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The Montceau-les-Mines Lagerstätte (Late Carboniferous, France)

Le Lagerstätte de Montceau-les-Mines (Carbonifère supérieur, France)

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ABSTRACT

The Montceau-les-Mines Lagerstätte (Late Stephanian, Late Carboniferous) is located north-east of the French Massif Central. Situated at equatorial latitudes during the Pennsylvanian, this Lagerstätte, probably a freshwater environment, preserves a rich and diverse flora (lycopsids, sphenopsids, ferns, pteridosperms, and cordaites) and fauna (bivalves, annelids, crustaceans, myriapods, insects, chelicerates, myxinoids, actinopterygians, sarcopterygians and tetrapods). These exceptionally preserved fossils can be found either flattened in shales or three-dimensionally preserved in sideritic nodules. The fossils from the nodules are exceptional for at least two reasons: the absence of major disarticulation of their body structure and the preservation of soft parts and extremely fragile cuticular structures. Such preservation was made possible by the combination of several factors: rapid burial in fine anoxic mud, early siderite precipitation (inducing the nodule formation) and phosphatization of cuticles and soft-bodied features.

RÉSUMÉ

Le Lagerstätte de Montceau-les-Mines (Stéphanien supérieur, Carbonifère supérieur) est situé au nord-est du Massif central (France). Positionné à des latitudes équatoriales durant le Pennsylvanien, ce Lagerstätte, probablement d'environnement d'eau douce, livre une flore (lycophytes, sphénophytes, fougères, ptéridospermales et cordaïtes) et une faune (bivalves, annélides, crustacés, myriapodes, insectes, chélicérates, myxines, actinoptérygiens, sarcoptérygiens et tétrapodes) riches et diversifiées. Ces fossiles exceptionnels sont trouvés soit compressés dans des argiles, soit en volume dans des nodules sidéritiques. Les fossiles des nodules sont exceptionnels, pour au moins deux raisons : l'absence de désarticulation majeure de leurs structures anatomiques et la préservation 3D de leurs parties molles et de structures cuticulaires extrêmement fragiles. Une telle préservation a été rendue possible par la combinaison de plusieurs facteurs : enfouissement rapide dans une boue fine et anoxique, précipitation précoce de sidérite (induisant la formation du nodule) et phosphatisation des cuticules et des parties molles.

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1. Palaeontological collection of the Montceau Lagerstätte

In the 1970s, the exploitation of coal in opencast mines in the Montceau-les-Mines basin allowed Daniel Sotty to collect sideritic concretions bearing exceptionally preserved animals and plants. Due to the scientific importance of his discovery, Daniel Sotty organized palaeontological excavations with a small team of amateur palaeontologists. In collaboration with the regional museum of Autun (close to Montceau-les-Mines), between 1979 and 1982 they collected more than 120,000 nodules (Sotty, 1980) in three opencasts mines: Saint-Louis, Sainte-Hélène and Saint-François (Fig. 1). The fossils collected at Montceau-les-Mines were quickly noticed by the palaeontologists from the Paris Museum and international collaborations developed between French, American, German and British scientists. The first synthesis of these pioneering works on the nodules was published by Poplin and Heyler (1994a).

In 1997, Daniel Sotty officially bequeathed his collection of thousands of nodules to the Muséum national d'histoire naturelle, Paris. The deposit of the collection for management in the regional Museum of Autun was validated by a contract signed between the MNHN and the city of Autun on November 5th, 1997. Now, under the MNHN direction, the Sotty collection is managed in the museum of Autun. It contains more than 100,000 nodules bearing three-dimensionally preserved animals and plants, including 300 types and figured specimens. These collections are computerized and regularly consulted and studied by international scientists. For more details about the history of the Sotty collection, see Chabard and Poplin (1999) and Charbonnier (2010a, b).

2. Geological background and palaeoenvironment

2.1. Montceau-les-Mines coal basin

The Montceau-les-Mines coal basin is located northeast of the French Massif Central (Morvan region) and is well exposed along the southern margin of the Late Stephanian (Pennsylvanian)–Permian Blanzy–Le Creusot–Bert graben, with numerous fossiliferous localities (Fig. 1). This intramontane basin forms a 40-km-long, continuous band of Late Pennsylvanian deposits, bounded by two Variscan fault systems. The basin is separated from Permian deposits by the East Fault and from crystalline basement by the Border Fault. Coal mining began in the mid-eighteenth century and fostered pioneering palaeobotanical studies (Grand'Eury, 1877; Manès, 1847; Zeiller, 1906). The general aspects of the stratigraphy and structural geology of the basin were first described by Delafond (1902). The stratigraphy was revised by Feys and Greber (1958) and successively improved by Branchet (1983) and Courel et al. (1985, 1994; see Fig. 2). From the base to the top, the Late Pennsylvanian Series of Montceau-les-Mines consists of:

- the Assise de Montceau (or Great Seams Formation);
- the Assise des Carrières (or Upper Seams Formation);
- the Assise du Ponsard (Late Pennsylvanian–Permian transition; see Fig. 2).

In the 1970s, the exploitation of coal in opencast mines allowed for more accurate sedimentological studies. Branchet (1983), Courel (1983) and Vallé (1986) distinguished several paludal-to-fluvial environments in the First Seam of the Assise de Montceau. These studies indicated that different facies are often juxtaposed in the basin because of numerous synsedimentary faults. For example, organic-rich deposits are typically interrupted by detrital inputs of fluvial and lacustrine origin. The coexistence, migration, and replacement of these environments through time largely resulted in partitioning of the depositional areas. The entire coal basin is affected by strong and differential subsidence, and early tectonics played an important role in understanding the dynamics of sedimentation (Courel and Paquette, 1981).

2.2. The nodule-rich beds

The approximately 120,000 sideritic nodules that were collected during successive field seasons (Sotty, 1980) from three opencast mines (Saint-Louis, Saint-François, and Sainte-Hélène) come from clayey siltstones and silty claystones that occur a few meters above the First Seam of the Assise de Montceau (Figs. 1 and 2). Nodule-bearing horizons are typically bounded by thin iron carbonate layers. The fossiliferous nodule-containing layers were numbered as they were discovered, from 0 to +5 and 0 to −12, layer 0 being the first layer discovered and the richest in nodules (Fig. 2). The majority of the nodules were collected from layer 0 and layer +2 of the Saint-Louis opencast mine (Chabard and Poplin, 1999; Pacaud and Sotty, 1994). The series of nodule-rich layers is demarcated at its base and top by thick sandstone units. Two fish-rich horizons also occur within the succession and allowed correlations between the three opencast mines (see Charbonnier et al., 2008, fig. 2). After mining operations closed down in the beginning of the 1990s, the opencast mines were banked up or flooded, making the nodule horizons inaccessible.

2.3. The Montceau Lagerstätte

The Montceau Lagerstätte was situated at equatorial latitudes during deposition (Cocks and Torsvik, 2011), allowing the development of a luxuriant vegetation, as demonstrated by abundant compression floras composed of lycopsids, sphenopsids, ferns, pteridosperms, and cordaites (see Section 4 and Fig. 3). Hygrophytic terrestrial plants flourished along the banks of water bodies, some of which being deep rooted in water, whereas more mesoxerophilic plants grew on the hills of the intermontane basin (Langiaux, 1994). A variety of freshwater habitats were occupied by a rich and diverse fauna. Major animal groups that have been identified include freshwater bivalves, annelids, crustaceans, myriapods, insects, spiders, merostomes, myxinoids, actinopterygian fishes, sarcopterygian fishes and tetrapods (see Section 5 and Fig. 4). The remarkable preservation of the fauna makes the Montceau-les-Mines Lagerstätte a major source of information for the

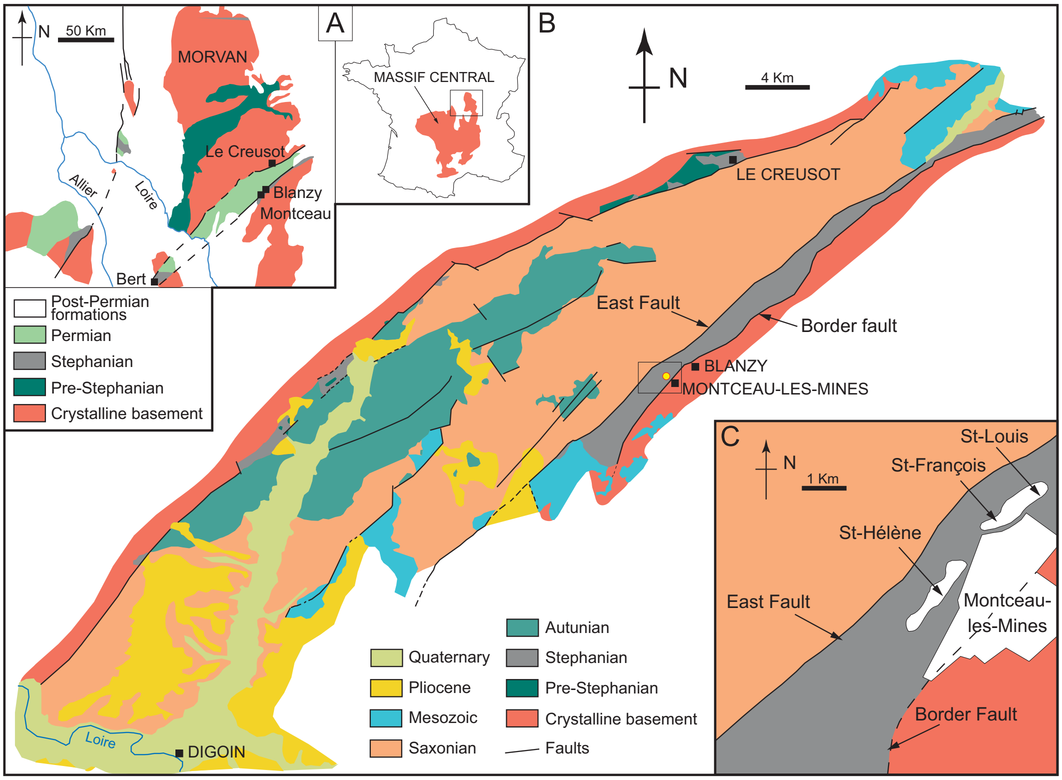

Fig. 1. (Colour online) Montceau-les-Mines coal basin: geological setting. A. Regional map (modified after Feys and Greber, 1958). B. Location of the Montceau coal basin in the Stephanian-Permian Blanzy–Le Creusot–Bert graben (modified after Charbonnier et al., 2008). C. Location of the three opencast mines yielding sideritic nodules (modified after Vallé, 1984).

Fig. 1. (Couleur en ligne) Bassin houiller de Montceau-les-Mines : contexte géologique. A. Carte régionale (modifié d'après Feys et Greber, 1958). B. Position du bassin houiller de Montceau au sein du graben stéphano-permien de Blanzy–Le Creusot–Bert (modifié d'après Charbonnier et al., 2008). C. Localisation des trois découvertes ayant livré des nodules sidéritiques (modifié d'après Vallé, 1984).

reconstruction of Pennsylvanian freshwater biotas (Heyler, 1981; Heyler and Poplin, 1988; Poplin, 1994a; Rolfe et al., 1982).

A freshwater continental setting is generally well accepted for the Montceau Lagerstätte (e.g. Charbonnier et al., 2008; Perrier et al., 2006; Racheboeuf et al., 2002, 2004, 2008). It is clear that there is no sedimentological, structural or palaeogeographical evidence of any Upper Carboniferous open marine deposits in the Montceau area. According to available data, the closest Upper Carboniferous marine deposits were located at least several hundred kilometres in the southwest of Montceau (Courel et al., 1994; Debelmas and Ellenberger, 1974). The hypothetical marine influence (Poplin, 1994a; Poplin et al., 2001; Rolfe et al., 1982; Schultze, 2009) has been suggested on the basis of an apparent 'mixture' of marine and freshwater faunal components. The 'marine bound taxa' include the possible craniate *Myxineidus* by Poplin et al. (2001; also considered by Germain et al. (in press) as a possible lamprey) and the annelid worm *Palaeocampa* by Pleijel et al. (2004). However, Racheboeuf et al. (2008) suggest that these animals are considered as marine mainly because the timing of their marine to freshwater transition is still under discussion. Racheboeuf et al. (2008) proposed an interesting Amazonian model with an early marine influence, and subsequent enclosure and evolution of marine forms to freshwater forms over 20–25 million years.

2.4. Other Carboniferous Lagerstätten

Several Late Carboniferous Lagerstätten displayed sideritic nodules; these include: Sosnowiec, Poland (Krawczyński et al., 1997; Pacyna and Zdebska, 2002), Coseley and Bickershaw, UK (Anderson et al., 1997; Wilson and Almond, 2001) and Mazon Creek, USA (Peppers and Pfefferkorn, 1970; Pfefferkorn, 1979). The deltaic setting is a common feature of all these Lagerstätten whether the environmental conditions were marine, brackish, or lacustrine. Pacyna and Zdebska (2002) suggested that the environment of the Sosnowiec Lagerstätte (Poland) was lacustrine and very shallow, probably situated in an alluvial plain between meanders. The Coseley and the Bickershaw Lagerstätten are thought to have been deposited in freshwater (Wilson and Almond, 2001) and in brackish fluviodeltaic settings (Anderson et al., 1997), respectively. The Mazon Creek Lagerstätte is a complex delta showing two different depositional settings and faunas, i.e. the marine Essex and the brackish to freshwater Braidwood faunas (Baird et al., 1985, 1986; Nitecki, 1979).

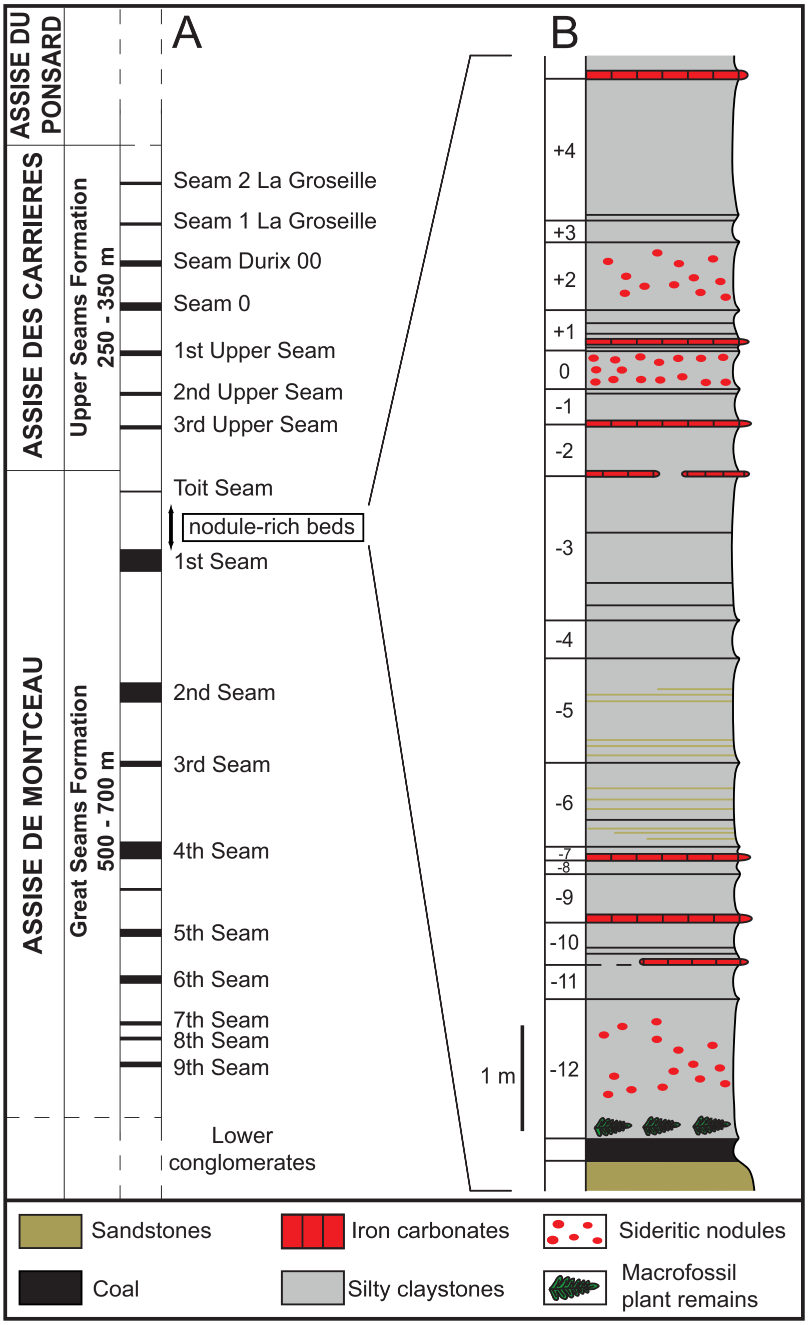

Fig. 2. (Colour online) Location of the Montceau Lagerstätte. A. Stephanian (Late Pennsylvanian) stratigraphic scale of the Montceau-les-Mines coal basin. B. Lithostratigraphic section in the nodule-rich beds from the Saint-Louis opencast mine.

Fig. 2. (Couleur en ligne) Position du Lagerstätte de Montceau. A. Échelle stratigraphique du Stéphanien (Pennsylvanien supérieur) du bassin houiller de Montceau-les-Mines. B. Coupe lithostratigraphique des couches à nodules dans la découverte Saint-Louis.

3. The exceptional preservation

The Montceau Lagerstätte displays exceptionally preserved fossils in the shales, where they are flattened, but the really remarkable flora and fauna come from the nodules on which we will concentrate in the following section. The fossils from the nodules are exceptional for at least two reasons: the absence of major disarticulation of their body structure and the 3D-preservation of soft parts, e.g., eggs, or extremely fragile cuticular features such as appendages, setae (Fig. 5). This kind of preservation enables precise morphofunctional interpretations (e.g. Perrier et al., 2006; Racheboeuf et al., 2002) and/or precise phylogenetic character analyses (Garwood et al., 2011).

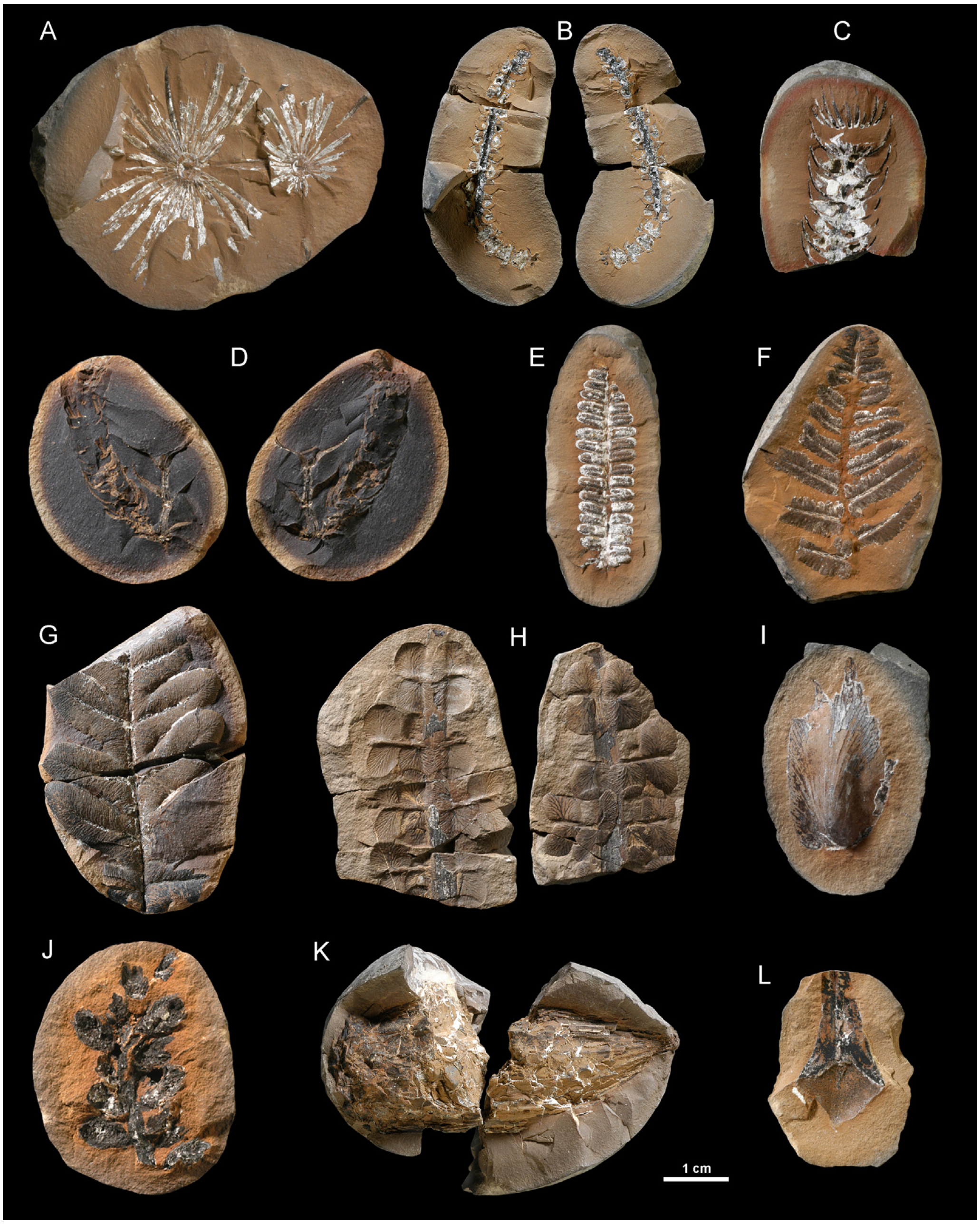

Fig. 3. (Colour online) Flora from the nodules of the Montceau-les-Mines Lagerstätte, Stephanian, France. A. *Annularia stellata* MNHN.F.SOT080920b. B. *Calamostachys tuberculata* MNHN.F.SOT093536ab. C. *Asterophyllites equisetiformis* MNHN.F.SOT091130. D. *Sphenophyllostachys* sp. MNHN.F.SOT005555ab. E. *Pecopteris unita* MNHN.F.SOT023653a. F. *Pecopteris* sp. MNHN.F.SOT087258a. G. *Alethopteris zeilleri* MNHN.F.SOT.025664a. H. *Odontopteris subcrenulata* MNHN.F.SOT025618ab. I. *Odontopteris minor* MNHN.F.SOT056492. J. *Cordaitanthus* sp. MNHN.F.SOT029128. K. *Sigillariostrobus* sp. MNHN.F.SOT099355. L. *Cyperites bicarinata* MNHN.F.SOT.007560a.

Fig. 3. (Couleur en ligne) Flore des nodules du Lagerstätte de Montceau-les-Mines, Stéphanien, France. A. *Annularia stellata* MNHN.F.SOT080920b. B. *Calamostachys tuberculata* MNHN.F.SOT093536ab. C. *Asterophyllites equisetiformis* MNHN.F.SOT091130. D. *Sphenophyllostachys* sp. MNHN.F.SOT005555ab. E. *Pecopteris unita* MNHN.F.SOT023653a. F. *Pecopteris* sp. MNHN.F.SOT087258a. G. *Alethopteris zeilleri* MNHN.F.SOT.025664a. H. *Odontopteris subcrenulata* MNHN.F.SOT025618ab. I. *Odontopteris minor* MNHN.F.SOT056492. J. *Cordaitanthus* sp. MNHN.F.SOT029128. K. *Sigillariostrobus* sp. MNHN.F.SOT099355. L. *Cyperites bicarinata* MNHN.F.SOT.007560a.

3.1. Absence of major disarticulation

Most fossils are preserved as complete specimens; sideritic nodules yielding only a fragment of the animal are extremely rare. In the case of the syncarids, it is the whole segmented body that is most frequently preserved, with its cephalic, thoracic and pleonal sections joined together (Perrier et al., 2006; Fig. 5C). On a smaller scale, numerous

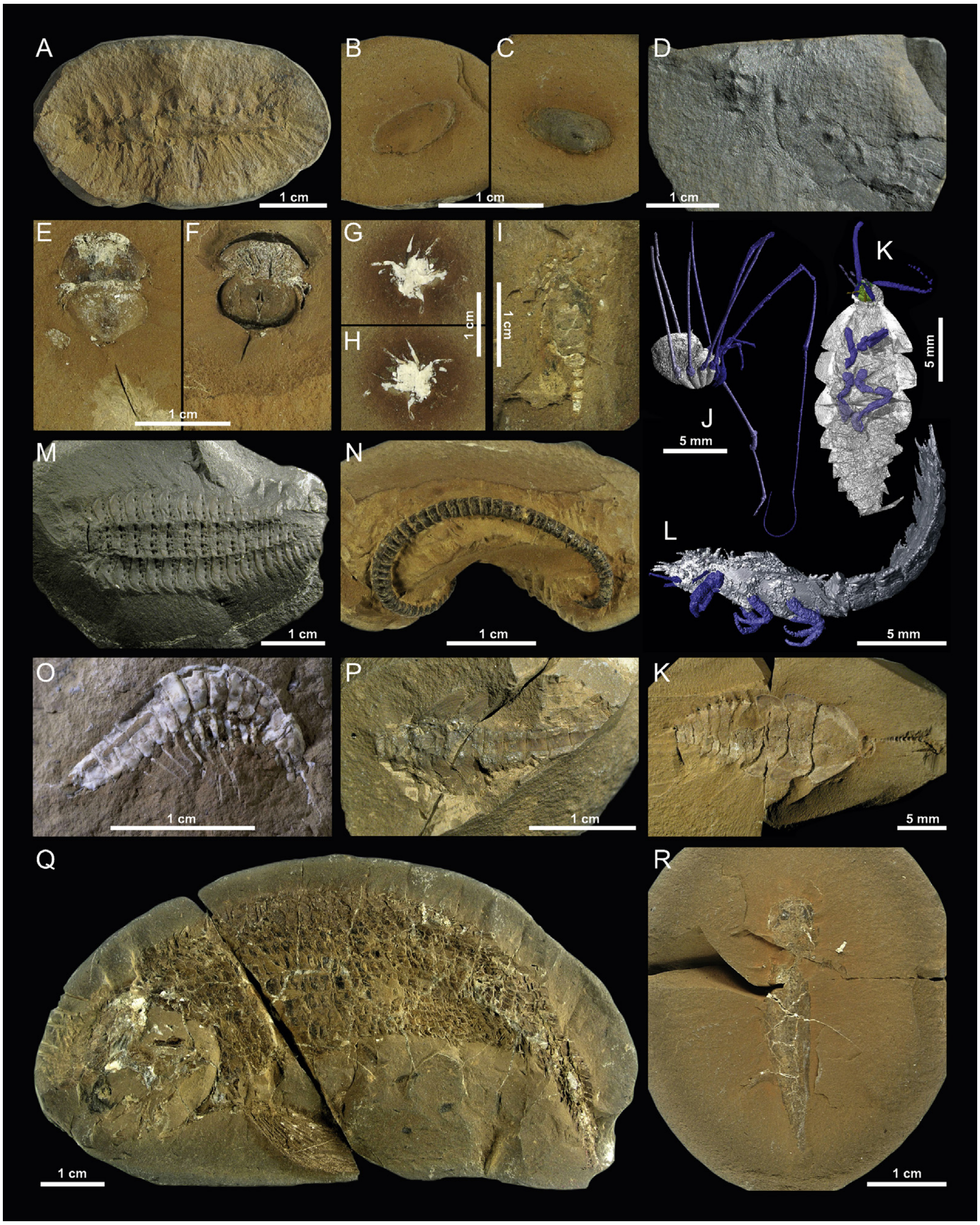

Fig. 4. (Colour online) Fauna from the nodules of the Montceau-les-Mines Lagerstätte, Stephanian, France. A. *Palaeocampa anthrax* MNHN.F.SOT003657a. B, C. *Anthraconaia lusitanica* MNHN.F.SOT004957ab. D. Undescribed onychophoran MNHN.F.SOT003121b. E, F. *Alanops magnificus* MNHN.F.SOT002154ab. G, H. Undescribed spider MNHN.F.SOT.095184ab. I. *Allobuthus pescei* MNHN.F.SOT003119a. J. Digital reconstruction of *Macrogyion cronus* MNHN.F.SOT079398. K. Digital reconstruction and external mould of an unnamed dictyopteran juvenile MNHN.F.SOT086502. L. Digital reconstruction of *Anebos phrixos* MNHN.F.SOT.005630. M. *Arthropleura* sp. MNHN.F.SOT002122a. N. Undescribed myriapod MNHN.F.SOT081522a. O. *Palaeocaris secretanae* MNHN.F.SOT024746a. P. Undescribed ephemeropter larva MNHN.F.SOT058176a. Q. Undescribed actinopterygian MNHN.F.SOT.001568a. R. *Branchiosaurus petrolei* MNHN.F.SOT007407b. J after Garwood et al. (2011); K, L after Garwood et al. (2012).

Fig. 4. (Couleur en ligne) Faune des nodules du Lagerstätte de Montceau-les-Mines, Stéphanien, France. A. *Palaeocampa anthrax* MNHN.F.SOT003657a. B, C. *Anthraconaia lusitanica* MNHN.F.SOT004957ab. D. Onychophore indéterminé MNHN.F.SOT003121b. E, F. *Alanops magnificus* MNHN.F.SOT002154ab. G, H. Arachnide indéterminé MNHN.F.SOT.095184ab. I. *Allobuthus pescei* MNHN.F.SOT003119a. J. Reconstitution digitale de *Macrogyion cronus* MNHN.F.SOT079398. K. Reconstitution digitale et moule externe d'un dictyoptère juvénile indéterminé MNHN.F.SOT086502. L. Reconstitution digitale d'*Anebos phrixos* MNHN.F.SOT.005630. M. *Arthropleura* sp. MNHN.F.SOT002122a. N. Myriapode indéterminé MNHN.F.SOT081522a. O. *Palaeocaris secretanae* MNHN.F.SOT024746a. P. Larve d'éphéméroptère indéterminé MNHN.F.SOT058176a. Q. Actinoptérygien indéterminé MNHN.F.SOT.001568a. R. *Branchiosaurus petrolei* MNHN.F.SOT007407b. J d'après Garwood et al. (2011) ; K, L d'après Garwood et al. (2012).

very fragile appendages are also complete, e.g., legs, pedipalps and chelicerae of harvestman (Garwood et al., 2011; Fig. 4E). Charbonnier et al. (2008) also note the excellent preservation of fine structures such as sporangia or the delicate veins of pinnules in Montceau flora (Fig. 3E–H). Most of the fossils, as they appear on the surface of split nodules or in digital reconstructions, show striking similarities to their living representatives (e.g., xiphosurids, Racheboeuf et al., 2002; diplopods, Racheboeuf et al., 2004; opiliones, Garwood et al., 2011; Fig. 4). This strongly suggests that the animals from Montceau were trapped and buried alive in situ.

Experimental studies on the decay of extant arthropods greatly help in understanding the post-mortem history of the arthropods from Montceau. Several authors have noted that microbial activity caused rapid (within days) disarticulation of crustacean/insect carcasses left unburied in oxic conditions (Duncan et al., 2003; Hof and Briggs, 1997). The first stage of decay in these experimental studies is the expansion of internal tissues, which is not observed in the Montceau fossils (Garwood et al., 2012; Perrier et al., 2006) thereby confirming a very low degree of pre-fossilization decay. Harding (1973) demonstrated that carcasses decomposed much less rapidly if buried immediately after death. Plotnick (1986) showed that carcasses buried under 5–10 cm of sediment were rapidly damaged by scavenging and bioturbation, whereas their preservation was largely undisrupted below 10 cm. The conditions (oxic–dysoxic) that prevail within the sediment play a crucial role in the preservation of the fauna. Additionally, decay (under anoxic conditions) is faster in marine environments than in freshwater (Allison, 1988). Consequently, rapid burial under more than 10 cm of sediment in anoxic conditions dramatically increases the chances of segmented bodies being preserved.

Decomposition in most Montceau fossils was minimal (Fig. 4) indicating that the carcasses were protected from both mechanical and biochemical (bacteria) damage by their rapid burial, the anoxic conditions that prevailed in the sediment, and the lack of physically disrupting agents, e.g., scavengers, bioturbators. Post-mortem transportation was probably neither vigorous nor extensive, as suggested by the lack of abrasion or post-mortem trauma to the Montceau flora (Charbonnier et al., 2008; Fig. 3). Freshwater conditions may have delayed decay. The factors that caused the death of animals are unknown. Oxygen depletion in the lower level of the water column may have killed aquatic animals that then settled gently within the flocculent mud (Perrier et al., 2006). More plausible though is the scenario in which animals got trapped by turbidity currents and were buried within a few centimetres of deposited mud (Racheboeuf et al., 2002). In this case, the death of the animals and their burial would have been almost simultaneous.

3.2. Three-dimensional preservation

Most fossils from Montceau preserve their original three-dimensional shape; even extremely fragile spherical syncarid eggs or poorly sclerotized insect nymphs were preserved in volume (Garwood et al., 2012; Perrier et al., 2006; Figs. 4F and 5G). The nodule flora and fauna show virtually no trace of collapse and flattening (e.g. xiphosurids, Racheboeuf et al., 2002; spinicaudatans, Vannier et al., 2003; flora, Charbonnier et al., 2008; euthycarcinoids, Racheboeuf et al., 2008; insect nymphs, Garwood et al., 2012; Figs. 4 and 5).

Although arthropod cuticular elements may be relatively resistant to decay (Hof and Briggs, 1997), the rapid destruction of underlying soft tissues via microbial activity usually accelerates the collapse of body features. Early mineralization prevents collapse and allows 3D-preservation. Numerous palaeontological and experimental studies show that phosphatization (apatite) is the most common of the mineralization processes (Briggs and Wilby, 1996). Microprobe-analysis confirmed that phosphatization (presence of apatite) was probably responsible for the cuticular and soft-bodied 3D-preservation of syncarids (Perrier et al., 2006; Fig. 5O, S). In these fossils, phosphatization typically occurs as a thin black layer (Fig. 5C, I) and led to the preservation of extremely fine structures, such as sensory pores (diameter approx. 5 μm). Phosphatic minerals can also be apparent as a thin black layer covering the Montceau fossils (Poplin and Heyler, 1994a).

Another factor that played a key role in the exceptional preservation of the Montceau biota was the formation of sideritic nodules (Poplin and Heyler, 1994a; Fig. 5). Precipitation of iron carbonate around the carcasses (as the possible result of chemical changes induced by microbial activity) prevented these fossils from being rapidly flattened and severely damaged by compaction (Fig. 5D–F, N, Q, U–V). This hypothesis is again supported by experimental taphonomy. For example, Hof and Briggs (1997) observed that water chemistry changed rapidly around dead crustaceans; i.e. after three days, the percentage of O_2 decreased from 50 to 3%, and the pH from 8.00 to 6.56, thus creating anoxic conditions around the carcass. Whether a nodule will form or not around a carcass largely depends on the iron concentration (Coleman, 1985; Coleman and Raiswell, 1993; Raiswell, 1987). If iron is available in sufficient quantity, the conditions are optimal for siderite precipitation, especially in freshwater conditions (Berner et al., 1979; Walter and Burton, 1990). The Montceau Lagerstätte is also remarkable because it allows the observation of the different stages of nodule formation (Fig. 5D–F). This formation is progressive; the siderite first precipitates on the surface of the biological remains, then spreads rapidly around it (in the sediment pores), until it forms a concretion that can be isolated from the sediment (Charbonnier, 2014; Fig. 5D–F, T–Y). In some nodules, the siderite precipitation was insufficient or incomplete, leading to the formation of a pseudo-nodule, which will be more affected by the compaction (Fig. 5A). Germain (2008a) describes swarms of small (about 1 μm in diameter; Fig. 5K) spherical structures interpreted as bacteria in the posterior portion of the skull of an aistopod vertebrate from Montceau Lagerstätte. This bacterial film might have surrounded the remains, causing a rapid diagenesis, i.e. causing the mineralization of soft tissues and the formation of the nodule by enhancing the absorption of metallic cations (Dunn et al., 1997).

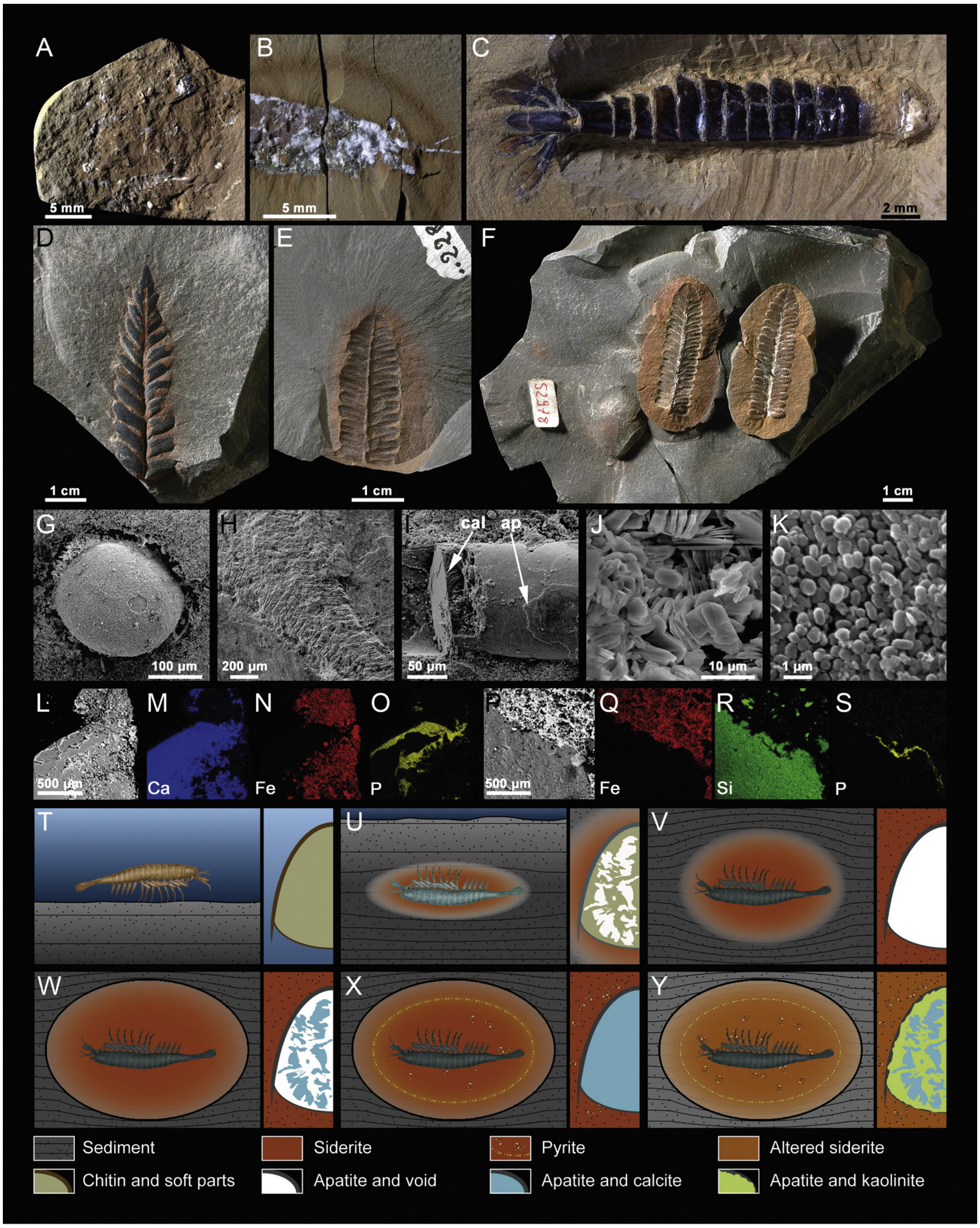

Fig. 5. (Colour online) Taphonomy of the Montceau-les-Mines Lagerstätte, Stephanian, France. A. MNHN.F.SOT023128a, pseudo-nodule bearing three compressed syncarids (*Palaeocaris secretanae*) and fragments of plant remains. B. MNHN.F.SOT096571a, cephalic region of *P. secretanae* showing a pyrite aureole and the pyrite and kaolinite body filling. C. MNHN.F.SOT005795a, dorsal view of *P. secretanae* demonstrating the apatite preservation of the cuticle in its posterior part and a kaolinite filling of the cephalic region. D–F. Successive stages of nodule formation in the Montceau Lagerstätte; D. MNHN.F.SOT027733a, *Odontopteris* sp. bordered by siderite; E. MNHN.F.SOT002282a, *Pecopteris unita* with immediate surroundings invaded by siderite; F. MNHN.F.SOT024054a-b, part and counterpart of *Pecopteris unita* in a nodule physically individualized from the sediment, left part still included in the rock matrix. G. MNHN.F.SOT074685a, *P. secretanae* egg preserved in three-dimensions. H. MNHN.F.SOT005795a, dorsal view of *P. secretanae* uropods bearing delicate setaes. I. MNHN.F.SOT0078506a, detail of *P. secretanae* epipodite showing the apatite (Ap) and calcite (Cal) mineralizations. J. MNHN.F.SOT003019a, close up of an egg section of *P. secretanae* showing the kaolinite mineralization. K. MNHN.F.SOT101076a, possible bacterial accumulation on the posterior portion of the skull of *Phlegethontia* sp. L–O. MNHN.F.SOT095664b, microprobe analysis of *P. secretanae* mandible in cross section; L, general view; M, calcium mapping showing the calcite filling; N, iron mapping showing the siderite surrounding; O, phosphate mapping showing the apatite cuticle. P–S. MNHN.F.SOT003685a, microprobe analysis of *P. secretanae* body/nodule interface; P, general view; Q, iron mapping showing the siderite surrounding; R, silicon mapping showing the kaolinite filling and the quartz grain in the sediment; S, phosphate mapping showing the remains of the apatite cuticle. T–Y. Successive stages of nodule formation and mineralizations in the Montceau Lagerstätte, general view and cross section of an arthropod carapace; T, living animal on the sediment; U, animal just buried and very early stage of apatite and siderite mineralization; V, immediate surroundings of the carrion invaded by siderite, cuticle mineralized, void in the fossils; W, final stage of nodule formation, calcite filling the fossil void; X, pyrite precipitation; Y,

3.3. Later taphonomic processes

Perrier et al. (2006) identified other minerals associated with syncarids. Calcite infillings were frequently observed; it seems to have crystallised preferentially in body cavities formerly occupied by soft tissues. By filling the cavities during or just after the cementation, the calcite may have facilitated the three-dimensional preservation of soft parts during the compaction (Fig. 5M, W, X). Pyrite occurs either as a ring around the fossil, as a thin layer on the surface of the cuticle, or in a disseminated form within the nodule (Fig. 5B, X, Y). One of the most frequent minerals in Montceau nodules is kaolinite (Fig. 5B, C, J, R, Y). It fills up the inside of fossils and is likely to have been produced by the alteration of rocks surrounding nodules. Chalcopyrite, baryte, celestine are also present (Perrier, 2003).

3.4. Taphonomy

Although the taphonomic evolution and the chronology of mineralization are not completely understood, major steps leading to the preservation of syncarids have been recognized and may apply to the majority of fossils found in nodules as follows (Fig. 5T–Y):

- rapid burial in fine anoxic mud inhibited decomposition and disarticulation;
- anoxia coupled with high iron concentration induced siderite (bacterial?) precipitation, thus creating a protective microenvironment around the carcass (initial stage of nodule formation);
- at the same time, phosphatization preserved cuticular and soft-bodied features (decaying organic material as a major source of phosphate);
- other minerals, mainly calcite and pyrite crystallized in cavities;
- kaolinite filled up cavities and replaced former minerals.

4. Palaeobotany

Late Palaeozoic floras from the Montceau-les-Mines coal basin preserved as compressions were studied from the nineteenth century onwards (Grand'Eury, 1877; Manès, 1847; Zeiller, 1906), while those from nodules did not receive attention until much later (Langiaux, 1984; Sotty, 1980). The increase of opencast coal mining at the beginning of the 1970s encouraged palaeobotanical research and led Langiaux (1984) to recognize 134 taxa throughout the Late Pennsylvanian Series at Montceau-les-Mines. Permineralized gymnospermous woods were also studied by Langiaux (1994), and Doubinger (1994) provided detailed information on palynology.

Charbonnier et al. (2008) studied the flora preserved in small sideritic concretions from the Saint-Louis, Saint-François and Sainte-Hélène opencast mines. Taphonomic and sedimentological data show that the flora contained in the nodules was hypoautochthonous to parautochthonous. Their qualitative and quantitative analyses of plant diversity and floristic composition in 6812 nodules indicate substantial variations in the floral composition of these opencast mines. More than 50 taxa are recognized and belong to groups that are typical of the Late Pennsylvanian flora (lycopsids, sphenopsids, tree ferns, and pteridosperms; Fig. 3). Arborescent sphenopsids and tree ferns were the major components at Saint-Louis, whereas the flora from Saint-François mainly consisted of pteridosperms; the Sainte-Hélène flora has a more balanced composition.

Charbonnier et al. (2008) also discussed the plant colonization in the Montceau Lagerstätte. The deltaic environment of Montceau, which was likely to have been relatively unstable and variable, allowed rapid colonization of swampy areas by opportunistic plants as soon as favorable conditions were restored. Sand bars produced by the prograding delta probably emerged in places and formed islets where vegetation could grow rapidly, such as the arborescent sphenopsids (e.g., *Calamites*, whose foliage is very abundant in the nodules; Fig. 3A). *Calamites* is known to have colonized deltaic areas, estuaries, and riverbanks in general (Scott, 1979). Similarly, in the Graissessac–Lodève basin (Massif Central, France), autochthonous calamiteans are associated with clastic floodplain facies (Martín-Closas and Galtier, 2005). Saint-Louis, with a flora of about 70% arborescent sphenopsids,

alteration of the nodule and fossil, replacement of apatite and calcite by kaolinite. A–C, G, H, P–S after Perrier et al. (2006); I, J, L–O, T–Y after Perrier (2003); D–F after Charbonnier, 2014; K after Germain (2008a).

Fig. 5. (Couleur en ligne) Taphonomie du Lagerstätte de Montceau-les-Mines, Stéphanien, France. A. MNHN.F.SOT023128a, pseudo-nodule montrant trois syncarides compressés (*Palaeocaris secretanae*) et des fragments de plantes. B. MNHN.F.SOT096571a, région céphalique de *P. secretanae* montrant une auréole de pyrite et le remplissage des cavités par la pyrite et la kaolinite. C. MNHN.F.SOT005795a, vue dorsale de *P. secretanae* montrant la cuticule préservée en apatite dans la partie postérieure et le remplissage de kaolinite dans la région céphalique. D–F. Étapes successives de la formation d'un nodule dans le Lagerstätte de Montceau ; D, MNHN.F.SOT027733a, *Odontopteris* sp. entouré de sidérite ; E, MNHN.F.SOT002282a, *Pecopteris unita* dont l'environnement immédiat est envahi par de la sidérite ; F, MNHN.F.SOT024054a-b, empreinte et contrempreinte de *Pecopteris unita* dans un nodule s'individualisant à partir du sédiment, la partie gauche est toujours incluse dans la matrice rocheuse. G. MNHN.F.SOT074685a, œuf de *P. secretanae* préservé en trois-dimensions. H. MNHN.F.SOT005795a, vue dorsale des uropodes *P. secretanae* montrant de délicates soies. I. MNHN.F.SOT078506a, détail d'une épipodite de *P. secretanae* montrant les minéralisations d'apatite (Ap) et de calcite (Cal). J. MNHN.F.SOT003019a, détail d'un œuf de *P. secretanae* montrant le remplissage kaolinitique. K. MNHN.F.SOT101076a, possible accumulation de bactéries dans la partie postérieure du crâne de *Phlegethontia* sp. L–O. MNHN.F.SOT095664b, analyses microsonde d'une mandibule *P. secretanae* en section ; L, vue générale ; M, carte du calcium montrant le remplissage calcitique ; N, carte du fer montrant la sidérite ; O, carte du phosphate montrant les restes de la cuticule minéralisée en apatite. P–S. MNHN.F.SOT003685a, analyses microsonde de l'interface corps/sédiment de *P. secretanae* ; P, vue générale ; Q, carte du fer montrant la sidérite ; R, carte de la silice montrant le remplissage kaolinitique et les grains de quartz dans le sédiment ; S, carte du phosphate montrant la cuticule minéralisée en apatite. T–Y. Étapes successive de la formation d'un nodule et des minéralisations dans le Lagerstätte de Montceau, vue générale et en coupe de la carapace d'un arthropode ; T, animal vivant sur le sédiment ; U, animal enterré juste après sa mort et stage précoce de minéralisation de l'apatite et de la sidérite ; V, environnement immédiat du cadavre envahi par de la sidérite, cuticule complètement minéralisée, intérieur du fossile vide ; W, stage final de la formation du nodule, remplissage calcitique du vide du fossile ; X, précipitation de la pyrite ; Y, altération du nodule et du fossile, remplacement de l'apatite et de la calcite par la kaolinite. A–C, G, H, P–S d'après Perrier et al. (2006) ; I, J, L–O, T–Y d'après Perrier (2003) ; D–F d'après Charbonnier, 2014 ; K d'après Germain (2008a).

corresponds to this type of environment. At Sainte-Hélène, the depositional environment is more varied and of higher energy; large sand bodies indicate the presence of a fluvial system with numerous channels. The occurrence of angular, decimetre-sized fragments of crystalline basement in these sandbars suggests that the relief was probably more proximal than at Saint-Louis, with steeper slopes allowing more efficient drainage and more powerful channelling of sediments. These dynamics probably hindered the development of swampy areas and the colonization by arborescent sphenopsids, but were beneficial to other plants, such as certain species of cordaitaleans, which are considered here, and in numerous intermontane basins of Europe (Doubinger et al., 1995), to be a seasonally dry soil species (sensu DiMichele et al., 2005). The absence of pond-dwelling fauna (e.g., conchostracans; see Vannier et al., 2003) in the Sainte-Hélène nodules may also relate to the high energy conditions (e.g., dominance of coarse sandstones) that prevailed at this locality. At Saint-François, the environmental conditions seem to have been intermediate, but were probably swampier than at Saint-Hélène, which is consistent with the numerical abundance of pteridosperms. In conclusion, despite the lack of recent and direct sedimentological observations, due to the flooding of the opencast mines, sedimentary dynamics are likely to have exerted a major control on the composition of the floras and may account for the compositional differences between the different localities. Numerous studies of various Carboniferous floras have reached the same conclusions (e.g., DiMichele et al., 2005; Gastaldo et al., 1995; Martín-Closas and Galtier, 2005). Nevertheless, the three localities studied were, at least occasionally, interconnected; for example, during flooding of the deltaic plain, deposition was uniform over the whole area (e.g., bituminous shales with fish-rich layers). In conclusion, the Montceau Basin displayed a mosaic of palaeoenvironments (e.g., deltaic lacustrine, paludal-to-fluvial), which favoured colonization by plants and animals.

5. Palaeozoology

During the last 40 years, a diverse and abundant fauna, including both invertebrates and vertebrates, was described in the Montceau Lagerstätte. A resurgence of interest began in the 1990s with the publication of an overview of the Lagerstätte (Poplin and Heyler, 1994a) followed by detailed studies focusing on specific taxa (e.g. Perrier et al., 2006; Racheboeuf et al., 2002, 2004). In recent years digital reconstruction, through such techniques as X-ray tomography (Garwood et al., 2011, 2012; Germain, 2008b; Germain et al., in press), has been shown to be a very valuable tool for the study of siderite-hosted fossils. For example, the fossil MNHN.F.SOT086502 (Fig. 4K) was first interpreted as an isopod, then as a leptostracan and is now known to be a dictyopteran insect nymph thanks to the tomographic reconstruction (Garwood et al., 2012). This technique can reveal the fossil's morphology in its entirety, allowing more accurate description, and hence a more informed picture, of a fossil's taxonomy, phylogeny and palaeoecology. The use of tomographic reconstruction is probably the future for studying the Montceau fossils. The following section summarizes the current state of researches on the different taxa recorded from the Montceau Lagerstätte.

5.1. Invertebrates

5.1.1. Annelids

According to Pacaud et al. (1981), several annelid forms occur in the Montceau Lagerstätte, including the amphinomid *Palaeocampa anthrax* Meek and Worthen, 1865 with preserved parapodia and chaetae (Pleijel et al., 2004; Fig. 4A). The rest of the annelid material is still unstudied.

5.1.2. Molluscs

Although they are very abundant (about 25% of the total fauna), molluscs are little diversified in Montceau, being represented almost entirely by the freshwater bivalve *Anthraconaia lusitanica* (Teixeira, 1943) (Babin, 1985, 1994; Fig. 4B–C). Very abundant in the Bed 0, some of them are thought to have been fossilised in life position with their valves connected. Strangely none of these bivalves seems to show any preserved soft part.

5.1.3. Onychophorans

Several specimens are present with well-preserved antennae. They may belong to the form found in Mazon Creek (*Helenodora inopinata* Thompson and Jones, 1980) reassigned to *Ilyodes* Scudder, 1890 by Pacaud et al. (1981). These forms are still undescribed (Fig. 4D).

5.1.4. Merostomes

The xiphosuran *Alanops magnificus* Racheboeuf, Vannier & Anderson, 2002 (= *Liomesaspis birtwelli* sensu Anderson, 1997) preserves unrecorded details of fossil xiphosuran ventral anatomy (Fig. 4E–F), and enable detailed interpretation of their phylogeny, functional morphology (locomotion, feeding, vision), lifestyle and palaeoecology (Racheboeuf et al., 2002).

5.1.5. Arachnids

About 50 nodules contain arachnid specimens (Poplin and Heyler, 1994a; Fig. 4G, H), among them Selden (1996 a, b; 2000) described the first fossil and oldest known mesothele spider (*Palaeothele montceauensis*) and commented upon its morphology and phylogeny. Two specimens of trigonotarbid arachnids (*Aphantomartus areolatus* Pocock, 1911 and *Trigonotarbus* sp. A) were also discussed by Dunlop (1999). Garwood (2010) and Garwood et al. (2011) described two harvestmen (*Ameticos scolos* and *Macrogyion cronus*; Fig. 4J) from X-ray micro-tomographic reconstructions. These very precise digital models allowed the first phylogenetic analysis of Palaeozoic opiliones and detailed comparisons with extant harvestmen. These comparisons showed strong morphological stasis in the order and permitted speculations about the lifestyle of the Carboniferous species. Volatier et al. (1994) recognized two scorpion species in the Montceau Lagerstätte, i.e. *Allobuthus pescei* (Vachon & Heyler, 1985; Fig. 4I) and *Coseleyscorpio lanceolatus* Kjellesvig-Waering, 1986, and discussed their systematic position, palaecology, and palaeobiogeography.

5.1.6. Myriapods

Only small juveniles assigned to *Arthropleura* sp. have yet been found in nodules (up to 45 mm, Briggs and Almond, 1994; Fig. 4M). The exceptional material includes some of the most complete specimens described so far, showing for the first time aspects of the cephalic morphology, thus allowing assumptions about its palaeoecology. In addition, large trackways indicate that some individuals were giant (up to 40 cm). One diplopod myriapod (*Amynilyspes fatimae*) was described by Racheboeuf et al. (2004) with a discussion about its terrestrial lifestyle, defence mechanisms and palaeogeographic distribution. Several other species are probably present including *Blanziulus parriati* (Langiaux and Sotty, 1976) – Fig. 4N.

5.1.7. Malacostracans

The syncarid crustaceans (*Palaeocaris secretanae* Schram, 1984; Schram and Secretan, 1994) are by far the most abundant animals in Montceau representing about 50% of the entire fauna (Figs. 4O, 5A–C). The abundance of syncarid specimens allowed very fine reconstruction and precise morphofunctional interpretation of their locomotion, feeding, reproduction (Perrier et al., 2006). J. Pollard (in Rolfe et al., 1982) identified two ostracod species in Montceau, however, Vannier et al. (2003) considered them to be conspecific (*Carbonita salteriana* (Jones and Kirby, 1890)) based on their morphology and the fact that they were recovered from a single concretion. One specimen bears a drill-hole that the authors interpreted as possible predation from a juvenile gastropod. Two spinicaudatan species (*Montcestheria orri* and *Eustheria feysi*) described by Poplin and Heyler (1994b) and Vannier et al. (2003) display some soft parts and resting eggs suggesting a lifestyle, reproduction and feeding comparable to that of recent representatives and possibly living in temporary aquatic environments. Based on recently cracked concretions, Racheboeuf et al. (2009) described a new palaeophreatoicid isopod, *Sottyella montcellensis* and a gorgonophontid stomatopod, *Chabardella spinosa*. The presence of the palaeophreatoicid isopod *Palaeocrangon* sp. (Pacaud et al., 1981; Schram, 1980) and other Montceau isopod-related specimens are also discussed by Racheboeuf et al., 2009.

5.1.8. Euthycarcinoids

There are two euthycarcinoids described in the Lagerstätte (*Schramixerxes gerem* and *Sottyxerxes multiplex*; Schram and Rolfe, 1982). Some new, three-dimensionally preserved material, allowed Schram and Rolfe (1994) and Racheboeuf et al. (2008) to reconstruct and interpret for the first time their lifestyle, functional morphology and their possible hexapod affinities.

5.1.9. Hexapods

Burnham (1994) reports that the Montceau Lagerstätte yields one of the most diverse Carboniferous insect fauna (Fig. 4K, L, P). Although most the material is fragmentary (mostly wings), the following insect groups are represented: Monura, Ephemeroptera, Palaeodictyoptera, Megasecoptera, Protorthoptera (Strephocladidae, Blattinopsidae), Caloneurodea, Odonoptera, Miomoptera, Rochdalia (Béthoux and Nel, 2010; Burnham, 1981, 1984, 1985; Langiaux and Parriat, 1974, 1975a, b; Oudard, 1980). These publications include discussions about taxonomy, palaeoecology and palaeobiogeography. In addition, a large proportion of the fossils are aquatic nymphs. Among them, Garwood (2010) and Garwood et al. (2012) reconstructed, using X-ray microtomography, polyneopteran insect nymphs (*Anebos phrixos* and an unnamed juvenile Dictyoptera; Fig. 4K, L). This work described the morphologically best-known Palaeozoic insect nymphs with preserved limbs in both specimens and discussed their lifestyle and the question of the origin of wings.

5.2. Vertebrates

5.2.1. Myxinoids/Lampreys?

Several fossils from Montceau-les-Mines are referred to a fossil hagfish (*Myxineidus gononorum*) by Poplin et al. (2001). This material displays strikingly similarities to modern hagfish and, as living hagfish are exclusively marine, the authors discussed the depositional environment of the Lagerstätte. However, new data from X-ray tomography (Germain et al., in press), do not exclude the possibility that these specimens belong to the lampreys. This would be more consistent with the generally accepted freshwater environment of Montceau.

5.2.2. Chondrichthyans

The group is only known from several isolated xenacanthiform spines (*Expleuracanthus* sp.; Heyler and Poplin, 1989; Langiaux and Sotty, 1977; Poplin and Heyler, 1989) found in the "couche de schistes à poissons" (fish shale bed). These freshwater predators might have occupied niches close to that of recent sharks (Heyler and Poplin, 1994).

5.2.3. Sarcopterygians

The only known sarcopterygian (dipnoan) from Montceau was described recently by Olive et al. (2012). It probably belongs to the genus *Sagenodus* Owen, 1867, thus indicating palaeobiogeographic links between France and Germany, but the fragmentary state of the material precludes further determination.

5.2.4. Acanthodians

Most of the Montceau acanthodians come from the "couche de schistes à poissons" although some specimens where found in nodules. All the specimens are very fragmentary and might belong to the genus *Acanthodes* Agassiz, 1833–44, (Heyler, 1980; Heyler and Poplin, 1994; Langiaux and Sotty, 1977).

5.2.5. Actinopterygians

The actinopterygians are by far the most diverse and abundant vertebrates in Montceau (Fig. 4Q). They are well represented in the nodules but it is in the "couche de schistes à poissons" that the preservation is the best and allows the most precise determinations. Altogether 12 species belonging to four orders (Palaeonisciformes, Brookvaliiformes, Paramblypteriformes and Aeduelliformes) are recognized and allow discussions about palaeobiogeography and taxonomy (Heyler, 1980; Heyler and Poplin, 1983, 1994).

5.2.6. Tetrapods

Present mostly in the nodules, temnospondyls are well represented but not very well-preserved. However some specimens show trace of soft parts such as muscles, gills and digestive tracks, and two larval stages can be observed. Two species from the Stephanian (*Branchiosaurus petrolei* (Gaudry, 1875; Fig. 4R) and *Micromelerpeton boyi* Heyler, 1994) and one Autunian form (Branchiosauridae *incertae sedis*) were recognized (Heyler, 1980, 1985, Heyler and Poplin, 1994) allowing the authors to discuss their anatomy and palaeobiogeography. Several fragments of temnospondyls (including *Actinodon* sp.) were also recorded by Dutuit and Heyler (1994). Lepospondyls are represented by nectrideans and aistopods. Three nectridean species (*Sauravus costei*, *S. spinosus* and *Montcellia longicaudata*; Civet, 1983; Descheaux, 1955; Dutuit and Heyler, 1994; Langiaux et al., 1974; Thévenin, 1906, 1910) are present in the shales and the nodules. One aistopod amphibian was described by Heyler (1980) on the basis of some 100 vertebrae and some ribs but the skull is missing. Dutuit and Heyler (1994) compared this material to *Phlegethontia longissima* (Fritsch, 1875) but could not offer a more precise identification because of a lack of diagnostic features. Another juvenile specimen, also possibly belonging to the genus *Phlegethontia* Cope, 1871 was digitally reconstructed using X-ray tomography by Germain (2008a, b). The new specimen allows a discussion about the possible terrestrial lifestyle of some aistopods and the origin of pedicellate teeth. A single fragment of pelycosaurian reptile (mandible + skull fragments) was recovered from the Lagerstätte (*Stereorachis*? *blanziacensis*; Dutuit and Heyler, 1994; Langiaux et al., 1974). The presence of this single specimen contrasts with the abundance of tracks present in the basin, and tentatively attributed to pelycosaurians. Based on the whole vertebrate fauna, Dutuit and Heyler (1994) discussed the palaeoecology of these different forms and the taphonomy of the vertebrates.

5.2.7. Tracks

The large open coal quarries of Montceau-les-Mines displayed a large number of footprints. These suggest the existence of microsaures, pelycosaurians and temnospondyls probably living in a fluvio-palustrine environment (Gand, 1994).

5.2.8. Coprolites

Coprolites are also common and contain actinopterygian scales and teeth. These were most probably produced by large actinopterygians/amphibians and give indications of predation levels and the trophic chain (Poplin, 1994b).

6. Conclusion

The Montceau-les-Mines Lagerstätte (Late Stephanian, Late Carboniferous, France) was located at equatorial latitudes and probably represents freshwater environments.

The Lagerstätte displays a rich and diverse flora (lycopsids, sphenopsids, ferns, pteridosperms and cordaites) and fauna (bivalves, annelids, crustaceans, myriapods, insects, chelicerates, myxinoids, actinopterygians, sarcopterygians and tetrapods).

The exceptionally preserved fossils found in nodules exhibit a high degree of structural articulation and the 3D-preservation of soft parts, as well as extremely fragile cuticular structures.

This preservation was made possible by the combination of several factors: rapid burial in fine anoxic mud, early siderite precipitation inducing the nodule formation, and phosphatization of cuticules and soft-bodied features.

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