Scientific Research Publishing

Open Journal of Geology, 2026, 16(8), 503-543
https://www.scirp.org/journal/ojg
ISSN Online: 2161-7589
ISSN Print: 2161-7570

On Dinosaur Reconstruction: The Body

Georgios A. Florides, Paul Christodoulides

Faculty of Engineering and Technology, Cyprus University of Technology, Limassol, Cyprus
Email: paul.christodoulides@cut.ac.cy

How to cite this paper: Florides, G.A. and Christodoulides, P. (2026) On Dinosaur Reconstruction: The Body. *Open Journal of Geology*, **16**, 503-543.
https://doi.org/10.4236/ojg.2026.168026

Received: May 18, 2026
Accepted: August 28, 2026
Published: August 31, 2026

Abstract

This is the fourth in a series of articles presenting the theoretical background for reconstructing dinosaurs in all scientific details, focusing on the body of *Amargasaurus cazaui*. Following the Extant Phylogenetic Bracket method, the musculature of the neck, pectoral girdle, forelimbs, hindlimbs and tail are reconstructed using comparative anatomy of extant archosaurs, primarily Alligator mississippiensis and Crocodylus porosus. The posture of the skeleton is critically evaluated against competing gait hypotheses, and a walking stance with the right forelimb and left hindfoot bearing the weight is adopted. The elongated neural spines of the neck are reconstructed with a sail blending smoothly with the rest of the body. For a full-scale physical reconstruction, the bones are formed from welded steel wire rods assembled on a steel armature, with iron reinforced concrete columns and beams providing structural support. Muscles are built up using wire mesh and plaster guided by metal templates, and the skin is finished with rolling stamps producing polygonal scale rosettes. The completed model is a scientifically informed, full-scale representation of *Amargasaurus*, ready for exhibition. This work aims to promote understanding of past life on earth and to motivate interaction with the art of paleontology.

Keywords

Dinosaur Reconstruction, *Amargasaurus cazaui*, Sauropoda, Musculoskeletal Reconstruction, Sauropod Posture, Locomotor Gaits, Full-Scale Model

1. Introduction

This is the fourth in a series of articles that presents the theoretical background on important Paleontological knowledge that will enable one to reconstruct Dinosaurs in all scientific details. The first article introduced important topics of Paleontology and Dinosaurs [1], the second examined the posture of dinosaurs [2], and the third focused on the reconstruction of the head [3]. As in the previous

articles, the series demonstrates in detail the reconstruction steps of a specific Dinosaur, in full scale, that of *Amargasaurus cazaui* [4]. The articles are written in a way that is comprehensible not only by specialists but also by the broader reader. Hence, the series can motivate people to interact with the Art of Paleontology and promote understanding of past life on earth.

While the previous papers dealt with skeletal posture and cranial reconstruction, the present article focuses on the body itself—specifically, the musculature of the neck, pectoral girdle, forelimbs, hindlimbs and tail, as well as the soft tissues that give a dinosaur a living appearance. The first and basic decision for any reconstruction is the posture of the animal, which was also examined in the previous paper [2]. Once the posture is decided, the next step is to reconstruct the soft tissues that surround the bones. Unlike skeletal elements, which are often preserved as fossils, muscles, tendons, skin, and keratinous structures rarely fossilize. Therefore, their reconstruction must be inferred through comparative anatomy with living relatives.

The evolutionary branch of archosaurs gave rise not only to dinosaurs but also to crocodilia (including caimans, alligators, and crocodiles) and to birds. Therefore, dinosaur myology can be studied and compared in relation to its extant relatives [5]. This approach, known as the Extant Phylogenetic Bracket (EPB), provides a rigorous methodology for reconstructing soft tissues in extinct taxa by using the anatomy of living archosaurs as analogs. Following this method, the present paper reconstructs the musculature of *Amargasaurus* by comparing the osteological evidence from the fossil remains with the myology of *Alligator mississippiensis* and various avian species.

The neck of *Amargasaurus* presents a particular challenge for reconstruction because of its unique morphology. Unlike other sauropods, *Amargasaurus* possessed two parallel rows of elongated neural spines projecting from the cervical vertebrae, reaching 60 cm in length on the middle of the neck [6]. These spines, which are subcircular in cross-section and taper towards a pointed tip, have been the subject of considerable debate regarding their function and soft tissue covering. Bailey [7] examined elongated neural spines of dinosaurs and compared them to those on the backs of buffalos, concluding that a single pad of 6 - 8 cm width was more plausible than twin crests, given the narrow 3 - 7 cm separation of the cervical spine pairs. Schwarz *et al.* [8] reconstructed the soft tissues of the neck in diplodocid and dicraeosaurid sauropods, presenting a transverse cross-section through the cervical vertebra of *Amargasaurus cazaui* and suggesting a keratinized horn sheath covering the dorsal two thirds of the cervical neural spines. More recently, Cerda *et al.* [9] performed osteohistological analysis of the hyperelongate hemispinous processes and found no evidence of high-magnitude stresses required for physical combat, supporting an inter-spinous pad or display structure. Militello *et al.* [10] reconstructed the craniocervical muscular insertions of *Amargasaurus* and suggested that the neural spines limited dorsiflexion while allowing the snout to reach the ground, consistent with a me-

dium-to-low browsing strategy.

The pectoral girdle and forelimb musculature of sauropods has been studied extensively through comparative anatomy. Wilhite [11] reconstructed the appendicular musculature of three North American Jurassic sauropods, namely *Apatosaurus*, *Diplodocus* and *Camarasaurus*, examining the functional morphology of both forelimbs and hindlimbs. Klinkhamer *et al*. [12] performed a comparative three-dimensional (3D) moment arm analysis of the forelimb in three neosauropods, quantitatively assessing the leverage of forelimb muscles in the transition from narrow to wide-gauge stances. For the forelimb musculature of archosaurs in general, Otero *et al*. [13] examined the forelimb muscle and joint actions in *Crocodylus johnstoni*, reconstructing 3D paths of 30 muscles around the shoulder, elbow and wrist joints. Klinkhamer *et al*. [14] provided interactive 3D models of the limb musculature of a dissected Australian estuarine crocodile (*Crocodylus porosus*), showing in great detail the musculature of both forelimbs and hindlimbs. These works serve as the primary analogs for the present reconstruction.

Concerning the hindlimb and tail musculature, Ibiricu *et al*. [15] note that to reconstruct the hind legs and tail musculature of sauropods it is necessary to refer to the group of crocodilians rather than birds, because birds show skeletal modification and fusion of the caudal vertebrae. Mallison *et al*. [16] showed tail dissections along the length of the tail of *Alligator mississippiensis*, demonstrating that extant crocodilian tails can be used as models for dinosaur tails since anatomically they are the closest approximation. Díez Díaz *et al*. [17] presented a detailed 3D volumetric reconstruction of the tail musculature of the Late Jurassic sauropod *Giraffatitan brancai*, digitally reconstructing the tail by applying photogrammetric 3D digitization and 3D modeling tools in combination with information provided by dissections of extant crocodilians.

The posture and gait of sauropods during walking have also received considerable attention, with implications for how the limbs should be articulated in a reconstruction. Bishop *et al*. [18] used predictive simulations of running gait to reveal a critical dynamic role for the tail in bipedal dinosaur locomotion. Lallensack and Falkingham [19] developed a new method to calculate limb phase from trackways, demonstrating that giant wide-gauged sauropods used diagonal couplet walks in lateral sequence, with the forefoot touching down just before the hindfoot on the opposite side. Sellers *et al*. [20] applied muscle properties derived from living animals to a musculoskeletal model of *Argentinosaurus huinculensis*, generating a gait control pattern that minimized metabolic cost. For the forelimb specifically, Christian *et al*. [21] studied the posture and mechanics of the forelimbs of *Brachiosaurus brancai* with biomechanical models, concluding that reasonable reconstructions are with the long limb bones perfectly in line or with the elbow joints flexed slightly.

Bearing in mind the above general knowledge, one can then proceed with specific details and decisions concerning the reconstruction of *Amargasaurus*. The

present article is structured as follows. Section 2 presents the posture of the skeleton, including a critical evaluation of competing gait hypotheses and the final foot arrangement chosen for the reconstruction. Section 3 examines the neck and scapulocoracoid musculature, incorporating recent histological and myological findings, and discusses the possible reconstructions of the elongated neural spines. Section 4 addresses the pectoral girdle and forelimb musculature, while Section 5 covers the hindlimb and tail musculature. For each anatomical region, the reconstruction follows a consistent protocol: osteological data from the holotype specimen provide the skeletal framework [4]; muscle attachment sites and volumes are inferred using the EPB approach, with primary reference to dissections of *Alligator mississippiensis* and *Crocodylus porosus*; and, biomechanical plausibility is assessed against trackway evidence and locomotor simulations [18]-[20]. The resulting reconstruction is presented through a set of figures and a description of the actual full-scale built in steel and concrete.

2. Materials and Methods

The reconstruction of the body of a dinosaur follows a similar methodological framework to that previously established for the head [3], but with a greater emphasis on the musculoskeletal system and locomotor biomechanics. The procedure begins with a decision on the overall posture of the animal, as this determines the relative positioning of the neck, trunk, limbs, and tail. Once the posture is fixed, the reconstruction proceeds region by region: first the neck and its associated musculature, then the pectoral girdle and forelimbs, followed by the hindlimbs and tail. For each region, osteological evidence from the fossil remains provides the skeletal framework, while soft tissues are inferred using the EPB method. This approach relies on the fact that dinosaurs share a common archosaurian ancestry with modern crocodilians and birds, whose anatomy can therefore serve as a reference for reconstructing muscles, tendons, and other soft structures in extinct taxa.

For the physical reconstruction of a full-scale dinosaur body, the same basic materials and techniques used for the head are extended to the entire skeleton. The bones are first constructed individually from welded steel wire rods and placed in their relevant position; they are assembled on a steel armature that holds the skeleton in the chosen walking posture. A steel and concrete basic support is constructed beneath the armature to provide a stable foundation capable of bearing the total weight of the reconstruction, which for a medium-sized sauropod like *Amargasaurus* can exceed several hundred kilograms. The basic support starts from the feet and extends inside the dinosaur body to bear the weight of the neck, body and tail. Once the skeletal framework is securely positioned, each muscle area is then coated with a fine wire mesh that serves as a base for the subsequent layering of plaster and the detailed musculature. The muscles are built up by applying additional plaster over the mesh-covered bones, carefully shaping each muscle group according to the attachment sites

identified on the osteological remains. The volume and external contours of the muscles are guided by comparisons with dissected crocodilians and birds, ensuring that the reconstructed anatomy is both visually realistic and biomechanically plausible.

The reconstruction of soft tissues extends beyond the muscles to include skin and, where present, keratinous structures. In sauropods, skin impressions preserved in the fossil record show that the body was covered with small, non-overlapping polygonal scales, typically arranged in rosette patterns. For the present reconstruction, these scale patterns are applied over the entire body surface using cylindrical stamps, either hand-sculpted from modeling clay or designed digitally and produced by 3D printing [3]. In the case of *Amargasaurus*, particular attention is given to the elongated neural spines of the neck. Several alternative reconstructions are considered for these structures, ranging from a double skin sail to a single keratinous pad or paired horn sheaths. The final choice is based on osteohistological evidence regarding the mechanical stresses experienced by the spines, as well as on comparisons with analogous structures in living and extinct vertebrates.

Throughout the reconstruction process, biomechanical plausibility is continuously assessed against available evidence from trackways, gait simulations, and functional models of the limbs. The final posture and limb articulation are selected to be consistent with the animal's estimated body mass, center of mass position, and likely locomotor behavior. The completed reconstruction is then painted with weather-resistant colors, with scale patterns highlighted to enhance the 3D appearance. The resulting model is a full-scale, scientifically informed representation of the dinosaur's body, ready for exhibition or further study.

3. Posture of the Skeleton

Every dinosaur reconstruction starts with a decision on the posture of the dinosaur in which the artist selects to show the animal. Details on the posture of dinosaurs are given in a previous authors' paper [2]. As in all previous papers on Dinosaur Reconstruction [2], [3], also here, *Amargasaurus* is chosen as an example to demonstrate the reconstruction procedure.

Additional information on acceptable movement of individual parts of a dinosaur skeleton will give the reconstruction a realistic posture. In recent years much work has been done to analyze the locomotion of animals and gain more insight into the relation of general shapes, bones and muscles and how these affect the animal's movements. Wampler *et al.* [22] analyzed a set of animal gaits to predict the gait of a new animal from its shape alone. Their method, which combines inverse optimization with sparse data interpolation, is applied on a wide range of bipeds and quadrupeds and adapts the motion style to the size and shape of the animal.

Permissible movement of forelimbs of nonavian theropod dinosaurs (Coelophy-

sis, cf. Coelurus, Allosaurus, Deinonychus, and Tyrannosaurus) in predation are shown in Carpenter [23]. With the use of realistic modeling that employs specimens and casts, coupled with CAT-scans and dissections of extant vertebrate forelimbs, it was shown that forelimb motion in theropods is considerably less than hypothetical models indicate.

Bishop and collaborators [18] [24] used computational biomechanics to mechanistically relate anatomy to whole-animal function and behavior for bipedal locomotion. Applying their method to Coelophysis, a theropod dinosaur, they generated 3D, muscle-driven simulations predicting the locomotion of the animal. They also observed the pronounced role of the tail movements during locomotion. The approach used applies quantitative techniques and physics-based principles that help maximize results, robustness and reproducibility.

Gait Animation and Analysis for Biomechanically Articulated Skeletons was studied by Wills [25]. Methods that allow limbs with any number of biomechanical degrees of freedom to be kinematically examined and mapped into a visualization space were presented.

Gaits generated for *Apatosaurus*, Triceratops, and Tyrannosaurus dinosaur models were then compared to those generated for dogs and reptiles.

Turning now to quadrupedal sauropods, permissible movement of sauropod forelimb was analyzed in detail by Klinkhamer *et al.* [12]. Reconstruction of the Orientation of the Pectoral Girdle in Sauropods and possible movement was studied by Schwarz *et al.* [26], where the inclination of the scapula to the horizontal plane was reconstructed for *Diplodocus* (60˚ - 65˚), *Camarasaurus* (60˚ - 65˚), and *Opisthocoelicaudia* (55˚ - 65˚). The orientation of the scapulocoracoid in sauropod dinosaurs proposed in the present paper is based on comparative anatomical investigations of pectoral girdles of extant amniotes.

Details of the evolution of the pectoral girdle and forelimb in sauropodomorpha (Dinosauria, Saurischia) relating to osteology myology and their function was presented by Remes [27]. The biomechanics of the shoulder girdle of Caiman crocodylus were investigated with regard to providing a basis for understanding locomotion in sauropod dinosaurs by Hohn *et al.* [28], who presented a plausible reconstruction of the shoulder girdle of the sauropod *Diplodocus* longus. The appendicular skeleton of three north American Jurassic sauropods was also biomechanically reconstructed by Wilhite [11]. The study included the digitizing of the large fossil skeletal elements of *Apatosaurus*, *Diplodocus*, and *Camarasaurus* for 3D applications and examination of the appendicular musculature of the American alligator, alligator mississippiensis. The functional morphology of the forelimb and hindlimb of the three north American Jurassic sauropods was then examined.

Sellers *et al.* [20] showed how *Argentinosaurus huinculensis*, 40 meters long and weighing 83 tonnes, may have moved. The study assigned muscle properties derived from living animals to a musculoskeletal model that was generated with 3D data of a laser scanned mounted skeleton. The locomotion considered

the accelerations produced by the muscle forces, coupled with machine learning techniques, and a control pattern was derived that minimizes metabolic cost.

Lallensack and Falkingham [19] presented a method to calculate limb phase from trackways of sauropod dinosaurs. They suggested that variation in trackways can be used to recover the timings of fore and hind footfalls. Their results showed that giant sauropod dinosaurs used diagonal couplet walks in lateral sequence and that high limb phases allowed for maintaining diagonal supports in wide-bodied trackmakers.

Wampler *et al.* [22], analyzed a set of animal gaits to predict the gait of a new animal from its shape alone. They introduced a new algorithm, the joint inverse optimization, which learns coherent patterns in motion style from a database of different animal-gait pairs. Then, they applied their method to predict the gaits of dinosaurs and other extinct creatures.

Christian *et al.* [21] studied the posture and mechanics of the forelimbs of *Brachiosaurus brancai* with the help of biomechanical models. They concluded that reasonable reconstructions are with the long limb bones perfectly in line or with the elbow joints flexed slightly. During fast walking, either the forelimbs were flexed at the elbows during the middle of the support phase, or the apparently rigid shoulder girdle allowed movements of the shoulder joints relative to the trunk.

Stevens and Wills [29] [30] kinematically presented their work on the role of the pectoral girdles and trunk in the walk of *Apatosaurus* (among others). They adopted a specific search algorithm to examine a very large "configuration space" of possible limb poses to find a step cycle that could achieve a smooth path with minimized lateral, vertical, and angular deviations of the anterior dorsals. Each limb had 8 functional degrees of freedom at the scapula (rotation and elevation), shoulder (flexion/extension, abduction/adduction, and humeral rotation), elbow (flexion/extension), antebrachium (pronation/supination), and wrist (flexion/extension). Their reconstruction of Triceratops and *Apatosaurus* walk was presented in the "Dinosaurs in their Time" exhibit of the Carnegie Museum of Natural History.

3.1. *Amargasaurus* Posture

In [2], Figure 32(a), a general walking posture for *Amargasaurus* was chosen that allows the observer to appreciate its full length. The walking posture, with any needed alterations, is produced with the various actual size bones constructed with steel wire rods and bars. The shapes and sizes of every bone, as found in the digging, are described in [4] and the mounted skeleton is shown in [2], Figure 28.

Here, it has been decided to reconstruct *Amargasaurus* with all four feet touching the ground while walking, for having a stable and robust reconstruction. A walking position could possibly be similar to that of a walking elephant, demonstrated in **Figure 1**.

Figure 1. Walking elephant, with the right forelimb and the left hindfoot bearing the weight of the animal, the left forelimb is extented to the front and just touching the ground, while the right hindfoot is extended backwards and preparing to lift off the ground (Berlin zoo).

The elephant walking style can be adopted and schematically presented for *Amargasaurus*, as shown in Figure 2.

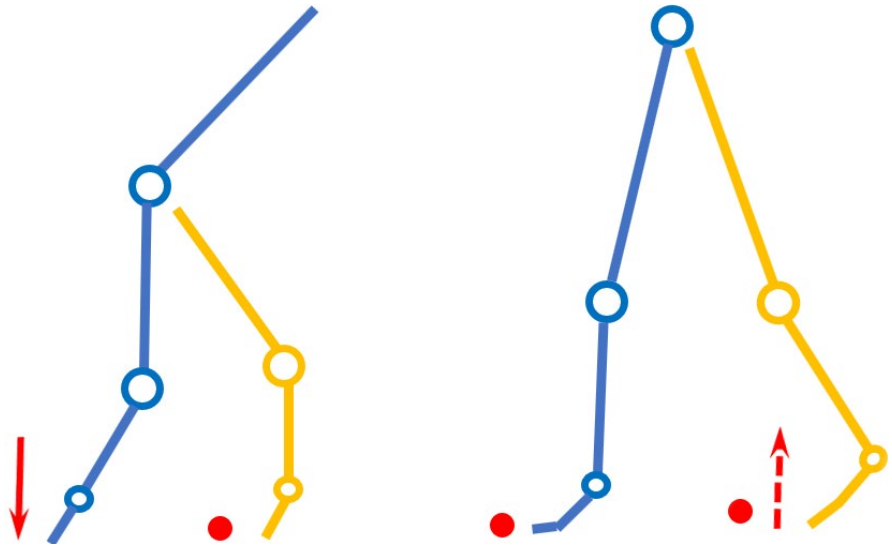


Figure 2. Elephant walking style, with the right forelimb and the left hindfoot bearing the weight of the animal, the left forelimb is extented to the front and just touching the ground, while the right hindfoot is extended backwards and preparing to lift off the ground. In blue the left forelimb and left hindfoot; in orange the right forelimb and right hindfoot; red circle, feet bearing animal weight; solid arrow indicating movement in progress; dashed arrow indicating movement to follow.

A similar style to the elephant walking is the reconstruction of the mounted skeleton of *Dicraeosaurus* presently on display in the Museum für Naturkunde,

Berlin (Figure 3).

Figure 3. *Dicraeosaurus* skeleton in an elephant walking style, presented in the Museum für Naturkunde, Berlin.

Relevant literature and available videos [13] [14] [17] [18] [20] can also be consulted for greater insight. Sellers *et al.* [20] in their study and simulation video for *Argentinosaurus* showed a produced gait that was typically diagonal, with lateral couplets: foot fall sequence left hindfoot, right forefoot, right hindfoot, left forefoot; and the ipsilateral forefoot and hind foot on the ground for a greater proportion of the gait cycle than the contralateral forefoot and hind foot. A better understanding of this way of walking can result from the video accompanying the study. Presenting this way of walking for *Amargasaurus* results in Figure 4.

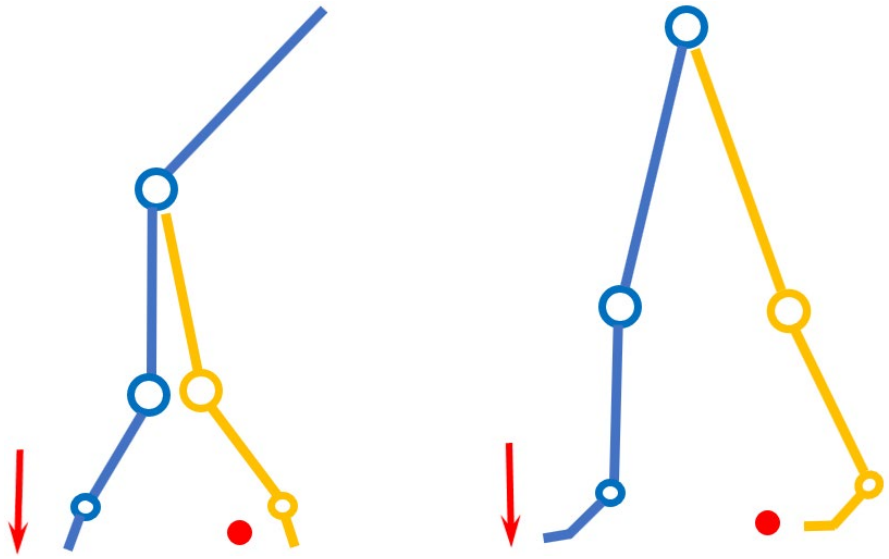


Figure 4. Walking style as suggested by Sellers *et al.* [20], applied for *Amargasaurus*. The right forelimb and the right hindfoot bearing the weight of the animal, and the left forelimb is extended to the front touching the ground nearly at the same time as the left hindfoot. In blue the left forelimb and left hindfoot; in orange the right forelimb and right hindfoot; red circle, feet bearing animal weight; solid arrow indicating movement in progress.

Stevens and Wills [29] [30], in their study and simulation videos, show *Apatosaurus* walking in a dissimilar way to an elephant. The forelimbs are in the same position as the elephant in Figure 1 and Figure 2, but this brings the rear limbs to opposite positions, *i.e.*, the left hind limb is extended backward, and the right is under the belly. This way of walking applied for *Amargasaurus* is shown in Figure 5.

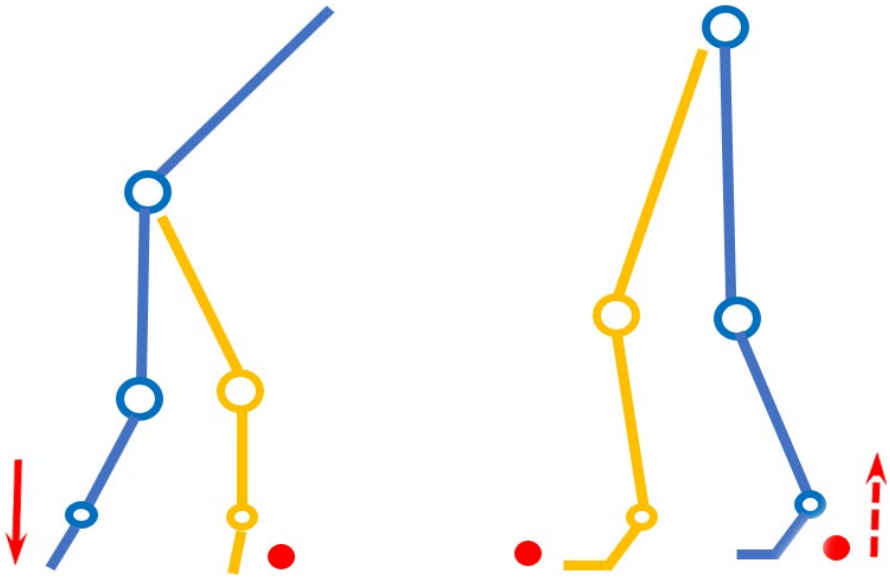


Figure 5. Walking style, as suggested by Stevens and Wills [29] [30], applied for *Amargasaurus*. The right forelimb and the left hindfoot bearing the weight of the animal, the left forelimb is extended to the front and just touching the ground, while the right hindfoot is extended backward and preparing to lift off the ground. In blue the left forelimb and left hindfoot; in orange the right forelimb and right hindfoot; red circle, feet bearing animal weight; solid arrow indicating movement in progress; dashed arrow indicating movement to follow.

A *Malawisaurus* skeleton mounted in a walking position as suggested by Stevens and Wills [29] [30] was exhibited in 2016 at the Victoria Memorial Museum of Ottawa (Figure 6).

Figure 6. *Malawisaurus* skeleton mounted in a walking position, as suggested by Stevens and Wills [29] [30]. Exhibition at the Victoria Memorial Museum of Ottawa (2016).

Lallensack and Falkingham [19] (see also video and report [31]), in their study present a new method for estimating the limb phase that is based on variation patterns in long trackways. When examining limb phases of giant wide-gauged sauropod dinosaurs, they observed that their tracks did not match any of the modern animals they checked. Instead, they showed that the forefoot touches down just before the hindfoot on the opposite side. Such a gait shows that these sauropods were actually doing the opposite of the elephants. In their walk the sauropods would have stabilized by always having at least one foot on the ground on each side. The result of applying this way of walking for *Amargasaurus* is shown in **Figure 7**.

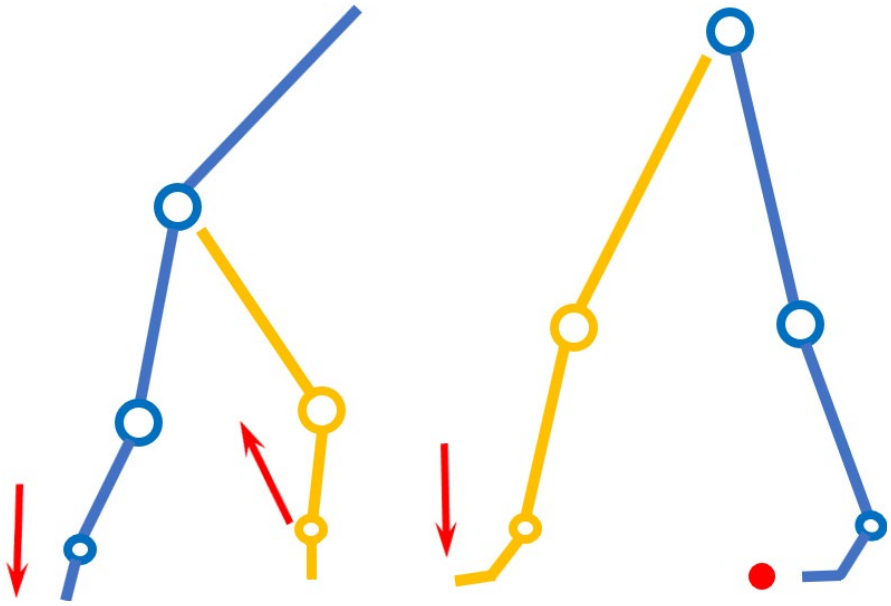


Figure 7. Walking style, as suggested by Lallensack and Falkingham [19], applied for *Amargasaurus*. The left forelimb has just touched the ground and the right hindfoot is about to touch the ground. The right forelimb is ready to lift off the ground moving to the front, while the right hindfoot is extended backward bearing the weight. In blue the left forelimb and left hindfoot; in orange the right forelimb and right hindfoot; red circle, foot bearing animal weight; solid arrows indicating movement in progress.

From the above observations, it is obvious that there is no agreement on the walking style. Considering that Stevens and Wills [29] [30] have matched *Apatosaurus* simulated style to actual footprints, and Lallensack and Falkingham [19] have presented evidence that sauropods were not walking in a similar way to elephants, a foot arrangement similar to **Figure 5** is followed here. Thus, the final foot arrangement for *Amargasaurus* is shown in **Figure 8**.

Another detail to consider is whether sauropods walked with the elbow joints straight or flexed. In a recent skeletal reconstruction of *Dicraeosaurus* in the Museum für Naturkunde, Berlin, the elbows were restored with the long limb bones in line or with the elbow joints flexed slightly, replacing the older restoration with an extended limb posture (**Figure 9**).

Relevant to the above is the study concerning the posture and mechanics of the forelimbs of *Brachiosaurus brancai* [21], which indicates that an extended limb

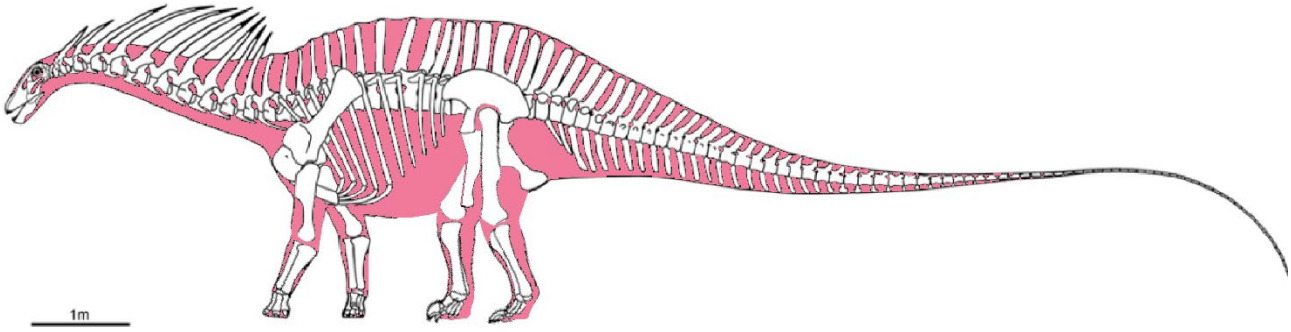


Figure 8. *Amargasaurus* shown in a walking posture. Foot arrangement will be followed in the reconstruction. Figure modified from [32].

posture (either with the long limb bones perfectly in line or with the elbow joints flexed slightly) was possible, but a semi-extended forelimb posture was not reasonable.

(a) (b)

Figure 9. Skeletal reconstruction of *Dicraeosaurus* in the Museum für Naturkunde, Berlin, (a) Old reconstruction with an extended limb posture and (b) Recent reconstruction with the long limb bones nearly in line.

Furthermore, to decide about the inclination of the limbs, it is necessary to examine whether *Amargasaurus* was a narrow gauge or a wide gauge animal. Narrow gauge trackways were left by sauropods with their limbs angling inwards in an elephant like fashion, while wide gauge trackways were imprinted by limbs that were held directly beneath the girdles. Farlow [33] mentions that it is uncertain that trackway patterns correlate with taxonomic differences. He suggests that the speed of walking or the consistency of the substrate could be responsible for the different trackway patterns that are found. Wilson and Carrano [34] suggest that body-size-related influences are not related to footprint gauges and that sauropods were probably restricted in locomotor behavior. They argue that skeletal morphology is responsible for gauge differences and suggest that titanosaurs were the wide gauge trackmakers. Finally, Henderson [35] studies the hypothesis that

the narrow- and wide-gauge trackways of sauropod dinosaurs is due to the relative positions of the sauropod centers of mass. He suggests that among sauropods, *Apatosaurus*, *Jobaria*, *Camarasaurus*, *Haplocanthosaurus*, *Brachiosaurus* and Titanosauria have body masses in excess of 12.5 tons and are predicted to have walked with a wide gauge. On the other hand, narrow-gauge gaits were the primitive state for not only sauropods, but also prosauropods and thus *Plateosaurus*, *Shunosaurus*, *Patagosaurus*, *Diplodocus* and *Dicraeosaurus* walked in a narrow-gauge gait. Having in mind the above *Amargasaurus* could be assumed to have walked in a narrow-gauge gait.

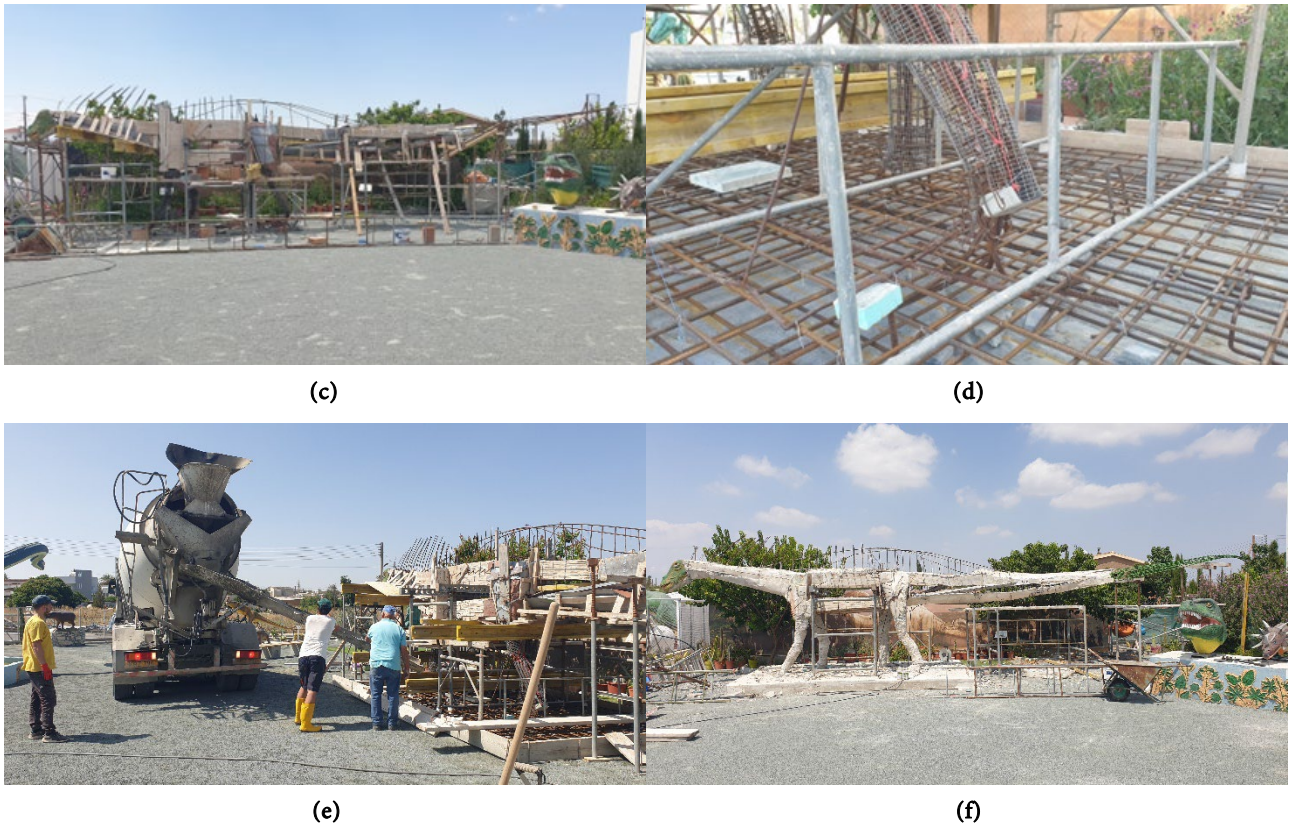
3.2. *Amargasaurus* First Reconstruction Steps: Structural Support for the Full-Scale Reconstruction

The chosen walking posture is implemented in full size using welded steel wire rods and bars that form each bone, assembled on a main steel armature that follows the exact pose of the skeleton (Figure 10(a)). To bear the weight of the final plaster musculature, the neck, body and tail, extra iron tube beams are placed at critical positions beneath the trunk and along the vertebral column (Figure 10(b)). More steel bars and straps as in building beams, are also added to withstand the stresses that will be present. Molds are then formed to create iron reinforced concrete columns and beams inside the body volume (Figure 10(c)). The base of the structure has to be also reinforced to stand the complete weight and balancing forces of the neck and tail that are far out of the base (Figure 10(d)). Once these are in place, concrete is poured, creating a stable foundation that starts from the feet and extends inside the dinosaur body to support the entire reconstruction (Figure 10(e)). When the concrete is cured there is a complete beam running from the head to the middle of the tail supported on four column-like feet standing on a base. There is also an intermediate beam connecting the four legs that will be hidden inside the lower part of the belly (Figure 10(f)).

3.3. Reconstruction Steps for All Individual Body Parts

All individual body parts thereafter follow the same procedure. First, the shape of each muscle is studied from the osteological evidence and comparative anatomy of extant archosaurs. Additional iron bars and wire mesh are then placed on the

(a) (b)



(c) (d)

(e) (f)

Figure 10. Structural support for the full-scale reconstruction. (a) Main steel armature with bones assembled in the chosen walking posture. (b) Extra iron tube beams added beneath the trunk and along the vertebral column. (c) Molds formed for iron reinforced concrete columns and beams inside the body volume. (d) Base reinforced to balance the neck and tail. (e) Concrete poured to create a stable foundation from feet to body. (f) Completed structure with a continuous beam from head to mid-tail supported on four column-like feet, plus an intermediate belly beam connecting the legs.

(a) (b)

Figure 11. Muscle contour construction. (a) Iron bars and wire mesh placed on the concrete skeleton, with plaster applied to form each muscle. (b) Metal templates used to guide the final shape, ensuring symmetry and accuracy.

existing concrete skeleton to form the exact contour of each muscle, and a concrete plaster is applied over this framework to achieve the final muscle shape (**Figure 11(a)**). To ensure symmetry and accuracy, metal templates shaped to the external muscle profile are employed to guide the final form (**Figure 11(b)**). The skin finish is produced using rolling stamps [3] that imprint the characteristic non-overlapping polygonal scales arranged in rosette patterns, as known from sauropod skin impressions. Finally, the complete structure is painted with weather-resistant colors appropriate for the exhibition environment.

4. The Neck and Scapulocoracoid Musculature

The evolutionary branch of archosaurs gave rise not only to dinosaurs, Sauropods and Theropods, but also to crocodilia (including caimans, alligators, and crocodiles) and to birds. Therefore, dinosaur myology can be studied and compared in relation to its extant relatives [5].

A detailed description of the anatomy of the neck in three species of vultures is presented in [36]. Excellent anatomical details of every neck muscle are presented together with clear photographs for each species. **Figure 12** and **Figure 13** show some of the presented muscles for one of the species, Gyps fulvus.

Boumans *et al.* [37] studied the muscular arrangement and muscle attachment sites in the cervical region of the American barn owl (*Tyto furcata pratincola*). They presented the complex structure of the S-shaped neck of the owl, in a semi-diagrammatic reconstruction as indicated in **Figure 14**, showing its fleshy and the tendinous or aponeurotic parts and their attachment sides on the relative vertebra.

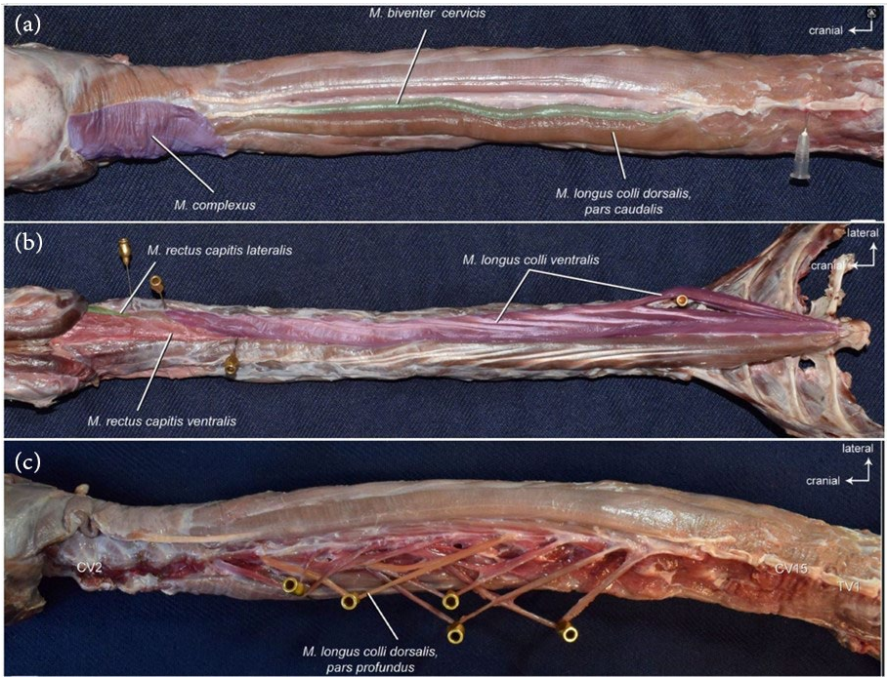


Figure 12. Gyps fulvus: (a) Dorsal view of the superficial muscles; (b) Ventral view of the muscle system; (c) Lateroventral view of dorsal, superficial muscles of the Craniocervical system [36].

Klingler [38], shows a dissection of Alligator mississippiensis of the cervical musculature (Figure 15) and the cervical and infrahyoid musculature (Figure 16).

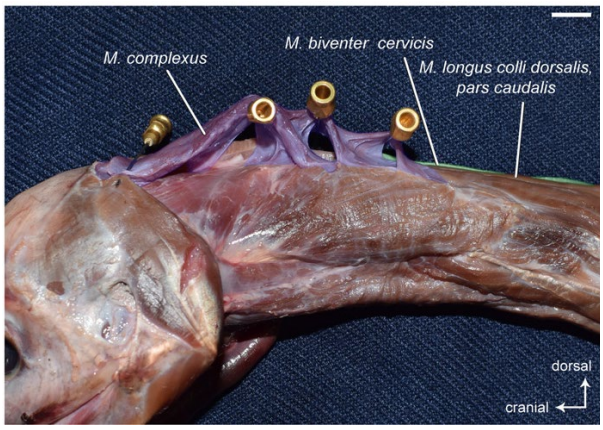


Figure 13. Dorsal system—deep muscles of Gyps fulvus [36].

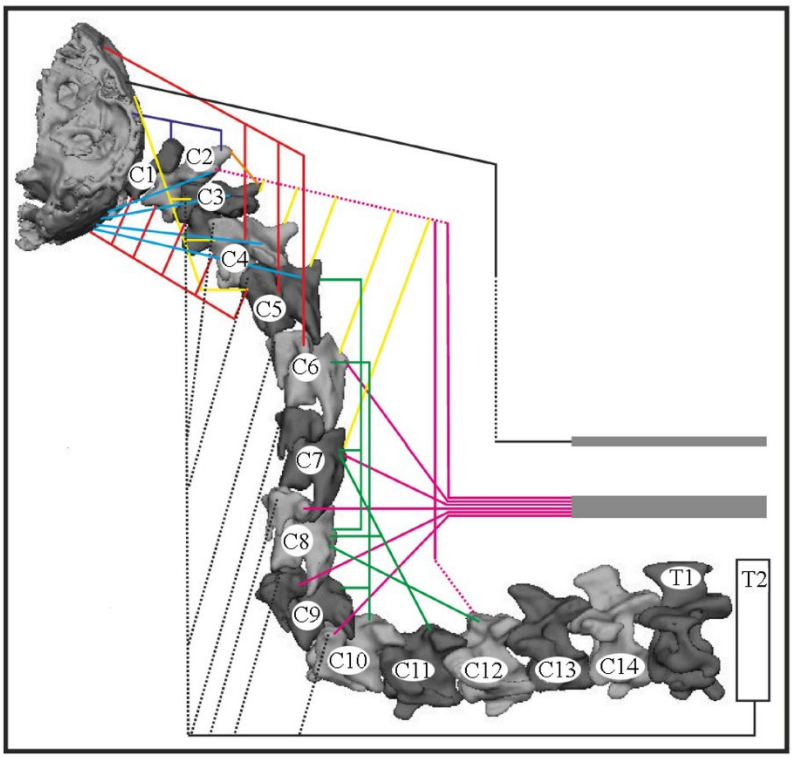


Figure 14. The reconstruction presents the back of the skull of the American barn owl, the 14 cervical vertebrae (C1 - C14) and the first two thoracic vertebra (T1 - T2). Fleshy parts are indicated with solid lines; broken lines represent tendinous or aponeurotic parts. The heavy lines above C14, T1 and T2 represent the aponeurosis notarii. Colours represent the individual muscles as listed below. Dorsally originating muscles: m. complexus (red), m. biventer cervicis (black), m. splenius capitis (purple), m. rectus capitis dorsalis (blue), m. longus colli dorsalis, pars caudalis (pink), m. longus colli dorsalis, pars cranialis (yellow), pars profunda (green), m. interspinalis (orange). Ventrally originating muscles: m. rectus capitis lateralis (yellow), m. rectus capitis ventralis (red), m. longus colli ventralis (black). Modified from [37].

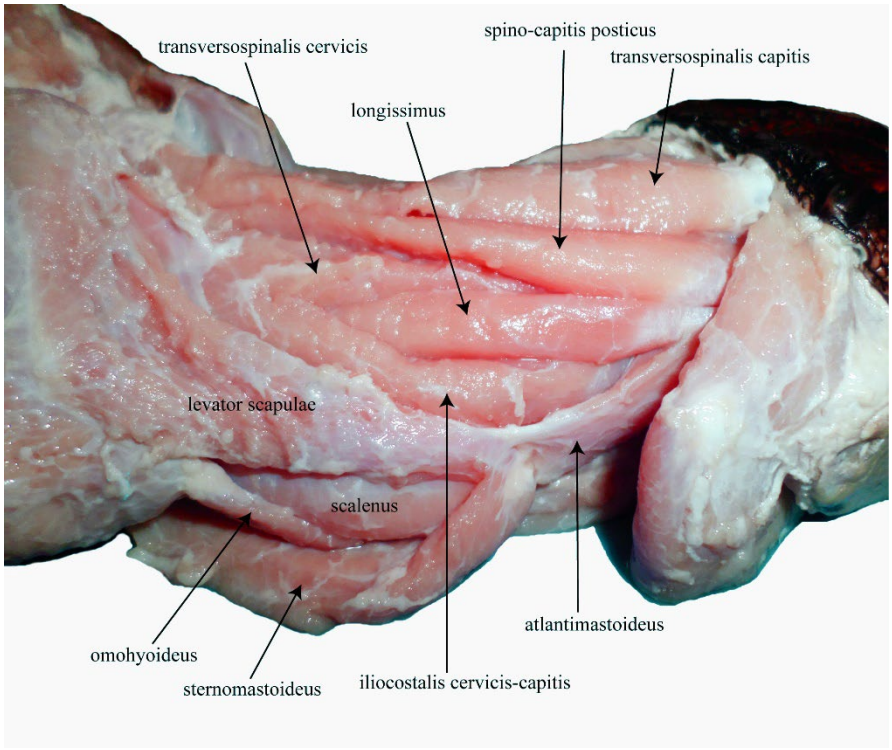
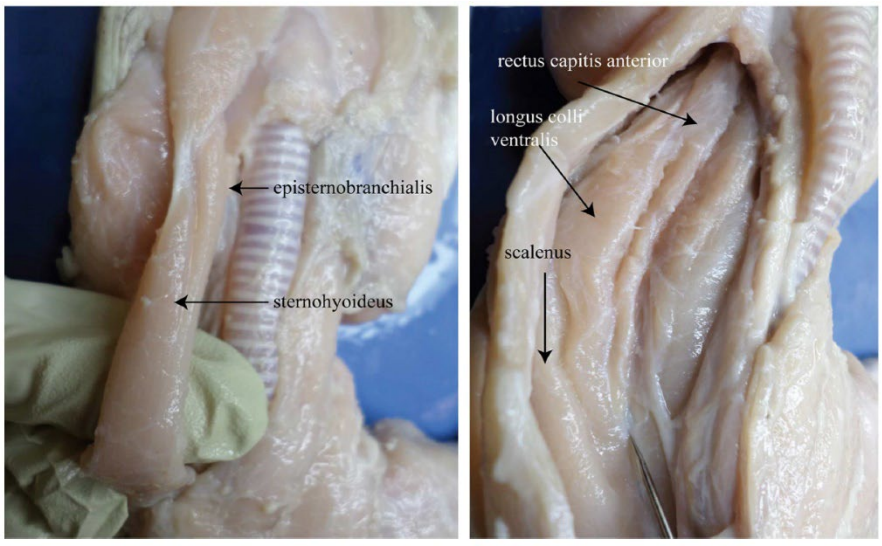


Figure 15. Lateral view of the cervical musculature of *Alligator mississippiensis*. M. sternomastoideus is reflected away ventrally to expose the m. omohyoideus and m. scalenus [38]. On the Morphological Description of Tracheal and Esophageal Displacement and Its Phylogenetic Distribution in Avia Jeremy J. Klingler-2016 plos one.



(a) (b)

Figure 16. A. mississippiensis cervical and infrahyoid musculature. (a) Ventral view of the m. episternobranchialis and m. sternohyoideus. (b) Ventral view of the ventralmost cervical muscles with the trachea, esophagus and infrahyoid muscles pushed aside [38].

One can also refer to the work of Tsuihiji [39], for studying musculature homologies in extant species. His study compared the neck muscle reconstruction in

three species, namely (a) Iguana iguana—Lepidosauria, (b) Alligator mississippiensis—Crocodylia, (c) Struthio camelus—Aves, and showed the homologies and specific details of every species.

The above presented information can give a good understanding of the complexity of the neck musculature and may be used for comparison and help to reconstruct the musculature in extinct species by analogies. This can be done only by experienced specialists and is not a straightforward job since every animal species has its own uniqueness.

Information for the neck musculature of large theropod dinosaurs can be found in Snively and Russell [40]. The study was carried out to determine the feeding style of theropods and for this reason, the neck musculature was reconstructed in every detail for each animal examined. A small part of their reconstructions is shown in **Figure 17**, where a lateral view reconstruction of the neck of Tyrannosaurus rex and Allosaurus fragilis is shown.

A similar study for allosaurids compared to sabre-tooth cats of Bakker [41], presents the reconstruction of neck, stern and scapula muscles.

Concerning the long necks of sauropods, Taylor and Wedel [42] assume that a realistic presentation of the cross section of the neck of *diplodocus* would show reduced soft tissue compared to that of the Ostrich neck but enlarged vertebra within. In this way, the mass is reduced by extensive pneumaticity in both the bone and the soft tissue (**Figure 18(a)**).

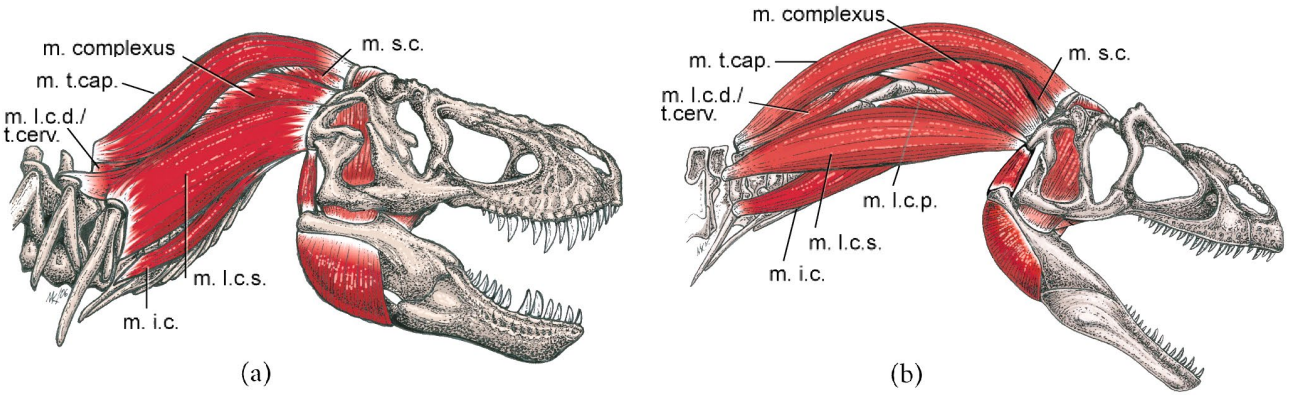
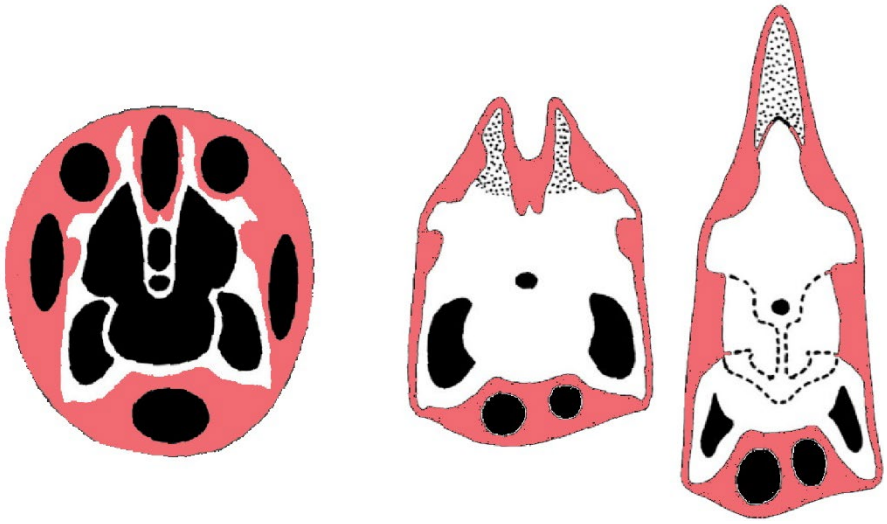


Figure 17. Lateral flesh reconstruction of the neck of (a) Tyrannosaurus rex and (b) Allosaurus fragilis (modified from [40]). Appreciations: m. t.cap., M. transversospinalis capitis; m. l.c.d./t.cerv, M. longus colli dorsalis/transversospinalis cervicis; m. i.c., M. iliocostalis capitis; m. l.c.s., M. longissimus capitis superficialis; m. l.c.p., M. longissimus capitis profundus.

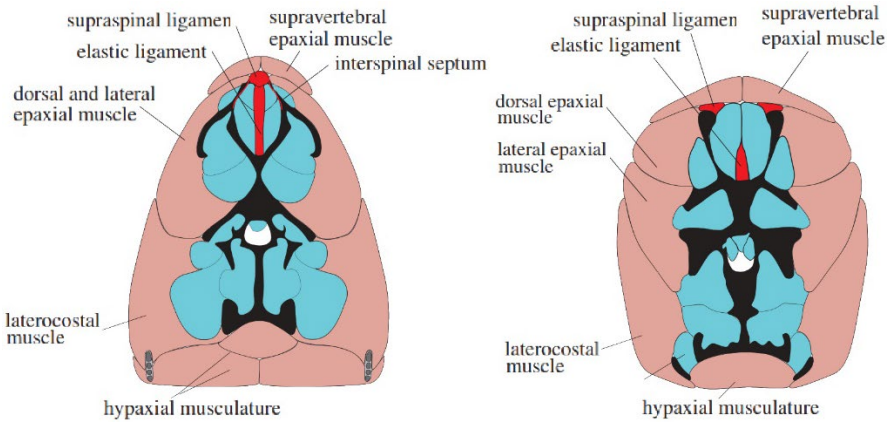
In his study describing the ligaments in sauropod, Paul [43] presents cross sections of *Diplodocus* and *Brachiosaurus* necks. Paul suggests that the cross-sectional shapes of sauropod necks were complex as shown in his restorations (**Figure 18(b)-(c)**) and not simple semi-circles as shown in most restorations. Additionally, in their study of the pneumatic diverticula systems in the sauropod necks and their role in the pneumatic stabilization of sauropod necks, Schwarz-Wings and Frey [44] present their soft-tissue reconstructions of the neck of sauropods as shown in **Figure 19**.

Also, Schwarz *et al.* [8] present a reconstruction of soft tissues, in lateral aspect, of the neck of *Diplodocus*, where the cervical ligaments and the cervical axial musculature are shown (**Figure 20**). It is noted that ligaments are fibrous elastic tissues that connect bones to other bones. More information about the complex connections of the cervical musculature of sauropods, based on the neck muscles of birds, can be found in Wedel and Sanders [45].



(a) (b) (c)

Figure 18. Sauropod necks in cross-section (a) according to [42]. A realistic presentation for *diplodocus* would show reduced soft-tissue compared to that of the Ostrich neck but enlarged vertebra within with extensive pneumaticity in both the bone and the soft-tissue. (b) and (c) according to [43] with (b) for *Diplodocus* and (c) for *Brachiosaurus*. Excavations that lightened the vertebra are shown in dotted lines, the restored gullet and trachea (smaller passage) are shown on the underside of each neck section. In sections (a) to (c) bone is shown in white, airspaces in black, and soft tissue in pink.



(a) (b)

Figure 19. Schematic cross-section of the cervical vertebra showing the muscles according to [26] (a) of *Brachiosaurus* (b) of *Apatosaurus*. Muscles are shown in pink, possible pneumatic diverticula in blue, dorsal neck ligaments in red and bone in black (for *Apatosaurus*, *Diplodocus*, *Dicraeosaurus* or *Camarasaurus*).

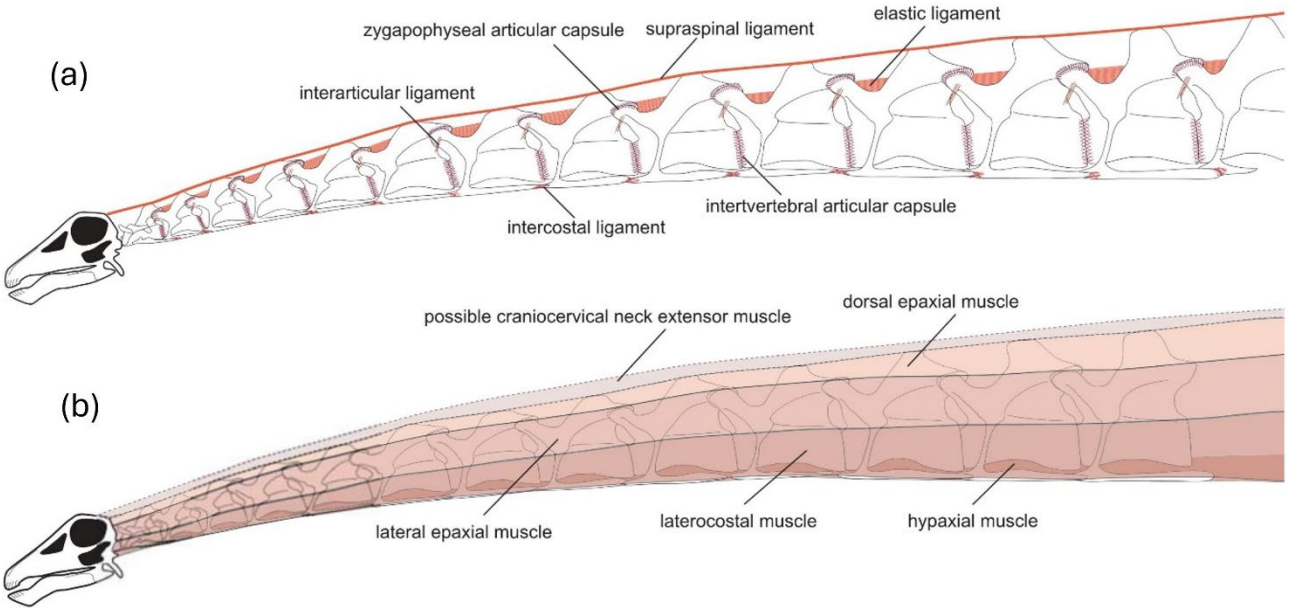


Figure 20. Reconstruction of soft tissues in the neck of *Diplodocus* [8]. (a) Reconstruction of cervical ligaments in left lateral aspect. (b) Reconstruction of cervical axial musculature in left lateral aspect. Not to scale.

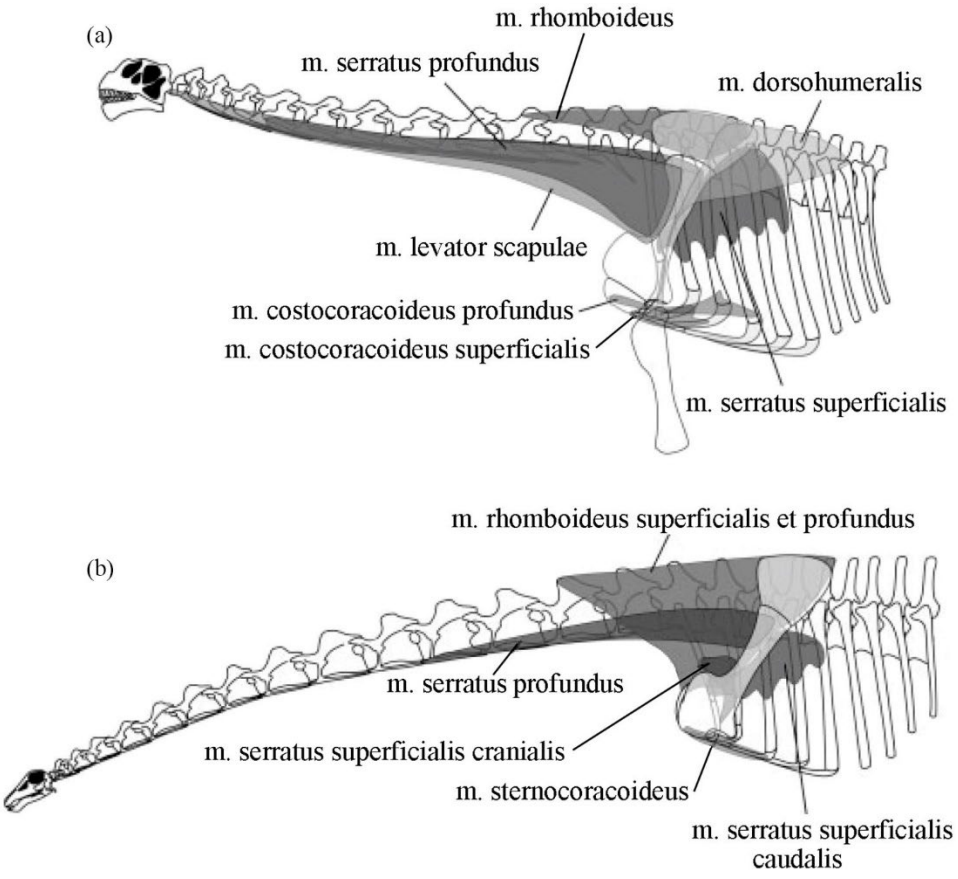


Figure 21. Reconstruction of the main muscles of scapulocoracoid and suspension of the trunk in sauropods. (a) Reconstruction of *Camarasaurus* main muscles, in left lateral view, with the crocodylian model of muscles around the scapulocoracoid. (b) Reconstruction of main muscles of scapulocoracoid in left lateral view of *Diplodocus* with the avian model [26].

The exact reconstruction of the myology of sauropods depends on the observations of their bones and the model to follow, either avian or crocodilian. As an example, Schwarz *et al.* [26] present the discussion concerning the correct angle of the scapula to the horizontal plane in sauropods that is difficult to conclude from taphonomy. Sauropod remains are usually found with displaced shoulder girdles because they are not firmly attached to the skeleton. The generally accepted position of the scapula to the horizontal plane is about 45˚ but their study resulted in an inclination of the scapula to the horizontal plane for *Diplodocus* and *Camarasaurus* at 60˚ - 65° and for *Opisthocoelicaudia* at 55˚ - 65˚. Additionally, they reconstructed *Camarasaurus* and *Diplodocus* in a crocodilian and an avian model, as shown in Figure 21, with obvious differences.

4.1. *Amargasaurus* Neck and Scapulocoracoid Musculature

Schwarz *et al.* [8] reconstructed the neck soft tissues of *Amargasaurus cazaui*, as shown in Figure 22.

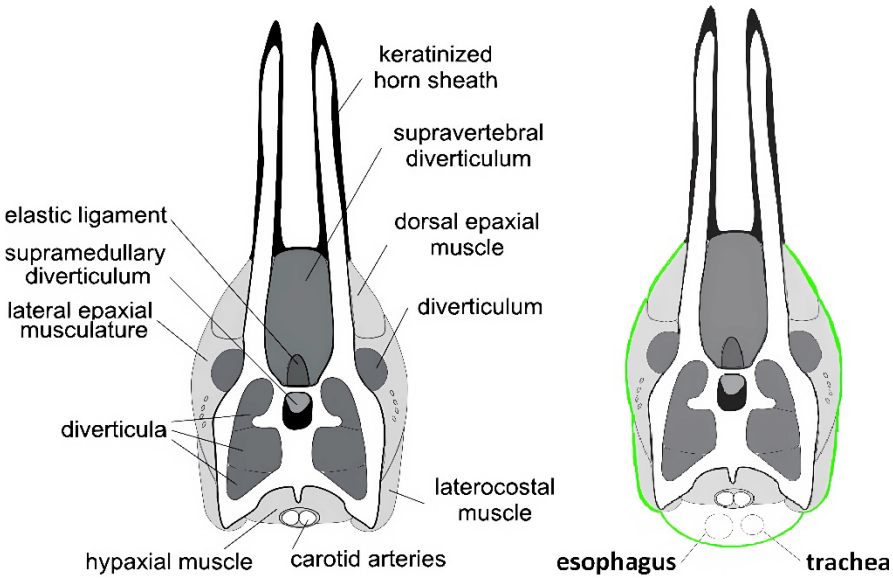


Figure 22. Transverse cross section through cervical vertebra in the diapophysis region of the neck of *Amargasaurus cazaui*. (a) Reconstruction of the soft tissue according to [8]. (b) In green color is presented the possible external shape of the neck, after the addition of the esophagus and trachea.

4.2. Elongated Neural Spines

Amargasaurus had elongated neural spines projecting from the back of its neck. Although the axis had only a single projection, from there on the neural spines branch into two long spikes to create a double row of bony projections from the back of the neck.

Each spike is subcircular in cross-section and tapered towards a pointed tip. The tallest spines are found on the middle part of the neck, where they reach 60

cm in length [6]. The bony spikes are bowed backward as if to repel an attack from behind (**Figure 23**). The tall, bony Spikes were originally thought to have been incorporated into twinned skin sails that ran along the length of the neck, used in sexual and social display, or in thermoregulation [46].

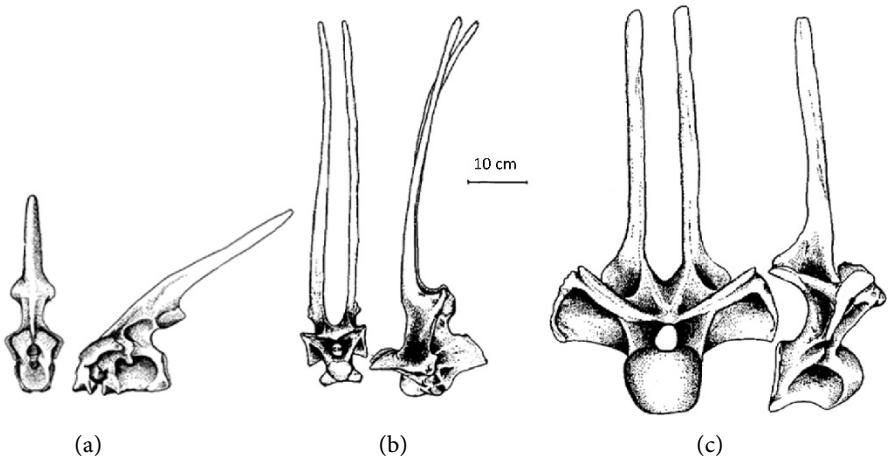


Figure 23. *Amargasaurus cazaui* elongated neural spines in anterior and lateral view. (a) Atlas and axis; (b) 6th cervical vertebra and (c) 1st dorsal vertebra. Scale bar 10 cm. Redrawn from [4].

Bailey [7] examined the elongated neural spines of dinosaurs and compared them to those on the backs of buffalos for determining their function. He concluded that in the case of *Amargasaurus*, it is probable that an elevated cervical crest above the epaxial ligaments and musculature could be present and this case was the only convincing case of a crested dinosaur in his study. He also suggests that a single pad 6 to 8 cm wide should have existed since the narrow separation of 3 - 7 cm of the cervical spine pairs could not account for a "twin crest". The function of such a pad although uncertain could be for display.

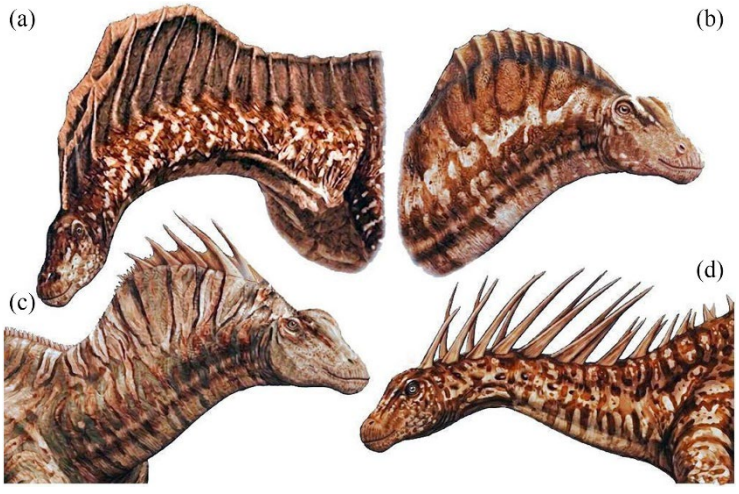


Figure 24. *Amargasaurus cazaui* in possible reconstructions: (a) a double sail, (b) a single pad 6 to 8 cm wide, (c) a narrow pad in the middle of the spines, ending in keratinized horns, (d) long keratinized horn sheath.

Schwarz *et al.* [26], on the other hand, suggest a keratinized horn sheath covering the dorsal two thirds of the cervical neural spines. In this case, the keratinized horns would form a sheath either for defense or display.

The above possibilities would allow for the following ways of reconstruction (Figure 24) of the neck: (a) a double sail, (b) a single pad 6 to 8 cm wide, (c) a narrow pad in the middle of the spines, ending in keratinized horns, (d) long keratinized horn sheath.

For the elongated neural spines, the reconstruction preferred here was with a double sail that internally is joined as a single pad resembling a buffalo back, rising from the neck and reaching full height after the eighth spine (Figure 25).

Figure 25. Reconstruction of the neck and sail of *Amargasaurus cazaui* showing the elongated neural spines covered by a double sail that internally is joined as a single pad resembling a buffalo back, rising from the anterior neck and reaching full height after the eighth cervical spine.

5. Pectoral Girdle and Forelimb Musculature

Jasinoski *et al.* [47] performed an investigation of dromaeosaur shoulder girdle musculature and forelimb function. Twenty-two shoulder girdle muscles were reconstructed, based on phylogenetic inference, which involved the comparison of lepidosaurian, crocodilian and avian musculature. The reconstruction with excellent sketches, provides the basis for subsequent investigation of differences in muscular attachment and function, based on scapulocoracoid morphology, across the theropod lineage leading to birds.

Burch [48] provided a complete reconstruction of dinosaurian forelimb musculature, including the antebrachial and intrinsic manual muscles. For the study data on the forelimb myology of an extensive sample of extant birds, crocodylians, lizards, and turtles, statistically analyzed using maximum likelihood ancestral state reconstruction, were considered. The obtained results, together with the osteology of the early theropod Tawa hallae from the Late Triassic, were used to formulate a complete plesiomorphic myology for the theropod forelimb. Com-

parisons with previous reconstructions showed that the shoulder musculature of basal theropods was closer to that of basal ornithischians and sauropodomorphs than to that of dromaeosaurids.

Reconstruction of the pectoral girdle and forelimb musculature of Megaraptora (Dinosauria: Theropoda) was presented by Aranciaga *et al.* [49]. Megaraptora is a group of carnivorous non-avian theropod dinosaurs from the Cretaceous of Asia, Australia, and especially South America. Their comprehensive reconstruction of the musculature is based on observations of the pectoral girdle and forelimb skeletons of Megaraptora and myological assessments of other archosaurian taxa.

Klinkhamer *et al.* [14] provide figures that show in detail the forelimb musculature of Crocodylus porosus (see **Figure 26**). Analogous musculature could be assumed present in dinosaurs and, therefore, reconstructions of the forelimb musculature are based on this animal.

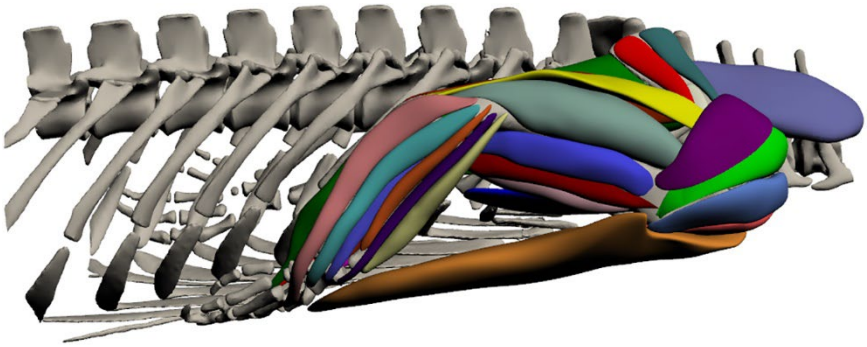


Figure 26. Three-dimensional model of forelimb musculature in Crocodylus porosus. Details can be found in [14].

As an example, Otero A. *et al.* [13] examined the forelimb muscle and joint actions in Archosauria by studying the musculature of Crocodylus johnstoni. They reconstructed the 3D paths of 30 muscles that are found around the shoulder, elbow and wrist joints and evaluated the forelimb joint mobility and muscle actions in respect to postural and anatomical alterations from basal archosaurs to early sauropodomorphs.

Wilhite [11] reconstructed the musculature of the pectoral girdle and forelimb muscles in three north American Jurassic sauropods, namely *Diplodocus*, *Apatosaurus* and *Camarasaurus*, from which **Figure 27** was extracted.

Klinkhamer et al [12] performed a comparative analysis on three neosauropods, namely the narrow-gauge diplodocid *Apatosaurus louisae*, the intermediate-gauge titanosariform *Giraffatitan brancai*, and the widegauge titanosaur *Diamantinasaurus matildae*. In their effort to quantitatively assess the leverage of forelimb muscles in the transition from the narrow-gauge stance of basal sauropods to a wide-gauge stance in titanosaurs, they used a 3D musculoskeletal modeling. For the modeling the muscle attachment sites on the forelimbs were identified and muscle paths were traced. Their work can be used in a reconstruction of a sauropod forelimb model (**Figure 28**).

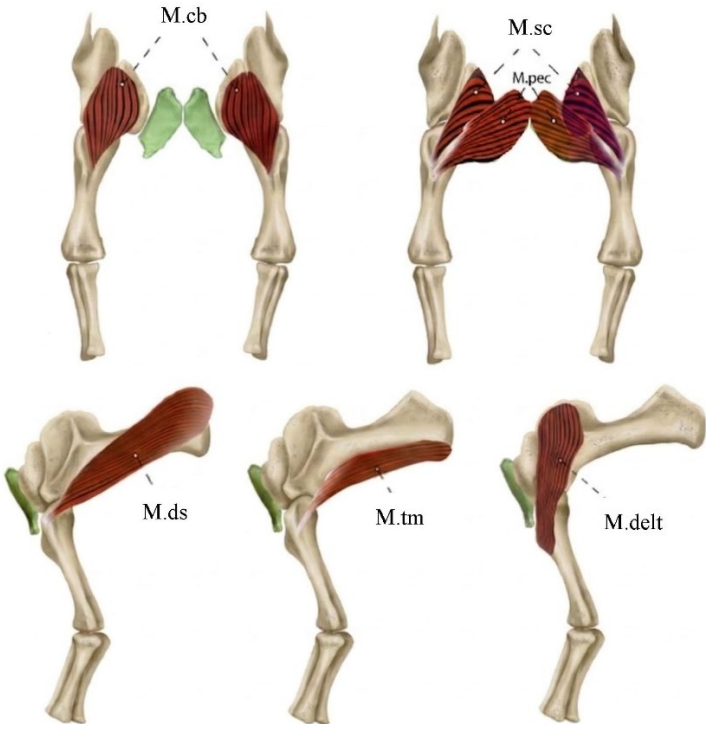


Figure 27. The musculature of the pectoral girdle of *Camarasaurus*, a north American Jurassic sauropod, suggested by Wilhite [11].

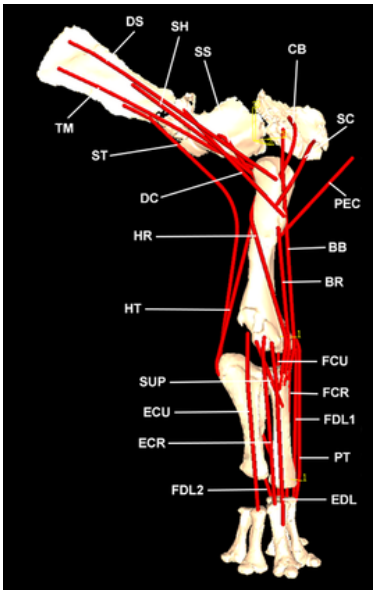


Figure 28. Map of identified muscle attachment sites and muscle paths on the right forelimb of *Diamantinasaurus matildae* in lateral view. Reconstructed muscles include: deltoideus scapularis (DS), teres major (TM), scapulohumeralis (SH), scapular triceps (ST), subscapularis (SS), deltoideus clavicularis (DC), coracobrachialis (CB), supracoracoideus (SC), pecoralis (PEC), humeroradialis (HR), biceps brachii (BB), brachialis (BR), humeral triceps (HT), flexor carpi ulnaris (FCU), supinator (SUP), extensor carpi ulnaris (ECU), extensor carpi radialis (ECR), flexor carpi radialis (FCR), flexor digitorum longus 1 (FDL1), flexor digitorum longus 2 (FDL2), pronator teres (PT), extensor digitorum longus (EDL) (Klinkhamer *et al.* [12]).

Following the guidelines above, the present reconstruction is shown in Figure 29.

6. The Main Body: Thorax and Abdomen

Between the pectoral girdle and the pelvic region lies the main body of the dinosaur, housing the vital organs and supporting the massive trunk. In sauropods like *Amargasaurus*, this region was very large, accommodating the massive digestive system necessary to process vast quantities of plant material. The accurate reconstruction of the main body requires careful consideration of the trunk musculature, the dorsal rib cage, the abdominal wall (including the gastral basket), and the resulting overall body contour.

(a) (b)

Figure 29. Musculature reconstruction of *Amargasaurus cazaui*. (a) Anterior view of the pectoral girdle musculature; (b) lateral view of the left forelimb showing the arrangement of major muscle groups.

6.1. Trunk Musculature

The muscles of the trunk in sauropods are divided into two main functional groups: the epaxial muscles (located dorsal to the transverse processes of the vertebrae) and the hypaxial muscles (ventral to the transverse processes). The reconstruction of these muscles relies heavily on the Extant Phylogenetic Bracket (EPB) method, mapping the osteological correlates of living archosaurs onto fossil bones.

Based on comprehensive muscle mapping in extant diapsids by Tsuihiji [39], the epaxial musculature, primarily the M. longissimus and M. iliocostalis, originated on the ilium and sacral ribs and inserted extensively along the dorsal vertebrae and ribs. In a sauropod like *Amargasaurus*, these muscles formed massive, longitudinal tracts that acted as a crucial tension system to support the heavy, bridge-like torso, resisting gravity and providing lateral stability during locomotion.

Conversely, the hypaxial muscles, including the M. rectus abdominis and the

external and internal obliques, formed the ventral body wall. As detailed by Carrier and Farme [50], these muscles were highly developed in archosaurs. Rather than being reduced, they formed a broad, robust muscular sling that was essential for supporting the immense weight of the abdominal viscera and actively assisting in costal ventilation.

6.2. The Dorsal Rib Cage and Respiratory Muscles

The dorsal ribs articulate with the vertebrae of the trunk region, forming the lateral and ventral walls of the thoracic cavity. In sauropods, these ribs are massive and curved, enclosing a voluminous body cavity. Because the parapophyses are located more anteriorly than the diapophyses on the dorsal vertebrae, the ribs articulate at an angle, sweeping backward as they descend [26].

The intercostal muscles, which fill the spaces between the ribs, were essential for both stabilizing the rib cage and driving respiration. In extant archosaurs, the external intercostals facilitate inspiration, while the internal intercostals assist in expiration [50]. Furthermore, the presence of postcranial skeletal pneumaticity, visible as pneumatic foramina or fossae in the dorsal vertebrae and ribs of many sauropods, indicates the presence of an avian-like air sac system [51]. This highly efficient respiratory system would have required well-developed intercostal and hypaxial trunk muscles to pump air through the rigid lungs and expansile air sacs.

The dorsal rib cage and respiratory muscles of sauropods are shown in **Figure 30**.

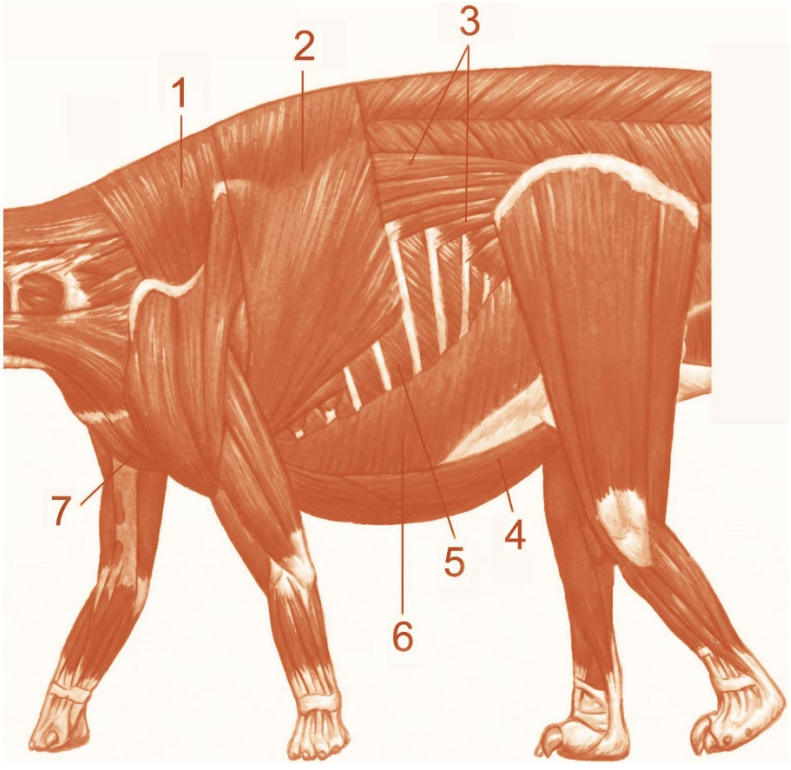


Figure 30. The dorsal rib cage and respiratory muscles of sauropods. 1, Trapezius; 2, Latissimus dorsi; 3, Iliocostalis serratus; 4, Rectus abdominis; 5, Intercostales; 6, Obliquus externis; 7, Pectoralis major (for more details see [52]).

6.3. Gastralia and Abdominal Musculature

Gastralia, or abdominal ribs, are dermal bones situated in the ventral body wall between the sternum and the pelvis. They do not articulate with the vertebral column but form a basket-like structure that stiffens the abdomen, supports the viscera, and provides vital attachment sites for the hypaxial musculature [53]. In modern crocodilians, gastralia anchor the M. rectus abdominis and oblique muscles, aiding in a specialized breathing mechanism known as cuirassal breathing.

The distribution of gastralia in sauropods has historically been difficult to trace due to their fragile nature and poor preservation. However, Tschopp and Mateus [54] definitively identified gastralia in diplodocids and Flagellicaudates, noting that while they may have been lost in later, wide-gauge titanosauriforms, they were present in non-neosauropod eusauropods. Because *Amargasaurus* is a dicraeosaurid belonging to Flagellicaudata, the presence of a gastral basket is highly probable. In the present reconstruction, the gastralia serve as the ventral anchor point for the heavy abdominal sling, though they would be entirely embedded within the hypaxial muscle and connective tissue, not visible externally.

6.4. Body Cavity Volume and Organ Reconstruction

The coelomic cavity in sauropods was immense. Franz *et al.* [55] applied allometric equations for organ masses from living amniotes to sauropod models, and they found that the estimated volume of the sauropod body cavity vastly exceeds the expected volume of their combined organs. This indicates that sauropod internal anatomy deviated conceptually from extant vertebrates: the extra space was likely filled by an expansive network of respiratory air sacs and a massive, specialized digestive tract.

To process low-nutrient vegetation, *Amargasaurus* likely relied on a massive fermentation chamber similar to hindgut fermenters like elephants. This biological reality necessitates reconstructing a highly capacious, deeply rounded abdomen. The M. rectus abdominis and the transverse abdominal muscles would have been incredibly thick to hold the tension of this outward and downward pressure (see **Figure 31**).

6.5. Soft Tissue and Body Contour

The external contour of the *Amargasaurus* main body is dictated by the underlying skeletal scaffold and the massive muscle groups described above. Because dinosaurs lacked mammalian subcutaneous fat layers, the skin and scales would have closely followed the underlying myology.

The epaxial muscles running along the dorsal vertebrae would have filled the space on either side of the neural spines, giving the back a smoothly rounded, robust contour rather than a starved, shrink-wrapped skeletal ridge. Ventrally, the massive hypaxial muscles and the internal pressure of the digestive tract would have created a deep, smooth, and rounded belly. The greatest width of the animal would be located in the anterior trunk, tapering slightly as it approaches the pelvis.

Figure 31. Reconstruction of the thorax and abdomen of *Amargasaurus cazaui*, showing the rounded dorsal contour and the deep, voluminous belly.

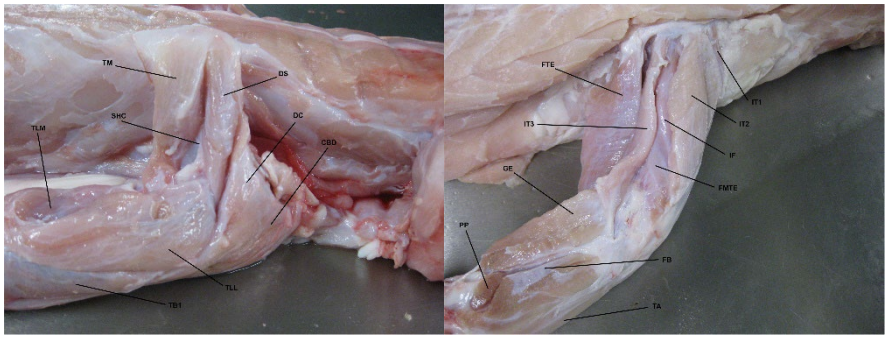
7. Hindlimb and Tail Musculature

According to Ibiricu *et al.* [15], to reconstruct the hind legs and tail musculature of sauropods it is necessary to refer to the group of crocodilians rather than birds because birds show skeletal modification and fusion of the caudal vertebrae. Furthermore, the hindlimb of extant birds includes a mix of ancestral dinosauromorph, theropod features and avian synapomorphies [12]. Therefore, it is necessary to study the musculature details of a crocodilian for the reconstructions of Dinosaurs.

Klinkhamer *et al.* [14] provide interactive 3D models of the limb musculature of a dissected Australian estuarine crocodile (Crocodylus porosus), where one can see in great detail the musculature (**Figure 32** and **Figure 33**).

Concerning the tail musculature, Mallison *et al.* [16] showed tail dissections along the length of the tail of Alligator mississippiensis (**Figure 34**). Extant crocodilian tails can be used as models for dinosaur tails since anatomically are the closest approximation of the tails of non-avian dinosaurs, and therefore a good starting point.

Having in mind the above Díez Díaz *et al.* [17] presented a detailed 3D volumetric reconstruction of the tail musculature of the Late Jurassic sauropod *Giraffatitan brancai*. They digitally reconstructed the tail of the sauropod by applying photogrammetric 3D digitization and 3D modeling tools in combination with information provided by dissections of extant crocodilians (Alligator mississippiensis) (**Figure 35** and **Figure 36**).



(a) (b)

Figure 32. (a) Fresh-tissue dissection with muscles identified around shoulder. Lateral view of right shoulder region of Crocodylus porosus (XCb Cp5). TM: Teres major, DS: Deltoideus scapularis, SHC: Scapulohumeralis caudalis, DC: Deltoideus clavicularis, CBD: Coracobrachialis brevis dorsalis, TLM: Triceps longus medialis, TLL: Triceps longus lateralis, TB1: Triceps brevis 1. (b) Fresh-tissue dissection with some hindlimb muscles identified. Dorsolateral view of right hindlimb of Crocodylus porosus (XCb Cp5). FTE: flexor tibialis externus, IT1-3: Iliotibialis 1 ± 3, IF: Iliofemoralis, FMTE: Femorotibialis externus, GE: Gastrocnemius externus, PP: Pronator profundus, FB: Fibularis brevis, TA: Tibialis anterior [14].

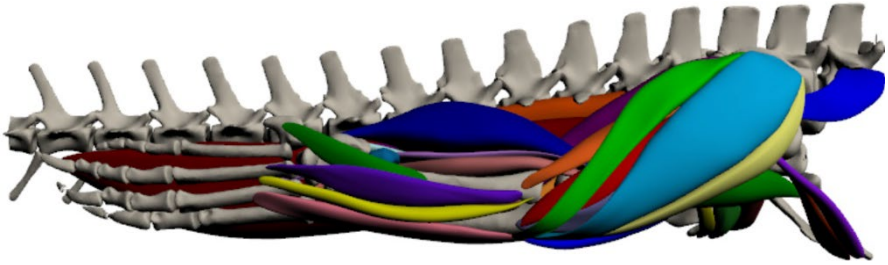


Figure 33. Three-dimensional presentation of the musculature of the hindlimb of Crocodylus porosus [14].

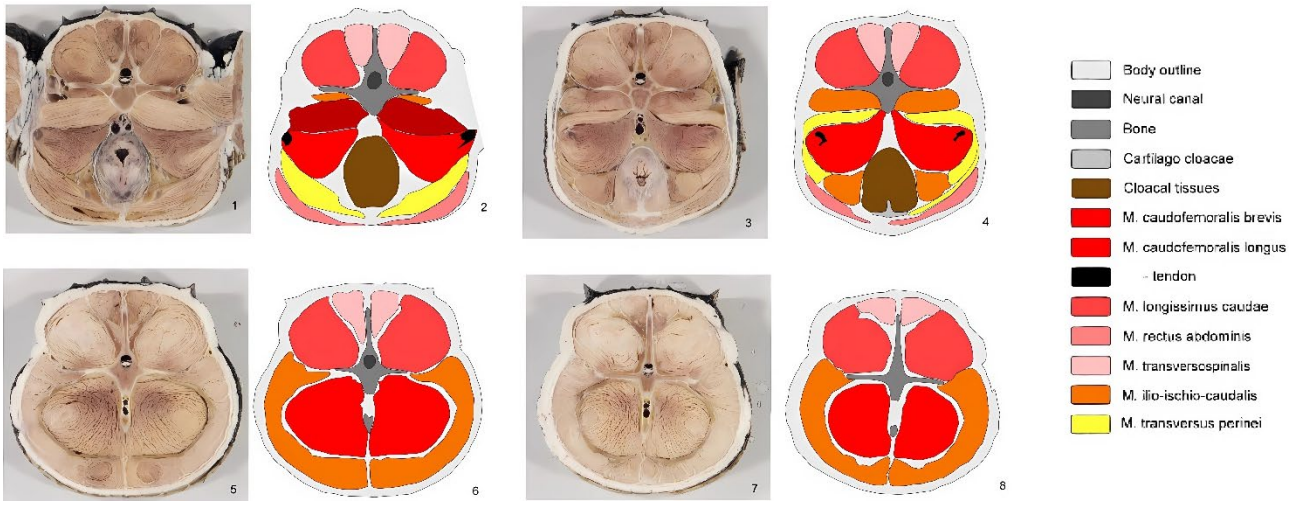


Figure 34. Alligator mississippiensis tomographic slices of the tail. Each physical slice is accompanied by an interpretative drawing. 1 & 2, slices just posterior to the pelvis showing the M. caudofemoralis brevis, 3 & 4, at the level of the M. transversus perinei, 5 & 6, just posterior to the M. transversus perinei, and 7 & 8, from ca. two-thirds down the tail showing the dorsal offset of the M. longissimus caudae/M. transversospinalis contact on the neural arch [16].

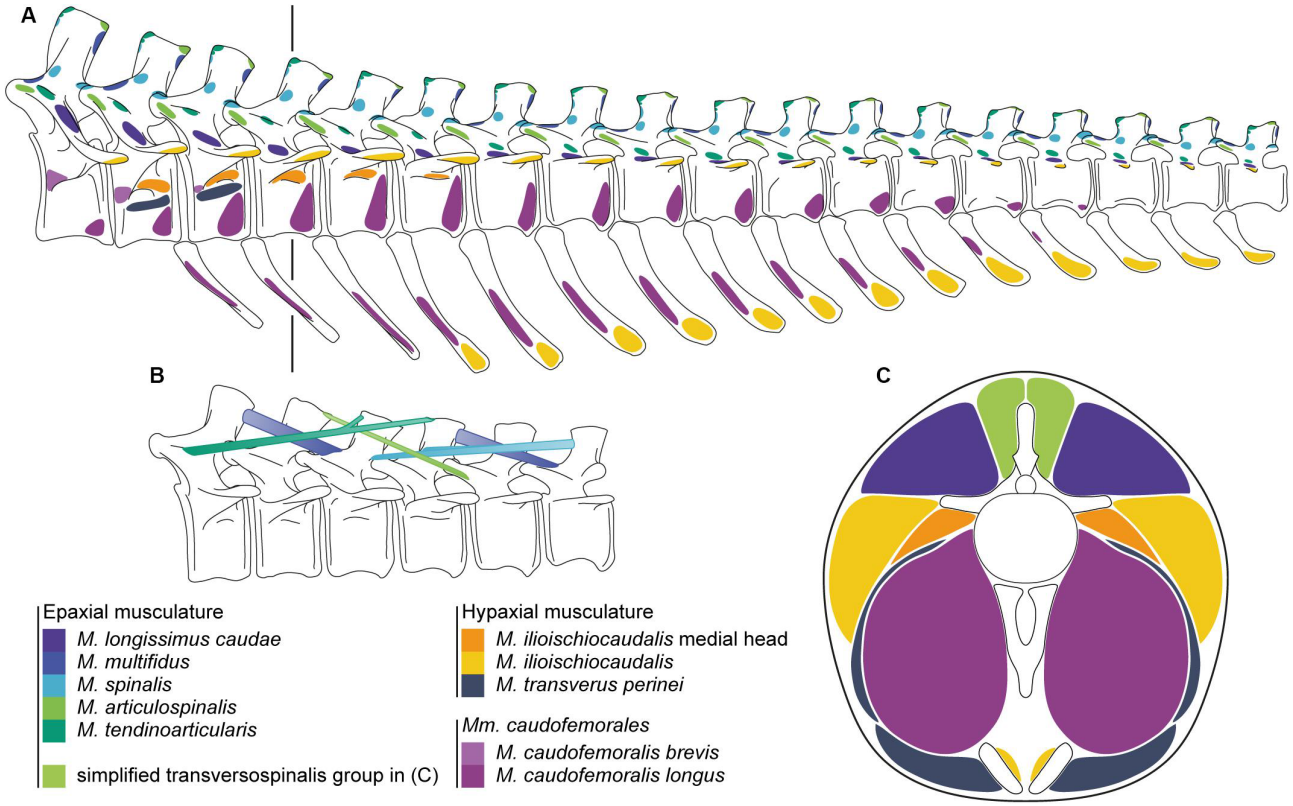


Figure 35. (A) Origins and insertions of the caudal musculature of the Late Jurassic sauropod *Giraffatitan brancai*. (B) Simplified muscle paths of the transversospinalis group of the epaxial musculature. (C) Cross-section of the tail at the fourth caudal vertebrae showing the lateral extent of the tail musculature. The line in A indicates the location of the cross-section through the musculature. Paired ventral elements represent the ischia [17].

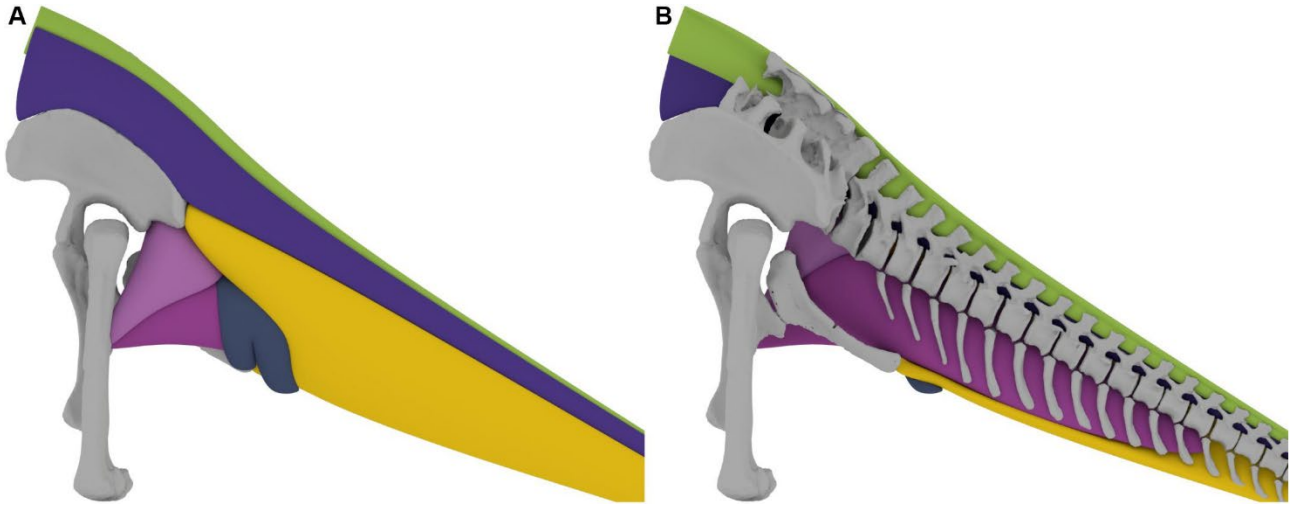


Figure 36. (A) 3D tail muscle reconstruction of the Late Jurassic sauropod *Giraffatitan brancai*. (B) Sagittal section of the tail musculature, showing the dorsal and ventral extent of the musculature in relation to the vertebrae [17].

Similar work for reconstructing the musculature of the appendicular skeleton in three north American Jurassic sauropods, namely *Diplodocus*, *Apatosaurus* and *Camarasaurus* was performed by Wilhite [11] (**Figure 37**).

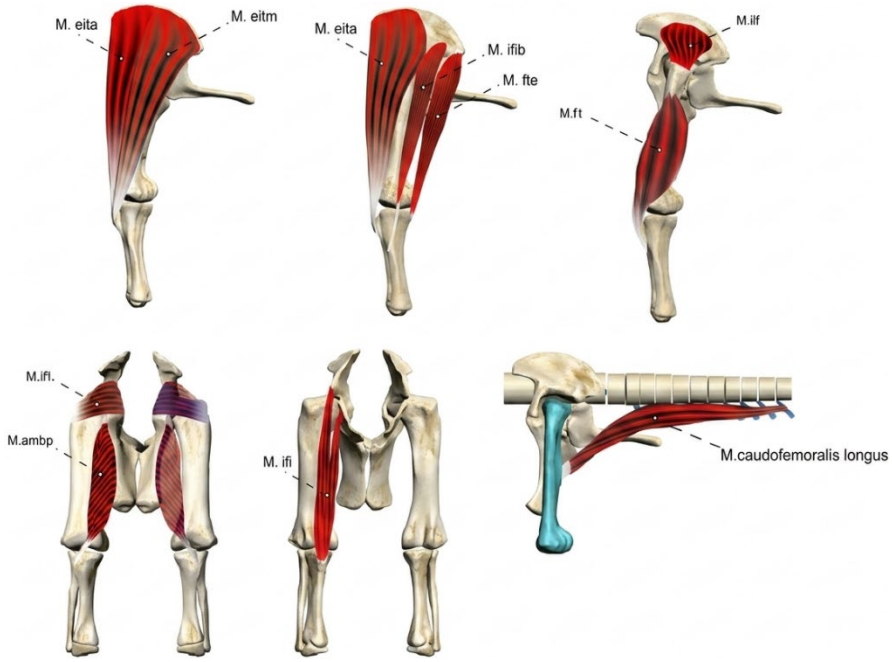


Figure 37. Musculature details of the appendicular skeleton of *Camarasaurus*, a north American Jurassic sauropod as suggested by Wilhite [11].

The reconstruction here of the *Amargasaurus* rmusculature of the appendicular skeleton and long tail is shown in **Figure 38**.

Figure 38. Musculature of the appendicular skeleton and long tail in the *Amargasaurus* reconstruction.

8. Manus and Pes Reconstruction

Footprint studies provide direct evidence for reconstructing the feet of extinct dinosaurs. For bipeds, such as theropods, tracks typically show a three-toed shape that records the impression of the hind foot only. White *et al.* [56] reconstructed the foot of the theropod Australovenator wintonensis by 3D-printing the bones, molding them into a flexible foot, and pressing it into simulated paleo-sediment to create actual footprints for comparison with fossil tracks at Lark Quarry, Australia. Lallensack *et al.* [57] experimented on a great number of outlines of theropod and ornithischian footprints, training a deep convolutional neural network to distinguish the two groups. Their software consistently outperformed human ex-

perts, identifying the majority of test tracks. For quadrupeds, such as sauropods, trackways preserve both manus (front foot) and pes (back foot) impressions together. Martill *et al.* [58] described well-preserved manus-pes couples from the Middle Jurassic of Yorkshire, England, where the pes print shows four to five toes and even preserves impressions of scaled integument (skin) around parts of the foot. These experimental and descriptive studies demonstrate how fossil footprints and experimental recreations directly inform the reconstruction of foot anatomy in both bipedal and quadrupedal dinosaurs.

Figure 39. Reconstruction of the manus (front foot) of *Camarasaurus* based on specimen SMA 0002 [60]. The claws are oriented with their outer sides facing downward. Because *Amargasaurus* belongs to Dicraeosauridae, the sister group to Camarasauridae, this manus reconstruction is adopted for the present work.

Figure 40. Reconstruction of the pes (hind foot) of *Camarasaurus* based on the exceptionally well-preserved skeleton SMA 0002 [60]. The pes is compact with five toes of different lengths. This reconstruction serves as the best available model for *Amargasaurus*, whose foot bones are not preserved.

Tschopp *et al.* [59] reconstructed the feet of *Camarasaurus* from an exceptionally well-preserved skeleton (specimen SMA 0002) with fully articulated bones. For the manus, the claws were oriented with their outer sides facing downward. The pes was compact with five toes of different lengths. Based on their 3D model,

they created a test footprint and found it did not match any known fossil tracks, suggesting misidentification of trackmakers. Because *Amargasaurus* belongs to Dicraeosauridae, the sister group to Camarasauridae within Neosauropoda, the *Camarasaurus* reconstruction represents the best available model for *Amargasaurus* (whose foot bones were not preserved) and was adopted in the present reconstruction (Figure 39 and Figure 40).

9. Reconstruction of the Cloaca in *Amargasaurus*

Following the EPB method, the cloaca of *Amargasaurus* was reconstructed here as a longitudinal vent oriented vertically to the ground, positioned immediately posterior to the ischia (Figure 41). This decision is supported by the only known fossilized dinosaur cloaca, preserved in Psittacosaurus sp., which confirms Romer's prediction that the cloacal aperture in extinct archosaurs opens where haemal arches are absent on the caudal vertebrae [60]. The Psittacosaurus specimen reveals a longitudinal vent with a crocodylian-style scale rosette, a condition we extended to *Amargasaurus* by phylogenetic inference [61]. A vertical orientation was additionally chosen for practical reasons in the full-scale reconstruction, as it allows for natural integration with the ventral body wall and the surrounding hypaxial musculature anchored to the gastral basket.

Figure 41. Reconstruction of the cloaca of *Amargasaurus cazaui*. Following the Extant Phylogenetic Bracket method, the cloaca is reconstructed as a longitudinal vent oriented vertically to the ground, positioned immediately posterior to the ischia.

10. The Complete Full-Scale Reconstruction

The complete full-scale reconstruction of *Amargasaurus cazaui* presented in this work (Figure 42) demonstrates that a scientifically informed reconstruction of a

dinosaur body is achievable through the systematic application of the EPB method, combined with careful engineering and artistic craftsmanship. From the initial decision on posture and gait, through the construction of the steel and concrete support structure, to the detailed layering of muscles, skin scales and paint, each step has followed a logical procedure grounded in comparative anatomy and biomechanical evidence. The resulting model stands as a tangible representation of the current state of paleontological knowledge, while also acknowledging the uncertainties that remain, particularly regarding the exact function of the elongated neural spines and the precise body contours of the living animal. It is hoped that this work, together with the previous papers in this series, will serve as a practical guide for future reconstructions and will inspire a deeper appreciation for the ancient life that once roamed planet Earth.

Figure 42. Complete full-scale reconstruction of *Amargasaurus cazaui* in the chosen walking posture, showing the final musculature, skin texture and the elongated neural spines of the neck covered with a sail.

11. Discussion

This paper makes the following contributions: i) a critical synthesis of sauropod musculoskeletal and locomotor literature; ii) a reproducible EPB-based reconstruction protocol from posture to skin texture; iii) documentation of the complete full-scale physical build of *Amargasaurus cazaui*—steel armature, reinforced concrete support, wire-mesh and plaster musculature with metal templates, and rolled polygonal scale rosettes. The work serves as a reference, a methodological guide, and a case study.

The following are not preserved in the *Amargasaurus* holotype and were therefore reconstructed from comparative taxa: the manus and pes (from *Camarasaurus* SMA 0002), all trunk soft tissues including epaxial and hypaxial musculature, intercostals, and abdominal wall, the gastral basket (by phylogenetic inference from diplodocids), the cloaca (from Psittacosaurus and crocodilians), and the sail covering of the elongated neural spines (inferred from osteohistology).

The selection of extant analogs followed the hierarchical logic of the EPB. For the neck, pectoral girdle, forelimb, hindlimb, and tail musculature, Alligator mississippiensis and Crocodylus porosus served as the primary analogs, where osteological correlates are present in both crocodilians and birds, yielding high confidence. For the trunk respiratory system, both crocodilian and avian patterns were also considered. For the covering of the cervical neural spines, no direct osteological correlate exists; thus upon examining all possibilities in the literature, the covering was reconstructed by a double sail. The sail is internally joined as a single pad resembling a buffalo back, rising from the anterior neck and increasingly reaching the full height of the back.

12. Conclusions

This paper has presented the current knowledge concerning the reconstruction of the body of dinosaurs, with particular emphasis on the musculature of the neck, pectoral girdle, forelimbs, hindlimbs and tail, as well as the soft tissues that give a dinosaur a living appearance. As a worked example, the full-scale reconstruction of the body of *Amargasaurus* has been presented, following the same methodological framework established for the head in a previous paper.

The first and basic decision for any reconstruction is the posture of the animal. The present paper has reviewed competing gait hypotheses for sauropod dinosaurs, including elephant-like walking, the diagonal couplet walks suggested by Sellers *et al*., the kinematic reconstructions of Stevens and Wills, and the limb phase analysis of Lallensack and Falkingham. After evaluating the available evidence, a foot arrangement similar to the Stevens and Wills model was adopted for *Amargasaurus*, with the right forelimb and the left hindfoot bearing the weight of the animal. A narrow-gauge gait was assumed, consistent with the phylogenetic position of dicraeosaurids, and the elbow joints were reconstructed with the long limb bones nearly in line or slightly flexed, following the recent skeletal reconstruction of *Dicraeosaurus* in the Museum für Naturkunde, Berlin.

The neck musculature of sauropods was reconstructed using the EPB method, with primary reference to dissections of Alligator mississippiensis and various avian species. The complex arrangement of cervical muscles in vultures, owls, and alligators provides a valuable comparative framework for understanding the neck anatomy of extinct sauropods. In the case of *Amargasaurus*, the elongated neural spines of the neck present a particular challenge. Four alternative reconstructions were considered: a double sail, a single pad 6 to 8 cm wide, a narrow pad ending in keratinized horns, and a long keratinized horn sheath. Based on the osteohistological evidence of Cerda *et al*. and the soft tissue reconstructions of Schwarz *et al*., a keratinized horn sheath covering the dorsal two thirds of the cervical neural spines was adopted for the present reconstruction.

The pectoral girdle and forelimb musculature of sauropods was examined through the works of Wilhite, Klinkhamer *et al*., and Otero *et al*. The 3D models of limb musculature in Crocodylus porosus provided by Klinkhamer *et al*. served

as the primary analog for reconstructing the forelimb muscles of *Amargasaurus*. The hindlimb and tail musculature, following the recommendations of Ibiricu *et al*., was reconstructed using crocodilian rather than avian models, because birds show skeletal modification and fusion of the caudal vertebrae. The tail dissections of Alligator mississippiensis by Mallison *et al*. and the 3D volumetric reconstruction of the tail of *Giraffatitan brancai* by Díez Díaz *et al*. provided detailed guidance for the tail musculature of *Amargasaurus*.

For the physical reconstruction of the full-scale *Amargasaurus* body, the bones were constructed individually from welded steel wire rods and assembled on a steel armature in the chosen walking posture. A steel and concrete support, starting from the feet, extends inside the body to bear the weight of the neck, trunk and tail. Each muscle area was coated with a fine wire mesh and plaster, with the volume and external contours of the muscles guided by comparisons with dissected crocodilians and birds. The skin was covered with small, non-overlapping polygonal scales arranged in rosette patterns, applied using cylindrical stamps. The main body was reconstructed with a voluminous and rounded contour, consistent with allometric evidence that sauropod organ volumes may have deviated significantly from those of extant animals. Gastralia were included in the abdominal region, following the evidence from diplodocids and the phylogenetic position of dicraeosaurids within Flagellicaudata.

The resulting reconstruction is a full-scale, scientifically informed representation of *Amargasaurus*, ready for exhibition or further study. The methods and materials described in this paper, together with those presented in the previous papers of this series, provide a comprehensive guide for the accurate reconstruction of dinosaurs in all scientific details. It is hoped that this work will motivate people to interact with the art of paleontology and promote understanding of past life on earth.

Acknowledgments

This work was funded by the Cyprus University of Technology.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

[1] Florides, G.A. and Christodoulides, P. (2021) On Dinosaur Reconstruction: An Introduction to Important Topics of Paleontology and Dinosaurs. *Open Journal of Geology*, **11**, 525-571. https://doi.org/10.4236/ojg.2021.1110028

[2] Florides, G.A. and Christodoulides, P. (2021) On Dinosaur Reconstruction: Posture of Dinosaurs. *Open Journal of Geology*, **11**, 756-793. https://doi.org/10.4236/ojg.2021.1112037

[3] Florides, G.A. and Christodoulides, P. (2022) On Dinosaur Reconstruction: The Head. *Open Journal of Geology*, **12**, 371-432. https://doi.org/10.4236/ojg.2022.126020

[4] Salgado, L. and Bonaparte, J.F. (1991) A New Dicraeosaurid Sauropod, *Amargasaurus cazaui* Gen. et. sp. nov., from the La Amarga Formation, Neocomian of Neuquen Province, Argentina. *Ameghiniana*, **28**, 333-346. (in Spanish)

[5] Rogers, S.W. (1999) *Allosaurus*, Crocodiles, and Birds: Evolutionary Clues from Spiral Computed Tomography of an Endocast. *The Anatomical Record*, **257**, 162-173. https://doi.org/10.1002/(sici)1097-0185(19991015)257:5<162::aid-ar5>3.0.co;2-w

[6] Novas, F. (2009) The Age of Dinosaurs in South America. Indiana University Press.

[7] Bailey, J.B. (1997) Neural Spine Elongation in Dinosaurs: Sailbacks or Buffalo-Backs? *Journal of Paleontology*, **71**, 1124-1146. https://doi.org/10.1017/s0022336000036076

[8] Schwarz, D., Frey, E. and Meyer, C.A. (2007) Pneumaticity and Soft-Tissue Reconstructions in the Neck of Diplodocid and Dicraeosaurid Sauropods. *Acta Palaeontologica Polonica*, **52**, 167-188.

[9] Cerda, I.A., Novas, F.E., Carballido, J.L. and Salgado, L. (2022) Osteohistology of the Hyperelongate Hemispinous Processes of *Amargasaurus cazaui* (Dinosauria: Sauropoda): Implications for Soft Tissue Reconstruction and Functional Significance. *Journal of Anatomy*, **240**, 1005-1019. https://doi.org/10.1111/joa.13659

[10] Militello, M., Otero, A. and Carballido, J.L. (2026) The Occiput of *Amargasaurus* (Sauropoda, Dicraeosauridae): Reconstruction of the Craniocervical Muscular Insertions with Comments on Feeding Strategy. *Journal of Anatomy*, **248**, 284-306. https://doi.org/10.1111/joa.70071

[11] Wilhite, D.R. (2003) Biomechanical Reconstruction of the Appendicular Skeleton in three North American Jurassic Sauropods. Ph.D. Thesis, Louisiana State University and Agricultural and Mechanical College. https://repository.lsu.edu/gradschool_dissertations/2677/

[12] Klinkhamer, A.J., Mallison, H., Poropat, S.F., Sloan, T. and 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

[13] Otero, A., Allen, V., Pol, D. and Hutchinson, J.R. (2017) Forelimb Muscle and Joint Actions in Archosauria: Insights from *Crocodylus johnstoni* (Pseudosuchia) and *Mussaurus patagonicus* (Sauropodomorpha). *PeerJ*, **5**, e3976. https://doi.org/10.7717/peerj.3976

[14] Klinkhamer, A.J., Wilhite, D.R., White, M.A. and Wroe, S. (2017) Digital Dissection and Three-Dimensional Interactive Models of Limb Musculature in the Australian Estuarine Crocodile (*Crocodylus porosus*). *PLOS ONE*, **12**, e0175079. https://doi.org/10.1371/journal.pone.0175079

[15] Ibiricu, L.M., Martínez, R.D. and Casal, G.A. (2020) The Pelvic and Hindlimb Myology of the Basal Titanosaur *Epachthosaurus sciuttoi* (Sauropoda: Titanosauria). *Historical Biology*, **32**, 773-788. https://doi.org/10.1080/08912963.2018.1535598

[16] Mallison, H., Pittman, M. and Schwarz, D. (2015) Using Crocodilian Tails as Models for Dinosaur Tails. *PeerJ*, **3**, e1339v1. https://doi.org/10.7287/peerj.preprints.1339v1

[17] Díez Díaz, V., Demuth, O.E., Schwarz, D. and Mallison, H. (2020) The Tail of the Late Jurassic Sauropod *Giraffatitan brancai*: Digital Reconstruction of Its Epaxial and Hypaxial Musculature, and Implications for Tail Biomechanics. *Frontiers in Earth Science*, **8**, Article ID: 160. https://doi.org/10.3389/feart.2020.00160

[18] Bishop, P.J., Falisse, A., De Groote, F. and Hutchinson, J.R. (2021) Predictive Simulations of Running Gait Reveal a Critical Dynamic Role for the Tail in Bipedal Dinosaur Locomotion. *Science Advances*, **7**, eabi7348.

https://doi.org/10.1126/sciadv.abi7348

[19] Lallensack, J.N. and Falkingham, P.L. (2022) A New Method to Calculate Limb Phase from Trackways Reveals Gaits of Sauropod Dinosaurs. *Current Biology*, **32**, 1635-1640.e4. https://doi.org/10.1016/j.cub.2022.02.012

[20] Sellers, W.I., Margetts, L., Coria, R.A. and Manning, P.L. (2013) March of the Titans: The Locomotor Capabilities of Sauropod Dinosaurs. *PLOS ONE*, **8**, e78733. https://doi.org/10.1371/journal.pone.0078733

[21] Christian, A., Heinrich, W.-D. and Golder, W. (1999) Posture and Mechanics of the Forelimbs of *Brachiosaurus brancai* (Dinosauria: Sauropoda). *Fossil Record*, **2**, 63-73. https://doi.org/10.1002/mmng.1999.4860020103

[22] Wampler, K., Popović, Z. and Popović, J. (2014) Generalizing Locomotion Style to New Animals with Inverse Optimal Regression. *ACM Transactions on Graphics*, **33**, 1-11. https://doi.org/10.1145/2601097.2601192

[23] Carpenter, K. (2002) Forelimb Biomechanics of Nonavian Theropod Dinosaurs in Predation. *Senckenbergiana Lethaea*, **82**, 59-75. https://doi.org/10.1007/bf03043773

[24] Bishop, P.J., Cuff, A.R. and Hutchinson, J.R. (2021) How to Build a Dinosaur: Musculoskeletal Modeling and Simulation of Locomotor Biomechanics in Extinct Animals. *Paleobiology*, **47**, 1-38. https://doi.org/10.1017/pab.2020.46

[25] Wills, E.D. (2008) Gait Animation and Analysis for Biomechanically Articulated Skeletons. Ph.D. Thesis, University of Oregon. https://scholarsbank.uoregon.edu/items/b6ff97c9-c0ca-41d9-83dc-76e025693d45/full

[26] Schwarz, D., Frey, E. and Meyer, C.A. (2007) Novel Reconstruction of the Orientation of the Pectoral Girdle in Sauropods. *The Anatomical Record*, **290**, 32-47. https://doi.org/10.1002/ar.20405

[27] Remes, K. (2008) Evolution of the Pectoral Girdle and Forelimb in Sauropodomorpha (Dinosauria, Saurischia) Osteology Myology and Function. Ph.D. Thesis, Universität München. https://edoc.ub.uni-muenchen.de/8395/1/Remes_Kristian.pdf

[28] Hohn, B., Klein, N., Remes, K., Gee, C.T. and Sander, P.M. (2011) Walking with the Shoulder of Giants: Biomechanical Conditions in the Tetrapod Shoulder Girdle as a Basis for Sauropod Shoulder Reconstruction. In: Wings, O., Borbély, A., Breuer, T., Christian, A., Clauss, M., Dumont, M. and Witzel, U., Eds., *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*, Indiana University Press, 182-196.

[29] Stevens, K. and Wills, E. (2011) Kinematic Constraints on the Reconstruction of Dinosaur Gaits. University of Oregon. http://ix.cs.uoregon.edu/~kent/paleontology/presentations/2007%20SVPCA.html

[30] Stevens, K.A. and Wills, E.D. (2011) Non-Parasagittal Yet Efficient: The Role of the Pectoral Girdles and Trunk in the Walk of *Triceratops* and *Apatosaurus*. University of Oregon. http://ix.cs.uoregon.edu/~kent/paleontology/presentations/SVP%202009%20Bristol/interactive.html

[31] Lesté-Lasserre, C. (2022) Long-Necked Dinosaurs Had a Gait Unlike Any Living Animal. New Scientist. https://www.newscientist.com/article/2310340-long-necked-dinosaurs-had-a-gait-unlike-any-living-animal/

[32] Hartman, S. (2022) *Amargasaurus cazaui*. Dr. Scott Hartman's Skeletal Drawing.com. https://www.skeletaldrawing.com/sauropods-and-kin/*amargasaurus*

[33] Farlow, J.O. (1992) Sauropod Tracks and Trackmakers: Integrating the Ichnological

and Skeletal Records. *Zubia*, **10**, 89-138.

[34] Wilson, J.A. and Carrano, M.T. (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

[35] Henderson, D.M. (2006) Burly Gaits: Centers of Mass, Stability, and the Trackways of Sauropod Dinosaurs. *Journal of Vertebrate Paleontology*, **26**, 907-921. https://doi.org/10.1671/0272-4634(2006)26[907:bgcoms]2.0.co;2

[36] Böhmer, C., Prevoteau, J., Duriez, O. and Abourachid, A. (2020) Gulper, Ripper and Scrapper: Anatomy of the Neck in Three Species of Vultures. *Journal of Anatomy*, **236**, 701-723. https://doi.org/10.1111/joa.13129

[37] Boumans, M.L.L.M., Krings, M. and Wagner, H. (2015) Muscular Arrangement and Muscle Attachment Sites in the Cervical Region of the American Barn Owl (*Tyto Furcata Pratincola*). *PLOS ONE*, **10**, e0134272. https://doi.org/10.1371/journal.pone.0134272

[38] Klingler, J.J. (2016) On the Morphological Description of Tracheal and Esophageal Displacement and Its Phylogenetic Distribution in Avialae. *PLOS ONE*, **11**, e0163348. https://doi.org/10.1371/journal.pone.0163348

[39] Tsuihiji, T. (2007) Homologies of the *Longissimus*, *Iliocostalis*, and Hypaxial Muscles in the Anterior Presacral Region of Extant Diapsida. *Journal of Morphology*, **268**, 986-1020. https://doi.org/10.1002/jmor.10565

[40] Snively, E. and Russell, A.P. (2007) Functional Variation of Neck Muscles and Their Relation to Feeding Style in Tyrannosauridae and Other Large Theropod Dinosaurs. *The Anatomical Record*, **290**, 934-957. https://doi.org/10.1002/ar.20563

[41] Bakker, R.T. (1998) Brontosaur Killers: Late Jurassic Allosaurids as Sabre-Tooth Cat Analogues. *Gaia*, **15**, 145-158. http://www.arca.museus.ul.pt/ArcaSite/obj/gaia/MNHNL-0000779-MG-DOC-web.PDF

[42] Taylor, M.P. and Wedel, M.J. (2013) Why Sauropods Had Long Necks; and Why Giraffes Have Short Necks. *PeerJ*, **1**, e36. https://doi.org/10.7717/peerj.36

[43] Paul, G.S. (1997) Dinosaur Models: The Good, the Bad, and Using Them to Estimate the Mass of Dinosaurs. In: *DinoFest International Proceedings*, Academy of Natural Science Philadelphia, 129-154. http://www.gspauldino.com/Models.pdf

[44] Schwarz-Wings, D. and Frey, E. (2008) Is There an Option for a Pneumatic Stabilization of Sauropod Necks? An Experimental and Anatomical Approach. *Palaeontologia Electronica*, **11**, 17A. https://palaeo-electronica.org/2008_3/155/

[45] Wedel, M. and Sanders, K. (2002) Osteological Correlates of Cervical Musculature in Aves and Sauropoda (Dinosauria: Saurischia), with Comments on the Cervical Ribs of *Apatosaurus*. *PaleoBios*, **22**, 1-6.

[46] Naish, D. (2009) The Great Dinosaur Discoveries. University of California Press.

[47] Jasinoski, S.C., Russell, A.P. and Currie, P.J. (2006) An Integrative Phylogenetic and Extrapolatory Approach to the Reconstruction of Dromaeosaur (Theropoda: Eumaniraptora) Shoulder Musculature. *Zoological Journal of the Linnean Society*, **146**, 301-344. https://doi.org/10.1111/j.1096-3642.2006.00200.x

[48] Burch, S.H. (2014) Complete Forelimb Myology of the Basal Theropod Dinosaur *Tawa hallae* Based on a Novel Robust Muscle Reconstruction Method. *Journal of Anatomy*, **225**, 271-297. https://doi.org/10.1111/joa.12216

[49] Aranciaga Rolando, A.M., Novas, F.E., Calvo, J.O., Porfiri, J.D., Dos Santos, D.D. and Lamanna, M.C. (2023) Reconstruction of the Pectoral Girdle and Forelimb Muscula-

ture of Megaraptora (Dinosauria: Theropoda). *The Anatomical Record*, **306**, 1804-1823. https://doi.org/10.1002/ar.25128

[50] Carrier, D.R. and Farmer, C.G. (2000) The Integration of Ventilation and Locomotion in Archosaurs. *American Zoologist*, **40**, 87-100. https://doi.org/10.1093/icb/40.1.87

[51] Wedel, M.J. (2003) The Evolution of Vertebral Pneumaticity in Sauropod Dinosaurs. *Journal of Vertebrate Paleontology*, **23**, 344-357. https://doi.org/10.1671/0272-4634(2003)023[0344:teovpi]2.0.co;2

[52] Hallett, M. and Wedel, M.J. (2016) The Sauropod Dinosaurs, Life in the Age of Giants. Johns Hopkins University Press.

[53] Claessens, L.P.A.M. (2004) Dinosaur Gastralia; Origin, Morphology, and Function. *Journal of Vertebrate Paleontology*, **24**, 89-106. https://doi.org/10.1671/a1116-8

[54] Tschopp, E. and Mateus, O. (2013) Clavicles, Interclavicles, Gastralia, and Sternal Ribs in Sauropod Dinosaurs: New Reports from Diplodocidae and Their Morphological, Functional and Evolutionary Implications. *Journal of Anatomy*, **222**, 321-340. https://doi.org/10.1111/joa.12012

[55] Franz, R., Hummel, J., Kienzle, E., Kölle, P., Gunga, H. and Clauss, M. (2009) Allometry of Visceral Organs in Living Amniotes and Its Implications for Sauropod Dinosaurs. *Proceedings of the Royal Society B*: *Biological Sciences*, **276**, 1731-1736. https://doi.org/10.1098/rspb.2008.1735

[56] White, M.A., Cook, A.G. and Rumbold, S.J. (2017) A Methodology of Theropod Print Replication Utilising the Pedal Reconstruction of *Australovenator* and a Simulated Paleo-Sediment. *PeerJ*, **5**, e3427. https://doi.org/10.7717/peerj.3427

[57] Lallensack, J.N., Romilio, A. and Falkingham, P.L. (2022) A Machine Learning Approach for the Discrimination of Theropod and Ornithischian Dinosaur Tracks. *Journal of The Royal Society Interface*, **19**, Article 20220588. https://doi.org/10.1098/rsif.2022.0588

[58] Martill, D.M., Smith, R.E. and Romano, M. (2024) Sauropod Manus and Pes Prints with Impressions of Integument from the Ravenscar Group (Middle Jurassic) of Whitby, Yorkshire, England. *Proceedings of the Geologists' Association*, **135**, 196-207. https://doi.org/10.1016/j.pgeola.2024.02.003

[59] Tschopp, E., Wings, O., Frauenfelder, T. and Brinkmann, W. (2015) Articulated Bone Sets of Manus and Pedes of *Camarasaurus* (Sauropoda, Dinosauria). *Palaeontologia Electronica*, **18**, 1-65. https://doi.org/10.26879/559

[60] Romer, A.S. (1956) Osteology of the Reptiles. University of Chicago Press.

[61] Bell, P.R., Pittman, M., Kaye, T.G. and Hendrickx, C. (2020) A Crocodylian-Style Cloaca in a Non-Avialan Dinosaur. https://doi.org/10.1101/2020.10.11.335398