

Constraining the body mass range of *Anzu wyliei* (Theropoda: Caenagnathidae) using volumetric and extant–scaling methods

Kyle L. Atkins-Weltman^{1*}, Eric Snively², and Patrick O'Connor^{3,4}

¹660 Gateway Court, Apt N2, Lawrence, KS, 66049, USA; flarginblarg@gmail.com

²OSU College of Osteopathic Medicine at the Cherokee Nation, 19500 E. Ross Street, Tahlequah, OK, 74464, USA; eric.snively@okstate.edu

³Department of Biomedical Sciences, 228 Irvine Hall, Ohio University Heritage College of Osteopathic Medicine, Athens, OH, 45701, USA; oconnorp@ohio.edu

⁴Ohio Center for Ecological and Evolutionary Studies, Irvine Hall, Ohio University, Athens, Ohio, 45701, USA

Abstract: The ability to accurately and reliably estimate body mass of extinct taxa is a vital tool for interpreting the physiology and even behavior of long-dead animals. For this reason, paleontologists have developed many possible methods of estimating the body mass of extinct animals, with varying degrees of success. These methods can be divided into two main categories: volumetric mass estimation and extant scaling methods. Each has advantages and disadvantages, which is why, when possible, it is best to perform both, and compare the results to determine what is most plausible within reason. Here we employ volumetric mass estimation (VME) to calculate an approximate body mass for previously described specimens of *Anzu wyliei* from the Carnegie Museum of Natural History. We also use extant scaling methods to try to obtain a reliable mass estimate for this taxon. In addition, we present the first digital life restoration and convex hull of the dinosaur *Anzu wyliei* used for mass estimation purposes. We found that the volumetric mass estimation using our digital model was 216–280 kg, which falls within the range predicted by extant scaling techniques, while the mass estimate using minimum convex hulls was below the predicted range, between 159–199 kg. The VME method for *Anzu wyliei* strongly affirms the predictive utility of extant-based scaling. However, volumetric mass estimates are likely more precise because the models are based on comprehensive specimen anatomy rather than regressions of a phylogenetically comprehensive but disparate sample.

INTRODUCTION

Body mass is an important characteristic of organisms, as it relates to many important life functions such as metabolic rate (Strotz et al. 2018), relative maturity, and biomechanics (Hutchinson et al. 2011; Sander et al. 2011; Schmidt-Nielsen 1984). However, it is much harder to estimate body mass of extinct taxa due to a variety of factors including a lack of soft tissues, and taphonomic distortion of bones. A wide range of techniques have been developed to try to solve this conundrum, reviewed comprehensively by Brassey (2017) and Campione and Evans (2020). Currently, there are two major categories into which mass estimation techniques fall — volumetric mass estimates, that use various

ways of estimating body volume and density, and extant scaling methods, which use relationships between measured osteological characters and body mass in modern taxa, and attempt to reconcile these relationships with extinct organisms. Each method has advantages and drawbacks, which is why using both can be informative (Campione and Evans 2020) for identifying potential errors in one method or the other and to provide what may be a more realistic range of values, and for tradeoffs of comparative sample size versus time investment.

We wanted to determine whether volumetric mass estimation could create a narrower range of body mass estimates than extant scaling for a taxon such as *Anzu wyliei* based on known specimens, using a class of techniques known

Published September 28, 2021

*corresponding author. © 2021 by the authors; submitted July 8, 2021; revisions received September 7, 2021; accepted September 7, 2021. Handling editor: Jordan Mallon. DOI 10.18435/vamp29375

as volumetric mass estimation (or VME), as well as using expanded extant scaling methods than those used in the original description (Lamanna et al. 2014). Many different methods have been used to estimate body mass from volume. Such methods have included using a scaled-down physical model of the animal of interest (Alexander 1985; Colbert 1962; Gregory 1905), and more recent techniques include 3D mathematical slicing (Henderson 1999; Snively et al. 2019), photogrammetry and parameterized computer modeling (Bates et al. 2009; Gunga et al. 2008, 1995; Hutchinson et al. 2007), and using minimum convex hulls to wrap around a digitized skeletal frame (Brassey and Sellers 2014; Sellers et al. 2012). See Brassey (2017) and Campione and Evans (2020) for a thorough review of each of these approaches.

Current published mass estimates for *Anzu wyliei* yield a range of 200–300 kg (Lamanna et al. 2014), based both on femoral circumference (Anderson et al. 1985) and femoral length measures (Christiansen and Fariña 2004; Zanno and Makovicky 2013). However, since the original publication more refined techniques for estimating body mass using stylopodial circumference have been developed that potentially allow for more rigor and further have the added benefit of yielding confidence ranges even for single-point estimates (Campione et al. 2014; Campione and Evans 2020). Such methods also do not resort to using multiple different techniques of mass estimation. Here, we derive new, updated mass estimates utilizing extant scaling methods developed by Campione et al. (2014) and further refined by Campione and Evans (2020). We then compare these to volumetric mass estimates obtained by digital scanning of *Anzu* specimens as well as manual digital modeling, similar to procedures presented by Romano et al. (2021) for the pareiasaur *Scutosaurus*. Furthermore, we estimated the animal's mass with minimum convex hulling, to see which of the applied methods yielded a range that was more congruent with that generated from the extant scaling method.

MATERIALS AND METHODS

Volumetric Mass Estimation

To conduct volumetric mass estimation, multiple elements of the paratype specimen of *Anzu wyliei* (CM 78001) and a second caenagnathid from the Hell Creek Formation (currently being described) were digitized using photogrammetry. Digital photographs were captured with a Canon EOS Rebel T3i DSLR, with point clouds derived from the photos using Agisoft Metashape. Imperfections in the resulting meshes were corrected manually in ZBrush 2020. To minimize unnecessary corrections related to taphonomic distortion, only the more complete and/or better preserved of paired elements was digitized, with the exception of the

femur. Elements of CM 78001 digitized using photogrammetry included the left ilium, left pubis, right ischium, both femora, left tibia, and right fibula. The elements of the second caenagnathid (CM 96523) that were digitized included the left metatarsal III and the right metatarsal IV. While not pertaining to *Anzu wyliei*, these elements were scaled to appropriate proportions using data from a currently unpublished specimen (M. Lamanna, pers. comm. 2020). 3D scans of a series of presacral vertebrae from both the holotype (CM 78000) and referred specimen (CM 78001) were provided by L. Roberts.

To surmount time constraints, the rest of the skeleton was not directly digitized using photogrammetry – instead, the remaining elements were manually sculpted using reference images of preserved elements from anterior, posterior, lateral, dorsal, and ventral perspectives. Manually sculpted elements included cervical and dorsal ribs, sacral and caudal vertebrae and chevrons, the entire pectoral girdle and forelimbs, and the proximal phalanges and unguals of the pes (Fig. 1).

An approximate life-restoration of *Anzu wyliei* was first constructed in ZBrush 2020 using the skeletal outline drawings created by Scott Hartman as a starting point, though the tail of the life restoration was straightened to make it easier to match the articulation of the caudal vertebrae once they were digitized. The skeletal reconstruction represents a sufficiently accurate starting point as it was used to illustrate in the original description (Lamanna et al. 2014). The digitized skeleton was then placed within this life restoration to mimic the position of the skeleton within the living organism, with corrections made to fit the skeleton where necessary (Fig. 2). To reconstruct the major pulmonary tissues, Dynamesh spheres were imported into the model space, then manually sculpted using Inflate, Move, and Dynamesh tools to shape into the lungs, trachea, and air sacs (Fig. 1).

To calculate volume and subsequently body mass, the model was exported to 3DS Max 2021, where the volume of the entire life model was calculated in addition to the volume of the lungs and air sacs. The composition, position, and estimated arrangement of lungs and air sacs were constrained using osteological correlates for air sac invasion and placement in theropods (O'Connor 2006; Sereno et al. 2008; Wedel 2006) (Fig. 1) – specifically, lungs, cervical and abdominal air sacs, and pneumatic diverticula (e.g., lateral cervical diverticula) were modeled along the cervical and dorsal vertebral series (Benson et al. 2012; O'Connor 2006; O'Connor and Claessens 2005). Since there are no well constrained osteological correlates for thoracic and clavicular air sacs, we utilized two calculations of body mass. First, we did a calculation using the most conservative model, with only the cervical air sacs, lungs, abdominal air sacs, and trachea present. Second was a more exten-

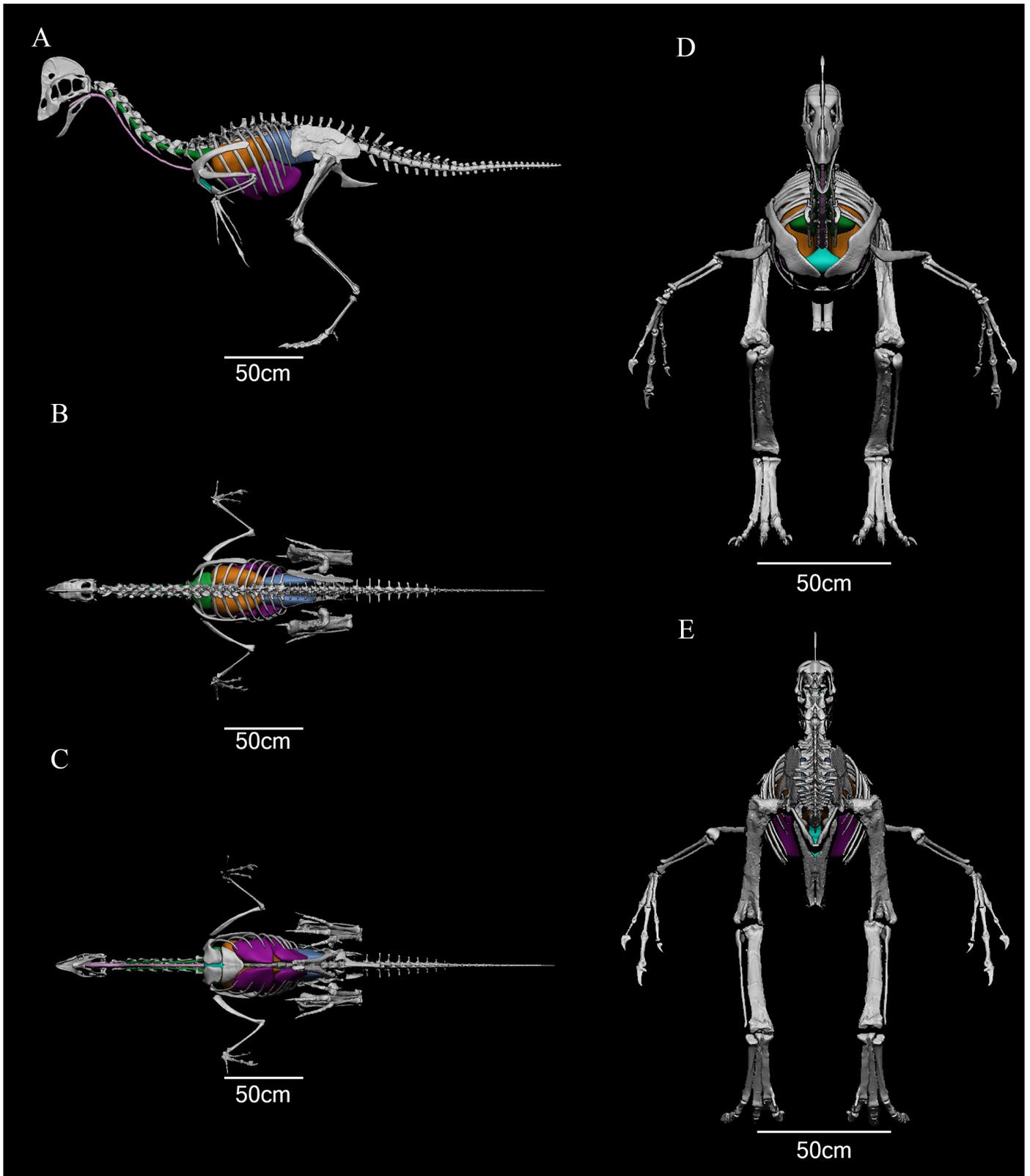


Figure 1. Digitized skeleton of *Anzu wyliei* with air sacs (“avian” model). Model shown in A, lateral; B, dorsal; C, ventral; D, anterior; and E, posterior views. Key: Green: cervical air sacs; orange: lungs; blue: abdominal air sacs; purple: thoracic air sacs; aquamarine: clavicular air sacs; pink: trachea. NOTE: Clavicular and thoracic air sacs were removed in the more conservative reconstruction.

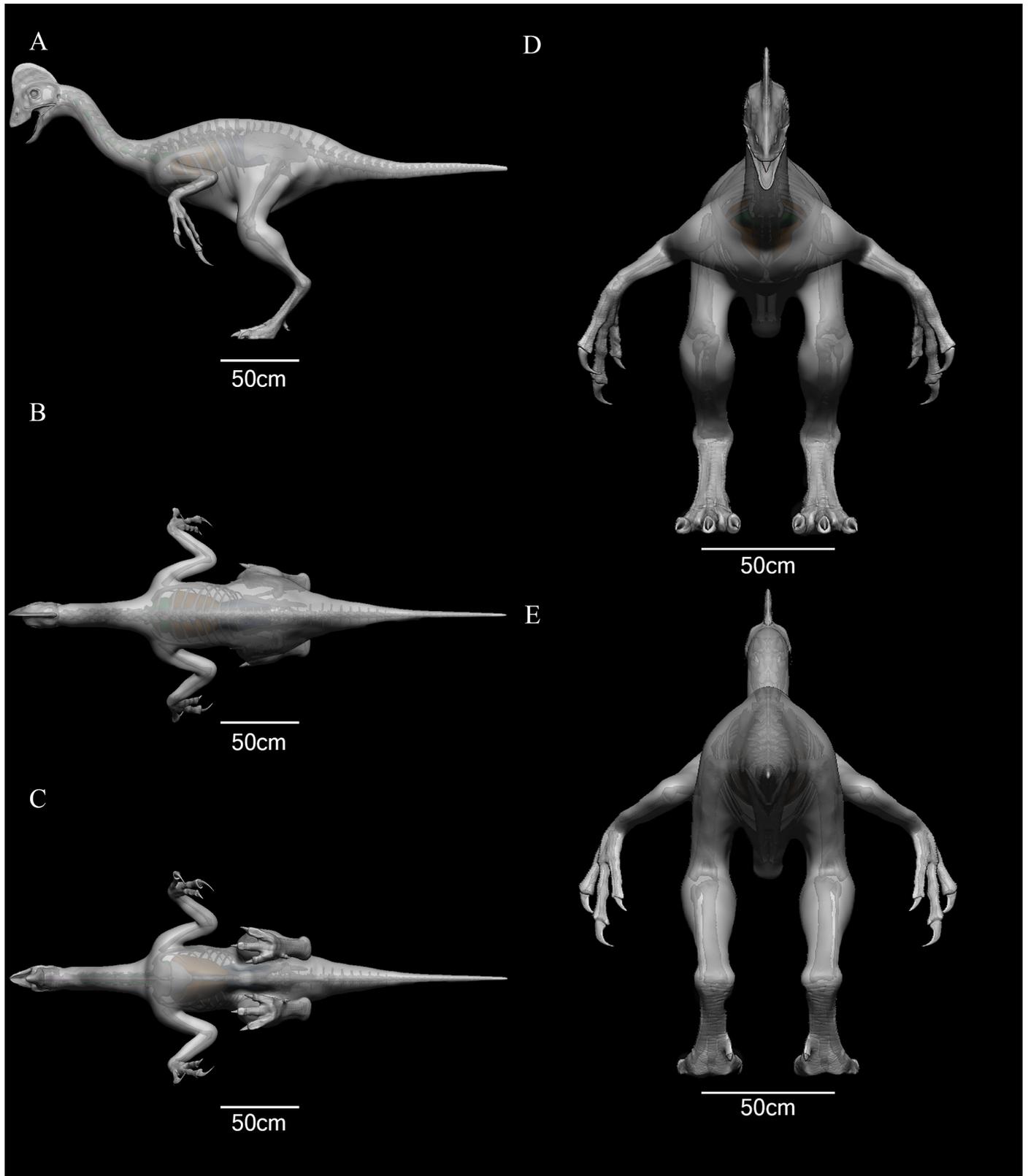


Figure 2. Life restoration of *Anzu wyliei*, with skeleton and air sacs semi-visible through transparency. Model shown in A, lateral; B, dorsal; C, ventral; D, anterior; and E, posterior views. Lungs and air sacs as in Figure 1.

sive air sac system (an “avian model”) that included both anterior and posterior thoracic air sacs, and a clavicular air sac, as are present in Avialae (Benson et al. 2012; Duncker 1971; O’Connor 2004, 2006). In this way we account for the uncertainty in presence or absence of such air sacs, and importantly, determine how modeling them affects our estimate of body mass.

Since the exact and overall tissue densities of extinct organisms are impossible to calculate with certainty, we used two different values for density of the body excluding pulmonary air space to create an upper and lower bound for the model. The lower bound used an estimated density of 800 kg/m³, as has been applied to large sauropods because the pneumaticity in their bones was assumed to lower their body density (Gunga et al. 2008), an issue that has been brought up for highly pneumatic saurischian taxa (Benson et al. 2012; Brassey and Sellers, 2014; Campione and Evans 2020). However, increasing skeletal pneumaticity does not appear to change the total mass of the bones relative to whole body mass—the skeletons of highly pneumatic birds weigh the same relative to total body mass as less pneumatic birds (Martin-Silverstone et al. 2015; Prange et al. 1979). This could mean that skeletal pneumaticity probably does not directly have an effect on whole body density. The negative relationship between density and body mass in birds is probably related to an increase in size of the air sacs relative to total body volume (S. Gutherz pers. comm.). Thus, to allow for these uncertainties, we used a value of 1000 kg/m³, which has been used in many previous studies

aiming to estimate body mass through volumetric methods (Bates et al. 2009; Henderson 1999; Hutchinson et al. 2007, 2011). The non-respiratory value of 1000 kg/m³ is closer to recent estimates for extant and extinct saurischian dinosaurs (Larramendi et al. 2020).

Since previous researchers have used convex hulling methods to estimate body mass of both extant and extinct taxa (Brassey and Sellers 2014; Sellers et al. 2012), we also used this method with *Anzu* for comparative purposes. To construct minimal convex hulls, first the skeleton was exported from 3DS Max into MeshLab. The skeleton was divided into multiple segments, each given its own convex hull (Fig. 3), with each hull used to estimate volume. Because exact scaling parameters did not transfer between programs, the Transform:Scale:Normalize function we employed to scale the skeleton as close as possible to the known actual size of the animal. Furthermore, MeshLab’s volume output was in cm³, and thus we converted these volumes to m³. The total volumes of all segments (Tab. 1) were summed together and multiplied by the two extremes of density used for the manually modeled estimate, to establish a range of body masses.

While feathers are known to be present in oviraptorosaurs based on direct preservation (Funston and Currie 2020; Qiang et al. 1998; Xu et al. 2010; Zhou et al. 2000), in addition to indirect inference based on quill knobs on the ulna (Kurzanov 1982), in many extant birds, feathers do not contribute significantly to overall body mass (Brassey and Sellers 2014; Hopps 2002; Larramendi et al. 2020;

Table 1. Volumes of the convex hulls used to generate a minimum convex hull estimate of body mass for *Anzu wyliei*.

Body segment	Volume (cm ³)	Volume (m ³)	Mass (800 kg/m ³)	Mass (1000 kg/m ³)
Torso	125274.625	0.125274625	100.2197 kg	125.274625 kg
Tail	12802.94043	0.01280294	10.24235234 kg	12.80294043 kg
Skull	10121.46387	0.010121464	8.097171094 kg	10.12146387 kg
Neck	12408.58691	0.012408587	9.926869531 kg	12.40858691 kg
L humerus	797.968811	0.000797969	0.638375049 kg	0.797968811 kg
L antebrachium	464.968689	0.000464969	0.371974951 kg	0.464968689 kg
L manus	1855.232666	0.001855233	1.484186133 kg	1.855232666 kg
R humerus	744.117065	0.000744117	0.595293652 kg	0.744117065 kg
R antebrachium	466.130646	0.000466131	0.372904517 kg	0.466130646 kg
R manus	4343.450684	0.004343451	3.474760547 kg	4.343450684 kg
L stylopod	4343.450684	0.004343451	3.474760547 kg	4.343450684 kg
L zeugopod	2814.483398	0.002814483	2.251586718 kg	2.814483398 kg
L autopod	7956.745605	0.007956746	6.365396484 kg	7.956745605 kg
R stylopod	4343.51416	0.004343514	3.474811328 kg	4.34351416 kg
R zeugopod	2792.091309	0.002792091	2.233673047 kg	2.792091309 kg
R autopod	7956.643555	0.007956644	6.365314844 kg	7.956643555 kg
Total	199486.4135 cm³	0.199486413 m³	159.5891308 kg	199.4864135 kg

L = left; R = right

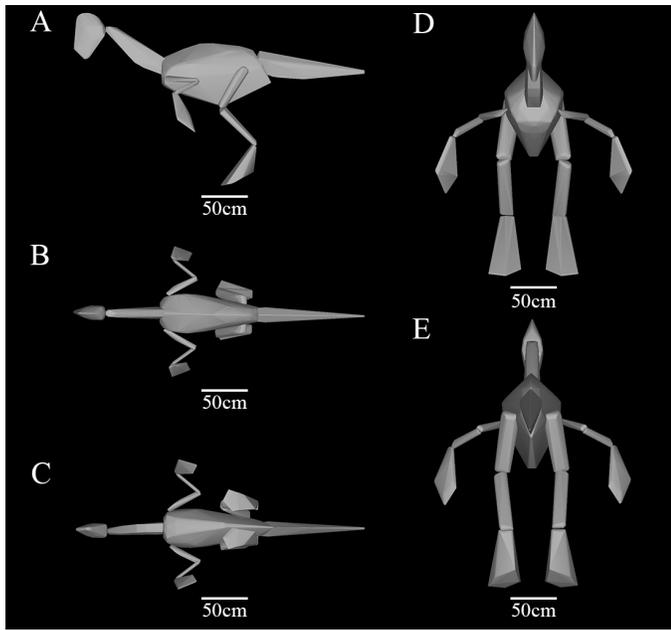


Figure 3. Convex Hull model of *Anzu wyliei*. Model shown in A, lateral; B, dorsal; C, ventral; D, anterior; and E, posterior views.

Wecke et al. 2017). In large, extant ratites, feathery integument comprises less than 2% of total body mass (Brassey and Sellers 2014). For this reason, we decided to construct our volumetric model without feathers, and infer that feathers would add up to an additional 2% to the volumetric body mass estimates reported in this paper.

Extant Scaling Methods

We provided data on femoral circumference of the holotype *Anzu wyliei* (CM 78000) to Dr. N. Campione, to use in his body mass regression analyses as has been done in previous works (Campione et al. 2014; Campione and Evans 2020) (Fig. 4). We also compared these to the values originally obtained by Lamanna et al. (2014), as using femoral length as an estimator could still be useful because actual femoral circumference can be easily distorted by taphonomic factors and be made impossible to measure.

RESULTS

Volumetric Mass Estimation

The volume of the complete life model was 0.30 m^3 (Tab. 2). The air sac volume differed between a more conservative (i.e., lungs and other pulmonary structures modeled at 0.02 m^3) and less conservative (i.e., lungs and other pulmonary structures modeled at 0.03 m^3). From these results, the conservative model is heavier at an estimated 224–280 kg, whereas the more speculative model is slightly lighter, ranging from 216–270 kg. Minimum convex hulling yielded a volume of 0.199 m^3 (Tab. 1), with a mass estimate between 159 and 199 kg, depending on which body density value was applied.

Extant Scaling Methods

Because the femoral circumference of CM 78001 was not available, we were only able to use femoral circumference of the *Anzu* holotype (CM 78000) for the extant scaling regression. However, while the two differ slightly in size, the difference is slight enough that the obtained femoral circumference is a somewhat reasonable proxy for CM 78001 (M. Lamanna, pers. comm. 2021), although see Table 3 for comparative measurements. The resulting regression yielded a body mass range of between 202 and 342 kg (Fig. 4), whereas the original point estimate based on femoral circumference was 193 kg (Lamanna et al. 2014).

DISCUSSION

The results obtained from volumetric mass estimates of *Anzu wyliei* fit within both the original mass range proposed in the original description (Lamanna et al. 2014) and that predicted by the corroboration plot using Campione's method (Campione et al. 2014; Campione and Evans 2012). Thus, current volumetric mass estimate of 216–280 kg provides a more precise range of body masses for this organism than those that use extant data alone (Tab. 2).

Table 2. Mass estimates resulting from different methods of estimation.

Note the increasing precision relative to earlier studies provided by the results presented herein. Further note the discrepancy of the minimum convex hull estimate relative to all other estimates.

Source:	Lamanna et al. 2014	Nicolás Campione	This paper	This paper
Estimation Type:	Femoral length	Log stylopodial circumference regression	VME from digitally reconstructed model	VME from minimum convex hulls
Result:	200–300 kg	202–342 kg	216–280 kg	159–199 kg

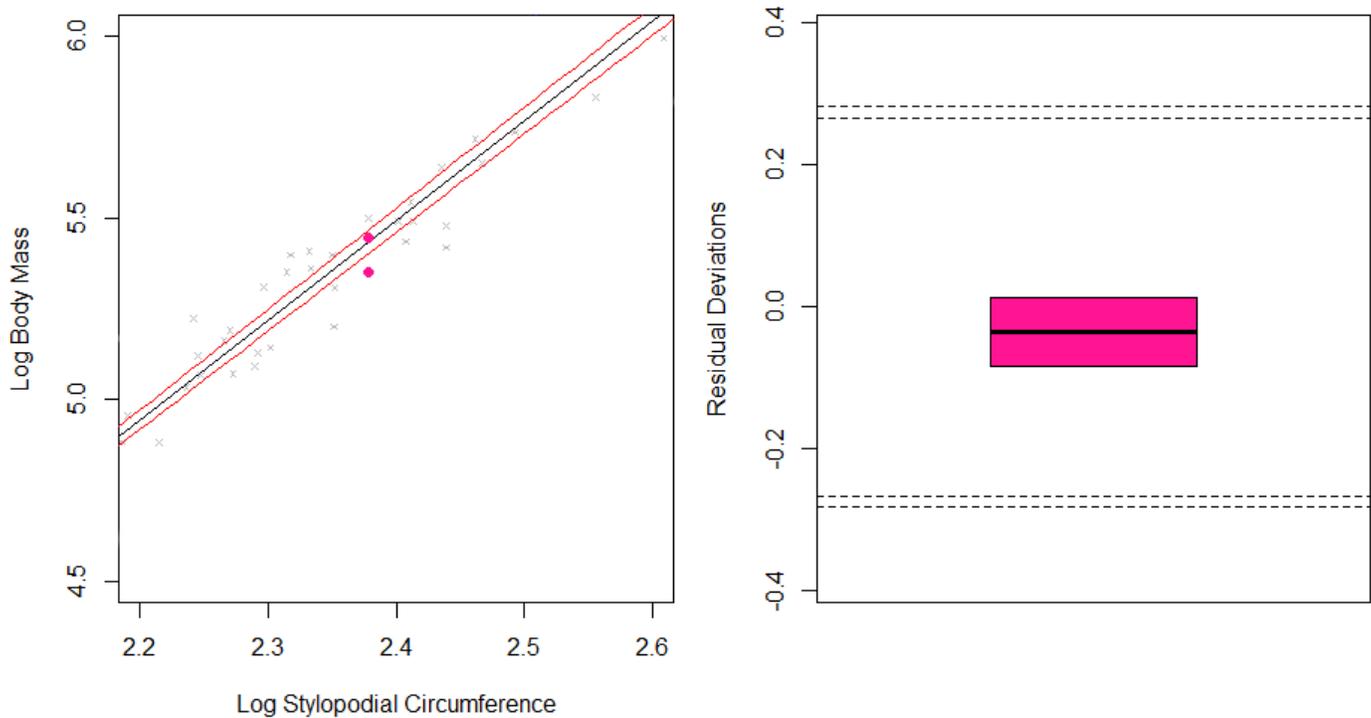


Figure 4. Logistic regression of stylopodial circumference versus body mass in dinosaurs, and residual deviance. Red lines represent the upper and lower bounds of the 95% confidence interval. The pink dots represent the upper and lower estimates for CM 78000 based on femoral circumference. Gray “x” marks represent other specimens of various taxa used to create the regression. Regressions and figure courtesy Nicolás Campione.

We also found that the minimum convex hulling method seems to lead to an underestimation of total body mass in this case, though this could be due to scaling errors when transferring between programs. However, if this is indeed a reflection upon minimum convex hulling as a method, it appears when comparing the convex hull model to the manually sculpted life restoration that much of the missing body mass relates to the extremely low volume of both the forelimbs and hind limbs using the hull approach (Figs. 2, 3). The convex hull model does not account for the *M. iliotibialis*, *M. iliofibularis*, or many of the other muscles connecting the pelvic bones to the femur, or the *M. caudofemoralis* spanning between the tail and the thigh. The same is true for many of the muscles in the upper forelimb. This could explain the much lower estimate and suggests that aspects of the convex hull method may make implausible biological assumptions. Feathers would add less than 2% (Brassey and Sellers 2014) to our estimate of the body mass of *Anzu*, regardless of method.

Moreover, it seems likely that with convex hulling, the choice of which elements to include in a particular convex hull may have a strong influence on the final result. Perhaps if the pelvic bones were included in the same hull as the femur, for example, the resulting hull would have added the muscles to the proximal hind limb. Yet, even if this

change were made, there is still the issue of the incredibly thin zeugopodia of both forelimbs and hind limbs, largely underrepresenting both the gastrocnemius and, to a lesser extent, the antebrachial muscles. However, whereas these areas are clearly given less volume than they would account for in life, both the head and the autopodia of both forelimbs and hind limbs account for a greater volume than they would in life. This is because separate elements are often hulled together - since the skull is modeled as a single element despite consisting of an upper and lower jaw (and the mouth being open in articulation), the hull included the gap between the jaws in its total volume which is biologically inaccurate. Similarly, since the individual fingers and toes were not added as separate hulls, the generated hull connected them in a single, wide structure (e.g., like a duck’s foot), which is not correct. Despite these three areas of greater-than-expected volume, they are not sufficient to balance out the underestimation of volume in other regions, resulting in a lower-than-expected body volume regardless of the density value selected.

Whereas the volumetric mass estimate using a manually constructed life restoration has worked well to narrow the plausible range of body masses for *Anzu wyliei*, we continue to argue for the use of integrated methods making use of both volumetric and extant scaling methods when possible.

Table 3. Comparative measurements of skeletal elements preserved in both CM 78000 and CM 78001, as reported in Lamanna et al. 2014. As reported in the original description, measurements greater than 205 mm were taken with tape measure and are therefore less precise, and provided only to the nearest 5 mm.

Element/dimension	CM 78000	CM 78001
Skull and mandible		
Braincase		
Height, occipital condyle midline, dorsoventral	10.4	12.3
Width of occipital condyle, transverse	20.9	21.7
Height of foramen magnum, dorsoventral	18.0	15.3
Width of foramen magnum, transverse	15.1	13.1
Femur		
Length, proximodistal	525 ^R	505 ^L , 500 ^R
Width of proximal end, mediolateral	121.7 ^{L*} , 127.4 ^R	136.3 ^L , 135.5 ^R
Width of distal end, mediolateral	94.1 ^{L*} , 112.4 ^R	110.0 ^R
Tibia		
Length, proximodistal	660 ^L	595 ^L
Width of proximal end, mediolateral	93.5 ^L , 101.7 ^{R*}	86.1 ^L
Depth of proximal end, anteroposterior	104.6 ^L	88.4 ^L
Width of distal end, mediolateral	101.7 ^L	110.3 ^L
Fibula		
Length, proximodistal	585 ^L , 580 ^R	570 ^L
Width of proximal end, anteroposterior	70.0 ^L , 65.0 ^R	74.7 ^L , 67.9 ^R
Width of proximal end, mediolateral	29.2 ^L , 27.5 ^R	25.0 ^L , 31.8 ^R
Astragalocalcaneum		
Length, proximodistal	133.1 ^{L*} , 141.8 ^{R*}	220 ^L
Width across distal condyles, mediolateral	98.5 ^L , 98.0 ^R	109.7 ^L
Metatarsal V		
Depth of proximal end, anteroposterior	16.0 ^{L*}	20.7 ^L

Abbreviations: aofe, antorbital fenestra; L, left; R, right; *, element incomplete, measurement as preserved

Volumetric body mass is only possible for taxa known from relatively complete remains (Campione and Evans 2020), which greatly reduces its utility in the vertebrate fossil record because many taxa are known only from incomplete skeletons. Furthermore, there are still great unknowns about body density, lung and air sac size and structure, and other soft tissue systems that no doubt convey sources of variation within volumetric mass estimates if not carefully accounted for a priori. This may be done by creating more than one model, to account for differing amounts of soft tissue as has been implemented by some researchers (Hutchinson et al. 2011), or as we have done here, simply by using a differing possible body density in the same model. We chose the latter, as the relatively small total volume of the model (0.30 m³) and the sensitivity of the software calculating the volume (± 0.01 m³) meant that it would

take the addition or subtraction of an immense amount of extra soft tissue relative to the model size to modify the body mass of the model by more than 10–20 kg in either direction. However, with larger taxa, even seemingly small changes may register due to the larger total volume, and thus, the smaller proportion of total volume 0.01 m³ represents. For this reason, we suggest that anyone attempting to replicate this method with larger taxa should use a lower sensitivity to volume changes, perhaps using this study as an approximation of what proportion of total body volume to use for the sensitivity. For example, for an animal with a body volume of 6.0 m³, the sensitivity would need to be twenty times lower (i.e., ± 0.20 m³). Researchers can use this in conjunction with a maximum and minimum body density to create a range of body mass estimates using body volume (Campione and Evans 2020). We reiterate that

these caveats apply to the precision of the specific software used, which yields lower relative error with larger volumes and greater relative error with smaller volumes. Software with greater precision, or consistent relative precision regardless of volume, will yield more equivalent relative precision with large and small volumes.

CONCLUSIONS

Using carefully sculpted digital models based on actual specimens, along with modeling a range of possible body densities, allows for a more realistic and accurate range of possible body masses than extant scaling alone. However, we note that this is only possible when specimens are sufficiently complete and well-known enough to reliably infer basic soft tissue anatomy, and as such, extant scaling is still critical for providing a bracket of reasonable values against which to compare those estimated by volumetric methods. Further, we show that there is a great sensitivity of minimum convex hulling to the selection of elements within the hull, making it difficult to determine reliability on animals with lower estimated body sizes.

ACKNOWLEDGEMENTS

We would like to thank Matt Lamanna and Ami Henrici of the Carnegie Museum of Natural History (Pittsburgh, PA, USA) for allowing access to the original *Anzu wyliei* type material, and Heinrich Mallison for providing advice on photogrammetry. We also thank Lucy Roberts for providing scans of *Anzu wyliei* presacral vertebrae, Evelyn Volmer for sculpting missing skeletal elements and articulating the skeleton, and Emma Schachner, who provided photographs of the axial skeleton of the CM *Anzu* specimens. Scott Hartman's skeletal diagrams proved invaluable for sculpting the initial basis of the life restoration and informing basic articulation of the skeletal elements. Nicolás Campione deserves acknowledgement for his assistance with extant-scaling regressions. Lastly, we acknowledge Samuel Guthertz for additional input regarding the air sac reconstruction.

LITERATURE CITED

- Alexander, R.M. 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society* 83:1–25. <https://doi.org/10.1111/j.1096-3642.1985.tb00871.x>
- Anderson, J.F., A. Hall-Martin, and D.A. Russell. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology* 207:53–61. <https://doi.org/10.1111/j.1469-7998.1985.tb04915.x>
- Bates, K.T., P.L. Manning, D. Hodgetts, and W.I. Sellers. 2009. Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. *PLoS ONE* 4:e4532. <https://doi.org/10.1371/journal.pone.0004532>
- Benson, R.B.J., R.J. Butler, M.T. Carrano, and P.M. O'Connor. 2012. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'-bird transition. *Biological Reviews of the Cambridge Philosophical Society* 87:168–193. <https://doi.org/10.1111/j.1469-185X.2011.00190.x>
- Brassey, C.A., and W.I. Sellers. 2014. Scaling of convex hull volume to body mass in modern primates, non-primate mammals and birds. *PLoS ONE* 9:e91691. <https://doi.org/10.1371/journal.pone.0091691>
- Campione, N.E., and D.C. Evans. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology* 10:60. <https://doi.org/10.1186/1741-7007-10-60>
- Campione, N.E., and D.C. Evans. 2020. The accuracy and precision of body mass estimation in non-avian dinosaurs. *Biological Reviews* 95:1759–1797. <https://doi.org/10.1111/brv.12638>
- Campione, N.E., D.C. Evans, C.M. Brown, and M.T. Carrano. 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods in Ecology and Evolution* 5:913–923. <https://doi.org/10.1111/2041-210X.12226>
- Christiansen, P., and R.A. Fariña. 2004. Mass prediction in theropod dinosaurs. *Historical Biology* 16:85–92. <https://doi.org/10.1080/08912960412331284313>
- Colbert, E.H. 1962. The weights of dinosaurs. *American Museum Novitates* 2076:1–16.
- Duncker, H.R. 1971. The lung air sac system of birds. A contribution to the functional anatomy of the respiratory apparatus. *Ergebnisse der Anatomie und Entwicklungsgeschichte* 45:7–171.
- Funston, G.F., and P.J. Currie. 2020. New material of *Chirostenotes pergracilis* (Theropoda, Oviraptorosauria) from the Campanian Dinosaur Park Formation of Alberta, Canada. *Historical Biology* 15 pp. <https://doi.org/10.1080/08912963.2020.1726908>
- Gregory, W.K. 1905. The weight of the *Brontosaurus*. *Science* 22:572–572. <https://doi.org/10.1126/science.22.566.572>
- Gunga, H.-C., T. Suthau, A. Bellmann, S. Stoinski, A. Friedrich, T. Trippel, K. Kirsch, and O. Hellwich. 2008. A new body mass estimation of *Brachiosaurus brancai* Janensch, 1914 mounted and exhibited at the Museum of Natural History (Berlin, Germany). *Fossil Record* 11:33–38. <https://doi.org/10.1002/mmng.200700011>
- Gunga, H.-Chr., K.A. Kirsch, F. Baartz, L. Röcker, W.-D. Heinrich, W. Lisowski, A. Wiedemann, and J. Albertz. 1995. New data on the dimensions of *Brachiosaurus brancai* and their physiological implications. *Naturwissenschaften* 82:190–192. <https://doi.org/10.1007/BF01143194>
- Henderson, D.M. 1999. Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology* 25:88–106.

- Hopps, E.C. 2002. Information on waterfowl feather characteristics. *Transactions of the Illinois State Academy of Science* 95:229–237.
- Hutchinson, J.R., K.T. Bates, J. Molnar, V. Allen, and P.J. Makovicky. 2011. A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLoS ONE* 6:e26037. <https://doi.org/10.1371/journal.pone.0026037>
- Hutchinson, J.R., V. Ng-Thow-Hing, and F.C. Anderson. 2007. A 3D interactive method for estimating body segmental parameters in animals: application to the turning and running performance of *Tyrannosaurus rex*. *Journal of Theoretical Biology* 246:660–680. <https://doi.org/10.1016/j.jtbi.2007.01.023>
- Kurzanov, S. 1982. Structural characteristics of the fore limbs of *Avimimus*. *Paleontological Journal* 1982:108–112.
- Lamanna, M.C., H.-D. Sues, E.R. Schachner, and T.R. Lyson. 2014. A new large-bodied oviraptorosaurian theropod dinosaur from the latest Cretaceous of western North America. *PLoS ONE* 9:e92022.
- Larramendi, A., G.S. Paul, and S. Hsu. 2020. A review and reappraisal of the specific gravities of present and past multicellular organisms, with an emphasis on tetrapods. *Anatomical Record* 2021:1–56. <https://doi.org/10.1002/ar.24574>
- Martin-Silverstone, E., O. Vincze, R. McCann, C.H.W. Jonsson, C. Palmer, G. Kaiser, and G. Dyke. 2015. Exploring the relationship between skeletal mass and total body mass in birds. *PLoS ONE* 10:e0141794. <https://doi.org/10.1371/journal.pone.0141794>
- O'Connor, P.M. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology* 267:1199–1226.
- O'Connor, P.M. 2004. Pulmonary pneumaticity in the postcranial skeleton of extant aves: a case study examining Anseriformes. *Journal of Morphology* 261:141–161.
- O'Connor, P.M., and L.P.A.M. Claessens. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436:253–256. <https://doi.org/10.1038/nature03716>
- Prange, H.D., J.F. Anderson, and H. Rahn. 1979. Scaling of skeletal mass to body mass in birds and mammals. *The American Naturalist* 113:103–122. <https://doi.org/10.1086/283367>
- Qiang, J., P.J. Currie, M.A. Norell, and J. Shu-An. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761. <https://doi.org/10.1038/31635>
- Sander, P.M., A. Christian, M. Clauss, R. Fechner, C.T. Gee, E.-M. Griebeler, H.-C. Gunga, J. Hummel, H. Mallison, S.F. Perry, H. Preuschoft, O.W.M. Rauhut, K. Remes, T. Tütken, O. Wings, and U. Witzel. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological reviews of the Cambridge Philosophical Society* 86:117–155. <https://doi.org/10.1111/j.1469-185X.2010.00137.x>
- Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge, 256 pp. <https://doi.org/10.1017/CBO9781139167826>
- Sellers, W.I., J. Hepworth-Bell, P.L. Falkingham, K.T. Bates, C.A. Brassey, V.M. Egerton, and P.L. Manning. 2012. Minimum convex hull mass estimations of complete mounted skeletons. *Biology Letters* 8:842–845. <https://doi.org/10.1098/rsbl.2012.0263>
- Sereno, P.C., R.N. Martinez, J.A. Wilson, D.J. Varricchio, O.A. Alcober, and H.C.E. Larsson. 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE* 3:e3303. <https://doi.org/10.1371/journal.pone.0003303>
- Snively, E., H. O'Brien, D.M. Henderson, H. Mallison, L.A. Surring, M.E. Burns, T.R. Holtz Jr., A.P. Russell, L.M. Witmer, P.J. Currie, S.A. Hartman, and J.R. Cotton. 2019. Lower rotational inertia and larger leg muscles indicate more rapid turns in tyrannosaurids than in other large theropods. *PeerJ* 7:e6432. <https://doi.org/10.7717/peerj.6432>
- Strotz, L.C., E.E. Saupe, J. Kimmig, and B.S. Lieberman. 2018. Metabolic rates, climate and macroevolution: a case study using Neogene molluscs. *Proceedings of the Royal Society B, Biological Sciences* 285:20181292. <https://doi.org/10.1098/rspb.2018.1292>
- Wecke, C., D.R. Khan, A. Sünder, and F. Liebert. 2017. Age and gender depending growth of feathers and feather-free body in modern fast growing meattype chickens. *Open Journal of Animal Sciences* 7:376–392.
- Wedel, M.J. 2006. Origin of postcranial skeletal pneumaticity in dinosaurs. *Integrative Zoology* 1:80–85. <https://doi.org/10.1111/j.1749-4877.2006.00019.x>
- Xu, X., X. Zheng, and H. You. 2010. Exceptional dinosaur fossils show ontogenetic development of early feathers. *Nature* 464:1338–1341. <https://doi.org/10.1038/nature08965>
- Zanno, L.E., and P.J. Makovicky. 2013. No evidence for directional evolution of body mass in herbivorous theropod dinosaurs. *Proceedings of the Royal Society, Biological Sciences* 280:1–8.
- Zhou, Z.-H., X.-L. Wang, F.-C. Zhang, and X. Xu. 2000. Important features of *Caudipteryx* - evidence from two nearly complete new specimens. *Vertebrata Palasiatica* 38:242–254.