The Origin and Early Radiation of Archosauriforms: Integrating the Skeletal and Footprint Record

Massimo Bernardi¹,²*, Hendrik Klein³, Fabio Massimo Petti¹, Martín D. Ezcurra⁴

¹ MuSe–Museo delle Scienze, Trento, Italy, ² School of Earth Sciences, University of Bristol, Bristol, United Kingdom, ³ Saurierwelt Paläontologisches Museum, Neumarkt, Germany, ⁴ School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom

* massimo.bernardi@muse.it

Abstract

We present a holistic approach to the study of early archosauriform evolution by integrating body and track records. The ichnological record supports a Late Permian–Early Triassic radiation of archosauriforms not well documented by skeletal material, and new footprints from the Upper Permian of the southern Alps (Italy) provide evidence for a diversity not yet sampled by body fossils. The integrative study of body fossil and footprint data supports the hypothesis that archosauriforms had already undergone substantial taxonomic diversification by the Late Permian and that by the Early Triassic archosauromorphs attained a broad geographical distribution over most parts of Pangea. Analysis of body size, as deduced from track size, suggests that archosauriform average body size did not change significantly from the Late Permian to the Early Triassic. A survey of facies yielding both skeletal and track record indicate an ecological preference for inland fluvial (lacustrine) environments for early archosauromorphs. Finally, although more data is needed, Late Permian chirotheriid imprints suggest a shift from sprawling to erect posture in archosauriforms before the end-Permian mass extinction event. We highlight the importance of approaching palaeobiological questions by using all available sources of data, specifically through integrating the body and track fossil record.

Introduction

Archosauriforms (crocodiles, birds, and multiple extinct taxa) became one of the most successful tetrapods on land during the Mesozoic, radiating into virtually all habitats in the aftermath of the end-Permian mass extinction event (EPME) [1]. The crown clade Archosauria comprises Pseudosuchia (all forms closer to crocodiles than to birds) and Avemetatarsalia (all forms closer to dinosaurs and birds than to crocodiles) [2–6], which together constitute one of the most taxonomically diverse clades of extant amniotes with about 10,000 species. Current continuous research efforts by both palaeontologists and molecular biologists seek for a better understanding of the early evolution of archosaurs, and specially the timing of evolutionary...
events and the macroevolutionary history of the group. Reliable knowledge of their early palaeobiogeography can provide hints about their plesiomorphic ecological preferences and, if compared with an independent source of data, may reveal biases in the fossil record. Finally, the understanding of the origin of archosauriforms is essential for depicting the dawn of dinosaur evolutionary history because features and fate of the first archosauriforms would have eventually set the course for the evolution of the Dinosauria [4,7].

The origin and early diversification of archosauriforms can only be comprehensively studied by looking at all available sources of palaeontological evidence. However, the possible contribution of ichnological data has rarely been taken into account when considering archosauriform origins. No recent macroevolutionary analyses on this topic use ichnology as a source of data [1,5,8,9], with the notable, but single, exception of the debate on dinosauromorph and dinosauriform origins (e.g., [10,11]). Trace fossils are considerably more abundant than body fossils, and are often preserved in those depositional environments not appropriate for the preservation of body fossils. Historical ichnological investigation has usually been based on extramorphological (substrate-related) rather than anatomical features, preventing many researchers from considering the track record as a reliable source of data.

Furthermore ichnological data often allow only a coarse taxonomic assignement and are therefore useless in fine-scale integrative analysis. Only a few recent studies have analyzed trackmaker identity based on synapomorphies identified in the skeletal record. When a cladistic approach is used, as first advised by Olsen ([12,13]; see also [14–16]), trace fossil occurrences can potentially be used as a reliable source of data in macroevolutionary studies, such as on biomechanics and locomotion (e.g., [17,18]), palaeobiogeography and palaeoecology (e.g., [19,20]), timing of evolutionary events [10], and other fundamental palaeobiological aspects, as recently reviewed by Bernardi et al. [21].

In this framework, we review Late Permian and Early Triassic archosauriform evolutionary history, considering both ichnological and body fossil records. We describe new specimens and re-interpret previously published records that allow us to document the presence of archosauriform footprints in the Late Permian of the southern Alps. These indentifications are based on synapomorphy-based approach and represent the oldest archosauriform fossil tracks documented globally. We also discuss their implications in the light of the oldest skeletal taxa, which have a comparable age [1,22–25]. Finally, we integrate track and body fossil records for the Early Triassic with the aim of building a holistic (“total-evidence”) understanding of the early evolutionary history of Archosauriformes.

Materials and Methods

Seven chirotheriid and chirotheriid-like manus and pes imprints from the Upper Permian of the southern Alps, northeastern Italy (PZO 5753 NMS 1235, MGR 0032, N.S. 34/82, R 6, MUSE 7446, NMS 1; PZO and NMS: Museo di Scienze Naturali dell’Alto Adige/Naturmuseum Südtirol, Bolzano/Bozen, Italy; MGR, Museo Geologico di Redagno, Bolzano/Bozen, Italy; N.S. and R: Museum of Paleontology of the “Sapienza” University of Rome, Rome, Italy; MUSE, Museo delle Scienze di Trento, Trento, Italy) were studied at first hand in their repositories. These specimens are the only Permian tracks currently known (i.e., published) worldwide that can be referred unambiguously to an archosauriform trackmaker (see discussion below). Specimen PZO 5753 is the best-preserved Permian footprint described here (1A–B) and was collected from the Deutschnofen/Nova Levante locality within the Arenaria di Val Gardena Formation (see S1 Text for other names of this formation), in the southern Alps region of the Bolzano Province (northeastern Italy). This locality is situated just a few kilometers from the well-known Bletterbach Gorge fossil locality, where all the other specimens here described
were found. The footprint-bearing levels can be dated as late Capitanian to Changhsingian [26] or Lopingian (Visscher, in [27]) based on palynological evidence (see S1 Text for more details). Tracks were mapped using the conventional method of tracing footprint outlines on transparent acetate overlays. Photographs were taken under artificial light conditions for documentation. Descriptions and measurements follow standard procedures and terminology of Leonardi and Thulborn [28,29]. Some specimens labeled as 75/18, 73/93/A12 and 75/2 in Conti et al. ([30]: Figs 20, 21, 24, pls. 6(1), 8(2)) were deposited in the collections of the N.S. and/or IGPF (Museum of Paleontology and Prehistory "Piero Leonardi", University of Ferrara, Ferrara, Italy), but they could not be re-located during our study conducted between 2013 and 2014, and are probably lost. Their published photographs and drawings were used here for comparative purposes.

## Results

### The Permian Track Record

The Palaeozoic archosauriform track record is very scarce; it is restricted to a few chirotheriid footprints from the Lopingian of the Dolomites region of the southern Alps (NE Italy) that are discussed here (see also [30]). Supposed archosauriform footprints from the Late Permian of Morocco [31] have recently been redated as Early Triassic [32].

A rich diversity of tetrapod trackways associated with a well preserved macroflora has been described in the last decades from the Upper Permian Dolomites (e.g., [30,33–42]). Conti et al. [30] suggested the presence of possible "archosaur footprints" from the Arenaria di Val Gardena of the Bletterbach (see below), but these authors did not describe them in detail, nor did they deal with their evolutionary implications. The same specimens (73/93/A12, 75/2) were subsequently cited in multiple papers (e.g., [40,43–45]) but, again, never discussed in the context of archosauriform evolution. We redescribe and discuss here these specimens and document new footprints using a synapomorphy-based approach for their attribution to trackmaker(s) [sensu 14].

**Restudy of previously reported chirotheriid tracks from the Arenaria di Val Gardena.**

PZO 5753 is the natural cast of a left footprint figured by Wopfner ([46]: Fig 2), but was never properly described (Fig 1A). It is 17.0 cm in length and 12.5 cm in width. The robust digits show rounded phalangeal pads and metatarsophalangeal pads proximally, forming a posteriorly concave margin. Digits increase in length from I to III. Only the distal portion of digit IV is preserved and its position indicates that it was slightly shorter than digit III. Digits I–III possess moderate divarication angles, whereas digit IV is more strongly abducted laterally. All digits terminate in rounded distal tips. Digit V consists of a massive subtriangular basal pad with a narrowing, laterally curved distal portion. Clawmarks are visible on digits I–III and they are robust and sub-triangular with a blunt tip. Digits and clawmarks possess medial and lateral striations, documenting the dynamics and movement of the pes in the substrate. All features, especially the shape of digit V and relative length of digit IV, closely resemble those observed in *Protochirotherium* [47], an ichnogenus particularly abundant in the Lower Triassic deposits of central Europe (Germany and Poland) and northern Africa [32,47–49]. Chirotheriid apomorphies are present in this specimen (e.g., massive posterolateral digit V, compact digit group I–IV), allowing an attribution to the ichnofamily Chirotheriidae [50]. However, the absence of an associated manus imprint prevents an unambiguous assignment to the ichnogenus level. PZO5753 is therefore assigne to cf. *Protochirotherium* (see S2 Text).

Conti et al. ([30]; see also [43]) assigned three footprints (75/18; 73/93/A12; 75/2) from the Bletterbach locality to “archosauirian trackmakers” ([30]: Figs 20, 21, 24, pl. 6(1), pl. 8(2)). These footprints were identified as “Proterosuchia indet., *Synaptichnium* isp., and
Chirotherium isp., respectively. Specimen 75/18 assigned to “Proterosuchia” indet. is not diagnosable beyond a diapsid non-chirotherian pes imprint: the arrangement of digit group I–IV with IV > III > II > I is plesiomorphic for diapsids, and a small, straight digit V is not consistent with a chirotheriid identification. The identification of Synaptichnium isp. for specimen 73/93/A12 cannot be evaluated here because there was no photograph published by Conti et al. [30] and the specimen could not be re-located during this study. As for specimen 75/2 ([30]: pl. 6 (1)), the compact digit group I–IV and the posterolaterally oriented and recurved massive digit V, is typical for chirotheriids. The interpretative drawing of Conti et al. [30: Fig 24] differs in several aspects from the published photograph of the specimen ([30]: plate 6(1)), and only

Fig 1. Pes and manus imprints of cf. Protochirotherium. A, left pes imprint PZO 1111 from the Arenaria di Val Gardena (Upper Permian) of the Deutschofen/Nova Levante locality in northern Italy preserved as a natural cast. B, interpretative drawing. C, Protochirotherium wolfhagensense pes-manus set (Holotype) from the Detfurth Formation (Lower Triassic, Olenekian) of Germany. D, interpretative drawing.

doi:10.1371/journal.pone.0128449.g001
digit V seems to reflect a congruent morphology in the photograph and drawing. Digit lengths increase from I to III, with digit IV (3.2 cm) being considerably shorter than digit III (4.2 cm) and even digit II (3.84 cm). Distal ends of digits have a blunt shape, with exception of that of digit I that is distinctly tapering. Further observations cannot be made based on the published photograph. Although the absence of the manus imprint prevents any definitive assignment, this footprint closely resembles those of the ichnogenus *Protochirotherium*.

A track from the Deutschnofen/Nova Levante locality NMS 1235 (Fig 2C) was originally figured by Wopfner ([46]: Fig 3). It is a fragmentary, strongly deformed tetradactyl-pentadactyl imprint of 12 cm in length and 8.5 cm in width, and represents a manus or pes with broad
digits. The middle digit (probably digit III) possesses a blunt distal end whereas the thinner?medially positioned digit? I is tapering. All the other digits are only partially preserved. Because of its incompleteness, digit proportions are unknown. No definitive chirotheriid apomorphies can be recognized in this imprint, but the overall shape suggests a chirotheriid affinity.

**New chirotheriid material from the Arenaria di Val Gardena Formation.** There are several other imprints from the Arenaria di Val Gardena Formation of the Bletterbach canyon that show chirotheriid morphology. They represent pes and manus imprints, but their isolated preservation prevents an unequivocal ichnotaxonomic attribution.

1. An isolated tetradactyl imprint (MGR 0032) (Fig 2A) is fan-shaped, short and broad. It possesses broad, robust digits finishing in blunt distal ends, with the exception of digit II that tapers distally. Digits increase in length from I to IV and digit IV is the longest. The proximal margin of the imprint is posteriorly convex. The proportionally short imprint resembles those of chirotheriid manus imprints, although no definitive assignement can be made.

2. N.S. 34/82: a pentadactyl, semi-plantigrade to plantigrade imprint with a length of ca. 6 cm (Fig 2B). Digits are relatively broad and rounded, with narrow claw traces. Digit I is the shortest and digit III the longest of the imprint. Digit IV is slightly shorter than digit III and digit V has a posterolateral orientation. N.S. 34/82 is a manus or pes impression and its
overall shape and digit proportions suggest chirotheriid affinities, resembling Protochirotherium. However, no more definitive assignment can be made.

3. R6: a tetradactyl manus or pes imprint with a length of ca. 10 cm (Fig 2D). It possesses short, rounded and broad digits, narrow claw marks, and a semicircular palmar or plantar surface. This imprint is very similar to chirotheriid footprints, but the absence of measurable characters prevents an unambiguous attribution.

4. MUSE 7446: a pentadactyl, semi-plantigrade, deeply impressed footprint (Fig 2E), with a length of ca. 13 cm. It possesses short and blunt digits, in which digits III and IV are the longest and subequal in length. Digit IV is laterally spread and digit V is large and laterally oriented, with a massive heel. This imprint strongly resembles a Protochirotherium pes because of digit proportions and the robustness of digit V.

5. NMS 1: a tetradactyl manus or pes imprint (Fig 2F) with a length of ca. 13 cm. This imprint possesses long anterior digits, probably representing digits II–IV. Digit V is posterolaterally oriented, short and oval. This specimen is a probable chirotheriid, but the absence of several characters (e.g., digit I) prevents attribution to a specific ichnogenus.

Trackmaker identification. It is commonly assumed that tracks can only be attributed with difficulty to their producers at a low taxonomic level [14,51]. However, there is wide consensus on the assignment of some footprint morphgroups to broad taxonomic categories (e.g., [14,52–55]) based on the physical association of track and body fossil material (e.g., [56]) or detailed comparisons between tracks and limb skeletal remains (e.g., [16,57–61]). A synapomorphy-based approach was established in the last two decades and represents a clear step forward from the previous rough shape comparisons [10,12,15,18,62–68]. This approach has considerably constrained potential trackmakers and allows testing of the taxonomic hypotheses of trackmakers.

The ichnofamily Chirotheriidae Abel, 1935 [50] comprises the ichnogenera Chirotherium Kaup, 1835 [69], Brachychirotherium Beurlen, 1950 [70], Isochirotherium Haubold, 1971 [58], Synaptichnium Nopcsa, 1923 [71], Parasynaptichnium Mietto, 1987 [72] and Protochirotherium Fichter and Kunz, 2004 [48]. These taxa have been consistently interpreted as produced by archosauriforms, including stem-archosaurs and pseudosuchians [57–59,61,73–83]. Previous studies have followed the approach of Haubold [57,58,74,75], who proposed the following characters as distinct archosaur (sensu lato, = archosauriform) features: (1) narrow trackway, (2) small manus relative to the pes, and (3) pes and manus imprints with compact anterior digit group I–IV and posterolaterally positioned, strongly reduced digit V. However, only character 3 represents a possible archosauromorph apomorphy.

A compact digit group I–IV is also present in non-archosauromorph diapsids, such as Youngina (SAM-PK-K7710, Iziko South African Museum, Cape Town, South Africa: [84]) and lepidosaurs (e.g., Dalungosaurus [85]). A posterolaterally positioned and divergent metatarsal and digit V is present in lepidosaurs and archauromaorphs (e.g., Dalungosaurus [85]; Prototherosaurus [86]), and probably some enigmatic basal diapsids (e.g., kuehneosaurids [87]). Nevertheless, the combination of a posterolaterally positioned, laterally oriented and robust digit V, and a massive metatarso-phalangeal region shorter than or as long as digit I seem to be unique to archauromaorphs among diapsids. Therefore, they are useful apomorphies for the identification of archauromaorph trackmakers.

Another apomorphy useful for the identification of archauromaorph imprints is a metatarsal IV shorter than or as long as metatarsal III. This character state has been recovered as a synapomorphy of the archauromaorph clade that includes Erythrosuchus and more crownward
archosauriforms ([5]: p. 191), and metatarsal length seems to be directly correlated with digit length ([5]: p. 177).

As a result, the chirotheriid imprints from the Upper Permian of the southern Alps and other chirotheriids (i.e., Protochirotherium, Brachychoirotherium, Chirotherium, and Isochirotherium, see [18]) can be confidently identified as produced by an archosauriform, based on the presence of a digit IV shorter than or as long as digit III and a proportionally short digit V. Footprints PZO 1111 and 75/2 (the latter from Conti et al. 1977) and possibly, although not conclusively, the other specimens discussed in the previous section (NMS 1235, MGR 0032, N. S. 34/82, R 6, MUSE 7446, NMS 1), represent the oldest ichnologic record of archosauriforms worldwide.

The Early Triassic Track Record

No Induan archosauriform tracks have been reported so far, contrasting with the relatively abundant body fossil record of the group in the Lystrosaurus Assemblage Zone of South Africa and its penecontemporaneous strata in China. Olenekian tracks are known from central Europe (Germany, Poland), northern Africa (Morocco) and North America (western USA). Track-bearing units in Germany are the Volpriehausen, Detfurth, Hardegsen and Solling formations (middle Buntsandstein). From the Volpriehausen Formation of southern Thuringia (Germany), Gümbel [88] figured chirotheriid footprints that have been assigned to the ichnogenus Protochirotherium by Klein et al. [47] and Klein and Niedźwiedzki [49]. The Detfurth and Hardegsen formations yielded assemblages with archosauriform footprints, including Protochirotherium (the type material, and the specimens previously referred to Palaeochirotherium which has been shown to be a junior synonym [49]), Synaptichnium, Rotodactylus and Prorotodactylus [48,89–92]. The Solling Formation, which represents the Olenekian-Anisian transition, yields a diverse archosauriform ichnofauna that has been referred to Chirotherium barthii, Chirotherium sickleri, Brachychoirotherium, Synaptichnium, Isochirotherium and Rotodactylus [57,58,74,76,78]. In particular, the “Thüringischer Chirotheriensandstein” [57,58,74], a unit that represents the uppermost part of the Solling Formation, preserves most of these footprints. It has to be noted here that the identification of Brachychoirotherium in the Early-Middle Triassic is doubtful, because of problems with the diagnosis of this taxon reported by Karl and Haubold [93] and Klein and Haubold [94].

Archosauriform tracks are also known from the upper Olenekian Wióry Formation, which crops out in the Holy Cross Mountains of Poland [95–97]. They have been revised recently by Klein and Niedźwiedzki [49], and assigned to the ichnogenera Protochirotherium and Synaptichnium. Prorotodactylus specimens, from the same unit and locality, have been interpreted as dinosaurmorph tracks by Brusatte et al. [10] and Niedźwiedzki et al. [11] (but see [49,98,99] for different views on trackmaker attribution). Klein et al. [32] reported from the Lower Triassic Timezgadiouine Formation of Morocco tracks of Protochirotherium and Synaptichnium. From the Lower Triassic Alpine Buntsandstein of Austria, Kainer et al. [100] figured chirotheriid imprints that they assigned to aff. Protochirotherium and cf. Synaptichnium. In North America, Early Triassic archosauriform tracks are known from the Wupatki Member of the lower Moenkopi Formation of Arizona, which is most probably late Olenekian in age [101,102], although no high-resolution dating is available. These footprints have been assigned to Chirotherium sickleri, Synaptichnium diabloense, Isochirotherium coltoni and Chirotherium rex [101,102]. The Moenkopi Formation of Utah (member 6 of [103]; Lower-?Middle Triassic); preserves footprints that have been assigned to chirotheriids and are very similar to Protochirotherium and Synaptichnium [103]. In South America, Melchor and de Valais [104] reported
Brachychirotherium isp. from the Early-Middle Triassic Tarjados Formation of Argentina, which was subsequently re-assigned to Synaptichnium by Klein and Lucas [105].

The Permian the Skeletal Record

Archosauromorpha includes crown diapsids more closely related to archosaurs than to lepidosaurs [106] (Fig 3). The minimum divergence time of the group based on the body fossil record is estimated at 255.7–259.9 Ma (middle-late Wuchiapingian) ([1] see also [107]), suggesting a minimum Permian evolutionary history for the group of 3.1–8.3 Ma. Only four archosauromorph nominal species are known from Permian units: Eorasaurus olsoni from the late Capitanian–Wuchiapingian of Russia [1,108]; Protorosaurus speneri from the middle Wuchiapingian of Germany and England [109–112]; Aenigmastropheus parringtoni from the middle–late Wuchiapingian of Tanzania [1]; and Archosaurus rossicus from the Changhsingian of Russia [1,22–24,113,114] (Fig 3). Protorosaurus and Aenigmastropheus have been recovered as very basal archosauromorphs in recent phylogenetic analyses [1,112]. Archosaurus represents the only unambiguous Permian archosauriform to date, and its holotype (PIN 1100/55, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia: premaxilla) and several of the formerly referred specimens (e.g., PIN 1100/48: skull roof; PIN 1100/66, 66a, 66b: cervical vertebrae; PIN 1100/78: dentary) possess a morphology extremely similar to that of Early Triassic proterosuchids [1,2,22–24]. Eorasaurus might represent the oldest archosauriform, but the very fragmentary condition of its hypodigm and similarities with tanystropheids force us to consider this assignment as tentative [1]. Potential Permian archosauromorph cranial bones and vertebrae have been reported from Uruguay ([115]; MDE pers. obs.), but substantial debate exists about the Permian or Triassic age of the fossil-bearing unit and therefore this record should be considered temporally ambiguous [1]. Regardless, multiple phylogenetic analyses suggest that the ghost lineages of some archosauromorph groups (e.g., tanystropheids, rhynchosaurs, potentially choristoderans) should extend back into the Permian [5,116], indicating an evolutionary history of several independent lineages before the EPME that is not currently sampled in the fossil record.

Most of these Permian archosauromorphs are known from fragmentary remains, mostly restricted to the axial skeleton [1]. However, Protorosaurus is an exception because is known from multiple articulated specimens, including all regions of the skeleton [112]. As a result, Protorosaurus is particularly relevant for the integration of skeletal and ichnological data because it is the only Permian archosauromorph with known autopodia (Fig 4).

The Early Triassic Skeletal Record

The archosauromorph record in the aftermath of the EPME is considerably more abundant and geographically widespread than that of the Permian [1,24]. Recent studies based on osteological evidence concluded that the early evolutionary radiation of archosauriforms and archosaurs occurred by the late Early Triassic or early Middle Triassic [5,117]. Nevertheless, the earliest phase of archosauriform history is still patchily understood, largely because of the paucity of the early record of several lineages [5,117,118]. In this regard, the presence of poposauroid archosaurs in uppermost Olenekian strata implies long ghost lineages, suggesting that all main archosauriform (and many archsaurian) lineages should already have been present by that time (e.g., protorochampsids, doswelliids, euparkeriids, phytosaurs, ornithosuchids, gracilisuchids, aetosaurs, and avemetatarsalians) [1,5,117–123].

Early Triassic non-archosauriform archosauromorphs are relatively taxonomically diverse and restricted to a handful of groups, including rhynchosaurs (Noteosuchus), 'prolactiforms/protorosaurs' (e.g., Prolacerta, Kadimakara, Boreopricea, Prolacertoides, Czatkowiella,
Malutinisuchus, Vritramimosaurus, Augustaburiania) and probable trilophosaurids (e.g., Coelodontognathus, Vitalia). Non-archosauriform archosauromorphs remains have been found in Lower Triassic units worldwide, namely South America, Africa, Antarctica, Europe, Asia, and Australia [1,22,25,116,124–139].

The Early Triassic archosauriform record is dominated in terms of taxonomic diversity by species historically referred to Proterosuchidae [25]. The proterosuchid record is particularly abundant in well sampled Induan–lower Olenekian beds of South Africa (Proterosuchus...
Erythrosuchids appear for the first time in the fossil record in the Olenekian beds of Russia and South Africa (Garjainia prima, Garjainia madiba [24,25,155–157]). In addition, several Early Triassic non-archosaur archosauriforms of uncertain or problematic phylogenetic affinities have been described from South America [138,139], South Africa [158], Antarctica [159], Europe (Osmolksina, Collilongus [137,160]), and the Early–Middle Triassic of China (Fugusuchus, Guchengosuchus [161,162]). The Early Triassic archosaur record is extremely scarce when it is compared with that of non-crown archosauromorphs, being restricted to poposaurus found in the uppermost Olenekian beds of Germany and Russia (Ctenosauriscus, Vytshegdoesuchus [23,24,117]), and upper Olenekian–lower Anisian beds of China (Xilousuchus [119]).

Discussion
Can Any Known Permian Archosauromorph Be the Producer of Chirotheriid Tracks?
Establishing if known Permian archosauromorphs can be considered potential candidates for Protochirotherium-like or chirotheriid trackmakers means establishing whether the track record supports recent fragmentary findings or provides hints to a diversity still not documented by skeletal remains. Three of the four currently recognized Permian archosauromorph species (i.e., Archosaurus rossicus, Eorasaurus olsoni and Aenigmastropheus parringtoni) are only known from fragmentary remains lacking autopodial bones [1,22,24,108]. The only Permian archosauromorph species with known autopodia is Protorosaurus speneri, a quadrupedal reptile with a body length of up to 1.5–2.0 m [112]. The foot of Protorosaurus possesses five metatarsals, of which metatarsal IV is the longest, followed by metatarsals III, II, I, and V, respectively. Pedal digit IV is the longest, clearly longer than III, and the pedal phalangeal formula is 2-3-4-5-4 [112]. The limb morphology of the latest Permian proterosuchid archosauriform Archosaurus and putative referred specimens is unknown. Nevertheless, their morphology is extremely similar to that of the earliest Triassic proterosuchids (e.g., Proterosuchus fergusi) and autopodial morphology may have been possibly similar to that of stratigraphically younger proterosuchids. Metatarsal IV (63.5 mm) is considerably longer than metatarsal III (57.0 mm) in Proterosuchus fergusi (SAM-PK-K140), resembling the condition in non-archosauriform archosauromorphs (the complete length of digit IV is unknown in collected proterosuchid specimens). In contrast, metatarsal III is as long as, or longer than, metatarsal IV in Erythrosuchus and more crownward archosauriforms [2,3,5,163].

Conti et al. [30] excluded Proterosuchus as the producer of some of the Permian tracks described here because in this taxon metatarsals I–IV strongly increase in length, suggesting footprints with a sharp cross-axis angle (i.e., defined as the angle between the metapodial-phalangeal axis and the long axis of the footprint along digit III; of the four angles formed by these two axes, the cross-axis angle is the lateral and anterior one; [28]). As a result, potential footprints of Proterosuchus would be strongly asymmetric or ectaxonic with digit IV being considerably longer than digit III, and with a very long digit V. In this respect they would probably be similar to those expected for Protorosaurus [86] (Fig 4A and 4B) and other non-archosauriform archosauromorphs. In contrast, the imprint pattern of Protochirotherium is mesaxonic.
The producer-taxon of *Synaptichnium* footprints had a digit IV longer than, or subequal to, digit III, resulting in a distinct ectaxonic shape of the pes imprint. Thus, early archosauromorphs, such as *Protorosaurus* [86] and *Proterosuchus* [25] are potential candidate trackmakers of *Synaptichnium* footprints, although extremely narrow *Synaptichnium* trackways, known for example from the Moenkopi Group (Lower-Middle Triassic) of Arizona ([101], [102]; p. 30, Fig 28), might contradict this possibility. Both protorosaurs/tanystropheids and proterosuchids are expected to have had more spread gaits [25,164]. Note also that digit IV subequal to digit III may indicate a trackmaker more derived than proterosuchids [25].

Klein and Niedźwiedzki [49] and Klein et al. [47] suggested erythrosuchids and/or pseudosuchian archosaurs as probable producers of Early Triassic *Protochirotherium* footprints. Limb position in early archosauriforms is poorly known, therefore any definitive conclusion cannot be reached. Nevertheless, articulated protorosuchid skeletons show a sprawling posture (e.g., *Chasmatosaurus* *yuani*: IVPP V4067, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) and the very similar morphology of the acetabulum and proximal end of femur in proterosuchids and erythrosuchids suggests a similar sprawling posture in life. All known *Protochirotherium* trackways are narrow, indicating that protorosuchids and erythrosuchids might be excluded as potential producers of chirotheriid footprints because they should have left broader trackways. Accordingly, we suggest that more crownward archosauriforms are the probable trackmakers of Late Permian and Early Triassic chirotheriid and chirotheriid-like imprints. The presence of a digit IV shorter than or subequal to digit III in *Protochirotherium* indicates that the producer is an archosauriform, or even a member of Archosauromorpha. Accordingly, the chirotheriid *Protochirotherium*-like footprints described here from the southern Alps are the oldest evidence of a mesaxonic foot within Archosauromorpha. The stratigraphically oldest archosauriform with a mesaxonic foot is *Euparkeria* from the early Middle Triassic of South Africa (see [122] and references therein; Fig 4C and 4D), but several Early Triassic archosauriforms may also have had mesaxonic feet based on their phylogenetic position (e.g., poposauroid archosaurs [5]). Interpretations of *Osmolskina czatkowicensis* as an euparkeriid [138] might imply the presence of mesaxonic taxa in the Early Triassic, but recent analyses recovered it further outside Archosauromorpha with respect to *Euparkeria* ([120]; see also [122]).

A number of other early archosauromorph clades which have their ghost lineages extending into the considered time span, should also be considered. Among these are tanystropheids, rhynchosaurs, trilophosaurids, and proterochampsids that all have well preserved limbs allowing full comparison with the track record. Tanystropheids have digit IV > III (e.g., [165]) and would have therefore produced ectaxonic imprints. Furthermore they were mainly marine and their footprints, named *Gwyneddichnium*, are known from the Upper Triassic of Pennsylvania and Colorado [53,166]. Rhynchosaurs can also be excluded as possible trackmakers of mesaxonic tracks, as their pes have digit IV > III (e.g., [167]). Furthermore the ichnospecies *Synaptichnium pseudosuchoides* was recently assigned to rhynchosaurs by Tresise and King [168]. *Trilophosaurus*, also had an ectaxonic pes. *T. buettneri* [169], for example, shows a pes digit IV clearly longer than III. Lockley et al. [170] dubitably attributed *Apatopus* ichnogenus to trilophosaurs, but more recently Padian et al. [60] discarded this possibility. When autopodia are preserved, as in *Chanareusuchus*, proterochampsids show digit III ≥ IV [171], an arrangement therefore compatible with a mesaxonic print. However their digit IV is extremely thin, and digit V is highly reduced, in the shape of a ‘hook’ without phalanges [3,171,172] making proterochampsids not suitable candidates as *Protochirotherium* trackmakers. Furthermore, other chirotheriid tracks, like *Isochirotherium delicatum*, have been attributed to proterochampsid trackmakers [173].

The discovery of Late Permian *Protochirotherium*–like footprints therefore represent also the oldest evidence of mesaxony, indicating the presence of archosauriforms more crownward...
than proterosuchids before the Permian-Triassic boundary, and predating the appearance of a mesaxonic foot in the body fossil record by ca. 10 My (Fig 5). Long ghost ranges in early archosauriform evolution were inferred because of the presence of the proterosuchid *Archosaurus* and the potential archosauriform *Eorasaurus* in the Late Permian of Russia [1]. *Eorasaurus* was recovered as more closely related to erythrosuchids and *Euparkeria* than to proterosuchids. As a result, *Protochirotherium*-like tracks provide independent evidence for a potentially taxonomically broader evolutionary radiation of archosauriforms in the Late Permian than previously recorded.

**Early Archosauriform Palaeobiogeography**

A recent revision of the early archosauromorph body fossil record found a rather palaeolatitudinally broad geographical distribution for the group during the Late Permian [1]. Current evidence indicates that early archosauromorphs spanned from few degrees north to the palaeo-Equator (Germany and England) to a palaeolatitude of 30°N (Russian localities) in the northern hemisphere to high palaeolatitudes of 55°S (Tanzania) in southern Pangaea (Fig 6).

The report here of Late Permian palaeo-Equatorial archosauriforms partially bridges the gap between the northern records of archosauromorphs and that of the Southern Hemisphere, representing the palaeolatitudinally lowest occurrence of the group. In addition, these imprints extend the geographic range of archosauriforms between palaeolatitudes of 0°–30°N before the EPME.

The Early Triassic body and footprint fossil record indicates a global geographic distribution of archosauromorphs, being considerably broader than that present in the Late Permian.

---

**Fig 5. Evolution of the mesaxonic pes in archosauromorphs.** Grey and black boxes indicate evolution of apomorphic characters: grey = ectaxony, black = mesaxony. Late Permian *Protochirotherium* pulls the evolution of mesaxony down the archosauriform tree and anticipates the oldest skeletal remain (*Euparkeria capensis*) by 10 Ma.

doi:10.1371/journal.pone.0128449.g005
In particular, tracksites in Arizona and Utah support the presence of archosauromorphs in central-western Pangaea during the Early Triassic, documented in the body fossil record by the single report of Nesbitt [178], while the best known evidence of the presence of the group in this region is Anisian in age (i.e., *Arizona-saurus* [179,180]).
Multiple non-archosaur archosauriform and archosaur lineages are inferred to have been present during the Early Triassic based on current phylogenetic hypotheses, and yet these remain unsampled (e.g., gracilisuchids, ornithosuchids, phytosaurs, proterochampsids [5,117,118,181]). The striking absence of crown archosaurs in the Early Triassic, with the exception of poposauroids, has led to the hypothesis that early archosaurs originated or, at least began to diversify, in areas that have a bias towards the non-preservation of body fossil remains or are not well sampled, such as the tropics [117,119]. The geographic palaeodistribution of archosauriform skeletal remains during the Early Triassic shows that most of them occur outside the tropical belt, with the sole exception of the three European taxa: *Ctenosauriscus* [117], *Osmolskina*, and *Collilongus* [137,160,166]. In contrast, archosauriform ichnoses are mainly concentrated in the tropics, namely between the palaeo-Equator and the Tropic of Cancer, in central and western Pangaea. The only possible exception is a single *Synaptichnium* footprint from northwestern Argentina [104,105], but the age of this record is poorly constrained and could be either Early or Middle Triassic. An uneven sampling or taphonomic bias are likely explanations for this distribution pattern, and future discoveries may reveal the presence of more chirotheriids at high palaeolatitudes in the northern and southern hemispheres as well as body fossils at low latitudes. Beyond these biases, footprints indicate that archosauriforms were distributed also at low latitudes soon after their origin. It is worth noting that Sun et al. [182] suggested that the absence of vertebrates from the Equatorial belt in the Early Triassic reflects lethally hot temperatures for five million years after the EPME. This conclusion however was based solely on the distribution of body fossils, and archosauriform track data reject this hypothesis.

**Body Size in Early Archosauriforms**

Studies of evolutionary changes in body size have long attracted the attention of researchers. After comparing ichnological and skeletal fossil evidence, we test here the effect of the new data on previously published studies. Although Permian chirotheriid footprints are rare, the body size of the trackmaker can be compared with that of the oldest archosauriforms. We estimated an approximate body length for *Archosaurus* using a linear regression (premaxillary body height vs. skull length) composed of ten Early Triassic proterosuchid specimens (see S3 Text). The total skull length of *Archosaurus* is estimated as ca. 460 mm and closely resembles that of the largest sampled specimens of the earliest Triassic *Proterosuchus fergusii* (GHG 231, Geological Survey, Pretoria, South Africa: 477.0 mm [120]). As a result, *Archosaurus* should have reached a total body length similar to that of *Proterosuchus fergusii*, being of approximately 3–3.5 m [142]. Therefore, *Archosaurus* is considerably larger than the only known complete Permian archosauromoph, *Prototosaurus speneri*, which reached a body length of up to 1.5–2 m [112]. The total body length of the Permian chirotheriid trackmakers from the southern Alps is calculated in approximately 2 m, following estimations conducted by Gand et al. [183] for Triassic chirotheriid footprints. As a result, the body size estimated for these Permian trackmakers fits the range expected for the oldest known archosauriforms based on the body fossil record.

**Evolutionary trends in early archosauriform evolution.** Trends in archosaur body size through time have been recently investigated using both skeletal [184,185,186] and ichnological data [18]. Footprint size (commonly measured as pes length) is a reliable parameter for such analysis because it correlates directly with body size [17,29], and can be easily measured from footprints, even if they are not arranged in trackways. In addition, when considering true tracks (or shallow undertracks—about 1 cm deep, [187]), pes length is less dependent on substrate consistency and taphonomic distortion with respect to other descriptive measurements.
(e.g., interdigital angle; \[188,189\]). Using a database of 125 published trackway occurrences, Kubo and Kubo \[18\] found a statistically significant increase in foot length between Early and Middle Triassic non-dinosauriform archosauriforms, and interpreted the result in the context of locomotory and biomechanical novelties that occurred during the early evolution of archosaurs.

We use here a modified version of the database of Kubo and Kubo \[18\] of Early and Middle Triassic chirotheriids, which was increased and updated with the addition of 17 new records from the Late Permian and Early Triassic (see S1 Table). Late Triassic occurrences were present in the original database, but they were excluded here because they are outside the main aims of our study, which are: (i) explore evolutionary trends with the addition of the Permian record and test for significant changes in size across the Permo-Triassic boundary, and (ii) test the effect of the inclusion of the so-called “Wióry Formation megaichnofauna” described by Niedźwiedzki and Ptaszyński \[97\] and not included in the original dataset. The megaichnofauna of the Wióry Formation represents the oldest known ichnological record of very large (ca. 6 m long) archosauriforms \[97\].

The small sample size of the Permian archosauriform track record prevents a robust statistical analysis of the data and full comparison with that from the Early and Middle Triassic. However, until further discoveries are made, a first set of analyses is valuable when testing for patterns and trends. Permian chirotheriids (mean pes length = 117.7 mm, median = 120 mm, 3σ = 33.4) are fully within the variance of the Early Triassic sample (mean pes length = 134.4 mm, median = 122 mm, 3σ = 78.1), and the latter distribution only partially overlaps that of the Middle Triassic. A Mann-Whitney U test showed that the difference in foot length between Late Permian and Early Triassic occurrences is non-significant (W = 197.5, p = 0.8594), but it is significant between the Early Triassic and Middle Triassic (W = 345, p = 0.0001), in which Middle Triassic footprints are significantly larger. Accordingly, the impact of the “Wióry megaichnofauna” on the analysis was not significant and bolsters the results recovered by Kubo and Kubo \[18\]. The extreme values (minimum and maximum) between Late Permian and Early Triassic ichnological samples are strikingly different, in which both upper and lower body size boundaries increased in Early Triassic archosauriforms (Fig 8). However, because the mean and median of the Late Permian sample are not significantly different from that of the Early Triassic, we can suggest that the average body size of archosauriforms did not change substantially across the Permo-Triassic boundary. However, more data is necessary for a strong test of the hypothesis that the EPME did not have a significant effect on archosauriform average body size. On the other hand, if maximum values only are taken into account, the large size of the Wióry ichnofauna \[97\] implies that maximum body size doubled in less than 10 My during the aftermath of the EPME.

**Palaeoecological Inferences**

Trace fossils may be preserved in environments that are not appropriate for the preservation of bones and teeth. Therefore, ichnological data can provide an independent source of information about the ecology of trackmakers, and allow evaluation of a potential bias in skeletal data (e.g., allochthonous association). To investigate this issue, the depositional environment of each Late Permian and Early Triassic geological formation that yielded skeletal and/or ichnological archosauriform records was surveyed. Strikingly, almost all specimens, including both body and trace fossils, were found in non-marine formations, ranging from fluvial (e.g., channel and braided systems) to lacustrine environments. The only two exceptions are *Protorosaurus*, [112] and the tanistrophid *Augustaburiania* [136]. However, the occurrences of *Protorosaurus* are very likely allochthonous, because at least one specimen possesses gut contents that are terrestrial in origin [190]. Although the fossil bearing horizon is not always well
constrained, resulting in uncertainties regarding the depositional environment for several taxa and ichnotaxa (e.g., fluvial/lacustrine, fluvial/aeolian) both body fossils and track fossils were mostly found in fluvial sediments (respectively 47% and 71% in our database, that when all possible fluvial influence on the depositional environment is considered goes up to 68% and 100%, respectively; see S2 Table for more details; Fig 9). Interestingly, no track fossil is known

**Depositional environment**

**Fig 8. Archosauriform body size through time as derived from track length.** Average track size indicates that archosauriform body size did not change significantly from the Late Permian to Early Triassic, although maximum values show a significant increase. The Permo-Triassic mass extinction might not have affected archosauriform body size. Based on data of S1 Table.

doi:10.1371/journal.pone.0128449.g008

**Fig 9. Depositional environment of late Permian and Early Triassic archosauromorph-bearing formations.** The common pattern exhibited by the body fossil and the track fossil record suggest a real environmental/ecological preference for inland-fluvial (lacustrine) environments for early archosauromorphs.

doi:10.1371/journal.pone.0128449.g009
from lacustrine deposits (or max 4% if the fluvial/lacustrine uncertainties are considered) while 23% of body fossils come from this depositional environment. We interpret this datum as a preservational bias. The whole predominance of early archosauromorphs in fluvial and lacustrine rocks may in fact reflect a preservational bias, as suggested for other taxa (see [191] and references therein). However, the common pattern exhibited in both the skeletal and track record may suggest a real environmental/ecological preference for inland-fluvial (lacustrine) environments for early archosauromorphs. The occurrence of early archosauromorphs in multiple fluvial (to lacustrine) subenvironments (e.g., floodplains, braided river systems) with a broad palaeolatitudinal range implies that they lived inland, inhabiting freshwater continental environments, irrespective of the local palaeoclimate, and they possibly possessed broad climatic tolerance.

Locomotory Features

The acquisition of an upright limb posture and a parasagittal gait was a key innovation in early archosauriform evolution [17,57,58,60,74,75]. The position of the legs under the body enabled fast running with low loss of energy compared with the gait of typical sprawlers. The classical view, expressed by Charig [192], maintained that Early Triassic archosaurs (sansu lato) were sprawlers, Middle Triassic ones were semi-erect (or "semi improved", as he termed it), and fully erect gait emerged in the late Middle to Late Triassic. However, in an analysis of compiled fossil trackway data, Kubo and Benton [16] showed that archosauriforms with erect posture originated and became common in the Early Triassic. The parasagittal gait is reflected in the narrow trackways of all chirotheriids, with occasional long strides [57,58,75]. Chirotheriid trackways are all characterized by a narrow gauge [18,57,58] and all known Early Triassic Protochirotherium trackways show a similar condition (see [49]: Figs 9, 12, 15). No unambiguous chirotheriid trackways have so far been discovered in the Late Permian of the southern Alps, but it is more parsimonious to hypothesise that Permian chirotheriid trackways would show the same pattern exhibited by all Triassic chirotheriids. Protochirotherium–like tracks from the southern Alps can therefore be considered as the earliest indirect evidence for narrow-gauge trackmakers, which walked with an erect gait. This suggests that at least some archosauriforms may have adopted an erect gait during the Late Permian. Together with the trends observed in some therapsid lineages [17], Late Permian Protochirotherium–like tracks may therefore support an earlier shift from a sprawling to an erect posture in archosauriforms, raising questions about the conclusions of Kubo and Benton [17], who linked the shift to the Permo-Triassic event. However, this conclusion does not contradict the hypothesis that erect walkers radiated soon after the mass extinction [17], and discoveries of Palaeozoic chirotheriid trackways are strictly necessary to support any conclusion on this issue.

Conclusions

The integrative study of body and track records allows a better understanding of the origin of archosauriforms. The ichnological record supports a Late Permian–Early Triassic radiation of archosauriforms not well documented by skeletal material, but implied by ghost ranges deduced from the most recent phylogenetic analyses and supported by the recent recovery of the Late Permian Eorasaurus as a possible non-proterosuchid archosauriform. Newly studied footprints from the southern Alps provide evidence of a Late Permian diversity not yet sampled by body fossils, which widens the geographical distribution of this clade before the Permo-Triassic boundary. Studied tracks provide evidence of several morphologically distinct archosauriform groups in central Pangaea in the Late Permian–Early Triassic and suggests that this region might be crucial also for future discoveries of body fossil remains.
The integration of footprint and body fossil data sheds light on early archosauriform evolution and suggests that:

1. Archosauriforms had already undergone substantial taxonomic diversification by the Late Permian. *Eorasaurus* (a derived archosauromorph with no appendicular skeleton preserved) and cf. *Protochirotherium* tracks are independent evidence of a taxonomically broader evolutionary radiation of archosauriforms in the Late Permian than currently expected.

2. The integration of body and track data suggests a broader geographical distribution of Early Triassic archosauromorphs. Footprints support body fossil data by indicating that archosauriforms were distributed also at low latitudes soon after their origin.

3. Tracks indicate that the archosauriform body size did not change significantly from the Late Permian to Early Triassic. The possibility that the Permo-Triassic event did not affect substantially archosauriform body size constitutes a new hypothesis that should be tested in the future with more data both from the body and footprint record.

4. Skeletal and track record suggest an environmental/ecological preference for inland fluvial (lacustrine) environments for early archosauromorphs. The broad palaeolatitudinal range occupied implies broad climatic tolerance.

5. Late Permian *Protochirotherium*-like imprints might support a shift from a sprawling to an erect posture in archosauriforms before the Permo-Triassic event (contra Kubo and Benton [16]). Although no Palaeozoic chirotheriid trackways are known to date, this constitute a new working hypothesis that will be tested as new specimens become available.

**Supporting Information**

**S1 Table.** Late Permian to Middle Triassic archosauriform track length database used in the statistical analysis.

(DOCX)

**S2 Table.** Depositional environment of the fossil-bearing formations.

(XLSX)

**S1 Text.** Geology and age of the Arenaria di Val Gardena Formation.

(DOCX)

**S2 Text.** Ichnostratigraphic remarks.

(DOCX)

**S3 Text.** *Archosaurus rossicus* body length estimation.

(DOCX)

**Acknowledgments**

We thank Evelyn Kustatscher (NMS, PZO); Roberta Pancaldi, Benedetto Sala (IGPF); Marigabriella Fornasiero (Museum of the Department of Geology of the University of Padova, Padova); Maria Rita Palombo, Umberto Nicosia (N.S.,R); Christian Weber (MGR); Bernhard Zipfel, Bruce Rubidge, Jonah Choiniere and Fernando Abdala (Evolutionary Studies Institute, University of the Witswatersrand, Johannesburg, South Africa); Markus Moser and Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany); Ellen de Kock (GHG); Jun Liu and Corwin Sullivan (IVPP); Elize Butler and Jennifer Botha-Brink (NM); Andrey Sennikov (PIN); Sheena Kaal (SAM) and Heidi Fourie (Ditsong National
Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa) for access to specimens. Discussion with Marco Avanzini (MUSE, Trento), Sebastian Voigt (Urweltmuseum GEOSKOP, Burg Lichtenberg) and Evelyn Kustatscher (NMB, Bolzano) improved our study. We thank Mike Benton (University of Bristol), Grzegorz Niedźwiedzki (Uppsala University) and an anonymous referee for the insightful reviews. We also thank the editor David Carrier for his constructive criticism. This study is part of the project “The Permian–Triassic ecological crisis in the Dolomites: extinction and recovery dynamics in Terrestrial Ecosystems” financed by the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano–South Tyrol.

**Author Contributions**

Conceived and designed the experiments: MB. Performed the experiments: MB HK FMP MDE. Analyzed the data: MB HK FMP MDE. Contributed reagents/materials/analysis tools: MB HK FMP MDE. Wrote the paper: MB HK FMP MDE.

**References**

1. Ezcurra MD, Scheyer TM, Butler RJ (2014) The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS ONE 9(2): e89165. doi: 10.1371/journal.pone.0089165 PMID: 24586565
2. Sereno PC, Arcucci AB (1990) The monophyly of crurotarsal ankle joints. Neu Jahrb Geol Paläont Ab 180: 21–52.
3. Sereno PC (1991) Basal archosaurs: phylogenetic relationships and functional implications. J Vert Pal 10: 1–53.
4. Benton MJ (1999) *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. Phil Trans R Soc London B 354: 1423–1446.
5. Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull Am Mus Nat Hist 352: 1–292.
6. Sereno PC (2005) The logical basis of phylogenetic taxonomy. Syst Biol 54: 595–619. PMID: 16109704
7. Benton MJ, Forth J, Langer MC (2014) Models for the Rise of the Dinosaurs. Curr Biol 24: R87–R95. doi: 10.1016/j.cub.2013.11.083 PMID: 24456985
8. Brusatte SL, Benton MJ, Lloyd GT, Ruta M, Wang SC (2011a) Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). Earth Environ Sci Trans R Soc Edinburgh 101: 367–382.
9. Nesbitt SJ, Desojo JB, Irmis RB (2013) Anatomy, phylogeny and palaeobiology of early archosaurs and their kin. Geol Soc London Spec Publ, 379 pp.
10. Brusatte SL, Nied wiedzi G, Butler RJ (2011b) Footprints pull origin and diversification of dinosaur stem-lineage deep into Early Triassic. Proc R Soc London B 278: 1107–1113. doi: 10.1098/rspb.2010.1746 PMID: 20926435
11. Nied wiedzi G, Brusatte SL, Butler RJ (2013). *Prorotodactylus* and *Rotodactylus* tracks: an ichnological record of dinosauromorphs from the Early–Middle Triassic of Poland. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 319–351.
12. Olsen PE (1995) A new approach for recognizing track makers. Geol Soc America Abstracts. pp. 72.
13. Olsen PE, Smith JB, McDonald NG (1998) Type material of the type species of the classic theropod footprint genera *Eubrontes, Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield basins, Connecticut and Massachusetts, USA). J Vert Pal 18: 586–601.
14. Carrano MT, Wilson JA (2001) Taxon distributions and the tetrapod track record. Paleobiology 27: 564–82.
15. Padian K (2003) Pterosaur stance and gait, and the interpretation of trackways. Ichnos 10: 115–26.
16. Farlow JO, Schachner ER, Sarrazin JC, Klein H, Currie PJ (2014) Pedal proportions of *Poposaurus gracilis*: convergence and divergence in the feet of archosaurs. Anat Record 297: 102–1046.
17. Kubo T, Benton MJ (2009) Tetrapod postural shift estimated from Permian and Triassic trackways. Palaeontology 52: 1029–1037.
18. Kubo T, Kubo M (2013) Analysis of Triassic archosauriform trackways: difference in stride/footprint ratio between dinosauromorphs and other archosauriforms. Palaios 28: 259–265.

19. Lockley MG, Meyer CA, Hunt AP, Lucas S (1994) The distribution of sauropod tracks and track-makers. In: Lockley MG, dos Santos VF, Meyer CA, Hunt AP, editors. Aspects of sauropod paleobiology. GAIA 10: 233–248.

20. Mannion PD, Upchurch P (2010) A quantitative analysis of environmental associations in sauropod dinosaurs. Paleobiology 36: 253–282.

21. Bernardi M, Petti FM, Piñuela L, García-Ramos JC, Avanzini M, Lockley MG (in press) The Mesozoic vertebrate radiation in terrestrial settings. In: Mangano M, Buatois L, editors. The trace-fossil record of major evolutionary events. Springer-Verlag, series Topics in Geobiology.

22. Tatarinov LP (1960) Otkrytie pseudozhukhii v verkhnei permi SSSR. Paleontologischeskii Zhurnal 4: 74–80.

23. Sennikov AG (1988) The role of the oldest thecodontians in the vertebrate assemblage of Eastern Europe. Paleontol J 1988: 78–87.

24. Gower DJ, Sennikov AG (2000) Early Archosaurs from Russia. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN, editors. The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge. pp. 140–159.

25. Ezcurra MND, Butler RJ, Gower DJ (2013) ‘Proterosuchia’: the origin and early history of Archosauriformes. In: Nesbitt SJ, Desojo JB, Irms RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 9–33.

26. Pittau P (2005) The microflora. In: Pittau P, Kerp H, Kustatscher E, editors. The Bletterbach canyon: “Let us meet across the P/T boundary”—workshop on Permian and Triassic Palaeobotany and Palynology, Bozen 16.-18.06.2005, Excursion guide. pp. 9–19.

27. Kustatscher E, van Konijnenburg-van Cittert JHA, Bauer K, Butzmann R, Meller B, Fischer TC (2012) A new flora from the Upper Permian of Bletterbach (Dolomites, N-Italy). Rev Palaeobot Palynol 182: 1–13.

28. Leonardi G (1987) Glossary and manual of tetrapod footprint palaeoichnology. Departamento Nacional de Produção Mineral, Brasilia, 117 pp.

29. Thuilbom T (1990) Dinosaur tracks. Chapman and Hall, London.

30. Conti MA, Leonardi G, Mariotti N, Nicosia U (1977) Tetrapod footprints of the “Val Gardena Sandstone” (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. Palaeont It NS 40: 1–91.

31. Hmich D, Schneider W, Saber H, Voigt S, El Wartiti M (2006) New continental Carboniferous and Permian faunas of Morocco: Implications for biostratigraphy, palaeobiogeography and palaeoclimate. Geol Soc London, S Publi 265: 297–324.

32. Klein H, Voigt S, Hminna A, Saber H, Schneider J, Hmich D (2010) Early Triassic Archosaur-Dominated Footprint Assemblage from the Argana Basin (Western High Atlas, Morocco). Ichnos 17: 215–227.

33. Leonardi P (1948) Contributi alla conoscenza delle flora delle Arenarie di Val Gardena (Permiano medio-inf.) dell’Alto Adige: la nuova flora di Redagno e una felce di Egna. Mem Ist Geol Min Univ Padova 16: 3–15.

34. Leonardi P (1951) Ricerche sulla geologia della regione dolomitica. La ricerca scientifica, 21: 783–786.

35. Leonardi P, Conti MA, Leonardi G, Mariotti N, Nicosia U (1975) Pachypes dolomiticus n. gen. n. sp.: Pareiasaur footprint from the “Val Gardena Sandstone” in the western Dolomites (N. Italy). Atti Acc Naz Lincei, Rend Cl Sci ff mm nn 57: 221–232.

36. Conti MA, Leonardi G, Mariotti N, Nicosia U (1975) Tetrapod footprints, fishes and molluscs from the Middle Permian of the Dolomites (N. Italy). Mem Geopal Univ Ferrara 3: 139–150.

37. Conti MA, Fontana D, Mariotti N, Massari F, Neri C, Nicosia U, et al. (1986) The Bletterbach-Butterloch section (VGS and Bellerosphon Formation). In: Italian IGCP Group 302, editors. Field Conference on Permian and Permain-Triassic boundary in the south-Alpine segment of the western Tethys, Brescia, June 1986, Gield guide book, SGI, pp. 91–110.

38. Ceoloni P, Conti MA, Mariotti N, Nicosia U (1988) New late Permian tetrapod footprints from the southern Alps. Mem Soc Geol It 34 (1986): 45–56.

39. Valentini M, Nicosia U, Conti MA (2009) A re-evaluation of Pachypes, a pareiasaurian track from the Late Permian. N Jb Geol Paläont Abh 251: 71–94.
40. Avanzini M, Bernardi M, Nicosia U (2011) The Permo-Triassic tetrapod faunal diversity in the Italian southern Alps. In: Ahmad Dar I, Ahmad Dar M, editors. Earth and Environmental Sciences. pp. 591–608.

41. Uhl D, Butzmann R, Fischer TC, Me r B, Kustatscher E (2012) Wildfires in the Late Palaeozoic and Mesozoic of the southern Alps: The Late Permian of the Bletterbach-Butterloch area (Northern Italy). Riv It Pal Strat 118: 223–233.

42. Bernardi M, Kustatscher E, Petti FM, Franz M, Wappler T, Labandeira CC, et al. (Submitted) The Bletterbach terrestrial biota: a reference equatorial ecosystem for the late Permian. Palaeogeogr, Palaeoclim, Palaeoe col.

43. Conti MA, Leonardi G, Mietto P, Nicosia U (2000) Orme di tetrapodi non dinosauriani del paleozoico e Mesozoico d’Italia. In: Leonardi G, Mietto P, editors. Dinosauri in Italia, Accademia Editoriale Pisa–Roma. pp. 297–320.

44. Avanzini M, Tomasoni R (2004) Giornate di Paleontologia 2004, IV edizione, Bolzano 21–23 maggio 2004, Guida all’escursione: la gola del Bletterbach. Stud Trent Sci Nat Acta Geol 79 (2002): 1–34.

45. Avanzini M, Breda A, Kustatscher E (2010) Day 1: The Permo-Triassic succession at Bletterbach Gorge. In: Gianolla P, Avanzini M, Breda A, Kustatscher E, Preto N, Roghi G, et al., editors. Dolomites. 7th International Triassic Field Workshop: Pan-European Correlation of the Triassic. Field trip to the World heritage site of the tethyan Triassic. pp. 20–59.

46. Wopfner H (1999) Über Tetrapoden-Fährten, Kohlen und versteinerte Hölzer aus dem Grödner Sandstein (Perm) bei Deutschnofen. Der Schlern 73: 23–32.

47. Klein H, Niedźwiedzki G, Voigt S, Lagnaoui A, Hminna A, Saber A, Schneider JW (2013) The Tetrapod Ichnogenus Protochirotherium Fichter and Kunz 2004, a characteristic Early Triassic morphotype of central Pangea. Ichnos 20: 24–30.

48. Fichter J, Kunz R (2004) New genus and species of chirotherioid tracks in the Detfurth Formation (Middle Bunter, Lower Triassic) of central Germany. Ichnos 11: 183–193.

49. Klein H, Niedźwiedzki G (2012). Revision of the Lower Triassic tetrapod ichnofauna from Wióry, Holy Cross Mountains, Poland. Cross Mountains, Poland. New Mexico Mus Nat Hist Sci Bull 56: 1–62.

50. Abel O (1935) Vorzeitliche Lebenssspuren. Fischer Verlag, Iena. pp. 644.

51. Farlow JO, Pianka ER (2000) Body form and trackway pattern in Australian desert monitors (Squamata: Varanidae): Comparing zoological and ichnological diversity. Palaios 15: 235–247.

52. Baird D (1980) A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In: Jacobs LL, editor. Aspects of vertebrate history: Essays in honor of Edwin Harris Colbert. Mus Northern Arizona Press, Flagstaff. pp. 219–230.

53. Olsen PE, Kent DV, Sues H-D, Koeberl C, Huber H, Montanari A, et al. (2002) Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary. Science 296: 1305–1307. PMID: 12016313

54. Sarjeant WAS (1990) A name for the trace of an act: approaches to the nomenclature and classification of fossil vertebrate fossils. In: Carpenter K, Currie PJ, editors. Dinosaur systematics: perspectives and approaches. Cambridge Univ Press, Cambridge. pp. 299–307.

55. Thulborn T (2006) On the tracks of the earliest dinosaurs: implications for the hypothesis of dinosaurian monophyly. Alcheringa 30: 273–311.

56. Voigt S, Berman DS, Henrici AC (2012) First well-established track-trackmaker association of Paleozoic tetrapods based on Ichniotherium trackways and diadectid skeletons from the Lower Permian of Germany. J Vert Pal 27: 553–570.

57. Haubold H (1971a) Die Tetrapodenfährten des Buntsandsteins in der Deutschen Demokratischen Republik und in Westdeutschland und ihre Äquivalente in der gesamten Trias. Paläont Abhand A, 4: 395–548.

58. Haubold H (1971b) Ichnia Amphibiorum et Reptiliorum fossillium. Handbuch der Paläoherpetologie, 18: 1–124.

59. Demathieu G, Demathieu P (2004) Chirotheria and other ichnotaxa of the European Triassic. Ichnos 11: 79–88.

60. Padian K, Li C, Pchelnikova J (2010) The trackmaker of Apatopus: early diversification of archosaur stance and gait. Palaeontology 53: 175–189.

61. Heckert AB, Lucas SG, Rinehart LF, Celeskey MD, Spielmann JA, Hunt AP (2010) Articulated skeletons of the aetosaur Typhothorax coccinarum Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: early-mid Norian), eastern New Mexico, USA. J Vert Pal 30: 619–642.
62. Olsen PE, Baird D (1986) The ichnogenus Atreipus and its significance for Triassic biostratigraphy. In: Padian K, editor. The beginning of the Age of Dinosaurs. Cambridge Univ Press, Cambridge. pp. 61–87.

63. Wilson JA, Carrano MT (1999) Titanosaurs and the origin of "wide gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology 25: 252–267.

64. Wright JL (2005) Steps in understanding sauropod biology: the importance of sauropod tracks. In: Curry Rogers KA, Wilson JA, editors. The sauropods: evolution and paleobiology. Univ California Press, Berkeley. pp. 252–284.

65. Wilson JA (2005) Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. Paleobiology 31: 400–423.

66. Haubold H, Klein H (2000) Die dinosauroiden Fährten Parachirotherium–Atreipus–Grallator aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, Nor) in Franken. Halle Jahr Geowiss B 22: 59–85.

67. Haubold H, Klein H (2002) Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. Halle Jahr Geowiss B 24: 1–22.

68. Haubold H (1999) Tracks of the Dinosauromorpha from the Lower Triassic. Zbl Geol Paläont Teil I 7–8: 783–795.

69. Kaup JJ (1835) Thier-Fährten von Hildburghausen: Chirotherium oder Chirosauro. N Jahrb Min Geogn Geol Petref 327–328.

70. Beurten K (1950) Neue Fährtenfunde aus der Fränkischen Trias. N Jahrb Geol Paläont, 308–320.

71. Nopcsa F (1923) Die Familien der Reptilien. Fortschr Geol Paläont Berlin 2: 1–210.

72. Mietto P (1987) Nopcsa F (1923) Die Familien der Reptilien. Fortschr Geol Paläont Berlin 2: 1–210.

73. Krebs B (1965) Die Triasfauna der Tessiner Kalkalpen. XIX. Ticusuchus ferox, nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Georgio. Schweiz Paläont Abhand 81: 1–140. PMID: 11563352

74. Haubold H (1967) Eine Pseudosuchier-Fährtenfauna aus dem Buntsandstein Südhüringsens. Halle Jahr Mittel Erd 8: 12–48.

75. Haubold H (1984) Sauierfährten. Wittenberg, Ziensen, 231 p.

76. Haubold H (1986) Archosaur footprints at the terrestrial Triassic-Jurassic transition. In: Padian K, editor. The beginning of the age of dinosaurs. Cambridge Univ Press, Cambridge. pp. 189–201.

77. Haubold H (1999) Tracks of the Dinosauromorpha from the Lower Triassic. Zentral Geol Palä 1999: 783–795.

78. Haubold H (2006) Die Saurierfährten Chirotherium barthii Kaup, 1835—das Typusmaterial aus dem Buntsandstein bei Hildburghausen/Thüringen und das Chirotherium-Monument. Veröf Nat Mus Schlesisengen, 21: 3–31.

79. Lockley MG, Meyer C (2000) Dinosaur tracks and other fossil footprints of Europe. Columbia Univ Press, New York.

80. Gand G, De La Horra R, López-Gómez J, Barrenechea JF, López-Gómez J, et al. (2010) New ichnites from the Middle Triassic of the Iberian Ranges (Spain): palaeoenvironmental and palaeo-geographical implications. Hist Biol 22: 40–56.

81. Bowden AJ, Tresise GR, Simkiss W (2010) Chirotherium, the Liverpool footprint hunters and their interpretation of the Middle Trias environment. Geol Soc, London, Spec Publ 343: 209–228.

82. Lucas SG, Heckert AB (2011) Late Triassic aeosauras as the trackmaker of the tetrapod footprint ichnotaxon Brachychotherium. Ichnos 18: 197–208.

83. Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, et al. (2013). Aetosauria: A clade of armoured pseudosuchians from the Upper Triassic continental beds. In: Nesbitt SJ, Desojo JB, Irims RB editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 203–239.

84. Smith RMH, Evans SE (1996) New material of Youngina: evidence of juvenile aggregation in Permian diapsid reptiles. Palaeontology 39: 289–303.

85. Evans SE, Wang Y (2005) Dalringsaurus, a lizard from the Early Cretaceous Jehol Biota of northeast China. Acta Pal Pol 50: 725–742.

86. Gottmann-Quesada A, Sander PM (2009) A redescription of the early archosauromorph Protorosaurus speneri Meyer, 1832 and its phylogenetic relationships. Palaeontographica A 287: 123–220.

87. Evans SE, Haubold H (1987) A review of the Upper Permian genera Coelurosauravus, Weigeltisaurus and Gracilisaurus (Reptilia: Diapsida). Zool J Linn Soc 90: 275–303.
88. Gümbel F (2009) Saurierspuren in der Rhön; Der Buntsandstein und seine Fährten vom Handtier "Chirotherium". Mitt Biosph Res Rhön 14: 7–16.
89. Demathieu G, Haubold H (1982) Reptifährten aus dem Mittleren Buntsandstein von Hessen. Hall JB Geowiss 7: 97–110.
90. Fichter J, Lepper J (1997) Die Fährtenplatte vom Heuberg bei Gieselwerder. Philippa 8: 35–60.
91. Fichter J, Kunz R (2011) Neue Nachweise chirotherioider Fährten in der Detfurth-Formation (Mittlerer Buntsandstein, Untere Trias) bei Wolfhagen. Geol Jahrb Hessen 137: 5–18.
92. Fichter J, Kunz R (2013) "Dinosauromorph" tracks from the Middle Buntsandstein (Early Triassic: Olenekian) of Wolfhagen, northern Hesse, Germany. LNEG, Com Geol 100: 81–88.
93. Karl C, Haubold H (1998) Brachychirotherium aus dem Coburger Sandstein (Mittlerer Keuper, Karn/Nor) in Nordbayern. Hall JB Geowiss B, 20: 33–58.
94. Klein H, Haubold H (2004) Überlieferungsbedingte Variation bei Chirotherien und Hinweise zur Ichnotaxonomie nach Beispielen aus der Mittel-bis Ober-Trias (Anisium–Karnium) von Nordbayern. Hall JB Geowiss B 26: 1–15.
95. Fuglewicz R, Ptaszyński T, Rdzanek K (1990) Lower Triassic footprints from the Swietokrzyskie (Holy Cross) Mountains, Poland. Acta Pal Pol 35: 109–164.
96. Ptaszyński T (2000) Lower Triassic vertebrate footprints from Wióry, Holy Cross Mountains, Poland. Acta Pal Pol 45: 151–194.
97. Nied wiezgik G, Ptaszyński T (2007) Large Chirotheriidae tracks in the Early Triassic of Wióry, Holy Cross Mountains, Poland. Acta Geol Pol 57: 325–342.
98. Padian K (2013) The problem of dinosaur origins: integrating three approaches to the rise of Dinosauria. Earth Env Sci Trans R Soc Edinburgh 103: 423–442.
99. Langer MC, Nesbitt SJ, Bittencourt JS, Irmis RB (2013) Non-dinosaurian Dinosauromorpha. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 157–186.
100. Krainer K, Lucas SG, Ronchi A (2012) Tetrapod footprints from the Alpine Buntsandstein (Lower Triassic) of the Drau Range (Eastern Alps, Austria). Jahrb Geol Bund 152: 205–212.
101. Peabody FE (1948) Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. Univ Calif Publ Bull Dept Geol 27: 295–468.
102. Klein H, Lucas SG (2010) Review of the tetrapod ichnofauna of the Moenkopi Formation/Group (Early-Middle Triassic) of the American Southwest. New Mexico Mus Nat Hist Sci Bull 50: 1–67.
103. Thomson TJ, Heckert AB, Chure DJ (2014) First report on reptile tracks from the Moenkopi Formation (Lower-Middle Triassic) in Dinosaur National Monument, Utah. New Mexico Mus Nat Hist Sci Bull 62: 129–134.
104. Melchor RN, de Valais S (2006) A review of Triassic tetrapod track assemblages from Argentina. Palaeontology 49: 355–379.
105. Klein H, Lucas SG (2010) Tetrapod footprints— their use in biostratigraphy and biochronology of the Triassic. Geol Soc London S Pub 334: 419–446.
106. Gauthier JA, Kluge AG, Rowe T (1988) Amniote phylogeny and the importance of fossils. Cladistics 4: 105–209.
107. Benton MJ, Donoghue PCJ (2007) Paleontological evidence to date the Tree of Life. Mol Biol Evol 24: 26–53. PMID: 17047029
108. Sennikov AG (1997) An enigmatic reptile from the Upper Permian of the Volga River Basin. Paleontol J 31: 94–101.
109. von Meyer H (1830) Protorosaurus. Isis von Oken 1830: 517–519.
110. Meyer H von (1832) Palaeologica zur Geschichte der Erde und ihrer Geschöpfe. Verlag Siegmund Schmerber, Frankfurt a. M., 1–560.
111. Evans SE, King MS (1993) A new specimen of Protorosaurus (Reptilia: Diapsida) from the Marl Slate (late Permian) of Britain. Proc Yorkshire Geol Soc 49: 229–234.
112. Gottmann-Quesada A, Sander PM (2009) A redescription of the early archosauromorph Protosaurus speneri Meyer, 1832 and its phylogenetic relationships. Palaeontographica A 287: 123–220.
113. Sennikov AG, Golubev VK (2006) Vyazniki biotic assemblage of the terminal Permian. Paleont J 40: S475–S481.
114. Krassilov V, Karasev E (2009) Paleoecological evidence of climate change near and beyond the Permian–Triassic boundary. Palaeogeogr Palaeoclimatol Palaeoecol 284: 326–336.
115. Piñeiro, G., Meneghel, M., Velozo, P., Ezcurra, M.D. (in press) First record of proterosuchid archosauriforms from the Late Permian-Early Triassic Buena Vista Formation of Uruguay. Congreso Uruguayo de Zoología.

116. Dilkes, D.W. (1998) The Early Triassic rhynchosaur *Mesosuchus brownii* and the interrelationships of basal archosauriform reptiles. Philos Trans R Soc Lond B 353: 501–541.

117. Butler, R.J., Brusatte, S.L., Reich, M., Nesbitt, S.J., Schoch, R.R., Hornung, J.J. (2011) The sail-backed reptile *Ctenosaurus* from the latest Early Triassic of Germany and the timing and biogeography of the early archosaur radiation. PLoS One 6(10): e25693. doi: 10.1371/journal.pone.0025693 PMID: 22022431

118. Butler, R.J., Sullivan, C., Ezcurra, M.D., Liu, J., Lecuona, A., Sookias, R.B. (2014) New clade of enigmatic early archosaurs yields insights into early pseudosuchian phylogeny and the biogeography of the archosaur radiation. BMC Evolutionary Biology 14: 128. doi: 10.1186/1471-2148-14-128 PMID: 24916124

119. Nesbitt, S.J., Liu, J., Li, C. (2011) A sail-backed suchian from the Heshanggou Formation (Early Triassic: Olenekian) of China. Earth Env Sci Trans R Soc Edinburgh 101: 271–284.

120. Ezcurra, M.D., Lecuona, A., Martinelli, A. (2010) A new basal archosauriform diapsid from the Lower Triassic of Argentina. J Vert Pal 30: 1433–1450.

121. Ezcurra, M.D. (2010) *Prolacerta broomi* gen. et spec. nov. from the Olenekian of the Orenburg Region. Paleontol J 39: 199–209.

122. Sennikov, A.G. (2011) New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. Vert. Paleontol 18: 340–347.

123. Sennikov, A.G. (2005) A new specialized prolacertilian (Reptilia: Archosauromorpha) from the Lower Triassic of Poland. Acta Pal Pol 65: 235–281.

124. Watson, D.M.S. (1912) The skull of the Early Triassic archosauriform reptile *Ctenosaurus* and its phylogenetic significance. Zool J Linn Soc 140: 225–234.

125. Parrington, F.R. (1935) On *Prolacerta broomi*, gen. et sp. n. and the origin of lizards. Ann Mag Nat Hist 16: 197–205.

126. Young, C.C. (1936) On a new *Chasmatosaurus* from Sinkiang. Bull Geol Soc China 15: 291–311.

127. Carroll, R.L. (1976) *Noteosuchus* – the oldest known rhynchosaur. Ann S Afr Mus 72: 37–57.

128. Bartholomai, A. (1979) New lizard-like reptiles from the Early Triassic of Queensland. Alcheringa 3: 225–234.

129. Watson, D.M.S. (1912) *Mesosuchus brownii*, gen. et spec. nov. Rec Albany Mus 2: 298–299.

130. Ezcurra, M.D. (2010) Bida S (2009)– Hydrozoa and its phylogenetic significance. Zool J Linn Soc 140: 335–351.

131. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

132. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

133. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

134. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

135. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

136. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

137. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

138. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

139. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

140. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

141. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.

142. Ezcurra, M.D. (2010)– Mesosuchus with its phylogenetic significance. Zool J Linn Soc 140: 335–351.
142. Ezcurra MD, Butler RJ (2015) Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology 58: 141–170.

143. Young C-C (1958) On the occurrence of Chasmatosaurus from Wuhsiang, Shansi. Vert PalAsiatica 2: 259–262.

144. Young C-C (1963) Additional remains of Chasmatosaurus yuani Young from Sinkiang, China. Vert PalAsiatica 7: 215–222.

145. Young C-C (1978) A complete skeleton of Chasmatosaurus yuani from Xinjiang. Mem Inst Vert Paleontol and Paleoanthro Acad Sinica B 13: 26–46.

146. Camp CL, Banks MR (1978) A proterosuchian reptile from the Early Triassic of Tasmania. Alcheringa 2: 143–158.

147. Thulborn RA (1979) A proterosuchian thecodont from the Rewan Formation of Queensland. Mem Queensland Mus 19: 331–355.

148. Thulborn RA (1986) The Australian Triassic reptile Tasmaniosaurus triassicus (Thecodontia: Proterosuchia). J Vert Pal 6: 123–142.

149. Kear BP (2009) Proterosuchid archosaur remains from the Early Triassic Bulgo Sandstone of Long Reef, New South Wales. Alcheringa 33: 331–337.

150. Ezcurra MD (2014) The Osteology of the Basal Archosauromorph Tasmaniosaurus triassicus from the Lower Triassic of Tasmania, Australia. PLoS ONE 9(1): e86864. doi:10.1371/journal.pone.0086864 PMID: 24497988

151. von Huene F (1940) Eine Reptilfauna aus der ältesten Trias Nordrusslands. N JB Min Geol Paläont 84: 1–23.

152. Sennikov AG (1992) Drevneyshye triasovye arkhosavry Vostochnoy Evropy. Doklady Akademii Nauk 326: 896–899.

153. Huxley TH (1865) On a collection of vertebrate fossils from the Panchet Rocks, Ranigunj, Bengal. Mem Geol Surv India 3: 1–24.

154. Satsangi PP (1964) A note on Chasmatosaurus from the Panchet Series of Raniganj Coalfield, India. Current Science 33: 651–652.

155. von Huene F (1860) Ein grosser Pseudosuchier aus der Orenburger Trias. Palaeontographica Abt A 114: 105–111.

156. Hancox PJ (2000) The continental Triassic of South Africa. Zentralblatt Geol Paläont 1, 1998: 1285–1324.

157. Gower DJ, Hancox PJ, Botha-Brink J, Sennikov AG, Butler RJ (2014) A new species of Garjainia Ochev, 1958 (Diapsida: Archosauriformes: Erythrosuchidae) from the Early Triassic of South Africa. PLoS One 9: e111154. doi: 10.1371/journal.pone.0111154 PMID: 25386937

158. Modesto SP, Botha-Brink J (2008) Evidence of a second, large archosauriform reptile in the Lower Triassic Katberg Formation of South Africa. J Vert Pal 28: 914–917.

159. Smith ND, Crandall JR, Hellert SM, Makovicky PJ (2011) Anatomy and affinities of large archosauromorphs from the lower Fremouw Formation (Early Triassic) of Antarctica. J Vert Pal 31: 784–797.

160. Borsuk-Bialynicka M, Evans SE (2003) A basal archosauriform from the Early Triassic of Poland. Acta Pal Pal 48: 649–652.

161. Cheng ZW (1980) Vertebrate fossils. Mesozoic Stratigraphy and Paleontology of the Shan-Gan-Ning Basin 2. Publishing House of Geology, Beijing. pp. 114–171.

162. Peng J-H (1991) A new genus of Proterosuchia from the Lower Triassic of Shaanxi, China. Vert PalAsiatica 29: 95–107.

163. Gower D. J. 1996. The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. Zoological Journal of the Linnean Society, 116, 347–375.

164. Wild R (1973) Die Triasfauna der Tessiner Kalkalpen: XXIII. Tanystropheus longobardicus (Bassani) (Neue Ergebnisse). Schweiz Paläontol Abh 95: 1–162. PMID: 11563352

165. Nosotti S (2007) Tanystropheus longobardicus (Reptilia, Protorosauria): Reinterpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, Northern Italy). Mem Soc It Sci Nat Mus Civ S Nat Milano 35: 1–88.

166. Lockley M, Hunt AP (1995) Dinosaur tracks and other fossil footprints of the Western United States. New York: Columbia University Press. 338 p.

167. Benton MJ (1990) The species of Rhynchosaurus, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans R Soc London B 328: 213–306.
168. Tresise G, King MJ (2012) History of Ichnology: The Misconceived Footprints of Rhynchosaurs. Ichnos 19: 228–237.

169. Gregory JT (1945) Osteology and relationships of Trilophosaurs. Univ Texas Publ 4401: 273–359.

170. Lockley M, Conrad K, Paquette M (1991) Distribution and significance of Mesozoic vertebrate trace fossils in Dinosaur National Monument. Univ Wyoming Nat Park Ser Res Center Annual Report 15: 16.

171. Trotteyn MJ, Arcucci AB, Raugust T (2013) Proterochampsia: an endemic archosauriform clade from South America. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 59–90.

172. Romer AS (1972) The Chañares (Argentina) Triassic reptile fauna XII. The postcranial skeleton of the thecodont Chañaresuchus. Breviora 385: 1–21.

173. Avanzini M, Lockley M (2002) Middle Triassic archosaur population structure: interpretation based on Ichnoichirotherium delicatum fossil footprints (Southern Alps, Italy). Palaeogeogr, Palaeoclim, Palaeoecol 185: 391–402.

174. Broom R (1903) On a new reptile (Proterosuchus fergusi) from the Karroo Beds of Tarkastad, South Africa. Ann South African Mus 4: 161–163.

175. Borsuk-Bialynicka M, Sennikov AG (2009) Archosauriform postcranial remains from the Early Triassic karst deposits of southern Poland. Pal Polonica 65: 283–328.

176. Modesto SP, Sues HD (2004) The skull of the Early Triassic archosauromorph reptile Protops amigus and its phylogenetic significance. Zool J Linn Soc 140: 335–351.

177. Kühn O (1964) Ungelöste Probleme der Stammesgeschichte der Amphibien und Reptilien. Jahr Ver Nat Württemberg 118/119: 293–325.

178. Nesbitt S (2005) Stratigraphy and tetrapod fauna of major quarries in the Moenkopi Formation (Early-Middle Triassic) along the Little Colorado River of northern Arizona. Mesa SW Mus Bull 11: 18–33.

179. Welles SP (1947) Vertebrates from the Upper Moenkopi Formation of northern Arizona. Univ Cal Pub Geol Sci 27: 241–294.

180. Nesbitt SJ (2003) Arizonasaurus and its implications for archosaur divergences. Proc R Soc London B 270: S234–S237.

181. Brusatte SL, Benton MJ, Desojo JB, Langer MC (2010) The higher-level phylogeny of Archosauromorpha (Tetrapoda: Diapsida). J Syst Pal 8: 3–47.

182. Sun Y, Joachimski MM, Wignall PB, Yan C, Chen Y, Jiang H, et al. (2012) Lethally Hot Temperatures During the Early Triassic Greenhouse. Science 338: 366–370. doi:10.1126/science.1224126 PMID: 23087244

183. Gande G, Demathieu G, Montenat C (2007) Les traces de pas d’Amphibiens, de dinosaures et autres reptiles du Mésozoïque français: inventaire et interprétations. Palaeovertebrata 35: 1–149.

184. Sookias RB, Butler RJ, Benson RBJ (2012) Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. Proc R Soc B 279: 2180–2187. doi:10.1098/rspb.2011.2441 PMID: 22298850

185. Turner A, Nesbitt SJ (2013) Body size evolution during the Triassic archosauromorph radiation. In: Nesbitt SJ, Desojo JB, Irmis RB (eds) Phylogeny and palaeobiology of early archosaurs and their kin. Geol Soc Spec Publ 379: 573–597.

186. Irmis RB (2011) Evaluating hypotheses for the early diversification of dinosaurs. Earth Environ Sci Trans R Soc Edinburgh 101:397–426.

187. Falkingham PL, Gatesy SM (2014) The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. PNAS 111: 18279–18284. doi: 10.1073/pnas.1416252111 PMID: 25489092

188. Miščan J, Bromley RG (2006) True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. Palaeoechoq, Palaeoclim, Paleocool 231: 253–264.

189. Falkingham PL, Bates KT, Margetts L, Manning PL (2011) The ‘Goldilocks’ effect: preservation bias in vertebrate track assemblages. J R Soc Interface 8: 1142–1154. doi: 10.1098/rsif.2010.0634 PMID: 21233145

190. Munk W, Sues H-D (1993) Gut contents of Parasaurus (Pareiasaura) and Protorosaurus (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany. Paläont Z 67: 169–176.

191. Irmis RB, Nesbitt SJ, Sues H-D (2013) Early Crocodylomorphs. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin. Geol Soc London Spec Publ 379: 275–302.
192. Charig AJ (1972) The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In: Joysey KA, Kemp TS, editors. Studies in vertebrate evolution. Oliver and Boyd, Edinburgh, p. 121–151.

193. Gradstein FM, Ogg JG, Schmitz MD, Ogg G (2012) The geologic time scale 2012. Boston: Elsevier. 1176 p.

194. Alroy J (2013) Online paleogeographic map generator. Available: http://fossilworks.org/?a=mapForm.