Evolution of the Semi-aquatic Lifestyle in Archosaurs – Evidence from the Tetrapod Footprint Record

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ABSTRACT

The semi-aquatic lifestyle in archosaurs is documented by skeletal remains of specialized ?proterosuchids, phytosaurians, poposauroids, crocodylomorphs and avemetatarsalians from the Late Permian–Early Triassic to the present. Correspondingly, tetrapod footprints of the ichnogenera Apatopus *(phytosaurs),* Batrachopus *and* Crocodylopodus *(Crocodylomorpha), as well as those of modern crocodylians, preserve adaptive features that provide evidence of a semi-aquatic lifestyle and preceding terrestrial habitus. Ichnofossils and body fossils have similar stratigraphic ranges:* Apatopus*/semi-aquatic phytosaurs (Late Triassic);* Batrachopus*/terrestrial crocodylomorphs (Late Triassic–Early Jurassic); footprints/skeletons of semi-aquatic crocodylomorphs (Jurassic–Recent). The earliest phase of phytosaurian evolution, including a presumed terrestrial stage in the Early–Middle Triassic, is unknown. Morphologically and temporally, the chirotheriid ichnogenus* Synaptichnium *from the Early–Middle Triassic, matches hypothetical footprints of terrestrial phytosaurians. Features shared by* Synaptichnium *and the phytosaur ichnotaxon* Apatopus *are: 1) elongate pes imprints, digits increasing in length from I to IV, digit IV longest, 2) extended, antero-laterally directed digit V, 3) relatively large manus, digit III longest and 4) relative position/orientation of imprints. Differences are the compact metatarsal-phalangeal axis and thick phalangeal pads in* Synaptichnium *due to cursorial habits, whereas* Apatopus *has a crocodilian appearance. Furthermore, the scarcity of* Apatopus vs. *abundance of swim traces is considered to reflect an aquatic environment and poor preservation potential. The footprint record thus provides important evidence of the evolution of terrestrial to semi-aquatic lifestyles in more than one group of Mesozoic archosauromorphs.*

INTRODUCTION

Direct interpretation of the skeletal record suggests that the Mesozoic evolution of semi-aquatic lifestyles took place in several different archosaur groups such as the ?proterosuchids, phytosaurians, poposauroids, crocodylomorphs and avemetatarsalians (Nesbitt, 2011; Ibrahim *et al.*, 2014; but *see* Botha-Brink and Smith, 2011 and Ezcurra *et al.*, 2013, who advocated a terrestrial lifestyle of proterosuchids). Amphibians, reptiliomorphs and therapsids dominated Late Permian tetrapod communities in aquatic habitats such as lakes and rivers. In contrast, archosaurs, such as proterosuchids, were relatively minor components of lake and river biotas until well into the Triassic, but are especially evident during the Late Triassic, when semi-aquatic phytosaurs were abundant and widespread, feeding on fish and other prey. In their overall morphology and inferred lifestyle, phytosaurs resembled modern crocodilians (*e.g.*, Hunt, 1989). However, in contrast, during the Late Triassic, crocodilians were small cursorial animals fully adapted to a terrestrial life (Lockley *et al.*, 2010). Based on their body fossil record, the first semi-aquatic and aquatic crocodilians occurred in the Jurassic.

Anatomical adaptations to a semi-aquatic lifestyle in phytosaurians and crocodylians involve elements of the skull as well as the locomotor apparatus. This suggests that evolutionary developments of the autopodia as well as different habitats might be reflected in the morphology of footprints. The wide distribution and abundance of fossil footprints, compared with fossil skeletal remains, offers a potential for the study of the evolution of the semi-aquatic lifestyle. Here, we compare the footprints of selected semi-aquatic archosaurs – phytosaurs and crocodylomorphs – with those of cursorial, terrestrial forms. Our conclusion is that studies of evolution from terrestrial to semi-aquatic habitus in archosaurs should employ the footprint record to assist in the understanding of these developments.

LIFESTYLE OF ARCHOSAURS – INDICATIONS FROM THE FOOTPRINT RECORD

THE TRIASSIC PHYTOSAUR ICHNOTAXON *APATOPUS LINEATUS*

The ichnogenus *Apatopus* (Fig. 1d–g) was erected by Baird (1957) based on material from the Passaic Formation (Norian) of the Newark Supergroup of New Jersey, USA. It was originally described by Bock (1952) as *Otozoum lineatus* and thereafter identified on other Triassic footprint surfaces in North America, Europe, North Africa and Southeast Asia (*see* Klein and Lucas, 2013 for a complete review). These are medium- to large-sized imprints of a quadruped. The plantigrade to semi-plantigrade, pentadactyl pes imprint has an elongate shape with slender digit traces, increasing in length from I to IV, that of digit IV being longest. The trace of digit V is straight and antero-laterally extended. Sharp, robust claws are visible on digits I–IV. The associated pentadactyl manus imprint, which is positioned anterior to the pes imprint, is short and rounded, with the trace of digit III being longest. Trackways are moderately broad, with strictly outward-rotated pes and less outward-rotated manus imprints

In the past, *Apatopus* footprints were attributed to different kinds of archosaurs, such as rhynchosaurs, trilophosaurids and phytosaurs (*see* Klein and Lucas, 2013). However, Padian and Pchelnikova (2010) demonstrated that the phytosaur interpretation is the most convincing one. As noted above, phytosaurs were crurotarsan archosaurs with a semi-aquatic lifestyle similar to modern crocodylians. Their skeletons are known from Triassic deposits in North America, Europe, Turkey, North Africa, Madagascar, India and South America (Lucas, 2010).

Baird (1957) illustrated *Apatopus lineatus* with distinct web traces between digits however, based on our own investigations of the type material, the presence of webbing could not be confirmed. Also, all other material referred to the ichnogenus from different localities does not show webbing (Klein and Lucas, 2013). Remarkable, however, is the general morphology of imprints and digit traces that often show elongated sinuous scratches or a transition to swim traces (*see* below). A striking feature is also that in most *Apatopus* specimens, anatomical details such as the traces of phalangeal pads are rather indistinct or faint (Fig. 1d–g). This might partly be due to preservational factors and different sediment consistency, indicating subaqueous formation of the footprints in a moist substrate. Alternatively, this could be interpreted as an anatomical feature that reflects the trace-maker's semi-aquatic lifestyle. In the pes of tetrapods, cushioning phalangeal pads protect the toe bones from ground reaction forces while walking, thereby stabilizing their normal function. It, therefore, can be expected that phalangeal pads are thicker and more distinctly developed in tetrapods that have a terrestrial lifestyle, than in aquatic or semi-aquatic forms, such as amphibians or extant crocodilians. However, this cannot be demonstrated at present and has to be tested by a larger sample of tetrapod feet. The pes of a land-dwelling komodo dragon (Fig. 2a and b) shows well-defined, thick pads, whereas in the semi-aquatic modern alligator (Fig. 1a–c), these are rather faint and indistinct, similar to those displayed in *Apatopus*. In the morphology of the latter, both preservational and anatomical components may overlap. Finally, the development of phalangeal pads and morphology of the plantar/palmar surface is linked to function and reflects limb kinematics and the distribution of load over the foot during progression (Farlow and Pianka, 2000; Farlow and Elsey, 2010).

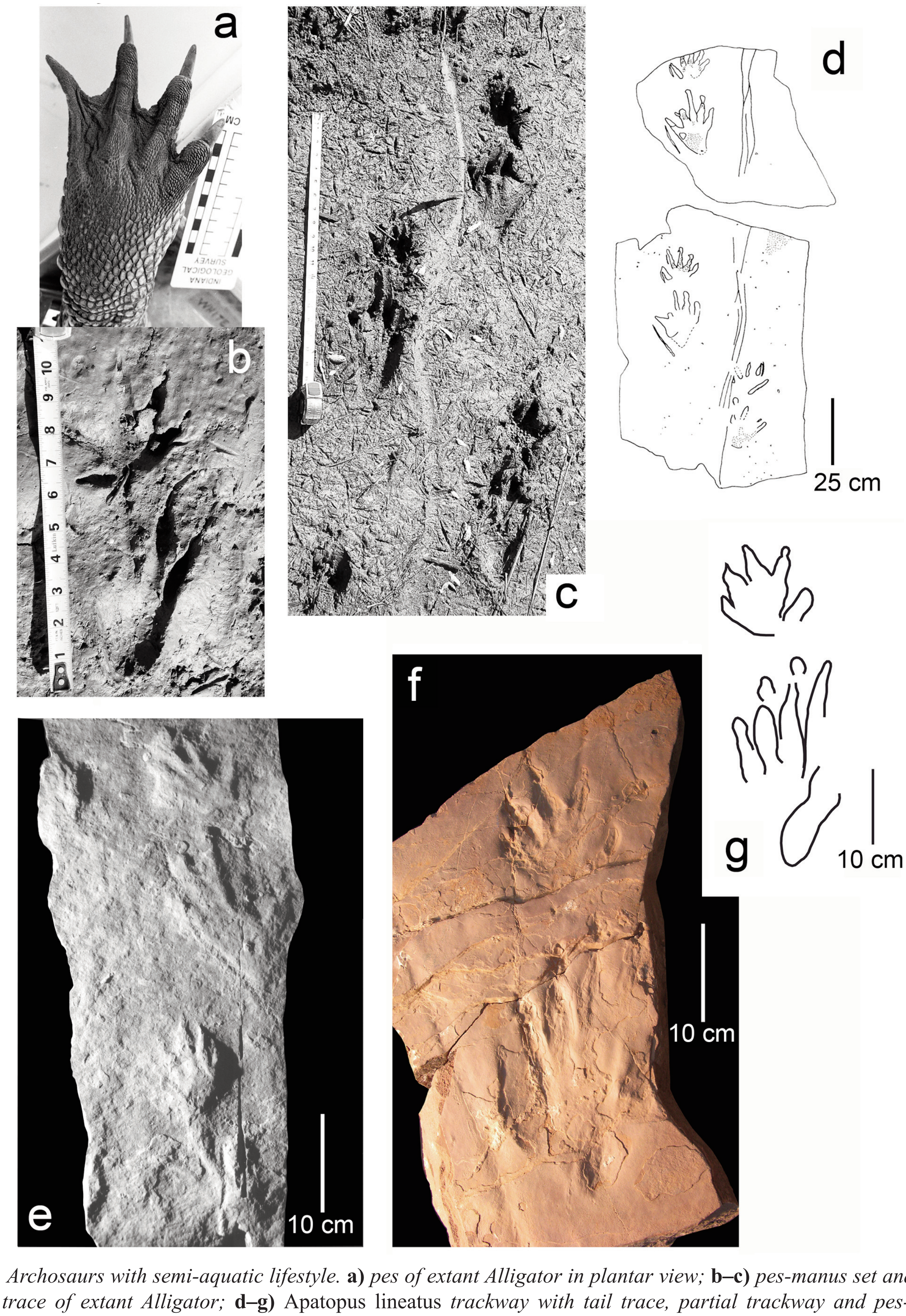

Figure 1. *Archosaurs with semi-aquatic lifestyle.* **a)** *pes of extant Alligator in plantar view;* **b–c)** *pes-manus set and trackway with tail trace of extant Alligator;* **d–g)** Apatopus lineatus *trackway with tail trace, partial trackway and pes-manus set (coloured photograph and sketch) from the Late Triassic of North America* **(d)**, *Germany* **(e)** *and Morocco* **(f–g)**. *Notice faint imprints and pes anatomy with weakly developed phalangeal pads. [***a–c)** *from Farlow and Elsey (2010);* **d)** *from Foster* et al. *(2003);* **e)** *from Klein and Lucas (2013);* **f–g)** *from Lagnaoui* et al. *(2012).]*

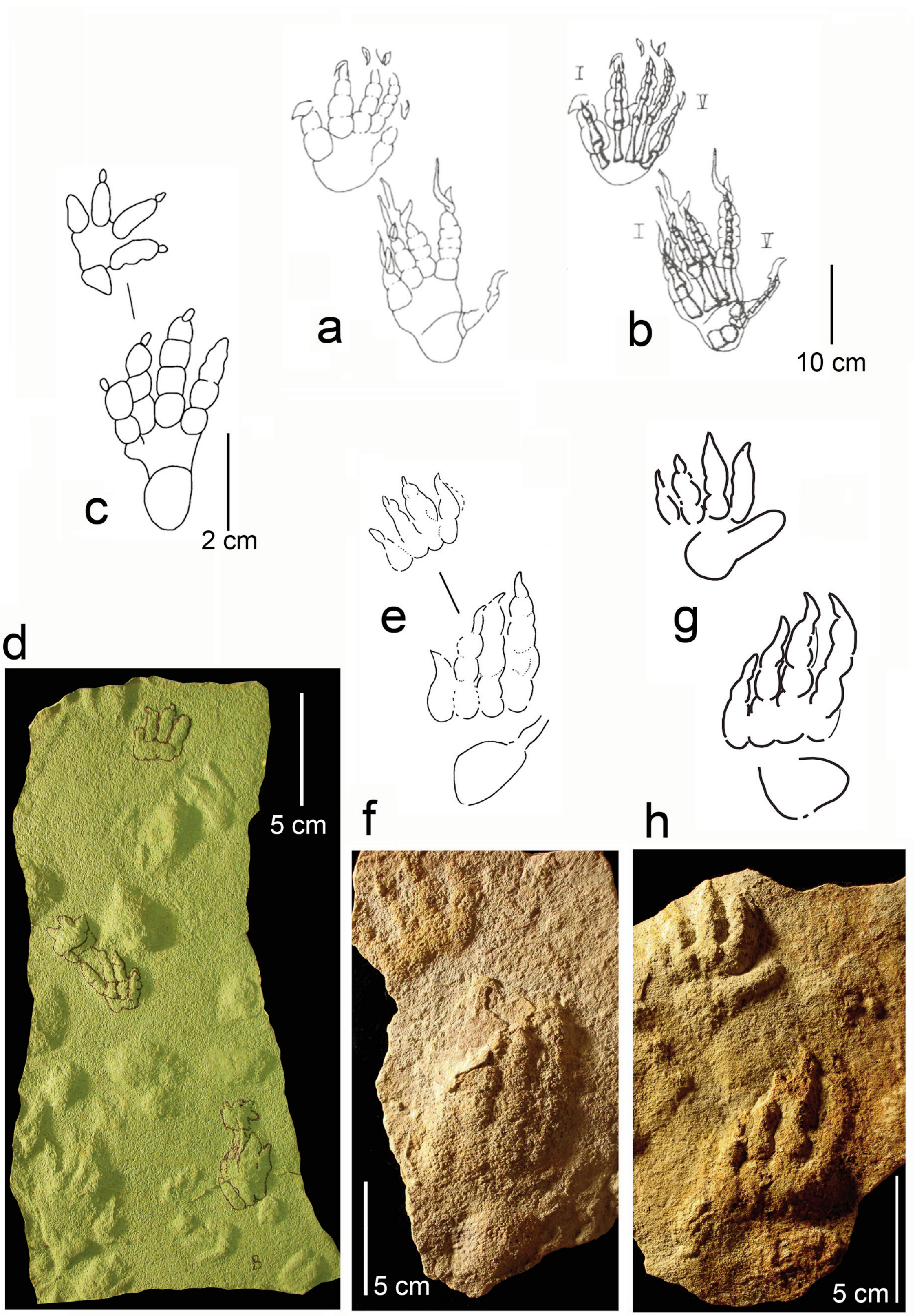

Figure 2. *Archosaurs with terrestrial lifestyle.* **a–b)** *pes-manus imprints and superimposed autopodial skeletons of a Komodo dragon in plantar view;* **c–d)** *footprints of crocodylomorphs (*Batrachopus*) from the Early Jurassic of North America;* **e–h)** *footprints of basal archosaurs from the Middle Triassic of Germany (*Synaptichnium*). Notice well-developed phalangeal pads. [***a–b)** *from Padian and Olsen (1984);* **c)** *from Olsen and Padian (1986);* **e–h)** *from Klein and Haubold (2004).]*

CROCODYLOMORPH FOOTPRINTS

Footprints of basal crocodylomorphs are represented by the ichnogenus *Batrachopus* (Fig. 2c and d) from the latest Triassic–Jurassic and possibly from Cretaceous deposits of North America, South America, Europe and southeastern Asia (Klein and Lucas, 2010a, 2013). These are small, tetradactyl footprints with small claws, sometimes resembling chirothere tracks lacking a fifth pedal digit. In the pes, the trace of digit III is longest, followed by IV, II and I. The manus imprint is pentadactyl, with the trace of digit III being longest. Trackways show a strongly outward-rotated manus imprint compared with the pes imprint and along digit III. *Batrachopus* can probably be attributed to small crocodylomorphs with a terrestrial lifestyle, such as *Protosuchus*, well known from nearly complete skeletal material (Colbert and Mook, 1951). Well-defined robust phalangeal pads in the imprints support this (*see* above).

Crocodylopodus refers to the footprints of possible semi-aquatic, small crocodylomorphs from the Late Jurassic of Spain. A semi-aquatic lifestyle is indicated by occasional swim traces that can be attributed to the same trackmaker (Avanzini *et al.*, 2010).

CHIROTHERIIDS

These are pentadactyl pes and manus imprints of Triassic archosaurs, characterized by a compact anterior digit group I–IV and a postero-laterally positioned and strongly reduced digit V that can be everted and recurved in a thumb-like manner. Trackways are narrow, with more or less outward-rotated imprints. Digit proportions and trackway pattern are used to differentiate the ichnogenera *Protochirotherium*, *Synaptichnium*, *Isochirotherium*, *Brachychirotherium* and *Chirotherium*, which include numerous ichnospecies. For consideration here, *Synaptichnium* (Fig. 2e–h) is of special importance. The pes imprints show digit proportions with digit traces I–IV increasing in length, and IV being longest. The trace of digit V is straight and antero-laterally elongated. Trackways show strongly outwardly rotated pes imprints and less outwardly rotated manus imprints.

Chirotherian footprints have well-defined, thick phalangeal pads similar to those seen in modern analogues of terrestrial cursorial tetrapods (compare Fig. 2a and b, and e–h). They are the most common and widespread tetrapod footprints of Triassic age (Klein and Lucas, 2010b).

ENVIRONMENTAL EFFECTS

Only rare co-occurrences of semi-aquatic *Apatopus lineatus* with chirotheriid and other footprints of terrestrial archosaurs are known. This is the case, for example, on the surface that preserves the type material of *A. lineatus* from the Passaic Formation (Norian) of Milford, New Jersey, where *Brachychirotherium parvum* is also preserved (Baird, 1957). Furthermore, in the Timezgadiouine Formation of the Argana Basin of Morocco, very few chirotheriid imprints could be documented in a succession of different track-bearing layers dominated by footprints of *Apatopus* and *Rhynchosauroides* (Fig. 1f and g). In contrast, surfaces with rich terrestrial tetrapod footprint assemblages in the same stratigraphic unit mostly lack *Apatopus* (Lagnaoui *et al.*, 2012). A similar pattern can be observed in the Stuttgart and Hassberge formations (Carnian) of Germany (Klein and Lucas, 2013). In these units, *Apatopus* occurs on surfaces forming the bottoms of thick sandstone channel fills (Fig. 1e), whereas thin-layered, fine-grained overbank deposits that have abundant *Brachychirotherium* and *Grallator* footprints, lack *Apatopus*. In the Chinle Group of North America (Redonda Formation), large surfaces and trampled layers that have thousands of archosaur footprints, such as *Brachychirotherium*, *Evazoum* and *Grallator*, thus far contain no *Apatopus* footprints despite the fact that phytosaur skeletal material is well known from this unit (Lucas *et al.*, 2010; Spielmann and Lucas, 2012).

Generally, *Apatopus* is a rare component in the global Triassic footprint record, although phytosaur skeletons are common and widely distributed. This points to a preservational bias due to the semi-aquatic lifestyle of phytosaurs and the minor preservation potential of their footprints associated with water-bodies. Only during their stay on land, along the shorelines, might phytosaurs have left distinctly preserved trackways that occasionally crossed those of other archosaurs. This view is supported by the presence of swim traces that have been assigned to buoyant phytosaurs touching and scratching the floor of a watercourse with their digits (Lockley and Milner, 2006). These kinds of archosaur swim traces were originally documented from Jurassic dinosaurs, and have been named *Characichnos* (White and Romano, 2001). Similar observations have been made, for example, in footprints of possibly semi-aquatic crocodylomorphs from the Late Jurassic of Asturia (Spain) (Avanzini *et al.*, 2010).

Phytosaur footprints are rare, but their bones are common in Upper Triassic non-marine rocks. This bias against preservation of their footprints is largely due to their semi-aquatic lifestyle. Significantly, a recent review of the fossil footprint record of crocodylomorphs by Lockley *et al.* (2010) identified less than 20 records in Jurassic and Cretaceous strata globally, whereas there are thousands of records of crocodylomorph bones in strata of these time periods. Indeed, a consideration of all of the crocodylomorph tracks documented in a volume devoted to this subject (Milàn *et al.*, 2010) indicates that most of these traces can be called ‘swim tracks', many of which are referred to the ichnogenus *Characichnos*. The body fossil record of crocodylomorphs thus indicates an early (latest Triassic–Early Jurassic) terrestrial phase, well documented by both footprint and skeletal material, followed by evolution of the semi-aquatic habitus during the Jurassic, which is also well documented by both footprints and bones.

EVOLUTION OF THE SEMI-AQUATIC LIFESTYLE IN ARCHOSAURS

The ichnological and body fossil record from the Mesozoic indicates the evolution of a semi-aquatic lifestyle in several different archosaur groups (Fig. 3). Based on the body fossil record, the early evolution of Phytosauria remains unknown. In a recent phylogenetic analysis of archosaurs by Nesbitt (2011), Phytosauria was removed from the crown-group, resulting in a new definition of Crurotarsi, now comprising Phytosauria as well as crocodile- and dinosaur-bird-line groups. Nesbitt (2011) considers that the long ghost-lineages of Phytosauria range back to the Middle or even Early Triassic. This may suggest a terrestrial stage preceded the evolution of known semi-aquatic phytosaurs. Up to now, no skeletal evidence exists to prove this, though the footprint record evidences a possible link. It has to be noted here that recent studies provide evidence of a possible secondarily terrestrial re-adaptation of the phytosaur *Nicrosaurus kapffi* from the Germanic Basin (Kimmig, 2013).

Archosaur footprints such as the chirotherian ichnogenus *Synaptichnium* show an overall morphology and trackway pattern similar to the phytosaur ichnotaxon *Apatopus lineatus* (compare Figs. 1d–g and 2e–h): 1) elongate, slender pes imprint with the digit traces increasing in length, that of digit IV being longest, 2) trace of digit V anterolaterally elongated, 3) manus imprint relatively large and with similar shape and digit proportions, 4) trackways relatively broad compared with other chirotherians, with strong outward rotation of the pes imprint and less outward rotation of the manus (*see* above). *Synaptichnium* footprints could thus (at least, in part) represent basal Phytosauria adapted to a terrestrial lifestyle based on both their morphology and their stratigraphic range (Early and Middle Triassic; Fig. 4).

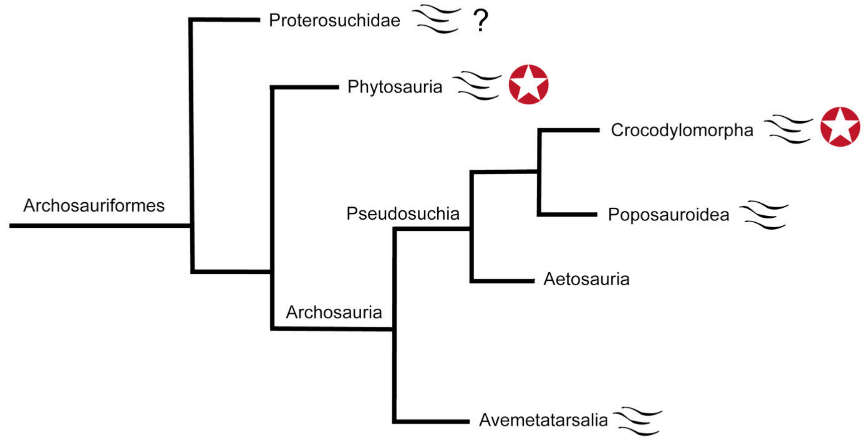

Figure 3. *Phylogenetic relationships of archosaurs with position of semi-aquatic groups (wave icon) and footprints (asterisk) discussed in this paper; simplified from Nesbitt (2011).*

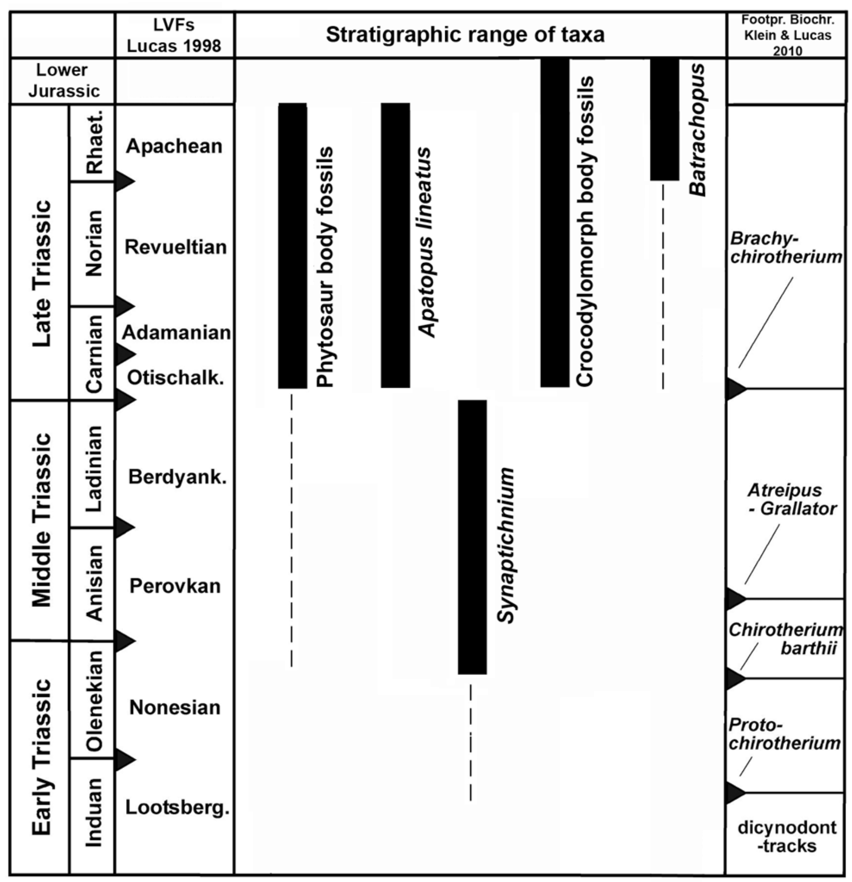

Figure 4. *Stratigraphic range of archosaur body fossils and footprints discussed in this paper;* after *Klein and Lucas (2010a, b).*

Similar evolutionary developments and a correspondence between the body and ichnofossil record can be demonstrated in crocodylomorphs between the Late Triassic–Jurassic and the Cenozoic, where skeletons of small terrestrial forms are coeval with the footprint ichnogenus *Batrachopus* and the association between semi-aquatic modern crocodylians and their footprints, which include the ichnogenus *Crocodylopodus* (Fig. 5). The footprint and body fossil record therefore reinforce each other in suggesting a latest Triassic–Early Jurassic dominance of terrestrial crocodylomorphs, followed by a Jurassic to recent interval with abundant semi-aquatic and aquatic crocodylomorphs.

The occupation of aquatic habits by archosaurs, including the expansion into marine environments, was likely controlled by climatic-ecological constraints as well as by the opportunistic filling of ecological niches. The latter is indicated by coincident events such as the extinction of different synapsid groups and the rise of archosaurs at the end of the Permian, and also the disappearance of semi-aquatic phytosaurs which corresponds to the occurrence of semi-aquatic crocodylomorphs during the Triassic–Jurassic transition.

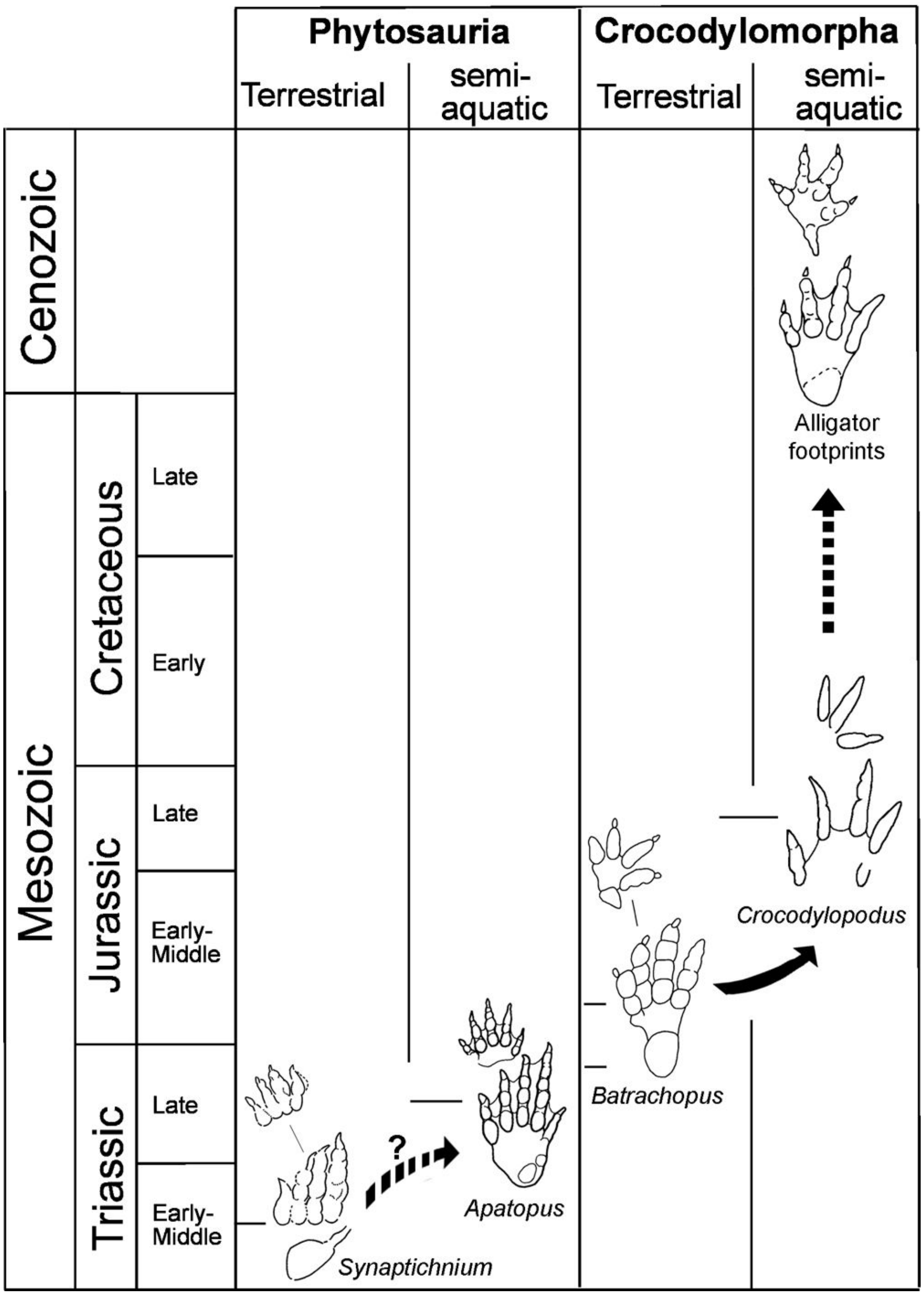

Figure 5. *Hypothetical evolution of the semi-aquatic lifestyle in archosaurs deduced from the footprint record (Klein and Lucas, 2013).*

CONCLUSIONS

The semi-aquatic and terrestrial lifestyle of trackmakers is indicated in the morphology of footprints of Triassic–Jurassic archosaurs. The Late Triassic phytosaur ichnogenus *Apatopus* is similar to the footprints of modern crocodilians in having a plantigrade pes with relatively indistinct and faintly impressed phalangeal pads and the lack of a compact metatarsophalangeal axis. This indicates the plantar anatomy of typical semi-aquatic tetrapods and/or the formation of footprints under subaqueous conditions in a saturate substrate prone to liquefaction failure. The latter may be limited only by a higher clay/mud content that enabled the preservation of, at least, some details. The transition of digit traces into elongate scratches, as well, as the occurrence of typical Late Triassic swim traces attributable to phytosaurs, supports this interpretation. Similar features can be observed in the footprints of crocodilians from the Jurassic up to the modern. Ichnological evidence and body fossil morphology and distribution document evolutionary developments in the group, with fully terrestrial forms preceding those adapted to a semi-aquatic lifestyle. In phytosaurians, body fossils of the terrestrial stage have not been discovered. The chirotheriid ichnogenus *Synaptichnium* combines features of the phytosaur footprint *Apatopus* with footprints of typical terrestrial tetrapods. *Synaptichnium* matches the hypothetical terrestrial ancestor of semi-aquatic phytosaurs both morphologically and temporally.

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