



## THE TRACKMAKER OF *APATOPUS* (LATE TRIASSIC, NORTH AMERICA): IMPLICATIONS FOR THE EVOLUTION OF ARCHOSAUR STANCE AND GAIT

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**Abstract:** For some decades, a major focus of research has been on how locomotor modes changed in some archosaurian reptiles from a more or less ‘sprawling’ to an ‘erect’ posture, whether there were discrete intermediate stages, and how many times ‘erect’ posture evolved. The classic paradigm for the evolution of stance and gait in archosaurs, a three-stage transition from sprawling to ‘semi-erect’ to erect posture, has been replaced by a subtler understanding of a continuum of changing limb joint angles. We suggest a further separation of terminology related to stance vs. gait so as not to entail different processes: ‘sprawling’ and ‘erect’ should refer to continua of stance; ‘rotatory’ and ‘parasagittal’ are more appropriate ends of a continuum that describes the motions of gait. We show that the Triassic trackway *Apatopus* best fits the anatomy and proportions of phytosaurs,

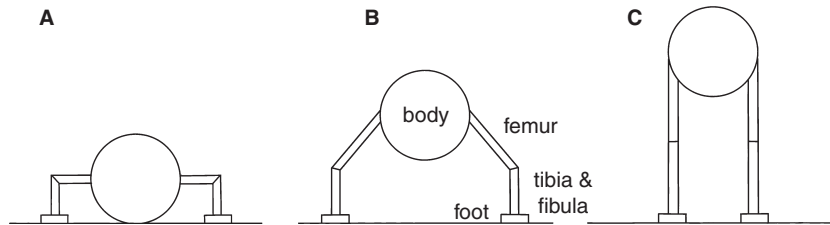
based on a new reconstruction of their foot skeleton; it is less likely to have been made by another pseudosuchian or non-archosaurian archosauromorph. Moreover, the trackmaker was performing the high walk. A phytosaurian trackmaker would imply that the common ancestor of pseudosuchians, and therefore archosaurs could approximate the high walk (depending on phylogeny), and if so, erect stance and parasagittal gait did not evolve independently in pseudosuchians and ornithosuchians, although the kinematic mechanisms differed in the two groups. It remains to be seen how far outside Archosauria, if at all, more or less erect posture and parasagittal gait may have evolved.

**Key words:** Archosauria, locomotion, functional morphology, paleoichnology, Dinosauria.

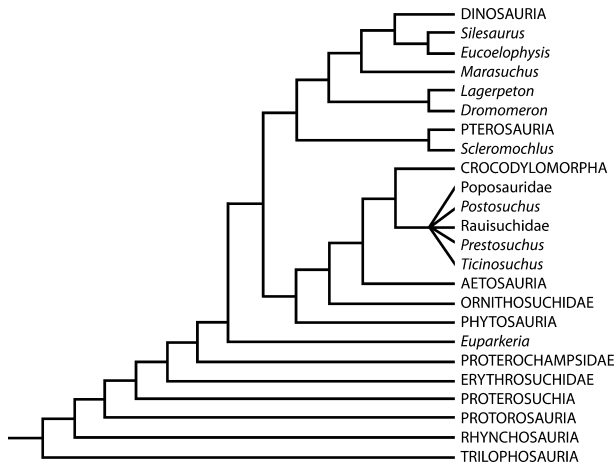
AMONG living tetrapods, a dichotomy in locomotor styles was long accepted. Birds and mammals, two different and highly derived amniote lineages, have an erect stance and a parasagittal gait (with the exception of some monotremes), whereas the more basal non-avian reptiles and amphibians sprawl their limbs and move them more laterally. Indeed, the term ‘reptile’ (which originally included amphibians) comes from the Greek word denoting ‘crawling’. But crocodiles do not merely sprawl; they also perform a gait called the ‘high walk,’ in which the hind limbs are adducted, so that the knees face nearly forward and the femur moves in a much more restricted anterior arc as the animal walks; the feet are placed close to the body midline (Brinkman 1980; Gatesy 1991a). Bakker (1971) and Charig (1972) embodied this as a ‘semi-erect’ or ‘semi-improved’ stance and gait, citing the alligator as a living representative, and inferred that many ‘thecodontians’ (most basal archosaurs and archosauriforms: Gauthier 1984, 1986) could also perform this stance and gait (Text-fig. 1). This problem was greatly clarified with Gauthier’s (1984; 1986) published cladistic

analysis of archosaurs, an updated version of which is given in Text-figure 2, because he separated archosaurs into those closer to crocodiles (pseudosuchians) and those closer to birds (ornithosuchians). Pseudosuchians seem to have included ‘sprawling’ forms and those that could at least facultatively perform the ‘high walk;’ ornithosuchians seem to have been exclusively ‘erect’ in their stance and ‘parasagittal’ in their gait, with some possible exceptions (Padian 1997).

Parrish (1986a, b; 1987) and Gatesy (1991a, 1995; see also Hutchinson and Gatesy 2000; 2006) showed that these classic trichotomous categories of posture and gait, tied to pre-cladistic ideas of archosaur relationships (Text-fig. 1), were actually parts of functional continua better characterized by limb joint angles and the kinematics of rotations of joints on other joints than by discrete functional categories. Kubo and Benton (2007) suggested the possibility of studying limb bone stress vectors to reconstruct reasonable postures in extinct archosauromorphs. The questions remain: where along the pseudosuchian lineage did the major changes in stance



**TEXT-FIG. 1.** Charig's (1972) conception of the evolution of archosaurian stance and gait, from a sprawling to 'semi-erect' to fully erect posture (modified from the original).



**TEXT-FIG. 2.** Cladogram of Archosauromorpha (after Gauthier 1984, 1986; Parrish 1993; Irmis *et al.* 2007).

and gait evolve, and what does the phylogenetic pattern tell us about the number of times that this evolution in stance and gait took place? This study attempts to approach these questions by examining the evidence for locomotor ability – functional, phylogenetic and ichnological – in basal pseudosuchian archosaurs.

## HISTORICAL HYPOTHESES OF THE EVOLUTION OF STANCE AND GAIT

In 1972, Alan Charig published a seminal paper in which he explored the evolution of the archosaur pelvis and hindlimbs in what he called functional terms. Although they were 'functional terms' for those times, the 'evolutionary' component did not constitute a fully independent test of phylogeny, as we would approach it today (Padian 2001). The small bipedal Argentinian archosaurs *Lagosuchus* (material now assigned to *Marasuchus*) and *Lagerpeton* (Romer 1971, 1972; Bonaparte 1975) were not yet published, so they did not figure in Charig's scenario. He proposed an evolution from a sprawling, lizard-like posture and gait to an upright, parasagittal dinosaurian stance and gait through an intermediate 'semi-improved' stage that was characterized by a crocodile (Text-fig. 1).

Charig equated the crocodile's 'high walk' with this 'semi-improved' gait, implying that their limbs were not as functionally advanced as those of dinosaurs. Bakker (1971) distinguished this from an 'erect gait', because the femur is allegedly held in a subhorizontal position and is angled 40 degrees or less below the horizontal plane. However, the angle at which the femur is held is largely a function of the size of the animal and the gait that it is using (within a given group) and in any case cannot be observed directly in extinct animals (Gatesy 1991a, b). Furthermore, as noted above, there is no phylogenetic evidence that the 'high walk' of crocodiles was an intermediate stage between sprawling reptiles and dinosaurs. The origin of this crocodilian mode of stance and gait is rooted more deeply in the Pseudosuchia (Parrish 1987) and may possibly be more generally distributed (see below).

More recently, stance and gait were studied using functional morphology in a more phylogenetic context and introducing evidence from ichnology when possible. Parrish (1986a, b; 1987) introduced a set of paradigms based on his analyses of the locomotor abilities of extant reptiles. Using studies by Brinkman (1980) and Rewcastle (1980), Parrish noted that, in sprawling animals, the proximal segment of the limbs proceeds almost laterally from the body, and that is why the animal cannot possess only simple hinge-like flexion and extension at the joints. Instead, movement involves rotation of adjacent limb segments as well as flexion and extension at the joints of both forelimbs and hindlimbs. The joint surfaces are usually oblique to the long axis of the limb element, 'allowing long-axis rotation of the proximal segment to be translated in part into flexion/extension of the distal segment' (Parrish 1986a, p. 10). Overall, locomotion of typically sprawling animals is characterized by modifications that allow less restriction and more rotation of the limb joints.

The hip joint also shows some differences between 'sprawling' and 'erect' taxa. Examining Charig's (1972) categories, Parrish (1986a) noted that in 'sprawling' species the acetabulum is shallow and laterally directed, and the proximal end of the femur lacks a distinct head or neck. These characteristics permit protraction and retrac-

tion of the femur as well as rotation about its long axis. Because the femur, crus and pes all rotate as the limb is retracted, the pes is laterally oriented for at least part of the step cycles.

At this point, we suggest the adoption of a distinction in terminology that is currently missing but necessary. Stance and gait are two different concepts in locomotion, yet some terms such as 'sprawling' and 'erect' are used to describe both aspects (often dichotomously, but more correctly as steps on a continuum: Gatesy 1991a). 'Sprawling' and 'erect' may more appropriately describe stance, a static condition that denotes posture, the geometric configuration of the limbs relative to the body and the ground. 'Gait' more appropriately refers to the kinematics of locomotion, such as moving in a parasagittal or horizontal plane, or to specific modes of locomotion such as walk, trot, or gallop.

We suggest restricting the use of the term 'sprawling' to stance (posture); we propose to describe the kinematic aspect of the gait of an animal in a sprawling posture that moves its limbs in a horizontal plane as 'rotary,' a term that appears apt because the limb segments rotate considerably about each other through several planes (Brinkman 1980; Parrish 1986a; Gatesy 1991a). An animal such as a crocodile can assume a sprawling posture but can variably use a rotary gait with the body close to the ground or perform the high walk. Most birds and mammals have an erect stance and a parasagittal gait, which appear to be functionally correlated; lizards do not habitually stand erect but some can adopt a parasagittal gait, so these distinctions should be maintained (Table 1).

Unfortunately, the living vertebrate biota does not reflect most transitional stages in the evolution of stance and gait, which leaves us with artificial distinctions from which evolutionary continua must be reconstructed. A major distinction in the morphology between living animals that use rotary or parasagittal gait is that in the latter, the movement consists of simple flexion and extension of limb segments in a parasagittal plane, whereas the long-axis rotation of limb segments is greatly reduced. In fact, the joints are modified so as to minimize

rotation around the long axes of the femur and crus. There are distinctive osteological correlates of this gait (Coombs 1978; Padian 1983, 1997). Animals with erect stance have a femur with a distinct, medially directed head. The pelvic girdle has a relatively deep acetabulum, elongated pubis and ischium and an expanded anterior iliac blade. The long axes of the ankle joints are parallel, favouring simple, hinge-like motion (Parrish 1986a, 1987). These features naturally result in a parasagittal gait (Padian 1983, 1997).

Gatesy (1991a) established a new paradigm for the problem of stance and gait by showing that the traditional categories of sprawling, semi-erect and erect posture were artificially trichotomized; the correct way to consider the problem was in terms of the joint angles between successive limb segments in three dimensions, and how the kinematics of the step cycle are actually influencing stance and gait. He showed, for example, that simply by varying the amount of femoral adduction (and the attendant kinematics of the lower limb), crocodiles can move from 'sprawling' to 'semi-erect' and even 'erect' locomotion. Gatesy correctly saw these not as discrete categories and also asked rhetorically whether it was not possible to move among these grades, and how we are to recognize and categorize such shifts. We suggest that, as usual, differential extinction has removed some intermediate stages of evolution from our extant biota (Hutchinson 2006), and therefore we are constrained to consider how important changes may have occurred based solely on extinct animals that cannot be subjected to experimental manipulation. Morphology alone cannot solve the problem, because a single morphological configuration can be capable of several locomotor modes (as crocodiles show by swimming, sprawling, high walking, bipedal running and even galloping). For these reasons, we use a combination of skeletal anatomy and trackways to analyse and evaluate hypotheses about stance and gait and their evolution.

## THE EVOLUTION OF CROCODYLIAN GAIT

In Parrish's (1986a; 1987) view, the evolution of an expanded anterior iliac blade and a much deeper acetabulum is among the characteristics associated with an erect stance that are first seen in Aetosauria (Text-figs 1, 2). Also for the first time in Aetosauria, the proximal surface of the tibia consists of a pair of distinct fossae separated by a median ridge. The articulation of this surface with the femoral condyles helps to restrict the movement in the crus to only flexion and extension of the femur; this is carried through to crocodiles. In lizards and phytosaurs, on the other hand, the proximal surface of the tibia

**TABLE 1.** Distinctions among stance, gait (kinematics and modes), and their structural correlates, with examples of features commonly cited in the literature. It appears preferable to avoid using the same adjectives for different aspects of locomotion.

Feature	Example descriptors
Stance	Sprawling, erect, bipedal, quadrupedal
Gait (kinematics)	Rotary, parasagittal, undulatory
Gait (mode)	Walking, trotting, galloping, flapping
Structural correlates	Ball-and-socket hip, hinge joints, crurotarsal ankle, bowed femur

is nearly planar, allowing a wider range of motions (Parrish 1986a, 1987).

A similar situation is observed with the distal end of the tibia: proterosuchians, phytosaurs and lizards have a nearly planar facet on the distal end of the tibia, whereas aetosaurs, 'rauisuchians' and crocodylians have a curving facet. The latter condition ensures a tight union between the tibia and the astragalus, thus restricting the range of movement to hinge-like motion. The morphology of aetosaurs, 'rauisuchians' and crocodylians also requires that the tibia 'sit vertically on the astragalus, such that the tibial long axis [is] perpendicular to the (horizontal) axis of the astragalocalcaneal joint. This arrangement restricts flexion and extension of the calcaneum on the astragalus to a parasagittal plane' (Parrish 1986a, p. 18). Corwin Sullivan (2007), in as yet unpublished research, has further clarified much of our understanding about the evolution of archosaur stance and gait.

Parrish (1987) applied another morphological aspect, described by Szalay (1984), to the problem of the tarsal mechanics. Three ankle joints were defined: the upper ankle joint (UAJ) – between the proximal tarsals and the crus; the middle ankle joint (MAJ) – between the two proximal tarsals; and the lower ankle joint (LAJ) – between the proximal and distal tarsal rows (Parrish 1987). The long axes of these three joints are all mutually oblique in sprawling animals, which results in considerable flexion and rotation (quantified by Gatesy 1991a). In dinosaurs, which have an erect stance, the axes are parallel, favouring hinge-like motion. Parrish (1987) showed that the long axes of the ankle joints of phytosaurs are mutually oblique, whereas they are parallel in Aetosauria, 'Rauisuchia', 'Sphenosuchia' (basal crocodylomorphs) and 'Protosuchia' (basal crocodyliforms). According to Parrish's (1986a) paradigms, these morphological observations suggest that the archosaurian features matching the paradigms for strictly 'sprawling' locomotion are last seen in phytosaurs, whereas adaptations for a parasagittal gait first appeared in Aetosauria (Text-fig. 1). As Gatesy (1991a) noted, these divisions may not be strict, and the correlates available in fossils to evaluate them may be ambiguous, which Parrish (1987) also acknowledged.

## METHODS

Morphology alone, especially when restricted to skeletal remains, is often not enough to make a conclusion about the gaits of living animals, let alone extinct ones. In such cases, when stance and gait cannot be witnessed directly, hypotheses of both stance and gait are most testable when (1) the motion-limiting parameters of contiguous joint surfaces are clearest, (2) diagnostic features of homologues and analogues are readily available in living forms

and (3) trackways referable to skeletal remains or their close relatives are available.

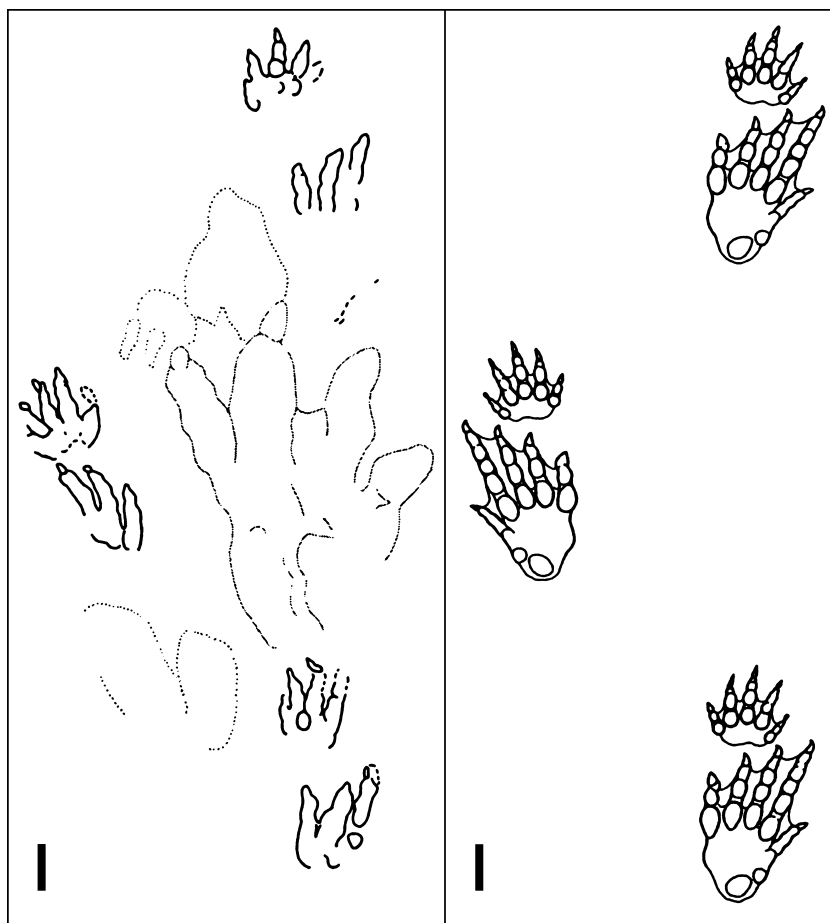
Trackways have long been used as a test of hypotheses about functional morphology and locomotor modes. Trackways can also test the likelihood that hypothesized trackmakers actually could have made the prints in question (e.g. Padian and Olsen 1984a, b, 1989; Olsen and Padian 1986; Padian 2003). We decided to test whether the manual and pedal skeletons of proposed archosaurian trackmakers would fit the trackway of *Apatopus lineatus* described and reconstructed by Baird (1957) and later by Olsen and Huber (1998). *Apatopus* may represent a somewhat pivotal point in the understanding of the evolution of stance and gait in archosaurs, depending on its presumed trackmaker (which has been a subject of dispute) as well as what it reveals about the stance and gait of its trackmaker.

Complete manus and pes skeletons of non-crocodylomorph pseudosuchians and non-archosaurian archosauriforms are few. There are also relatively few reconstructions of complete skeletons in dorsal view, which are essential for comparing manus and pes size, gleno-acetabular length, and trackway 'wheelbase' measurements (the approximate gleno-acetabular length, taken as the anteroposterior length between the centroid of a manus and its contralateral pes). Dorsal reconstructions of skeletons are also necessary to test whether the limbs were in erect or sprawling stance when the trackways were made.

In reptiles with a more sprawling stance and rotary gait, the limbs are normally positioned lateral to the body and so are conspicuous in dorsal view (Parrish 1987; Gatesy 1991a). In animals with erect stance and parasagittal gait, however, the limbs are more nearly tucked underneath the girdles or are closer to them by as much as a body radius and are not as conspicuous in dorsal view. If phytosaurs had a parasagittal gait, the quadrangle that connects the centroids of the four manus and pedes prints should be narrower mediolaterally than if it had a rotary gait: its limbs, especially the propodia, would be expected to be oriented more vertically than laterally, and the manus and pedes placed almost beneath the girdle during locomotion.

*Apatopus lineatus* (Bock) (Text-fig. 3) has historically been regarded as the trackway of a phytosaur, as first identified by Baird (1957, pp. 490–494; Haubold 1971; see also Parrish 1987; Olsen and Huber 1998). The type specimen was identified by Wilhelm Bock (1952) as a possible new species of *Otozoum*; Baird (1957) erected the genus *Apatopus*, diagnosed the taxon and redescribed and restored the tracks based on a successive left–right manus–pes set. In so doing, Baird reconstructed parts of pedal digits IV and V from 'other specimens' and had to calculate stride, pace angulation and gleno-acetabular

**TEXT-FIG. 3.** *Apatopus lineatus*, the presumed track of a phytosaur, as drawn from the slab (left) and reconstructed by Baird (1957); from Olsen and Huber (1998). Scalebar represents 5 cm.



length by adding a third manus–pes set at the same relative distance that is found between the preserved pairs of tracks. Thus, there is some uncertainty about some of the morphology of the holotype specimen and its reconstruction. We proceed on the basis of Baird’s work, because it has never been questioned, and in fact has been supported by Olsen and Huber (1998). Nevertheless, further diagnostic specimens would be highly desirable.

Baird suggested that the trackmaker was using the high walk, but he did not test this hypothesis against skeletal remains. Parrish (1986b), however, raised some potential difficulties in attributing *Apatopus* to a phytosaur. The relative position and size of the fifth metatarsal and the calcaneum seem to vary between *Apatopus* and known phytosaur material. Parrish (1986b) constructed an inferred phytosaur track from the restored *Rutiodon adamanensis* (specimen USNM 18313 now referred to *Smilosuchus gregorii*) foot, in which the proximal part of its fifth metatarsal makes a much larger, mediolaterally elongate pad impression than the nearly circular impression that represents the fifth metatarsal in *Apatopus*. The fairly large, posterolaterally directed calcaneal tuber in *Smilosuchus* also makes a pad impression. However, Parrish (1986b) argued that even if the tarsus is positioned

such that the calcaneal tuber in *Smilosuchus* is directed posteriorly, the pad that was made by the tuber would still be posterior and slightly lateral to the fifth metatarsal pad. This would not correspond to *Apatopus*, in which the pad made by the tuber is positioned posteromedial to the fifth metatarsal pad. Olsen and Huber (1998, p. 83) judged that Parrish’s ‘model of a phytosaur track based on known osteology... is as close to *Apatopus* as can be expected given the limitations of the method.’ They countered that ‘a functional argument is inherently weaker than one based on anatomical similarity’ and therefore concurred with Baird’s (1957) original assignment of *Apatopus* to a phytosaurian trackmaker. We test these inferences below.

As noted, the presumed phytosaur trackway examined was *Apatopus lineatus* (Baird 1957; Olsen and Huber 1998). Our assessment of the rhynchosaur skeleton was based on *Hyperodapedon gordonii* and *Rhynchosaurus articeps* as reconstructed by Benton (1983, 1990); the trilophosaur used was *Trilophosaurus buettneri* (Gregory 1945); ornithosuchids were based on *Ornithosuchus* (Walker 1964) and *Riojasuchus* (Bonaparte 1971); the phytosaur skeleton was based on *Parasuchus hislopi* (Chatterjee 1978); the aetosaur skeletons were based on *Aetosaurus*

*ferratus* (Schoch 2007) and *Stagonolepis robertsoni* (Walker 1961), with comparison to *Desmatosuchus spurensis* (Parker 2008); and the basal 'rauisuchian' was *Ticinosuchus ferox* (Krebs 1965). We assumed that even if the sizes of the animals represented by the skeletons were not identical to those of the animals that made the trackways, they would be more or less geometrically similar (with some variation expected for species, ontogenetic stage and other factors). We estimated that the mediolateral difference between the feet in a sprawling animal versus an upright animal would approximate 1–2 body radii, a significant difference, and so the hypothesis of correspondence between skeletal remains and *Apatopus* footprints could inform the inference of erect or sprawling posture, or some intermediate stance. We therefore define an ichnological correlate of erect posture by the placement of the pedes no farther than one body radius lateral to the girdles (where body radius equals the distance from the vertebral midline to the shoulder or hip socket, respectively). We cannot, of course, account for the possible role of the tail in magnifying lateral undulations of the body during walking, which may have affected placement of the feet. However, absent any compelling evidence of this effect in crocodiles (living pseudosuchians), it seems reasonable not to invoke it for extinct pseudosuchians.

Images of the skeletons and trackways in question were taken from the publications cited above. The images were resized and compared using Adobe PhotoShop CS3 and MB-Ruler 3.3 (Markus Bader). The skeleton of the phytosaur was reconstructed in dorsal view using Chatterjee's (1978) descriptions and illustrations. The phalanges were sometimes individually separated as images and repositioned to test their fit to the digit impressions of the trackway in different ways. The image of the *Apatopus* trackway was transparently overlain on reconstructions of the dorsal views of the skeletons, and the size of the manus and pes prints manipulated until a best fit was reached. The best fit was approximated by the distance from the tarso-metatarsal impression to the ends of the pedal digits, maintaining proportional similarity between the manual and pedal prints. A 'wheelbase' (approximate gleno-acetabular distance) fit between the skeletons and the *Apatopus* trackway was then assessed.

We mainly considered Late Triassic archosaurs as potential trackmakers, because *Apatopus* is only known from deposits of the Late Carnian and Norian stages of the Triassic (Olsen and Huber 1998). Rainforth (2007) determined that all referred *Apatopus* specimens from the Newark Supergroup are not referable to that genus and instead represent brachychirotheres. As a result, in the eastern U.S., *Apatopus* is restricted to the type trackway and therefore is known only from a single locality. Foster *et al.* (2003, p. 165) described what they called the 'best preserved *Apatopus* trackway reported from the Western

U.S.' from the Chinle Formation of Utah. However, they note that this specimen differs from the type specimen in that digit IV is shorter than digit III, although they suggest that this could be as a result of substrate, injury or another cause. (We are grateful to Bill Parker (Petrified Forest National Park, Arizona) for this information.)

## RESULTS

The type specimens of *Apatopus lineatus* consist of a left manus–pes set (Bock's original 1952 holotype of *Otozoum(?) lineatus*, Lafayette College Museum S 489) plus 'the succeeding right set of the same trackway' (Museum of Comparative Zoology, Harvard University, MCZ 212) as amended by Baird (1957, p. 487). It is from these specimens that Baird originally reconstructed the trackway, and his reconstruction has been accepted by later workers (e.g. Parrish 1986b; Olsen and Huber 1998). The stride length of the *Apatopus* trackmaker, measured by the distance between the centroids of successive pedal footprints, is roughly 70 cm, and the distance between the left and right limbs, measured horizontally between pedal centroids, is 21 cm. The 'wheelbase' or approximate gleno-acetabular length (see above) was estimated at 55 cm (Baird (1957) estimated this at 52 cm; the difference is insignificant). In order to compare the skeletons to the trackways, the proportions of the manus and pedes first have to be adjusted to fit the prints of the manus and pedes in *Apatopus*. This made it possible to ask whether the relative distances between the footprints (anteroposterior and lateral) match the distances between the feet of the fossil skeleton. For example, the gleno-acetabular distance in *Parasuchus hislopi* was approximately 60.5 cm (Chatterjee 1978) and that of *Aetosaurus ferratus* was 20 cm (Schoch 2007); these were scaled to fit the *Apatopus* trackway. The animals represented by the fossil skeletons that we used are unlikely to be the exact species represented by the trackway, but it is expected that they will be more or less geometrically similar because strong proportional allometry has never been demonstrated in pseudosuchian skeletons.

### *Crocodylomorpha*

The first well-recognized crocodylomorph ichnogenus is *Batrachopus*, known from the Early Jurassic and ascribed to a trackmaker such as *Protosuchus*, from the Moenave Formation of Arizona (Olsen and Padian 1986). The fifth pedal digit is absent in both crocodylomorphs and *Batrachopus*, whereas it is present in *Apatopus*. We therefore eliminated crocodylomorphs from consideration.

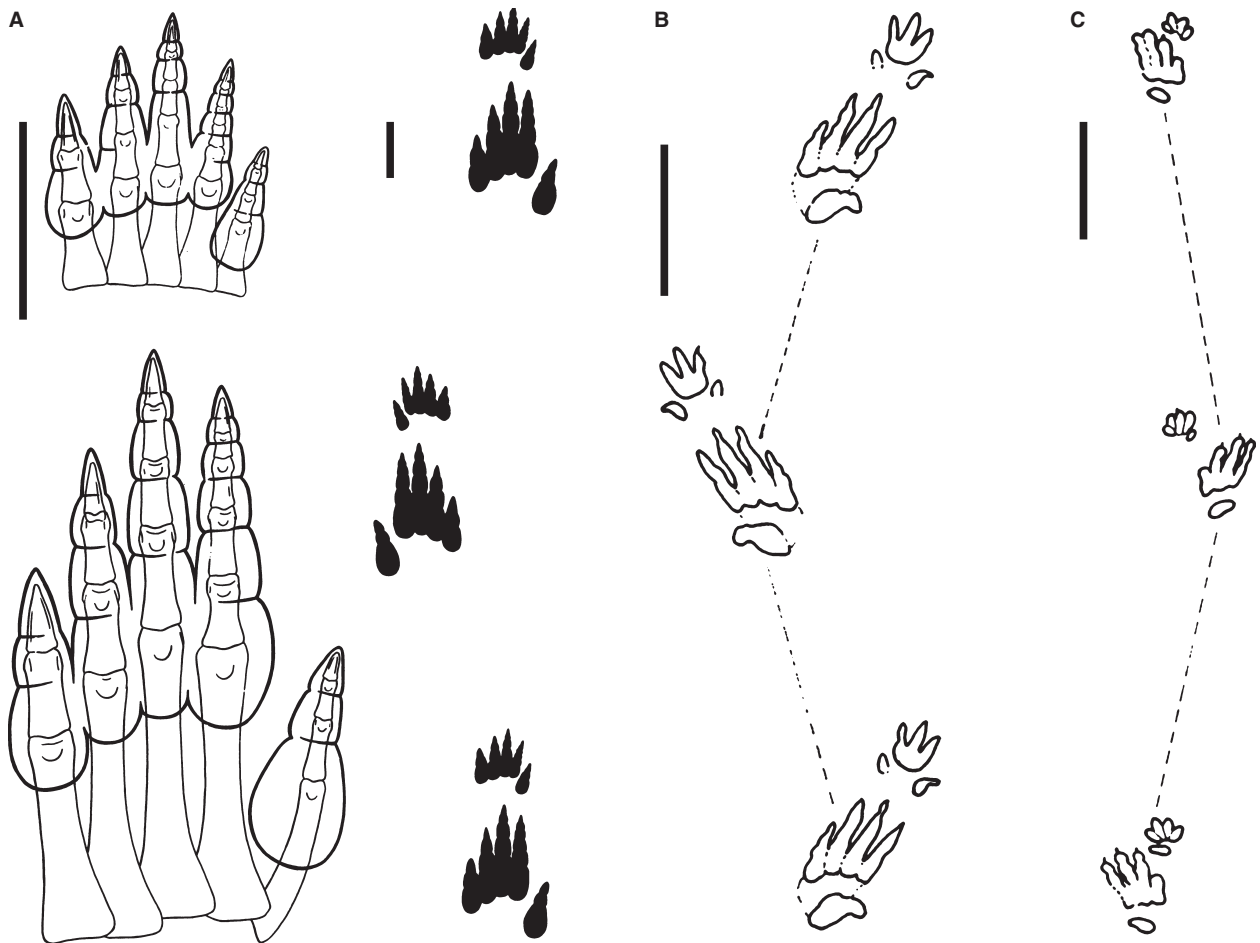
'Rauisuchia'

Although this taxon is now regarded as paraphyletic as traditionally constituted (Parrish 1993; Gower 2000; Gower and Nesbitt 2006; Nesbitt 2007; Weinbaum and Hungerbuehler 2007), most of its members, such as Poposauridae and related forms, are usually considered the closest known sister taxa to Crocodylomorpha, although published phylogenies vary. These animals have conspicuous fifth pedal digits; trackways that reflect this, in the Ichnofamily Chirotheriidae, are generally ascribed to 'rauisuchians' (Krebs 1965; Haubold 1971, 1986). However, the fifth digits are generally more divergent and more posteriorly oriented than in other pseudosuchians (Haubold 1986). *Postosuchus alisonae*, recently described by Peyer *et al.* (2008), has a very well-preserved manus and pes; pedal digit IV is significantly shorter than digits II and III, so it is unlikely to have been the trackmaker of *Apatopus*.

Although the manual and pedal skeletal elements of 'rauisuchians' do not fit the *Apatopus* trackways (Text-fig. 4A), there is substantial evidence that these animals had an erect stance and parasagittal gait (Krebs 1965). Aside from functional morphological evidence (Parrish 1986a), the trackway *Chirotherium* (Text-fig. 4B), commonly attributed to 'rauisuchians' (Haubold 1984, 1986; Lockley and Meyer 2000) is very narrow compared to the width of the body, and its trackmaker was presumably performing the high walk.

Aetosauria

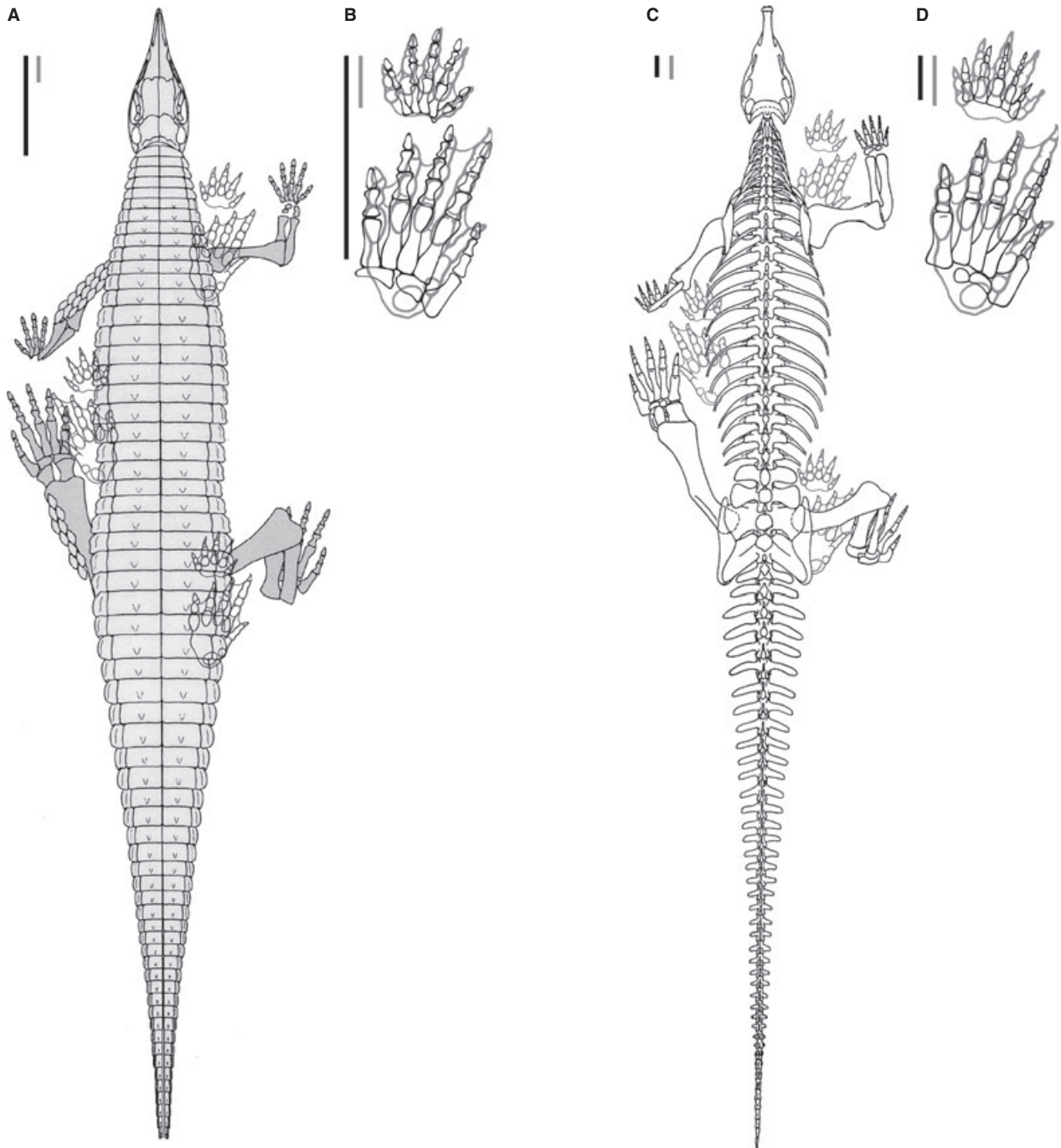
As far as we know, no trackways have been formally attributed to an aetosaurian trackmaker, with the possible exception of *Brachychirotherium* (Haubold 1986, p. 198, fig. 15.10), although Avanzini *et al.* (2007) considered aetosaurs a likely trackmaker for some *Apatopus*-like



**TEXT-FIG. 4.** A, *Ticinosuchus ferox*, a basal 'rauisuchian.' Left, manus and pes, as reconstructed by Krebs (1965), with outlines to show his hypothesis of the footprints that it would make; right, Krebs's reconstruction of a hypothesized *Ticinosuchus* trackway. B, A trackway of *Chirotherium barthi* (after Haubold 1984, fig. 105.5). C, *Brachychirotherium* (after Haubold 1971, fig. 36.3); chirotheriid tracks are often referred to 'rauisuchians,' although not always specifically *Ticinosuchus*. Scalebar represents 5 cm.

traces from the Triassic of Italy. However, *Brachychirotherium* (Text-fig. 4C) lacks the impression of pedal digit V, a digit that is present in aetosaurs (Text-fig. 5). Baird (1957) considered crocodylomorphs (negatively) and phytosaurs (positively) as trackmakers of *Apatopus*, but

he did not consider aetosaurs. As is true for phytosaurs, foot skeletons are poorly known for aetosaurs, but Schoch's (2007) recent restudy of *Aetosaurus ferratus* provides an opportunity to reassess the question. As Text-figure 5 shows, when the hand and foot of



**TEXT-FIG. 5.** A, the aetosaur *Aetosaurus ferratus* in dorsal view, superimposed over the *Apatopus* trackway. B, detail of manus and pes of *A. ferratus* as superimposed. C, the aetosaur *Stagonolepis robertsoni* in dorsal view, superimposed over the *Apatopus* trackway. D, detail of manus and pes of *S. robertsoni* as superimposed. Skeletal drawings in A and B adapted from Schoch (2007), in C and D adapted from Walker (1961). Scalebar represents 5 cm. In B and D, dark bold scale is for the skeleton, light grey scale is for the footprints.



*Aetosaurus* are scaled to optimize overall fit to *Apatopus*, the overall size of the skeletal hand fits the manus print with strong proportional similarity. One difference is that in the skeleton, manual digit I is larger than digit V, whereas in the trackway they are subequal. This might be explained by kinematics (Padian and Olsen 1984a; Olsen and Huber 1998); but details of the pes differ importantly in that in the reconstructed pedal print of *Apatopus* the fourth digit is the longest, whereas the third digit is the longest in *Aetosaurus*. The *Apatopus* trackway from the Chinle Formation, if assigned correctly, may have a digit III that is longer than digit IV (Foster *et al.* 2003); if so, it is more similar to the aetosaur pes than is the Newark specimen. Also, the overlay shows that skeletal pedal digit V is outside the trackway impression of digit V by the width of a digit, although if in life there were overlap of the proximal metatarsals, it would have condensed the width of the foot as illustrated.

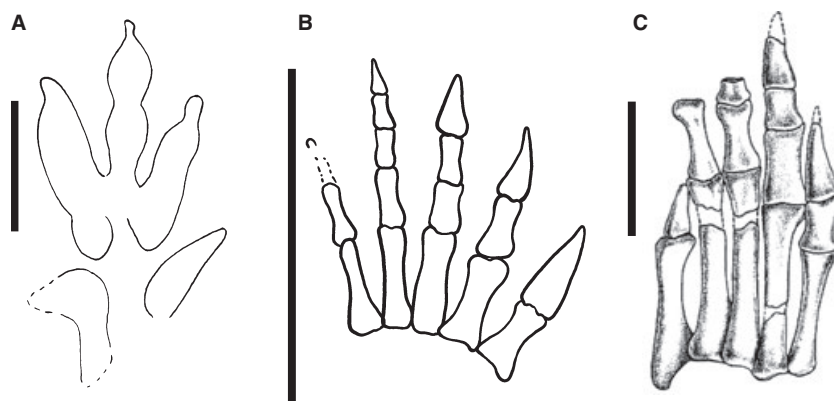
A considerable difficulty is that the preserved material of *Aetosaurus ferratus* is generally held to represent immature individuals (Schoch 2007); younger individuals tend to be more gracile than larger ones, if crocodiles are any indication. Moreover, the 'wheelbase' of a typical *Aetosaurus* is only about 15 cm, whereas that of the *Apatopus* trackways is 52–55 cm, as noted above.

*Stagonolepis robertsoni* is a much larger animal, with a wheelbase of about 67 cm, much closer to the size of the *Apatopus* trackmaker. However, as reconstructed by Walker (1961), *Stagonolepis* only fits the *Apatopus* tracks if the feet are held very close underneath the limb girdles (Text-fig. 5C), which could only work if the limb posture were fully columnar (vertical). Whereas Desojo (2004) determined that several different aetosaurs had acetabula that faced laterally, ventrally and ventrolaterally, this is not

the same as determining that their limbs were columnar. Consequently, because the fourth pedal digits vary proportionally with respect to other digits, and because the feet would have to be placed too far under the body, the candidacy of aetosaurs as trackmakers of *Apatopus* is weakened.

#### *Ornithosuchidae*

Ornithosuchidae have not been proposed as the trackmakers of *Apatopus*, but Haubold (1986) suggested them as the makers of *Parachirotherium* trackways (Text-fig. 6A). *Parachirotherium* lacks a manus print, suggesting that its maker was either bipedal or barely impressed its manus while walking. The pedal tracks have an anterior tridactyl configuration of digits II–IV, and digits I and V are more posterior and more divergent, so if Haubold's hypothesis is correct, ornithosuchids bear no further relevance to our question. The skeletal manus of *Ornithosuchus longidens* does not appear completely enough known for a reconstruction, although the pes is partly preserved in disarticulation (Walker 1964, fig. 10; Text-fig. 6B), and suggests that the fourth digit is the longest; however, the claws of the medial digits appear too large for the impressions in *Apatopus*. In *Riojasuchus tenuiceps* (Bonaparte 1971, fig. 20; Text-fig. 6C), the pedal digits are better preserved, though incomplete; but digit III is clearly the longest, whereas digit IV is longest in the *Apatopus* trackmaker, so this would seem a critical factor in rejecting ornithosuchids as candidates. Finally, no ornithosuchid skeletal fossils have yet been discovered in North America, perhaps corroboration (although only by negative evidence) that they were not likely the makers of *Apatopus*.



**TEXT-FIG. 6.** A, *Parachirotherium* left pes print (from Haubold 1986, p. 192, fig. 15.2E). B, hypothesized reconstruction of the left pes of *Ornithosuchus longidens* (based on Walker 1964, fig. 13). The specimen (Natural History Museum R 2410) would seem to come from a relatively small individual, perhaps with a skull length of 115 cm. C, Left pes of *Riojasuchus tenuiceps* (based on Bonaparte 1971, fig. 20). Scalebar represents 5 cm.

*Parasuchia (Phytosauria)*

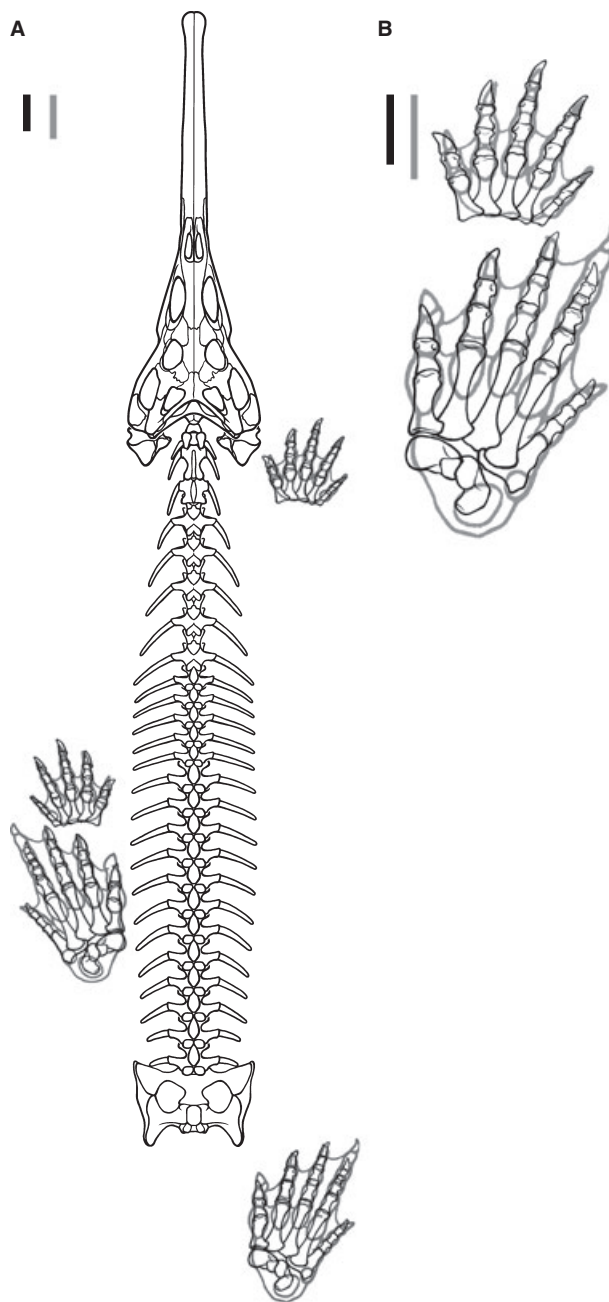
When the manual and pedal skeletal outlines of the reconstruction of *Parasuchus hislopi* (Chatterjee 1978) are scaled optimally, the fit to the *Apatopus* trackway is much as it was for *Aetosaurus* (Text-fig. 7A–B). As noted earlier, the ‘wheelbase’ calculated for *P. hislopi* is approximately 60.5 cm, and for *Apatopus* 52–55 cm, so they are proportionally very close. A similar difficulty as for the aetosaurs is that according to Chatterjee’s restoration the third pedal digit of the phytosaur, not the fourth, is the longest, whereas in *Apatopus* pes impressions the fourth digit is longer than the third, a condition primitive for diapsids (Parrish 1986b).

However, Chatterjee’s (1978) reconstruction of the pes of *Parasuchus* (Text-fig. 8A) raises questions. He gave the phalangeal formula as 2-3-4-5-4, and he restored digit III as the longest, but his drawing of the specimens ISI R 42 and ISI R 43 (Indian Statistical Institute) does not depict a complete foot. The most complete foot drawn is the left pes of ISI R 42 (Text-fig. 8B), but the preserved phalanges as illustrated would give a formula of 2-3-3-4-3; no other pes suggests more phalanges for any digit, although that does not mean that a complete set is preserved. As preserved, however, based on Chatterjee’s drawing of the skeleton, the metatarsal and four phalanges of the fourth digit are already 25% longer than the metatarsal and three phalanges of the third digit. Because the preserved penultimate phalanges of the third and fourth digits are approximately equal in length, it is difficult to see how the addition of a further phalanx to each digit could make the third digit longer than or even as long as the fourth.

If this line of reasoning is correct, then the fourth digit was longer than the third in *Parasuchus*, and it would have conformed more closely to the *Apatopus* trackway than Chatterjee’s (1978) reconstruction of the foot would suggest. Our revised reconstruction is given in Text-figure 8C. This configuration conforms better than the aetosaur foot or any other foot considered here. Furthermore, when the manus and pes are scaled to fit skeleton with tracks, the ‘wheelbases’ correspond closely. In all respects that we can determine, phytosaurs are a consistent match with the *Apatopus* tracks.

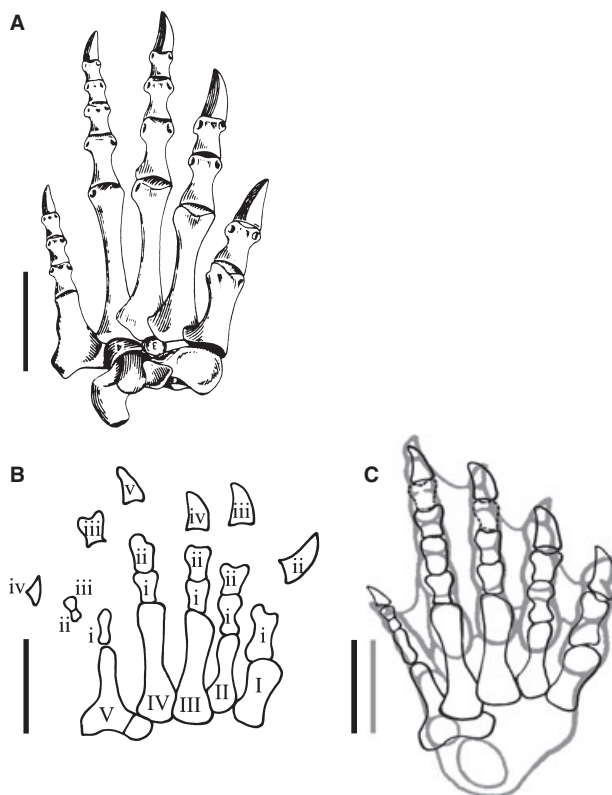
*Non-archosaurian archosauromorphs*

Although we considered mainly pseudosuchian candidates for the *Apatopus* trackmaker, Parrish (1986b) cited Woodward (1907) that the rhynchosaur manus is often restored with the fourth digit longer than the third, which corresponds to the restored condition in *Apatopus*. Thus, the possibility that *Apatopus* could have been made by a



**TEXT-FIG. 7.** A, the phytosaur *Parasuchus hislopi* in dorsal view, superimposed over the *Apatopus* trackway. B, detail of manus and pes of *P. hislopi* as superimposed. Skeletal drawings based in part on Chatterjee (1978). Scalebar represents 5 cm. In A and B, dark bold scale is for the skeleton, light grey scale is for the footprints.

rhynchosaur cannot be disregarded (Parrish 1986b). However, based on *Hyperodapedon gordonii* (Benton 1983) and *Rhynchosaurus articeps* (Benton 1990), this is unlikely (Text-fig. 9A). In *Hyperodapedon* pedal digit V is much longer than in *Apatopus*; manual digit IV, not digit III, is the longest; and the hands and feet are more nearly equal



**TEXT-FIG. 8.** A, Reconstruction of the left foot (dorsal view) of the phytosaur *Parasuchus hislopi* (from Chatterjee 1978). B, Chatterjee's drawing of the best preserved foot skeleton (left pes of ISI R 42), on which we have indicated presumed identifications of phalanges. C, Our reconstruction of the foot of *P. hislopi*, assuming Chatterjee's reconstructed phalangeal formula of 2-3-4-5-4 and relative equivalence of proportions of the missing phalanges; this is superimposed over the trackway of *Apatopus*. According to this reinterpretation the fourth digit would now be longer than the third, and would fit the *Apatopus* trackways better than other pseudosuchians would. Scalebar represents 5 cm.

in size. In *Rhynchosaurus*, the hand is too large for the *Apatopus* trackways and the third and fourth digits too long. Furthermore, the body is too wide and the wheel-base too short for *Rhynchosaurus* to fit the trackway of *Apatopus* (Text-fig. 9B). Moreover, the pedal claws are enlarged in rhynchosaurs (Benton 1983, fig. 39), which is not evident in *Apatopus*.

*Trilophosaurus buettneri*, named by Case and redescribed by Gregory (1945), is an unusual reptile from the Late Triassic. The manus alone excludes it from authorship of the *Apatopus* tracks, because its fourth manual digit is much longer than the third (even if the penultimate phalanx were not as long as in Gregory's reconstruction). The manus is too nearly the same size as the pes to qualify (Text-fig. 9C). Also, the fifth digit of the *Trilophosaurus* pes is much longer than the corresponding impres-

sion of the digit in the *Apatopus* trackway. So *Trilophosaurus* may be eliminated as a possible trackmaker.

## DISCUSSION

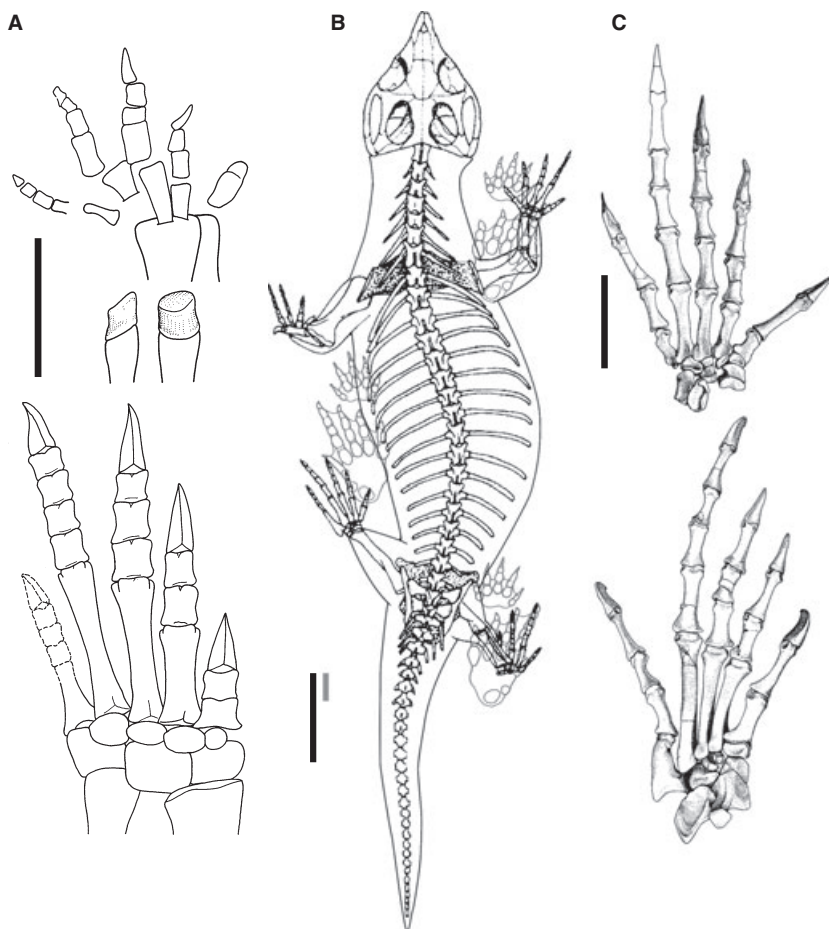
All available evidence points to a narrow-gauge, parasagittal gait for the *Apatopus* trackmaker, because the distance between left and right footprints is small compared to the size of the tracks; this implies an erect or nearly erect stance as the animal performed the high walk (Baird 1957), which we have confirmed using skeletal restorations. The question is who could have left the tracks. We have considered non-archosaurian archosauromorphs known to have been abundant during the Late Triassic, namely pseudosuchians, trilophosaurs and rhynchosaurs. Most other non-archosaurian archosauromorphs lived earlier in the Triassic or have skeletons that are not suitable for the *Apatopus* trackmaker (Kuhn 1976).

### *Aetosaurian trackmaker*

If *Apatopus* tracks were made by aetosaurs, it would preserve Parrish's (1986a) separation of phytosaurs from other pseudosuchians capable of performing (approximately) the high walk seen in crocodiles, which he argued on functional morphological grounds was not likely. Several functional features that first arise in Aetosauria, such as a deep acetabulum and the modification of the distal and proximal ends of the tibia to restrict movement to a simple, hinge-like motion (Parrish 1987), are shared by groups with a parasagittal gait. However, digit III of the foot in *Aetosaurus* is the longest (a derived condition relative to basal archosauriforms), whereas in *Apatopus* it is the fourth; and for this and other reasons, aetosaurs are not the most likely trackmakers.

### *Non-archosaurian trackmaker*

If *Apatopus* were made by a trilophosaur, rhynchosaur or other non-archosaurian archosauriform, another interesting implication would arise: the ability to execute the high walk, involving erect stance and parasagittal gait, evolved outside Archosauria proper. If so, the common ancestor of Archosauria would have inherited this ability, as it would have if *Apatopus* were made by a phytosaur. However, correlations of footprints with non-archosaurian archosauriform skeletal remains are unfortunately few, and it is difficult to find the necessary synapomorphies to link tracks to trackmakers (Carrano and Wilson 2001). Those that are preserved, such as rhynchosaurs



**TEXT-FIG. 9.** A, left manus and pes of *Hyperodapedon gordonii* (from Benton 1983). B, Skeletal restoration of *Rhynchosaurus articeps* (from Benton 1990, fig. 38) superimposed on the trackway of *Apatopus*. Dark bold scale is for the skeleton, light grey scale is for the footprints. C, left manus and pes of *Trilophosaurus buettneri* (from Gregory 1945, figure reversed). Scalebar represents 5 cm.

and trilophosaurs, do not fit the footprints of *Apatopus* sufficiently well to merit further consideration.

#### *Phytosaurian trackmaker*

If *Apatopus* tracks were made by phytosaurs, which appears most likely among all known possibilities from a reconsideration of the foot skeleton of *Parasuchus* (Text-fig. 7C), then phytosaurs could have performed or approximated the high walk (i.e. with strongly adducted femora) and hence would have been capable of erect or nearly erect stance and parasagittal gait (although this does not exclude additional options of stance and gait, as for living crocodiles). That would imply that pseudosuchians basally shared this ability, whereas up to now phytosaurs have been considered incapable of performing the high walk on functional morphological grounds (Parrish 1986b; *pace* Baird 1957 and Chatterjee 1978).

Because the prints of *Apatopus*, when the skeleton of *Parasuchus* is superimposed over them, are so close to the body wall, could not have been situated anywhere near the distance of a body radius from the girdles, it is difficult to see how the animal could have been using

any mode of locomotion except one very much like the crocodylian high walk, as has been inferred for aetosaurs and other pseudosuchians closer to and including crocodylomorphs (Bonaparte 1984; Parrish 1986a, 1987). In this case, erect stance, parasagittal gait and the ability to do the high walk would have evolved only once in pseudosuchians; and because all known ornithosuchians were limited to erect stance and parasagittal gait (Padian 1997), the common ancestor of Archosauria would have shared these features. To this argument can be added: the point that there are no morphological features, such as trochanters or ridges that would prevent phytosaurs, or the common ancestor of archosaurs from executing the movements that could produce the *Apatopus* tracks.

We would have to look to non-archosaurian archosauriforms to understand the transition between obligate sprawling stance with rotary gait and the archosaurian condition of erect stance and parasagittal gait. Some of this depends on the phylogenetic position of Ornithosuchidae, on the discovery of complete skeletal manus and pedes, and on precise identification of other Triassic reptile tracks (Carrano and Wilson 2001). Kubo and Benton (2007) suggested that erythrosuchids may have also been

capable of a parasagittal gait, based on inferences of load vectors on the hind limbs. If so, these features may have appeared in archosauriforms more basal than archosaurs; however, corroboration of this on functional and ichnological grounds still requires testing.

## CONCLUSIONS

Ornithosuchians (dinosaurs and their relatives) could not sprawl, or walk other than with erect stance and parasagittal gait (Padian 1997). They therefore show a different modification than that of pseudosuchians, and Bonaparte (1984) linked this to differences in the morphology of the pelvis and proximal femur between the two groups: pseudosuchians dorsally flared the ilium over the acetabulum to help hold the weakly offset femoral head in the hip socket, whereas ornithosuchians favoured a well offset femoral head, a deeper acetabulum and no lateral flaring of the dorsal ilium. There is no evidence that the derived pseudosuchian condition was intermediate between the basal tetrapod condition and that seen in ornithosuchians (Gatesy 1991a). Therefore, the obligate erect stance of ornithosuchians is a secondary (apomorphic) feature of this clade, which apparently evolved independently from animals already capable of executing it facultatively. It remains to be seen, then, where in the lineage of (non-archosaurian) archosauromorphs this faculty first evolved. That will require the difficult exercise of matching those skeletons with Triassic footprints, and determining stance and gait therefrom.

The evidence available to us, given new analyses and reconstructions, indicates that *Apatopus* tracks were most likely made by phytosaurs; those phytosaurs were using an erect stance and parasagittal gait, much as crocodiles do today and as Parrish (1986a; 1987) has inferred for 'rauisuchians' and aetosaurs. Consequently, we hypothesize that erect stance and parasagittal gait were present in the common ancestor of all archosaurs, and possibly outside the crown-group Archosauria, depending on further investigations.

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*Editor.* P. David Polly

## REFERENCES

- AVANZINI, M., DALLA VECCHIA, F. M., MIETTO, P., PIUBELLI, D., PRETO, N., RIGO, M. and ROGHI, G. 2007. A vertebrate nesting site in Northeastern Italy reveals unexpectedly complex behavior for late Carnian reptiles. *Palaios*, **22**, 465–475.
- BAIRD, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology, Harvard College*, **117**, 449–520.
- BAKKER, R. T. 1971. Dinosaur physiology and the origin of mammals. *Evolution*, **25**, 636–658.
- BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, B*, **302**, 605–720.
- 1990. The species of *Rhynchosaurus*, a rhynchosaurian (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London, B*, **320**, 213–306.
- BOCK, W. 1952. Triassic reptilian tracks and trends of locomotive evolution. *Journal of Paleontology*, **26**, 395–433.
- BONAPARTE, J. F. 1971. Los tetrapodos del sector superior de la Formacion Los Colorados, La Rioja, Argentina (Triasico Superior). I. Parte. *Opera Geologica Lilloana*, **22**, 3–185.
- 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia – Pseudosuchia) y su significado en el origen de los Saurischia. Chañarensis inferior, Triasico Medio de Argentina. *Acta Geologica Lilloana*, **13**, 5–90.
- 1984. Locomotion in raiuisuchid thecodonts. *Journal of Vertebrate Paleontology*, **3**, 210–218.
- BRINKMAN, D. 1980. The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Canadian Journal of Zoology*, **58**, 2187–2200.
- CARRANO, M. T. and WILSON, J. A. 2001. Taxon distributions and the tetrapod track record. *Paleobiology*, **27**, 564–582.
- CHARIG, A. J. 1972. The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. 121–155. In JOYSEY, K. A. and KEMP, T. S. (eds). *Studies in vertebrate evolution: Essays presented to Dr. F. R. Parrington, FRS*. Oliver & Boyd, Edinburgh, 284 pp.
- CHATTERJEE, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology*, **21**, 83–128.
- COOMBS, W. P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly Review of Biology*, **53**, 393–418.
- DESOJO, J. B. 2004. Los aetosaurios (Amniota: Diapsida) de America Del Sur: sus relaciones y aportes a la biogeografía y bioestratigrafía del Triasico continental. PhD Dissertation, Universidad de Buenos Aires, Buenos Aires, 176 pp.
- FOSTER, J. R., HAMBLIN, A. H. and LOCKLEY, M. G. 2003. *Apatopus* trackway and other footprints from the Chinle Group of southern Utah: an update. *Ichnos*, **10**, 165–167.
- GATESY, S. M. 1991a. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *Journal of Zoology (London)*, **224**, 577–588.
- 1991b. Hind-limb scaling in birds and other theropods – implications for terrestrial locomotion. *Journal of Morphology*, **209**, 83–96.

- 1995. Functional evolution of the hindlimb and tail from basal theropods to birds. 219–234. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate evolution*. Cambridge University Press, New York, 277 pp.
- GAUTHIER, J. A. 1984. *A cladistic analysis of the higher systematic categories of the Diapsida*. Unpublished PhD Dissertation, University of California, Berkeley, 564 pp.
- 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, **8**, 1–55.
- GOWER, D. J. 2000. Rausuchian archosaurs (Reptilia: Diapsida): an overview. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **218**, 447–488.
- and NESBITT, S. J. 2006. The braincase of *Arizonasaurus babbitti* – further evidence for the non-monophyly of “rauisuchian” archosaurs. *Journal of Vertebrate Paleontology*, **26**, 79–87.
- GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus*. *University of Texas Contributions to Geology*, **4401**, 273–361.
- HAUBOLD, H. 1971. *Encyclopedia of Paleoherpology, Part 18: Ichnia Amphibiorum et Reptiliorum Fossilium*. Gustav Fischer Verlag, Stuttgart, 124 pp.
- 1984. *Saurierfahrten*. A. Ziemsen Verlag, Wittenberg, 232 pp.
- 1986. Archosaur footprints at the terrestrial Triassic–Jurassic transition. 190–201. In PADIAN, K. (ed.). *The beginning of the Age of Dinosaurs: Faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, Cambridge, 378 pp.
- HUTCHINSON, J. R. 2006. The evolution of locomotion in archosaurs. *Comptes Rendus PalEvol*, **5**, 519–530.
- and GATESY, S. M. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology*, **26**, 734–751.
- 2006. Beyond the bones. *Nature*, **440**, 292–294.
- IRMIS, R. B., NESBITT, S. J., PADIAN, K., SMITH, N. D., TURNER, A. H., WOODY, D. and DOWNS, A. 2007. A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science*, **317**, 358–361.
- KREBS, B. 1965. *Ticinosuchus ferox* nov. gen., nov. sp., Ein neuer Pseudosuchier aus der Trias der Monte San Giorgio. *Schweizerische Paläontologische Abhandlungen*, **81**, 1–140.
- KUBO, T. and BENTON, M. J. 2007. Evolution of hindlimb posture in archosaurs: limb stresses in extinct vertebrates. *Palaeontology*, **50**, 1–11.
- KUHN, O. (ed.) 1976. *Encyclopedia of Paleoherpology, Part 13: Thecodontia*. Gustav Fischer Verlag, Stuttgart, 136 pp.
- LOCKLEY, M. J. and MEYER, C. 2000. *Dinosaur tracks and other fossil footprints of Europe*. Columbia University Press, New York, 323 pp.
- NESBITT, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History*, **302**, 1–84.
- OLSEN, P. E. and HUBER, P. 1998. The oldest Late Triassic footprint assemblage from North America (Pekin Formation, Deep River Basin, North Carolina, USA). *Southeastern Geology*, **38**, 77–90.
- and PADIAN, K. 1986. Earliest records of *Batrachopus* from the Southwest U.S., and a revision of some early Mesozoic crocodylomorph ichnogenera. 259–274. In PADIAN, K. (ed.). *The beginning of the Age of Dinosaurs: Faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, Cambridge, 378 pp.
- PADIAN, K. 1983. A functional analysis of flying and walking in pterosaurs. *Paleobiology*, **9**, 218–239.
- 1997. Bipedality. 68–70. In CURRIE, P. J. and PADIAN, K. (eds). *The encyclopedia of dinosaurs*. Academic Press, San Diego, 869 pp.
- 2001. Cross-testing adaptive hypotheses: phylogenetic analysis and the origin of bird flight. *American Zoologist*, **41**, 598–607.
- 2003. Pterosaur stance and gait, and the interpretation of trackways. *Ichnos*, **10**, 115–126.
- and OLSEN, P. E. 1984a. The track of *Pteraichnus*: not pterosaurian, but crocodylian. *Journal of Paleontology*, **58**, 178–184.
- — 1984b. Footprints of the Komodo dragon and the trackways of fossil reptiles. *Copeia*, **1984**, 662–671.
- — 1989. Ratite footprints and the stance and gait of Mesozoic theropods. 231–241. In GILLETTE, D. D. and LOCKLEY, M. (eds). *Dinosaur tracks and traces: Proceedings of the First International Conference on Dinosaur Tracks and Traces*. Cambridge University Press, New York, 454 pp.
- PARKER, W. G. 2008. Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. *PaleoBios*, **28**, 1–40.
- PARRISH, J. M. 1986a. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. *Hunteria*, **1**, 2–35.
- 1986b. Structure and function of the tarsus in the phytosaurs (Reptilia: Archosauria). 35–43. In PADIAN, K. (ed.). *The beginning of the Age of Dinosaurs: Faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, Cambridge, 378 pp.
- 1987. The origin of crocodylian locomotion. *Paleobiology*, **13**, 396–414.
- 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsal monophyly. *Journal of Vertebrate Paleontology*, **13**, 287–308.
- PEYER, K., CARTER, J., SUES, H.-D., NOVAK, S. and OLSEN, P. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology*, **28**, 363–381.
- RAINFORTH, E. C. 2007. Ichnotaxonomic updates from the Newark Supergroup. 49–59. In RAINFORTH, E. C. (ed.). *Field Guide and Proceedings of the XXIV Annual Conference and Fieldtrip of the Geological Association of New Jersey, Contributions to the Paleontology of New Jersey (II)*. Geological Association of New Jersey, New Jersey Geological Survey, Trenton, 124 pp.
- REWCASLE, S. 1980. Form and function in lacertilian knee and mesotarsal joints: a contribution to the analysis of sprawling locomotion. *Journal of Zoology*, **191**, 147–170.
- ROMER, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. *Breviora*, **378**, 1–10.

- 1972. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. *Breviora*, **394**, 1–7.
- SCHOCH, R. R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **246**, 1–35.
- SULLIVAN, C. S. 2007. Function and evolution of the hind limb in Triassic archosaurian reptiles. PhD Dissertation, Harvard University, 267 pp.
- SZALAY, F. 1984. Arboreality: is it homologous in metatherian and eutherian mammals? *Evolutionary Biology*, **18**, 215–258.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London*, **B 244**, 103–204.
- 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London*, **B 248**, 53–134.
- WEINBAUM, J. C. and HUNGERBUEHLER, A. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern USA. *Palaeontologische Zeitschrift*, **81**, 131–145.
- WOODWARD, A. S. 1907. On *Rhynchosaurus articeps* (Owen). *Reports of the British Association for the Advancement of Science*, **1906**, 293–329.