The Late Triassic archosaur ichnogenus *Brachychirotherium*: First complete step cycles from Morocco, North Africa, with implications for trackmaker identification and ichnotaxonomy

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Abstract:

Trackways of Late Triassic *Brachychirotherium* (archosaur) are known from few specimens, mostly from North America. Complete step cycles have been found on the upper and lower bedding surface in laminated mudstone and fine sandstone of the upper Oued Oum Er Rbiaa Formation (Late Triassic). This is the first trackway of the ichnogenus in North Africa. It consists of 7 successive pes (pl = 12 cm, pw = 8 cm) and manus (ml = 5-6 cm, mw = 5-6 cm) tracks. Imprints show the characteristic broad pes, with digit proportions III > II > IV> I > V, with digit V preserved as a large oval basal pad. Skin impressions are present in several tracks. Striking feature is the large distance between pes and manus imprints, possibly due to the early ontogenetic stage of the small individual.

In some associated isolated tracks, pedal digit V is oriented in line with digit IV. These tracks are similar to *Brachychirotherium parvum* (Hminna et al., 2013), whereas pes imprints from the trackway show similarities to *B. thuringiacum* and *B. hassfurtense* from the Hassberge Formation (Carnian) of Germany (Beurlen, 1950; Karl & Haubold, 2000), with pedal digit V, being laterally spread.

The footprints from Morocco are determined as *Brachychirotherium parvum* and *B. thuringiacum* based on the presence of features diagnostic of the ichnospecies such as the orientation of pedal digit V (Hunt & Lucas, 2007a). Probable trackmakers are archosaurs of the crocodylian stem-group (Crurotarsi). Associated tetrapod ichnofauna from the unit consists of small *Rhynchosauroides* (archosauromorph/lepidosauromorph) tracks.

Keywords: North Africa, chirothere footprints, Crurotarsi, Rhynchosauroides, Archosauromorpha

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Why ornithopod feet rotate inward

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Abstract:

Inward rotation of hindfoot axis (orientation of digit III relative to the trackway midline) is commonly observed in both bipedal and quadrupedal trackways of ornithopods, suggesting in-toed gait of the trackmakers. The origin of quadrupedalism of ornithopods has been often discussed in previous research, but the cause of in-toed orientation of the pes is largely unknown.

We investigated 14 ornithopod trackways, all showing inward rotation of the hindfoot. The average pace angulation of 14 trackways based on the measurement connecting the center of the footprints is 158°. In contrast, the value based on the measurement connecting the tip of digit III is 166°. The latter value is close to that of the average pace angulation of theropods.

The observation of shorebirds has proven that birds with long legs and high-positioned acetabular joints do not have inward rotated feet. In contrast, birds with short legs and low positioned acetabular joints have inward rotated feet.

Based on these data, we interpret this as follows. The inward rotation of the hindfoot axis: 1) increases the stability of the body against the lateral overturning moment; 2) compensates for the short distance between knee and ground, and resolves the disadvantage of short legs when placing the foot closer to the trackway midline (center of mass) for maintaining body balance.

Keywords: dinosaur, footprint, trackway, in-toed, pronation