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Locomotor reassessment of *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* (Dinosauria, Ornithopoda) using osteological correlates

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Abstract

Large ornithopod dinosaurs have been successively described as quadrupeds, bipeds and facultative bipeds. Here we study the case of three ankylopollexians (*Iguanodon bernissartensis*, *Ouranosaurus nigeriensis* and *Lurdusaurus arenatus*) for which locomotion remains debated. We examine in detail their appendicular skeleton, focusing on osteological features that were previously associated with either bipedality or quadrupedality in dinosaurs. We compare our observations with data obtained for 12 saurischians and 32 ornithischians whose bipedal or quadrupedal locomotion is unambiguous. *Iguanodon* and *Ouranosaurus* score as quadrupeds for nine of the eleven correlates used in this study and are therefore best interpreted as obligate quadrupeds—contrasting with previous hypotheses of facultative bipedalism in Ankylopollexia—although this is sensitive to how hadrosaur locomotion is assessed. *Lurdusaurus* is found among quadrupeds for all the osteological correlates employed and is thus considered as an obligate quadruped, implying that obligate quadrupedality in ornithopods arose long before the hadrosaurs. Moreover, its extreme humeral and femoral eccentricity, along with its very short metatarsus, indicate graviportality, making *Lurdusaurus* the first graviportal ornithopod. Further biomechanical investigations are definitely needed to fully appreciate the locomotion of this unique taxon. Osteological correlates appear to be useful tools for investigating the transition to quadrupedalism in ornithopods, and may provide a basis for more comprehensive reconstructions of locomotor and postural evolution across diverse dinosaur lineages.

Key Words

Ankylopollexia, dinosaur locomotion, facultative bipedalism, functional morphology, graviportality, quadrupedality

Introduction

While the first dinosaurs were bipedal (Sereno 1999; Hutchinson 2006; Persons and Currie 2017), evolution led them to experience several reversals to quadrupedalism (Fig. 1). This is the case in saurischian dinosaurs, with sauropods, which are also graviportal (Coombs 1978; Carrano 2005; Wilson 2005). For sauropods, this means that they have appendicular skeletal adaptations related to their characteristic high body mass, such as columnar limbs and reduced distal limb segments (Goussard 2009; Rauhut et al. 2011). Gregory (1912) and, more recently, Carrano (1999) described this particular quadrupedal condition as the morphological extreme of a multivariate continuum, as opposed to the cursorial morphology.

However, while sauropods exemplify quadrupedalism associated with extreme graviportal adaptations, quadrupedalism does not necessarily imply graviportalism, nor does bipedalism necessarily imply cursoriality. For example, some quadrupedal mammals, most notably horses, are cursorial (Jones 2016). Similarly, several early crocodylomorphs, such as *Terrestrisuchus*, are reconstructed as cursors (Spiekman et al. 2024). In dinosaurs, however, these traits generally covary: quadrupedal taxa show reduced cursoriality and more robust, load-bearing limb morphologies, though they do not reach the extreme condition seen in sauropods, whereas bipedalism and cursoriality largely overlap, particularly among theropods and small ornithopods (Carrano 1999). Even large taxa like *Tyrannosaurus* retain key cursorial features (e.g., proximally placed trochanters, relatively long distal limb segments; Farlow et al. 1995; Hutchinson and Garcia 2002). In this manuscript, comparative references to "cursorial" and "graviportal" are explicitly restricted to dinosaurs and framed along a morpho-functional continuum, sensu Carrano (1999), allowing discussion of relative locomotor adaptations without assuming a perfect correspondence between locomotion and functional specialisation.

Beyond sauropods, repeated independent shifts to obligate quadrupedalism occurred in Ornithischia, notably in Thyreophora (stegosaurs, ankylosaurs) and in derived Marginocephalia (ceratopsids). Within Ornithopoda, small taxa are bipedal, while recent studies tend to support obligate quadrupedalism in hadrosaurs, the most derived ankylopollexians (Barrett and Maidment 2017; Dempsey et al. 2023; Pintore et al. 2025). However, the locomotion and posture adopted by many early branching ankylopollexians remains unclear (Maidment and Barrett 2014).

The case of *Iguanodon* (Mantell 1825), one of the very first dinosaurs to be named, perfectly illustrates this long-lasting debate on ankylopollexian locomotion. First thought to be a type of large iguana, its first representations in the mid-19th century showed it as a quadruped (Michel and Witton 2022). Dollo (1883), following the discovery of several dozen almost complete skeletons of *Iguanodon* in Bernissart, Belgium, reconstructed this dinosaur bipedal with an upright posture, leaning on its tail like a gigantic kangaroo. This is the position in which it is still presented to the public today in many museums around the world. Almost a century later, Norman (1980) re-examined the remains of *Iguanodon bernissartensis* (Boulenger 1881). Based on a functional analysis of the forelimbs, he concluded that *Iguanodon* was primarily quadrupedal, while claiming that it was most likely capable of standing on its hindlimbs to run and defend itself. This image of a facultatively bipedal animal was gradually extended to all large ornithopods (Dilkes 2001; Organ 2006; Persons and Currie 2017).

In 1965, Taquet discovered in Niger the nearly complete skeletons of two atypical ankylopollexians that he named *Ouranosaurus nigeriensis* (Taquet 1976) and *Lurdusaurus arenatus* (Taquet and Russell 1999). The skeleton of *Ouranosaurus* is slender and its relatively short forelimbs suggest that it may have been bipedal. *Ouranosaurus* was originally presented as a morphological intermediate between early branching ankylopollexians and hadrosaurids (Taquet 1976). Unlike that of *Ouranosaurus* and all Early Cretaceous ankylopollexians, the skeleton of *Lurdusaurus* is excessively robust, which makes it unique among ornithopod dinosaurs and raises questions about its locomotion and posture. However, only a handful of studies—notably the unpublished PhD thesis of Chabli (1988) and the brief description of its general anatomy (Taquet and Russell 1999)—followed its discovery. The distinctive features of *Lurdusaurus* have led to it being compared to giant ground sloths (Taquet and Russell 1999), or depicted as a semi-aquatic organism (Holtz 2007).

Maidment and Barrett (2014) reviewed a list of previously proposed osteological correlates in dinosaurs, that is osteological features associated with bipedal or quadrupedal locomotion. They tested their relevance in Ornithischia using unambiguously bipedal and quadrupedal taxa from all lineages in which secondary quadrupedalism is documented (thyreophorans and marginocephalians). In addition, they used these osteological correlates to infer locomotion in some ornithopod taxa, including some ankylopollexians. The present study builds on this work. We investigated osteological correlates in *Ouranosaurus*, *Iguanodon* and *Lurdusaurus*, three ankylopollexians with different morphologies (slender, heavy and super-heavy, respectively), in an attempt to better constrain their still discussed locomotor preferences and thus improve our understanding of the evolution of locomotion and posture in this lineage.

Material and methods

Material

We examined the appendicular skeletons of the ankylopollexians *Iguanodon bernissartensis*, *Ouranosaurus nigeriensis* and *Lurdusaurus arenatus*. Observations of character states and osteological measurements were taken directly on specimens of *Iguanodon* (MNHN.F.1899-1, IRSNB R 51), *Ouranosaurus* (MNHN GDF 300 [holotype cast]) and *Lurdusaurus* (MNHN.F.1966-15 GDF 1700) in the palaeontology collection of the Muséum national d'histoire naturelle (MNHN) and the Institut royal des sciences naturelles de Belgique (IRSNB), and were also retrieved from the literature (Table 1, Suppl. material 1).

Osteological correlates

Poole (2022) recently proposed that styracosternans (a clade within Ankylopollexia including *Iguanodon*, *Ouranosaurus*, *Lurdusaurus* and hadrosaurids) were most likely obligate quadrupeds. The author relied on only four of the eight osteological correlates previously assessed by Maidment and Barrett (2014)—who tested their relevance using a sample of uncontroversial ornithischian bipeds and quadrupeds, including thyreophorans, ceratopsids and ornithopods—because these characters were also present in her phylogenetic matrix (femur longer than tibia, flange on proximal ulna, tab-shaped fourth trochanter, rounded manual unguals). Here we employed a combination of eleven osteological correlates to infer the locomotion of *Iguanodon*, *Ouranosaurus* and

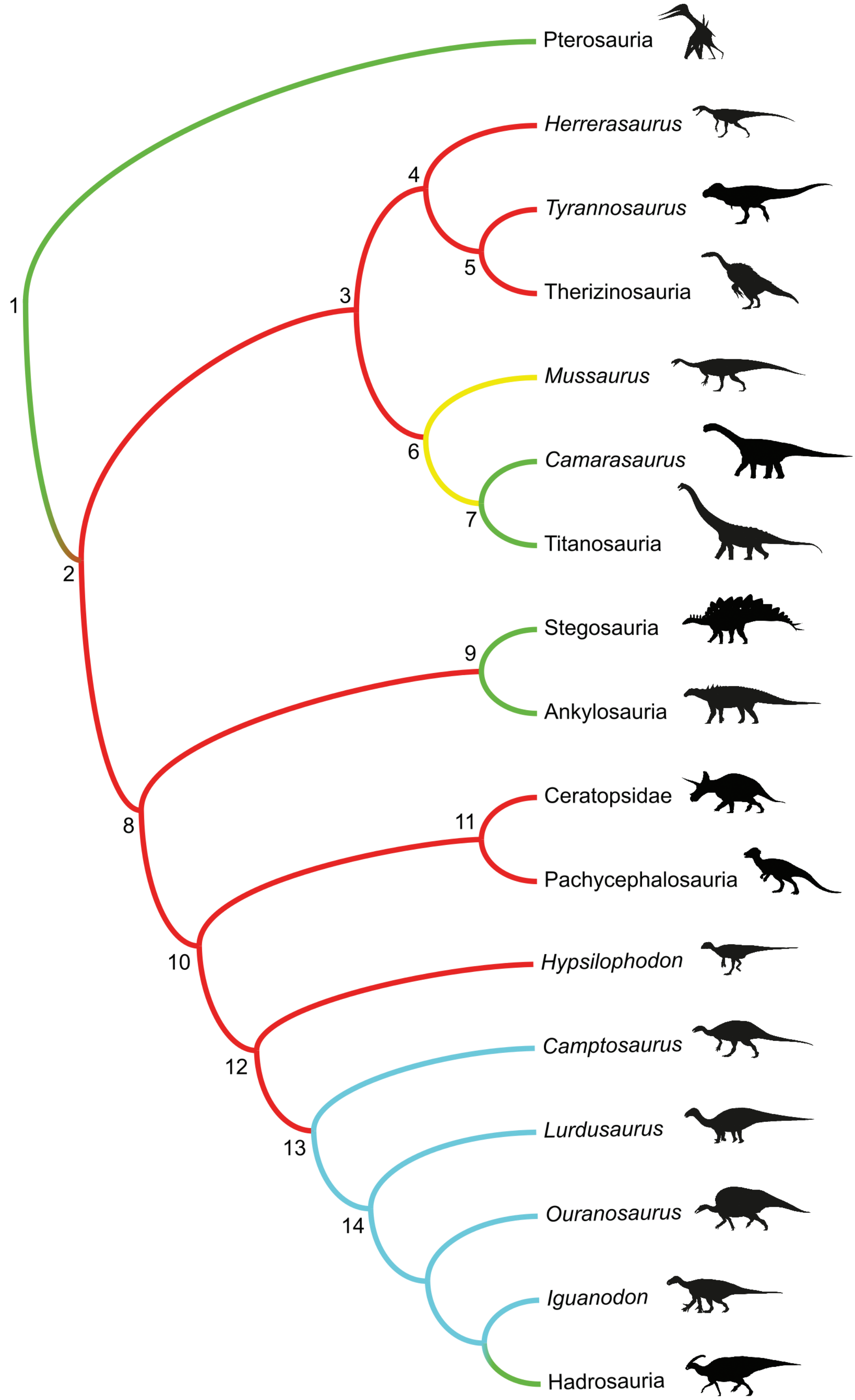

Figure 1. Simplified cladogram of avemetatarsalians, compiled from multiple sources (Benton 2004; Butler et al. 2008; Allain and Läng 2009; Poole 2022). Bipedal and quadrupedal lineages appear in red and green, respectively, and facultative quadrupeds and taxa with ambiguous locomotion are shown in yellow and blue, respectively. While a return to quadrupedalism occurred at least four times independently in dinosaurs, the locomotion of many early branching ankylopollexians remains debated. Node numbers: 1. Avemetatarsalia; 2. Dinosauria; 3. Saurischia; 4. Theropoda; 5. Coelurosauria; 6. Sauropodomorpha; 7. Sauropoda; 8. Ornithischia; 9. Thyreophora; 10. Cerapoda; 11. Marginocephalia; 12. Ornithopoda; 13. Ankylopollexia; 14. Styracosterna. Silhouettes from https://www.phylopic.org/.

Table 1. List of the dinosaurian taxa included in this study and their preferred locomotion.

Taxon			Locomotion
Saurischia	Sauropoda	*Apatosaurus ajax*	Graviportal
		Camarasaurus supremus	Graviportal
		Giraffatitan brancai	Graviportal
		Omeisaurus maoianus	Graviportal
		Tazoudasaurus naimi	Graviportal
		Vouivria damparisensis	Graviportal
	Theropoda	*Acrocanthosaurus atokensis*	Biped
		Allosaurus fragilis	Biped
		Eoraptor lunensis	Biped
		Herrerasaurus ischigualastensis	Biped
		Torvosaurus tanneri	Biped
		Tyrannosaurus rex	Biped
Ornithischia		*Abrictosaurus consors*	Biped
		Lesothosaurus diagnosticus	Biped
	Ankylosauria	*Ankylosaurus magniventris*	Quadruped
		Dyoplosaurus acutosquameus	Quadruped
		Edmontonia longiceps	Quadruped
		Edmontonia rugosidens	Quadruped
		Euoplocephalus tutus	Quadruped
		Hoplitosaurus marshi	Quadruped
		Panoplosaurus mirus	Quadruped
		Polacanthus foxii	Quadruped
		Sauropelta edwardsi	Quadruped
	Stegosauria	*Dacentrurus armatus*	Quadruped
		Hesperosaurus mjosi	Quadruped
		Huayangosaurus taibaii	Quadruped
		Kentrosaurus aethiopicus	Quadruped
		Loricatosaurus priscus	Quadruped
		Stegosaurus stenops	Quadruped
	Ceratopsia	*Centrosaurus apertus*	Quadruped
		Chasmosaurus belli	Quadruped
		Styracosaurus albertensis	Quadruped
		Vagaceratops irvinensis	Quadruped
	Ornithopoda	*Brachylophosaurus canadensis*	Quadruped
		Corythosaurus casuarius	Quadruped
		Edmontosaurus regalis	Quadruped
		Gryposaurus notabilis	Quadruped
		Hypacrosaurus altispinus	Quadruped
		Hypsilophodon foxii	Biped
		Iguanodon bernissartensis	Debated
		Jeholosaurus shangyuanensis	Biped
		Lambeosaurus lambei	Quadruped
		Lurdusaurus arenatus	Debated
		Ouranosaurus nigeriensis	Debated
		Parasaurolophus walkeri	Quadruped
		Parksosaurus warreni	Biped
		Thescelosaurus neglectus	Biped

Lurdusaurus (Fig. 2). Among those are the complete set of eight osteological correlates from Maidment and Barrett (2014). These correlates correspond to either continuous (e.g., forelimb vs hindlimb length; iliac mediolateral width vs iliac blade length) or discrete (e.g., presence/absence of an ulnar anterolateral process; presence/absence of a femur that is straight in lateral view) characters, and their functional significance is addressed below (see also Fig. 2, Table 2):

- Longer forelimbs. A lengthening of the forelimbs relative to the hindlimbs is supposedly associated with quadrupedalism, since it facilitates quadrupedal locomotion by reducing the distance between the manus and the ground (Galton 1970; Yates et al. 2010; Maidment and Barrett 2014). This is assessed using the ratio of forelimb to hindlimb length (Table 2). Forelimb length rarely exceeds hindlimb length (ratio > 1), while a forelimb that is at least half as long as the hindlimb (ratio > 0.5) is generally associated with quadrupedal locomotion.
- Broader ilium. Maidment and Barrett (2014) showed that quadrupedal ornithischians present a broader ilium than bipedal ones. Ilium breadth can be quantified using the ratio of its maximum width to the length of the iliac blade (Table 2). A value above 0.2 generally indicates quadrupedalism. A broad ilium, showing marked lateral expansion of the iliac blade, modifies the lines of action of the different muscles attaching to it, such as the *m. iliofemoralis* or *m. iliofibularis*, resulting in increased abduction moment at the hip (Romer 1927; Dilkes 1999; Maidment and Barrett 2011). The latter would be needed in taxa that place their feet lateral to the centre of mass to counteract the adduction moment generated by the ground reaction force (Maidment and Barrett 2014). Lateral foot placement necessarily implies quadrupedalism. In bipedal taxa, the feet are typically placed directly under the pelvis to maintain balance during locomotion. When the feet are positioned more laterally, this balance cannot be maintained without additional support, so that stability can only be ensured if the forelimbs touch the ground (Maidment et al. 2012).
- Shorter metatarsals. Quadrupeds tend to present a shorter metatarsus relative to hindlimb length (Colbert 1964; Galton 1970; Yates and Kitching 2003; Maidment and Barrett 2014). This can be quantified using the ratio of the length of metatarsal III to the combined length of the femur and tibia, with values below 0.2 generally indicating quadrupedal locomotion (Table 2). From a biomechanical standpoint, shorter distal limb segments enhance stability and reduce mechanical stress by bringing the centre of mass closer to the foot, which in turn lowers limb oscillation speed during locomotion (Gregory 1912; Carrano 1999). Quadrupedal dinosaurs were generally large herbivores within their respective lineage that probably did not require fast oscillation speeds in their daily activities, unlike carnivorous bipeds, which exhibit a more cursorial morphology adapted to their hunting lifestyle, or small herbivorous bipeds, which probably relied mainly on fleeing to escape predators.
- Anterolateral process on the ulna. Bonnan (2003), echoed by Yates and Kitching (2003) and Yates et al. (2010), suggested that the presence of a

well-developed anterolateral process on the proximal ulna of sauropods is related to a medial shift of the radius leading to complete pronation of the hand during quadrupedal locomotion. Maidment and Barrett (2014) demonstrated that the presence of this processus is also associated with quadrupedalism in ornithischians, although the functional implications in this clade might differ from those in sauropods. For example, the presence of a well-developed anteromedial process on the proximal ulna of many large ornithopods, such as hadrosaurids, reportedly prevents complete pronation (Senter 2012). This is supported by ichnological evidence from ornithopod tracks with manus impressions (Díaz-Martínez et al. 2015). Alternatively, the presence of an anterolateral process on the ulna could provide forearm reinforcement for body support.

- Hoof-like manual unguals. The term “hoof-like” refers to any terminal phalanx of the manus with the following features: (1) the dorsoventral height to mediolateral width ratio is less than 1; (2) distally, the phalanx extends laterally, taking the shape of an arrow with a rounded tip. The presence of hoof-shaped unguals suggests that the forelimbs were used, at least occasionally, to support the body and thus indicates quadrupedalism (Galton 1970; Maidment and Barrett 2014).
- Short tibiae. Dinosaur quadrupeds typically have a tibia shorter than the femur (Colbert 1964; Galton 1970). As with short metatarsals (see above), short tibiae enhance stability and reduce mechanical stress by lowering the centre of mass and decreasing limb oscillation speed. This shortening of distal limb segments is part of the suite of adaptations associated with graviportal habits. Quadrupedal large-bodied herbivores most likely did not require rapid limb movements in routine activities, unlike more cursorial or predator-escape specialists.
- Straight femora in lateral view. A femur with minimal curvature is better at withstanding the increased compressive forces resulting from a larger body mass and generally indicates quadrupedal locomotion (Chinnery 2004; Yates et al. 2010). Indeed, dinosaurian lineages that evolved secondary quadrupedalism often did so as body masses increased (Maidment and Barrett 2012; Campione et al. 2014).
- Crest-like or reduced fourth trochanter. Quadrupedal ornithischians often show a modified fourth trochanter, which is typically smaller or crest-like, in contrast to the large, pendant trochanter seen in bipeds (Galton 1970; Yates and Kitching 2003; Maidment and Barrett 2014). In ornithopods, increasing trochanter asymmetry has been linked to a gradual shift toward quadrupedalism (Pintore et al. 2025), and a distal displacement of the trochanter—perhaps driven by the mechanical demands of herbivory—may have rendered the pendant process obsolete. Indeed, the fourth trochanter, as a key muscle attachment, is interpreted to reflect locomotor performance relevant to foraging, such as sustained walking, stability while browsing, and movement between feeding patches (Persons and Currie 2020). Although the precise functional relationship between trochanter shape and stance remains to be fully resolved, the repeated trochanter reduction in heavier, secondarily quadrupedal lineages highlights the relevance of using this morphological correlate for inferring locomotion.

Two additional correlates (manus vs forelimb length ratio and radius vs humerus length ratio) were tested by Maidment and Barrett (2014) as potential indicators of locomotor posture in ornithischians, but were eventually rejected as reliable metrics. This is because bipeds in their sample did not exhibit a relatively longer radius or manus compared to quadrupeds. However, the absence of manus elongation in bipeds is not unexpected. Unlike the hindlimb, where foot elongation can improve the efficiency of limb oscillation during locomotion, the forelimb in bipeds is not involved in propulsion. It is therefore subject to different functional constraints, depending notably on the forelimb usage, which likely explains the lack of common morphological patterns with the hindlimb.

Table 2. List of the osteological correlates used in this study

Osteological correlate for quadrupedality	Ratio/Coding	References
Longer forelimbs	Humeroradial length vs femorotibial length	Galton 1970; Yates et al. 2010; Maidment and Barrett 2014
Broader pelvis	Iliac mediolateral width vs iliac blade length	Maidment and Barrett 2014
Shorter metatarsals	Metatarsal III length vs femorotibial length	Colbert 1964; Galton 1970; Yates and Kitching 2003; Maidment and Barrett 2014
Presence of an ulnar anterolateral process	0 = absence; 1 = presence	Bonnan 2003; Yates and Kitching 2003; Yates et al. 2010; Maidment and Barrett 2014
Presence of hoof-like manual unguals	0 = absence; 1 = presence	Galton 1970; Maidment and Barrett 2014
Shorter tibiae	0 = absence; 1 = presence	Colbert 1964; Galton 1970; Maidment and Barrett 2014
Straight femora	0 = curved; 1 = straight	Chinnery 2004; Yates et al. 2010; Maidment and Barrett 2014
Crest-like or reduced fourth trochanter	0 = pendant; 1 = a crest; 2 = reduced	Galton 1970; Yates and Kitching 2003; Maidment and Barrett 2014; Persons and Currie 2020; Pintore et al. 2025
Distal fourth trochanter	0 = proximal; 1 = distal	Persons and Currie 2020; this study
Eccentric humeral and femoral diaphysis	Humeral (femoral) mediolateral width vs anteroposterior width	Carrano 2001; Yates and Kitching 2003; this study

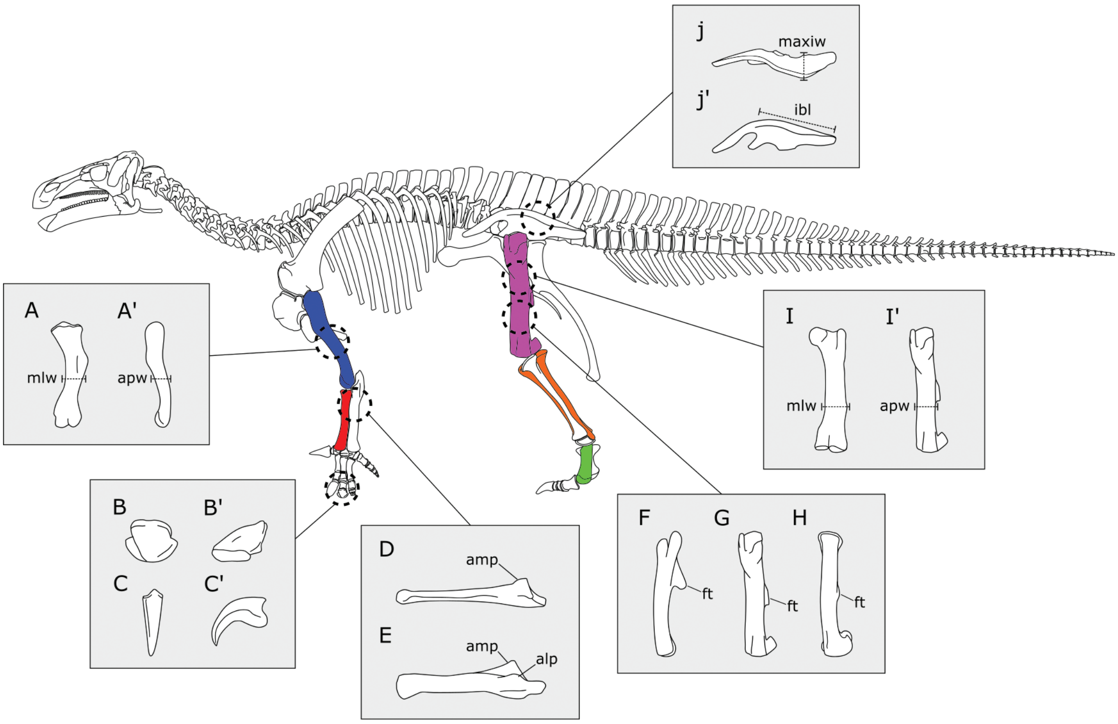

Figure 2. Illustration of the osteological correlates used in this study. **A.** Left humerus of *Iguanodon* in anterior view; mlw—mediolateral width; **A'.** Lateral view; apw—anteroposterior width. Humeral eccentricity is the ratio of mlw to apw at midshaft. **B.** Hoof-like ungual phalange of *Iguanodon* in dorsal view; **B'.** Lateral view; **C.** Claw-shaped ungual phalange of *Herrerasaurus* in dorsal view; **C'.** Lateral view. Hoof-like manual unguals: absent (0); present (1); **D.** Reduced ulnar anterolateral process in *Herrerasaurus*; amp—anteromedial process; **E.** Well-developed ulnar anterolateral process in *Iguanodon*; alp—anterolateral process. Ulnar anterolateral process: absent (0); present (1); **F.** Left femur of *Lesothosaurus*; ft—fourth trochanter. The femur is curved in lateral view (0) and the proximal fourth trochanter (0) is pendant (0); **G.** Left femur of *Iguanodon*. The femur is straight in lateral view (1) and the mid-diaphyseal fourth trochanter (1) forms a crest (1); **H.** Left femur of *Camarasaurus*. The femur is straight in lateral view and the mid-diaphyseal fourth trochanter is reduced (2); **I.** Left femur of *Iguanodon* in anterior view; **I'.** Lateral view. Femoral eccentricity is the ratio of mlw to apw; **J.** Left ilium of *Iguanodon* in dorsal view; maxiw—maximum iliac width; **J'.** Lateral view; ibl—iliac blade length. Iliac width is the ratio of maxiw to ibl. Relative forelimb length: ratio of humerus (blue) + radius (red) to femur (pink) + tibia (orange); relative foot length: metatarsus III (green) to femur + tibia. Femur shorter than tibia: 0; longer: 1. Skeletal representation of *Iguanodon* adapted from Slate Weasel (CC BY-SA 4.0). We removed metatarsal and digit IV to expose metatarsal III. Drawings based on Baron (2018), Norman (1980, 1986), Osborn and Mook (1919) and Sereno (1994). Drawings not at scale.

In this study, we used three additional osteological correlates:

- Distal placement of the fourth trochanter on the femoral diaphysis. Persons and Currie (2020) previously discussed the association between a distally placed fourth trochanter and quadrupedalism in dinosaurs. From a biomechanical point of view, the caudofemoralis muscle, which originates from the anterior caudal vertebrae and attaches on the fourth trochanter, operates as a femoral retractor (Hutchinson and Gatesy 2000). The position of the fourth trochanter on the femoral diaphysis modifies the moment arm of the caudofemoralis muscle. Proximal muscle insertions are generally found in cursorial organisms, whereas more distal insertions characterise graviportal organisms (Gregory 1912; Carrano 1999). In addition, Pintore et al. (2025) considered that the distal shift of the fourth trochanter is linked to body mass increase in ornithopods. As quadrupedal dinosaurs tend to be heavier than bipedal taxa (Maidment and Barrett 2012; Campione et al. 2014), we suspect that a mid-diaphyseal fourth trochanter could be indicative of quadrupedal locomotion.
- Eccentric humeri and femora. An eccentric femur was previously associated with obligate, graviportal quadrupedalism (Wilson and Carrano 1999; Carrano 2001; Yates and Kitching 2003). Indeed, a marked femoral eccentricity is thought to result from several factors increasing mediolateral bending, such as high body mass or lateral placement of the feet relative to the midline (Wilson and Carrano 1999). Lateral foot placement inherently implies a quadrupedal stance (see above). The same reasoning applies to the humerus.

Comparative dataset

We determined the state or value of each osteological correlate for *Iguanodon*, *Ouranosaurus* and *Lurdusaurus*. Then, we compared them to those of a sample of 44 dinosaurs with uncontroversial bipedal or quadrupedal locomotor habits (Table 1, Suppl. material 1). This sample comprises 32 ornithischian taxa used in Maidment and Barrett (2014) and Maidment et al. (2012), including 7 hadrosaurids (*Brachylophosaurus canadensis*, *Corythosaurus casuarius*, *Edmontosaurus regalis*, *Gryposaurus notabilis*, *Hypacrosaurus altispinus*, *Lambeosaurus lambei* and *Parasaurolophus walkeri*) that exhibit the full suite of osteological correlates originally identified by Maidment and Barrett (2014) as indicative of quadrupedal locomotion. Over the past decade, hadrosaurs have increasingly been regarded as obligate quadrupeds (Barrett and Maidment 2017; Dempsey et al. 2023; Pintore et al. 2025), while the possibility that they were instead facultative bipeds—allowing both bipedal and quadrupedal locomotion—continues to be discussed (e.g., Sereno et al. 2025). The latter interpretation is supported by ichnological evidence, including trackways preserving bipedal footprints (e.g., Vila et al. 2013; Fiorillo and Tykoski 2016), as well as by biomechanical studies suggesting that at least some taxa were capable of facultatively switching between bipedal and quadrupedal gaits (e.g., Sellers et al. 2009). However, converging anatomical evidence strongly supports predominantly quadrupedal habits in the subset of taxa considered here (Maidment and Barrett 2014). This, together with their close phylogenetic relationship to *Iguanodon*, *Ouranosaurus* and *Lurdusaurus*, makes them particularly well-suited for inclusion in our comparative sample.

The sample also comprises 12 saurischian dinosaur taxa (6 bipedal theropods and 6 quadrupedal sauropods). We included saurischians due to the apparent similarity between *Lurdusaurus* humeri and femora and those of sauropods, especially regarding shaft eccentricity (Ullmann et al. 2017; Klinkhamer et al. 2019; Lefebvre et al. 2022). We were able to assess all the osteological correlates in saurischians except for the iliac mediolateral width vs iliac blade length ratio: lateral expansion of the ilium is largely absent in saurischians and therefore not measurable for most taxa. This absence likely reflects a fundamentally different overall pelvic morphology (Iijima and Kobayashi 2016). For this reason, this osteological correlate should be treated with caution in broad, inter-clade comparisons. It appears most informative within Ornithischia and may not be homologous or directly comparable across saurischian taxa. We note one exception: some bipedal therizinosaurids show lateral ilium expansion, but their pelves are highly derived and therefore warrant dedicated study (Zanno et al. 2009; Smith 2021).

To minimise the potential impact of ontogenetic variation, only specimens interpreted as subadults or adults were considered, with one explicit exception discussed below. The specimens of *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* included in this study are interpreted as adults based on skeletal maturity and size. For comparative taxa taken from Maidment and Barrett (2014) and Maidment et al. (2012), the original datasets excluded small individuals (defined as less than 50% of the size of the largest conspecific), ensuring that no skeletally immature specimens were included and thus are part of our sample. For the remaining taxa (saurischians), none of the consulted publications explicitly identified juvenile specimens among the material considered here. The only exception is *Tazoudasaurus* (specimen MHNM To2-112), for which the morphology of the terminal manual phalanges is known exclusively from a juvenile individual, as no adult manus has been described to date. This specimen was therefore included solely to score the presence or absence of hoof-shaped terminal manual phalanges in this taxon, a character that is not expected to vary ontogenetically.

For length ratios, measurements were gathered from the literature or taken directly on published photographs of the bones using Fiji (Schindelin et al. 2012). When the left and right sides were present in the same individual, we used the mean of both sides. When several individuals were available, we first calculated ratios for each individual, then we used the mean of all individuals. Numerical values and coded states of the osteological correlates for each taxon in our comparative dataset are available in Suppl. material 1.

Taxonomic considerations on the sample

Part of our dataset is directly derived from the specimens provided in Maidment et al. (2012) and Maidment and Barrett (2014). In these studies, taxa such as *Stegosaurus armatus* and *Stegosaurus mjosi* were used following the taxonomic views of the authors at that time. To ensure consistency with current taxonomic consensus, we have updated these names in our study: *Stegosaurus armatus* is replaced by *Stegosaurus stenops*, and *Stegosaurus mjosi* is referred to *Hesperosaurus mjosi*, in accordance with more recent revisions (Maidment et al. 2015; Raven and Maidment 2017). These updates do not modify the underlying specimen-level data; they simply align nomenclature with current usage so that our dataset remains fully comparable with both the original sources and modern taxonomical attributions.

In addition, *Stormbergia dangershoeki*, listed as a distinct taxon in Maidment and Barrett (2014), is now widely interpreted as the adult form of *Lesothosaurus diagnosticus* and treated as its junior subjective synonym (Knoll et al. 2010; Baron et al. 2017). We therefore follow this interpretation and refer *Stormbergia* material to *Lesothosaurus diagnosticus*.

Results

Forelimb vs hindlimb

The bipeds in our sample have shorter forelimbs than the quadrupeds (Fig. 3A). Indeed, they present lower ratio values, ranging from 0.23 to 0.50, indicating that their forelimbs are generally less than half the length of the hindlimbs. In contrast, quadrupeds show higher ratios, from 0.56 to 1.04, meaning their forelimbs are at least half as long as their hindlimbs and, in some cases, nearly equal in length. This trend can be observed in both saurischians and ornithischians, although the gap between bipeds and quadrupeds is greater in saurischians. *Lurdusaurus*, *Ouranosaurus* and *Iguanodon* show typical quadruped values (0.58, 0.60 and 0.62, respectively).

Metatarsal III vs hindlimb

A relatively shorter metatarsus is found in quadrupeds (Fig. 3B). The latter show ratio values ranging from 0.08 to 0.19, with sauropods and *Hesperosaurus mjosi* presenting the lowest values. Bipeds show values ranging from 0.20 to 0.28. *Iguanodon* and *Ouranosaurus*, with a value of 0.18, fall within the range of quadrupeds. *Lurdusaurus* shows the lowest value of the entire sample (0.05).

Iliac width

A laterally expanded ilium seems to indicate quadrupedalism (Fig. 3C). This is observed at least in ornithischians; in saurischians, this osteological correlate could not be assessed because it is absent (see Material and Methods). Bipeds range from 0.03 to 0.06, while quadrupeds range from 0.20 to 0.95. *Ouranosaurus*, *Iguanodon* and *Lurdusaurus*, with values of 0.20, 0.21 and 0.35 respectively, all fall within the quadrupedal range.

Femoral eccentricity

The quadrupeds in our sample exhibit significantly more eccentric femora compared to the bipeds (Figs 3D, 4A), although several quadrupedal taxa—including *Panoplosaurus*, *Dyoplosaurus*, *Hoplitosaurus*, *Centrosaurus*, and most hadrosaurids—overlap with bipeds. The latter present values below 1.19. *Parasaurolophus*, a hadrosaurid, exhibits the lowest value in the sample (0.58). At the other extreme, graviportal sauropods reach values as high as 2.06. *Iguanodon* and *Ouranosaurus* have intermediate values (1.10 and 1.30, respectively), while *Lurdusaurus* presents one of the highest values (1.88), rivalling *Stegosaurus stenops* and *Tazoudasaurus* (1.82 and 1.88, respectively).

Humeral eccentricity

The quadrupeds in our sample display significantly greater humeral eccentricity than bipeds (Figs 3E, 4B). Bipeds present ratio values of no more than 1.26, with the exception of *Parksosaurus* (1.64). Ornithischian quadrupeds show higher values, but largely overlap with bipeds (1.06 to 1.80). Sauropods present values higher than 1.54. Eccentricity in *Ouranosaurus* is comparable to that of some bipeds (1.22). *Iguanodon* has a relatively more eccentric humerus (1.50), while *Lurdusaurus* has the fourth most eccentric humerus in the sample (1.75).

Ulnar anterolateral process

All bipedal dinosaurs in our sample (both saurischians or ornithischians) have a reduced anterolateral process, while all quadrupedal dinosaurs (graviportal or not) have a well-developed process. *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* all have a well-developed process.

Hoof-shaped manual unguals

No saurischian, biped or quadruped, has hoof-shaped manual unguals. Among ornithischians, all quadrupeds as well as *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* have hoof-shaped manus phalanges, whereas all bipeds lack them.

Femur longer than the tibia

All the saurischians in our sample, whether bipedal or quadrupedal, have a femur longer than the tibia, with the exception of *Eoraptor*, in which the femur is slightly shorter. The situation is different in ornithischians: the femur is systematically shorter than the tibia in bipeds, whereas it is longer in quadrupeds. *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* all have a femur that is longer than the tibia.

Straight femur in lateral view

The femur is curved in all bipedal saurischians and straight in all quadrupedal ones. The same pattern is observed in ornithischians. *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* all present a straight femur.

Reduced fourth trochanter

In our sample of saurischian dinosaurs, the fourth trochanter forms a crest in bipeds, whereas it is reduced in graviportal sauropods. In ornithischians, the fourth trochanter is pendant in all bipeds except *Parksosaurus*, where it forms a crest, and forms a crest or is reduced in all quadrupeds. The fourth trochanter is a crest in *Iguanodon*, *Ouranosaurus* and *Lurdusaurus*, as in hadrosaurids.

Mid-diaphyseal fourth trochanter

The majority of saurischian and ornithischian quadrupeds have a mid-diaphyseal fourth trochanter, with the exception of *Giraffatitan*, *Vouivria*, *Sauropelta* and *Vagaceratops*, in which it is more proximal. In all saurischian and ornithischian bipeds, the fourth trochanter is proximal on the femur. *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* all present a mid-diaphyseal fourth trochanter.

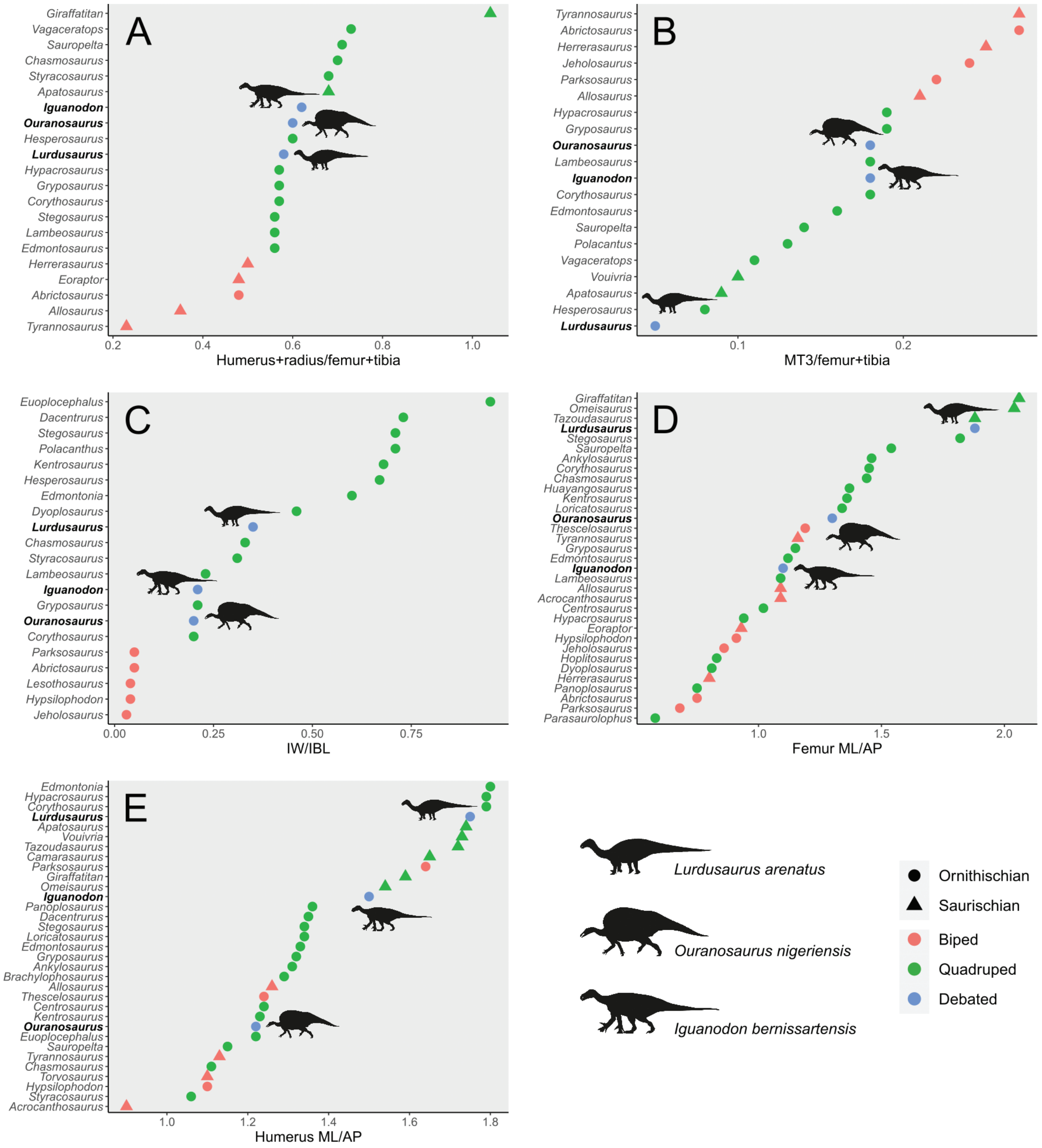

Figure 3. Graphical representation of continuous osteological correlates in our dinosaur sample. **A.** Forelimb to hindlimb length ratio; **B.** Metatarsal III to femur + tibia length ratio; **C.** Ratio of maximum iliac width to iliac blade length; **D.** Ratio of femur mediolateral width to anteroposterior width; **E.** Ratio of humerus mediolateral width to anteroposterior width. *Lurdusaurus* is consistently found among quadrupeds, unlike *Iguanodon* and *Ouranosaurus*, whose femoral and humeral eccentricities fall in the overlap between locomotor categories. Silhouettes from https://www.phylopic.org/.

Discussion

Regarding forelimb elongation, *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* present typical quadruped values (Fig. 3A), similarly to hadrosaurs (Maidment and Barrett 2014), such as *Lambeosaurus* (0.56), *Edmontosaurus* (0.56) or *Hypacrosaurus* (0.57). It should be noted that the specimens of *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* examined in this study are adults. Thus, our conclusions do not necessarily apply to juveniles. Indeed, several authors proposed that an allometric growth of the forelimbs could trigger a shift from bipedalism to quadrupedalism during the ontogeny of various dinosaurian taxa, including the ornithopods *Iguanodon* (Norman 1980) and *Maiasaura* (Dilkes 2001). However, subsequent works on *Iguanodon* (Verdú et al. 2017), *Maiasaura* (Chapelle et al. 2020) and *Edmontosaurus* (Wosik et al. 2017) found no significant change in forelimb-to-hindlimb proportions or limb robusticity between subadult and adult individuals. Taken together, the limb proportions observed in our adult specimens of *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* are fully consistent with habitual quadrupedalism in these taxa.

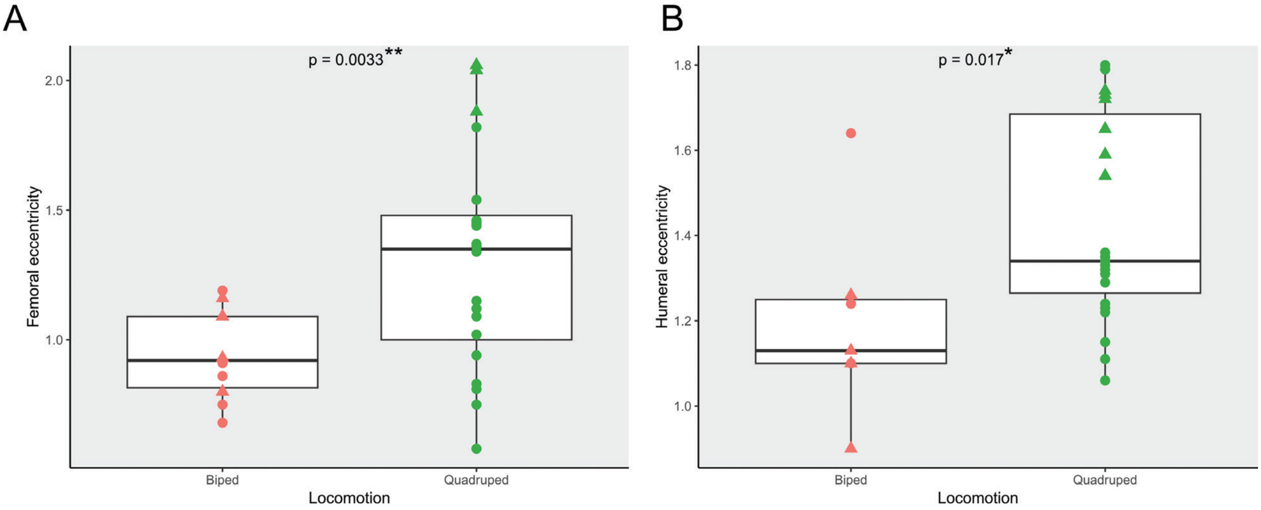

Figure 4. Comparison of femoral and humeral eccentricity between bipedal and quadrupedal dinosaurs. **A.** Femoral eccentricity; **B.** Humeral eccentricity. Based on our comparative sample of dinosaurian taxa, femoral and humeral eccentricity are significantly higher in quadrupeds than in bipeds ($p < 0.05$ [Welch's t-test for A and Wilcoxon-Mann-Whitney test for B]). Species are distinguished by locomotor mode (red = bipeds; green = quadrupeds) and clade (triangles = saurischians; circles = ornithischians). Box plots summarise group distributions: the horizontal line represents the median, the box indicates the interquartile range, and the whiskers extend to the most extreme values.

Elongated forelimbs occur in all quadrupeds of our sample, but the gap between bipeds and quadrupeds is larger in saurischians. This is most likely due to sampling bias. Indeed, our comparative dataset contains only uncontested bipeds and quadrupeds, effectively excluding taxa with mixed locomotor habits, such as early-branching sauropodomorphs, which are thought to be mostly facultative quadrupeds (Bonnan and Senter 2007). In many of these taxa, the forelimb-to-hindlimb ratio—although based on ulna length rather than radius length as in the present study—showed intermediate values between those of the bipeds and quadrupeds of our sample: e.g., 0.55 in *Lufengosaurus*, 0.57 in *Mussaurus*, 0.58 in *Adeopapposaurus* or 0.69 in *Riojasaurus* (Peyre de Fabrègues et al. pers. comm.). Nevertheless, forelimb proportions in *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* fall within the range of the other quadrupeds in our sample, suggesting that these taxa were also quadrupedal.

The metatarsals of *Lurdusaurus* are exceptionally short—even shorter than those of the largest hadrosaurs (e.g., 0.18 in *Magnapaulia*; Prieto-Márquez et al. 2012), and markedly more reduced than in the thyreophorans and sauropods of our sample (Fig. 3B). Short metatarsals are often linked to quadrupedalism in dinosaurs (Colbert 1964; Galton 1970; Yates and Kitching 2003; Maidment and Barrett 2014) and common in graviportal tetrapods (Gregory 1912; Carrano 1999). In *Lurdusaurus*, this extreme reduction suggests a strong adaptation toward both quadrupedalism and graviportal locomotion. By contrast, *Iguanodon* and *Ouranosaurus* show metatarsal proportions that fall within the quadrupedal range in our sample and are comparable to those of hadrosaurids (e.g., 0.18 and 0.19 in *Corythosaurus* and *Hypacrosaurus*, respectively). These proportions are consistent with quadrupedal locomotion, without indicating either cursorial or graviportal specialisation.

A broad Ilium characterises quadrupedal ornithischians (Fig. 3C). Both *Iguanodon* and *Ouranosaurus* exhibit a pelvic width comparable to those of quadrupedal hadrosaurids. This, while indicating quadrupedalism in *Iguanodon* and *Ouranosaurus*, also suggests that their feet were positioned closer to the midline than in ceratopsids or thyreophorans, which have wider pelves, as suggested for hadrosaurids by Maidment et al. (2012), a pattern consistent with observations from hadrosaurid trackways (Lockley and Wright 2001). *Lurdusaurus*, in turn, exhibits a typical quadrupedal value. It far surpasses values found in all other ornithopods, even exceeding the value reconstructed at the Ceratopsidae node (0.25), although without reaching the condition observed in Thyreophora (0.43; Maidment et al. 2014). This would indicate a more lateral placement of the feet relative to the midline in this taxon.

Regarding femoral eccentricity, some quadrupedal taxa among the ornithischians in our sample fall within the bipedal range. These include the thyreophorans *Panoplosaurus*, *Dyoplosaurus* and *Hoplitosaurus*, the eratopsids *Centrosaurus*, and several hadrosaurids (Fig. 3D). In the thyreophorans and *Centrosaurus*, their relatively lower body mass could explain this result, as femoral eccentricity was previously associated with graviportality and therefore high body mass (Wilson and Carrano 1999; Carrano 2001). Indeed, if we were unable to find body mass estimates for these taxa in the literature, based on femur lengths (Maidment et al. 2012), they are indeed those with the shortest femora in their respective clades (see Suppl. material 1). By contrast, the low values observed in hadrosaurids do not seem to be related to low body mass. For instance, *Parasaurolophus* exhibits the lowest value in the sample (0.58) despite possessing a femur over one meter in length (see Suppl. material 1). This may instead result from pronounced limb flexion combined with medial foot placement, which shift peak stresses from a mediolateral to an anteroposterior orientation, producing an inverted eccentricity pattern (anteroposterior width > mediolateral width; Maidment et al. 2012).

Wilson and Carrano (1999) also mentioned that limb obliquity (humerus or femur arched medially) can contribute to increasing eccentricity, as it moves the feet away from the midline. Extreme femoral eccentricity in *Lurdusaurus*, comparable to that of sauropods, could therefore be induced by both high body mass and its particularly high femoral obliquity. This supports the interpretation that *Lurdusaurus* had a wide-gauge stance—with its feet positioned farther from the body's midline—as observed in titanosaur sauropods (Wilson and Carrano 1999), and consistently with the aforementioned interpretation of *Lurdusaurus*' broad pelvis. Based on this correlate, *Lurdusaurus* is thus considered an obligate, graviportal quadruped. Interpreting moderate femoral eccentricity in *Iguanodon* and *Ouranosaurus* is more challenging. Unlike large hadrosaurids, which show low femoral eccentricity likely due to pronounced limb flexion, *Iguanodon* and *Ouranosaurus* exhibit somewhat higher values, which may reflect a more upright posture.

Humeral eccentricity broadly follows the same pattern as femoral eccentricity, with several quadrupedal ornithischians overlapping with bipeds (Fig. 3E), and is similarly influenced by factors such as body mass and limb obliquity. Shifts in the centre of mass due to anatomical features (e.g., skull size in ceratopsids or dermal armour distribution in stegosaurs) could further affect forelimb eccentricity (Maidment et al. 2012). Indeed, such shifts would alter the loading patterns on the forelimbs, particularly at the humeral midshaft, influencing its cross-sectional shape. Moreover, particular forelimb postures in quadrupedal ornithischians might also affect the orientation of humeral eccentricity. Indeed, the forelimbs of ceratopsids, for example, are more splayed (with the elbow rotated slightly outwards and the anterior humerus facing more medially) than those of other quadrupedal taxa (Paul and Christiansen 2000; Fujiwara 2009; Dempsey et al. 2023). Such a forelimb posture would result in the mediolateral stresses not being fully aligned with the mediolateral axis of the humerus, leading to anteromedial-posterolateral eccentricity. As a result, using the mediolateral-to-anteroposterior width ratio alone would not fully capture the eccentric loading pattern.

One last, but by no means least, factor that could affect both humeral and femoral eccentricity is taphonomy. It is illustrated here with *Parksosaurus* (from Maidment et al. 2012), which present one of the most eccentric humeri in our comparative sample likely due to taphonomic deformation and subsequent repair of the humerus. Indeed, the humerus is crushed and presents extensive plaster reconstruction (Sues et al. 2023).

Overall, interpreting femoral and humeral eccentricity in the fossil record remains challenging. Factors such as body size, locomotor habits, limb posture and taphonomic distortion introduce substantial overlap and confounding effects, limiting the use of these metrics as strict proxies for quadrupedality. Nevertheless, our sample reveals a significant difference in eccentricity between bipeds and quadrupeds (Fig. 4) and identifies clear empirical upper limits for unequivocal bipeds: no biped—whether saurischian or ornithischian—exceeds a femoral eccentricity of 1.19 (*Thescelosaurus*), and, apart from *Parksosaurus* (see above), none exceeds a humeral eccentricity of 1.26 (*Allosaurus*). Therefore, taxa with eccentricity values above these thresholds can be considered non-bipeds, although this does not necessarily indicate obligate quadrupedalism, particularly in taxa with intermediate eccentricity values. Consequently, the locomotor habits of *Iguanodon* and *Ouranosaurus* remain inconclusive based on their moderately eccentric humeri and femora. By contrast, the extreme eccentricity of both the humeri and femora in *Lurdusaurus*, underpinned by strong biomechanical arguments, helps overcome these uncertainties and supports its interpretation as an obligate, graviportal quadruped with a wide-gauge stance.

Both quadrupedal and bipedal saurischians possess a femur that is longer than the tibia (with the exception of the bipedal *Eoraptor*). However, this is most likely due to sampling bias. Indeed, the femur is shorter than the tibia in many coelurosaurians (Christiansen 1999), including birds (Gatesy and Middleton 1997). Moreover, the fact that this osteological correlate was coded as a two-state character by Maidment and Barrett (2014) prevents any quantitative discrimination between the saurischian quadrupeds and bipeds in our sample. Indeed, if we calculate the tibia vs femur length ratio in the saurischians in our sample, we observe that quadrupeds present ratio values below 0.64 and bipeds above 0.81 (see Suppl. material 1). Therefore, the femur of quadrupedal saurischians, without necessarily being shorter than the tibia, is generally "less short" than in bipeds. In contrast, in ornithischians, the femur is longer than the tibia in quadrupeds, while it is shorter in bipeds (Maidment and Barrett 2014). *Iguanodon*, *Ouranosaurus* and *Lurdusaurus* all have a femur longer than the tibia. They are therefore considered quadrupeds based on this correlate.

Based on our sample, a mid-diaphyseal fourth trochanter seems to indicate quadrupedal locomotion in dinosaurs. Yet, some quadrupeds show a more proximal trochanter, possibly reflecting autapomorphies related to functional specialisation (e.g., *Vagaceratops*; see Holmes 2014). Recent studies based on geometric morphometrics also showed that the position of this trochanter along the diaphysis in non-avian theropods and ornithopods is influenced by body mass, with a more distal placement in heavier taxa (Pintore et al. 2024, 2025). However, body size alone does not fully account for the observed variation. Indeed, even the largest bipeds, such as *Tyrannosaurus rex*, retain a fourth trochanter that is more proximal than in all the quadrupeds in our sample, or at least never more distal. Additionally, quadrupeds such as *Scelidosaurus* also exhibit a mid-diaphyseal trochanter

Table 3. Summary of the osteological correlates for *Iguanodon*, *Ouranosaurus* and *Lurdusaurus*. The check mark symbol indicate quadrupedalism. Abbreviations: FL—forelimb relative length; MT3—metatarsus III relative length; IW—iliac width; Fecc—femoral eccentricity; Hecc—humeral eccentricity; Antlat—anterolateral process on the ulna; Hoof—hoof-shaped manual unguals; F>T—femur longer than tibia; FC—femoral curvature in lateral view; 4TS—fourth trochanter shape; 4TP—fourth trochanter position. Silhouettes from https://www.phylopic.org/.

Taxon	FL	MT3	IW	Fecc	Hecc	Antlat	Hoof	F>T	FC	4TS	4TP
Iguanodon	✓	✓	✓			✓	✓	✓	✓	✓	✓
Ouranosaurus	✓	✓	✓			✓	✓	✓	✓	✓	✓
Lurdusaurus	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

despite their relatively small size (Norman 2020). Altogether, these observations suggest that *Iguanodon*, *Ouranosaurus* and *Lurdusaurus*, which possess a mid-diaphyseal fourth trochanter, were obligate quadrupeds, while acknowledging that trochanter position can be influenced by multiple factors.

Importantly, the position of the fourth trochanter should be considered separately from its shape, as each reflects a distinct functional aspect of the caudofemoralis system. Shape indicates the nature and extent of the muscle insertion, while position affects the lever arm and mechanical advantage (Persons and Currie 2020). In our sample, a mid-diaphyseal trochanter can be either reduced (e.g., in ceratopsids) or crest-like (e.g., in hadrosaurids), showing that shape and position are not always correlated. Treating them independently allows for a more nuanced understanding of potential functional variation.

To summarise, both *Iguanodon* and *Ouranosaurus* are found among quadrupeds for nine of the eleven osteological correlates used (Table 3). They differ from each other mainly in humeral and femoral eccentricity, *Iguanodon* falling within quadrupeds with respect to humeral eccentricity, while *Ouranosaurus* is found in the overlap between bipeds and quadrupeds. *Iguanodon* is included in the overlap between bipeds and ornithischian quadrupeds for femoral eccentricity and the *Ouranosaurus* femur, although more eccentric than that of *Iguanodon* and all the bipeds in the sample, remains in the interval between the bipeds and quadrupeds. We tentatively attribute these eccentricity results to a more upright limb posture compared with large hadrosaurids. However, femoral and humeral eccentricity must be interpreted with caution, as it is influenced by body mass, locomotion, limb posture and taphonomy (see above). Other osteological features—including elongated forelimbs, a relatively short metatarsus, a moderately enlarged ilium, hoof-like manual unguals, and a mid-diaphyseal fourth trochanter—consistently indicate habitual quadrupedalism in these taxa. Taken together, these traits suggest that, while likely obligate quadrupeds, *Iguanodon* and *Ouranosaurus* retained substantial locomotor versatility.

It should be noted, however, that when hadrosaurs are treated as facultative bipeds rather than obligate quadrupeds (see the Material and Methods section), *Iguanodon* and *Ouranosaurus* fall between unambiguous bipeds and quadrupeds for traits such as pelvic width and relative metatarsal length. Under this alternative coding, the number of osteological correlates supporting quadrupedalism in these taxa decreases from nine out of eleven to seven, producing a more balanced signal. This, in turn, supports a more conservative interpretation in which *Iguanodon* and *Ouranosaurus* were predominantly quadrupedal while retaining some capacity for bipedalism. More broadly, these results highlight the sensitivity of comparative inferences to the definition of reference taxa, especially hadrosaurs, and underscore the need for further integrative studies of locomotion within this clade.

Lurdusaurus is found among quadrupeds for all the osteological correlates used in this study (Table 3). It is therefore considered an obligate quadruped. The appendicular skeleton of *Lurdusaurus* is illustrated by a set of anatomical features that are unique among ornithischians (highly eccentric humeri and femora, extremely reduced metatarsals), but which are typical of graviportal organisms. This would make *Lurdusaurus* the first known graviportal ornithopod. Also, the high obliquity of the humerus and femur must have resulted in a wide-gauge stance during the animal's lifetime, comparable to the condition seen in some titanosaurs.

Conclusion

Based on the comparisons of eleven osteological correlates, this study clarifies the locomotion and posture of three ankylopollexian ornithopods with previously controversial locomotor habits. *Iguanodon* and *Ouranosaurus* appear quite similar in their inferred locomotor patterns. They were likely obligate quadrupeds, contrasting with previous hypotheses suggesting that ankylopollexians retained some capacity for occasional bipedalism, although this interpretation depends on whether hadrosaurs are coded as obligate quadrupeds in our comparative sample. The uniquely massive *Lurdusaurus* clearly deviates from the typical ornithopod bauplan, exhibiting traits of an obligate, graviportal quadruped, the first known among ornithopods. These findings suggest that ankylopollexians were trending toward obligate quadrupedalism—a locomotor pattern likely already established in *Iguanodon* (Barremian) and *Ouranosaurus* (Aptian), and most certainly in *Lurdusaurus* (Aptian)—predating some hadrosaurs by at least 30 million years. Our results contribute to a better understanding of the evolutionary trajectories of locomotion within

Ornithopoda. Expanding the use of osteological correlates to a broader range of ornithopods for which locomotion remains debated would allow for a more comprehensive reconstruction of their locomotor evolution, and further clarify how morphological diversity influenced functional adaptations in this clade.

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Authors' contributions

Jordan Gônet: Conceptualisation, methodology, formal analysis, data curation, writing—original draft, writing—review and editing. Ronan Allain: Conceptualisation, methodology, writing—review and editing, supervision. Alexandra Houssaye: Conceptualisation, methodology, writing—review and editing, supervision, funding acquisition.

Competing interests

The authors declare that they have no conflict of interest.

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References

Allain R, Aquesbi N (2008) Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. Geodiversitas 30 : 345–424. https://sciencepress.mnhn.fr/fr/periodiques/geodiversitas/30/2/anatomie-et-relations-phylogenetiques-de-tazoudasaurus-naimi-dinosauria-sauropoda-de-la-fin-du-jurassique-inferieur-du-maroc

Allain R, Läng E (2009) Origine et évolution des saurischiens. Comptes Rendus Palevol 8: 243–256. https://doi.org/10.1016/j.crpv.2008.09.013

Baron MG (2018) The Origin and Early Evolution of the Dinosauria. PhD Thesis, University of Cambridge, Cambridge, UK. https://doi.org/10.17863/CAM.18898

Baron MG, Norman DB, Barrett PM (2017) Postcranial anatomy of *Lesothosaurus diagnosticus* (Dinosauria: Ornithischia) from the Lower Jurassic of southern Africa: Implications for basal ornithischian taxonomy and systematics. Zoological Journal of the Linnean Society 179: 125–168. https://doi.org/10.1111/zoj.12434

Barrett PM, Maidment SCR (2017) The evolution of ornithischian quadrupedality. Journal of Iberian Geology 43: 363–377. https://doi.org/10.1007/s41513-017-0036-0

Benton MJ (2004) Origin and relationships of Dinosauria. In: Weishampel DB, Dodson P, Osmólska H (Eds) The Dinosauria. University of California Press, Oakland, 7–19. https://www.ucpress. edu/books/the-dinosauria-second-edition/paper

Bonnan MF (2003) The evolution of manus shape in sauropod dinosaurs: Implications for functional morphology, forelimb orientation, and phylogeny. Journal of Vertebrate Paleontology 23: 595–613. https://doi.org/10.1671/A1108

Bonnan MF, Senter P (2007) Were the basal sauropodomorph dinosaurs *Plateosaurus* and *Massospondylus* habitual quadrupeds? Special Papers in Paleontology 77 : 139–155.

Boulenger GA (1881) Sur l'arc pelvien chez les dinosauriens de Bernissart. Bulletins de l'Académie Royale de Belgique 1 : 600–608.

Butler RJ, Upchurch P, Norman DB (2008) The phylogeny of the ornithischian dinosaurs. Journal of Systematic Palaeontology 6: 1–40. https://doi.org/10.1017/S1477201907002271

Campione NE, Evans DC, Brown CM, Carrano MT (2014) Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. Methods in Ecology and Evolution 5: 913–923. https://doi.org/10.1111/2041-210X.12226

Carrano MT (1999) What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. Journal of Zoology 247: 29–42. https://doi.org/10.1111/j.1469-7998.1999.tb00190.x

Carrano MT (2001) Implications of limb bone scaling, curvature and eccentricity in mammals and non-avian dinosaurs. Journal of Zoology 254: 41–55. https://doi.org/10.1017/S0952836901000541

Carrano MT (2005) The evolution of sauropod locomotion: Morphological diversity of a secondarily quadrupedal radiation. In: Curry Rogers KA, Wilson JA (Eds) The Sauropods: Evolution and Paleobiology. University of California Press, Oakland, 229–251. https://doi.org/10.1525/california/9780520246232.003.0009

Chabli S (1988) Étude anatomique et systématique de *Gravisaurus tenerensis* n.g. n.sp. (Dinosaurien, Ornithischien) du gisement de Gadoufaoua (Aptien du Niger). PhD Thesis, Université Paris 7, Paris, France. https://theses.fr/1988PA077030

Chapelle KE, Benson RB, Stiegler J, Otero A, Zhao QI, Choiniere JN (2020) A quantitative method for inferring locomotory shifts in amniotes during ontogeny, its application to dinosaurs, and its bearing on the evolution of posture. Palaeontology 63: 229–242. https://doi.org/10.1111/pala.12451

Chinnery B (2004) Morphometric analysis of evolutionary trends in the ceratopsian postcranial skeleton. Journal of Vertebrate Paleontology 24: 591–609. https://doi.org/10.1671/0272-4634(2004)024[0591:MAOETI]2.0.CO;2

Christiansen P (1999) Long bone scaling and limb posture in non-avian theropods: Evidence for differential allometry. Journal of Vertebrate Paleontology 19: 666–680. https://doi.org/10.1080/02724634.1999.10011180

Colbert EH (1964) Relationships of the saurischian dinosaurs. American Museum Novitates: 1–24. https://digitallibrary.amnh.org/items/25d371ff-e34c-43f3-b1f7-311444be0b63

Coombs WP (1978) Theoretical aspects of cursorial adaptations in dinosaurs. The Quarterly Review of Biology 53: 393–418. https://doi.org/10.1086/410790

Cooper MR (1984) A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. Palaeontologica Africana 25: 203–231.

Dempsey M, Maidment SCR, Hedrick BP, Bates KT (2023) Convergent evolution of quadrupedality in ornithischian dinosaurs was achieved through disparate forelimb muscle mechanics. Proceedings of the Royal Society B: Biological Sciences 290: 20222435. https://doi.org/10.1098/rspb.2022.2435

Díaz-Martínez I, Pereda-Suberbiola X, Pérez-Lorente F, Canudo JI (2015) Ichnotaxonomic review of large ornithopod dinosaur tracks: Temporal and geographic implications. PLoS ONE 10: e0115477. https://doi.org/10.1371/journal.pone.0115477

Dilkes DW (1999) Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Transactions of the Royal Society of Edinburgh: Earth Sciences 90: 87–125. https://doi.org/10.1017/S0263593300007185

Dilkes DW (2001) An ontogenetic perspective on locomotion in the Late Cretaceous dinosaur *Maiasaura peeblesorum* (Ornithischia: Hadrosauridae). Canadian Journal of Earth Sciences 38 : 1205–1227. https://doi.org/10.1139/e01-016

Dollo L (1883) Troisième note sur les dinosauriens de Bernissart. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 2 : 85–120. https://biblio.naturalsciences.be/rbins-publications/bulletin-of-the-royal-belgian-natural-history-museum/bulletin-of-the-royal-belgian-natural-history-museum-1930-1948/fec52c520c5b4e1b94bc923ce47602aa

Farlow JO, Smith MB, Robinson JM (1995) Body mass, bone "strength indicator," and cursorial potential of Tyrannosaurus rex. Journal of Vertebrate Paleontology 15: 713–725. https://doi.org/10.1080/02724634.1995.10011257

Fiorillo AR, Tykoski RS (2016) Small hadrosaur manus and pes tracks from the Lower Cantwell Formation (Upper Cretaceous) Denali National Park, Alaska: Implications for locomotion in juvenile hadrosaurs. Palaios 31: 479–482. https://doi.org/10.2110/palo.2016.049

Fujiwara SI (2009) A reevaluation of the manus structure in *Triceratops* (Ceratopsia: Ceratopsidae). Journal of Vertebrate Paleontology 29: 1136–1147. https://doi.org/10.1671/039.029.0406

Galton PM, Jensen JA (1979) A new large theropod dinosaur from the Upper Jurassic of Colorado. Brigham Young University Geology Studies 26: 1–12.

Gatesy SM, Middleton KM (1997) Bipedalism, flight, and the evolution of theropod locomotor diversity. Journal of Vertebrate Paleontology 17 : 308–329. https://doi.org/10.1080/02724634.1997.10010977

Goussard F (2009) Etude morpho-fonctionnelle de la main des dinosaures sauropodomorphes : Implications évolutives et apport de l'analyse en éléments finis. PhD Thesis, Muséum National d'Histoire Naturelle, Paris, France. https://theses.fr/2009MNHN0009

Gregory WK (1912) Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Annals of the New York Academy of Sciences 22: 267–294. https://doi.org/10.1111/j.1749-6632.1912.tb55164.x

Holmes RB (2014) The postcranial skeleton of *Vagaceratops irvinensis* (Dinosauria, Ceratopsidae). Vertebrate Anatomy Morphology Palaeontology 1: 1–21. https://doi.org/10.18435/B5159V

Holtz TR (2007) Dinosaurs: The Most Complete, Up-to-Date Encyclopedia for Dinosaur Lovers of All Ages. Random House Books for Young Readers, New York, 432 pp. https://www.penguinrandomhouse.com/books/82233/dinosaurs-by-dr-thomas-r-holtz-jr-illustrated-by-luis-v-rey/

Hutchinson JR (2006) The evolution of locomotion in archosaurs. Comptes Rendus Palevol 5 : 519–530. https://doi.org/10.1016/j.crpv.2005.09.002

Hutchinson J, Garcia M (2022) *Tyrannosaurus* was not a fast runner. Nature 415: 1018–1021. https://doi.org/10.1038/4151018a

Hutchinson JR, Gatesy SM (2000) Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology 26: 734–751. https://doi.org/10.1666/0094-8373(2000)026<0734:AAATEO>2.0.CO;2

Iijima M, Kobayashi Y (2016) Convergences and trends in the evolution of the archosaur pelvis. Paleobiology 40: 608–624. https://doi.org/10.1666/13053

Jones KE (2016) New insights on equid locomotor evolution from the lumbar region of fossil horses. Proceedings of the Royal Society B: Biological Sciences 283: 20152947. https://doi.org/10.1098/rspb.2015.2947

Klinkhamer AJ, Mallison H, Poropat SF, Sloan T, Wroe S (2019) Comparative three-dimensional moment arm analysis of the sauropod forelimb: Implications for the transition to a wide-gauge stance in titanosaurs. The Anatomical Record 302: 794–817. https://doi.org/10.1002/ar.23977

Knoll F, Padian K, de Ricqlès A (2010) Ontogenetic change and adult body size of the early ornithischian dinosaur *Lesothosaurus diagnosticus*: Implications for basal ornithischian taxonomy. Gondwana Research 17: 171–179. https://doi.org/10.1016/j.gr.2009.03.010

Lefebvre R, Houssaye A, Mallison H, Cornette R, Allain R (2022) A path to gigantism: Three-dimensional study of the sauropodomorph limb long bone shape variation in the context of the emergence of the sauropod bauplan. Journal of Anatomy 241: 297–336. https://doi.org/10.1111/joa.13646

Lockley MG, Wright JL (2001) Trackways of large quadrupedal ornithopods from the Cretaceous: A review. In: Tanke DH, Carpenter K (Eds) Mesozoic Vertebrate Life. Indiana University Press, Bloomington, 428–442.

Maidment SCR, Barrett PM (2011) The locomotor musculature of basal ornithischian dinosaurs. Journal of Vertebrate Paleontology 31: 1265–1291. https://doi.org/10.1080/02724634.2011.606857

Maidment SCR, Barrett PM (2012) Does morphological convergence imply functional similarity? A test using the evolution of quadrupedalism in ornithischian dinosaurs. Proceedings of the Royal Society B: Biological Sciences 279: 3765–3771. https://doi.org/10.1098/rspb.2012.1040

Maidment SCR, Barrett PM (2014) Osteological correlates for quadrupedality in ornithischian dinosaurs. Acta Palaeontologica Polonica 59: 53–70. https://doi.org/10.4202/app.2012.0065

Maidment SCR, Linton DH, Upchurch P, Barrett PM (2012) Limb-bone scaling indicates diverse stance and gait in quadrupedal ornithischian dinosaurs. PLoS ONE 7: e36904. https://doi.org/10.1371/journal.pone.0036904

Maidment SCR, Brassey C, Barrett PM (2015) The postcranial skeleton of an exceptionally complete individual of the plated dinosaur

Stegosaurus stenops (Dinosauria: Thyreophora) from the Upper Jurassic Morrison Formation of Wyoming, U.S.A. PLoS ONE 10: e0138352. https://doi.org/10.1371/journal.pone.0138352

Mantell GA (1825) Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of Tilgate forest, in Sussex. Philosophical Transactions of the Royal Society 115: 179–186. https://doi.org/10.1098/rstl.1825.0010

Michel E, Witton MP (2022) Art and Science of the Crystal Palace Dinosaurs. The Crowood Press, Ramsbury, 192 pp. https://www.crowood.com/products/art-and-science-of-the-crystal-palace-dinosaurs-by-mark-witton-ellinor-michel

Norman DB (1980) On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). Mémoires de l'Institut Royal des Sciences Naturelles de Belgique 178 : 7–83. https://biblio.naturalsciences.be/rbins-publications/memoirs-of-the-royal-belgian-institute-of-natural-sciences-first-series/178-1980

Norman DB (1986) On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 56 : 281–372. https://biblio.naturalsciences.be/rbins-publications/bulletin-of-the-royal-belgian-institute-of-natural-sciences-earth-sciences/bulletin-of-the-royal-belgian-institute-of-natural-sciences-earth-sciences/norman_anatomy_1986

Norman DB (2020) *Scelidosaurus harrisonii* from the Early Jurassic of Dorset, England: Postcranial skeleton. Zoological Journal of the Linnean Society 189: 47–157. https://doi.org/10.1093/zoolinnean/zlz078

Organ CL (2006) Biomechanics of ossified tendons in ornithopod dinosaurs. Paleobiology 32: 652–665. https://doi.org/10.1666/05039.1

Osborn HF, Mook CC (1919) *Camarasaurus*, *Amphicoelias*, and other sauropods of Cope. Bulletin of the Geological Society of America 30: 379–388. https://doi.org/10.1130/GSAB-30-379

Paul GS, Christiansen P (2000) Forelimb posture in neoceratopsian dinosaurs: Implications for gait and locomotion. Paleobiology 26: 450–465. https://doi.org/10.1666/0094-8373(2000)026<0450:FPINDI>2.0.CO;2

Persons WS, Currie PJ (2017) The functional origin of dinosaur bipedalism: Cumulative evidence from bipedally inclined reptiles and disinclined mammals. Journal of Theoretical Biology 420: 1–7. https://doi.org/10.1016/j.jtbi.2017.02.032

Persons WS, Currie PJ (2020) The anatomical and functional evolution of the femoral fourth trochanter in ornithischian dinosaurs. The Anatomical Record 303: 1146–1157. https://doi.org/10.1002/ar.24094

Prieto-Márquez A, Chiappe LM, Joshi SH (2012) The lambeosaurine dinosaur *Magnapaulia laticaudus* from the Late Cretaceous of Baja California, Northwestern Mexico. PLoS ONE 7: e38207. https://doi.org/10.1371/journal.pone.0038207

Pintore R, Hutchinson JR, Bishop PJ, Tsai HP, Houssaye A (2024) The evolution of femoral morphology in giant non-avian theropod dinosaurs. Paleobiology 50: 308–329. https://doi.org/10.1017/pab.2024.6

Pintore R, Houssaye A, Hutchinson JR (2025) How femoral morphology informs our understanding of the evolution of ornithopod locomotion and body size. Palaeontology 68: e70016. https://doi.org/10.1111/pala.70016

Poole KE (2022) Phylogeny of iguanodontian dinosaurs and the evolution of quadrupedality. Palaeontologia Electronica 25: a30. https://doi.org/10.26879/702

Rauhut OWM, Fechner R, Remes K, Reis K (2011) How to get big in the Mesozoic: The evolution of the sauropodomorph body plan. In: Klein N, Remes K, Gee CT, Sander PM (Eds) Biology of the Sauropod Dinosaurs: Understanding the Life of Giants. Indiana University Press, Bloomington, 119–149. https://iupress.org/9780253013552/biology-of-the-sauropod-dinosaurs/

Raven TJ, Maidment SCR (2017) A new phylogeny of Stegosauria (Dinosauria, Ornithischia). Palaeontology 60: 401–408. https://doi.org/10.1111/pala.12291

Romer AS (1927) The pelvic musculature of ornithischian dinosaurs. Acta Zoologica 8: 225–275. https://doi.org/10.1111/j.1463-6395.1927.tb00653.x

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez JY, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardona A (2012) Fiji: An open-source platform for biological-image analysis. Nature Methods 9: 676–682. https://doi.org/10.1038/nmeth.2019

Sellers WI, Manning PL, Lyson T, Stevens K, Margetts L (2009) Virtual palaeontology: Gait reconstruction of extinct vertebrates using high performance computing. Palaeontologia Electronica 12: 11A. https://palaeo-electronica.org/2009_3/180/index.html

Senter P (2010) Evidence for a sauropod-like metacarpal configuration in stegosaurian dinosaurs. Acta Palaeontologica Polonica 55: 427–432. https://doi.org/10.4202/app.2009.1105

Senter P (2012) Forearm orientation in Hadrosauridae (Dinosauria: Ornithopoda) and implications for museum mounts. Palaeontologia Electronica 15: 30A. https://doi.org/10.26879/330

Sereno PC (1994) The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. Journal of Vertebrate Paleontology 13: 425–450. https://doi.org/10.1080/02724634.1994.10011524

Sereno PC (1999) The evolution of dinosaurs. Science 284 : 2137–2147. https://doi.org/10.1126/science.284.5423.2137

Sereno PC, Saitta ET, Vidal D, Myhrvold N, Real MC, Baumgart SL, Bop LL, Keillor TM, Eriksen M, Derstler K (2025) Duck-billed dinosaur fleshy midline and hooves reveal terrestrial clay-template "mummification". Science 0. https://doi.org/10.1126/science.adw3536

Smith DK (2021) Hind limb muscle reconstruction in the incipiently opisthopubic large therizinosaur *Nothronychus* (Theropoda; Maniraptora). Journal of Anatomy 238: 1404–1424. https://doi.org/10.1666/13053

Spiekman SN, Butler RJ, Maidment SCR (2024) The postcranial anatomy and osteohistology of *Terrestrisuchus gracilis* (Archosauria, Crocodylomorpha) from the Late Triassic of Wales. Papers in Palaeontology 10: e1577. https://doi.org/10.1002/spp2.1577

Sues HD, Evans DC, Galton PM, Brown CM (2023) Anatomy of the neornithischian dinosaur *Parksosaurus warreni* (Parks, 1926) from the Upper Cretaceous (lower Maastrichtian) Horseshoe Canyon Formation of Alberta, Canada. Cretaceous Research 141: 105369. https://doi.org/10.1016/j.cretres.2022.105369

Taquet P (1976) Géologie et Paléontologie du Gisement de Gadoufaoua (Aptien du Niger). CNRS Éditions, Paris, 191 pp. https://www.cnrseditions.fr/catalogue/ecologie-environnement-sciences-de-la-terre/geologie-et-paleontologie-du-gisement-de-gadoufaoua-aptiendu-niger/

Taquet P, Russell DA (1999) A massively-constructed iguanodont from Gadoufaoua, Lower Cretaceous of Niger. Annales de Paléontologie 1: 85–96. https://doi.org/10.1016/S0753-3969(99)80009-3

Ullmann PV, Bonnan MF, Lacovara KJ (2017) Characterizing the evolution of wide-gauge features in stylopodial limb elements of titanosauriform sauropods via geometric morphometrics. The Anatomical Record 300: 1618–1635. https://doi.org/10.1002/ar.23607

Verdú FJ, Godefroit P, Royo-Torres R, Cobos A, Alcalá L (2017) Individual variation in the postcranial skeleton of the Early Cretaceous *Iguanodon bernissartensis* (Dinosauria: Ornithopoda). Cretaceous Research 74: 65–86. https://doi.org/10.1016/j.cretres.2017.02.006

Vila B, Oms O, Fondevilla V, Gaete R, Galobart A, Riera V, Canudo JI (2013) The latest succession of dinosaur tracksites in Europe: Hadrosaur ichnology, track production and palaeoenvironments. PLoS ONE 8: e72579. https://doi.org/10.1371/journal.pone.0072579

Weishampel DB, Dodson P, Osmólska H (2004) The Dinosauria. University of California Press, Oakland, 880 pp. https://www.ucpress.edu/books/the-dinosauria-second-edition/paper

Wilson JA (2005) Overview of sauropod phylogeny and evolution. In: Curry Rogers KA, Wilson JA (Eds) The Sauropods: Evolution and Paleobiology. University of California Press, Oakland, 15–49. https://doi.org/10.1525/california/9780520246232.003.0002

Wilson JA, Carrano MT (1999) Titanosaurs and the origin of “wide-gauge” trackways: A biomechanical and systematic perspective on sauropod locomotion. Paleobiology 25: 252–267. https://doi.org/10.1017/S0094837300026543

Wosik M, Goodwin MB, Evans DC (2017) A nestling-sized skeleton of *Edmontosaurus* (Ornithischia, Hadrosauridae) from the Hell Creek Formation of northeastern Montana, USA, with an analysis of ontogenetic limb allometry. Journal of Vertebrate Paleontology 37: e1398168. https://doi.org/10.1080/02724634.2017.1398168

Yates AM, Kitching JW (2003) The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. Proceedings of the Royal Society B: Biological Sciences 270: 1753–1758. https://doi.org/10.1098/rspb.2003.2417

Yates AM, Bonnan MF, Neveling J, Chinsamy A, Blackbeard MG (2010) A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. Proceedings of the Royal Society B: Biological Sciences 277: 787–794. https://doi.org/10.1098/rspb.2009.1440

Zanno LE, Gillette DD, Albright LB, Titus AL (2009) A new North American therizinosaurid and the role of herbivory in “predatory” dinosaur evolution. Proceedings of the Royal Society B: Biological Sciences 276: 3505–3511. https://doi.org/10.1098/rspb.2009.1029

Supplementary material 1

Dataset

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Data type: xlsx

Explanation note: Numerical values and coded states of osteological correlates for *Iguanodon*, *Ouranosaurus*, *Lurdusaurus*, and 44 comparative dinosaur taxa with established locomotor modes.

Link: https://doi.org/10.3897/fr.29.173614.suppl1