

Reptile tracks (*Rotodactylus*) from the Middle Triassic of the Djurdjura Mountains in Algeria

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In 1983, during stratigraphic investigations in the Djurdjura Mountains, vertebrate tracks were discovered in the Middle Triassic Haizer–Akouker Unit at the Belvédère (Bkherdous) locality in Algeria. The footprints are about 2 cm long and consist of impressions of four clawed digits (I–IV), plus a reverted digit V. Manus imprints were overstepped by those of the pes. Originally interpreted as lizard footprints, they have been recently diagnosed as *Rotodactylus* cf. *bessieri* Demathieu 1984. In the current literature, *Rotodactylus* trackmakers are regarded as a group closest to dinosaurs among stem archosaurs. The footprints demonstrate a terrestrial sedimentary regime in the Maghrebids area during the ?late Anisian.

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INTRODUCTION

In spring of 1983, one of us (Z. K.) was looking for Middle Triassic diplopores near a road along the main ridge of the Djurdjura (Jurjura) Mountains in Grand Kabylie (Great Kabylia), Algeria. The tracks described herein were discovered in the Haizer–Akouker Unit at the Belvédère (Bkherdous) locality (Fig. 1). Two slabs of fine-grained sandstone were delivered to an expert on Triassic reptilian tracks, Prof. P. Ellenberger (Université de Montpellier II) in summer 1985, with the help of Dr. J.-L. Reille from the same university. P. Ellenberger commented that the numerous traces look like lizard footprints; he promised to diagnose them further and send the specimens together with detailed descriptions to Warsaw.

In 1986 at the Polish Geological Institute in Warsaw, in a presentation of results of research on the Kabylia Triassic of the Tellian chain in Northern Algeria, including the finds of diplopores (Kotański, 1987a), the reptile tracks from the Middle Triassic of Djurdjura were reported as lizard footprints (*vide* Ellenberger). After this presentation, one of us (G. G.) diagnosed the best preserved specimens, based on a colour photograph of the larger slab (No. 1), taken in 1983 (Fig. 2), as a natu-

ral cast of a left pes imprint of the ichnogenus *Rotodactylus* Peabody, 1948, cf. *Rotodactylus matthesi* Haubold, 1967, attributable to ornithosuchian archosaurs. The presence of *Rotodactylus* tracks was noted in the geological section from the Djurdjura Mountains in a symposium presentation on diplopores from the same sequence (Kotański, 1995).

To resolve the discrepancy between this determination of tracks by G. G. and the preliminary opinion of P. Ellenberger, the original specimens and the final determination of the fossils by P. Ellenberger were necessary. In summer of 1995, G.G. visited P. Ellenberger in Montpellier to arrange the delivery of the loaned specimens to Warsaw. P. Ellenberger promised him to find the specimens and to send them, together with determinations. Later, P. Ellenberger (letter to G. G. dated December 22, 1995), explained that the specimens had been transferred to the basement of the Department of Nature at the University in Montpellier and placed together with other similar Triassic tracks. The palaeontological museum had been flooded and documents accompanying the specimens had been destroyed by water. When P. Ellenberger attempted to find the Djurdjura specimens, he could not locate them. Only much later, the specimens were discovered in mud on the floor of cellar. Fortunately, they survived in very good condition and were safely delivered to Warsaw in December 1995. The material has been

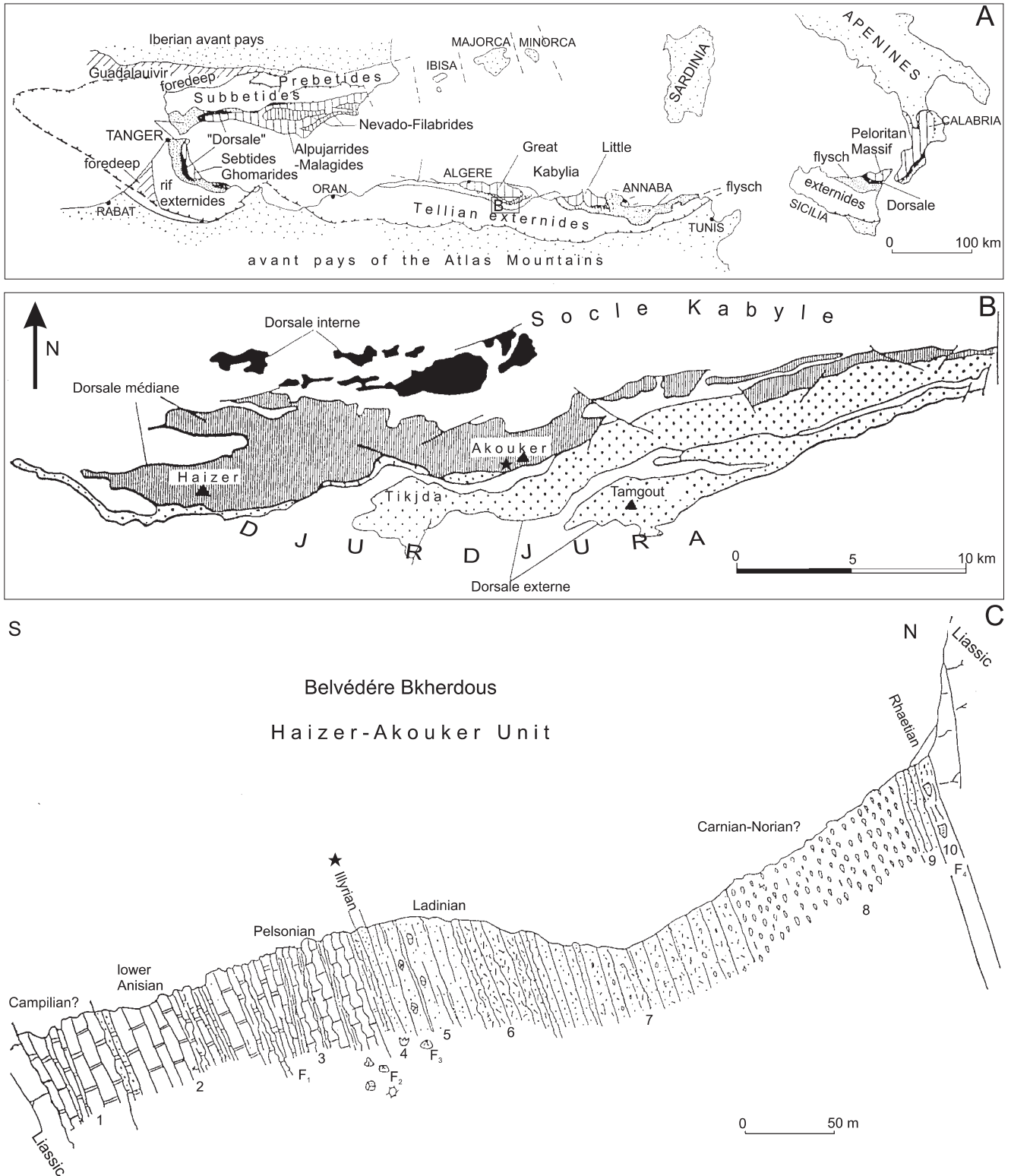


Fig. 1. A — the position of the Tellian Atlas in the structural context of the Betides and Maghrebides (Durand-Delga and Fontboté, 1980 from Mišik, 1984); B — sketch map of the calcareous ridge (Dorsale Kabyle) in the Djurdjura after Kotański, 1995; the *Rotodactylus* tracks at the Belvédère–Bkherdous locality (Haizer–Akouker Unit) are marked with an asterisk; C — detailed profile of the Triassic strata at the Belvédère (Bkherdous) locality; succession of strata 1–10 are described in the text; F₁–F₄ — stratigraphic positions of the faunal assemblages; position of *Rotodactylus* tracks marked with an asterisk

deposited in the Geological Museum of the Polish Geological Institute (abbreviated Muz. PIG).

P. Ellenberger attached to his letter of December 1995 a drawing with determinations and labels made by him back in 1986 (Fig. 3). On slab No. 1 he identified *Rhynchosauroides* cf. *rectipes* Maidwell, 1911, and *Batrachopus* cf. *deweyi* Hitchcock, 1843 on slab No. 2. The first slab is certainly one of the two specimens found by Z. K. in the Triassic of Djurdjura, photographed in Bejaia in 1983. Its photograph was attached to letters from Z. K. to P. Ellenberger in 1990 and 1995. The origin of the second slab with reptile tracks is uncertain. The sandstone of this slab differs from the sandstone of the first slab and it is not certain whether it came from the Triassic of Djurdjura. Unfortunately, no photographs of the second slab were taken before its delivery to P. Ellenberger. Since the documents accompanying the specimens were submerged and partly damaged in Montpellier, the drawings and determinations enclosed to the letter from Ellenberger to G. G. could have been produced by P. Ellenberger only in 1995, after the slabs with tracks and original documents had been recovered from the mud. If that was the case, it is uncertain whether the slab No. 2, with tracks completely different from those on slab No. 1, indeed originates from the Triassic of Djurdjura.

In January 1997, at a scientific conference on vertebrate tracks was held in Geological Museum of the PGI. Z. K. and G. G. presented the specimens from Djurdjura, attributed by G. G. to the ichnogenus *Rotodactylus* (*Rotodactylus* cf. *bessieri* Demathieu 1984). Other reports at that meeting concerned reptilian tracks from the Middle Buntsandstein from Wióry in the Holy Cross Mountains in Poland in 1980s and 1990s (Fuglewicz *et al.*, 1981, 1990; Ptaszyński, 2000), including *Protodactylus* tracks (Ptaszyński, 2000), similar to those of the ichnogenus *Rotodactylus*.

STRATIGRAPHIC AND TECTONIC SETTING OF *ROTODACTYLUS* TRACKS

The Triassic of the Djurdjura Mountains is well known thanks to the studies of Fallot (1942), Lambert (1942), and especially Flandrin (1952). The Djurdjura Mountains belong to the "limestone chain" (dorsale calcaire), being the Mesozoic–Eocene cover of the internal massifs of the Great and Little Kabylia. The limestone chain, documented by Durand-Delga and his team (Durand-Delga, 1962, 1978, 1980, 1981; Caire, 1971; Raoult 1974; Bouillin, 1977; Vila, 1980; Durand-Delga and Fontboté, 1980; Obert, 1981; Bouillin *et al.*, 1986) belongs to the Maghrebids, spanning the Betic Alps in southern Spain, Gibraltar, the Rif in Northern Morocco, the Tellian Atlas in Algeria, Northern Sicily (the Peloritian range) and Calabria (Fig. 1A). The Triassic of Kabylia (with the Djurdjura Mountains) belongs to the internal part of the Maghrebids (Mišik, 1984).

The morphological-tectonic zonation of the Djurdjura Mountains by Flandrin (1952) comprises: the internal (Kouriet), the middle (Haizer–Akouker) and the external (Tikjda and Tamgout) units, differing in their facies development. All of these are thrust south on to Cretaceous flysch. The best sec-



Fig. 2. Photograph of the entire slab No. 1, Muz. PIG 1672.II.1 with reptile footprints made by Kotański in Bejaia in 1983

tions of the Middle Triassic occur in the Haizer–Akouker Unit, where it is developed mainly as Muschelkalk facies.

The most fully developed Triassic section can be observed in the middle unit, the Haizer–Akouker. Clastic deposits of the Lower Triassic are preserved only partly (Flandrin, 1952), because they are mostly left below the surface of the overthrust. The best section of the Middle Triassic sediments belonging to this unit outcrops at Belvédère (Bkherdous), above the asphalt road from Tikjda, at the foot of the main ridge of Djurdjura. The section through the Middle Triassic is crossed obliquely by the road, but crops out best along the path leading through the slope of Epaule de Akouker to the Belvédère pass in the main ridge.

The section of the outcrop at Belvédère (Bkherdous) is as follows (Fig. 1C):

1. Yellow, platy dolomites without fauna, about 40 m thick, thrust onto massive, light Liassic limestones of the lower Tikjda Unit. In their upper part, quartz-quartzite conglomerates with sandstone intercalations are present. They possibly mark the Montenegro fold phase, near the Anisian boundary (Kotański, 1987). All these carbonate Triassic sediments were up to now considered as part of the Muschelkalk, but possibly belong to the uppermost Lower Triassic (Campilian).

2. Lower Anisian grey saccharoid dolomites and platy dolomites about 80 m thick, with local evidence of flow disturbances and landslides. In sequence stratigraphy terminology, they are designed as SMW/LST (Tefiani *et al.*, 1994).

3. The succession of vermicular and platy limestones with intercalations of yellow, thin-bedded dolomites and dolomitic shales is a single deepening upwards parasequence (TST — Tefiani *et al.*, 1994), about 70 m thick. In its upper part (condensed interval, F₁ in the section, Fig. 1C), fossil gastropods (*Neritaria*, *Omphaloptycha*, *Loxonema*), bivalves (*Myophoria*), ostracods and benthic foraminifers (*Meandrospira deformata*, *Ammodiscus*, and *Tetrataxis*) were found (Tefiani, 1993; Tefiani *et al.*, 1994). This succession was deposited in lagoonal, hypersaline environment, as evidenced

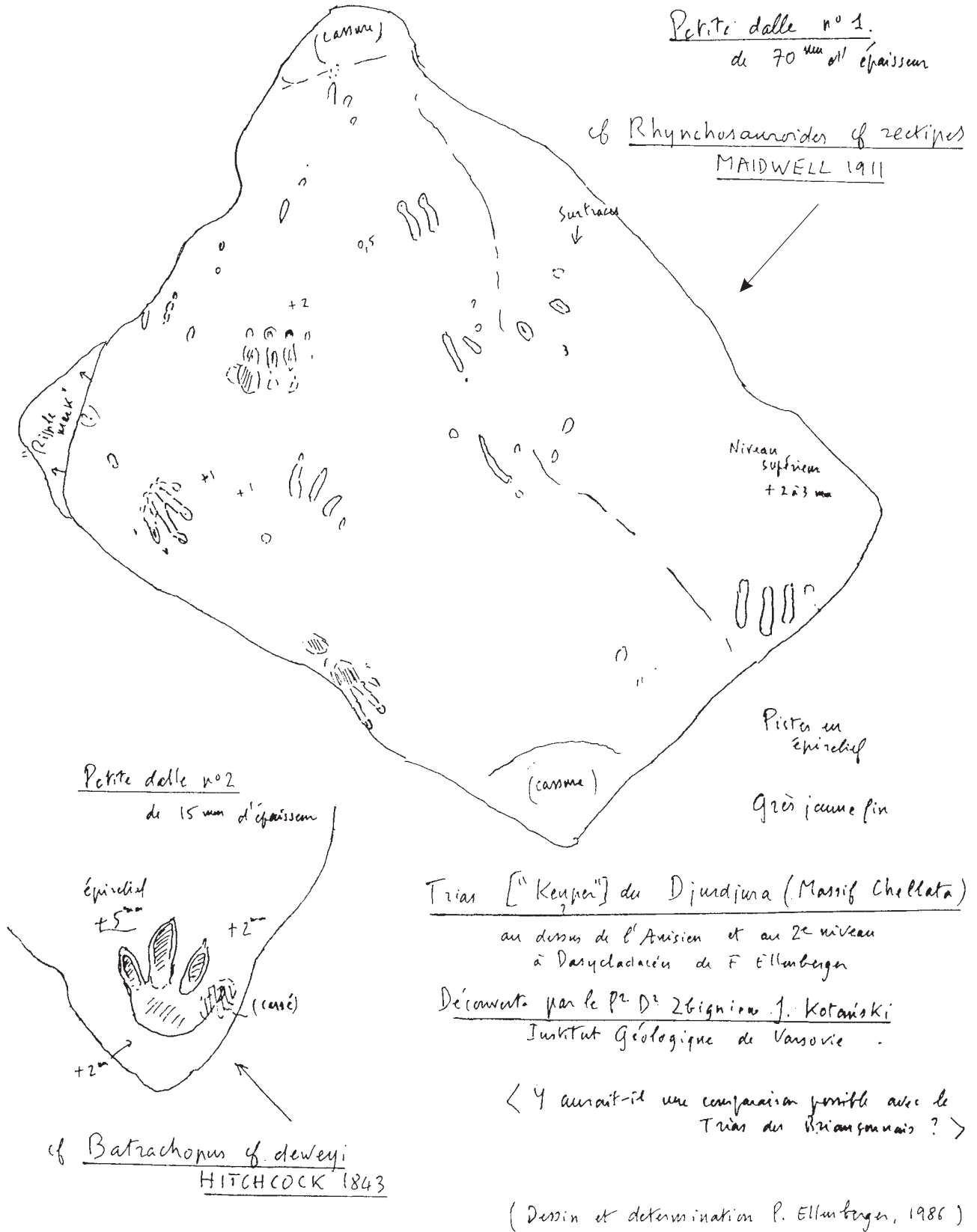


Fig. 3. Photocopy and determination of the footprints from slab No. 1 in the sketch by P. Ellenberger, attached to his letter of 22.12.1995 to Gierliński

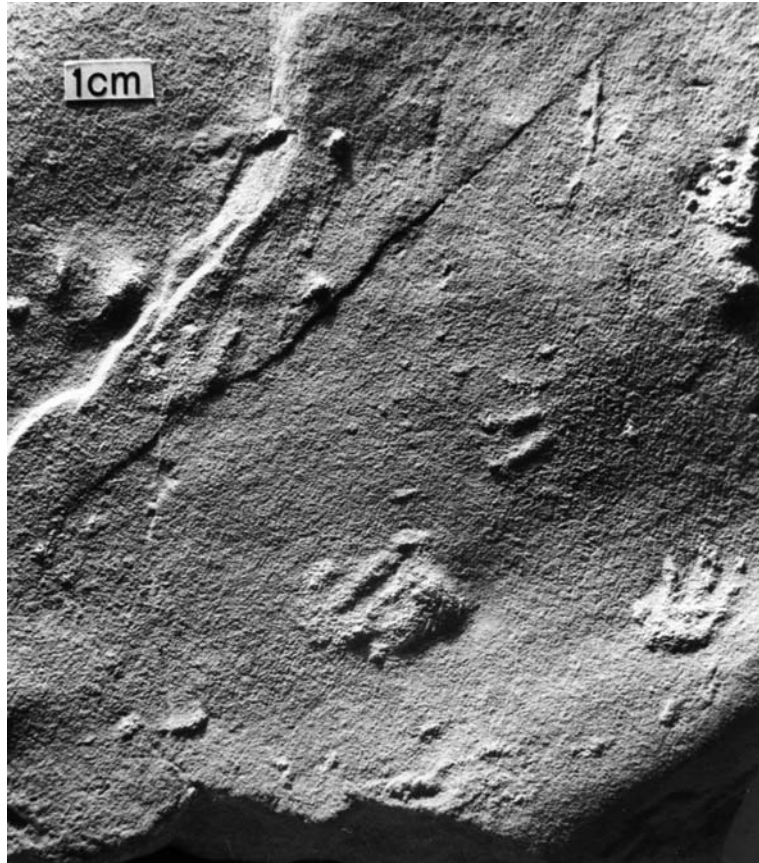


Fig. 4. Slab No. 1, Muz. PIG 1672.II.1 with footprints

Numbers are compatible with descriptions in the text

e.g., by Dasycladales (Kotāński 1984, 1987, 1994a, b, 1995), representing both “double-row” physoporellae (*Physoporella praealpina*, *Ph. dissita*, *Ph. minutula*), and “single-row” types (*Ph. pauciforata*) (Kotāński, 1995). Hagdorn (in Tefiani *et al.*, 1994) regarded the species *Neoschizodus orbicularis* Bronn as characteristic of the upper Anisian (lower Illyrian) of Germany (*Orbicularis* Schichten). However, benthic foraminifers are characteristic of the lower and middle Anisian (Pelsonian), whereas palynomorphs from the TST sequence (*Hexasaccites muehleri* and *Cristanisporites* sp.) indicate a Lower and Middle Anisian age (Tefiani *et al.*, 1994). The presence of physoporellae and lack of *Diplopora annulatissima*, an index fossil of the Illyrian, restricts the age of the vermicular limestones to the Pelsonian (Kotāński, 1987, 1994), equivalent to the lower part of the II *Diplopora* Zone of Ellenberger (1958) from the Briançonnian Alps.

4. In the uppermost part of the vermicular limestone succession sandy shale intercalations appear, indicating a supply of clastic material from nearby land. Tefiani *et al.* (1994) noted here a thin layer of marly palaeosol (HST). Above them there are situated pale, fine-grained quartz sandstones, 2–3 m and thick containing parallel ripplemarks, bioturbations and tracks of small reptiles, described below. In the section (Fig. 1C) this level is marked F2. The presence of reptile tracks is unquestionable evidence of the terrestrial origin of the sediments near the Anisian–Ladinian boundary. Because of the Pelsonian age of the vermicular limestones, the age of continental sediments

containing reptile tracks may be equivalent to the Illyrian; the overlying deposits belong to the Ladinian.

5. Brown ferruginous sandstones and white sandstones with intercalations of green, yellow and red shales about 50 m thick, containing a bivalve fauna (F3 in Fig. 1). Sandstones display delicate horizontal stratification with numerous surfaces showing traces of erosion. Overlying the intraformational erosional surfaces there are deposits packed with fragments of red and brown shales with numerous surfaces bearing ripplemarks. On surfaces of white sandstones occur parallel, interfering and partly eroded ripples. In white saccharoidal sandstones there are bioturbational structures. This assemblage of fluvial sediments contains the Ladinian palynomorph *Ovalipollis pseudoalatus* (Tefiani *et al.*, 1996).

6. A succession of red clastic sediments about 150 m thick: distinctly stratified thick-bedded red sandstones. Also present are pebbly sandstones with red, white and black quartzite pebbles (lydites) and conglomerate intercalations of the same composition. On erosional surfaces fragments of red and green shales can be observed.

7. Conglomerates with pebbles of lydite and multi-coloured quartz. There are intercalations of yellowish saccharoidal sandstones, especially numerous in the uppermost part of this succession. Its thickness attains about 100 m.

8. Yellowish saccharoidal sandstones, about 20 m thick. They continue to the steep wall built of Liassic limestones, but the contact is covered by talus debris.



Fig. 5. *Rotodactylus* cf. *bessieri* Demathieu, 1984

Muz. PIG 1672.II.1, specimen No. 1; enlargement from Figure 4

9. In other places of the Triassic section, Flandrin (1952) found in its uppermost part sandstones and shales with *Rhaetavicula contorta* (F4 in Fig. 1C), proving their Rhaetian age (10).

Strata 7–9, situated in the Ladinian and Rhaetian, can be assumed to be Carnian and Norian. Less probably, the red beds 7–9 belong to that Ladinian, the Upper Triassic being absent (Tefiani *et al.*, 1994).

FOOTPRINT DESCRIPTIONS

The small slab of fine-grained grey-yellowish sandstone, Muz. PIG 1672.II.1 (Figs. 2 and 4), is 14 by 11 cm across, and 7 cm thick. It shows about 12 vertebrate footprints preserved as natural casts on its bottom side. The imprints are isolated; no trackway pattern can be recognised except for possible manus and pes sets of imprints. It is often difficult to determine imprints made by hands or by feet. Most of them are incomplete or show only digit traces. All imprints are similar in size.

The most fully preserved imprint, No. 1 (Fig. 5), is pentadactyl. Digits II–IV are similar in length. Digit I is relatively short. Metapodial–phalangeal pads are distinctly placed along the straight line and therefore the metapodial–phalangeal axis is well defined. The first four digits are clawed. The fifth digit tip imprint clearly shows its rotated position relative to the digit group I–IV; 3 mm long, 10 mm distant from the basal part of the IV, a little less than the length of digit IV. The whole imprint is 22 mm long by 11 mm wide; the digit group I–IV is 15 by 11 mm. Lengths of digits are: I — 6 mm; II — 10 mm; III — 13

mm; IV — 13 mm. Digits I–IV diverge at 43° one from another; that value of digits II–IV equals 20°, and that of IV–V attains 167°. The crossing axis equals 65°. Other specimens show digit IV somewhat longer than III but both are very similar in length.

Other specimens, No. 5 and 2 are similar in size and shape to specimen No. 1 and may represent the same ichnospecies. Specimen No. 4, also similar in size, shows a larger angle between axes of digits II and IV, 34°; the digit V tip is in a more lateral position in relation to the digit group I–IV, but this may be the result of an atypical impression of the foot. The partial imprint No. 3 showing only distal parts of digits II–IV, is somewhat larger in size and may represent a hind foot imprint of the same set as No. 4; the angle between their axes equals 16°. The same applies to the somewhat larger, but problematic No. 7, showing only poorly visible distal parts of digit IV and V imprints, situated before the relatively well impressed specimen No. 6 which shows the digit group I–IV. If No. 6 and 7 indeed belong together, the manus imprints are overstepped by those of the pes. On the other hand, the poorly preserved specimen No. 3 could be a manus imprint representing the same set as the poor imprint No. 12, being close to specimen No. 1 in size.

Measurements of specimen No. 6, which has a state of preservation typical of other *Rotodactylus* (see Demathieu, 1984), are (in mm): I — 6(?); II — 8; III — 11; IV — 11; length of the digit group I–IV: 13; width of the digit group I–IV: 12. The imprint of digit V is not visible.

Possibly all well preserved imprints represent only one ichnotaxon, made by trackmakers of the same size and passing at approximately the same time, perhaps as a group.

The lack of any trackway pattern makes the exact determination of the ichnospecies difficult. The distinct rotation of

digit V imprints and the arrangement of digits allow identification of specimens No. 1 and 2 as representatives of the ichnogenus *Rotodactylus* Peabody, 1948 known from Lower and Middle Triassic deposits of Europe and America.

The imprints examined show the largest similarity to the relatively large ichnospecies *R. bessieri* Demathieu 1984, described from the Middle Triassic of France. *R. bessieri* Demathieu 1984 differs from specimens from Djurdjura in having pedal digit IV distinctly longer than III (this does not apply to manus imprints), but their whole shape and size are similar, and therefore the Djurdjura in prints should be identified here as *Rotodactylus* cf. *bessieri* Demathieu 1984.

DISCUSSION

In comparison with pes and manus the imprints of *Rotodactylus cursorius* Peabody, 1948 and *R. mckeei* Peabody, 1948, the imprints from Djurdjura are wider and have shorter digits IV. Manual digits V of *R. mckeei* and *R. bradyi* Peabody, 1948 are closer to the longitudinal axis of the entire imprint. Imprint No. 1, possibly also No. 2 and, especially, No. 4 show the digit V imprint situated distinctly outwards from the digit IV axis; this feature distinctly differentiates them from *R. matthesi* (Haubold, 1967).

The low value of the transverse axis and somewhat lateral situation of the digit V in the specimens discussed, distinguishes them from rotodactylids such as *R. rati* and *R. kronachense* Demathieu and Leitz, 1982. *R. velox* Demathieu and Gand, 1974 (see Gand, 1975) and *R. lucasi* are also much bigger in size; specimens illustrated by Gand (1975) are too poorly preserved to allow exact comparison, but suggest a higher value of the transverse axis, close to 90°.

The affinity of *Rotodactylus* trackmakers has been considerably discussed (Peabody, 1948; Haubold, 1967; Thulborn, 1990) as a track record of Pseudosuchia or dinosaur-like forms among thecodonts (e.g., lagosuchids). According to Haubold (1998), *Rotodactylus* corresponds perfectly with the Dinosauromorpha. Ptaszyński (2000) interpreted the posteriorly reversed digits V of both manus and pes, a unique feature of *Rotodactylus*, as evidence of arboreal specialisation.

CONCLUSIONS

The footprints discovered in Belvédère (Bkherdous) locality in Algeria demonstrate a terrestrial origin for the ?upper Anisian deposits in the Djurdjura Mountains, improving our understanding of the Mid-Triassic palaeogeography of Algeria. They also indicate the presence there of advanced, dinosaur-like basal archosaurs.

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