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ABSTRACT
The Carboniferous-Permian is a key period concerning the emergence and diversification of major tetrapod clades such as amphibians and amniotes. This is particularly the case of the Seymouriamorpha Watson, 1917. Some seymouriamorphs are well-known, such as *Seymouria* Broili, 1904 from North America and Germany, but the ecology of most taxa remains debated. This is the case of *Discosauriscus* Kuhn, 1933 from the early Permian of Europe. Here we provide a preliminary study of new specimens from the early Permian Lagerstätte of Franchesse (Allier, France) whose exceptionally well-preserved soft tissues including skin and intestinal casts provide valuable insights into the palaeoecology of *Discosauriscus*. We describe for the first time the complete skin external and histological features of a seymouriamorph indicating that juvenile discosauriscids already displayed epidermal scalation. This suggests a skin adapted towards terrestrial lifestyle in juvenile *Discosauriscus*. The recovery of an *in situ* cololite facilitates the identification of seymouriamorph coprolites found *ex situ*, and thus, future interpretations of the specific diet of this taxon. In order to better understand how these soft tissues have been preserved, we also conducted a taphonomic study including a stratigraphic and palaeoenvironmental analysis of the fossil layer deposits. Our results suggest that pronounced volcanic activity at work during the early Cisuralian of the Bourbon-l'Archambault Basin may be the cause of the multiple Permian mass mortality assemblages found at Franchesse, as well as the exceptional preservation of the fossil remains from this site.

KEY WORDS
Permian,
Seymouriamorpha,
skin,
cololite,
palaeoecology.

RÉSUMÉ
Paléoécologie et paléoenvironnement de Discosauriscus *Kuhn, 1933 avec préservation exceptionnelle des moules de peau et d'intestin du Permien précoce de Franchesse (Allier, France).*
Le Carbonifère-Permien est une période clé en ce qui concerne l'émergence et la diversification des principaux clades de tétrapodes tels que les amphibiens et les amniotes. C'est notamment le cas des Seymouriamorpha Watson, 1917. Certains seymouriamorphes sont bien connus, comme *Seymouria* Broili, 1904 d'Amérique du Nord, mais l'écologie de la plupart des taxons reste débattue. C'est le cas de *Discosauriscus* Kuhn, 1933 du Permien inférieur d'Europe. Ici, nous étudions de manière préliminaire de nouveaux spécimens provenant du Lagerstätte du Permien inférieur de Franchesse (Allier, France) dont les tissus mous exceptionnellement bien conservés, y compris la peau et le moulage des intestins, permettent d'en apprendre davantage sur la paléoécologie de *Discosauriscus*. Nous décrivons pour la première fois la morphologie externe et interne de la peau d'un seymouriamorphe, indiquant que les discosauriscidés juvéniles présentaient des écailles épidermiques. Cela suggère une peau adaptée à un mode de vie terrestre chez les *Discosauriscus* juvéniles. La découverte d'un cololithe *in situ* facilite l'identification des coprolithes de seymouriamorphes trouvés *ex situ* et ainsi de futures interprétations sur le régime alimentaire de ce taxon. Afin de mieux comprendre comment ces tissus mous ont été préservés, nous avons également mené une étude taphonomique comprenant une analyse stratigraphique et paléoenvironnementale des dépôts des couches fossilifères. Nos résultats suggèrent qu'une activité volcanique marquée au cours du Cisuralien inférieur dans le bassin de Bourbon-l'Archambault pourrait être à l'origine des multiples assemblages de mortalité massive trouvés à Franchesse, ainsi que de la préservation exceptionnelle des restes fossiles de ce site.

MOTS CLÉS
Permien,
Seymouriamorpha,
peau,
cololithe,
paléoécologie.

INTRODUCTION

Complementary to the study of mineralised tissues in fossil vertebrates, new palaeoecological traits can be inferred from fossilised soft tissues, such as skin (e.g. Vincent *et al.* 2017; Hendrickx *et al.* 2022; Jagielska *et al.* 2024), and bromalites (Hoffmann *et al.* 2020; Halaçlar *et al.* 2023; Qvarnström *et al.* 2024). Indeed, the skin, as first barrier between the organism and the external environment, shows several adaptations such as protection against mechanical stress, UV-radiation or predatory attacks (Vickaryous & Sire 2009). It can also prevent desiccation (Alibardi 2003), favour thermoregulation (Lindgren *et al.* 2014), and is a main component of behavioural displays such as camouflage and/or sexual display, for example through colouration (e.g. McNamara *et al.* 2021). Fossilised digestive remains, preserved either within (e.g. consumulites) or outside the body (e.g. coprolites, regurgitalites), also provide valuable information regarding palaeoecology (e.g. environmental factors; Hunt 1992; Northwood 2005) or palaeobiodiversity (some floral and faunal elements are only preserved in bromalites; Byrne *et al.* 2022). Especially, consumulites such as gastrolites or cololites are the most compelling evidence in the fossil record of the predator-prey interactions (e.g. Qvarnström *et al.* 2024). Furthermore, fossilised gut content is precious evidence allowing to directly link a predator with its prey and environment, at a relatively precise temporal and spatial resolution (Kriwet *et al.* 2008; Mondini 2023). However, as both soft tissues and bromalites fossilise more rarely than mineralised tissues, these key aspects of the palaeoecology of Palaeozoic tetrapods are poorly known (e.g. Eliason *et al.* 2017; Hunt & Lucas 2021).

The Discosauriscidae Romer, 1947 is a clade of Seymouriamorpha Watson, 1917. Their palaeoecology is debated between mainly aquatic or more amphibious/terrestrial lifestyle (Klembara 1995; Malakhov 2000; Kriloff *et al.* 2008; Sanchez *et al.* 2008; Calábková *et al.* 2022). Mainly, external gills are frequently preserved in discosauriscids (Ivakhnenko 1987; Klembara 1995; Bulanov 2003). Cololites have been described in association with discosauriscid remains, suggesting putative cannibalism (Klembara & Meszároš 1992). Dermal coverage has been described but only assigned to ossified dermal scales, without palaeoecological implications (Špinar 1952; Klembara & Bartík 1999). Thus, almost no skin soft tissue is known for this clade, and even for all Seymouriamorpha (Olson 1965).

The Permian *Lagerstätte* of Franchesse (Allier, France), discovered by Prof. Roger-Paul Dechambre (MNHN) in 1964, yielded hundreds of sub-complete to complete specimens of *Discosauriscus* Kuhn, 1933, preserving soft-tissue remains (Steyer *et al.* 2012: fig. 2). From 2007, one of us (J.-S.S.) organised regular systematic excavations at the Les Charbonnières site in Franchesse, under a working convention with Epona Society, owner of the site. These fieldworks led to the discovery and description of a very rich flora and fauna including numerous aeduellids, one partial *Bohemiacanthus* Schneider, 1996 shark, numerous exquisite *Discosauriscus* Kuhn, 1933 specimens, and a larval eryopoid temnospondyl (Steyer *et al.* 2012). Then A.L. co-organised further fieldworks (2021, 2022, 2024) in order to collect more palaeontological data, to better understand the soft tissue preservation and to precise the stratigraphic log of the locality (Houée *et al.* 2022a, b; Logghe *et al.* 2023a).

Here we describe new *Discosauriscus* specimens from the latest fieldworks, with exceptionally preserved complete skin coverage identified as epidermal skin, and a cololite recovered *in situ* within a complete skeleton. We also precise the stratigraphic log of the locality. These new discoveries allow: 1) the identification of seymouriamorph skin soft tissues and its comparison with the cutaneous coverage of other Palaeozoic tetrapods; 2) the study of a seymouriamorph cololite; 3) the discussion of these new data in terms of palaeoecology (e.g. skin adaptation to an aquatic or amphibious/terrestrial life), and palaeoenvironment; and 4) to better understand the mass mortality of *Discosauriscus* from Franchesse and the exceptional quality of preservation of the described soft-tissue and cololite remains.

GEOLOGICAL SETTING

The Les Charbonnières site in Le Pontet, 4 km near the village of Franchesse, is located in the north of the Bourbon-l'Archambault Basin (Allier, Massif Central, France), approx. 10 km away from the early Permian historic site of La Queue-de-l'Étang (de Saint-Seine 1949; Heyler 1969). More precisely, this site belongs to the Souvigny sub-basin (Steyer *et al.* 2012; Fig. 1A). As with the other Carboniferous-Permian basins of Autun, Blanzy-Le Creusot and Decize-La Machine, the Bourbon-l'Archambault Basin is located in the northern part of the Massif Central (Debriette 1992), belonging to the Variscan Belt of the Central Pangea (Châteauneuf & Farjanel 1989). The fossil-bearing horizons of the Les Charbonnières site come from the upper-most shale sequence of the Renière B Member of the Renière Formation (Steyer *et al.* 2012). The Renière Formation has been identified from the site of Buxières-les-Mines, south of the Aumance sub-basin of the Bourbon-l'Archambault Basin (Steyer *et al.* 2000, 2012; Kaulfuss 2003; Fig. 1B). The underlying Buxières Formation may be of early Artinskian age (288 ± 4 Ma; Kaulfuss 2003 according to the International Chronostratigraphic Chart 2024-12) but recent U-Pb dating in the Buxières Formation rather proposed a lowermost Asselian age (Cisuralian, lower Permian) of 298.592 ± 0.075/0.15/0.35 Ma (Mercuzot *et al.* 2023). An absolute age of the Les Charbonnières site has not been calculated so far, but a Sakmarian age has been proposed based on the previously assigned Sakmarian age of the Buxières Formation (Steyer *et al.* 2012, based on the ICC 2010-09). An older age of the Les Charbonnières site is in this way possible regarding the new radiometric ages of the Buxières Formation.

Valli (2007) conducted the first stratigraphic survey of the Les Charbonnières site (Steyer *et al.* 2022: fig. 2A) and observed a strong horizontal variability of the layers in the span a of few meters, with changes in both sedimentology and fossil remain contents. Our recent fieldworks (excavations

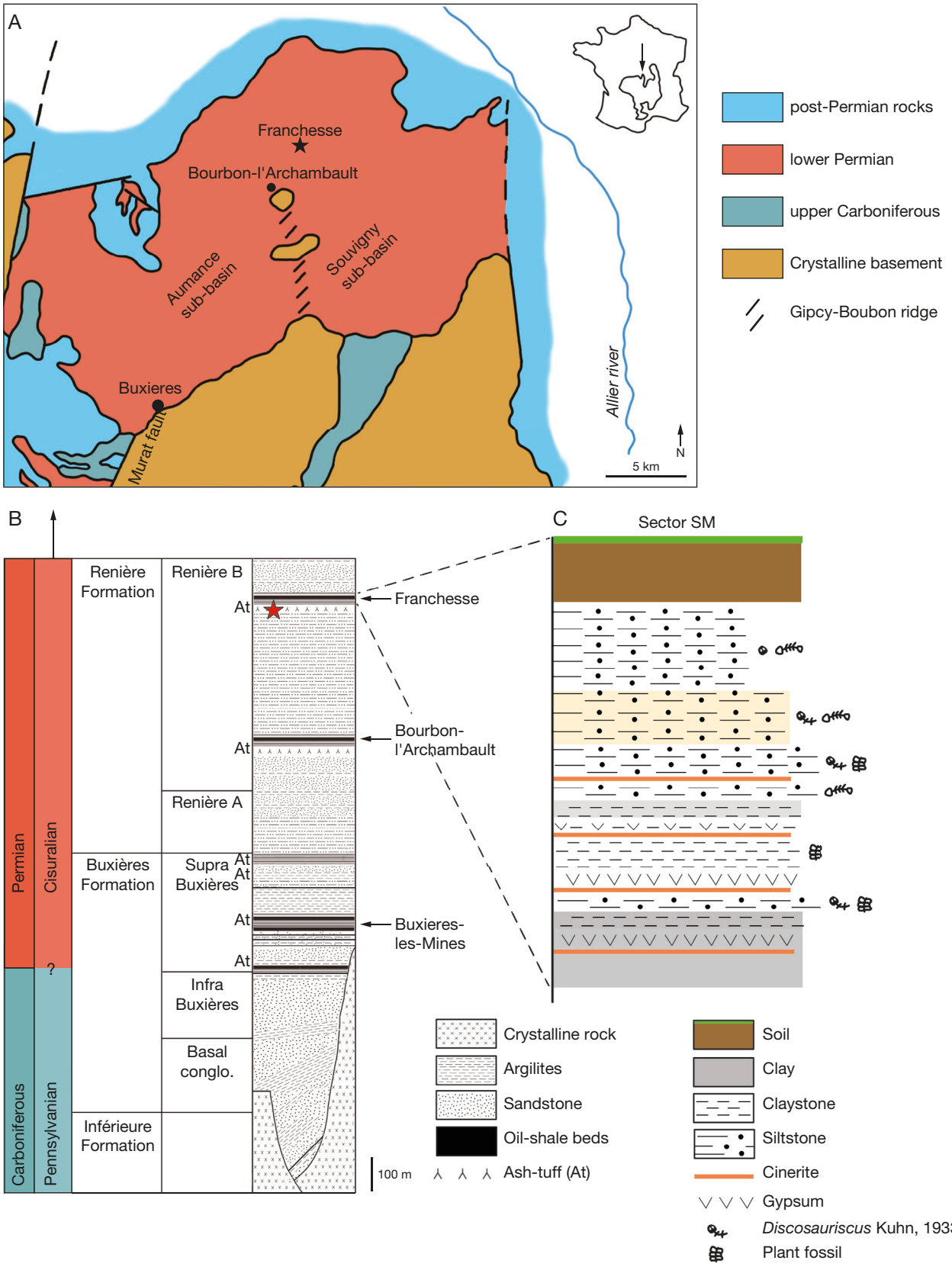

FIG. 1. — Geological context of the Les Charbonnières site near Franchesse, Bourbon-l'Archambault Basin (Allier, France) with locations of the main fossiliferous deposits of La Queue-de-l'Étang, Buxières-les-Mines and the early Permian *Lagerstätte* of Franchesse: **A**, simplified map of the Carboniferous and Permian Bourbon-l'Archambault Basin (modified after Paquette & Feys 1989); **B**, log of the main localities, from bottom to top: Buxières-les-Mines, Franchesse, La Queue-de-l'Étang; **red star**, stratigraphic position of the Les Charbonnières site (modified after Debriette 1992); **C**, detailed stratigraphic log of the SM sector of the Les Charbonnières site near Franchesse.

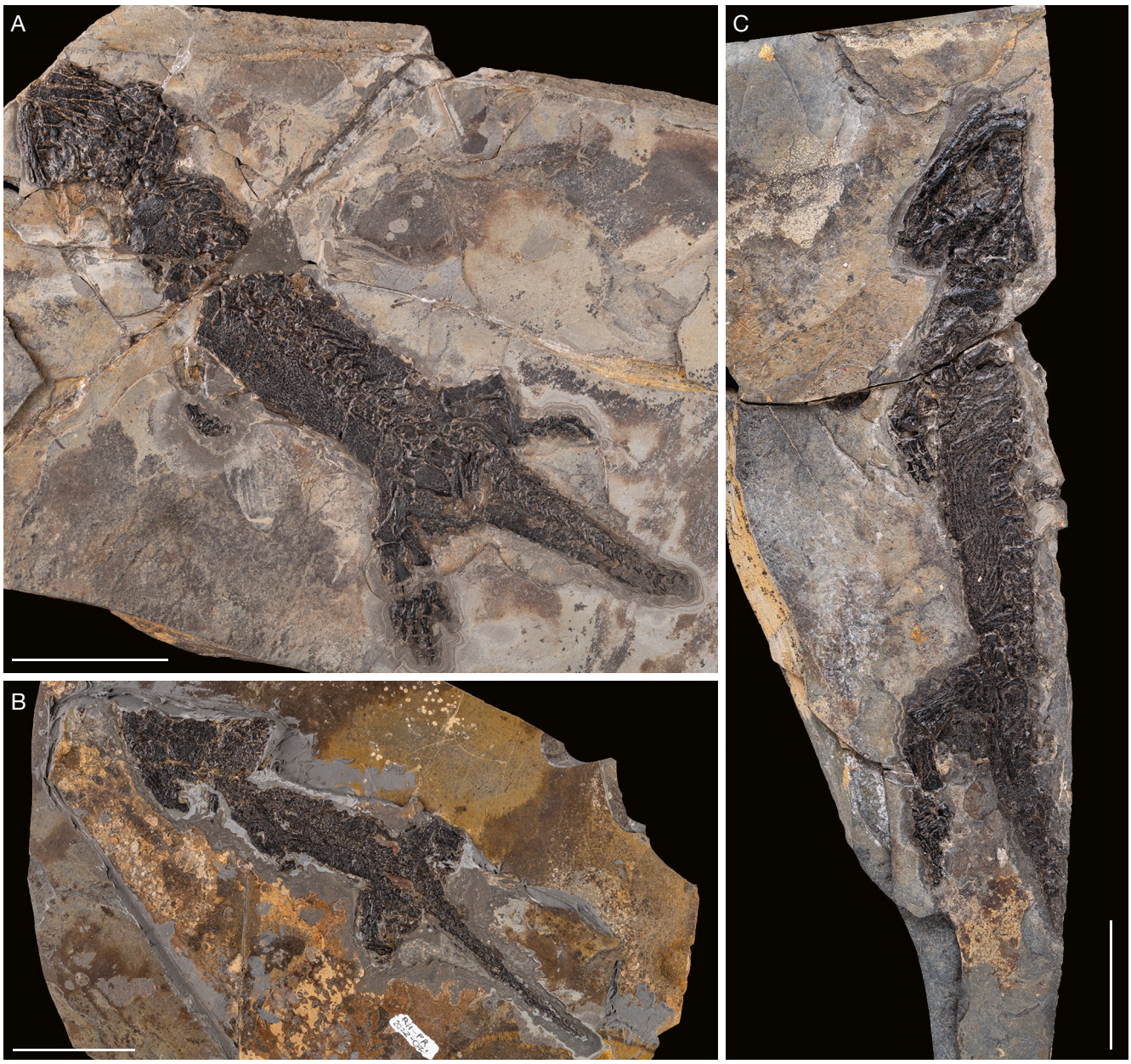

Fig. 2. — New specimens of *Discosauriscus* sp. from the Permian of Franchesse: **A**, RH-FR-2022-01, complete and articulated juvenile individual (only the right forelimb is missing) preserving dermal soft-tissue alongside the whole body; **B**, RH-FR-2022-07, sub-complete individual of poor cranial and soft-tissue preservation but yielding an *in situ* mold of the intestine; **C**, RH-FR-2022-03, sub-complete individual preserving dermal soft-tissue alongside the whole body. Scale bars: A, B, 5 cm; C, 3 cm. Credits: Lilian Cazes (CR2P).

and detailed stratigraphy; Fig. 1C) have been realised in the sector SM (see Steyer *et al.* 2022: fig. 2A), which showed a high potential for recovering *Discosauriscus* specimens through drillings (Valli 2007; Steyer *et al.* 2022). The stratigraphy of this sector is composed of, from bottom to top (Fig. 1C): an alternance (15 cm) of crystallised gypsum, a possible cinerite and shales; an alternance (4 cm) of claystones, clays and a dark indurated shale level (3 cm) with numerous well-preserved *Discosauriscus* remains of various sizes. From this layer, rare plant fragments and four slabs containing (sub)complete *Discosauriscus* – their taphonomy will be the subject of another article – were sampled. Above, a thin (0.5 cm) orange cinerite, sampled for absolute age investigations, is associated with crystallised gypsum and white to grey clay. It is topped by a dark indurate claystone (10 cm) rich in plant fragments, recovered in association with another possible cinerite layer (1 cm, also sampled). This plant layer is topped by an alternance of clay (1 cm) with crystallised gypsum, paper shale layers (5 cm), then a darker thin claystone layer (4 cm) with numerous actinopterygian remains. Above this "fish"-layer, numerous specimens of *Discosauriscus* have been found in a grey shale level (10 cm). They are exceptionally well-preserved and abundant, with several complete specimens exposed side by side (e.g. Steyer *et al.* 2012, 2022; Houée *et al.* 2022a; Logghe *et al.* 2023a). The material described here comes from this layer. It has been recovered in association with an

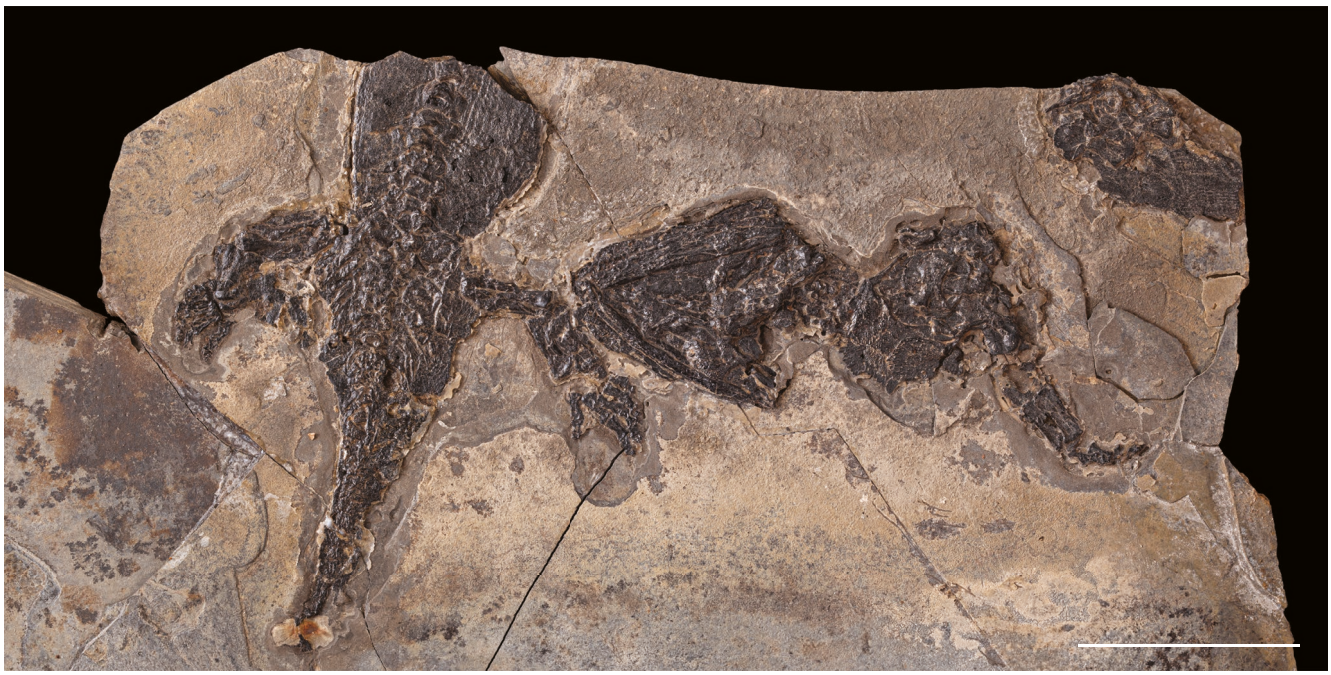

Fig. 3. — New specimen (RH-FR-2022-02) of *Discosauriscus* sp. from the Permian of Franchesse, preserving dermal soft-tissues: posterior body region (**left**), and anterior body region (**right**) of a probable unique individual. Scale bar: 5 cm. Credits: Lilian Cazes (CR2P).

orange dusty layer, possibly another cinerite (2 cm), sampled as well to precise its nature and run absolute dating analyses. Above was observed a grey-yellowish claystone (17 cm) with mostly well-preserved actinopterygians, rare chondrichthyan spines and some large and sub-complete *Discosauriscus* at the base. Finally, this layer is topped by dark and weathered claystones (20 cm) with isolated small *Discosauriscus* fragments and numerous more or less complete actinopterygians, and then the grass soil.

MATERIAL AND METHODS

We sampled four specimens of articulated *Discosauriscus* (RH-FR-2022-01, RH-FR-2022-02, RH-FR-2022-03 and RH-FR-2022-07; Figs 2; 3) whose soft tissues are preserved, including a specimen containing a cololite found *in situ* in the abdomen (RH-FR-2022-07; Fig. 2B). All these specimens were collected from the Permian of Franchesse (see the Geological Setting section for more details) and are part of the collections of the Rhinopolis Association, which aims to promote and preserve the palaeontological heritage of the Département de l'Allier (Allier county, France). All specimen images were taken using a Nikon D800 camera (apn full-frame 36 Mpx) with a lens Makro-Planar Zeiss 50 mm. For macro, we used a Canon 5DSR camera (apn full-frame 50Mpx) with a Canon MP-E65 mm lens mounted on micrometer rail and illuminated using cold light on fiber. The images were processed in Focus Stacking using Helicon Focus (v. 8.3.0). The images were taken and processed by Lilian Cazes (CR2P). The specimens are stored in the collections of the Rhinopolis Association in Varennes-sur-Allier (Allier, France).

IDENTIFICATION

Systematics

The studied specimens show an exquisite preservation of the soft tissues but a very poor preservation of the skeletal elements, especially those from the skull: this renders their systematic identification very difficult at the species level. The aim of this paper is not to give a detailed systematic palaeontological description of the whole skeletal elements. However, some skeletal elements allow an identification at the family and genus level:

1) all the specimens have relatively short trunks and stout limbs. RH-FR-2022-02 preserves at least 24 presacral vertebrae (Fig. 2C), and RH-FR-2022-01 small ribs at the level of the cervical vertebrae and a left foot with a phalangeal formula of 2-3-4-5-3 (Fig. 2A). Also, RH-FR-2022-03 shows swollen neural arches, large cylindrical pleurocentra, and haemal arches at the level of the tail (Fig. 3): these characters are often seen in Discosauriscidae (e.g. Klembara & Bartík 1999; Laurin 2010).

2) these specimens have relatively short snouts, rounded orbits lying anteriorly to the middle of the skull length, and a relatively high skull in the region of the otic notches when preserved: these characters are typical of the genus *Discosauriscus*, e.g. Klembara 1997. Unfortunately, as mentioned above, the peculiar preservation of these specimens does not allow to identify the species: pending a more thorough systematic study of the whole material of Franchesse (composed of hundreds of specimens), we therefore prefer to stay prudent and to refer the studied specimens as to *Discosauriscus* sp. This identification is consistent with that of Steyer *et al.* (2012, 2022).

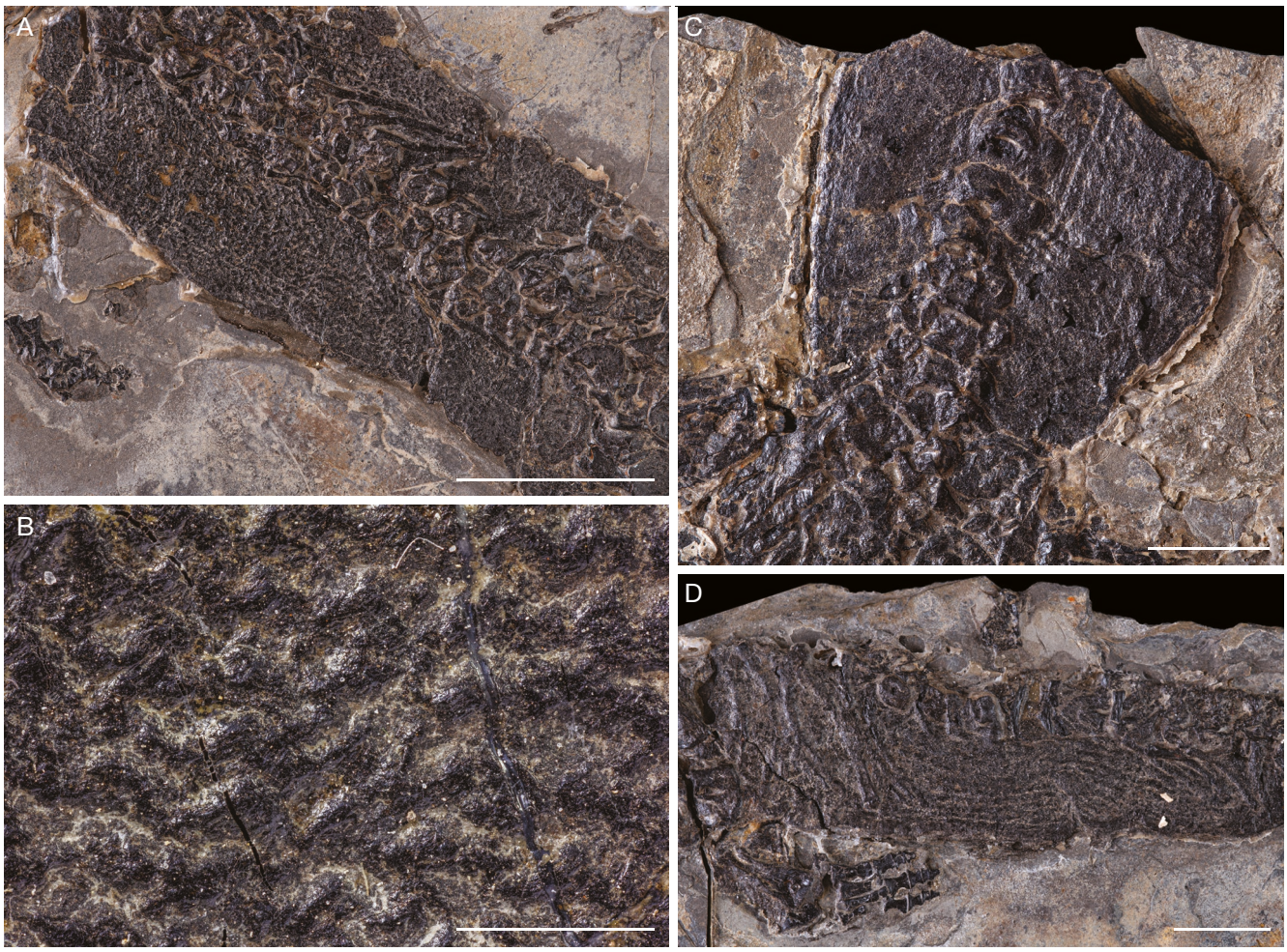

Fig. 4. — Close-ups on dermal soft-tissues of *Discosauriscus* sp. specimens from the Permian of Franchesse: **A**, RH-FR-2022-01, showing arrangement in longitudinal and transversal rows; **B**, macrophotography of the scales of RH-FR-2022-01 showing the triangular (to quadrangular in some regions) shape of the scales. The arrangement in longitudinal and transversal rows is well visible here; **C**, RH-FR-2022-02, showing a similar arrangement of the scales as in the other specimens, preserving however a more quadrangular shape of the scales; **D**, RH-FR-2022-03, showing the longitudinal and transversal arrangement of the scales. The rows seem less straight than those in RH-FR-2022-01 but display a more 'wavy' arrangement alongside the body. Scale bars: A, D, 2 cm; B, 2 mm; C, 1 cm. Credits: Lilian Cazes (CR2P).

Growth stage

The high ossification degree of the preserved long bones, ribs and vertebrae; the well-developed ornamentation pattern of the dermal bones; the fact that the orbits are relatively anteriorly located within the skull; the relatively long postorbital region; and the robust mandibles preserving well-developed teeth are typical for a late juvenile ontogenetic stage (Klembara 1997; Steyer 2000; Sanchez *et al.* 2008). However, according to Klembara (2009) who distinguished ontogenetic stages based on skull length only, these specimens might be younger in somatic age. Considering all the characters together, we prefer to stay prudent and to give an "average" juvenile age for the studied specimens.

DESCRIPTION OF THE SOFT TISSUES

Putative epidermal scales (Figs 4, 5)

Several rows of scales are well-preserved on RH-FR-2022-01 (Fig. 4A, B). These scales seem to be positioned on the flanks and/or dorsal side of the specimen as they do not appear to be below the vertebral column but rather constrained around it. These scaly skin remains are mostly preserved on the body region of the other *Discosauriscus* skeletons, and less detailed skin remains are visible around the tails. Skin remains from the shoulder girdles and pelvic regions are seldomly visible (see RH-FR-2022-03; Fig. 4C), and overall appear smoother than in the thoracic region, and deprived of scales. These skin remains present a blackish coloration, consistent with that of the rest of the skeleton and with other tetrapod skin remains recovered from the Franchesse locality, and contrasting with the grey colour of the substrate. They are preserved in thee-dimensions (Fig. 4B), and are therefore not the result of the impression of the skin on the substrate. The scales are mostly triangular (Fig. 4B), although some seem rather quadrangular (Fig. 4C). They measure between 1 and 1.5-1.7 mm. No concentric rings seem to be preserved within the scales. However, they seem to preserve ridges, that follow the overall shape of the scales (Fig. 5A). Some kind of tubercule-like ornamentation is also seen on some scales, however without definite

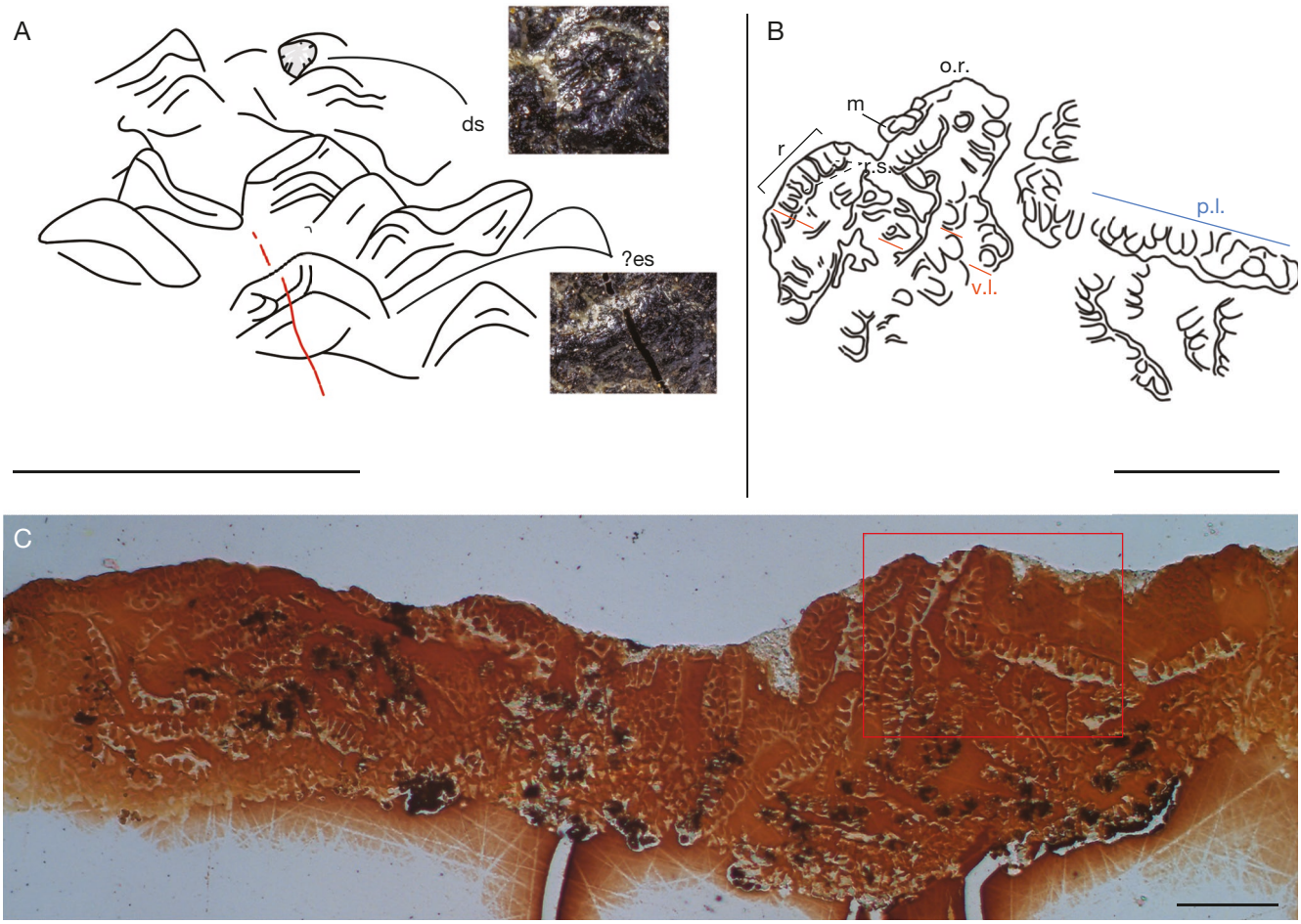

FIG. 5. — **A**, Drawing of section of the skin remains of specimen RH-FR-2022-01 showing both dermal (**ds**) and putative epidermal scales (**es**). The putative epidermal scalation present a more triangular to quadrangular shape. They display structural differences with dermal scales: absence of concentric rings and swollen margins, presence of ridges and ornamentations; **B**, drawing of part of the thin section of the skin remains of specimen RH-FR-2022-02; **C**, thin section of part of the skin remains of specimen RH-FR-2022-02 through optical microscopy. **Red square** indicates the zone of interest drawn in **B**. Abbreviations: **m**, membrane; **o.r.**, outer rim; **p.l.**, perpendicular layer compared to the outer rim outline; **r**, row; **r.s.**, round structure; **v.l.**, vertical layer compared to the outer rim outline. Scale bars: 100 µm. Credits: Antoine Logghe.

shape (Fig. 5A). They are closely arranged in longitudinal and transversal rows and seem to overlap ventro-dorsally. Almost no interstitial space is visible between the scales (this is especially the case on RH-FR-2022-01; Fig. 4A). No scales nor skin remains are observable near the skull and limb regions (see Figs 2; 3; 4D).

A preliminary thin section of 15 µm of the skin remains of specimen RH-FR-2022-02 have been performed (Fig. 5B). The skin remains present an orange colouration in optical microscopy. The thickness of the skin varies from between 200 and 300 µm depending on the local preservation. Several layers of round to rectangular structures can be observed, either perpendicular or parallel to the skin outer rim. Each of the structures seem to be surrounded by whitish contour. These layers are not observed in different quantity and orientation depending on the local preservation. These round to quadrangular structures measure around 10 µm. They are completely different from spindle-shape lacunae and canaliculi in their close arrangement to one another and in rows forming several distinct layers. No fibres or circumferential growth marks can be observed.

COLOLITE (Fig. 6)

In addition to the skin preservation, RH-FR-2022-07 also preserves part of its intestines in three-dimensions (Fig. 6). This cololite, more precisely an intestinelite *sensu* Hunt & Lucas (2012) as it is preserved inside the body cavity of the producer, has a shiny texture compared to the surrounding blackish scaly skin. This cololite is preserved in two parts separated by around 1 cm: we named them cololite A and cololite B (see Fig. 6) for the following description.

Cololite A is elongated and tubular. Its distal-most part forms a "turn", being oriented laterally, roughly perpendicular to the length of the specimen, in contrast to the proximal part, oriented anterioposteriorly. This cololite is positioned at the posterior end of the body in the pelvic region and seems to exhibit minimal deformation and/or displacement. Its distal part is preserved in three dimensions, while the proximal part is not. Still, the morphology of the intestine is visible, and can be taken into consideration in the following measurements. Cololite A has a length of approximately 12.6 mm and a maximum width of 2.9 mm. Its surface is smooth, with blackish inclusions visible.

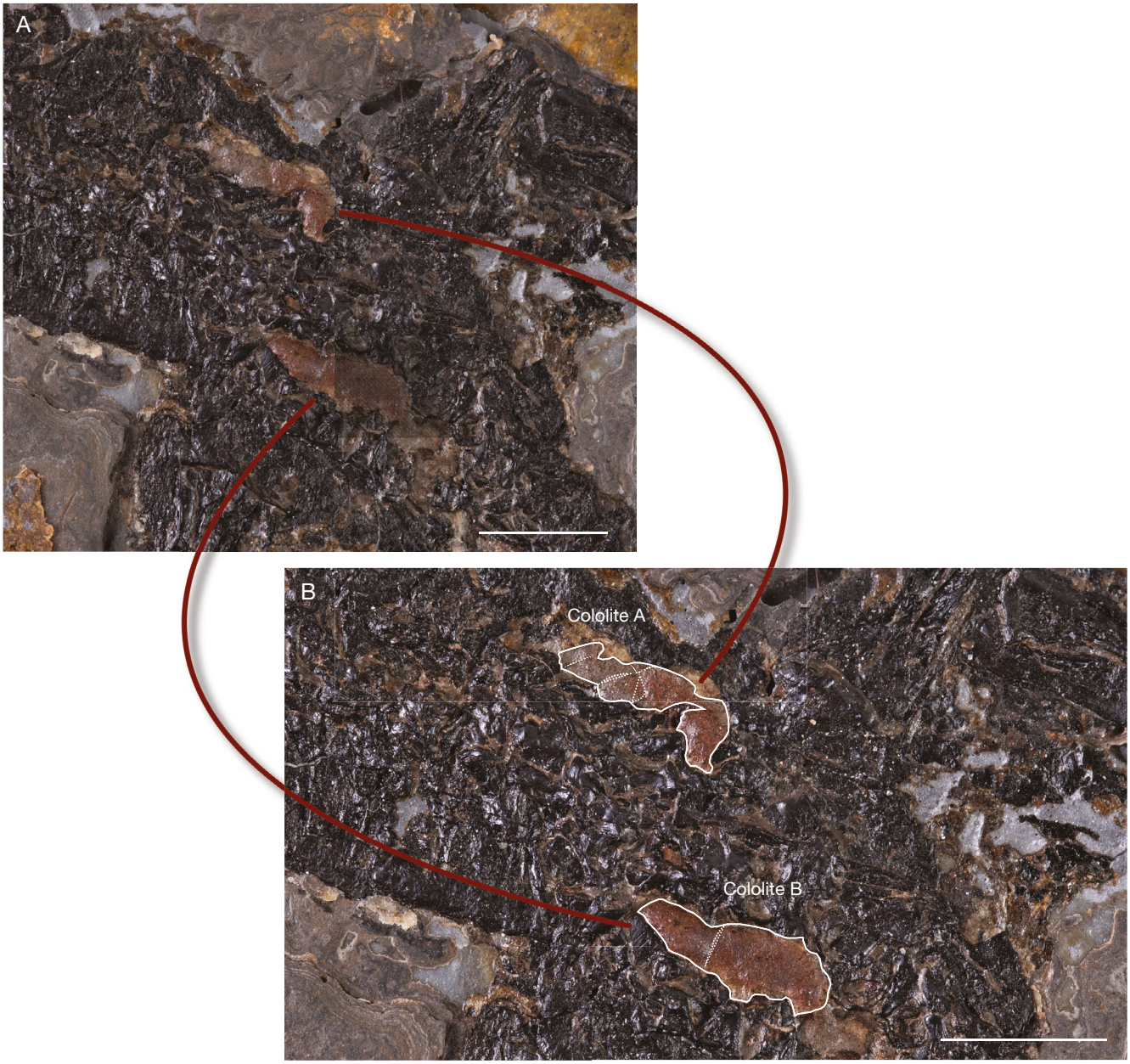

FIG. 6. — Close-ups on the pelvic region of RH-FR-2022-07 preserving *in situ* molds of the intestines: **A**, photography; **B**, with superimposed interpretative drawings. Scale bars: 1 cm. Credits: Lilian Cazes (CR2P).

Cololite B is elongated, tubular, oriented anterioposteriorly to the body, and preserved in three dimensions. It is positioned in the pelvic region, distally to cololite A. It seems to exhibit minimal deformation and/or displacement. It has a length of approximately 12.3 mm and a maximum width of 3.7 mm. No coil can be distinguished but a pinch (a narrower portion) is visible (Fig. 6). Its surface is smooth, with blackish inclusions also visible.

DISCUSSION

SKIN SOFT-TISSUE PRESERVATION

Scales have been described from numerous discosauriscid seymouriamorphs (e.g. Špinar 1952; Klembara & Meszároš 1992; Klembara & Bartík 1999). The most comprehensive description of *Discosauriscus* scales was made by Špinar (1952), who found scales to cover the whole body, including the tail and the limbs, contrasting with the lack of skin remains around the limb regions in the Franchesse specimens. Špinar (1952) described the scales of *Discosauriscus* as forming sheets of thin, oval or rounded structures with concentric rings, both on the ventral and dorsal surfaces of the body. Klembara & Bartík (1999) provided detailed drawings of the scale pattern related to the skeletal region of *Discosauriscus* from the Lower Permian of the Boskovice Furrow (Czech Republic). These scales were recovered from the ventral surface of the body, mainly from the pectoral and pelvic regions. The scales observed on the Franchesse specimens do not display an oval shape with

TABLE 1. — Summary of the occurrences of epidermal scales recovered in the Carboniferous and Permian fossil record, in body fossils (**BF**) and ichnofossils (**IF**).

Taxons	Shape	Arrangement	Overlapping	Fossil type	Age	Reference
Lepospondyli von Zittel, 1887 cf. Diplocaulidae Cope, 1881	Quadrangular	Longitudinal rows	Yes	IF	Asselian – Oberhof Formation (Thurigian Forest Basin)	Walter & Werneburg 1988
Seymouriamorpha Watson, 1917 Discosauriscidae Romer, 1947	Triangular-quadrangular	Longitudinal-transversal rows	Yes	BF	Early Permian – Renière Formation (Bourbon-l'Archambault Basin)	This paper
Diadectomorpha Watson, 1917 cf. Diadectidae Cope, 1880	Quadrangular	Longitudinal-transversal rows	No	IF	Asselian – Slupiec Formation (Intra-Sudetic Basin)	Voigt *et al.* 2024
Synapsida Osborn, 1903 cf. Sphenacodontidae Marsh, 1878	Rhomboidal-rectangular	Longitudinal-transversal rows	Yes	IF	Asselian – Tambach Formation (Thuringian Forest Basin)	Pabst 1908; Haubold 1972
Varanopidae Romer & Price, 1940	Rectangular elongated	Apparent. transversal rows	Yes	BF	Sakmarian – Leukersdorf Formation (Chemnitz Basin)	Spindler *et al.* 2018
Parareptilia Lawrence, 1868 cf. Bolosauridae Cope, 1878	Rhomboidal-rectangular	Longitudinal-transversal rows	Yes	IF	Asselian – Goldlauteur Formation (Thurigian Forest Basin)	Haubold 1972; Martens 1991; Marchetti *et al.* 2025
Captorhinomorpha Watson, 1917 Captorhinidae Case, 1911	Ovoid elongated	Non-polarised tuberculate scales (pebbled structures)	No	BF	Artinskian – Richard Spurs Cave System	Mooney *et al.* 2024

concentric ring structures and with swollen margins, such as recovered from most of the lower Permian material of Czech Republic (see Klembara & Meszároš 1992: fig. 11; Klembara & Bartík 1999: fig. 16A). This type of scales has been associated to bony dermal scales as seen in temnospondyls (e.g. Witzmann 2007 and references therein). At least one "true" dermal scale was recovered within the skin remains of the Franchesse specimens (see Fig. 5).

The putative epidermal scales described here from the Franchesse specimens appear rather triangular to rectangular, forming longitudinal and transversal rows and closely patched (i.e., without interstice between them) (Fig. 5). Thus, they overall organization of scales within the scale patches is somewhat reminiscent with that figured by Klembara & Bartík (1999: fig. 16F). However, these authors do not provide information on the extension of these scale remains which seem to be mostly patches attached to the interclavicle and pubis. In the specimens of Franchesse, these scales probably covered the side and dorsal parts of the thoracic region, thus differing from the ventral ones described by Klembara & Bartík (1999). These small and rectangular scales of *Discosauriscus* from Franchesse also differ from the chevron-like pattern of the thin and elongated (dermal) gastral scales seen on the other seymouriamorph *Utegenia* Kuznetsov & Ivakhnenko, 1981, from the Permo-Carboniferous of Kazakhstan (Laurin 1996; Klembara & Ruta 2003). The absence of such arranged scalation in *Discosauriscus* suggests the absence of gastralia within this genus, as proposed by Laurin (1996).

The histology of the skin remains of the *Discosauriscus* of Franchesse also highly differs from that of dermal scales observed in other Palaeozoic tetrapods (e.g. Dias & Richter 2002; Witzmann 2011). The presence of aligned cell-like structures and their arrangement are forming a sort of pseudoepithelium, which is not compatible with typical bone tissue structure. The absence of growth lines and spindle-shaped lacunae (osteocyte lacunae) is unlike what is observed in the bone tissues of *Discosauriscus* (Sanchez *et al.* 2008). The absence of fibres (Sharpey's fibres or interwoven structural fibres) is inconsistent with a bony dermal element (e.g. dermal scales such as gastralias) or osteoderm. On the contrary, the presence of round to quadrangular structures arranged in rows and forming layers can be reminiscent of cells forming the epidermal layers of the skin of tetrapods (e.g. Alibardi 2003; Alibardi *et al.* 2009). More thin sections and detail descriptions of the inner-pattern of the skin remains of the *Discosauriscus* of Franchesse are needed to thoroughly assess with certainty if we observe an alignment of cells forming an epithelium (which would represent of very rare care of fossil preservation, especially regarding Palaeozoic tetrapods) further test comparisons with the epidermal skin pattern of extant tetrapods (both amniote and amphibians).

The scaly skin external and internal morphologies of the Franchesse material is therefore inconsistent with bony dermal scales. This would then be the first description of epidermal scales in seymouriamorphs. It has indeed only been mentioned (as skin soft-tissues) in a recent report focused on the larval specimens from the lower Permian historic Malá Lhota locality, Czech Republic (Calábková *et al.* 2024). In the Franchesse specimens, the skin is not solely the result of the impression of the integument on the substrate as regularly observed in temnospondyls, such as dissorophoids (e.g. Werneburg 2019, 2021), although many dermal scales recovered within these skin remains are preserved as true body fossils, allowing palaeohistological studies (see Witzmann 2011). Motifs and scale-like structuration (i.e., tubercules, scales), have been observed on these skin remains whose dermal or epidermal origin have yet to be determined (e.g. Fritsch 1879; Werneburg 2007, 2019, 2021). In other non-amniote tetrapods, similar scale pattern was recovered in the ichnofossil record, with a body impression attributed to the diplocaulid lepospondyl amphibian *Hermundurichnus fornicates* (Walter & Werneburg, 1988; Asselian of Germany). This body impression displays non-overlapping, rectangular scale impressions arranged in longitudinal rows. These scaly impressions have

TABLE 2. — Occurrences of vertebrate groups from the main Permian fossil deposits of the northern Massif Central. Data computed from the Rhinopolis Association collections and Steyer *et al.* 2012 for Franchesse; the Muséum national d'Histoire naturelle catalogue of the Heyler material of the Massif Central studied from 1955 to 1995 and Štamberg & Steyer 2021 for the La Queue-de-l'Étang locality (https://science.mnhn.fr/catalogue/pal-raof-poiss-massifcentralheyler/); the Rhinopolis Association collections for the Buxières-les-Mines locality; the Muséum national d'Histoire naturelle catalogue of the fossil fishes of the Permian of Autun (https://science.mnhn.fr/catalogue/pal-poiss-raof-autun/), Štamberg & Steyer 2021 and Falconnet 2014 for the Autun Basin.

Locality	Actinopterygians	Acanthodians	Chondrichtyans	Temnospondyls	Seymouriamorphs	Amniotes
Franchesse	50	6	5	3	140	0
La Queue-de-l'Étang	520	300	55	20	5	0
Buxières-les-Mines	420	80	450	190	0	0
Autun	1000	50	120	150	0	5

been attributed to epidermal scales because of their position on the external part of the skin (contra dermal scales which are embedded in the dermis). Further analyses on these soft tissue remains of *Discosauriscus* from Franchesse are needed to confirm their attribution as epidermal scales. However, the recovery of a scaly skin pattern similar to that of other non-amniote tetrapods from the early Permian and attributed to epidermal scales is consistent with the appearance of such scalation in Palaeozoic non-amniote tetrapods, as also suggested by a scaly body impression of a diadectomorph from the lower Permian Słupiec Formation of the Czech-Polish Intra-Sudetic Basin (Voigt *et al.* 2024).

The scales of *Discosauriscus* from Franchesse also differ from the elongated scales of the early Permian varanopid amniote *Ascendonanus* of Chemnitz, but both present overlap (Spindler *et al.* 2018). This overlapping triangular pattern of the scales in the *Discosauriscus*-specimens from Franchesse and their possible epidermal origin, has never been observed in the Permian fossil record so far. The overall morphology of this presumed epidermal scalation, pending more in-depth investigations in cross sections, especially regarding overlapping, is more reminiscent of the scalation seen in early amniotes, especially reptiles, rather than amphibians (Table 1) (Alibardi 2003). Such epidermal scales in seymouriamorphs could have served as protection against mechanical abrasion, when dwelling on land, and therefore represent a higher adaptation to terrestrial environments (Alibardi 2003). They could also have served as protection against predatory attacks.

Implications for the cololite

The recovery of cololites is rare in the fossil record (Hunt & Lucas 2021). Only two specimens of cololites preserved in *Discosauriscus* were published until now, from the lower Permian of the Boskovice Furrow, Czech Republic (Klembara & Meszároš 1992): the remains of another *Discosauriscus* within the "coprolite" of one of the specimens led to a discussion on cannibalism within discosauriscids. Specimen RH-FR-2022-07 from Franchesse presents parts of its intestines, fossilised *in situ*, within its body cavity. We hypothesize that this intestinelite was previously a single complete section of the gastrointestinal tract, posterior to the stomach, which got partly eroded, thus creating this gap between the two parts. The "turn", observable on the distalmost part of "Cololite A" also aligns with the hypothesis of a connection between the two isolated fragments. Its shape closely resembles the morphology and arrangement of an intestinal cast documented from a small Carboniferous temnospondyl (Milner 1982), suggesting comparable gastrointestinal configuration.

The studied cololite morphology is elongated, tubular and no spiral valve can be observed, which corroborates studies arguing that a spiral or scroll valve in the posterior part of the intestine is a plesiomorphic feature shared only amongst chondrichthyans (including most acanthodians), non-teleostean actinopterygians, non-tetrapod sarcopterygians and likely placoderms (McAllister 1987; Argyriou *et al.* 2016; Trinajstic *et al.* 2022). Hence, non-spiralled coprolites found at the Franchesse locality can be attributed to *Discosauriscus* based on its gastrointestinal tract morphology. Blackish inclusions are visible on the surface of both cololites (A and B). A more in-depth study on the internal content of these cololites could reveal their nature and therefore bring more data on the feeding strategy and palaeoecology of *Discosauriscus*.

Palaeoenvironment of Franchesse

More than 40 fossils of seymouriamorphs, in addition to dozens of actinopterygians and chondrichthyans, were recovered during the excavations of 2021, 2022 and 2024 (see Houée *et al.* 2022a, b; Steyer *et al.* 2022; Fig. 7). Almost 150 specimens (including disarticulated remains) of seymouriamorphs have been recovered since the first excavations and stored in the collections of the Rhinopolis Association in Varennes-sur-Allier and the Musée des Confluences in Lyon, France (Table 2). Well-preserved skin has already been recovered from Franchesse in an eryopoid temnospondyl (Steyer *et al.* 2012; Logghe *et al.* 2023b) whose skin structure is currently under study by two of us (A.L. and J.-S.S.). The actinopterygian fauna is currently under description by one of us (S.Š.). The first observations seem to indicate the presence of at least one species of Aeduellidae in Franchesse, close to the genus *Neslovicella,* currently known from the Permian of the Czech Republic and from the Weissig Basin in Germany (Štamberg 2010, 2020; Steyer *et al.* 2022). This, along with the recovery of *Discosauriscus* from both the Bourbon-l'Archambault and the Czech Republic basins (Klembara 1997; Steyer *et al.* 1998; Klembara & Mikudíková 2019; Klembara *et al.* 2020) suggests similarities in palaeoenvironments.

The main palaeoevironnment of the Permian fossil deposits of the non-marine basins of the Massif Central is that of a freshwater lake (although marine influence have been suggested based on the presence of some taxa such as xenacanthid sharks, see Schultze & Soler-Gijón 2004; Schultze

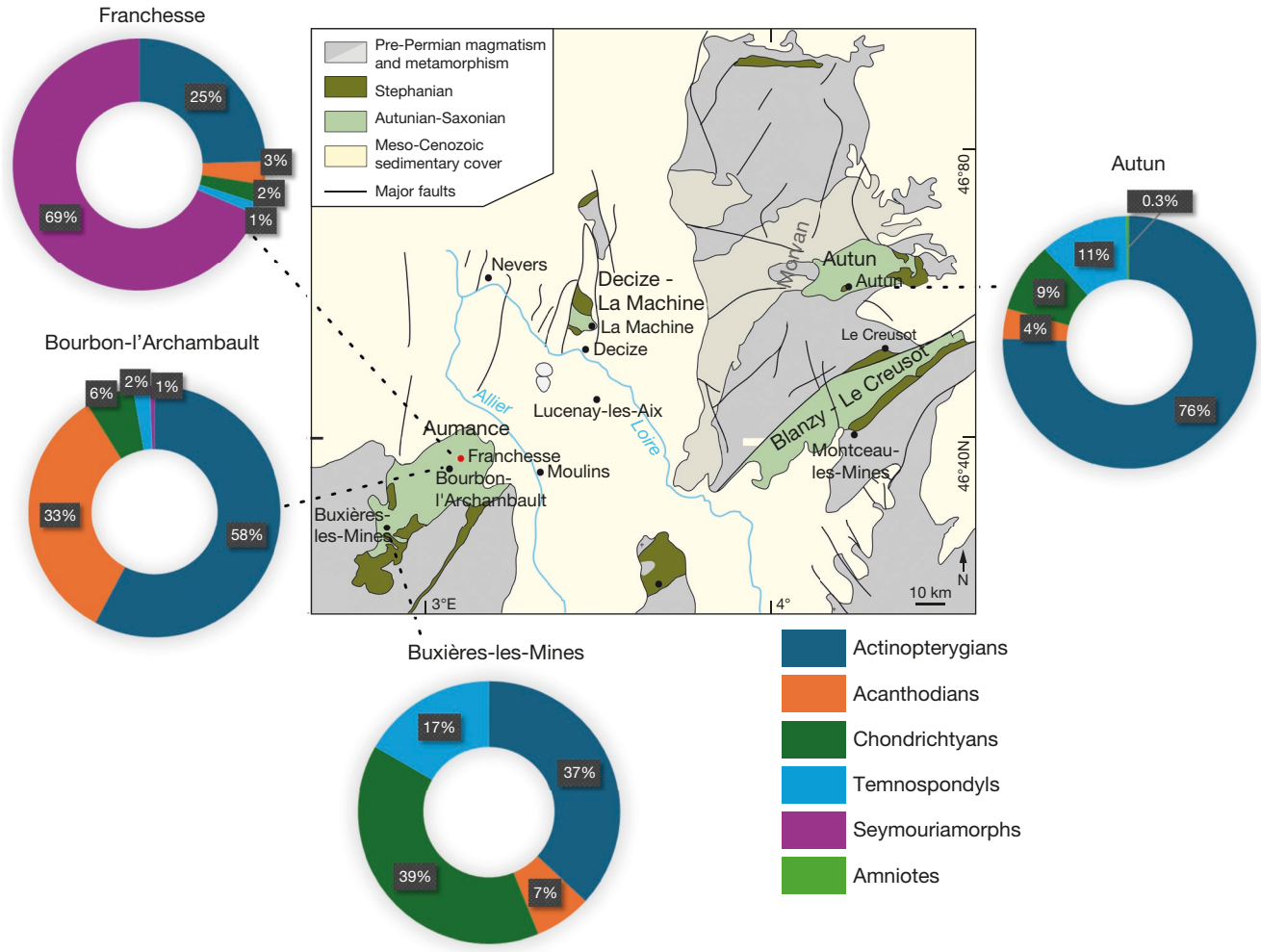

FIG. 7. — Map of the main Permian fossil localities of the northern Massif Central with occurrences of vertebrate remains, computed from Table 1 (and see references in table captions for diagrams). Geological map of the northeastern Massif Central modified from Elass-Damon 1977; Mercuzot *et al.* 2022.

2009; Laurin 2024; hypothesis challenged by Luccisano *et al.* 2023). More precisely, the palaeoenvironnment of Franchesse is suspected to be that of a shallow lake, like in the La Queue-de-l'Étang (Bourbon-l'Archambault Basin) and other inferred palaeoenvironnments of the *Discosauriscus*-yielding sites of the Massif Central (Heyler 1969), Thuringia Forest, and Saar-Nahe basins of Germany (Werneburg 1989, 2001; Boy 2007), as well as the Krkonoše and Intra-Sudetic basins of the Czech Republic (Fritsch 1879; Klembara 1997; Klembara & Mikudíková 2019; Klembara *et al.* 2020), which are often attributed to shallow lacustrine palaeoenvironments. The fauna of La Queue-de-l'Étang (or Bourbon-l'Archambault) is composed of small branchiosaurid temnospondyls, discosauriscids, xenacanthiform and hybodont chondrichthyans, acanthodians, acrolepids (*Progyrolepis* Fritsch, 1895), numerous aeduellid and amblypterid actinoptergyians (de Saint-Seine 1949; Heyler 1969; Štamberg & Steyer 2021; Fig. 7). The fauna of Franchesse differs from the fossil deposits of Buxières-les-Mines (Bourbon-l'Archambault Basin) in which bigger sized tetrapods, such as eryopoids and large sized xenacanthiforme chondrichthyans have been recovered (Steyer *et al.* 2000; Werneburg 2003; Schultze & Soler-Gijón 2004; Štamberg 2018; Fig. 7). Even though no seymouriamorphs have been recovered in the Autun Basin so far (Fig. 7), the palaeoenvironments of the Franchesse and La Queue-de-l'Étang sites of the Bourbon-l'Archambault Basin would be closer to the marginal aquatic to swampy environment identified from the Muse OSB (Heyler 1969; Luccisano *et al.* 2021, 2022) than the open and deep lake palaeoenvironment suggested for the Buxières-les-Mines site (Bourbon-l'Archambault Basin) (Steyer *et al.* 2000; Luccisano *et al.* 2023).

Steyer *et al.* (2012) suggested that the mass mortality of the seymouriamorphs (and actinopterygians) recovered in the Les Charbonnières site of Franchesse could be due to a global flooding event of the Bourbon-l'Archambault Basin (Debriette 1992) or the temporary arrival of salty water. Here we suggest, based on the new data from the stratigraphic log, that the mass mortality recovered in Franchesse could also have been due to volcanic events in the Bourbon-l'Archambault Basin at that time, explaining why rich fossiliferous layers are found right above and below supposed cinerites. This could also favour the explanation for the exceptional preservation of the fossils from Franchesse, with the recovery of extremely rare soft tissue in the Palaeozoic tetrapod fossil record (Steyer *et al.*

2012; Logghe *et al.* 2023a, b). The late Carboniferous-early Permian Variscan Belt was indeed marked by an intense inter-plate volcanism (Neumann *et al.* 2004), identifiable from the Bourbon-l'Archambault Basin by the deposit of the early Asselian Buxières Formation correlated "Quartzite de Meillers", corresponding to a thick hydrothermal siliceous sinter and probably resulting from intense volcanic activity within the basin (Marcoux *et al.* 2004; Debriette & Legrand 2021).

CONCLUSION

The first recovery in *Discosauriscus* of three-dimensionally preserved scaly skin is very useful to better infer the palaeoecology of seymouriamorphs and evolution of the skin of late Palaeozoic tetrapods. The subtriangular, overlapping probable epidermal scales are reminiscent of amniote, especially reptile, scalation. This preliminary histological description of the skin of *Discosauricus* from Franchesse provides the first possible inner-structuration of the epidermis visible within Palaeozoic tetrapods. The inner-pattern described here resembles that of the epidermis of extant tetrapods, including reptiles. This could mean that *Discosauriscus* is more terrestrially-adapted than previously thought and suggests that sauropsid-like epidermal scalation appeared earlier, in stem-amniotes or stem-tetrapods, as suggested in recent investigations in epidermal scalation evolution in non-amniote tetrapods. Moreover, the discovery of the intestinelite showing parts of the *Discosauriscus* gastrointestinal tract, gives a unique insight into its arrangement and morphology, highlighting the exceptional preservation seen in Franchesse. It allows to attribute the non-spiralled coprolites found at Franchesse to *Discosauriscus* based on its gastrointestinal tract morphology. This can lead to a re-evaluation of discosauriscids as trace-makers of early Permian coprolites in other Variscan sites. Further three-dimensional scans of the cololite will help to know more about its inclusions and have an even more precise picture of the gut anatomy and diet of discosauriscid seymouriamorphs. The recovered cinerites will be investigated as to whether or not they can be dated with precision to verify their link with the late Carboniferous-early Permian Variscan inner-plate volcanism. This intense volcanism could be linked to the exceptional preservation of the soft tissues recovered in fossils of the Franchesse site.

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