

A new vertebrate Lagerstätte from the Lower Permian of France (Franchesse, Massif Central): palaeoenvironmental implications for the Bourbon-l'Archambault basin

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Key-words. – Mass mortality, Seymouriamorpha, *Discosauriscus*, Exceptional preservation, Taphonomy, Cisuralian, Autunian, Palaeozoic.

Abstract. – A new vertebrate locality from the Lower Permian (Cisuralian) of the Bourbon-l'Archambault basin (Massif Central, France) is reported and its associated flora and fauna preliminarily described. This locality corresponds to a mass mortality assemblage deposited in an aquatic environment. Interestingly, it has yielded hundreds of exceptionally well preserved seymouriamorph specimens, all referred to *Discosauriscus austriacus*. This exquisite assemblage corresponds to the first seymouriamorph Lagerstätte and the first record of *D. austriacus* outside the Boskovice basin in Czechia. It enlarges the geographical distribution of the species during the Early Permian, and has new palaeoenvironmental implications regarding the Palaeozoic Bourbon-l'Archambault basin.

Un nouveau gisement de vertébrés à conservation exceptionnelle dans le Permien inférieur de France (Franchesse, Massif central) : implications paléoenvironnementales dans le bassin de Bourbon-l'Archambault

Mots-clés. – Mortalité en masse, *Discosauriscus*, Tétrapode, Conservation exceptionnelle, Taphonomie, Cisuralien, Autunien, Paléozoïque.

Résumé. – Une nouvelle localité fossilifère a été découverte dans le Permien inférieur (Cisuralien) du bassin de Bourbon-l'Archambault (Massif central, France). Il s'agit d'un gisement de concentration et de conservation exceptionnelles, livrant des centaines de squelettes sub-complets et articulés, attribués au seymouriamorphe *Discosauriscus austriacus*. La faune et la flore associées, également décrites ici, livrent d'intéressantes données sur le paléoenvironnement aquatique. Ce gisement correspond au premier Lagerstätte de seymouriamorphes (groupe de tétrapodes anciens) et à la première occurrence de *D. austriacus* à l'extérieur du bassin de Boskovice, Tchéquie. Cette découverte élargit l'aire de répartition de l'espèce pendant le Permien inférieur et permet de nouvelles interprétations paléoenvironnementales concernant le bassin paléozoïque de Bourbon-l'Archambault.

INTRODUCTION

This article corresponds to a report of a new tetrapod Lagerstätte discovered in the Lower Permian of Franchesse (Allier, France), in the northern part of the Bourbon-l'Archambault basin, Massif Central (fig. 1A), preserving hundreds of exquisite specimens of *Discosauriscus austriacus*.

Discosauriscus austriacus is a seymouriamorph known only from the Lower Permian lacustrine deposits of the Boskovice basin, Czechia [Klembara and Meszároš, 1992;

Laurin, 2000]. Up to now, seymouriamorphs from France have been little known and poorly documented: historically, the very first specimen comes from the “Autunian” (Lower Permian according to Gand *et al.* [1997]) of Bourbon-l'Archambault and was briefly described by de Saint-Seine [1949], who considered it as a branchiosaur temnospondyl based on its size, and who named it “*Melanerpeton sacheti*”. Later, Heyler [1969] redescribed the specimen and attributed it to the genus *Discosauriscus* KUHN, 1933 based on its peculiar vertebral, cranial and scapular morphology. Other poorly preserved specimens

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were referred to as *Discosauriscus* sp. in the “Autunian” of the Autun basin, or as “Discosauriscidae” in the “Autunian” of the Sarre-Lorraine / Palatinat basin [Steyer *et al.*, 1998]. These were the only records of seymouriamorphs in France.

The tetrapod Lagerstätte reported here was discovered in 1964 by one of us (RPD), but systematic excavations only started in June 2007 under a working convention between the CNRS (JSS, SS, RV) and the Eldonia Society (FE, BP, AV), and after the use of a mechanical digger.

MATERIAL AND METHOD

Hundreds of specimens have been collected during the recent systematic excavations. The best preserved ones have been selected for description: they are preserved on a large sedimentary slab (104 x 56 x 4 cm, fig. 2) belonging to the collection of the “Musée des Confluences” (Lyon) under the reference number MHNL 20269991.

The slab corresponds to a grey claystone (argilite), very rich in organic matter, and preserving 14 subcomplete skeletons and other remains. All the specimens are articulated (figs 2, 3). They have been mechanically prepared with a micro-abrasive blasting machine. To keep the skeletons in connection, they have been only half removed from the rock. Consequently, only one view of each fossil (dorsal, ventral or lateral) is visible.

Institutional abbreviations – MHNL, Musée des Confluences, Lyon, France ; WDC, Wyoming Dinosaur Center.

Anatomical abbreviations – Fr: frontal; Ju: jugal; Na: nasal; Pa: parietal; PFr: prefrontal; PoFr: postfrontal; PoOr: postorbital; Sl: skull length.

SYSTEMATIC PALAEOLOGY

Seymouriamorpha WATSON, 1917
Discosauriscidae ROMER, 1947

Discosauriscus KUHN, 1933

Type species. – *Discosauriscus pulcherrimus* (FRITSCH, 1879)

Other species. – *Discosauriscus austriacus* (MAKOWSKY, 1876)

Repartition. – ?Upper Carboniferous – Early Permian of Czeckia [Makowsky, 1876; Klembara and Meszároš, 1992], Germany [e.g., Credner, 1883], Poland [e.g., Klembara, 2005] and France [summarized in Steyer *et al.*, 1998].

Discosauriscus austriacus (MAKOWSKY, 1876) (figs 2-3)

Type Locality. – Boskovice basin, Moravia, Czeckia [Klembara and Meszároš, 1992].

New Locality. – Les Charbonnières, Franchesse village, Allier, France [this paper].

Figured specimens. – Fourteen articulated subcomplete skeletons of different individual ages, preserved on an argilite slab Nr. MHNL 20269991 [this paper].

Horizon and age. – The specimens come from laminated dark siltstone horizons (35 cm thick) composed of thin (maximum 5 mm) black silts intercalated with discontinuous brownish carbonates (maximum 3 mm in thickness). The horizons belong to the uppermost shale sequence (20 m in thickness) of the Renière B Member (the “Charlerie Member” of mining geologists), Renière Formation, upper section of the “Autunian Group”, Sakmarian, Lower Permian

(Cisuralian) (fig. 1B). A Sakmarian age is proposed here for Franchesse because this locality is stratigraphically younger than Buxières-les-Mines, where a cinerite (called “Lien vert”) has been dated at 288 ± 4 Ma, i.e. at the Asselian-Sakmarian limit [Kaufuss, 2003].

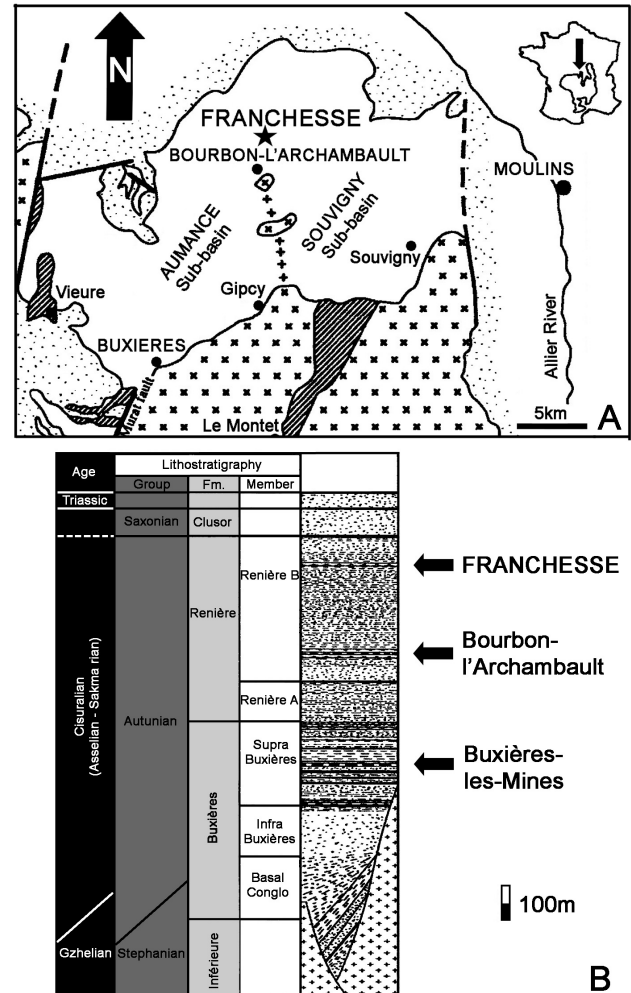


FIG. 1. – A. Carte géologique simplifiée du bassin carbonifère et permien de Bourbon-l'Archambault montrant la localisation du nouveau gisement de Franchesse [modifiée d'après Paquette and Feys, 1989]. Symboles : points, roches post-permiennes ; croix, socle cristallophylien ; blanc, Permien inférieur ; zébré, Carbonifère supérieur (« Stephanien ») ; croix horizontales, ride de Gipy-Bourbon (séparant le bassin en deux sous-bassins). B. Log stratigraphique synthétique du bassin montrant la position verticale du gisement dans la dernière séquence bitumineuse du Membre « Renière B » (ou Membre « Charlerie » des géologues miniers), Formation de Renières, partie supérieure du groupe « Autunien », Permien inférieur (Cisuralien) [modifié d'après Debriette, 1992]. Abréviations et symboles : Conglo, conglomérats de base ; croix, socle cristallophylien ; vagues, cinérites ; pointillés, grès ; ligne noire, charbon ; tirés, argilites ; rectangle blanc, « schistes » bitumineux.

Diagnosis. – We referred to the detailed description of Klembara [1997] regarding the cranial diagnostic characters of *Discosauriscus austriacus*.

(We also referred to Laurin [2000]; and Klembara and Ruta [2005] for the characters of the seymouriamorphs; to Klembara and Bartík [2000]; Klembara and Ruta [2004]; and Klembara [2005] for the characters of the family Discosauriscidae and of the genus *Discosauriscus*).

Preservation. – Hundreds of exceptionally well-preserved specimens have been found. The specimens described here are 3D preserved, as is the case of those from the type locality in Czeckia. They are slightly dorso-ventrally compressed, notably in the skull region. As mentioned above, they are preserved on a metre-long siltstone slab but they do not show any preferential orientation to indicate a possible palaeocurrent. Most lie on their dorsal or ventral side (figs 2, 3A), but one is visible in lateral view (fig. 3E).

PRELIMINARY DESCRIPTION

As a detailed analysis of the *Discosauriscus* from Franchesse is under preparation by SS and colleagues, we give here only a preliminary description of the specimens.

General outlines. – The skull is subtriangular in shape and relatively flattened, with large, rounded orbits and a short snout. The skull roof bones show an ornamentation composed of deep pits and ridges. The postorbital region is broader than long. The otic notch is dorso-ventrally broad and antero-posteriorly deep (figs 3B-C). In ventral view, the pterygoids exhibit a large, transverse flange (fig. 3D). Twenty-four presacral vertebrae are visible, but only one sacral vertebra, connected to one sacral rib, is present. Ribs are preserved from the atlas to the anterior caudal segment. The mid-presacral ribs are elongated (fig. 3A). The scapular girdle is well preserved with its dermal and endochondral elements. The stem of the interclavicle is elongated but with a

broad anterior portion (fig. 3E). The limbs are stout. The humerus, relatively long, possesses massive proximal and distal heads, a high ectepicondyle and a broad entepicondyle (fig. 3A). Both the manus and the pes exhibit five digits with a phalangeal formula of 2-3-4-5-3 (fig. 3F).

Identification. – The specimens from Franchesse show the following cranial features which assign them to the species *Discosauriscus austriacus* (KLEMBARA, 1997): the pre-frontal and postfrontal meet around the midlength of the frontal; the postorbital-jugal suture is relatively long; the skull table is elongated (figs 3B-C); and ridges bearing small denticles run radially on the ventral surface of the pterygoids (fig. 3D).

Ontogeny. – Different individual or somatic ages are recognized among the specimens:

– Specimens Nr. 20269991.-1 to -4 (SI=26-37.5 mm) show semi-elliptical skulls which are not as well-preserved as the older ones. The preorbital and postorbital regions are very short. The orbits are proportionally large. The nasals and lacrimals are short, by comparison with the length of the frontals. The frontals are slightly longer than the parietals. The pineal foramen lies in the anterior half of the interparietal suture. The otic notches are shallow and dorso-ventrally broad. The ornamentation of the skull roof bones is radial. All these features characterise larval or metamorphic individuals [Klembara, 1995, 1997].

– Specimens Nr. 20269991.-5 to -8 (SI= 38-45 mm) show more triangular skulls, with a more elongated preorbital region, even if the orbits remain placed in the first anterior half of the skull. The length of the postorbital region also increases. The nasal and lacrimal are longer but the nasals stay nevertheless smaller than the frontals. The frontals are about the same size as the parietals. The pineal foramen slightly moves posteriorly in 20269991.7. The otic notches are deeper. The cranial ornamentation is less radial. All these features characterise juvenile individuals [Klembara, 1995, 1997; Steyer, 2000].

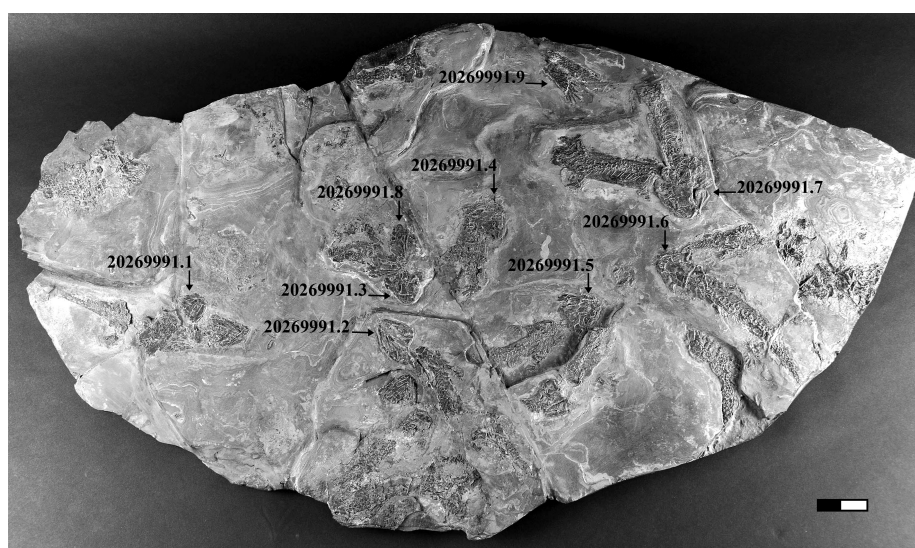


FIG. 2. – New specimens of *Discosauriscus austriacus* from the Lower Permian of Franchesse, exceptionally well preserved on an argillite slab Nr. MHN 20269991 (collection “Musée des Confluences”, Lyon, France). Note that all the specimens are preserved in connection. Scale bar 5cm. Numbered specimens are referred to in the text (section ontogeny) and figure 3. Photo Didier Berthet (Musée des Confluences, Lyon, France).

FIG. 2. – Nouveaux spécimens de *Discosauriscus austriacus* du Permien inférieur de Franchesse exceptionnellement bien préservés sur une plaque d'argillite N° MHN 20269991 (collections “Musée des Confluences”, Lyon, France). Tous les spécimens sont en connection. Echelle 5 cm. Les numéros sur certains spécimens renvoient au texte (section “ontogeny”) et à la figure 3. Photo Didier Berthet (Musée des Confluences, Lyon, France).

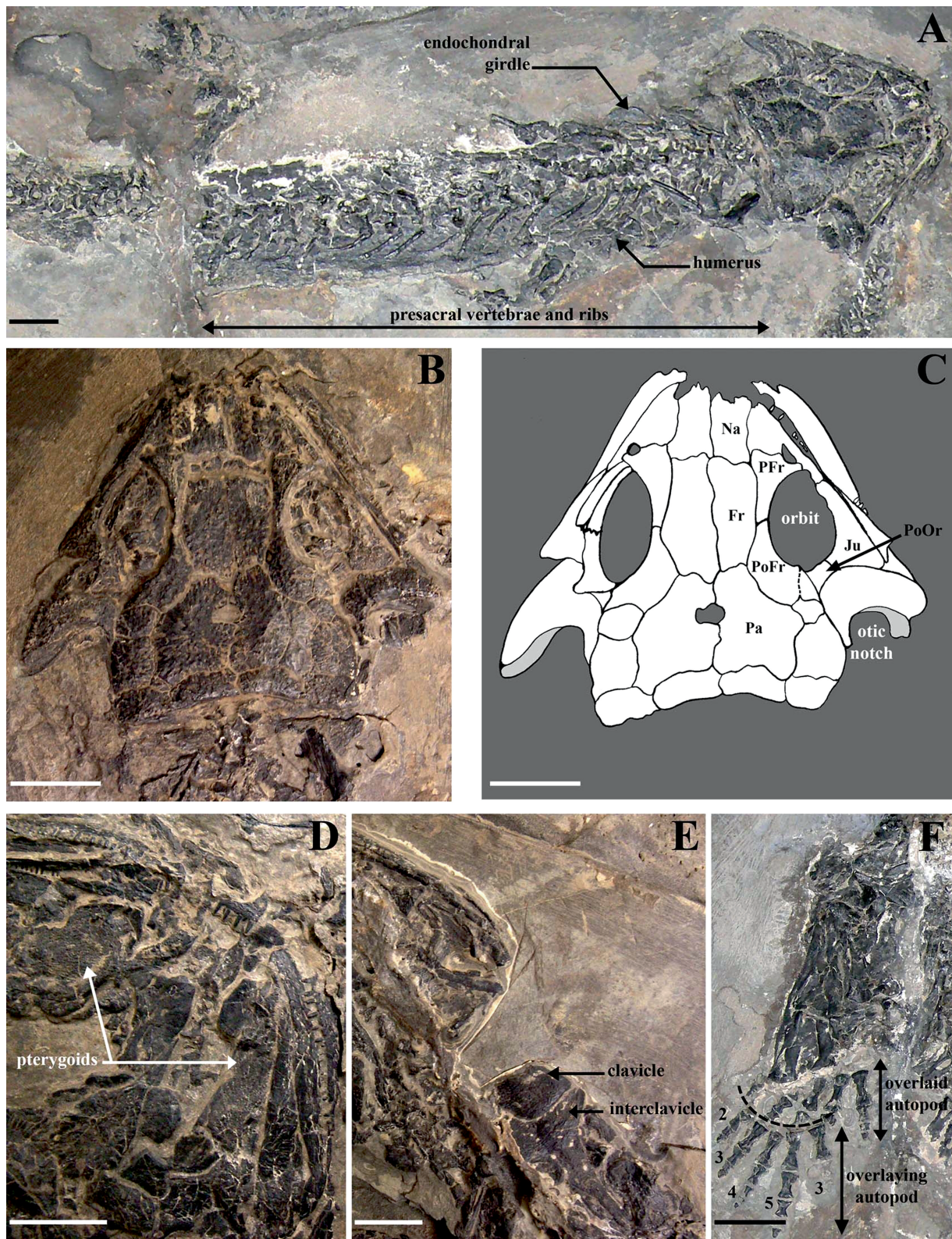


FIG. 3. – Anatomical details of specimens of *Discosaurus autriacus* from the Lower Permian of Franchesse. A: complete articulated specimen (Nr. 20269991.6) in dorsal view; with details of the skull (B: photo; C: interpretative drawing – the dash line indicates a break in the right postfrontal; both postorbitals are partly overlapped by surrounding bones, hiding partly their outlines); D: palatal view of specimen 20269991.8, showing denticles running on the pterygoids; E: ventral view of the pectoral girdle of specimen 20269991.2; F: lateral view of the hindlimbs of specimen 20269991.9, illustrating the phalangeal formula 2-3-4-5-3. Scale bars 1 cm. Photos Didier Berthet (Musée des Confluences, Lyon, France).

FIG. 3. – Détails anatomiques des spécimens de *Discosaurus autriacus* du Permien inférieur de Franchesse. A : spécimen complet et articulé (N° 20269991.6) en vue dorsale, avec détails du crâne (B : photo ; C : dessin interprétatif - les pointillés correspondent à une fissure du postfrontal ; les postorbitaux sont en partie recouverts par les os limitrophes, masquant partiellement leurs contours) ; D : vue palatale du spécimen 20269991.8 montrant des denticules ptérygoidiennes ; E : vue ventrale de la ceinture pectorale du spécimen 20269991.2 ; F : vue latérale des membres postérieurs du spécimen 20269991.9 présentant la formule phalangienne 2-3-4-5-3. Echelles 1 cm. Photos Didier Berthet (Musée des Confluences, Lyon, France).

**ASSOCIATED FLORA, FAUNA, AND
PALAEOENVIRONMENT (PLATE 1)**

In 1858, a coal well around Franchesse yielded the very first fossils of this Lagerstätte. They consist of plant remains

attributed to *Callipteris conferta* and *Calamodendron* by de Launay [1888]. This coal well is the source of the name given to this locality, “Les Charbonnières”. Since the 60s’, prospections and excavations have been carried out by one of us (RDP) who found the very first fossil vertebrates from



PLATE I. – Associated floral and faunal elements. A: sterile coniferal branch (photo JSS, identification A. Bercovici, CNRS Rennes and MNHN Paris); B: estherid (photo JSS); C: partial postcranial skeleton of *Aeduella* sp. showing articulated scales (photo JSS); D: postcranial portion of *Bohemiacanthus* sp. (photo AV, Nr. WDC-FR03-PermBPFE001); E: subcomplete larval eryopoid (photo P. Loubry, CNRS and MNHN Paris, Nr. RPD-17IX02, identification R. Schoch, Naturkunde Museum Stuttgart). Scale bars 5 mm.

PL. I. – Eléments de la faune et flore associées. A : rameau stérile de conifère (photo JSS, identification A. Bercovici, CNRS Rennes and MNHN Paris) ; B : esthéride (photo JSS) ; C : squelette postcrânien partiel d'*Aeduella* sp. avec ses écailles en connexion (photo JSS) ; D : partie postcrânienne de *Bohemiacanthus* sp. (photo AV, Nr. WDC-FR03-PermBPFE001) ; E : spécimen subcomplet d'une larve d'eryopoïde (photo P. Loubry, CNRS and MNHN Paris, Nr. RPD-17IX02, identification R. Schoch, Naturkunde Museum Stuttgart). Echelles 5 mm.

this locality. Now, since June 2007 and with the help of a mechanical digger, systematic excavations have been organized with French students and volunteers. Beyond *Discosauriscus*, this Lagerstätte also yields a rich associated flora and fauna (plate I). They are of special interest to explain the taphonomy and to reconstruct the paleoenvironment of this mass-mortality locality. The flora is mostly represented by small fragments of coniferal (Bercovici, pers. com. 2010) (plate IA), whereas the fauna consists of numerous estherids, coprolites, orthacanthid remains (cf. *Bohemiacanthus*), acanthodian spikes (cf. *Acanthodes*), palaeoniscoid actinopterygians of various sizes, and a subcomplete temnospondyl skeleton attributed to a larval eryopoid (Schoch, pers. com. 2010). The large palaeoniscoids are signalled by isolated centimetric scales, whereas the small ones are subcomplete and relatively abundant. They are referred to as *Aeduella* sp. according to their size (maximum 15 cm in total body length) and scale ornamentation. Interestingly, the scales of *Aeduella* are articulated along the body. All these vertebrate taxa, including *Discosauriscus austriacus*, are aquatic.

The palaeontology of the Bourbon-l'Archambault basin has been intensively studied since the end of the nineteenth century [e.g., de Launay, 1888], and thanks notably to various coal exploitations [e.g., Debriette, 1992; Heyler, 1969]. The last one was the large opencast mine of Buxières-les-Mines which closed in 2001. The localities of Buxières-les-Mines, Bourbon-l'Archambault, Souvigny, Coulandon, Meillers, and now Francheville are the main fossiliferous localities in the Bourbon-l'Archambault basin: Meillers and Coulandon have mostly yielded plant remains [de Launay, 1888]. Souvigny yielded stromatolites [Legrand and Debriette, 2007], ostracods [Damotte *et al.*, 1992], as well as an *Orthacanthus* tooth, actinopterygian (palaeoniscoid) scales, acanthodian and temnospondyl (cf. *Onchiodon*) scapular elements [Steyer, Heyler *et al.*, 2000]. The locality of Bourbon-l'Archambault, property of the Muséum national d'Histoire naturelle (Paris), also yielded an aquatic fauna represented by actinopterygian scales, a subcomplete acanthodian, and some branchiosaurs [e.g., Heyler, 1969]. Buxières-les-Mines yielded by far the most diversified flora and fauna of the basin: stromatolites, macro- and micro-flora, ostracods, insects (blattoid wings), elasmobranchs (orthacanthids, possible hybodonts, and xenacanthids) [Schultze and Soler-Gijón, 2004], acanthodians, actinopterygians (palaeoniscoids) [Heyler and Poplin, 1983], and temnospondyl amphibians (eryopids, archegosaurids, branchiosaurids) [Werneburg, 2003] have been described

[Steyer, Escuillié *et al.*, 2000]. Most of these taxa suggest an Asselian-Sakmarian age and a relatively deep, freshwater environment, although local and temporary marine influences are not excluded [Schultze and Soler-Gijón, 2004].

The new Francheville locality is less diversified than that of Buxières-les-Mines (in term of taxonomy), but it is the most abundant site of the Bourbon-l'Archambault basin (in terms of fossil number), and the first seymouriamorph Lagerstätte in France. Its aquatic fauna, composed of small vertebrates, as well as some desiccation marks occurring in the same sedimentary sequence, suggest a shallow water environment of low energy (suggested by the skeletons being articulated). This sedimentary sequence is the youngest fossiliferous sequence of the Bourbon-l'Archambault basin, and corresponds to the last global flooding episode of the basin [Debriette, 1992]. The rapid flooding of this shallow and quiet northern border of the basin (contrary to the deep southern border documented by Buxières-les-Mines) might explain the mass mortality of the vertebrate fauna. Another scenario to explain this mass mortality could also be a temporary and sudden arrival of salty waters from the sea. In this case, the salty waters would have been toxic for most of the freshwater and stenohaline components of this fauna. Several palaeogeographical reconstructions indeed suggest temporal and local connections between the North Sea and the European Hercynian basins during the Late Carboniferous and the Early Permian [Héry, 1990; Mascle, 1990]. If this is confirmed, the Bourbon-l'Archambault basin would resemble geomorphologically a palaeo-fjord rather than a palaeo-lake [*contra* Roscher and Schneider, 2006].

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