Evidence of an Early Triassic age (Olenekian) in Argana Basin (High Atlas, Morocco) based on new chirotherioid traces

Évidence de l’âge Trias inférieur (Olénékien) dans le Bassin d’Argana (Haut Atlas, Maroc) basée sur des traces chirothérioïdes

Abdelilah Tourani, Naima Benaouissa, Georges Gand, Sylvie Bourquin, Nour-Eddine Jalil, Jean Broutin, Bernard Battail, Damien Germain, Fatima Khaldoune, Soumaya Sebbana, Jean-Sébastien Steyer, Renaud Vacant

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**Abstract**

New chirotherioid traces (Synaptichnium, Chirotherium, Brachychirotherium, Isochirotherium), are described in the Argana Basin (High Atlas of Morocco). Seeing that these ichnotaxa are frequent in the Triassic, their occurrence in outcrops formerly mapped as Permian (T2 Member) has required detailed sedimentological and paleontological studies of the fossiliferous site. These studies clearly show that the ichnite-bearing strata belong actually to the T3 Member of the “regional Triassic”, i.e., lower member of the Timezgadwine Formation, the age of which was, in fact, unknown up to now. The description of these ichnospecies and their statistical comparison with those of other Early and Middle Triassic areas, suggest an Olenekian age for this footprint site, and consequently for the T3. The trackmakers were Archosauriformes, some of which had autopodia less evolved than those of Anisian age. With Lepidosauria, they lived in a floodplain close to alluvial-fans.
1. Introduction

The stratigraphic study of the Permian and Triassic series of the Argana basin was made by Roch (Roch, 1930), and their cartography carried out by Tixeront (Tixeront, 1973; Tixeront, 1974). Within this framework, several sedimentological works, quoted in Medina et al. (Medina et al., 2000, 2001), Tourani et al. (Tourani et al., 2000) and Hofmann et al. (Hofmann et al., 2000), were elaborated among which that of Jones who discovered the first footprints (Rhynchosauroides) in the Argana Basin, on Permian outcrops, south-east of Timezgadiwine (Jones, 1975). Later, others were found by Dutuit (Dutuit, 1976) in the Triassic T5 Member of this same area, and by Beauchamp (in Biron (Biron, 1982)) in the Triassic of the Ourika valley (High Atlas). All these tracks, studied by Biron and Dutuit (Biron and Dutuit, 1981), are currently stored in the collections of the Faculty of Sciences Semlalia (Department of Geology) and the Muséum national d’histoire naturelle (Paris).

Recently, since the 2000s, the first two authors of this work found other footprint sites and gathered new traces during their sedimentological studies of the Argana Basin and neighbouring Permian and Triassic Formations of High Atlas Mountains (Fig. 1A). One of these track places, the Iggui Aouglef mapped as Permian by Tixeront (Tixeront, 1974) yielded Triassic chirotherioid footprints. Thus, this discrepancy justified a new detailed cartographic, sedimentological and paleontological study of these Permian-Triassic beds. The aim of this paper is:

- to replace them within their geological and stratigraphic contexts;
- to describe the tracks themselves;
- to propose a chronological attribution based on a comparison with European Permian-Triassic series.

2. Geological and stratigraphic context of the tracksite

Because of numerous uses of the lithostratigraphic term Formation and Member, these will be replaced by the abbreviations Fm and Mb.

The track site of Iggui Aouglef is located about 50 km to the south of Imin’ Tanout, 8 km SSW of Timezgadiwine, and 2 km south of Irerhi village, along the Assif Aït Messaoud (Fig. 1B, star). According to the geological map, it is located in the terminal part of the unit T2 (Tourbihine Mb), the upper member of the Ikakern Fm (Tixeront, 1973, 1974) dated as Late Permian on the basis of vertebrate remains (Jalil and Dutuit, 1996; Jalil and Janvier, 2005). However, the precise sedimentological study of this footprint site made by the first two authors showed that it rather belongs to the basal Triassic and especially to the unit T3 (Tanameurt Mb) of the Timezgadiwine Fm (Fig. 1C). The footprint level is about 2.5 m above the Permian-Triassic boundary.

In Iggui Aouglef locality, the Triassic succession is divided into the unit T3 and the overlying unit T4 (Agelgal Mb) (Fig. 1C). The Tanameurt conglomerates, 11 m thick, overlaid unconformably the Late Permian T2 unit (Fig. 1C). Their first meter consists of laterally discontinuous beds up to 40 cm thick of crudely stratified matrix-supported breccias deposited by debris flows. This unit is followed by sheet-like beds composed of matrix-supported conglomerates. They are interpreted as sheet-flood and debris flow deposits in alluvial-fan setting. Carbonate nodules or continuous carbonate beds are frequent features of this part of T3. They are interpreted as pedogenic carbonate accumulations in semi-arid paleosols. Moreover, interbedded light brown to light red sheet sandstone and red to chocolate sandy mudstone, with some mudcracks, are frequent. The very coarse- to medium-grained sandstone facies dominate. They are composed of horizontal laminated, subordinate ripple laminated, or massive layers. This facies association is interpreted as overbank deposits laid...
Fig. 2. Chirotheroid traces (Argana Basin, T3 unit). A: trackway n° 1 (5-6 FM), Brachychotherium. sp.; B: 11 FM, unnamed; C, D, F: footprints of trackway n° 1, respectively: 5 FM = CP1M1, 6 FM = CP2M2, 8 FM = P4; E: 4 FM, unnamed; G: 7 FM, Isochirotherium cf. gierlinskii; H: 2 FM, cf. Synaptichniun; I: 10 FM, Chirotherium barthii; J: 1 FM, Isochirotherium cf. gierlinskii; K: 3 FM, CPM Synaptichnium cf. pseudosuchoides; L: pes 5 FM = P1, Brachychotherium sp.; M: 9 FM, C. barthii, possible CPM; N: possible relation between 4 and 2 FM; O: Fossiliferous site (F); P: Footprint level (F). Scale-bar = 1 cm for B-L.

Fig. 2. A: piste n° 1 (5-6 FM), Brachychotherium. sp.; B: 11 FM, non nommé; C, D, F: traces de la piste n° 1, respectivement: 5 FM = CP1M1, 6 FM = CP2M2, 8 FM = P4; E: 4 FM, non nommé; G: 7 FM, 1 cf. gierlinskii; H: 2 FM, cf. Synaptichnium; I: 10 FM, C. barthii; J: 1 FM, 1 cf. gierlinskii; K: 3 FM, CPM Synaptichnium cf. pseudosuchoides; L: 5 FM = P1, Brachychotherium sp.; M: 9 FM, C. barthii, possible CPM; N: possible relation entre 4 et 2 FM; O: site fossilière (F); P: Niveau à traces (F). Barre d’échelle = 1 cm pour B-L.
Fig. 3. Chirotherioid traces (Argana Basin, T3 unit). A: trackway n° 1 (5, 6, 8 FM), Brachychirotherium sp.; B: 10 FM, Chirotherium barthii; C: 7 FM, Isochirotherium cf. gierlinskii; D: 3 FM, CPM Synaptichnium cf pseudosuchoides; E: 2 FM, cf. Synaptichnium; F: 5 FM=CP1M1, Brachychirotherium sp., e = scales; G: 8 FM=P4, Brachychirotherium sp.; H: 4 FM, chirotheriod trace; I: 6 FM=CP2M2, Brachychirotherium sp.; J: detail of the scale traces of the digit I in fig. F; K: 9 FM, possible CPM, Chirotherium barthii; L: 1 FM, CPM, Isochirotherium cf. gierlinskii. Scale-bar = 1 cm, except for A and J; ? = doubtful link.

3. Palaeontological study

The footprint site is located at the base of a little cliff (Fig. 2O). Traces are convex hyporeliefs which appear, on 2.25 m², at the basal surface of a conglomeratic sandstone forming an overhang. The original trace fillings were various, made of gravels to silts, explaining the poor quality of several of them. Among these traces were distinguished about twenty footprints which may fit in the Nopcsa (Nopcsa, 1923) crocodiloid group and more precisely in that of Chirotherioid as defined by Lessertisseur (Lessertisseur, 1955) or in the Chirotheriidae ichnofamily (Abel, 1935). Some others are lacertoid and close to Rhynchosauroides Maidwell, 1911 (Maidwell, 1911).

3.1. Description of the footprints

The following abbreviations will be P and M = pes and manus traces often named only pes or manus, CPM = associated pes-manus; I, II, III, IV, V: digits numbering; L and W = footprint length and width; LD and WD = I–IV part length and width; LP and LM = pes and manus length, Q = cross-axis angle in degrees = angle between the metapodial-phalangeal axis and the long axis of the footprint (see Fig. 3B); L/W, LD/WD, L/LM, L/LD, III/II, III/IV, II/I: various characters ratios often statistically tested; 1-10 FM = collection numbering.

Unlike the Rhynchosauroides track site already mentioned (Jones, 1975) in the Permian of the Argana Basin, most of the traces observed in the Iggui Aouglef site are chirotherioid in aspect. This term indicates pentadactyl, heteropod, quadruped tracks of which digits I–IV form a distal part more or less separated from the digit V. This later is reduced or absent, and extended by a large metapod trace. It constitutes the posterior part of the footprint, which often has a lateral posterior outer position.

As a whole, this morphological organisation characterizes the ichnogenera Chirotherium Kaup, 1835 (Kaup, 1835), Brachychirotherium Beurlen, 1950 (Beurlen, 1950) in which the pes digit III is the longest whereas it is IV for Synaptichnium Nopcsa, 1923 (Nopcsa, 1923), and Isochirotherium Haubold, 1971 (Haubold, 1971b) characterized by subequal II and III.
3.1.1. The manus-pes couple 3 FM (Figs. 2K, 3D)

The pes trace dimensions are as follows: L × W = 136 × 48 mm; LD × WD = 80 × 48 mm; I–IV lengths successively equal to 38, 56, 69, 77 mm; cross-axis angle Q = 48°; angle III–V = 40°. The whole is therefore lacertoid in aspect with toes close to each other (angle I–IV = 15°). They are ended by rather strong claws directed towards the footpath inside. An oblong metatarsal mark without the digit V is only present at the back of the I–IV digital part.

The manus is located to 97 mm ahead of the pes. The digit IV is not visible. It seems to be torn off, or its trace was erased by the later passage of another animal which made a print covering partially the preceding footprint. Digits are ended by short claws. II and III are rather broad and the first (I) is present only by the claw mark; recorded dimensions are: L × W = 45 × 40 mm; II and III are subparallel, with III = 47 mm, II = 41 mm; digito-metacarpal pad V = 37 mm; Q = 75°. III–V angle = 50°.

3.1.2. The 2 FM trace (Figs. 2H, 3E)

Longer than broad, it is a pes trace of which the digital lengths decrease from IV to I digits. Q is low: 60° and the angle III–V = 40°. L × W must be close to 135 × 70 mm.

3.1.3. The trackway n° 1 (5, 6, 8 FM traces) (Figs. 2, 3)

It is made of two consecutive couples P1–M1 and P2–M2 (Figs. 2A, C, D), and an incomplete pes P4 (Fig. 2F); P3–M3 seems to be destroyed or removed. The pes traces show a planigrad support (Figs. 2C, D, F, L and 3F, G, I). The digits I–IV are broad, squeezed and only a little separated (angle I–IV = 22°). I and IV are right whereas II and III are bent laterally to the outside of the trackway. They are ended by rather discrete claws. That of III is clear and constant. The IV is short on P2 and P4, not very printed on P1. The digit II is present in P4, but not preserved in P1.

The I–IV part is complete only in P1 where it appears transverse, broader than long, with LD × WD = 79 × 93 mm. It is extended backwards by the quadrangular toe V, without claw, which comes from a broad triangular to ovoid sole representing the metatarsal pad print.

Based on P1, L × W = 170 × 91 mm and digital lengths, without claws, are as follows: I = 65, II = 75, III = 70, IV = 59 mm (II > III > I > IV). This order is the same for P2 and P4. The II is thus the longest, a few millimeters longer than the III, and the IV is the smallest. The length of V is respectively 39, 28 and 11 mm for P1, P2 and P4. The pes length mean is 161 mm. The P1 trace is the best preserved, its surface is covered by transversal or oblique furrows. Those of the internal border partly correspond to a slight autopodium skid. The others are cutaneous folds and round-scale band traces which are quite visible on the toe I and a part of the II (Figs. 2L, 3F, E, J).

The M1 and M2 traces are located at 156 and 180 mm ahead of their respective pes. They show a digitigrad support. On M1, the I–IV part is as long as broad (LD × WD = 62 × 54 mm). The digits IV–II appear there broad, right, a little divergent from each other (angle IV–II = 90°), clawed and enough strong, unlike the I which is thin and not very visible because of it is stuck against the II. The digital lengths are: I = 729, II = 45, III = 57, IV = 50 mm; III is thus the longest with III > IV > II > I. The V trace is not distinguished from those of metacarpals. This V whole is located back to the I–IV part. It is 43 mm long and the angle III–V is 55°. M1 is as long as broad (L × W = 77 × 74 mm). The M2 trace shows the same organisation and dimensions as M1: L = 82 mm; LD × WD = 62 × 60 mm; I = ? 35, II = 48, III = 57, IV = 49 mm. The little thin digit I is not clearly marked. V is the partial metapodium trace, not clearly readable because of a print superposition. Angle II–IV = 12°.

3.1.4. The 1, 4, 7, 9, 10 FM traces (Figs. 2, 3)

These footprints seem isolated on the surface. Among the best preserved, we distinguished two CPM: 9 and 1 FM (Figs. 2M, J, 3K, L) and two pes traces: 10 and 7 FM (Figs. 2I, G, 3B, C). The four pes length mean equal 113 mm. These traces are typically chirotheriid in aspect as those of the trackway n° 1. But there the I–IV toes, ended by short claws and are more spread (angle II–III = 31° against 15°). As a rule, also the digit V is much shorter than its neighbours (length mean = 20 mm). It is extended inside by metatarsal pads expanded strongly behind the I–IV part, especially for 1 and 7 FM. The manus is located ahead of the pes, outside for 9 FM (Figs. 2M, 3K) and just in front of for 1 FM (Figs. 2J, 3L). The digit V and associated metacarpal pads traces of 1 FM were covered by the pes during the moving. The small 4 FM print could be that of a pes but there is no trackway allowing to know it with certainty (Figs. 2E, 3H).

3.2. Ichnotaxonomy

3.2.1. The 3 FM manus-pes couple: Synaptichnium cf. pseudosuchoides

Several chirotheriid ichnospecies were mentioned in the Lower and Middle Triassic of the USA (lower part of the Moenkopi Fm (Peabody, 1948)) and Europe where they were found in various formations: Keuper Sandstone of England (Habold, 1971b), Middle and Upper Buntsandstein of Germany (Detfurth, (Fichter and Kunz, 2004; Kunz and Fichter, 2000), Hardegsen, Solling and Röt Fms (Demathieu and Habold, 1982; Demathieu and Leitz, 1982; Fichter, 1995; Habold, 1967, 1971a, 1971b, 1983), and Poland (Labyrinthodontid beds, (Fuglewicz et al., 1990; Ptaszyński, 2000)).

A comparison of the 11 FM footprints with the various ichnospecies described in the formations quoted above, shows that they more resemble the ichnospecies Synaptichnium pseudosuchoides Nopsca, 1923. The type comes from the English Lower Triassic, and similar forms have been described in the Solling Folge and the Lower Röt (Demathieu and Habold, 1982; Demathieu and Leitz, 1982). So the Synaptichnium ichnogenus is known now in Arguna Basin, but only from a CPM whose the pes is very narrow (LD/WD = 1.67).

3.2.2. The 2 FM trace: cf. Synaptichnium

We report with doubt to this ichnogenus the 2 FM pes which is not entirely visible in situ (Figs. 2H, 3E). Nevertheless the decreasing of the IV–I digital lengths and the low values of Q (= 60°) and that of the angle III–V (= 40°), plead for this generic attribution.
3.2.3. The trackway n° 1 (5, 6, 8 FM traces) FM traces: Brachychirotherium sp.

In addition to Synaptichnium, the Chirotherium, Isochirotherium and Brachychirotherium ichnogenera are also present in the Early Triassic palichn fauna. Few years ago, the Chirotheriidae ichnotaxa grew with Protochirotherium wolfhagense Fichter and Kunz 2004 (Fichter and Kunz, 2004), described in the Detfurth Fm (Middle Bunter, Germany).

Although the trackway n°1 footprints show II–IV digital lengths virtually subequal, they cannot be assigned to Isochirotherium because of the manus size. Indeed, the ratio (LP/LM = 2.2) of these footprints differs significantly from that of Isochirotherium which is included between 2.6 and 3.7, but fits with those of Chirotherium (1.9–2.7) and Brachychirotherium (1.4–3.1) (calculus by authors). Based on the LP/LM ratio mean equal to 2.2, the trackway traces can thus be regarded as Chirotherium or Brachychirotherium. But in respect to the distal tip of the broad subparallel II–IV toes, which are rounded in shape and ended by narrow claws, we ascribe them to Brachychirotherium. Moreover these traces of the Argana Basin have similar measurements with B. hauboldi (Ptaszyński 1990 in Fuglewicz et al., 1990; Ptaszyński, 2000) from the Labyrinthodontid Beds of Poland. In each case, the pes prints are directed outside of the trackway, by nearly the same value, respectively 17° and 20° for B. hauboldi and those of the trackway. The pace angulation is variable in B. hauboldi: 157° (Ptaszyński, 2000), 120° to 65° (Fuglewicz et al., 1990), and 110° for the trackway n° 1 of the Argana Basin. But whereas the longest toe of the trackway n° 1 is the II (sample n=3), it is the III in B. hauboldi where, for n = 11, III/II mean = 1.17 (1.12–1.22) with confidence interval at 5% level, and III/IV mean = 1.19 (1.16–1.22).

The pes of the trackway n° 1 was also compared to that of Protochirotherium wolfhagense. At first sight, they are rather close by a LD/WD ratio equal to 0.93 and 0.97. Thus the I–IV part appears a little broader for B. hauboldi and those of the trackway. The pace angulation is variable in B. hauboldi: 157° (Ptaszyński, 2000), 120° to 65° (Fuglewicz et al., 1990), and 110° for the trackway n° 1 of the Argana Basin. But whereas the longest toe of the trackway n° 1 is the II (sample n=3), it is the III in B. hauboldi where, for n = 11, III/II mean = 1.17 (1.12–1.22) with confidence interval at 5% level, and III/IV mean = 1.19 (1.16–1.22).

The pes prints of the trackway n°1 are placed close to those of Protochirotherium wolfhagense. At first sight, they are rather close by a LD/WD ratio equal to 0.93 and 0.97. Thus the I–IV part appears a little broader for P. wolfhagense. Nevertheless the latter differs from the trackway n° 1, by its claws stronger and directed inwards (towards inside of the trackway), and by the absence of round digital ends. It is the reason why P. wolfhagense is closer to Chirotherium than to Brachychirotherium. But with the III toe hardly longer than the IV, its autopodium pes has a rather archaic organisation.

Brachychirotherium hauboldi (Ptaszyński, 2000) of which the pedal I–IV part is almost as broad as long, was then statistically compared with ichnospecies sharing this characteristic, namely B. gallicum Willruth, 1917 (Willruth, 1917), B. pachydaactylum Demathieu and Gand, 1973 (Middle Triassic, France) (Demathieu and Gand, 1973), I. soergeli (Haubold, 1967) and C. sickleri Kaup, 1835 (Solling Folge, Early Triassic, Germany) (Haubold, 1967; Haubold, 1971b). The means and variances tested at 5% level showed that B. hauboldi shares similarities with B. gallicum Willruth, 1917, concerning the ratios values of III/IV, II/I and the Q angle, but they differ for I/W, LD/WD, L/LD. With B. pachydaactylum Demathieu and Gand, 1973, of the French Middle Triassic (Demathieu and Gand, 1973), there is only the Q value (= 67°) which is not significant. Using the measurements made by Haubold (Haubold, 1971a), the III/II, LD/WD, L/LD values of B. hauboldi and C. bartihii Kaup, 1835, are also no significant. Except LD/WD, all the other ratio values are significantly different between I. soergeli (Haubold 1967) (Haubold, 1967) and B. hauboldi, the latter being fully different of C. sickleri Kaup, 1835 for all the ratios.

In the absence of sufficient measurement series for P. wolfhagense and the trackway n° 1 traces, we also executed a statistical comparison of the outlines of the I–IV part between the pes P1 of the trackway n° 1, 3 pes of P. wolfhagense, and 11 specimens B. hauboldi. For this, the complex discrete Fourier analysis clarified in Navaro et al. (Navarro et al., 2004) was used. The Dommergues program (Dommergues, 2001) was selected. Then 200 points, 11 and 20 pairs of harmonics were chosen in order to reconstitute the outlines. They were successively restored at 94 and 97% values. The results were analysed by a CPA (Components Principal Analysis) and visualized by a group of points traces in the two graphs Fl/F2 and F2/F3; the factor F representing the factorial weight.

From the two Fl/F2 graphs, P1 of the trackway and one P. wolfhagense pes are outside of the B. hauboldi cloud, two others being on the limit, and similar by their shape with two C. hauboldi traces. In the two Fl/F3 graphs, the three P. wolfhagense points and the P1 of Argana are external. Thus, there is a certain morphological similarity between two P. wolfhagense samples and the B. hauboldi whole (= population traces) inferred from the Fl/F2 graphs, but none between the Argana traces and the two preceding ichnospecies. Thus, it does not seem appropriate to have synonymise B. hauboldi with Protochirotherium as made Klein and Haubold (Klein and Haubold, 2007).

3.2.4. The 1, 7 FM traces: Isochirotherium cf gierlinskii; 9, 10 FM: Chirotherium bartihii

The 1 and 7 FM pes prints have subequal digits II–III, with a slight prevalence for the III, a characteristic favourable to its attribution to Isochirotherium. This hypothesis is also corroborated by the LP/LM value = 2.7, but the manus is not quite complete. Based on the II–IV lengths, which exceed faintly those of II and IV in the CPM 1 FM, it appears that these last tracks are neither Isochirotherium archaeum and Haubold, 1982 (Demathieu and Haubold, 1982), from Hardegse Fm (Germany, Early Triassic) nor I. soergeli, I. hessbergense, I. jenense and I. herculis from the Solling Fm (Germany, Early Triassic) (Haubold, 1967; Haubold, 1971b; Haubold, 1983). On the other hand, except for the IV length, smaller for the two Argana traces, the length ratios I/III, taken two by two, are close to those of I. gierlinskii from the Labyrinthodontid Beds of Poland. This species also has important posterior digito-metatarsal pads (Fuglewicz et al., 1990; Ptaszyński, 2000).

Following a mean and variance statistical comparison, the 9 and 10 FM pes (Fig. 3B, K) have more common points with Chirotherium bartihii than with C. sickleri. Eight tested characters (Q and I–IV angles, L/W, LD/WD, L/LD, II/I, III/IV, and III/II ratios) are similar to those of C. bartihii whereas three (Q, L/W and III/I) differ from those of C. sickleri.
4. Palaeontological, palaeoenvironmental and stratigraphic results

The osteological interpretation of Synaptichnium, Chirotherium, Isochirotherium and Brachychirotherium has long been discussed (Demathieu, 1970; Demathieu and Haubold, 1974; Haubold, 1971b; Peabody, 1948). This led, in the 1970s, to a general agreement that ascribes them to Archosaurus Pseudosuchia, or Archosauriformes Crurotarsi in cladistic nomenclature (Sereno, 1991). In such a phylogenetic concept, Synaptichnium would have been made by a basal Archosauruslike form as Euparkeria, and the other ichnogenera by different undetermined Crurotarsi. From the autotopod structure inferred from the pes traces of the trackway n° 1, it seems that the author of these Argana footprints was an archaic Crurotarsi. By using various methods quoted in Gand et al. (Gand et al., 2007), the analysis of the trackway characters and measurements allow to reconstitute a pentadactyl quadruped animal, approximately 2 m long, with forelimbs shorter than the posterior ones, a measured (from the trackway) and calculated trunk length about 50 cm, and a barycentre position located between 1/3 and 1/4 from the acetabulum (Demathieu, 1970). The pace angle value (110°) is indicative of semi-erected members. Nevertheless, this stance could be occasional as for the B. hauboldi trackmakers. Aside these Crurotarsi, Lepidosauria were also present as indicated by the Rhynchosauroides footprints.

The sedimentologic characters of the beds bearing the footprints level are indicative of an alluvial plain under the influence of alluvial fan inputs. As it was suggested, this environment was therefore inhabited by a tetradopec community dominated by Archosaurus Crurotarsi. The measured orientation of their traces in the Iggui Aouchel site indicates that animals walked west-east in both directions.

Until now the unit T3 (Tanameurt Mb) of the Timezgadiwine Fm was only tentatively referred to the Triassic. It overlies unconformably the unit T2 (Tourbihine Mb) of the Ikakern Fm, assigned to the Upper Permian thanks to stratigraphic results (Beurlen, 1950). It is overlain by the unit T4 (Aglegal Mb), dated as Middle Triassic by charophytes and ostracods (Medina et al., 2001) and as Anisian by Heylerosaurine Cyclotosauridae remains (Jalil et al., 2009). The tetradopec footprint assemblage studied here provides new element for biostratigraphic dating of the T3 unit.

Any of the ichnospecies described in the Middle Triassic of France (Anisian-Ladinian “Grès inférieurs” Fm) (Demathieu, 1970; Gand et al., 2007) and Germany (Röt Fm (Haubold, 1967; Haubold, 1971a; Haubold, 1971b) dated Lower Anisian (Bourquin et al., 2006) have been identified in the present study. Moreover, the closeness of the Argana ichnospecies to the German Synaptichnium cf. pseudosuchoides and Chirotherium barthii (Solling Fm., Upper Olenekian (Bourquin et al., 2006), and to the Polish Isochirotherium cf. Gierlinskii (Labyrinthodontid beds, Upper Olenekian (Bourquin et al., 2006; Niedźwiedzki and Ptaszyński, 2007) is clearly indicative of an Early Triassic age of this Moroccan ichnofauna, probably Upper Olenekian (Spathian). An Early Triassic age, possibly later than mid-Olenekian, could also be deduced from the Brachychirotherium sp. trackway, which suggests Crurotarsi with autopodia less advanced than those known in the Anisian.

5. Conclusions

The Iggui Aouchel ichnites are represented by Rhynchosauroides sp. and chirotheroid footprints: Synaptichnium cf pseudosuchoides, Synaptichnium sp., Brachychirotherium sp., and Isochirotherium cf gierlinskii. They have been identified above all at the generic level, except Chirotherium which is clearly present by the ichnospecies C. barthii. Animals were Archosauriformes Crurotarsi, and Lepidosauria represented by Rhynchosauroides. On the footprint surface, it could be shown that all these animals moved in east–west opposite directions. From the sedimentological characters of the fossiliferous site, we deduced that the palaeoenvironment they run through was a floodplain periodically invaded by braided channels during wet periods. These last alternated with dryness phases during which vertisols could develop.

According to the closeness of the aforesaid footprints with Lower Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic ichnospecies, and the relative archaic pes bony structure of the Brachychirotherium sp. trackmaker, an Upper Triassic

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