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Angolan ichnosite in a diamond mine shows the presence of a large terrestrial mammaliamorph, a crocodylomorph, and sauropod dinosaurs in the Early Cretaceous of Africa

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A R T I C L E I N F O

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A B S T R A C T

We report here new and the first mammaliamorph tracks from the Early Cretaceous of Africa. The tracksite, that also bears crocodylomorph and sauropod dinosaurian tracks, is in the Catoca diamond mine, Lunda Sul Province, Angola. The mammaliamorph tracks have a unique morphology, attributed to *Catocapes angolanus* ichnogen. et ichnosp. nov. and present an anterolateral projection of digit I and V. The tracks with an average length of 2.7 cm and width of 3.2 cm are the largest mammaliamorph tracks known from the Early Cretaceous unmatched in size in the skeletal fossil record. The crocodylomorph trackways and tracks are attributed to *Angolaichnus adamanticus* ichnogen. et ichnosp. nov. ('ichnofamily' Batrachopodidae) and present a functionally pentadactyl pes, an extremely outwardly rotated handprint, and an unusual tetradactyl and plantigrade manus. One medium-sized sauropod dinosaur trackway preserved skin impressions of a trackmaker with stride length of 1.6 m; a second is that of a small-sized sauropod trackmaker with a pace length of 75 cm.

1. Introduction

The Catoca Mine near Saurimo in Lunda Sul Province, Angola, is the fourth largest diamond mine in the world (Fig. 1A). Within sediments preserved in a crater associated with the kimberlite pipe that created the resource are mammaliamorph, crocodylomorph, and dinosaur footprints, with one sauropod dinosaur print preserving the skin impression (Marzola et al., 2014, 2015). The kimberlite pipe is located along the Lucapa Fault Zone and has a U-Pb radiometric date on zircons from the kimberlite of ~118 Ma (Late Aptian), providing a maximum age for the lacustrine fill preserving the tracks (Robles-Cruz et al., 2012; Nikitina et al., 2012), thus making the Catoca tracksite the most precisely numerically constrained Early Cretaceous terrestrial fossil locality in Africa (Fig. 1B–C). Datation to 118 Ma on zircons must be considered the maximum estimate, because of the xenogenic origin of the mineral in kimberlite magma: an error of about 2 Ma is possible, and the date 118 Ma is only the peak value of many individual measurements between 114 and 123 Ma (Robles-Cruz et al., 2012).

Moreover, the Lucapa Fault Zone can be traced southwestward to the coast, where it influenced the setting for Late Cretaceous marine vertebrate fossil deposition on the continental shelf, and it can be traced further to the Mid-Atlantic Ridge (Eagles, 2007; Guiraud et al., 2010). The age of the Catoca kimberlite indicates it was emplaced as little as 2 My after the beginning of seafloor crust accretion north of the Walvis Ridge in the South Atlantic Ocean (Real, 1958; Gaina et al., 2013). Our purpose is to describe the Catoca tracks and identify them as precisely as possible. Fossils are not necessarily rare in volcanic craters globally. However, because of the geologic setting of the Catoca tracks, and because of their precise dating, we can relate this fossil locality to events

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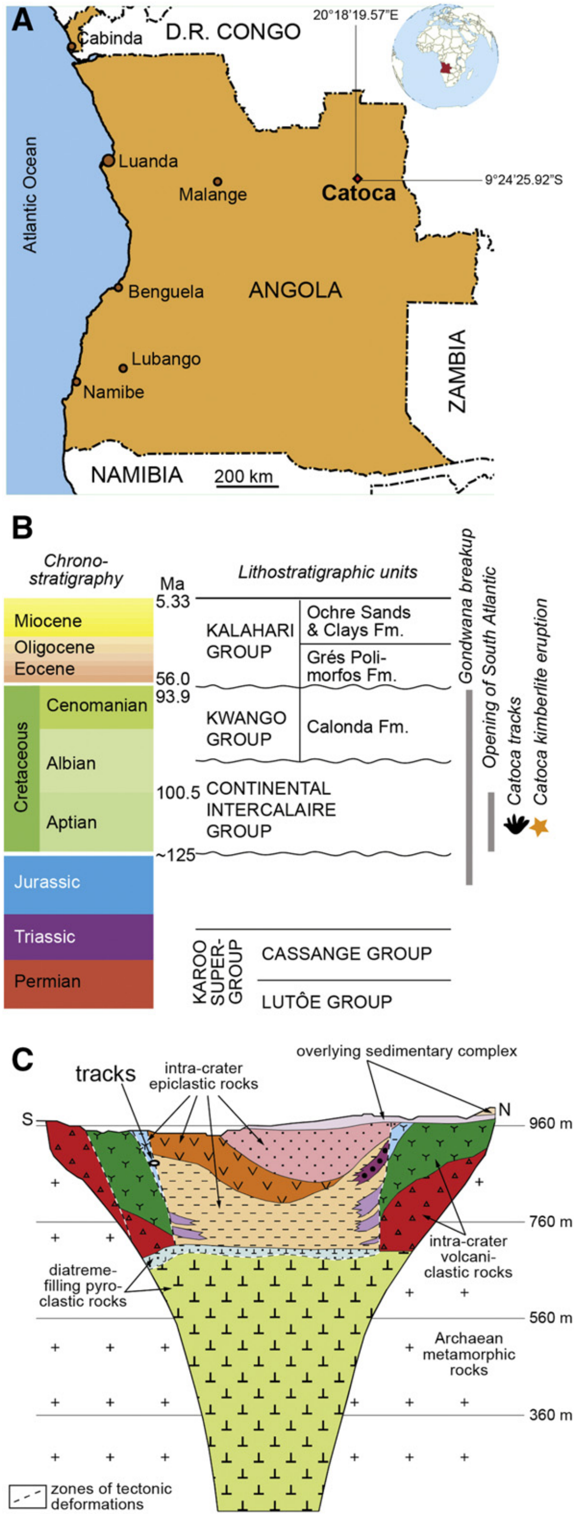

Fig. 1. (A) Catoca global position; (B) Chrono-litho-stratigraphy of "Catoca beds"; (C) Model of the Catoca sedimentary basin (modified after Pervov et al., 2011).

and structures in the breakup of Gondwana, and we can determine the paleolatitude of the locality, which provides a first order indication of the paleoenvironment in which it was formed.

2. Geological setting

Cretaceous outcrops in Angola are mainly distributed along the coast, and are related to the Late Cretaceous opening and growth of the South Atlantic (Jacobs et al., 2006, 2009). The Cretaceous vertebrate fauna known from Angola is summarized in Mateus et al. (2012). Among the marine amniotes from the Cretaceous of Angola are turtles (Mateus et al., 2009), mosasaurs (Schulp et al., 2006; Polcyn et al., 2007, 2010, 2012), and plesiosaurs (Araújo et al., 2015). Dinosaurs and a pterosaurs are the only terrestrial amniotes reported previously from the Angolan Cretaceous (Mateus et al., 2011; Mateus et al., 2012). The Catoca crater is the only completely terrestrial Cretaceous fossil locality known in Angola.

Volcanic craters are usually filled initially by a coarse-grained material from the collapse of the crater walls, followed by lacustrine sediments (White and Ross, 2011). The lake filling the Catoca crater was no >500–600 m in diameter.The tracks were encountered around the southern periphery of the Catoca crater at several levels within a 25–30 m thick section of sediments (Figs. 1C, 2A–F). Sedimentary structures include graded bedding, load casts, mud-cracks, ripple marks, crescentic scour marks, and flame structures, indicating shallow-water alluvial and turbidity flow deposition in a shallow-water intermittent lake (Pervov et al., 2011) (Fig. 2A–B, F–H). At Catoca, the track-bearing strata dip 60°–70° toward the crater center indicating *syn*- and post-depositional subsidence and faulting (Fig. 2A).

The tracks are preserved in three different horizons of fine-grained, shaly, purple-red mudstones (Figs. 2D–F, 3–7). Two horizon yielded 70 distinct crocodylomorph and mammaliamorph tracks (Figs. 2E–F, 3–4); an upper horizons preserved the dinosaur tracks with the skin impression (Figs. 2D, 5–7). In close proximity to the slab MGUAN-PA601 bearing the mammaliamorph tracks (Fig. 2F, see chapter 3 Material and methods), three well-preserved *Scolicia*-like snail trails were associated with a mud-cracked surface (Fig. 2G–H). Sparse coalified relics of sedge-like plants were encountered in mudstone at this stratigraphic level.

3. Material and methods

The tracks collected in Catoca Mine are preserved as true tracks (negative epireliefs), distributed on three bedding planes, made by crocodylomorph, sauropod dinosaur, and mammaliamorph trackmakers. The site (Fig. 2C) was discovered by one of us (VP) in December 2010; the Catoca Diamond Mine Company management remarkably decided to suspend mining operations at that sector of the mine, pending the follow-up field trip in July 2011 by OM and VP. During this visit the track-site was mapped in detail, and a selection of some of the small tracks was excavated, including a chaotically trampled surface bearing mammaliamorph and crocodylomorph tracks (Figs. 2F, 3) and one crocodylomorph trackway (Figs. 2E, 4). A sample of skin impression of a sauropod dinosaur track was recovered (Fig. 6B). The large size of the dinosaur tracks so far precluded recovery of the dinosaur trackways (Figs. 5–7).

The material will be housed in the collections of the Geological Museum of Universidade Agostinho Neto-PaleoAngola Project (Catoca collection) in Luanda, Angola, under the acronym MGUAN-PA. Registration number has been assigned as follows: MGUAN-PA600 is a slab bearing one crocodylomorph trackway (trackway 1) (Fig. 4); MGUAN-PA601 is a slab bearing the main chaotically trampled surface with mammaliamorph and crocodylomorph isolated tracks and one crocodylomorph trackway (trackway 2) (Fig. 3); MGUAN-PA602 is a sauropod dinosaur foot skin impression (Fig. 6B).

In the text, two sauropod dinosaur trackways will be also described as trackway 3 (Figs. 5, 6) and trackway 4 (Figs. 5, 7). Because of the weak preservation of both trackways, the size of each track, and the lack of time, these tracks were not collected during the visit in July 2011, and, up to date, have gone lost by the mining activity. Their description is based on field observation and photographs. Skin impression MGUAN-PA602 was collected from one track 4 of trackway 3 (see chapters 5.2 and 5.3).

To avoid confusion between the text and the images, in the manuscript we kept the field numbers attributed to each track.

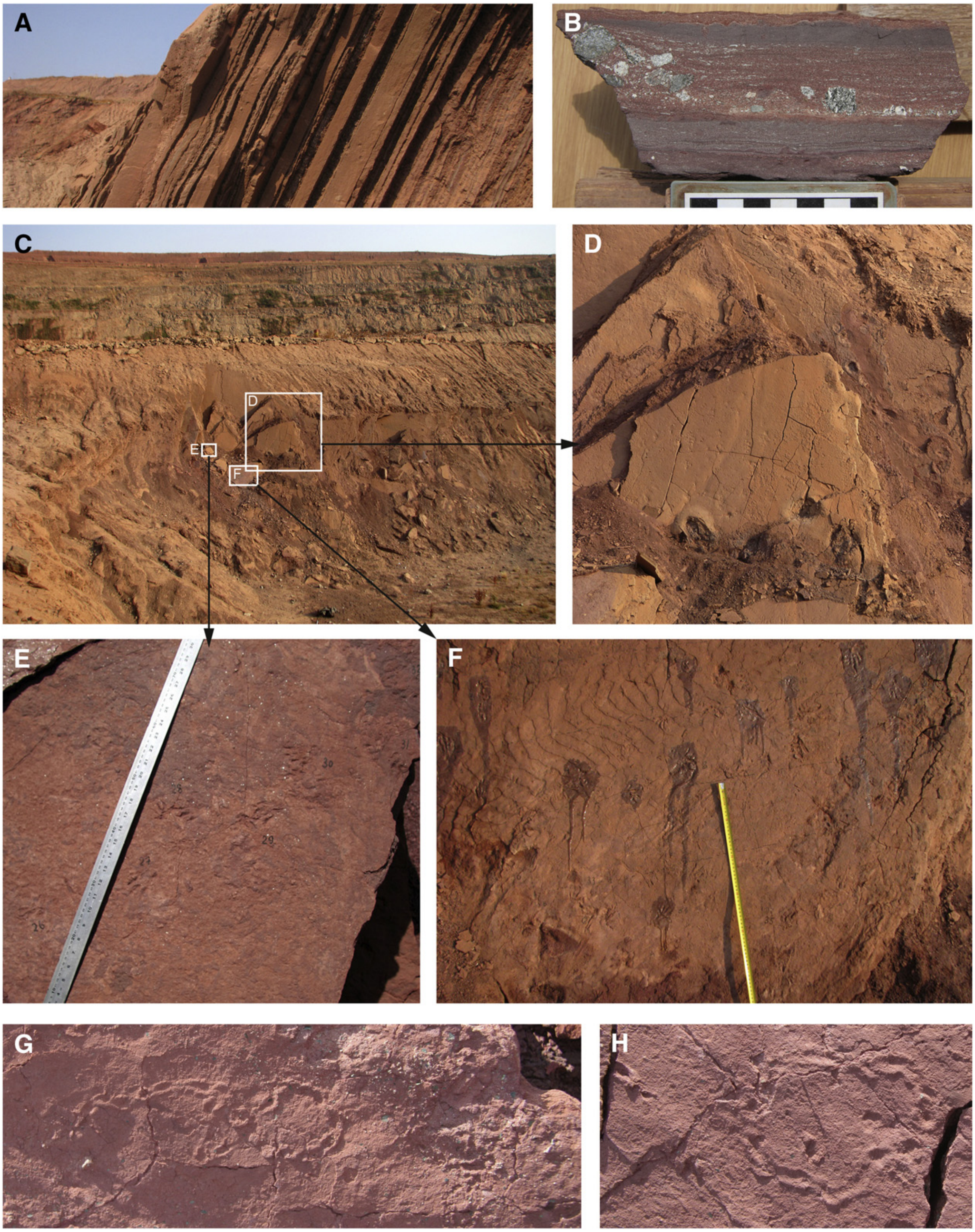

Fig. 2. (A) The sedimentary sequence including footprints of various Mesozoic animals. Intercalation of sand, silt and mudstones. The thickest layer in the center is 15 cm thick. Steep inclination is related to intra-crater tectonic processes; (B) Cross section of a sample with mammal-like animal footprints on its surface. Intercalation of tuffaceous sand-, silt and mudstones. Tuffaceous sandstone includes metamorphic rock clasts and numerous phlogopite flakes. The upper mudstone surface shows desiccation cracks; (C) Overview of the Catoca outcrop in July 2011; photographs in perspective of (D) the two sauropod dinosaur trackway 3 and trackway 4, (E) slab MGUAN-PA600 bearing the crocodylomorph trackway 1, and (F) the chaotically trampled surface MGUAN-PA601 bearing mammaliamorph and crocodylomorph isolated tracks and trackway 2 with evident ripple marks in the upper part; (G) and (H) Scolicia-like snail trails associated with a mud-cracked surface.

Digit, track, and trackway measurements were taken directly in the field or on the original material when collected. In crocodylomorph trackways, pace and stride lengths, and pace angulation, were measured between points defined by the junction of digit III with the metacarpal or metatarsal, while pes-manus rotation was measured along digit III axis of each track. For the outline drawings, the specimens were traced

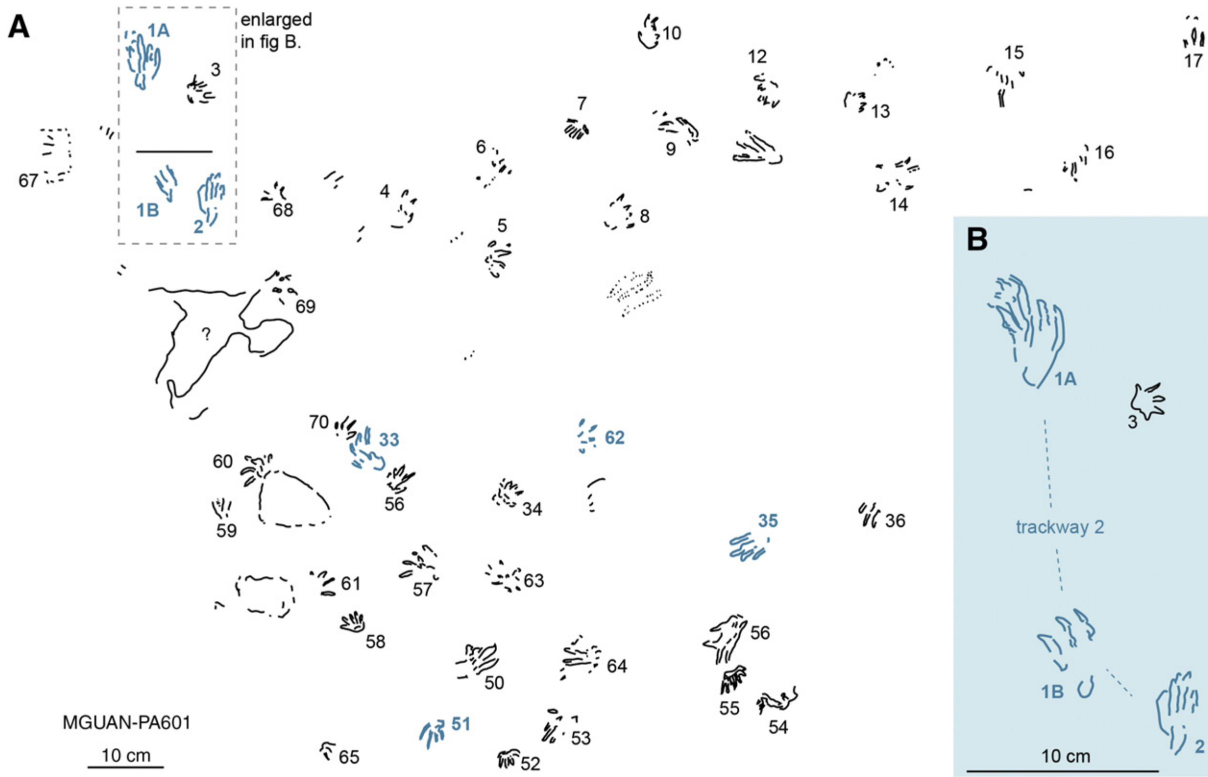

Fig. 3. (A) Drawing based on the field sketch made by OM of the chaotically trampled surfaced bearing mammaliamorph (black) and crocodylomorph (blue) tracks. The broken rectangular line, zoomed in (B), enlightens the possible crocodylomorph trackway 2 and the mammaliamorph track 03.

on transparent plastic films at their original scale. 3D digital photogrammetric models were reconstructed based on photographs taken directly from the stored material at ML.

Mesozoic mammal-like tracks (Leonardi, 1987; Lockley et al., 2004a; De Valais, 2009; Contessi, 2013) are identified by pentadactyl and mesaxonic morphology of the relative small-sized track, digit length up to 1.5 cm, divergent central digits (II–IV) with shorter and more divergent lateral digits I and V, typical for ancient eutherians, multituberculates, and triconodonts (Lockley and Foster, 2003) (Fig. 8). No phalangeal formula can be calculated for the Catoca tracks, due to the absence of preserved phalangeal pad impressions, but the symmetry and relative lengths of digits is consistent with a 2-3-3-3-3 formula rather than that of lepidosaurs, which have greatly varying digit lengths due to their phalangeal formulae (Lockley and Foster, 2003). Mammal tracks present straight

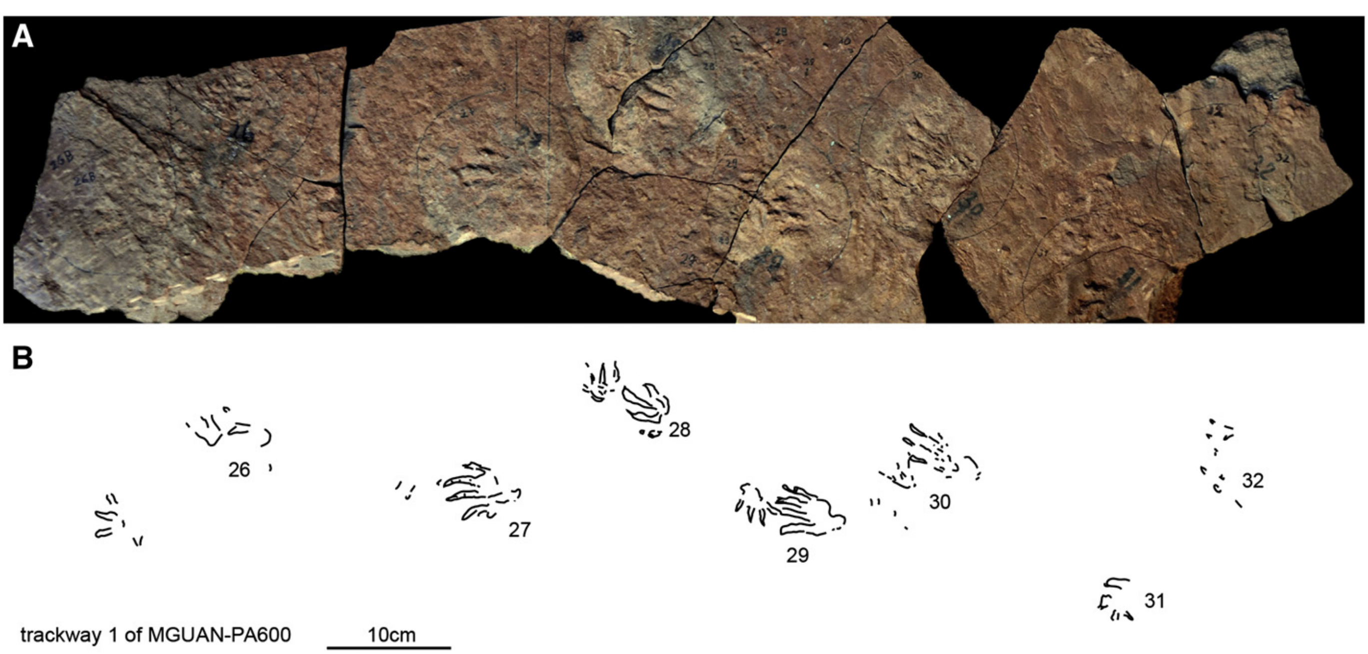

Fig. 4. *Angolaichnus adamanticus* ichnogen. et ichnosp. nov. holotype trackway 1 in MGUAN-PA600. (A) photograph; (B) interpretative drawing.

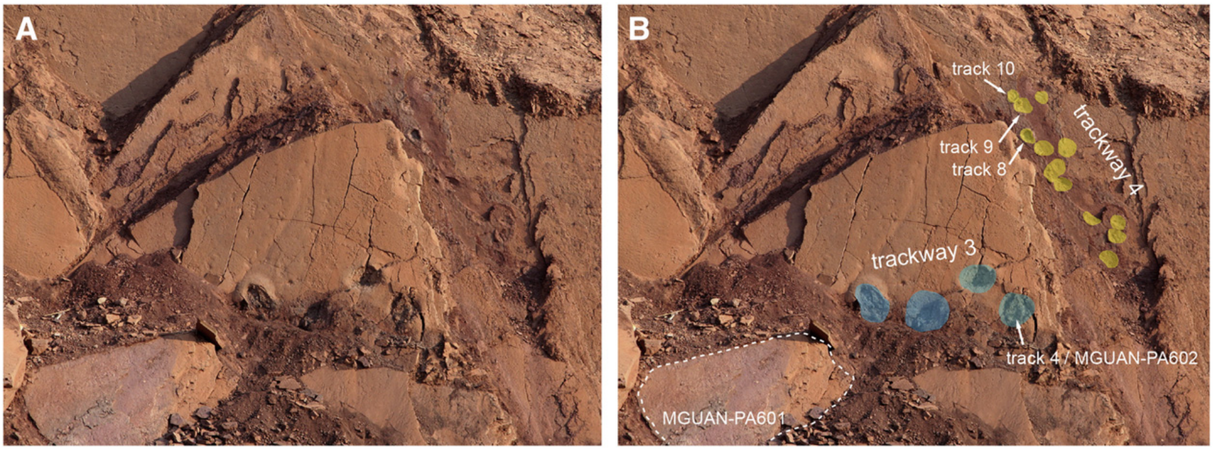

Fig. 5. (A) Overview of the dinosaur trackways from the Catoca mine; (B) annotated version of (A) with the chaotically trampled surface MGUAN-PA601 indicated with the dashed line and sauropod trackway 3 (blue) and sauropod trackway 4 (yellow) with relatively best preserved tracks and the skin impression MGUAN-PA602.

and relatively robust digits, compared to other small pentadactyl tracks, such as the ichnogenus *Rhynchosauroides* (Lockley et al., 2004a), which have slender, curved digits.

3.1. Ichnological abbreviations

ANG = pace angulation; L = track length; LI = length of digit I; LII = length of digit II; LIII = length of digit III; LIV = length of digit IV; LV = length of digit V; I–II = angle between digits I and II; II–III = angle between digits II and III; III–IV = angle between digits III and IV; IV–V = angle between digits IV and V; I–IV = angle between digits I and IV; I–V = angle between digits I and V; PL = pace length; PLm = manus pace length; PLp = pes pace length; SL = stride length; SLm = manus stride length; SLp = pes stride length; TWe = external pes width; TWi = internal pes width; TWm = manus trackway width; TWp = medial pes width; W = track width.

4. Mesozoic crocodylomorph and mammalian records

4.1. Mesozoic crocodylomorph track record

Mesozoic crocodylomorph and crocodilian tracks and trackways are attributed to the ichnofamily Batrachopodidae Lull, 1904. It extends from the Triassic of France (Lapparent and Montenat, 1967), Lesotho (Ellenberger and Ellenberger, 1960) and North America (Hitchcock, 1889; Wanner, 1889; Bock, 1952; Silvestri and Szajna, 1993) to the end of Mesozoic era, as testified by the Early Cretaceous ichnogenus *Crocodylopodus* Fuentes Vidarte and Meijide Calvo, 1999, and Late Cretaceous batrachopodid tracks from Brazil (Leonardi, 1994) and Morocco (Ambroggi and Lapparent, 1954a).

Many different ichnogenera and ichnospecies are attributed to this ichnofamily, leaving the debate on a proper classification still open and under debate (see i.e., Olsen and Padian, 1986; Lockley and Meyer, 2004; Lockley et al., 2004b, 2010). The mostly representative morphotype, *Batrachopus* Hitchcock, 1845, has been tentatively attributed to 'true crocodilian or to a crocodylomorph with a pedal digit V reduced to the state seen in crocodilians' by Olsen and Padian (1986) and is described from a Lower Jurassic ichnofauna of the United States (Hitchcock, 1845; Olsen and Padian, 1986; Milner and Lockley, 2006). *Batrachopus* presents a functionally tetradactyl and plantigrade manus and pes, with a foot length between 2 cm and 8 cm, the presence of claw marks, and a minimal total digital divarication (Fig. 9B, E–F).

Ichnogenus *Antipus* Hitchcock, 1858, is considered a distinct morphotype from *Batrachopus*. They differ to one another for the digit morphology, stout digits, and with minimal digital divarication in *Batrachopus*, much more slender, with sharpen digits, and widely

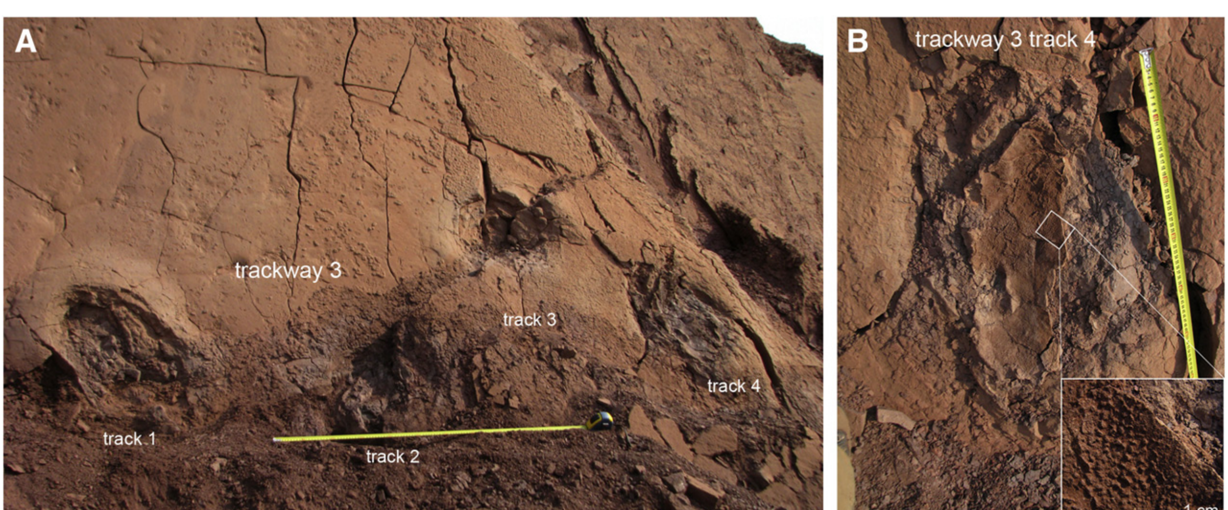

Fig. 6. Sauropod trackway 3. (A) photograph in perspective; (B) photograph of track 4 with the preserved skin impression MGUAN-PA602.

Fig. 7. Sauropod trackway 4 as seen from below in perspective view.

divaricated in *Antipus* (Lockley and Meyer, 2004) and for the inner trackway width, close to 0 in *Batrachopus* (the right and left pedes touch the trackway midline), and about 4 cm in *Antipus* (Lockley and Meyer, 2004). However, Lockley and Meyer (2004) pointed out that this difference in the trackway width could be due to the walking speed of an identical trackmaker, with *Antipus* representing a slower version of *Batrachopus*.

A third common morphotype, *Sustenodactylus* Lull, 1904 (previously named *Stenodactylus* by Hitchcock, 1858), presents slender pes digits, pes and manus dimensions, and a relative rotation of the manus to the pes (Fig. 9C) that allow it to be considered a synonym of *Batrachopus* by Olsen and Padian (1986) or of *Antipus* by Lockley and Meyer (2004).

The Jurassic–Cretaceous boundary morphotype *Crocodylopodus* was originally ascribed by Fuentes Vidarte and Meijide Calvo (1999) to the new ichnofamily Crocodilopodidae (see also Avanzini et al., 2007) (Fig. 9D). Lockley and Meyer (2004) made a complete comparison between *Batrachopus* and *Crocodylopodus*, considering the distinction between the two morphotypes valid, but refusing the existence of the ichnofamily Crocodilopodidae and including *Crocodylopodus* in the ichnofamily Batrachopodidae.

Finally, crocodylomorph tracks attributed to large neosuchian crocodilomorph and to the morphotype *Hatcherichnus* Foster and Lockley (1997) are reported from the Late Jurassic of Utah and Spain (see also Avanzini et al., 2007, 2010).

4.2. Mesozoic mammalian track record

A complete scheme with Mesozoic mammalian tracks is reported in Fig. 8.

With the caveat that "Many of the Late Triassic to Early of Middle Jurassic reports could represent various non-mammalian synapsids rather than true mammals[…]" (Lockley and Foster, 2003: p. 269), the Triassic mammal trackway record includes a plethora of ichnospecies from southern Africa (Ellenberger, 1972, 1974; see review and summary in Lockley et al., 2004a), and "unnamed mammal tracks" from the Triassic–Jurassic of Gateway, western Colorado, USA (Lockley et al., 1996). In Lockley et al. (2004a, 2004b: pp. 91–92) the authors once more "[…] advocate caution in the interpretation of these isolated footprints [from Gateway] pending further discoveries", also because of the potential of confusion of mammal-like pes tracks with *Rhynchosauroides*-like manus tracks.

The Jurassic record is similarly limited. Sarjeant (1975) described the mammal-like track *Pooleyichnus burfordensis* from the Bajocian Stonesfield Slate from the UK. Leonardi (1994) reported tracks from the Lower Jurassic Botucatu Fm of Brazil (but see Tamrat and Ernesto (2006) for a younger dating); Rainforth and Lockley (1996:p.266) suggested these tracks to be of possible mammalian affinity. Olsen (1980: p.369) reported "possible advanced therapsid […] or early mammal" tracks from the Hettangian of the Towaco Formation of New Jersey, USA. Additionally, Lucas and Tanner (2007:p.249) mention a "synapsid (or mammal?) footprint […]" from the Early Jurassic of Gateway, Colorado. Casamiquela (1964) named *Ameghinichnus patagonicus* from the Middle Jurassic La Matilde Formation of Argentina, which, according to the review by Rainforth and Lockley (1996:p.267) "[…] represent[s] one of the most convincing examples of mammal tracks known from the Mesozoic." Gierliński et al. (2004) reported Hettangian mammal-like ("cf. *Ameghinichnus*") tracks from Poland, UK occurrence. *Brasilichium* is a mammal morphotype reported both from the Upper Jurassic of North America (Hamblin and Foster, 2000; Hamblin et al., 2000; Engelmann, 2010; Lockley, 2011) and from the Lower Cretaceous of Brazil (Leonardi, 1980, 1994; reviewed in Adorna Fernandes and De Souza Carvalho, 2008) and Mexico (Rodriguez-de la Rosa, 2003).

From the Cretaceous, probable marsupial tracks *Duquettichnus kooli* were described from the Aptian-Albian of British Columbia, Canada (Sarjeant and Thulborn, 1986; see also Lockley and Foster, 2003: p. 273). Tracks of "[…]possible mammalian origin" (Stanford and Lockley, 2002) from the Lower Cretaceous Patuxent Formation of Maryland, USA, were reported in more detail in Stanford et al. (2007). McCrea and Sarjeant (2001) described *Tricorynopus? brinkmani* from the early Albian of Alberta, Canada; however, McCrea et al. (2004, 2014) both suggested that *Tricorynopus brinkmani* prints could be partially impressed or preserved avian prints, or possibly a product of two or more overlapping avian prints: *Tricorynopus brinkmani* should be considered a *nomen dubium* and its association to mammalian trackmaker is highly speculative. Lockley and Foster (2003) described the Maastrichtian *Schadipes crypticus* from the Laramie Formation of Golden, Colorado, USA. In the same paper, they also tentatively suggested that *Agadirichnus elegans* (see Ambroggi and Lapparent, 1954b) from the Maastrichtian of North Africa could be of mammalian origin. Certain mammal-like tracks from Africa have been recently reported from the Cenomanian of the Kerker Member of the Zebbag Formation of Tunisia (Contessi, 2013).

4.3. Mesozoic mammalian body fossil record suitable for identification of track-makers

The Mesozoic mammalian body fossil record consists for the greater part of jaws, teeth and ear bones, which are of limited use in the study of trackways. Significant material reported so far includes discoveries from North America (e.g., Cifelli, 1993, 1999), South America (Bonaparte and Rougier, 1987; Rauhut et al., 2002), China (e.g., Ji et al., 2002; Luo et al., 2003; Hu et al., 2010), Mongolia (Rougier et al., 1998; Prieto-Márquez et al., 2012), and Australia (Archer et al., 1985; Flannery et al., 1995). From Africa, mammal material has been reported from Libya (Nessov et al., 1998), Cameroon (Jacobs et al., 1988; Brunet et al., 1990), Tanzania

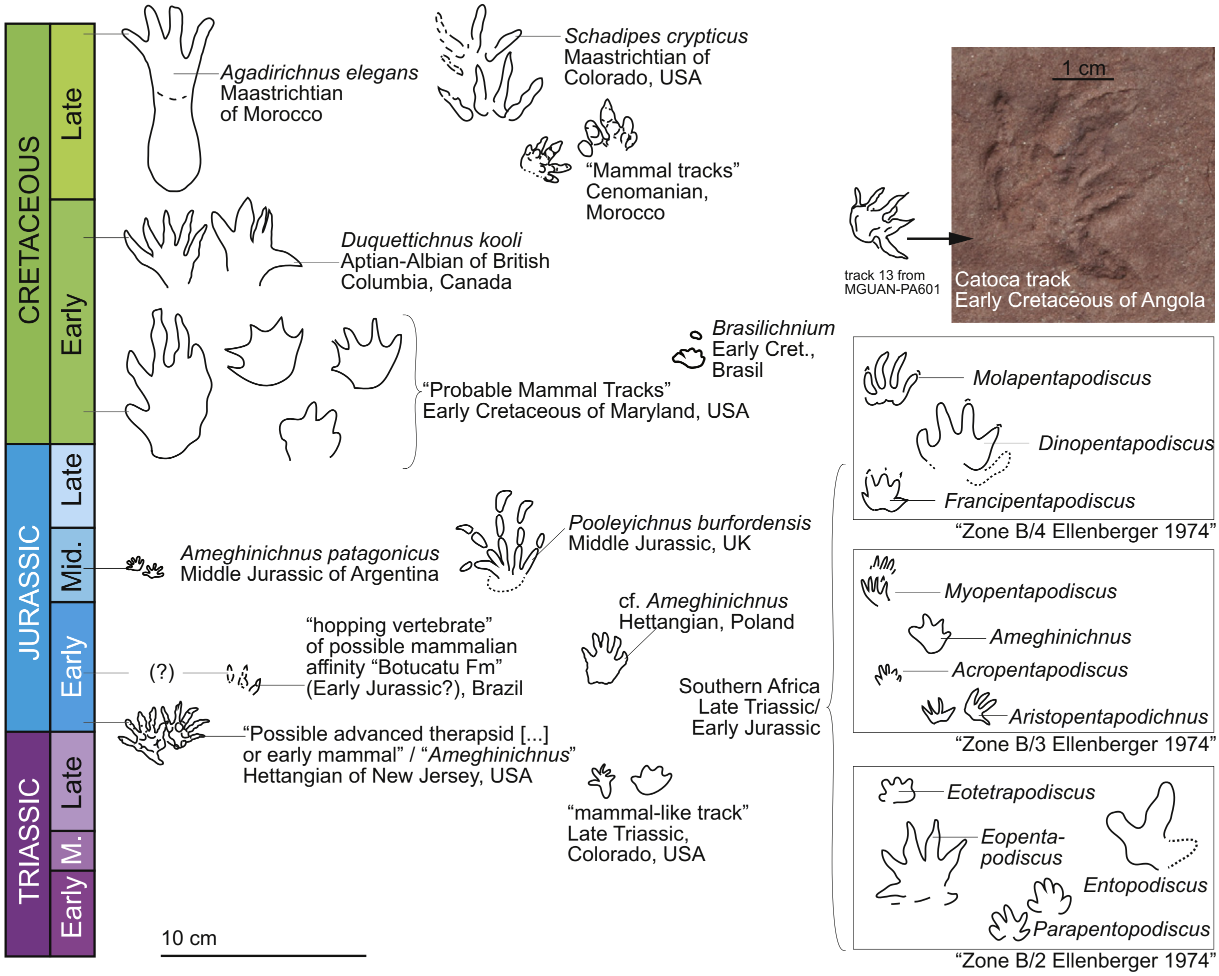

Fig. 8. Mesozoic mammalian track record with *Catocapes angolanus* ichnogen. et ichnosp. nov. holotype track 13 photograph (right) and interpretative drawing (left).

(Krause et al., 2003, 1997), and Morocco (Sigogneau-Russell et al., 1988; Haddoumi et al., 2015). Very little postcranial material of Mesozoic mammals has been described so far. We are not aware of any published Early Cretaceous mammalian postcranial material from Africa beyond the caudal vertebra reported from Libya by Nessov et al. (1998), nor of any mammal track from the same period on this continent.

Early Cretaceous mammals with preserved postcranial material are known mostly from the Liaoning Province of China, all represented by small, 'squirrel-sized' species: the triconodont *Jeholodens jenkinsi* Ji and Luo (1999) and the symmetrodont *Zhangheotherium quinquecuspidens* Hu et al. (1997) from the Late Jurassic/Early Cretaceous boundary of the Yixian Formation; the spalacotheriid *Akidolestes cifelli* Li and Luo (2006) (see also Chen and Luo, 2012) and the eutriconodont *Yanoconodon allini* Luo et al. (2007) from the Barremian of the Yixian Formation; the eutherian *Eomaia scansoria* Ji et al. (2002) and the boreosphenidan *Sinodelphys szalayi* Luo et al. (2003) from Berriamian/Aptian boundary of the Yixian Formation; the medium-sized eutriconodont *Liaoconodon hui* Meng et al. (2011) from the Aptian of the Jiufotang Formation.

The largest known Mesozoic mammals are from the family Gobiconodontidae Jenkins and Schaff (1988). Postcranial remains *Gobiconodon ostromi* Jenkins and Schaff (1988) are reported from the Early Cretaceous of the Cloverly Formation of Montana, USA, represented by two specimens including mandibles, maxillary and other cranial fragments, parts of the vertebral column and ribs, shoulder and pelvic girdles, limb bones, but no autopod. From the Early Cretaceous of the Liaoning Province of China, postcranial remains have been found and associated to the species *Repenomamus robustus* Li et al. (2001) and *Repenomamus giganticus* Hu et al. (2005); the latter holotype, bigger in size than *R. robustus*, consists of a partial skull with complete right upper dentition, associated right mandible with complete lower dentition, and articulated postcranium with pes and manus missing; head-body length of *R. giganticus* is estimated at 42 to 68 cm.

5. Systematics and description of tracks

Complete track and trackway measurements, when available, are provided in Tables 1, 2, and 3.

5.1. Crocodylomorph tracks

Parasystematics	Systematics
	Crocodylomorpha Walker, 1970
	Crocodyliformes Hay, 1930
Ichnofamily Batrachopodidae Lull, 1904	Crocodyliformes indet.
Angolaichnus adamanticus ichnogen. et ichnosp. nov.	

Diagnosis. Narrow trackway of a small-medium sized crocodylomorph. The manus is mesaxonic, functionally tetradactyl and plantigrade, wider than longer (length is 3.0 cm, width is 3.4 cm). Manus digits are slender, with claw marks, and increase in length from digit I (1.1 cm) to digit V (1.8 cm), with a total divarication I–IV of 79.5°. The pes is mesaxonic, functionally tetradactyl and plantigrade, longer than wider (length is 5.3 cm, width is 3.7 cm). Pes digits are

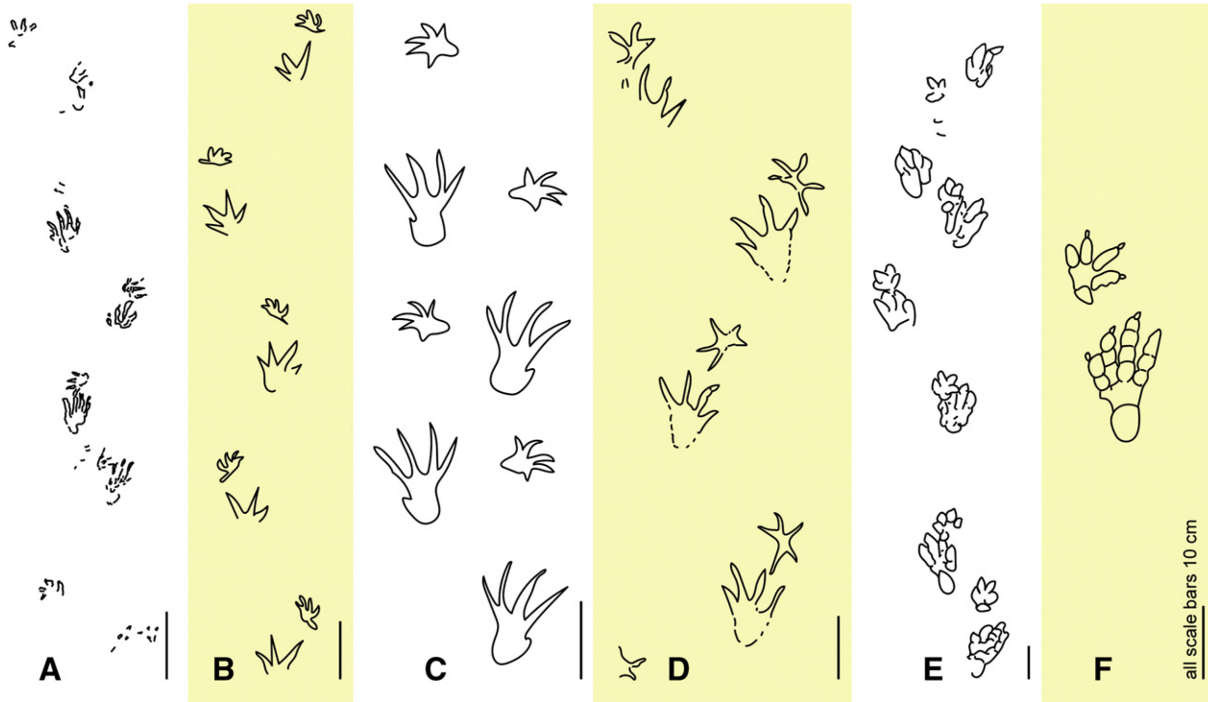

Fig. 9. Interpretative drawings of crocodylomorph trackways. (A) *Angolaichnus adamanticus* ichnogen. et ichnosp. nov. from the Early Cretaceous of Catoca, Angola; (B) trackway associated to *Batrachopus* from the Early Jurassic of France; (C) trackway associated to *Sustenodactylus* from the Early Jurassic of North America; (D) trackway associated to *Crocodylopodus* from the Jurassic–Cretaceous boundary of Spain; (E) trackway and (F) succession associated to *Batrachopus deweyi* from the Early Jurassic of North America. B–D after Lockley and Meyer (2004), E and F after Klein and Lucas (2010).

slender, with claw marks, tend to increase in length from digit I (2.6 cm) to digit III (3.0 cm), with digit IV being the shortest (2.4 cm) and a total divarication I–IV of 38°; digits II and III are slightly bent outward. Manus pace angulation of 148°, and manus pace and stride lengths of respectively 13.9 cm and 23.8 cm. Pes pace angulation is of 145°, and pes pace and stride lengths of 14 cm and 25.1 cm, respectively. Manus tracks presents an average extreme outward rotation of 118° respect to the pes.

Etymology. The generic name *Angolaichnus* is derived from Angola and *ichnus*, meaning track in Latinized Greek. The specific name *A. adamanticus* is Latin for diamond, referred to the diamond mine of Catoca where the holotype was collected.

Holotype. Trackway 1 in MGUAN-PA600 (Fig. 4).

Stratigraphic context. Congo Basin, Kalahari Group, Calonda Formation. Lower Cretaceous: mid Late Aptian age.

Locality. Catoca Diamond Mine, Catoca, Lunda Sul, Catoca, Angola (9°24′25.92″S–20°18′19.57″E).

5.1.1. Description

Slab MGUAN-PA600 bears trackway 1, comprising track 26 to track 32. Track 26 to track 30 are composite prints of one manus and one pes (Fig. 4). The manus is mesaxonic, functionally tetradactyl and plantigrade, with average Lm of 3.0 cm, Wm of 3.4 cm, and L/W equal to 0.88. Average digital angles are I–II of 29°, II–III of 17.5°, III–IV of 33.5° and the total divarication I–IV of 79.5°. Manus digits have a slender shape, with a pointed tip, due to claw marks. Manus digit length increases from digit I to digit IV with an average LI of 1.1 cm, LII of 1.2 cm, LIII of 1.5 cm, and LIV of 1.8 cm. In the two best-preserved manus prints, digit III is slightly bent medially in left manus print 29, but not in the right manus print 28. The manus presents an average extreme outward rotation of 118° respect to the pes.

The pes is mesaxonic, functionally tetradactyl and plantigrade, with average L of 5.3 cm, W of 3.7 cm and L/W of 1.43. Average digital angles are I–II of 10°, II–III of 11°, III–IV of 17°, and the total divarication I–IV of 38°. Pes digit lengths tend to increase from digit I to digit III, with digit IV

Table 1
Crocodylomorph track main measurements and ratios from slabs MGUAN-PA600 and MGUAN-PA601. Lengths and widths are in centimeters. Data not available are indicated by a hyphen (−). Average values are given for trackway-1 in slab MGUAN-PA600. ANG = pace angulation; L = track length; LI = length of digit I; LII = length of digit II; LIII = length of digit III; LIV = length of digit IV; I-II = angle between digits I and II; II-III = angle between digits II and III; III-IV = angle between digits III and IV; I-IV = angle between digits I and IV; PL = pace length; SL = stride length; TWe = external pes width; TWi = internal pes width; TWm = manus trackway width; TWp = medial pes width; W = track width.

	L	W	L/W	LI	LII	LIII	LIV	I-II	II-III	III-IV	I-IV	ANG	TW	TWe	TWi	PL	SL
MGUAN-PA600																	
Handprint	3.0	3.4	0.88	1.1	1.2	1.5	1.8	29°	17.5°	33.5°	79.5°	148°	4.0	–	–	13.9	23.8
Footprint	5.3	3.7	1.43	2.6	2.8	3.0	2.4	10°	11°	17°	38°	145°	7.0	11.6	4.6	14.0	25.1
MGUAN-PA601																	
Track-1A	7.6	4.5	1.69	3.1	3.7	4.7	3.7	10°	8°	14°	32°	–	–	–	–	–	–
Track-2	5.9	3.7	1.60	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Track-33	3.7	2.7	1.37	1.0	2.1	2.2	1.3	26°	18°	18°	62°	–	–	–	–	–	–
Track-35	5.7	3.7	1.54	2.1	2.9	3.7	3.1	6.5°	7.5°	8°	22°	–	–	–	–	–	–
Track-51	4.1	3.0	1.37	1.3	1.6	2.6	2.3	14°	15°	14°	41°	–	–	–	–	–	–
Track-62	4.7	4.1	1.15	1.6	2.4	2.9	2.1	35°	23°	21°	79°	–	–	–	–	–	–

Table 2
Sauropod trackway-3 from Catoca. Tracks measurements (in centimeters) and ratios. L = track length; W = track width.

Sauropod trackway-3	L	W	L/W
Track-1	42	51	0.82
Track-2	47	47	1
Track-3	48	45	1.07
Track-4	48	50	0.96

being the shortest: digits average measurements are LI of 2.6 cm, LII of 2.8 cm, LIII of 3.0 cm, and LIV of 2.4 cm. Digits II and III are slightly bent outward and all the digits generally present a claw mark.

Trackway 1 is narrow, with manus pace angulation of 148°, and manus pace and stride lengths of respectively 13.9 cm and 23.8 cm; pes pace angulation is of 145°, and pes pace and stride lengths of 14 cm and 25.1 cm, respectively.

Crocodylomorph tracks are present also at a lower level than trackway 1 and are preserved on the chaotically trampled surface bearing also mammaliamorph tracks MGUAN-PA601. Trackway 2 (Fig. 3B) and isolated track 33, track 35, track 51, and track 62 (Fig. 3A) are similar to the crocodylomorph morphotype described for footprints in trackway 1, with a mesaxonic, functionally tetradactyl and plantigrade pes, slender and slightly curved pes digits and a narrow digital divarication.

Trackway 2 is made of the left footprint track 1A, the right footprint track 02, and track 1B, that might be interpreted as a manus print. Tracks-1A and track 2 present an average L of 6.8 cm, a W of 4.1 cm and a ratio L/W of 1.65. Track 1A is a left footprint and the only one complete in the trackway; digit length tends to increase from digit I to digit III, with digit IV subequal in length to digit II. Digits are slightly bent outward and all the digits generally present the claw mark both on track 1A and track 02. Track 02 is poorly preserved.

MGUAN-PA601 also bears some isolated crocodylomorph tracks. The best preserved track 33, track 35, track 51, and track 62 have a mesaxonic, functionally tetradactyl, and plantigrade morphology, with an average FL of 4.6 cm, an average W of 3.4 cm, and L/W of 1.35. Digits are short, straight, distally rounded, and with claw impressions. Digit I is the shortest, digit III is the longest, and digits II and IV are subequal in size; average LI is 1.5 cm, LII is 2.3 cm, LIII is 2.9 cm, and LIV is 2.2 cm. Digits are slender and usually end with an acuminate claw mark. The footprints are narrow, with an average total divarication of 51°, while average digit divarication I–II is 20°, II–III is 16°, and III–IV is 15°.

5.1.2. Comparison and interpretation

Angolaichnus adamanticus presents an unique functional morphology of the manus, tetradactyl and plantigrade, that allows it to be classified as a new ichnogenus. Batrachipodid manus tracks are usually pentadactyl and functionality digitigrade (see Lockley et al., 2004b; Avanzini et al., 2007).

A. adamanticus can be ascribed to the ichnofamily Batrachopodidae because of the functionally tetradactyl and plantigrade pes, the foot length value (between 3.7 and 7.6 cm), and the presence of claw marks. *A. adamanticus* has a total digital divarication similar to *Batrachopus-Antipus* morphotype (<40°), with exception to tracks 33 and 62 in MGUAN-PA601, which wider total digital divarication (respectively 62° and 72°) allow them to be compared to the Early Cretaceous morphotype *Crocodylopodus*.

A. adamanticus trackway shares similarities with other known batrachopodid trackways, such as the narrowness (with a TWp about twice the pes W and a PLp 2–3 times the pes L) and a pes ANG of 145° (Lockley and Meyer, 2004). Similar to *Antipus* trackways, *A. adamanticus* has an inner width of 4.6 cm. Moreover, the peculiar extreme outward rotation of the handprint in *A. adamanticus* is distinctive of other trackways attributed to crocodylomorph ichnospecies (Fig. 9) from the Early Jurassic of North America and France, and from the Jurassic–Cretaceous boundary of Spain (see Fuentes Vidarte and Meijide Calvo, 1999; Lockley and Meyer, 2004; Klein and Lucas, 2010).

5.2. Dinosaur tracks

Two narrow-gauge dinosaur trackways, trackway 3 and trackway 4, were also found close to the chaotically trampled surface bearing mammaliamorph and crocodylomorph tracks (Fig. 5).

Trackway 3 (Fig. 6) comprised four true tracks, subcircular in shape, with no appreciable digits, and an average depth of 6–7 cm. Track average L was of 46.3 cm, W of 48.3 cm, and ratio L/W of 0.96 (see Table 2). The SL calculated between track 1 and track 3 was 172 cm, while the SL calculated between footprints track 2 and track 4 was 150 cm; average trackway SL was of 161 cm and TW_p was of 116 cm. Inside the relief of track 4 a 35 × 8 cm patch preserved skin impressions (MGUAN-PA602, Fig. 6B).

Trackway 4 (Fig. 7) comprised 12 ellipsoid tracks preserved as true tracks and undertracks, with an average SL of 75 cm and a total trackway length of about 330 cm. The best preserved footprints were tracks 8, 9, and 10, with average L of 18 cm and W of 15 cm (Figs. 10, 11).

5.2.1. Interpretation

Because of their dimensions, their morphology, and their age we interpret both trackway 3 and trackway 4 as made by sauropod dinosaur track makers. Trackway 3 trackmaker can be identified as a medium-sized sauropod, also thanks to the preservation of the skin impression.

Trackway 4 presents a poor preservation that does not allow to distinct clearly the dinosaurian group to which its trackmaker belongs. Because of its morphology and dimensions, the trackmaker might be identified in a small-sized sauropod.

5.3. Dinosaur skin impression

The preservation of skin impression is rare in most dinosaur trackways except to some degree in hadrosaurs. In sauropods, skin impression and preservation is known in *Barosaurus* sp. AMNH (Brown, 1935), *Cathetosaurus lewisi* SMA0002 (reported by Ayer, 2000:p.91 as *Camarasaurus* but see Mateus and Tschopp, 2013 reclassification as *Cathetosaurus lewisi*), *Camarasaurus lentus* CM 11338 (Gilmore, 1925) *Diplodocus* sp. (Ayer, 2000), *Haestasaurus* (="*Pelorosaurus*") *becklesii* BMNH R1868 (Upchurch et al., 2015), *Saltasaurus loricatus* PVL 4017-118 (Bonaparte and Powell, 1980), *Tehuelchesaurus benitezii* MPEF-PV 1125 Rich et al. (1999), and indeterminate titanosaur embryos PVPH-126; PVPH-130; PVPH-131 (Chiappe et al., 1998). Sauropod tracks with preserved skin impressions are more common, either with the

Table 3
Tracks measurements from Catoca. Slab MGUAN-PA601. Mammaliamorph tracks main measurements and ratios of tridactyl footprints. Lengths and widths are in centimeters. L = track length; LI = length of digit I; LII = length of digit II; LIII = length of digit III; LIV = length of digit IV; LV = length of digit V; I–II = angle between digits I and II; II–III = angle between digits II and III; III–IV = angle between digits III and IV; IV–V = angle between digits IV and V; I–V = angle between digits I and V; W = track width.

MGUAN-PA601	L	W	L/W	LI	LII	LIII	LIV	LV	I–II	II–III	III–IV	IV–V	I–V
Track-3	1.5	1.7	0.88	0.7	1.3	1.2	0.8	0.6	61°	30°	26°	55°	172°
Track-13	3.2	4.1	0.78	1.6	1.5	1.8	1.4	0.9	40°	24°	20°	31°	112°
Track-22	3.3	3.9	0.85	1.8	2.1	1.8	1.9	1.4	36°	13°	12°	25°	83°
Track-58	2.7	3.1	0.87	1.1	1.5	1.5	1.6	1.1	30°	20°	16°	17°	80°
Track-68	2.9	3.4	0.85	1.1	1.3	1.4	1.3	1.1	59°	36°	22°	34°	150°

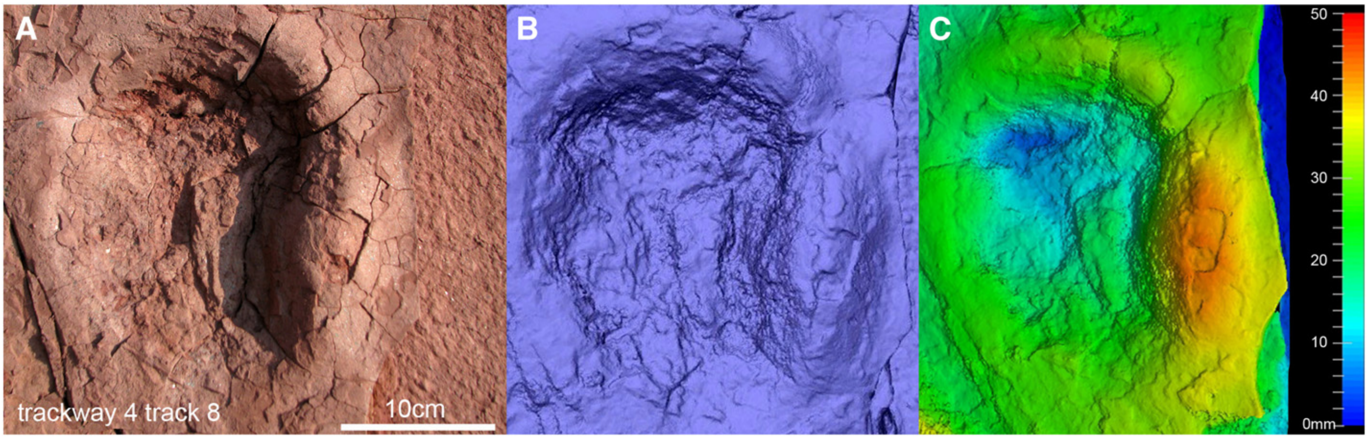

Fig. 10. Sauropod track 8 in trackway 4. (A) photograph; (B) 3D image; (C) photogrammetry derived 3D model in colour-code.

palmar impression (i.e., Mateus and Milàn, 2010) or the striation in natural infill casts resulting of the skin dragging in the mud (Czerkas, 1994; Milàn et al., 2005; Foster and Hunt-Foster, 2011).

The near-absence of preserved skin impressions in non-avian dinosaurs associated to the conservative anatomy of little variation has been the main reasons for neglecting skin for taxonomical identification within Dinosauria. Dinosaurs, including pedal skin in modern birds, consistently shows irregular non-imbricating polygonal tubercles, which differs from other archosaurs (i.e., crocodiles) that often possess regular square or rhombus non-imbricated skin tubercles, often aligned in rows.

The skin impression of the Catoca sauropod MGUAN-PA602 (Fig. 6B) shows irregular non-imbricating polygonal to round tubercles, as known in most dinosaurs (i.e., Davis, 2014).

5.4. Mammaliamorph tracks

Parasystematics	Systematics
	Mammaliamorpha Rowe, 1988
	Mammaliaformes Rowe, 1988
Ameghinichnidae Casamiquela, 1964	Mammaliaformes indet.
Catocapes angolanus ichnogen. et ichnosp. nov.	

Diagnosis. Relatively big in size tracks of a mammaliamorph. Mesaxonic, functionally pentadactyl and plantigrade track, wider than longer (length is 2.7 cm, width is 3.2 cm). Digits are short, straight, distally rounded, with no claw marks. The orientation of digits is autapomorphic, with medial digits II–IV projecting anteriorly and lateral digits I and V more divergent and anterolaterally projected. Interdigital angle I–II is 43°, II–IV is 43.5°, and IV–V is 33°. Digits II and III are the longest (1.5 cm), while digit V is the shortest (1.0 cm).

Etymology. The generic name *Catocapes* is derived from the locality of Catoca, where the type material was collected and the Latin word *pes*, meaning foot. The specific name *C. angolanus* refers to Angola.

Holotype. Specimen MGUAN-PA601 Track 13 (Fig. 8). The track MGUAN-PA601-58 (Fig. 12) is elected as paratype.

Stratigraphic context. Congo Basin, Kalahari Group, Calonda Formation. Lower Cretaceous: mid Late Aptian age.

Locality. Catoca Diamond Mine, Catoca, Lunda Sul, Catoca, Angola (9°24′25.92″S–20°18′19.57″E).

5.4.1. Description

At least 45 mammaliamorph tracks, preserved as concave epireliefs (true tracks) are distributed on slab MGUAN-PA602, a chaotically trampled bedding plane. The general state of preservation is poor. The best preserved isolated tracks are track 03, track 13, track 22, track 58, and track 68 (Figs. 3, 8, 12) (Table 3) present a mesaxonic, functionally pentadactyl, and plantigrade morphology, with an average L of 2.7 cm, an average W of 3.2 cm, and L/W of 0.8. Digits are short, straight, distally rounded, and with no claw impressions. Digit V is the shortest, digits II and III are the longest and equal in size. Average digit lengths LI of 1.3 cm, LII of 1.5 cm, LII of 1.5 cm, LIV of 1.4 cm, and LV of 1.0 cm. Medial digits (II–IV) are directed anteriorly; digit I is more divergent than digit

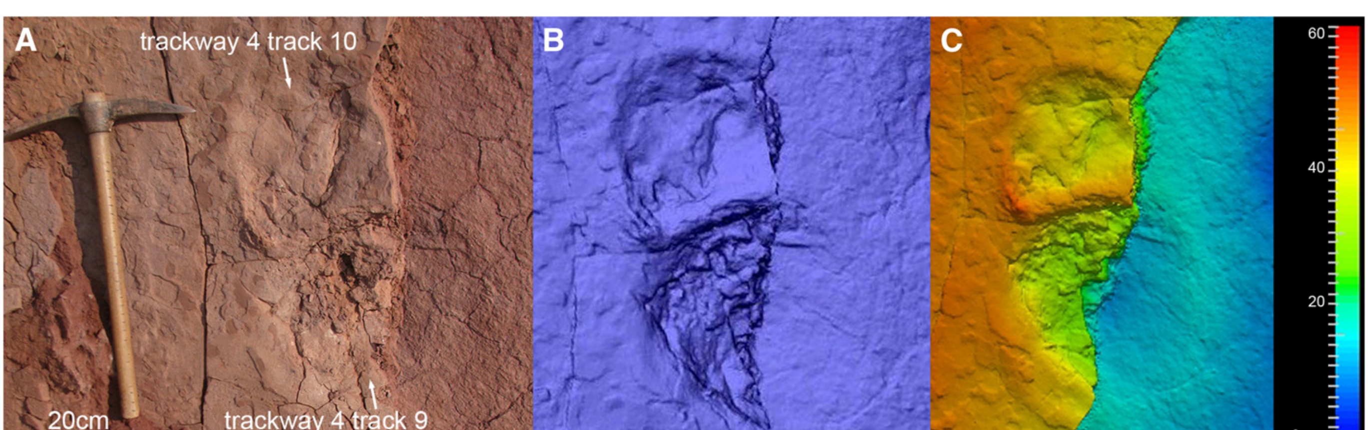

Fig. 11. Sauropod track 9 and track 10 in trackway 3. (A) photograph; (B) 3D image; (C) photogrammetry derived 3D model in colour-code.

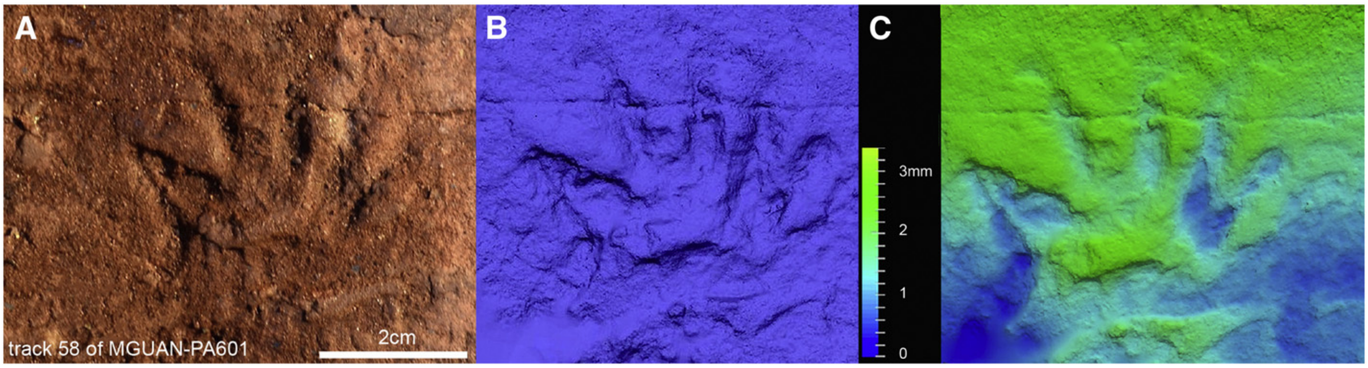

Fig. 12. *Catocapes angolanus* ichnogen. et ichnosp. nov. paratype track 58 in MGUAN-PA601. (A) photograph; (B) 3D image; (C) photogrammetry derived 3D model in colour-code.

II and is directed anterolaterally, while digit V diverges slightly from digit IV and is directed anterolaterally. The footprint average total divarication is 118°, while average digital divarications I–II is 43°, II–III is 24.5°, III–IV is 19°, and IV–V is 33°.

5.4.2. Comparison and identification

Although being comparable in size, digits length, and total digital divarication to *Ameghinichnus* Casamiquela, 1961, reported from the Hettangian of New Jersey, USA (Early Jurassic, ~200 Mya) to the Callovian-Oxfordian boundary of Argentina (Middle-Late Jurassic, ~163.5 Mya) (Casamiquela, 1964; Leonardi and Oliveira, 1990; Olsen, 2002), Catoca morphotype is not associable to any known Cretaceous mammal-like track morphotype (Ambroggi and Lapparent, 1954a; Leonardi, 1981; Sarjeant and Thulborn, 1986; McCrea and Sarjeant, 2001; Stanford and Lockley, 2002; Lockley and Foster, 2003; Stanford et al., 2007; Marzola et al., 2015), and so can be classified as a new ichnogenus: *Catocapes*. *Catocapes angolanus* resembles an exceptionally large in size Early Cretaceous gondwanan mammaliamorph, with an unique track characterized by mesaxonic, functionally pentadactyl and plantigrade morphology with external digits (I and V) more divergent and anterolaterally projecting than medial digits (II–IV) (see also Marzola et al., 2015).

6. Conclusions

The vertebrate tracks from the diamond mine of Catoca are the first tetrapod fossils ever found from the inlands of Angola, as well as the first Angolan vertebrate tracks. They were formed about 118 Ma in a shallow lacustrine environment, today represented by a small sedimentary basin, preserved inside the crater of the Catoca kimberlite pipe.

The majority of the tracks from Catoca are preserved on a chaotically trampled surface and are ascribed to the largest known mammaliamorph from the Early Cretaceous and to the new ichnospecies *Catocapes angolanus*. The mammaliamorph trackmaker from Catoca is unmatched in size by the coeval skeletal fossil record and is comparable to a modern raccoon.

One short trackway and few isolated tracks preserved on the same surface of the *C. angolanus*, plus one single long trackway from a different level are attributed to small to medium size crocodylomorphs attributed to the new batrachopodid ichnospecies *Angolaichnus adamanticus*, presenting an unique tetradactyl and plantigrade handprint.

Close to the surface bearing the mammaliamorph and crocodylomorph tracks, two dinosaurian trackways were also recognized, one assigned to a medium-sized sauropod trackmaker with stride length of 1.6 m, the other tentatively attributed to a small-sized sauropod trackmaker with a pace length of 75 cm. Inside one of the sauropod tracks, a preserved skin impression was also found.

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