Refining the evolutionary path of hadrosaurinoformes: An analysis of the *Caudofemoralis* muscle retractor

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Personal Section

My project originated long ago, when I was barely an infant. Almost every day I visited the Museum of Natural History and had lunch underneath the blue whale after touring the museum, paying special attention to the dinosaurs. Ever since I was young, dinosaurs have held that special interest for me, not in the sense of big scary monsters of a world long gone, but more in the sense of marvels of nature, amazing creatures at the zenith of evolution. My favorite recent addition to the museum is the moving *Triceratops* skull. I would spend days (and still do) imagining what these creatures looked like, how they moved, and other details that by all reasoning are impossible to know. However, when the time came to design my research project, I knew there was only one choice. I had to try and find out how dinosaurs moved. The culmination of this project isn't the just the culmination of the program, or time spent in science class; it's the culmination of 13 years of dreaming about dinosaurs.

I was fortunate enough to perform my research at the prestigious Yale Peabody Museum in New Haven, Conneccticut. After obtaining permission from Professor Daniel Brinkman, I visited the museum with my mentor, Walter Scott Persons IV. We went into their underground fossil collections where we were lucky enough to measure a complete *Dryosaurus* skeleton.

While I was working with my mentor to establish a protocol, I noticed I was missing some vital math skills that I needed to complete my study. Nothing major, just simple vector-based physics, but as I was completing my work during the summer leading into senior year, and was scheduled to take Physics in senior year, I had not yet learned it. Thus, I had to teach physics to myself.

A bigger problem was teaching myself how to use Rhinoceros NURBS, a modeling program that I used in my work. The program is very robust, and is used to create 3d models of anything imaginable, from houses to boats. However, barring a small tutorial from my mentor, I had to teach myself how to use the program all on my own, which was incredibly difficult and tedious. Pulling and pushing thousands of vertices into place, trying to make it match my measurements, was very difficult, as any deviation from the true measurements could throw off my results. Luckily, my statistical data was qualitative and not quantitative, so the possible minute deviations did not turn out to be detrimental to my study.

For other high school researchers looking into projects that combine science and math, I have but one bit of advice. Make sure you are passionate about your project. In my entire research program, the most successful people are those who are most passionate about their projects, and choose a topic that they are truly interested in. If you choose a topic that you're truly interested in, and one that you can study for the love of the topic rather than to finish a paper, no amount of daunting science or mathematics will stop you.

Research Section

Review Of Literature

Ornithopods are a clade of ornithiscian dinosaurs named for their bird-like feet and hind legs. All ornithopods are thought either to be obligate bipeds (animals that always move on their two hind limbs) or facultive bipeds (animals that move on

four legs when walking and feeding, but rear back onto two legs when running).

Because bipedal dinosaurs are anatomically dissimilar to modern terrestrial

mammals, which the bulk of previous muscle research has focused upon, dinosaur

muscles are poorly understood. Specifically, we have not elucidated the locomotive

properties of the main dinosaur hind limb retractor muscle, the *Caudofemoralis*.

The large *Caudofemoralis* muscles of non-avian dinosaurs have been

recognized since 1833, when their existence was inferred from a proportionately

massive fourth trochanter in the herbivorous ornithopod hadrosaur, *Iguanodon*

(Dollo, 1883). Gatesy's 1990 study of *Caudofemoralis* argues that the muscle shrank

over time as theropod dinosaurs evolved into extant birds, shifting the emphasis

from powered locomotion to stabilization during flight. He further states that this

regression occurred slowly over time in a noticeable relationship with the

emergence of powered flight as the primary means of locomotion for avian

dinosaurs. Gatesy argued that in dinosaurs the presence of a large *Caudofemoralis*

(absent in birds and mammals) together with a parasagittal gait (parallel to the

anatomical sagittal plane, absent in extant reptiles) made dinosaur's locomotion

fundamentally different from other modern animals.

To accurately analyze the muscle, I chose to use two different specimens

from different points in history so that I could not only look at the muscle in the

context of two different physiologies, but also I could track the muscle's evolution.

To this end, I decided to use *Dryosaurus altus,* a primitive hadrosaurinoform, and

Ouranosaurus nigeriensis, a more evolved hadrosaur.

Dryosaurus altus was a Late Jurassic ornithopod whose particular importance to this study is that it is an early ancestor for almost all species of ornithopoda.

Fig. 1. The basal ornithopod ancestor all hadrosaurinoformes, *Dryosaurus altus* (Seus and Norman, 1990)
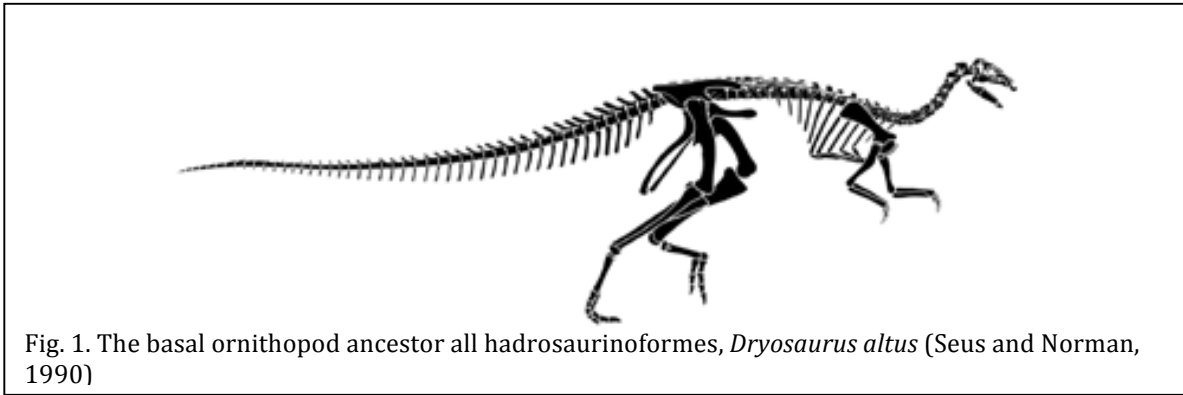
Dryosaurus was of average stature for an ornithopod of the time, with its two most unique characteristics being its unusually long legs for its size, and its long, stiff tail (Marshall, 1999). The tail was strengthened by a latticework of tendons, which kept the tail aloft as a counterbalance, and made the tail useful for powered locomotion.

Ouranosaurus nigeriensis (fig 2), a large iguanodont, is commonly depicted with a sail on its back, the result of disproportionately high vertebral neural spines

Fig. 2. *Ouranosaurus nigeriensis*, the species in question on neural spine evolution (Bailey, 1997; modified by author)
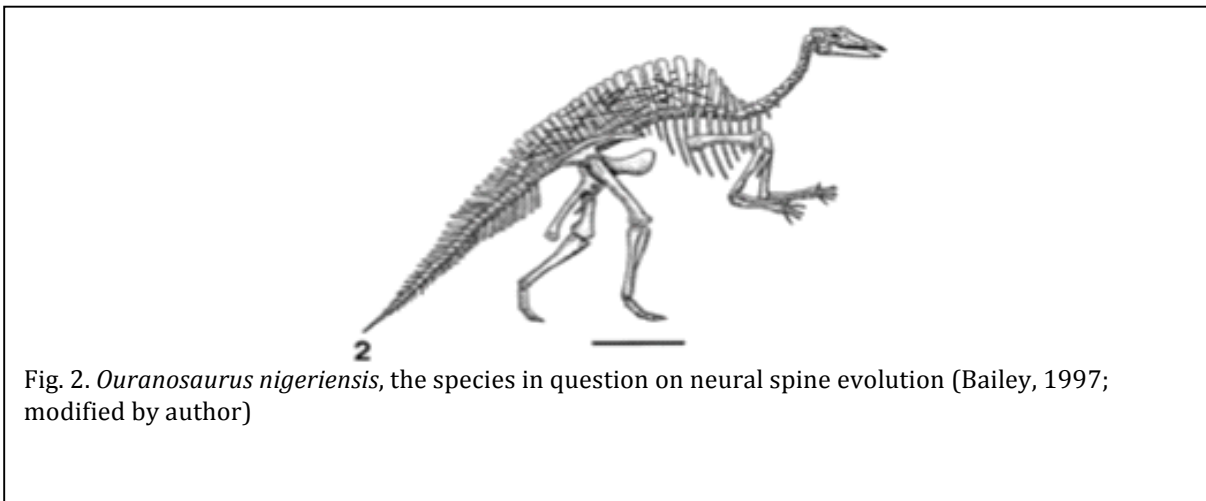
with seemingly few muscular attachments, and no modern analogues. This osteological peculiarity in such close proximity to the tail and spine deserved special

examination, since *Ouranosaurus* is the step immediately preceding the appearance of the true hadrosaur.

Examination of the neural spines which make up the back of *Ouranosaurus* show they are short and thick, similar to those of a bison, while the neural spines of the sail-backed *Dimetrodon* are longer, rod-shaped, and jut up from a low-set backbone. This loosely suggests that *Ouranosaurus* may have had a slight hump, akin to a bison.

My study further elaborated on the musculoskelature of the spine. By assessing the unique skeletal structures of *Ouranosaurus* and *Dryosaurus,* I elucidated the evolutionary path of the ornithopod *Caudofemoralis.*

Methods

Using the modeling software Rhinoceros (McNeel Robert and Associates, 2007), the hips and caudal series of the *Ouranosaurus nigeriensis* (GDF 300) and *Dryosaurus altus* (YPM 1884) were digitally sculpted based on skeletal measurements. Digital muscle models were then created overtop of the skeletal models. From these muscle models, basic properties of volume and cross-sectional area were calculated using the Rhinoceros software, using simple functions in Rhinoceros NURBS, according to the osteological relations described and determined from dissections of modern reptiles (Persons and Currie, 2011). The software then calculated the volume of each restored muscle. Because muscle is known to have a fairly constant density of 1.06 g/cm3 (Mendez and Keys, 1960), the muscle volume estimates were multiplied by this density value to obtain estimates of muscle mass.

To evaluate the potential contribution of the *Caudofemoralis* to femoral retraction, the muscle reconstructions of *Ouranosaurus* and *Dryosaurus* were used in combination with a series of biomechanical equations. First, the mass of the *Caudofemoralis* was calculated using a standard muscle density of 1.06 g/cm3 (Mendez and Keys, 1960). Then, the physiological cross-sectional area (PCSA) of the *Caudofemoralis* was calculated according to the following equation:

$$PCSA = m \cos \sigma / dl$$

(Sacks and Roy, 1982; Snively and Russell, 2007), where *m* is the mass of one *Caudofemoralis*); σ is the pennation angle of the muscle fibers within the *Caudofemoralis*, (based on dissected specimens, this is assumed to be approximately 1.00 (0.95) (Persons and Currie, 2011)), *d* is muscle density (assumed to be 1.06 g/cm3), *l* is the average fascicle length within the *Caudofemoralis*. However, due to data constraints, I had to use Anatomical Cross-Sectional Area (ASCA) instead of PCSA. ACSA is simply the cross-sectional area of the muscle at its greatest width. The difference in the final results is very small, a one or two percent difference. Specific tension (ST), also sometimes referred to as specific force (Brooks and Faulkner, 1994), is a ratio of the strength of a muscle to its area and has been shown to vary among different muscles and among different taxa (ref in table 1).

Table 1. Summary of previously reported specific tension values for hind limb muscles of extant animals (Persons and Currie, 2011)

Animal	Muscle(s)	ST (N/cm²)	Source
Domestic cat	Caudofemoralis	31.2	Brown et al. (1997)
Human	Thigh average	27.3–30.0	Storer et al. (2003)
Quarter horse	Gluteus medius	25.9	Marx et al. (2005)
White rhinoceros	Hamstring	34.4	Marx et al. (2005)

Known ST values for hind limb muscles likely offer the best basis for estimating the appropriate ST values for the *Caudofemoralis* of ornithopods. Estimates within the range of 25–35 N/cm2 would seem reasonable. Here, ST is assumed to be 25 N/cm2 for all ornithopoda (a conservative estimate).

The total contractile force (F_t) of *Caudofemoralis* was estimated by multiplying the calculated ACSA by the assumed ST (25 N/cm2):

$$F_t = \text{ACSA ST}$$

Although the contractile force of the *Caudofemoralis* is useful, a more accurate measure of its true contribution to locomotion is its torque-generating capacity. A muscle's torque-generating capacity is proportional to the force exerted in a direction orthogonal to its moment arm (which here is from the head of the femur in the femoral joint to the fourth trochanter). This force is here termed the effective force (F_e). The F_e of the *Caudofemoralis* is calculated with the following equation:

$$F_e = F_t \cdot \cos\theta$$

where θ is the angle between the vector of line of pull of the *Caudofemoralis* and a vector orthogonal to the moment arm, calculated for a femur positioned perpendicular to the ground

Finally, the potential torque generation of the *Caudofemoralis* is calculated with the equation:

$$\tau_m = R \cdot F_e \cdot \sin\Phi$$

Here, Φ is the angle between the vectors of the moment arm and the effective force (this angle is assumed to be 90 and the $\sin\Phi$ is, therefore, equal to 1), and R is the length of the moment arm.
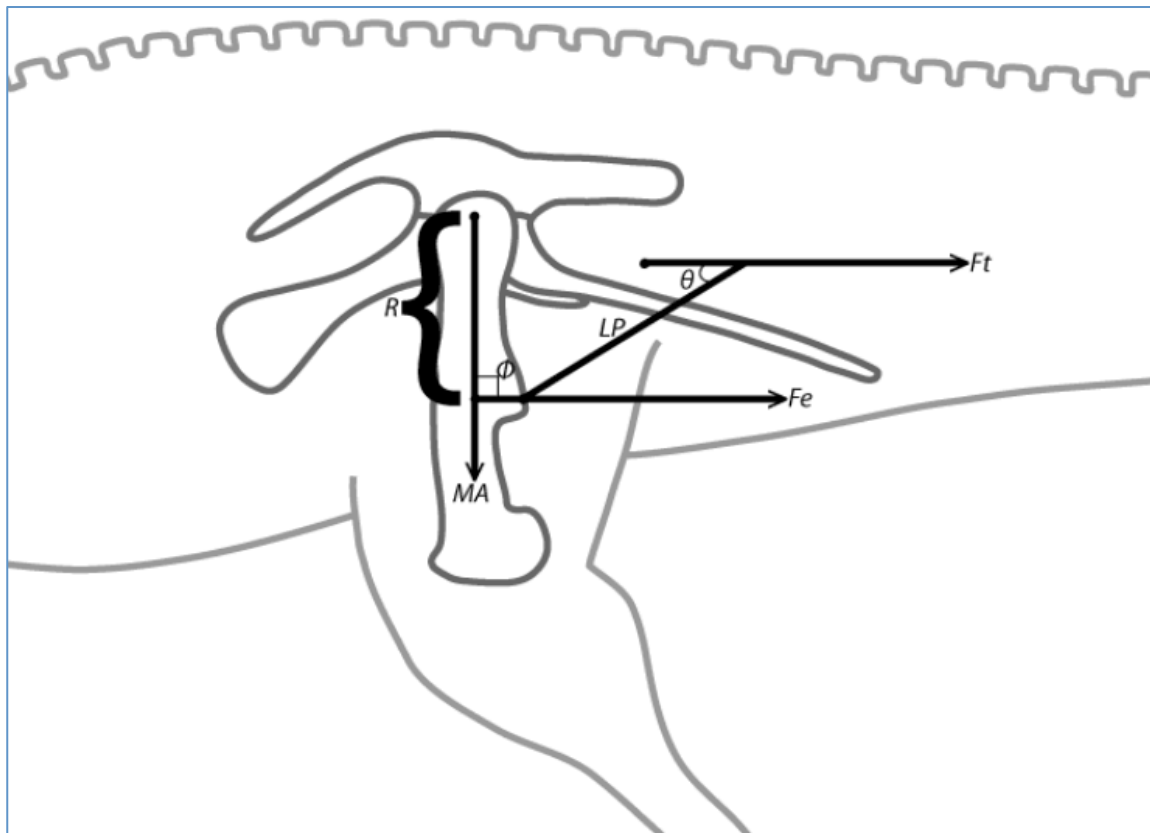
Fig. 3. The various vectors and angles used in the physics-calculations, using precedent set forth in earlier articles. Note: Diagram is not to scale. (Persons and Currie, 2011)

Results

Ouranosaurus nigeriensis and *Dryosaurus altus* have proportionately smaller *Caudofemoralis* to body mass ratios (2.6% and 3.9% respectively) (Table 2) than do theropods and hadrosaurs. I propose that the exceptional *Caudofemoralis* size seen in hadrosaurs, as evidenced by the *Lambeosaurus lambei Caudofemoralis* to body mass ratio of 5.6% (Persons and Currie, in press), is a characteristic that evolved

Table 2. Summary of estimated biomechanics of two species of ornithopoda (single leg)

	Ouranosaurus nigeriensis	*Dryosaurus altus*
Mass (kg)	29.635	1.66
ACSA (cm²)	418.53	59.28
Total Contractile Force (N)	1,046,325	148,200
Effective Muscle Pull (N)	923,850	136,419
Moment arm (m)	.51	.165
Torque (Nm)	471,164	22,509
Mass of Caudofemoralis in relation to body mass	2.6 %	3.9 %

within hadrosauria. A full 115% increase in *Caudofemoralis* to body mass ratio

indicates that the expanded *Caudofemoralis* muscle retractor evolved within the

hadrosauria clade, not before.

Aside from the math, I could also look at the raw models themselves to gather even

more information about my results, and hopefully look for visual cues to explain

why I had received such numbers.

The *Ouranosaurus'* neural spines also arced more smoothly from anterior to

posterior, peaking slightly over the pectoral girdle, and remaining tall well into the

anterior portion of the tail. The spines pulled on the base of the tail, indicating that

they indeed had muscles that fed into that area, but since the spines were not

directly in the hips, they could not change the basic locomotive patterns.
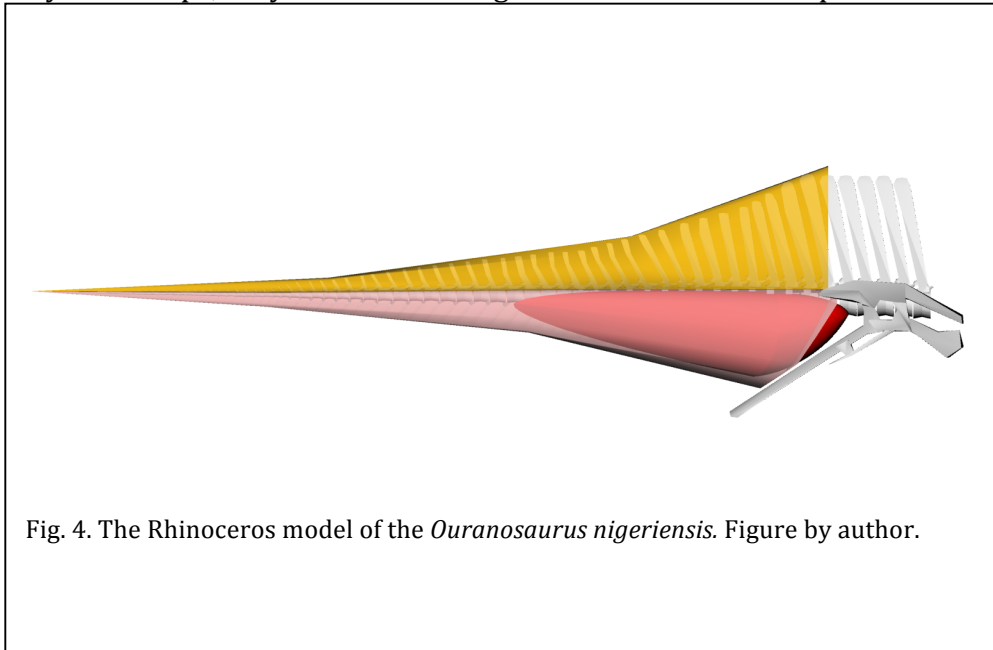

Fig. 4. The Rhinoceros model of the *Ouranosaurus nigeriensis.* Figure by author.

The neural spines of *Ouranosaurus* were also structurally poorly equipped to

carry as large a muscle mass as the *Bison*'s were. The transverse processes were not

as proportionately wide as its neural spines, indicating unexpanded epaxial muscles.

This corroborates the timeframe of *Ouranosaurus* in history, immediately prior to

true hadrosaurian evolution. Another skeletal characteristic of *Ouranosaurus'* neural spines was that their chevrons were not very deep, and certainly not deep enough to sturdily support large musculature. These multiple skeletal features all point to the statement that an *Ouranosaurus* did not have a heavily muscled back.

Dryosaurus' musculature can be seen as a starting point for many evolutionary lines, including Rhabdodontidae and Anklyopollexia, which eventually become hadrosauriformes. The *Caudofemoralis* is estimated to be proportionately smaller than that of true hadrosaurs but still larger than those observed in modern reptiles. This possibly indicates that while the *Caudofemoralis* was enlarged in the advanced hadrosaurs, within ornithopoda it started out as a strong muscle retractor well suited for bipedal locomotion.

Fig. 5. Rhinoceros model of *Dryosaurus altus.* Figure by author
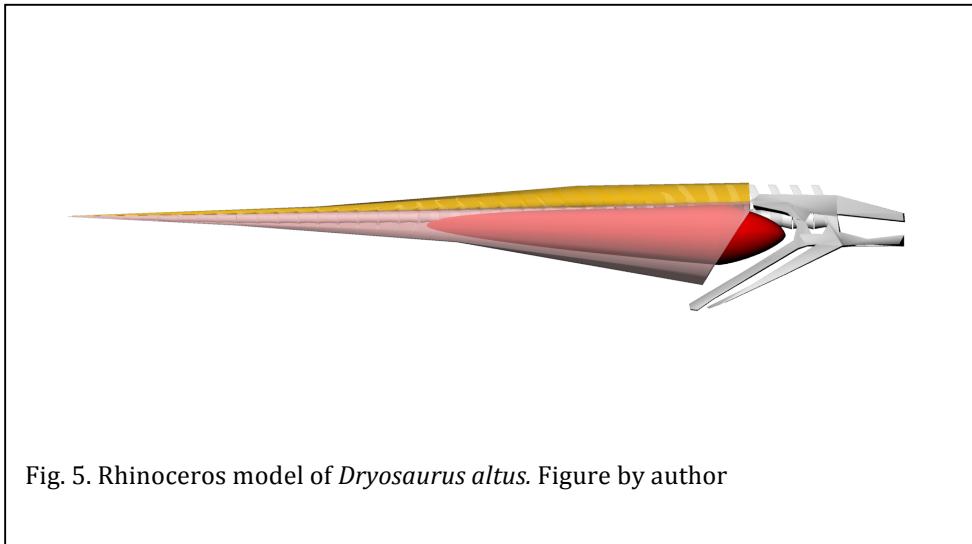
Dryosaurus altus has been previously stated to be an agile and quick runner, but it's true, adult musculature, is unknown. This is because despite numerous skeletons, especially from the Morrison Formation, no complete adult skeleton has been found (Horner, de Ricqles, Padian, Scheetz, 2009). Despite this, it has been studied intensively because of its prevalence. *Dryosaurus* is known to be smaller

than later ornithopods, with unusually long legs for its size. This unique skeletal structure among ornithopods would lead to the presumption that their *Caudofemoralis* would indeed be bigger to act upon their proportionally longer legs. Thus, their higher *Caudofemoralis* to body mass ratio does make sense in relation to *Ouranosaurus nigeriensis* and ornithopoda as a whole.

Conclusions

In this study I looked at the evolution of the *Caudofemoralis* retractor muscle from basal ornithopoda to its full extent in hadrosauria. I found that *Dryosaurus altus,* an ornithopod indicative of a common ancestor to may later clades, was an obligate biped. I also found that the *Caudofemoralis* of *Ouranosaurus nigeriensis* wasn't nearly as developed as that of true hadrosaurs, as shown by a 115% jump in *Caudofemoralis* to body mass ratio between *Ouranosaurus* and a hadrosaur, *Lambeosaurus lambei*. I reject the null hypothesis. I propose that the exceptional *Caudofemoralis* retractor muscle is a derived characteristic from within hadrosauria.

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