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Comparison of the Functional Morphology of *Appalachiosaurus* and *Albertosaurus*

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Abstract: In order to assess how similar *Appalachiosaurus* and *Albertosaurus libratus* are, their functional morphology was compared with emphasis on bite force, velocity, dentition, and skull construction with implication on possible feeding behaviors. It was found that despite their skeletal similarities and velocities, they likely filled two different ecological niches which may or may not have influenced a possible retention of basal features in *Appalachiosaurus*.

Keywords: *Appalachiosaurus, Albertasaurus*, Alabama dinosaurs, tyrannosaurids.

INTRODUCTION

Since its discovery in the 1980s, *Appalachiosaurus* has been the center of debate regarding arm length and the number of digits on the manus. Proponents on both sides offer compelling evidence in the form of cladistical analysis and a supposed fossilized humerus from the large theropod. The humerus, which has yet to be confirmed as belonging to *Appalachiosaurus*, suggests that this tyrannosaur retained primitive features well into the Cretaceous while others of the same period lost them. Arms aside, *Appalachiosaurus* is very similar structurally to its western cousin, *Albertosaurus libratus* (which will now be referred to as only *Albertosaurus*), which possessed short arms with two manus digits.

During the Campanian, North America was divided by the Western Interior Seaway, isolating dinosaur populations on either side, including *Albertosaurus* from its Appalachian cousin in the east [1]. Due to this isolation, it is likely that differences outside of arm length and digit number could have arisen, separating the two behaviorally despite structural similarities. Based on fossilized botanical evidence, the environment of eastern North America differed considerably from that of the western half. Large seeds found in Alabama suggest *Appalachiosaurus* lived in a rainforest-like environment with a closed canopy. *Albertosaurus* lived in a flat, open temperate forests dominated by conifers [2]. As a result, prey availability would have differed, possibly drastically. The differences in environment and prey availability could have affected the ecological niche inhabited by each of these theropods, meaning they could have inhabited very different ones.

Furthermore, dinosaurs exhibited diverse feeding mechanisms, which would have resulted in niche partitioning [3]. These feeding behaviors strongly influence other aspects of the animal's biology, including energy for reproduction, life-history strategies, population ecology, habitat preference, and behavioral ecology, which directly affect niche partitioning [4]. To infer feeding habits, two methods are often used: ahistorical and historical. For this study, we have focused on ahistorical which includes functional morphology and comparisons to extant analogue taxa [5]. In order to assess how similar *Appalachiosaurus* and *Albertosaurus* are, their functional morphology was compared with emphasis on velocity, hindlimb dimensions, skull dimensions, and bite force with implications on arm length and possible feeding behaviors.

Since the only known specimen of *Appalachiosaurus* is suspected to be a juvenile [1], in some cases we compare it to a juvenile *Albertosaurus*. This specimen, discovered by Lambe in 1917, was originally classified as a *Gorgosaurus.* Some researchers continue to classify the specimen as a *Gorgosaurus* (sister to *Albertosaurus*) while others have moved on to classifying it as an *Albertosaurus* [6]. In this project we consider this specimen to be an *Albertosaurus libratus*, not a separate genus. To expound the data set for analysis we also use Albertosaurus measurements found in Carr *et al*. [1].

It has been shown that three equations can be used to calculate velocity: Bakker's equation, Thulborn's equation, and Alexander's method [7-9]. For Bakker's equation, errors in estimating body mass generally have relatively small effects on this equation. Hindlimb length, however, can cause large changes in the predicted top velocity. For example, animals with long limbs, such as the giraffe, will have erroneously high velocities [10]. Due to the possibility of errors, the other equations, were used as a comparison and a check.

A variety of methods have been used to calculate the bite force of theropods, particularly *Tyrannosaurus rex*. These methods range from reconstructions, measuring tooth mark depth, measuring skull dimensions, and graphically mapping the maxilla and calculating angles to calculate bite force [11-14]. However, due to the lack of equipment we found Meers' [15] bite force extrapolation to be the most suitable to the study. Meers used a combination of predators from several

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taxa to determine bite force for *Tyrannosaurus rex*. The best predictions were those based on all taxa instead of just crocodylians or mammals.

METHODS AND MATERIALS

The author's collected original measurements from the *Appalachiosaurus montgomeriensis* (RMM 6670) type specimen held at the McWane Science Center in Birmingham, AL. Those measurements included: right femur, metatarsal, tibia, astragalus, toe, humerus, jaw depth, skull length, snout width, jaw length, and tooth size (Tables **1** and **2**). This type specimen is the only known skeleton of *Appalachiosaurus montgomeriensis* and data from this skeleton is used in the proceeding equations. Where needed, Carr *et al*. [1] provided other necessary measurements for *Appalachiosaurus montgomeriensis*. Because the repositories for the *Albertosaurus libratus* (ROM678, ROM1247, TMP 86.144.1) and *Albertosaurus sarcophagus* (CMN 5601) are held at the Royal Ontario Museum (Ontario, Canada), Royal Tyrrell Museum of Palaeontology (Alberta, Canada), and Canadian Museum of Nature (Ottawa, Canada), respectively, we used measurement data provided by Carr *et al*. [1] and Lambe [16]. Therefore, the data provided in Tables **1-3** indicate single measurements for *Appalachiosaurus* and average values for *Albertosaurus*. This is the sample set we used when conducting statistical analysis.

Using observations by Carr *et al*. [1], comparisons were made between skull construction and dentition. These measurements of the hindlimb and foot were used to calculate possible velocities using three different methods (Table **3**). The first was Bakker's Equation where v=4.132(RHL)-14 (m/s) where RHL is relative hindlimb length. Relative hindlimb length is the total length of the hind limb from the end of the third toe to the tip of the femur in centimeters divided by the cube root of the animal's body mass in kilograms [8]. Carr *et al*. [1] calculated *Appalachiosaurus* to weight 623 kg which was used in this equation. Thulborn's Equation (v=0.25(gravitational acceleration in meters/second)$^{0.5}$(stride length in meters)$^{1.67}$(limb length in meters)$^{-1.17}$) requires stride length which was estimated from the *Appalachiosaurus* cast at the Tellus Museum in Catersville, Georgia. This stride length was most likely a walking stride due to its small size [9]). Alexander's method, however, results in two velocities: the velocity (m/s) at which the animal transitions from a walk to a jog/trot (v=√6.12H where H is hindlimb length from the tip of the third metatarsal to the end of the femur in m) and the velocity at which the animal transitions from a trot/jog to a run (v=√33.13H) [7]. The velocity of both *Appalachiosaurus* and *Albertosaurus* were calculated using these equations and compared using a T-Test.

To calculate bite force, Meers' equations were used. For the best comparison, all three equations (all taxa - y=0.9182x+4.3829; crocodylians - y=0.7848x+5.3789; mammals - y=0.725x+5.0308) were used. These three equations use the natural log of the body mass to find the natural log of the bite force in Newtons. To convert back to the actual bite force a correction factor (RE), which is the ratio of the mean of observed values to the dependent variable divided by the mean values predicted by transformation back from logarithms that define an exponential relationship, were used [17], in this case 1.1038, 1.0002, and 1.1369 respectively. Bite force was calculated for both *Appalachiosaurus* and *Albertosaurus* and compared using a T-test.

Since there is only one specimen of *Appalachiosaurus* known to the world, statistical analysis of the skull dimensions and hindlimb dimensions cannot be done. Because of this, "lollipop" graphs were constructed

Table 1. Hindlimb Lengths of *Appalachiosaurus* and *Albertosaurus*. *Albertosaurus* Measurements are Applied from Lambe

Species	Femur (mm)	Tibia (mm)	Astragulus (mm)	3rd Metatarsuus (mm)
Appalachiosaurus	840	792	75	528
Albertosaurus	930	842	158	594

Table 2. Skull Dimensions of *Appalachiosaurus* and *Albertosaurus*. *Albertosaurus* Measurements are Applied from Lambe

Species	Alexander *Walk to Trot*	Alexander *Trot to Run*	Thulborn	Bakker
Appalachiosaurus	13 km/hr	31 km/hr	6.5 km/hr	101 km/hr
Albertosaurus	13 km/hr	30 km/hr	6.2 km/hr	122 km/hr

Table 3. Velocity of *Appalachiosaurus* and *Albertosaurus*. Estimates of Limb Lengths for *Albertosaurus* are Applied from Lambe. Stride Length for Both *Appalachiosaurus* and *Albertosaurus* was Estimated at 3.24 m. This is Most Likely Walking Stride for Both Since Limb Size is Similar

Species	Total Length (mm)	Jaw Depth (mm)	Jaw Length (mm)
Appalachiosaurus	968	188	502
Albertosaurus	560	196	180

regarding the skull dimensions and bite force and the hindlimb dimensions and velocity since these dimensions directly affect the outcome of bite force or velocity. These were plotted to visually represent the data to see if anything significant was occurring that could not be found with statistics. For the size of the "lollipop", bite force and velocity was used. For velocity, however, an average of Alexander's method was used to reduce errors.

RESULTS AND DISCUSSION

Hindlimb Length and Velocity

Using Alexander's Method, the velocities for *Appalachiosaurus* and *Albertosaurus* are not significantly different with the transition from walking to trotting being 13 km/hr and the transition from a trot to run being about 30-31 km/hr (Table **2**). Thulborn's equation also resulted in lower transitional velocities from walking to trotting;6.5 km/hr for *Appalachiosaurus* and 8.2 km/hr for *Albertosaurus* (Table **4**). Bakker's equation, while drastically different from the other methods, yielded much higher velocities for the two species during a trot to run transition at 101 km/hr and 122 km/hr respectively (Table **3**). These high velocities may be implausible, especially when considering the forested environment these theropods lived in during the Campanian.

Comparing *Appalachiosaurus* and *Albertosaurus*, there was not a significant difference in hindlimb dimensions nor in velocity (Table **2** and Fig. **1**). For the sake of comparison, two adult *Albertosaurus* were also used. These adults had longer hindlimbs and higher velocities than the juveniles. Again for comparison purposes, *Ornithomimus*, which has short hindlimbs in comparison, had a greater velocity. This may imply that shorter hindlimbs translate to lower velocity.

SKULL, JAW, AND BITE FORCE

The nasal of *Appalachiosaurus* lacks bony papillae projecting from the dorsal surface which is found in other tyrannosaurids, including *Albertosaurus libratus*. However, the nasal does have a row of 6 low bumps that travel along the midline and end at the maxillary processes. Midline bumps are also present, to a lesser extent, in *Albertosaurus libratus* (ROM 1247) [1]. On the maxilla of *Appalachiosaurus*, there are 5 dental alveoli with the longest being the seventh. In *Albertosaurus libratus*, the longest is in the fourth or fifth position. Both species have maxillary fenestra that are small and do not approach the rostrodorsal margin of the antorbital fossa. This fenestra is also separated from the rostral margin of the maxillary antorbital fossa by a wide apron of bone (Fig. **1**) [1]. The base of the ventral jugal process is slightly shallower in *Appalachiosaurus* at 20 mm compared to similar sized *Albertosaurus* which are roughly 32 mm (ROM 683) and 34 mm (ROM 1247) deep [1].

The ridge of the lacrimal of *Appalachiosaurus* does not assist the corneal process as it does in *Albertosaurus*, but the apex of the ridge is rostral to the lacrimal recess in both species [1]. However, the lacrimal recess is small in *Appalachiosaurs* compared to *Albertosaurus* (Fig. **2**) [1].

The carinae of the teeth of *Appalachiosaurus* are denticulate which is common in tyrannosaurids [1]. The serrations on the teeth in *Applachiosaurus* are the same as those found in *Albertosaurus* which are 5 mm apart [1, 16]. However, unlike *Albertosaurus*, the basal crown lengths of some of the teeth are elongated.

The length of the skull and jaw length are considerably longer in *Appalachiosaurus* than in *Albertosaurus* (Table **3**). However, jaw depth is very similar between the two species at 188 mm and 196 mm respectively.

Using an extrapolation based on all taxa the bite force of *Appalchiosaurus* was found to be roughly 32,500 Newtons (Figs. **3**, **4**). When using only mammals, bite force dropped considerably to 18,000 Newtons, but increased slightly to 33,800 Newtons when using only crocodylians (Table **4**). *Albertosaurus* has a slightly higher bite force at 42,000 Newtons when using all taxa and crocodylians (Fig. **3**; Table **4**). Like *Appalachiosaurus*, the bite force decreased considerably when applying method to mammals. (Fig. **3**; Table **4**). Using a paired T-Test with a confidence interval of 95%, there is a significance difference between the bite forces of *Appalachiosaurus* and *Albertosaurus* (p-value=0.0459; t=4.5077).

Despite the similarities in bite force, the skull of *Appalachiosaurus* is much longer and the jaw longer, but the jaw depth only slightly deeper. In comparison, *Tyrannosaurus rex* had a much larger skull and a much large bite force (7x greater) than that of both *Appalachiosaurus*

Table 4. Predicted Bite Force from Exponential Relationships for *Appalachiosaurus* and *Albertosaurus*

Appalachiosaurus					
Equation	**Body mass**	**Ln Body Mass**	**Exponential Bite Force (N)**	**Correction Factor (RE)**	**Corrected Bite Force (N)**
All taxa	623	6.42	29,469	1.1038	32,528
Crocodylians			33,817	1.0002	33,824
Mammals			16,250	1.1369	18,475
Albertosaurus					
Equation	**Body Mass**	**Ln Body Mass**	**Exponential Bite Force (N)**	**Correction Factor (RE)**	**Corrected Bite Force (N)**
All taxa	823	7.50	38,053	1.1038	42,003
Crocodylians			42,076	1.0002	42,084
Mammals			19,884	1.1369	22,607

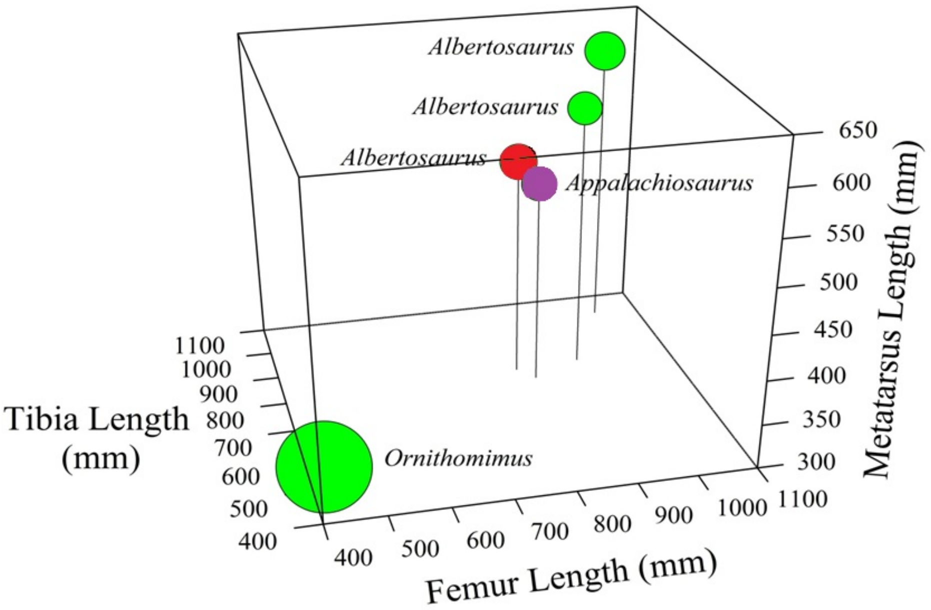

Fig. (1). Bite force compared to skull dimensions. Size of the lollypop is the average velocity using Alexander's method. *Appalachiosaurus* is represented as purple and *Albertosaurus* as red. The other *Albertosaurus* featured in the graph are adults used for the sake of comparison. The *Ornithomimus* was also used for comparison.

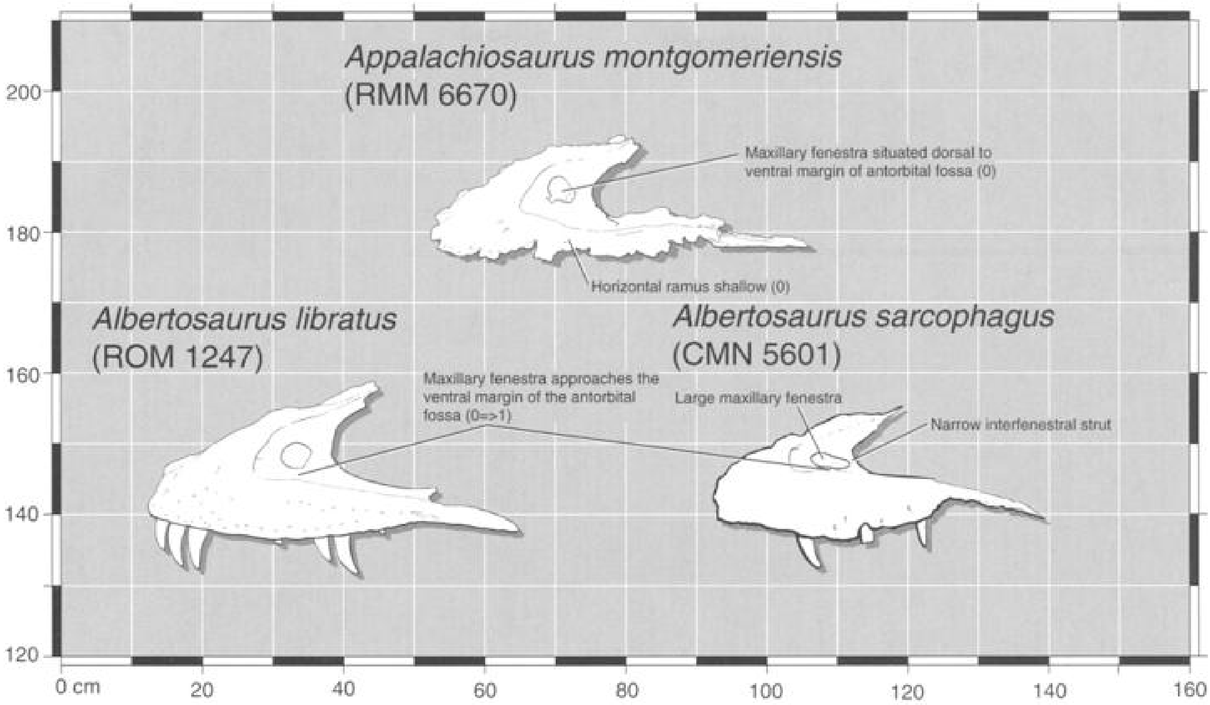

Fig. (2). Taxonomic characters of *Appalachiosaurus* and *Albertosaurus maxillae.* Adapted from Carr *et al.* [1]. The scale of the images can be measured in cm starting at the lower left corner.

and *Albertosaurus* [15]. It is interesting to note the similar size in skull and jaw length in *Appalachiosaurus* and *Tarbosaurus*, but the significant difference in jaw depth.

CONCLUSION

Similarities in the skull construction of *Appalachiosaurus* and *Albertosaurus* suggest they are closely related species, as suggested by Carr *et al.* [1]. However, differences in these skulls suggest differences in feeding mechanisms. Snively *et al.* [18] found that vaulting of the nasal, which is present in both specimens, increased the cross-sectional area of the skull which would have ultimately increased the strength of the skull in regards to bending and torsion. However, based on the skull dimensions, *Albertosaurus* would have been stronger than that of *Appalachiosaurus* which is supported by the differences in bite force. Snively *et al.* [18] also predicted *Albertosaurus*'*s* cranium to be no less than 1.5 times stronger in vertical bending than that of *Allosaurus*.

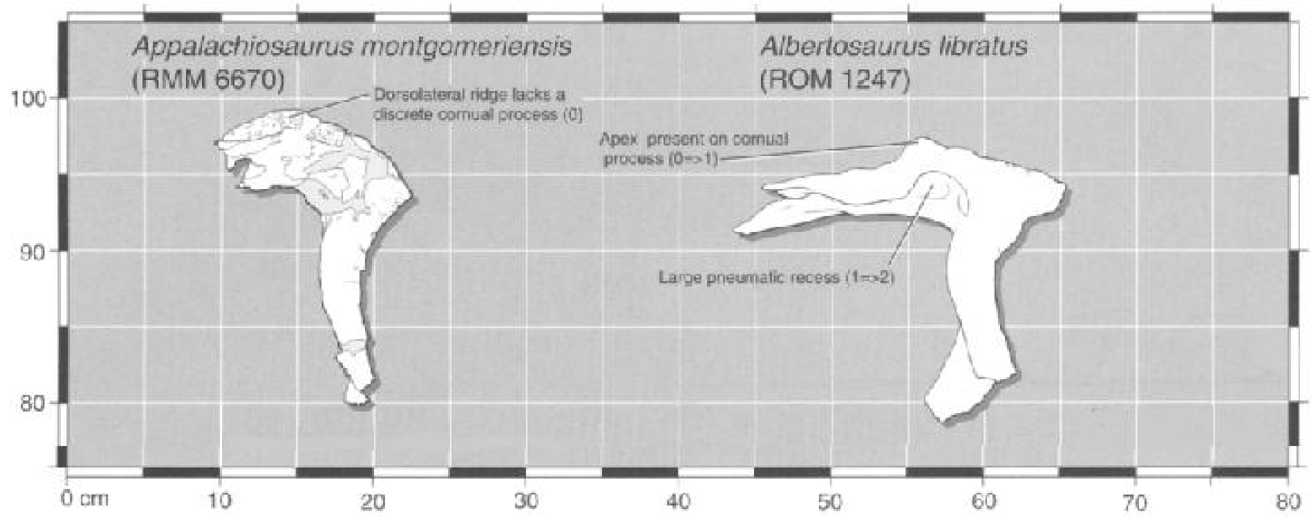

Fig. (3). Taxonomic characters of *Appalachiosaurus* and *Albertosaurus lacrimals*. Adapted from Carr *et al*. [1]. The scale of the images can be measured in cm starting at the lower left corner.

The slightly longer cranium of *Allosaurus* likely contributed to this reduced strength, which could translate to *Appalachiosaurus*, which has a longer cranium than *Albertosaurus*, having at least 1.5 times weaker vertical bending than *Albertosaurus*. The interlocking nasal-maxilla present in these specimens and other large theropods would help brace the joint against high concentrations of shear stress, ultimately acting as a shock absorber [19]. However, because we focused on juvenile specimens, their skulls are much weaker in vertical bending than adults, supporting the hypothesis that juveniles filled a different dietary niche than the adults. *Appalachiosuarus* which has a relatively taller and narrower skull than *Albertosaurus* would have been better equipped raking down and backwards into the flesh of prey [19, 20]. However, *Albertosaurus* most likely practiced a similar behavior. Based on their bite forces, they likely did not break bone often as did other large theropods such as *Tyrannosaurus rex*. It is more likely they left the bone and focused on the flesh of their prey. However, the high bending strength [6] of the tyrannosaurid cranial, including those of *Appalachiosaurus* and *Albertosaurus*, are consistent with biting into bone [18]. Furthermore, jaw depth is significantly correlated to typical prey size, but it is likely that based on regressions, overestimates are produced, especially for theropods [21]. For example, the regressions predict *T-rex* consuming an animal that weighed 10^6 kg, which is larger than any maximum weight estimates for dinosaurs. Despite the overestimates, jaw depth is potentially useful in determining ecological separation among theropods [21]. For this reason, *Appalachiosaurus* probably fed on slightly smaller prey than *Albertosaurus.* Skulls that feature increased skull length, as seen in both specimens, generally have increased strength of the maxillary teeth [5]. This means *Appalachiosaurus* and *Albertosaurus* would have been able to dispatch prey of equal or greater body size. However, because of their small skulls they likely used lateral shaking to dismember their prey rather than repeated biting.

These differences exhibited in cranium strength and bite force (Table **4**) suggest *Appalachiosaurus* and *Albertosaurus* fed on similar prey but were designed to feed differently. Two different killing styles are present in theropods: ambush and long-distance pursuit [21]. The moderate size of both *Appalachiosaurus* and *Albertosaurus* suggest they were likely ambush killers, but would have been able to engage in long-distance pursuit. Based on finds near the location of *Appalachiosaurus*, their prey was likely to be heavily armored or as large as them. Furthermore, the densely wooded area would have prevented *Appalachiosaurus* from reaching its potential top speeds. Therefore, it is likely *Appalachiosaurus* reached a max speed of around 13 km/hr when chasing prey, never transitioning from a trot to a run due to the enclosed area. The environment would have likely forced *Appalachiosaurus* to be an ambush predator, hiding behind dense vegetation. *Albertosaurus*, on the other hand, would have been able to easily engage in both ambush and long-distance pursuit as their environment was less densely vegetated. Therefore, they were likely to engage in speeds up to 30 km/hr when chasing prey, transitioning from a trot to a run. Although Bakker's equation produced speeds congruent with other tyrannosaurids he studied, these velocities are likely exaggerated due to discrepancies in limb length. van Valkenburgh and Molnar [21] suggest theropods are more similar to canids than felids based on skull size relative to body mass. Like canids, theropods have relatively larger skulls and smaller body mass. Snout width correlates with the choice of prey canids pursue. For example, larger snouted wolves and African hunting dogs often take down prey much larger than themselves where as the narrower snouted Ethiopian wolf hunts smaller prey such as rodents. The narrower snout suggests a weaker bite force (Fig. **5**). Although we were unable to find the snout width for *Albertosaurus*, it is likely its width was greater than that of *Appalachiosaurus*, but not significantly enough to delineate a difference in prey size. They likely took on smaller prey compared to *T-rex* which would have been able to take down larger prey such as sauropods alone. Furthermore, the serrations on the teeth would have aided in hunting as they

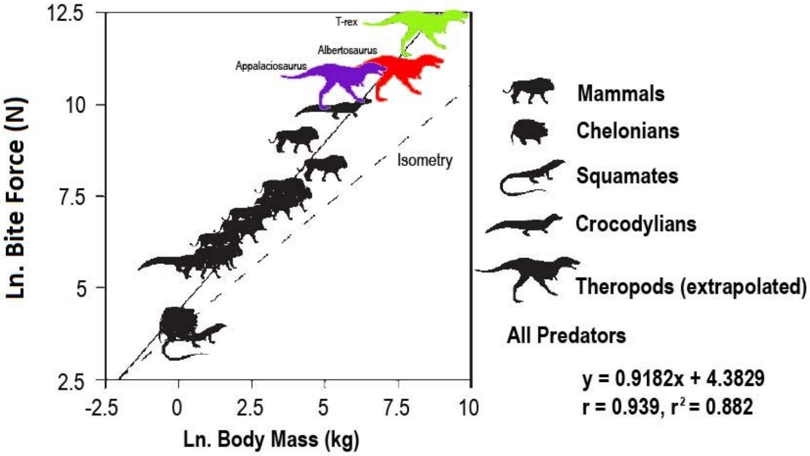

Fig. (4). Extrapolation of all taxa to determine potential bite force of *Appalachiosaurus* (purple) and *Albertosaurus* (red).

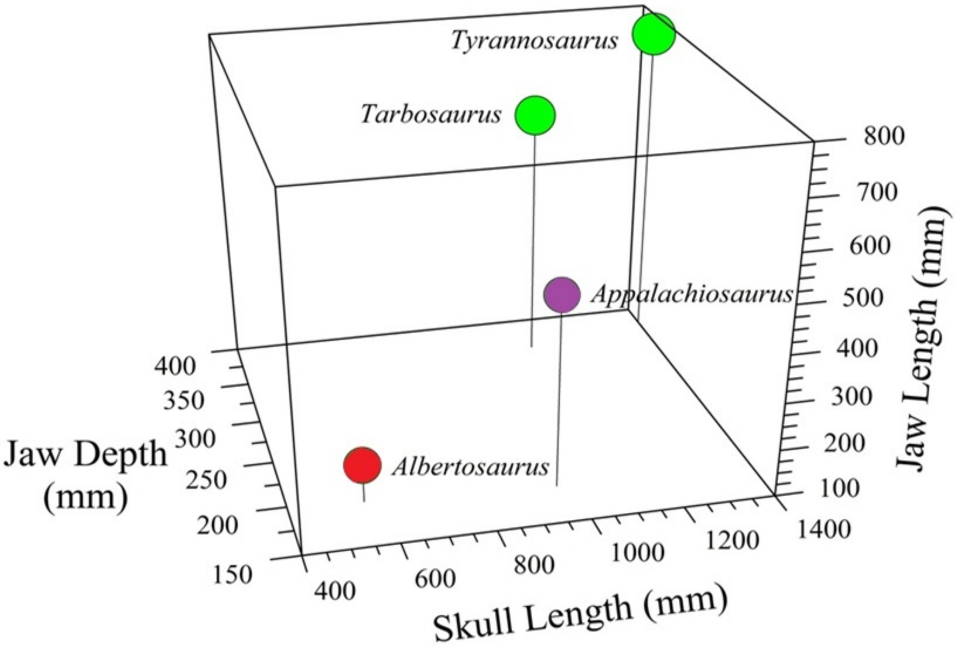

Fig. (5). Bite force compared to skull dimensions of selected dinosaurs. *Appalachiosaurus* is in purple and *Albertosaurus* in red. For comparison purposes, *Tyrannosaurus rex* and *Tarbosaurus*, a relative, were used.

would likely capture food that would later putrefy, making their bite a lethal dose of bacteria like the modern day Komodo dragon [14]. Understanding these functional differences allows us to partition *Appalachiosaurus* and *Albertosaurus* into two similar yet different ecological niches based on their feeding habits, despite their structural similarities.

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CONFLICT OF INTEREST

The authors confirm that this article content has no conflicts of interest.

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