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General palaeontology, systematics and evolution (Palaeoichnology)

Biometric and morphometric approaches on Lower Hettangian dinosaur footprints from the Rodez Strait (Aveyron, France)

Approches biométriques et morphométriques des traces de pas de Dinosaures de l'Hettangien basal du Détroit de Rodez (Aveyron, France)

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ABSTRACT

Along the southern crystalline border of the Rouergue, the detrital Sandstones-variegated Mudstones Formation and the Dolomitic Formation yields numerous dinosaur footprints from the Earliest Hettangian. Among the 25 sites distributed along the 40 km-long transect between Marcillac-Vallon and Saint-Geniez-d'Olt, two of them, Puech de Castres and Le Bouyssou, have yielded abundant ichnites in various well-defined stratigraphic units. The combined analysis of these footprints with biometric and morphometric methods (Fourier analysis) warrants their identification to *Grallator, Eubrontes* and *Dilophosauripus*. The dual methodological approach also reveals two new morphotypes previously unknown in the Causses Basin. Moreover, the footprints assigned to *Grallator* and *Eubrontes* tend to be morphologically similar, suggesting that they might correspond to a same taxon of Coelophysoidea theropod at different growth stages. This dinosaur fauna was living in a vast floodplain, in which fluvial channels carried southward the detrital material coming from the Rouergue substratum. The Dolomitic Formation was deposited in the context of a northward marine transgression during which shallow and aerial environments prevailed in the area.

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Mots clés :
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Théropodes
France

RÉSUMÉ

Sur la bordure cristalline méridionale du Rouergue, la Formation des Grès et Argilites bariolées et la Formation Dolomitique contiennent de nombreuses traces de pas de dinosaures datées de l'Hettangien basal. Parmi les 25 sites répartis sur une quarantaine de kilomètres entre Marcillac-Vallon et Saint-Geniez-d'Olt, deux d'entre eux, Puech de Castres et Le Bouyssou, ont livré des ichnites abondantes dans plusieurs niveaux stratigraphiques bien repérés. L'étude combinée de ces traces par des méthodes biométriques et morphométriques (analyse de Fourier) permet de les attribuer aux ichnogenres *Grallator, Eubrontes* et *Dilophosauripus*. La complémentarité des analyses révèle deux nouveaux morphotypes jusqu'alors inconnus dans le bassin des Causses. De plus, des similitudes morphologiques sont mises en évidence entre *Grallator* et *Eubrontes*. Ces ichnites sont

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attribuées à des théropodes Coelophysoidea et pourraient représenter un même taxon à différents stades de croissance. La faune dinosauriennne à l'origine de ces traces évoluait dans une plaine d'inondation parcourue par un réseau fluviatile transportant vers le sud des matériaux détritiques issus de l'érosion proximale du socle du Rouergue, en marge de la transgression marine provenant du sud.

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1. Introduction

Trace fossils are essential to our understanding of the spatio-temporal distribution of dinosaurs, especially in the Early Jurassic where many dinosaur occurrences are ichnites rather than body fossils (Weishampel et al., 2004). Many localities with Early Jurassic dinosaur footprints are known in France, mainly in the Hettangian Dolomitic Formation of the "Grands Causses" area in which different ichnogenera were identified (Demathieu et al., 2002; Gand et al., 2007). However, in the northwestern part of this region known as the Rodez Strait, older dinosauroid footprints were found by Fuchs (1964) near Cruéjouls in the underlying Sandstones-variegated Mudstones Formation that rests on the basement. This site supplies traces for amateur collectors, but some ichnites were made available to science by J. Sciau despite the absence of detailed contextual data (Demathieu et al., 2002; Gand et al., 2005; Sciau, 2003). The discoveries of numerous new footprints by one of us (AM) in the historical site of "Cruéjouls" (named here Le Bouyssou), but also in 25 other places distributed along a 40 km west-east transect, permit an in-depth study of this megatracksite. Two specific sites offer large outcrops and lend themselves to precise investigations: Le Bouyssou and Puech de Castres. The aim of this article is to define the morphological characteristics of these footprints and to know what palaeoenvironmental inferences can be drawn from them and their associated sedimentological context. We provide a stratigraphical and sedimentological account for these two sites, we investigate the footprints using both biometric and morphometric methods, and we compare our samples with those from other Hettangian localities in France and in the USA.

2. Geological setting, age of the footprint-bearing formations and palaeoenvironments

The Causses Basin is located southwest of the Massif Central. Its northwestern part forms the Rodez Strait in which are located the ichnological sites "Puech de Castres" and "Le Bouyssou" (Causse Comtal, Aveyron, Fig. 1). Both localities belong to the basal detrital Sandstones-variegated Mudstones Formation described by Alabouvette et al. (1989), Burg et al. (1992), Defaut et al. (1990), Fuchs (1964, 1969), Rousset and Becq-Giraudon (1989), Simon-Coinçon (1989). This formation is composed by alternations of rubefied lenticular channelized sandstones and variegated argillites that show marked lateral variation in facies. The outcrops of Le Bouyssou and Puech de Castres show cross stratifications, desiccation cracks, palaeosols (root casts), local carbonaceous or lignitous layers and plant remains (Fig. 2). The upperlaying Dolomitic Formation also displays desiccation cracks. At Puech de Castres, footprints were found in two sandstone dolomitic layers (Fig. 2: A1, A6) and in one limestone layer (Fig. 2: B3). Only one lenticular sandstone level yielded footprints at Le Bouyssou (Fig. 2: C2). Based on palynological data (presence of *Classopolis* without Triassic species), the Sandstones-variegated Mudstones Formation is considered to be Early Hettangian in age (Alabouvette et al., 1989; Burg et al., 1992; Grigniac and Taugourdeau-Lantz, 1982). The presence of *Cardinia* (Bivalvia) at the base of this formation at Le Bouyssou agrees with this dating (Fuchs, 1969 in Alabouvette et al., 1989). The Dolomitic Formation started being deposited during the Hettangian transgression (Grigniac and Taugourdeau-Lantz, 1982).

The sedimentological features of the Sandstones-variegated Mudstones Formation suggest a continental palaeoenvironment bordering the Rouergue Hercynian peneplain. The area was a vast floodplain in which fluvial channels periodically occurred.

Some sandstone levels correspond to crevasse splays and they alternate with argillites that represent temporary calm deposits. Palaeosoils and desiccation cracks indicate periods of aerial exposure probably under a dry climate with alternate seasons. These palaeosoils are affected locally by an intense alteration resulting from dolomitization processes. The latter sometime form vertical conducts (dolocretes) interpreted as root casts (Grigniac, 1983; Spy-Anderson, 1980). The north-south orientation of casts of tree trunks in several sandstone units at Puech de Castres suggests detrital inputs from the crystalline northern border of the Rouergue, where these plants originally lived. The petrography of the pebbles at Puech de Castres confirms this nearby erosional phenomenon that was accompanied with silicification and dolomitization processes (Simon-Coinçon, 1989). In this locality, a thin argillite layer rich in bivalves and containing some gastropods suggests a lagoon-like environment that preceded the northward marine transgression at the origin of the overlying Dolomitic Formation. The latter witnessed the installation of a shallow environment that has left evaporitic facies locally (Alabouvette et al., 1989; Moreau, 2011). More to the south, in the Lodève area, the Dolomitic Formation is interpreted as marine swamps with a propensity to emersion (Arrondeau, 1982, Marza, 1995), as testified by the vertical frequency of levels with dessication cracks and dinosaur footprints (Demathieu et al., 2002).

3. Materials and methods

A total of 70 tridactyl II–IV footprints, mainly convex hyporeliefs were discovered: 10 at Puech du Castres and 60 at Le Bouyssou. This last site actually yielded 6 assemblages

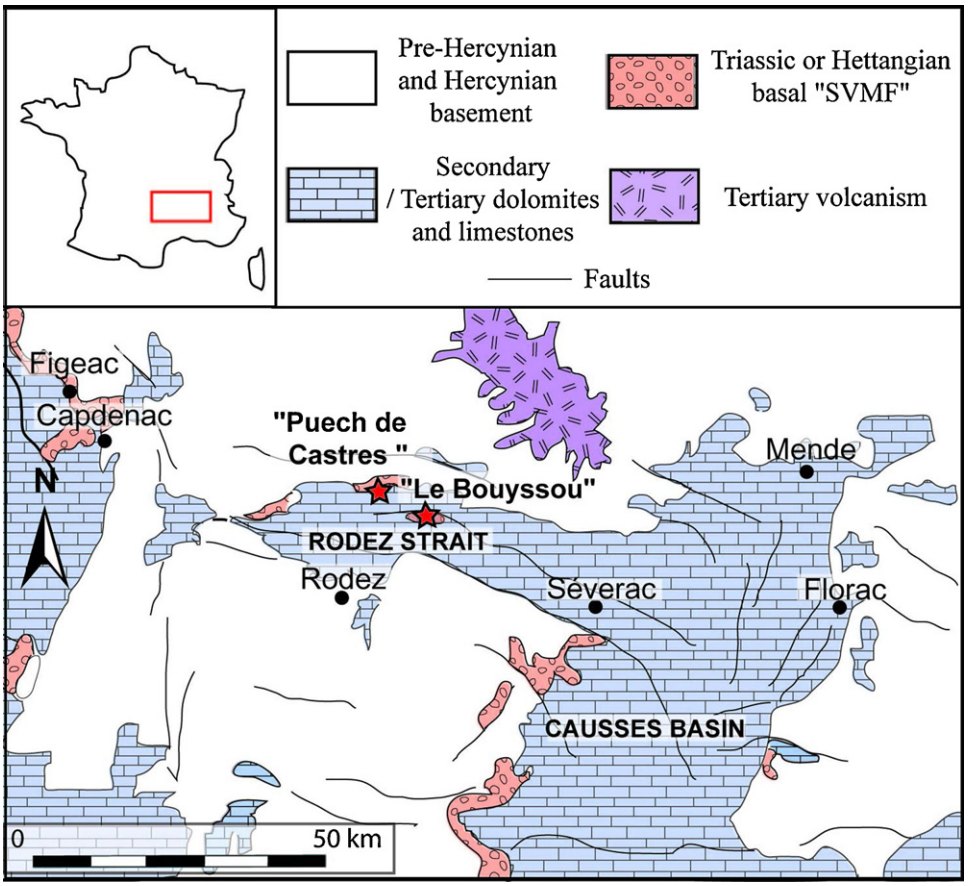

Fig. 1. Location of "Puech de Castres" and "Le Bouyssou" near Cruéjouls on the geological map of Grigniac and Taugourdeau-Lantz (1982), modified. SVMF: Sandstones and Variegated Mudstones Formation.
Fig. 1. Localisation des sites d'étude sur la carte géologique de Grigniac and Taugourdeau-Lantz (1982), modifiée. SVMF : Sandstones and Variegated Mudstones Formation.

(A to F) from level C2 (Fig. 2), but they cannot be joined into a continuous surface. The largest assemblage is shown in Fig. 3, and several footprints are detailed in Fig. 4. Although there are 32 traces, no trackway could be observed. Most of these specimens are conserved temporarily in the scientific collection of Alain Michelin.

Biometric measurements were taken as shown on Fig. 5. Ratios were computed on a selection of 25 footprints from Le Bouyssou and Puech de Castres. This sample is constituted of the best preserved footprint and is representative of the overall morphological diversity. It is compared with the Hettangian footprints from the Dolomitic Formation (Causses) studied by Demathieu et al. (2002). Biometric measurements were used to identify different morphotypes that were then evaluated by a morphometric approach. The latter is a Fourier analysis (Complex Discrete Fourier Transform [CDFT]) applied on 19 footprints whose outline is closed and well defined. Using the MATLAB Toolbox CDFT (Dommergues, 2001, Dommergues et al., 2007; Navarro et al., 2004), 200 points were used for reconstructing the outline and the amplitudes of the first 11 extracted harmonics (they capture about 95% of the original outline for our sample). For comparison, we applied the same procedure to a dataset on the ichnogenus *Eubrontes* from other places of the Causses Dolomitic Formation (Demathieu et al., 2002) and from the Hitchcock collection (Pratt Museum, Amherst, USA; Lull, 1953; Olsen et al., 1998; Rainforth, 2005). Harmonic amplitudes were chosen rather than coefficients because they are less sensitive to variation in footprint orientation and to the location of the starting point for the outline reconstruction (Dommergues et al., 2007). Amplitude values were then explored with a Principal Component Analysis (PCA), and among morphotypes, significant differences in amplitude were tested with a one-way NPMANOVA (Bray-Curtis distance). Because statistical significance is evaluated after 10,000 permutations, 20 successive runs were made and the highest probability found during this procedure is reported. Pairwise post hoc NPMANOVAs were computed with the very conservative Bonferroni correction and with α set at 5%. All computations were made with PAST v2.09 (Hammer et al., 2001).

4. Results

Several biometric parameters (L/W, L/D, [L-D]/L, T and L), together with other morphological criteria (e.g., the

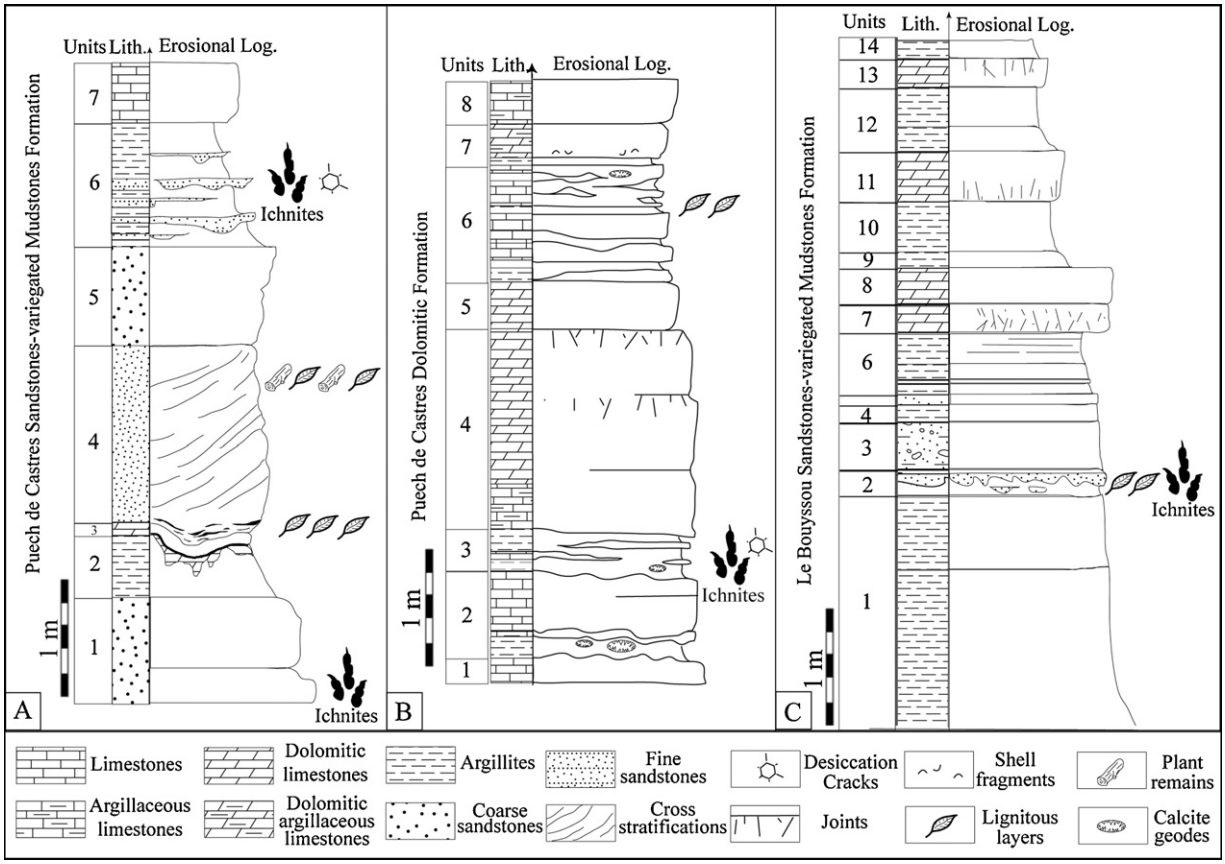

Fig. 2. Position of footprint-bearing layers in the Sandstones–variegated Mudstones Formation at Puech de Castres (A) and Le Bouyssou (C); and in the Dolomitic Formation at Puech de Castres (B).
Fig. 2. Localisation des traces de pas dans la Formation des Grès et Argilites bariolées à Puech de Castres (A) et près de Le Bouyssou (C) ; et dans la Formation Dolomitique de Puech de Castres (B).

relative position of digits, digit width, pad shape), suggest the existence of seven morphotypes M1–M7. Because they tend to differ in size, most of them can be recognized on a simple bivariate diagram confronting T with L (Fig. 6A). Puech de Castres yielded the smallest morphotypes M1, M2 (Fig. 4, no. 25) and M3, whereas the whole morphotype size range is present at Le Bouyssou: M1 (Fig. 4, no. 10), M4 (Fig. 4, nos. 3, 8, 9 and 13), M5, M6 (Fig. 4, nos. 12, 14, 15, 17, 19 and 22), and M7 (Fig. 4, nos. 11, 13, 18 and 21). A previous study on dinosaur footprints from the Dolomitic Formation classified ichnites into 3 biometric groups, each containing specific ichnospecies (Demathieu et al., 2002): group I, *Grallator variabilis*, *Grallator sauclierensis*; group II, *Grallator lescurei*, *Grallator minusculus*, *Dilophosauripus williamsi*; and group III, *Eubrontes giganteus*. Fig. 6B represents the position of footprints from the Rodez Strait in the biometric space of these 3 ichnological groups. The latter are all occupied by footprints from either (or both) Puech de Castres and Le Bouyssou, although a few ichnites fall slightly outside the morphological envelops defined by Demathieu et al. (2002). Morphotype M1 (from Puech de Castres and Le Bouyssou) belongs to the group of the smallest ichnospecies and it can be attributed to *G. variabilis* or *G. sauclierensis* (Fig. 6B). No previously described morphotype from the Dolomitic Formation is comparable to M2. Morphotype M4 falls into group II but its biometric values, especially L/W≈1, refine its attribution to *D. williamsi*. Although M5 is located into group II because of its length, it has L/W and T values (respectively 1.25 and 59°) that are characteristic of *E. giganteus*. M6 can be attributed to *D. williamsi*, but its mean length is the largest ever found in the Causses Basin (28.8 cm, to be compared with 19.8 cm reported by Demathieu et al., 2002). M7 can be assigned to *E. giganteus* and its mean length (34 cm) places it among large ichnites.

Fig. 7 shows the PCA scatter plot based on Fourier-derived harmonic amplitudes, without morphotypes 3 and 5 because their outline was too poorly preserved. The two first axes represent 45.2 and 25.9% of the total variance. The interpretation of the PCA components is difficult, but Component 1 seems to express mainly the L/W ratio. The convex hulls for M1, M6 and M7 overlap with the one of *Eubrontes* from the Dolomitic Formation along the first three PCA components. Along Component 1, they occupy a rather intermediate position between a pole formed by M2 and M4, and one with the *Eubrontes* ichnites

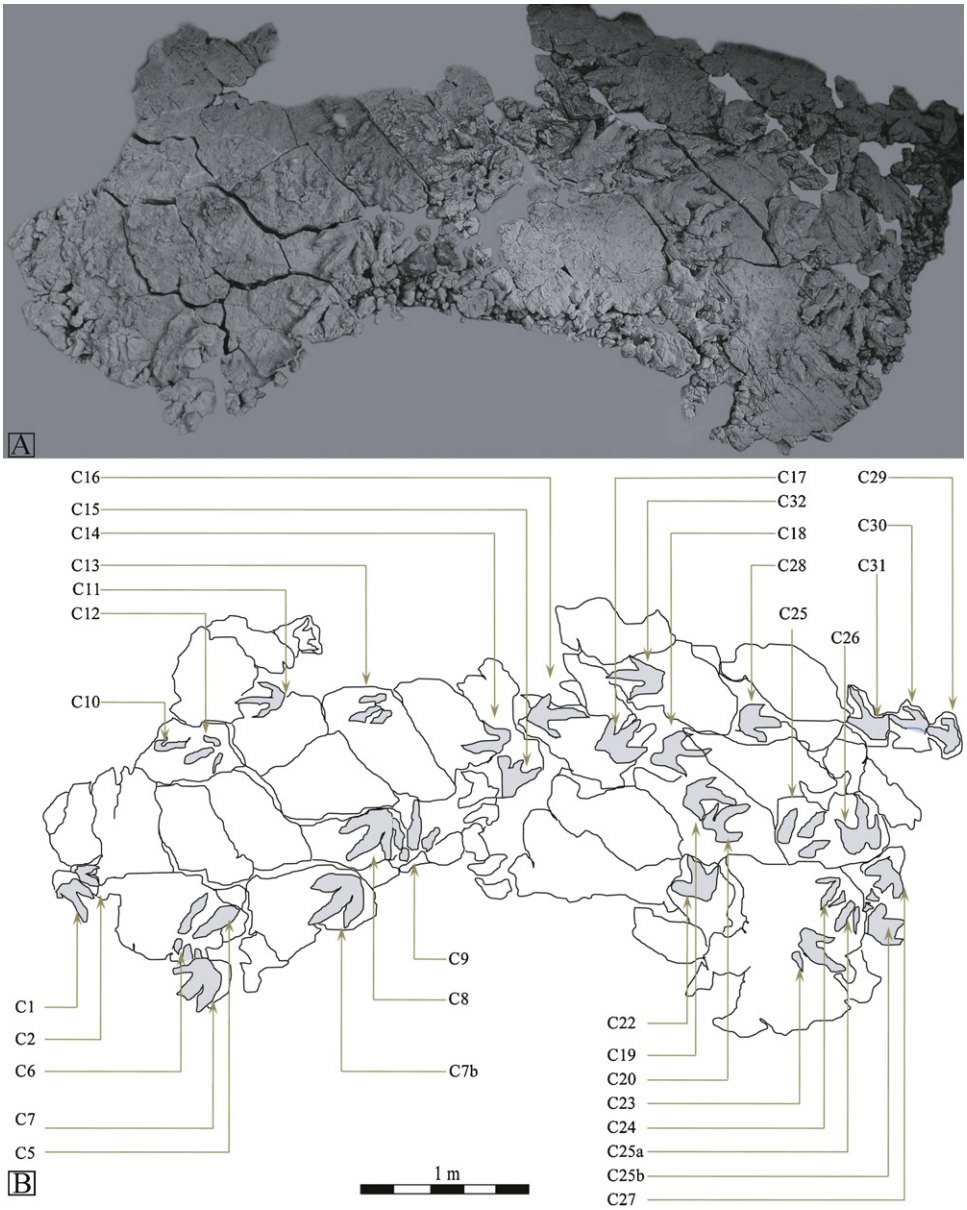

Fig. 3. A: Assemblage C made by AM showing 32 dinosauroid footprints *Eubrontes* from slabs of layer 2 at Le Bouyssou (C Fig. 2); **B:** Interpretative schematic sketch with ichnite names. Some of them are figured in fig. 4.
Fig. 3. A : Assemblage C constitué par AM montrant 32 traces dinosauroïdes *Eubrontes* (hyporeliefs convexes) à partir de dalles du niveau 2 de Le Bouyssou (C Fig. 2) ; **B :** interprétation schématique avec repérage des ichnites dont certaines sont représentées sur la Fig. 4.

from the USA (Fig. 6). The NPMANOVA corroborates this pattern as it shows an overall significant difference among morphotypes ($F = 3.262$, $p < 0.0001$), and post hoc pairwise comparisons are only significant between USA *Eubrontes* and both M2 and M4 ($0.0189 < p < 0.048$ and $0.0021 < p < 0.0168$, respectively). The p value between USA *Eubrontes* and *Eubrontes* from the Causses Dolomitic Formation is also significant ($0.0033 < p < 0.0059$). The same analysis carried only on Rodez Strait's morphotypes suggests a marginally significant difference among their amplitudes ($0.0432 < p < 0.05$), which is essentially caused by the peculiarity of M2.

5. Discussion and conclusion

Both approaches help to distinguish M2 and M4 from the other morphotypes, and they both suggest an assignment of M7 to *Eubrontes* (Fig. 6B and 7). Biometry places M6 in the range of *D. williamsi* (Fig. 6B), whereas morphometry suggests an assignment to *Eubrontes* for

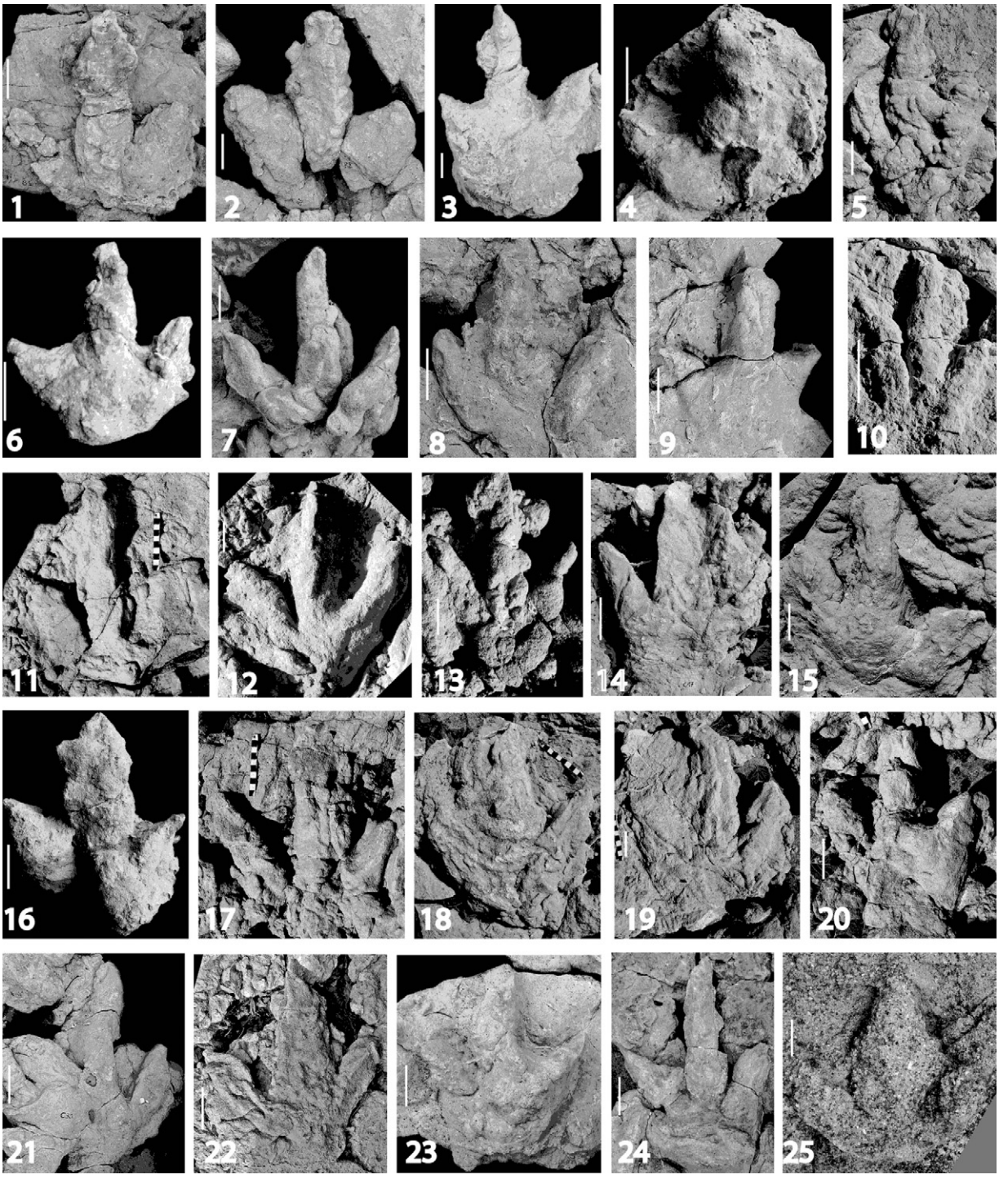

Fig. 4. Dinosauroïd tridactyl II-IV footprints of the assemblages B to F (Le Bouyssou), level 2 and P (Puech de Castres), levels 1, 6, Sandstones-variegated Mudstones Formation; no. **1-2** = footprints B1 and B2; no. **3-4, 6-9, 16, 23** correspond respectively to D1, D4, D7, D12, D16, D17, D3, D18; no. **5, 11-15, 17-22** = C20, C7B, C8, C9, C17, C19, C25 bis, C25, C26, C27, C30, C32; no. **10** = F1, **24** = E2, **25** = P6 of assemblages F, E and P; F1, E2 = *Grallator sensu* Demathieu et al. (2002), D1, D7–D18 = *Dilophosauripus*, C7B, C9–C17, C18, C20-C31 = *Eubrontes*; white scale bare = 5 cm, other = 10 cm.

Fig. 4. Traces de pieds dinosauroïdes des assemblages B à F (Le Bouyssou), niveau 2 et P (Puech de Castres), niveaux 1, 6, Formation des Grès et Argilites bariolées ; nº **1-2** = traces B1 et B2 ; nº **3–4, 6–9, 16, 23** correspondent respectivement à D1, D4, D7, D12, D16, D17, D3, D18 ; n° **5, 11–15, 17–22** = C20, C7B, C8, C9, C17, C19, C25 bis, C25, C26, C27, C30, C32 ; n° **10** = F1, **24** = E2, **25** = P6 des assemblages F, E et P ; F1 et E = F1, E2 = *Grallator sensu* Demathieu et al. (2002), D1, D7–D18 = *Dilophosauripus*, C7B, C9-C17, C18, C20-C31 = *Eubrontes* ; Barre d'échelle blanche = 5 cm, Barre d'échelle noire et blanche = 10 cm.

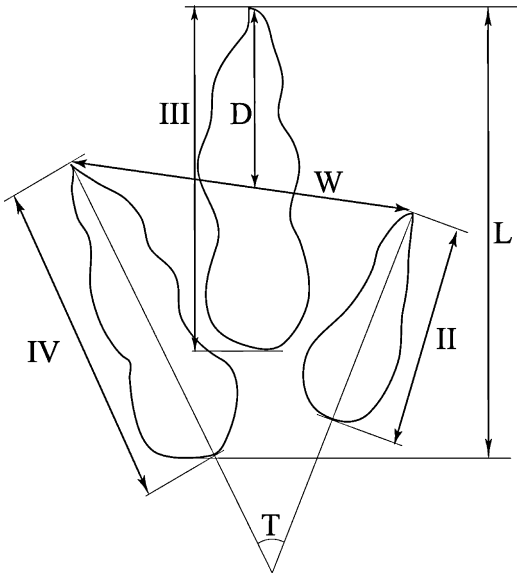

Fig. 5. Biometric measurements taken on dinosauroid footprint ; L: pes length; W: II–IV distal interdigit width; II, III, IV: digit lengths; D: length of the free part of III; T: angle between II–IV.
Fig. 5. Caractères mesurés ; L : Longueur du pied ; W : distance entre les extrémités distales II–IV ; II, III, IV : longueurs des orteils ; D : dimension libre de l'orteil III ; T : angle II–IV.

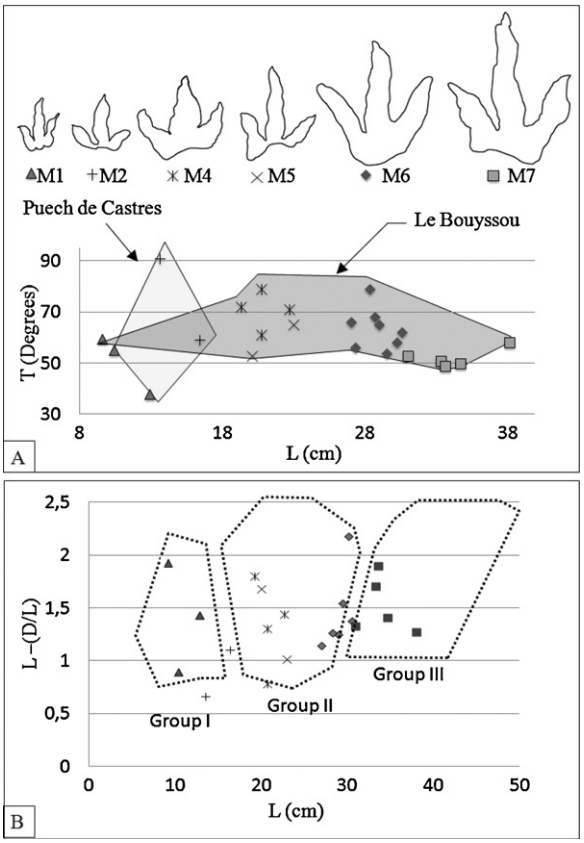

Fig. 6. Footprints from Puech de Castres and Le Bouyssou in a bivariate diagram L vs. T (**A**) and in a bivariate diagram L vs L-(D/L) (**B**); Groups I, II, III correspond to the biometrical envelops defined by Demathieu et al. (2002) based on Causses footprints.
Fig. 6. Localisation des empreintes de Puech de Castres et de Le Bouyssou dans un diagramme bivarié L par rapport à T (**A**) et dans un diagramme bivarié L par rapport à L-(D/L) (**B**). Les groupes I, II et III correspondent aux espaces biométriques définis par Demathieu et al. (2002) pour les empreintes des Causses.

this morphotype (Fig. 7). This is because M6 presents a combination of dimension and morphology that was previously unknown among the Hettangian ichnotaxa reported from the Causses. M6 occupies an intermediate position between *Dilophosauripus* and *Eubrontes*.

Although biometry places M1 and M7 in the respective range of *Grallator* group I and of *E. giganteus* group III (Demathieu et al., 2002; Sciau, 2003), PCA and NPMANOVA do not discriminate these two morphotypes. Lapparent and Montenat (1967) have already mentioned some resemblance between *Eubrontes* and some large *Grallator*, such as *G. minusculus*. Thus, the hypothesis of similar trackmakers leaving footprints at different growth stages cannot be excluded, as it was shown for other traces found in the Dolomitic Formation of the Causses (Demathieu et al., 2002: pp. 95–96).

The significant difference between the outline amplitudes of *Eubrontes* from the USA and from the Causses may indicate different trackmakers. As a whole, our study warrants the occurrence of *Grallator, D. williamsi* and *Eubrontes* at Puech de Castres and at Le Bouyssou. It also reveals two new morphotypes previously unknown in the Hettangian of the Causses Basin: M2 (Fig. 4, no. 25) and M6 (Fig. 4, nos. 12, 14, 15, 17, 19, 22). However, the limited size of the sample impedes the erection of new ichnotaxa as the variability in footprint outline cannot be properly characterized statistically.

Footprint outline analyses are not as discriminant as those incorporating biometric data because they dismiss differences in size, notably for digital surface. Despite this, our data underline the proximity of *Eubrontes* and *Grallator* and they testify to the presence of original morphotypes in the Causses area (M2 and M6).

Finally, the same Hettangian ichnofauna (*Grallator, Eubrontes* and *Dilophosauripus*) occurs in both the carbonated Dolomitic Formation and the detrital Sandstones-variegated Mudstones Formation in northern Causses. These two first ichnotaxa have led Demathieu et al. (2002) to infer the presence of Cerotosaurian theropods at different life stages (trackmakers of *Grallator* and *Eubrontes*). However, the trackmakers most probably belong to Coelophysoidea because all body fossils of theropods known in Europe before the end of the Early Jurassic belong to that clade. In addition, although *Dilophosauripus* was ascribed to ornithopods by Demathieu et al. (2002), its trackmaker is certainly a theropod because of the frequent presence of strong claw traces. This paleozoological assignation was formerly made by Welles (1971). The presence of *Dilophosauripus* has also been inferred recently in the Dolomitic Formation from the northeastern part of the Causses, in the Lozère Département (Moreau, 2011). Further investigations on the geographical and temporal

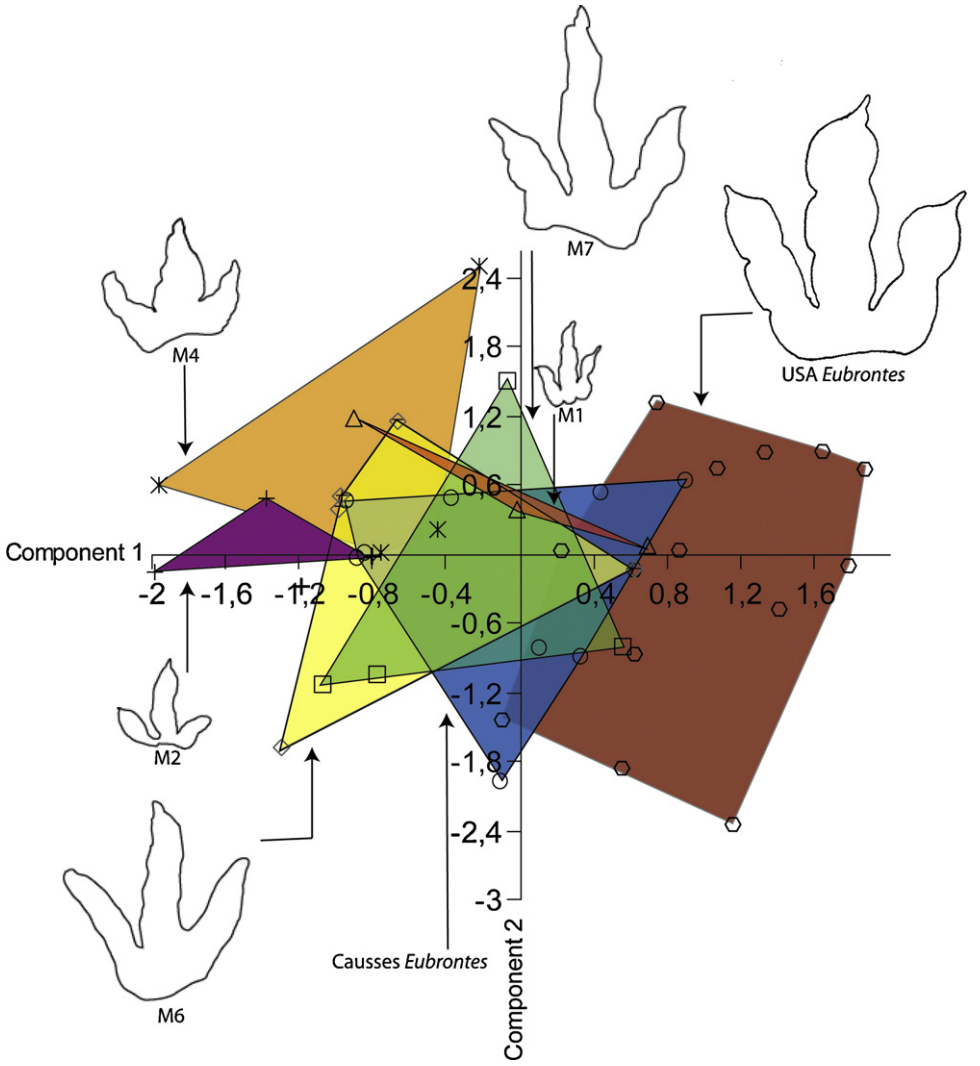

Fig. 7. Principal Component Analysis (PCA) based on the amplitudes of footprint morphotypes from Puech de Castres and Le Bouyssou, together with those of *Eubrontes* from the Causses Dolomitic Formation and from the USA.
Fig. 7. Analyse en composantes principales (ACP) réalisée à partir des amplitudes des contours des traces de pas de Puech de Castres et de Le Bouyssou et de ceux d'*Eubrontes* des USA et de la Formation Dolomitique des Causses.

distribution of these ichnotaxa will undoubtedly reveal more about their biological interpretation, and the Causses will assuredly be a key area in that perspective.

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