An exceptional *Dimetropus* pes imprint with scalation pattern from the lower Permian of Lodève and its broader implications for early synapsid palaeobiogeography and skin evolution

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Dimetropus is one of the most widespread tetrapod ichnogenera of the Permian, known from several Cisuralian units of Euramerica and North Africa. Generally attributed to pelycosaur-grade synapsid trackmakers, two ichnospecies are currently considered valid: *D. leisnerianus* and *D. osageorum*. A revision of a well-preserved *Dimetropus* pes footprint from the lower Permian (upper Artinskian) Rabéjac Formation of the Lodève Basin highlights the first definitive presence of *D. osageorum* from the Variscan Belt. A synapomorphy-based track–trackmaker correlation suggests ophiacodontids, such as *Ophiacodon*, as potential tracemakers of *D. osageorum*. Therefore, this potentially extends the palaeobiogeographic distribution of ophiacodontids in the upper Cisuralian in both North American and European basins. Moreover, the presence of well-preserved epidermal scale imprints on the *D. osageorum* pes of Lodève precises the evolution of epidermal scalation in pelycosaur-grade synapsids and suggests the presence of both dermal and epidermal scales in ophiacodontids. This occurrence is time-equivalent with the Artinskian Warming Event, strengthening the scenario of epidermal scale evolution in light of palaeoclimatic changes in the Variscan Belt, from everwet-adapted biotas to seasonal drought-adapted biotas.

Key words: Ophiacodontidae, *Dimetropus osageorum*, epidermal scales, track-trackmaker correlation, Artinskian Warming Event.

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Introduction

The earliest diverging synapsids from the Permo-Carboniferous, hereafter called "pelycosaur-grade synapsids" for consistency with older literature (therein often called "pelycosaurs"; see Sumida 2025), are essential for understanding the evolution of early terrestrial clades, representing one of the earliest groups of terrestrial amniotes (Bolton et al. 2025). They form a paraphyletic assemblage of stem-mammals that represent the earliest-diverging members of Synapsida Osborn, 1903 (Romer and Price 1940; Sumida 2025). The earliest members of synapsids appeared during the middle Pennsylvanian but their diversity drastically increased in the early Permian (Romer and Price 1940; Reisz 1980, 1986; Sumida 2025). They are represented by the Eothyrididae Romer & Price, 1940, and the Caseidae Williston, 1911, both forming the clade Caseasauria Williston, 1912, as well as the Varanopidae Romer & Price, 1940, the Ophiacodontidae Nopsca, 1923, and the two sailed-back clades Edaphosauridae Cope, 1882, and Sphenacodontidae Marsh, 1878, including the apex predators of the early Permian of northern Pangea. Recent studies have suggested reptilian affinities for varanopids (Ford and

Benson 2020; Buffa et al. 2024), although most subsequent analyses have once again recovered them as pelycosaur-grade synapsids (Benoit et al. 2021; Simões et al. 2022; Jenkins et al. 2025). Fossil discoveries in North and South America, Europe, Russia and South Africa (only Varanopidae for the latter) indicate a nearly global distribution of these early-derived synapsids (MacRae 1999; Angielczyk and Kammerer 2018; Sumida 2025 and references therein; Angielczyk et al. 2026). Pelycosaurian-grade synapsids exhibit a great morphological and ecological diversity (e.g., Canoville and Laurin 2010; Angielczyk and Kammerer 2018; Singh et al. 2024), from small insectivorous eothyridids to large herbivorous caseids, and predatory sphenacodontids (Romer and Price 1940; Berman et al. 2023; Sumida 2025). Their north American fossil record reveals the establishment of the first amniote-dominated food webs as early as the early Permian (~290 Ma) (Sumida 2025). In Europe, terrestrial food webs were mostly dominated by temnospondyls (e.g., Buxières-les-Mines; Steyer et al. 2000; Luccisano et al. 2023), with few small-sized pelycosaur-grade synapsids (e.g., Falconnet 2014; Berman et al. 2020). In one case, the ecosystem was dominated by herbivorous diadectids (Berman et al. 2023). Moreover, several key anatomical and ecological innovations, including herbivory, heterodont dentition, and even parental, social, or aggregation behaviours (Jasinoski and Abdala 2017; Smith et al. 2021; Marchetti et al. 2025a), first appeared within early synapsids, foreshadowing the evolutionary trends that would later culminate in mammals (Reisz 1986; Brocklehurst et al. 2016; Mann and Paterson 2019; Bolton et al. 2025; Sumida 2025).

The ichnofossil record of late Palaeozoic tetrapods is crucial to get further insights into their palaeoecology and behaviour. The tetrapod fossil record of pelycosaur-grade synapsids reflects the abundance seen in trace fossil occurrences, both in the Carboniferous (Lucas 2022; Lucas et al. 2022; Lucas and Stimson 2025) and Permian (Lucas 2018; Marchetti et al. 2025b). The most abundant track associated with early-diverging synapsid trackmakers is the ichnogenus *Dimetropus* Romer & Price, 1940, recovered from Pennsylvanian and Cisuralian strata (see Marchetti et al. 2025b, and references therein). Precise synapomorphy-based track-trackmaker correlation helped us decipher the biostratigraphic and palaeobiogeographic range of the *Dimetropus* producers, as well as permitting inferences on locomotion (e.g., Hunt and Lucas 1998; Voigt 2005; Sacchi et al. 2014; Hopson 2015; Romano et al. 2016; Calábková et al. 2023). Furthermore, *Dimetropus* tracks and associated body impressions, *Bromackerichnus requiescens*, allowed precisions on the behaviour and soft tissue anatomy of sphenacodont synapsid producers (Marchetti et al. 2025a). So, trace fossils can be a reliable data source for the understanding of the early evolution of soft tissues in synapsids, which is scattered or non-existent in the body fossil record (e.g., Romer 1956; Reisz 1972).

Here we re-describe some *Dimetropus* specimens from the Rabéjac Formation of the Lodève Basin (southern Massif Central, France) which allow us to: (i) perform a thorough systematic assignment at the ichnospecies level based on well-preserved material; (ii) carry out a precise anatomy-based track-trackmaker correlation at the family level; (iii) evaluate the biostratigraphical range of the family producer in the Variscan Belt in comparison to that of North America; (iv) improve our knowledge regarding epidermal scale evolution in Palaeozoic synapsids; and (v) verify whether the acquisition of epidermal scales is related to the Carboniferous–Permian palaeoenvironmental and palaeoclimatic changes linked to the demise of the Late Palaeozoic Ice Age and the resulting global warming and aridification.

Institutional abbreviations.—ML, Musée de Lodève, Hérault, France; FMNH, Field Museum of Natural History, Chicago, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNG, Friedenstein Stiftung Gotha, Germany; MNHN, Muséum national d'Histoire naturelle, France; UR, University "La Sapienza" of Rome, Italy.

Geological setting

Geology and lithology of the Rabéjac Formation.—The Rabéjac Formation can be found on the whole East to West extent of the Lodève Basin (Odin 1986), in the south part of the Massif Central (Fig. 1). It is composed of the St-Xist (deltaic conglomerates), Rabéjac and Lafont facies (Odin 1986). The Rabéjac Formation, 280 m thick, starts with a thick conglomeratic deposit (Gand et al. 2003; Schneider et al. 2006). This layer is overlain by alluvial red beds that correspond to the majority of the formation sedimentation. The top of the Rabéjac Formation is composed of alluvial sandstones, progressively transgressing into red bed siltstones, characteristic of the playa environments of the overlying Salagou and La Lieude formations (Lopez et al. 2008).

Sedimentation marks have been described from the Rabéjac Formation, such as the dendritic surge mark '*Dendrophycus*' (Heyler & Gand, 2000) as well as raindrops and current marks (Heyler and Gand 2000).

The age of the Rabéjac Formation is well constrained, with a tuff bed (N°III of Michel et al. 2015) from the lower part of the underlying Viala Formation dated to 290.96 ±0.19 Ma with $^{206}Pb/^{238}U$ (therefore approximately at the base of the Artinskian). Several tuff beds from the lower part of the overlying Octon Member (150 m above the upper boundary of the Rabéjac Formation) of the Salagou Formation have been dated to respectively 284.40 ±0.13 Ma and 284.46 ±0.10 Ma with $^{206}Pb/^{238}U$ (Michel et al. 2015), corresponding to the uppermost Artinskian. The Rabéjac Formation has thus an age comprised between uppermost Sakmarian and uppermost Artinskian, but considering the deposition of the Viala Formation, the basal unconformity of the Rabéjac Formation and the deposition of the overlying Salagou Formation, it was likely upper but not uppermost Artinskian. Although

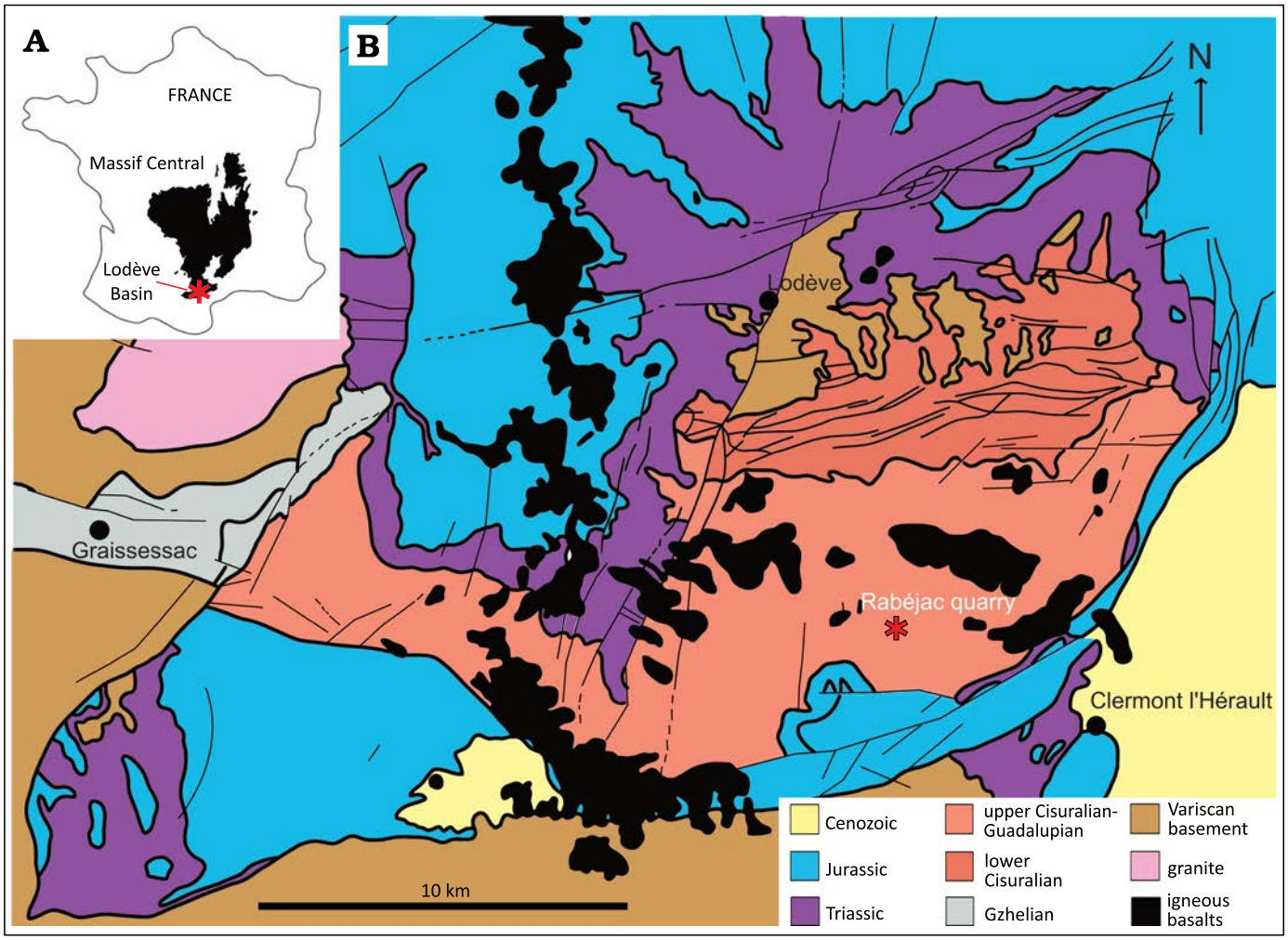

Fig. 1. Location (**A**) and geological map (**B**) of the Lodève Basin with the locality of the studied specimens (asterisk) (redrawn from Lopez et al. 2005).

tuff beds have been recognised from the Rabéjac Formation (Nmila et al. 1989), they have yet to be dated to propose a more precise absolute age of the formation.

Geomagnetic data suggested a global upper Cisuralian–lower Guadalupian age for the Rabéjac Formation: Sakmarian–Artinskian (Kruseman 1962; Maillol and Evans 1992) and Artinskian–Wordian (Mérabet and Guillaume 1988). Further constraints come from the tetrapod footprint record. Haubold and Lucas (2001) considered an upper Artinskian age for the Rabéjac Formation based on tetrapod footprints. This formation includes the base of the *Erpetopus* tetrapod footprint biochron, which is now considered late Artinskian–Kungurian (Voigt and Lucas 2018; Marchetti et al. 2025b). An upper Artinskian–Kungurian age has also been proposed based on the palaeofloral assemblage (Galtier and Broutin 2008). This is consistent with the upper but not uppermost Artinskian age from radiosiotopic ages.

Palaeontology of the Rabéjac Formation.—The Rabéjac Formation is the most fossil-rich Permian unit of the Lodève Basin, and preserves diverse plants, invertebrates, and tetrapod trace fossils (Schneider et al. 2006) which were recovered for the great part from the Rabéjac quarry (Fig. 1). Its palaeoflora, including conifers (*Autunia*), callipterids (*Supaia*), and *Taeniopteris* leaves, shows lower diversity than the underlying formations, likely due to taphonomic biases (Galtier and Broutin 2008). Invertebrate traces include burrows (*Scoyenia*, *Beaconites*; Gand et al. 2003, 2004; Lopez et al. 2005), trackways (*Isopodichnus furcosus*, *Cruziana*, *Acripes*; Gand 1987, 1994; Gand et al. 2008), and abundant notostracan feeding/resting traces (*Rusophycus minutus*; Debriette and Gand 1990; Gand et al. 2008).

The palaeoichnofauna of the Rabéjac Formation was first described by Heyler and Lessertisseur (1963). The Rabéjac tetrapod ichnofauna forms the Association III of the Lodève Basin (Gand and Durand 2006) characteristic of deltaic palaeoenvironment (Odin 1986). It is one of the most diverse in the region and includes nine ichnogenera (Heyler and Lessertisseur 1963; Haubold 1971, 1973; Ellenberger 1983a, b; Gand 1987; Heyler and Gand 2000; Gand and Durand 2006; Marchetti et al. 2021b): *Batrachichnus*, attributed to small-sized temnospondyls or lepospondyls, including "microsaurs" (Voigt 2005; Petti et al. 2014; Allen et al. 2022; Marchetti et al. 2025b), *Limnopus*, attributed to large-sized temnospondyls such as eryopoids (Marchetti 2019; Marchetti et al. 2025b),

Table 1. Trace fossil measurements (in mm) of the *Dimetropus osageorum* from the Rabéjac Formation. FL, foot length; FW, foot width; I–V D, divarication (angle in degrees) of digits I–V; I–V L, digit I–V length; × , no measurement was possible.

	FL	FW	I L	II L	III L	IV L	V L	I–V D	FL	FW	I L	II L	III L	IV L	V L	I–V D
Specimen	manus								pes							
2001.1453.1	×	×	×	×	×	×	×	×	224.2	120.6	47.2	51.9	55.8	60.5	51.4	67.54
2001.1482.1	~101	>43.9	×	×	×	×	×	×	183.3	61.6	38.6	46.4	50.6	63.5	44.6	58.92

Dimetropus, attributed to pelycosaur-grade synapsids (Gand 1987; Haubold 2000; Voigt 2005; Marchetti et al. 2025b), *Tambachichnium*, attributed to varanodontine varanopids (Marchetti et al. 2021a, 2025b), *Erpetopus*, attributed to small "parareptiles" such as nyctiphrutetids and acleistorhinids (Marchetti et al. 2022b, 2025a), *Pachypes*, attributed to pareiasauromorphs (Marchetti et al. 202b, 2025b), *Notalacerta*, attributed to non-diapsid stem reptiles (Marchetti et al. 2020, 2025b), *Hyloidichnus*, attributed to captorhinids (Logghe et al. 2021; Matamales-Andreu et al. 2023; Marchetti et al. 2025b), and *Dromopus*, which upper Pennsylvanian–Guadalupian occurrences are attributed to araeoscelid diapsids and non-varanodontine varanopids (Marchetti et al. 2021a, 2025b). Key discoveries from the Rabéjac Formation include the first appearance of *Pachypes ollieri* (upper Artinskian; Marchetti et al. 2021b) and the introduction of the *Erpetopus* footprint biochron base (Voigt and Lucas 2018; Schneider et al. 2020). The Rabéjac Formation is thus a key unit for the understanding of the late Cisuralian reptile radiation in the footprint record (e.g., Marchetti et al. 2013, 2019b; Voigt and Lucas 2017) and the change of continental floras and faunas that is part of the Artinskian Warming Event (Marchetti et al. 2022a).

Material and methods

The specimens described in this study are housed in the Musée de Lodève (Hérault, France) (ML 2001.1453.1; 2001.1482.1; 2001.1483.1) and the Muséum national d'Histoire naturelle (Paris, France) (MNHN.F.LOD59). All track specimens were studied first-hand and photographed with adequate light conditions (artificial oblique light). The studied specimens were evaluated based on the preservation of their diagnostic features (e.g., Marchetti et al. 2019a). Photo series in full light were taken to obtain 3D models by using the photogrammetry technique (e.g., Mujal et al. 2020). Photographs were done using a Nikon D5300 and a Canon EOS 2000D (with a camera lens EFS-S 18–55 mm) digital cameras. The 3D models were built using the software Agisoft Metashape Professional (v. 2.1.3), and contour lines and colour depth maps were obtained using the software Cloud Compare (v. 2.7.0.) and ParaView (v.5.9.1.). The 3D models were uploaded to the digital repository MorphoSource (https://www.morphosource.org). The material was digitally measured with ImageJ2, and the measurements are reported in Table 1.

Systematic palaeontology

Ichnogenus *Dimetropus* Romer & Price, 1940

Type ichnospecies: *Dimetrodon berea* (Tilton, 1931); Waynesburg Formation, Cisuralian, west Virginia, USA.

Included ichnospecies: *Dimetropus leisnarianus* (Geinitz, 1863) and *Dimetropus osageorum* Sacchi et al., 2014. Sacchi et al. (2014) recognised five valid ichnospecies of *Dimetropus*: *D. leisnerianus*, *D. osageorum*, *D. berea* (Tilton, 1931), *D. salopensis* Haubold & Sarjeant, 1973, and *D. nicolasi* Gand & Haubold, 1984. Voigt (2005) synonymised *D. berea*, *D. salopensis* and *D. nicolasi*, with *D. leisnerianus*. Lucas et al. (2016) discussed the validity of *D. osageorum*, based on the similarity with the historical material of *D. berea* and concluded on the impossibility in deciphering *Dimetropus* ichnospecies (Voigt and Lucas 2015; Lucas et al. 2016).

Diagnosis (after Marchetti et al. 2025b, emended after Voigt 2005).—Plantigrade to semiplantigrade pentadactyl ectaxonic tracks of a quadruped. Large tracks (50–200 mm in length). Plantigrade pes significantly larger than the manus, with a fully impressed large sole extended proximally and laterally. Pedal digits relatively short compared with the palm/sole size. Digits end in thin and acuminate claw impressions, often bifurcated. Medial parts of digits from fully to non-impressed, resulting in paw-like impressions. Basal pads of the digits large, in an arcuate disposition, with evident hemispherical shape when visible. Manual digit proportions: I<II=V<III<IV. Pedal digit proportions: I<II≤V≤III≤IV. Total digit divergence low in the pes (about 50–70°). Trackway showing a simple pes-manus alternating arrangement pattern. Secondary overstep possible in case of lower pace angulation. Footprints are aligned to the trackway midline, with the pes slightly turned outwards in rare occasions.

Remarks.—Waiting for a comprehensive revision, we follow Voigt (2005) and Marchetti et al. (2025b), recognising only *D. leisnerianus* and *D. osageorum* as valid, considering the wide range of extramorphological variations of *Dimetropus* and the need of a comprehensive revision study (e.g., Gand 1987; Haubold et al. 1995; Hunt et al. 1995; Voigt and Lucas 2015).

Stratigraphic and geographic range.—Definite *Dimetropus* occurrences are known from Pennsylvanian and Cisuralian units (Marchetti et al. 2025a). It has been recovered from the USA (Arizona, Colorado, New Mexico, Oklahoma, Texas, West Virginia, Pennsylvania), Canada (Nova Scotia), Spain, France, Italy, Germany, Poland, Czech Republic, and Morocco. See Marchetti et al. (2025b) and Lucas and Stimson (2025) and references therein for complete bibliography of *Dimetropus* occurrences.

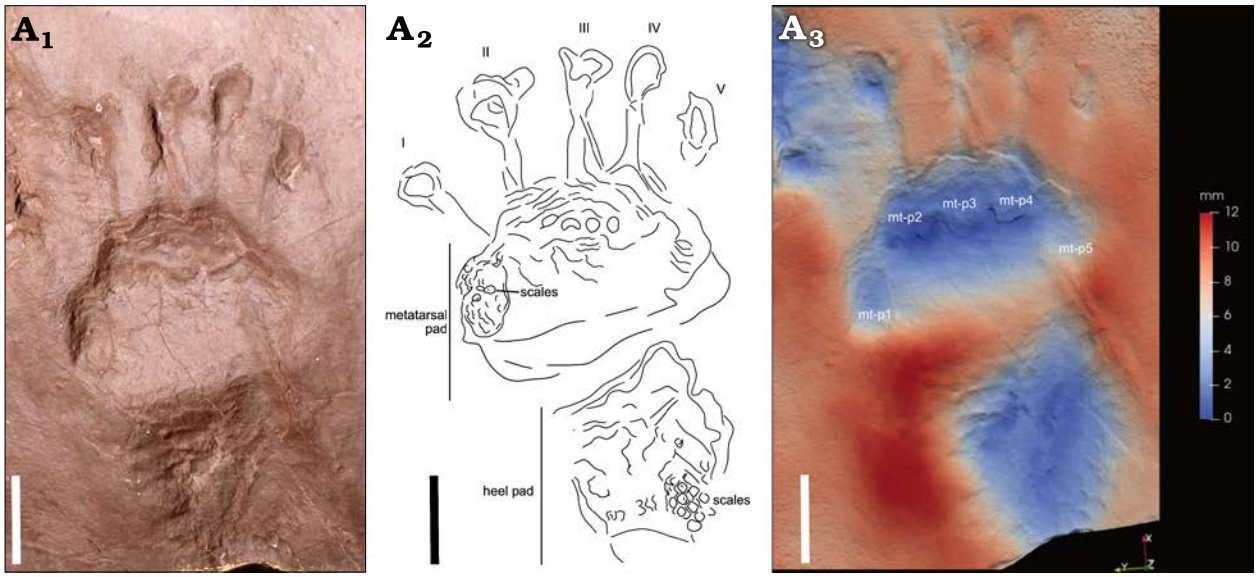

Fig. 2. Right pes of *Dimetropus osageorum* Sacchi et al., 2014 (ML 2001.1453.1, concave epirelief) from Rabéjac Formation, Lodève Basin, Rabéjac quarry, France; upper Artinskian (Permian). Exceptionally preserved skin folds and scale impressions on the digits, metatarsal and heel pads. Photograph (A_1), explanatory drawing (A_2), false-colour height map (A_3). I–V, digit numbers; mt-p1–5, metatarsal-phalangeal pads 1–5. Scale bars 40 mm.

Dimetropus osageorum Sacchi et al., 2014

Figs. 2–5; Table 1.

1983 '*Pseudanthropopus egregrius*'; Ellenberger 1983a: 557, pl. 1: 11.
1983 '*Pseudanthropopus insolitus*'; Ellenberger 1983a: 557, pl. 1: 12.
1987 *Dimetropus leisnerianus*; Gand 1987: 168, text-fig. 47H., pl. 6: c.
1987 *Dimetropus leisnerianus*; Gand 1987:168, text-fig. 47I.
2000 *Dimetropus leisnerianus*; Heyler and Gand 2000: 15, fig. 25.
2006 *Dimetropus leisnerianus*; Gand and Durand 2006:160, fig. 2D3.
2025 *Dimetropus* isp.; Marchetti et al. 2025a: 2755, supplementary figure S3.

Material.—ML 2001.1453.1 (Figs. 2–5), original specimen track of a right pes, concave epirelief; MNHN.F.LOD59 (Fig. $5A_2$), plaster cast of the track of a right pes, concave and convex hyporelief; 2001.1482.1 (Fig. $3A_1$), original specimen right manus-pes couple, concave epirelief; 2001.1483.1 (Fig. $3A_2$), counterpart of specimen 2001.1482.1, original specimen manus-pes-couple, convex hyporelief. All from Rabéjac Formation, Lodève Basin, Rabéjac quarry, France; upper Artinskian, Cisuralian (Permian).

Description.—Plantigrade, pentadactyl footprint of a quadrupedal tetrapod. The pes is 224.2 mm long and 100.5 mm wide. It is weakly ectaxonic (i.e., digit IV is the longest) and digits I and V are more proximal compared to digits II–IV (Figs. $2A_2$ and $3A_2$). Digit impressions are relatively short (I, 47.2 mm; II, 51.9 mm; III, 55.8 mm; IV, 60.5 mm; V, 51.4 mm) compared to the metatarsal pad (68 mm long) (Table 1). Digits present more or less the same length, with only a slight increase from digit I to IV. Digits II–IV are closely grouped, subparallel compared to each other, presenting a low divarication angle. They are not superimposed at their base. Digit I is the shortest. Digit V is slightly shorter than digit II. The divergence angle between digits I and V is about 67.54° (Table 1). Digits are straight, thin and end in enlarged impressions, sometimes bifurcated. The digits are more impressed proximally and distally, the metapodial-phalangeal pads of the pes (i.e., metatarsal-phalangeal pads) I to V are visible, especially I (Figs. $2A_2$ and $3A_2$). These pads are arranged along a symmetric semicircle, with metatarsal-phalangeal pads I and V positioned in a significant distal position compared to the digit bases than metatarsal-phalangeal pads II–IV (Figs. $2A_2$, $3A_2$, SOM: fig. 1; Supplementary Online Material available at http://app.pan.pl/SOM/app71-Logghe_etal_SOM.pdf). The metatarsal-phalangeal pads I and V are significantly larger than the metatarsal-phalangeal pads II–IV (Fig. $2A_2$). They also present an ovoid shape (Figs. $2A_2$ and $3A_2$), contrary to the circular shape of the metatarsal-phalangeal pads II–IV.

The sole is longer than wide. It consists of two parts, a metatarsal pad and a heel pad (Figs. $2A_2$ and $3A_2$). The metatarsal pad impression is ovoid, wider (68 mm) than long (61.6 mm). A large heel pad impression, longer (95.7 mm) than wide (30 mm) is visible posteriorly to the metatarsal pad impression. It is separated from it by a marked expulsion rim impression (~2 mm wide). The heel pad impression is more impressed medially. The sole imprint has a hourglass-shape: it is wider in its distal (middle of the metatarsal pad) and proximal (middle of the heel pad) parts and thinner to non-impressed in its middle part, between the two pads.

ML 2001.1482.1 (Fig. 3) preserves an incomplete manus imprint, at least 1/3 of the size of the pes footprint. The digit imprints are short and straight. As for the pes, they are thin. They are closely grouped and sub-parallel. They do not seem to be superimposed at their base. Only digits II to IV seem to be preserved. The manus is superimposed by the pes imprint, blurring anatomical features.

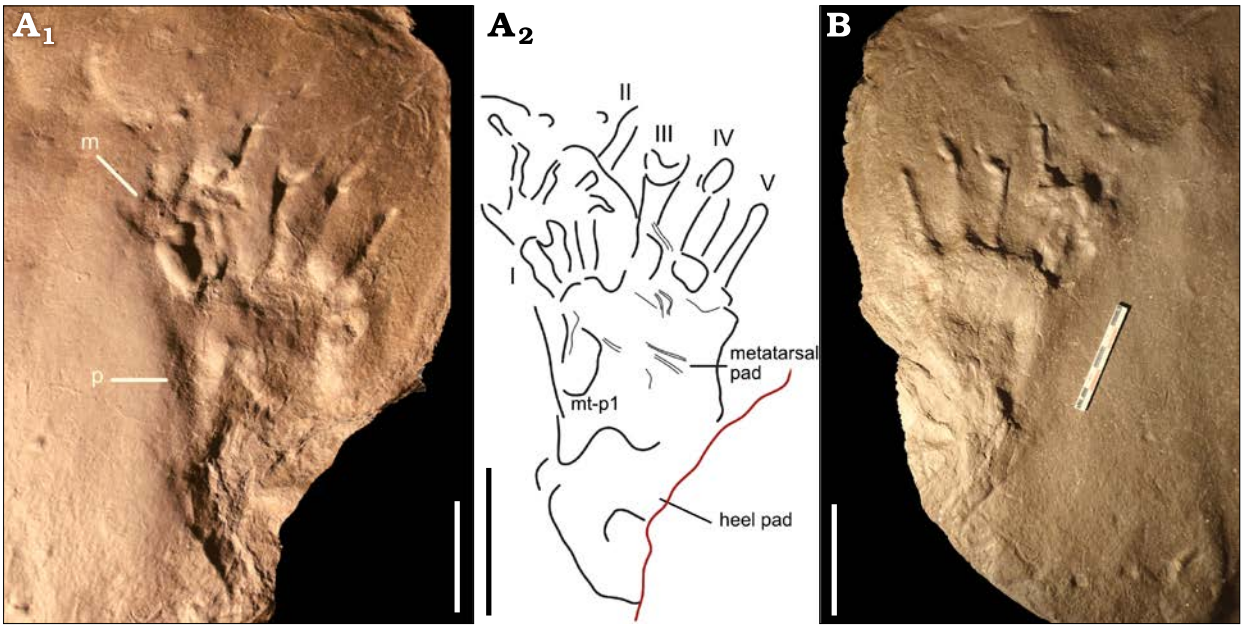

Fig. 3. Right manus-pes couple of cf. *Dimetropus osageorum* Sacchi et al., 2014, described as '*Pseudanthropopus insolitus*' Ellenberger, 1983, from Rabéjac Formation, Lodève Basin, Rabéjac quarry, France; upper Artinskian (Permian). **A**. ML 2001.1482.1, concave epirelief, photograph (A_1), explanatory drawing (A_2). **B**. ML2001.1483.1, counterpart of A, convex hyporelief. I–V, digit numbers; m, manus; mt-p1, metatarsal-phalangeal pad 1; p, pes. Scale bars 50 mm. Photos by Stéphane Fouché.

Scale impressions in ML 2001.1453.1 (Figs. $2A_2$, 4, 5) are present on the metatarsal pad, forming a small patch at the base of digits III and IV (Fig. 4), on the metatarsal-phalangeal pad I (Figs. $2A_2$ and 5), and on the proximal right part of the heel pad (Fig. $2A_2$). Scales on the metatarsal-phalangeal pad I and at the base of the digits are ovoid to circular, approx. 1 mm long. They do not appear evenly arranged. Skin creases are also present on the metatarsal impression, at the base of the digits in ML 2001.1453.1 and 2001.1482.1 (Fig. 4). Scales on the right part of the heel pad are hexagonal, approx. 2.5–5 mm long (Figs. $2A_2$, 5). They are especially visible on the plaster cast of the original specimen, MNHN.F.LOD.59 (Fig. $5A_2$). The hexagonal scales of the heel impression are more prominent and tightly arranged, in a bee-hive like configuration, and present thick margins of equivalent thickness. No ornamentation is visible on the scale impressions. In this way, the scales on the heel impression are larger than those present on the metatarsal impression. They are also organised in a specific configuration, contrary to the metatarsal scale impressions.

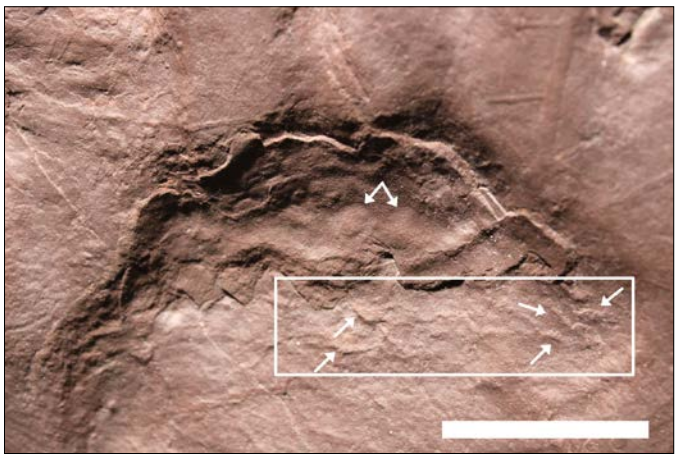

Fig. 4. Skin folds on the metatarsal pad of *Dimetropus osageorum* Sacchi et al., 2014, ML 2001.1453.1 (concave epirelief) from Rabéjac Formation, Lodève Basin, Rabéjac quarry, France; upper Artinskian (Permian). White rectangle highlighting the base of digits III–V, where skin creases are visible. Arrows point at the scale impressions. Scale bar 20 mm.

Remarks.—ML 2001.1453.1 was first figured by Ellenberger (1983a) as "*Pseudanthropopus egregerius*", then by Dutuit and Heyler (1985) as '*Feraequadigitipes parallelus*' in a popular science journal. Gand (1987) discarded these two ichnogenera as nomen nudum, as they did not have a diagnosis. Gand (1987) and Heyler and Gand (2000) referred this material to *Dimetropus leisnerianus*.

The material described here presents the following features that allow its attribution to *Dimetropus osageorum*: a pes weakly ectaxonic, the proportionally shorter digits compared to the sole impression, digits II–IV of about the same length, lacking the marked increase in digits I–IV (well-visible in "*Dimetropus salopensis*" material, here considered as synonym to *D. leisnerianus*) (Haubold and Sarjeant 1973) and a digit V shorter than digit II. Also, the symmetric semi-circle arrangement of the metatarsal-phalangeal pads is present, a key feature of *D. osageorum*. The only difference seems to be the thinner digit imprints in the Lodève material, but this is probably a taphonomic artifact, especially in the case of *Dimetropus* which can vary considerably the depth of impression of the middle part of digits (e.g., Voigt 2005).

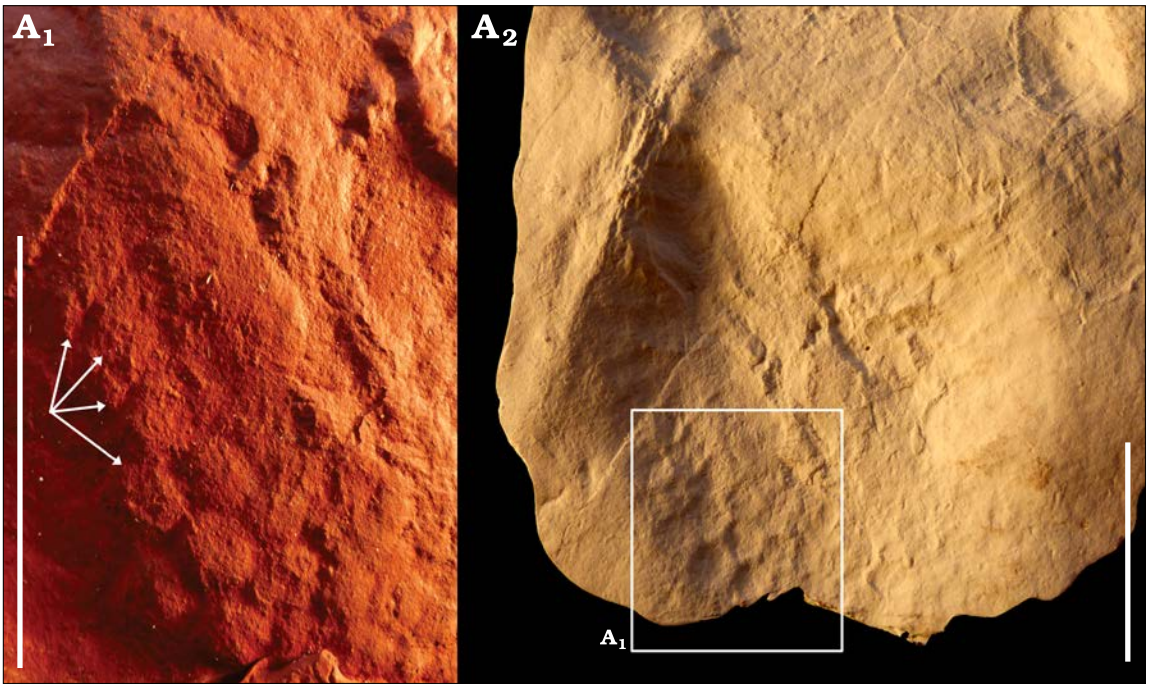

Fig. 5. Epidermal scalation on the heel pad of the right pes of *Dimetropus osageorum* Sacchi et al., 2014, from Rabéjac Formation, Lodève Basin, Rabéjac quarry, France; upper Artinskian (Permian). MNHN.F.LOD59 (ML 2001.1453.1), latex mould, convex epirelief, arrows are pointing at the epidermal scale impressions (A_1); plaster cast, concave epirelief, showing the epidermal scale impressions within the heel-pad impression (A_2). Scale bars 20 mm.

These specimens represent the first definite occurrence of *D. osageorum* from the Lodève Basin. Also, this represents the first occurrence of *D. osageorum* outside the type locality of the lower Artinskian Wellington Formation (Oklahoma, USA), although Sacchi et al. (2014) assigned several specimens from the Lodève Basin to *D.* cf. *osageorum*, without an official description (and not including the specimens re-assigned herein). This further supports the presence of *D. osageorum* from the Lodève Basin.

ML 2001.1482.1 (Fig. 5) was figured as *Dimetropus leisnerianus* by Gand (1987: fig. 47I). The pes impression of this specimen shows similarities with ML 2001.1453.1 (e.g., digits shorter compared to the sole impression, digit II to IV of similar size). It also presents an incomplete manus impression placed in front of the pes, partly overlapped by it and at least three times shorter than the pes impression. Based on these elements, we hereby assign this specimen to *D. osageorum*, pending complete description of the *Dimetropus* material of the Rabéjac Formation. Finally, the ichnospecies '*D. nicolasi*' was raised from material of the early Permian of the St-Affrique Basin (Massif Central, France; Gand and Haubold 1984; Gand 1987). Voigt (2005) considered most of the '*D. nicolasi*' material as undertracks of *D. leisnarianus.* However, several specimens from the Cisuralian St-Affrique and Lodève basins of France (e.g., Gand and Haubold 1984: fig. 11a from the Mas d'Alary Member, Viala Formation), the Robledo Mountains Formation of New Mexico (e.g., Haubold et al. 1995: fig. 24C), and the Carboniferous–Permian Cape John Formation of Canada (Van Allen et al. 2005: fig. 6) present similarities with *D. osageorum*. These similarities include: (i) the pes imprints markedly larger than the manus imprints, (ii) the symmetrical semi-circular arrangement of the metatarsal-phalangeal pads, (iii) the extensive sole impression and the weak pedal ectaxony. Here, we suggest that *D. osageorum* might be the correct assignment for several specimens previously classified as '*D. nicolasi*' and also some material previously assigned to *D. leisnerianus* (e.g., Gand 1986: fig. 5; Gand 1991: pl. 1: d; Voigt et al. 2012: fig. 5A), suggesting broader biostratigraphic and palaeogeographic occurrences for this ichnospecies. As such, although material referred to '*D. nicolasi*' clearly includes undertracks of *Dimetropus* (Gand and Haubold 1984; Gand 1987; Haubold et al. 1995; Voigt 2005; Gand and Durand 2006), further revision of this ichnospecies (as suggested by Sacchi et al. 2014) is needed to support putative *D. osageorum* assignments.

One of the most conspicuous differences between *D. leisnerianus* and *D. osageorum*, in addition to the clearly smaller manus compared to the pes, is the overall arrangement and morphology of the metapodial-phalangeal pads of the pes (see SOM: fig. 1). Contrary to *Dimetropus leisnerianus* where the metatarsal-phalangeal pads are arranged in an asymmetric configuration, those of *D. osageorum* are arranged along a symmetric semi-circle, with metatarsal-phalangeal pads I and V positioned way more distally in regard to the base of the digits than metatarsal-phalangeal pads II to V (SOM: fig. 1). Moreover, the shape of metatarsal-phalangeal pads I and V are ovoid, contrary to the circular shape recovered in the metatarsal-phalangeal pads II to IV, and the shape of all metatarsal-phalangeal pads of *Dimetropus leisnerianus*. In *D. leisnerianus*, the metatarsal-phalangeal

pad IV is the biggest, whereas in *D. osageorum*, the metatarsal-phalangeal pads I and V are the biggest (SOM: fig. 1).

The described scales on ML 2001.1453.1 are the only known occurrence from sole impressions of *Dimetropus*, and were only illustrated but not described in previous studies (Ellenberger 1983a; Heyler and Gand 2000; Marchetti et al. 2025a). Scales associated with *Dimetropus* digit imprints have been reported or figured previously (e.g., Pabst 1908; Voigt 2005). They are wider than long, as wide as the digits and perpendicular to the digit axis (Voigt 2005; Marchetti et al. 2025a). Thin digital, plantar and transverse creases on the sole of *Dimetropus* material from Czech Republic were also described (Calábková et al. 2023). They are not as pronounced as the skin folds described here (Fig. 4). More recently, exceptional skin impressions of the limbs, trunk and tail, associated with *Dimetropus* have been described (Marchetti et al. 2025a), supporting the presence of epidermal scales in sphenacodontids. These body impressions have been assigned to the ichnogenus *Bromackerichnus requiescens* Marchetti et al., 2025a.

Stratigraphic and geographic range.—Lower to upper Artinskian, Wellington Formation (USA) and Rabéjac Formation (France)

Results

Trackmaker attribution

Synapomorphy-based track-trackmaker correlation.— The trackmaker of *Dimetropus* has been historically assigned to pelycosaur-grade synapsids (Gand 1987; Haubold 2000; Voigt 2005; Marchetti et al. 2025b), mostly based on the antero-posteriorly elongated sole pad impression, corresponding to a "fleshy pad" positioned at the level of the ovoid calcaneum of pelycosaur-grade synapsids (Reisz 1986; Sacchi et al. 2014). *Dimetropus leisnerianus* and the associated *Bromackerichnus requiescens* were correlated to sphenacodontid synapsids through a synapomorphy-based attribution (Marchetti et al. 2025a, b). Sacchi et al. (2014) assessed the trackmaker of *D. osageorum* as caseids or, potentially, putative edaphosaurids. In particular, they noted a congruence with the uniform digit lengths of both manus and pes in the caseid *Cotylorhynchus romeri*, although no caseid autopodia strictly matched the footprints of *D. osageorum*. In addition, Sacchi et al. (2014) noted biostratigraphic discrepancies between the tracks of *D. osageorum* and the younger large-sized caseids such as *Cotylorhynchus*. Romano et al. (2016) conducted a thorough investigation of the trackmaker and locomotion of both *Dimetropus leisnerianus* and *Dimetropus osageorum*, supporting their attribution to pelycosaur-grade synapsids. Marchetti et al. (2025a) noted that the high heteropody observed in *D. osageorum* rather indicated a trackmaker group different from sphenacodontids, potentially belonging to caseids, edaphosaurids and ophiacodontids. In the following section, we will compare the autopodial morphology of these three groups with that of *Dimetropus osageorum* tracks, thanks to the well-preserved material from the Rabéjac Formation (Lodève Basin).

In their discussion of the track-trackmaker attribution for the *D. osageorum* of the Wellington Formation, Sacchi et al. (2014) noted that early caseids such as *Casea* or *Oromycter* were markedly smaller than the putative trackmakers of the footprints, and that only younger giant caseids such as *Cotylorhynchus* were a match in absolute size. A similar situation occurs in the Rabéjac Formation, where the *D. osageorum* pes tracks are more than 220 mm long (Table 1). This is at least 1/3 longer than the pes of the putative early caseid *Callibrachion gaudryi* from the Sakmarian Millery Formation, Autun Basin, northern Massif Central, France (Spindler et al. 2016) or the early caseid *Martensius bromackerensis* from the upper Asselian Tambach Formation, Thuringian Forest Basin, central Germany (Tables 2, 3, Fig. 6A–C). The absolute size range could conform to that of the larger *Euromycter rutenus* and especially *Ruthenosaurus russellorum* from the Grès Rouge Group of the Rodez Basin (Massif Central, France), currently considered Asselian–lower Kungurian (Werneburg et al. 2022), though no pes is known from either taxon. Among early caseids, a complete foot is only known in *Martensius* (Fig. 6A, C), which displays a long digit I and a clear increase in digit length from digit I to IV (Table 3). This contrasts with the short digit I impression, markedly shorter than digit II, and similarly long digits

Table 2. Skeletal measurements (in mm) of the manus of synapsids from lower Permian units of Euamerican Variscan Belt. DML, digit metapodial length; FL, autopodium length; FW, autopodium width; MCL, metacarpal-carpal length; I–V D, divarication (angle in degrees) of digits I–V; I–V L, digit I–V length; × , no measurement was possible. Measurements from Marchetti et al. (2025a).

Family	Species	Specimen	FL	DML	MCL	FW	I L	II L	III L	IV L	V L	I–V D
Caseidae	*Martensius bromackerensis*	MNG 13814	152.6	122.6	61.2	83.8	22.7	42.2	46.2	67.2	53.5	43.07
		MNG 10595	91.4	82.2	55.0	63.1	23.5	33.3	45.5	46.3	40.9	30.06
		MNG 14320	81.6	67.8	35.4	39.1	×	26.5	39.3	44.6	32.6	×
Edaphosauridae	*Edaphosaurus pogonias*	FMNH	199.7	162.6	110.8	189.8	48.3	69.9	85.0	88.9	70.0	88.86
	Edaphosaurus boanerges	MCZ 1366	163.0	128.4	88.2	117.8	40.9	53.1	68.5	78.4	52.2	50.65
Ophiacodontidae	*Ophiacodon mirus*	FMNH	109.4	90.3	67.7	86.8	15.0	22.1	31.7	47.5	24.6	91.84
		FMNH 240	108.7	90.7	72.6	91.7	16.5	23.1	33.5	47.5	27.5	76.59
	Ophiacodon retroversus	FMNH 458	165.8	116.8	108.3	112.5	26.3	39.5	51.5	68.5	36.0	63.77
	Ophiacodon uniformis	MCZ 1366	110.1	78.7	72.3	105.5	11.7	29.0	37.4	45.0	24.8	99.82

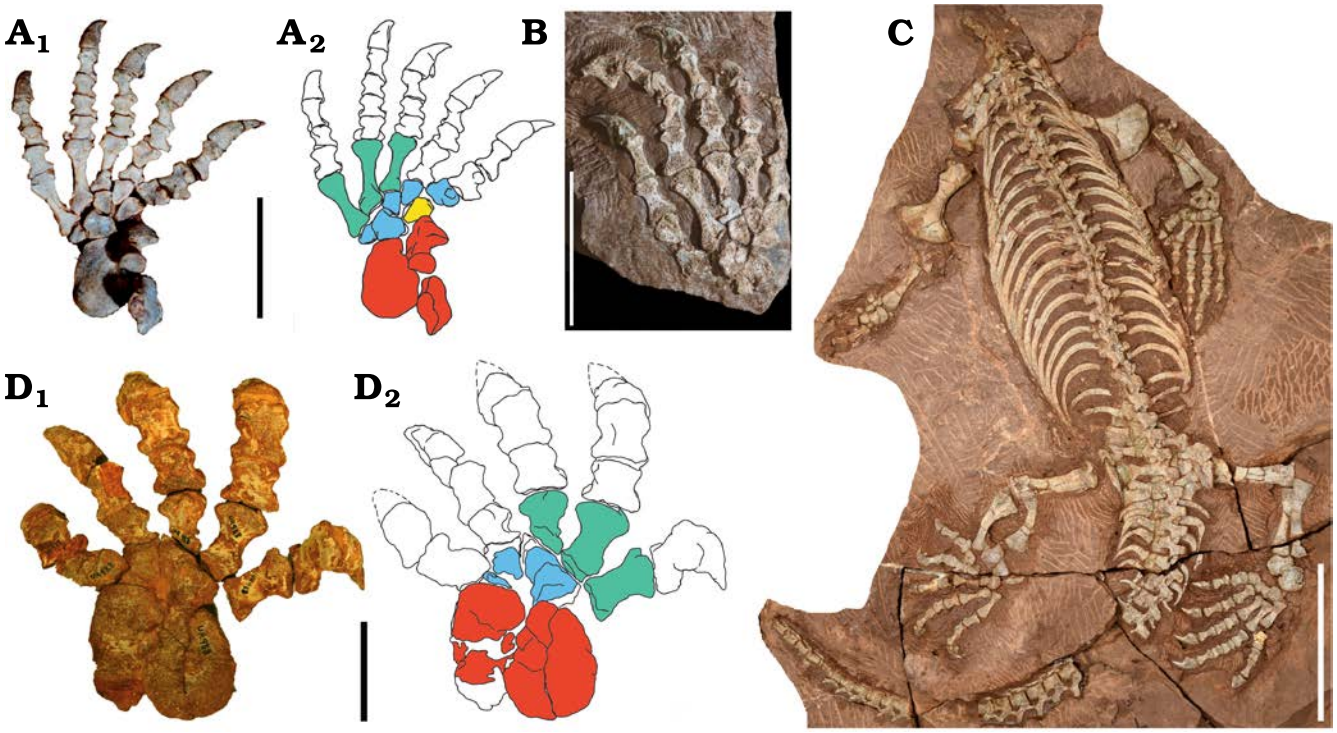

Fig. 6. Caseidae manus and pes bodyfossils: *Martensius bromackerensis* Berman et al., 2020, Tambach Formation, Bromacker (Germany), upper Asselian (Cisuralian) (A–C) and *Cotylorhynchus bransoni* Olson and Barghusen, 1962, Chickasha Formation, Omega quarry, Oklahoma (USA), early Roadian (Guadalupian) (D). **A**. MNG 13814, left pes in dorsal view; photograph (A_1), explanatory drawing (A_2). **B**. MNG 10595, left manus in dorsal view. **C**. MNG 14230, sub-complete skeleton of a juvenile individual in dorsal view. **D**. FMNH UR 988, described in Romano and Nicosia (2015), stored at the Field Museum of Natural History; right pes in dorsal view; photograph (D_1), explanatory drawing (D_2). Red, astragalo-calcaneal complex; yellow, centrale; blue, distal tarsals (1–5); green, metatarsals III–V. Scale bars 50 mm, except C 100 mm.

II–IV impressions of *D. osageorum*. In contrast, later-diverging caseids present a shorter digit I (though not markedly smaller than digit II) and subequal digits II–IV, comparable to *D. osageorum*, including the relatively early diverging *Ennatosaurus tecton* from the middle Permian of Russia (Table 1; Olson 1962). Phylogenetic bracketing under recent topologies suggests that this might also have been the case at least for *Ruthenosaurus* (Werneburg et al. 2022). In addition, complete skeletons of the early caseids *Callibrachion*, *Martensius* and *Ennatosaurus* show no marked heteropody (Olson 1962; Spindler et al. 2016; Berman et al. 2020), contrary to *D. osageorum*. Also, larger, later diverging caseids such as *Cotylorhynchus* lack this heteropody and contrast with *D. osageorum* (as suggested by Sacchi et al. 2014). It is unknown whether *Euromycter* or *Rhuthenosaurus* showed heteropody. However, all late-diverging caseids show thick manual and pedal digits, including *Ennatosaurus*, *Euromycter* or *Cotylorhynchus* (Fig. 6D; Olson 1962; Stovall et al. 1966; Sigogneau-Russell and Russell 1974). This is different from the rather gracile digits observed in *D. osageorum*, especially in the well-preserved tracks of the Rabéjac Formation described herein. Moreover, the thickness of the first phalanges in these later caseids caused a high divarication angle between the base of the digits, especially digits IV

Table 3. Skeletal measurements (in mm) of the pes of synapsids from lower Permian units of Euamerican Variscan Belt. DML, digit metapodial length; FL, autopodium length; FW, autopodium width; MTL, metatarsal-tarsal length; I–V D, divarication (angle in degrees) of digits I–V; I–V L, digit I–V length. Measurements from Marchetti et al. (2025a).

Family	Species	Specimen	FL	DML	MTL	FW	I L	II L	III L	IV L	V L	I–V D
Caseidae	*Martensius bromackerensis*	MNG 13814	123.2	89.9	76.4	104.7	34.0	38.5	39.3	50.0	43.0	65.25
		MNG 10595	138.3	104.1	72.0	75.8	23.9	38.1	56.1	68.5	56.1	28.36
		MNG 14320	93.6	75.6	47.0	65.5	23.3	31.2	38.5	46.7	37.7	59.28
	Cotylorhynchus bransoni	UR 988	170.1	88.5	57.4	165.7	>31.3	52.5	>62.2	>61.4	>36.3	123.49
Edaphosauridae	*Edaphosaurus pogonias*	FMNH	231.8	177.1	134.8	189.1	36.8	58.7	81.5	106.9	85.8	52.44
	Edaphosaurus boanerges	MCZ 1366	172.2	121.0	100.9	116.8	36.3	56.7	67.4	78.6	57.6	55.55
Ophiacodontidae	*Ophiacodon mirus*	FMNH	158.4	116.8	103.4	133.7	25.9	39.4	48.7	63.6	55.8	71.58
		FMNH 240	159.5	109.4	97.0	131.6	21.3	35.5	52.9	68.4	52.3	85.85
	Ophiacodon retroversus	FMNH 458	128.1	92.8	84.3	104.1	22.9	37.0	44.5	46.8	38.3	68.60
	Ophiacodon uniformis	MCZ 1366	224.7	166.2	147.1	177.4	37.0	54.1	68.8	90.6	65.4	52.44

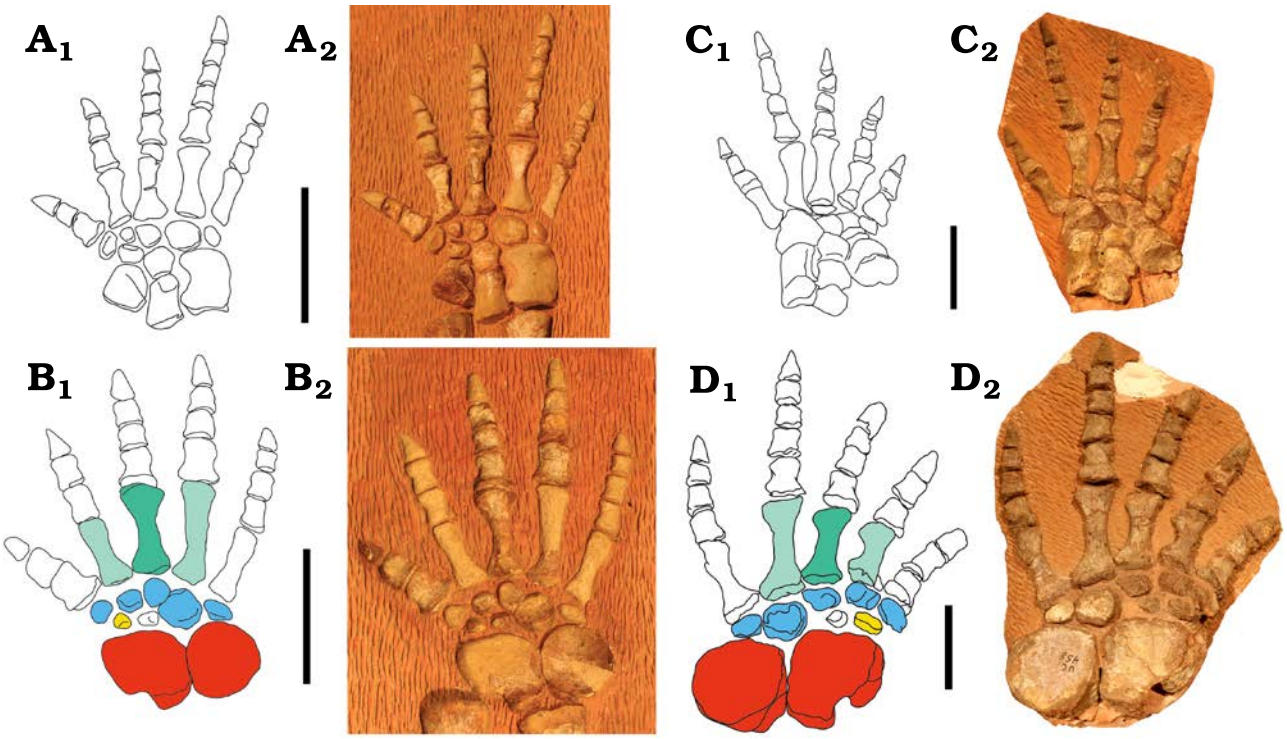

Fig. 7. Manus and pes of Ophiacodontidae species. **A**, **B**. *Ophiacodon mirus* Marsh, 1878, Conemaugh Group, Linton (Ohio, USA), Gzhelian (upper Carboniferous), FMNH 240, manus (**A**) and pes (**B**) in dorsal views. **C**, **D**. *Ophiacodon retroversus* Cope, 1878, Nocona Formation, Mount Barry, Wichita County (Texas, USA), Asselian–Sakmarian (lower Permian), FMNH 458, manus (**C**) and pes (**D**) in dorsal views. Photographs (A_1–D_1), explanatory drawings (A_2–D_2). Red, astragalo-calcaneal complex; blue, distal tarsals; yellow, centrale; green, metatarsals II–IV; dark green, metatarsal III. Scale bars 50 mm.

and V, as is the case in *Ennatosaurus* and *Cotylorhynchus* (Fig. 6D; Olson 1962; Stovall et al. 1966). This contrasts with the parallel digits I to V and the low divarication angle of the autopods observed in *D. osageorum*. Lastly, digit V of the pes of *Cothylorhynchus* is smaller than digit II (Table 3), comparable to a key characteristic of *D. osageorum*. However, this character cannot be assessed in other late-diverging caseids. In light of all this, we think that *D. osageorum* is unlikely to have been made by a caseid trackmaker, contrary to Sacchi et al. (2014).

The autopodia of edaphosaurids is not well known (Spindler et al. 2020). The manus of *Edaphosaurus* seems to present gracile straight and parallel digits (Kummell et al. 2020), potentially congruent with the footprints of *D. osageorum*, although gracile digit imprints in *D. osageorum* are mostly in the pes. We note that most European edaphosaurid specimens are relatively small compared to their North American counterparts (Spindler et al. 2020), and in turn, to *D. osageorum*. However, this may reflect the scarcity of the European edaphosaurid fossil record. To sum up, we provisionally exclude an edaphosaurid trackmacker attribution for *D. osageorum*.

The manus and pes of Ophiacodontidae has been poorly studied compared to caseids, and no complete autopods are known from European ophiacodontids (Falconnet 2014). However well-preserved *Ophiacodon mirus* and *Ophiacodon retroversus* material from the lower Permian of North America showing sub-complete to complete autopodia are known (Fig. 7), as well as some subcomplete pedes of *Varanosaurus* (Case, 1910). Amongst pelycosaurian-grade synapsids, ophiacodontids present the best case of heteropody, especially in *O. retroversus* (Fig. 7C, D), with a pes at least 1/3 larger than the manus, similar to *D. osageorum* (Fig. 5). Also, the digits of the manus of *Ophiacodon* species (Table 2) display an increase in length from digits I to IV, with digit V of similar size as digit II, which seems consistent with the manus of ML 2001.1482.1 from the Rabéjac Formation (Fig. 5). The pes of *Ophiacodon retroversus* also displays an increase in length of digits I to IV, although digits II–IV remain rather similar in size (Table 3). Digit I is clearly smaller than digit II. Digit V appears to be of similar size, only very slightly longer than digit II (Table 3), in accordance with a key feature of *D. osageorum*. The metatarsal-phalangeal pads in the herein described *D. osageorum* specimens are arranged along a symmetric semi-circle (SOM: fig. 1), with the metatarsal-phalangeal pads of digits I and V more proximal compared to that of digits II–IV. In *Ophiacodon*, the metatarsal-phalangeal articulations of digits I and V are also more proximal than those of digits II–IV (SOM: fig. 1). This is also the case, to a lesser degree, in *Varanosaurus* (Case, 1910). In contrast, in sphenacodontids, the metatarsal-phalangeal articulations of digits I and II are positioned more closely to those of digits III–V, and so in a more distal position compared to those of ophiacodontids (SOM: fig. 1), which instead conforms to the asymmetric

configuration of the metatarsal-phalangeal pads of *D. leisnerianus* (Marchetti et al. 2025a, b).

The position of the metatarsal-phalangeal pads in *D. leisnerianus* pes thus seems to match the metatarsal-digit articulation of some of their trackmakers (e.g., sphenacodontid synapsids, SOM: fig. 1). Moreover, the placement of the metatarsal-phalangeal pads in *Dimetropus* footprints might also reflect the functional prevalence of their tracemakers: median in *D. osageorum* (median digits II–IV more predominantly used during the locomotor cycle) and lateral in *D. leisnerianus* (lateral digits III–V more predominantly used during the locomotor cycle). The differences in functional prevalence recovered from both *Dimetropus* ichnospecies is therefore consistent with that of their trackmakers considering the metatarsal-phalangeal articulations, and suggest a weak lateral to median functional prevalence in the locomotor cycle of ophiacodontids. Moreover, the proximal phalanx of digit III of *Ophiacodon* (Fig. 7: green) is also thicker compared to the phalanges of digits V and IV, with more prominent distal processes. This might suggest higher surface for articulation and muscle attachments. This would have led to a medial-median functional prevalence with a high utility of digit III in the locomotor cycle, congruent with the medial functional prevalence, weak ectaxony and deep impression of the basal part of digit III in *D. osageorum*. In contrast, our observations of the proximal phalanges of sphenacodont synapsids and other small caseids correlated with *D. leisnarianus*, reveal thicker proximal phalanges in the digits III–V (Fig. 6), congruent with the marked ectaxony of these taxa. Further investigation on the proximal phalanges shape in relation to functional prevalence is needed to back up these observations.

In conclusion, we discard *Cotylorynchus* and other large caseids as a possible trackmaker of *D. osageorum* because of the lack of heteropody, the thick proximal phalanges and the resulting high divarication of the digits, features contrasting the morphological features of this ichnospecies. We also discard large but earlier diverging caseids such as *Rhutenosaurus*, for which autopodia are incompletely known, based on their inferred morphology for the aforementioned characters. Edaphosaurids are also tentatively discarded due to the relatively smaller size of all known European early Permian edaphosaurids (although there are large edaphosaurid remains from the USA). Ophiacodontidae may represent the better fit for a *D. osageorum* trackmaker amongst pelycosaurian-grade synapsids, by presenting a high heteropody, especially in some *Ophiacodon* species. The metatarsal-phalangeal pad arrangement in *D. osageorum* is also consistent with the metatarsal-digit articulation in *Ophiacodon* and *Varanosaurus* with a more proximal articulation of the metatarsal-phalangeal pad impressions of digits I and V coupled with a deepened impressions of digits II–IV, probably reflecting the weak lateral functionality and ectaxony of *D. osageorum*. This is also supported by preliminary observations of the proximal phalanges of ophiacodontids that may reveal a median functional prevalence in their locomotor cycle, as in *D. osageorum*. In conclusion, we support and add ophiacodontids to the list of putative trackmakers of *D. osageorum*.

Early-diverging synapsid occurrences in the Massif Central and Ophiacodontidae palaeobiogeoraphy.—The Carboniferous–Permian formations of the Massif Central, in France, yield a surprising diversity and disparity of synapsids (Fig. 8). In the Permian, indeterminate sphenacodontids have been described from the bone breccia of the lower Sakmarian lower Viala Formation of the Lodève Basin (Falconnet 2014, 2015) but also from the coeval Millery Formation of the Autun Basin, with the historic description of *Haptodus baylei* Gaudry, 1886. Numerous Caseidae occurrences are known (Fig. 8), with the recovery of: *Callibrachion gaudryi*, from the Sakmarian Millery Formation of the Autun Basin (Boule and Glangeaud 1893), *Ruthenosaurus russelbrum* and *Euromycter ruterus* from the Asselian–lower Kungurian Red Sandstone Group of the Rodez Basin (Sigogneau-Russell and Russell 1974; Reisz et al. 2011) and *Lalieudorhynchus gandi*, from the lower Guadalupian La Lieude Formation of the Lodève Basin (Werneburg et al. 2022). Other putative pelycosaur-grade synapsid occurrences from the Massif Central are given through the presence of *Dimetropus leisnerianus* from several formations. It has been described from: the upper Sakmarian Meissac Formation of the Brive Basin (Gand 1987), the Asselian-lower Kungurian Red Sandstone Group of the Rodez Basin (Gand 1987), the Asselian Saint-Rome, Sakmarian Grès du Dourdou and upper Asselian–lower Kungurian Saint Pierre formations of the Saint-Affrique Basin (Gand 1993), and the lower Asselian Usclas-Saint Privas, upper Asselian Tuilières-Loirat, Sakmarian Viala and upper Artinskian Rabéjac formations of the Lodève Basin (Gand and Durand 2006).

The ichnotaxon *Dimetropus osageorum* was previously only known from the type locality, the Wellington Formation in Oklahoma, dated to the lower Artinskian (Sacchi et al. 2014; Marchetti et al. 2022a). The *D. osageorum* from the Rabéjac Formation, dated to the upper Artinskian thus represents a younger occurrence of this ichnospecies and extends its stratigraphic range (Fig. 8). The only known body fossils of similar age in the French basins are the relatively smaller and older caseids *Callibrachion*, *Euromycter* and *Ruthenosaurus* from the Sakmarian, or the younger large caseid *Lalieudorhynchus*, the only taxon of comparable size to *D. osageorum*. None of the taxa above are, however, considered as potential tracemakers of *D. osageorum* (see section above). Rather, the synapomorphy-based track-trackmaker correlation carried out here suggests, for the first time, the presence of ophiacodontid synapsids in the Massif Central (France), and more generally, within the lower Permian of the Variscan Belt, leading to several implications regarding ophiacodontid palaeobiogeography.

Ophiacodontidae are rare from Palaeozoic basins of the Variscan Belt, where only assessed Carboniferous early-

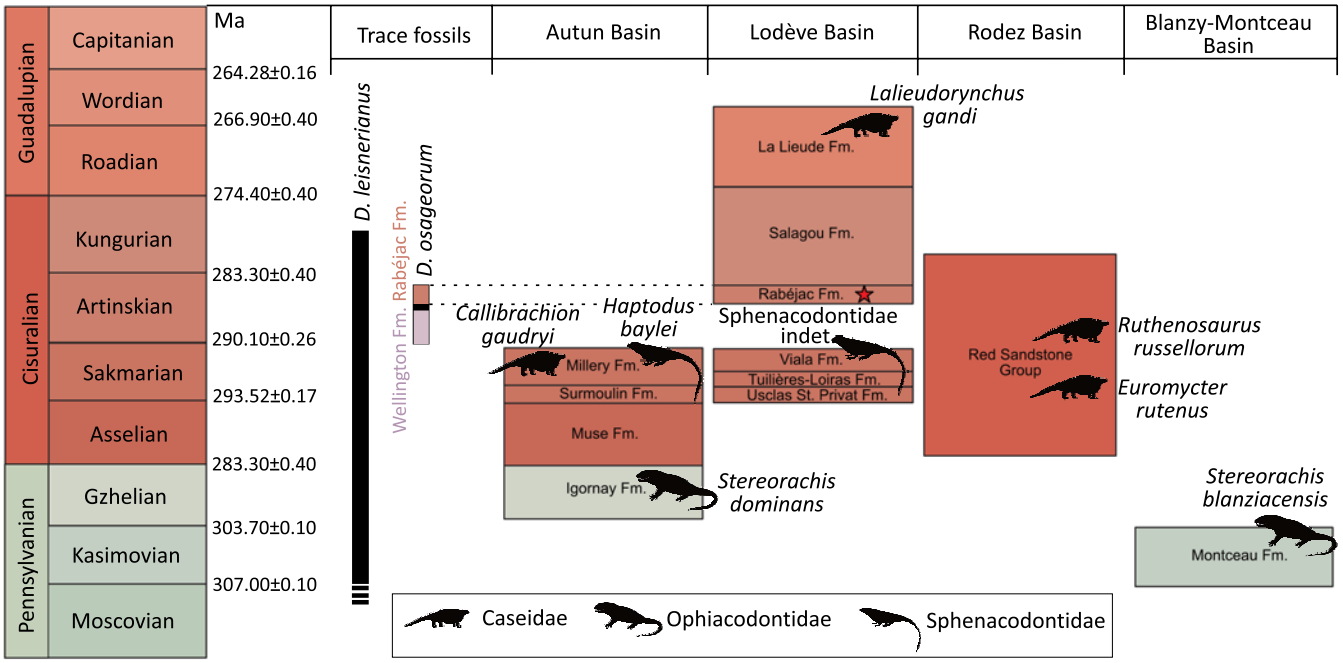

Fig. 8. Global stratigraphic range of *Dimetropus osageorum*, with occurrences of synapsids (Caseidae, Ophiacodontidae, and Sphenacodontidae) in Carboniferous–Permian basins of the Massif Central (France). Red star indicates *D. osageorum* occurrence (after Falconnet 2014; Marchetti et al. 2025a). Stratigraphic position of the Rabéjac Formation after Michel et al. (2015), the Wellington Formation after Marchetti et al. (2022). Silhouettes from PhyloPic (https://www.phylopic.org/): *Cotylorhynchus* (Caseidae) by Nobu Tamura, vectorized by Roberto Díaz Sibaja; *Stereorhachis* (Ophiacocodontidae) by Dmitry Bogdanov; *Haptodus* (Sphenacodontidae) by Dmitry Bogdanov, vectorized by T. Michael Kessey.

diverging forms are known (e.g., Reisz 1975; Falconnet 2013, 2014; Spindler et al. 2020). *Archaeothyris* has been described from the Carboniferous of the Pilsen Basin (Czech Republic) (Reisz 1975), and two occurrences from the Massif Central (Fig. 8) are also known: *Stereorhachis dominans*, from the Gzhelian (see Pellenard et al. 2017; Mercuzot et al. 2023 for datations) Igornay Formation of the Autun Basin (Gaudry 1880; Thévenin 1910), and *Stereorhachis blanziacensis*, from the Kasimovian Montceau Formation of the Blanzy-Montceau Basin (Langiaux et al. 1974). A putative occurrence has been described from the Kenilworth Sandstone Formation of the late Gzhelian to early Asselian Pennine Basin of England (Paton 1974; Spindler 2020). Considering ophiacodontids as potential trackmakers of the *D. osageorum* tracks of Rabéjac, this would support a Permian presence of the family Ophiacodontidae in the Variscan Belt. On the contrary, Ophiacodontidae are widespread in the lower Permian of North America with most of the occurrences come from marginal marine units of Texas, spanning from the Asselian to the late Artinskian (e.g., Lucas 2006, 2018). Several occurrences are known from Oklahoma as well, from floodplain environments spanning from the Sakmarian to the late Artinskian (e.g., Lucas 2006, 2018). Other occurrences are from the Asselian–Sakmarian floodplain units of Arizona and New Mexico and are generally more scattered (e.g., Lucas 2006, 2018). Contrary to caseids, ophiacodontids well-overlap the lower Artinskian *D. osageorum* occurrence in North America.

Interestingly, the late Artinskian Rabéjac occurrence of putative ophiacodontid trackmaker is immediately preceding the "Redtankian events" (Benton 1989; Lucas 2016, 2018) associated with an extinction of "microsaurs", anthracosaurs and ophiacodontids in the late Cisuralian (which has been associated to the Olson's gap by some authors, see Sahney and Benton 2008; Benton 2012). The track-trackmaker correlation between *D. osageorum* and ophiacodontids could therefore suggest that the "Redtankian events" might be extended to western Europe. More evidence of actual bodyfossils and a review of the *Dimetropus* occurrences at the ichnospecies level are however needed to support his hypothesis.

The extreme scarcity of ophiacodontids, such as *Ophiacodon*, in the lower Permian of Europe (only one dubious occurrence, see Spindler 2020) was so far puzzling: ophiacodontids from North America are indeed the only pelycosaur-grade synapsids that do not share European counterpart (Spindler 2020). It has thus been suggested that their morphotype was linked to specific extensive coastal lowland or continuous floodplain environmental conditions, which differed from the isolated intramontane basins of the late Palaeozoic of Europe (Schneider 1993; Pardo et al. 2019; Spindler 2020). The recovery of putatively derived ophiacodontids, such as *Ophiacodon*-like trackmakers, in the upper Artinskian of the Lodève Basin, within the Variscan Belt, could support the W–E lag in the Permian increase of dryland suggested by Pardo et al. (2019), during

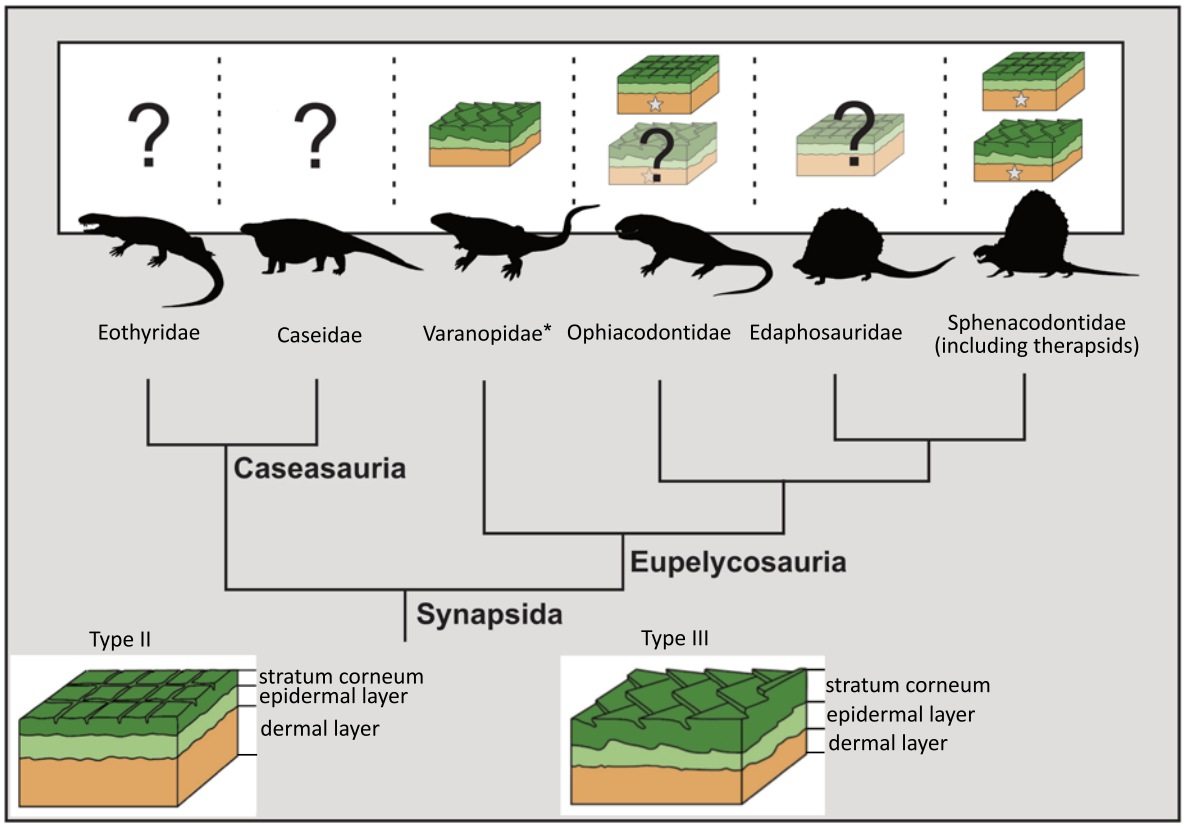

Fig. 9. Epidermal scalation evolution in Palaeozoic synapsids. Phylogeny after Sumida (2025): *, the phylogenetic position of Varanopidae is still unclear as either synapsids or early diverging reptiles. Skin three-dimensional sections after Marchetti et al. (2025b): Type II, non-overlapping thin epidermal scalation; Type III, thickened epidermal scales/overlapping scales; stars indicate the presence of dermal scales. Silhouettes from PhyloPic (https://www.phylopic.org/): *Eothyris* (Eothyridae), *Edaphosaurus* (Edaphosauridae) by Nobu Tamura; *Cotylorhynchus* (Caseidae) by Nobu Tamura, vectorized by Roberto Díaz Sibaja; *Varanops* (Varanopidae), *Stereorhachis* (Ophiacodontidae), *Dimetrodon* (Sphenacodontidae) by Dmitry Bogdanov.

the Artinskian Warming Event (e.g., Marchetti et al. 2022a). This change in palaeoclimate might actually have been advantageous for the dispersal of ophiacodontids from North America to Europe (contra Spindler 2020; although it must be noted that earlier *D. osageorum* occurences in France are possible, so more studies are needed to further verify dispersal hypotheses). The Rabéjac Formation, characterised by a dry tropical floodplain (Lopez et al. 2008) might have been therefore a favourable palaeoenvironment for Ophiacodontidae within the Variscan Belt.

Epidermal scale evolution in Palaeozoic synapsids

Epidermal scalation of Palaeozoic synapsids.—The material of *D. osageorum* from the Rabéjac Formation displays well-preserved epidermal scale impressions (Figs. 4, 5). The shape and organisation of the scales is consistent with that of the forelimb impressions of *Bromackerichnus recquiensens* from the upper Asselian of Bromacker (Tambach Formation, Thuringia Forest Basin, Germany) (Marchetti et al. 2025a, 2026b). The epidermal scales of *Bromackerichnus requiescens* show a remarkably well-preserved organisation and morphology, allowing a detailed reconstruction of the skin of this early Permian synapsid. The belly is covered with rhomboidal to rectangular scales, arranged in a regular grid of transverse and longitudinal rows that are slightly curved backward and laterally. The lateral parts of the trunk bear slightly more prominent scales. On the forelimbs, which are short and robust, the scales become hexagonal, smaller and arranged in oblique rows, suggesting greater flexibility in these areas. The hindlimbs display rectangular scales, often overlapping on the ventral side, following the curvature of the limb. Finally, the tail is covered with longitudinal rows of rectangular, prominent scales showing well-defined hinge regions. *Bromackerichnus* has been assigned to sphenacodontid synapsids.

Putative ophiacodontids as trace makers of *Dimetropus osageorum* would then suggest similar epidermal scalation in the autopods and hindlimbs in both sphenacodontids and ophiacodontids. Indeed, the epidermal scalation type II (following Marchetti et al. 2025b; see Fig. 9) is also recovered in the sphenacodontid body impression *Bromackerichnus requiescens* in the forelimb impression. In this way, a possible presence of more cornified epidermis (epidermal scalation type III of Marchetti et al. 2025a; see Fig. 9) could have also been present in ophiacodontids in other body parts (belly, tail, etc.) In Marchetti et al. (2025a), the *Dimetropus* pes

described here was assigned to a caseid trackmaker, following Sacchi et al. (2014) and Romano et al. (2016). The new attribution to putative ophiacodontid trackmakers changes the interpretation pattern of these groups. The earliest occurrences of epidermal scales in synapsids would then be from the upper Asselian Tambach Formation (Germany), in sphenacodontids (Marchetti et al. 2025a, 2026b), and from the upper Artinskian Rabéjac Formation (France), in ophiacodontids (this study). Both groups belong to pelycosaur-grade synapsids, suggesting reptile-like epidermal scalation as ancestral in non-therapsid synapsids. No scales are known from edaphosaurids, however its presence in this group is likely considering the recovery of reptile-like epidermal scalation as ancestral in pelycosaur-grade synapsids (Marchetti et al. 2025; this study).

Further conclusions regarding the ancestral state of skin scalation in synapsids would depend on the findings on skin remains or skin impressions attributed to caseids. It also depends on the phylogenetic position of Varanopidae, as either early synapsids (Romer 1956; Reisz 1975; Reisz and Dilkes 2003; Benson 2012; Jenkins et al. 2025) or early diverging diapsid reptiles (Spindler et al. 2018; Ford and Benson 2020). Also, some taxa previously attributed to Varanopidae, such as *Ascendonanus*, might represent neoreptiles instead (Jenkins et al. 2025). The exceptionally preserved *Ascendonanus* from the Leukersdorf Formation (Chemnitz Basin, Germany) presents a highly organised pattern of tetragonal to rectangular epidermal scales, covering the trunk, limbs and tail. These scales are small, often overlapping (this is especially seen on the tail region, see Spindler et al. 2018: figs. 14 and 24; Marchetti et al. 2026a: supplementary figure 4), and form longitudinal and transverse rows similar to the scalation of extant non-avian reptiles such as lizards and crocodilians (Spindler et al. 2018; Marchetti et al. 2025a).

The great similarities between early synapsid epidermal scalation and stem reptile epidermal scales (see Marchetti et al. 2026a) could therefore suggest a convergent evolution of integumentary adaptation in both groups or the appearance of reptile-like epidermal scalation as ancestral in amniotes. The latter scenario is also supported by the finding of putative epidermal scales in body fossils of the non-amniote seymouriamorph *Discosauriscus* from the lower Permian of the Renière Formation (Bourbon-l'Archambault Basin, northern Massif Central, France) (Logghe et al. 2025) as well as scale impressions on body traces attributed to Diplocaulidae (Walter and Werneburg 1988) and Diadectomorpha (Voigt et al. 2024).

Dermal scalation of Palaeozoic synapsids and the transition from dermal to epidermal scales.—The recovery of epidermal scalation in ophiacodontids is moreover interesting as presence of gastral scales sensu Witzmann (2007) have been described from this group, early-diverging ophiacodontid *Archeothyris* from the upper Carboniferous of Linton (Ohio) (Reisz 1975). These finely striated elongated-narrow ventral scales display a chevron-like organisation forming parallel oblique rows (Reisz 1975), reminiscent of that of other Palaeozoic tetrapods (e.g., Witzmann 2007). Ventral dermal scales have purportedly been reported associated with the sphenacodontid *Dimetrodon milleri* (Reisz, 1975). Gastralia or "abdominal ribs" sensu Witzmann (2011) are also known in ophiacodontids, in *Ophiacodon* (Romer 1956: 433) and differ from the scales reported in *Archeothyris*.

Dermal ventral scales possibly played a protective role (Witzmann 2007). They are ancestral in tetrapods (e.g., Jarvik 1952; Romer 1972; Witzmann 2011), and present in most late Palaeozoic lineages such as temnospondyl amphibians (e.g., Romer and Witter 1941; Findlay 1968; Boy and Sues 2000; Dias and Richter 2003; Witzmann 2007), lepospondyls (Caroll and Gaskill 1978; Mann et al. 2021), reptiles (Credner 1889; Caroll and Baird 1972; Bickelmann et al. 2009) and synapsids (e.g., Romer 1956; Reisz 1975; Berman et al. 2020). During the late Carboniferous and early Permian, a reduction in dermal scalation is observed in tetrapods, mainly in both amniote clades, sauropsids and synapsids, which conversely displayed an increasingly keratinised epidermis through the presence of thick epidermal scalation (Mooney et al. 2024; Marchetti et al. 2025a, 2026a). The replacement of a putatively protected skin through dermal scalation by a thicker epidermis happened in the late Carboniferous–late Permian, probably already in non-amniote crown tetrapods (Logghe et al. 2025). The presence of both scalation-type in late Palaeozoic tetrapods, such as ophiacodontids, is therefore not surprising. The epidermal scales, without ossified component, are formed through cornified-beta proteins in sauropsids and keratin-associated proteins in mammalian synapsids (Alibardi 2022; Holthaus et al. 2025, and references therein). Their increased cornification throughout the amniote evolutionary history provided protection against mechanical stress, desiccation and higher locomotor flexibility than dermal scalation, embedded deep into the dermis (Witzmann 2007). In comparison to dermal scalation, epidermal scales provided clear terrestrial adaptations in amniotes.

Skin evolution in light of early Permian palaeoclimate.—This new finding adds to our knowledge of the evolution of epidermal skin of Palaeozoic tetrapods, recently explored through the description of both ichno- (Voigt et al. 2024; Marchetti et al. 2025a, 2026a) and bodyfossils (Spindler et al. 2018; Logghe et al. 2025), and specifically on the epidermal scale of early synapsids (Table 4).

The time interval between the Gzhelian and the Artinskian was characterised by global warming, aridification and the progressive demise of the South Polar ice sheets of the Late Palaeozoic Ice Age (e.g., Montañez and Poulsen 2013; Richey et al. 2020). This caused more seasonal, hotter and drier climate at low palaeolatitudes of Pangaea, considerably changing the floras and the faunas in order to resist these new conditions. This includes the development of new integumentary structures such as epidermal scales in stem amniotes and amniotes, adaptations for fossoriality

Table 4. Skin preservation of late Palaeozoic synapsids in the bodyfossil (BF) and ichnofossil (IF) record. *The phylogenetic position of Varanopidae is still unclear as either synapsids or early diverging reptiles.

Group (Taxon)	Stratigraphy; locality	Scale morphology	Arrangement pattern	Body regions with skin preserved	BF/IF	References
Eothyridae	Upper Carboniferous–lower Permian	no scales preserved	N/A	N/A	N/A	N/A
Caseidae	Lower Permian; North America and Europe	no scales preserved	N/A	N/A	N/A	N/A
Varanopidae* (*Tambachichnium* footprints/*Ascendonanus nestleri*)	Lower Permian (Sakmarian), Leukersdorf Formation; Germany	rhomboidal, rectangular or hexagonal (1–3 mm), sometimes overlapping and laterally tapering	oblique or alternating rows	trunk, tail, limbs	BF	Spindler et al. 2018
Ophiacodontidae (*Dimetropus osageorum*)	Lower Permian (Artinskian), Rabéjac Formation; France	hexagonal	irregular rows	pes	IF	Marchetti et al. 2025b, this study
Edaphosauridae	Lower Permian; North America	no scales preserved	N/A	N/A	N/A	N/A
Sphenacodontidae (*Bromackerichnus requiescens*, *Dimetropus leisnerianus*/*Dimetrodon teutonis*)	Lower Permian (Sakmarian), Tambach Formation; Germany	rhomboidal, rectangular or hexagonal (4–5 mm), with hinge zones, sometimes overlapping	transverse and longitudinal rows, slightly curved caudolaterally	trunk, tail, limbs, pes, manus	IF	Marchetti et al. 2025b

to be able to aestivate and in general a replacement of wet-adapted biotas by drought-adapted biotas (e.g., Marchetti et al. 2024, 2025a; Voigt et al. 2024). This culminated with the Artinskian Warming Event (AWE), a global warming peak induced by the release of large volcanic quantities of CO_2 that affected both the floras and the faunas at low palaeolatitudes (Montañez et al. 2007; Richey et al. 2020; Marchetti et al. 2022a). This was also coupled with further warming mechanisms and an important sea-level transgression (Sun et al. 2022, 2026; Hou et al. 2023; Li et al. 2025; Wu et al. 2025). The Rabéjac Formation is time-equivalent with the AWE, therefore the effects of this event are observable in its footprint record, with an increase of diversity of reptilian footprints. Also, from this unit, we record epidermal scales in both reptilian, with a scaly body and tail impression associated with *Erpetopus* isp. (Ellenberger 1983a; Marchetti et al. 2025b: fig. 4.12D), and synapsid traces (this study). So, it is clear that the Rabéjac Formation is a key unit for the understanding of this climatic event on the continental realm, including the biota composition and also and foremost the evolution of integumentary structures.

Conclusions

In this study we therefore support:

- the first occurrence of *Dimetropus osageorum* from the Rabéjac Formation (upper Artinskian, France), extending the ichnospecies range beyond North America;
- a new track-trackmaker correlation for this ichnospecies, which strongly suggests an ophiacodontid-grade synapsid trackmaker based, among other features, on heteropody;
- thus, the presence of ophiacodontids in the Variscan Belt (Europe) during the late Artinskian, first such evidence outside North America and a possible dispersal of ophiacodontids across Pangaea during the Artinskian Warming Event (AWE);
- the presence of well-preserved epidermal scale imprints—earliest direct evidence of reptile-like epidermis in ophiacodontids;
- that integumentary adaptations towards more cornified, water-retentive skin were already established in early pelycosaur-grade synapsids, supporting correlation between climatic aridification, selective pressures for water-conserving integument, and synapsid terrestrial expansion.

Overall, this study highlights the Rabéjac Formation, which was deposited under dry tropical floodplain conditions, contemporaneous with the Artinskian Warming Event, as a key continental archive for studying early amniote adaptation to climate stress.

Authors' contribution

AL and LM designed the original project, described and interpreted the fossils. AL wrote the manuscript with the help of all authors. LM did the 3D-model. AL prepared the figures. All authors reviewed the manuscript.

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