

Walking -- and running and jumping -- with dinosaurs and their cousins, viewed through the lens of evolutionary biomechanics

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24	Abstract		

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Archosauria diversified throughout the Triassic period before experiencing two mass extinctions near its end ~201 Mya, leaving only the crocodile-lineage (Crocodylomorpha) and bird-lineage (Dinosauria) as survivors; along with the pterosaurian flying reptiles. About 50 years ago, the 'locomotor superiority hypothesis' (LSH) proposed that dinosaurs ultimately dominated because their locomotion was superior to other archosaurs'. This idea has been debated continuously since, with taxonomic and morphological analyses suggesting dinosaurs were "lucky" rather than surviving due to being biologically superior. However, the LSH has never been tested biomechanically. Here we present integration of experimental data from locomotion in extant archosaurs with inverse and predictive simulations of the same behaviours using musculoskeletal models, showing that we can reliably predict how extant archosaurs walk, run and jump. These simulations have been guiding predictive simulations of extinct archosaurs to estimate how they moved, and we show our progress in that endeavour. The musculoskeletal models used in these simulations can also be used for simpler analyses of form and function such as muscle moment arms, which inform us about more basic biomechanical similarities and differences between archosaurs. Placing all these data into an evolutionary and biomechanical context, we take a fresh look at the LSH as part of a critical review of competing hypotheses for why dinosaurs (and a few other archosaur clades) survived the Late Triassic extinctions. Early dinosaurs had some quantifiable differences in locomotor function and performance vs. some other archosaurs, but other derived dinosaurian features (e.g. metabolic or growth rates, ventilatory abilities) are not necessarily mutually exclusive from the LSH; or maybe even an opportunistic replacement hypothesis; in explaining dinosaurs' success.

Keywords: archosaur, locomotion, biped, posture, digitigrady, moment arm, simulation,

morphological disparity, Triassic-Jurassic transition

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52 Introduction

Casual observation of a crocodile and a bird might not suggest any profound evolutionary proximity, but Crocodylia and Aves are each other's closest extant relatives in the vertebrate clade Archosauria. Archosauria originated very late in the Permian period about 252 Mya and diversified tremendously in the Triassic period (e.g., Benton, 2016). Archosaurs faced the mass extinctions around the Triassic-Jurassic boundary ~201 Mya, leaving only two surviving lineages: Crocodylomorpha, which now includes only Crocodylia as a shadow of its Mesozoic diversity, and Ornithodira (slightly more inclusively, Avemetatarsalia; Nesbitt et al., 2017), including the winged reptiles Pterosauria (extinct by the end of the Cretaceous 66 Mya) along with Dinosauria, which now includes only Aves (Figure 1). Archosauria is united as a clade by conspicuous postcranial osteological traits, including a caudoventral portion of the coracoid bearing a tuber, an internal tuberosity of the humerus that is distinctly separated from the proximal articular surface, an olecranon process of the ulna that is prominent but lower than its craniocaudal depth at its base, a lateral "radius" tuber on the proximal ulna, a craniomedial tuber on the proximal femur, a longest metacarpal that is about half the length of the longest metatarsal, and a more caudally oriented calcaneal tuber (~50-90° relative to the transverse plane) (Nesbitt, 2011; Ezcurra, 2016). These traits are of likely functional relevance to terrestrial locomotion as they suggest enlarged/concentrated attachments for limb muscles or ligaments, greater dominance of the hindlimbs in locomotion (i.e., shortened metacarpals), and leverage for the ankle extensor muscles that is shifted more toward parasagittal function (e.g., Bonaparte, 1984; Sereno, 1991; Parrish, 1986; Sullivan, 2010, 2015).

Indeed, archosaurs have long fascinated morphologists and biomechanists because they evolved numerous locomotor specialisations in the Triassic, some of which extant archosaurs retain. First, the ancestral archosaur had limbs that, to some degree, seem to have been more erect (adducted: drawn closer to the body); unlike the more sprawling posture in earlier tetrapod ancestors. Limb joint morphology along with fossilised trackways together provide strong evidence of this postural shift (Charig, 1972; Kubo and Benton, 2009), corroborated by the somewhat erect "high walk" that Crocodylia often use, and the quite erect hindlimb posture of Aves. Erect limb posture is strongly associated with a more parasagittal gait (Nyakatura et al., 2019), although it remains uncertain if a highly erect hindlimb posture was ancestral for Archosauria or not (Figure 1A; Parrish, 1986; Sereno, 1991; Padian et al., 2010; Sullivan, 2015; Demuth et al., 2020). Second, archosaurs repeatedly evolved bipedalism (Figure 1C); at least once in the crocodile-lineage Pseudosuchia (for example, the bizarre, dinosaur-like Triassic poposauroids; Gauthier et al., 2011; Bates and Schachner, 2012; also likely *Smok wawelski* and *Postosuchus* spp.); and at least once (possibly multiple times) in Avemetatarsalia (controversially, pterosaurs; and certainly some or all early dinosaurs and their cousins; Padian, 1983, 2012; Novas, 1996; Langer et al., 2010, 2013; Pintore et al., 2022). Again, limb morphology and fossilised trackways demonstrate the antiquity of bipedalism in archosaurs (e.g., Brusatte et al., 2011; Kubo & Kubo, 2013). Third, foot posture transformed multiple times in archosaurs from the ancestral plantigrade ('flat-footed') pose to a digitigrade ('tip-toed') pose (Figure 1); possibly multiple times in Pseudosuchia (e.g., Crocodylomorpha and poposauroids; Farlow et al., 2014; Schachner et al., 2020; Turner and Gatesy, 2021) and once in Ornithodira (Padian, 1983; Kubo & Kubo, 2016). Digitigrade foot posture has potential benefits for functionally lengthening the limb to increase stride length and perhaps speed (Kubo & Kubo, 2012, 2013, 2016), and aligning limb forces with the joints to increase effective mechanical advantage, aiding in support against gravity

(Biewener, 1989). These and other benefits of digitigrady might also make locomotion more
economical, accompanied by less well understood tradeoffs in terms of muscle 'gearing'
(Carrier et al. 1994). Erect posture and parasagittal gait, bipedalism, and digitigrade foot
posture are but three of many remarkable locomotor specialisations of archosaurs -famously, archosaurs also radiated into many habitats by evolving enhanced swimming or
climbing abilities or (twice; in pterosaurs and birds) powered flight.

These locomotor specialisations of archosaurs have excited palaeontologists even since the 1800s, leading Richard Owen to coin the name Dinosauria based in part on their apparently advanced locomotion (Owen, 1942; Padian, 2012). Yet in the 1960s-1970s, new evidence and thinking transformed our view of the importance of archosaur locomotion — and led to debates that continue today. Discoveries of small Triassic forebears of dinosaurs in Argentina helped scientists such as Romer (1971, 1972a,b) and Bonaparte (1969, 1975) to realise that dinosaurs began as small, long-legged (cursorial), perhaps fleet-footed animals; rather than the giants they later became. Bakker and Galton (1971) recognised that early dinosaurs were united by having major muscle attachments on their humerus and femur that should have increased their leverage relative to Triassic Pseudosuchia, and this led them to re-establish the monophyly of Dinosauria, returning to Owen's (1842) ideas after decades of uncertainty about dinosaur origins. Charig (1972) proposed that there was a sequential 'improvement' of limb posture in Triassic archosaurs, from sprawling to 'semi-erect' to erect, linked to the ultimate success of dinosaurs and their survival across the Triassic-Jurassic boundary (also see Bonaparte, 1984). Parrish (1986) conducted the first real comparative, quantitatively morphometric and "paradigm"-based functional morphology analysis across archosauriforms. He found support for diversity of locomotor function, from more sprawling posture non-archosaurian archosauriforms and phytosaurs to independent origins of erect gaits in the

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crocodile lineage, the "crocodile-reversed" ankle-bearing Ornithosuchidae and Dinosauria, inferring that there were competitive advantages of erect postures. Earlier concerns about the possible non-monophyly of Dinosauria were finally fully dismissed as these discoveries and the advent of phylogenetic systematics helped scientists recognise that numerous hindlimb and other synapomorphies unite Dinosauria and its closest relatives (Novas, 1996; Langer et al. 2010). These ideas congealed into what can be called the 'locomotor superiority hypothesis' (LSH) for dinosaurian evolutionary success. However, that hypothesis soon had one main challenger.

Benton (1983, 1986, 1994) surveyed the global diversity of Triassic-early Jurassic archosaurs and other organisms and inferred that the pattern of originations and extinctions did not match predictions of the LSH (or similar ideas that could be said to centre on differential survival/competition between taxa) that dinosaurs should have increased in diversity while other archosaurs declined during the Triassic. Instead, he favoured an opportunistic (ecological) replacement hypothesis (ORH): as other Triassic species went extinct due to "random" processes (e.g., at the Triassic-Jurassic boundary's mass extinction), dinosaurs radiated into the vacant ecological space as fortunate "chance" beneficiaries; not superior competitors. Benton's ideas were expanded by Brusatte et al. (2008a,b), who compiled osteological phylogenetic characters into a morphospace analysis of Pseudosuchia vs. Dinosauria/Ornithodira across the Triassic-Jurassic boundary. They proposed that dinosaurs benefitted from "good luck": starting with low disparity (morphological diversity) and diversity that gradually increased throughout the Triassic/early Jurassic, whereas Pseudosuchia radiated into more disparity and diversity during the Triassic, which crashed by the Jurassic as the clade almost completely "died out by chance." Hence there was no correlation between Dinosauria/Ornithodira's rise and Pseudosuchia's fall from ecological

dominance. Further discoveries of possible Early/Middle Triassic dinosaurs (or close relatives) reinforced the notion that dinosaurs were not latecomers to the Triassic (Irmis et al., 2007; Nesbitt et al., 2010, 2013; Brusatte et al., 2011), having coexisted with other archosaurs for many millions of years, in low abundance, until their ascendance late in the Triassic. Thus some consensus was reached that dinosaur origins and gradual diversification early in the Triassic probably had nothing to do with any adaptive superiority they might have had (or not) versus other archosaurs (e.g., Brusatte et al. 2010a; Bernardi et al., 2018; Foth et al., 2021).

Soon enough, however, concerns were raised that the ORH or 'lucky dinosaurs' might not be so clear-cut of a conclusion. Irmis (2010) countered that many of the potential hypotheses for dinosaur success (versus extinction of most Pseudosuchia) were not mutually exclusive, and the hypothesis of chance or opportunistic replacement was not truly a null or default hypothesis, plus that competition or lack thereof was almost impossible to truly test; views broadly echoed by Padian (2012), Langer et al. (2010) and Marsicano et al. (2016). Brusatte et al. (2008a,b, 2010a,b) had likewise acknowledged that dinosaur diversity or disparity patterns were not simple, morphospace trends of phylogenetic characters were not evidence of or against any biotic interactions, and there was some risk of circularity in that these characters were the basis for Pseudosuchia and Ornithodira being recognised as sister clades; thus divergence of disparity between them was almost a foregone conclusion. Foth et al. (2021) found greater disparity in 2D geometric morphometrics of archosaur crania vs. pelves, inferring that the latter might have been more morphofunctionally constrained; yet both anatomical regions exhibited "early burst" high evolutionary rates in the Triassic. In the meantime, Kubo and Kubo (2012, 2013, 2016) presented a series of studies hinting again at locomotor superiority for Dinosauria: compared with Triassic Pseudosuchia, Triassic

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dinosaurs overall had longer limbs and stronger digitigrady along with a greater tendency for bipedalism, and fossil trackway evidence suggested this gave them some speed advantages. Benton (e.g., 2016) and colleagues (e.g., Brusatte et al., 2010a; Sookias et al., 2012; Benton et al., 2014; Bernardi et al., 2018) continued to produce studies in favour of the ORH, but did not directly address these critiques and potentially contradictory evidence (yet see Benton, 2021). Here we return to points raised by Irmis (2010) and colleagues, and Kubo and Kubo (2012, 2013, 2016), aiming to reassess the LSH, ORH and other contenders for explaining trends in archosaurian disparity and diversity across the Triassic to the early Jurassic. We do this via a synthesis of understanding, especially studies from the past decade, of the locomotor biomechanics of extant and extinct archosaurs. These studies help address what, if anything, was different between the locomotor functions of Pseudosuchia and Avemetatarsalia/Ornithodira; and how any differences evolved. We begin with a summary of how extant Archosauria (Crocodylia and Aves) move, then examine what the latest studies have taught us about locomotor function, performance and behaviour in Triassic to early Jurassic archosaurs. Finally, we will return to the LSH and ORH with a critical reappraisal and prospectus for these ongoing debates. **Extant Archosauria** The locomotor dynamics of extant archosaurs give hints about what mechanisms might be ancestral for all Archosauria (e.g., Manafzadeh et al. 2021) versus which mechanisms divergently evolved in the lineages to Crocodylia or Aves. We begin here with research we have done recently on the terrestrial gaits of Nile crocodiles (Crocodylus niloticus), focusing

on the 'high walk' during steady state locomotion. However, more sprawling limb postures or faster, even asymmetrical, running gaits are common in this and other species of Crocodylia; duty factors (= stance phase; foot-ground contact time; divided by stride time; total duration of a cycle of footfalls) can get as low as 0.25 and speeds $> 4 \text{ ms}^{-1}$ / Froude numbers > 10(Zug, 1974; Webb & Gans, 1982; Renous et al., 2002; Hutchinson et al. 2019; Wiseman et al. 2021). All experimental protocols were conducted in the Structure and Motion Laboratory of the Royal Veterinary College, via prior approval by the College's Ethics and Welfare Committee (approval number 2016-0089 N) and under a project licence (P0806ABAD) granted by the Home Office (United Kingdom). For ease of comparison with birds, we focus on hindlimb function but some data on forelimb function exist for Crocodylia (e.g., Baier et al. 2013; Otero et al., 2017; Paschenko, 2018; Nyakatura et al. 2019). A representative high walk involves a duty factor ~0.70. Each hindlimb primarily generates propulsive (craniad, horizontal) and medial GRFs (Figure 2A). As the crocodile moves forward, the hindlimb retracts, with the hip joint extending (then flexing in later stance), medially rotating around its longitudinal axis and adducting, while the knee has fairly linear flexion and the ankle (dorsi)flexes, then extends (plantarflexes) after mid-stance and the third metatarsophalangeal joint mostly dorsiflexes in late stance (Figure 2B; Table 1). Intriguingly, our representative trial had similarities to the fourth subject described by Gatesy (1991) that tended to adduct its hip in stance; unlike the other, more abducted alligators; but our subject did not extend its knee in the same way. These motions and forces otherwise compare favourably with data from high-walking alligators (Gatesy 1991; Blob & Biewener, 2001; Reilly et al., 2005; Tsai et al. 2020; Manafzadeh et al., 2021; Iijima et al., 2021), so the general patterns observed in *C. niloticus* appear to be ancestral for Crocodylia. How, then, do these hindlimb dynamics compare with those of birds?

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Elegant-crested tinamous (Eudromia elegans) are small paleognath birds closely related to ostriches and other traditional ratites. They are ground birds that prefer to run rather than engage in brief bouts of burst flight. Our studies of Eudromia elegans (Bishop et al., 2021a,b,c), combined with prior work by Hancock et al. (2007, 2014) and Stoessel and Fischer (2012) established the following locomotor dynamics. In normal walking, these tinamous alternate braking/propulsion and mostly pushing medially (Figure 3A). Hindlimb retraction during the stance phase consists of the hip extending, medially rotating and adducting while the knee, ankle and third metatarsophalangeal joints show fairly coordinated flexion (mainly after mid-stance; dorsiflexion for the toe) then extension (late stance; plantarflexion for the toe), with the toe adding a second dorsiflexion motion latest in stance (Figure 2B; Table 1). Vaulting (walking) mechanics transitions to bouncing (running) mechanics without an aerial phase at Froude numbers ~0.4-0.6, but tinamous can run with aerial phases eventually, reaching speeds >2.78 ms⁻¹ and duty factors <0.39 / Froude numbers > 4, with peak vertical GRFs > 2.5 BW (Hancock et al., 2007; Bishop et al., 2021c). The tinamous exhibit some traits that are slightly unusual relative to other small cursorial birds (Movie S1). They hold their toes and tarsometatarsus rotated inwards by 10-15°, rather than facing more straight cranially, in standing and while walking and running. The tibiotarsus (knee joint) shows long-axis rotation (LAR) of $\sim 24^{\circ}$ in external rotation early in stance phase, shifting to about 0° by the end of stance (i.e., internal LAR throughout stance),

which decreases with increasing speed. Compared with Helmeted guineafowl (*Numida*

meleagris), whose locomotor kinematics are best-studied for birds, tinamous seem to have

248 more hip abduction (the hip adducts thru stance $\sim 9^{\circ}$ vs. $\sim 3^{\circ}$ in *Numida*; Kambic et al., 2015),

which increases with speed (e.g., 14° in a fast run up to 2 ms⁻¹). We speculate that these

250 kinematic differences in part arise from the unusual foot morphology of *Eudromia*: the first

toe (hallux) has been lost, and similar kinematics seem evident in the ostrich *Struthio* (Rubenson et al., 2007), which has also lost its hallux. However, it is possible that all Paleognathae and Neognathae species have derived aspects of their locomotor dynamics in particular ways. Bishop et al. (2021b) used dynamic computer simulations to study vertical jumping in tinamous, estimating that these birds could jump about 0.3m high (vs. 0.133 standing height), with dynamics and muscle functions that mostly qualitatively matched other birds'. The simulated tinamous used a countermovement during pre-launch and landing, respectively with peak vertical GRFs > 2.6 BW and 4.3 BW; and jump height performance was most strongly sensitive to ankle extensor muscle force capacity. As it is difficult to get other species such as Crocodylia to jump and impossible for extinct taxa, this predictive simulation approach holds promise for future comparative studies of jumping performance and general dynamics.

Considering the above walking dynamics for Crocodylia and Aves (including other studies by Gatesy, 1991; Rubenson et al., 2004, 2007; Willey et al. 2004; Reilly et al. 2005; Kambic et al., 2015), there are common general patterns for Archosauria studied to date (see also Manafzadeh et al. 2021). Most notably, vertical GRFs are approximately double-peaked during a stance phase of walking, and the mediolateral GRF vector is medially oriented, of comparable peak magnitude to the horizontal GRF vector (Table 1). Hips extend and medially rotate through stance. The knee, ankle and toe share some similar sagittal motions for archosaurs through stance: knee extension at least late in stance and possibly flexion earlier in stance, ankle flexion then extension, and at least some toe dorsiflexion.

274 However, there certainly are major divergent patterns for extant archosaur locomotor275 dynamics at similar duty factors for apparently preferred walking speeds. Individual limb

GRFs, unsurprisingly, are relatively greater in bipeds; and bipeds must use their hindlimbs to brake and propel rather than specialising them more for propulsion (e.g., Willey et al. 2004). Variation is present in whether hip abduction (e.g., most crocodylian subjects?) or adduction (e.g., some birds; Rubenson et al., 2007) prevails in stance. Knee motion may be more concentrated on extension in Crocodylia, and the toe tends to have a second flexion cycle late in stance in Aves (vs. Crocodylia), as may the ankle (e.g., Stoessel and Fischer, 2012; Kambic et al., 2015), although some birds such as ostriches deviate from those ankle motions (Rubenson et al., 2007). So far we have focussed purely on stance (not swing) phase dynamics and joint rotations, not translations (see Manafzadeh et al., 2021, 2022). We will continue to do so in this study, as almost all prior literature on our topic has done so as well. Furthermore, stance phase is arguably simpler to analyse because it imposes severe geometric (the substrate) and biomechanical (supporting the body vs. gravity; as opposed to swinging the limb mainly vs. inertia) constraints. Nonetheless these other phenomena (and others neglected here) certainly deserve further study and integration into our understanding of archosaur locomotor evolution. It is important to stress, however, that we have overly simplified our treatment of archosaur feet (distal to the ankle joint) above, reducing them to a single (third) toe joint (a weakness of the predictive simulations as noted by Bishop et al., 2021a,b,c). Turner et al. (2020), Turner and Gatesy (2021) and Turner et al. (2022) have revealed detailed 3D kinematics of the feet in extant archosaurs, and a series of studies by Falkingham et al. (e.g., 2020; also Falkingham and Gatesy, 2014) have integrated kinetic data as well via models and simulations, offering promise of greater insight into 3D foot dynamics even in extinct archosaurs. Together, these

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studies show that plantigrade archosaurs should tend to exhibit substantial intrapedal 3D motions such as metatarsal spreading, pitching and rolling (Turner et al., 2020) whereas digitigrade taxa, via their tightly bound, more vertically oriented metapodials, have shared similar phalangeal motions since at least the Early Jurassic period including "looping" patterns (adduction and flexion coordinated between digits). This reinforces earlier work by Gatesy et al. (1999) showing continuity of theropod dinosaur foot function since the Late Triassic, although the latter study noted that digitigrade early theropods seem to have used foot postures closer to plantigrade (i.e., less vertical than in Aves) early in stance phase. The dynamic simulation research holds much promise for integrating 3D foot form and kinematics with substrate properties to (in)form better animal-ground contact models used in simulations of whole-organism locomotion (extant and extinct). This remains an exciting frontier. Knowledge of neuromuscular control in relation to locomotor dynamics is vital for better linking locomotor dynamics with morphology (e.g., muscle moment arms; see below) and with methods such as computational models and simulations where control is a necessary input or output parameter. Gatesy (1990,1994,1999), Hutchinson and Gatesy (2000) and Cuff et al. (2019) have synthesised data on how neuromuscular control of archosaur hindlimbs during stance phase evolved. While there were some conserved patterns of activation such as "antigravity" extensors (related to conserved joint extension patterns in stance noted above), there are interesting divergences. As Hutchinson and Gatesy (2000) noted, quadrupedal, less erect archosaurs use hip adductor muscles more to support their hindlimbs; whereas bipedal birds use mainly internal rotator muscles. Via simulation studies, Rankin et al. (2016) found that hip abductors were still important in Aves, consistent with Hutchinson and Gatesy's inference that early bipedal dinosaur(iform)s should have relied on hip abductors for single-

leg support, as a transition from adductor- to internal rotator-based control mechanisms. Cuff et al. (2019) used experimental electromyographic data and phylogenetic character mapping (following up on Gatesy, 1990, 1994, 1999) to show that archosaurs ancestrally switched their M. iliotibialis 2 (hip flexor/extensor and abductor, and knee extensor) from swing to stance phase activity. Birds, and possibly earlier dinosaur(iform)s, have switched their M. iliofibularis (hip extensor and abductor, and knee flexor) to stance phase activity as well, and shifted their M. gastrocnemius pars lateralis (knee flexor and ankle extensor) to start activity just before stance phase, as knee and ankle flexion begin (unlike in typical Crocodylia).

335 Extinct Archosauria

Recent studies of locomotor function in extinct Triassic Archosauria have focussed either on qualitative characterisation of posture, stance or gait, or (more rarely) quantification of locomotor function. We cover these two types of approaches in sequence here. The first type sometimes has used statistical (e.g., morphometric) methods to categorise "locomotor mode" (e.g., bipedal/quadrupedal stance). Given the multiple origins of some sort of bipedalism in early Archosauria, three recent studies of this type have tried to estimate which taxa were bipedal and how many times or when this capacity (facultative or obligate) evolved. Grinham et al. (2019) used phylogenetic comparative methods and literature-based assessments of bipedal capacity to reconstruct the evolution of bipedalism in Archosauromorpha and found seven origins of obligate bipedalism vs. 14 of facultative bipedalism; only one of the latter being a 'transitional' state between quadrupedalism and obligate bipedalism (in the close dinosaur relatives Silesauridae). Bishop et al. (2020) used a combination of morphometric, statistical and biomechanical/functional methods to test, based on body/limb form, which archosauromorphs might have been bipedal vs. quadrupedal. They found support for the notion that the pseudosuchian archosaur Postosuchus, potentially a close relative of

3 4	351	Crocodylomorpha, was bipedal (e.g., Parrish, 1986; Weinbaum, 2013). However, they
5 6 7	352	obtained a similar result for the enigmatic Riojasuchus, which had been presumed
7 8 9	353	quadrupedal yet some studies have reconstructed it or its close relatives as perhaps
10 11	354	facultatively, if not obligately, bipedal (Walker, 1964; von Baczko et al., 2019). Clearly such
12 13	355	approaches deserve application to a broader range of archosauromorph taxa and body forms.
14 15 16	356	Pintore et al. (2022) applied 3D geometric morphometrics, including phylogenetic
17 18	357	approaches, to the femur of archosauromorphs, testing for shapes typical of bipedal vs.
19 20	358	quadrupedal taxa, as well as characterisation of femora into more cursorial/gracile vs.
21 22 23	359	graviportal/robust forms. They obtained categorisations broadly in agreement (Figure 4) with
23 24 25	360	those of Bishop et al. (2020), also demonstrating that the femur has a stronger epiphyseal
26 27	361	offset, a less curved shaft and a more symmetrical fourth trochanter in quadrupedal
28 29 20	362	archosauriforms than in bipedal avemetatarsalians and pseudosuchians from the Late
30 31 32	363	Triassic. However, they also found some taxa to be ambiguous in bipedal/quadrupedal
33 34	364	locomotor mode (e.g., some of the dinosaur/pterosaur cousins Lagerpetidae; some
35 36	365	Silesauridae; also Postosuchus and Riojasuchus). As Pintore et al. (2022) determined femur
37 38 30	366	shape to converge on similar forms along with body size in different gracile or robust species,
40 41	367	why locomotor mode was not so clearly reflected in femoral shape of some taxa remains to
42 43	368	be explained. Nevertheless, disentangling the impact of locomotor mode vs. body size
44 45	369	increase in the femoral shape of Triassic archosaurs within a phylogenetic framework
46 47 48	370	broadens our understanding of how locomotor mode might correlate with archosaurian
49 50	371	extinctions across the Triassic-Jurassic transition.
51 52	372	
53 54 55	373	Functional morphology is another qualitative (or partly quantitative) approach for
55 56 57	374	categorising locomotor modes or other aspects of function, and has a history almost as
58 59	375	lengthy as palaeontology itself. It could be seen as bridging the two types of approaches: the

aforementioned statistical/morphometric methods are more pattern-based, seeking common trends in form that correlate with higher-level biological properties, whereas the second, quantitative type is more process-based, seeking or using biological mechanisms and first principles to infer function using form and other data. Functional morphology certainly uses qualitative form to infer function but may also draw on quantitative morphometric and/or biomechanical data. Most recently in Triassic-Jurassic archosaur functional morphology, Demuth et al. (2020) used 3D digital scans and models of the early archosauriform Euparkeria capensis to quantify its hindlimb joint axes and mobility. They found that its hip articulation resembles the "pillar-erect" morphology (e.g., Figure 1A; Bonaparte, 1984; Parrish, 1986), yet the hip joint was fairly mobile except for the most sprawling postures, and its ankle joint had an oblique axis that was inconsistent with a more erect limb posture, so overall they favoured limb poses between very sprawling and erect (mostly consistent with earlier inferences; e.g., Parrish, 1986,1987; Sereno, 1991; Sullivan, 2015; Figure 1A). Sullivan (2010) argued that a lateral tarsal process present in varanid lizards is an analogue of the calcaneal tuber in archosaurs, and used 3D digital models with experimental X-ray measurements of walking Varanus exanthematicus to quantify how this process increased ankle extensor leverage (e.g., M. peroneus/fibularis longus). Granatosky (2020) measured the muscle excitation patterns of this and other ankle muscles in the same species via electromyography and confirmed that there was some likely propulsive function. It would be valuable to know how these ankle muscles produce force, torque, work and/or power through a walking stride; so far studies have only tested muscle function more indirectly. Regardless, digital modelling approaches such as Sullivan (2010) and Demuth et al. (2020) have gone beyond simply classifying taxa as quadrupedal/bipedal or sprawling/erect; thereby giving explicit insights into how parts of the skeleton work together, including with muscles.

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Bates and Schachner (2012) used very similar 3D modelling methods with the Late Triassic bipedal pseudosuchian *Poposaurus* to quantify its hindlimb muscle moment arms (leverages) and compare them with those of other archosaurs (also see Bates et al. 2015). They found abundant convergence in hip muscle actions with bipedal theropods and other dinosaurs. However, they also noted that Poposaurus and Alligator (an extant pseudosuchian) were divergent from ornithodiran archosaurs (dinosaurs) in having lower muscle leverage for hip flexion, whereas Poposaurus also had low leverage for hip long-axis rotation and abduction/adduction vs. high leverage for ankle extension (from its large calcaneal tuber; ancestral for Pseudosuchia). They made the reasonable inference that these specialisations of hip muscles in pseudosuchians like *Poposaurus* relate to an emphasis of parasagittal limb control linked to that clade's seemingly restrictive "pillar-erect" hip articulations; so modern quantitative approaches reinforced and illuminated more classical inferences from functional morphology. Farlow et al. (2014) focussed on the pes morphology of *Poposaurus*, using a morphometric approach that led them to infer that it was digitigrade; another convergence with ornithodirans. This also concurs with the functional inferences of Turner and Gatesy (2021), who noted that some pseudosuchians with parallel, rather than splayed, metatarsal bones should have been digitigrade; adducing *Poposaurus* as an exemplar. Allen et al. (2021) used the same kind of 3D musculoskeletal modelling as Bates and Schachner (2012), across a larger sample of archosaurs (but not *Poposaurus*), including the Middle Triassic ornithodiran *Marasuchus*. They made the unexpected, tentative discovery that hip medial (internal) long-axis rotation leverage was low (relative to abduction leverage) in ornithodirans (specifically, Dinosauriformes). Like Bates and Schachner's (2012) findings, this result reinforced the idea raised by Hutchinson and Gatesy (2000); using qualitative

425 functional morphology; that early bipedal archosaurs relied on hip abductors for support

during stance phase, and only later shifted (within theropod dinosaurs) to the long-axis-rotation-based mechanism that extant birds use.

Here we present some previously unpublished data using essentially the same 3D musculoskeletal modelling approach as Bates and Schachner (2012) and Allen et al. (2021), but with a codified method presented by Bishop et al. (2021d) to maximise repeatability and transparency as well as comparability between taxa (also see Gatesy et al. 2022 on joint axes and landmarks for archosaur hindlimbs). We will not detail the methods here, which are fully presented by Bishop et al. (2021d; and see Gatesy et al. (2022)); with extant archosaur examples in Bishop et al. (2021a-c) and Wiseman et al. (2021). Briefly, we: (1) scanned the hindlimb skeletons of 8 representative Triassic/Jurassic archosauriforms including *Euparkeria*, *Batrachotomus* and *Poposaurus* (plus 4 extant representatives; Table 2), (2) reconstructed their major hindlimb muscles (Figure 5A,B) and (3) quantified their leverages, then (4) compared gross patterns across the hip (flexor-extensor) and ankle (extensor-only) joints for major muscle groups. Hip leverages were computed from -65° (flexed) to 45° (extended) hip joint angles (similar to Allen et al., 2021; but -90° to 0° for Aves due to more restricted hip mobility). Ankle leverages were calculated from 0° (dorsiflexed; normally to vertical metatarsus pose but also beyond this to -45° for Crocodylia which use more dorsiflexed angles during stance phase in vivo; e.g., Wiseman et al., 2021) to 90° (extended; plantarflexed to plantigrade pose). Leverages were then averaged for simplicity (per taxon, then across clades as needed for comparisons). We chose the hip and ankle because these have the most obvious morphological differences (e.g., pelvis and calcaneal tuber size) that might influence leverage (e.g., Bates and Schachner 2012). Considering the huge body size range of archosauriforms, the issue of dimensional comparison and scaling must be

 addressed; we divided moment arms by femur length (e.g., Hutchinson et al., 2005; Bates and
Schachner, 2012) to normalise for body size effects.

> We describe qualitative differences in quantitative results of these modelling studies, pending acquisition of a larger sample that would enable more conclusive (e.g., statistical) tests. Hence these findings are preliminary and tentative. Hip extensor moment arms overall did not differ appreciably (~3-5% average) for Pseudosuchia (here with *Euparkeria* data included) vs. Dinosauriformes (Figure 5C: "Pseudosuchia" = *Euparkeria through Poposaurus*); unsurprising as the postacetabular ilium can have a similar caudad extent in both groups (e.g., Hutchinson, 2001). Yet we found that Pseudosuchia had about 30% larger hip flexor moment arms vs. Dinosauriformes for the important M. pubo-ischio-femoralis internus 1+2 (PIFI1+2) deep dorsal thigh muscle group (Figure 5D). This difference is evident anatomically from the position of those muscles in Crocodylia (well craniad to the hip, especially for PIFI2) and similar inferred positions in most extinct Pseudosuchia based on the short preacetabular ilium which has not captured the PIFI1+2 origins as occurred in later Dinosauriformes (e.g., Hutchinson, 2001). Surprisingly, ankle extensor (plantarflexor) muscles did not emerge as having greater leverage for the pseudosuchians sampled, despite their large calcaneal tubers, which Dinosauriformes lack; indeed, the latter lineage tended to have 48% greater ankle extensor moment arms (Figure 5E), which might be attributable to their digitigrade foot postures. These differences are also illuminated by closer comparison of models of two somewhat closely related pseudosuchians: quadrupedal, plantigrade *Batrachotomus* vs. bipedal, digitigrade *Poposaurus* differ by (latter vs. former taxon) 28%, 55% and 90% greater in their hip flexor, hip extensor and ankle extensor leverages respectively (Figure 5F-H), likely linked to their different stance and apomorphic pelvis in Poposaurus (Bates and Schachner, 2012) despite their similar body sizes. Size-related morphological transformations

also alter muscle leverages in complex ways. "Graviportal" archosaurs such as the large early sauropodomorphs *Plateosaurus* and *Mussaurus* have large hip extensor moment arms (~30%-210% greater vs. average for Dinosauriformes) for M. caudofemoralis longus (and its brevis part) due to its insertion on the distally displaced fourth trochanter (see Pintore et al., 2022), but other hip extensor leverages are more unexceptional; attributable to their fairly plesiomorphic dinosaurian pelvic morphology (Figure 5I). These are just a few examples of how 3D musculoskeletal modelling can reveal basic aspects of archosaur hindlimb biomechanics and evolution. 3D musculoskeletal modelling has also been used, to a lesser degree, to study forelimb function in early archosaurs; and 3D models have been used in more biomechanical, functional studies to infer bipedalism. Otero et al. (2017) modelled forelimb muscles in a crocodile and the early (but already >1000 kg) sauropodomorph dinosaur *Mussaurus* patagonicus. They inferred that the forelimb joints were unable to put the forelimbs into a fully pronated position for quadrupedalism, and that muscle leverages (and overall functions) in the more sprawling crocodile vs. erect sauropodomorph were heavily influenced by limb posture. While many forelimb muscles conserved their morphology and presumed functions, others transformed both. For example, M. scapulohumeralis posterior was a supinator of the shoulder joint in Crocodylus (and Archosauria ancestrally?) but a pronator in Mussaurus; and M. coracobrachialis brevis ventralis was a shoulder extensor vs. flexor, respectively, in those taxa; and M. pronator teres was an elbow extensor vs. flexor. Furthermore, quadrupedalism vs. bipedalism was assessed across ontogeny in Mussaurus using 3D digital modelling-based estimates of centre of mass (COM) position (Otero et al., 2019), following the logic that to stand on one leg a biped must be able to place its COM over its foot. From hatchling to adult Mussaurus, the COM shifted caudally (with enlarged tail and reduced head/neck relative

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size), bringing the COM from a position too far craniad to enable bipedalism to one much
more amenable to such behaviour. This study thus supported the inference of Otero et al.
(2017) that adult *Mussaurus* were bipedal; but added the insight that this was a secondary
ontogenetic transformation. More studies have found similar patterns in other early dinosaurs
such as the sauropodomorph *Massospondylus carinatus* (Reisz et al., 2012; but see Chapelle
et al., 2020).

Some of the most recent studies of archosaur locomotion and evolution have used more cutting-edge biomechanical methods that enable deeper, more specific insights into function, performance and behaviour in extinct taxa. Polet and Hutchinson (2022) adopted Polet's (2021) perspective of the "Murphy number" and 2D trajectory optimisation-based optimal control simulations to reconstruct how the quadrupedal early "rauisuchian" Batrachotomus may have moved, recognising that it should, like archosaurs ancestrally, have had a large pitch moment of inertia due to its long, heavy body. They tested the validity of their simulation approach vs. empirical data for dogs, finding good agreement. They then compared the predicted limb phase patterns for *Batrachotomus* at different relative speeds to the manus vs. pes footprint positions in fossil trackways assigned to Brachychirotherium and Isochirotherium (e.g., Apesteguía et al., 2021; Klein et al., 2006; Petti et al., 2009); both large Middle/Late Triassic ichnotaxa presumed to be "rauisuchians" or roughly similar, heavily built quadrupedal taxa such as aetosaurs (Lucas and Heckert, 2011). Polet and Hutchinson (2022) found that the simulations, in light of the trackways, best supported two gait transitions: from a slow walking trot to a "tölt"-like quasi-run with bouncing forelimbs but vaulting hindlimbs, then a full diagonal sequence run with all four limbs bouncing.

Similar optimal control-based simulations have also been used lately to study locomotion of the Late Triassic theropod dinosaur Coelophysis (Bishop 2021c,d). First, Bishop et al. (2021d) used a more static, inverse approach to infer what hindlimb postures it may have used, concluding that more vertical 'buttress-like' orientations were favoured. Second, Bishop et al. (2021c) advanced this approach into fully predictive, forward simulations of 3D locomotor dynamics, obtaining similar maximal running speeds to the static approach (~7 ms⁻ ¹). They unexpectedly discovered that the tail swung laterally toward each retracting hindlimb during its stance phase, acting to conserve angular momentum like humans swing their arms to do. Additionally, the simulation found muscle excitation and activation patterns supporting earlier conclusions that these early dinosaurs used their hip abductors as important stance phase supportive muscles. Figure 7 shows the major muscle groups and their activations across a stride. These broadly fall into "stance phase" and "swing phase" active muscles, similar to excitations of homologous archosaurian muscles (Gatesy, 1999; Cuff et al., 2019). Yet as Bishop et al. (2021c) noted, quite a few muscles show secondary bursts of activity in the opposite phase from their main burst (e.g., ITCa,p; IFE; PIFI2; ADD1; FTE; AMB). Similar biphasic or pulsatile bursts also are evident in some extant archosaurian muscles (Gatesy, 1997, 1999; Reilly et al., 2005; Cuff et al., 2019).

Muscles in these dynamic simulations tend to be activated in ways that match their apparent optimal actions (i.e., major moment arms; see above). For example, muscles with large hip extensor moment arms such as Mm. flexores tibiales internus et externus, adductores femores and caudofemorales are most active around mid-stance; as are hip abductors/internal rotators such as Mm. iliotrochantericus caudalis, iliofemoralis externus and puboischiofemoralis internus 2. Hip flexors and external rotators/adductors (e.g., Mm. puboischiofemoralis interni 1-3, ischiotrochantericus, puboischiofemoralis internus 1) tend to be more active in swing

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phase. Muscles with predominantly knee extensor actions (Mm. iliotibialis 2+3, femorotibiales) are likewise active around mid-stance whereas knee extensors (Mm. iliotibialis 1, ambiens) that also have some hip flexor leverage are more active around mid-swing. Lower hindlimb muscles can broadly be differentiated into stance phase ankle extensors/digital flexors (Mm. flexores digitorum longus et hallucis longus, gastrocnemii medialis et lateralis, fibularis longus) vs. swing phase ankle flexors/digital extensors (Mm. tibialis anterior, extensores digitorum longus et hallucis longus, fibularis brevis). Bishop et al. (2021c) even obtained a late swing phase burst for M. gastrocnemius lateralis that matches electromyographic muscle excitation data for extant archosaurs (Cuff et al., 2019; see above). Indeed, the general congruence of these results for muscle functions vs. those previously inferred using simpler methods (e.g., general morphology and moment arms; and comparisons with extant taxa) gives some reciprocal confidence to the usage of those methods (e.g., Figure 5; Bates and Schachner, 2012; Allen et al., 2021). Additionally, there are good prospects for harnessing new methods to estimate muscle sizes and incorporate these into dynamic models (e.g., Bishop et al., 2021d; Demuth et al., 2022). LSH, ORH or something else? The above results from recent studies of archosaur locomotion suggest that the LSH for dinosaur success across the Triassic-Jurassic boundary cannot so easily be dismissed, but also that extensive convergent evolution between Pseudosuchia and Ornithodira defies simple scenarios of locomotor superiority. This convergence ranges widely across different levels of biological organisation, including basic skeletal form such as femur shape (Pintore et al., 2022), to muscle functions and leverage (Bates and Schachner, 2012; Figure 5), to limb and foot posture (sprawling-erect continuum; buttress/pillar-erect; plantigrade/digitigrade), and

even to behaviours such as quadrupedalism/bipedalism (Otero et al., 2019; Bishop et al., 2020) and perhaps gaits (Polet and Hutchinson, 2022). Yet it is timely to also take a fresh look at the fossil record of Archosauromorpha across the Triassic-Jurassic, in terms of other evidence most relevant to the LSH (and ORH). For example, how did body size and metabolism evolve, why did some crocodylomorphs (and pterosaurs) survive along with dinosaurs, how did dinosaur diversity and disparity change, and finally what was the nature of the end-Triassic mass extinctions in terms of overall environmental changes? This final synthesis will enable us to revisit the LSH, ORH and other hypotheses related to faunal turnover around the Triassic-Jurassic boundary. Many locomotor parameters depend on (and scale with) body size (i.e., mass; e.g., Biewener, 1989; Campione and Evans, 2020), so knowing how body size has evolved is important for

reconstructing locomotor evolution. The evolution of early Archosauromorpha seems to show an increase in disparity of body sizes through the Triassic, then a Triassic-Jurassic extinction of larger forms (Turner and Nesbitt, 2013; Pradelli et al., 2021; but contradicted by Allen et al. 2018 although perhaps because of sampling limitations). In contrast to this general trend, dinosaurs did not change size disparity around the Triassic-Jurassic boundary (but see Irmis, 2010). Turner and Nesbitt (2013) found that dinosaurs increased their range of body sizes while Pseudosuchia decreased theirs; inferring that this pattern was indicative of disruptive selection with an adaptive radiation. Benson et al. (2018) generally agreed, finding evidence for an early burst in ornithodiran body size evolution followed by a Triassic-Jurassic transition with multiple size optima (e.g., larger body size for Sauropodomorpha; vs. Benton et al., 2014). Sookias et al. (2012), however, concluded that increases in dinosaurian body masses during their early evolution were driven by "passive processes", not Cope's Rule-like active processes (i.e., selection), but still benefitted from rapid growth rates enabling large

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maximal body sizes. Intriguingly, small-bodied pterosaurs and early crocodylomorphs 599 survived the mass extinctions, but not their closest relatives, some of which were also small-600 bodied (e.g., Lagerpetidae). Allen et al. (2018) suggested hat there was clade-level selection 601 including against traits such as semi-aquatic habits. Turner and Nesbitt (2013) showed that 602 Crocodylomorpha was the only clade to reduce body size across the Triassic-Jurassic 603 boundary, raising the question of whether pseudosuchians experienced selection against 604 605 larger body sizes (Pradelli et al., 2021)? The latter study noted that this pattern is combined with a reverse Bergman's rule in which higher palaeolatitudes evidenced smaller body sizes, 606 607 perhaps implicating heterothermy and ectothermy rather than homeothermy and endothermy in Triassic Pseudosuchia. 608

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The issue of archosauromorph metabolic strategies is one with a long and complex history of 610 scientific study and we do not attempt to cover it in depth here, much as it is highly relevant 611 to the LSH, ORH and other hypotheses. Dunne et al. (2020) found that Pseudosuchia was 612 more species-rich around warmer equatorial regions, whereas Ornithodira was more 613 cosmopolitan in global distribution; fitting a scenario in which the former were ectothermic 614 and the latter endothermic or mesothermic (also see Mannion et al., 2015; Pradelli et al., 615 2021). Similarly, Whiteside et al. (2015) inferred that dinosaurs did not become dominant in 616 the tropics of the Triassic period because their high metabolic rates and endothermy were 617 618 maladaptive in those unstable "hothouse", wildfire-prone palaeoenvironments. Benton (2021) considered archosaurs to have been ancestrally endothermic and this key to their survival 619 across the Permo-Triassic boundary (a time of major environmental stresses such as global 620 anoxia). Pontzer et al. (2009) used a biomechanical/metabolic model to assess locomotor 621 physiology. They inferred a link between long (hind)limbs and muscle fascicles, leading to 622 wide aerobic scope (especially in larger-bodied taxa) and greater likelihood of endothermy in 623

dinosauriforms; also consistent with improved endurance and potential for dispersal (see below). Brocklehurst et al. (2020) reconstructed the evolution of the archosaur ventilatory system, inferring a dorsally rigid lung as ancestral for Dinosauria. Rapid growth and metabolic rates, advanced ventilatory systems and improved locomotor mechanisms might even be inextricably linked in dinosaurian success: the former two physiological specialisations benefit each other and would be advantageous to fuel widened aerobic scope (Pontzer et al., 2009). Arguably, no hypothesis for ornithodiran or dinosaurian success is robust unless the question of why some crocodylomorphs survived the Triassic period is also resolved. The basic data needed to resolve this are beginning to accumulate at last. As Irmis (2010) noted, Brusatte et al. (2008a,b) excluded Crocodylomorpha from their analyses, thus overestimating the crash of pseudosuchian disparity across the mass extinctions (acknowledged by Brusatte et al., 2010a; Foth et al., 2021). Stubbs et al. (2013) inferred that Triassic crocodylomorphs were "subordinate" to other Pseudosuchia, then became dominant in the Early Jurassic (when there were no large carnivores), 'revisiting' pseudosuchian ecological roles. Furthermore, Crocodylomorpha experienced lower disparity in the Triassic vs. Jurassic (Toljagic and Butler, 2013; Foth et al., 2021), partly due to the origin of more aquatic Jurassic lineages. Stockdale and Benton (2021) found correlations between Crocodylomorpha diversity and warm temperatures, concluding that diversity and body size disparity conferred evolutionary opportunities around the Triassic-Jurassic boundary (also hinted at by Dal Corso et al., 2020). Bronzati et al. (2015) instead concluded that the diversification of Crocodyliformes (a less inclusive clade) was linked to the Triassic-Jurassic boundary.

The small, cursorial early crocodylomorphs had their own novelties that might explain their survival into the Jurassic period. They convergently evolved "buttress-erect" hip joints with dinosaurs (Figure 1), as well as apparently digitigrade foot postures (e.g., Parrish, 1987; Irmis et al., 2013; Turner and Gatesy, 2021). Yet it remains far from "fact" (contra Benton, 2021; also Seymour et al., 2004) that they were bipedal; their locomotor modes are still poorly studied (e.g., Parrish, 1986; Kubo & Kubo, 2012; Pintore et al., 2022). This leaves claims of Cretaceous "crocodylomorph" bipedal fossil trackways (Kim et al., 2020) highly suspect, as no such trackmakers are known after Late Triassic taxa such as Poposaurus and Postosuchus. Crocodylomorpha had high evolutionary rates (opposite early dinosaurs) in terms of pelvic 2D geometric morphometrics early in their history (Foth et al. 2021), which surely led to some locomotor and ventilatory novelties. It is generally agreed now that ancestral Archosauria had advanced ventilatory systems including unidrectional airflow and heterogeneous parabronchial lungs with a post-pulmonary septum (Brocklehurst et al., 2020). There is tantalizing evidence that some crocodylomorphs might have had pneumatised postcranial skeletons, but the extent or importance of such pneumaticity is controversial (e.g., O'Connor, 2006; Butler et al., 2012; Irmis et al., 2013; Brocklehurst et al., 2020). This is an important issue as it might indicate increased ventilatory capacities, convergent with Ornithodira/Dinosauria, consilient with evidence for somewhat rapid growth (Ricgles et al., 2008; Cubo et al., 2012; Irmis et al., 2013; Legendre et al., 2016; Legendre and Davesne, 2020; Klein et al., 2017; Garcia Marsà et al., 2020). If early crocodylomorphs did converge with some ornithodirans in this way, this might even explain their survival into the early Jurassic. It is thought that any such novelties were secondarily lost with aquatic habits in later (Jurassic) Crocodyliformes (Seymour et al., 2004; Ricgles et al., 2008; Legendre et al., 2016; Legendre and Davesne, 2020; Benton, 2021).

How did dinosaurs evolve? A first, controversial issue is when they evolved; without firmly establishing this it is difficult to resolve how (or why) their diversification relates to that of other lineages. There are undoubted Carnian stage (Late Triassic) trackways (e.g., Carrano and Wilson, 2001; Porchetti et al., 2008; Bernardi et al., 2018); firmly consistent with body fossils of true dinosaurs. Purported dinosauromorph footprints as old as Early Triassic (e.g., Olsen and Baird, 1986; Marsicano et al., 2004, 2007, 2010; Brusatte et al., 2011; Niedzwiedzki et al., 2013; Bernardi et al., 2018; Citton et al., 2020; Marchetti et al., 2021) have been challenged; are they other avemetatarsalians or even non-archosauromorphs (e.g., Padian 2012; Fichter and Kunz, 2013; Marsicano et al., 2016; Mancuso et al., 2020)? Diagnostic skeletal remains of Dinosauriformes such as Marasuchus are known from the Middle Triassic (e.g., Sereno and Arcucci, 1994; Irmis et al., 2007; Novas et al., 2010; Langer et al., 2013; Benton et al., 2014; Mancuso et al. 2014;). As dinosaurs originated, body size exhibited complex evolutionary patterns. Body fossils of Ornithischia are rare, and small in body size until the Early Jurassic (Brusatte et al., 2010b; Benson et al., 2018). Theropoda were mostly small-bodied (but increasing in size; Irmis, 2010; Turner and Nesbitt, 2013), and not very diverse in the Triassic. Sauropodomorpha became abundant and attained very large (>500 kg) body sizes; perhaps benefitting from extinctions of other herbivores in the Late Triassic (e.g., "ecological release" of Langer et al., 2010; from extinction of rhynchosaurs, etc.). Apaldetti et al. (2021) uncovered an expansion of sauropodomorph disparity through the Late Triassic ("early burst" evolution), shifting toward herbivory, seeming unaffected in disparity or diversity by the mass extinctions except that small-bodied taxa went extinct. Hence there are contradictory patterns even just for dinosaur survival into the Jurassic, in which larger-bodied Sauropodomorpha survived vs. smaller-bodied Ornithischia and Theropoda did; and this phenomenon remains unexplained.

The fossil record reveals stepwise extinctions of many archosaurs from the Late Triassic to Early Jurassic (Rigo et al. 2020), but two major events stand out as likely causal mechanisms (e.g., Benton, 1994). The Late Triassic's Carnian stage witnessed the Carnian Pluvial Event (CPE), involving pulses of global increases of humidity and temperature caused by huge volcanic pulses (perhaps four in total, ~234-232 Mya) of the Wrangellia and other large igneous provinces (Dunhill et al., 2018; Lu et al. 2021; Figure 8). The CPE was roughly concurrent with a phase of dinosaur diversification that seems to have happened during quasiglobal aridity in between CPE pulses (Langer et al., 2010; Bernardi et al., 2018; Klausen et al., 2020; Mancuso et al., 2020; Dal Corso et al., 2020; Benton, 2021). Hence one major environmental change is correlated with dinosaur success, although this idea is not without challengers (e.g., Dunne et al., 2020). Second, it is now generally accepted that Central Atlantic Magmatic Province (CAMP; Figure 8) eruptions (~201.5 Mya) caused the final Triassic-Jurassic mass extinction via global warming, elevated greenhouse gases and rising sea levels (He et al., 2020; Petryshyn et al., 2020; Tegner et al., 2020; Wignall & Atkinson, 2020; Benton, 2021; Fox et al., 2022; Kaiho et al., 2022; Shen et al., 2022), although there may be added complexity (Klausen et al., 2020; Rigo et al., 2020; Ruhl et al., 2021). These changes eradicated coastal lowland ecosystems; a pattern reversed and repeated in a second CAMP phase (Lindström, 2021).

Might these major environmental changes give clues to why dinosaurs survived vs. almost all other Archosauriformes did not? Klausen et al. (2020) noted that semi-aquatic Pseudosuchia in coastal areas had "biomechanical inability to cope with flooding" during sea level changes such as those wrought by the CPE and CAMP; i.e., they could not migrate inland, having limited dispersal ability. In contrast, they pointed out that dinosaurs favoured "marginal ecosystems in the continental interior" (e.g., Brusatte et al., 2011) so they did not suffer so

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much or could recover faster. Furthermore, Klausen et al. (2020) raised the speculation that dinosaur bipedalism may have conferred advantages on land as sea levels changed, although such advantages have not been demonstrated. Yet their general point about Triassic-Jurassic survival fits with a trend noted by Allen et al. (2018): slower dispersers are poor at surviving mass extinctions, and the expected dispersal performance and related locomotor morphology of most Pseudosuchia appears inferior vs. Ornithodira (e.g., Pontzer et al., 2009; Klausen et al., 2020). This generalisation fits with the finding of Dunhill & Wills (2015) that increased geographic range stopped conferring extinction resistance around the Triassic-Jurassic boundary: perhaps Theropoda survived vs. Phytosauria went extinct because the kinds of environments they favoured and their dispersal abilities, not how broadly distributed they were. If more conclusive methods for testing dispersal ability for different archosaurs were found, that could be more powerful for addressing the LSH vs. other hypotheses.

The literature on archosaurs and the Triassic-Jurassic crisis may see similar data in quite different ways, or at least use different words to describe it (see Irmis, 2010). Brusatte et al. (2010b) concluded that dinosaurs likely survived the Triassic "due to differences in growth, metabolism or locomotion" but that these were "not key innovations"; they merely "came in handy". Benson et al. (2018), however, argued that dinosaurian body size evolution indicated they had "key innovations" behind their early success. Pradelli et al. (2021) likewise wondered if the survival of dinosaurs past the mass extinctions might have been due to selective benefits of their erect bipedal gait, for example. Benton (2014) contended that dinosaur success was not an "accident" but was attributable to a "range of adaptations" advantageous in environmental crises, yet limb posture was "not a factor", as dinosaurs were bipedal since the Early Triassic. As stated previously, this depends on whether fossil trackways and fragmentary body fossils are accepted as dinosaurian. Langer et al. (2010)

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3 4	748	surmised that competition around the Triassic-Jurassic boundary might still have played a
5 6 7	749	role in differential survival, and that dinosaurs had "key adaptations" in a changing
7 8 0	750	environment giving them "circumstantial superiority" in the short term during environmental
9 10 11	751	crises; just not throughout the Triassic. Perhaps there is more agreement emerging. Benton
12 13	752	(2021) acknowledged Kubo and Kubo's (2012, 2013) inference that dinosaurs' long legs
14 15	753	related to long relative stride lengths, lower locomotor costs, and higher stamina; then
16 17 19	754	accepted that, as higher activity levels in the Triassic led to an "arms race", posture and gait
19 20	755	were thus key to dinosaurian success. While dinosaur taxonomic diversity and morphological
21 22	756	disparity seem decoupled in the Triassic (e.g., Brusatte et al., 2008a,b, 2010a,b),
23 24	757	biomechanical analyses could better test how well morphological vs. functional (e.g.,
25 26 27	758	locomotor performance) disparity were coupled (as assumed by Kubo & Kubo, 2012, 2013)
28 29	759	or not; an issue that is fairly pivotal for conclusively testing the LSH. There seems to be a
30 31	760	long way to go yet to fully understand the Triassic-Jurassic transition and archosaurian
32 33	761	palaeobiology, but a wide range of perspectives will be valuable in achieving improved
34 35 36	762	understanding. Even if the LSH ends up disfavoured by a strong consensus, it would be
37 38	763	exciting to gain confident insight into what the consequences of morphological changes
39 40	764	evident in Triassic archosaurs were for higher level functions and performance and which of
41	704	evident in Thassie arenosaurs were for higher-level functions and performance, and which of
42	765	these remain in extant archosaurs as ancient legacies.
44 45 46	766	
40 47 48	767	
49 50	768	Funding
51 52	769	This work was supported by the European Research Council (ERC) under the European
53 54	770	Union's Horizon 2020 research and innovation programme [grant agreement #695517]; the
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3 4 5	798	
5 6 7	799	Data Availability Statement
8 9	800	The data underlying this article are available in the article and in its online supplementary
$\begin{array}{c} 10\\ 11\\ 12\\ 13\\ 14\\ 15\\ 16\\ 17\\ 18\\ 19\\ 20\\ 21\\ 23\\ 24\\ 25\\ 26\\ 27\\ 28\\ 29\\ 30\\ 31\\ 32\\ 33\\ 34\\ 35\\ 36\\ 37\\ 38\\ 39\\ 40\\ 41\\ 45\\ 46\\ 47\\ 48\\ 49\\ 50\\ 51\\ 52\\ 53\\ 54\\ 55\\ 56\\ 57\\ 58\\ 9\\ 60\\ \end{array}$	801	naterial.

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3	802			
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5	803	TABLES		
6 7	805	INDEES		
7 8	804			
9	001	Parameter	Crocodvlus	Eudromia
10		Hip extension min	-32	-52
11		Hip extension max	-20	-30
12		Hip extension 50%	-30	-29
13		Hip abduction min	30	3
15		Hip abduction max	40	15
16		Hip abduction 50%	34	11
17		Hip internal LAR min	-19	4
18		Hip internal LAR max	2	14
19 20		Hip internal LAR 50%	2	4
21		Knee extension min	-105	-122
22		Knee extension max	-65	-39
23		Knee extension 50%	-87	-83
24		Ankle extension min	-40	-102
25 26		Ankle extension max	-1	-20
20		Ankle extension 50%	-39	-31
28		Toe extension min	-56	13
29		Toe extension may	-90	120
30		Toe extension 50%	-15	120
31		GRE vertical max1 (BW)	88	150
33		GRE vertical max1 (0 vv)	52	26
34		GRE vertical max? (BW)	52 75	105
35		GRE vertical max2 (0 vv)	75	72
36		GRE cranial min (BW)	-0.07	-35
37		GRE cranial min (%stance)	-0.07	-33 57
38 39		GPE granial max (PW)	42	0.06
40		GRF cranial max (bw)	11	0.00
41		CDE modial min (DW)	10	<u>22</u> 0.19
42		CPE modial min (BW)	-19 12	-0.18
43		CRF medial min (%stance)	15	0.19
44 45		GRF medial max (BW)	U	0.05
45 46		GRF medial max (%stance)	98	0
40	805			

806 Table 1. Kinematics and kinetics of representative extant archosaur (*C. niloticus* and *E.*

807 *elegans*) walking trials (see text for details; data from Wiseman et al., 2021 and Bishop et al.,

⁵³ 808 2021a,c). No statistical comparisons are made. "min" = minimal, "max" = maximal and 50%

 $^{55}_{56}$ 809 = mid-stance values during stance phase. Kinematics for hip (3 rotational degrees of

5758 810 freedom), knee, ankle and "toe"/third metatarsophalangeal (single degrees of freedom) joints.

60 811 GRF "max1" and "max2" values are for first and second peaks during stance; and "%stance"
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2 3	812	is when these occur; for all 3 components of the GRF vector (vertical, craniocaudal,
4 5	813	mediolateral).
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2 3 4 5 6	815	Taxon	Specimen #s	Museum	Body mass (kg)	Femur L (m)	Reference
7 8		Euparkeria capensis	SAM PK 6047A+others	Iziko South African Museum	0.8287	0.054	Demuth et al. 2020
9 10		Batrachotomus kupferzellensis	52970+others	Staatliches Museum für Naturkunde, Stuttgart	161.2	0.425	Bishop et al. 2020
11 12 13		Poposaurus gracilis	YPM 57100	Yale Peabody Museum, New Haven	67.5	0.37	(Bates and Schachner, 2012)
14 15		Crocodylus niloticus	JRHRVC- DDNC06	RVC	2.9	0.067	Wiseman et al. 2021
16 17		Crocodylus johnstoni	n/a	RVC	20.9	0.112	Allen et al. 2021
18 19 20		Marasuchus lilloensis	PVL 3870	Paleontología de Vertebrados, Instituto "Miguel Lillo," San Miguel de Tucumán	0.288	0.047	Allen et al. 2021
21 22 23		Lesothosaurus diagnosticus	NHMUK RUB 17	Natural History Museum, London	6.3	0.102	Allen et al. 2021
23 24 25		Plateosaurus engelhardti	GPIT1 & GPIT2	Eberhardt-Karls- Universitat, Tubingen	753	0.57	Allen et al. 2021
26 27		Mussaurus patagonicus	MLP 68-II- 27-1+others	Museo de La Plata, La Plata	1073.3	0.70	Otero et al. 2019
28 29		Coelophysis bauri Euducenia	CMNH 10971 IDUDVC	Cleveland Museum of Natural History, Ohio	13.9	0.16	Bishop et al. 2021c,d Dishor et al.
30 31		elegans Gallus gallus	DDT09	RVC	0.534	0.034	2021a-c Allen et al
32 33	816	(junglefowl)	11/ u	RVC	2.57	0.105	2021
34 35	010	T-11-2 Amelia	: C-	1			
36 37	817	Table 2. Archos	auriform musci	uloskeletal models used	d nere. E	sody mas	sses are measured
38 39	818	extant archosau	rs, or estimated	from volumetric mode	els or fen	noral (ar	id humeral for
40 41	819	quadrupeds) cir	cumference foll	lowing Campione and	Evans (2	.020), bu	t are purely for
42 43 44	820	comparative con	ntext here. Fem	ur L = length, used for	moment	t arm not	rmalisation.
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FIGURE CAPTIONS

, 8 9	824	Figure 1. Postural evolution of Archosauromorpha. A, Evolution of the different hip joint
10 11	825	articulations and limb postures superimposed onto a consensus tree (foreground) following
12 13	826	Nesbit (2011), Nesbit et al. (2017), von Baczko et al. (2019) and Ezcurra et al. (2020), and
14 15 16	827	alternative tree topology (shadowed) following Ezcurra (2016), Garcia et al. (2019) and
17 18	828	Müller & Garcia (2020). "Erect" postures necessitate both relatively parasagittal hip and
19 20	829	ankle joints while "sprawling" lack both, and "semi-erect" possess a rotatory ankle joint or
21 22 22	830	lack a relatively parasagittal hip articulation (e.g., Parrish, 1986; Demuth et al., 2020; but see
23 24 25	831	Gatesy, 1991). B, Skeletal illustrations of various archosauriforms; from top to bottom:
26 27	832	Euparkeria, Paleorhinus (Phytosauria), Stagonolepis (Aetosauria), Poposaurus,
28 29	833	Batrachotomus, Postosuchus, Caiman (Crocodylia), Teleocrater (Aphanosauria),
30 31 32	834	Rhamphorhynchus (Pterosauromorpha), Marasuchus (Lagosuchidae), Silesaurus
33 34	835	(Silesauridae), Heterodontosaurus, Plateosaurus (basal Sauropodomorpha), Coelophysis.
35 36	836	Drawings not to scale and courtesy of Scott Hartman (https://www.skeletaldrawing.com/;
37 38	837	except Euparkeria, illustrated by Oliver E. Demuth). C, Evolution of bipedalism in
39 40 41	838	archosauromorphs following Grinham et al. (2019), Bishop et al. (2020) and Pintore et al.
42 43	839	(2022), superimposed on the same trees as in A. See text for discussion (e.g., Postosuchus
44 45	840	likely a biped). Clades: 1, Archosauromorpha; 2, Eucrocopoda/Archosauriformes; 3,
46 47 48	841	Archosauria; 4, Pseudosuchia; 5, Crocodylomorpha; 6, Avemetatarsalia; 7, Ornithodira; 8,
49 50	842	Dinosauriformes, 9, Dinosauria; 10, Saurischia; 11, Theropoda.
51 52	843	
53 54	844	Figure 2. Three-dimensional hindlimb dynamics of a representative Nile crocodile
55 56 57	845	(Crocodylus niloticus) high-walking trial during the stance phase (some data from Wiseman
58 59 60	846	et al., 2021). A, Kinematics: joint angles vs. % stance phase; B, Kinetics: ground reaction

847	forces (GRFs) normalised by body weight (BW); GRFx = craniocaudal (horizontal); GRFy =
848	dorsoventral (vertical); GRFz = mediolateral (transverse).
849	
850	Figure 3. Three-dimensional hindlimb dynamics of a representative Elegant-crested tinamou
851	(Eudromia elegans) walking trial during the stance phase (data from Bishop et al., 2021a,c).
852	A, Kinematics: joint angles vs. % stance phase; B, Kinetics: ground reaction forces (GRFs)
853	normalised by body weight (BW); GRFx = craniocaudal (horizontal); GRFy = dorsoventral
854	(vertical); GRFz = mediolateral (transverse).
855	
856	Figure 4. Comparison of results for the same four archosauriform taxa in Pintore et al. (2022)
857	vs. Bishop et al. (2020). "Locomotor index": 0 = quadrupedal; 1 = bipedal. Silhouettes in
858	dark grey represent taxa with uncertain locomotor habit. Taxon abbreviations: Eu =
859	<i>Euparkeria</i> ; Mu = <i>Mussaurus</i> (H = hatchling, A = adults), Pl = <i>Plateosaurus</i> , Po =
860	<i>Postosuchus</i> , Ri = <i>Riojasuchus</i> . Silhouettes from J. Conway, J. Gonzalez, S. Hartman & A.
861	Otero. Theoretical femoral morphology of quadrupedal (left) and bipedal (right) Triassic
862	archosauriforms from Pintore et al. (2022).
863	
864	Figure 5. 3D musculoskeletal modelling of archosaur right hindlimbs, with muscle moment
865	arms normalised by femur length. A, Batrachotomus and B, Marasuchus in lateral view. C,
866	Comparison of averaged hip extensor moment arms (see panels F,I for muscles included). D,
867	Averaged hip flexor moment arms (for PIFI1+2 muscles see main text). E, Averaged ankle
868	extensor moment arms: GE = M. gastrocnemius externus; GI = M. gastrocnemius internus;
869	FDL = M. flexor digitorum longus. F, Averaged hip extensor moment arms for individual
870	muscles compared between two Triassic Pseudosuchia. Muscle acronyms: ADD1, ADD2 =

871 Mm. adductores femores 1+2; CFB+CFL = Mm. caudofemorales brevis+longus;

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872	FTE+FTIs1-3 = Mm. flexores tibiales interni externus et internus 1-3; ILFB = M.
873	Iliofibularis; ISTR = M. ischiotrochantericus; IT2p+3 = Mm. iliotibiales 2 (posterior part)+3.
874	G, Hip flexors PIFI1+2 = Mm. puboischiofemorales interni 1+2 compared between the same
875	taxa as in F. H, Three ankle extensors (as in E) compared between the same taxa as in F, G. I,
876	Hip extensor moment arms (excluding IT2p; negligible/hip flexor moment arm) compared
877	between two early sauropodomorphs; especially note the large moment arms for Mm.
878	caudofemorales (CFB+CFL). For details on muscle homologies see Bishop et al. (2021d).
879	
880	Figure 6. Brachychirotherium trackways with increasing stride length compared to dynamic
881	simulation results from Polet and Hutchinson (2022). At the shortest stride lengths (A,B), the
882	simulation closely matches fossil track phase (distance from pes to manus divided by stride
883	length), and corresponds to a walking trot. To maintain this gait, limb phase must decrease
884	with increased stride length (speed). However, at intermediate stride lengths, track phase
885	becomes constant in the fossil trackways, shown as a static manus position between (C) and
886	(D), and resulting in an increase in limb phase. Simulations predict a shift in gait to a slow
887	run, and an increase in track phase. At the longest stride lengths (D), and therefore fastest
888	speeds, track phase again decreases, representing a maintenance of limb phase, and
889	simulations predict a transition to a fast run. Trackways were reproduced using averaged
890	trackway data from (A,B) Apesteguía et al. (2021) tracks R1 and R2-t5, (C,D) Petti et al.

891 (2009) tracks BsZ-A and BsZ-D, and (E) Klein et al. (2006) trackway NMMNH P-48756.

892 Track width is not representative of width in the fossil tracks. Footprint drawings from
 893 <u>https://commons.wikimedia.org/wiki/File:Brachychirotherium.svg</u>, used under a CC-BY 3.0

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896	Figure 7. Biomechanical modelling and simulation of the Triassic theropod dinosaur
897	Coelophysis (from Bishop et al., 2021a,c). Superficial (A) and deep (B) right hindlimb
898	muscles in a musculoskeletal model, with muscle acronym labels. C-F: Muscle activations
899	from the fast-running nominal simulation results from Bishop et al. (2021c); activation levels:
900	1.0 = 100% active; $0.0 =$ inactive, plotted against % gait (stride) cycle (0-100% = 0.0-1.0).
901	Muscle acronyms correspond to those in A+B. Vertical dashed lines at 80% stride = start of
902	stance phase (ends at 100% stride). Panels correspond to approximate functional/anatomical
903	groups: C, Hip external rotators/abductors; D, Hip extensors; E, Knee extensors (and hip
904	flexors/extensors); F, Lower limb muscles (mainly ankle flexors/extensors). See Figure 5 for
905	muscle acronyms plus: AMB = M. ambiens; FMTE+FMTI = Mm. femorotibiales
906	externus+internus; EDL = M. extensor digitorum longus; EHL = M. extensor hallucis longus;
907	FHL = M. flexor hallucis longus; $FB+FL = Mm$. fibulares brevis+longus; $IFE = M$.
908	iliofemoralis (externus); ISTR = M. ischiotrochantericus; ITCa,p = M. iliotrochantericus
909	caudalis (anterior, posterior parts); PIFE1-3 = Mm. puboischiofemorales externi 1-3; TA =
910	M. tibialis anterior.
911	
912	Figure 8. Upper/Late and Lower/Early Jurassic palaeogeography and palaeoclimate (from
913	Boucot et al., 2013; used with permission). Brown outlines: maximal extents of Wrangel
914	Large Igneous Province (WLIP) and other LIPs (based on Lu et al., 2021) in the Carnian

stage, and Central Atlantic Magmatic Province (CAMP; based on Fox et al., 2022) in the

Rhaetian stage of Upper Triassic strata. Differences in palaeoclimate are emphasised with

917 purple arrows ("cool temperature" zones absent in Upper Triassic); examples of regions with

- 918 more exposed land (i.e., lower sea levels) in Lower Jurassic vs. Upper Triassic are
- ⁶ 919 emphasised with light blue arrows. Legend shows symbols corresponding to lithological and
- $_{59}^{58}$ 920 other evidence for palaeoclimate as per Boucot et al. (2013).

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9 10 11	924	Movie S1. XROMM data for tinamou walking at 0.48 ms ⁻¹ , shown from dorsal view in body
12 13	925	(pelvis) frame of reference. Recorded at 750 Hz, playback at 25 Hz (i.e., slowed to 3.33%).
14 15	926	Right hindlimb axes visible for hip, knee and ankle follow convention of red = longitudinal
16 17 18	927	(LAR), green = craniocaudal (abduction/adduction), blue = mediolateral (flexion/extension).
19 20	928	LAR of the tibiotarsus is conspicuous.
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3 4	930	References
5 6	931	
7 8 0	932	Allen, B. J., Stubbs, T. L., Benton, M. J., & Puttick, M. N. (2019). Archosauromorph
9 10 11	933	extinction selectivity during the Triassic-Jurassic mass extinction. Palaeontology, 62(2), 211-
12 13	934	224.
14 15 16	935	
17 18	936	Allen, V.R., Kilbourne, B.M., Hutchinson, J.R. 2021. The evolution of pelvic limb muscle
19 20	937	moment arms in bird-line archosaurs. Science Advances 7:eabe2778.
21 22	938	
23 24 25	939	Apesteguía, S., Riguetti, F., Citton, P., Veiga, G. D., Poiré, D. G., de Valais, S., et al. (2021).
26 27	940	The Ruditayoj-Tunasniyoj Fossil Area (Chuquisaca, Bolivia): a Triassic chirotheriid
28 29	941	megatracksite and reinterpretation of purported thyreophorantracks. Hist. Biol. 33, 2883-
30 31 22	942	2896.
32 33 34	943	
35 36	944	Baier, D. B., & Gatesy, S. M. (2013). Three-dimensional skeletal kinematics of the shoulder
37 38 30	945	girdle and forelimb in walking <i>Alligator</i> . Journal of Anatomy, 223(5), 462-473.
39 40 41	946	
42 43	947	Bakker, R. T., & Galton, P. M. (1974). Dinosaur monophyly and a new class of vertebrates.
44 45	948	Nature, 248(5444), 168-172.
46 47 48	949	
49 50	950	Bates, K. T., & Schachner, E. R. (2012). Disparity and convergence in bipedal archosaur
51 52	951	locomotion. Journal of the Royal Society Interface, 9(71), 1339-1353.
53 54	952	
55 56 57		
58 59		
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2		
3 4	953	Bates, K., Maidment, S. C., Schachner, E. R., & Barrett, P. M. (2015). Comments and
5 6	954	corrections on 3D modeling studies of locomotor muscle moment arms in archosaurs. PeerJ,
7 8	955	3, e1272.
9 10 11	956	
12 13	957	Benson, R. B., Hunt, G., Carrano, M. T., & Campione, N. (2018). Cope's rule and the
14 15	958	adaptive landscape of dinosaur body size evolution. Palaeontology, 61(1), 13-48.
16 17	959	
18 19 20	960	Benton, M. J. (1983). Dinosaur success in the Triassic: a noncompetitive ecological model.
20 21 22	961	The Quarterly Review of Biology, 58(1), 29-55.
23 24	962	
25 26	963	Benton, M. J. 1986. The Late Triassic tetrapod extinction events. <i>The Beginning of the Age of</i>
27 28 20	964	Dinosaurs (ed. Padian, K.). Cambridge: Cambridge Univ. Press. 303–320.
29 30 31	965	
32 33	966	Benton M. I. (1994). Late Triassic to Middle Jurassic extinctions among continental
34	500	Benton, W. S. (1993). Eule Thussie to Wiedle Sullasie extinctions unlong continental
35 36 37	967	tetrapods: testing the pattern. In Fraser, N. C. and Sues, HD. (eds), In the Shadow of the
37 38 39	968	Dinosaurs, pp. 366-397. Cambridge University Press, Cambridge
40 41	969	
42 43	970	Benton, M. J. (2016). The Triassic. Current Biology, 26(23), R1214-R1218.
44 45	971	
46 47	972	Benton, M. J. (2021). The origin of endothermy in synapsids and archosaurs and arms races
40 49 50	973	in the Triassic. Gondwana Research, 100, 261-289.
51 52	974	
53 54	975	Benton, M. J., Forth, J., & Langer, M. C. (2014). Models for the rise of the dinosaurs. Current
55 56	976	Biology, 24(2), R87-R95.
57 58	977	
60		

Page 45 of 76

1 2		
2 3 4	978	Bernardi, M., Gianolla, P., Petti, F. M., Mietto, P., & Benton, M. J. (2018). Dinosaur
5 6 7	979	diversification linked with the Carnian Pluvial Episode. Nature Communications, 9(1), 1-10.
, 8 9	980	
10 11	981	Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle
12 13 14	982	mechanics. Science, 245(4913), 45-48.
15 16	983	
17 18	984	Bishop, P.J., Bates, K.T., Allen, V.R., Henderson, D.M., Randau, M., Hutchinson, J.R. 2020.
19 20 21	985	Relationships of mass properties and body proportions to locomotor habit in terrestrial
21 22 23	986	Archosauria. Paleobiology 46:550-568.
24 25	987	
26 27	988	Bishop, P.J., Michel, K.B., Falisse, A., Cuff, A.R., Allen, V.R., De Groote, F., Hutchinson,
28 29 30	989	J.R. 2021a. Computational modelling of muscle fibre operating ranges in the hindlimb of a
31 32	990	small ground bird (<i>Eudromia elegans</i>), with implications for modelling locomotion in extinct
33 34	991	species. PLOS Computational Biology 7:e1008843.
35 36 27	992	
37 38 39	993	Bishop, P.J., Falisse, A., De Groote, F., Hutchinson, J.R. 2021b. Predictive simulations of
40 41	994	musculoskeletal function and jumping performance in a generalized bird. Integrative
42 43	995	Organismal Biology obab006.
44 45 46	996	
47 48	997	Bishop, P.J., Falisse, A., De Groote, F., Hutchinson, J.R. 2021c. Predictive simulations of
49 50	998	running gait reveal a critical dynamic role for the tail in bipedal dinosaur locomotion. Science
51 52 53	999	Advances 7: abi7348.
54 55	1000	
56 57		
58 59 60		

2 3 4	1001	Bishop, P.J., Cuff, A.R., Hutchinson, J.R. 2021d. How to build a dinosaur: musculoskeletal
5 6	1002	modelling and simulation of locomotor biomechanics in extinct animals. Paleobiology 47:1-
7 8	1003	38.
9 10 11	1004	
12 13	1005	Blob, R. W., & Biewener, A. A. (2001). Mechanics of limb bone loading during terrestrial
14 15 16	1006	locomotion in the green iguana (Iguana iguana) and American alligator (Alligator
17 18	1007	mississippiensis). Journal of Experimental Biology, 204(6), 1099-1122.
19 20	1008	
21 22 23	1009	Bonaparte, J. F. (1969). Comments on early saurischians. Zoological Journal of the Linnean
23 24 25	1010	Society, 48(4), 471-480.
26 27	1011	
28 29	1012	Bonaparte, JF (1975). Nuevos materiales de Lagosuchus talampayensis Romer (Thecodontia-
30 31 32	1013	Pseudosuchia) y su significado en el origen de los Saurischia: Chañarense inferior, Triásico
33 34	1014	medio de Argentina. Acta Geológica Lilloana 13 (1): 5–90.
35 36	1015	
37 38 30	1016	Bonaparte, J. F. (1984). Locomotion in rauisuchid thecodonts. Journal of Vertebrate
40 41	1017	Paleontology, 3(4), 210-218.
42 43	1018	
44 45 46	1019	Boucot, A. J., Chen Xu, & Scotese, C. R. 2013. Phanerozoic Paleoclimate: An Atlas of
40 47 48	1020	Lithologic Indicators of Climate, SEPM Concepts in Sedimentology and Paleontology,
49 50	1021	(Print-on-Demand Version), No. 11, 478 p, ISBN 978-1-56576-289-3, October 2013, Society
51 52	1022	for Sedimentary Geology, Tulsa, OK. doi: 10.2110/sepmcsp.11
53 54 55	1023	
56 57		
58 59		
60		

2		
3 4	1024	Brocklehurst, R. J., Schachner, E. R., Codd, J. R., & Sellers, W. I. (2020). Respiratory
5 6	1025	evolution in archosaurs. Philosophical Transactions of the Royal Society B, 375(1793),
/ 8 9	1026	20190140.
10 11	1027	
12 13	1028	Bronzati, M., Montefeltro, F. C., & Langer, M. C. (2015). Diversification events and the
14 15 16	1029	effects of mass extinctions on Crocodyliformes evolutionary history. Royal Society Open
17 18	1030	Science, 2(5), 140385.
19 20 21	1031	
21 22 23	1032	Brusatte, S. L., Benton, M. J., Lloyd, G. T., Ruta, M., & Wang, S. C. (2010a).
24 25	1033	Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida).
26 27 28	1034	Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 101(3-4),
28 29 30	1035	367-382.
31 32	1036	
33 34 25	1037	Brusatte, S. L., Nesbitt, S. J., Irmis, R. B., Butler, R. J., Benton, M. J., & Norell, M. A.
35 36 37	1038	(2010b). The origin and early radiation of dinosaurs. Earth-Science Reviews, 101(1-2), 68-
38 39	1039	100.
40 41	1040	
42 43 44	1041	Brusatte, S. L., Niedźwiedzki, G., & Butler, R. J. (2011). Footprints pull origin and
45 46	1042	diversification of dinosaur stem lineage deep into Early Triassic. Proceedings of the Royal
47 48	1043	Society B: Biological Sciences, 278(1708), 1107-1113.
49 50 51	1044	
51 52 53	1045	Brusatte, S. L., Benton, M. J., Ruta, M., & Lloyd, G. T. (2008a). Superiority, competition,
54 55	1046	and opportunism in the evolutionary radiation of dinosaurs. Science, 321(5895), 1485-1488.
56 57 58 59 60	1047	

Brusatte, S. L., Benton, M. J., Ruta, M., & Lloyd, G. T. (2008b). The first 50 Myr of dinosaur

evolution: macroevolutionary pattern and morphological disparity. Biology Letters, 4(6),

Butler, R. J., Barrett, P. M., & Gower, D. J. (2012). Reassessment of the evidence for

Campione, N. E., & Evans, D. C. (2020). The accuracy and precision of body mass

Carrano, M. T., & Wilson, J. A. (2001). Taxon distributions and the tetrapod track record.

Carrier, D. R., N. C. Heglund and K. E. Earls. (1994). Variable gearing during locomotion in

Chapelle, K. E., Benson, R. B., Stiegler, J., Otero, A., Zhao, Q., & Choiniere, J. N. (2020). A

application to dinosaurs and its bearing on the evolution of posture. Palaeontology, 63(2),

quantitative method for inferring locomotory shifts in amniotes during ontogeny, its

estimation in non-avian dinosaurs. Biological Reviews, 95(6), 1759-1797.

the human musculoskeletal system. Science 265, 651-653.

Italian Journal of Geosciences, 139(2), 309-320.

postcranial skeletal pneumaticity in Triassic archosaurs, and the early evolution of the avian

3 4	1048
5 6	1049
7 8	1050
9 10 11	1051
12 13	1052
14 15	1053
16 17 18	1054
19 20	1055
21 22	1056
23 24 25	1057
26 27	1058
28 29	1059
30 31 32	1060
33 34	1061
35 36	1062
37 38 30	1063
39 40 41	1064
42 43	1065
44 45	1066
46 47 48	1067
49 50	1068
51 52	1069
53 54 55	1070
56 57	1071
58 59	1072
60	

1

733-736.

respiratory system. PloS one, 7(3), e34094.

Paleobiology, 27(3), 564-582.

229-242.

Citton, P., Ronchi, A., Nicosia, U., Sacchi, E., Maganuco, S., Cipriani, A., ... & Romano, M.

(2020). Tetrapod tracks from the Middle Triassic of NW Sardinia (Nurra region, Italy).

1 2		
3 4	1073	
5 6 7	1074	Cubo, J., Le Roy, N., Martinez-Maza, C., & Montes, L. (2012). Paleohistological estimation
7 8 9	1075	of bone growth rate in extinct archosaurs. Paleobiology, 38(2), 335-349.
10 11	1076	
12 13	1077	Cuff, A.R., Daley, M.A., Michel, K.B., Allen, V.R., Lamas, Luis P., Adami, C., Monticelli,
14 15 16	1078	P., Pelligand, L., Hutchinson, J.R. 2019. Relating neuromuscular control to functional
17 18	1079	anatomy of limb muscles in extant archosaurs. Journal of Morphology 280:666-680.
19 20	1080	
21 22 22	1081	Dal Corso, J., Bernardi, M., Sun, Y., Song, H., Seyfullah, L. J., Preto, N., & Benton, M. J.
23 24 25	1082	(2020). Extinction and dawn of the modern world in the Carnian (Late Triassic). Science
26 27	1083	Advances, 6(38), eaba0099.
28 29	1084	
30 31 32	1085	Demuth, O.E., Rayfield, E.J., Hutchinson, J.R., 2020. 3D hindlimb joint mobility of the stem-
33 34	1086	archosaur Euparkeria capensis with implications for postural evolution within Archosauria.
35 36	1087	Scientific Reports 10:15357.
37 38 20	1088	
39 40 41	1089	Demuth, O.E., Wiseman, A.L.A., Mallison, H., van Beesel, J., Hutchinson, J.R. 2022. Three-
42 43	1090	dimensional polygonal muscle modelling and line of action estimation in living and extinct
44 45	1091	taxa. Scientific Reports 12:3358.
46 47 48	1092	
49 50	1093	Dunhill, A. M., & Wills, M. A. (2015). Geographic range did not confer resilience to
51 52	1094	extinction in terrestrial vertebrates at the end-Triassic crisis. Nature Communications, 6(1), 1-
53 54 55	1095	8.
55 56 57 58 59 60	1096	

2		
3 4	1097	Dunne, E. M., Farnsworth, A., Greene, S. E., Lunt, D. J., & Butler, R. J. (2021). Climatic
5 6 7	1098	drivers of latitudinal variation in Late Triassic tetrapod diversity. Palaeontology, 64(1), 101-
/ 8	1099	117.
9 10 11	1100	
12 13	1101	Ezcurra, M. D. (2016). The phylogenetic relationships of basal archosauromorphs, with an
14 15 16	1102	emphasis on the systematics of proterosuchian archosauriforms. PeerJ 4:e1778
17 18	1103	
19 20	1104	Ezcurra, M. D., Nesbitt, S. J., Bronzati, M., Dalla Vecchia, F. M., Agnolin, F. L., Benson, R.
21 22 23	1105	B., & Langer, M. C. (2020). Enigmatic dinosaur precursors bridge the gap to the origin of
23 24 25	1106	Pterosauria. Nature, 588(7838), 445-449.
26 27	1107	
28 29	1108	Falkingham, P. L., & Gatesy, S. M. (2014). The birth of a dinosaur footprint: subsurface 3D
30 31 32	1109	motion reconstruction and discrete element simulation reveal track ontogeny. Proceedings of
33 34	1110	the National Academy of Sciences, 111(51), 18279-18284.
35 36	1111	
37 38 30	1112	Falkingham, P. L., Turner, M. L., & Gatesy, S. M. (2020). Constructing and testing
40 41	1113	hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation.
42 43	1114	Palaeontology, 63(6), 865-880.
44 45 46	1115	
40 47 48	1116	Farlow, J. O., Schachner, E. R., Sarrazin, J. C., Klein, H., & Currie, P. J. (2014). Pedal
49 50	1117	proportions of <i>Poposaurus gracilis</i> : convergence and divergence in the feet of archosaurs.
51 52	1118	The Anatomical Record, 297(6), 1022-1046.
53 54 55 56 57 58 59 60	1119	

1 2		
2 3 4	1120	Foth, C., Sookias, R. B., & Ezcurra, M. D. (2021). Rapid initial morphospace expansion and
5 6 7	1121	delayed morphological disparity peak in the first 100 million years of the Archosauromorph
7 8 9	1122	evolutionary radiation. Frontiers in Earth Science, 763.
10 11	1123	
12 13 14	1124	Fox, C. P., Whiteside, J. H., Olsen, P. E., Cui, X., Summons, R. E., Idiz, E., & Grice, K.
15 16	1125	(2022). Two-pronged kill mechanism at the end-Triassic mass extinction. Geology. doi:
17 18	1126	10.1130/G49560.1
19 20	1127	
21 22 23	1128	Garcia, M. S., Müller, R. T., Da-Rosa, A. A. S., & Dias-da-Silva, S. (2019). The oldest
24 25	1129	known co-occurrence of dinosaurs and their closest relatives: A new lagerpetid from a
26 27 28	1130	Carnian Upper Triassic) bed of Brazil with implications for dinosauromorph biostratigraphy,
28 29 30	1131	early diversification and biogeography. Journal of South American Earth Sciences 91:302-
31 32	1132	319
33 34	1133	
35 36 37	1134	García Marsà, J. A., Agnolin, F., & Novas, F. E. (2020). Comparative bone microstructure of
38 39	1135	three archosauromorphs from the Carnian, Late Triassic Chañares Formation of Argentina.
40 41	1136	
42 43	1137	Gatesy, S. M. (1990). Caudofemoral musculature and the evolution of theropod locomotion.
44 45 46	1138	Paleobiology, 16(2), 170-186.
47 48	1139	
49 50	1140	Gatesy, S. M. (1991). Hind limb movements of the American alligator (Alligator
51 52 53	1141	mississippiensis) and postural grades. Journal of Zoology, 224(4), 577-588.
54 55	1142	
56 57	1143	Gatesy, S. M. (1994). Neuromuscular diversity in archosaur deep dorsal thigh muscles. Brain,
58 59 60	1144	Behavior and Evolution, 43(1), 1-14.

1 2		
2 3 4	1145	
5 6 7	1146	Gatesy, S. M. (1997). An electromyographic analysis of hindlimb function in Alligator during
7 8 9	1147	terrestrial locomotion. Journal of Morphology, 234(2), 197-212.
10 11	1148	
12 13	1149	Gatesy, S. M. (1999). Guineafowl hind limb function. II: Electromyographic analysis and
14 15 16	1150	motor pattern evolution. Journal of Morphology, 240(2), 127-142.
17 18	1151	
19 20	1152	Gatesy, S.M., Manafzadeh, A.R., Bishop, P.J., Turner, M.L., Kambic, R.E., Cuff, A.R.,
21 22 22	1153	Hutchinson, J.R. 2022. A proposed standard for quantifying 3-D hindlimb joint poses in
25 24 25	1154	living and extinct archosaurs. Journal of Anatomy, published online.
26 27	1155	
28 29	1156	Gatesy, S. M., Middleton, K. M., & Shubin, N. H. (1999). Three-dimensional preservation of
30 31 32	1157	foot movements in Triassic theropod dinosaurs. Nature, 399(6732), 141-144.
33 34	1158	
35 36	1159	Gauthier, J. A., Nesbitt, S. J., Schachner, E. R., Bever, G. S., & Joyce, W. G. (2011). The
37 38 30	1160	bipedal stem crocodilian Poposaurus gracilis: inferring function in fossils and innovation in
39 40 41	1161	archosaur locomotion. Bulletin of the Peabody Museum of Natural History, 52(1), 107-126.
42 43	1162	
44 45	1163	Granatosky, M. C. (2020). Testing the propulsive role of m. peroneus longus during
46 47 48	1164	quadrupedal walking in Varanus exanthematicus. Journal of Experimental Zoology Part A:
49 50	1165	Ecological and Integrative Physiology, 333(5), 325-332.
51 52	1166	
53 54 55	1167	Grinham, L. R., VanBuren, C. S., & Norman, D. B. (2019). Testing for a facultative
55 56 57	1168	locomotor mode in the acquisition of archosaur bipedality. Royal Society Open Science, 6(7),
58 59 60	1169	190569.

1		
2 3 4	1170	
5 6 7	1171	Hancock, J. A., Stevens, N. J., & Biknevicius, A. R. (2007). Whole-body mechanics and
7 8 9	1172	kinematics of terrestrial locomotion in the Elegant-crested Tinamou Eudromia elegans. Ibis,
10 11	1173	149(3), 605-614.
12 13 14	1174	
15 16	1175	Hancock, J. A., Stevens, N. J., & Biknevicius, A. R. (2014). Elegant-crested Tinamous
17 18	1176	Eudromia elegans do not synchronize head and leg movements during head-bobbing. Ibis,
19 20 21	1177	156(1), 198-208.
22 23	1178	
24 25	1179	He, T., Dal Corso, J., Newton, R. J., Wignall, P. B., Mills, B. J., Todaro, S., & Dunhill, A.
26 27 28	1180	M. (2020). An enormous sulfur isotope excursion indicates marine anoxia during the end-
29 30	1181	Triassic mass extinction. Science Advances, 6(37), eabb6704.
31 32	1182	
33 34 35	1183	Hutchinson, J. R. (2001). The evolution of pelvic osteology and soft tissues on the line to
36 37	1184	extant birds (Neornithes). Zoological Journal of the Linnean Society, 131(2), 123-168.
38 39	1185	
40 41	1186	Hutchinson, J. R., & Gatesy, S. M. (2000). Adductors, abductors, and the evolution of
42 43 44	1187	archosaur locomotion. Paleobiology, 26(4), 734-751.
45 46	1188	
47 48	1189	Hutchinson, J. R., Anderson, F. C., Blemker, S. S., & Delp, S. L. (2005). Analysis of
49 50 51	1190	hindlimb muscle moment arms in Tyrannosaurus rex using a three-dimensional
52 53	1191	musculoskeletal computer model: implications for stance, gait, and speed. Paleobiology,
54 55	1192	31(4), 676-701.
56 57 58 59 60	1193	

1 ว		
2 3 4	1194	Hutchinson, J.R., Felkler, D., Houston, K., Chang, YM., Brueggen, J., Kledzik, D. and
5 6 7	1195	Vliet, K.A. 2019. Divergent evolution of terrestrial locomotor abilities in extant Crocodylia.
7 8 9	1196	Scientific Reports 9:19302.
10 11	1197	
12 13	1198	Iijima, M., Munteanu, V. D., Elsey, R. M., & Blob, R. W. (2021). Ontogenetic changes in
14 15 16	1199	limb posture, kinematics, forces and joint moments in American alligators (Alligator
17 18	1200	mississippiensis). Journal of Experimental Biology, 224(23), jeb242990.
19 20 21	1201	
21 22 23	1202	Irmis, R. B., Nesbitt, S. J., Padian, K., Smith, N. D., Turner, A. H., Woody, D., & Downs, A.
24 25	1203	(2007). A Late Triassic dinosauromorph assemblage from New Mexico and the rise of
26 27 28	1204	dinosaurs. Science, 317(5836), 358-361.
28 29 30	1205	
31 32	1206	Irmis, R. B. (2010). Evaluating hypotheses for the early diversification of dinosaurs. Earth
33 34 25	1207	and Environmental Science Transactions of the Royal Society of Edinburgh, 101(3-4), 397-
35 36 37	1208	426.
38 39	1209	
40 41	1210	Irmis, R. B., Nesbitt, S. J., & Sues, H. D. (2013). Early Crocodylomorpha. Geological
42 43 44	1211	Society, London, Special Publications, 379(1), 275-302.
45 46	1212	
47 48	1213	Kaiho, K., Tanaka, D., Richoz, S., Jones, D. S., Saito, R., Kameyama, D., & Fujibayashi,
49 50 51	1214	M. (2022). Volcanic temperature changes modulated volatile release and climate fluctuations
52 53	1215	at the end-Triassic mass extinction. Earth and Planetary Science Letters, 579, 117364.
54 55 56 57 58 59	1216	
60		

1 2		
2 3 4	1217	Kambic, R. E., Roberts, T. J., & Gatesy, S. M. (2014). Long-axis rotation: a missing degree
5 6 7	1218	of freedom in avian bipedal locomotion. Journal of Experimental Biology, 217(15), 2770-
7 8 9	1219	2782.
10 11	1220	
12 13 14	1221	Kim, K. S., Lockley, M. G., Lim, J. D., Bae, S. M., & Romilio, A. (2020). Trackway
15 16	1222	evidence for large bipedal crocodylomorphs from the Cretaceous of Korea. Scientific
17 18	1223	Reports, 10(1), 1-13.
19 20 21	1224	
21 22 23	1225	Klausen, T. G., Paterson, N. W., & Benton, M. J. (2020). Geological control on dinosaurs'
24 25	1226	rise to dominance: Late Triassic ecosystem stress by relative sea level change. Terra Nova,
26 27	1227	32(6), 434-441.
28 29 30	1228	
31 32	1229	Klein, H., Lucas, S. G., and Haubold, H.(2006). "Tetrapod Track Assemblage of the Redonda
33 34	1230	Formation (Upper Triassic, Chinle Group) in East-central New Mexico – Reevaluation of
35 36 27	1231	Ichnofaunal Diversity from Studies of New Material," in The Triassic-Jurassic Terrestrial
37 38 39	1232	Transition. Editors J. D. Harris, S. G. Lucas, J. A. Speilmann, M. G. Lockley, A. R. C.
40 41	1233	Milner, and J. I. Kirkland (Albuquerque, New Mexico: New Mexico Museum of Natural
42 43	1234	History and Science), 241–250.
44 45 46	1235	
47 48	1236	Klein, N., Foth, C., & Schoch, R. R. (2017). Preliminary observations on the bone histology
49 50	1237	of the Middle Triassic pseudosuchian archosaur Batrachotomus kupferzellensis reveal fast
51 52 53	1238	growth with laminar fibrolamellar bone tissue. Journal of Vertebrate Paleontology, 37(4),
54 55	1239	e1333121.
56 57 58 59 60	1240	

1 2		
2 3 4	1241	Kubo, T., & Benton, M. J. (2009). Tetrapod postural shift estimated from Permian and
5 6 7	1242	Triassic trackways. Palaeontology, 52(5), 1029-1037.
, 8 9	1243	
10 11	1244	Kubo, T., & Kubo, M. O. (2012). Associated evolution of bipedality and cursoriality among
12 13 14	1245	Triassic archosaurs: a phylogenetically controlled evaluation. Paleobiology, 38(3), 474-485.
15 16	1246	
17 18	1247	Kubo, T., & Kubo, M. O. (2013). Analysis of Triassic archosauriform trackways: Difference
19 20 21	1248	in stride/foot ratio between dinosauromorphs and other archosauriforms. Palaios, 28(4), 259-
22 23	1249	265.
24 25	1250	
26 27 28	1251	Kubo, T., & Kubo, M. O. (2016). Nonplantigrade foot posture: A constraint on dinosaur body
29 30	1252	size. PLoS One, 11(1), e0145716.
31 32	1253	
33 34 35	1254	Langer, M. C., Ezcurra, M. D., Bittencourt, J. S., & Novas, F. E. (2010). The origin and early
36 37	1255	evolution of dinosaurs. Biological Reviews, 85(1), 55-110.
38 39	1256	
40 41 42	1257	Langer, M. C., Nesbitt, S. J., Bittencourt, J. S., & Irmis, R. B. (2013). Non-dinosaurian
42 43 44	1258	Dinosauromorpha. Geological Society, London, Special Publications, 379(1), 157-186.
45 46	1259	
47 48 40	1260	Legendre, L. J., Guénard, G., Botha-Brink, J., & Cubo, J. (2016). Palaeohistological evidence
50 51	1261	for ancestral high metabolic rate in archosaurs. Systematic Biology, 65(6), 989-996.
52 53	1262	
54 55 56	1263	Legendre, L. J., & Davesne, D. (2020). The evolution of mechanisms involved in vertebrate
50 57 58	1264	endothermy. Philosophical Transactions of the Royal Society B, 375(1793), 20190136.
59 60	1265	

2		
3 4	1266	Lindström, S. (2021). Two-phased mass rarity and extinction in land plants during the end-
5 6	1267	Triassic climate crisis. Frontiers in Earth Science, 9, 1079.
/ 8 9	1268	
10 11	1269	Lu, J., Zhang, P., Dal Corso, J., Yang, M., Wignall, P. B., Greene, S. E., & Hilton, J.
12 13	1270	(2021). Volcanically driven lacustrine ecosystem changes during the Carnian Pluvial Episode
14 15 16	1271	(Late Triassic). Proceedings of the National Academy of Sciences, 118(40).
17 18	1272	
19 20	1273	Lucas, S. G., & Heckert, A. B. (2011). Late Triassic aetosaurs as the trackmaker of the
21 22 23	1274	tetrapod footprint ichnotaxon Brachychirotherium. Ichnos, 18(4), 197-208.
24 25	1275	
26 27	1276	Manafzadeh, A. R., Kambic, R. E., & Gatesy, S. M. (2021). A new role for joint mobility in
28 29 30	1277	reconstructing vertebrate locomotor evolution. Proceedings of the National Academy of
31 32	1278	Sciences, 118(7).
33 34	1279	
35 36 37	1280	Manafzadeh, A. R., & Gatesy, S. M. (2022). Advances and challenges in paleobiological
38 39	1281	reconstructions of joint mobility. Integrative and Comparative Biology. doi:
40 41	1282	10.1093/icb/icac008
42 43	1283	
44 45 46	1284	Mancuso, A. C., Benavente, C. A., Irmis, R. B., & Mundil, R. (2020). Evidence for the
47 48	1285	Carnian Pluvial Episode in Gondwana: New multiproxy climate records and their bearing on
49 50	1286	early dinosaur diversification. Gondwana Research, 86, 104-125.
51 52 53	1287	
55 54 55	1288	Marsicano, C. A., & Barredo, S. P. (2004). A Triassic tetrapod footprint assemblage from
56 57	1289	southern South America: palaeobiogeographical and evolutionary implications.
58 59	1290	Palaeogeography, Palaeoclimatology, Palaeoecology, 203(3-4), 313-335.
60		

1 ว		
2 3 4	1291	
5 6 7	1292	Marsicano, C. A., Domnanovich, N. S., & Mancuso, A. C. (2007). Dinosaur origins: evidence
7 8 9	1293	from the footprint record. Historical Biology, 19(1), 83-91.
10 11	1294	
12 13	1295	Marsicano, C. A., Mancuso, A. C., Palma, R. M., & Krapovickas, V. (2010). Tetrapod tracks
14 15 16	1296	in a marginal lacustrine setting (Middle Triassic, Argentina): Taphonomy and significance.
17 18	1297	Palaeogeography, Palaeoclimatology, Palaeoecology, 291(3-4), 388-399.
19 20 21	1298	
21 22 23	1299	Marsicano, C. A., Irmis, R. B., Mancuso, A. C., Mundil, R., & Chemale, F. (2016). The
24 25	1300	precise temporal calibration of dinosaur origins. Proceedings of the National Academy of
26 27	1301	Sciences, 113(3), 509-513.
28 29 30	1302	
31 32	1303	Michel, K.B., West, T.G., Daley, M.A., Allen, V.R., Hutchinson, J.R. 2020. Appendicular
33 34	1304	muscle physiology and biomechanics in Crocodylus niloticus. Integrative Organismal
35 36 37	1305	Biology obaa038.
37 38 39	1306	
40 41	1307	Müller, R. T., & Garcia, M. S. (2020). A paraphyletic 'Silesauridae' as an alternative
42 43	1308	hypothesis for the initial radiation of ornithischian dinosaurs. Biology Letters, 16: 20200417
44 45 46	1309	
47 48	1310	Nesbitt, S. J., Barrett, P. M., Werning, S., Sidor, C. A., & Charig, A. J. (2013). The oldest
49 50	1311	dinosaur? A Middle Triassic dinosauriform from Tanzania. Biology Letters, 9(1), 20120949.
51 52 53	1312	
54 55	1313	Nesbitt, SJ (2011). The early evolution of archosaurs: relationships and the origin of major
56 57	1314	clades. Bulletin of the American Museum of Natural History. 352: 1–292.
58 59 60	1315	

1 2		
2 3 4	1316	Nesbitt, S. J., Butler, R. J., Ezcurra, M. D., Barrett, P. M., Stocker, M. R., Angielczyk, K. D.,
5 6	1317	& Charig, A. J. (2017). The earliest bird-line archosaurs and the assembly of the dinosaur
/ 8 9	1318	body plan. Nature, 544(7651), 484-487.
10 11	1319	
12 13	1320	Nesbitt, S. J., Sidor, C. A., Irmis, R. B., Angielczyk, K. D., Smith, R. M., & Tsuji, L. A.
14 15 16	1321	(2010). Ecologically distinct dinosaurian sister group shows early diversification of
17 18	1322	Ornithodira. Nature, 464(7285), 95-98.
19 20	1323	
21 22 23	1324	Niedźwiedzki, G., Brusatte, S. L., & Butler, R. J. (2013). Prorotodactylus and Rotodactylus
24 25	1325	tracks: an ichnological record of dinosauromorphs from the Early-Middle Triassic of Poland.
26 27	1326	Geological Society, London, Special Publications, 379(1), 319-351.
28 29 30	1327	
31 32	1328	Novas, F. E. (1996). Dinosaur monophyly. Journal of Vertebrate Paleontology, 16(4), 723-
33 34	1329	741.
35 36 37	1330	
37 38 39	1331	Novas, F. E., Ezcurra, M. D., Chatterjee, S., & Kutty, T. S. (2010). New dinosaur species
40 41	1332	from the Upper Triassic Upper Maleri and Lower Dharmaram formations of central India.
42 43	1333	Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 101(3-4),
44 45 46	1334	333-349.
47 48	1335	
49 50	1336	Nyakatura, J. A., Melo, K., Horvat, T., Karakasiliotis, K., Allen, V. R., Andikfar, A., &
51 52 53	1337	Ijspeert, A. J. (2019). Reverse-engineering the locomotion of a stem amniote. Nature,
54 55	1338	565(7739), 351-355.
56 57 58 59	1339	
60		

1 2		
3 4	1340	O'Connor, P. M. (2006). Postcranial pneumaticity: an evaluation of soft-tissue influences on
5 6 7	1341	the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. Journal
7 8 9	1342	of Morphology, 267(10), 1199-1226.
10 11	1343	
12 13 14	1344	Olsen, P. E., & Baird, D. (1986). The ichnogenus Atreipus and its significance for Triassic
15 16	1345	biostratigraphy. The Beginning of the Age of Dinosaurs. Cambridge University Press,
17 18	1346	Cambridge, 61-87.
19 20	1347	
21 22 23	1348	Otero, A., Allen, V., Pol, D., Hutchinson, J.R. 2017. Forelimb muscle and joint actions in
24 25	1349	Archosauria: insights from Crocodylus johnstoni (Pseudosuchia) and Mussaurus patagonicus
26 27 28	1350	(Sauropodomorpha). PeerJ 5:e3976.
20 29 30	1351	
31 32	1352	Otero, A., Cuff, A.R., Allen, V., Sumner-Rooney, L., Pol, D., Hutchinson, J.R. 2019.
33 34	1353	Ontogenetic changes in the body plan of the sauropodomorph dinosaur Mussaurus
35 36 37	1354	patagonicus reveal shifts of locomotor stance during growth. Scientific Reports 9:7614.
38 39	1355	
40 41	1356	Owen, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association
42 43 44	1357	for the Advancement of Science, 11, 60–204.
45 46	1358	
47 48	1359	Padian, K. (1983). A functional analysis of flying and walking in pterosaurs. Paleobiology,
49 50	1360	9(3), 218-239.
51 52 53	1361	
54 55	1362	Padian, K. (2012). The problem of dinosaur origins: integrating three approaches to the rise
56 57	1363	of Dinosauria. Earth and Environmental Science Transactions of the Royal Society of
58 59 60	1364	Edinburgh, 103(3-4), 423-442.

1 2		
2 3 4	1365	
5 6 7	1366	Padian, K., Li, C., & Pchelnikova, J. (2010). The trackmaker of Apatopus (Late Triassic,
7 8 9	1367	North America): implications for the evolution of archosaur stance and gait. Palaeontology,
10 11	1368	53(1), 175-189.
12 13	1369	
14 15 16	1370	Parrish, J. M. (1986). Locomotor adaptations in the hindlimb and pelvis of the Thecodontia.
17 18	1371	Hunteria 1, 1–35.
19 20	1372	
21 22 23	1373	Parrish, J. M. (1987). The origin of crocodilian locomotion. Paleobiology, 13(4), 396-414.
24 25	1374	
26 27	1375	Pashchenko, D. I. (2018). A new interpretation of the crocodile forelimb morphological
28 29 30	1376	features as adaptation to parasagittal quadrupedal locomotion on the ground. Doklady
31 32	1377	Biological Sciences 483(1):235-238.
33 34	1378	
35 36 27	1379	Petryshyn, V. A., Greene, S. E., Farnsworth, A., Lunt, D. J., Kelley, A., Gammariello, R.,
37 38 39	1380	& Corsetti, F. A. (2020). The role of temperature in the initiation of the end-Triassic mass
40 41	1381	extinction. Earth-Science Reviews, 208, 103266.
42 43	1382	
44 45 46	1383	Petti, F. M., Avanzini, M., Nicosia, U., Girardi, S., Bernardi, M., Ferretti, P., et al. (2009).
47 48	1384	Late Triassic (Early-middle Carnian) Chirotherian Tracks from the Val Sabbia Sandstone
49 50	1385	(Eastern Lombardy, Brescian Prealps, Northern Italy). Riv. Ital. di Paleontol. e Stratigr. 115,
51 52 53	1386	277–290.
54 55	1387	
56 57	1388	Pintore, R., Houssaye, A., Nesbitt, S.J., Hutchinson, J.R. 2022. Femoral specializations to
58 59 60	1389	locomotor habits in early archosauriforms. Journal of Anatomy, published online.

1390	
1391	Polet DT. 2021. The Murphy number: how pitch moment of inertia dictates quadrupedal
1392	walking and running energetics. J Exp Biol 224:jeb228296.
1393	
1394	Polet DT, Hutchinson JR. 2022. Estimating gaits of an ancient crocodile-line archosaur
1395	through trajectory optimization, with comparison to fossil trackways. Front Bioeng Biotech:
1396	1514.
1397	
1398	Pontzer, H., Allen, V., & Hutchinson, J. R. (2009). Biomechanics of running indicates
1399	endothermy in bipedal dinosaurs. PLoS One, 4(11), e7783.
1400	
1401	Porchetti, S. D., Nicosia, U., Mietto, P., Petti, F. M., & Avanzini, M. (2008). Atreipus-like
1402	footprints and their co-occurrence with <i>Evazoum</i> from the upper Carnian (Tuvalian) of
1403	Trentino-Alto Adige. Studi Trentini Di Scienze Naturali: Acta Geologica, 83, 277-287.
1404	
1405	Pradelli, L. A., Leardi, J. M., & Ezcurra, M. D. (2022). Body size disparity of the
1406	archosauromorph reptiles during the first 90 million years of their evolution. Ameghiniana,
1407	59(1), 47-77.
1408	
1409	Rankin, J. W., Rubenson, J., & Hutchinson, J. R. (2016). Inferring muscle functional roles of
1410	the ostrich pelvic limb during walking and running using computer optimization. Journal of
1411	the Royal Society Interface, 13(118), 20160035.
1412	
	 1390 1391 1392 1393 1394 1395 1396 1397 1398 1399 1400 1401 1402 1402 1403 1404 1405 1406 1407 1408 1409 1410 1411 1412

2		
3 4	1413	Reilly, S. M., Willey, J. S., Biknevicius, A. R., & Blob, R. W. (2005). Hindlimb function in
5 6	1414	the alligator: integrating movements, motor patterns, ground reaction forces and bone strain
/ 8 9	1415	of terrestrial locomotion. Journal of Experimental Biology, 208(6), 993-1009.
10 11	1416	
12 13	1417	Reisz, R. R., Evans, D. C., Roberts, E. M., Sues, H. D., & Yates, A. M. (2012). Oldest known
14 15 16	1418	dinosaurian nesting site and reproductive biology of the Early Jurassic sauropodomorph
17 18	1419	Massospondylus. Proceedings of the National Academy of Sciences, 109(7), 2428-2433.
19 20	1420	
21 22 23	1421	Renous, S., Gasc, J. P., Bels, V. L., & Wicker, R. (2002). Asymmetrical gaits of juvenile
24 25	1422	Crocodylus johnstoni, galloping Australian crocodiles. Journal of Zoology, 256(3), 311-325.
26 27	1423	
28 29 30	1424	Rigo, M., Onoue, T., Tanner, L. H., Lucas, S. G., Godfrey, L., Katz, M. E., & Bertinelli, A.
31 32	1425	(2020). The Late Triassic Extinction at the Norian/Rhaetian boundary: Biotic evidence and
33 34	1426	geochemical signature. Earth-Science Reviews, 204, 103180.
35 36 27	1427	
37 38 39	1428	Romer, A. S. (1971). The Chanares (Argentina) Triassic reptile fauna. X. Two new but
40 41	1429	incompletely known long-limbed pseudosuchians. Breviora. 378: 1–10.
42 43	1430	
44 45 46	1431	Romer, A. S. (1972a). The Chañares (Argentina) Triassic reptile fauna. XV. Further remains
47 48	1432	of the thecodonts Lagerpeton and Lagosuchus.
49 50	1433	
51 52 53	1434	Romer, A. S., (1972b). The Chañares (Argentina) Triassic reptile fauna. XIV. Lewisuchus
54 55	1435	admixtus gen. et sp. nov., a further thecodont from the Chañares beds.
56 57 58 59 60	1436	

3 4	1437	Rubenson, J., Heliams, D. B., Lloyd, D. G., & Fournier, P. A. (2004). Gait selection in the
5 6 7	1438	ostrich: mechanical and metabolic characteristics of walking and running with and without an
, 8 9	1439	aerial phase. Proceedings of the Royal Society of London. Series B: Biological Sciences,
10 11	1440	271(1543), 1091-1099.
12 13	1441	
14 15 16	1442	Rubenson, J., Lloyd, D. G., Besier, T. F., Heliams, D. B., & Fournier, P. A. (2007). Running
17 18	1443	in ostriches (Struthio camelus): three-dimensional joint axes alignment and joint kinematics.
19 20	1444	Journal of Experimental Biology, 210(14), 2548-2562.
21 22 23	1445	
24 25	1446	Ruhl, M., Bonis, N. R., Reichart, G. J., Damsté, J. S. S., & Kürschner, W. M. (2011).
26 27	1447	Atmospheric carbon injection linked to end-Triassic mass extinction. Science, 333(6041),
28 29 30	1448	430-434.
31 32	1449	
33 34	1450	Schachner, E. R., Irmis, R. B., Huttenlocker, A. K., Sanders, K., Cieri, R. L., & Nesbitt, S. J.
35 36 37	1451	(2020). Osteology of the Late Triassic bipedal archosaur <i>Poposaurus gracilis</i> (Archosauria:
38 39	1452	Pseudosuchia) from Western North America. The Anatomical Record, 303(4), 874-917.
40 41	1453	
42 43 44	1454	Sereno, P. C. (1991). Basal archosaurs: phylogenetic relationships and functional
45 46	1455	implications. Journal of Vertebrate Paleontology, 11(S4), 1-53.
47 48	1456	
49 50	1457	Sereno, PC; Arcucci, AB. (1994). Dinosaurian precursors from the Middle Triassic of
51 52 53	1458	Argentina: Marasuchus lilloensis, gen. nov. Journal of Vertebrate Paleontology. 14 (1): 53-
54 55	1459	73.
56 57 58 59 60	1460	

1 2		
2 3 4	1461	Seymour, R. S., Bennett-Stamper, C. L., Johnston, S. D., Carrier, D. R., & Grigg, G. C.
5 6	1462	(2004). Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution.
/ 8 9	1463	Physiological and Biochemical Zoology, 77(6), 1051-1067.
10 11	1464	
12 13	1465	Shen, J., Yin, R., Algeo, T. J., Svensen, H. H., & Schoepfer, S. D. (2022). Mercury evidence
14 15 16	1466	for combustion of organic-rich sediments during the end-Triassic crisis. Nature
17 18	1467	Communications, 13(1), 1-8.
19 20 21	1468	
21 22 23	1469	Sookias, R. B., Butler, R. J., & Benson, R. B. (2012). Rise of dinosaurs reveals major body-
24 25	1470	size transitions are driven by passive processes of trait evolution. Proceedings of the Royal
26 27 28	1471	Society B: Biological Sciences, 279(1736), 2180-2187.
28 29 30	1472	
31 32	1473	Stockdale, M. T., & Benton, M. J. (2021). Environmental drivers of body size evolution in
33 34	1474	crocodile-line archosaurs. Communications Biology, 4(1), 1-11.
35 36 37	1475	
38 39	1476	Stoessel, A., & Fischer, M. S. (2012). Comparative intralimb coordination in avian bipedal
40 41	1477	locomotion. Journal of Experimental Biology, 215(23), 4055-4069.
42 43	1478	
44 45 46	1479	Stubbs, T. L., Pierce, S. E., Rayfield, E. J., & Anderson, P. S. (2013). Morphological and
47 48	1480	biomechanical disparity of crocodile-line archosaurs following the end-Triassic extinction.
49 50	1481	Proceedings of the Royal Society B: Biological Sciences, 280(1770), 20131940.
51 52 53	1482	
54 55	1483	Sullivan, C. (2010). The role of the calcaneal 'heel' as a propulsive lever in basal archosaurs
56 57	1484	and extant monitor lizards. Journal of Vertebrate Paleontology, 30(5), 1422-1432.
58 59 60	1485	

3 4	1486	Sullivan, C., (2015). Evolution of hind limb posture in Triassic archosauriforms. In Dial, K.
5 6	1487	P., Shubin, N., & Brainerd, E. L., Eds. Great Transformations In Vertebrate Evolution, 107-
7 8 9	1488	124.
10 11	1489	
12 13	1490	Tegner, C., Marzoli, A., McDonald, I., Youbi, N., & Lindström, S. (2020). Platinum-group
14 15 16	1491	elements link the end-Triassic mass extinction and the Central Atlantic Magmatic Province.
17 18	1492	Scientific Reports, 10(1), 1-8.
19 20 21	1493	
22 22 23	1494	Toljagić, O., & Butler, R. J. (2013). Triassic–Jurassic mass extinction as trigger for the
24 25	1495	Mesozoic radiation of crocodylomorphs. Biology Letters, 9(3), 20130095.
26 27 20	1496	
20 29 30	1497	Tsai, H. P., Turner, M. L., Manafzadeh, A. R., & Gatesy, S. M. (2020). Contrast-enhanced
31 32	1498	XROMM reveals in vivo soft tissue interactions in the hip of <i>Alligator mississippiensis</i> .
33 34 25	1499	Journal of anatomy, 236(2), 288-304.
35 36 37	1500	
38 39	1501	Turner, A. H., & Nesbitt, S. J. (2013). Body size evolution during the Triassic archosauriform
40 41 42	1502	radiation. Geological Society, London, Special Publications, 379(1), 573-597.
42 43 44	1503	
45 46	1504	Turner, M. L., & Gatesy, S. M. (2021). Alligators employ intermetatarsal reconfiguration to
47 48	1505	modulate plantigrade ground contact. Journal of Experimental Biology, 224(11), jeb242240.
49 50 51	1506	
52 53	1507	Turner, M. L., Falkingham, P. L., & Gatesy, S. M. (2020). It's in the loop: shared sub-surface
54 55	1508	foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track
56 57 58	1509	diversity. Biology Letters, 16(7), 20200309.
59 60	1510	

1 2		
3 4 5 6 7 8	1511	Turner, M. L., Falkingham, P. L., & Gatesy, S. M. (2022). What is stance phase on
	1512	deformable substrates?. Integrative and Comparative Biology. doi:10.1093/icb/icac009
	1513	
9 10 11	1514	von Baczko, M. B., Desojo, J. B., & Ponce, D. (2019). Postcranial anatomy and osteoderm
12 13	1515	histology of Riojasuchus tenuisceps and a phylogenetic update on Ornithosuchidae
14 15	1516	(Archosauria, Pseudosuchia). Journal of Vertebrate Paleontology, 39(5), e1693396.
16 17 18	1517	
19 20	1518	Walker, A. D. (1964). Triassic reptiles from the Elgin area: Ornithosuchus and the origin of
21 22	1519	carnosaurs. Philosophical Transactions of the Royal Society of London. Series B, Biological
23 24 25	1520	Sciences, 248(744), 53-134.
26 27	1521	
28 29	1522	Webb, G. J. & Gans, C. (1982) Galloping in Crocodylus johnstoni- a reflection of terrestrial
30 31 22	1523	activity? Rec. Austral. Mus. 34, 607–618.
33 34	1524	
35 36	1525	Weinbaum, J. C. (2013). Postcranial skeleton of Postosuchus kirkpatricki (Archosauria:
37 38	1526	Paracrocodylomorpha), from the upper Triassic of the United States. Geological Society,
39 40 41	1527	London, Special Publications, 379(1), 525-553.
42 43	1528	
44 45	1529	Whiteside, J. H., Lindström, S., Irmis, R. B., Glasspool, I. J., Schaller, M. F., Dunlavey, M.,
46 47 48	1530	& Turner, A. H. (2015). Extreme ecosystem instability suppressed tropical dinosaur
49 50	1531	dominance for 30 million years. Proceedings of the National Academy of Sciences, 112(26),
51 52	1532	7909-7913.
53 54 55	1533	
56 57	1534	Wignall, P. B., & Atkinson, J. W. (2020). A two-phase end-Triassic mass extinction. Earth-
58 59	1535	Science Reviews, 208, 103282.
60		

1		
2 3 4	1536	
5 6	1537	Willey, J. S., Biknevicius, A. R., Reilly, S. M., & Earls, K. D. (2004). The tale of the tail:
7 8	1538	limb function and locomotor mechanics in Alligator mississippiensis. Journal of
9 10 11	1539	Experimental Biology, 207(3), 553-563.
12 13	1540	
14 15 16	1541	Wiseman, A.L.A., Bishop, P.J., Demuth, O.E., Cuff, A.R., Michel, K.B., Hutchinson, J.R.
16 17 18	1542	2021. Musculoskeletal modelling of the Nile crocodile (Crocodylus niloticus) hindlimb:
19 20	1543	effects of limb posture on leverage during terrestrial locomotion. Journal of Anatomy
21 22 22	1544	239:424-444.
23 24 25	1545	
26 27	1546	Zug, G. R. (1974). Crocodilian galloping: an unique gait for reptiles. Copeia, 1974(2), 550-
28 29 20	1547	552.
30 31 32		
33 34		
35 36		
37 38		
39 40		
41 42		
42 43		
44 45		
46		
47 48		
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