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Virtual skeleton and body mass for revealing the life strategies of *Sinosaurus*

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Abstract

Sinosaurus from the Lufeng Basin, Yunnan Province, is the largest and most famous predatory dinosaur from the Early Jurassic in China. Although a number of specimens have been discovered in the past, no studies to date have focused exclusively on complete skeletal articulation, estimation of mass, or life strategies. Based on surface scans of a new well-preserved specimen, a digital skeleton of *Sinosaurus* was produced in two poses: osteologically neutral pose, and extended pose. We estimated the possible living body mass by three volumetric-density methods, advocating the use of the expanding convex hulls method of 849.6 kg with the COM (0.41, 1.31, 0.00) as a more reliable result, which is greater than the mass of traditional regression formulas. The body shape and skull/body length suggested that *Sinosaurus* was a great runner, and this, combined with the weak crests and large forelimbs, further led to the conclusion that both the head and forelimbs were required to prey. This finding is also consistent with the finding that *Sinosaurus* has a moderate ability to metabolize body heat in the skin, as reflected by the surface/volume ratio.

Keywords: *Sinosaurus*, digital models, mass estimation, locomotion, prey

1 Introduction

When it comes to carnivorous dinosaurs, ferocious scenarios of giant theropods hunting undoubtedly come to mind (e.g., Coria and Salgado 1995; Therrien and Henderson 2007; Hutchinson et al. 2011), but the fossil records suggest that medium-sized hunters were far more common (e.g., Gilmore 1920; Young 1948; Welles 1984; Xing 2012; Zhang et al. 2023). *Sinosaurus* is one such ‘medium-sized’ theropod, yet is also the hugest predatory animal known to have lived on land in China and across Asia during the Early Jurassic (Young 1948; Hu 1993; Dong 2003; Xing 2012; Zhang et al. 2023), exhibiting a suite of advanced carnivorous traits, such as blade-like teeth with serrations and a perforated crest (Carrano et al. 2012; Xing et al. 2013, 2014; Hendrickx and Mateus 2014). In recent decades (Table 1), much attention has been given to *Sinosaurus* osteology and a hitherto inconclusive phylogenetic analysis based on skull anatomy (Young 1948; Welles 1984; Hu 1993; Dong 2003; Xing 2012; Xing et al. 2013, 2014; Marsh and Rowe 2020; Xu et al. 2021; Zhang et al. 2023), while the whole skeleton, osteologically neutral pose or relative extended pose, and body mass (BM) of this dinosaur remain unclear. BM is

undoubtedly one of the most important biomechanical factors of vertebrates and not only explains physiological and ecological traits such as metabolism and home ranges (e.g., Martin and Palumbi 1993; Hillebrand and Azovsky 2001; Gillooly et al. 2006; Pontzer and Hutchison 2009; Grady et al. 2014; Reolid et al. 2021) but also provides an impetus to study these characteristics in a macroevolutionary context (e.g., LaBarbera 1989; Calder 1996; Allen et al. 2013; Gates et al. 2016; D'Emic et al. 2023). Here, we estimate the possible living BM of a new well-preserved *Sinosaurus* specimen (ZLJ0057) by the volumetric density method (Figure 1) (Campione and Evans 2020). We generate three volumetric models based on the digital skeleton in osteologically neutral pose and extended pose (Bates et al. 2009b; Mallison 2010a; Sellers et al. 2012; Hart et al. 2022; Macaulay et al. 2023), and compare the results obtained by traditional regression formulas based on extant scaling (Christiansen and Farina 2004; Campione et al. 2014; Gates et al. 2016).

BM estimation via - three dimensions (3D) digital reconstruction models has been common for many bipedal theropod taxa, including prosauropod *Plateosaurus* (Mallison 2010a; Macaulay et al. 2023), the basal theropods *Coelophysis bauri* (Allen et al. 2013; Bishop et al. 2021; Macaulay et al. 2023) and *Dilophosaurus wetherelli* (Reolid et al. 2021; Macaulay et al. 2023), the ceratosauria *Ceratosaurus nasicornis* and *Carnotaurus sastrei* (Reolid et al. 2021), the allosauroids *Allosaurus fragilis* (Bates et al. 2009a, 2009b; 2012; Macaulay et al. 2023), *Acrocanthosaurus atokensis* and *Giganotosaurus carolinii* (Bates et al. 2009b; 2012; Reolid et al. 2021), the spinosauridae *Baryonyx walker* (Reolid et al. 2021), the tyrannosauroids *Tyrannosaurus rex* (Hutchinson et al. 2007, 2011; Bates et al. 2009b; Reolid et al. 2021; Macaulay et al. 2023) and *Struthiomimus sedens* (Bates et al. 2009b). There are limited physiological and ecological traits that mass alone directly provides. Therefore, we provide skull-to-body length ratios, which will aid in identifying simplified major evolutionary trends (Therrien and Henderson 2007; Gates et al. 2016; Reolid et al. 2021). We 3D scanned specimens of *Sinosaurus* to produce digital volumetric models and provide morphometric measurements that were not available from bones alone, such as surface/volume ratios (S/V), which help to characterize the metabolism of extinct taxa that are closely related to heat dissipation (Reolid et al. 2021). These traits, along with cranial ornaments and BM, are important for our understanding of convergent evolution between theropod dinosaurs at macroevolutionary scales (Gates et al. 2016; Reolid et al. 2021; D'Emic et al. 2023).

Institution abbreviations

IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China;
KMV, Kunming City Museum, Kunming, Yunnan, China;
LDM, Lufeng Dinosaurian Museum, Lufeng, Yunnan, China;
LFKL, Dinosaur Fossil Research and Protection Center of Lufeng City, Lufeng, Yunnan, China
ZLJ/ZLJT, Lufeng World Dinosaur Valley Park, Yunnan, China.

2 Materials and methods

2.1 Materials

A well-preserved *Sinosaurus* skeleton (ZLJ0057) was discovered in Heilongtan Village, Songjiapo, Jinshan Township, Yunnan, and the biostratigraphy corresponds to the Shawan member of the lower Lufeng Formation (Hettangian) (Xing et al. 2015). The specimen was found almost complete and articulated in situ, with broken 12 to 31 caudal vertebrae, ribs and chevrons that were manually repaired when it was first collected in the museum. There was a small amount of bone loss in the right forelimb, and plaster replicas were recast based on the left forelimb of ZLJ0057 and other unpublished *Sinosaurus* specimens in the exhibition hall. This low degree of symmetrical restoration for the right forelimb elements did not affect the discussion of volumetric reconstruction in this paper. It conforms to the diagnostic features of *Sinosaurus triassicus* summarised by Xu et al. (2021), such as: the rostrum is elevated on both sides, forming a pair of sagittal fan-shaped crests, with a divergent herringbone in parietal view; the presence of the main body height of the premaxilla greater than the length and its ventral portion located dorsal to the ventral margin of the maxilla; and it possesses 9 cervical, 14 dorsal, 5 sacral, and about 40 caudal vertebrae. The skeletal specimen ZLJ0057 is housed in the Lufeng World Dinosaur Valley Site Hall (Figure 1A). The skull mounted on the displayed skeleton is a cast of a real fossil prepared as the cranium and the left and right mandibles, housed in the Excellence Hall as specimen ZLJ0109.

2.2 Methods

2.2.1 Extracting Fossil Morphology

Rather than scanning the mount directly (e.g. as in Bates et al 2009a, 2009b), we removed each of the nearly 200 bones of *Sinosaurus* from the supporting bracket that presented the display posture, and scanned each one individually with a Blu-ray Artec Space Spider scanner (Figure 1B). The digitized surface of each bone was processed in the supporting Artce Studio 15 professional version, and exported as Object file (*obj.) for easy execution in general 3D modelling software. The above digital morphology at a higher level of detail may also save time for the same or other research groups; avoiding the harmful processing of fossils re-digitization (Bishop et al. 2020). In practice, however, several single exported files of specimen ZLJ0057 are more than 1GB, for example the skull. Volumetric reconstruction could be performed with just the skeleton contours (Bates 2009a, 2009b, 2012; Mallison 2010a; Sellers et al. 2012; Macaulay et al. 2023), so we focused more on the whole than on fine detail parts. High-polygon representations of bone models have no benefit over downsampled models for volumetric reconstructions, and so these files were downsampled using Zbrush (2021) to reduce computational overhead.

2.2.2 Mounting Digital Skeletons

The alignment of the digitally mounted *Sinosaurus* skeleton followed what Stevens and Parrish (1999) described as the osteologically neutral pose (Figure 2A, 3A), a posture where there was perfect overlap between the articular surfaces of parallel centra, especially in the zygapophyses. The appendages, ribs and chevrons were all mostly mounted in positions of maximum overlap with the articular surfaces of the parental skeletal elements , except for the feet, which were in contact with the ground when standing (Mallison 2010a; Bates 2012; Sellers et al. 2012; Bishop et al. 2021). A second pose followed the more favourable configuration proposed by Macaulay et al. (2023), and a detailed comparison of the advantages and disadvantages of these methods is given in the Discussion section. Note that these postures are not meant to represent life-poses, but rather to present the skeleton in an objective, reproducible way that facilitates volumetric reconstruction.. Based on the observations of Macaulay et al. (2023), we chose a more extended posture in neck, tail, forelimbs and hindlimbs based on the first pose (Figure 4A). In mounting manipulation, we ignored the joint articulation of these elements and only considered aligning their shafts in a straight line. The digital bone models were manually articulated one by one in multi-view 3ds MAX (2018) (Figure 1C, D). The above two mounted models of *Sinosaurus* (ZLJ0057) were subsequently divided into functional regions using 3ds MAX (2018), including head, neck, torso (which included the attached scapulocoracoids and ilia), tail, thigh and arm, shank and forearm, hands and feet.

2.2.3 Generating Body Volume

We used three methods to generate volumes (Figure 1E). (1) Best lofting models (Figures 2B, C): multiple closed spline lines were created surrounding the osteologically neutral articulated skeletal model in computer-aided design (CAD, 3Ds MAX 2018 in this case), and the best estimated volume model was generated by the lofting command (Bates et al. 2009b; Mallison 2010a; Otero et al. 2019; Bishop et al. 2020). (2) Minimum convex hulls (Figure 3B): each segment of the osteologically neutral articulated skeletal model was converted to first minimum convex hulls polygon using the 'Convex Hull' function in Meshlab (2020.09) (Sellers et al. 2012; Hart et al. 2022). (3) Expanding convex hulls (Figure 4B, D): the second minimum convex hulls volume of the extended skeletal model was created as method (2), but also had to multiply by the average dilatation factors to obtain expanding convex volume (Macaulay et al. 2023). The convex hulling method is now really the standard, and is simpler and quicker than making closed splines. We also choose lofting models here, which create a more streamlining body and respiratory structures around and within the 3D skeletal model, as a comparative reference to convex hulling. The enclosed volume was calculated using the Python (3.11.9) (https://www.python.org/) trimesh tool (@software), along with the area and COM value (Figure 2G, 3C, 4C, E).

2.2.4 Estimating Body Mass

The density and volume sensitivity analysis of the lofting body segments suggested that the BM were extremely uncertain with a wide range of plausible values (Bates et al. 2009a, 2009b; Mallison 2010a). Therefore, the BM generated for *Sinosaurus* following method (1) used the single best

lofting model, without trying to create a minimum or maximum model. The best lofting models for each region were multiplied by 1000kg·m^{-3}, while the air cavity lofting model density was taken as 0 kg·m^{-3} (Hutchinson et al. 2007; Bates et al. 2009b; Reolid et al. 2021). An additional note here is that the respiratory structures suffer from uncertainties about precise articulation of the skeleton. A sensitivity analysis was conducted to investigate the effects with reference to Bates et al. (2009a). The best estimate of thoracic volume was adjusted via increasing and decreasing of the medial-lateral rib flare by +/-10°. The total BM for this model was the difference between these two components of mass (Figure 1D-F).

The minimum convex hull method (2) is not meant to be a 1:1 representation of the animal's *in vivo* morphology, (Figure 3B, C) and generally underestimates the true volume (living animals are not "shrink wrapped"). Sellers et al. (2012) applied this technique to obtain masses of a range of extant large-bodied mammals (90~3000 kg), consistently underestimating by approximately 21% those obtained from the literature of extant exemplars. For this reason, here we summed the first minimum convex hull volumes from each region, and then multiplied the total volume by 121% to obtain more accurate convex envelope results. This volume was then multiplied by 1091, 1206, and 1322 kg m^{-3} (as per the 95% confidence interval) to obtain lower, mean, and upper BM estimates of *Sinosuarus*, respectively (Sellers et al. 2012; Hart et al. 2022).

Apart from the difference in posture, the first step in method (3) to obtain the minimum skeletal convex hulls for each segment of the body was consistent with that of method (2) (Figure 4B). Subsequent enlargements of the second minimum convex hulls for the 20 segments were referenced to the average factor in Macaulay et al. (2023) (Figure 4D). These volumes did not deform along the long axis of the body during this process, and only expanded along the other two directions. The expanding convex hulls volume were obtained by summing the each expanding region, and then multiplied by 1000 kg m^{-3} to obtain the BM estimates in a more relative extended pose of *Sinosuarus* (Macaulay et al. 2017, 2023).

The other two BMs for comparison were calculated based on traditional regression formulas for femoral length and circumference (Christiansen and Farina 2004; Campione et al. 2014; Gates et al. 2016).

3 Results of the virtual models

3.1 Virtual skeleton mount

Since a more complete skeleton, such as specimen ZLJ0057, makes realistic physical or digital volumetric models, it offers a chance to examine the mass properties of extinct species (Hutchinson et al 2007; Bates et al 2009). The cranium and mandible (52 cm in length and 36 cm in height) of ZLJ0057 in the display were a compacted cast, but we scanned the real fossil

(ZLJ0109) and then digitally mounted it to better reflect the true condition. The vertebral series of ZLJ0057 consists of 9 cervical, 13 dorsal, and more than 31 caudal vertebrae. The challenge in accurately determining the number of sacral vertebrae in ZLJ0057 arises from sediment compaction and the overlap of the sacral vertebrae and ilia. Here, based on the more distinct anterior sacral centrum 1-3 and the more clearly defined posterior neural spine 3-5, as well as the lengths of the anterior and posterior dorsal and caudal vertebrae of ZLJ0057, we suggest that this specimen has 5 sacral vertebrae. Preservation frequently has an impact on the body of fossilized organisms, and they are not symmetrical. Therefore, when a skeletal element on a side of the body is missing or severely distorted, the corresponding element on the other side could be taken as a substitute after being mirror symmetrized for further study.

Based on nearly 200 skeletal models obtained by scanning the fossil surfaces, the first rebuilt *Sinosaurus* possesses an S-shaped neck, an arched dorsum, and a rigid anteriorly and flexible distal tail, a form similar to that of a number of early primitive predatory theropods (Figure 2A, 3A). In accordance with the morphology of the scapulocoracoids and the position of the posterolateral expansion of the prothoracic ribs, we estimated that the distal end of the scapulocoracoids would have begun at the point immediately beneath the dorsal 1 and that the curvature of the blade tightly hugs but does not meet the ribs (Hu 1993; Senter and Sullivan 2019; Xu et al. 2021). Both the distal tibiotarsus and the proximal metatarsus of ZLJ0057 exhibit a subrectangular articular surface that is perpendicular to the long axis of the shank, which suggests that the mesotarsal ankle joint in *Sinosaurus* is more vertical block-like structure. In early theropods, the inwardly curved ‘S’ femur was mostly upright in pillar-erect hip morphology with a low adductor angle and maximum extension limited by the pubis, which implies a more adducted hindlimb combining with the above ankle (Carrano 2000; Tsai and Holliday 2015; Tsai et al. 2018; Demuth et al. 2020). The second rebuilt *Sinosaurus* is based on the osteologically neutral articulated skeleton above, and has more straightened vertebrae, forelimbs and hindlimbs (Figure 4A) (McCauley et al. 2023).

3.2 Mass and center of mass

Here, we employed hybrid methods to get a more comprehensive picture of *Sinosaurus* BM. The two BMs obtained by the traditional method were 429kg (based on femur length, Christiansen and Farina 2004; Gates et al. 2016) and 537kg (based on femur circumference, Campione et al. 2014). In the following, we discuss the biomechanical factors under the digital mounting skeleton of *Sinosaurus* in osteologically neutral pose and extended pose.

3.2.1 Spline Lofting Models

In this model, we adopted 3ds MAX (2018) to create a closed spline near the outline of the skeleton (Figure 2B), transformed it into an editable form with the right number of vertices for adjustment, and then utilized the lofting command in the composite object to generate the best lofting models

(Figure 2C). It is important to note that the combination of ZLJ0057 thoracic rib motion and the fact that both theropods and sauropods developed lungs similar to those of extant birds, as has been demonstrated by Witmer (1995) based on the extant phylogenetic bracket, reflects the respiratory capacity of *Sinosaurus*. Therefore, it is equally necessary to simulate the air sacs of the head cavity, trachea, and lungs during spline lofting volume creation to obtain a more realistic mass and mass distribution (Figure 2D-F) (Bates et al. 2009b; Mallison 2010a).

The best lofting model of *Sinosaurus* based on the osteologically neutral articulated skeleton of ZLJ0057 is 0.8700 m^{-3} (Table 2). The volume of air sacs occupied by the head cavity, trachea, and lungs has a total volume range of 0.0530-0.0795 m^{-3}, and sensitivity analyses of this segment mainly done by the flare of ribcage. It can be concluded that ZLJ0057 has a total net mass range of 790.51-817.05 kilograms (kg). The best lofting models with a 'best guess' air sac of 0.0617 m^{-3} is 808.30 kg with an average density of 929.1 $kg \cdot m^{-3}$. We locate the origin of the COM coordinate system for all volume models at the midpoint of the two feet line right below the hip joint similar to previous studies (Bates et al. 2009a). The best net COM is calculated by Boolean subtraction in 3ds MAX (2018) as (0.36, 1.34, 0.00) (Figure 2G).

3.2.2 Two Convex Hulls Models

The osteologically neutral articulated and extended skeleton of *Sinosaurus* was separated into various anatomical segments in 3ds MAX (2018), and the latter was subdivided into three more segments of tail, metacarpals and digits (Sellers et al. 2012; McCauley et al. 2023). The 3D minimum envelopes (Figure 3B, 4B) of the above regions were calculated by the filters in Meshlab (2020.09). Based on the osteologically neutral articulated skeleton of ZLJ0057, the first minimum convex hulls volume of *Sinosaurus* sum up to 0.5285 m^{-3} with a COM as (0.36, 1.31, 0.00) (Figure 3C). Multiplying the first minimum convex hulls volume by the corresponding exact values (121%) yields a more accurate volume of 0.6395 m^{-3} (Sellers et al. 2012), giving a total mass range of 697.7-845.4 kg (Table 3). Based on the extended skeleton, the second minimum convex hulls volume (Figure 4A-C) were obtained for *Sinosaurus* sum up to 0.4769 m^{-3} with a COM as (0.46, 1.36, 0.00). Afterwards, the expanding convex hulls volume of those regions have been multiplied by the average dilatation factors (Figure 4D), which is measured from individual body segments of three extant phylogenetic bracket groups (lizards, crocodiles, and birds) (McCauley et al. 2023). The expanding convex hulls volume sum up to 0.8946 m^{-3} (894.6 kg) and a COM as (0.41, 1.36, 0.00) (Table 4), which is more caudally orientated than the COM of the minimum envelopes in that pose (Figure 4C, D).

4 Discussion

4.1 Body Mass Inference of Fossils

The mass of terrestrial organisms is readily and directly accessible through weighing. With respect to current research, weight assessment of extinct archosaurs is more challenging. The mass assessment methodologies that have been employed for extinct organisms since the last century can be categorized into extant scaling (large datasets for macroevolutionary and palaeoecological studies) and volumetric density (whole-body palaeoreconstruction for biomechanics and physiology studies) approaches (Christiansen and Farina 2004; Bates et al. 2009b; Sellers et al. 2012; Campione et al. 2014; Campione and Evans 2020; McCauley et al. 2023; Romano et al. 2023).

The extant scaling approaches have a lower demand for primary fossil data, derived from standardised measurements of various body parts (Anderson et al. 1985; Alexander 1989; Campione and Evens 2012; Campione et al. 2014; Bates et al. 2015; Campione 2017), allowing it to be almost universally for estimating body mass of extinct clades. Here, we only used two independent, extant species-based extant scaling approaches related to non-avian bipeds based on femur length and circumference to estimate the body mass of *Sinosaurus* (ZLJ0057) at 429 kg and 537 kg, respectively (Christiansen and Farina 2004; Campione et al. 2014). However, it will never be possible to test the assessment mass in the fossil record. The errors can only be influenced by applying extant scaling approaches or the direct use of a proxy to as many extinct members of crown clades as possible where evolutionary relationships are more certain (Christiansen and Farina 2004; Campione et al. 2014; Campione and Evens 2020). Because the phylogenetic analysis of *Sinosaurus* has not been widely recognized (Xing 2012; Gates et al. 2016; Marsh and Rowe 2020; Xu et al. 2021; Zhang et al. 2023), the body mass determined by the extant scaling approaches is not a reliable value; instead, it can only be used as a reference.

The volumetric density approaches have been further divided by Campione and Evans (2020) into three methods: i) physical scale models (Alexander 1985; Christiansen and Farina 2004; Romano et al. 2023); ii) two-dimensional mathematical models (Jerison 1969; Mazzetta et al. 1998); iii) three-dimensional virtual models (Bates et al. 2009b; Mallison 2010a; Sellers et al. 2012; Otero et al. 2019; Bishop et al., 2020; Hart et al. 2022; McCauley et al. 2023). In previous three-dimensional virtual model studies, the 3D slicing method (Henderson 1999; Bates et al. 2016), the convex hull method (Sellers et al. 2012; Romano et al. 2021; Hart et al. 2022) and the spline- or hoop-based method (Bates et al. 2009b; Mallison 2010a; Otero et al. 2019; Bishop et al., 2020) were mostly used in the reconstruction of extinct organism volumes. In next section, we present a synopsis of the chief spline- or hoop-based and convex hull method, the above methods should be referred to the original authors for a more detailed explanation.

4.2 Best estimation of mass

The spline- or hoop-based method has the advantage of maximizing the information content of the complete skeleton, but they are not perfect. Previous attempts have been made to perform sensitivity analysis of lofting body mass (Bates et al. 2009a; Mallison 2010a). The best lofting models *Plateosaurus* were considered to represent a basic body mass of 739.26 kg, with a range of 660.24-837.50 kg by multiplying a density value between 900-1000 $kg \cdot m^{-3}$ (Mallison 2010a). The best lofting models for *Allosaurus* was calculated to be 1500.91 kg by a density of 1000 $kg \cdot m^{-3}$ after producing a 'best estimate model' (Bates et al. 2009a). The volume of neck, thoracic, sacral, tail and hind limb segments were then changed to create a single gracile (- 7.5%) and two larger models (+ 7.5% and +15%) with a mass range of 660.24-837.50 kg. However, the sensitivity analysis results suggest that body mass are highly uncertain values and fail to be reasonably qualified by conditional constraints. Nonetheless, the COM location is strictly restricted just in front of and beneath the hip joint (Henderson 1999; Hutchinson et al. 2007; Bates et al. 2009a, 2009b; Mallison 2010a), even in the motion of dorsal ribs and an increase of 5 mm in inter-vertebral spacing. The location of the COM between the feet facilitates the maintenance of body stability in bipedal theropods; and the COM near the acetabulum reduces the need for the femur to rotate in order to maintain the balance of the body, which in turn reduces the limitation on the hindlimb locomotor ability of the predator (Carrano 2000; Tsai and Holliday 2015; Tsai et al. 2018; Demuth et al. 2020).

In this manuscript, we first generated best lofting models of *Sinosaurus* based on the digitally reconstructed ZLJ0057 in the osteologically neutral articulated skeleton, following the overall workflow of the Spline or hoop-based method (Bates et al. 2009a, 2016). Although the spline lofting method is too time-consuming and labor-intensive, it produces body and air sac model closely aligned with the organism's body morphology. The best body mass of *Sinosaurus* was 808.30 kg, with air cavities ranging from 11.97-19.90% of the trunk volume. The latter is slightly larger than in *Allosaurus* because *Sinosaurus* has relatively more slender but long dorsal ribs, which means that they can accommodate lung development in a more longitudinally extended direction. However, variation in air cavity did not significantly affect body mass assessment and centre of mass (0.36, 1.34, 0.00) (Figure 2G), which is consistent with previous studies (Henderson 1999; Hutchinson et al. 2007; Bates et al. 2009a, 2009b).

When constraining the thickness of missing soft tissue, the Spline or hoop-based method is frequently criticized for involving excessive amount of subjective input to generate the body outline. The other strategy, the minimum convex hull method (2) is faster and more objective with less user intervention (Sellers et al. 2012). It rapidly automatically generates volume in Meshlab software for estimating body mass of a digital mounted skeleton. However, due to the tightly fitted volume to the skeleton, this method assesses in a lower value. Sellers et al. (2012) compared the summed segment volumes and derived body masses of 14 relatively large-bodied mammalian

and demonstrated that this value proved to underestimate body mass by 21%. The first minimum convex hulls volume for the osteologically neutral articulated skeleton of *Sinosaurus* was 0.5285 m^{-3}, which was multiplied by 121% to give a more accurate volume 0.6699 m^{-3}. Although this volume is slightly lower than the volume derived by the spline lofting method (0.8700 m^{-3}), it will be assigned to a more realistic and higher density obtained from extant animals. The mass of expanding convex hulls model (697.7-845.4 kg) ultimately approximates to the best lofting models (790.51-817.05 kg), and the former's COM (0.41, 1.36, 0.00) is slightly further down and cranial than the latter (0.36, 1.34, 0.00).

The minimum convex hull method (2) combines the segment volumes obtained from a digital osteologically neutral articulated skeleton with predictive regression to produce faster and better mass estimates in comparison to the Spline or hoop-based method. However, the large-bodied mammalian taxa used to predict the regression are poorly related to bipedal dinosaur, making the reliability of the multiple factor questionable. Predictions of extant dinosaur kin taxa would significantly improve the confidence of the factors. Macaulay et al. (2023) investigated 3D skeletal, minimum convex hull and skin volume models of 17 extant non-avian sauropsids and 33 extant birds to predict factors between volume models, and used it to estimate mass of extinct archosaurian. Those models were obtained from CT scans using physical CoM - suspension methodology (Macaulay et al. 2017, 2023), and were separated into various segments of head, neck, thoracic, tail and sectional limbs to generate volume. The average dilatation factors between real skin volumes and minimum skeletal convex hulls were successfully refined, which could be employed even further to accurately expand segments and whole-body mass characteristics in fossilized archosaurians. The only point to note is that the digital skeletons in osteologically neutral pose and extended pose of *Sinosaurus* not only have different postures, but also allow the COM position to change. Therefore, the COM comparisons between the osteologically neutral pose and the extended pose model are somewhat distorted. Based on the extended skeleton, the total minimum volume of *Sinosaurus* was 0.4784 m^{-3} with a COM of (0.46, 1.36, 0.00). The sum of expanding convex hulls body volume was 0.8946 m^{-3} with a more caudal COM of (0.41, 1.36, 0.00), thereby yielding a whole-body dilatation factor of 1.87. For *Sinosaurus* here in both postures, this factor is much larger than that for generation of the first minimum convex hulls volume (121%) from mammals.

The BM of *Sinosaurus* was estimated from three 3D volume model to range from 711.0-894.6 kg when the densities ranged from 929.1-1322.0 $kg \cdot m^{-3}$. Changes in the air cavity volume of the spline lofting method had little effect on the ultimate total mass (790.51-817.05 kg), with body mass fluctuations of only -18 to +10 kg (-1.08~+2.20% using the best lofting model as a reference). However, the first minimum convex hulls method density alternative had a much larger effect on BM (697.7-845.4 kg), with a fluctuation of about ±80 kg (-9.54~+9.62%, using the mean mass as a reference). This suggests that within and between the BMs generated by three volumetric density

methods (Figure 5) (more detailed data are provided in Supplementary Table 1), the BM was more affected by the choice of density than by changes in volume. The BMs derived from three volumetric density methods was far heavier than the other two calculated from the femur length equation (Christiansen and Farina 2004; Campione et al. 2014; Gates et al. 2016), which were 537.04 kg and 429 kg, respectively.

To avoid being influenced by individual differences, we compared the BM obtained by the best lofting models, plaster reconstructions, expanding convex hulls method and regression formulas of typical non-avian theropods (Figure 6) (more detailed data in Supplementary Table 2), with data sourced mostly from previous studies (Bishop et al. 2009a, 2009b, 2021; Allen et al. 2013; Gates et al. 2016; Reolid et al. 2021; D'emic et al. 2023; Macaulay et al. 2023). The two traditional regressions performed here based on femur size (length and circumference) yielded BMs that did not differ significantly (grey line in Figure 6, correlation fluctuates at 100%). This is due to the fact that as theropod dinosaurs became massive, the femurs in the hindlimbs, which were used to support the weight of the body, thickened and lengthened simultaneously. The same species generated by the best lofting models, plaster reconstructions and expanding convex hulls method showed less mass correlation with each other (triangles, squares and circles in Figure 6), and only a certain amount of convergence could be observed between best lofting and expanding convex hulls volume models. Here, we advocate the use of the expanding convex hulls method, which can automate the fitting of convex hulls to segments of the skeleton to reconstruct soft tissue volumes. More convincing is the fact that this method applies empirically derived post hoc correction factors derived from extant relatives rather than mammals (Sellers et al. 2012; Macaulay et al. 2023). Thus, it is preferable and recommended to use the expanding convex hulls model as an optimal BM of 894.6 kg in the case of *Sinosaurus* with an adequately complete fossil skeleton (ZLJ0057).

4.3 Locomotor and feeding strategies

The skull-length/body-length ratio was estimated with data sourced mostly from Reolid et al. 2021 (Figure 7, the squares represents) (more detailed data are provided in Supplementary Table 3). The theropod skulls, including fossils and 3D models, tended to be proportionally larger in this ratio, including the Late Triassic more primitive genus, *Coelophysis* (0.093), the Early Jurassic *Sinosaurus* (0.099) and *Dilophosaurus* (0.103), and the Cretaceous largest form of *Tyrannosaurus rex* (0.119) (Therrien and Henderson, 2007). The ratio of *Sinosaurus* followed a trend of increasing with BM in previously studied genera (Reolid et al. 2021), but only *Carnotaurus* (0.067) did not follow this trend owing to its particularly short skull.

To enhance body and skull scale while maintaining an acceptable level of agility, advanced biped carnivorous theropods, such as the best-known *Tyrannosaurus rex*, have progressively shorter arms. Causing the changes in the COM at osteologically neutral pose (Table 5) in some taxonomic

groups, such as *Tyrannosaurus* (23.88, %COM cranial to Head-Neck-and-Trunk (HNT) length), *Acrocanthosaurus* (17.36) and *Allosaurus* (16.04), and *Struthiomimus* (23.05) (Bates et al. 2009a, 2009b), it would be more cranial than *Sinosaurus* (11.31) to balance the increased body and skull size with the reduced arm (Bates et al. 2009a, 2009b). Although there is a tendency for the COM to shift anteriorly, the derived traits actually differ between each taxon and even between individuals. In fact, we are more likely to encounter an elevated forepart of the body, as in the case of the long-necked *Struthiomimus sedens* (Bates et al. 2009b), or an enlarged tail and hind limbs, as in the case of the giant *Giganotosaurus carolinii* (Reolid et al. 2021).

The COM of *Sinosaurus* is more hypoventral, which somewhat reduces the degree of flexibility of the hip to a certain degree, as a robust joint is required to maintain body stability. However, the lower functional demands on the hind limbs for balancing decreases the limitation on the speed of locomotion (Mallison 2010a, 2010b). Beginning with the most primitive genus, *Coelophysis* from the late Triassic (Rinehart et al., 2009) to the slender *Sinosaurus* and *Dilophosaurus* from the Early Jurassic, all had relatively proportionally large limbs to its slender body with a narrow pelvis. The long hindlimbs and relatively high ratio (1.44) between the lengths of the tibia + metatarsus to femur of medium-sized *Sinosaurus* are considered suitable for fast operation, as is the case for *Carnotaurus* (Persons and Currie, 2011; Persons and Currie 2016; Dececchi et al. 2020; Reolid et al. 2021).

Locomotion characteristics in general could be materialized into life strategies. *Baryonyx* had very strong forelimbs and distinctive large claws on the thumbs that may have aided in catching fish (Amiot et al. 2010). The slender and long tail of *Allosaurus* indicates that it is adept at ambushing and pursuing predators (Reolid et al. 2021). In contrast, during the heyday of dinosaur dominance on the terrestrial Earth, such as with progressively shortened forelimbs, *Ceratosaurus* relied exclusively on biting power and muscular necks (Reolid et al. 2021). *Giganotosaurus* and *Tyrannosaurus* are constrained by their massive size and are unsuitable for running due to high skeletal loads, but the main hunter weapon is the skull, or perhaps the scavenger (Stevens 2006; Hone and Watabe 2010; Sellers et al. 2017).

The teeth of ZLJ0057 are consistent with the curved blade-like according to Xing's (2012) observation in LDM-L10. Denticles that function as sharp 'serrations' are developed on both the anterior and posterior carinae, which are typical of carnivorous theropods. The maximum depth of the mandible is 61 mm, while the length of the skull is 520 mm. There is weak biting in *Sinosaurus*, confirming that it possibly feeds small- to medium-sized vertebrates. A larger body size corresponds to a larger and deeper jaw to better meet the increase in size and energy demands (Kane et al. 2016). A finite element analysis of the skull of *Sinosaurus* by Xing et al. (2015) showed that paired cranial crests with perforated cavities were too weak to resist mechanical loads during combat. The

forelimbs also do not have structural features conducive to hunting, as in the case of *Baryonyx* (Amiot et al. 2010). In terms of the feeding strategy of *Sinosaurus*, its relatively larger forelimbs could be simultaneously employed with slender skulls to attack slightly larger prey, along with long legs, proving them to be good at running in pursuit (Paul 2016). The optimization of forelimbs and skulls in predation maintains the nutrition required for the trend toward gigantism in the body size of nonavian theropods.

4.4 Body design and metabolism

Metabolic activity generates body heat and requires the skin, respiratory system and digestive system to eliminate excess body heat (e.g., O'Connor and Dodson 1999; Henderson 2013; Porter and Witmer 2020). In particular, the skin is known to be the most crucial and largest metabolic organ of the body. With the gradual increase in the size of theropods, S/V decreased (e.g., Henderson 2013), and the efficiency of metabolic heat dissipation also decreased (Gillooly et al. 2006; Lucas 2007; Reolid et al. 2021). Based on previous genera as well as the 3D volume models of *Sinosaurus* we reconstructed, the scatterplots (Figure 7, the circles represents) (more detailed data in Supplementary Table 3) show that S/V is strongly correlated with body mass, including the anomalous *Carnotaurus* in the preceding section, which suggests the metabolism of extinct taxa. Of course, other objective conditions that affect the efficiency of metabolic heat on the surface are skin color, temperature difference from the environment, and the feathers beneath the skin. S/V showed an overall trend of slower heat dissipation with increasing body mass. *Coelophysis* (36.00) had the fastest heat metabolism, and *Sinosaurus* (11.81) had a moderate heat dissipation rate, while *Tyrannosaurus* (5.08) had the lowest heat dissipation efficiency.

Larger theropods may be incapable of strenuous exercise, which would generate a large amount of body heat in a short period of time, echoing the inference in the previous section that they are not good at running. Or they may need to rest for a long time after feeding activities, which could also indicate that enormous-bodied theropods are not active hunters and may all be scavengers (Horner 1994; Carpenter 1998; Stevens 2006; Hone and Watabe 2010; Kane et al. 2016). *Sinosaurus* is from the most famous lagerstätten found in the Lufeng Formation and is at the top trophic level of the Lufeng food chain (Xing 2012). Based on the $\delta^{13}C$ and $\delta^{18}O$ compositions of sauropodiform and *Sinosaurus* tooth enamel and compact bones, Shen et al. (2021) proposed a relatively arid tropical savanna climate for this family. This warmer climate ($\geq 21 \pm 3°C$) favours thermoregulation. From the point of view of heat dissipation, body temperature may have increased with mass, corroborating the inference that large dinosaurs may be endotherms.

4.5 Convergent macroevolution

The phylogenetic analysis of *Sinosaurus* has mostly relied on the anatomy and morphology of the skull (Xing 2012; Marsh and Rowe 2020), but there are still no widely recognized conclusions. As

we can find from most of the previous mainstream related studies (e.g., Carrano et al. 2002; Smith et al. 2007; Xing 2012; Marsh and Rowe 2020), there is a high threshold for such attempts to explain phylogenetic mechanisms or evolution through the lens of individual species. As far as *Sinosaurus* is concerned, it has been more than 70 years since its discovery (Young 1948). However, due to the limitations of low availability of holotype specimen and imperfect preparation of additional specimens (Young 1948; Welles 1984; Hu 1993; Dong 2003; Xing 2012; Xing et al. 2013, 2014), detailed morphological descriptions, not to mention phylogenetic analyses based on morphology, have not yet been completed (Marsh and Rowe 2020; Xu et al. 2021; Zhang et al. 2023). A detailed and precise description of the diagnostic characters is the basis for phylogeny based on anatomy. Consequently, large datasets, calculated by the extant scaling regression equations (Christiansen and Farina 2004; Campione et al. 2014), have been employed in macroevolutionary and palaeoecological studies of the extinct members of crown clades in nonavian dinosaurs (Campione and Evans 2020; D'Emic et al. 2023). Gates et al. (2016) argued that a dichotomy between large size and cranial ornaments reveals that *Sinosaurus* and *Cryolophosaurus* belong to an advanced branch, each forming a distinct clade from *Ceratosaurus*, *Abelisaurus*, and *Carnotaurus*, which are all derived from a more basal branch formed by *Dilophosaurus*, *Coelophysis*, and *S. kayentakatae*.

However, we did not intend to discuss the phylogenetic analysis of *Sinosaurus* here or to compare the advantages and disadvantages of the phylogeny from the individual species or the convergent macroevolution of features. Instead, in the absence of comprehensive anatomical and taxonomic information, it is also possible to explore the macroevolution of organisms in terms of physiological and ecological traits such as body mass and metabolism (Gates et al. 2016; D'Emic et al. 2023). Overall, these factors require a more solid and plausible body mass as a foundation, and BM estimates using individual or fragmentary bones can be implausible and misleading (Figures 5-6). In the presence of sufficiently complete and well-preserved fossil skeletons, volumetric density methods derived from 3D reconstruction can generate more reliable estimates of body mass that reflect natural size (Macaulay et al. 2017, 2023; Bishop et al. 2020; Campione and Evans 2020; Reolid et al. 2021; Romano et al. 2023). Finally, we look forward to the future use of mass datasets not only for correcting/or standardising mass values based on 3D reconstructions or single skeletal elements, but also as the idea that mass datasets could be used for the study of macroevolution in theropods. We suggest that phylogeny using the mass datasets could be used as a forerunner to identify developmental locations of species that have not been precisely described yet (Gates et al. 2016; D'Emic et al. 2023). In the future, it is expected that the evolutionary relationships obtained by the two approaches, morphological phylogeny and mass datasets, could prospectively validated against each other.

5 Conclusions

We used non-contact scanning techniques to capture 3D morphology data from near 200 bones of a near-complete specimen of *Sinosaurus* and first mounted the digital skeleton according to the osteologically neutral position between joints. The first rebuilt *Sinosaurus* possesses an S-shaped neck, an arched dorsum, and a rigid anteriorly but flexible distal tail. For the shoulder joints, the distal end of the scapulocoracoids began immediately beneath the dorsal 1, and the blade arcs tightly hugs the ribcage. The hip joint was mostly upright with the vertical block-like ankle. It was then also digitally mounted with more extended vertebrae, forelimbs and hindlimbs posture based on the above.

We present a synopsis of the volumetric models of *Sinosaurus* generated by the spline- or hoop-based and convex hull method. The best lofting models with the time-consuming total volume of 0.8700 m^{-3} had a mass of 808.30 kg. The sensitivity analysis by flare of the dorsal ribs yielded air cavities in the range of 0.0530-0.0795 m^{-3}, but without significant effect on the COM of (0.36, 1.34, 0.00). The first minimum convex hulls volume rapidly automatically generated the more accurate convex envelope of 0.5285 m^{-3} with COM (0.36, 1.31, 0.00), getting a mass range of 697.7-845.4 kg. The sum of expanding convex hulls body volume was 0.8946 m^{-3} (894.6 kg) with a more caudal COM of (0.41, 1.36, 0.00) than before expansion. The whole-body dilatation factor of 1.87 is much larger than that for generation of the first minimum convex hulls volume from mammals. Here, we advocate the use of the expanding convex hulls method, which can automate the fitting of convex hulls to segments of the skeleton to reconstruct soft tissue volumes. We estimated the possible living BM of a new well-preserved ZLJ0057 by three volumetric density method to range from 711.0-894.6 kg when the densities ranged from 929.1-1322.0 $kg \cdot m^{-3}$. By comparing the results obtained by traditional regression formulas, it was concluded that the best estimate of body mass of *Sinosaurus* was 894.62 kg with the COM (0.41, 1.31, 0.00) in the expanding convex hulls model.

The skull/body length of *Sinosaurus* is consistent with the gigantification of theropod body size, and its narrow pelvis, relatively high lower leg ratio, and slender body make it a great runner. Combining these features with the shallow lower jaw, weak crest and large forelimbs, we suggest that *Sinosaurus* requires the skull and forelimbs to cooperate in the pursuit of prey. The S/V ratio indicated that *Sinosaurus* has a moderate ability to generate body heat from locomotion through cutaneous metabolism. This parameter is useful for studying locomotor patterns and body temperature changes but is less pronounced in medium-sized theropods such as *Sinosaurus* than in giant theropods. There are no widely recognized conclusions about the phylogenetic analysis of *Sinosaurus* through the lens of individual species. The macroevolution of skull ornaments and traditional calculated body mass datasets provides a new phylogenetic comparative framework in the absence of comprehensive anatomical and taxonomic information. It is hoped that the more

precise mass estimation derived from 3D reconstruction will provide more solid and plausible datasets for further convergent macroevolution.

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Figures

Figure 1. The overall workflow for generating a three-dimensional (3D) volumetric model of fossil taxa, in this case, *Sinosaurus*. (A), photograph of mounted skeleton ZLJ0057 by Wang Tao; (B), the 3D geometry of each fossil bone is digitally captured using laser surface scanning; (C), ; (D), the osteologically neutral pose; (E), the convex hulls volumetric model; (F), the fully defined volumetric model then provides the basis for a wide range of analyses.

Figure 2. The best lofting model of ZLJ0057 *Sinosaurus*. (A) upper body area of the osteologically neutral articulated skeleton, surrounded by spline circles (B); (C) lateral view of the best lofting model volume; D-F, sensitivity analysis of sac air with the ribcage reduced (D) and increased (F) by 10° relative to the osteologically neutral articulated skeletal mount (E); (G) black dots indicating the position of the COM. Note that some of the sternal ribs may protrude from the volumetric model, mainly because the elements are deformed and therefore ignored during volumetric model creation.

Figure 3. The first minimum convex hulls volume models of ZLJ0057 *Sinosaurus*. (A), the entire osteologically neutral articulated skeleton; (B), lateral view of the first minimum convex hulls volume, automatically generated in Meshlab; (C), black dots indicating the position of the COM.

Figure 4. The expanding convex hulls model of ZLJ0057 *Sinosaurus*. (A), the entire virtual extended skeleton; (B) and (D) lateral view of the second minimum and expansion convex hulls volume; (C) and (E) black dots indicating the position of the COM.

Figure 5. Bar graph of mass estimates obtained with two traditional regression methods and three volumetric models. (I) value obtained using the equation of Campione et al. (2014); (II) value taken from the Supplement to Gates et al. (2016) using the equation of Christiansen and Farina (2004); (III) values calculated from the best lofting model, (IV) first minimum convex hulls volume model (Sellers et al. 2012), and (V) expanding convex hulls model (Macaulay et al. 2023).

Figure 6. Comparison of BM estimates derived from different methods for theropods from representative families (standardised using the BM values from Gates et al. 2016, estimated using the femoral length equation from Christiansen and Farina 2004). Gray line is calculated by another traditional regression equations (mass values derived from D'emic et al. 2023 using the femoral circumference equation from Campione et al. 2014), and triangle, square and circle are estimated by the best lofting model, plaster reconstructions and expanding convex hulls methods, respectively (Bishop et al. 2009a, 2009b; 2021; Sellers et al. 2012; Allen et al. 2013; Reolid et al. 2021; Macaulay et al. 2023).

Figure 7. Scatter plot showing the relationships among the skull length/body length ratio (square) and surface/volume ratio (circle) with body mass for 3D model species, mainly from Reolid et al. (2021). Note that the dinosaur taxon legend on the right is only used to illustrate the decrease in body size from the bottom up, not the true proportions. Abbreviations: *Co*, *Coelophysis*; *Di*, *Dilophosaurus*; *Si*, *Sinosaurus*; *Ce*, *Ceratosaurus*; *Ba*, *Baryonyx*; *Ca*, *Carnotaurus*; *Al*, *Allosaurus*; *Gi*, *Giganotosaurus*; *Ty*, *Tyrannosaurus*.

Tables

Table 1. The research history of *Sinosaurus*

Table 2. Results of the best lofting model in the osteologically neutral pose of *Sinosaurus* ZLJ0057

Table 3. The volumetric models of the minimum convex hull method (2) in the osteologically neutral pose of *Sinosaurus* ZLJ0057 (Multiple factor from Sellers et al. 2012).

Table 4. Results of the expanding convex hulls model in a more relative extended pose of *Sinosaurus* ZLJ0057 (Average dilatation factors from McCauley et al. 2023).

Table 5. COM for precise mass estimation derived from the best lofting volumetric reconstruction (Bates et al. 2009a, 2009b)

Supplementary Table 1-3.