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Crocodylomorph, turtle and mammal tracks in dinosaur-dominated Middle–?Upper Jurassic and mid-Cretaceous ichnoassemblages of Morocco

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ABSTRACT

We report tetrapod traces from two stratigraphic intervals in Morocco, and discuss their palaeoecological implications. In the first interval, crocodylomorph footprints assigned to *Crocodylopodus meijidei* are described from Middle–?Upper Jurassic continental fluvial red beds of the Isli Formation in the Imilchil region, Central High Atlas, Morocco. These traces are associated with a diverse dinosaur-dominated ichnofauna, including the footprints of theropods, ornithischians, sauropods and pterosaurs, together with numerous invertebrate traces. In the second interval, we report crocodylomorph swim traces assigned to *Hatcherichnus* isp., turtle trackways assigned to *Emydhipus* isp. and isolated mammal footprints in the mid-Cretaceous Midelt Formation, in the High Moulouya region, Morocco. These traces are, also, associated with a diverse dinosaur-dominated ichnofauna including theropods and ornithopods as well as pterosaurs and abundant invertebrate traces. Together with plant remains, conchostracans and fishes, findings indicate a diverse community populating a fluvial-brackish environment.

1. Introduction

Jurassic–Cretaceous tetrapod footprint assemblages are essentially dominated by dinosaurs, with theropods and sauropods representing the major components of the Jurassic ichnofaunas (Lockley and Hunt, 1995; Lockley and Meyer, 2000). Less abundant are ornithischians, although they can be more frequent on some surfaces (Olsen and Rainforth, 2003). In Lower Cretaceous strata, the most abundant ornithischian- and theropod-dominated ichnofaunas are known from North America, Europe and East Asia (e.g., Lockley, 1987; Pérez-Lorente, 2001, 2015; Lockley et al., 2006; Matsukawa et al., 2006; McCrea et al., 2014; Xing et al., 2015). Sauropod ichnofaunas can be more abundant locally (Farlow et al., 1989), as is the case for pterosaurs and birds (Lockley and Rainforth, 2002).

Generally, minor components in both ichnofaunas include crocodylians, turtles and mammals. In the case of crocodylians and turtles, this scarcity is partly related to the semi-aquatic lifestyle of many Jurassic–Cretaceous groups and the low preservation potential in subaqueous and inundated substrates (Klein and Lucas, 2015). Mammal tracks are generally rare in the Mesozoic, and crocodylomorph tracks have mainly been reported from small terrestrial forms and by traces of swimming individuals, in particular from the Jurassic–Cretaceous of Europe and North America (Olsen and Padian, 1986; Lockley and Meyer, 2004).

From the African continent, crocodylomorph tracks are scarcely known (Hadri et al., 2015; Mateus et al., 2017). Also, turtle tracks thus far have rarely been reported from this region (Belvedere et al., 2013). In recent years, Morocco has become one of the most important places for the study of Paleozoic–Mesozoic tetrapod footprint assemblages. Nearly complete successions with tetrapod footprints from this region

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have been documented from the Carboniferous to the Triassic (e.g. Lagnaoui, 2014; Lagnaoui et al., 2016). Middle Jurassic–Cretaceous (Bathonian-Maastrichtian) assemblages mostly yield theropod, sauropod and ornithischian tracks as well as the footprints of pterosaurs (Ishigaki, 1989; Gierliński, 2016; Gierliński et al., 2009, 2017a, 2017b; Marty et al., 2010; Hadri and Pérez-Lorente, 2012; Belvedere and Mietto, 2010; Belvedere et al., 2010, 2013; Ibrahim et al., 2014; Masrour and Pérez-Lorente, 2015; Masrour et al., 2013, 2017a, 2017b, 2018). However, most of those works focused on the western and central part of the Central High Atlas, leaving the studied area in the eastern part, the Imilchil and Midelt region, less recognized ichnologically. Here, we present a detailed study of crocodylomorph and turtle footprints from Jurassic–Cretaceous deposits of this region (Klein et al., 2017).

2. Geological setting

The fossils reported here were found in two separate regions of Morocco: a Middle Jurassic site near Imilchil, representing the Isli Formation, and a mid-Cretaceous site near Midelt, representing the lower part of the Midelt Formation.

2.1. Isli Formation (Middle Jurassic, Bathonian–?Upper Jurassic)

The Imilchil region, where some of the footprint localities are situated, lies in the heart of the Central High Atlas, Morocco (Fig. 1A, B). Here, the Jurassic marine succession overlies the widespread Central Atlantic Magmatic Province (CAMP) basalts (Youbi et al., 2003). Based on Charrière et al. (2011), the Jurassic deposits comprise, from base to top (Fig. 1C), as follows: (i) Tassent Formation (=Agoudim 1; Toarcian–Aalenian), consisting of platform carbonates, marls and shales (> 600 m), overlying shallow water limestones (~300–400 m) of Hettangian–Sinemurian age; (ii) Bab n'Ouayad Formation (=Agoudim 2; lower Bajocian), dominated by reefal limestones or “Calcaire corniche” and exposed mostly along the ridge of the anticline (> 200 m); and (iii) Tislit Formation (=Agoudim 3, upper Bajocian), consisting of shallow water limestones and marls (~600 m). These three formations constitute a marine sequence of about 2000 m thickness. This is overlain by (iv) Imilchil Formation (=Anemzi 1; upper Bajocian–Bathonian; ~200 m), which represents a marine-continental transitional facies, and (v) continental red beds of the Isli Formation (=Anemzi 2; upper Bathonian–?Upper Jurassic; ~250 m), the latter containing the tetrapod traces reported here.

The exact age of the trackway-bearing Isli Formation is uncertain. The Isli Formation, which unconformably overlies the Imilchil Formation locally, did not yield any body-fossils of biostratigraphic value; only small characean charophytes (Porocharaceae) have been found (A. Charrière, pers. com.). Also, vertebrate fossil remains have not been found thus far. Dinosaur footprints from the Isli Formation, such as *Carmelopodus* (theropod) and *Polyonyx* (sauropod), are characteristic Middle Jurassic ichnotaxa, although at present these are not well-established as biostratigraphic markers. The lower part of the Isli Formation is probably Bathonian in age, and the middle-upper part could possibly range into the Upper Jurassic. The age can be constrained based on its direct position above the Imilchil Formation, which has been dated to the early Bathonian based on brachiopods (Charrière and Haddoumi, 2016). In cyclostratigraphic terms, the red beds of the Isli Formation correspond to the end of the regressive Jurassic cycle.

The ichnological data presented in this paper refer to localities on the north flank of the Aït Ali Ou Ikkou Syncline, about 10 km east of Imilchil village (N 32° 9′ W 5° 33′; Fig. 1B). The material comes from the lower and middle parts of the Isli Formation, which mainly consist of alternating red sandstones, siltstones and claystones (Fig. 1C b–c). The track-bearing layers are fine-to medium-grained red sandstones, sometimes with mudstone intercalations, which are laminated and contain mud-cracks, current ripples and rain drop marks associated with diverse invertebrate and vertebrate ichnoassemblages.

2.2. Lower part of Midelt Formation (mid-Cretaceous, upper Barremian–?Aptian)

The Midelt region, with the second footprint locality described here, is located between the High Atlas and the Middle Atlas of Morocco, precisely termed High Moulouya (N 32° 52′ W 4° 46′; Figs. 1A, 2A). Here, the pre-Cenomanian Cretaceous series lie in angular unconformity on Triassic and/or Jurassic deposits (geological map of Rabat 1/500,000). In this paper, the Cretaceous series of the Midelt region (Fig. 2B) is subdivided into two lithostratigraphic units based on previous work (Charrière et al., 1998; Ciszak et al., 1999) as follows: The Midelt Formation is a transgressive megasequence subdivided into three members. (i) The lower member, consisting of up to 40 m of red clastic deposits, in which the bed thickness and grain size decrease towards the top. (ii) The intermediate member, which consists of dolomites at its base, comprises mostly 130 m of gypsum and marl. (iii) The upper member consists mainly of marls that become more ferruginous at the top of the succession with massive gypsum and reworked beds (Ciszak et al., 1999). The Amghourzif Formation, consisting mainly of upper Cenomanian bioclastic limestones and lower Turonian platy limestones. The age is based on ₣ foraminifera and ammonites (Charrière et al., 1998).

A well-dated level is the upper member of the Midelt Formation, which yields marine ostracods indicating an upper Cenomanian age while the base of the series is assigned to the Albian (Ciszak et al., 1999). Charophytes and foraminifers collected recently about 100 km east of Midelt, in the infra-Cenomanian conglomerates and the levels above, suggest an upper Barremian–?Aptian age (A. Charriére, pers. comm.). In summary, the red beds of the Midelt Formation correspond to the beginning of the Cretaceous cycle. Based on the dinosaur footprint record, the Mibladen assemblage, with the theropod ichnogenera *Deferrariischnium* and *Bressanichnus*, is characteristic of Albian–Cenomanian ichnofaunas, and the ornithopod ichnogenus *Iguanodontipus* is known from Barremian–Albian deposits. This allowed Gierliński et al. (2017a) to suggest the Albian as the most probable age of the track-bearing horizon in the Midelt Formation.

The vertebrate ichnoassemblage described here comes from the lower member of the Midelt Formation (Fig. 2B), which contains several fluvial sequences. It consists of conglomerates forming the bases of channels and anastomosed channel sandstone bars, prograding towards the east, alternating with red and/or green floodplain claystones. The lower member yielded diverse ichnofossils and body fossils, including plant roots, invertebrate traces, conchostracans, fish scales, fish and bone remains. The vertical evolution of sedimentation reflects a decrease in hydrologic energy levels as a consequence of reduction in topography that likely took place on the southwestern edge of the Midelt area (Ciszak et al., 1999). The track-bearing beds consist mainly of fine- to medium-grained sandstones with muddy surfaces. Preserved tetrapod swim traces indicate occasional highwater levels. We note the co-occurrence of invertebrate- and dinosaur-dominated vertebrate ichnoassemblages in the beds, which contain lamination, mud-cracks, current ripples and rain drop marks.

3. Material and methods

The described material comprises crocodylomorph walking traces assigned to *Crocodylopodus* isp., crocodylomorph swimming traces assigned to *Hatcherichnus* isp., turtle trackways assigned to *Emydhipus* isp., and isolated mammal footprints. All specimens were left in the field. In this paper the following abbreviations are used: Chouaïb Doukkali University, El Jadida, Morocco (CDUE); Imilchil, Morocco (Imil); Mibladen, Morocco (Mibl).