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Jean-David Moreau, Naima Benaouiss, Abdelilah Tourani, Nour-Eddine Jalil, Sylvie Bourquin. Tetrapod tracks from the Middle/Late Triassic of the Ourika and Yagour basins (Morocco): new ichnotaxonomical data based on the Biron collection. *Journal of African Earth Sciences*, 2024, 212, pp.105202. 10.1016/j.jafrearsci.2024.105202 . insu-04452136

HAL Id: insu-04452136

<https://insu.hal.science/insu-04452136v1>

Submitted on 12 Feb 2024

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Journal Pre-proof

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PII: S1464-343X(24)00035-9

DOI: <https://doi.org/10.1016/j.jafrearsci.2024.105202>

Reference: AES 105202

To appear in: *Journal of African Earth Sciences*

Received Date: 9 October 2023

Revised Date: 9 February 2024

Accepted Date: 9 February 2024

Please cite this article as: Moreau, J.-D., Benaouiss, N., Tourani, A., Jalil, N.-E., Bourquin, S., Tetrapod tracks from the Middle/Late Triassic of the Ourika and Yagour basins (Morocco): new ichnotaxonomical data based on the Biron collection, *Journal of African Earth Sciences* (2024), doi: <https://doi.org/10.1016/j.jafrearsci.2024.105202>.

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

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13
 14 **Abstract:** Palaeontological prospecting organized in the Ourika and Yagour basins
 15 (Marrakech High Atlas, Morocco) in the 1980's, have yielded abundant and exquisitely
 16 preserved tetrapod tracks, some of them preserving thinly detailed skin traces (Collection
 17 Biron, Cadi Ayyad, Marrakech, Morocco). Based on this material, diverse morphologies of
 18 tracks were described and six new ichnotaxa were erected. However, these trackways have
 19 never been reinvestigated in detail from an ichnotaxonomic point of view. Here, the Biron
 20 collection is reevaluated using modern photogrammetric imaging techniques. The fine-
 21 grained sandstone slabs bear trackways ascribed to *Apatopus lineatus*, *Isochirotherium* isp.
 22 and *Rhynchosauroides* isp. whose trackmakers are possible phytosaurs, crocodylian-stem
 23 archosaurs or non-crown-group archosauriforms and lepidosauromorphs/archosauromorphs,
 24 respectively. “*Chirotherium atlensis*”, “*Enigmatopus atlensis*”, “*Hyloidichnus triasicus*”,
 25 “*Prochirotherium triasicum*”, “*Pseudochirotherium oukaïmedensis*” and “*Rectilinetopus*
 26 *ourikensis*” are considered as invalid. The palaeoichnological assemblage includes a mixture
 27 of Early to the Middle Triassic (*Isochirotherium*) and Late Triassic (*Apatopus lineatus*) tracks.
 28 This result corroborates the biostratigraphic data recently obtain from the base of the
 29 Oukaïmeden Sandstone Formation, suggesting a Middle-Late Triassic age. The living
 30 environment was a semi-arid alluvial plain with ponds and ephemeral rivers.

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

33

34 **1. Introduction**

35 In Morocco, significant ichnofossils including abundant and diverse vertebrate and
36 invertebrate tracks were reported from Triassic deposits of the Argana Basin (Klein et al.,
37 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020), the Sidi
38 Saïd Maachou Basin (Hminna et al., 2013, 2020, 2021) and the Yagour Plateau (Biron and
39 Dutuit, 1981; Biron, 1982). They constitute a key for the reconstruction of continental early
40 Mesozoic palaeoecosystems (Biron and Dutuit, 1981; Klein et al., 2010, 2011; Tourani et al.,
41 2010; Lagnaoui et al., 2012, 2016; Zouheir et al., 2020; Hminna et al., 2013, 2020, 2021).
42 Whereas tracks from the Triassic deposits of the Argana Basin were abundantly studied
43 (Biron and Dutuit, 1981; Klein et al., 2010, 2011; Tourani et al., 2010; Lagnaoui et al., 2012,
44 2016; Zouheir et al., 2020), those from the Ourika and Yagour basins clearly appear to be
45 underestimated. In 1981, Pierre-Eymard Biron discovered several tracksites (Biron and
46 Dutuit, 1981; Biron, 1982). This material was described by Biron and Dutuit (1981) who
47 dated it as Late Triassic. In this study, they described two slabs bearing exquisitely preserved
48 tracks that they attributed to *Apatopus lineatus* and a new species of *Chirotherium*: “*C.*
49 *atlensis*”. Then, based on isolated pes or manus tracks, they briefly described five additional
50 new ichnotaxa: “*Enigmatopus atlensis*”, “*Hyloidichnus triasicus*”, “*Prochirotherium*
51 *triasicum*”, “*Pseudochirotherium oukaimedensis*” and “*Rectilinetopus ourikensis*”. Except for
52 a tentative discussion by Klein and Lucas (2013, 2021) of some of these ichnospecies, the
53 tracks from the Ourika and Yagour basins have never been reinvestigated in detail. Here, we
54 revised Biron’s material housed at the Cadi Ayyad University (Marrakech). We describe it
55 using photogrammetric imaging techniques, update the ichnotaxonomy of the tracks and
56 discuss their age.

57

58 **2. Geographical and geological setting**

59

60 The study area is located in the Marrakech High Atlas (Fig. 1A), 60 to 80 km
61 southeast of Marrakech. At the south of the Carboniferous Ourika-Zat anticline (Fig. 1B), the
62 Permian and Triassic outcrops overlie the deformed Variscan basement, represented by
63 Precambrian volcanic rocks, Cambrian series, granitoids and metamorphic rocks, or
64 Carboniferous deposits. The Permian and Triassic rift area is related to the NW-SE-oriented
65 extension, which generated N-S trending normal faults (Van Houten, 1977; El Arabi et al.,
66 2003; Qarbous et al., 2003; Baudon et al., 2009) and reactivated pre-existing NE-SW to ENE-
67 WSW Variscan structures (Fig. 1B). These dip-slip and strike-slip faults are reactivated
68 (Baudon et al., 2009; El Arabi, 1988; El Arabi et al., 2003; Laville and Petit, 1984; Laville
69 and Piqué, 1991) and controlled the Triassic sedimentation (Benaouiss et al., 2023). The
70 Permian and Triassic sedimentary successions are represented by elongated and narrow
71 tectonic belts with an ENE-WSW orientation (Fig. 1B), up to 17 km wide and up to 35 km
72 long. These Permian and Triassic deposits are subdivided into six formations (fms), noted F1
73 to F6 (Biron, 1982; Fig. 1C), corresponding to the Permian Anrar Conglomerate (F1), dated
74 by radioactive and zircon method (Van Houten, 1977 and Perez et al., 2019) and the Cham-
75 El-Houa Siltstone (F2), located below the Permian-Triassic unconformity, is attributed to the
76 Permian age by correlation with the Argana t2 Unit (e.g. Benaouiss et al., 2023). The F3
77 (Timalizène Conglomerate), F4 (Anouffig Siltstone), F5 (Oukaïmeden Sandstone), and F6
78 (Tafilalt Siltstone) fms of Biron (1982) correspond respectively to the Basal Conglomerate,
79 Ramuntcho Siltstone, the Oukaïmeden Sandstone and Upper Siltstone fms of Mattis (1977).
80 The F3 Formation (Fm) is attributed to Early Triassic (e.g. Benaouiss et al., 2023) by
81 correlation with the t3 Unit in the Argana Basin, dated by Tourani et al. (2010) with tetrapod
82 tracks. Based on pollen analyses, the lower part of F4 Fm is middle Anisian age (El Arabi et
83 al., 2006) and the F5 Fm is dated middle Carnian at its lower (Biron and Courtinat, 1982) and
84 upper parts (Cousminer and Manspeizer, 1976) (Fig. 1C). The base of the Oukaïmeden
85 Sandstone Fm was recently dated by pollen grains and conchostracans as Ladinian-early
86 Carnian (Benaouiss et al., 2018). This part of F5 Fm represents the equivalent of the lower
87 part of the t5 Unit in the Argana Basin which is dated as Julian-Tuvalian (mid-Carnian) by
88 Tourani et al. (2023). The F6 Fm is attributed to the Norian, by correlation to the t8 Unit in
89 the Argana Basin which is dated by conchostracans according to Weems and Lucas (2015).
90 The Triassic series is overlain by Early Jurassic basalts, representing a good stratigraphic
91 marker across Morocco (Bertrand et al., 1982; Blackburn et al., 2013; De Pachtère, 1983;
92 Marzoli et al., 2004).

93 Two main Triassic outcrops are of interest to this study (Fig. 1B); (1) those of the
94 Ourika Basin, which is limited at the north by the Sidi Ali-Ou-Fars fault and at the south by
95 the Oukaïmeden fault (Fig. 1B), (2) those of the Yagour Basin, which is limited by the Sidi
96 Ali-Ou-Fars and Tafrawt faults at the north and the Meltsene fault at the south (Fig. 1B).
97 Biron and Dutuit (1981) reported three tracksites on the Ourika and Yagour basins, at the East
98 of Aghbalou, at the North-East of Anammer and at the North-West of the Yagour Plateau
99 (Star symbol in Fig. 1B). The historical tracksites are located at the base of the Oukaïmeden
100 Sandstone Fm (Fig. 1B and C). This formation is up to 600 m thick and outcrops mainly as
101 cliffs, accessible along streams and tracks, and is mainly characterized by channel sandstone
102 bodies alternating with lenticular fluvial bar sandstones and overbank mudstone deposits
103 (Benaouiss et al., 1996; Fabuel-Perez et al., 2009). The Oukaïmeden Sandstone Fm is
104 subdivided into three units (Benaouiss et al., 1996; Fabuel-Perez et al., 2009), called lower-,
105 middle- and upper Okaïmeden units. The lower unit, which yields the fossil tracks, is 30 to
106 110 m thick. It is richer, than the middle and upper units, in red clay-stones and siltstones, and
107 was deposited in an ephemeral fluvial system under dry climate. The middle unit is 25 to 80
108 m thick, and corresponds to a distal braided system associated with more humid conditions
109 (Fabuel-Perez et al., 2009). The upper unit, which is 30 to 80 m thick, corresponds to the
110 comeback of ephemeral conditions with the installation of aeolian dunes corresponding to arid
111 conditions (Benaouiss et al., 1996; Fabuel-Perez et al., 2009).

112

113 3. Material and methods

114

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

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

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

137 3D photogrammetric reconstructions were produced with the software Agisoft
 138 Metashape Professional 2.0. Pictures of the surfaces were taken with a Nikon D5200 camera
 139 coupled with an AF-S Nikkor 18–105 128 mm f/3.5–5.6G ED lens. The same software was
 140 used to produce photogrammetric digital elevation models and contours.

141

142 4. Systematic palaeoichnology

143

144 *Isochirotherium* isp.

145 Fig. 2A–F

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

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

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

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

162 Manus imprints are pentadactyl, quite symmetrical, smaller than pes tracks (PL/ML=
 163 2.6), wider than long (ML=6.5 cm, MW=7.3 cm, ML/MW ratio = 0.9; Fig. 2D–F). The digit
 164 imprints are moderately elongated, straight and apically pointed. The impression of the digit
 165 III is the longest. The impression of digit V is shallower than others. The impression of the
 166 digit I is the shortest. The divarication angle of digits I-V is up to 120°. Proximal pads of
 167 digits I–V form a posteriorly concave margin. Manus tracks sometimes show a poorly marked
 168 sole. On pes and manus tracks, phalangeal nodes, skin detailed-structures and large triangular
 169 claws are very well-preserved (Fig. 2D–F). The slab UCA.82 bears thin, elongated and
 170 straight to curved ridges that could be possible tail marks (Fig. 2C).

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

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

210

211 *Apatopus lineatus* Bock, 1952

212 Fig. 3A–G

213

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

216 *Description.* The slab UCA.83 bears eight plantigrade to semi-plantigrade and quadrupedal
 217 tracks, with four pes tracks and three manus imprints (including three pes/manus sets; Fig.
 218 3A–C). Two pes/manus sets are part of a trackway (Fig. 3C). Pes and manus tracks from the

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

222 Pes imprints are pentadactyl, longer than wide, 10.0–10.5 cm long and 4.7–6.0 cm wide (Fig.
223 3D–G). The PL/PW ratio varies from 1.7 to 2.1. Digit imprints are elongated, straight and
224 apically pointed. The impressions of digit increase in length from I to IV. The impression of
225 digit V is shallower than others, nearly absent. Digits I-IV shows a sub-parallel arrangement.
226 The divarication angle of digits I-V varies from 40 to 41°. Pes tracks show a large and
227 triangular plantar-like impression (Fig. 3D–G).

228
229 Manus imprints are pentadactyl, smaller than pes tracks, longer than wide to as long as wide
230 (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.
231 Digit imprints are short, straight and apically pointed. The impression of the digit III is the
232 longest. The divarication angle of digits I-V varies from 68 to 70°. Manus tracks sometimes
233 show a poorly impressed sole. Marks of phalangeal nodes and claws are very well-preserved
234 on both pes and manus tracks (Fig. 3D–G).

235
236
237 **Remarks.** Based on the following characters, these tracks match with the diagnostic features
238 of *Apatopus lineatus*: quadrupedal trackways; pes long and narrow, plantigrade, pentadactyl
239 with slender digits increasing in length from I to IV; digits with well-developed articular
240 swellings and sharp claw impressions; manus pentadactyl, semi-plantigrade, short, and quite
241 symmetrical around digit III, which is the longest. Biron and Dutuit (1981) correctly ascribed
242 these tracks to *Apatopus lineatus*. However they committed several mistakes in their
243 interpretations of the tracks: (1) their interpretative sketch of the trackway (Biron and Dutuit,
244 1981; fig. 9B p. 412) is not concordant with what can be seen on the slab - although Biron and
245 Dutuit (1981) noted a problem of laterally of right /left sets, it appears that they erroneously
246 associated two manus/pes sets to a same trackway - this misinterpretation explained why the
247 order of digits I-V is inverted on their stretch (Biron and Dutuit, 1981; fig. 9B p. 412; digit I
248 towards the outside of the trackway whereas digit V was located towards the inside); (2)
249 although they mentioned five digits on manus tracks, they drew only up to four digits on
250 their interpretative sketch (Biron and Dutuit, 1981; fig. 9 p. 412) of the trackway. The gross
251 morphologies of *Apatopus* and *Synaptichnium* show many similarities. However,

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

255

256 ***Rhynchosauroides isp.***

257 Fig. 4A–D

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

260 *Description.* The tracks are small, pentadactyl, digitigrade to plantigrade and consist of
261 numerous isolated pes and manus imprints (Fig. 4A–D) forming a trampled surface on slab
262 UCA.82 (Fig. 2C). Tracks are so abundant that it was not possible to distinguish a trackway
263 nor to clearly identify pes/manus sets. Morphology of tracks varies a lot. Only some tracks
264 display well marked impression of all digits. In most of tracks only two or three traces of
265 digits are present (II–IV mainly). Tracks showing five traces of digits are longer than wide, up
266 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
267 imprints are slender, elongated, curved (sometimes straight) and show sharp claw traces. The
268 impressions of digit increase in length from I to IV. When preserved, the impression of digit
269 V is clearly more curved than others (Fig. 4A–D). Digits I–IV are curved inward showing a
270 sub-parallel arrangement. Digit V is oriented outward compared to the group I–IV. The
271 position of the impression of digit V is more proximal than those of digits I–IV. The
272 divarication angle of digits I–V varies from 63 to 88°.

273

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

280

281 **5. Discussion**

282

283 5.1. Ichnotaxonomic remarks on the other tetrapod tracks described by Biron and Dutuit
284 (1981)

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

312

313 5.2. Age of the tracksite

314 All tracksites reported by Biron and Dutuit (1981) and Biron (1982) are
315 stratigraphically located at the base of the Oukaïmeden Sandstone Fm (F5 Fm *sensu* Biron,
316 1982). Based on pollen analyses (Cousminer and Manspeizer, 1976; Biron and Courtinat,
317 1982), these deposits were considered as Late Triassic. However, based on conchostracans
318 and new palynological data, Benaouiss et al. (2018) proposed a Ladinian-early Carnian age
319 for the base of the Oukaïmeden Sandstone Fm. In Morocco, *Rhynchosauroides* was reported
320 from Middle to Late Triassic in the Argana Basin (Klein et al., 2011; Lagnaoui et al., 2012,
321 2016; Zouheir et al., 2020). Possible *Rhynchosauroides* were also described in the Early
322 Triassic from the same basin (Klein et al., 2010). Although *Rhynchosauroides* shows a broad
323 stratigraphic range, extending from the middle Permian (e.g. Marchetti et al., 2022) to the
324 Late Jurassic (Avanzini et al., 2010), the stratigraphic distribution of *Apatopus lineatus* and
325 *Isochirotherium* are more restricted. *Apatopus lineatus* is characteristic of the Late Triassic
326 being known from the Carnian to the Rhaetian (Klein and Lucas, 2013). In Morocco, this
327 ichnospecies was reported from the Carnian deposits of the Argana Basin (Lagnaoui et al.,
328 2012, 2016). *Isochirotherium* is characteristic of the Lower to the Middle Triassic with a large
329 geographic distribution (France, Italy, Germany, Great Britain, Spain, and the USA; Klein and
330 Haubold, 2007; Klein and Lucas, 2021 and references therein). In Morocco, *Isochirotherium*
331 *coureli* was reported by Klein et al. (2011) from the Anisian-Ladinian (Middle Triassic)
332 deposits of the Argana Basin. In conclusion, the palaeoichnological assemblage described
333 here, as well as the palynological and conchostracean content (Benaouiss et al., 2018) from
334 the base of the Oukaïmeden Sandstone Fm suggest a Middle-Late Triassic age. The
335 ichnoassemblage described here displays the first documented co-occurrence of *Apatopus* and
336 *Isochirotherium*.

337

338 5.3. Trackmakers and their paleoenvironment

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

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

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

357

358 **6. Conclusions**

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

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

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

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

373

374 **Declaration of competing interest**

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

377

378 **Data availability**

379 Data will be made available on request.

380

381 **Acknowledgments**

382 The authors are grateful to Moulay Ahmed Boumehdi, head of the department of
383 Geology at Cadi Ayyad University Marrakech for the access to the collection room housing
384 the studied slabs. We also thank Spencer G. Lucas and the anonymous reviewer for their
385 constructive and thoughtful reviews on the manuscript.

386

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542 **Figure captions**

543

544 **Fig. 1.** Geological and stratigraphical setting of Marrakech High Atlas around the Ourika and
 545 Yagour basins. **A**, Permian and Triassic outcrops throughout the High Atlas:

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

556

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

563

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

569

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

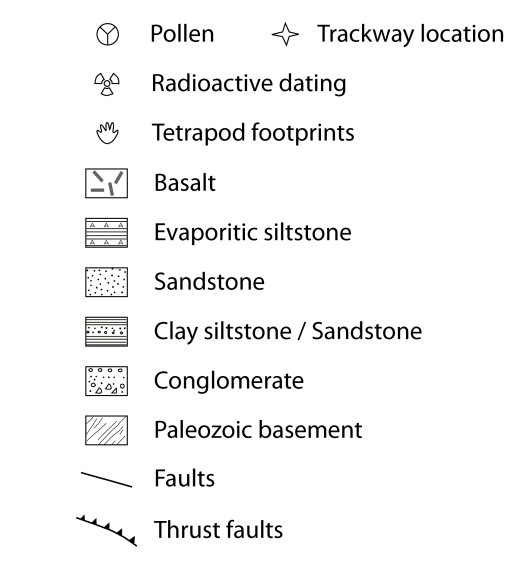
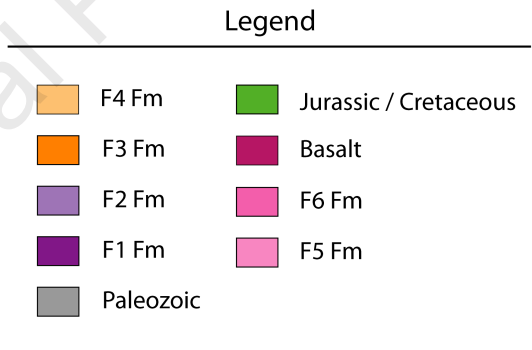
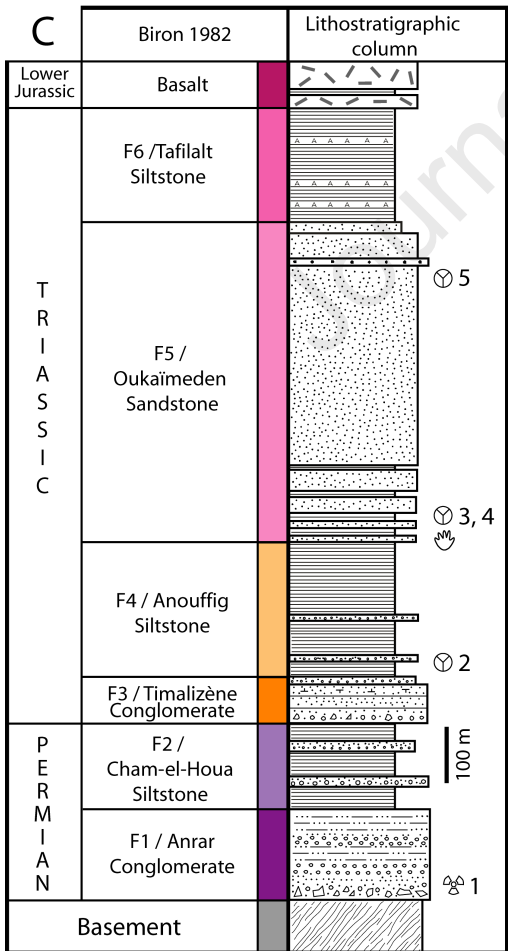
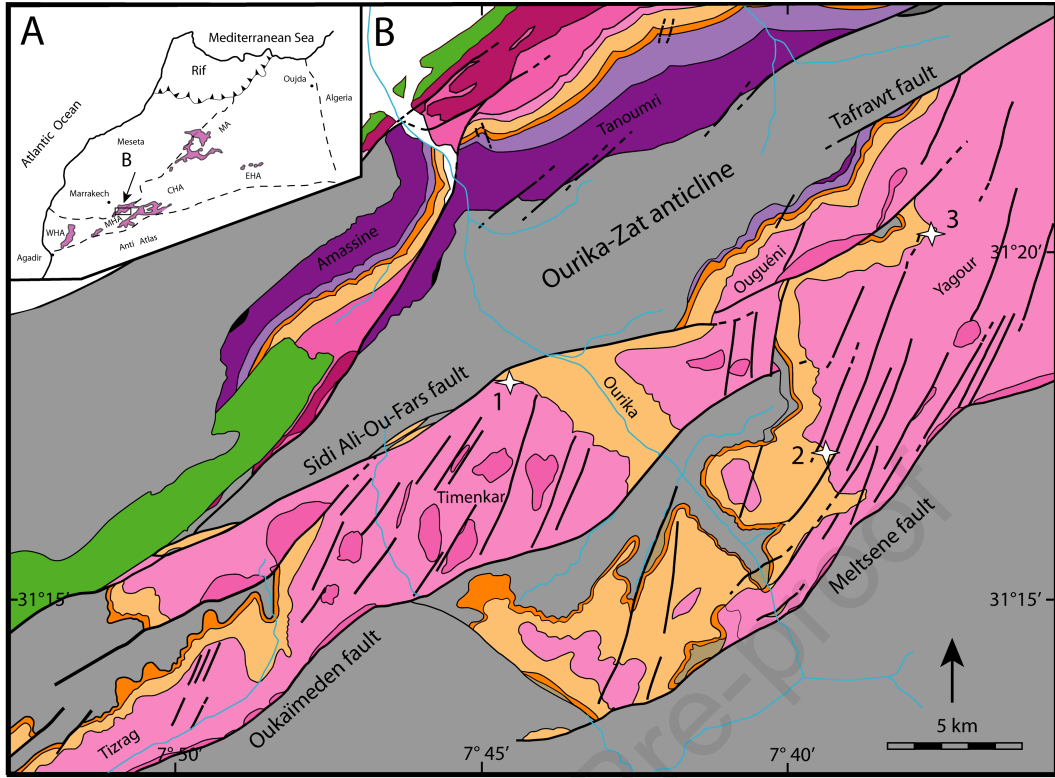
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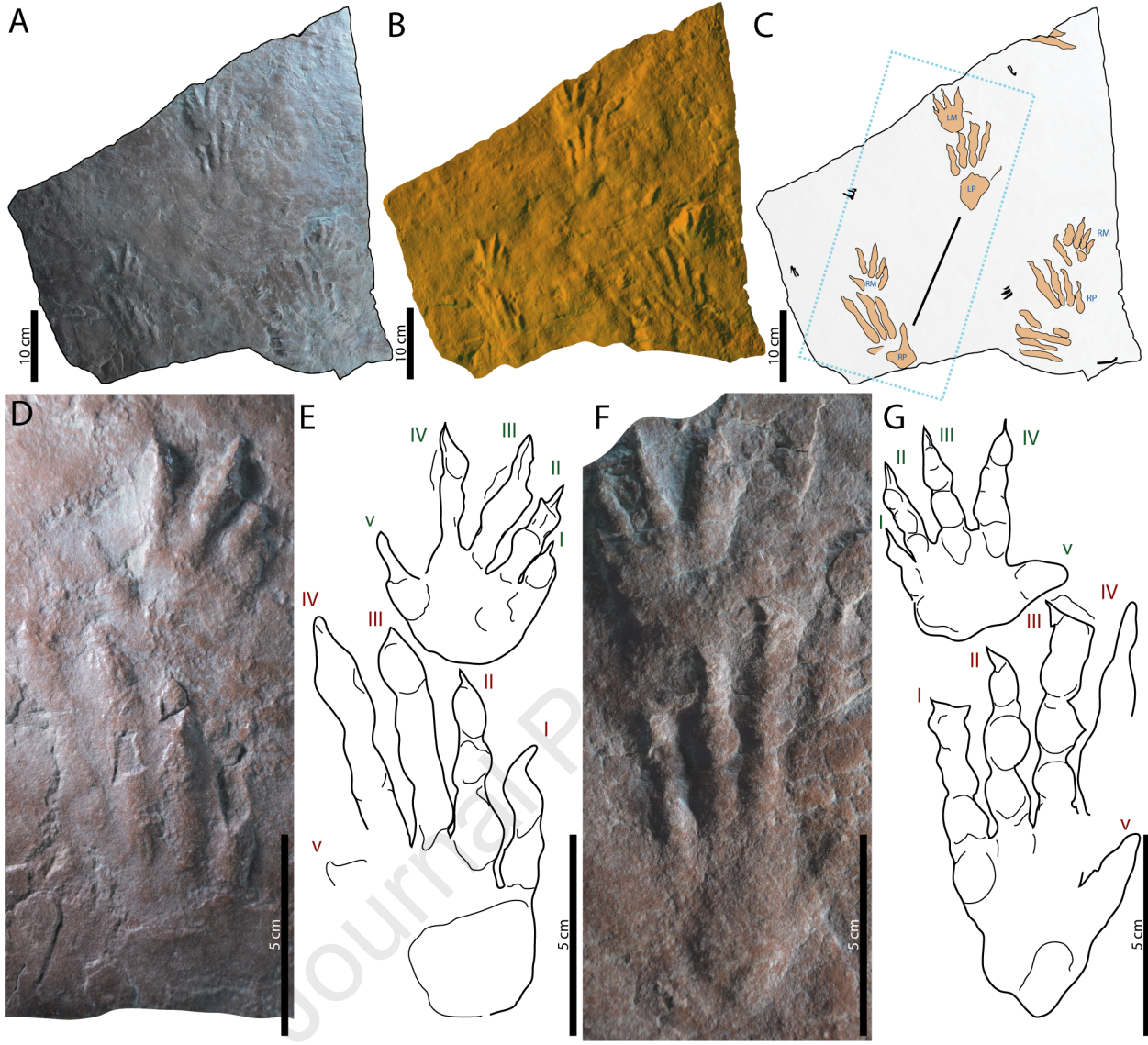
573 **Fig. 5.** Invalid or problematic ichnotaxa reported by Biron and Dutuit (1981) in the Triassic of
574 the Ourika-Yagour basins. **A**, “*Enigmatopus atlensis*” (invalid ichnotaxon in this study). **B**,
575 “*Hyloidichnus triasicus*” (nomen dubium in this study). **C**, “*Rectilinetopus ourikensis*”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

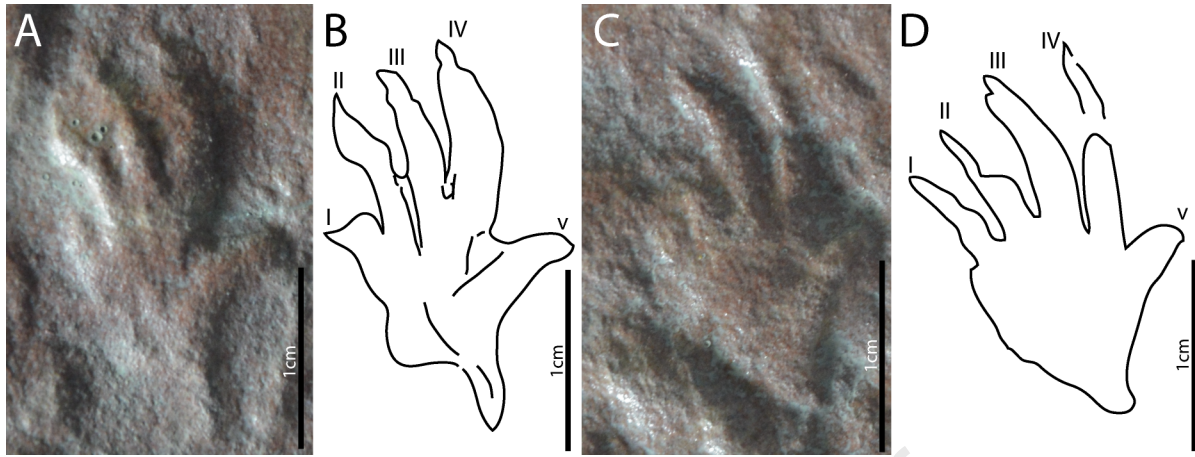
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579 **Fig. 6.** Comparison between some Triassic Chirotherian tracks. **A**, *Brachychirotherium*, Late
580 Triassic, Germany. **B**, *Isochirotherium lomasi*, Middle Triassic, Great Britain. **C**,
581 *Chirotherium* (“*Parachirotherium*”), Middle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

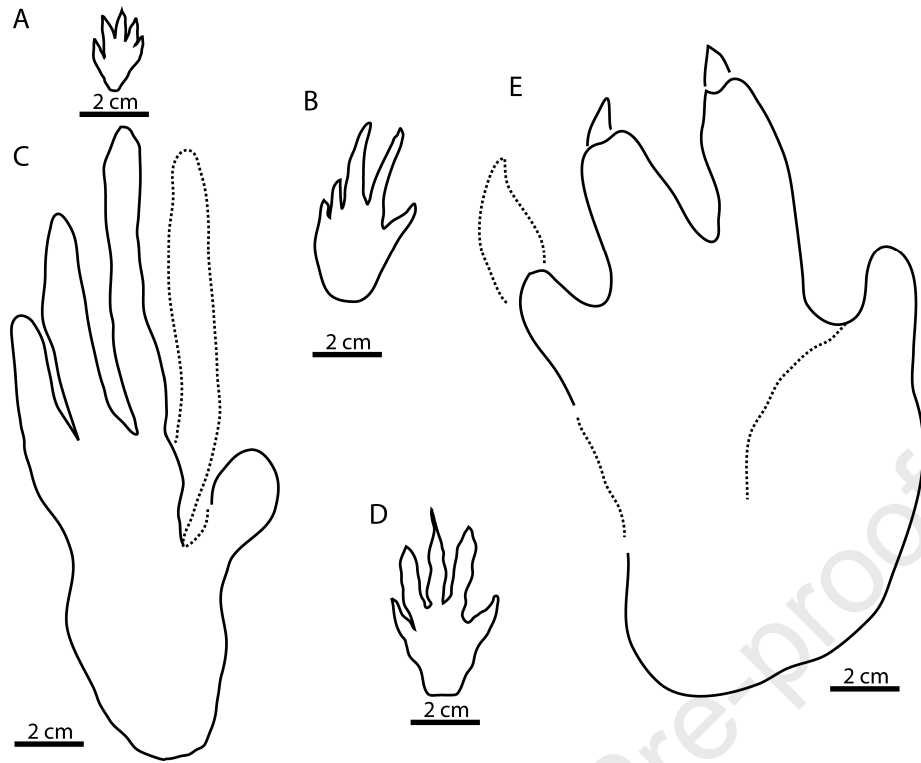
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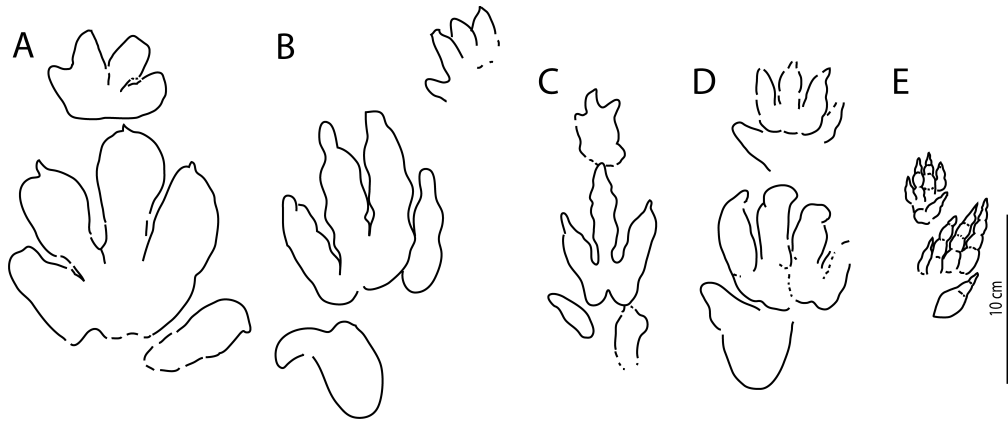




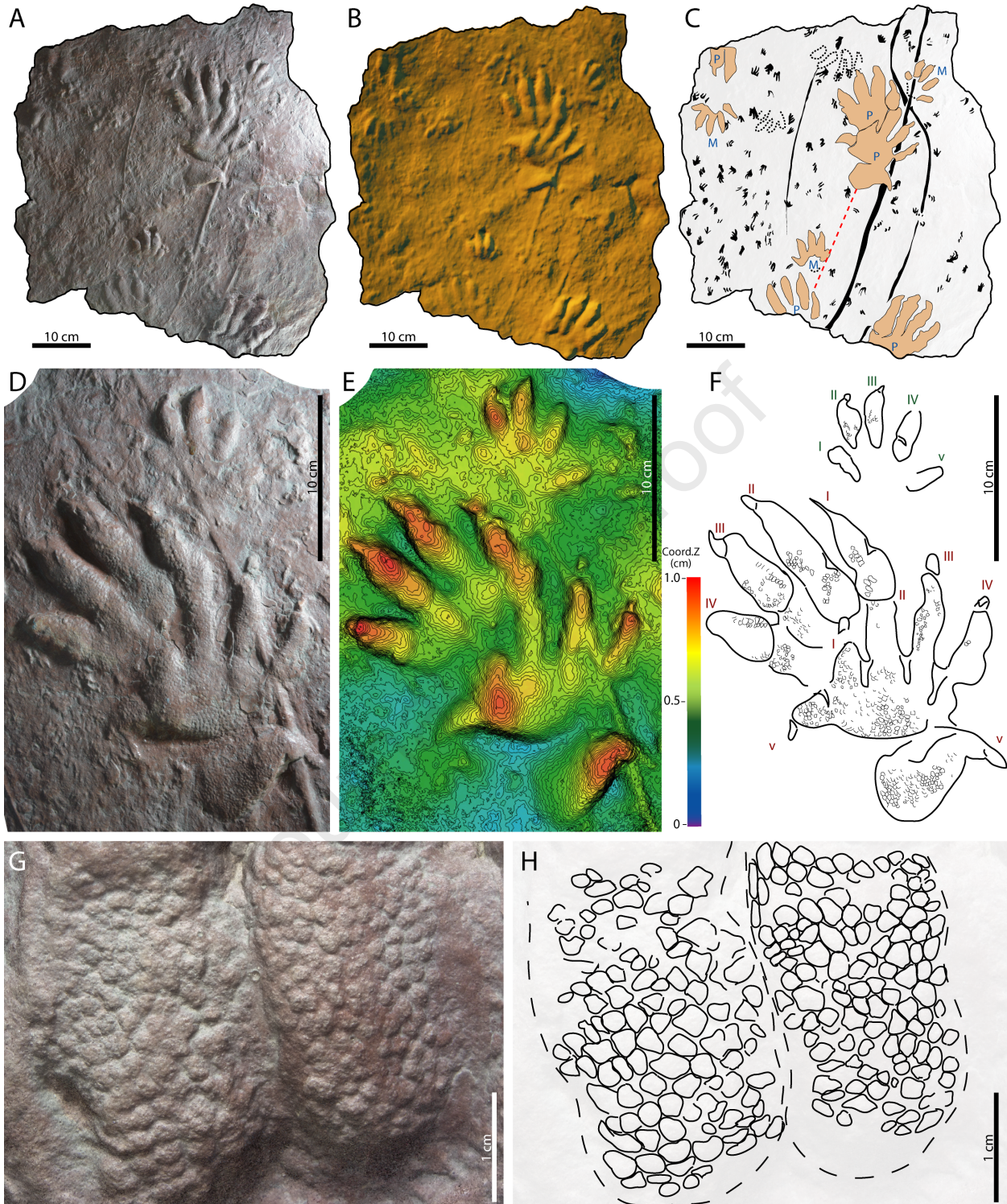


Journal Pre-proof





Journal Pre-proof



- 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