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Re-assessment of *Arthropleura mammata* from the Moscovian of Northern France: new anatomical information and adaptations to terrestrial environments

Mickaël LHÉRITIER[a,1], Bruno VALLOIS[b,c], and Claudie DURAND[b]

The fossil record of *Arthropleura*, distributed in the Nord-Pas-de-Calais coalfield (France) and some Belgian localities, is reassessed and compared to new material discovered in new localities of the Bruay Formation. Based on tergite ornamentation, the Bruay specimens are attributed to *Arthropleura mammata*. Two specimens are preserved with their head, allowing the description of the head anatomy of this species for the first time. We estimated the size of the most complete remains from the newly investigated localities, with a maximum length probably reaching 50 centimetres. The geographical extension of *A. mammata* can be extended to the Nord-Pas-de-Calais and to the Saarland coal basins. Some specimens from the Bruay Formation consist of K-plates, typical ventral plates of arthropleurids displaying well-preserved pierced tubercules. These pierced tubercules are also found in K-plates of *Arthropleura cristata*, found in the Mazon Creek Lagerstätte, and could represent spiracles similar to the ones found in millipedes. This suggests that *Arthropleura* possessed a tracheal system for respiration and, combined with other anatomical factors, would confirm it as a terrestrial arthropod.

Arthropleura | Bruay Formation | Moscovian | Nord-Pas-de-Calais coalfield | K-plates

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Introduction

Arthropleura Jordan & Von Meyer 1854 has long been an iconic myriapod due to the gigantic size of some of its representatives, that may have reached nearly 3 metres long (Davies et al. 2021), making them the largest land arthropod of all time. *Arthropleura* thrived from the Early Carboniferous (Rößler & Schneider 1997) to the Early Permian (Rößler et al. 2012), with an Euro-American distribution (Hannibal 1997). Their most prominent feature is the division of their tergites between a central syntergite and lateral paratergites. Among members of *Arthropleura*, *A. mammata* Salter 1863 is recognisable by its characteristic tuberculation - a first row of four tubercles under the keel of the paratergite and a second row of smaller tubercles behind the first row. *Arthropleura mammata* was known from the Bashkirian (323.2 Ma – 315.2 Ma) of the United Kingdom, Belgium and France (Salter 1863; Pruvost 1919, 1922, 1930).

In Northern France, knowledge of *Arthropleura* is largely the result of very limited opportunistic collections, housed in the Natural History Museum of Lille (Hauts-de-France, France). Specimens were found during coal mining at the end of the 19th century and at the beginning of the 20th century (Pruvost 1912, 1919). These fragmentary remains of *Arthropleura* were examined by Pruvost and already considered as important references for studying the genus *Arthropleura*. They are deposited under Gosselet collections (acronym MGL, see Appendix 1) and consist of 34 specimens, among which only eight specimens were actually collected during coal exploitation in Nord-Pas-de-Calais localities (Fig. 1). The fossils were determined as *Arthropleura mammata* (i.e. Pruvost 1912, 1919). Because of a lack of complete specimens, knowledge of this animal has been scarce and characterised by very fragmentary remains examined by Pruvost in 1919. For example none of the examinations include an estimation on the animal size. Based on previous records, *A. mammata* has been described as inhabiting the coal marshes of Nord-Pas-de Calais in the locality of Anzin (Pruvost 1912, 1919). This study aims to revisit the biostratigraphy of *A. mammata* in accordance with plant biozones of Moscovian age, with new material acquired during fieldwork in 1995 to 2012 in the western part of the Nord-Pas-de-Calais coal basin (see Vallois & Nel 2023) (Fig. 1). This material comes from three new localities from the Bruay Formation, forming the upper part of the coal layers. These new occurrences confirm the presence of *Arthropleura mammata*, already known in the Westphalian B (Duckmantian, late Bashkirian), through Westphalian C (Bolsovian, early to middle Moscovian, see Lucas et al. 2022 for the equivalence between Western Europe and Global stages) and allow a more precise estimation of the size of *A. mammata*. These new occurrences extend the biostratigraphical span of *A. mammata* well beyond the Bashkirian age, that would complete a vertical extension of this species (i.e. Fig. 2, red hexagon). A focus is made on samples previously studied by Pruvost (1912, 1919), which correspond to

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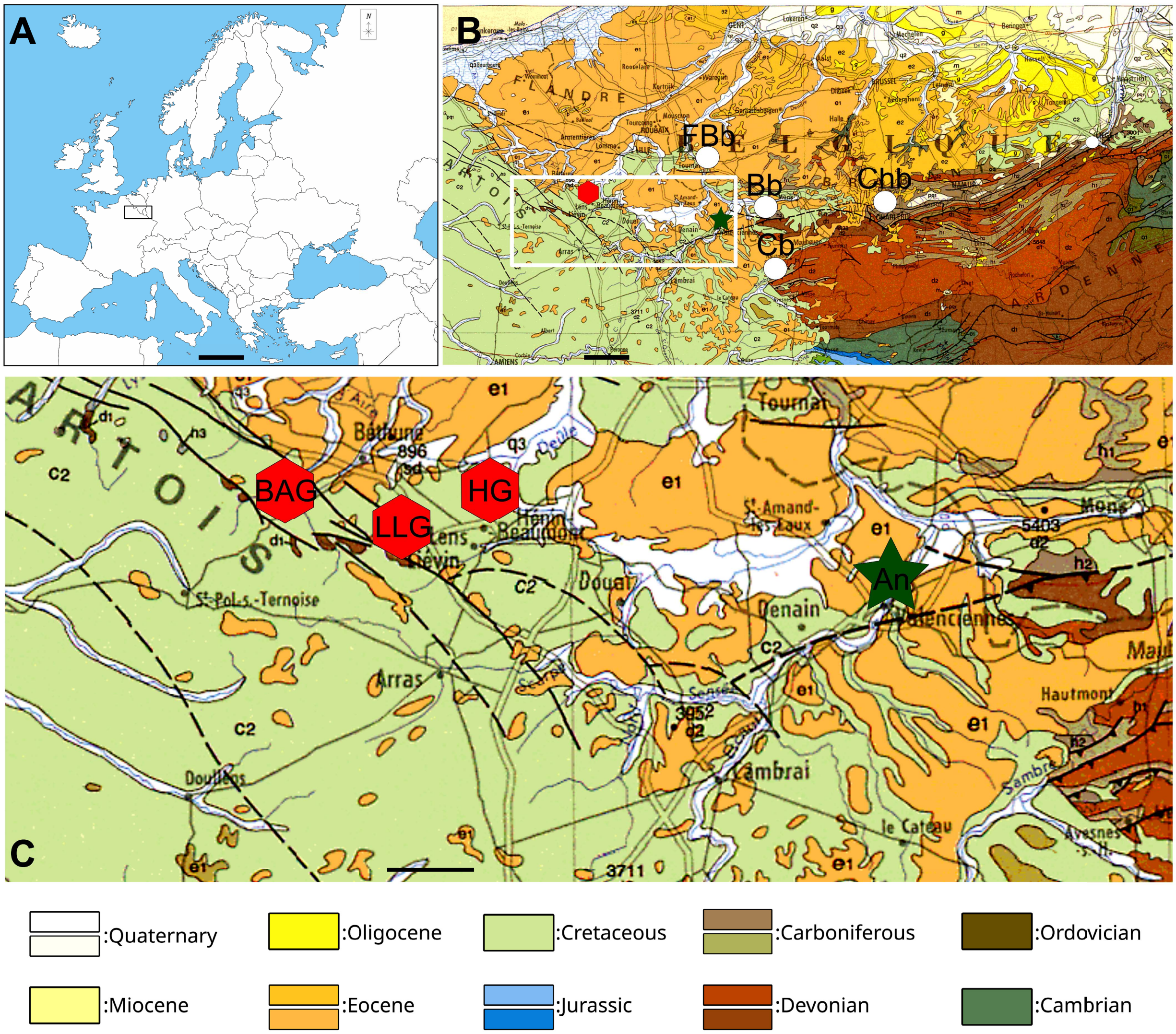

Figure 1. Location of the studied material. **A**: position of the French and Belgian coalfields. **B**: position of the Pas-de-Calais basin, where the 'ancient material' (Pruvost, 1919, Anzin Formation, Westphalian B i.e. Baskhirian-Moscovian, green star) and the new specimens from the Bruay Formation (Westphalian C i.e. Moscovian, red hexagon) were found. **C**: details of the position of the Bruay Formation in the Pas-de-Calais basin. The Bruay specimens come from three different zones exploited by different mining companies: the Bruay-Auchel Group (BAG), the Lens-Liévin Group (LLG) and the Hénin Group (HG). Note that the coalfields are not visible on the map at this scale, being covered by Cretaceous sediments and located in underground mines. An, Anzin; Bb, Borinage basin; Cb, Center basin; Chb, Charleroi basin; FBb, Franco Belgian basin. Scale bars = 10 km (B, C), 500 km (A). Vectorised map in A from © d-maps.com.

localities in the Valenciennes coal basin of Zeiller 1886 (Anzin Formation). Morphology and ecology of *A. mammata* is also discussed thanks to the discovery of the first heads observed for this species and ventral plates displaying a possible tracheal system.

Geological setting

The foreland coal basin (covering Northern France and dating from the Moscovian, Fig. 2) is defined by an elongated region of sediment accumulation formed between a compressional orogenic belt and the adjacent craton. The growth of the Variscan mountain range increased sediment supply to the basin due to syn-orogenic erosion, leading to thick sediment accumulations during the Westphalian (Corsin & Corsin 1970). These accumulations are divided into three Formations (locally called Assises): the Vicoigne Formation (*Assise de Vicoigne*), the Anzin Formation (*Assise d'Anzin*) and the Bruay Formation (*Assise de Bruay*). These formations are themselves subdivided into members, following their plant fossil record. Among them, the members of the Bruay Formation are not well differentiated. They are the Six Sillons member, the Ernestine member, the Du-souich member and the Edouard member which are made of a rhythmic succession of parasequences. These sequences include from the base to the top a paleosol, a coal seam, shales rich in plant fossils and conglomerates and sandstones both with a decreasing sorting (Bouroz 1969; Dollé 1970; Le Gall 1994).

The Bruay Formation, where *Arthropleura* was most abundant, is separated from the preceding Formation (Anzin) by the Rimbert marine band (Fig. 2) indicating the last marine transgression. The Bruay Formation includes a repetition of parasequences, which enabled the formation of 37 coal seams with a thickness varying from 770 to 1490 metres (Corsin & Corsin 1970). These parasequences are an indicator of a subsidence directed by climatic, eustatic and

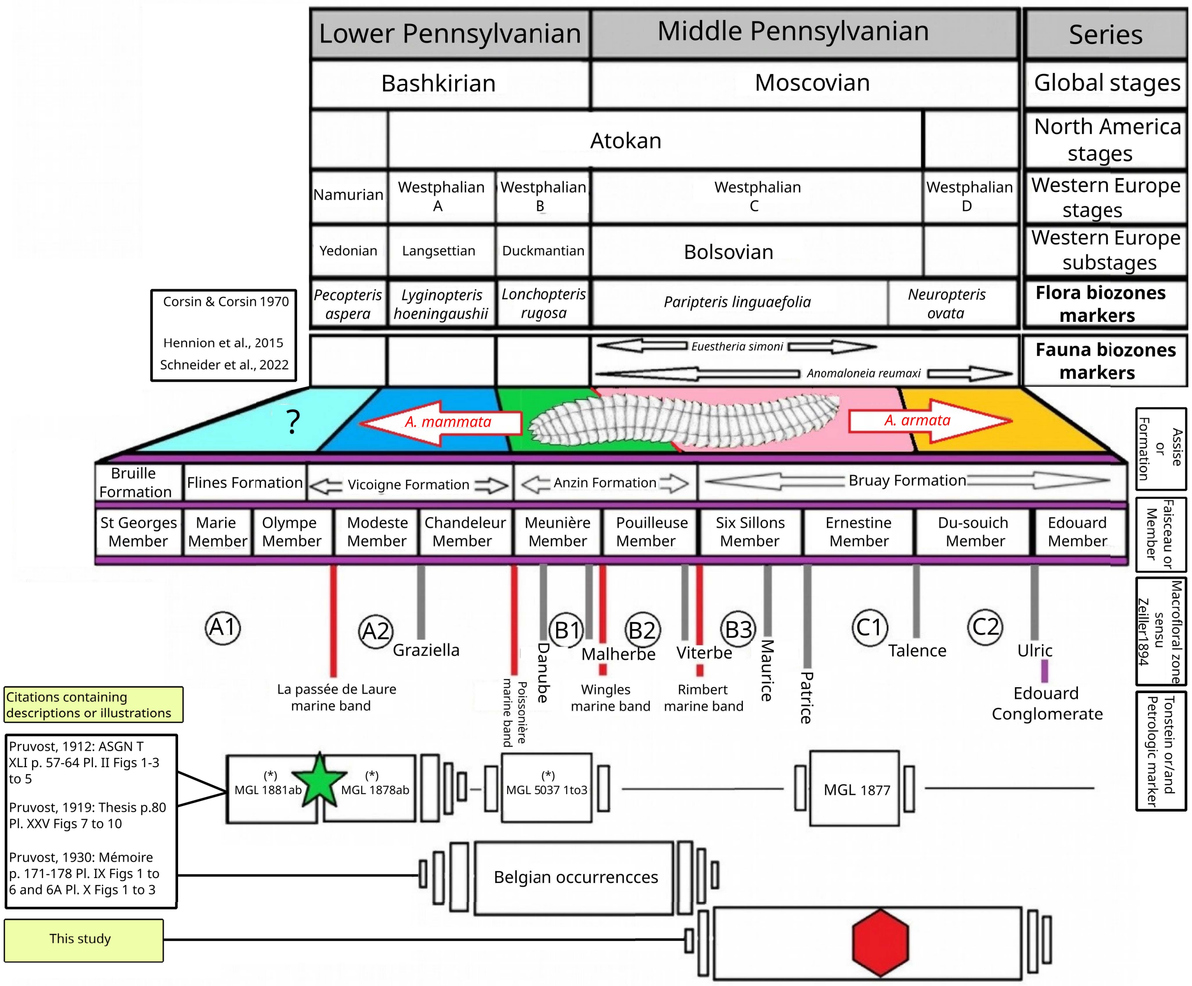

Figure 2. Biostratigraphical ranges of key *Arthropleura* species from northern France basins (including Belgian occurrences). Correlation with plant biozone markers from Zieller (1894) and faunistic biozone markers from Hennion et al. (2015) and Schneider et al. (2021). Each sequence of formation, successively Vicoigne, Anzin, Bruay, refers to eponymous localities and is adapted from the stratigraphic column figured in Corsin & Corsin (1970). Green star: eight old historical references (Pruvost, 1919, Anzin Formation). Red hexagon: Bruay Formation.

tectonic conditions. Within each sequence the organic deposit responsible for the coal seams accumulated in a calm, shallow and anoxic environment similar to modern bogs or mangroves. These seams were covered by sedimentary material with decreasing sorting. This sedimentary material is composed from the bottom to the top of shales deposited during the transgressive context of a deltaic plain, then flooding plain sandstones deposited in a more regressive context.

Zeiller (1894) was among the first to use fossil plants for stratigraphy in these basins. His monography on the Carboniferous of the Valenciennes basin (Zeiller 1886) introduced a new macrofloral approach, that successfully correlated formations based on the plant fossils abundance and similarity of plant sequences, see in Figure 2 (B3, C1, C2 subzones). The productive coal seams in the subzones B1 and B3, exploited in the Anzin area, led to the designation of Anzin as the type locality of the Anzin Formation. This formation is considered a typical series of Westphalian B (Bertrand 1914), equivalent to the late Bashkirian in international time scale. These coal seams are located in underground mines and not in outcrops.

Although the Bruay-les-Mines locality and adjacent areas (e.g., Lens-Liévin and Hénin-Liétard coal districts, Pas-de-Calais, France) have been exploited since the 19th century, the Bruay Formation was defined more recently (Corsin & Corsin 1970; Vallois & Lebrun 2010). This formation includes the C1 and C2 subzones of Zeiller (Fig. 2). These plant sequences were later identified as belonging to the Westphalian C or the equivalent Early Moscovian. In the Nord-Pas-de-Calais coal basin, correlations between different formations and members are based on plant remains and tonsteins (Bouroz et al. 1963; Bouroz 1967), which are fine deposits, often of volcanic origin, which could cover large areas (grey vertical boundaries in Figure 2).

Materials and methods

The studied material comes from the Anzin and Bruay Formations. Specimens from the Anzin Formation mainly come from outcrops in the vicinity of the Valenciennes area. This material was described in previous literature (Pruvost 1912, 1914, 1919, 1930), that we refer to as “ancient material” (green star in Figs 1 and 2) and is housed in Lille Museum (Gosselet Collections, acronym = MGL). Reassessment of Lille specimens made by previous authors (Pruvost 1912, 1919) and by the curator of Gosselet collections (Oudoire, pers. comms.) gave a clear view on the disparity of *Arthropleura* (see Appendix 1 for the re-assessment of this material and Appendix 2 for additional data on Lille collections). Lille specimens consist of leg fragments (MGL.1874 and MGL.5037-3, Pruvost 1912), ventral plates (MGL.1877, Pruvost 1919), a syntergite fragment (MGL.1878a-b, Pruvost 1919), another syntergite fragment associated with finely wrinkled soft parts (MGL.1881a-b, Pruvost 1919) and a paratergite fragment (MGL.5057-1). Specimens from the Bruay Formation were collected from three localities between 1995 and 2019:

- Slag heap of pit N° 5 of Bruay-Auchel group (acronym: BAG - 50° 28’ 49” N, 2°31’ 10” E)
- Slag heap at pit N° 4 East (50° 24’ 48” N, 2° 59’ 48” E) and N° 3 East of Henin Group (acronym: HG - 50° 24’ 46” N, 2° 56’ 22” E)
- Slag heap at pit N° 7 of Lens-Liévin Group (acronym LL - 50° 24’ 09.98” N, 2° 48’ 50.61” E)

This newly investigated material (red hexagon in Figs 1 and 2) is housed at the Museum of Natural History of Grenoble (Isère, France), under label MHNGr.PA.

Systematic palaeontology

Subphylum **Myriapoda** Latreille, 1802
Total-group **Diplopoda** de Blainville in Gervais, 1844 or total-group **Pectinopoda** Benavides, Edgecombe and Giribet, 2023

Remarks. This systematic position is based on the position of *Arthropleura* obtained in the latest total-evidence analyses from Lhéritier et al. (2024).

Subclass **Arthropleuridea** Waterlot, 1934

Diagnosis (emended from Edgecombe in Minelli, 2015). Myriapoda with diplosegmentation and paired anal valves. Paratergal lobes separated from the syntergal axis by sutures. Sclerotized plates (K, B and rosette plates) buttressing the leg.

Order **Arthropleurida** Waterlot, 1934

Diagnosis (modified from Wilson, 1999 and Edgecombe in Minelli, 2015 and adapted from the observations in Lhéritier et al. 2024). Arthropleuridea with ventral sclerites at the front of the head. Eyes stalked. Antennae with eight articles. Mandible with gnathal lobe separated from the distal part of the mandible base. First maxillae reduced with short palp. Second maxillae present. At least 23 trilobed dorsal plates bearing irregular large and small tubercles. Two sternites per dorsal tergite. Sternites with a rounded posterior margin and a more pointed anterior margin. Groove crossing the sternites midline.

Remarks. Contrary to what was said in Lhéritier et al. 2024, the antennae of *Arthropleura* (notably those observed in Montceau-les-Mines juveniles) bear eight articles (not seven).

Family **Arthropleuridae** Von Zittel, 1885

Diagnosis. Same as order.

Remarks. Monogeneric family.

Genus ***Arthropleura*** Jordan in Jordan and Von Meyer, 1854

Type species. *Arthropleura armata* Jordan 1854. Holotype K_{13-14} deposited in the Museum für Naturkunde, Berlin.

Diagnosis. Same as family.

Arthropleura mammata Salter 1863
1912 *Arthropleura mammata* Pruvost: 57-64, pl.II figs 1-3, 5
1919 *Arthropleura mammata* Pruvost: 81, pl. XXV figs 7-8, 10, 20

Type material. Lectotype UKBGS.GSM 25381 deposited in the British Geological Survey.

Type stratum and locality. Upper Carboniferous, Westphalian B, top of the *Modiolaris* Zone in the Ferny Metal, beneath the Seven Foot Coal of Rams Mine; Pendleton Colliery, near Manchester, Lancashire, UK.

Referred Material. MHNGr.PA.39321 (Figs 3A, B and 4).
MHNGr.PA.39322 (Fig. 5A)
MHNGr.PA.39324 (Fig. 5C)
MHNGr.PA.39327 (Fig. 6F)
MHNGr.PA.39328-1 (Fig. 5B)
MHNGr.PA.39347 (Fig. 6E)
MHNGr.PA.39551-1 (Fig. 7A, C)
MHNGr.PA.39551-11 (Fig. 7B, D)
MGL.1878 (Fig. 6A, B)
MGL.5057-1 (Fig. 6C)
MGL.5057-3 (Fig. 6D)

Origin of the material. Slag heap N°1A, pit N° 5 of Bruay at Bruay-Auchel group (50° 28’ 49” N, 2° 31’ 10” E), near Divion, Pas-de-Calais- France. See the Material and methods section for the other pits.

Age and stratigraphy. Early Moscovian, Westphalian C or Bolsovian (Substages Western Europa) – Bruay Formation.

Diagnosis (modified after Salter 1863). *Arthropleura* with round and heavily ornamented head. Collum without paratergites. Trunk paratergites bearing very granulated furrow and no tubercle behind the keel. Posterior part of paratergites with one row of large and one row of smaller tubercles. Middle to front part of the syntergite granulated.

Description. Head rounded anteriorly, ranging in length from 23.2-33.8 mm and in width from 41.7-50 mm, and bearing 50 (MHNGr.PA.39321, Fig. 3AB) to 61 (MHNGr.PA.39322, Fig. 5A) tubercles (1.1-6.4 mm in width). Tubercles round with a diameter of 1.4 to 5.4 mm. Number of tubercles decreasing from the anterior to the posterior part. Ventral sclerites (maximum width of 4.9 mm in MHNGr.PA.39322) at the front of the head (Fig. 5A) in the shape of flattened plates beginning on the sides of the head and rejoining at the centre. Ventral sclerites wider laterally and decreasing in width at the centre.

Specimen MHNGr.PA.39321, the most complete, comprises nine body segments (Fig. 3). First segment modified into a collum (13.1 mm long and 41.7 mm wide) and different from the following segments by being composed of only a syntergite (Figs 3 and 4). Segments two to nine divided into a central syntergite and lateral paratergites (Fig. 3). Average syntergite length and width: 14.5 and 39.4 mm, respectively. Middle to front part of the syntergite granulated (Figs 3, 4, 5). Only left paratergite (37.2 mm wide and 28.6 mm long) of segment five observed (Fig. 3). Paratergite with a row of two visible tubercles (diameter 5 to 7 mm) (Figs 3, 4, 6E) followed by a second row of smaller tubercles (diameter 4,4 to 3 mm) (Figs 3, 4, 6E).

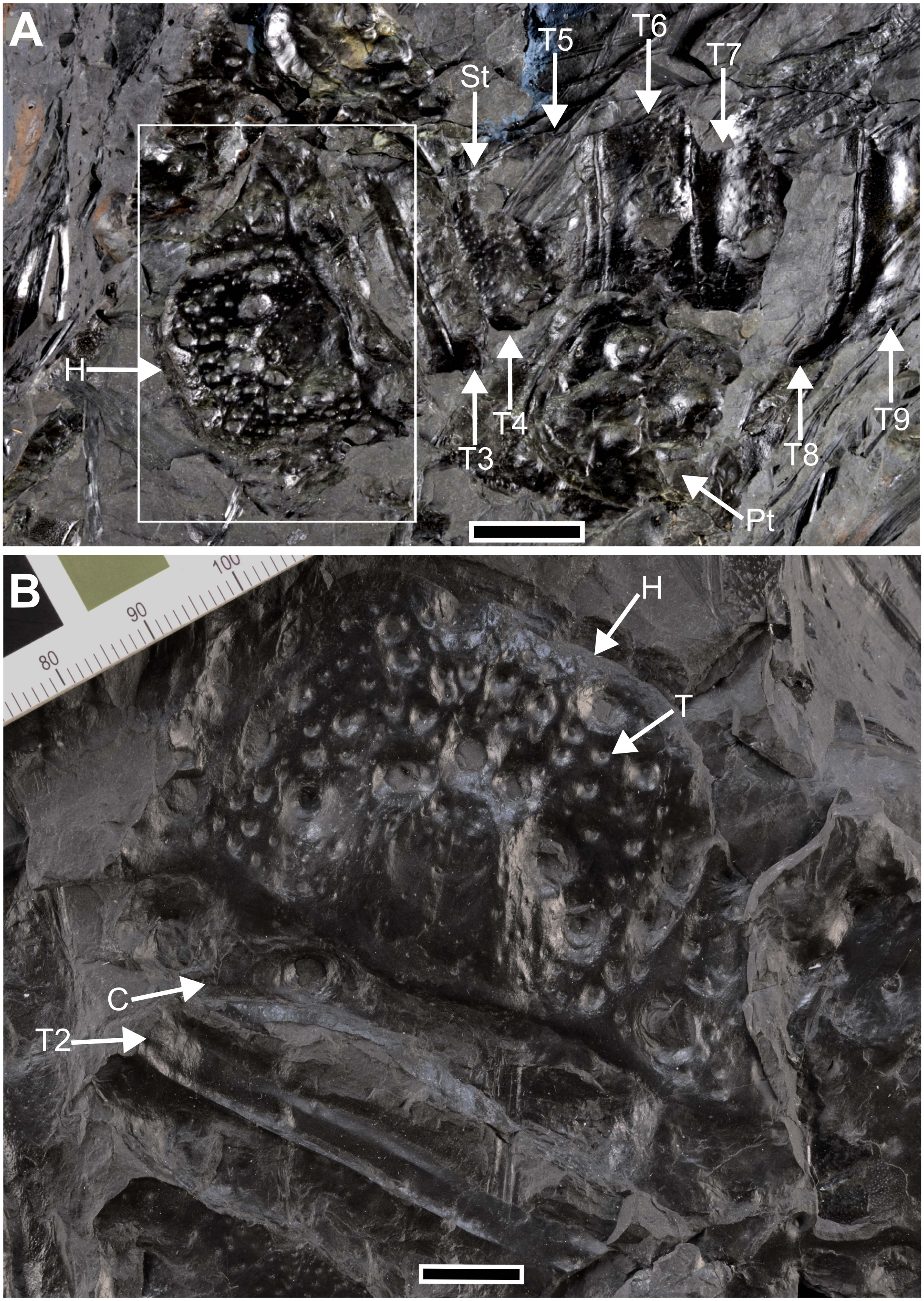

Figure 3. ***Arthropleura mammata*, specimen MHNGr.PA.39321**. **A**: whole specimen. **B**: detail of the head. C = collum; H = head; Pt = paratergite; St = syntergite; T = tubercule; T# = tergite number #. White rectangle on A corresponds to the position of B. Scale bars = 10 mm (B), 20 mm (A). Photos by C. Durand, Muséum d'Histoire Naturelle de Grenoble.

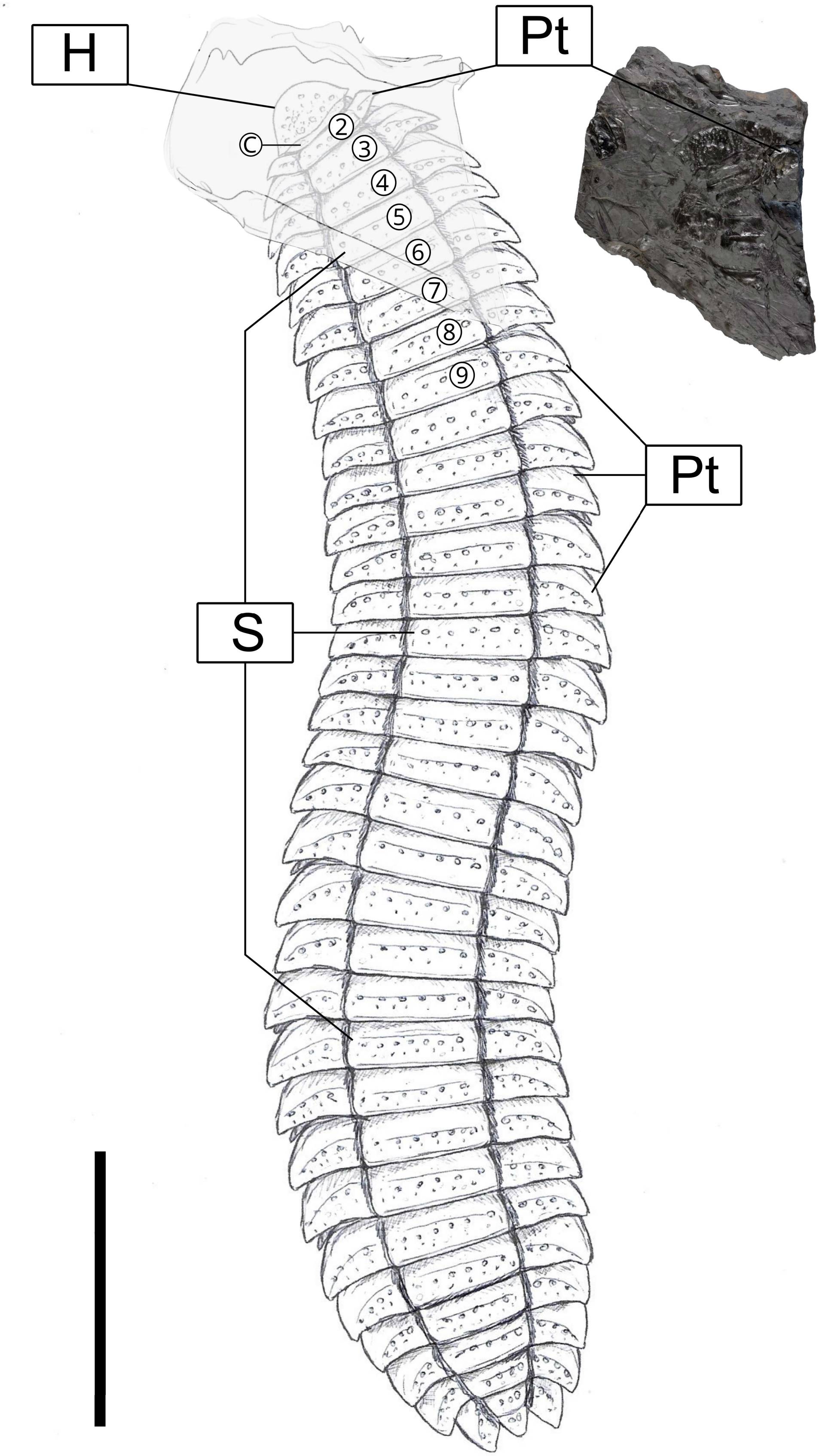

Figure 4. Reconstruction of *Arthropleura mammata*. Based on MHNGr.PA.39321. C, collum; H, head; Pt, paratergite; S, syntergite. Numbers indicate the segments observable on the specimen. Scale bar = 120 mm.

MHNGr.PA.39551-5 and MHNGr.PA.39551-11 are K-plates. These plates are 10 mm long and 5 mm (MHNGr.PA.39551-5) (Fig. 7A, C) to 6 mm (MHNGr.PA.39551-11) (Fig. 7B, D) wide. They are divided into five parts (Fig. 7). The first one (more proximal part to the leg) is triangular and the largest one, with a maximum length and width of 6 mm and 5 mm respectively. It is elongated toward the leg (Fig. 7). The second part (middle of the plate, 3 mm in length and 5 mm in width), is also triangular pointing toward the sternite (Fig. 7). The third part (most distal part to the leg and closer to the sternite), is sub-triangular (2 mm long and 5 mm wide; Fig. 7). The fourth part (behind the third part) is sub-triangular (2 mm long and 1 mm wide), pointing toward part three (Fig. 7B, D), and seems to be located at the boundary between the K-plate and the sternite. The fifth part (only observed in MHNGr.PA.39551-11), is anterior to the first and second parts (Fig. 7). It is trapezoidal (length of 5 mm and a width of 1 mm) and seems to be located at the boundary between the K-plate and the coxa (B-plate) of the next leg in front. Multiple pierced tubercles are present on all parts of the plates (from 91 to 103 on the first part, from 32 to 38 on the second part, 21 on the third part, eight on the fourth part and 12 on the fifth part) (Fig. 7). Tubercle roughly round with a diameter of 0.2 to 0.63 mm. Opening of the tubercle also round with a diameter of 0.07 mm.

Discussion

Extent of Ancient specimens

Several fragments of *Arthropleura mammata* have been discovered in the past, the stratigraphical extent of these ancient specimens is represented by a green star in Figure 2. Most were found near the eponymous locality of the Anzin Formation, Anzin. The discovery of these specimens seems to be linked to the historical context of coal mining in this region during the 19th and 20th century. *Arthropleura mammata* was considered as living in a spatially restricted zone with occurrence in the fossil record also restricted stratigraphically. These coal exploitations seemed to be limited geographically near Anzin and Valenciennes localities (Nord Department, Hauts-de-France region) and in excavation dumps, comprising material from the type locality of the Anzin Formation. The coal exploitations are mainly located in the eastern part of the Nord-Pas-de-Calais coal basin. Dated from the late Bashkirian (Westphalian A and B), these deposits are located between “La Passée de Laure marine band” and the “Rimbert marine band”, corresponding to a time interval in which a rich flora arose (Molina-Solís et al. 2024), qualified by Zeiller as the “Valenciennes basin” flora (Zeiller 1886) (Fig. 2). However, It should be noted that *A. mammata* discoveries remained rare even during coal mining times, during which the majority of *A. mammata* specimens near the locality of Anzin were found (Pruvost 1912, 1919).

New extent in Bruay Formation

The new occurrences from Bruay are younger than previous occurrences of *A. mammata* found in Northern France (Anzin locality), extending the range of this species in the Nord-pas-de-Calais coal basin from the Bashkirian to the early Moscovian (Westphalian C). Its stratigraphy could possibly extend also into the late Moscovian (Westphalian D), based on the macroflora assemblage observed in the excavation dump n°76 from Liévin (Fig. 6C). Among the Bruay occurrences, specimen MNHGr.PA.39321 (Fig. 3) is among the most complete specimens of *Arthropleura mammata* found yet and can be compared to specimen MTB 1220 of *A. armata* found in equivalent chronostratigraphic ranges in the Saar basin (Brauckmann et al. 1997; Wilson 1999).

Congruent extents in European localities

A. mammata, like other arthropleurid species, is mostly known in continental paleo-equatorial environments (Schneider et al. 2010). The stratigraphical extension of *A. mammata* goes from the Bashkirian (Pruvost 1912, 1919, 1930) to the early Moscovian (new Bruay occurrences). We propose that its extension was uninterrupted from the Bashkirian to the Moscovian even through the Carboniferous rainforest collapse, recorded by four major marine transgressions (Fig. 2, Corsin & Corsin 1970; Molina-Solís et al. 2024). The oldest occurrences of the genus *Arthropleura* are known from the Visean in the Hainichen basin in Germany (Rößler & Schneider 1997). No *Arthropleura* occurrence from this age is found in the Nord-Pas-de-Calais basin (acronym HBNPC), which during this stage was a marine environment with a scarce Namurian continental flora assemblage. In the lower part of the HBNPC, the marine nature of the deposits is confirmed by the presence of *Goniatites* (Chalard 1960). Some rare continental outcrops yield remains of *Pecopteris aspera* Brongniart 1828, indicating the existence of some islands bearing flora at this time.

Among older records, occurrences are found during the Serpukhovian in the Lower and Upper Silesian basins in Poland (Pacyna et al. 2018) and a large specimen of *Arthropleura* was described in the Stainmore Formation from the Serpukhovian of England (Davies et al. 2021). Disparate elements of *Arthropleura* have been described in the Bashkirian in the Ostrava-Karvina basin in Czechia (Řehoř & Řehořova 1972), the Charleroi Formation in Belgium (Pruvost 1930), the Donets Basin in Ukraine (Dernov 2019), the Pennine Lower and Middle Coal Measures Formation in the United Kingdom (Vernon 1912; Andrée 1913; Pruvost 1930; Anderson et al. 1997), the Lower Silesian Basin (Zacler Formation) and the Upper Silesian Basin (Ruda Beds) in Poland (Pacyna et al. 2012; Pavela 2018) and the Emma Mine in the Netherlands (Pruvost 1930). Localities increase in abundance in the upper part of the HBNPC with a maximum of recorded occurrences in the Moscovian with specimens in Germany (Jordan & Meyer 1854; Andrée 1913; Guthörl 1934, 1935; Hahn et al. 1986; Kraus & Brauckmann 2003; Kraus 2005), the United Kingdom (Salter 1863; Woodward 1907; Andrée 1913; Pruvost 1930; Hahn et al. 1986; Proctor 1998), France (Waterlot 1934), the Netherlands (Pruvost 1930), Sardinia (Pillola & Zoboli 2021) and in Czech Republic (Pavela 2018). This rise in recording is not simply correlated with the generalised coal mining in localities from this age in Europe and North America and the associated sampling bias. This peak of *Arthropleura* occurrences is not in contradiction with the new described material. 105 fragments of *Arthropleura* from the early Moscovian were already described in the Saar basin (Waterlot 1934; Guthörl 1936). The extension of *A. mammata* seems to be in congruence with a peak of macrofloral diversity that characterises the wet environments of Variscan foreland basins (Molina-Solís et al. 2024). Recently, Pillola & Zoboli (2021) described a paratergite of *Arthropleura armata* in Sardinia (Italy). This occurrence is the most meridional one found so far, and confirms a late Moscovian extension for the genus.

Chronostratigraphic implications

Until now, most *Arthropleura* specimens found in the HBNPC were grouped under the species *Arthropleura mammata*, based on eight

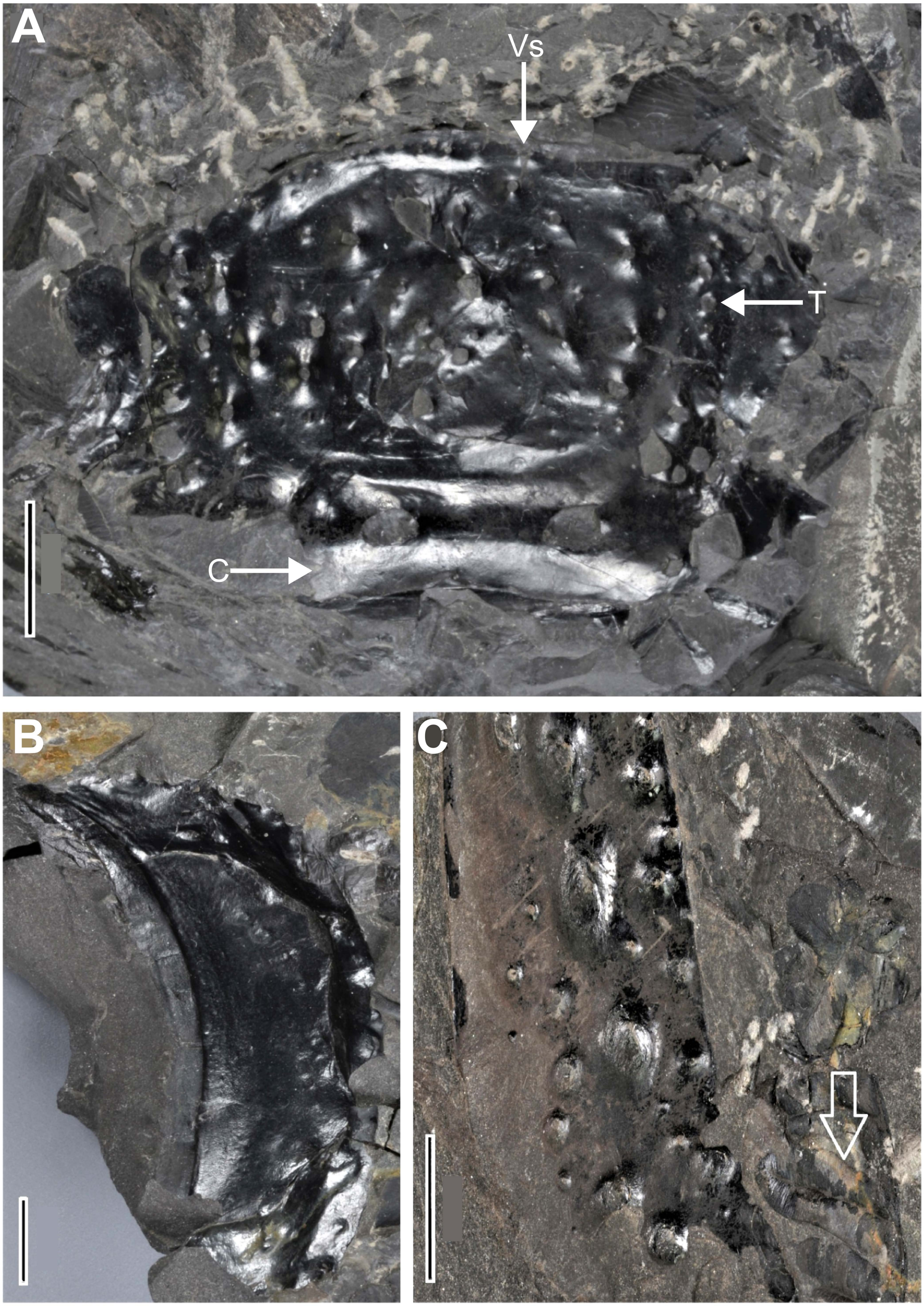

Figure 5. *Arthropleura mammata*, other specimens from La Bruay Formation. **A**: head, specimen MHNGr.PA.39322. **B**: syntergite fragment, specimen MHNGr.PA.39328-1. **C**: paratergite fragment, specimen MHNGr.PA.39324. C = collum; T = tubercule; Vs = ventral sclerites. White arrow in C indicates an *Alethopteris serlii* pinnule. Scale bars = 10 mm. Photos from C. Durand, Museum d'Histoire Naturelle de Grenoble.

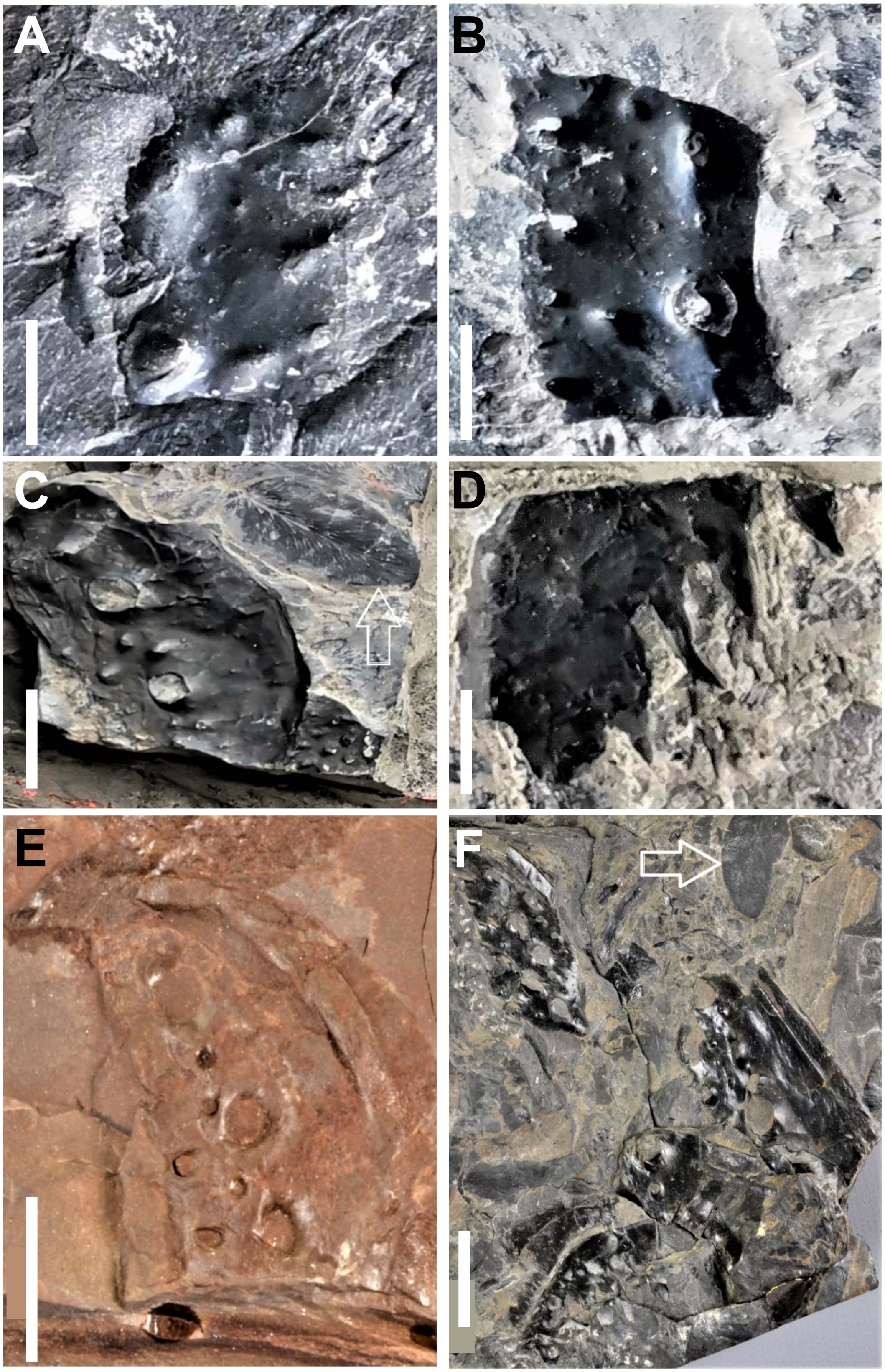

Figure 6. ***Arthropleura mammata*, specimens from the Anzin and Bruay formations**. **A-D**: Anzin Formation. **A-B**: part and counterpart of a syntergite, specimen MGL.1878 (same as in Pruvost, 1919, pl. XXV, fig. 8). **C**: paratergite, specimen MGL.5057-1, Vicq locality, Pit Cuvinot, Westphalian B, Meunière member, seam Boulangère. **D**: fragment of leg segment, specimen MGL.5057-3, same locality as MGL.5057-1. **E-F**: Bruay Formation, Lens-Lievin Group. **E**: paratergite, specimen MHNGr.PA.39327. **F**: fragments of paratergite and syntergites, specimen MHNGr.PA.39347. White arrows on C and F indicate a *Linopteris subbrongniartii* pinnule. Scale bars = 10 mm. E and F made by C. Durand, Muséum d'Histoire Grenoble.

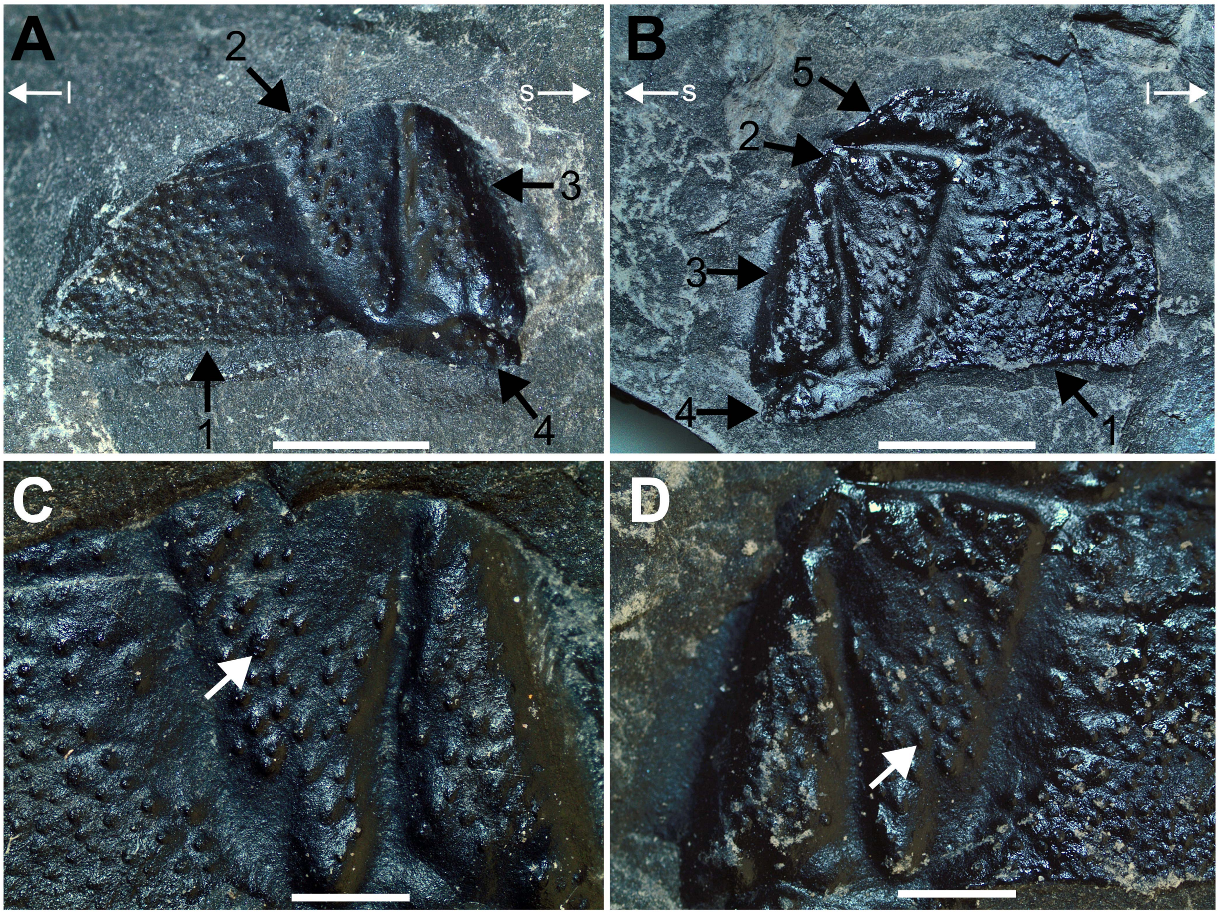

Figure 7. ***Arthropleura mammata*, K-plates**. **A**: right K-plate, specimen MHNGr.PA.39551-5. **B**: left K-plate, specimen MHNGr.PA.39551-11. **C**: details of the central part of MHNGr.PA.3955-1. **D**: details of the central part of MHNGr.PA.39551-11. 1 = part proximal to the leg; 2 = middle part; 3 = part most distal to the leg; 4 = connexion between K-plate and sternite; 5 = connexion between K-plate and B-plate. Small white arrows indicate the orientation of the plate: l = leg; s = sternite. White arrows on C and D indicate pierced tubercles. Scale bars = 2 mm (C, D); 5 mm (A, B).

isolated elements (MGL collection), found solely in the Anzin Formation (Pruvost 1912, 1914, 1919, 1930). The stratigraphical extent of *A. mammata* is thoroughly described in multiple monographs and theses (Brongniart 1828; Boulay 1876, 1879; Zeiller 1886; Carpentier 1913; Danzé-Corsin 1953; Danzé 1956; Buisine 1961; Crookal 1964, 1969; Laveine 1967; Laveine et al. 1978, 1987, 1992; Laveine & Goubet 1995; Izart et al. 1998; Laveine & Belhis 2007).

Plant remains associated with *Arthropleura* specimens known in the Anzin Formation are also present in the Bruay Formation (Vallois & Lebrun 2010; Vallois & Nel 2023; Molina-Solís et al. 2024). Some seed fern specimens can be identified (Bertrand 1907), indicating in the Bruay Formation a *Paripteris linguaefolia* (Bertrand 1930) biozone (Fig. 2). It seems that the increase of macroflora diversity is synchronous with the increase in *Arthropleura* occurrences from the Bashkirian to the late Moscovian.

The successive Westphalian series characterising the HBNPC in the Vicoigne, Anzin and Bruay Formations are not very differentiated. They are formed of a rhythmic succession of parasequences, consisting from the base to the top of a paleosol, a coal seam, shales rich in plant fossils and conglomerates and sandstones with a decreasing sorting (Bouroz 1969; Dollé 1970). The repetition of these sedimentary sequences highlights rapid changes of the hydrodynamic conditions, which have been controlled by variations of climatic, eustatic (Fig. 2, red lines indicating marine transgressions), and tectonic conditions. The climax of these variations was reached during the Asturian (Westphalian D), identified in the HBNPC by the Du-souich and Edouard members (Fig. 2). With each cycle, the organic matter which produced the coal seams accumulated below stagnant water or a shallow bog or mangrove, forming an anoxic environment. This organic matter, including possible *Arthropleura* exuviae was covered by transgressive clay (becoming shales with diagenesis) from deltaic plains, then by fluviatile sandstones from flood plains, which have been deposited in a regressive context.

As seen in Molina-Solís et al. 2024, the specific richness of plants increases exponentially and corroborates with *A. mammata* occurrences in the Bruay Formation. We disagree with the idea that an *Arthropleura* association was strictly limited to the Valenciennes basin in the Anzin-Valenciennes basin during the Bashkirian like said in ancient studies (Pruvost 1912, 1919, 1930). The occurrences in the Bruay-Auchel mining group extend the stratigraphy of *Arthropleura*. This extension affirms that *Arthropleura* was present along the whole stratigraphical sequence of the basin from the Bashkirian to the Moscovian nearly without interruption. The remains of *Arthropleura* have been found starting from the Olympe member (Fig. 2), where plant richness reaches around 60 species at the base of the Vicoigne Formation (marked by *Lyginopteris*

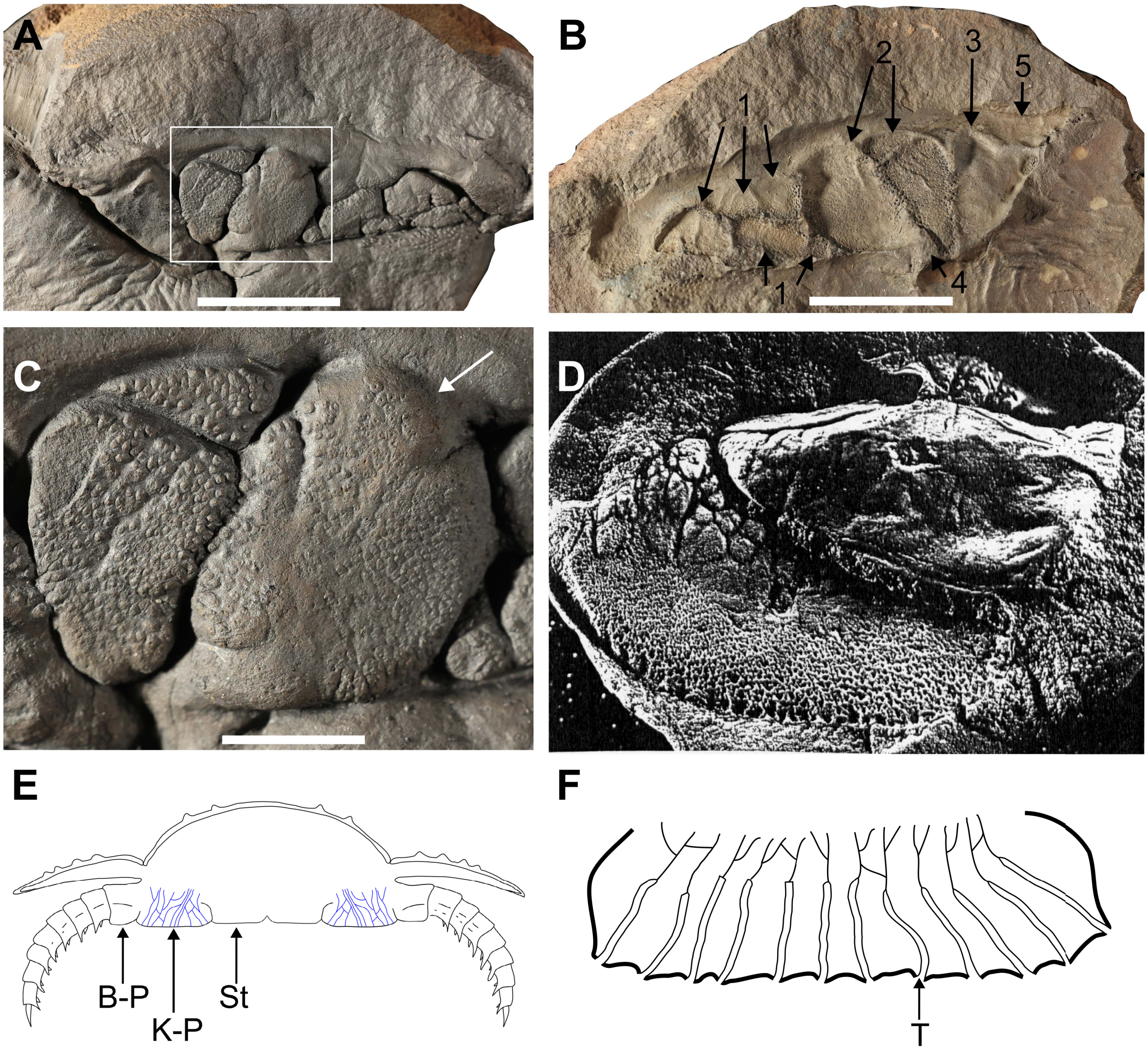

Figure 8. ***Arthropleura cristata*, Mazon Creek, Moscovian-Kasimovian and reconstitution of the tracheal system**. **A-C**: specimen FMNH PE9304. **A**: part. **B**: counterpart. **C**: details on the pits. **D**: unnumbered specimen (named specimen FMNH 1 in Wilson 1999). **E-F**: reconstitution of the tracheal system. **E**: position of the supposed tracheal system (blue) on the K-plate. **F**: Details on the K-plate, highlighting the pierced tubercules as possible tracheal openings. Square in A indicates the position of C. 1 = part most proximal to the leg; 2 = middle part; 3 = part most distal to the leg; 4 = connexion between K-plate and sternite; 5 = connexion between K-plate and B-plate. B-P = B-plate; K-P = K-plate; St = sternite; T = pierced tubercule. White arrow on C indicates pierced tubercules. Scale bars = 1 cm (C); 2 cm (A, B). A, B and C taken by Mane Pritza and provided by Paul Meyer. D from Wilson 1999.

hoeninghausii Potonié 1897, Fig. 2). The swampy environment of this time is characterised by an increase of pteridosperms and non-marattialean ferns, observed with occurrences on specimens MGL.1878 and MGL.1881 (Figs 2 and 6A-D). The diversity of plants still increased progressively in the Vicoigne and Anzin Formations (Langsettian-Duckmantian i.e. Westphalian A-B or late Bashkirian), reaching around a hundred species in the late Westphalian B, as seen in the Pouilleuse member (Fig. 2), ending with the marine transgression of the "Rimbert Marine band".

The floral diversity seems in accordance with *Arthropleura* ecology, as a detritivorous and/or possibly herbivorous (Lhéritier et al. 2024) myriapod feeding on abundant plant biomass available in swamp areas in Northern France (Rolfe 1985) (see Appendix 2 for additional knowledge of presumed *Arthropleura* diet). A new increase of plant diversity is recorded in the lower part of the Bruay Formation (Bolsovian i.e. Westphalian C or early Moscovian). This occurs starting from the floristic zone B3 *sensu* Zeiller 1896 (Molina-Solís et al. 2024, Fig. 2). A diversity peak is observed in the upper part of the Six-Sillons member (> 110 plant species), including a high number of non-marattialean ferns and medullosalean pteridosperms. This interval is correlated with the presence of *A. armata* (specimen MGL.1877), considered here as a preliminary occurrence from the upper part of the member but also from the same age as *A. mammata* specimens from the Bruay Formation.

Size and ontogeny

The animal is reconstructed in Figure 4, on the basis of *Arthropleura armata* from Sulzbach (Saarland, Germany; Moscovian; Davies et al.

2021), it is estimated to be 50 centimetres long. The old specimens from the Anzin Formation in the Gosselet collection of the Lille Museum seem to indicate that there were already large specimens (probably adult fragments) since the Bashkirian. Comparable large *Arthropleura* have been assigned to *A. mailleuxi* Pruvost 1930, but the lack of preserved appendages, head, or detailed ornamentation in the *A. mailleuxi* specimens precludes confident species-level comparisons. Specimens MHNGr.PA.39321 and MHNGr.PA.39322 document the first complete head cuticle of adult *Arthropleura mammata*. Complete heads are only known in Montceau juvenile specimens (Lhéritier et al. 2024), only fragments are preserved in other localities (Kraus & Brauckmann 2003). The head of *Arthropleura* seems to keep the same shape during ontogeny, as it is the case for extant centipedes and millipedes that are its closest relatives (Lhéritier et al. 2024). In these two groups, there is no drastic morphological change of the head during ontogeny, the major change being an increase in size (Minelli 2011, 2015). The presence of ventral sclerites at the front of specimen MHNGr.PA.39322 (Fig. 5A), also observed in Montceau juveniles (Lhéritier et al. 2024), confirms that these structures are persistent throughout ontogeny. No other appendages (antennae, feeding apparatus or eyes) were observed in the Bruay specimens. *A. mammata* head morphology is very close to that of Montceau specimens and may have displayed comparable head appendages (i.e., stalked eyes, antennae, mandibles and maxillae; Lhéritier et al. 2024). *A. mammata* could have followed an hemianamorphic development (i.e., the addition of new segments at each mould until the sexual maturity followed by multiple moulds with an increase in size; Minelli 2015) like seen in the Montceau juveniles. Ontogenetic development is quite stable among myriapod clades (e.g., all millipedes follow an anamorphic ontogeny), hence it is plausible that all arthropleurids followed the same developmental pattern. As the posterior part of MHNGr.PA.39321 and MHNGr.PA.39322 are not preserved, we cannot see if the posterior segment and legs were not fully developed as in juveniles (Lhéritier et al. 2024) and assess if the specimens were fully matured or juveniles.

Habitat

The association of *Arthropleura* species with plant remains of the *Lonchopteris rugosa* Brongniart 1822 zone (e.g., *Alethopteris davreuxii* (Brongniart 1836), *Mariopteris muricata* (Brongniart), *Sphenophyllum miriophyllum* (Crepin)) (Bouroz 1940 and Corsin & Corsin 1970) suggest that these *Arthropleura* inhabited wetlands during the Bashkirian. The presence of *Paripteris pseudogigantea* (Potonié) Gothan 1953, *P. linguaefolia* and *Laveineopteris rarinervis* (Bunbury) Cleal et al., 1990, typically found in early Moscovian (Bolsovian) deposits, may indicate environmental changes in *Arthropleura*'s habitat. In the western part of the HBNPC, no *Arthropleura* specimens are known prior to the Moscovian surely because it was a marine environment as indicated by the Rimbert marine band (Fig. 2). It is only after this marine band that we observe *Arthropleura* along with the increase of neuropterid plants occurrences (Corsin & Corsin 1970; Vallois & Nel 2023). *Arthropleura* was also recovered in Belgium, in coal series that developed between the Quaregon Marine Band and the Petit-Buisson Marine Band (Westphalian A and B; Pruvost 1930; Paproth et al. 1983). The occurrences of *Arthropleura mammata* in the two coalfield series, recorded in the French and Belgian sites, are dated of the same time interval. Due to the occurrence of *Arthropleura* in both series before and after the submergence by the sea, we consider that the geographical extension of *Arthropleura* may have been reduced due to environmental changes, limiting its presence to the coalfields. This new discovery of *A. mammata* in the Bruay Formation helps to build a better understanding of the Carboniferous terrestrial fauna of the HBNPC. The scarcity of animal remains in the Carboniferous of Northern France could be linked to these dynamic changes of their habitats (Molina-Solís et al. 2024). Taphonomic parameters could also explain this stratigraphic pattern, as coalfields are the most suitable Carboniferous environments for preserving *Arthropleura* and other fauna remains, compared to other drier environments.

Respiration

All extant myriapods are terrestrial and breathe through a tracheal system or cuticle diffusion (Minelli 2011, 2015). The respiratory system of *Arthropleura* is still debated as there is still no fossil evidence of spiracles (tracheal openings). The K-plates, observed here in MHNGr.PA.39551-5 and MHNGr.PA.39551-11, are usually interpreted as being associated with possible tracheal pouches based on the fact that the so-called "K-plates" are in fact not plates but bag-like structures (Wilson 1999; Kraus & Brauckmann 2003). Multiple specimens of *Arthropleura cristata* Richardson 1959 from the Kasimovian Mazon Creek Lagerstätte show the same pierced tubercles on the K-plates (Fig. 8A-C) and one shows internal details of the K-plates (Wilson 1999), especially a network of reticulated structures composed of small interconnected chambers and circular cavities (Wilson 1999) (Fig. 8D). In this context, the tubercles with openings observed in our specimens may represent the outer surface of such cavities (Fig. 8E, F). One major counter-argument to the presence of a tracheal system in *Arthropleura* is the lack of spiracles observed on the sternites (where they are located in extant millipedes, Minelli 2015). However, Wesener et al. 2014 discovered that the spiracles of glomeridesmids are not present on the sternites but on another plate they called the "stigmatic plate" which is connected to the coxa. As *Arthropleura* is a stem-relative of Diplopoda (i.e. millipedes; Lhéritier et al. 2024), the spiracles, if present in *Arthropleura* may not be located on the sternites but on another plate equivalent to the stigmatic plate (in this case the K-plate). Even if a tracheal system can also be found in aquatic arthropods like aquatic insects, the general anatomy of *Arthropleura* is really similar to extant myriapods (that are all terrestrial) and with no clear adaptations to life in water (modified tracheae, swimming setae on legs). This would imply that *Arthropleura* was not an aquatic but a truly terrestrial arthropod.

Conclusions

Arthropleura mammata from the Bruay Formation (early Moscovian) reveals important information of the head and ventral K-plates of this species' adult specimens. This new material extends the stratigraphic range of *A. mammata* to the Moscovian. The presence of the same group of plants associated with *A. mammata* throughout its stratigraphic range and its disappearance in the fossil record in intervals with sea submergence could suggest that *A. mammata* preferentially lived in low altitude wetlands. The heads of the Bruay specimens are also among the most complete adult heads of the genus, and can be compared to the better-preserved ones of Montceau-les-Mines juvenile specimens. The presence of ventral head sclerites (previously only seen in Montceau specimens) in adult representatives confirm their persistence throughout their development. The presence of multiple pierced tubercles on K-plates suggests that *Arthropleura* had a tracheal system, with the holes being its openings towards the exterior surroundings. This interpretation is supported by comparable features found in Mazon Creek *Arthropleura cristata* specimens displaying the same pierced tubercles on their K-plates. If the respiratory function of these structures is confirmed, then *Arthropleura* is likely to have been an air breathing terrestrial arthropod, as all extant myriapods. The Mazon Creek Lagerstätte bears interesting material for the detailed study of the ventral plates and the possible 3D reconstruction of the respiratory system of *Arthropleura*.

Data availability

Specimens of *Arthropleura mammata* are deposited in the Lille Museum and the Museum of Natural History of Grenoble. Specimens from the Bruay Formation can be found in an online database (https://paleo-collections.museum-grenoble.fr/fr/collections/arthropleura-collection-museum-grenoble). Specimens of *Arthropleura cristata* figured in Figure 8A-C are deposited in the Field Natural History Museum of Chicago. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary data.

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Author contributions

M.L. and B.V. contributed to the design of this study. B.V. and C.D. provided the specimens for this study. B.V. and C.D took photos of the specimens. M.L and B.V. conducted the preparation and improvement of data visualisation. All authors prepared the original draft.

Competing interests

The authors declare no competing interests.

Ethics and AI use

No AI was used for this study.

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Minor amendment

In the respiration section, we compare the K-plates of *Arthropleura mammata* found in the Bruay locality to ventral plates of *Arthropleura cristata* from Mazon Creek (figured in Fig. 8A–C). We use this comparison to defend the fact that the pierced tubercules we observe on *A. mammata*are also present on other *Arthropleura* species. However, the ventral plates of *A. cristata* that we figured are in fact not K-plates but Rosette plates, another type of ventral plates present in arthropleurids, located not under the body but at the top of the leg in a vertical axis. The ventral plates from Bruay that we describe in Fig. 7 have a similar shape compared to the Rosette plates from Mazon Creek but we still consider them as K-plates. They have not the same number of triangular lobes that we observe in Rosette plates (Wilson 1999; Schneider et al. 2010) and they bear a peculiar large subtriangular lobe (that we called part 1 in Figs 7 and 8) at the front that is not observed on Rosette plates. Also, what we call part 3 has an apex oriented in opposition to the other lobes, another feature not seen in Rosette plates (Wilson 1999; Schneider et al. 2010). Our main argument to identify these ventral plates as K-plates were the numerous pierced mounds, that were also described by Wilson in 1999, while she described the Rosette plates as being less tuberculated with the tubercules only present on some lobes. In the Bruay specimens, we can see that the pierced tubercules are present on all triangular lobes. The ventral plate with a reticulated system figured in Fig. 8D is a K-plate (Wilson 1999), so the idea of the K-plate bearing the respiratory system, with the pierced tubercules equivalent to spiracles, is not invalidated. We would like to thank Bruno Agostinho for informing us on the misidentification of the Mazon Creek ventral plates.

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