendron minutifolium (Boulay, 1876) Zeiller, 1879, *Cyperites bicarinatus* Lindley et Hutton, 1832, *Halonia* sp., *Lepidodendron lycopodioides* Sternberg, 1820, *Lepidophloios laricinus* (Sternberg, 1820) Goldenberg, 1857, *Lepidostrobophyllum* sp., *Syringodendron* sp., *Stigmaria ficoides* (Sternberg, 1820) Brongniart, 1822, *Asterophyllites grandis* (Sternberg, 1825) Geinitz, 1854, *As. longifolius* (Sternberg, 1825) Brongniart, 1828, *Calamites carinatus* Sternberg, 1823, *C. undulatus* Sternberg, 1825, *C. cistii* Brongniart, 1828, *Pinnularia capillacea* Lindley et Hutton, 1834, *Sphenophyllum cuneifolium* (Sternberg, 1821) Zeiller, 1879, *Corynepteris coralloides* (Gutbier, 1835) Zeiller, 1888, *Dictyoxylon* sp., *Eusphenopteris* cf. *obtusiloba* (Brongniart, 1830–1831) Novik, 1947, *Neuralethopteris schlehanii* (Stur, 1877) Cremer, 1893 (Fig. 3, *b*), *Paripteris gigantea* (Sternberg, 1823) Gothan, 1941 (Fig. 3, *c*), etc., was collected at this fossil site (Dernov, Udovychenko, 2019). Plant fossils sometimes bear biodamages (e.g., galls, ovipositions, and margin feedings) (Dernov, 2021). The trace fossils *Planolites beverleyensis* (Billings, 1862) and *Cochlichnus anguineus* Hitchcock, 1858 (Fig. 3, *k*) were also found here (Dernov, 2019b, 2023).

Stratigraphy. The arthropleurid-bearing rocks lie in the middle part of the Mospyne Formation (see Fig. 2, *a, b*), which consists of a 315 to 730-m-thick sequence of mudstones, siltstones, sandstones, limestones, and coals (Aisenverg et al., 1963, 1975; Feofilova, Levenstein, 1963; Dunaeva, 1969; Poletaev et al., 2011; Nemyrovska, Yefimenko, 2013). The formation corresponds to the lower part of the Zuyivkian Horizon (lower half of the Kayalian Regional Stage) of the Regional stratigraphic scheme of the Don-Dnipro Trough (Poletaev et al., 2011; Nemyrovska, Yefimenko, 2013). The lower part of the formation (below the g_1 coal bed) in the study area is replaced by the shale-dominated succession, which is very poor in fossils. Apparently, this part of the Mospyne Formation should be referred to the Dyakove Group (late Visean–late Bashkirian) (Dernov, 2022b; Dernov, Poletaev, 2024).

The Mospyne Formation contains typical Langsettian terrestrial plants (Novik, 1974; Dernov, Udovychenko, 2019) and ammonoids (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), the late Bashkirian conodonts *Declinognathodus noduliferus* (Ellison et Graves, 1941) s.l., ?*D. pseudolateralis* Nemyrovska, 1999, *Idiognathodus praedelicatus* Nemyrovska, 1999, *Id. primulus* Higgins, 1975, *Id. sinuosus* Ellison et Graves, 1941, and *Idiognathoides lanei* Nemirovskaya in Kozitskaya et al., 1978 (Nemyrovska, 1999), and other marine and terrestrial biota such as miospores, foraminiferans, corals, bryozoans, brachiopods, scaphopods, gastropods, horseshoe crabs, insects, and fishes.

Taphonomy and palaeoecology. As the studied fossils were collected in the dumps of a small coal mine, they probably originate from different parts of the roof shale of the g_1^2 coal seam. As a rule, roof shales of coal beds in the Donets Basin consist of several palaeoenvironmental "zones" 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 mudstone and siltstone with frequent plant debris, non-marine bivalves, and conchostracans; (2) Shallow marine and brackish black mudstone and siltstone with lingulide brachiopods, marine bivalves, and ostracods; (3) Offshore marine shale with marine bivalves, gastropods, ammonoids, and other normal marine fauna. The remains of *Arthropleura* apparently originate from the lacustrine black shale of the swamp/lacustrine "zone".

The trace fossils assigned to *Cochlichnus anguineus* Hitchcock, 1858 (see Fig. 3, *k*), which are interpreted as locomotion traces of nematodes, insect larvae, or annelids (Gluszek, 1995; Metz, 1995; Buatois et al., 1996, 1997; Lucas et al., 2004), were found at the site. In addition, feeding traces of unidentified "worm-like organisms" (Mikuláš, Dronov, 2006), *Planolites beverleyensis* (Billings, 1862), have been found at several stratigraphic levels of the studied section. In the roof of the sandstone unit (Bed No. 1; see Fig. 2, *c*), myriapod locomotion traces assigned to *Diplopodichnus biformis* Brady, 1947 were found; arthropod locomotion traces *Diplichnites* isp. have been found in the Bed No. 6. The horseshoe crab resting traces *Selenichnites hundalensis* (Romano et Whyte, 1987) with *Planolites beverleyensis* were found at the base of the Bed No. 7.

The remains of bivalves from the roof shales of the g_1^2 coal bed are often represented by shell fragments. The formation of shell debris is probably not related to the influence of abiotic environmental factors (*e.g.*, high water activity), since, on the basis of the lithological features, mudstone was formed under conditions of low water dynam-

ics. It is possible that sclerophagous fishes that fed on molluscs were the producers of shell debris. Together with bivalves, a single tooth plate of the bradyodont fish belonging to the genus *Helodus* and scales of sarcopterygians were found in the Bed No. 4. In the same mudstones, elongated clusters of small fish scales and bone debris are often observed, which may be fish bromalites (see Fig. 3, *j*).

Bivalves of the studied locality existed in shallow eutrophic freshwater or brackish lakes located on the coastal accumulative lowland. These palaeobasins were characterized by a significantly depleted composition of aquatic organisms, low sedimentation rate, dysaerobic environments, and an active supply of nutrients from the adjacent lowland wetland (Dernov, 2022a).

The representatives of the genus *Curvirimula* probably led a pseudoplanktonic lifestyle, attaching themselves to various floating (*e.g.*, wood fragments) or bottom-located objects (*e.g.*, benthic macroscopic algae) (Warth, 1967; Wignall, Sims, 1990). In this way, these molluscs rose above the oxygen-depleted water column zone. It should be noted that the pseudoplanktonic lifestyle may be optional for these molluscs and under more favorable conditions they could lead a benthic lifestyle. The coastal zone of these lakes was covered by dense, but systematically monotonous, hydrophilic vegetation represented by monotaxon assemblages of the arborescent sphenopsid genus *Calamites* (Fissunenko, 1987). Bivalves of the genus *Curvirimula* existed in brackish water basins (Betekhtina, 1974; 1979; Anderson et al., 1997).

Material and methods

Two newly collected, poorly preserved fragmental impressions of supposed paratergites of *Arthropleura* sp. preserved in carbonaceous, black mudstone (specimen GMLNU-19/01) and siltstone (specimen NMNH-G 8640/01) together with rare plant debris were examined in this study. One fossil described below has been previously figured by the author (Dernov, 2019b: Fig. 3.6), but not formally described. Studied fossils, collected by the author during fieldwork in 2013–2014, are stored in the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (specimen NMNH-G 8640/01) and in the Geological Museum of the Luhansk Taras Shevchenko National University, Poltava (specimen GMLNU-19/01).

Systematic palaeontology

Phylum Arthropoda von Siebold, 1848
Subphylum Myriapoda Latreille, 1802
Order Arthropleurida Waterlot, 1934
Family Arthropleuridae von Zittel, 1885
Genus *Arthropleura* Jordan in Jordan et von Meyer, 1854

Type species. *Arthropleura armata* Jordan in Jordan et von Meyer, 1854; by original designation.

Arthropleura sp.
Fig. 4

Material. Two poorly preserved fragmental impressions of probable paratergites with partially preserved carbonized cuticle from the roof shale of the g_1^2 coal bed, late Bashkirian-aged Mospyne Formation (fossil site near the village of Makedonivka, Luhansk Region, Ukraine).

Description. Specimen NMNH-G 8640/01 (Fig. 4, *a*) is a fragment of a weakly convex sub-triangular left lateral (?)paratergite, about 10 mm long and 6 mm wide, preserved as a thin carbonized film in siltstone together with small carbonized plant debris. Two short, slightly curved faint furrows, 3–4 mm long and *c.* 1 mm thick, are situated on the outer surface of the (?)paratergite, in the area close to the supposed medial tergite. Four sharp, rounded and slightly ellipsoidal tubercles (three clearly visible and one faintly visible), 1 mm in diameter at the base, spaced about 2.0–2.5 mm apart, are arranged in a checkerboard pattern near the narrow (lateral) margin of the (?)paratergite. One or two tubercles have broken-off tips and are therefore truncated. The surface of the (?)paratergite between the tubercles is smooth and shows no evidence of the surface fine ornamentation.

Specimen GMLNU-19/01 (Fig. 4, *b*) is a sub-triangular fragment of a flattened (?)paratergite, about 14 mm long and 9 mm wide at its widest part, preserved as a thin carbonized film in mudstone. The outer surface of the (?)paratergite bears four well-defined ellipsoidal and rounded tubercles, 1–2 mm in diameter, spaced 3.0–3.5 mm apart and arranged in a checkerboard pattern, and one barely visible slightly larger ellipsoidal tubercle 2.5 mm in length along the long axis. Most of the tubercles are truncated because they have broken-off tips. The surface of the (?)paratergite between the tubercles is smooth and shows no evidence of the surface fine ornamentation.

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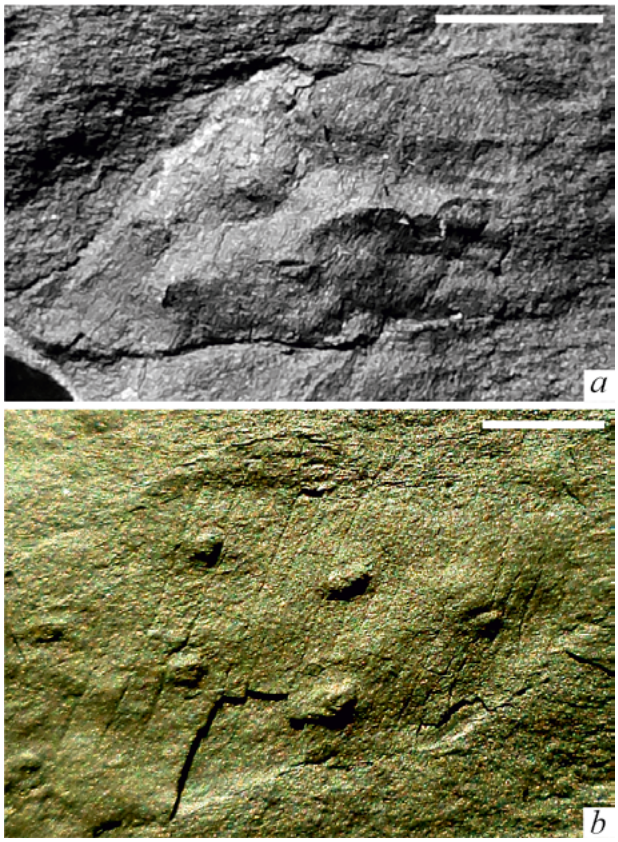

Fig. 4. *Arthropleura* sp. from the Mospyne Formation of the Donets Basin: *a* – specimen NMNH-G 8640/01, *b* – specimen GML-NU-19/01. Scale bars = 5 mm

Remarks. It is not possible to compare the specimens of *A.* sp. described here with reliably identified remains of species of the genus *Arthropleura*, since the available material, limited in quantity, is very poorly preserved and may belong to juvenile individuals of this genus, which, unfortunately, are less frequently described (*e.g.,* Calman, 1915; Almond, 1985; Briggs, Almond, 1994) than the remains of adults.

Occurrence. Late Bashkirian-aged Mospyne Formation of the central Donets Basin, Ukraine.

Discussion

The previously reported occasional finds of the trackway *Diplichnites cuithensis* from the Donets Basin (Dernov, 2019a: Fig. 8.9) confirm the opinion of Schneider et al. (2010) that the limited record of these large trace fossils in Central and Eastern Europe, where *Arthropleura* body remains are very common, is simply due to the lack of large exposure surfaces in Upper Palaeozoic fluvial sandstone units. In the recent past, laminated marine and rarely deltaic sandstones have been actively mined in the Donets Basin. Alluvial sandstones, in which *Diplichnites cuithensis* is most commonly preserved (see (Schneider et al., 2010)) for a review, have hardly been mined, thus there are no large areas of exposed alluvial sandstone bedding planes.

It should be noted that the only figured specimen of *Diplichnites cuithensis* from the Donets Basin (Dernov, 2019a: Fig. 8.9) is rather poorly preserved, probably caused by wave erosion, and is also represented by a small fragment of a trackway. In terms of preservation, this specimen is similar to traces of *Diplichnites cuithensis* from the Pennsylvanian of Kentucky, USA (Martino, Greb, 2009). However, unlike the trace fossils from Kentucky, *Diplichnites cuithensis* from the Donets Basin are located on an erosion surface that was probably not covered with microbial mats, which may greatly enhance the preservation of animal surface tracks (Seilacher, 2008; Marty et al., 2009; Carmona et al., 2012), including the trackways *Diplichnites cuithensis* (Prescott et al., 2014).

It is impossible to attribute the described probable paratergites to a specific species of the genus *Arthropleura*, since they are very poorly preserved and represented by only two specimens. Externally, the two specimens of *Arthropleura* sp. described above differ somewhat from each other, so it is likely that they belong to different species of the genus *Arthropleura*, although this cannot be proven based on the available material.

The specimens of *A.* sp. described above differ from most arthropleurid fossils described and figured by previous researchers (*e.g.,* Pruvost, 1912, 1930; Waterlot, 1934; Copeland, 1957; Castro, 1997; Pacyna et al., 2012; Pillola, Zoboli, 2021) by their much smaller size, far fewer tubercles on the surface of the probable paratergites, and the absence of a significant size gradation of the tubercles. However, the latter feature may be caused by the small size of the studied fossils and their poor preservation. It should be noted that the paratergite of *Arthropleura armata* Jordan in Jordan et von Meyer, 1854 from the Visean of Germany (Rößler, Schneider, 1997: Fig. 16a, b; Schneider et al., 2010: Fig. 9B) bears tubercles arranged in a staggered pattern and differing slightly in size.

It is likely that the described material represents the remains of juvenile individuals of *Arthropleura*. The paratergites of juvenile arthropleurids from the latest Stephanian–earliest Autunian of Montceaules-Mines in France (see (Schneider et al., 2010: Fig. 10A, B; Schneider, Werneburg, 2010: Fig. 11; Lhéritier et al., 2024: Fig. 6)), bear rare tubercles of approximately the same size. The same applies to the

juvenile specimen of *Arthropleura* described under the name *A. moyseyi* Calman, 1915 from the Westphalian of England (Calman, 1915). These tubercles are sometimes staggered, although more often they are arranged linearly. In addition to spines, the paratergites also have a broad longitudinal ridge. Schneider et al. (2010) also reported very long and thin, spike-like sculpture cones on the paratergites of *A. moyseyi*, which are only observed on silicon rubber casts, but are not visible on the holotype of *A. moyseyi* (see GB3D Type Fossils).

On the other hand, it should be noted that the small size of the arthropleurid remains described here could be a collecting artifact, as the *Arthropleura*-bearing fossil site is an old mine dump composed of weathered small (up to 5 cm) pieces of rock. Under such conditions, large fragments of *Arthropleura* exoskeletons could not have been preserved.

Juvenile and adult arthropleurids may have inhabited different habitats and the preferred habitat of adult arthropleurids could be characterized as loosely vegetated sandy areas in open river landscapes under a year-round wet climate in coastal environments to seasonally wet, semi-humid climates in continental settings (Schneider et al., 2010). Therefore, the absence of remains of adult arthropleurids in the material described here could also be due to these reasons, although the small amount of material studied does not allow us to determine this with certainty.

Another morphological feature of the fossils described above that distinguishes them from the remains of *Arthropleura* described by previous authors (*e.g.,* Pillola, Zoboli 2021) is the absence of fine ornamentation on the surface of the exoskeleton fragments, which cannot be explained by the insufficient preservation of the described fossils, which were preserved in fine-grained rocks (siltstone and mudstone) as positive impressions with partially preserved carbonized cuticle. The absence of surface texture on fragments of the exoskeleton is characteristic of arthropleurid remains buried in coarse-grained psammite rocks (Davies et al., 2021).

Conclusions

The study of new finds of remains of terrestrial arthropods of the genus *Arthropleura* from the Pennsylvanian of the Donets Basin demonstrated the great importance of the so-called collecting artifact in the completeness of collections of arthropleurid remains and the age structure of representatives of these arthropods in these collections. The absence of complete trackways of arthropleurids belonging to the ichnospecies *Diplichnites cuithensis* in the Upper Palaeozoic of Central and Eastern Europe is probably due to the lack of large areas of exposed fluvial sandstones of this age in these macroregions. The arthropleurid fossils and locomotion traces from the Mospyne Formation of the Donets Basin described in this paper and studied earlier may indicate different living conditions for juvenile and mature arthropleurids, as proposed by some previous researchers.

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З континентальних (ймовірно, озерних) порід моспинської світи (верхня частина башкирського ярусу, нижній пенсильваній) півдня Луганської області описано нові знахідки решток, вірогідно, ювенільних особин гігантських наземних багатоніжок роду *Arthropleura* Jordan in Jordan et von Meyer, 1854, визначених за відкритою номенклатурою лише до родового рівня (*A.* sp.). Вивчені рештки *A.* sp. відрізняються від більшості скам'янілостей артроплеврид, описаних і зображених попередніми дослідниками, значно меншими розмірами, значно меншою кількістю горбків на поверхні паратергітів і відсутністю значної градації розмірів цих горбків. Нові знахідки підтверджують припущення деяких дослідників щодо того, що молоді та дорослі особини роду *Arthropleura* могли обирати різні біотопи для свого існування.

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