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Investigating the quadrupedal abilities of *Scutellosaurus lawleri* and its implications for locomotor behavior evolution among dinosaurs

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Abstract

A reversion to secondary quadrupedality is exceptionally rare in nature, yet the convergent re-evolution of this locomotor style occurred at least four separate times within Dinosauria. Facultative quadrupedality, an intermediate state between obligate bipedality and obligate quadrupedality, may have been an important transitional step in this locomotor shift, and is proposed for a range of basal ornithischians and sauropodomorphs. Advances in virtual biomechanical modeling and simulation have allowed for the investigation of limb anatomy and function in a range of extinct dinosaurian species, yet this technique has not been widely applied to explore facultatively quadrupedal gait generation. This study places its focus on *Scutellosaurus*, a basal thyreophoran that has previously been described as both an obligate biped and a facultative quadruped. The functional anatomy of the musculoskeletal system (myology, mass properties, and joint ranges of motion) has been reconstructed using extant phylogenetic bracketing and comparative anatomical datasets. This information was used to create a multi-body dynamic locomotor simulation that demonstrates that whil quadrupedal gaits were physically possible, they did not outperform bipedal gaits is any tested metric. *Scutellosaurus* cannot therefore be described as an obligate biped, but we would predict its use of quadrupedality would be very rare, and perhaps restricted to specific activities such as foraging. This finding suggests that basal thyreophorans are still overwhelmingly bipedal but is perhaps indicative of an adaptive pathway for later evolution of quadrupedality.

KEYWORDS
biomechanics, bipedalism, dinosaur, musculoskeletal system, quadrupedalism

1 | INTRODUCTION

A locomotor transition can be defined as an evolutionary event wherein a taxon acquires a new locomotor stance. Since the colonization of land by quadrupedal tetrapods in the Late Devonian (Ahlberg & Clack, 2006), several groups including some marsupials, the common ancestors of dinosaurs, and hominids evolved a bipedal gait. Far rarer is a transition in the opposite direction: a reversion to secondary quadrupedality following the evolution of a bipedal gait. Such a reversion occurred on at least four separate occasions within Dinosauria; sauropods, thyreophorans, ornithopods, and ceratopsians each shared a bipedal basal dinosaurian ancestor, but independently returned to quadrupedality (see Figure 1; Maidment, Henderson, & Barrett, 2014). For this reason, dinosaurs are a key target for research that seeks to understand how and why locomotor transitions occur, knowledge that could then be applied to explore this phenomenon on a wider taxonomic scale. Furthermore, a deeper understanding of facultative quadrupedality would also shed additional light on how bipedal and quadrupedal gait generation differs as a whole, highlighting how disparity in body form and function impacts upon locomotor mode. In this study, we reconstruct the myology of one such "model dinosaur", the Early Jurassic thyreophoran *Scutellosaurus*, and provide an example of how virtual locomotor simulation techniques may be applied to explore dinosaurian locomotor transitions in greater depth.

The dinosaurian reversions to obligate quadrupedality are also thought to have occurred over millions of years (Barrett & Maidment, 2017), and as such, we would expect to find intermediate transitional locomotor forms within their evolutionary history. These species may have made use of a locomotor style somewhere between obligate bipedality and obligate quadrupedality. Facultative quadrupeds (sometimes used interchangeably with "facultative bipeds") are species that make regular use of both bipedal and quadrupedal gaits within their ecological niche. Extant examples include kangaroos (*Macropus* sp.) that show fast bipedal saltation and a slower quadrupedal hop, and the giant pangolin (*Smutsia gigantea*) that can recruit all four limbs into a walking gait or utilize just the hindlimbs. Some form of facultative quadrupedality is currently proposed for a range of basal thyreophorans (Colbert, 1981; Norman, 2021), ceratopsians (Zhao et al., 2013), and sauropodomorphs (Otero et al., 2019; Reisz et al., 2005). Some of the earliest speculation about the use of facultative quadrupedality in dinosaurs came from the examination of iguanodontids, with the conclusion that the vertebral column was held in a relatively horizontal position (Norman, 1980). This finding suggested that these dinosaurs, previously concluded to be obligate bipeds by preserved trackways (Beckles, 1862), would have
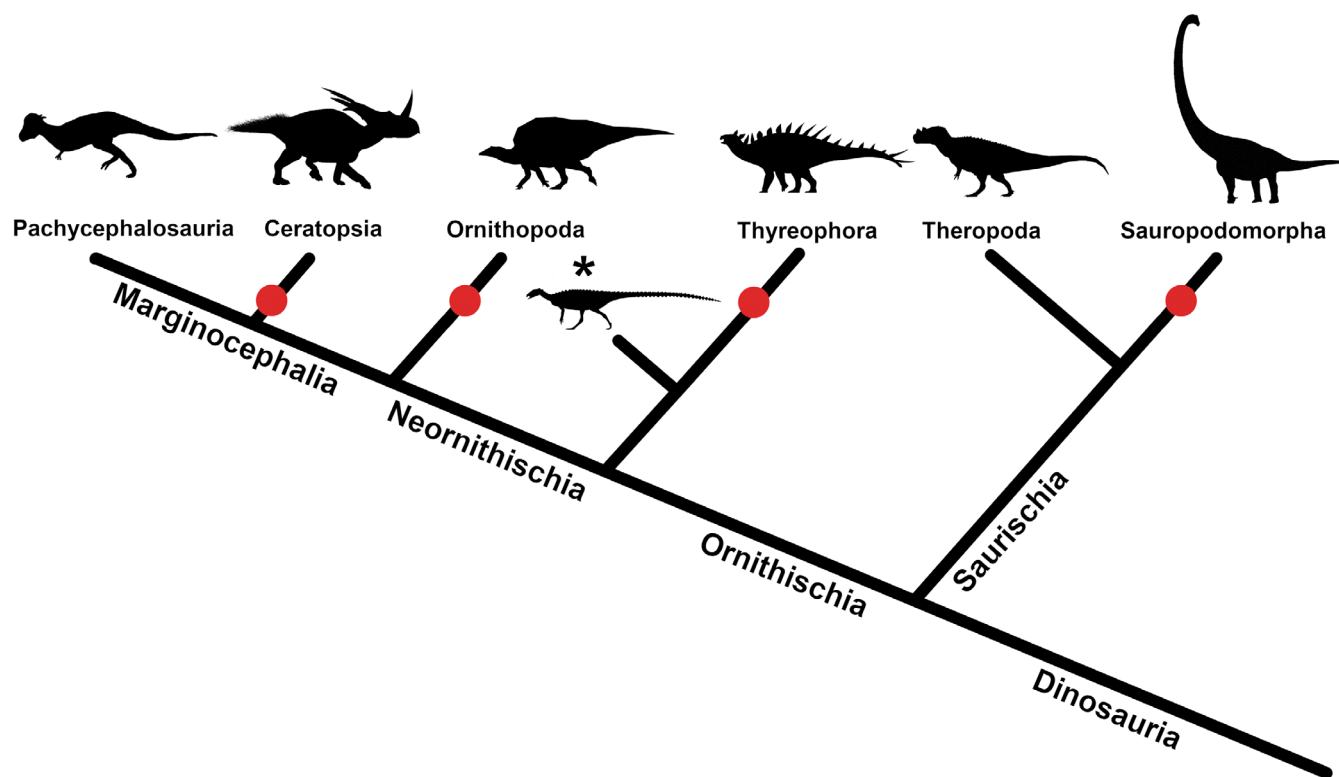

FIGURE 1 A simplified cladogram of Dinosauria showing the lineages that convergently evolved quadrupedality (red). *Scutellosaurus* (*) is herein assumed to be an obligate biped, a theory that this study aimed to test. Silhouettes obtained from PhyloPic http://www.phylopic.org/. Adapted from Maidment & Barrett (2012).

been physically capable of adopting a quadrupedal stance. In the decades since, a range of evidence including osteological correlates (Maidment & Barrett, 2012), trackways (Dalman & Weems, 2013; Gierlinski, 1999; Meyer & Thuring, 2003), and observed limb ratios (Colbert, 1981) has been used to infer facultative quadrupedal gaits for an increasing number of species.

This study places its focus within Thyreophora, a clade of armored ornithischians that acquired obligate secondary quadrupedality sometime in the Early-Mid Jurassic (Barrett & Maidment, 2017). Though some authors explore the possibility of a tripodal, tail-assisted stance for use in feeding and mating in stegosaurs (Bakker, 1978; Isles, 2009), derived eurypodan thyreophorans are widely considered to be obligate quadrupeds (Maidment & Barrett, 2012). Evidence from osteological correlates for stance support this conclusion: possession of a femur which is longer than the tibia, a reduced fourth trochanter, a transversely broadened ilium, hoof-like manual unguals and an anterolateral process on the ulna are all thought to be robust predictors of quadrupedal gait among ornithischians, and both *Ankylosaurus* and *Stegosaurus* possessed all five (Maidment & Barrett, 2012).

The locomotor behavior of the more basal non-eurypodan members of Thyreophora, including *Scutellosaurus*, is less well understood. For several species such as *Emausaurus*, very little material from the limbs has been recovered, rendering the evaluation of their habitual neutral stance and gait impossible (Norman et al., 2004). *Scelidosaurus* is known from far more complete skeletons (Norman, 2021). Examination of the proposed osteological correlates for ornithischian quadrupedality reveals that *Scelidosaurus* possessed a mixture of characters indicative of both quadrupedal and bipedal gaits (Maidment & Barrett, 2012). As such, several authors interpret *Scelidosaurus* as potentially being a facultative quadruped with some capability of walking on just its hindlimbs, perhaps using a bipedal gait more habitually as a juvenile (Maidment & Barrett, 2012; Norman, 2021). Currently, *Scelidosaurus* has been suggested to be the earliest known thyreophoran to make use of a quadrupedal gait with the absence of a robust olecranon to which forelimb extensors could attach has been cited as evidence to suggest that the recruitment of forelimbs to locomotion was relatively new within the clade (Norman, 2021).

Scutellosaurus is one of the most basal species which can be confidently assigned to Thyreophora (Baron et al., 2017; Boyd, 2015) and is the target of this study. In the 40 years since *Scutellosaurus* was first formally described, several revisions have been made to its proposed locomotor style. The species was originally classified within Fabrosauridae as it shared several characteristics with the obligate biped *Lesothosaurus* such as relatively gracile long limb bones, particularly in the forelimb, and a

hindlimb of a greater length than the forelimb (Colbert, 1981). However, the original description of the holotype also highlighted several *Scutellosaurus* autapomorphies that may suggest a different style of locomotion to *Lesothosaurus*. The length of the forelimb with respect to the hindlimb was much greater than that of other basal ornithischians which may have allowed for the adoption a quadrupedal stance (Colbert, 1981). With this supporting evidence, it was concluded that *Scutellosaurus* may have been a facultative quadruped. Subsequent descriptions of additional *Scutellosaurus* remains have criticized this hypothesis. First, the proposed limb ratios, initially estimated using an incomplete radius, were found to exaggerate the true condition after a complete set of limb long bones was recovered (Breeden et al., 2021; Rosenbaum & Padian, 2000). Considered alongside the gracile nature of the forelimbs where muscular attachments were probably less robust, the authors conclude that the forelimbs were unlikely to have played a significant role in locomotion (Rosenbaum & Padian, 2000). Nevertheless, the limb ratios in the *Scutellosaurus* holotype do not deviate significantly from those seen in the most recent reconstructions of *Scelidosaurus*, for which a primarily quadrupedal gait is proposed (Norman, 2021; Rosenbaum & Padian, 2000). It should be noted however that limb long bone length ratios alone are not always the most powerful predictors of habitual locomotor mode in extant amniotes, thus use of such measurements to make conclusions about dinosaurian locomotion may result in the erroneous assignment of a particular gait (Chapelle et al., 2020). Instead, the ratio of humeral to femoral circumference may be a more robust predictor of amniote gait (Chapelle et al., 2020). However, the methodology has yet to be applied to thyreophorans thus the predictive power that these measurements hold over this clade in particular is unknown. Overall, the limb ratios of *Scutellosaurus* neither definitively support nor refute the possibility of the species adopting a quadrupedal gait.

Colbert's (Colbert, 1981) original description of the *Scutellosaurus* manus has also received criticism; Colbert reconstructed a broad manus that may have represented an adaptation for bearing weight (Colbert, 1981). While many individual metacarpals and phalanges are known, none have been found in full articulation, hence confident assignment to specific digits is near impossible and consequently, the length of the digits and overall shape of the manus that Colbert (1981) proposed may not accurately reflect the anatomy of the living animal (Breeden et al., 2021). As a result, use of the manus morphology to support the possibility of a quadrupedal gait remains largely invalid until a specimen with the manus in articulation can be found to reveal its true size and shape.

Further evidence that has been used to refute claims of facultative quadrupedality comes from the fact that several of the osteological correlates associated with

ornithischian quadrupedality are absent in *Scutellosaurus*, which may indicate that this species had a closer affinity to obligate bipeds (Maidment & Barrett, 2012). However, there are also several correlates that cannot be scored in *Scutellosaurus* because they are not preserved in any currently known specimens (Breeden et al., 2021; Maidment & Barrett, 2012); these features, if eventually recovered, could potentially support either hypothesis. An additional anatomical feature lending some credence to the theory of obligate bipedality in *Scutellosaurus* is its exceptionally long tail; at almost twice the length of the rest of its body, the tail would have contributed a significant mass posterior to the acetabulum, the most obvious purpose for which being a counterbalance to support bipedal locomotion. To confirm its effect on center of mass (COM), Maidment, Henderson & Barrett (2014) used a 3D reconstruction of the animal to examine weight distribution, and as predicted, the COM lies very close to the hips, even when the distribution and size of dense dermal armor is altered or removed entirely. While an extremely rostral COM precludes stable obligate bipedalism (Bates et al., 2010), the relatively caudal position in *Scutellosaurus* does not confirm that it was definitely an obligate biped. Indeed, current estimates for the location of the center of mass suggest that it remains relatively caudal in the obligate quadrupeds *Ankylosaurus* and *Stegosaurus* (Maidment, Henderson, & Barrett, 2014; Mallison, 2014). Overall, most evidence used to make inferences about the locomotor behavior of *Scutellosaurus* is either incomplete or has been subsequently questioned. The current consensus is that this basal ornithischian was primarily, if not entirely, bipedal, but the possibility of some facultative quadrupedal ability still remains open. What remains is to explore additional computational techniques and lines of evidence in the context of this species that may be able to help resolve the locomotor mode of *Scutellosaurus*, something which this study aims to address.

Beyond examination of the physical evidence, dinosaur locomotion is increasingly being investigated through the use of theoretical models and virtual simulation. Previous studies of both ornithischians and saurischians have made use of Multi-body Dynamic Analysis (MDA) (Sellers et al., 2009, 2013), a technique that allows elements such as the bones, joints, muscles, and tendons to be rendered as fully 3D objects and simulated using a wider array of control parameters (Lautenschlager, 2020). This allows for the integration of more complex models of muscular force generation and metabolic energy cost (e.g., Minetti & Alexander, 1997) that are closer to the processes taking place in real skeletal muscle, thus bringing simulated gaits closer to mirroring what is seen in extant specimens. In addition, increases in computational power mean that

fewer simplifications to the number of muscles and joints need to be made. Two distinct options exist for deriving gaits from virtual models: firstly, kinematic data obtained from extant specimens or trackways which are an exact or close match to the species of interest can be applied, so that the model can attempt to recreate the step cycles known to be physically possible and practical for these living animals (e.g., Bishop, Michel, et al., 2021; van den Bogert et al., 1989). Where no analogous kinematic data can be obtained, as is arguably the case for many extinct species such as *Scutellosaurus*, an alternative option is to use machine learning (e.g., Sellers et al., 2009). An optimization algorithm can be employed to search through muscle control parameters to create activation patterns, and thus gaits, de novo. These generated gait solutions can be visualized to determine their stability and overall plausibility when compared with extant analogues whose kinematics are fully explorable. The simulations can also be set to maximize a chosen locomotor outcome such as speed or metabolic efficiency to explore gait repertoire in the absence of a living animal whose speed could be controlled via a treadmill and whose oxygen consumption could be measured directly. The key advantage to using virtual locomotor simulation techniques is the high degree of control and customization that can be applied to the models, something which is not afforded by living animals or real-world environments. For example, altering the force per unit area of skeletal muscle to investigate how this affects top speed (Bates et al., 2010) or reducing the force of gravity to investigate locomotion in extraterrestrial settings (Ackermann & van den Bogert, 2012) is made relatively simple within modeling software.

Within Dinosauria, MDA has provided unique insights into a variety of long-standing palaeobiological questions. For example, quantification of theropod top speeds and bite forces has supported the conclusion that *Tyrannosaurus* could indeed have been an active pursuit or ambush predator (Bates & Falkingham, 2012, 2018; Sellers et al., 2017) and not limited to scavenging as has been previously argued (Carpenter, 2013). Gait simulation has also aided understanding about how sauropods were able to support massive weights during walking, the results revealing that reduction of the range of motion in the ankle would have been necessary for the limb extensors to function with reasonable efficiency (Sellers et al., 2013). Sensitivity analyses have also begun to disentangle the relationships between various parameters such as COM, muscle force per unit area, and total body mass to examine what effect each of these has on locomotor outcomes when considered in isolation: the results suggesting that for bipedal dinosaurs, altering mass and COM within a realistic range has a lesser effect on locomotor function than altering the muscle parameters

(Bates et al., 2010). In terms of facultative quadrupedality, simulations of a musculoskeletal model of *Edmontosaurus* have investigated the gait repertoire achievable by this species and produced both bipedal and quadrupedal gaits which could be classified into various types including walks, trots, runs and gallops (Sellers et al., 2009). The results validate theories about hadrosaur locomotion originally drawn from ichnological (Meyer & Thuring, 2003) and osteological (Maryanska & Osmólska, 1984) evidence and highlights the utility of MDA when attempting to diagnose facultative quadrupedality. What remains is for a similar methodology to be applied to additional dinosaurian taxa that underwent a locomotor transition, especially targeting other species which may have been facultative quadrupeds to assess whether this locomotor mode is indeed made physically possible by their anatomy and physiology. By extension, if the locomotor mode of several species within a clade can be more definitively resolved by this method, the point in evolutionary time at which obligate quadrupedality first reappeared will become clearer.

Among Thyreophora, previous virtual reconstruction and simulation studies of locomotion have almost exclusively targeted eurypodans and especially stegosaurs. 3D skeletal models of *Kentrosaurus* have been used to explore the range of motion of the limb joints (Mallison, 2010) and reconstructions of various thyreophorans including *Scelidosaurus* have recreated the locomotor musculature that serviced the more proximal of these joints (Maidment, Bates, et al., 2014). Muscle function also has been explored through quantification of the moment arms that the limb muscles had over the hip, shoulder, knee, and elbow in *Stegosaurus* (Brassey et al., 2017). What is currently absent from the literature is a study which ties all of these individual elements together to investigate how range of motion and moment arms impact upon locomotion in thyreophorans. In addition, further emphasis on distal limb function and the locomotor biology of more basal species is required to understand how limb form and function changed as thyreophorans developed secondary quadrupedality.

The primary aim of this study was to apply an MDA approach to the biomechanics of *Scutellosaurus* and perform this more comprehensive type of analysis to explore gait production. MDA can show whether quadrupedal gaits would have been physically possible for this species to maintain and by extension, how the speed and efficiency of such gaits may have compared with bipedal ones. The results can then provide evidence to help to determine whether some form of quadrupedality existed early in the thyreophoran lineage or whether *Scutellosaurus* is better described as an obligate biped. To perform such an analysis requires a full myology of *Scutellosaurus*, incorporating both proximal and distal soft tissue elements as well as estimates of segment mass properties and joint ranges of motion.

2 | MATERIALS AND METHODS

For this study, a *Scutellosaurus* skeletal model was created using the MNA[1] V175 holotype remains as a reference. The specimen was recorded using photogrammetry and was photographed from multiple angles under ambient room lighting using a Canon E0S 40D camera. Images were processed using Agisoft Photoscan Standard Edition Version 1.4.3 build 6529 using methodology based on that of Mallison and Wings (2014). Meshes generated from the photogrammetry were imported into Cinema 4D R20.030, where they were scaled and individual bones digitally reconstructed where possible. Where elements were incomplete in the holotype, such as the skull and parts of the axial skeleton, reconstructions of other basal ornithischians such as *Lesothosaurus* (Sereno, 1991) and *Emausaurus* (Haubold, 1990) have been used to supplement the missing data. The digitally reconstructed bones were scaled based on reconstructions by Hartman (2016) and Colbert (1981). In order to reduce processing overheads and reduce polygon density, meshes were retopologized in Pixologic zBrush 2019 using the zRemesher function. This process results in a loss of some fine detail that would be superfluous for this analysis, but the bones retain their gross morphology. The osteoderms included follow the morphotypes defined in the holotype description, but their arrangement is speculative, inspired in part by Colbert's original proposed arrangement (Colbert, 1981) and also by the arrangement reconstructed for the related thyreophoran *Scelidosaurus* (Norman, 2021). The initial articulation of the skeletal model was performed in Blender (www.blender.org). The model used a bipedal neutral stance rather than a quadrupedal stance for consistency with the majority of previous *Scutellosaurus* reconstructions. The selected stance was in part based upon Colbert's original reconstruction of the MNA V175 remains (Colbert, 1981). This representation features a dragging tail characteristic of bipedal dinosaur reconstructions from this time (Oldham, 2018; Paul, 2005); this has been corrected to a more horizontal positioning in the model, following more modern reconstructions. As no other three-dimensional skeletal reconstructions of *Scutellosaurus* yet exist, front views of an *Edmontosaurus* 3D model (Sellers et al., 2009) and the mounted *Stegosaurus* NHMUK PV R36730 were used to reconstruct the positioning of the radius and ulna. As the forearm was treated as a single, non-rotating segment, any inaccuracies in the selected pose for the radius and ulna with respect to one

another should not have impacted significantly upon the locomotor ability of the model.

The posing of the pes was informed by the pedal prints of the ichnotaxon *Anomoepus*, which closely resemble the pedal anatomy of several basal ornithischian dinosaurs including *Scutellosaurus* (Dalman & Weems, 2013).The estimated size of the *Scutellosaurus* pes suggests that the known specimens, some of which are considered to be juveniles, would have been too large to be the trackmaker for the known North American prints (Rosenbaum & Padian, 2000), though recent hatchlings and very young juveniles were certainly much smaller than the individuals currently known, and larger prints attributed to the same ichnotaxon are known from Lesotho (Wilson et al., 2009). Regardless of whether *Scutellosaurus* was the trackmaker, the consistency in pes shape among basal ornithischians of different sizes suggests that the pedal prints they produced were likely of a consistent form as well (Dalman & Weems, 2013). The *Anomoepus* prints preserve evidence of a digitigrade foot that showed a slight medial rotation relative to the direction of travel. The degree of divarication between the pedal digits is inconsistent between prints, and so a value within the range observed was chosen for the *Scutellosaurus* model. To simplify the model, the pedal digits of the model were left completely flat. In life, dinosaurian pedal digits likely flexed and extended during the step cycle in a comparable way to many modern birds. Modeling virtual digits that move in the same way is challenging as various small distal muscles and joints must be added and moreover, the additional complexity impacts upon computation time. Previous studies have selected somewhat arbitrary foot poses somewhere in the middle of the full range of flexion and extension (Sellers et al., 2009, 2017), and significant simplifications with respect to foot anatomy (Bishop, Cuff, & Hutchinson, 2021) and this is currently a necessary compromise in full body locomotor simulations. As such, we cannot make any robust conclusions about motion within the *Scutellosaurus* foot and how this impacted upon gait appearance during forward locomotion.

The posing of the manus was more problematic as this element is not preserved in articulation in any known specimens (Breeden et al., 2021; Rosenbaum & Padian, 2000). It has been hypothesized that quadrupedal eurypodan thyreophorans may have held their manus in a semi-tube conformation similar to sauropods wherein the metacarpals are held vertically and fit together tightly into a c-shape.(Senter, 2011), but whether this would have been the case for a hypothetical quadrupedal *Scutellosaurus* is unclear. Dinosaurs hypothesized to have used this stance appear more graviportal, with metacarpals of a consistent length and very truncated digits; the

currently proposed *Scutellosaurus* manus morphology is much more cursorial with longer digits, though as previously mentioned, the original reconstruction of the manus has been repeatedly called into question but not definitively revised (Breeden et al., 2021; Rosenbaum & Padian, 2000). As a compromise, the model used in this study was posed and articulated so that it would be capable of holding the metacarpals vertically similar to this proposed semi-tube arrangement but was also able to make use of other more diagonal or horizontal positions if these proved to be more stable. The assumption was made that the manus could indeed be held in a more pronated position as in obligate quadrupeds; the original holotype description places the manus in this pose, and descriptions of more recent material do not provide definitive revisions to this reconstruction. However, *Scutellosaurus* may also have stood with a fully supinated manus and the ability to switch between poses has yet to be investigated in this species. While simplifications and assumptions made during the posing of the manus may well impact upon the appearance of the quadrupedal gaits generated by the simulations, the primary aim of this study was to determine whether any kind of quadrupedalism was made possible by *Scutellosaurus*' myology at all; future studies that spend additional time studying the manus posing are required to qualify what effect the posing has on generated gait mechanics.

Another area of equivocality is the placement of the scapulae; the pectoral girdle is not preserved in articulation in any known *Scutellosaurus* specimen (Breeden et al., 2021), thus the exact position in which this element sat is uncertain. The scapulae are preserved in approximate articulation in the *Scelidosaurus* BRSMG LEGL 0004 (Norman, 2021), though this species is rarely reconstructed in a bipedal stance and so the position of where the pectoral girdle should sit in a bipedal *Scutellosaurus* is hard to infer from this species. As a result, the positioning was inferred from previous *Scutellosaurus* reconstructions. The position of the scapulae impacts upon how closely the forelimbs can be held to the ground; should the true position be higher or lower than that which we have reconstructed for our model, the quadrupedal gait appearance and efficiency would likely be impacted. Further experiments testing the effects of scapulae position are required to fully understand the magnitude of these potential effects until the true position of the pectoral girdle in *Scutellosaurus* is discovered.

After posing as described above, the skeletal elements were imported into GaitSym2019 (https://github.com/wol101/GaitSym2019), an open source software package that provides a GUI interface for the integration of skeletal CAD models with the various other parameters required for MDA simulation. Four joints were added to

each limb, modeled as hinges permitting only two degrees of freedom (flexion and extension). This effectively limited the model to movement in only the parasagittal plane and removed the need to consider the complex control mechanisms involved in spherical joints, common simplifications made in similar studies to reduce computational demand (for review see Lautenschlager, 2020). This necessary simplification means that the results of this study will not reveal how abduction-adduction and/or long axis rotation of limb segments may have impacted upon the forward locomotion of *Scutellosaurus*, nor how agility during turning may have differed between bipedal and quadrupedal gaits. These are both factors that require specific investigation in future studies if we are to fully understand how this species navigated its environment. Removing the ability of the hip and shoulder to abduct, adduct and long-axis rotate means that some muscles exclusively supporting these functional roles can be excluded from the model, making individual repeats of the simulation faster to complete. The degree to which the *Scutellosaurus* manus could actively pronate and supinate has not been analyzed previously, and so this study considered the radius and ulna to be static with respect to one another and the wrist to be incapable of rotation. As mentioned earlier, additional joints existed between the phalanges within each digit, permitting additional toe flexibility in life; these were excluded from the model to reduce complexity. The small length and diameter of the phalanges suggest that the small muscles here would not have been capable of exerting a significant force anyway, and thus likely did not have as great an effect on locomotion as the larger more proximal muscles. To determine the location of the joint centers, first, construction markers were affixed to the medial and lateral surfaces of the proximal and distal ends of each bone to be linked. For each articular surface, an approximate centroid was estimated via the creation of a marker equidistant to the respective lateral-most and medial-most markers. To approximate the center for a given joint, a final marker was created equidistant from the respective articular surface centroid markers. Range of motion was tested after selection of these manually selected joint centers to ensure that broadly realistic range of flexion and extension was possible without bone–bone collision. While more sophisticated mathematical approaches can be used to define joint centers (see Bishop, Cuff, & Hutchinson, 2021), we chose this method partly because the simplification made to joint rotations (i.e., flexion-extension only) and because bone articulations within joints must be estimated anyway (see below). Both the pelvic and pectoral girdles were modeled as static elements. In reality, the pectoral girdle is a free-floating element not skeletally attached to the trunk,

and thus it is likely that some degree of scapular movement was possible in life. However, any estimate of joint range of motion (ROM) would be highly speculative as there are no skeletal obstacles that clearly define movement limits in cranial and ventral directions. For the purpose of the simulation, the neck, trunk, and tail were considered to be a single rigid element. Previous simulations of a small bipedal theropod suggest lateroflexion of the tail may have played a significant passive role on the regulation of whole-body angular momentum, but the consideration of the tail as a static element is likely not significantly impede the overall locomotor ability of the model (Bishop, Falisse, et al., 2021).

Relative bone positions and joint articulation in models such as ours requires estimation of the size and shape of unfossilized articulation cartilage. In real animals, these factors play a complex role in the 3D range of motion permitted and potentially favored during locomotor tasks. However, in our simplified model and in the simulations carried out, the primary influence of the cartilage size/shape estimations are on body segment lengths and subsequently masses. Previous sensitivity analyses on digital body mass reconstructions of *Allosaurus* found that more generous cartilaginous spacing between vertebrae than are typically used in mounted dinosaur skeletons result in a body mass increase of approximately 2.5% (Bates et al., 2009), suggesting a relatively modest effect on mass properties. Examination of extant archosaur limb articular cartilage has previously been used to estimate the changes in dinosaurian limb long bone dimensions resulting from the inclusion of such cartilage (Holliday et al., 2010). Even if a thick crocodilian-like cartilage (adding an average additional 10.8% to hindlimb bone length; Holliday et al., 2010) is assumed, the estimated length of *Scutellosaurus'* hindlimbs would only increase by around 2.4 cm compared with our current model, a change unlikely to considerably impact limb length, mass or function.

Estimations of ROM were created via manual rotation of the bones about each joint; the ROM limits were considered to be points at which the joint was clearly disarticulated or where two or more skeletal elements collided. Judging by this estimated maximum ROM alone, the adoption of a relatively erect quadrupedal stance appeared to be physically possible for the model. Due to time constraints, our analysis of joint ROM was relatively simplistic, considering each joint separately rather than the entire limb holistically. More rigorous studies of ROM in a running bird have examined the interactivity of joints within the entire hindlimb, revealing that the poses adopted by the living animal typically only occupied between 50% and 80% of the range estimated from the maximal and minimal rotation of the individual

joints. (Kambic et al., 2017). As a result of our simplification, some of the recovered joint postures seen in the simulations may not accurately reflect those used most habitually by the living dinosaur.

When reconstructing locomotor musculature in dinosaurs, the rarity of soft tissue preservation means that researchers almost exclusively rely upon extant analogues in order to make inferences (Witmer, 1995). For dinosaurs that were obligate bipeds, the hindlimb morphology of modern running palaeognaths is a useful comparison as the gross limb anatomy goes relatively unchanged (compared with the forelimb) from their non-avian theropod ancestors (Hutchinson, 2002). For obligate or facultative quadrupeds, the application of bird data is more limited; the specialized anatomy and function of avian forelimbs means that the location and primary function of several muscles has changed as well, reducing the number of inferences that can be made about dinosaurian forelimbs. The inclusion of crocodilian data can overcome some of these limitations, although there are still key functional differences between these extant animals and dinosaurs; the sprawling gait of crocodiles places emphasis on different muscles to the more erect stance of quadrupedal dinosaurs, and the aquatic propulsion role of the tail is not shared by the majority of dinosaurs. Nevertheless, comparison to extant species with similar anatomy and locomotor behavior remains the only real option for the reconstruction of dinosaurian muscle physiology.

The reconstruction of the limb musculature in this study was largely based on previous reconstructions in basal ornithischians wherein the *Scutellosaurus* holotype material is referenced specifically (Maidment & Barrett, 2011); areas of rugose scarring on these remains are considered to be indicative of areas of muscular attachment and provide support for the sites of origin and insertion inferred from extant phylogenetic bracketing. In cases where scarring was not found on the holotype remains, descriptions of more recent *Scutellosaurus* material were referred to in order to assess whether scarring could be found in another specimen (Breeden et al., 2021) as well as scarring found on the closely related and anatomically similar *Lesothosaurus* (Rosenbaum & Padian, 2000). Previous reconstructions of basal ornithischian and derived thyreophoran musculature have not included the more distal muscles of the feet (Brassey et al., 2017; Maidment & Barrett, 2011; Maidment, Bates, et al., 2014), thus additional reconstructions of a large hadrosaur (Dilkes, 2000), and a small coelophysoid (Bishop, Cuff, & Hutchinson, 2021) with more comparable pedal anatomy to *Scutellosaurus*, were also used to inform the reconstruction. As a result, the origin and insertion points for the muscles of the

manus and pes reconstructed for our model may not be an exact match for those in the living animal. However, the small size of the Scutellosaurus manus and pes (an estimated 3.8 and 10.6 cm, respectively; Rosenbaum & Padian, 2000) means than inaccuracies in muscle attachment position are unlikely to be out by much more than a few centimeters, thus any inaccuracies in the simulated muscle moment arms are likely to be similarly small.

There are currently two commonly used methods for the integration of reconstructed muscles to locomotor models. One first option is to sculpt the individual muscles as fully 3D objects, reconstructing their approximate volume and shape as well as their origin and insertion (Allen et al., 2013; Bates et al., 2012; Demuth et al., 2022; Díez Díaz et al., 2020; Hutchinson, Bates, Molnar, et al., 2011; Persons & Currie, 2011). This method requires significant anatomical knowledge acquired from extensive dissections of extant archosaurs, and they have produced mixed results where tests of their accuracy and repeatability have been conducted. For example, where osteology provides a reasonable constraint on muscle geometry, such as with the caudofemoralis longus muscle in crocodilians, independent research groups have shown that muscle sculpting can produce accurate estimates of muscle volume (Hutchinson, Bates, Molnar, et al., 2011; Persons & Currie, 2011). However, in anatomical systems where muscle geometry is less well constrained by osteology, validation assessments have demonstrated high levels of absolute error and inter-investigator subjectivity/variability (Broyde et al., 2021). The second method, and the one employed by this study, is to reconstruct muscles as muscle-tendon units (MTUs) which simplify the shape of muscles into a single line of action that can be guided across bones and joints from origin to insertion, with properties relevant to contractile dynamics estimated separately based "average" values from extant taxa (see below). Following previous dinosaur MDA studies small intrinsic muscles such as those between the radius and ulna were excluded from the model as these bones were reconstructed as a single element incapable of any pronation or supination. Pectoralis muscles were also excluded from the model; various sources reconstruct this muscle running from the sternum to the deltopectoral crest of the humerus (Ballell et al., 2021; Maidment & Barrett, 2011), and despite the presence of a prominent tubercle to support the site of insertion (Maidment & Barrett, 2011), no sternal plate is evident from the known *Scutellosaurus* remains (Breeden et al., 2021). Material that may have represented a sternal plate has subsequently been lost from reconstructions of the closely related *Scelidosaurus* (Norman, 2021), so speculation as to the position of the sternum in *Scutellosaurus*

would have had to borrow from more distantly related species. As the model used in this study limited the motion of the shoulder to only flexion and extension, the primary humeral adductor role of the pectoralis would have been largely redundant, and any role it may have played in shoulder flexion is covered by various other muscles.

Muscle origins and insertions were placed within the approximate centroids of their attachment area. Large muscles with broad areas of attachment were only split into multiple MTUs if the resulting subunits were deemed to play significantly different functions; for example, the anterior and posterior sections of the large fan-shaped latissimus dorsi insert at the humerus at very different angles, providing very different amounts of leverage over the shoulder joint. In previous thyreophoran reconstructions, this muscle has been modeled using five lines of action to account for the variation in moment arm that separate parts of this large muscle produced (Brassey et al., 2017). This study further simplified this reconstruction to only include two lines of action: an anterior section attaching to the caudal most cervical vertebrae and a posterior section attaching to the dorsal vertebrae. As the metacarpals and manual phalanges are treated as single fused elements as opposed to individual bones and digits that move independently, muscles such as the extensor carpi ulnaris that would have attached to each digit in life were simplified to only attach to the central digit. As previously alluded to, further study with a more complex, fully muscled, multi-jointed foot is required to understand how toe flexion and extension impacted upon dinosaurian locomotion as this is not explored within this study. The same procedure was used when reconstructing muscles that acted on the metatarsals and pedal digits. In total, 86 MTUs were reconstructed with 19 servicing each forelimb and 24 controlling each hindlimb. Wrap cylinders and via points were used sparingly to model more realistic paths for certain MTUs, ensuring that they passed over the appropriate joints and did not clip through the bones over the full ROM (see Figure 2).

The proportion of body mass that is made up of muscle differs between animals of different locomotor styles. For arboreal mammals such as small primates, muscles can make up as little as 25% of body mass, while active terrestrial species such as greyhounds and agoutis have musculature that represents up to 50% of their total body mass (Grand, 1977). Selecting a suitable value within this range is difficult for extinct species whose locomotor specialization (speed, stamina or all-round) and ecological niche are impossible to know with certainty. Previous dinosaur simulation studies focusing on theropods, which are proposed to be active pursuit predators, have opted to use the high estimate of 50% (Sellers et al., 2017). The vast majority of non-maniraptoran dinosaurs are not thought to have had an arboreal climbing lifestyle, thus the lower estimate of 25% derived from extant mammals with this niche is likely inapplicable. For the purposes of this study, the 50% upper estimate was used.

Inferences about muscle mass distribution across the limbs are hard to make from phylogenetic bracketing because of the stark differences in the terrestrial locomotion of birds and crocodiles. Quadrupedal mammals with erect gaits closer to a hypothetical quadrupedal *Scutellosaurus* are not a perfect fit either since the species that mammalian locomotor data is most commonly drawn from including horses and dogs that have forelimbs and hindlimbs of a more consistent length and do not include muscles such as the caudofemoralis longus that contribute to limb retraction in dinosaurs. A previous study of dinosaur facultative quadrupedalism elected to make arbitrary assignments of mass to the forelimbs and hindlimbs reflecting the geometry of the limbs, and to divide masses equally among the joints (Sellers et al., 2009) but other simulations of quadrupedal dinosaurs have opted to use mammalian data in spite of its limitations (for discussion see Sellers et al., 2013) and this latter approach was followed in this study using the reindeer proportions as an exemplar quadruped (Wareing et al., 2011). Thus 58% of the muscle mass is distributed within the hindlimb with the remaining 42% allocated to the forelimb. Within the limbs, 56% of the mass acts over the most proximal joints, 31% acts over the intermediate joints, and the remaining 13% services the distal joints. Since the current model incorporates two distal joints per limb, the assumption was made that the 13% share of mass was distributed with 2/3 at the proximal joint and 1/3 at the distal joint. 59% of the muscles were considered to play the functional role of an extensor, 30% as joint flexors and 11% as performing other functional roles such as rotators, adductors, and abductors. Since the joints in this model permitted only flexion and extension, the 11% of mass belonging to muscles with other roles was reallocated to flexors and extensors in equal amounts. By tabulating the muscles implemented and their functions it is thus possible to assign a muscle mass to each muscle. This is a pragmatic approach that should provide the correct functional weighting but cannot be used to identify the individual importance of specific muscles since the muscle mass is distributed equally across all muscles that have the same primary function.

Sensitivity analysis surrounding a virtual locomotor model of *Allosaurus* has revealed that the physiological parameters of the reconstructed muscles make a greater impact on locomotor performance than the body mass
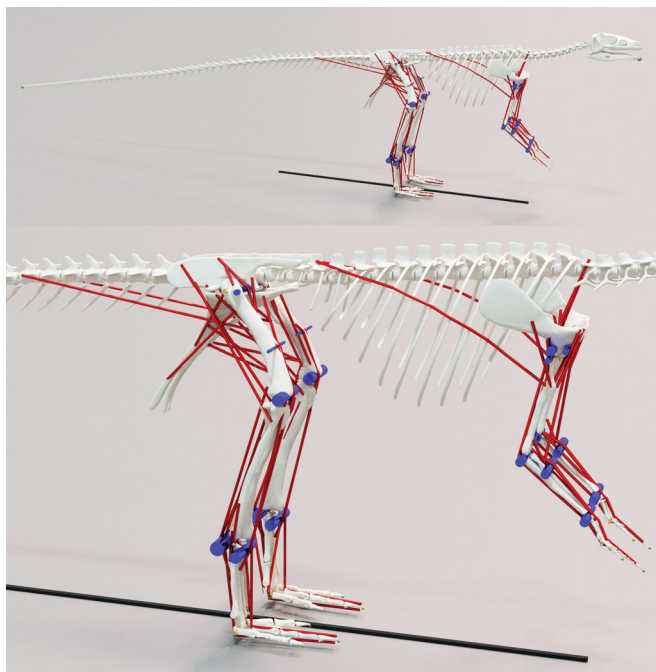
FIGURE 2 The completed musculoskeletal model including the muscle-tendon units (red), joints (yellow), wrap cylinders for guiding the muscles over the bones (blue), and contact spheres for interacting with the floor (green). This bipedal stance was used as the starting point for the initial simulations. The final rendering was produced using NVIDIA Omniverse. Scale bar = 0.5 m, total body length ≈1.35 m.

parameters (Bates et al., 2010). More specifically, changing the values for maximum muscle force (*F*max), fiber length or force per unit area (FPUA) can significantly alter bipedal top speed. Selecting appropriate physiological parameters for extinct species is complicated by the inconsistency in values reported in the literature, both between species of similar locomotor behavior and between different muscle groups within a species. This study made use of a FPUA value of 300,000 N m^{-2}. In the literature, this value has been applied to dinosaurian models of varying sizes and inferred locomotor modes including a sauropod (Sellers et al., 2013), and large and small theropod (Bishop, Cuff, & Hutchinson, 2021; Sellers et al., 2017; Sellers & Manning, 2007) however it is clear that a case can be made for a range of both considerably lower and higher values (for discussion see Alexander, 2003).

In addition to individual muscle mass, the fiber length over which this mass operates is key to defining the contribution of a specific muscle. As a result, the selection of appropriate fiber length values is imperative to improving the accuracy of the model. Again following previous work (Sellers et al., 2013), it was assumed that muscles typically operate between 75% and 125% of their

resting fiber lengths. The MTU lengths in the model were measured over the full joint ranges of motion and the fiber length set to half of the length change seen. While many muscles differ from this fiber length to extension ratio (Bishop, Michel, et al., 2021; Sellers et al., 2013), this relationship is favored here as muscles have been simplified into a reduced number of functional groups and this reduced redundancy means it is sensible to ensure these simplified actuators are capable for force generation over a relatively wide range of motion. The tendon lengths were set so that the fiber length plus the tendon length equaled the mean MTU length. Setting fiber lengths this way means that the models performance is largely independent of the muscle moment arms. Muscle performance is also influenced by its fiber type composition but there is currently no way to estimate this for a fossil animal and so the model in this study used a 50:50 split, with maximum contraction velocity (*V*max) set to 8.4 resting length per second. Muscle volume was calculated from the mass using a density of 1056 kg m^{-3} (Winter, 1990) and then physiological cross section area (PCSA) by dividing the volume by the fiber length. The Minetti–Alexander model (Minetti & Alexander, 1997) was then used to calculate the force and metabolic energy use of the individual muscles within the model.

The next step of model creation involves the calculation of mass, center of mass, and moments and products of inertia for each body segment. This can be achieved by scaling pre-existing inertial property datasets from extant specimens (e.g., DeLeva, 1996; Vilensky, 1979), though most studies instead attempt to estimate values from the model directly by generating an approximation of body volume and applying a suitable value for tissue density (Bishop, Cuff, & Hutchinson, 2021; Sellers et al., 2009, 2013). This study used a minimum convex hulling method which has been well-documented previously (Brassey & Sellers, 2014; Sellers et al., 2012). It involves the creation of hulls which shrink-wrap the bones and provide an estimate of the minimum volume required to contain the skeletal elements (see Figure 3). This method can be performed quickly and easily using an algorithm such as "convex hull" in Blender or "qhull" in MeshLab. These hulls are far from the true segment volumes in life, as the additional girth provided by the musculature and skin is not taken into account. To correct for this, data from extant taxa can be used to estimate the quantity of missing dinosaurian soft tissue. By producing minimum convex hulls for a range of extant archosaurs and comparing them to the true volumes of each segment quantified through medical imaging (Macaulay et al., 2017), expansion factors can be derived for each segment which can then be applied to the minimum convex hulls of extinct species to estimate their body volumes in life

(Macaulay et al., 2023) applied this approach to derive body segment specific convex hull expansions for dinosaurs based on extant birds, crocodilians and lizards, where simply percentage or allometric expansions for skeletal convex hulls could be applied to each body segment using one or a combination (i.e., an average) of these extant outgroups. Where possible, the *Scutellosaurus* segments were scaled using an average expansion factor derived from the whole dataset, however, as birds lack the long muscular tail seen in dinosaurs, the expansion factor for this segment was calculated from the crocodile and lizard data only. The mass estimation made use of the same limb segments as the locomotor model, though the head, neck tail and trunk were split into their own segments. Segmental masses and inertial properties from the expanded hulls and the mass parameters were added to the musculoskeletal model for simulation. However, to examine alternative reconstructions on overall we also applied the three other expansion methods used by Macaulay et al. (2023), where allometric relationships between skin and convex hull volumes for birds-only, crocodile+lizard-only and the full merged extant data set are used. The choice of extant outgroup and expansion method (allometric equation versus average percentage expansion) made little difference to total mass or mass distribution in *Scutellosaurus*: body mass across the four iterations varied by a maximum of 6% compared with our simulated model, and a total craniocaudal range in CoM position of 0.014 m (equivalent to a 6.4% range in craniocaudal CoM position normalized by gleno-acetabular distance).

Once the model has been constructed, we used a distributed machine learning system to generate the activation patterns required to drive the simulation to perform either bipedal or quadrupedal gait. This was implemented using the University of Manchester's Condor Cluster and a custom asynchronous genetic algorithm implementation (https://github.com/wol101/AsynchronousGA2022). The model was implemented as a quadruped, but bipedalism was easily enforced setting abort constraints on the forelimb contacts so that the simulation was aborted and penalized as soon as the forelimbs touched the ground. The optimizer was set to either maximize the distance forward in a given time (maximizing speed), or for a given amount of metabolic energy (maximizing metabolic efficiency), and we used our previously described gait morphing protocol (Sellers et al., 2004) where we initially start from a neutral pose and then use the results from the previously most successful trials as the starting points for subsequent trials. This protocol means that early trials require acceleration but eventually for later trials the model is maximizing its steady state performance.

3 | RESULTS

As anticipated from previous reconstructions of *Scutellosaurus*, the simulation was able to generate effective bipedal gaits. The most metabolically efficient bipedal gait generated, as illustrated in Figure 4 and Video 1, allowed the model to cover 8.7 m of forward distance at a speed of 1.6 ms^{-1}. The total energy expenditure for this run was limited to 100 J, thus the metabolic cost of transport was approximately 2.5 J kg^{-1} m^{-1}. With no energy limit and a 3 s time limit, the simulation, as illustrated in Figure 5 and Video 2, was able to progress 23.9 m forward giving a running speed of 8.0 ms^{-1} with an increased cost of transport of 8.1 J kg^{-1} m^{-1}. The metabolic cost of locomotion for a 4.65 kg animal, the mass estimated for *Scutellosaurus* by this study, would be expected to be 6.7 J kg^{-1} m^{-1} (Full et al., 1990) but the data drawn from extant species does show a degree of variability in metabolic cost for animals of similar mass, thus the higher expenditure seen in the running gait is still be a plausible value for *Scutellosaurus*. Depending on the equation used, the maximum running speed for this animal might be expected be 8.4 or 11.7 ms^{-1} depending on the equation used (Garland, 1983). As a result, the maximum speed recovered from the bipedal running simulations also falls within the bounds of realistic plausibility.

During the initial simulations stable quadrupedal gaits were also generated although much more infrequently. In many iterations the forelimbs did not produce a true stepping motion, but instead bounced along the ground in synchrony. The most metabolically efficient quadrupedal gait generated (Figure 6 and Video 3) managed to move the body 4.3 m forward for 100 J at a speed of 1.1 ms^{-1}, thus incurring a metabolic cost of transport of 5.1 J kg^{-1} m^{-1}. With no metabolic energy limit and a 3 s time limit (Figure 7 and Video 4), the quadrupedal simulation was able to progress 17.4 m giving a running speed of 5.8 ms^{-1} but incurred a much greater cost of transport at approximately 14.5 J kg^{-1} m^{-1}. Thus, while physically possible, quadrupedal running appears less energetically efficient to maintain than the bipedal alternative.

Through examination of the generated bipedal and quadrupedal gaits, it was clear that gait cycle time and duty factor acted as two key determinants on the recovered gait appearance and function. Between the most metabolically efficient walking gaits and the highest speed running gaits, there is a considerable reduction in gait cycle time in both the bipedal and quadrupedal models (Figure 8a), suggesting that cycle time is a major factor affecting the differences in walking and running gait appearance. As expected from their morphology, the forelimbs of *Scutellosaurus* appear to play a much lesser
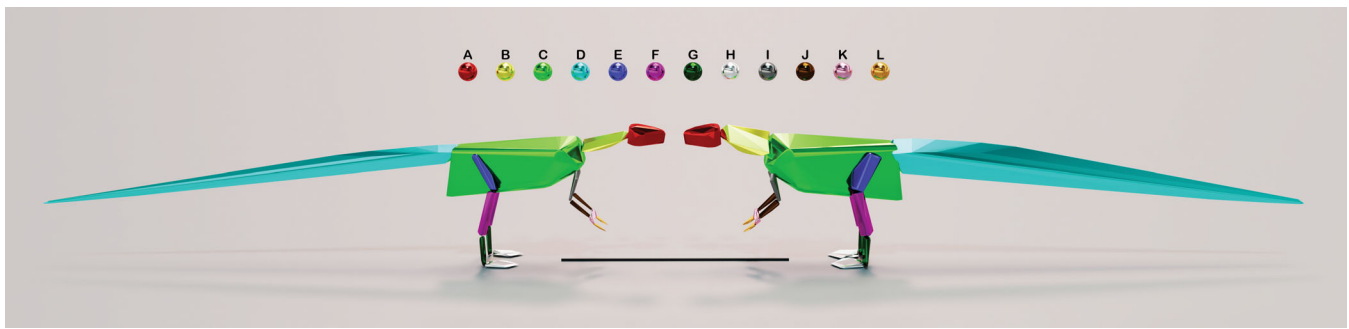
FIGURE 3 The segment convex hulls used to estimate body volume, mass, and inertial properties. Left, before and right, after expansion using extant archosaur data. A head; B neck, C torso, D tail, E upper leg, F lower leg, G metatarsals, H pedal digits, I upper arm, J lower arm, K metacarpals, L manual digits. The final rendering was produced using NVIDIA Omniverse. Scale bar = 0.5 m.
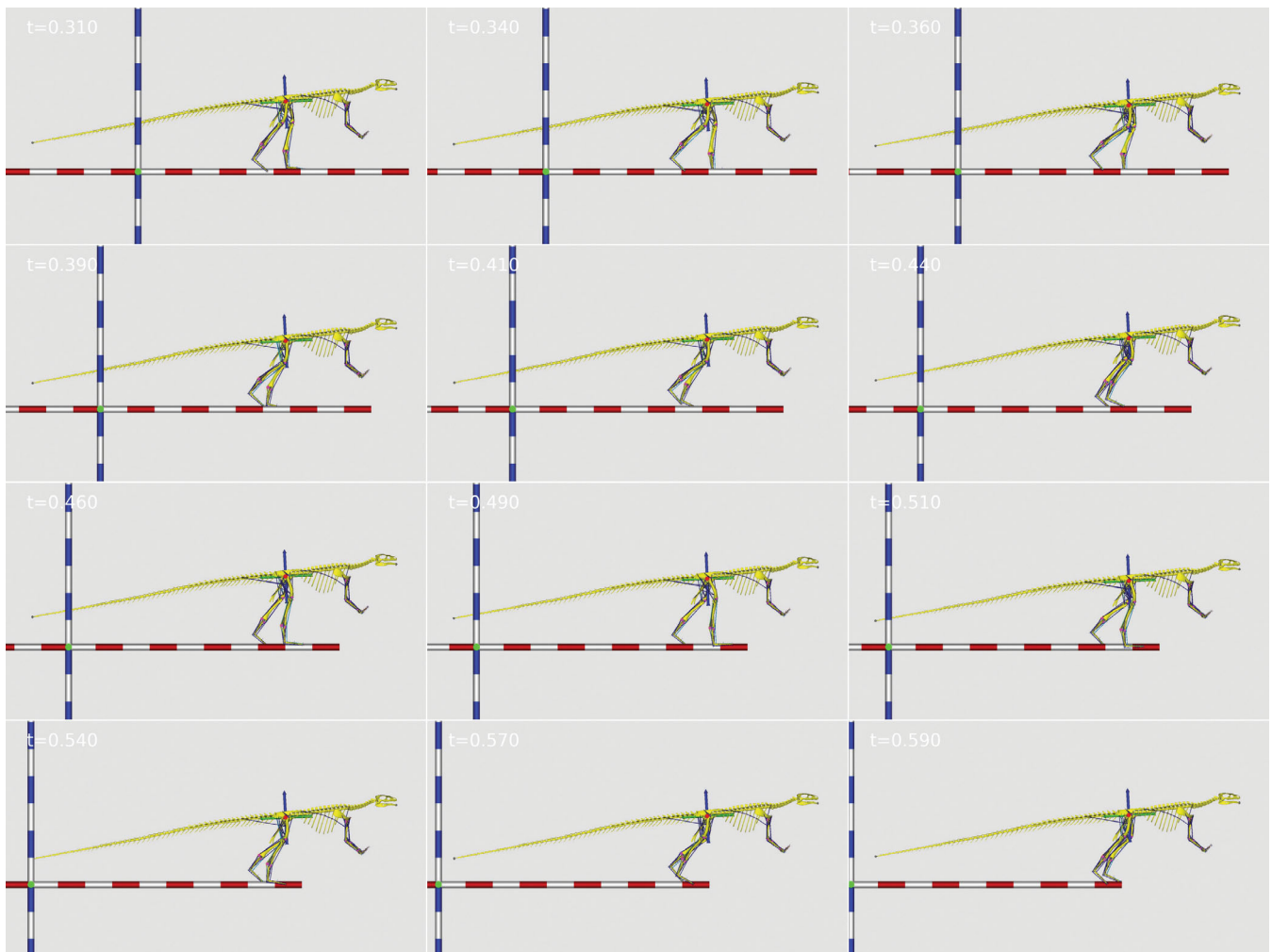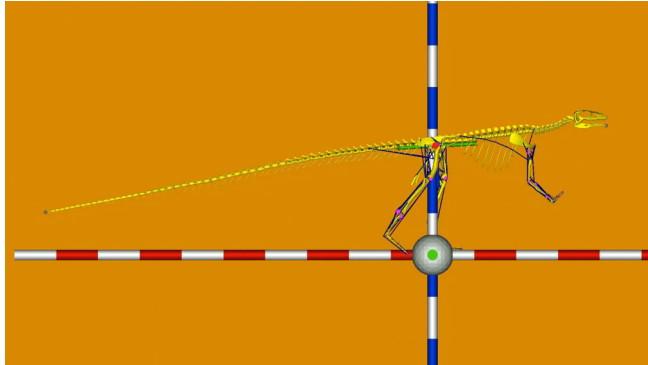

FIGURE 4 Snapshots from the bipedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled with 100 J of metabolic energy available. *t* indicates time in seconds.

role in active locomotion. Throughout the entire quadrupedal walking and running gaits, the forelimbs showed a greatly reduced duty factor, and thus longer aerial phase, than the hindlimbs (Figure 8b). To compare the forces at play, we recorded the mean ground reaction forces (GRFs) exerted at each stance phase (Figure 9a) as well as over the entire gait cycles (Figure 9b). During both walking and running, the average amount of force exerted each time a limb contacted the ground was slightly higher in the forelimbs, though because of their

greatly reduced duty factor, the average total force they exerted across the entire gait was much lower than in the hindlimbs.

Overall, the average total forces recorded during both bipedal and quadrupedal gaits appear to meet the expected values; when doubled to incorporate both

VIDEO 1　Video sequence of the bipedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled with 100 J of metabolic energy available.
Video content can be viewed at https://onlinelibrary.wiley.com/doi/10.1002/ar.25189
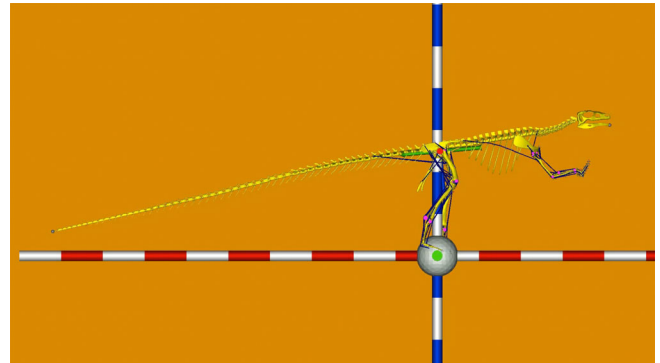
VIDEO 2　Video sequence of the bipedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled in 3 s with no constraint on metabolic energy available.
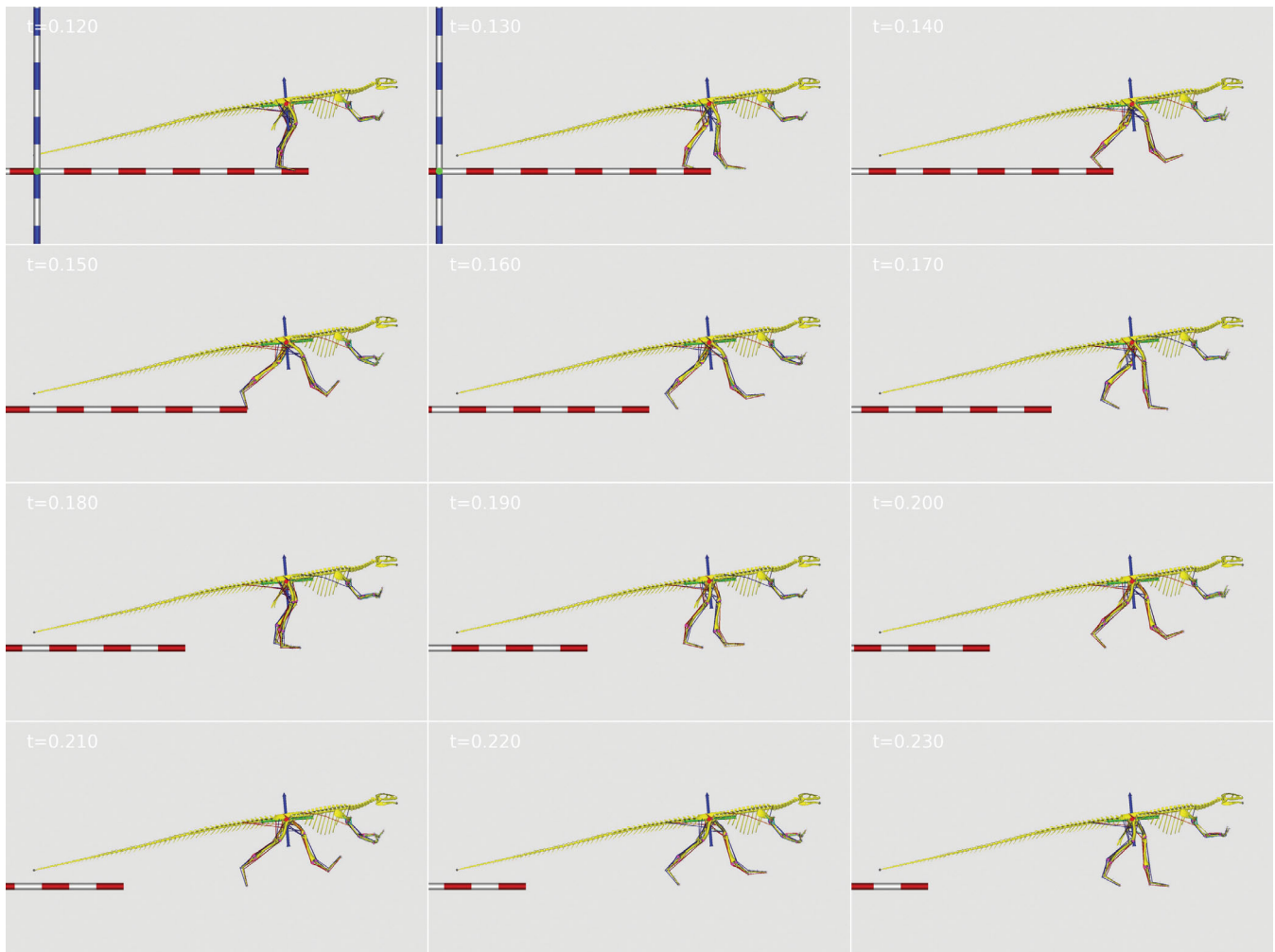Video content can be viewed at https://onlinelibrary.wiley.com/doi/10.1002/ar.25189

FIGURE 5　Snapshots from the bipedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled in 3 s with no constraint on metabolic energy available. *t* indicates time in seconds.
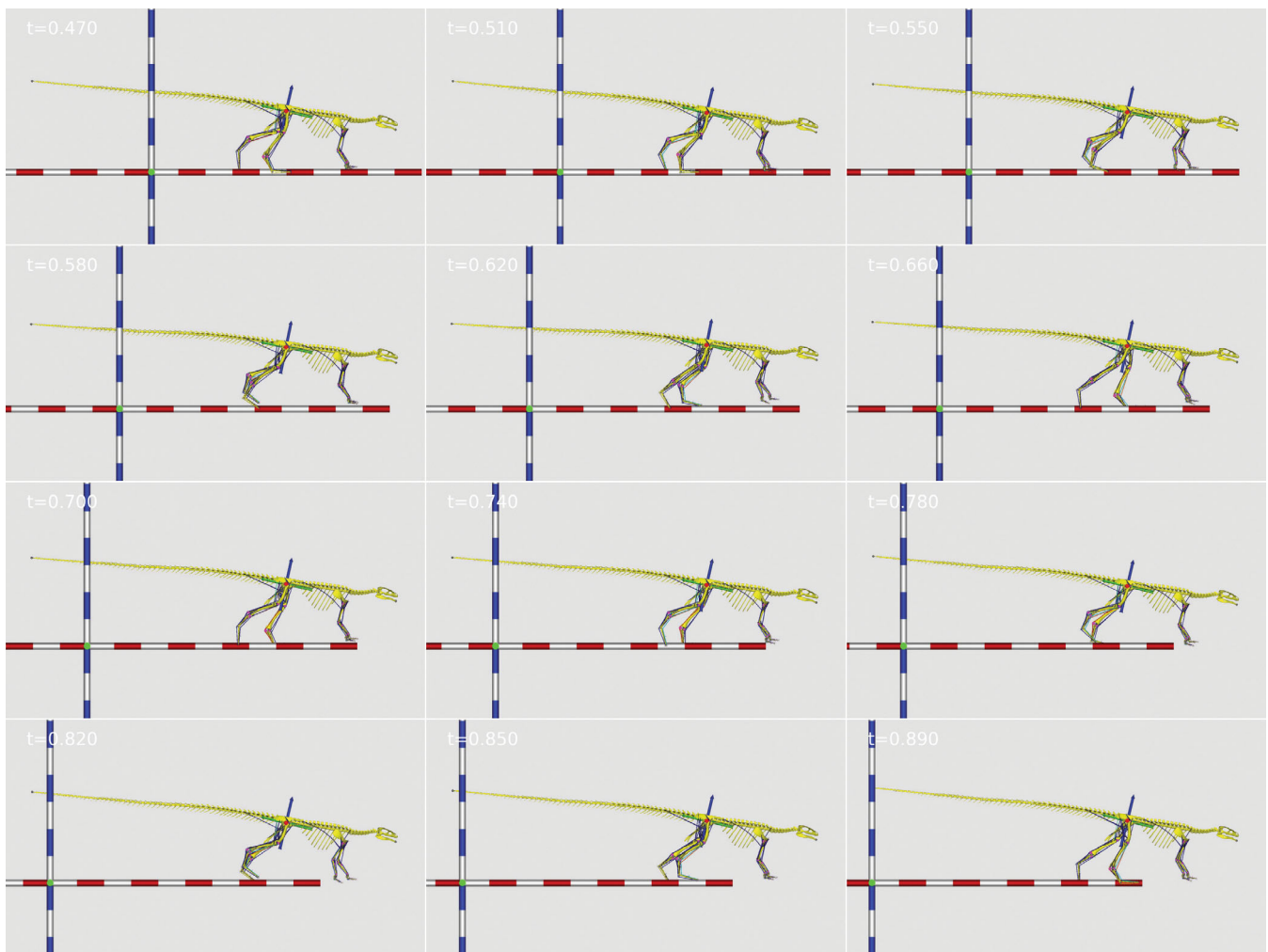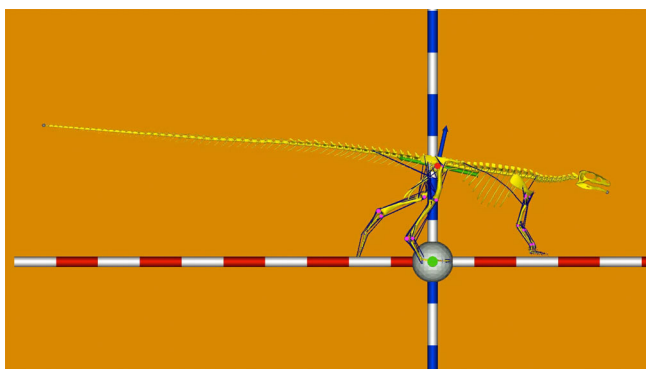
FIGURE 6   Snapshots from the quadrupedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled with 100 J of metabolic energy available. *t* indicates time in seconds.

VIDEO 3   Video sequence of the quadrupedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled with 100 J of metabolic energy available.
Video content can be viewed at https://onlinelibrary.wiley.com/doi/10.1002/ar.25189

produced forces that were realistic for an animal of this size, lending support to the plausibility of the recovered gaits.

A further way of evaluating the quality of a synthesized gait is to investigate the degree of wobble in the torso (Nyakatura et al., 2019; Sellers & Hirasaki, 2018). In particular (Nyakatura et al., 2019) developed what they term a "balance metric" from the pitch and roll velocities of the body, and this metric should be maximized to minimize the compromising effects of body wobble on vestibular and optical perception. They define this measure (M_B) as:

$$M_B = 1/\left(\frac{1}{T_F - T_0} \int_{T_0}^{T_F} |\dot{u}| + |\dot{v}|\,dt\right)$$

where T_0 and T_F define the start and end of the simulation, and $\dot{u}$ and $\dot{v}$ are the roll and pitch rates. Figure 10a

sides of the body, the outcome is approximately 46 N, a value in line with our estimated mass for the living animal. This suggests that our simulated myology
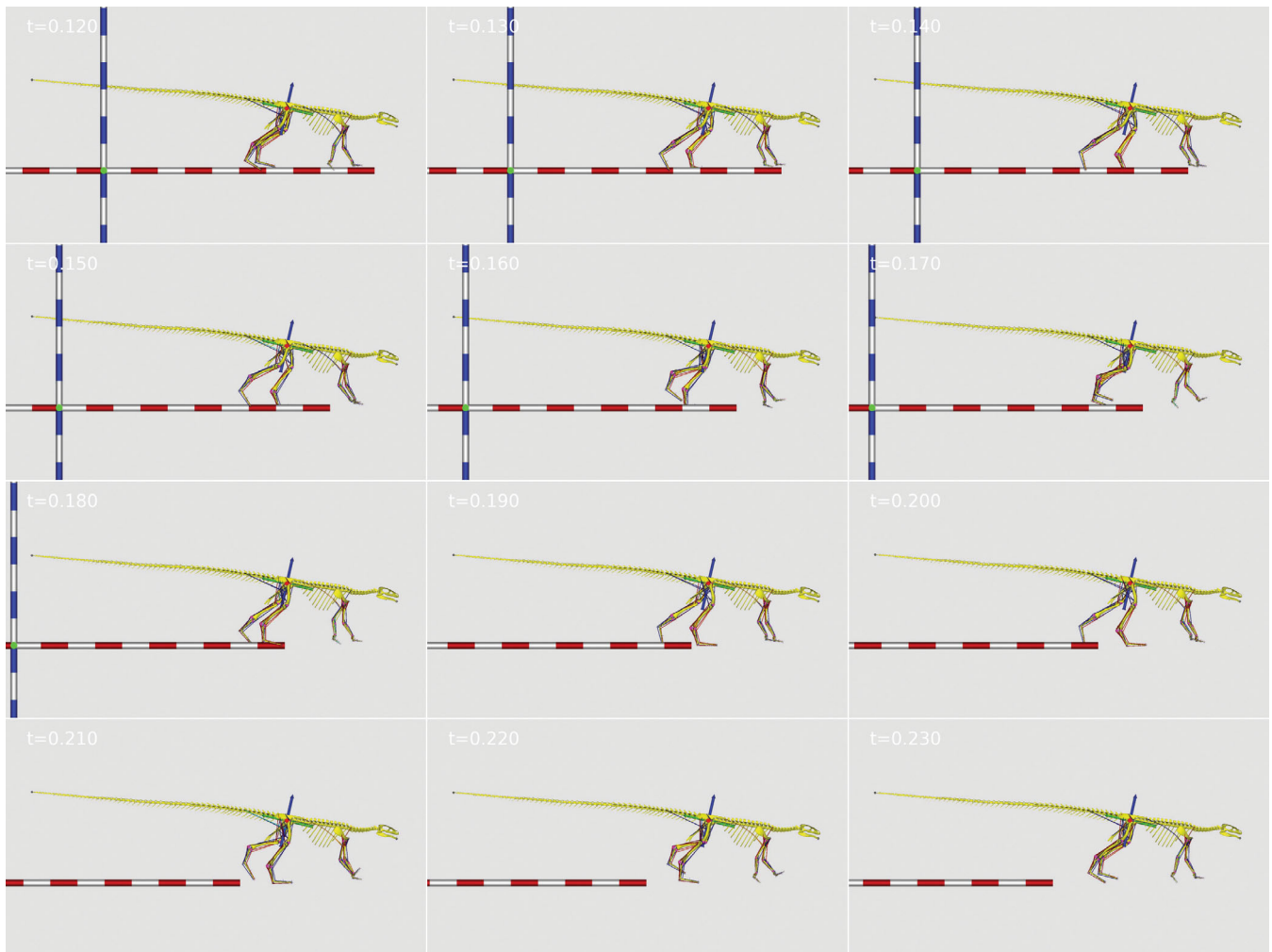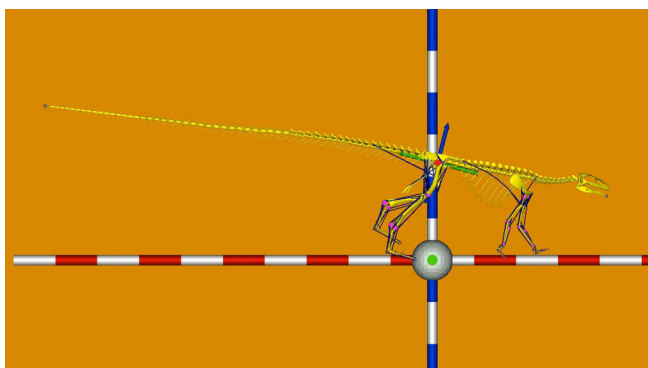
FIGURE 7 Snapshots from the quadrupedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled in X seconds with no constraint on metabolic energy available. t indicates time in seconds.

VIDEO 4 Video sequence of the quadrupedal simulation of *Scutellosaurus* where gait was optimized for the maximum distance traveled in 3 s with no constraint on metabolic energy available. Video content can be viewed at https://onlinelibrary.wiley.com/doi/10.1002/ar.25189

shows how the pitch velocity in the simulation varies for the different gait conditions with the peak pitch velocities being appreciably higher for the quadrupedal examples.

This is shown more clearly in Figure 10b where the balance metric is calculated for the different gaits. Interestingly the gait with the least wobble is the fast bipedal simulation, with relatively little difference between the others. There is so certainly no benefit in terms of improved balance for quadrupedal gaits at the speeds generated by the simulations.

4 | DISCUSSION

The principal aim of this study was to determine what quadrupedal ability, if any, *Scutellosaurus* may have possessed, and by extension, to determine whether some form of quadrupedality may have appeared within Thyreophora earlier than previously suggested. Following the initial set of simulations, intended to explore gait repertoire before further constraints were imposed, both bipedal and quadrupedal gaits were recovered. The fact that the model did not exclusively produce bipedal gaits in spite of its relatively caudal COM at the very least
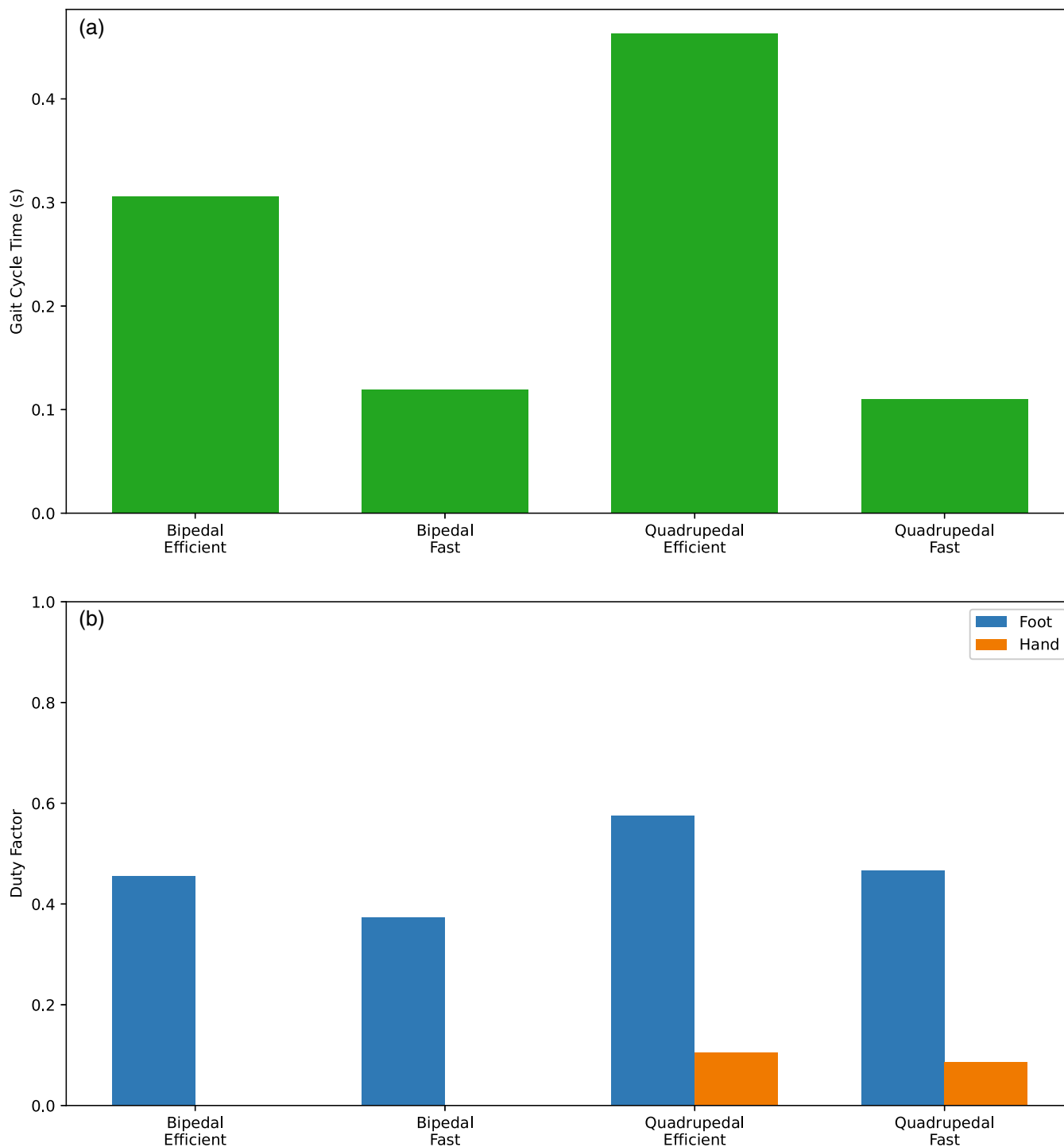
FIGURE 8 (a) Gait cycle times and (b) duty factors achieved for the most optimal bipedal and quadrupedal gaits optimized for metabolic energy cost and maximum speed.

implies that the adoption of a stable, stationary quadrupedal stance was physically possible for *Scutellosaurus*. The optimized results further show that maintenance of a slow quadrupedal walk as well as a faster quadrupedal run are certainly possibilities for this small dinosaur. However, neither quadrupedal gait is as effective as the equivalent bipedal gait as measured by maximum speed

or minimum cost of transport. Physical or mechanical possibility does not equate to a gait being ecologically useful in a real-life setting so it is important to consider what purposes these gaits could have served for *Scutellosaurus*. The bipedal top speed of 8 ms^{-1} may have been suitable for predator escape although estimates suggest that the contemporaneous predators may have been
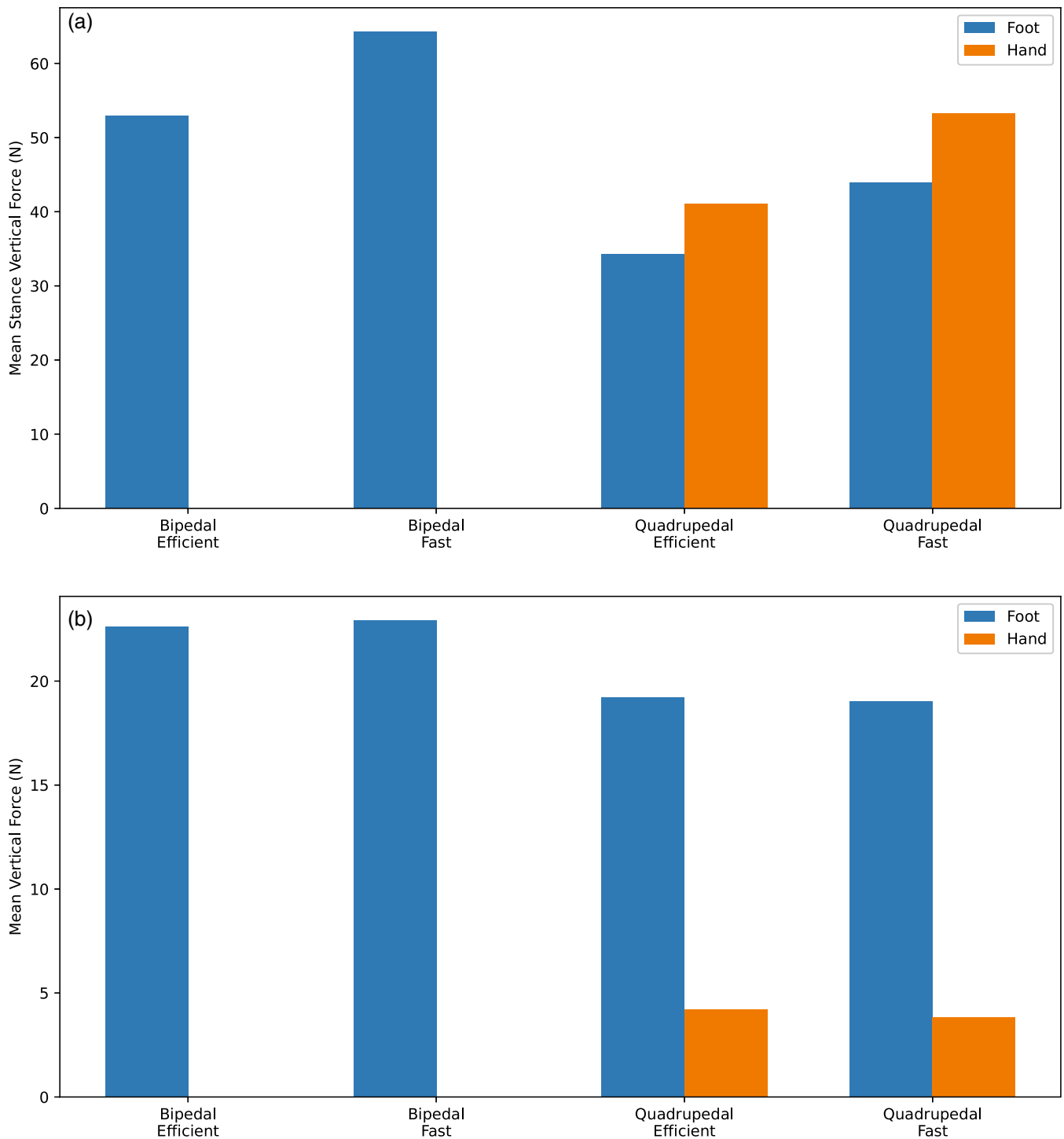
FIGURE 9 Mean vertical ground reaction force (a) during the time a limb is in contact with the ground and (b) averaged over the gait cycle. Values are for the left side of the body.

capable of reaching 6.5 ms^{-1} (Bishop, Falisse, et al., 2021, p. 202) and 10.5 ms^{-1} (Sellers & Manning, 2007), respectively, which would exceed what our model suggests *Scutellosaurus* was capable of as a quadruped. Similarly, the calculated balance metric shows no advantage of the quadrupedal gait with higher values found for the bipedal gaits. Nevertheless, the quadrupedal gait may have been

more practical for lower speed behaviors even though it is considerably less energy efficient than the bipedal gaits. The quadrupedal gait allows the head to be held closer to the ground than a bipedal gait and therefore a quadrupedal walk could have been used during feeding and drinking, reducing the amount of neck flexion needed to reach low plants. If the gait was used during
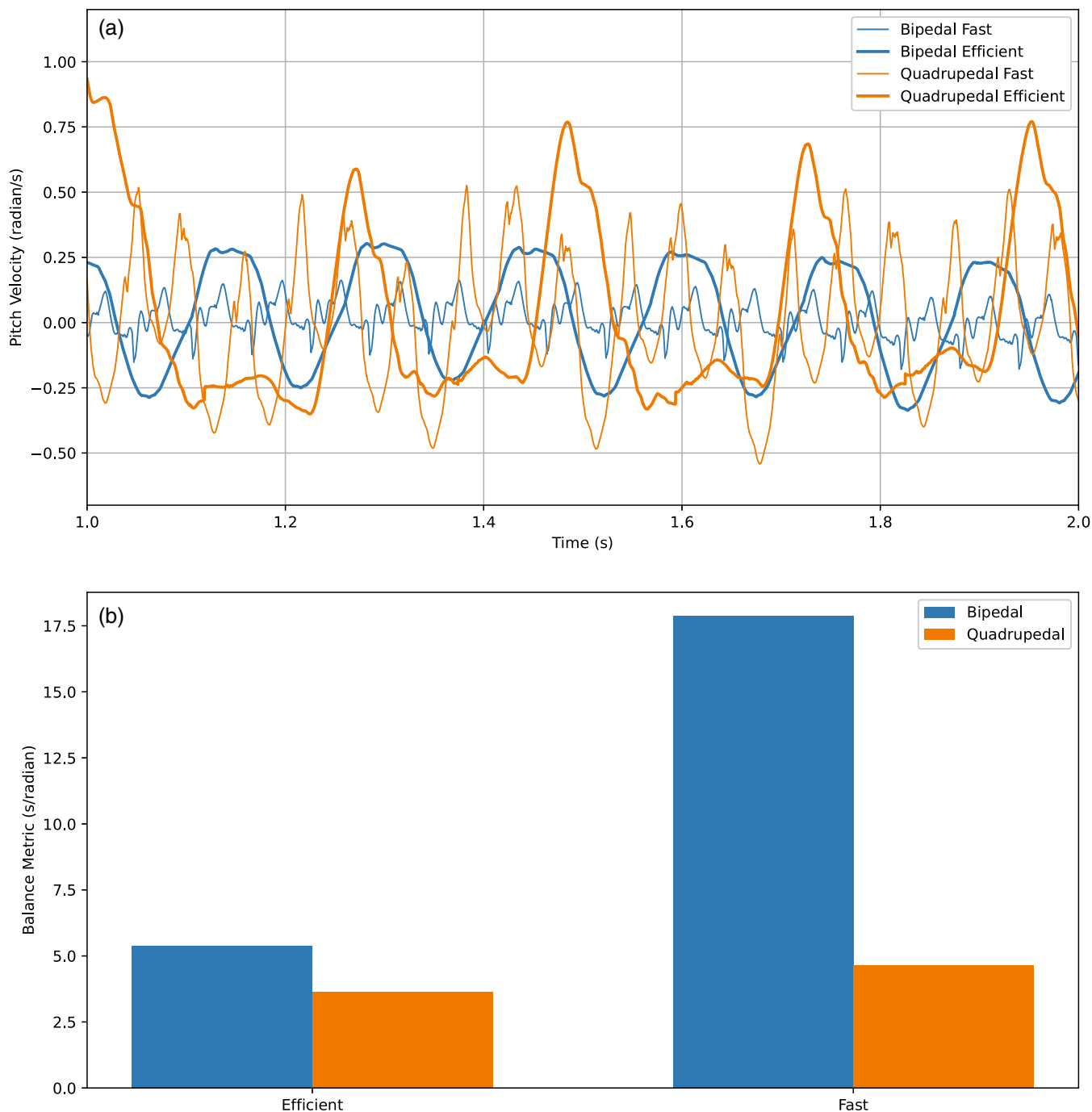
FIGURE 10 (a) Pitch velocities over time for the four different gait conditions. (b) Balance metric for the different gait conditions.

foraging rather than traveling, then the relatively poor cost of transport may well be less important.

Allowing some form of quadrupedal gait as an option for *Scutellosaurus* does provide some evidence for the time course of the recruitment of forelimbs into locomotion within Thyreophora. Evidence such as the more robust morphology of the humerus and the broad manus has been interpreted as indicating that *Scelidosaurus* may be the earliest true quadruped in this lineage (Norman, 2021) whil the more gracile appearance of the

Scutellosaurus forelimb has been interpreted as indicative of bipedalism (Breeden et al., 2021). While there is believed to be a degree of temporal overlap between *Scutellosaurus* and *Scelidosaurus*, *Scelidosaurus* remains are known from the Early Sinemurian (Breeden et al., 2021), while *Scelidosaurus* is known exclusively from the Late Sinemurian (Norman, 2021) suggesting that *Scutellosaurus* could have been making use of quadrupedal gaits several million years before its more derived relative. A clear next step is to perform similar

investigative locomotor simulations on *Scelidosaurus* to determine whether it could have possessed any bipedal ability or whether it may represent the first obligate quadrupedal thyreophoran.

There are several important caveats to the findings of this study. Firstly, the use of obligate quadrupedal mammal data when assigning muscle mass to the forelimbs presents a key inaccuracy. Reindeer are obligate quadrupeds, and as such, their forelimbs are well-adapted to support long distance quadrupedal locomotion. It is unlikely that the muscle mass distribution in a facultative quadruped would exactly mirror that of obligate quadrupeds as the dimensions of the forelimb and hindlimb differ more dramatically, and a more posterior COM means that the forelimbs would not be required to support as much weight. It might be preferable to make inferences from the muscle mass distribution in extant facultative quadrupeds that do not have specialized hindlimbs such as the giant pangolin whose locomotor anatomy and behavior is a closer fit to what was hypothesized for *Scutellosaurus*. Unfortunately, a comprehensive investigation into giant pangolin locomotor muscle distribution and mass does not yet exist. The method used in this study may have exaggerated the muscle mass ratio between the forelimbs and hindlimbs in *Scutellosaurus*; if the simulations were repeated with a 70:30 split as in a previous study of *Edmontosaurus* (Sellers et al., 2009), the forelimb muscles may then have insufficient power to support a quadrupedal gait, which would completely reverse the interpretation of *Scutellosaurus* as a facultative quadruped. As well as potentially enhancing the model's quadrupedal ability, the muscle mass distribution used may also have limited bipedal ability by allotting too little power to the hindlimbs. Previous simulations have attempted to quantify the effect that changing muscle mass has on achievable top speed (Bates et al., 2010; Sellers & Manning, 2007), and ideally, this type of sensitivity analysis needs to be repeated with dinosaur models of different sizes and locomotor modes.

A great amount of time could also be spent attempting to justify more specific physiological values for *Scutellosaurus*, but with so little preserved thyreophoran soft tissue, and certainly nothing from which values such as FPUA could be derived, there is almost no solid evidence to justify the use of one value over another. Furthermore, though the effects of parameters such as FPUA, fiber length and mass on dinosaurian models as a whole are known (Bates et al., 2010), identifying specific muscles that have the greatest impact upon locomotion when incorrectly estimated is near impossible unless a sensitivity analysis can be applied on a muscle-by-muscle basis. In this respect, dinosaurian simulation will always have to rely upon relatively limited data from extant animal

studies until more focus is given to extracting comprehensive quantitative datasets from extant taxa to better inform the reconstruction of extinct species. However, the conclusions of this study do not rely of precise quantitative values since the goal is simply to determine whether bipedal and quadrupedal gaits are possible with our best estimates for physiological values.

An additional source of error arises from the reconstruction of the joint centers and the exclusion of articular cartilage. Preservation of thyreophoran articular cartilage is scarce and none is preserved in any known *Scutellosaurus* remains; in the related thyreophoran *Kentrosaurus*, forelimb cartilage known from MFN MB. R.4800.33 causes this left ulna to be around 18% larger than other preserved ulnae from this species (Mallison, 2014). It is unclear how much of this actually corresponds to articular cartilage, and *Scutellosaurus* does not share the robust olecranon of the more derived thyreophoran. However, the *Kentrosaurus* specimen illustrates that cartilage made a significant contribution to the skeletal anatomy of thyreophorans, thus the exclusion of this tissue type may have resulted in the location of the joint centers being incorrect, impacting upon ROM. When estimating ROM from the bones alone, a further source of error arises from lack of knowledge about the soft tissue girth of the torso. Eurypodans, especially ankylosaurs, had broad torsos suitable for housing the extensive gut required for a herbivorous lifestyle (Norman, 2021). A broad midriff may have obstructed protraction of the hindlimbs somewhat, imposing limits on ROM. The width of *Scutellosaurus*' posterior torso was less exaggerated than more derived forms, though the pectoral girdle and anterior dorsal ribs are relatively broad and would have almost certainly have obstructed forelimb retraction beyond the limit estimated by this study. In addition, the presence of osteoderms may have inhibited limb range of motion depending on their placement in life; the arrangement reconstructed in this study assumed ample room would be left for the hindlimbs to retract and protract without colliding with the scutes, but the true placement may have been more restrictive. The small size of the scutes does however suggest that significant obstruction of the limbs was unlikely. Lack of knowledge about how these factors could have impacted upon ROM may again lead to the parameters used in the model exaggerating the true condition.

An important anatomical feature of *Scutellosaurus* that almost certainly requires additional focus in future studies is the exceptionally long tail. Reconstruction of dinosaurian tails has long been a point of contention within paleontology (Hutchinson, Bates, & Allen, 2011; Persons & Currie, 2011), and the functional roles of this anatomical feature are only just beginning to be

understood in detail. The tail is known to have a key role in the regulation of whole-body angular momentum, affecting both the degree of pitch and yaw in the various body segments as well as the phase in which it occurs (Bishop, Falisse, et al., 2021). Consideration of the tail as rigid with respect to the trunk has been shown to increase body yaw, an effect likely augmented by the sheer size of the tail in *Scutellosaurus*. Some of the simulations in this study involved the tail coming very close to the ground which is unlikely to have been the case in life as most trackways preserve no evidence of a dragging tail. These observations suggest that additional mobility of the tail would have played an important role in the various gaits of *Scutellosaurus*. Extant archosaurs with muscular tails of a comparative length with respect to their body drag them along the ground at low speeds (Willey et al., 2004), and during runs and gallops the tail still makes regular contact with the ground (Zug, 1974). As a result, extant kinematic data is unlikely to significantly aid understanding of tail function in dinosaurs with a more erect stance and horizontally held tails. Further experimentations within biomechanical simulations are therefore needed to understand how dinosaurian tail dimensions impacted upon their functional role during locomotion.

Another area that requires additional attention is the implementation of asymmetrical drivers into dinosaurian locomotor models. In extant quadrupeds, high speed gaits such as gallops are characterized by asymmetrical limb motion where the left and right-side limbs show more variable stance and swing phase durations and hence duty factors between successive steps (Robilliard et al., 2007). The type of drivers used in this study as well as previous quadrupedal dinosaur simulations in theory do not allow for the generation of asymmetrical gaits, though such gaits have still been observed in an *Edmontosaurus* model that used exclusively symmetrical drivers (Sellers et al., 2009). This previous finding suggests that galloping gaits could have been plausible for even very large-bodied dinosaurs and thus asymmetrical gaits in other ornithischians including *Scutellosaurus* warrant further investigation. By excluding asymmetrical drivers from this study, the fast quadrupedal gait repertoire as well as top speed of the model may have been reduced. If a faster asymmetrical quadrupedal gait was possible for *Scutellosaurus*, the interpretation of quadrupedal gaits being unsuitable for high-speed behaviors like predator escape may change.

In conclusion, the simulations of this study provide tentative evidence that suggests *Scutellosaurus* was able to make use of both slow and fast quadrupedal gaits and this feeds into the evolutionary narrative for secondary quadrupedal gaits. This implies that some form of quadrupedal locomotion within Thyreophora may have first evolved in some of its most basal members. Further investigation into the muscular anatomy and physiology of facultative quadrupeds as well as the role of exceptionally long tails in locomotion is required to fully understand how *Scutellosaurus'* anatomy supported its locomotor mode.

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ENDNOTE

[1] Institutional Abbreviations: MNA: Museum of Northern Arizona, AZ, USA; BRSMG: Bristol City Museum, Bristol, UK; NHMUK: Natural History Museum, London, UK; MFN, M.BR: Museum Für Naturkunde, Berlin, Germany, collection M.BR.

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