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**Tetrapod tracks from the Middle/Late Triassic of the Ourika and Yagour basins (Morocco): new ichnotaxonomical data based on the Biron collection**

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**Abstract:** Palaeontological prospecting organized in the Ourika and Yagour basins (Marrakech High Atlas, Morocco) in the 1980's, have yielded abundant and exquisitely preserved tetrapod tracks, some of them preserving thinly detailed skin traces (Collection Biron, Cadi Ayyad, Marrakech, Morocco). Based on this material, diverse morphologies of tracks were described and six new ichnotaxa were erected. However, these trackways have never been reinvestigated in detail from an ichnotaxonomic point of view. Here, the Biron collection is reevaluated using modern photogrammetric imaging techniques. The fine-grained sandstone slabs bear trackways ascribed to *Apatopus lineatus*, *Isochirotherium* isp. and *Rhynchosauroides* isp. whose trackmakers are possible phytosaurs, crocodylian-stem archosaurs or non-crown-group archosauriforms and lepidosauromorphs/archosauromorphs, respectively. “*Chirotherium atlensis*”, “*Enigmatopus atlensis*”, “*Hyloidichnus triasicus*”, “*Prochirotherium triasicum*”, “*Pseudochirotherium oukaïmedensis*” and “*Rectilinetopus ourikensis*” are considered as invalid. The palaeoichnological assemblage includes a mixture of Early to the Middle Triassic (*Isochirotherium*) and Late Triassic (*Apatopus lineatus*) tracks. This result corroborates the biostratigraphic data recently obtain from the base of the Oukaïmeden Sandstone Formation, suggesting a Middle-Late Triassic age. The living environment was a semi-arid alluvial plain with ponds and ephemeral rivers.

**Keywords:** tetrapod tracks; Mesozoic; Ladinian; Carnian; Marrakech High Atlas; photogrammetry

## 1. Introduction

In Morocco, significant ichnofossils including abundant and diverse vertebrate and invertebrate tracks were reported from Triassic deposits of the Argana Basin (Klein et al., 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020), the Sidi Saïd Maachou Basin (Hminna et al., 2013, 2020, 2021) and the Yagour Plateau (Biron and Dutuit, 1981; Biron, 1982). They constitute a key for the reconstruction of continental early Mesozoic palaeoecosystems (Biron and Dutuit, 1981; Klein et al., 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020; Hminna et al., 2013, 2020, 2021). Whereas tracks from the Triassic deposits of the Argana Basin were abundantly studied (Biron and Dutuit, 1981; Klein et al., 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020), those from the Ourika and Yagour basins clearly appear to be underestimated. In 1981, Pierre-Eymard Biron discovered several tracksites (Biron and Dutuit, 1981; Biron, 1982). This material was described by Biron and Dutuit (1981) who dated it as Late Triassic. In this study, they described two slabs bearing exquisitely preserved tracks that they attributed to *Apatopus lineatus* and a new species of *Chirotherium*: “*C. atlensis*”. Then, based on isolated pes or manus tracks, they briefly described five additional new ichnotaxa: “*Enigmatopus atlensis*”, “*Hyloidichnus triasicus*”, “*Prochirotherium triasicum*”, “*Pseudochirotherium oukaïmedensis*” and “*Rectilinetopus ourikensis*”. Except for a tentative discussion by Klein and Lucas (2013, 2021) of some of these ichnospecies, the tracks from the Ourika and Yagour basins have never been reinvestigated in detail. Here, we revised Biron’s material housed at the Cadi Ayyad University (Marrakech). We describe it using photogrammetric imaging techniques, update the ichnotaxonomy of the tracks and discuss their age.

## 2. Geographical and geological setting

The study area is located in the Marrakech High Atlas (Fig. 1A), 60 to 80 km southeast of Marrakech. At the south of the Carboniferous Ourika-Zat anticline (Fig. 1B), the Permian and Triassic outcrops overlie the deformed Variscan basement, represented by Precambrian volcanic rocks, Cambrian series, granitoids and metamorphic rocks, or Carboniferous deposits. The Permian and Triassic rift area is related to the NW-SE-oriented extension, which generated N-S trending normal faults (Van Houten, 1977; El Arabi et al., 2003; Qarbous et al., 2003; Baudon et al., 2009) and reactivated pre-existing NE-SW to ENE-WSW Variscan structures (Fig. 1B). These dip-slip and strike-slip faults are reactivated (Baudon et al., 2009; El Arabi, 1988; El Arabi et al., 2003; Laville and Petit, 1984; Laville and Piqué, 1991) and controlled the Triassic sedimentation (Benaouiss et al., 2023). The Permian and Triassic sedimentary successions are represented by elongated and narrow tectonic belts with an ENE-WSW orientation (Fig. 1B), up to 17 km wide and up to 35 km long. These Permian and Triassic deposits are subdivided into six formations (fms), noted F1 to F6 (Biron, 1982; Fig. 1C), corresponding to the Permian Anrar Conglomerate (F1), dated by radioactive and zircon method (Van Houten, 1977 and Perez et al., 2019) and the Cham-El-Houa Siltstone (F2), located below the Permian-Triassic unconformity, is attributed to the Permian age by correlation with the Argana t2 Unit (e.g. Benaouiss et al., 2023). The F3 (Timalizène Conglomerate), F4 (Anouffig Siltstone), F5 (Oukaïmeden Sandstone), and F6 (Tafilalt Siltstone) fms of Biron (1982) correspond respectively to the Basal Conglomerate, Ramuntcho Siltstone, the Oukaïmeden Sandstone and Upper Siltstone fms of Mattis (1977). The F3 Formation (Fm) is attributed to Early Triassic (e.g. Benaouiss et al., 2023) by correlation with the t3 Unit in the Argana Basin, dated by Tourani et al. (2010) with tetrapod tracks. Based on pollen analyses, the lower part of F4 Fm is middle Anisian age (El Arabi et al., 2006) and the F5 Fm is dated middle Carnian at its lower (Biron and Courtinat, 1982) and upper parts (Cousminer and Manspeizer, 1976) (Fig. 1C). The base of the Oukaïmeden Sandstone Fm was recently dated by pollen grains and conchostracans as Ladinian-early Carnian (Benaouiss et al., 2018). This part of F5 Fm represents the equivalent of the lower part of the t5 Unit in the Argana Basin which is dated as Julian-Tuvalian (mid-Carnian) by Tourani et al. (2023). The F6 Fm is attributed to the Norian, by correlation to the t8 Unit in the Argana Basin which is dated by conchostracans according to Weems and Lucas (2015). The Triassic series is overlain by Early Jurassic basalts, representing a good stratigraphic marker across Morocco (Bertrand et al., 1982; Blackburn et al., 2013; De Pachtère, 1983; Marzoli et al., 2004).

Two main Triassic outcrops are of interest to this study (Fig. 1B); (1) those of the Ourika Basin, which is limited at the north by the Sidi Ali-Ou-Fars fault and at the south by the Oukaïmeden fault (Fig. 1B), (2) those of the Yagour Basin, which is limited by the Sidi Ali-Ou-Fars and Tafrawt faults at the north and the Meltsene fault at the south (Fig. 1B). Biron and Dutuit (1981) reported three tracksites on the Ourika and Yagour basins, at the East of Aghbalou, at the North-East of Anammer and at the North-West of the Yagour Plateau (Star symbol in Fig. 1B). The historical tracksites are located at the base of the Oukaïmeden Sandstone Fm (Fig. 1B and C). This formation is up to 600 m thick and outcrops mainly as cliffs, accessible along streams and tracks, and is mainly characterized by channel sandstone bodies alternating with lenticular fluvial bar sandstones and overbank mudstone deposits (Benaouiss et al., 1996; Fabuel-Perez et al., 2009). The Oukaïmeden Sandstone Fm is subdivided into three units (Benaouiss et al., 1996; Fabuel-Perez et al., 2009), called lower-, middle- and upper Oukaïmeden units. The lower unit, which yields the fossil tracks, is 30 to 110 m thick. It is richer, than the middle and upper units, in red clay-stones and siltstones, and was deposited in an ephemeral fluvial system under dry climate. The middle unit is 25 to 80 m thick, and corresponds to a distal braided system associated with more humid conditions (Fabuel-Perez et al., 2009). The upper unit, which is 30 to 80 m thick, corresponds to the comeback of ephemeral conditions with the installation of aeolian dunes corresponding to arid conditions (Benaouiss et al., 1996; Fabuel-Perez et al., 2009).

### 3. Material and methods

The palaeontological collection of the department of Geology (Cadi Ayyad University) includes two large fine-grained sandstone slabs bearing tetrapod tracks, described and figured in Biron and Dutuit (1981) (Figs. 2 and 3). These slabs called “Dalle 1” and “Dalle 2” in Biron and Dutuit (1981), bear currently the collection numbers UCA.82 and UCA.83, respectively. The slab UCA.82 (Fig. 2), was collected at the base of the Yagour Plateau whereas the geographical origin of the slab UCA.83 (Fig. 3) was not indicated in Biron and Dutuit (1981). The slab UCA.82 (63 cm long and 58 cm wide) bears eight large and exquisitely preserved tracks briefly described by Biron and Dutuit (1981) for which they erected the new ichnospecies “*Chirotherium atlensis*”. The slab UCA.82 also bears numerous (around one hundred) small lacertoid tracks (*Rhynchosauroides*) undescribed by Biron and

Dutuit (1981) but briefly mentioned in Biron (1982). The slab UCA.83 (44 cm long and 41 cm wide) bears eight large tracks briefly described by Biron and Dutuit (1981) who ascribed them to *Apatopus lineatus* (Fig. 3). This slab also bears four isolated and partial small lacertoid tracks ascribed to *Rhynchosauroides* (Fig. 4). On both slabs, tetrapod ichnofossils are preserved as convex hyporeliefs. The tracks that Biron and Dutuit (1981) described as “*Enigmatopus atlensis*”, “*Hyloidichnus triasicus*”, “*Prochirotherium triasicum*”, and “*Rectilinetopus ourikensis*” (Fig. 5) were preserved on large isolated blocs left in place on the field (unfortunately not precisely located in Biron and Dutuit, 1981).

The descriptive terminology and biometric parameters used in this study follow those of Haubold (1971) and Leonardi (1987). We used the following standard abbreviations: ML, manus track length; MW, manus track width; ML/MW, length to width ratio of manus track; PL, pes track length; PW, pes track width; and PL/PW, length to width ratio of pes track.

3D photogrammetric reconstructions were produced with the software Agisoft Metashape Professional 2.0. Pictures of the surfaces were taken with a Nikon D5200 camera coupled with an AF-S Nikkor 18–105 128 mm f/3.5–5.6G ED lens. The same software was used to produce photogrammetric digital elevation models and contours.

#### 4. Systematic palaeoichnology

##### *Isochirotherium* isp.

Fig. 2A–F

**Material.** Eight tracks preserved as convex hyporeliefs on slab UCA.82, Cadi Ayyad University (Marrakech).

**Description.** The slab UCA.82 bears eight semi-plantigrade and quadrupedal tracks, including five pes tracks and three manus imprints (including three pes/manus sets; Fig. 2A–C). Two pes/manus sets are part of a trackway (Fig. 2A–C). Pes and manus tracks from the same set form a small divergent angle of 12 to 15°. Pes and manus track paces are 34.5 cm and 36.0 cm long, respectively. The pes and manus tracks are strongly oriented outward.

Pes imprints are pentadactyl, longer than wide, 16–17 cm long and 10.7–11.8 cm wide (Fig. 2D–F). The PL/PW ratio varies from 1.4 to 1.5. Digit imprints I–V are elongated, robust,

straight and apically pointed. They form a group oriented outward, whereas imprint of digit V is curved rearward. The position of the impression of digit V is more proximal than those of digits I–IV. Traces of digit V show a well-imprinted, oval and longer than wide proximal pad that is in line with impression of digit IV (Fig. 2D–F). The impressions of the digit II and III (that are similar in length) are the longest. The impressions of digits I and IV are shorter than those of II and III. The divarication angle of digits I–IV and digits I–V varies from 20 to 35° and 52 to 54°, respectively.

Manus imprints are pentadactyl, quite symmetrical, smaller than pes tracks (PL/ML=2.6), wider than long (ML=6.5 cm, MW=7.3 cm, ML/MW ratio = 0.9; Fig. 2D–F). The digit imprints are moderately elongated, straight and apically pointed. The impression of the digit III is the longest. The impression of digit V is shallower than others. The impression of the digit I is the shortest. The divarication angle of digits I–V is up to 120°. Proximal pads of digits I–V form a posteriorly concave margin. Manus tracks sometimes show a poorly marked sole. On pes and manus tracks, phalangeal nodes, skin detailed-structures and large triangular claws are very well-preserved (Fig. 2D–F). The slab UCA.82 bears thin, elongated and straight to curved ridges that could be possible tail marks (Fig. 2C).

**Remarks.** Biron and Dutuit (1981) identified these tracks as a new species, they named “*Chirotherium atlensis*”. The gross morphologies of *Chirotherium* and *Isochirotherium* are very similar. However, *Isochirotherium* differs from *Chirotherium* by the size of pedal digits II and III that are quite similar in length (Klein et al., 2011, 2013). In *Chirotherium* the digit III is the longest. For this reason, we attribute the tracks from the slab UCA.82 to *Isochirotherium* and consider the ichnospecies “*Chirotherium atlensis*” as an invalid name. Chirotherian tracks (*Brachychirotherium*, *Parachirotherium*, *Protochirotherium*, and *Synaptichnium*), were abundantly described from the Triassic of Morocco: in the Sidi Saïd Maachou (Hminna et al., 2013, 2021) and Argana basins (Klein et al., 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020). They all differ from the tracks of the slab UCA.82: *Brachychirotherium* (Fig. 6A) differs by broad pes that has short and broad digits and the oval basal pad of digit V that is in a postero-lateral position relatively to the anterior digit group I–IV; *Parachirotherium* (Fig. 6C) differs by the pentadactyl, functionally tridactyl pes tracks with a wide divarication angle I–V, reduced imprints of digits II and IV, and a posteriorly shifted digit I. Lagnaoui et al. (2012, 2016) mentioned the occurrence of *Parachirotherium* in the Late Triassic of the Argana Basin. Nevertheless, according to Klein and Lucas (2021) *Parachirotherium* should be regarded as a junior synonym of *Chirotherium*;

*Protochirotherium* (emended in Klein and Lucas, 2021 after Fichter and Kunz, 2004) differs from the tracks of the slab UCA.82 by larger manus tracks compared to the size of pes track and digit V of pes with strongly elongated pad proximally (Fig. 6D); *Synaptichnium* differs by a more slender overall shape, a less massive pedal digit V, and a pedal digit IV that is subequal with or even longer than digit III (Fig. 6E). In Morocco, Tourani et al. (2010) and Klein et al., (2011) reported *Isochirotherium* cf. *gierlinskii* and *Isochirotherium coureli* from the Triassic of the Argana Basin. The tracks described as *Isochirotherium* cf. *gierlinskii* in Tourani et al. (2010) were tentatively renamed *Protochirotherium* by Klein et al. (2013). The tracks of the slab UCA.82 has no distinctive character supporting the creation of a new species nor can it be confidently assigned to any of the known species of *Isochirotherium*. According to Klein and Lucas (2021), the valid *Isochirotherium* ichnospecies are *I. coltoni*, *I. coureli*, *I. delicatum*, *I. herculis*, *I. lomasi*, *I. marshalli* and *I. soergeli*. *I. coureli* differs from the tracks of the slab UCA.82 in showing higher PL/PW ratio (up to 1.9). *I. soergeli* differs in showing pes tracks with as long as wide to slightly longer than wide group I-IV. *I. delicatum* shows more elongated pes tracks with long traces of digits II-III as well as very short traces of digits I and IV. *I. marshalli* differs from the tracks of the slab UCA.82 in showing a bigger ovoid metatarsal-phalangeal pad on the digit V of pes tracks. *I. herculis* shows strongly bigger pes (PL can be more than 30 cm) and a group I-IV which is wider than long. *I. coltoni* and *I. soergeli* are clearly smaller than the tracks of the slab UCA.82. Similar to the tracks we describe here, the pes track of *I. lomasi* shows a longer than wide group I-IV. However, *I. lomasi* displays a higher PL/PW ratio (more than 1.6) and a shorter trace of digit IV on pes track.

### ***Apatopus lineatus* Bock, 1952**

Fig. 3A–G

**Material.** Eight tracks preserved as convex hyporeliefs on slab UCA.83, Cadi Ayyad University (Marrakech).

**Description.** The slab UCA.83 bears eight plantigrade to semi-plantigrade and quadrupedal tracks, with four pes tracks and three manus imprints (including three pes/manus sets; Fig. 3A–C). Two pes/manus sets are part of a trackway (Fig. 3C). Pes and manus tracks from the

same set form divergent angle of 22 to 40°. Pes and manus track paces are 22.5 cm and 19.0 cm long, respectively. The pes tracks are oriented outward whereas manus tracks are oriented forward to inward.

Pes imprints are pentadactyl, longer than wide, 10.0–10.5 cm long and 4.7–6.0 cm wide (Fig. 3D–G). The PL/PW ratio varies from 1.7 to 2.1. Digit imprints are elongated, straight and apically pointed. The impressions of digit increase in length from I to IV. The impression of digit V is shallower than others, nearly absent. Digits I–IV shows a sub-parallel arrangement. The divarication angle of digits I–V varies from 40 to 41°. Pes tracks show a large and triangular plantar-like impression (Fig. 3D–G).

Manus imprints are pentadactyl, smaller than pes tracks, longer than wide to as long as wide (ML=5.1–6.0 cm, MW=4.4–5.2 cm; Fig. 3D–G). The ML/MW ratio varies from 0.8 to 1.2. Digit imprints are short, straight and apically pointed. The impression of the digit III is the longest. The divarication angle of digits I–V varies from 68 to 70°. Manus tracks sometimes show a poorly impressed sole. Marks of phalangeal nodes and claws are very well-preserved on both pes and manus tracks (Fig. 3D–G).

**Remarks.** Based on the following characters, these tracks match with the diagnostic features of *Apatopus lineatus*: quadrupedal trackways; pes long and narrow, plantigrade, pentadactyl with slender digits increasing in length from I to IV; digits with well-developed articular swellings and sharp claw impressions; manus pentadactyl, semi-plantigrade, short, and quite symmetrical around digit III, which is the longest. Biron and Dutuit (1981) correctly ascribed these tracks to *Apatopus lineatus*. However they committed several mistakes in their interpretations of the tracks: (1) their interpretative sketch of the trackway (Biron and Dutuit, 1981; fig. 9B p. 412) is not concordant with what can be seen on the slab - although Biron and Dutuit (1981) noted a problem of laterally of right /left sets, it appears that they erroneously associated two manus/pes sets to a same trackway - this misinterpretation explained why the order of digits I–V is inverted on their stretch (Biron and Dutuit, 1981; fig. 9B p. 412; digit I towards the outside of the trackway whereas digit V was located towards the inside); (2) although they mentioned five digits on manus tracks, they drew only up to four digits on their interpretative sketch (Biron and Dutuit, 1981; fig. 9 p. 412) of the trackway. The gross morphologies of *Apatopus* and *Synaptichnium* show many similarities. However,

*Synaptichnium* displays a compact metatarsal-phalangeal axis, which is absent amongst *Apatopus* imprints (Klein and Lucas, 2013). *Apatopus lineatus* was described from the Triassic deposits of the Argana Basin (Lagnaoui et al., 2012, 2016).

### ***Rhynchosauroides isp.***

Fig. 4A–D

**Material.** Numerous tracks (around a hundred) preserved as convex hyporeliefs on slabs UCA.82 and UCA.83, Cadi Ayyad University (Marrakech).

**Description.** The tracks are small, pentadactyl, digitigrade to plantigrade and consist of numerous isolated pes and manus imprints (Fig. 4A–D) forming a trampled surface on slab UCA.82 (Fig. 2C). Tracks are so abundant that it was not possible to distinguish a trackway nor to clearly identify pes/manus sets. Morphology of tracks varies a lot. Only some tracks display well marked impression of all digits. In most of tracks only two or three traces of digits are present (II–IV mainly). Tracks showing five traces of digits are longer than wide, up to 2.3 cm long and up to 1.6 cm wide (Fig. 4A–D). The L/W ratio varies from 1.4 to 1.9. Digit imprints are slender, elongated, curved (sometimes straight) and show sharp claw traces. The impressions of digit increase in length from I to IV. When preserved, the impression of digit V is clearly more curved than others (Fig. 4A–D). Digits I–IV are curved inward showing a sub-parallel arrangement. Digit V is oriented outward compared to the group I–IV. The position of the impression of digit V is more proximal than those of digits I–IV. The divarication angle of digits I–V varies from 63 to 88°.

**Remarks.** These tracks can be confidently ascribed to *Rhynchosauroides* on the basis of the following characters: small, pentadactyl, digitigrade to plantigrade tracks; length impressions of digits increasing from I to IV; impressions of digits I–IV usually curved inward; postero-laterally positioned short digit V impression that is oriented antero-laterally. *Gwyneddichnium* differs from *Rhynchosauroides* in showing a digit proportion  $III > II \geq IV > I$  (Klein and Lucas, 2021).

## **5. Discussion**

### 5.1. Ichnotaxonomic remarks on the other tetrapod tracks described by Biron and Dutuit (1981)

Based on a single, small and pentadactyl lacertoid footprint, Biron and Dutuit (1981) described a new ichnotaxon, “*Enigmatopus atlensis*” (Fig. 5A). Showing some resemblance to *Rhynchosauroides* and *Procolophonichnium*-like latertoid forms, Klein and Lucas (2021) considered this track as a *nomen dubium*. We agree with this proposition. Based on a track with bifurcated digit impressions, Biron and Dutuit (1981) erected the ichnospecies “*Hyloidichnus triasicus*” (Fig. 5B). *Hyloidichnus* being a Permian ichnogenus (Voigt and Lucas, 2018) with a different digit arrangement and given the fact that the description and the illustrations of Biron and Dutuit (1981) are of very poor quality without any valid arguments supporting their hypothesis, we do not consider “*H. triasicus*” as a valid ichnospecies. Biron and Dutuit (1981) described an isolated track they ascribed to a new species, “*Rectilinetopus ourikensis*” (Fig. 5C), in spite of similarities with the tracks they identified as *Apatopus lineatus*. Klein and Lucas (2013) synonymized “*Rectilinetopus ourikensis*” with *Apatopus lineatus*. We agree with this proposition since this track shares strong similarities with pes tracks of the slab UCA.83 (pes imprints pentadactyl, longer than wide; with digit imprints elongated, strait and apically pointed; impressions of digit increasing in length from I to IV; digits I-IV with a sub-parallel arrangement; large and triangular plantar-like impression). Biron and Dutuit (1981) erected the ichnospecies “*Prochirotherium triasicum*” (Fig. 5D), for an isolated, small, pentadactyl, longer than wide, quite symmetrical track with a wide sole, and with straight and apically pointed digit impressions (impression of the digit III being the longest). They justified this assignment by similarities with tracks described as *Prochirotherium* from Permian deposits of Italy. Due to the poorness of the material described by Biron and Dutuit (1981) and the absence of diagnostic features, we consider “*P. triasicum*” as a *nomen dubium*. Based on a single isolated semi-plantigrade to plantigrade tetradactyl imprint, Biron and Dutuit (1981) erected the new species “*Pseudochirotherium oukaïmedensis*” (Fig. 5E). Due to the partial preservation of tracks and the absence of diagnostic features, we consider this ichnotaxon as a *nomen dubium*. Klein and Lucas (2021) proposed that it consists of a chirotheriid track of indeterminate affinity.

### 5.2. Age of the tracksite

All tracksites reported by Biron and Dutuit (1981) and Biron (1982) are stratigraphically located at the base of the Oukaïmeden Sandstone Fm (F5 Fm *sensu* Biron, 1982). Based on pollen analyses (Cousminer and Manspeizer, 1976; Biron and Courtinat, 1982), these deposits were considered as Late Triassic. However, based on conchostracans and new palynological data, Benaouiss et al. (2018) proposed a Ladinian-early Carnian age for the base of the Oukaïmeden Sandstone Fm. In Morocco, *Rhynchosauroides* was reported from Middle to Late Triassic in the Argana Basin (Klein et al., 2011; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020). Possible *Rhynchosauroides* were also described in the Early Triassic from the same basin (Klein et al., 2010). Although *Rhynchosauroides* shows a broad stratigraphic range, extending from the middle Permian (e.g. Marchetti et al., 2022) to the Late Jurassic (Avanzini et al., 2010), the stratigraphic distribution of *Apatopus lineatus* and *Isochirotherium* are more restricted. *Apatopus lineatus* is characteristic of the Late Triassic being known from the Carnian to the Rhaetian (Klein and Lucas, 2013). In Morocco, this ichnospecies was reported from the Carnian deposits of the Argana Basin (Lagnaoui et al., 2012, 2016). *Isochirotherium* is characteristic of the Lower to the Middle Triassic with a large geographic distribution (France, Italy, Germany, Great Britain, Spain, and the USA; Klein and Haubold, 2007; Klein and Lucas, 2021 and references therein). In Morocco, *Isochirotherium coureli* was reported by Klein et al. (2011) from the Anisian-Ladinian (Middle Triassic) deposits of the Argana Basin. In conclusion, the palaeoichnological assemblage described here, as well as the palynological and conchostracean content (Benaouiss et al., 2018) from the base of the Oukaïmeden Sandstone Fm suggest a Middle-Late Triassic age. The ichnoassemblage described here displays the first documented co-occurrence of *Apatopus* and *Isochirotherium*.

### 5.3. Trackmakers and their paleoenvironment

Trackmakers of *Apatopus* are considered as phytosaurs (Klein and Lucas, 2013). Morphology of *Apatopus* shares similarities with crocodylian imprints, suggesting a semi-aquatic mode of life (Klein and Lucas, 2013). This contrast with the compact metatarsal-phalangeal axis typically observed amongst *Synaptichnium* whose trackmakers are supposed to be a terrestrial archosauriforms (Klein and Lucas, 2013). *Isochirotherium* is usually referred to possible crocodylian-stem archosaurs or non-crown-group archosauriforms (Klein

and Lucas, 2021). Trackmakers of *Rhynchosauroides* is considered as lepidosauromorph and/or archosauromorph trackmakers (Avanzini and Renesto, 2002).

As mentioned by Biron and Dutuit (1981), vertebrate tracks from the Triassic deposits of the Ourika and Yagour basins are commonly associated with *Scoyenia*. This ichnogenus is interpreted as a feeding or a combined feeding and locomotion trace, produced by arthropods or annelids (Bromley and Asgaard 1979; Frey et al., 1984). The co-occurrence of these protostomian burrows and traces with tetrapod tracks matches with the *Scoyenia* ichnofacies. This latter is observed in non-marine formations commonly interpreted as subaqueous freshwater sediments (Buatois and Mángano, 1995; Buatois et al., 1997). According to Fabuel-Perez et al. (2009), the lower part of the Oukaïmeden Sandstone Fm was deposited in an ephemeral fluvial system. As a result, the living environment was semi-arid, with ponds and ephemeral sediment supply.

## 6. Conclusions

-The two slabs from the Cadi Ayyad University collection bear tetrapods tracks ascribed to *Apatopus lineatus*, *Isochirotherium* isp. and *Rhynchosauroides* isp. whose trackmakers are possible phytosaurs, crocodylian-stem archosaurs or non-crown-group archosauriforms and lepidosauromorphs/archosauromorphs, respectively.

-All ichnotaxa created by Biron and Dutuit (1981) ("*Chirotherium atlensis*", "*Enigmatopus atlensis*", "*Hyloidichnus triasicus*", "*Prochirotherium triasicum*", "*Pseudochirotherium oukaïmedensis*" and "*Rectilinetopus ourikensis*") are considered as invalid.

- The lithological features of the base of the Oukaïmeden Sandstone Fm as well as the presence of tetrapod walking tracks indicate that the depositional environment was a semi-arid alluvial plain with ponds, periodically flooded by ephemeral fluvial system.

- The palaeoichnological assemblage includes a mixture of Early to the Middle Triassic (*Isochirotherium*) and Late Triassic (*Apatopus lineatus*) tracks. This result corroborates the biostratigraphic data recently obtained from the base of the Oukaïmeden Sandstone Fm, suggesting a Middle-Late Triassic age.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### **Data availability**

Data will be made available on request.

#### **Acknowledgments**

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## Figure captions

**Fig. 1.** Geological and stratigraphical setting of Marrakech High Atlas around the Ourika and Yagour basins. **A**, Permian and Triassic outcrops throughout the High Atlas: CHA = Central High Atlas, EHA = Eastern High Atlas, MA = Middle Atlas, MHA = Marrakech High Atlas and WHA = Western High Atlas (modified after Beauchamp, 1988; Laville and Piqué, 1991). Rectangle indicates the study area. **B**, geological map modified after Biron (1982), showing tetrapod trackway sites marked by stars with number: (1) East of Aghbalou, (2) North-East of Anammer, and (3) NW of Yagour Plateau. **C**, Simplified lithostratigraphic column of the MHA area (F1 to F6 Fm). The studied interval is localised at the base of the F5 Fm. (1) early Permian (radioactive and zircon method, Van Houten, 1977); (2) middle Anisian (from pollens, El Arabi et al., 2006); (3) middle Carnian (from pollens, Biron and Courtinat, 1982); (4) Ladinian-early Carnian (from pollens and conchostracans; Benaouiss et al., 2018); (5) middle Carnian (from pollens; Cousminer and Manspeizer, 1976).

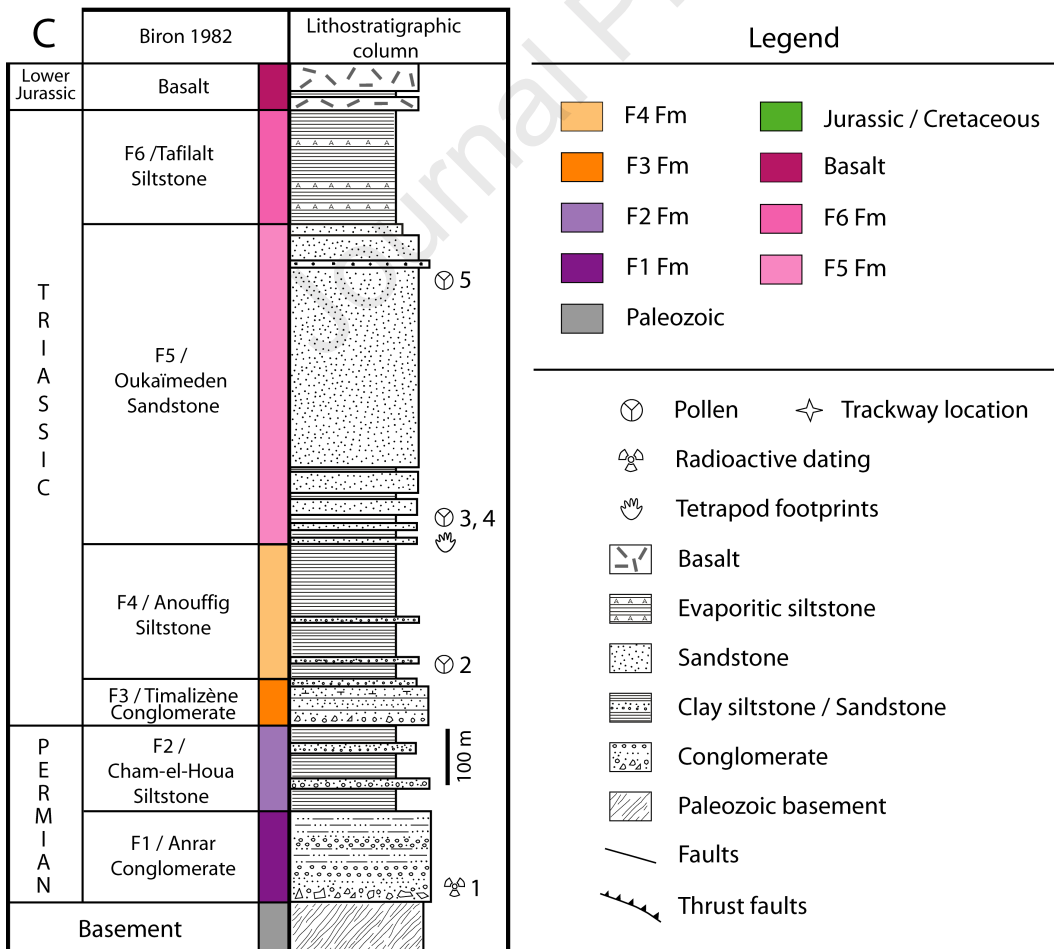
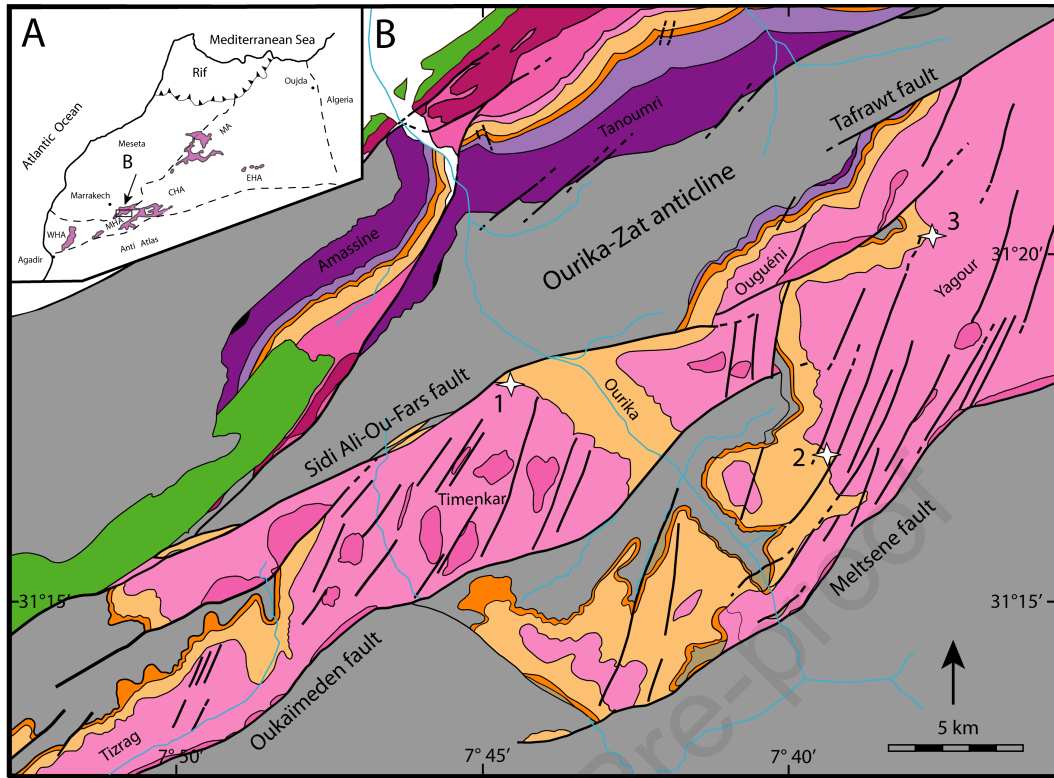
**Fig. 2. *Isochirotherium*.** **A–C**, Slab UCA.82 bearing several consecutive pes/manus sets (P., pes track; M., manus track), photograph (A), photogrammetric 3D mesh (B) and interpretative sketch (C); the red dotted line indicates the axis of the partial trackway. **D–F**, Pes/manus set; photograph (D), digital elevation model in false colours (E) and interpretative sketch (F). Convex hyporeliefs. **G–H**, details of the skin trace; photograph (G), and interpretative sketch (H).

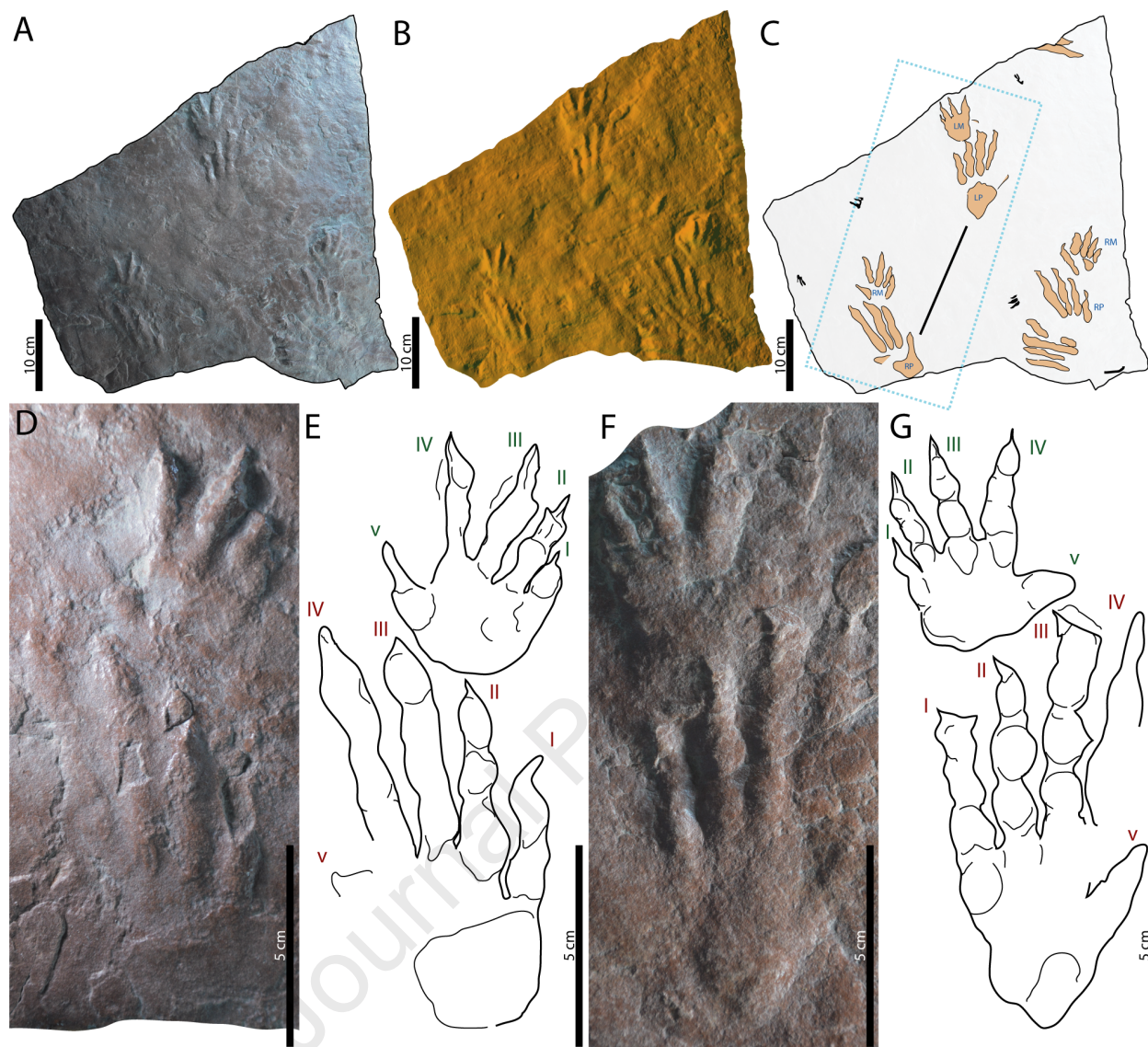
**Fig. 3. *Apatopus lineatus*.** **A–C**, Slab UCA.83. bearing several consecutive pes/manus sets, two of them forming a trackway (blue dots) (LP. left pes track, LM. left manus track, RP. right pes track, RM. right manus track), photograph (A), photogrammetric 3D mesh (B) and interpretative sketch (C). **D–G**, Two pes/manus sets; photograph (D, F) and interpretative sketches (E, G). Convex hyporeliefs.

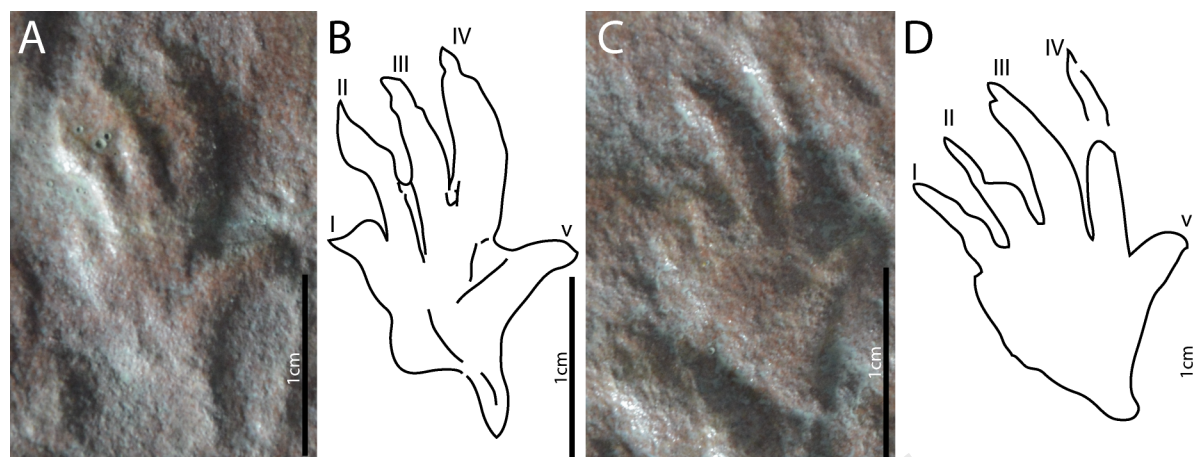
**Fig. 4.** *Rhynchosauroides* isp., two tracks from the slab UCA.82. **A–D**, Isolated tracks, photographs (A, C) and interpretative sketch (B, D). Convex hyporeliefs.

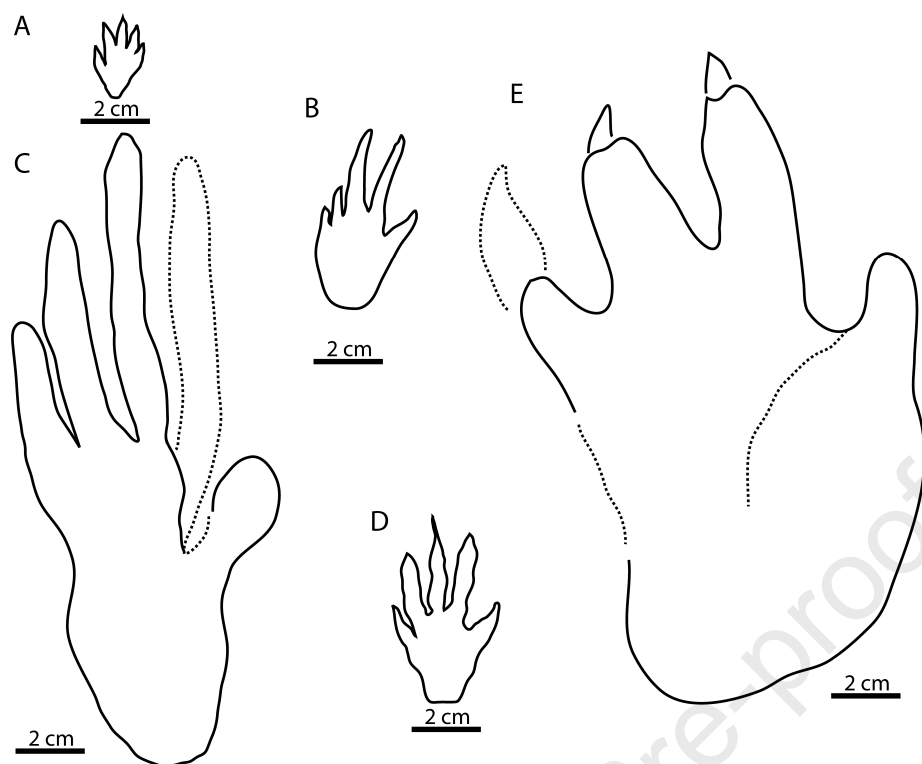
**Fig. 5.** Invalid or problematic ichnotaxa reported by Biron and Dutuit (1981) in the Triassic of the Ourika-Yagour basins. **A**, “*Enigmatopus atlensis*” (invalid ichnotaxon in this study). **B**, “*Hyloidichnus triasicus*” (nomen dubium in this study). **C**, “*Rectilinetopus ourikensis*” (*Apatopus lineatus* in this study). **D**, “*Prochirotherium triasicum*” (nomen dubium in this study). **E**, “*Pseudochirotherium oukaïmedensis*” (nomen dubium in this study).

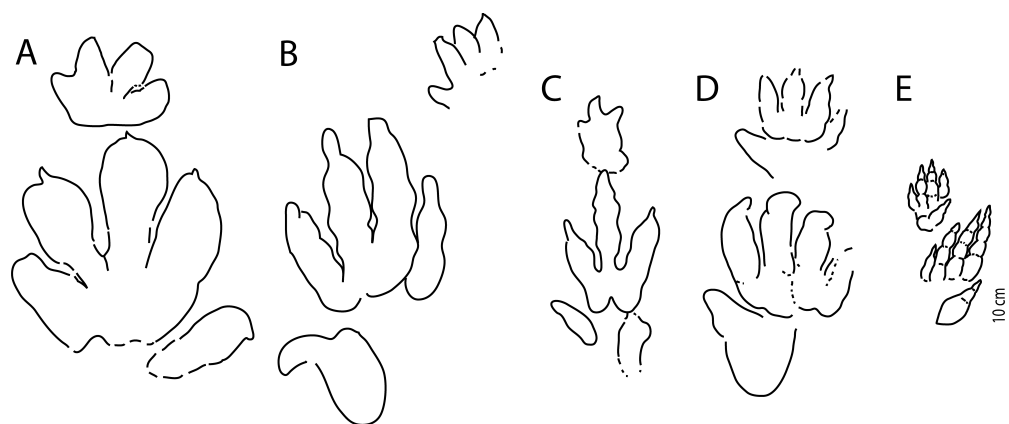
**Fig. 6.** Comparison between some Triassic Chirotherian tracks. **A**, *Brachychirotherium*, Late Triassic, Germany. **B**, *Isochirotherium lomasi*, Middle Triassic, Great Britain. **C**, *Chirotherium* (“*Parachirotherium*”), Middle Triassic, Germany. **D**, *Protochirotherium*, Early Triassic, Germany. **E**, *Synaptichnium*, Middle Triassic, Great Britain. Modified after Klein and Lucas (2021).

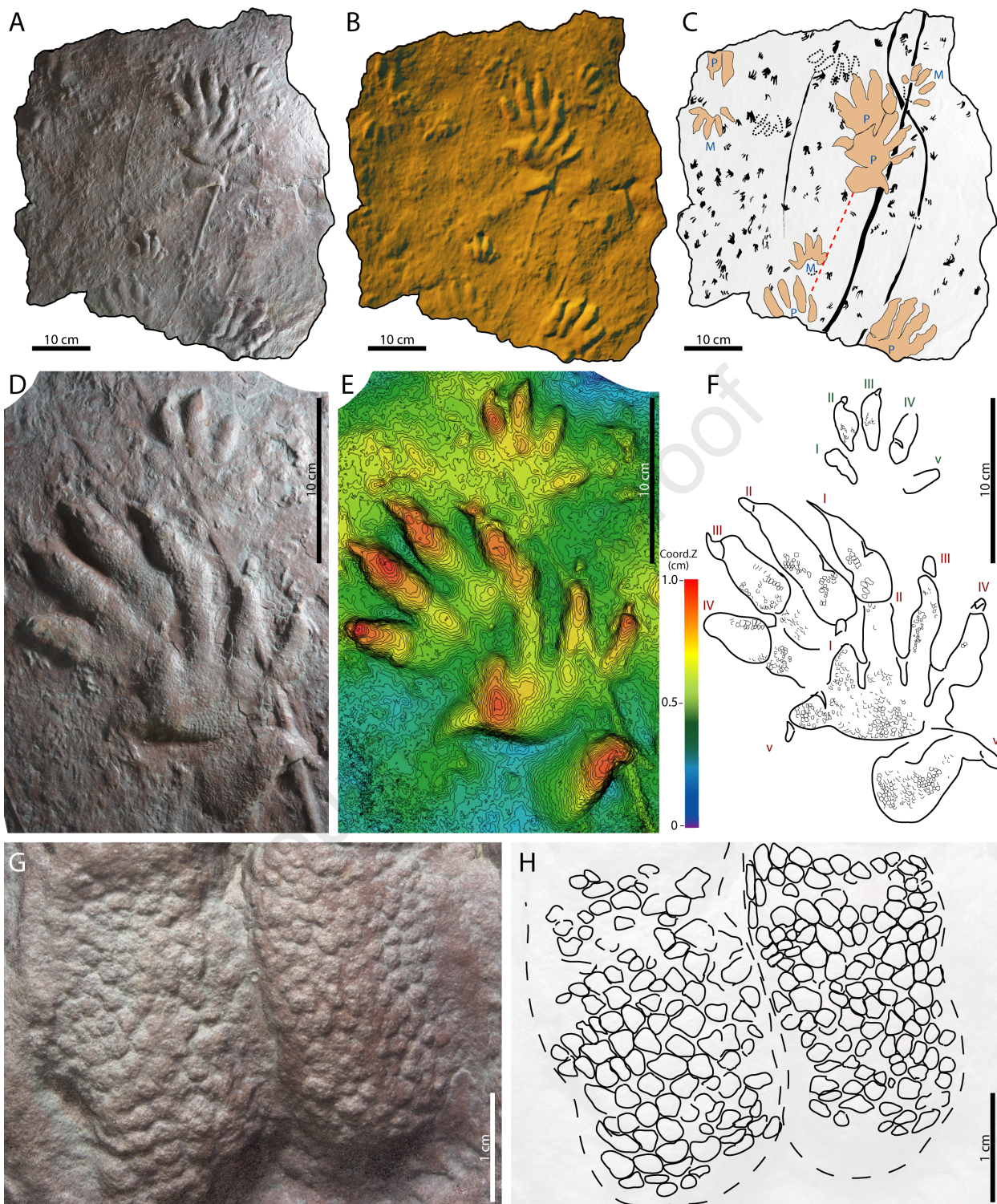












- Triassic tetrapod tracks from the Ourika-Yagour basins (Morocco) are studied.
- The historical collection of Pierre-Eymard Biron is ichnotaxonomically revised.
- These exquisitely preserved trackways are studied using 3D photogrammetric technique.
- Tracks include *Apatopus lineatus*, *Isochirotherium* isp. and *Rhynchosauroides* isp.
- They suggests a Middle-Late Triassic age for the Oukaïmeden Sandstone Formation.

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To Editor-in-Chief of *Journal of African Earth Sciences*

Dear Editor-in-Chief,

**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Yours sincerely,

Dr. Jean-David Moreau  
for the authors