Bird-like tracks from the Imilchil Formation (Middle Jurassic, Bajocian-Bathonian) of the Central High Atlas, Morocco, in comparison with similar Mesozoic tridactylous ichnotaxa

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INTRODUCTION

Footprints of birds or avian theropods are abundantly known from Cretaceous and Cenozoic deposits of North America, Europe and East Asia. In particular shorebirds have left their tracks on numerous surfaces variously co-occurring with those of non-avian theropods, ornithopods or pterosaurs (Lockley et al., 1992, 2006; Lockley, 1999; Lockley & Rainforth, 2002; Kim et al., 2012; McCrea et al., 2014; Xing et al., 2015). Bird-like footprints are known from the Jurassic but were poorly recognized in comparison with avian theropod body fossils, which include new finds from the Callovian-Oxfordian of China (e.g., Godefroit et al., 2013) as well as the classic material of Archaeopteryx von Meyer, 1861, from the Tithonian Solnhofen Limestone of Germany. The stratigraphically oldest bird-like footprints are reported from deposits that are latest Triassic and Early Jurassic in age. They come from the Lower Elliot Formation of Lesotho, southern Africa (Ellenberger, 1970, 1972), the Newark Supergroup of Massachusetts and Virginia, USA (Hitchcock, 1858) and from the Przysucha Formation of Poland (Gierliński, 1996). Younger records are known from the latest Jurassic-earliest Cretaceous Tuchengzi Formation of Liaoning Province, China (Lockley et al., 2006), an area famous for its discoveries of avian theropods. Ichnotaxonomically all
these footprints were assigned to different ichnogenera and ichnospecies. Hitchcock (1858) introduced the ichnotaxon *Plesiornis pilulatus* for specimens from the Newark Supergroup while those from the Lower Elliot Formation were named *Trisauropodiscus* by Ellenberger (1970). For the footprints from Liaoning the new ichnotaxon *Pullornipes aureus* was erected by Lockley et al. (2006). Unnamed bird tracks were also reported from the Late Jurassic of Asturias, Spain (Pinuela et al., 2002). From Middle Jurassic deposits of Msemrir, Morocco, Belvedere et al. (2011) reported small tridactyl bird-like imprints similar to the footprints from Imilchil described here.

The latter material was found during two field trips to the Central High Atlas of Morocco, in September 2009 and October 2016. First finds came from the vicinity of Imilchil in 2009 and were mentioned by Gierliński et al. (2009) as tracks similar to *Carmelopodus* Lockley, Hunt, Paquette, Bilbey & Hamblin (1998), an ichnogenus also recognized in Middle Jurassic strata of this region. In 2016, authors collected more material from the original site and also found similar bird-like footprints near Soumtate, co-occurring with the invertebrate traces *Selenichnites* and *Kouphichnium* in the same stratigraphic unit (Lagnaoui et al., 2016) (Fig. 1).

We focus here on the ichnotaxonomic status of the studied material, leaving the problem of the affinity to distinct biological groups open for future debates. Prospective detailed analyses of bird-like footprints especially from the Lower and Middle Jurassic and comparison with known skeletal material might enlighten the dark ages of bird evolution and help to better discriminate between bird and non-avian theropod feet.

Fig. 1 - Location of described bird-like tracks from the Middle Jurassic of the Central High Atlas, Morocco. a) Map showing study area in Morocco. b) Geological map of the Imilchil region with position of tracks. c) Stratigraphic section showing Middle Jurassic succession near Imilchil with position of tracks and invertebrate body fossils.
MATERIAL, METHODS AND SPECIMENS REPOSITORY

All ichnites, described herein, are preserved as natural casts and molds. Artificial casts to replicate specimens were produced by using Sculpey polymer clay (polyvinyl chloride). Photographs were taken strictly parallel to the surface by ultra low distortion Carl Zeiss lens, under controlled artificial low-key lighting diffused by an additional filter. All measurements are based on standard methods proposed by Haubold (1971) and Leonardi (1987). Track images with cropped matrix around footprints were made using few photos (taken with different lighting or virtually obtained from a single picture) as background layers and then hand shaped and drawn (usually combined with re-drawing of track replicas) using a graphic tablet, employing vector-based drawing software. This method combined few different techniques of illustrating the footprints in order to reduce subjectivity of interpretation.

Institutional abbreviations of specimens' repository

AC: Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, USA;
CDUE: Chouaïb Doukkali University, El Jadida, Morocco;
CMN: Canadian Museum of Nature, Ottawa, Canada;
CU-MWC: Joined collection of the University of Colorado and the Museum of Western Colorado, Boulder and Grand Junction, Colorado, USA;
GNM: Georgian National Museum Tbilisi, Georgia;
JuraPark: collection of Stowarzyszenie “Delta”, Ostrowiec Sw., Poland;
LES: Laboratoire de Paléontologie, Institut de Sciences de l’Évolution, University of Montpellier II, Montpellier, France;
Muz. PIG: Muzeum Geologiczne, Państwowy Instytut Geologiczny - Państwowy Instytut Badawczy, Warsaw, Poland;
UCM: University of Colorado Museum of Natural History, Denver, Colorado, USA.

GEOLOGICAL SETTING

The Imilchil region is situated in the heart of the Central High Atlas that was formed through inversion of former Triassic-Liassic rift basins during the Africa-Eurasia convergence, which consists of different anticlinal-synclinal structures (Frizon de Lamotte et al., 2008). The studied area lies in an elliptically-shaped basin of the Ait Ali Ou Ikko Syncline, about 2 km northeast of Imilchil village and 500 m east of Sountate Village near the road R317 (Fig. 1b). The material comes from the middle and uppermost parts of the Imilchil Formation that mainly consist of alternating red and green sandy marls and sandy limestones laid down in a brackish depositional environment. Characteristic features of the track-bearing layers are lamination, mud-cracks, and diverse invertebrate ichnoassemblages, including the ichnogenus Selenichnites (Lagnaoui et al., 2016).

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
Ichnofamily Trisauropodiscidae Lockley, Yang, Matsukawa, Fleming & Lim, 1992

Ichnogenus Trisauropodiscus Ellenberger, 1970
Type ichnospecies Trisauropodiscus aviforma
Ellenberger, 1970
(Fig. 3)

Emended diagnosis - Functionally tridactyl (with main digit group II-IV) footprints of small to medium-sized bipeds with occasional presence of a trace of the reversed semi functional hallux. Footprints mesaxonich, symmetrical with digit III being longest and lateral digits are subequal in length. Tracks lack metatarsophalangeal pads of digits II and IV, while that one of digit III is occasionally present, but not clearly separated from phalangeal portion of digit III. Digits are very narrow and widely divaricated (> 90°).


Remarks - Trisauropodiscus is slightly different from other Triassic and Jurassic tracks of supposed avian origin. It differs from Plesiornis Hitchcock, 1858 by being larger and much wider with relatively shorter claws and is distinguished from Pulloripes Lockley, Matsukawa, Ohira, Li, Wright, White & Chen, 2006 by being more gracile in its morphology and showing more narrow digits.
However, contrary to *Trisauropodiscus*, the most important feature of *Plesiornis* and bird tracks is the well-developed and separated metatarsophalangeal pad of digit III. The reversed hallux and swollen proximal pad of digit III extends the main gripping surface axially from digit III to the hallux. This adaptation observed in modern flying birds enhances foot grasping ability and evolved probably parallel to wings’ development compensating for the deterioration of the forelimbs’ grasping functions (Gierliński & Sabath, 1998; Gierliński, 2000).

*Trisauropodiscus* does not exhibit a clearly separated proximal pad of digit III and the reversed hallux is not well visible or is absent. Thus, *Trisauropodiscus* is less bird-like than *Plesiornis, Pullornipes* and the Cenozoic avian ichnogenus *Gruidipeda* Panin & Avram, 1962. The latter was considered as a junior synonym of *Trisauropodiscus* by Valais & Melchor (2008), which is not widely accepted (Abrahams et al., 2017).

On the other side, *Trisauropodiscus* was considered as the junior synonym of *Anomoepus* (e.g., Lockley & Harris, 2010), or as a separate ichnogenus, but close to *Anomoepus* (Abrahams et al., 2017). Recently described *Trisauropodiscus*-like footprints from the Early and Middle Jurassic of China are assigned directly to *Anomoepus* (Xing et al., 2016a, 2017), whereas Abrahams et al. (2017) argued to keep *Trisauropodiscus* as a separate ichnogenus from *Anomoepus*, but similar to the latter and of ornithischian origin as well (precisely of heterodontosaurid origin). In our opinion however, *Trisauropodiscus* does not exhibit any of the typical anomoepodid nor ornithischian foot patterns (see, discussion chapter).

*Trisauropodiscus* corresponds quite well with the morphology of seemingly non-avian theropod tracks of *Carmelopodus* Lockley, Hunt, Paquette, Bilbey & Hamblin, 1998, which in turn are very similar to Cretaceous tracks assigned to the ichnogenus *Ornithomimipodidae* by Lockley et al. (2011).

**Occurrence** - Late Triassic to Middle Jurassic of southern and northwestern Africa, and southeastern Asia.

**Trisauropodiscus** isp. (Fig. 2)

**Material** - Collected specimens from Imilchil vicinity CDUE 700 and CDUE 701 (Fig. 2c-d); casted specimen from Imilchil vicinity Muz. PIG 1816.II.1 (Fig. 2a); uncollected and not casted specimen from Sountate vicinity located at N32°9’58.56” and W5°36’31.82” (Fig. 2b); uncollected and not casted specimen located at N32°7’19.72” and W5°32’50.54” (Fig. 2e).

**Localities** - Vicinity of Imilchil and Sountate, Moroccan High Atlas (Fig. 1).

**Description** - The small pes imprints are functionally tridactyl with the reversed and reduced hallux shallowly impressed. Their length, excluding the trace of the hallux, varies from 5.4 cm up to 7.3 cm and their width is 6 cm to 9.3 cm depending on the varying digit divarication. The length/width ratio can be calculated with 0.8-0.9 indicating imprints that are slightly wider than long. Digits II, III and IV are relatively long and narrow and continuously tapering distally. Digit III is about twice as long when compared to lateral digits II and IV. The latter are equal...
in length representing 44-61% of the length of digit III. Digit I (hallux) is about 22% up to 32% in length when compared to the length of digit III. The projection of digit III above the tips of the lateral digits is very high and amounts to 52-73% of the footprint length excluding the hallux trace. The total divarication (the angle measured between the long axes of digits II and IV) varies between 98° and 127°.

Remarks - The morphology is comparable to the type material of *Trisauropodiscus* from the Lower Elliot Formation of Lesotho (Fig. 3) which comprises mesaxonic footprints, symmetrical with narrow and widely divaricated digits II-IV (> 90°) and characterized by lack of metatarsophalangeal pads of digits II and IV, very long digit III, digits II and IV of about half the length of digit III, occasional presence of a trace of the short and clearly reversed semi functional digit I.

Stratigraphy and age - Imilchil Formation, Middle Jurassic (Bajocian-Bathonian).

DISCUSSION

Morphologically similar footprints from the Middle Jurassic of Morocco have been described from the Msemrir region by Belvedere et al. (2011). They show widely divaricated, slender digits and a prominent middle toe strongly resembling the material from Imilchil. Belvedere et al. (2011) are uncertain about the presence of a hallux (digit I) trace questionably preserved in some imprints. Indeed these tracks from Msemrir seem to lack this feature. In this respect and by the absence of a metatarsophalangeal pad they are morphologically closer to the ichnogenus *Carmelopodus* (see below).

Described footprints from Imilchil strongly resemble the Late Triassic ichnogenus *Trisauropodiscus*. The latter was originally introduced by Ellenberger (1970) based on material from the Lower Elliot Formation (latest Triassic) of Lesotho, southern Africa (Fig. 3). Ellenberger (1970, 1972) erected different ichnosppecies such as *T. aviforma*, *T. galliforma*, *T. superaviforma* and several others, which seem to be junior synonyms of *T. aviforma* and *T. galliforma*. It was apparent that *Trisauropodiscus* is distinct from other tridactyl theropod tracks occurring in the same unit, mostly small to large grallatorid forms that were described by Ellenberger (1970, 1972, 1974) under various new names. However, the exact status and the affinity of *Trisauropodiscus* were questioned and widely discussed by several authors.


Presently, most authors consider *Trisauropodiscus* as the junior synonym of *Anomoepus* (e.g., Lockley & Harris, 2010), or distinct morphotype similar to *Anomoepus* (Abrahams et al., 2017). Originally *Anomoepus* was described from Early Jurassic deposits of the Newark Supergroup of eastern North America (Hitchcock, 1848; Olsen & Rainforth, 2003). The well-preserved type material shows footprints of a functionally tridactyl and facultative biped with moderately divaricated, relatively short and slightly cigar-shaped digits that are subequal in length. The pes of *Anomoepus* is asymmetrical because of the presence of a metatarsophalangeal pad in digit IV. This is similar to the pad configuration in the classic theropod ichnotaxon *Grallator* Hitchcock, 1858 and in most of non-avian dinosaur tracks. The relatively short digits being subequal in length, or with digit IV being longest when including the metatarsophalangeal pad impression, is the characteristic feature of all anomoepodid-like pes imprints that can be comprised in the *Anomoepus-Moyenisauropus-Shenmuichnus* plexus (Fig. 4), which combines morphologically similar tracks of basal ornithischians and basal thyreophorans.

Whatever the biological affinity of the *Trisauropodiscus* trackmaker might be, this ichnospecies comprises tracks of small bipeds with relatively long, elongate, widely divaricated digits, and with the pes being symmetrical - V or U shaped (Gierlinski, 2016; Abrahams et al., 2017). Similar to *Grallator* and all grallatorid tracks (Fig. 5), and contrary to *Anomoepus* and other *Anomoepus*-like footprints (Fig. 4), *Trisauropodiscus* shows a prominent, very long middle digit III and lateral digits II and IV of about half the length of the middle digit and nearly equal in their extension.

Looking at the osteological record and the skeletons of preserved theropod feet, such a long digit III is found among abelisaurid theropods. An exceptionally long digit III is seen in the abelisaurid *Velocisaurus* Bonaparte,
1991 from the Upper Cretaceous of Argentina (Gierlinski et al., 2017). Grallatorid tracks that reflect that feature come from the mid-Cretaceous of Argentina (Fig. 5a) and very recently it has been also found by the authors in mid-Cretaceous deposits of Morocco (Fig. 5b). This distinguished type of theropod footprints was named *Deferrariischnium* by Calvo, 1991 (see also Calvo, 2007).

However, in contrast to *Deferrariischnium* (as well as to *Grallator* and *Anomoepus*), *Trisauropodiscus*, has no metatarsophalangeal pad of the fourth digit. The proximal pad of *Trisauropodiscus* is located centrally below the middle toe, but not well separated from digit III. Sometimes when no hallux is visible, *Trisauropodiscus* tracks are not much distinguishable from *Carmelopodus* ichnites. This is why *Trisauropodiscus* tracks from Imilchil were previously reported as *Carmelopodus* by Gierlinski et al. (2009). On the other hand, *Carmelopodus* is consistent morphologically with tracks of the ichnofamily Ornithomimipodidae Lockley, Cart, Martin & Milner, 2011. *Ornithomimipodidae* comprises the ichngenera *Irenichnites* Sternberg, 1932, *Columbosauripus* Sternberg, 1932, *Magnoavipes* Lee, 1997, *Ornithomimus* Sternberg, 1926 and *Xiangxipus* Zeng, 1982. The latter ichnogenus *Xiangxipus* was referred recently to *Ornithomimipodidae* by Xing et al. (2016b). However, *Xiangxipus* is rather comparable to *Saurexallopus* Harris, 1997, as shown by Gierlinski & Lockley (2013) and that view was not disproved by Xing et al. (2016b), nor *Saurexallopus* was added to *Ornithomimipodidae*. So, here we consider the ornithomimipodid morphotype as *Irenichnites-Columbosauripus-Magnoavipes-Ornithomimus* plexus of tridactylous ichnotaxa only, excluding similar tetradactyl forms like *Xiangxipus* and *Saurexallopus*.

Ornithomimipodid tracks are symmetrical with the middle digit III being longer than the lateral ones. Digits are widely divaricated and slender. More precisely, Lockley et al. (2011) listed ornithomimipodid diagnostic features as follows: 1) digit II separated from the rest of the footprint; 2) proximal pad connected to digit III and IV, centrally located and separated from the phalangeal portion of digit III. *Carmelopodus* does not share those features concerning the proximal pad because its characteristic is the lack of those pads. However, it shares some ornithomimipodid characteristics such as the widely divaricated slender digits with the prominent middle toe and digit II separated from the rest of the footprint, which is well visible in the holotype of *Carmelopodus untermannorum* Lockley, Hunt, Paquette, Bilbey & Hamblin, 1998 (specimen CU-MWC 184.12; Fig. 6a), in *Carmelopodus* tracks from the Middle Jurassic of Morocco (Fig. 6b) and in cf. *Carmelopodus* from the...
Lower Cretaceous of Utah reported by Lockley et al., 2014 (Fig. 6c).

The *Carmelopodus-Irenichnites-Columbosauripus-Magnoavipes-Ornithomimipus* plexus (Fig. 6) seems to be more closely related to the *Trisauropodiscus* morphotype than the *Anomoepus-Moyenisauroopus-Shenmuichnus* plexus (Fig. 4).

*Carmelopodus* and ornithomimipodid are similar, but this does mean that *Carmelopodus* should be referred to the ichnofamily Ornithomimipodidae. Both types of tracks, *Carmelopodus* and ornithomimipodid footprints, are rather produced by two different groups of derived theropods with similar foot morphologies. *Carmelopodus* footprints are supposed to be of alvarezsaurid origin (Niedźwiedzki et al., 2017) and Ornithomimipodidae are widely considered as ornithomimosaurid tracks (e.g. Lockley et al., 2011; Xing et al., 2016b). However, it is also noteworthy that some researchers suggest more complicated picture of *Carmelopodus* and ornithomimipodid affinities. Hunt-Foster supposed ornithomimosaurid affinity of *Carmelopodus*-like tracks from the Early Cretaceous Cedar Mountain Formation of Utah (Rebecca Hunt-Foster personal comm., 2017). On the other hand, ornithomimosaurid footprints (possibly *Ornithomimipus* misidentified as *Magnoavipes*) from the Late Cretaceous Cantwell Formation of Alaska are supposed of direct avian origin (see Fiorillo et al., 2011).

**CONCLUSIONS**

*Trisauropodiscus* comprises tracks of small bipeds with the symmetrical pes, with widely divaricating digits, prominent middle toe and lateral digits shorter and subequal in length. Similar to *Grallator* and all grallatorid tracks and contrary to *Anomoepus* and other *Anomoepus*-like footprints, *Trisauropodiscus* shows a prominent, very long middle digit III and lateral digits II and IV of about half the length of the middle digit and nearly equal in their extension.

*Trisauropodiscus* is morphologically different from *Anomoepus-Shenmuichnus-Moyenisauroopus* plexus footprints. This ichnogenus represents a distinct morphotype most similar to the plexus comprising *Carmelopodus, Irenichnites, Columbosauripus, Magnoavipes* and *Ornithomimipus*.

We suggest *Trisauropodiscus* morphotype as a hypothetical predecessor of *Carmelopodus* and ornithomimipodid morphotypes.

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