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BIOMECHANICAL MODELING OF *COELOPHYSIS BAURI*: POSSIBLE FEEDING METHODS AND BEHAVIOR OF A LATE TRIASSIC THEROPOD

STEVEN E. JASINSKI[1,2]

[1] Section of Paleontology and Geology, State Museum of Pennsylvania, 300 North Street, Harrisburg, PA 17120-0024;
[2] Department of Biology, East Tennessee State University. Johnson City, TN 37614-1700

ABTRACT—*Coelophysis bauri* is a small theropod dinosaur from the Late Triassic of the southwestern United States. The Whitaker (= Ghost Ranch) quarry, which preserves hundreds to perhaps thousands of individuals, has led to many hypotheses about its behavior and feeding strategies. The beam theory allows for a quantitative approach to reconstruction of the feeding mechanism of *Coelophysis*. The *Coelophysis* mandible behaves as a simple lever, similar to that of *Varanus komodoensis*, and thus is more inclined to produce slashing bites. The mid-dentary region of the *Coelophysis* mandible has the greatest labiolingual strength, suggesting that this would have been the region most important to live prey capture. Comparisons of the juvenile and adult specimens of *Coelophysis bauri* show remarkable similarities in the relative mandibular strengths, suggesting juveniles would have been apt predators. Further study of the biomechanics of theropod dinosaurs such as *Coelophysis bauri* may lead to a better understanding of how they lived and behaved.

INTRODUCTION

The behaviors of extinct animals are often impossible to understand, although clues can be gathered as to how they once lived and behaved. In 1947, Edwin H. Colbert led a field party from the American Museum of Natural History to a hillside in Rio Arriba County in northern New Mexico after fossils were discovered there by George Whitaker (Schwartz and Gillette, 1994; Sullivan et al., 1996; Nesbitt et al., 2006, 2007). On this hillside, Colbert and his field crew recovered an amazing concentration of dinosaur skeletons. Colbert assigned these specimens to *Coelophysis bauri* Cope, 1887, which had previously been known only from incomplete material (Colbert, 1947, 1964, 1972, 1989, 1995; Schwartz and Gillette, 1994; Sullivan et al., 1996; Sullivan and Lucas, 1999; Lucas et al., 2005). Because of the large concentration found, *Coelophysis* has been part of a number of studies, especially as of late (e.g., Nesbitt et al., 2006; Rinehart et al., 2009). *Coelophysis* occupies a critical position in the early evolution of the Dinosauria, the Theropoda, and Aves because it is at the base of the clade leading to birds (Padian, 1986; Sereno et al., 1993; Schwartz and Gillette, 1994; Padian et al., 1999; Nesbitt et al., 2007).

The Whitaker quarry (also known as the Ghost Ranch quarry and the AMNH *Coelophysis* quarry) is located on Ghost Ranch, northwest of Abiquiu, Rio Arriba County, New Mexico (Schwartz and Gillette, 1994; Sullivan et al., 1996). The quarry is placed in the Upper Triassic Rock Point Formation (Chinle Group) and is of Apachean (late Norian-Rhaetian) age (Sullivan et al., 1996; Rinehart et al., 2009). The Whitaker quarry suggests an overall drier climate with heavy seasonal precipitation in a depositional environment consisting of a floodplain or a meandering river system that was part of western Pangaea (Schwartz and Gillette, 1994). A specimen (UCMP 129618) from the Petrified Forest Formation was reported by Padian (1986) as *Coelophysis bauri* and, while this identification has been called into question by some (Nesbitt et al., 2007), others (Spielmann et al., 2007) have agreed with the original referral. A number of streams have been suggested as part of the depositional environment around the *Coelophysis* Ghost Ranch specimens (Schwartz and Gillette, 1994). Rinehart et al. (2009) felt the *Coelophysis* specimens had been washed into a topographic low (i.e., a pond) and had been buried. The presence of numerous articulated skeletons, estimated to represent hundreds to thousands of individuals, is suggestive of a catastrophic event with relatively little transport (Colbert, 1989, 1995; Schwartz and Gillette, 1994; Rinehart et al., 2009). The Whitaker quarry *Coelophysis bauri* specimens, displaying a wide range of ontogenetic and individual variation among a single species, offer a large sample for comprehensive study.

Conclusions concerning *Coelophysis*, its phylogenetics, histology, and behavior, are still open to debate and reinterpretation even with all the research that has centered on this taxon. For example, one of the early specimens kept at the American Museum of Natural History (AMNH 7223) seemed to contain the remains of a "juvenile *Coelophysis*" within the rib cage of an adult, suggesting that *Coelophysis* may have been cannibalistic (Colbert, 1989, 1995; Rinehart et al., 2009). Recently this association has been reinterpreted; demonstrating that the remains were not of a juvenile *Coelophysis*, but those of an early crocodylomorph (Nesbitt et al., 2006). However, Rinehart et al. (2009) studied a single quarry block in great detail and felt they had other evidence for cannibalism in *Coelophysis*, including evidence from coprolites and regurgitalites. The large accumulation of skeletal remains is also suggestive of *Coelophysis* being gregarious and the Ghost Ranch individuals having been killed off by a single catastrophic event (Schwartz and Gillette, 1994; Rinehart et al., 2009). This concept has been critical in attempting to understand the behavior of *Coelophysis*.

In this paper I present an analysis of the biomechanical modeling of the *Coelophysis* mandible to determine probable feeding and social behaviors for this early theropod. This study employs the biomechanical modeling technique utilized by Therrien et al. (2005). Measurements of length and width were taken at landmarks along the mandible, which is treated as a "solid beam" that undergoes loads during food ingestion (Biknevicius and Ruff, 1992; Therrien et al., 2005). Dorsoventral and labiolingual strengths were calculated and then analyzed. Preferences of mandibles for shearing and slashing versus torsion and flexure were studied for several theropods, but specifically focusing on *Coelophysis*, and helped provide a more comprehensive understanding of this theropod.

Institutional Abbreviations: AMNH-American Museum of Natural History, New York, New York; CM-Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNH-Cleveland Museum of Natural History, Cleveland, Ohio; DMNS-Denver Museum of Nature and Science, Denver, Colorado; FMNH-Field Museum of Natural History, Chicago, Illinois; NMMNH-New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; RHMP-Ruth Hall Museum of Paleontology, Abiquiu, New Mexico; SMP-State Museum of Pennsylvania, Harrisburg, Pennsylvania; UCMP-University of California Museum of Paleontology, Berkeley, California; USNM-United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

METHODS AND MATERIALS

By looking at the amount and distribution of bone found around a given point in the mandible, calculations can be made to find strength towards shearing and slashing (on the horizontal axis), towards torsion and flexure (on the vertical axis), and relative strength throughout. An animal with higher strengths in the horizontal plane of the mandible should be better suited for slashing and shearing due to greater resistance to bending in this plane. In contrast, one with higher strength values in the vertical plane of the mandible should be better able to deal with torsion and flexure of struggling prey or crushing of bones and shells. Relative strength values provide an overall indication of the strengths in both planes throughout the mandible. *Coelophysis* mandible biomechanics are compared to other theropods and two extant varanids. Overall analysis suggests possible feeding methods and, in turn, a more comprehensive understanding of *Coelophysis*. As a note, Ivie et al. (2001) found that *Syntarsus* Raath 1969 was a generic homonym of the zopherid beetle *Syntarsus* Fairmaire, 1869, so they provided the replacement name *Megapnosaurus* for the dinosaur taxon.

Therrien et al. (2005) utilized a biomechanical modeling method that gives a measure of resistance to bending in lower jaws. In this study, two extant taxa were utilized, the Komodo dragon (*Varanus komodoensis*) and the adult Nile monitor (*Varanus nilocticus*), to portray modern analogs of large terrestrial predatory diapsids (Rieppel and Labhardt, 1979; Auffenberg, 1981; Losos and Greene, 1988; Molnar and Farlow, 1990; Therrien et al., 2005). Several theropod taxa, including *Coelophysis Megapnosaurus*, *Monolophosaurus*, *Ceratosaurus*, *Struthiomimus* and *Gorgosaurus* (see Table 1), were also compared to each other and to the extant varanid taxa utilizing this technique. External mandibular dimensions (width, depth, and length) were taken on the theropod mandibles in the dorsoventral and labiolingual planes, which were subsequently used to calculate the bending resistance strengths of the lower jaws (Fig. 1C). The lower jaw responds to feeding stresses and loads by depositing or reabsorbing bone, thus affecting its cross-sectional properties. Thus, the amount and distribution of bone can give an indication of the strength of the lower jaw. Data were collected using digital calipers and/or elephant calipers. Original specimens of the extinct theropod taxa were utilized and, in cases when original specimens were not available, museum-quality casts were measured. A very brief overview of the method, together with how and why it was used will be given below; for a more detailed description see Therrien et al. (2005).

TABLE 1. Properties of theropod mandibles in this study. **L** = total length of skulls and **(c)** indicates specimen was a museum-quality cast.

Genus	Species	#	landmark	log Zx/L	log Zy/L	Zx/Zy
Coelophysis	*bauri*	CM 81765	1	-2.19	-2.66	2.92
			2	-1.86	-2.19	2.17
(L=23.04)			3	-1.69	-2.14	2.79
			4	-1.61	-2.16	3.61
			5	-1.56	-2.24	4.85
Coelophysis	*bauri*	CM 82931	1	?	?	2.04
			2	?	?	2.02
(L=?)			3	?	?	?
			4	?	?	?
			5	?	?	?
Coelophysis	*bauri*	AMNH 7241	1	-2.52	-3.12	3.92
			2	-2.30	-2.75	2.85
(L=13.88)			3	-2.18	-2.63	2.86
			4	?	?	?
			5	?	?	?
Megapnosaurus	*kayentakatae*	USNM 442404 (c)	1	-1.55	-2.13	3.78
			2	-1.19	-1.61	2.59
(L=21.83)			3	-1.14	-1.56	2.57
			4	-0.96	-1.31	2.25
			5	-0.72	-1.33	4.10
Ceratosaurus	sp.	AMNH 27631 (c)	1	-0.04	-0.59	3.56
			2	0.04	-0.38	2.62
(L=61.6)			3	0.39	-0.31	4.97
			4	0.57	-0.01	3.81
			5	0.71	0.19	3.26
Monolophosaurus	*jiangi*	AMNH 652 (c)	1	-0.03	-0.54	3.21
			2	-0.07	-0.47	2.54
(L=64.64)			3	-0.04	-0.70	4.60
			4	0.51	-0.32	6.85
			5	0.72	-0.02	5.40
Struthiomimus	sp.	USNM 487137 (c)	1	-1.47	-2.05	3.80
			2	-1.29	-1.91	4.15
(L=19.46)			3	-1.03	-1.78	5.58
			4	-0.81	-1.58	5.83
			5	-0.72	-1.46	5.46
Gorgosaurus	*libratus*	USNM 012814 (c)	1	0.27	0.04	2.04
			2	0.51	0.15	2.27
(L=76.96)			3	0.50	-0.69	15.31
			4	0.95	-0.07	10.51
			5	1.02	0.03	9.73

Mandibles were measured approximately in an *in vivo* orientation by aligning the symphyseal surface along the vertical plane prior to measurement (Fig. 1). The mandibular depth (= dorsoventral dimension) was measured with the caliper blades oriented labiolingually, and the mandibular width (= labiolingual dimension) was measured with the caliper blades oriented dorsoventrally. To construct the beam models and compare them for the different taxa, measurements were made at homologous and easily identifiable landmarks along the mandible. As in Biewener (1992) and Therrien et al. (2005), five landmarks were identified: (1) at the second tooth alveolus; (2) at the mid-dentary (midway between the anterior limit of the mandibular symphysis and the superior dentary suture with the surangular); (3) at the upper dentary suture with the surangular; (4) at the lower dentary suture with the angular; and (5) at the location of the maximum mandibular depth (Fig. 1A-B), and values of “a” and “b” (dorsoventral radius and labiolingual radius, respectively, Fig. 1C), were taken at each. These data were used in the following calculations (from Therrien et al., 2005) to determine distributions of bone around a given axis:

1) $I(x) = \pi b a^3/4$,

distribution of bone about the labiolingual axis (in cm^4);

2) $I(y) = \pi a b^3/4$,

distribution of bone about the dorsoventral axis (in cm^4). The values gained from these equations were subsequently put into another set of equations:

3) $Zx = I(x)/a$,

bending strength in the dorsoventral plane (or about the labiolingual axis, in cm^3);

4) $Zy = I(y)/b$,

bending strength in the labiolingual plane (or about the dorsoventral axis, in cm^3).

The values of Z are measures of strength in bending, and are determined by the amount of bone present at different points along the lower jaw. Distances were also measured to the anterior- and posterior-most points of the mandible from each given landmark, aiding in the calculations for bite strengths at given points.

The main tooth-bearing section of the mandible, and therefore the portion most involved in feeding, was subdivided into two separate sections; (1) a pre-mid-dentary section between landmarks 1 and 2, and (2) a post-mid-dentary section, found between landmarks 2 and 3 (Figs. 1A-B). Relative changes along the tooth row can be found by division between the two sections, and these can be used for simpler comparisons. When more than one specimen was available for a taxon, an average was taken, and the results are presented as semi-log plots to reduce the effect of allometry (see Smith, 1984, 1993; Therrien et al, 2005). The graphs of log Zx/L represent the dorsoventral strength of the mandible, based on the torsions from the posterior to the anterior portion. The

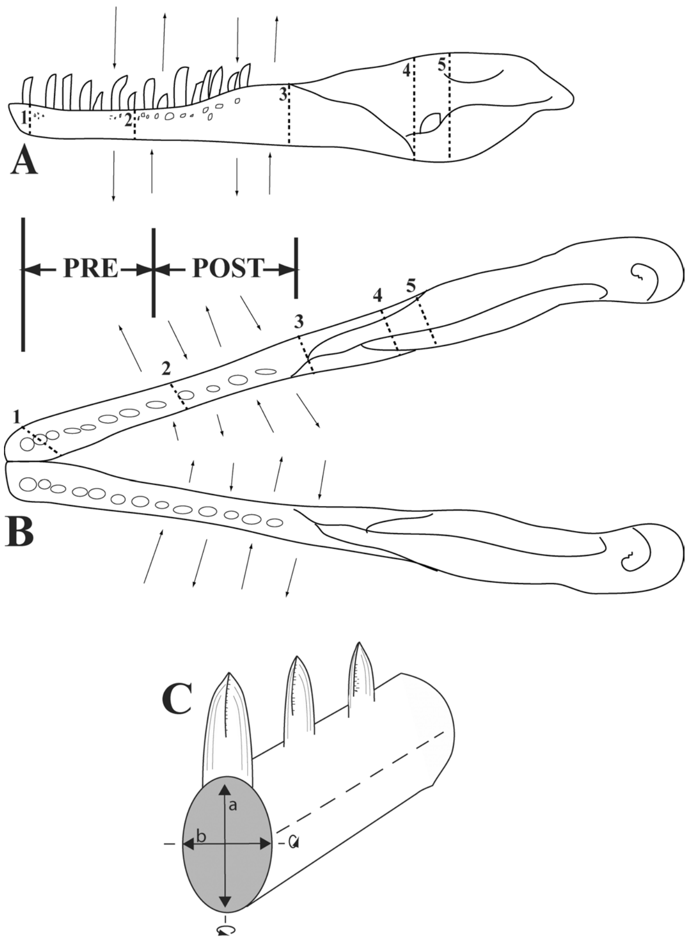

FIGURE 1. **A-B**, landmarks on theropod mandibulae in **A**, lateral view showing dorsoventral strengths and loads; and **B**, occlusal view showing labiolingual strengths and loads; **1**, landmark 1 at the second tooth alveolus, **2**, landmark 2 at mid-dentary, **3**, landmark 3 at upper dentary suture with the surangular, **4**, landmark 4 at lower dentary suture with the angular, and **5**, landmark 5 at the location of maximum mandibular depth. **PRE**, pre-mid-dentary region and **POST**, post-mid-dentary region are also marked. More detailed explanations are available in the text and in Therrien et al. (2005); **C**, Cross-section of hypothetical mandible showing dimensions measured and orientation of cross-sectional properties evaluated, with Ix and Zx in the dorsoventral plane (about x axis) and Iy and Zy in the labiolingual (or mediolateral) plane (about y axis); (modified from Therrien et al., 2005).

graphs of log Zy/L represent the labiolingual strength throughout the mandible, derived from the strength from the inside to outside of the mandible and help convey strength from flexure and torsion of the mandible. The relative strength profiles (Zx/Zy) give the relative proportions of the mandible (depth and width).

RESULTS

Three specimens of *Coelophysis bauri* were measured: one complete adult specimen (CM 81765), one incomplete adult specimen (CM 82931), and one nearly complete juvenile or sub-adult specimen (AMNH 7241). The complete adult specimen (CM 81765) allowed for accurate data of all needed measurements. CM 82931, from the same block as CM 81765, is only a partial skull, with only relative strength values able to be derived from the second tooth alveolus and the mid-dentary, and these are suspect due to the preservation and taphonomy of the skull and mandible. The third *Coelophysis* specimen (AMNH 7241) is a juvenile or sub-adult, as suggested by the proportionately larger orbit size and overall shorter skull length. Precise measurements were obtained from AMNH 7241, except for those of the depth of the mandible at the lower dentary suture and the place of maximum depth. Therefore, values were calculated at the second tooth alveolus, mid-dentary, and upper dentary suture only.

CM 81765 shows a decrease anteriorly along the mandible in dorsoventral strength (Fig. 2A). While the decrease in Zx/L is nearly uniform from the maximum depth to the second tooth alveolus, the profile gives a slightly convex curve ranging from -1.56 to -2.19, respectively (see Table 1 for values and properties of studied theropod mandibles). The labiolingual strength profile behaves in much the same way as the dorsoventral plane, but the curve is far shallower until the mid-dentary is reached, after which the slope is greater to the second tooth alveolus, ranging from -2.24 at the maximum depth to -2.66 at the second tooth alveolus. The Zx/Zy ratio for the adult has a positive slope in the post-mid-dentary region and a negative slope in the pre-mid-dentary region. Values range from 4.85 at the maximum depth position, to 2.17 at the mid-dentary, up to 2.92 at the second tooth alveolus.

CM 82931 represents a smaller individual whose dorsoventral and labiolingual strengths cannot be calculated due to incompleteness along the length of the lower jaw from the articular fossa to the anterior extremity. A negative slope in the Zx/Zy profile is shown from the mid-dentary to the second tooth alveolus, with the second tooth alveolus being slightly greater than the mid-dentary. The juvenile (or sub-adult) *Coelophysis* (AMNH 7241) shows remarkably similar profiles to the adult in its dorsoventral, labiolingual, and relative strength profiles (Fig. 2B) from the upper dentary suture to the second tooth alveolus. Both the dorsoventral strength profile and the labiolingual strength profile begin with convex curves running from the upper dentary suture to the second tooth alveolus, with a positive slope overall. The relative strength profile is also similar to the adults, with a concave curve and a negative slope from the upper dentary suture to the second tooth alveolus. The biggest differences between the two deal with the absolute force values of the differing strength profiles. The dorsoventral strengths are -1.69 to -2.19 (adult) vs. -2.17 to -2.53 (juvenile) anteriorly along the mandible (from the upper dentary suture to the second tooth alveolus). The labiolingual strengths range from -2.13 to -2.66 vs. -2.63 to -3.12 anteriorly along the mandible (from the upper dentary suture to the second tooth alveolus). The relative strengths range from 2.79 to 2.92 vs. 2.86 to 3.92 anteriorly along the mandible (from the upper dentary suture to the second tooth alveolus).

Careful analyses of dorsoventral strength, labiolingual strength, and relative strength of a number of extinct theropod taxa can be found in Therrien et al. (2005), including those of *Dilophosaurus wetherlii*, *Ceratosaurus nasicornis*, *Majungasaurus atopus*, *Carnotaurus sastrei*, *Suchomimus tenerensis*, "*Antrodemus valens*," *Allosaurus fragilis*, *Acrocanthosaurus atokensis*, *Giganotosaurus carolinii*, *Dromaeosaurus albertensis*, *Deinonychus antirrhopus*, *Velociraptor mongoliensis*, *Saurornitholestes langstoni*, *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Daspletosaurus torosus*, and *Tyrannosaurus rex*. The bite strength profiles of these can be compared to those from this study for a more detailed analysis. *Megapnosaurus kayentakatae* (= *Syntarsus kayentakatae* Rowe, 1989) was a theropod from the Early Jurassic of Arizona with the dorsoventral strength of the mandible having a fairly constant slope (Fig. 2C). The only major deviation is at the mid-dentary, which is higher than would be expected if the mandible was used as a simple lever during feeding. This makes a convex curve about the mid-dentary, with values of -0.72 at the maximum depth to -1.55 at the second tooth alveolus. The labiolingual applied force profile shows a slightly convex curve, with values ranging from -1.33 at the maximum depth to -2.12 at the second tooth alveolus. The Zx/Zy profile shows a concave curve with values at the maximum depth and the second tooth alveolus both being around 4.00. *Megapnosaurus* is one of the closest known relatives of *Coelophysis*.

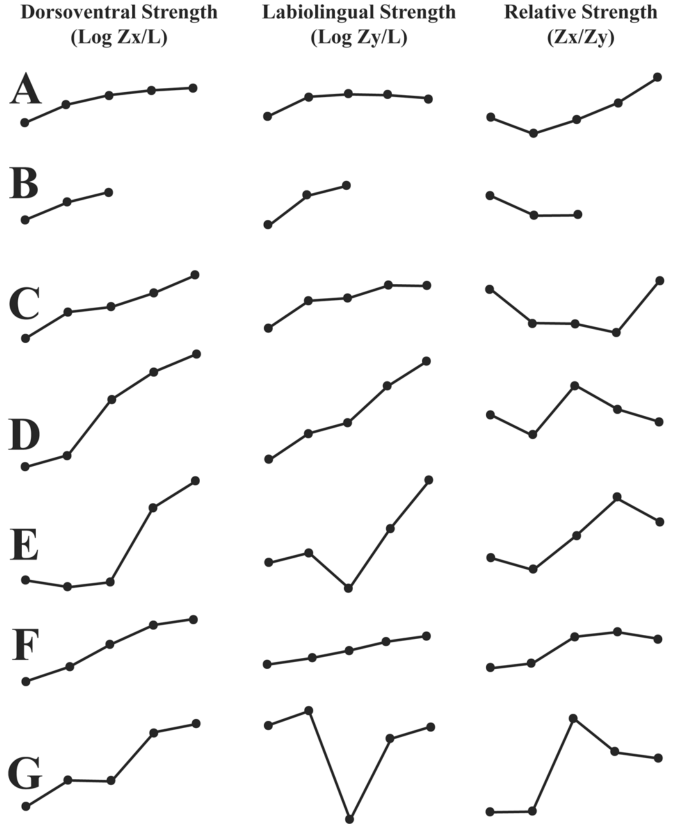

FIGURE 2. Properties of selected theropods. Proceeding left to right, dots represent values from Table 1 for landmarks 1-5, respectively. **A**, CMN 81765 (adult *Coelophysis bauri*), **B**, AMNH 7241 (juvenile *Coelophysis bauri*), **C**, USNM 442404 (*Megapnosaurus kayentakatae*), **D**, AMNH 27631 (*Ceratosaurus* sp.), **E**, AMNH 652 (*Monolophosaurus jiangi*), **F**, USNM 487137 (*Struthiomimus* sp.), and **G**, USNM 012814 (*Gorgosaurus libratus*). For more detailed specimen information and values see Table 1.

Ceratosaurus, a ceratosaurid from the Late Jurassic of the western United States, had dorsoventral and labiolingual forces decreasing in similar fashions (Fig. 2D). While there is a small concave curve around the mid-dentary in the dorsoventral strength, the small curve is convex in the labiolingual force profile of the mandible. The absolute values, in comparison, show larger values for the possible dorsoventral forces. The Zx/Zy values of the *Ceratosaurus* mandible demonstrate a stronger portion at the second alveolus than at the mid-dentary, followed by the upper suture of the dentary being far stronger than both, and finally lowering in strength posterior to the upper suture.

Monolophosaurus jiangi was a carnosaur from the Late Jurassic of China whose mandibular force decreases slowly in the post-mid-dentary region; on the other hand, the mandible is stronger at the second tooth alveolus than at the mid-dentary, producing a slightly positive pre-mid-dentary slope (Fig. 2E). The labiolingual force profile is very similar to that of the dorsoventral strength, with nearly the same slope in the post-mid-dentary. The major difference is anterior to the upper suture of the dentary, with the labiolingual strength profile having a concave curve (versus the convex curve of this portion of the mandible in the dorsoventral strength profile) and the mid-dentary being stronger then the second tooth alveolus. The absolute applied force values for the dorsoventral strength are most similar to the *Giganotosaurus* and *Acrocanthosaurus* (Allosauroidea). The mandible of *Monolophosaurus* has Zx/Zy decrease from 5.40 to 3.21, with increases being found from the maximum depth to the lower suture of the dentary and from the mid-dentary to the second tooth alveolus.

The dorsoventral strength of *Struthiomimus* shows a nearly uniform decrease in its rate anteriorly along the mandible, with the post-mid-dentary and pre-mid-dentary slopes being nearly equal (Fig. 2F). The labiolingual strength profile has a fairly constant slope anteriorly along the mandible. This, like those of the two varanid species, shows that the mandible behaves like a simple lever in *Struthiomimus*. The relative applied force profile that could be withstood by the mandible is not quite as simple, though. The profile shows a gradual decrease anteriorly along the mandible, with the maximum applied force being present around the lower dentary suture.

Gorgosaurus libratus (= *Albertosaurus libratus* of some authors, but maintained here per Currie, 2003) was a large tyrannosaurid from the Late Cretaceous of Alberta. Anteriorly, the dorsoventral strength (Zx/L) is relatively uniform, except for a slightly abnormally low value at the upper suture of the dentary (Fig. 2G). The dorsoventral force decreases rapidly when moving from the location of maximum mandibular depth to the lower suture of the dentary and from the mid-dentary to the second tooth alveolus. The labiolingual forces show a drastic decrease moving from the lower suture of the dentary to the upper suture of the dentary, followed by a dramatic increase to the mid-dentary. The relative strength profile of *G. libratus* shows a decrease anteriorly overall from 9.73 to 2.04, with a dramatic maximum of over 15 at the upper suture of the dentary. This infers the mandible of *Gorgosaurus* becomes rounder posteriorly.

INTERPRETATION AND DISCUSSION

Mandibular force profiles reveal relative maximum force distributions along the length of the mandible. Two varanid species, *Varanus komodoensis* and *V. nilocticus*, reveal relative maximum force distributions similar to those of theropods (Therrien et al., 2005, fig. 35). The Komodo dragon (*V. komodoensis*) has values greater than 2.00 in its post-mid-dentary, indicating that the mandible, in this region, is at least twice as deep as it is wide and, consequently, that dorsoventral loads are twice as essential as labiolingual loads, while labiolingual loads become more important toward the mandibular symphysis (Therrien et al., 2005). Therefore, the post-mid-dentary portion of the mandible of *V. komodoensis* is adapted for slicing and the pre-mid-dentary portion is slightly better adapted toward labiolingual loading and torsion that may occur during biting, prey handling, and food acquisition or prehension (Therrien et al., 2005). These patterns are consistent with the ambush-style feeding behavior described for *V. komodoensis* (Rieppel, 1979; Auffenberg, 1981; Losos and Greene, 1988; Therrien et al., 2005).

Varanus nilocticus has a Zx/Zy value of roughly 1.00 at the second tooth alveolus, which has been interpreted as an adaptation to resisting torsional loads while crushing hard shells with the posterior teeth (Hylander, 1979, 1981; Therrien et al., 2005). So, while the *V. komodoensis* mandible is well suited for dorsoventral loads along the tooth row and for sustaining labiolingual loads that may be exerted by struggling prey or during food ingestion near the mandibular symphysis, *V. nilocticus*, a creature that uses slower, more powerful crushing bites, is nearly as strong in the labiolingual plane of the mandible as in the dorsoventral plane, and uses this strength for the great resistance against torsional moments generated in the crushing of shells (Therrien et al., 2005). Therefore, mandibular properties, particularly those in the anterior extremity of the mandible, can and do mirror changes in behavior and/or diet.

Coelophysis bauri (CM 81765) has relatively simple dorsoventral and labiolingual strength profiles (Fig. 2A). The strength values in the dorsoventral and labiolingual planes most closely resemble the values obtained by Therrien et al. (2005) for dromaeosaurs, specifically those of *Saurornitholestes* (fig. 38), and *Varanus komodoensis* (fig. 35). The dorsoventral values for *Coelophysis* (-2.19 to -1.55, anteriorly to posteriorly) are rather intermediate between *V. komodoensis* (-2.39 to -0.99) and dromaeosaurids (-1.87 to -0.77). The labiolingual strengths for *Coelophysis* (-2.66 to -2.24) are weaker than those of the dromaeosaurs (-2.24 to 1.27) studied by Therrien et al. (2005) and closer to *V.*

komodoensis (-2.60 to -1.39). This suggests that stresses and loads endured from flexure and torsion (i.e., struggling prey) were more significant for *Coelophysis* than those endured during slashing and shearing. The greater values found in the posterior portion of the mandible for both planes show that this region incurred higher stress during feeding. The anterior of the mandible, showing the least strength, was apparently subjected to lower stress.

The Zx/Zy profile of *Coelophysis* (Fig. 2A) shows a drop in relative strength in the post-mid-dentary, compared to a rise in strength in the pre-mid-dentary. It shows a relatively important anterior extremity of the mandible, and a relatively strong posterior portion of the mandible compared to the central region. With a drop from the second tooth alveolus to the mid-dentary, a relatively strong point in the mandible is anterior. The posterior of the mandible becomes more elliptical, inferring more importance for slashing and shearing. *Coelophysis* potentially could have used its mandible for slashing and shearing based on having more strength in the dorsoventral plane. The mandible at the mid-dentary is rounder than the rest of the mandible, showing that, while the torsion and flexure resulting from struggling prey wasn't very characteristic of *Coelophysis*, the mid-dentary portion of the mandible would have been the most useful region for coping with this type of behavior. *Coelophysis* could have taken prey with quick, fast bites without a lot of prey manipulation. The high Zx/Zy values show that the mandible could have been used almost exclusively for slashing and shearing of flesh, and that the anterior portion of the mandible could have been used for some prey manipulation.

In *Coelophysis*, the anterior teeth are smaller, become larger towards the mid-dentary, and decreasing in size again posteriorly, as is generally the case in theropods. The relative size of the teeth tends to follow the patterns seen in the dorsoventral and labiolingual strengths of the mandible. *Coelophysis*, with teeth smaller in front and becoming slightly larger for slicing flesh more posteriorly, could have potentially preyed in another way, possibly taking prey much larger then itself. In live prey capture, *Coelophysis* could have opened up wounds on its prey, much as *Varanus komodoensis* does to some of its large mammalian prey today (Rieppel, 1979; Auffenberg, 1981; Losos and Greene, 1988; Therrien et al., 2005; Moreno et al., 2008; Fry et al., 2009). A similar mechanism has been proposed for dromaeosaurids by Therrien et al. (2005), among others.

Although data could not be obtained for the posterior portion of the juvenile jaw, anteriorly, the juvenile *Coelophysis* (AMNH 7241) jaw shows many similarities to that of the adult. The overall shape of the dorsoventral and labiolingual strength profiles is very similar, with the greatest change of the juvenile just after the mid-dentary (Figs. 2A-B). All strength values in the juvenile are lower than those of the adult, even though overall size should not be a cause due to the use of ratios. It is noted that the relative positions of the landmarks in the juvenile and adult are similar, suggesting further similarities between the two. In the dorsoventral strength profile, the adult has an increase by a factor of 1.18 from the second tooth alveolus to the mid-dentary and an increase of 1.10 from the mid-dentary to the upper dentary suture, compared to 1.10 and 1.06 in the juvenile, respectively. For labiolingual strengths, the values show an increase by a factor of 1.20 from the second tooth alveolus to the mid-dentary and an increase of 1.02 from the mid-dentary to the upper dentary suture, compared to 1.13 and 1.04 in the juvenile, respectively. In the relative strength profiles, the juvenile, like the adult, shows a propensity toward shearing and slicing of flesh. The upper dentary suture region in the juvenile is of more relative importance for the acquisition of live prey in comparison to the adult. The factor of decrease in the anterior-most portion of the relative strength profiles is 1.35 in the adult compared to 1.38 in the juvenile, while the factor of change from the mid-dentary to the upper dentary suture increases by a factor of 1.29 in the adult compared to roughly 1.00 in the juvenile. The parallels seen between the adult and juvenile of *Coelophysis* mean that both age groups could have used many of the same feeding behaviors. The difference in strength values suggests that juveniles may have taken relatively smaller prey then older individuals. Therrien et al. (2005) suggested a similar idea with tyrannosaurids and felt that similarities in different ontogenetic stages meant that juveniles were probably apt predators as well. The relatively greater labiolingual strength at the upper dentary suture means that juvenile *Coelophysis* were capable of live prey capture. Juvenile *Coelophysis*, therefore, may have been precocial.

Megapnosaurus (= *Syntarsus* Raath, 1969) has been suggested by Yates (2005) as possibly being synonymous with *Coelophysis* (specifically referring to *M. rhodesiensis*). Other authors have also argued that "*Megapnosaurus*" was actually a junior synonym of *Coelophysis* (Paul, 1988, 1993; Bristowe and Raath, 2004; Bristowe et al., 2004). Estimates of the size and weight of *Megapnosaurus* are essentially the same as those of *Coelophysis*, although *Megapnosaurus* is a younger taxon biostratigraphically. The dorsoventral strengths seen in *Megapnosaurus kayentakatae* (USNM 442404, Fig. 2C) are all higher than those seen in *Coelophysis bauri* (CM 81765). The same is true of the labiolingual strength profiles of *Megapnosaurus* and *Coelophysis*. Again, while *Coelophysis* shows a more uniform change throughout the mandible, a relatively weak point is found at the upper dentary suture in the labiolingual and dorsoventral strength profiles of *Megapnosaurus*. The dorsoventral strengths of the *Megapnosaurus* mandible are very similar to those of the dromaeosaurs, although they may be a bit higher. The labiolingual strengths of the *Megapnosaurus* mandible show values similar to dromaeosaurs as well, although the labiolingual strengths of *Dromaeosaurus albertensis* (Therrien et al., 2005, fig. 38) are a bit higher. The most glaring difference between *Coelophysis* and *Megapnosaurus* is in the Zx/Zy profiles (Fig. 2A, C). *Megapnosaurus* heavily favors dorsoventral strength and, therefore, slicing and shearing in the mandible at the second tooth alveolus and the position of maximum depth in the mandible. The entire middle portion is far more important in the possible torsion and flexure from prey capture, although these three points are less important for live prey capture in *Megapnosaurus* then at the mid-dentary of *Coelophysis*.

Ceratosaurus sp. (AMNH 27631), while not identified to species level, had dorsoventral and labiolingual strength profiles similar in shape to *Ceratosaurus nasicornis* studied by Therrien et al. (2005, fig. 36). Values were higher in both the dorsoventral and labiolingual strengths (Fig. 2D) of AMNH 27631. The Zx/Zy profile shows a large degree of variability throughout the mandible, with regions at the mid-dentary and the posterior being more relevant to live prey capture, or manipulation, or both. The lower values of Zx/Zy towards the back of the mandible could be an indication of crushing, such as in *Varanus nilocticus*. *Ceratosaurus* was one of the relatively larger predators of the Late Jurassic of the American West, although not nearly as numerous as *Allosaurus*. This could mean that ceratosaurs were more specialized than allosaurs. This specialization suggests some degree of predation on live prey, although higher values in the relative strength profiles suggest prey that offered fairly little resistance.

Monolophosaurus jiangi, similar in size and weight to *Ceratosaurus*, roamed China roughly 20 million years before *Ceratosaurus* prowled the American West. Not surprisingly, values for the dorsoventral and labiolingual strengths (Fig. 2E) of *Monolophosaurus* (AMNH 652) are very similar to those of *Ceratosaurus* sp., with relatively close profile shapes. The biggest difference is around the mid-dentary and upper dentary suture. The upper dentary suture of *Monolophosaurus* has lower strength values in both profiles compared to *Ceratosaurus*. *Ceratosaurus* was more dorsoventrally and labiolingually buttressed in this portion of the mandible than was *Monolophosaurus*. The Zx/Zy profile follows this same general trend. The upper dentary suture of *Monolophosaurus* is slightly more inclined to torsional and flexural loads than *Ceratosaurus*. At the lower dentary suture, *Monolophosaurus* becomes far more dorsoventrally supported, while *Ceratosaurus* is more labiolingually buttressed at this point. Both theropods have a negative slope of the Zx/Zy profiles posteriorly toward the position of maximum depth, but *Ceratosaurus* (value = 3.26, Table 1) is still more inclined to prey manipulation and flexure at this point than *Monolophosaurus* (= 5.40). This is interesting in that both genera are relatively similar in dorsoventral and labiolingual strength profiles, which could be a reflection of the size relationship between the two.

Struthiomimus sp. was a Late Cretaceous edentulous theropod. While its exact diet is not known, the toothless nature of its jaw suggests its diet would have been fairly simple. Not surprisingly, the dorsoventral and labiolingual strength profiles of *Struthiomimus* sp. (USNM 487137, Fig. 2F) show a fairly constant change throughout the mandible and take on the properties of a simple lever. The dorsoventral strength profile shows greater strengths than the labiolingual profile, indicating that vertical forces and loads were greater during feeding in *Struthiomimus*. The shapes of the Zx/L and Zy/L profiles of *Struthiomimus* are very similar to that of *Coelophysis*, although strengths are higher throughout the *Struthiomimus* mandible, undoubtedly due to its larger comparative size. The relative strength profile of *Struthiomimus* shows an overall convex shape, versus the overall concave relative strength profile of *Coelophysis*. The anterior portion of the mandible is important for the flexure and torsion from possible live prey capture, while the posterior portion is more dorsoventrally buttressed. While this doesn't directly demonstrate that *Struthiomimus* was a carnivore, herbivore, or omnivore, it does document relative mandible strengths, and utilization of the beam theory on some herbivores such as similarly-sized ornithopods and other theropods, which can possibly help show what its diet may have been.

Gorgosaurus libratus was a large tyrannosaurid with interesting mandibular profiles when compared to other non-tyrannosaurid theropods. The dorsoventral strength profile of *G. libratus* (USNM 012814, Fig. 2G) continuously increases posteriorly, except from the mid-dentary to the upper dentary suture, where both values are virtually equal. The labiolingual strength profile is more complicated, showing an increase from the second tooth alveolus to the mid-dentary, followed by a large drop to the upper dentary suture. This is followed by a large rise in labiolingual strength to the lower dentary suture, and finally a smaller rise to the position of maximum depth. The values in both are similar to those of other tyrannosaurids studied by Therrien et al. (2005), further suggesting similarities in the feeding habits of tyrannosaurids. The Zx/Zy profile of *Gorgosaurus* suggests a drop in labiolingual strength at the upper dentary suture. The anterior portion of the mandible is close to a ratio of 2.00 with dorsoventral versus labiolingual strengths. This is followed by a dramatic rise, and then a less considerable drop through the posterior of the mandible. The anterior of the mandible was more inclined to cope with stresses and loads from torsion and flexure, followed by more slicing and shearing moving posteriorly on the mandible. One possibility is that *Gorgosaurus* could have caught live prey with the anterior of its mandible, and used the posterior portion to slice the prey apart, although it could have also scavenged, preyed on larger or smaller prey animals, or any number of other possible behaviors.

CONCLUSIONS AND SUMMARY

The beam theory used by Therrien et al (2005) allows for a quantitative approach to determining how *Coelophysis* may have fed and behaved. Extinct theropods show variability between taxa, while the relative shapes are all reasonably analogous. Values change throughout, but dorsoventral strengths are virtually always stronger and more important in the mandibles of theropods. The mandible of *Coelophysis* behaved like a simple lever, with the mid-dentary being the most important in terms of live prey capture and manipulation. The overall shape of the mandible strength profiles and values were most similar to and lie between those of *Varanus komodoensis* and the dromaeosaurs. It has been suggested that dromaeosaurs took part in live prey capture, probably in groups or packs, and it is known that *V. komodoensis* take both carrion and large mammalian prey at times. It is thus suggested that *Coelophysis* did take part in live prey capture, specifically referring to prey larger than insects or small vertebrates. The mandible of the juvenile *Coelophysis* closely resembles that of the adult specimen of *Coelophysis*, with the former showing lower strength values throughout. The juvenile shows relatively high labiolingual strengths, suggesting juveniles may have taken part in live prey capture as well. A thorough study of more specimens of *Coelophysis* across all sizes and age ranges would provide greater insight into the possibilities of *Coelophysis* living in smaller groups and taking larger prey, but more study is needed to confirm or deny this.

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