The French Middle Jurassic dinosauroid trackways: interpretation and nomenclatural re-evaluation[†]

Georges Gand[*], Georges Demathieu

UMR 5561 du CNRS Biogéosciences, Centre des Sciences de la Terre, Université de Bourgogne, 6, boulevard Gabriel, Dijon 21000, France
Received 1 July 2003; accepted 6 October 2004
Posted in the internet 05 October 2005

1. Introduction

In the French Triassic, the oldest dinosauroid (sensu Nopcsa, 1923) traces were found in 1960 by Georges and Germaine Demathieu. They were initially in the Mont d'Or of Lyon and then in the Autunois. They included several isolated prints of tridactyl feet that were described under the names *Anchisauripus bibractensis* Demathieu, 1971 and *Coelurosaurichnus* sp. (Demathieu, 1970, 1971).

After 1969, the excavation, by Georges Gand, of a footprint-bearing locality in the Autunois—the la Pissoire quarry—permitted extracting large surfaces with footprints and the discovery of numerous trackways of tridactyl bipeds that were referred to the preceding ichnogenera (Gand, 1971; Demathieu and Gand, 1972a, 1972b). Subsequently, the researches undertaken in Bourgogne at several other localities (Gand, 1971, 1979d; Gand et al., 1973, 1976a, 1976b; Demathieu and Gand, 1981a, 1981b, 1986), but also in Ardèche (Demathieu and Samama, 1968; Montenat, 1968; Courel and Demathieu, 1976) led to the discovery of others. All these dinosauroid traces are associated with those of "pseudosuchians" = Crurotarsi and of lepidosaurians, together forming a characteristic Middle Triassic paleoichnofauna.

Based on palynological, micropaleontological, and ichnological data, the vertebrate footprint levels of the Grès inférieurs Formation were dated to the Middle Triassic. This makes it possible to currently consider the French Triassic dinosauroid traces as the oldest. The great paleontological interest in their measurement makes it possible to discuss the origin of dinosaurs.

Their morphometric comparison with younger tridactyl prints, French and German, will also permit discussing again the questions of nomenclature.

2. Middle Triassic dinosauroid trackways and traces

[†] Original citation: Gand, G. & G. Demathieu. 2005. Les pistes dinosauroïdes du Trias moyen français: interprétation et réévaluation de la nomenclature. *Géobios*38:725-749. Translated by Matthew Carrano, Smithsonian Institution, 2006-2007.

[*] Corresponding author.
E-mail address: georges.gand@wanadoo.fr (G. Gand).

2.1. Location

These imprints were collected in diverse formations at the base of the Triassic called "Grès inférieurs"[1] (Figs. 1 and 2). In Bourgogne and the Lyonnais, these sandstones were excavated, in the 19th century and in the first half of the 20th century, in the numerous "arkose" quarries opened for the fabrication of paving stones. These are the ichnological sites (Courel, 1970; Demathieu, 1970; Gand, 1971, 1979d). Farther south, in Ardèche, the galleries of the silver-bearing galena (Largentière) and their natural outcrops also furnish a great number of imprints (Demathieu and Samama, 1968; Courel and Demathieu, 1976).

The majority of them correspond to convex hyporeliefs. They were observed in elementary sequences, associated with salt pseudomorphs, dessication cracks, wrinkles, and some ichnotaxa attributed certainly to Crurotarsi (*Synaptichnium* Nopcsa, 1923; *Chirotherium* Kaup, 1835; *Isochirotherium* Haubold, 1971; *Brachychirotherium* Beurlen, 1950, and *Sphingopus* Demathieu 1966: Figs. 4 and 5), others to lepidosaurians (*Rhynchosauroides* Maidwell, 1911), Dinosauromorpha (*Rotodactylus* Peabody, 1948: Fig. 3), small cotylosaurians (*Circapalmichnus* Gand, 1977a; *Procolophonichnium* Nopcsa, 1923), and small indeterminate microvertebrates (*Minutipes* Demathieu, 1970; *Longipes*, *Furcapes*, *Paraophidichnium*: all three from Demathieu, 1977) (Demathieu, 1966, 1970, 1971, 1977; Demathieu and Gand, 1974; Gand, 1974c, 1977a, 1977b, 1979b). The ensemble constitutes a characteristic paleoichnofauna of the "Grès inférieurs" known from the Mâconnais in Bourgogne, the Lyonnais (NW of Lyon), and Roubreau, in Ardèche. They were emplaced during the Middle Triassic transgression onto the Paleozoic base along the eastern border of the Massif Central (Courel, 1970, 1973; Courel et al., 1984).

2.2. Ages of the footprint localities

2.2.1. In Bourgogne

2.2.1.1. In the Côte-de-Beaume, the Châlonnais, and the Mâconnais (Fig. 2(2)). The Grès inférieurs Formation is subjacent to the Calcaires gréseux Formation of Milly, which was dated as Ladinian by a rich microfauna with remains of bivalves, gastropods, crinoid stem segments, bryozoans, fish teeth, and foraminiferans such as *Ophthalmidium chiialingchiangense* Ho, 1959 (Fig. 2(2), FO, P) (Courel, 1970, 1973; Courel et al., 1984: 78-79). But as the summit part of this carbonate formation also contains a palynological association from the Upper Ladinian (Adloff and Doubinger, 1979), these Grès inférieurs are therefore earlier than the Upper Ladinian.

"According to the reptile imprints, the Grès inférieurs of the Mâconnais are situated in the upper part of the Anisian and/or the base of the Ladinian," according to Courel in Courel et al. (1984:79). They were dated to the Upper Anisian or Lower Ladinian by Demathieu in Courel et al. (1984:64) and by Courel and Durand in Courel et al. (1984:70).

[1] "lower sandstone" (MTC)

2.2.1.2. In the Charolais and the Autunois. The Brosses-Thillots quarry (Mont-Saint-Vincent, Nord-Charolais), those of the Plateau d'Antully, in the Autunois (notably La Pissoire, Pont d'Argent; Fig. 2(1)), which have furnished the greatest number of dinosauroid traces are more difficult to date because microflora and microfauna have not been found.

In these regions, located west of the Mâconnais, the Grès inférieurs Formation of the Mâconnais and the Calcaires gréseux Formation of Milly are reduced in thickness and are not clearly distinguishable there. In the Mont-Saint-Vincent sector, they were regrouped under the term "Grès fin à pseudomorphoses de sel gemme et empreintes de reptiles"[1] (Courel, 1970:32; Courel, 1973:19) and, in the Autunois, under that of "Grès d'Antully"[2] or "Grès fin à empreintes de Reptiles et pseudomorphoses de sel gemme"[3] (Courel, 1970:47-51; Courel, 1973:24).

2.2.2. In the Lyonnais (Fig. 2(3))

The Grès inférieurs of the Lyonnais are subjacent to the "Calcaires roses de la Font-Poivre", which revealed a fauna with vertebrate teeth, lamellibranchs (*Myophoria*), gastropods, brachiopods, and a Ladinian microfauna (Courel, 1970, 1973; Courel in Courel et al., 1984:81). Being based on the association of vertebrate foot traces, these Grès inférieurs have the same age as those of the Mâconnais (Courel et al., 1984:64 and 81; cf. supra).

2.2.3. In Ardèche

In Ardèche, the Grès inférieurs Formation of Roubreau sensu Finelle (1981) (= Grès à empreintes in Courel et al., 1984, = Grès du Roubreau in Razin et al., 1996; Courel et al., 1998) has revealed in the environs of Largentière and Daüs, several levels with traces of vertebrates which are localized in the lower and middle parts of this formation (Fig. 2(4)) (Demathieu and Samama, 1968; Montenat, 1968; Courel and Demathieu, 1976, 2000; Courel et al., 1980; Finelle, 1981).

Based on palynological data, the levels specified by numbers in column F in Fig. 2(4) were dated, in 2, to the Anisian-Ladinian (Doubinger and Adloff, 1977) and, from 1 to 3, to the Anisian to Lower Ladinian inclusive (Fauconnier et al., 1996). The conodonts (Fig. 2(4), column C) specify the base of the Ladinian (Hirsh in Courel et al., 1998).

By crossing these various datings, the Grès inférieurs of Roubreau were therefore deposited during the Anisian and the top of the Lower Ladinian. They surmount the Grès Formation with basal Buntsandstein facies, which has not been dated in this department (Fig. 2(4)), nor moreover, farther south, in Gard, where it is known under the name "Formation inférieure"[4] (Perrissol, 1990).

We also specify, that from palynological data (Fig,. 2(4)), levels 7 and 8 were dated as Carnian (Fauconnier et al., 1996). No. 5, from the Upper Ladinian, no. 6 from the Ladinian-Carnian boundary, and no. 7 were arranged in the Lower Carnian, according to Doubinger and Adloff (1977): 10 was not dated.

---

[1] "final sandstone with rock salt pseudomorphs and reptile prints" (MTC)
[2] "Antully sandstone" (MTC)
[3] "final sandstone with reptile prints and rock salt pseudomorphs" (MTC)
[4] "lower Formation" (MTC)

2.3. Description

2.3.1. Presentation

The dinosauroid traces were described by Demathieu (1970) for the Lyonnais; by Demathieu (1970, 1970); Demathieu and Gand (1972a, 1972b, 1981a, 1981b); Gand (1971, 1975a, 1976, 1978b, 1979c, 1979d); Gand et al. (1976b) for the Autunois; Gand (1973, 1974a); Gand et al. (1973) for the Nord-Charolais; Gand (1977a); Gand (1978a) for the Châlonnais; Demathieu and Gand (1986) for the Mâconnais; Gand et al. (1976) for the Auxois, and Courel and Demathieu (1976) for the Ardèche. These are several hundred footprints in total that have been recovered, most of them coming from the quarries of La Pissoire and Pont d'Argent of the Plateau d'Antully in the Autunois.

Based on their morphological characters, often supplemented with a statistical study when the number of samples permitted, several ichnospecies were distinguished. They are *Anchisauripus bibractensis*, *Coelurosaurichnus perriauxi* Demathieu and Gand, 1972a; *Coelurosaurichnus sabinensis* Gand et al., 197a; *Coelurosaurichnus palyssii* Gand, 1976, and *Coelurosaurichnus largentierensis* Courel and Demathieu, 1976. These dinosauroid traces were associated with other ichnospecies, schematized in Figs. 3 and 4, among which *Sphingopus ferox*, *Chirotherium barthi*, *Brachychirotherium circaparvum* Demathieu, 1971, and *B. tintanti* Demathieu, 1971 are always encountered.

In order to take account of the new discoveries of prints occurring after the description of the ichnotypes *C. perriauxi* and *A. bibractensis*, the specimens were re-measured using the method of Lull (1953). The results are in Tables 1 and 2, which contain the statistical parameters for each of them.

In the text, the following abbreviations are used: L = length, l = width, P = pes, M = manus, E = stride length, CPM = length of manus-pes pair. These are also reported in the legend for Table 1.

After calculating of traditional parameters, average, standard deviation, etc., we used the Cramer test based on asymmetry to appreciate the distribution of each character (Van der Waerden, 1967; Courel and Demathieu, 1976; Gand, 1987). This follows the normal law as much better than the probability of exceeding the reduced variable (= VR) is higher than the threshold 5%; that is, VR = 1.96. To compare the specimens, Fisher's or Snédecor's tests of the ratio of the variances and Student's for the averages, clarified in Monjallon (1968) and Moroney (1970), will be used.

2.3.2. Anchisauripus bibractensis Demathieu, 1971

2.3.2.1. Traces of autopodia (Fig. 5(9); 6(1-3, 6-16); 7(12-21, 45-47); 8(7, 9, 11, 12); 9(11, 13, 14)). This ichnospecies is represented by prints of tridactyl feet with rather slender and well-separated digits, comprising generally well-drawn pads. Digits II, III, and IV always show 2, 3, and 3 successively, but for IV, the digito-metatarsal pad can exist. This is nevertheless rare.

Referring to Table 1(2) of measurements of the reference sample made up of traces coming from levels well fixed in the Triassic stratigraphy of the Autunois (La Pissoire and Pont d'Argent quarries), one sees that *A. bibractensis* corresponds to small prints whose length is less than one decimeter. The II-IV angle is weak, and the size of digit IV is nearly equal to that of III. The result is that III slightly exceeds the lateral

digits (character D; L/D = 2.77), contrary to that noted in the same-sized prints of *Grallator* sensu Lull (1953); Olsen et al., (1998). We also note that the coefficients of variation of the ratios are remarkably weak except for L/D. In addition, the ichnopopulation is homogeneous because P > 5%. The two characters are correlated.

We attribute two manus prints to this ichnospecies, associated with a trace of a plantigrade pes that perhaps falls within this ichnopopulation according to the Discriminant Analysis (Fig. 5(13)). In this half-trackway, discovered in the Châlonnais (Gand, 1978a), one of the two forefoot prints, clearly smaller than that of the pes, has a typically chirotheroid aspect. Thus it is paraxonic, pentadactyl, and possesses short, large digits bearing narrow claws, except for V.

2.3.2.2. Trackways. They were studied by Gand (1971); Demathieu and Gand (1972b, 1981a); Gand (1979d). The longest belong to a surface that was extracted from the La Pissoire quarry (level BF2) bordering approximately 16 m^2 (Gand, 1971, 1974b, 1979d).

The principal characteristics of these trackways, in which there are only pedal traces, are the following. The step angle is on average 175° within an interval of 173-178°; E/P = 1.3., the value included between 13 and 14. The orientation O of the pes with the trackway axis equals 1.70° with 0° < O < -3.3°(Fig. 6(1-3)).

2.3.3. Coelurosaurichnus perriauxi Demathieu and Gand, 1972a, 1972b

2.3.3.1. Traces of autopodia (Fig. 5(3-6); 6(4, 5, 27-49); 7(1-7, 22-44); 8(1-5, 10); 9(2-7); Table 1(1)). This ichnospecies regroups, essentially, the pedal traces Ii-IV that were often observed in the Autunois. They are a little larger (average L = 82.46 mm) than in *A. bibractensis*. The digits there are also larger and less loose with less well-drawn pads. Digito-metatarsal pad IV is more frequent than in *A. bibractensis*. The dimensions of digits III and IV are subequal. With L/D = 2.95, III slightly exceeds the lateral digits.

In the Grès inférieurs Formation, the greatest length of *C. perriauxi* does not exceed 109 mm, except in the Nord-Charolais where some of them reach 142 mm (Fig. 8).

The manus trace is very rarely associated with that of the pes. We have noted it in 4% of the cases, and only in the Pont d'Argent quarry (Autunois) (Figs. 5 and 9(3-5)). When it is complete (Figs. 5(3-6) and 7(37)), it also has a chirotheroid aspect, pentadactyl with short and large digits, lacking claws. I is also reduced, II and III are subequal, and V is small but longer than I.

In another example, it is also tetradactyl but by the absence of V (Fig. 7(37)). In two other cases, it appears tridactyl with IV clearly shorter than I-II. This last morphology is also regularly observed in *Coelurosaurichnus grancieri* Courel and Demathieu, 2000.

2.3.3.2. Trackways. The most numerous and complete also come from the Pissoire quarry (Gand, 1974b). They were often observed on levels AF1 (Gand, 1978b) and BF2 (Gand, 1971, 1979d; Demathieu and Gand, 1972b).

The angle of the foot averages 173° ranging between 161 and 180°; the pes length/leg length ratio (L/E) equals 11.9 in an interval of 8.5–14.66 with n = 12, and the pes axis/trackway axis equals –4.5 (interval –7.5°; +10°).

2.3.4. Coelurosaurichnus sabinensis *Gand et al., 1976a,* Coelurosaurichnus palyssii *Gand, 1976 and* Coelurosaurichnus largentierensis *Courel and Demathieu, 1976*

The first two ichnospecies correspond to several tridactyl II-IV footprints, the third to two trackways observed in the roof of a gallery in the Largentière mine (Ardèche).

The value of angle T clearly discriminates (Fig. 10(1)) *C. sabinensis* from the other ichnospecies (Fig. 9(9, 12)). This is not the case for *C. palyssii* (Fig. 9(8)) and *C. largentierensis*, which were founded using the identification key proposed by Baird (1957).

2.4. Interpretation

The preceding data relative to the trackways and footprints of *Coelurosaurichnus perriauxi* and *Anchisauripus bibractensis* agree in evoking semi-permanently bipedal reptiles with functionally tridactyl feet and having elongate and well straightened hind limbs. Based on the orientation of their feet relative to the trackway axis, Demathieu and Gand (1972b) evoked for the authors of *C. perriauxi* animals of rather heavy movement, perhaps of carnosaurian aspect, and for those of *A. bibractensis*, more slender and mobile reptiles. The size of the first were estimated between 2.50 and 3 m long and those of the second between 1.40 and 2.50 m (Demathieu and Gand, 1972b, 1981a; Gand, 1975a, 1979d).

All the bony pedal structures deduced from the better-preserved prints culminate in the same organization of the acropodium, which was functionally tridactyl II-IV with II slightly inferior to IV, this last being smaller than III. From II to IV, the phalangeal formula of each digit was respectively 3, 4, and 5. This is in sum a banal formula and typical which is common among Upper Triassic bipedal dinosaurs: ceratosaurians (ex. "coelurosaurians") such as *Coelophysis* Cope, 1889 from the United States, Mexico, and South Africa, younger than *Procompsognathus triassicus* Fraas, 1913 and *Halticosaurus liliensterni* Huene, 1908, both from the German Keuper (Norian) (Württemberg and Thuringia) (Piveteau, 1955; Steel, 1970; Haubold, 1989). For this reason, the authors of *Coelurosaurichnus perriauxi* and *Anchisauripus bibractensis* were referred, if not regularly attributed, to "coelurosaurians" by Demathieu and Gand (1972b, 1981a, 1986); Gand (1975a, 1979d); Demathieu (1985, 1989) with, nonetheless, the possibility that the first could have also been paleopods sensu Colbert (1964) (Demathieu and Gand, 1972b). But as there exists an important temporal gap between the Upper Triassic ceratosaurians (Norian) and the French Aniso-Ladinian dinosauroid traces, it is reasonable that these animals may not have been the authors of these ichnites. The discoveries of reptiles arising in the Middle Triassic of Argentina and Brazil has progressively permitted seeing more clearly and better apprehending the origin of the dinosaurs.

In the Chañares Formation of Argentina, dated from the Ladinian, were thus found "thecodonts" (Bonaparte, 1993), an artificial group (Sereno, 1991) that currently contains the Crurotarsi Sereno and Arcucci, 1990 besides the Dinosauromorpha Benton, 1985. This last phylum includes *Lagerpeton* Romer, 1971; Sereno and Arcucci 1993 besides the Dinosauriformes Novas, 1992 (Novas, 19960 within which this last author

distinguishes *Marasuchus* Sereno and Arcucci, 1994 (= *Lagosuchus talampayensis*), *Pseudolagosuchus*, and the Dinosauria. The primitive dinosaurs are represented by *Staurikosaurus* Colbert, 1970 from the Santa María Formation of Brazil (basal Carnian or upper Ladinian-lower Carnian), *Herrerasaurus* Reig, 1963 and *Eoraptor* Sereno et al., 1993, from the Ischigualasto Formation (Argentina) of middle Carnian age (Carroll, 1988; Haubold, 1989; Norman, 1991; Bonaparte, 1993; Cuny, 1993). *Staurikosaurus* seems to be the most ancient remains of Dinosauria. And although it lacks it forelimbs and feet, based on the characters of other parts of the skeleton, it is considered as a bipedal animal with hollow bones, speedy, having affinities with *Herrerasaurus*, attributed as a theropod.

Currently, it seems admissible that the Dinosauriformes, appearing at the end of the Ladinian (Bonaparte, 1982), formed the stem group of the Dinosauria (Sereno and Arcucci, 1994; Novas, 1996). This last group is represented by several incomplete skeletons of small animals, about thirty centimeters long, who share several synapomorphies with the Dinosauria at the levels of the skull, vertebral column, acetabulum, and limbs; the tarsus shows a mesotarsal articulation.

According to the reconstructions in Carroll (1988:272), the pes is pentadactyl but with a predominant dinosauroid tridactyl II-IV mass. These animals also had pentadactyl manus whose digits IV and V were very reduced (in Carroll, 1988) as they were equally in *Eoraptor* (Cuny, 1993). These reptiles with long hind limbs, adapted to running and predation, were occasionally bipedal quadrupeds according to Bonaparte (1978), Carroll (1988) or rather exclusively bipedal according to Bonaparte (1993:30).

Being founded on the preceding characters and on their age, could these reptiles themselves have been the authors of *Anchisauripus bibractensis* and *Coelurosaurichnus perriauxi*? This is anatomically and chronologically possible although the French dinosauroid prints are older (cf. supra). Nevertheless, is this were the case, these Dinosauriformes would have appeared in the Anisian and been clearly larger and more diverse than had been thought from the known skeletons. The discovery of a tridactyl II-IV dinosauroid print in the Anisian of the "Valle di Non" in Italy (Avanzini, 2002) agrees with this hypothesis.

The print of the pentadactyl manus, of chirotheroid structure, associated with several pedal prints of *Anchisauripus bibractensis* and *Coelurosaurichnus perriauxi* (Fig. 5) shows that their trackmakers could have had an ornithosuchian origin, which is possible to specify when one compares them with *Sphingopus ferox*. This ichnite, which is their contemporary, is represented by prints of the pes and pentadactyl manus, with digits IV and V reduced, suggesting the existence of a crurotarsal articulation. It was attributed to principally bipedal ornithosuchians (Demathieu, 1967, 1970), with well straightened limbs (Gand, 1971, 1979d) from which could have come the authors of *Anchisauripus bibractensis* and *Coelurosaurichnus perriauxi*. Their emergence could have occurred in the lower Anisian truly during the upper Olenekian. It was characterized by a strong reduction in the lateral digits and by the acquisition of a mesotarsal pedal articulation which gave great speed to the reptiles who would become "dinosauriforms".

Such an "ornithosuchian" hypothesis is different from that of Haubold and Klein (2000), who considered that the authors of the German dinosauroid prints from the Ladinian–Carnian came from the Dinosauromorpha, such as *Lagerpeton* Romer, 1971.

3. Reevaluation of the nomenclature

3.1. Morphometric comparisons

3.1.1. The ichnites concerned

The choice of the ichnospecies was dictated by the nature of the characters utilized by paleoichnologists and by the existence of a series of measurements and/or statistical data; rather rare in the literature.

The method of measurement followed in this study is that of Lull (1953). The morphometric comparisons concern:

- *Anchisauripus bibractensis* Demathieu, 1971; *Coelurosaurichnus perriauxi* Demathieu and Gand, 1972a, 1972b; *C. palyssii* Gand, 1976; *C. sabinensis* Gand et al., 1976a, and *Coelurosaurichnus largentierensis* Courel and Demathieu, 1976 (Fig. 5) (French Middle Triassic);
- various ichnospecies of *Grallator* (Hitchcock, 1858) Lull, 1904 from the Hettangian of the Hartford basin (Massachusetts, USA);
- *Grallator variabilis* de Lapparent and Montenat, 1967 from the Sinemurian of Causses (France) in Demathieu et al. (2002);
- the ichnospecies of *Coelurosaurichnus* from Franconia measured by GD at the Geologisches Institut of Erlangen. These are *C. metzneri* Heller, 1952 (Steigerwald F., Ansbacher Sandstein, middle Carnian), *C. ziegelangernensis* Kuhn, 1958 (Semiotensandstein Formation, Carnian), *C. kehli* Beurlen, 1950 (Coburger Sandstein Formation, upper Carnian), and several *Coelurosaurichnus* sp. All these ichnospecies correspond to footprints except *C. metzneri* which is a manus-pes pair;
- *Coelurosaurichnus grancieri* Courel and Demathieu, 2000 and *Grallator* sp. which was found by Max Grancier in the environs of Payzac, SW of Largentière (Ardèche, France). According to Courel and Demathieu (2000), the fossiliferous levels are localized in the lower third of the gray sandy-dolomitic ensemble (Egdg), included between the "middle Barre limestone" and the variegated Ucel Formation (Fig. 2(4)). Their age is lower Carnian according to palynological associations from the horizons noted in Fig. 2(4) (Doubinger and Adloff, 1977; Fauconnier et al., 1996).

3.1.2. Statistical study: discriminant analysis (AD); Student's t-test and Snédecor's F-test

3.1.2.1. Methods utilized. The AD was performed with the program Statistica (Anonymous, 1997). It concerned, successively, the character-variables (raw data = L, W, I, II, II, D, T) and certain of their ratios. We indicated on graphics R1/R2, the better characters, or ratios, discriminants, in decreasing order and specify the proper values as a percentage of each axis.

The AD was also completed, according to the ichnospecies, by the Student's test (comparison of means) and by Snédecor's test (comparison of variances).

3.1.2.2. Analysis of graphics R1/R2 and Tables 3 and 4; nomenclatural discussion. The analysis of Fig. 10(1, 2) shows first that the ichnospecies are better discriminated by the raw data than by their ratios because the value of these latter minimize well the effects of the allometry of growth or size. It also results that *C. sabinensis* and *Anchisauripus* sensu Lull, 1953 form two groups clearly separated from one another and from two others: that with *A. bibractensis* and *C. perriauxi*, and the other with *Grallator* (G + Gv) containing the *Coelurosaurichnus* from Franconia (Aal). These two last groups or clouds are rather well discriminated because the classification values are 85% for *C. perriauxi* and 93% for *G. variabilis*.

C. perriauxi and *A. bibractensis* seem well interspersed but the classification value of 78% for the second ichnospecies suggests that these two ichnopopulations are separated in a significant manner. This interpretation is supported by the results of comparison tests between the means and variances because for all the ratios considered, t calculated is greater than t at the 5% threshold (Table 3(1)).

The AD obtained from these ratios, for the reasons indicated above, show that the differences between the four groups of prints are a little attenuated but remain significant, notably between the *Grallator* cloud (G + Gv) and that formed by *C. perriauxi* and *A. bibractensis* (Fig. 10(2)). The classification value of this last ichnospecies is weak: 49% but the differences between *C. perriauxi* and *A. bibractensis* remain significant, for several ratios (III/II, L/W) and character T, at the level of means and variances (Table 3(2)). These diverse statistical analyses agree that the validation of these two ichnospecies which are also differentiated by morphological characters (Demathieu, 1971, 1985; Demathieu and Gand, 1972a, 1972b).

3.1.3. Nomenclatural consequences

Referring to the preceding results, which are founded only on the morphometric considerations of the footprints, it appears that the various ichnospecies of *Coelurosaurichnus* from Franconia could be arranged within the ichnogenus *Grallator* sensu Lull, 1953 and de Lapparent and Montenat, 1967 (cloud G + Gv, Fig. 10). But as this is not the case for the great majority of specimens of *C. perriauxi* and *A. bibractensis*, it seems to us logical to conserve these binomials. Nevertheless, one sees that new observations concerning the ichnogenera *Anchisauripus* (Olsen et al., 1998) and *Coelurosaurichnus* (Leonardi and Lockley, 1995) are amenable to reconsidering their utility.

3.1.3.1. Anchisauripus. *Anchisauripus* was defined successively and, in the same manner, by Lull (1904, 1915, 1953) as an ichnogenus that includes dinosauroid footprints with dominant tridactyl II-IV mass, with the regular imprint of the hallux claw (digit I). But during its frequent absence and the difficulties there are in distinguishing certain ichnospecies of *Anchisauripus* and *Grallator*, Baird (1957:470-471) imagined discriminating them based on "characters…which reflect the bony structure". These would be founded on the relative positions of the digital pads, the relative lengths of the digits, which clearly differentiate between *Anchisauripus*, *Grallator*, and *Eubrontes* sensu Lull, 1953. Their new diagnoses permit distinguishing fairly easily prints of similar

length, and to attribute them by an identification key to *Anchisauripus* sensu Baird, 1957 or *Grallator* sensu Lull, 1953, according to the case.

It is this method that led GD to attribute some of the dinosauroid prints from the French Middle Triassic (cf. supra) within the ichnogenus *Anchisauripus* (Demathieu, 1971). Thus why have them subsequently arranged within *Grallator* with the trinomial *Grallator* (*Anchisauripus*) *bibractensis* (Demathieu, 1989:203; Courel and Demathieu, 1995:88)? This because of the very irregular presence (including absence) of the hallux in *Anchisauripus* and also following the observations of Olsen (1980), who suggested conserving only the ichnogenus *Grallator* ("senior name") after having remarked that certain characters of *Grallator*, *Anchisauripus*, and *Eubrontes*, sensu Lull, 1953, were connected by a growth allometry. Olsen and Galton (1984) followed this suggestion by including there the 16 ichnogenera defined by Ellenberger (1972, 1974) based on the dinosauroid ichnites from the Upper Triassic of South Africa.

The simplifying concept of Olsen (1980) seems to have been favorably received but it is right to specify that it had been preceded by the approach of de Lapparent and Montenat (1967) who generalized the use of *Grallator* for the name of the tridactyl II-IV prints reaching thirty centimeters in length. And besides this is progressively the concept of *Grallator* Hitchcock, 1858 sensu Lull, 1904, 1953 modified well with *Grallator* sensu Baird (1957); *Grallator* sensu de Lapparent and Montenat (1967); *Grallator* (*Anchisauripus* and *Eubrontes*) sensu Olsen (1980), sensu Olsen and Galton (1984); *Grallator* (*Anchisauripus*) sensu Demathieu (1989); *Grallator* (*Eubrontes*) sense Weems (1992); *Grallator* (*Anchisauripus* and *Eubrontes*) sensu Gierlinski (1994); *Grallator* sensu Olsen et al. (1998).

During this imbroglio, due to a lack of measurements, the heterogeneity of measurement methods, and the absence of statistical treatments of data, the general subjective tendency is currently toward simplification. That is the utilization of *Grallator* as the name for tridactyl II-IV footprints, small to moderate, with digits that are rather slender or not too wide!, whose II-IV angle is less open; the angle of the pes being close to 180°. *Eubrontes* is reserved for large dinosauroid imprints with wide, thick digits. Viewed from this angle, the footprints *Coelurosaurichnus perriauxi*, *C. grancieri*, and *Anchisauripus bibractensis* could be arranged within *Grallator*. This is what was done for *A. bibractensis*.

3.1.3.2. Remaining case of Coelurosaurichnus *which was established by Huene (1941) as the type species* C. toscanus. It is represented by a single print figured by a sketch that suggests a dinosauroid footprint. This ichnogenus was subsequently utilized to name numerous ichnospecies. Kuhn (1963:86-87) inventoried some ten to which it is necessary to add that from the Triassic border of the Massif Central (cf. supra) as *Coelurosaurichnus perriauxi* Demathieu and Gand, 1972a, 1972b. And this is besides ahead of the stability and frequent usage of this ichnogenus, specified by a short diagnosis in Demathieu (1985:57), it seems to us logical to continue to use it for the name of the Bourguignon dinosauroid prints in our work. But, in relating to *C. perriauxi*, we judge the taxa *C. palyssii* and *C. largentierensis* synonymous with the preceding ichnospecies because they are morphometrically continuous within the *C. perriauxi* cloud (Fig. 10).

In the critiques of our contribution, Umberto Nicosia (University of Rome) affirmed that *Coelurosaurichnus* "is invalid not because it lacks a type species but due to the only specimen of the type species (*C. toscanus*) is most probably nothing and thus it is a *nomen vanum*". He also considered that "Subsequent addition of many ichnospecies cannot be considered validation of an invalid taxon"; "Changes in *Coelurosaurichnus* diagnosis by Demathieu (1985) cannot be considered a formal revision".

By his refusal to use *Coelurosaurichnus*, U. Nicosia also rejoins the proposition of Leonardi and Lockley (1995), who recommended abandoning usage of *Coelurosaurichnus*. But he did not approve of the preceding authors' suggestion to synonymize it with *Grallator* Hitchcock, 1858 because U. Nicosia specified to us, "I believe that to invalidate *Coelurosaurichnus* as done by Leonardi and Lockley, without examining the position of the many species (more than 17) included was a mistake, but this real problem cannot be solved by maintaining an already invalidated ichnotaxon. Thus the author's suggestion cannot be applied. Moreover an opinion of the international zoological committee requires that a formal question be posed." And U. Nicosia said to use a thesis that is in process on the revision of *Coelurosaurichnus*.

For what concerns us, we recall (cf. supra) that according to our AD (Fig. 10), we come to propose to arrange within *Grallator* several ichnospecies of *Coelurosaurichnus* from Franconia, rejoining also the identifications of Haubold and Klein (2000). What we do not authorize to reject, for as much, *Coelurosaurichnus* whose current invalidation is evident for certain but not established by the authors of this work. All depends on the reading made under the nomenclatural code.

In all ways, as we have specified in the preceding paragraph, the concept of *Grallator* was so modified following several synonymies and diagnoses that this ichnogenus currently includes the great majority of functionally tridactyl II-IV dinosauroid footprints. Morphometrically, *C. perriauxi* could thus be made part if founded on the results of the AD since the imprints-points of this ichnospecies are mixed with those of *A. bibractensis* (Fig. 10) which were arranged within this ichnogenus (Demathieu, 1989).

3.2. Remarks on Atreipus *Olsen and Baird, 1986*

In 1986, Olsen and Baird described the ichnogenus *Atreipus* in the following manner: "Habitually quadrupedal ichnites; pes tulip-shaped with digit three longest; manus small, digitigrade, tridactyl or tetradactyl". Furthermore the older American ichnospecies *Anchisauripus milfordensis* Baird, 1957; *Grallator sulcatus* Baird, 1957, and the new *Atreipus acadianus* Olsen and Baird, 1986, all from the "late Carnian to early Norian", the authors judged "the European exception" *Coelurosaurichnus metzneri* Hellern, 1952. But in their work, *C. perriauxi* nevertheless figured by several manus-pes pairs in Demathieu and Gand (1981a), redefined by Demathieu (1985), is purely and simply ignored! In comparing the manus prints of various ichnospecies of *Atreipus* with those of *C. perriauxi*, it is Thulborn (1993) who would note these Bourguignon manus, entirely suggesting to arrange then within *Atreipus*. This would be correct because the footprint of *C. metzneri* is included within the *Grallator* Hitchcock, 1858 sensu Lull, 1904, 1953 cloud (G, Fig. 10), an ichnogenus which has priority over *Coelurosaurichnus*.

But, other than these manus-pes pairs from the Middle Triassic, in France, there exists a great number of others in the Ardechois Upper Triassic of Payzac whose age and geographic origin are more highly specified. The paleontological material was found in three levels included within a 1 m interval. The oldest, level F1, furnished a great slab of several meters square (no. 18 A-C) on which existed only tridactyl II-IV footprints, with slender digits whose well-marked pads are often separated. The II-IV angle is weak (29°). Digit III rather clearly exceeds its neighbors (L/D = 2.8) (Fig. 12(13-22); Table 1(4)) and, for this reason, we have named them *Grallator*.

On the other two levels E and F2, one encounters mostly *Coelurosaurichnus grancieri*: tridactyl II-IV footprints associated with those of the manus. They are exclusively on E (Fig. 11(3-40)) and accompanied by several *Grallator* sensu Lull on F2 (Fig. 12(9-12)).

One-third of the first ichnites from level E served to define *C. grancieri* (Courel and Demathieu, 2000) but like the material then available for these authors is much enriched since their study, we have measured a new specimen of this ichnospecies only from level E (Table 1(3)). It thus appears that the *C. grancieri* pedes are a little smaller than those of *Grallator* from level F (85 mm long versus 110 mm on average), but the values of the II-IV angle, the length ratios of digits III/II, III/IV, and IV/II, L/D are very close. To such a point, that Student's and Snédecor's tests, calculated to the 5% level, are not significant between these two ichnopopulations. Only III/D is for the averages (calculated t = 2.49 POUT t read = 1.96 to the 5% level (Table 4(1))) with a more elevated value for *Grallator* from level F1 than for *C. grancieri*.

The AD permits specifying the preceding (Fig. 13(1, 2)). For the raw data, the majority of *Grallator* points from level F1 are contained within the *Grallator* cloud (G + Gv), and those of *C. grancieri* are above all from *A. bibractensis*. But when one considers the ratios, *Grallator* from Payzac are a little more *A. bibractensis* than *Grallator* (G + Gv) whereas *C. grancieri* are at once *A. bibractensis*/*C. perriauxi* and of *Grallator* (G + Gv). Finally, considering the trinomial *Grallator* (*Anchisauripus*) *bibractensis* adopted by Demathieu (1989), all these Ardèchois footprints can be considered as *Grallator* sensu lato.

But *Coelurosaurichnus grancieri* appears above all characterized by the existence of the manus: tridactyl II-IV, small, with LP/LM = 4, with wide, short digits and small claws with IV < III–II and present in 66% of the cases, if one considers the footprints individually, and in 82% of the cases if one observes them only within trackways. As the successive diagnoses of *Grallator* (cf. supra) are only concerned with the footprints, the use of *Atreipus* is necessitated to name the manus-pes pairs with the inconvenience of being amenable to using the *Grallator*/*Atreipus* pair for the trackways whether the imprint of the manus is present or not. This bias could be easily lightened if one specifies its possible existence within a new diagnosis of the ichnogenus *Grallator* which in fact and following the numerous synonymies now regroup the great majority of dinosauroid footprints.

Although, here and now, the usage of *Atreipus* to name the manus-pes pairs of *C. grancieri* and *C. perriauxi* imposes that its vertical placement (Carnian-Norian according to Lockley and Hunt, 1995), includes furthermore the period upper Anisian-lower Ladinian.

4. Phylogenetic suggestion (Fig. 14)

Coelurosaurichnus grancieri shares morphometric characters with the groups *C. perriauxi*/*A. bibractensis* from the Middle Triassic and *Grallator* from the Hettangian and Sinemurian PRIS as referenced. This is clearer from the ratios than from the raw data (Fig. 13).

Such a note is not without suggesting a possible affiliation between the authors of these prints. In summary, from the results of the AD, it seems logical to deduce, from the title of the hypothesis, that the ichnospecies *C. grancieri* could be issued from the Dinosauriformes which left *C. perriauxi* and *A. bibractensis*. This evolution was characterized, by what we can perceive from the prints, by a progressive elongation of digit III, and by the generalized regression of digits I and V.

There is also a return to quadrupedalism because the authors of *C. perriauxi* and *A. bibractensis* are essentially bipedal. The frequency of manus prints of *C. grancieri* seems to indicate this. But when one examines the position of the manus in the pes-manus pairs, it appears strongly variable relative to the pes. As it is, besides, very small, Courel and Demathieu (2000) thought, with good reason, that it could not have played a preponderant role in locomotion. Quadrupedalism in these reptiles could therefore have been occasional and depended much on environmental conditions.

As we have specified above, below level F2 with *C. grancieri*, there also exists another *Grallator* sp., without trace of the manus, whose horizontal extension deserves to be confirmed. If such is the case, this ichnogenus would testify to the existence of exclusively bipedal reptiles in the basal Carnian. Were they already Dinosauria? This is entirely possible if one refers to the osteological evidence from the upper Ladinian and Carnian that is attributed to these animals (Bonaparte, 1993; Cuny, 1993; Sereno and Arcucci, 1994).

In the rest of the French Upper Triassic (variegated Ucel Formation sensu Courel et al., 1998) (Fig. 2(4)), dinosauroid traces are preponderant and become larger and more numerous after the lower Norian, exceeding a dozen centimeters in length at the base of the Carnian, to 20-30 cm in the middle Norian (Ellenberger et al., 1970; Gand et al., 2000), to reach 50 cm in the Rhaetian (Gand et al., 2005). Their authors seem thus to have rapidly developed after the lower Norian to the detriment of the Crurotarsi, whose traces have not been found in France; contrary to other regions of the USA (Lockley and Hunt, 1995).

Such a paleoichnological report recounts the great lineages which were established according to osteological data (Cuny, 1993). It specifies that from the end of the Carnian, the fauna went from only 2% Dinosauria to 80% at the end of the Norian, six million years later.

5. Conclusions

In the Grès inférieurs Formation of the eastern border of the Massif Central, dated as upper Anisian-lower Ladinian, numerous dinosauroid traces were recovered. Their interpretation leads to evoke bipedal digitigrade reptiles with parasagittal hind limbs,

having pentadactyl manus and II-IV tridactyl pedes whose bony architecture is similar to those of theropod dinosaurs. As the skeletons of these animals appeared only at the top of the upper Ladinian and/or in the lower Carnian, the Aniso-Ladinian footprints have been attributed to their probably ancestors, the Dinosauriformes, whose skeletons are found in the Ladinian of South America.

The chirotheroid manus of the authors of the French ichnites testifies to a "pseudosuchian" origin that could go back to the upper Olenekian; the transformations of the pes having been characterized by a reduction in the lateral digits (I, V) and by the acquisition of a mesotarsal articulation.

The great majority of dinosauroid footprints from the French Middle Triassic (II-IV tridactyl pedes sometimes associated with those of the manus), were arranged among the ichnospecies *Coelurosaurichnus perriauxi* and *Anchisauripus bibractensis*. The discriminant analysis realized only from the foot traces of these ichnospecies, of those from the Upper Triassic and Hettangian show that the French ichnotaxa differ in a significant manner from *Grallator* sensu Lull, 1953 but also from the ichnospecies of *Coelurosaurichnus* from Franconia of which certain ones show also the manus episodically.

Coelurosaurichnus perriauxi and *Anchisauripus bibractensis* are therefore quite original, and we could continue to arrange certain of them within the ichnogenus *Coelurosaurichnus* if Leonardi and Lockley (1995) had not proposed to invalidate *Coelurosaurichnus* because of a very poorly preserved ichnotype; a case, besides general for a lot of others. This nomenclatural problem is complex and finally concerns only *C. perriauxi* because in an enlarged concept of *Grallator*, it is possible, currently, to arrange the majority of II-IV tridactyl dinosaur foot traces within this latter ichnogenus. Haubold and Klein (2000) have already done so for the *Coelurosaurichnus* from Franconia but by utilizing the *Grallator/Atreipus* pair. This is undoubtedly logical, but less parsimonious because two ichnogenera are needed to name the foot traces of one trackway according to whether it is associated with the manus.

The results of the discriminant analysis from this work suggest that it is also possible to include *C. largentierensis* in the *Grallator/Atreipus* group and, to a lesser degree, *C. perriauxi*. According to *A. bibractensis*, an already old synonymy attributes this ichnospecies to *Grallator*.

Acknowledgments

The authors thank emeritus Prof. Louis Courel of the Université de Bourgogne for his remarks and suggestions, and Annie Bussière who improved the effectiveness of the many tables and figures (UMR 5561 of the CRNS Biogéosciences, Université de Bourgogne). We are also grateful to Gilles Cuny of the Université Pierre et Marie Curie (Paris-VI) and Ronan Allain of the Muséum d'Histoire Naturelle de Paris for their information, and to two reviewers: Prof. Nicosia of the Università di Roma and an anonymous colleague for having read our contribution very attentively.

The realization of this work benefited from the support of UMR 5561 of the CNRS, under Director Bruno David.

References

[Not listed.]

FIGURE CAPTIONS

Fig. 1. Locations of sites with dinosauroid traces from the Middle Triassic in France; Frame 2: Bourgogne and Lyonnais, with A = Auxois, Au = Autunois, CC = Côté Châlonnais and Charolais, M = Mâconnais, L = Mt. d'Or Lyonnais; Frame 3: A + G = Ardèche and Gard.

Fig. 2. Vertical arrangement and age of dinosauroid traces from the Grès inférieurs Formation from the Triassic of the eastern border of the Massif Central. **1** = Autunois, Antully Plateau in Gand (1979a); **2** = Mâconnais, log from drill MA10; **3** = Mont d'Or Lyonnais, 2 and 3 in Courel (1970, 1973); Courel et al. (1984), slightly modified; **4** = Ardèche, from Crussol aux Vans; after Finelle (1981); Courel et al. (1984, 1998); Gand et al. (2000); FORM. = Formation with Egdg = gray sandy dolomitic ensemble; Lithology with A = clays, AB = variegated clays, AN = black clays, B = breccias, D = dolomite, CA = limestone, G = sandstone, GC = conglomeratic sandstone, GB = yellow sandstone, Ps = salt pseudomorphs; Gy = gypsum; Paleontology with Pe = *Pellatia*, Ac = *Avicula contorta*, T.V - vertebrate traces, INV = invertebrates, M = flora, C = conodonts, FO = foraminifera, and P = microflora.

Fig. 3. **1** = *Rhynchosauroides petri* Demathieu, 1966, Chasselay, Mont d'Or Lyonnais, (Demathieu, 1970); **2** = *R. triangulus* Gand, 1977b (Autunois, la Pissoire, level EF2); **3** = *R. sphaerodactylus* Demathieu, 1971, Chasselay; **4** = *Rhynchosauroides lutevensis* Demathieu, 1984, inférieur Formation, Lodévois; **5** = *Rhynchosauroides majus* Demathieu, 1970, Chasselay; **6** = *R. virgiliae* Demathieu, Ramo, and Sopeña, 1978, Pont d'Argent, Autunois (Demathieu and Gand, 1981, 1981b); **7** = *Rhynchosauroides maximus* Gand, 1974c, les Brosses-Thillots, Charolais; **8** = *Rotodactylus bessieri* Demathieu, 1984, inférieur Formation, Lodévois; **9** = *Rotodactylus lucasi* Demathieu and Gand, 1973, pes, la Pissoire; **10** = P-M pair of *Rotodactylus velox* Demathieu and Gand, 1974, la Pissoire; **11** = *Rotodactylus rati* Demathieu, 1971, pes, Pont d'Argent; **1-11** = holotypes; P = pes, M = manus; scale = 1 cm.

Fig. 4. Type ichnospecies of *Synaptichnium*, *Chirotherium*, *Brachychirotherium*, and *Isochirotherium*. **1.** *Synaptichnium priscum*, Demathieu, 1970, Chasselay; **2.** *S. argantobrivense* Demathieu and Gand, 1981b, Pont d'Argent; **3.** *S. cameronensis* Peabody, 1948, Pont d'Argent (Demathieu and Gand, 1981b); **4.** *S. diabloense* Peabody, 1948, Saint-Vérand quarry, Mâconnais (Demathieu and Gand, 1986); **5.** *Chirotherium barthi* Kaup, 1835, les Brosses-Thillots (Gand, 1975b); **6.** *C. mediterraneum* Demathieu and Durand, 1991, Carnoulés near Alès, Argiles noires inférieures ensemble (Perrissol, 1990) = Argiles silteuses, grès à moulages ensemble (Courel et al., 1984); **7.** *Brachychirotherium tintanti* Demathieu, 1971, Chasselay; **8.** *B. gallicum* (Demathieu, 1984), inférieur Formation, Lodévois; **9.** *B. circaparvum* Demathieu, 1971, Chasselay; **10**. *B. pachydactylum* Demathieu and Gand, 1973, la Pissoire; **11.** *B. lorteti* Lortet, 1891, les Brosses-Thillots (Gand, 1974a); **12.** *Isochirotherium coureli* Demathieu, 1970, Chasselay; **13.** *I. felenci* Courel and Demathieu, 1976, Grès du Roubreau Formation, Ardèche; **14.** *I. circademathieui* Gand, 1979b, Culles-les-Roches; **15.** *I. demathieui*

Haubold, 1970, Chasselay (Demathieu, 1970); **16.** *I. comblei* Gand, 1979b, la Pissoire; **17.** *I. delicatum* Courel and Demathieu, 1976, Pont d'Argent (Gand, 1979a); scale = 1 cm for 1-4; = 5 cm for 5-17; P = pes, M = manus.

Fig. 5. **1-15.** Traces of *Sphingopus*, *Coelurosaurichnus*, *Anchisauripus*, and *Grallator* from the Grès inférieurs Formation (Middle Triassic). **1, 2.** *Sphingopus ferox* Demathieu, 1966 with 1 = trackway, 2 = PM pair, level BF2, la Pissoire, Autunois (Gand, 1971, 1979d); **3-6.** *Coelurosaurichnus perriauxi* Demathieu and Gand, 1972a, 1972b, 3, 4, 6 = CPM, Pont d'Argent and 5 = holotype, la Pissoire (Autunois); **7.** *C. largentierensis* Courel and Demathieu, 1976, holotype, Largentière; **8.** *C. palyssii* Gand, 1976; **p.** *Anchisauripus bibractensis* Demathieu, 1971, holotype, Pont d'Argent; **10, 11, 14.** Unnamed, Grès à Orthose rose Formation (Autunois) (Gand, 1979c); **12.** *C. sabinensis* Gand et al., 1976a, Sainte-Sabine, Auxois; **13.** cf. *Anchisauripus*, Culles-les-Roches, Côte-Châlonnais (Gand, 1978a); **15.** *Grallator* sp., Ardèche, (Montenat, 1968); **16-21.** Dinosauroid traces from the Upper Triassic; **16, 17.** *C. grancieri* Courel and Demathieu, 2000, Payzac, Ardèche; **19.** *Grallator andeolensis* Gand et al., 2000, la Grand-Combe, Gard; **20, 21.** Cruéjouls, Aveyron (Gand et al., 2005); scale = 10 cm for 1 and 1 cm for 2-21.

Fig. 6. *Anchisauripus bibractensis* and *Coelurosaurichnus perriauxi* from the la Pissoire quarry (Autunois). Grès d'Antully Formation; *Anchisauripus bibractensis* Demathieu, 1971: **1-3, 6-26**; level BF2, **1, 13-17** = trackway M; **2, 9-12** = trackway B; **6-8** = trackway A, **26** = isolated; level CF2, **3, 18-21** = trackway; level AF1, **22**; level EF1, **23, 24**; EF4, **25**; *Coelurosaurichnus perriauxi* Demathieu and Gand, 1972a, 1972b: **4, 5, 27-49**: level AF1, **27-29** = trackway A; **30, 31** = trackway B; **32, 33** = trackway D; **34** = trackway F; level BF2, **35** = trackway E; **5, 36-40** = trackway O; **41-44** = trackway X; **4, 45-48** = trackway Y1; **49** = trackway Y3; scale = 10 cm for 1-5 and 5 cm for 6-49; Gand collection, Muséum d'Histoire Naturelle d'Autun.

Fig. 7. **1-7.** *Coelurosaurichnus perriauxi*, la Pissoire quarry (Autunois) suite: level BF2, **1, 2** = trackway Y3; **3** = trackway Y2; level EF1, **4**; level EF3, **5**; **6** isolated; **7** = Grolliers quarry, isolated; **12-47.** *Coelurosaurichnus perriauxi* and *Anchisauripus bibractensis* from the Pont d'Argent quarry (Autunois) (Demathieu and Gand, 1981a, 1981b); **12-21, 45-47.** *Anchisauripus bibractensis*; **22-44.** *Coelurosaurichnus perriauxi*; scale = 10 cm for 44-47, = 5 cm for 1-43; Gand collection, Muséum d'Histoire Naturelle d'Autun.

Fig. 8. *Coelurosaurichnus perriauxi*, *C. sabinensis*, and *Anchisauripus bibractensis* from the Charolais (Brosses-Thillots quarry = BT; Gand, 1974a, 1975b), Mâconnais, and Châlonnais (Culles-les-Roches quarry = CR and St.-Vérand quarry = SV; Gand, 1977a, 1978a; Demathieu and Gand, 1986); *C. perriauxi*: **1-5, 10:** BT; *C. sabinensis* Gand et al., 1976a: **6,** BT; *A. bibractensis*: **8**, BT; Gand collection, Muséum d'Histoire Naturelle d'Autun.

Fig. 9. **1** = *Sphingopus ferox* pes, level BF2, la Pissoire; **2-7**: *Coelurosaurichnus perriauxi* with **1** = holotype, pes, level AF1, la Pissoire, **3, 4, 5** = PM pairs, Pag 15, Pag 52, Pag 50 from Pont d'Argent, **6** = pes, GL1, les Grolliers; **7** = pes, Pag 56, Pont

d'Argent; **8**: *Coelurosaurichnus palyssii*, holotype, Rg2, Repas; **9, 12**: *Coelurosaurichnus sabinensis*, **9** = holotype, pes, St Sg1, Sainte-Sabine; **12** = pes, BT4, les Brosses-Thillots; **10**: *Coelurosaurichnus* sp with scales, SVg1, Saint-Vérand; **11, 13, 14**: *Anchisauripus bibractensis*, pes with **11** = Cp5, Culles-les-Roches, **13** = level BF2, la Pissoire, **14** = trackway, level CF2, la Pissoire; **15**: cf. *Anchisauripus*, Cg3, PM pairs, Culles-les-Roches; scale = 1 cm; Gand collection, Muséum d'Histoire Naturelle d'Autun.

Fig. 10. Discriminant analysis concerning the ichnopopulations *Coelurosaurichnus perriauxi* (CP), *C. sabinensis* (CS), *Anchisauripus bibractensis* (AB) from the Grès inférieurs Formation (Middle Triassic), the various ichnospecies of *Coelurosaurichnus* from Franconia (Aal), *Grallator* (G), and *Anchisauripus* (A) sensu Lull (1953) and *Grallator variabilis* (Gv); **1, 2**: successive analysis of the character dimensions then their ratios.

Fig. 11. Dinosauroid traces from the gray sandy dolomitic ensemble (Egdg), figure 2(4), lower Carnian; *Grallator* sp.: **1** = trackway 1, level F1, la Salindre, Payzac, Ardèche; *Coelurosaurichnus grancieri* Courel and Demathieu, 2000: level E, la Salindre, **2** = trackway A, GR15, **3, 4** = trackways GR6, **5** = trackway GR1, **6-40** = on slabs SalEGR1, 3-5, 7-10, 12-15, 17, 19-23, 36-37; scale = 10 cm for 1-5 and 5 cm for 6-40.

Fig. 12. Dinosauroid traces from the gray sandy dolomitic ensemble (Egdg) (suite); *Coelurosaurichnus grancieri*, level F2, la Salindre, **1-8**, on slabs SalFGR 26-28, 33-34, 37; *Grallator* sp., level F2, **9-12** on slabs SalFGR 27, 30-32; level F1, **13-22** on slabs 18 A-C.

Fig. 13. Discriminant analysis concerning the ichnopopulations *Coelurosaurichnus perriauxi* (CP), *Anchisauripus bibractensis* (AB) from the Grès inférieurs Formation (Middle Triassic), the various ichnospecies of *Coelurosaurichnus* from Franconia (Aal), *Grallator* (G) sensu Lull (1953), *Grallator variabilis* (Gv).

Fig. 14. Possible phylogeny of the trackmakers (Dinosauriformes) of the dinosauroid traces from the French Middle Triassic. Comparisons with the trances from the French Upper Triassic (Rhaetian and/or Hettangian) and with various skeletons; abbreviations: S. a = *Synaptichnium argantobrivense*, S. p = *S. priscum*, E. c = *Euparkeria capensis*, C. b = *Chirotherium barthi*, C. m = *C. mediterraneum*, S. f = *Sphingopus ferox*, C. p = *Coelurosaurichnus perriauxi*, C. s = *C. sabinensis*, A. sp = *Anchisauripus* sp., A. b = *A. bibractensis*, C. g = *C. grancieri*, G. sp = *Grallator* sp., G. a = *Grallator andeolensis*, E. v = *Eubrontes veillonensis*, E. sp = *Eubrontes* sp., G. m = *G. minusculus*, G. v = G. *variabilis*, A. p = *Anatopus palmatus*, S. i = *Saltopoides igalensis*, G. o = *G. olonensis*.

TABLES

Table 1
Frequency distribution parameters of the measures, in mm and degrees, of the characters and ratios of the pedes. **1** = *Coelurosaurichnus perriauxi*, **2** = *Anchisauripus bibractensis*, **3** = *C. grancieri*, **4** = *Grallator* sp.; General legend valid for the tables: characters: II, III, IV = lengths of the digits; D = free dimension of digit III exceeding the line of unguals II-IV; L = length of the print and W = width; T = angle between digits II and IV; Statistical parameters: N = effective, M = median, B1 and B2 = Limit 1 and Limit 2 = confidence interval on the median at the 5% limit, E-T = ECART-type, C-T = coefficient of variation; Cramer test with asymmetry (AS), VR = reduced variable and P% = probability of exceeding VR in percentage; CC = calculated coefficient of correlation; CL = read coefficient.

Table 2
Frequency distribution parameters of the measures, in millimeters and degrees, of the characters and ratios of the pedes. **1** = *Coelurosaurichnus* from Franconia; **2.** = *Grallator variabilis*.

Table 3
Statistical comparisons between the means (calculated t = Student's test) and ratios of variances (calculated F = Snédecor's test) of characters (**1**) and pedal ratios (**2**) of *Coelurosaurichnus perriauxi* (CP) and *Anchisauripus bibractensis* (AB); t at 5% (1%) = values of t = Student's test at the 5% and 1% thresholds, F at 5% (1%) = values of the ratio of the variances at the 5% and 1% thresholds.

Table 4
Statistical comparisons between the means (calculated t = Student's test) and ratios of variances (calculated F = Snédecor's test) of characters (**1**) and pedal ratios (**2**) of *Coelurosaurichnus grancieri* (Cg) and *Grallator* sp., level F1, Payzac (GP); (**2**) of *C. grancieri* and *C. perriauxi* (CP).