

FIRST RECORDS OF CROCODYLE AND PTEROSAUR TRACKS IN THE UPPER JURASSIC OF PORTUGAL

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Abstract—The Upper Jurassic of Portugal has a rich vertebrate fauna well documented from both body and trace fossils. Although the occurrence of crocodiles and pterosaurs is well documented from body fossils, trace fossils from both groups were unknown until now. Here we describe an isolated crocodile-like track from Praia da Peralta and pterosaur tracks from the Kimmeridgian of Pedreira do Avelino, Sesimbra (Azóia Fm.) and Porto das Barcas, Lourinhã (Lourinhã Fm.). An enigmatic track suggests the possible presence of a small, tail-dragging tetrapod. Possible track-makers are suggested based on the known Late Jurassic vertebrate fauna of Portugal.

INTRODUCTION

The Mesozoic of Portugal has yielded a rich vertebrate fauna comprising fish, amphibians, turtles, pterosaurs, crocodiles, dinosaurs and mammals (Antunes and Mateus, 2003; Mateus, 2006, 2007; Mateus et al., 2006, 2009), as well as dinosaur nests, eggs and embryos (Antunes et al., 1998; Mateus et al., 1998). The trace fossil record, however, has hitherto only comprised tracks from all the major Jurassic and Cretaceous Laurasian clades of dinosaurs, including stegosaurs, sauropods, theropods, ornithomorphs and possible ankylosaur (Santos et al., 1994; Antunes and Mateus, 2003; Mateus and Antunes, 2003; Mateus and Milàn, 2008, in press).

Strangely enough, the other major Mesozoic clades, like crocodiles, pterosaurs and turtles, have so far not been documented by tracks in Portugal, although these groups are well documented from skeletal material. The nearby, Upper Jurassic deposits of Asturias, Spain, in addition to dinosaurs, have preserved abundant tracks and trackways of crocodiles, turtles, lizards and pterosaurs (García-Ramos et al., 2002, 2006; Avanzini et al., 2005, 2007; Lockley et al., 2008). Here we describe the first record of suspected crocodile and pterosaur tracks from the Mesozoic of Portugal (Fig. 1), as well as a small indeterminate trackway, possibly from a small, tail-dragging tetrapod. Institutional abbreviation ML: Museu da Lourinhã.

DESCRIPTION OF TRACKS

Crocodile or Pterosaur Tracks

A small sandstone slab containing a complete pes track and an eroded manus track was collected north of Praia da Peralta (39° 14.784'N, 9° 20.401'W) by Ben Pabst in 2001 and integrated into the Museum of Lourinhã collection by O.M. under the collection number ML801 (Fig. 2). The locality is at the top of the Amoreira-Porto Novo Member of the Lourinhã Formation (Kimmeridgian/Tithonian). The track is preserved as a natural cast on the underside of a thin, fluvial sandstone layer. The dimensions of the pedal print are 8.1 cm long and 4.9 cm at the widest across the outer digit impressions. The track is tetradactyl with impressions of three short, clawed digits, and a fourth digit without a claw trace. The cast of the digits is the most deeply protruding part of the track. The elongated “heel” area gives the track a roughly triangular appearance. The remains of the manual print are preserved in front of the pes track, but appear only as an amorphous cast, approximately 1/4 the size of the pes, and reveal very little anatomical information, except that the manus is smaller than the pes.

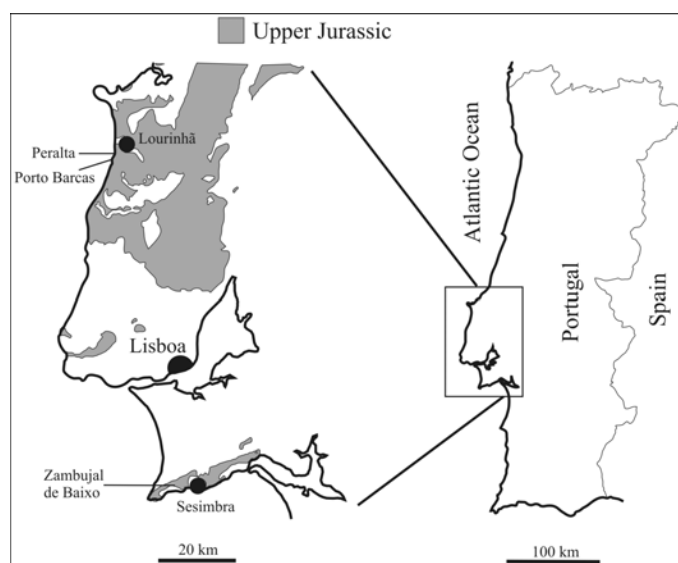


FIGURE 1. Map of Portugal with the locations of the finds indicated. The Upper Jurassic deposits are indicated by shaded areas.

Pterosaur Tracks

We report pterosaur tracks from two Late Jurassic localities: Zambujal de Baixo (Sesimbra) and Porto das Barcas (Lourinhã). A few pes and manus tracks are preserved on a rock slab at Zambujal de Baixo, at 38° 27.371N, 9° 07.297W, 161 m alt., near the Pedreira do Avelino sauropod trackway locality. The tracks are preserved in a limestone bed at the top of the Azóia Formation, dated to Kimmeridgian (Lockley and Santos, 1993; Antunes, 1990; Manuppella et al., 1999; Antunes and Mateus, 2003) (Fig. 3). Very recently, the locality of Peralta with the crocodile track also provided pterosaur tracks (work in progress).

In the rock slab (still preserved in place), several structures are interpreted as tracks (including sauropod-like and theropod-like) but are dubious. Contrary to other tracks, two clear pterosaur manus tracks are preserved as natural casts of the original track (Fig. 3). The shallow marine carbonate limestone rock slab surface is very regular, with little bioturbation, therefore any unusual form is strikingly visible. The positive identification as pterosaur manus prints is based on the general shape of a pterosaur manus (see Mazin et al., 2003 for a general overview of pterosaur tracks): long third digit oriented posteriorly, short second

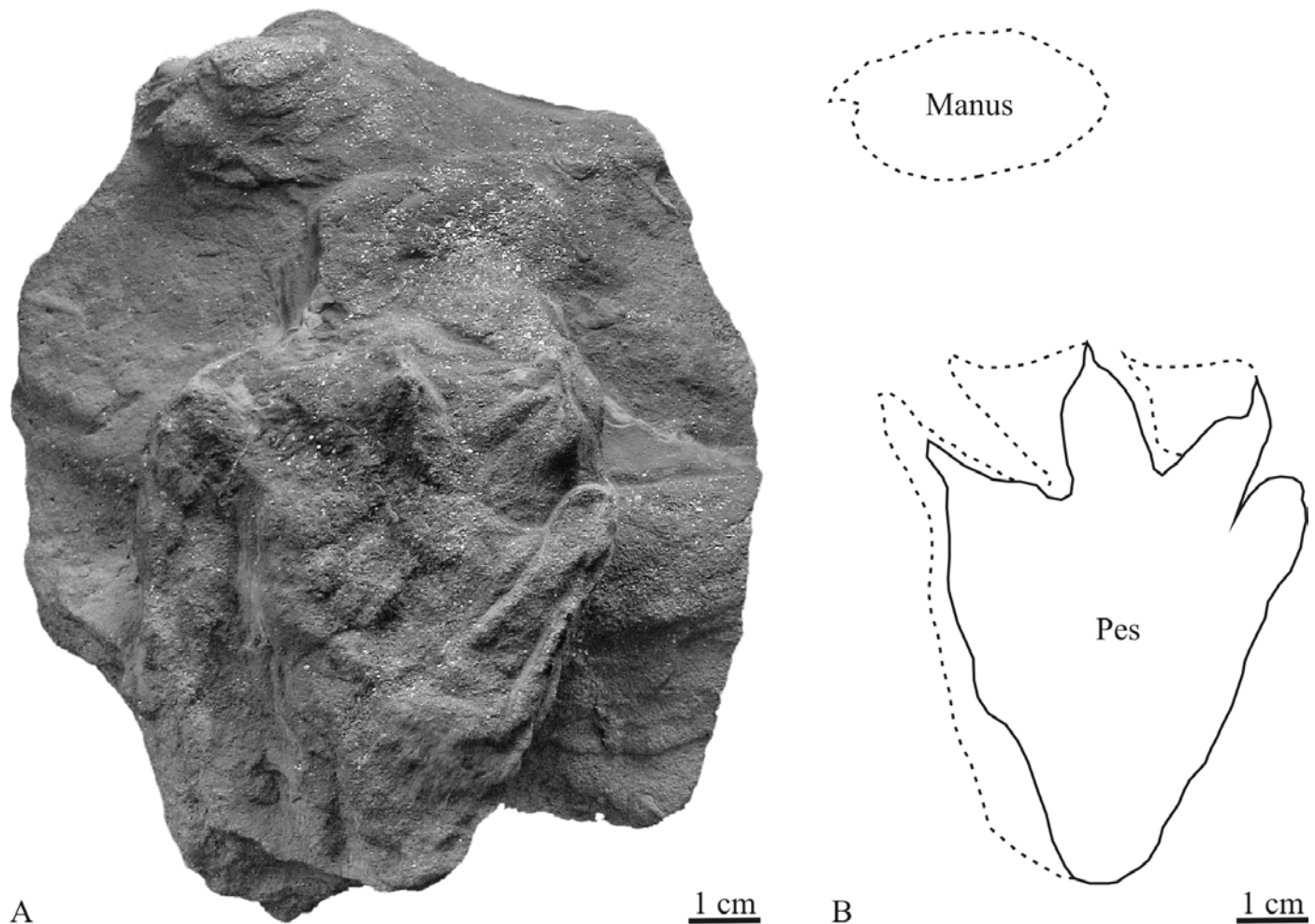


FIGURE 2. Crocodile pes and manus track found at Peralta, near Lourinhã. **A**, Sandstone slab containing the natural cast of a complete pes and a partial manus imprint (ML 801). The pes is deeply imprinted in the substrate and has slid sideways through the mud. The digits are the most deeply impressed parts. The manus imprint is eroded and reveals no anatomical details. **B**, Interpretive drawing.

digit facing posterolaterally, short first digit oriented lateroanteriorly, and medial rim curving outwards (Fig. 3). The two manus tracks are aligned as expected in a trackway, but no other elements can be positively ascribed to the same trackmaker.

The long axis of the two manus tracks measures 85 mm and 75 mm, and due to the morphology of the tracks, they can be assigned to the ichnogenus *Pteraichnus* (see Mazin et al., 2003). A few other poorly preserved tracks are visible on the same surface. A pes track is 24 cm long and 11 cm wide with three very long and thin digits. It may be interpreted as an incompletely preserved crocodile track or even a theropod track. A few other tracks from the locality seem to have been produced by the same trackmaker but with long drag marks from the toes.

A loose sandstone slab found at Porto Barcas (39° 14.236'N, 9° 20.241'W, 159 m. alt.) near Lourinhã (Sobral Member, Lourinhã Fm., Lower Tithonian) has preserved the natural cast of a manus print and the shallow cast of three digits of a pes (Fig. 4). Until more complete material is found at the locality, we tentatively assign these tracks to *Pteraichnus*.

Small Tail-dragging Tetrapod?

A small slab of sandstone (ML455) from Peralta (39° 14.678'N, 9° 20.279'W; Sobral Member, Lourinhã F, Lower Tithonian), near Lourinhã, bears a sinuous track comparable with tail drag marks in Paleozoic slabs shown by Martin and Peyson (2005, fig. 4) and Haubold et al. (2005), but with much less distinct autopodium tracks. The slender

furrow runs for approximately 45 cm across the surface of the slab (Fig. 5). The track preservation is very poor, and the possibility of it being an inorganic tool mark or a fish trail (i.e., *Undichna*) cannot be definitively excluded.

DISCUSSION – THE POSSIBLE TRACKMAKERS

Crocodyles

Crocodyle pes tracks bear strong resemblances to pterosaur pes tracks, in that they are both plantigrade, elongated, tetradactyl with a roughly triangular outline and have the greatest width across the digit impressions. Confusion between these two kinds of tracks is possible when footprints are badly preserved. However, the position of the manus track relative to the pes track is different between crocodyles and pterosaurs, and the morphology of the pterosaurian and crocodylian manus differs significantly. In crocodyles, the manus gait width equals the pes gait width, whereas in pterosaurs the manus gait width exceeds that of the pes gait width up to three times (Mazin et al., 2003; Kubo, 2008). In the specimen from Peralta, the remains of the manus track in close proximity to the pes print supports the interpretation of the track as crocodylian (Fig. 2). In addition, the Peralta pedal track shows relatively short and stout digits that are typical of crocodylian feet as reported by Foster and Lockley (1997) for the crocodylian ichnogenus *Hatcherichnus*, and by Pasqual Arribas et al. (2004) from large unnamed crocodylian foot-

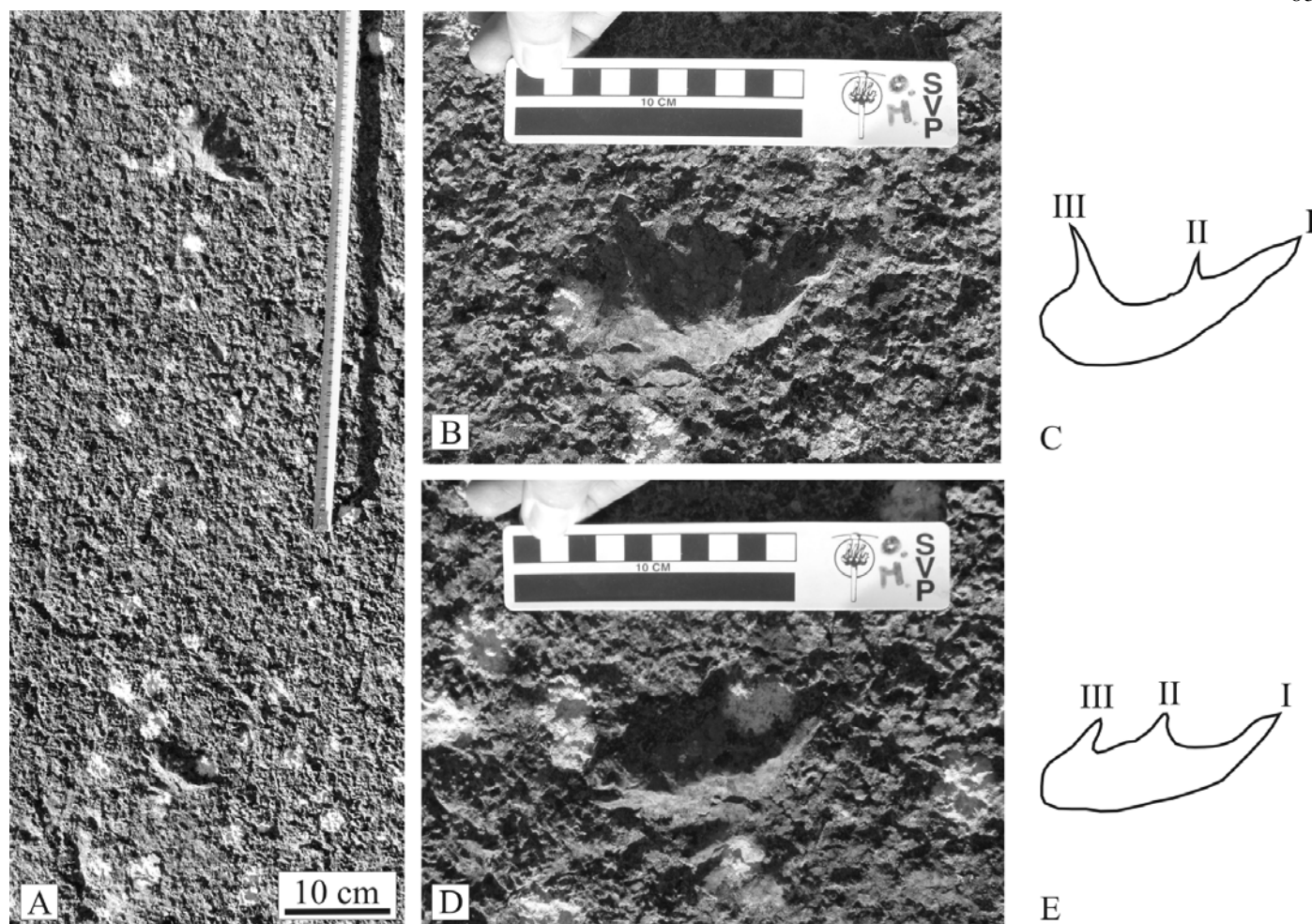


FIGURE 3. **A**, Two consecutive pterosaur manus tracks found at the Pedreira do Avelino tracksite, at Zambujal de Baixo, near Sesimbra. **B-C**, Closeup photo and interpretive drawing of the upper manus print. **D-E**, Closeup and interpretive drawing of the lower track in the trackway. Both tracks show impressions of short, forward-oriented digits II and III, and an elongated, laterally-directed impression of digit I. These tracks remained in situ.

prints. Similar tracks, but with better preservation of the digits, were reported by Fuentes-Vidarte and Meijide-Calvo (1999) from the Tithonian-early Berriasian of Spain and Portugal (Avanzini et al., 2007). Unlike the Portuguese material, the Spanish tracks clearly show four long digits on the pes and a pentadactyl manus with widely diverging digits. However, future finds of additional material, and preferably in situ trackways, will help to confirm the status of the Portuguese tracks as crocodylian.

Thus far, about nine crocodyliforms are known from the Late Jurassic of Portugal (Schwarz and Fechner, 2004), and are thus possible candidates trackmakers:

- Lisboasaurus estesi* Seiffert, 1973
- Lusitanisuchus mitrocostatus* Seiffert, 1975
- Teleosauridae: *Machimosaurus hugii*
- Goniopholididae: *Goniopholis* cf. *simus*,
- Goniopholis baryglyphaeus* Schwarz, 2003
- Bernissartiidae: cf. *Bernissartia*
- Atoposauridae: *Theriosuchus guimarotae* Schwarz and Salisbury 2005
- Theriosuchus* sp. indet. (*Macellodus* sensu Seiffert, 1973), cf. *Alligatorium*
- Undescribed ziphodont taxon (ML739)
- Metriorhynchidae: *Metriorhynchus* sp.

Lisboasaurus, *Theriosuchus*, *Alligatorium* and *Bernissartia* are small-sized crocodyles (<40 cm), so they cannot be regarded as possible

trackmakers of the Peralta crocodile track if crocodylian. With a pes length of 8.1 cm, *Goniopholis* is a larger animal but still smaller than the trackmaker. This leaves *Machimosaurus hugii* and *Metriorhynchus* sp. as the only plausible trackmaker candidates according to the size of the feet. However, the autopodium of *Machimosaurus* is unknown, and the related teleosaurid thalatosuchians *Mystrisaurus*, *Pelagosaurus*, *Steneosaurus* and *Teleosaurus* were mainly marine and had paddle-like limbs (Mueller-Töwe, 2006). This makes *Metriorhynchus* the most likely trackmaker candidate for the Peralta track.

Pterosaurs

Pterosaurs are not that well known from the Upper Jurassic of Portugal. Thus far, only two taxa ascribed to aff. *Rhamphorhynchus* sp. and aff. *Pterodactylus* sp. are known from single finds of isolated teeth and bones in the Guimarota coal mine (Weichmann and Glory, 2000; Mateus, 2006).

Small Tetrapods

Based on what is known from the Late Jurassic skeletal record, the possible candidates for the small tail-dragging tetrapods were the amphibians Albanerpetontidae *Celtesaurus*, the Squamata scincoids such as *Saurillodon*, the anguimorphs *Parviraptor* and *Dorsetisaurus*, the choristoderan *Cteniogenys*, and small atoposaurid crocodyles like *Theriosuchus* (Mateus, 2006). The tail trace from Peralta is insufficient for a more resolved classification. As a possible trackmaker for the small

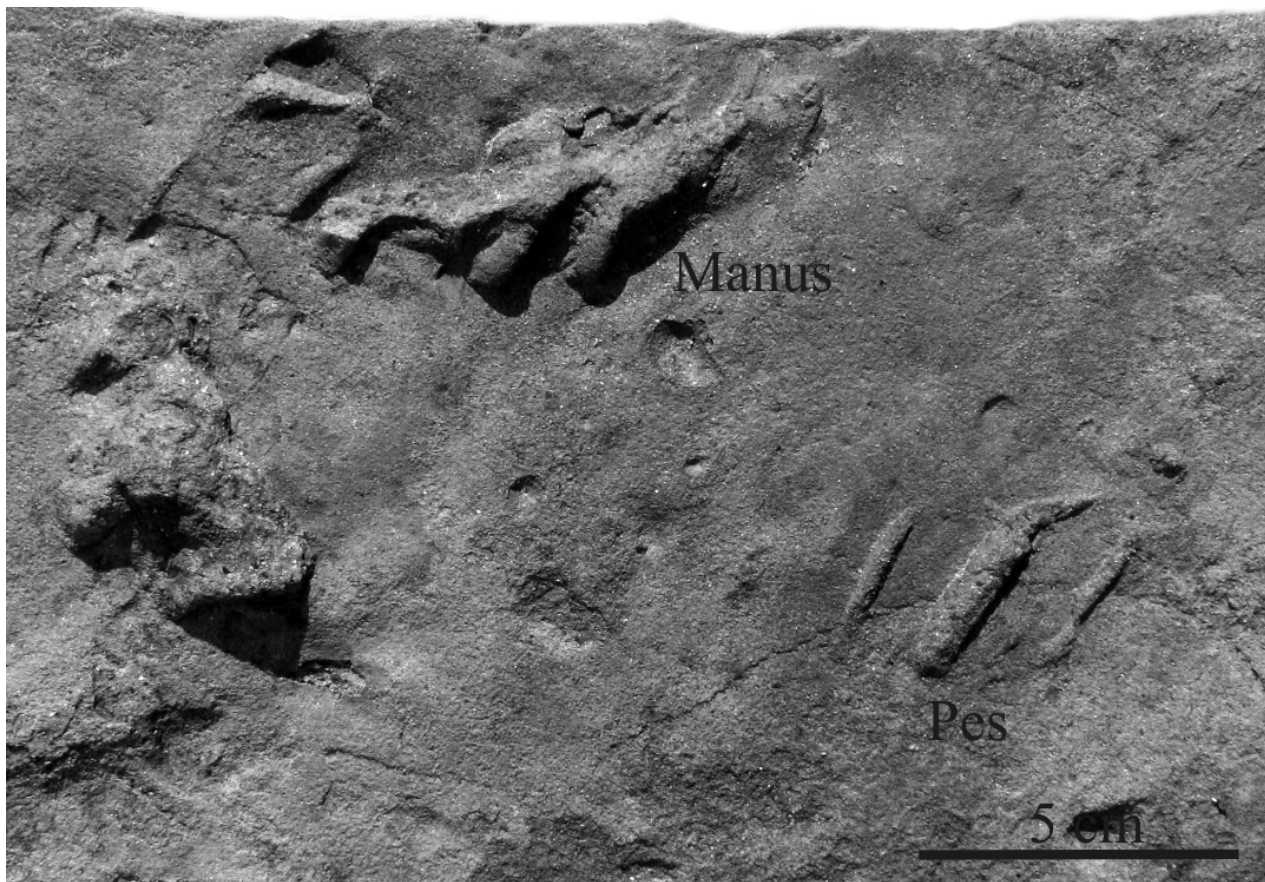


FIGURE 4. Sandstone slab containing the natural casts of pterosaur manus track and a partial pes track from Porto das Barcas (ML 1402). The tracks were found at 39°14' 13.71"N, 9°20'14.40"W, 159 m. alt.

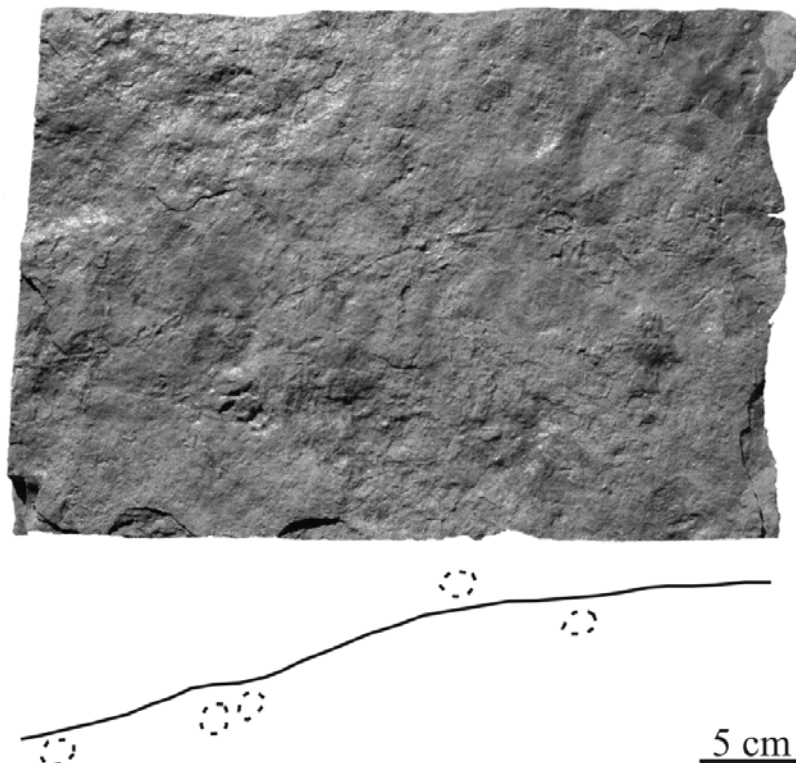


FIGURE 5. Sinusoidal traces found on a mudstone slab (ML 455). This trace is interpreted as a possible tail trace from a small, tail-dragging tetrapod. A few faint impressions on each side of the trace are interpreted as badly preserved traces of the autopodia.

tail dragging trace (Fig. 5) we can exclude dinosaurs and adult crocodyles as possible trackmakers and leave open the possibility of it having been made by a member of Caudata (salamander-like tetrapods), Squamata or a very small or juvenile crocodile. Albanerpetontids are too small. The closest match to the morphology of the trace comes from tracks and trackways of salamanders (Peabody, 1954, 1959).

CONCLUSION

A manus and pes track found on a loose sandstone slab from the Upper Jurassic Lourinhã Formation at Praia da Peralta, near Lourinhã is here putatively interpreted as crocodylian. Two consecutive pterosaur manus tracks are described from the Upper Jurassic Pedreira do Avelino

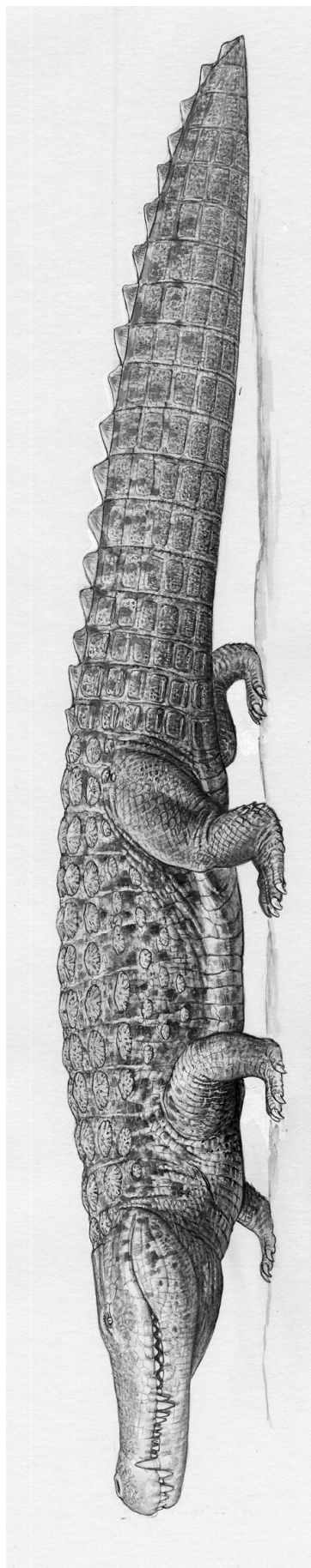
tracksite near Sesimbra, and a manus and partly preserved pes tracks are reported from the Upper Jurassic Lourinhã Formation at Porto das Barcas, near Lourinhã, and both are interpreted as pterosaurian. A sinusoidal, enigmatic trace from Peralta could represent the track of a small tail dragging tetrapod, possibly a salamander-like amphibian. This is the first ichnological evidence of crocodyles, pterosaurs and small, tail-dragging tetrapods from the Mesozoic of Portugal.

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Flesh reconstruction of *Deinosuchus* in left lateral view. Art by John Sibbick.