



# Digital 3D models of theropods for approaching body-mass distribution and volume

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## Abstract

The aim of this work is to obtain diverse morphometric data from digitized 3D models of scientifically accurate palaeoreconstructions of theropods from eight representative families. The analysed polyvinyl chloride (PVC) models belong to the genera *Coelophysis*, *Dilophosaurus*, *Ceratosaurus*, *Allosaurus*, *Baryonyx*, *Carnotaurus*, *Giganotosaurus*, and *Tyrannosaurus*. The scanned 3D models were scaled considering different body-size estimations of the literature. The 3D analysis of these genera provides information on the skull length and body length that allows for recognition of major evolutionary trends. The skull length/body length in the studied genera increases according with the size of the body from the smallest *Coelophysis* with a ratio of 0.093 to ratios of 0.119–0.120 for *Tyrannosaurus* and *Giganotosaurus*, the largest study theropods. The study of photogrammetric 3D models also provides morphometric information that cannot be obtained from the study of bones alone, but knowing that all reconstructions begin from the fossil bones, such as the surface/volume ratio (S/V). For the studied theropod genera surface/volume ratio ranges from 35.21 for *Coelophysis* to 5.55 for *Tyrannosaurus*. This parameter, closely related to the heat dissipation, help in the characterization of the metabolism of extinct taxa. Accordingly, slender primitive forms of the Early Jurassic (i.e. *Coelophysis* and *Dilophosaurus*) had relatively smaller skulls and higher mass-specific metabolic rates than the robust large theropods of the Cretaceous (i.e. *Giganotosaurus* and *Tyrannosaurus*). This work presents a technique that, when applied to proper dinosaur models, provides extent and accurate data that may help in diverse study areas within the dinosaur palaeontology and palaeobiology.

**Keywords** Dinosaurs · Bipeds · Body-mass · Surface/volume ratio · Mesozoic

## Resumen

El objetivo de este trabajo es la obtención de diversos datos morfométricos a partir de la digitalización de maquetas 3D realizadas en base a reconstrucciones científicamente elaboradas de especies representativas de ocho familias de terópodos. Las maquetas de PVC analizadas corresponden a los géneros *Coelophysis*, *Dilophosaurus*, *Ceratosaurus*, *Allosaurus*, *Baryonyx*, *Carnotaurus*, *Giganotosaurus*, y *Tyrannosaurus*. Los modelos digitales 3D fueron escalados teniendo en cuenta las estimaciones de tamaño publicadas por otros autores para estos taxones. El análisis 3D de estos géneros proporciona información de las variaciones en el modelo funcional de los terópodos, principalmente en cuanto a la longitud de la cabeza y el cuerpo, así como algunas características de las extremidades que permiten inferir tendencias evolutivas y de modo de vida de estos organismos. La relación de tamaños cabeza/cuerpo incrementa de acuerdo con la talla del terópodo, con los valores más bajos obtenidos para *Coelophysis* (0.093) y los más altos para *Tyrannosaurus* y *Giganotosaurus* (0.119 a 0.120).

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Los modelos digitales obtenidos también proporcionan información que no puede obtenerse solo con el estudio de los huesos, aunque éstos son la base de toda reconstrucción, tales como la relación superficie/volumen (S/V). Para los especímenes estudiados, y basándonos en la fidelidad de las maquetas, la S/V varía desde 35.21 en *Coelophysis* a 5.55 en *Tyrannosaurus*. Este parámetro, estrechamente relacionado con la disipación de calor por parte del organismo, ayuda a interpretar el metabolismo de taxones extintos. Así, formas primitivas y ligeras del Jurásico inferior (ej. *Coelophysis* y *Dilophosaurus*) tuvieron cráneos pequeños y posiblemente una tasa metabólica mayor que los grandes terópodos del Cretácico (ej. *Giganotosaurus* y *Tyrannosaurus*). Este trabajo, además, presenta una técnica que, cuando es aplicada a reconstrucciones científicamente cuidadas, proporciona aproximaciones que pueden ser de utilidad en el estudio paleontológico y paleobiológico de los dinosaurios.

**Palabras clave** Dinosaurios · Bípedos · Masa corporal · Relación superficie/volumen · Mesozoico

## Abbreviations

AMNH	American Museum of Natural History, New York
BHI	Black Hills Institute of Geological Research, Hill City, USA
BMNH	British Museum of Natural History, London, UK
CM	Carnegie Museum, Pittsburgh USA
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina
FMNH	Field Museum of Naural History, Chicago, USA
MOR	Museum of the Rockies, Bozeman, USA
MUCPv	Museo de la Universidad Nacional del Comahue, Neuquén, Argentina
MWC	Museum of Western Colorado, Fruita, USA
NHM	Natural Hostory Musem, London, UK
NMMNH	New Mexico Museum of Natural History, Albuquerque, USA
UCMP	University of California Museum of Paleontology, Berkeley
USNM	United States National Museum (Natural History), Smithsonian Institution, Washington, USA
UUVP	University of Utah Vertebrate Paleontology Collection, Utah, USA
YPM	Peabody Museum Yale University, New Haven, USA

## 1 Introduction

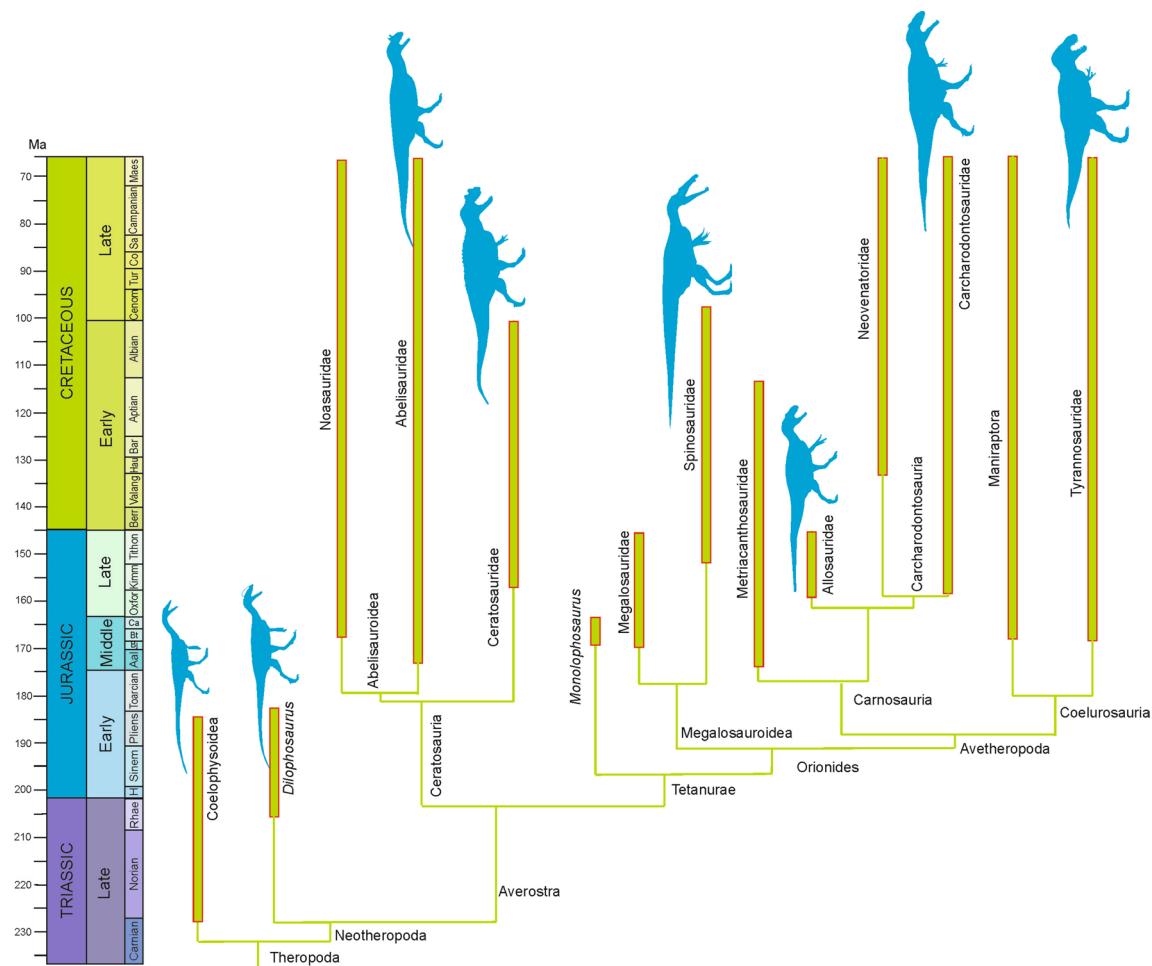
The Suborder Theropoda is a monophyletic group traditionally included within the Order Saurischia (e.g. Seeley, 1888; Ferigolo and Langer, 2006). However, recently Theropoda was included in the clade Ornithoscelida (Baron et al., 2017) that also comprises the Order Ornithischia, but there is a controversy about this proposal (Langer et al., 2017). All theropods were clawed biped with sharp, sometimes serrated teeth. Hollow bones, in both vertebrae and limbs, are a common feature of theropods. The size of theropods ranged from less than half meter (e.g. *Microraptor* and *Iberomesornis*)

to genera growing over 12 m in length (e.g. *Carcharodontosaurus*, *Giganotosaurus*, *Spinosaurus*, and *Tyrannosaurus*; Therrien and Henderson, 2007; Hutchinson et al., 2011). The nearly horizontal position of the vertebral column for balancing the body over the pelvis, took advantage of the centre of gravity being positioned near the hip. The presence of large and deep jaws and consequently large heads is distinctive of the group as carnivorous tetrapods. The increasing head size, mainly in large theropods of Ceratosauria, Carnosauria, and Tyrannosauroidea, among others, required downsizing of other parts of the front half of the body to remain balanced with the back half at the hip, therefore, some groups had notoriously short arms. The clearest example is the Family Abelisauridae. The tail is an important counterbalance in theropods.

The Suborder Theropoda is divided into three major groups (Fig. 1): Coelophysoidea (e.g. *Coelophysis*), Neoceratosauria (e.g. *Ceratosaurus* and *Carnotaurus*) and Tetanurae (rest of theropods). In tetanuran evolution, there is a tendency to decrease the flexibility of the tail except close to the hip (Sereno et al., 1994; Fastovsky and Weishampel, 2012; Pittman et al., 2013), and some groups present back half of the tail stiffened such as dromaeosaurid *Deinonychus* (Benton, 2005). Tetanurae constitutes a very diverse group of theropods of the Superfamily Megalosauroidea (families Megalosauridae and Spinosauridae) and the Avetheropoda that includes the infraorders Carnosauria (families Allosauridae and Carcharodontidae) and Coelurosauria (families Alvarezsauridae, Caenagnathidae, Caudipteridae, Compsognathidae, Deinocheiridae, Dromaeosauridae, Megaraptoridae, Ornithomimidae, Oviraptorsauridae, Proceratosauridae, Therizinosauridae, Troodontidae, Tyrannosauridae, and the Avialae).

The body plan of the large theropods was successful because those theropods that evolved to large sizes from different families, periods, and continents, independently developed same features (e.g. Brusatte et al., 2010a; Benson, 2018). Only Therizinosauroids (Coelurosauria) are clearly differentiated with respect to the other large theropods in morphology but also feeding habit, being herbivorous.

Different methods have been proposed to calculate the body-mass of extinct tetrapods that can be grouped into



**Fig. 1** Phylogeny and stratigraphic distribution of the main theropod clades, modified and simplified from Hendricks et al. (2015). Silhouettes for studied groups in this research

allometric and volumetric techniques also called extant-scaling and volumetric-density respectively (see Campione and Evans, 2020). Both approaches have been used for investigate a suite of biological properties (e.g. Fariña et al., 1998; Delson et al., 2000; Bates et al., 2009a, b; Mallison, 2010; Hutchinson et al., 2011; Vizcaíno et al., 2011; Campione and Evans, 2012; Serrano et al., 2015; Basu et al., 2016; Hopkins, 2018). The allometric methods for calculating dinosaur body-mass are based on the mathematical relationships between measurements of distinct bones and the body-mass of the tetrapod. This method relies on allometric scaling relationships resulting from skeletal metrics of extant taxa. In this approach, a large number of animals are measured and the results are represented on a scatter plot for obtaining a regression line to generate the mathematical formula to be applied to ancient taxa (e.g. Hurlbut, 1999). This extrapolation is just a raft approach because of the complexity of the body plans of some dinosaurs that contrast with the sizes and proportions observed in recent tetrapods. According to Campione and Evans (2012), scaling relationships between

body-mass and skeletal measurements in mammals and birds are usually applied to predict body-mass in extinct members of these crown clades. Although the applicability for predicting mass in more distantly related stem taxa, such as non-avian dinosaurs, has been criticized on biomechanical grounds. Some examples of body-mass estimations for dinosaurs based on allometric methods can be found in Anderson et al. (1985), Seebacher (2001), Christiansen and Fariña (2004), Therrien and Henderson (2007), Campione et al. (2014), and Grillo and Delcourt (2017).

The volumetric methods for estimating dinosaur body-mass are based on physical and digital models. The estimation of body-mass may be based on reconstructed body volume involving three-dimensional imaging and ranging techniques applied to skeletons using, for example, photogrammetry, laser or structured light scanning, and computed tomography (Gunga et al., 1999, 2007, 2008; Bates et al., 2009b). Other possibility is to work directly on models of the organism instead of on skeletons as Colbert (1962) that used plastic casts. The fidelity of this method depends on

the accuracy of the reconstruction, which must be based on scientifically anatomical data. Post-processing of the generated 3D models allows for the easy calculation of volume, but some works have used the Archimedes Principle for determining the volume (Colbert, 1962; Walker, 2020). When the volume from the model is obtained, this is scaled to the real size of the fossil taxon. At the end, the body-mass is calculated multiplying the volume by the inferred density of the animal when living. However, there are uncertainties concerning body density, skeletal articulation, and soft-tissue distribution (Brassey, 2017). Some examples of body-mass estimations based on volumetric methods are Colbert (1962), Gunga et al., (2007, 2008), and Bates et al. (2009a, b). Campione and Evans (2020) apply a hybrid approach that combines the accuracy of the allometric method or extant-scaling, with the precision provided by the volumetric method or volumetric-density.

The volumetric body-mass estimation method based on accuracy models of dinosaurs is therefore, a potential and easy approach that also allows calculating the body-surface, which is very useful for interpreting heat dissipation (heat tolerance and thermal stress) in large dinosaurs. The objective of this work is to approach the body-size, body-mass and volume from scanned 3D models of scientifically accurate palaeoreconstructions of theropods from eight representative families. The analysis of the surface/volume ratio in the selected theropod species is especially useful due to this ratio is directly related to efficiency for dissipating metabolic heat (Spotila et al., 1973; Gillooly et al., 2006). In this work the surface/volume ratio is also studied and discussed in terms of implications for theropod ecology.

## 2 Material and methods

### 2.1 Scanned models

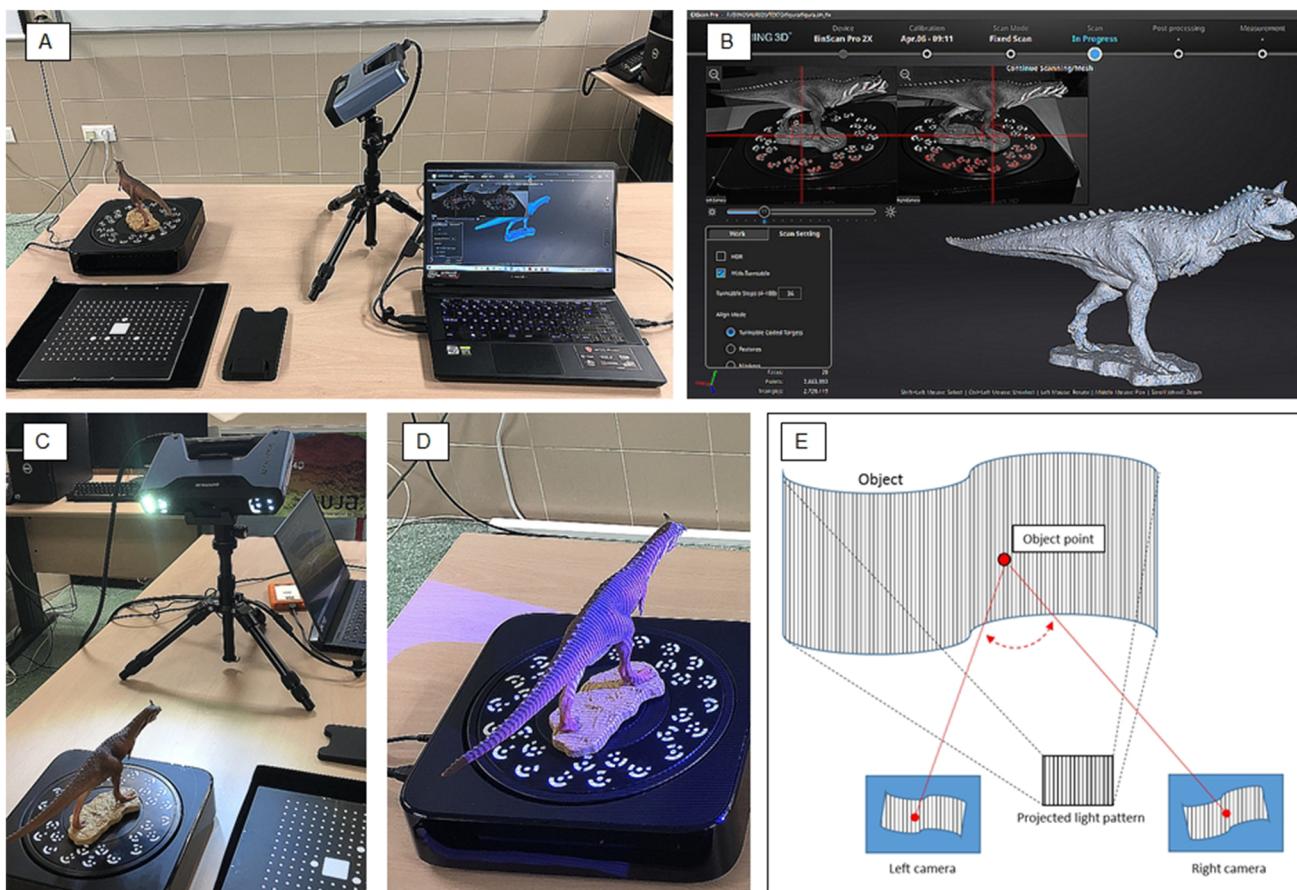
A total of 8 theropod models made up of PVC (polyvinyl chloride) were analysed. The models are based on some of the most recent and scientifically accurate palaeoreconstructions and are manufactured by Papo® (*Allosaurus* and *Ceratosaurus*), Safari Ltd® (*Coelophysis*, *Dilophosaurus*, and *Giganotosaurus*), Rebor® (*Tyrannosaurus*), and CollectA® (*Baryonyx* and *Carnotaurus*). These genera are selected as representatives of the main clades of the Order Theropoda (Fig. 1). First of all, approximations to the skull-size/body-size ratio of diverse models of the different species were done in order to control the accuracy of the reconstruction with respect to the available skeletal information in literature. Out of the models with right ratios, the final 8 theropod models were selected for their accuracy based on the reconstruction principles for guts, muscles, and fatty tissues proposed by Wiiton (2018) for dinosaurs and other extinct

animals. However, there are few aspects that should be considered for the use the selected figures as realistic models. Firstly, with the exception of *Coelophysis*, the figures were selected without feather entanglement even if some similar taxa have been proposed to have it from different kinds of theropods included small-sized relatives of *Tyrannosaurus rex* (Xu et al., 2004; Xu and Norell, 2005; Brusatte et al., 2010b). It was intentionally done to avoid overestimation of the body-mass based on the volume. In the case of *Allosaurus*, the pronated position of the manus of the model of Papo® is not scientifically accurate according to actual reconstruction of theropods forelimbs (Carpenter, 2002), but it is an assumption that can be done for the calculations of volume and weight. Finally, recent reconstructions based on exhaustive analysis of the muscular impressions in bones suggest that the tails of the theropods, at least from Coelurosauria, were thick and subrounded in section and not flattened as commonly displayed for most theropods (Persons and Currie, 2011a, b). These authors suggest that such reconstructions may underestimate the actual weight of theropods. The reported weight overestimation in *Tyrannosaurus rex* in this work might be explained by its accurate tail reconstruction without lateral flattening.

We used the estimations of Therrien and Henderson (2007) and reference specimens in this work for calculating the maximum length and weight of the different selected species of theropods. The scanned 3D models were also scaled considering the body-size and body-mass estimations of other authors and specimens. The models were scaled according to the length proposed by Therrien and Henderson (2007) in most of the cases. For testing accuracy of the models, they were also scaled using an average scale-factor based on the data of the skull-length and the body-length of Therrien and Henderson (2007). In the case of *Carnotaurus sastrei* the body-length used was that calculated by Grillo and Delcourt (2017).

### 2.2 Instruments and methods

All models have been scanned with an EinScan Pro 2X scanner (SHINING 3D®). This is a handheld structured light 3D scanner. Structured light scanners use projected light patterns (usually parallel stripes) and one or more cameras to measure the object surface (Fig. 2). After identification of the projected light stripes in the digital images, a dense point cloud is computed by means of triangulation. The EinScan Pro 2X is a close range scanner with a working distance of 0.4 m and a depth of field of  $\pm 100$  mm, so it is specially adapted for small-medium size objects. The scanning accuracy in fixed mode operation (with or without turntable) is 0.04 mm with a resolution (point distance) of 0.16 mm. With this mode, the scanner is set up on a tripod and the object is rotated between different scans covering the whole



**Fig. 2** **A** EinScan Pro 2X scanner (SHINING 3D®) with automatic turntable and markers. Scanner calibration board is shown at the lower left corner. **B** Left and right images with initial 3D point cloud. **C** Front view of EinScan Pro 2X in operation. Illumination LEDs

from left and right cameras are visible. **D** Light stripes pattern projected onto the *Carnotaurus* model. **E** Geometric principle of a two camera scanner and a pattern projector

object surface (Fig. 2). In fixed mode, the scanning speed is about 1 s per scan, but due to the complexity of the models, between 50 and 60 single scans were needed to avoid hidden areas. In the case of the *Tyrannosaurus*, 85 single scans were necessary to complete the whole model because of the size and complex shape of this model (Table 1). At first, a general scan with an automatic turntable (with a scan each 10°) allowed to generate an initial, although incomplete, model. Next, additional scans were necessary to complete hidden areas and/or areas out of the depth of field in the first scans with the turntable. Alignment of all scans were performed with SHINING 3D® 3.4.0.2 software by means of markers for those scans in the turntable and with feature matching techniques for the rest of scans. After merging all scans of the model, the resulting point cloud was edited to generate the final mesh. The meshes were watertight models by closing all holes allowing further volume calculations. Since coloured models were considered unnecessary for this work, no photogrammetric techniques for photorealistic textured models were employed, thus minimizing the total time employed

in data acquisition. As average, the total time to scan and generate the final mesh of a single model was about 1 h.

Once meshes were generated and exported in OBJ file format, we used CloudCompare V2 for further data processing. CloudCompare is an open source software for 3D point cloud and mesh processing (CloudCompare, 2021). This processing consisted mainly in the scale adjustment of the models to the real size proposed by Therrien and Henderson (2007). The scale factors were computed from measurements of the skull sizes and the total length of the scanned models. For the skull size, the length from the snout to the quadratojugal was measured at both sides of the head selecting the mean value as the final skull length of the model (Table 2). For the total length, a polyline from the snout to the tip of the tail was outlined, although neglecting the spines, crests and horns. Then the lengths of these lines and polylines were compared with the real length estimations of the different authors, mainly estimations of Therrien and Henderson (2007), and final scale factors were calculated (Table 2). The accuracy of the models using, skull-length

**Table 1** Main technical data of the scanned samples and 3D models: number of scans, size of the final mesh (expressed as the dimensions in mm of the sample bounding boxes) and the number of faces per 3D model

Specimens	No. of scans	Mesh (no. of triangles/faces)	Mesh size (bounding box) (mm)		
			X	Y	Z
<i>Coelophysis bauri</i>	49	459,558	196.5	64.8	502.2
<i>Dilophosaurus wetherelli</i>	51	1,894,910	170.7	59.8	52.9
<i>Ceratosaurus nasicornis</i>	74	4,997,990	180.2	65.8	131.2
<i>Carnotaurus sastrei</i>	52	2,854,878	270.7	104.3	111.3
<i>Allosaurus fragilis</i>	54	6,326,744	199.3	114.6	158.9
<i>Giganotosaurus carolinii</i>	60	4,096,258	266.6	154.2	109.4
<i>Baryonyx walkeri</i>	24	2,630,352	168.3	59.8	78.3
<i>Tyrannosaurus rex</i>	85	5,520,880	294.5	128.5	164.6

as scale factor is variable for the models. The difference between skull-size in Therrien and Henderson (2007) and the skull-size of the model taking into account the total body-size of the species inform us about the accuracy of these models expressed as % (Table 2). According to this *Coelophysis* (0.08%) and *Baryonyx* (0.09%) are the most accurate models whereas *Ceratosaurus* (0.40%) is the less accurate model.

Since meshes were watertight, the volume calculations were direct with CloudCompare, as well as the model surfaces by considering the single triangle surfaces and the total number of triangles of each mesh model. Final volumes and surfaces were computed from the scale factor (Table 3). The body-mass of the different genera was calculated after applying the scale factor following the densities proposed by Molina-Pérez and Larramendi (2019), with 0.9 g/cm<sup>3</sup> for small theropods such as *Coelophysis*, 0.925 g/cm<sup>3</sup> for medium size theropods such as *Dilophosaurus*, and 0.95 g/cm<sup>3</sup> for large theropods (*Ceratosaurus*, *Carnotaurus*, *Allosaurus*, *Baryonyx*, *Giganotosaurus* and *Tyrannosaurus*) (Table 3).

### 2.3 Studied genera: a short review

*Coelophysis* (Infraorder Neotheropoda, Superfamily Coelophysoidea, Family Coelophysidae) is a medium-size theropod of the Late Triassic to earliest Jurassic (Norian to Pliensbachian) of North America and Africa (Fig. 3; Schwartz and Gillette, 1994; Yates, 2005; Rinehart et al., 2009), with a maximum length around 3 m and around 1 m to the hip (Schwartz and Gillette, 1994; Therrien and Henderson, 2007; Paul, 2016). The *Coelophysis bauri* Cope 1887 is a well-known dinosaur with numerous complete skeletons (i.e. UCMP 129,618; NMMNH P-54620; AMNH 7223, AMNH 7224, NMMNH P-4200 and many other specimens from Ghost Ranch Quarry; New Mexico). Moreover, there are both gracile forms such as the specimen AMNH 7223, and robust forms such as the specimens AMNH 7224 y NMMNH P-42200 interpreted as sexual dimorphism (Rinehart et al., 2001). The skull is elongated reaching 26.8 cm in the AMNH 7223 (Therrien and Henderson, 2007) with big eyes and the deep jaw presents numerous curved, serrated teeth. The neck was very long. Despite being an early dinosaur, the theropod bodyplan is clearly

**Table 2** Measurements on the 3D models and those proposed by Therrien and Henderson (2007) for skull and size

Species	Real size		Model size			Body-size (mm)	Skull size 1 (mm)	Skull size 2 (mm)	Skull (mm)	Body-size (mm)	Estimated skull size (m)	Skull scale factor	Skull-size	Difference	%	Skull-body average factor
	Skull (m) <sup>a</sup>	Body-size (m)	Skull	2 (mm)	Skull											
<i>Coelophysis bauri</i>	0.268	2.860	22.701	22.199	22.450	222.313	0.012	0.289	0.021	0.08	0.012					
<i>Dilophosaurus wetherilli</i>	0.523	5.070	15.501	15.441	15.471	186.348	0.034	0.421	-0.102	-0.20	0.030					
<i>Ceratosaurus nasicornis</i>	0.625	5.900	33.700	33.474	33.587	226.744	0.019	0.874	0.249	0.40	0.022					
<i>Carnotaurus saurei</i>	0.520	7.750	25.979	25.723	25.851	292.136	0.020	0.686	0.166	0.32	0.023					
<i>Baryonyx walkeri</i>	0.910	8.190	23.960	24.459	24.209	200.321	0.038	0.990	0.080	0.09	0.039					
<i>Allosaurus fragilis</i>	0.682	6.360	37.373	36.830	37.102	302.296	0.018	0.781	0.099	0.14	0.019					
<i>Giganotosaurus carolinii</i>	1.560	13.000	51.590	51.279	51.435	378.384	0.030	1.767	0.207	0.13	0.032					
<i>Tyrannosaurus rex</i>	1.390	11.710	56.810	53.820	55.315	385.382	0.025	1.681	0.291	0.21	0.027					

Note that in the 3D model skull size was measured from snout to the quadratejugal in both sides (skull size 1 and 2) of the head, for obtaining an average value (skull size). The accuracy of the models is expressed as %

<sup>a</sup>Therrien and Henderson (2007)

developed. *Coelophysis* displays four digits in the forelimbs. It was a slender runner characterized by a narrow pelvis, forelimbs adapted to caught preys, and very narrow feet. The hindlimbs are large, with a femur shorter than tibia. The tail is long and semirigid, and worked as a counterweight as well as a rudder for favouring maneuverability (Gay, 2001).

Different approach to the weight of *C. bauri* proposed this species as lightly built, therefore, Paul (1988) proposed a weight of 15.3 kg, Seebacher (2001) proposed 15 kg, Therrien and Henderson (2007) proposed 24.23 kg and 2.86 m length, and finally Molina-Pérez and Larramendi (2019) proposed 32 kg for specimens with 2.75 m (Table 4).

*Dilophosaurus* (Infraorder Neotheropoda, Superfamily Coelophysoidea, Family Dilophosauridae) is a primitive theropod recorded in the Lower Jurassic (Sinemurian and Pliensbachian) of North America (Welles, 1984). It is more robustly constructed and larger than other coelophysoids (more than 5 m; Therrien and Henderson, 2007; Paul, 2016; Molina-Pérez and Larramendi, 2019). The neck is shorter and thicker than in *Coelophysis*. *Dilophosaurus wetherilli* Welles 1970 is a slender theropod with a relatively large, elongated skull but delicate that presents two large snout crests (Fig. 4). The deep jaw has large, thin curved teeth. The forelimbs are powerful, and had deep pits and stout processes for attachment of muscles and ligaments. The humerus is large and the manus have four fingers, the fourth of them was vestigial. The hindlimbs are large, with a slighter longer femur than tibia and long, stout feet with three well-developed toes that bore large claws.

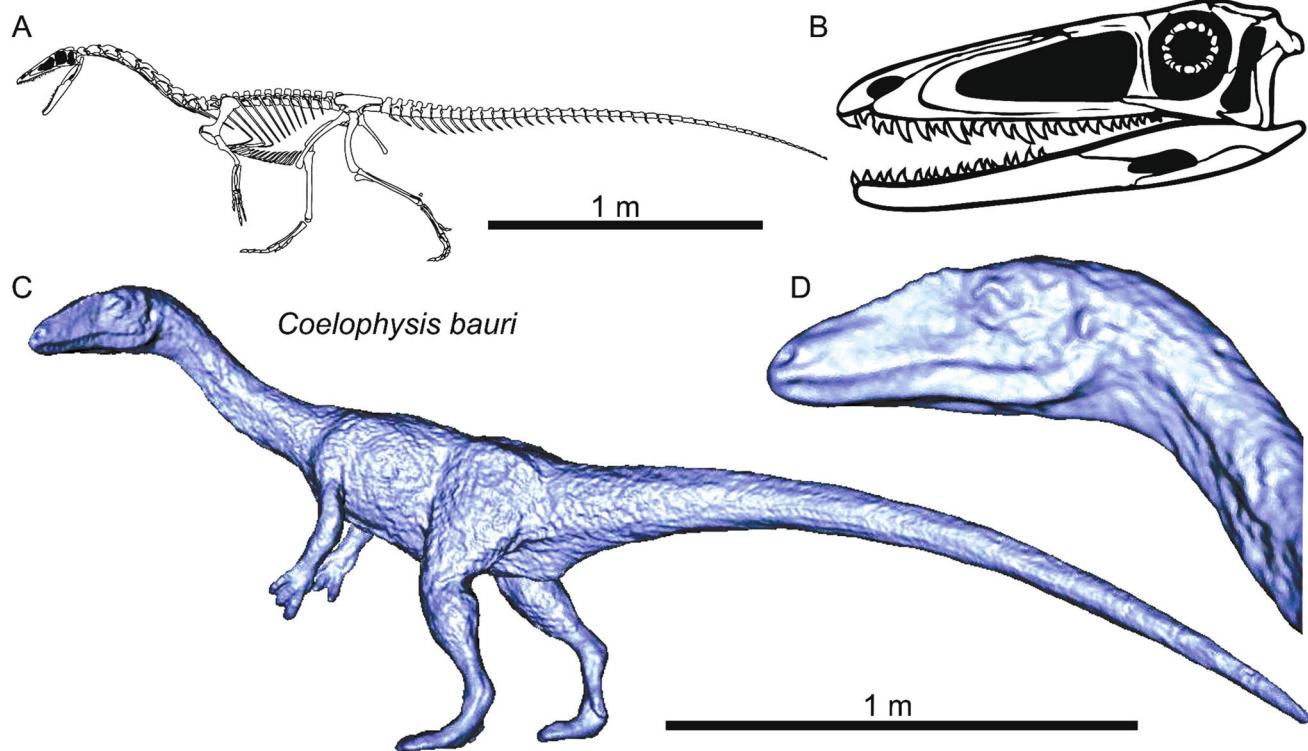
The largest specimen is UCMP 77,270 represented by a partial skull and skeleton (Welles and Pickering, 1995) and probably reached 400 kg weight and 7 m length with a skull of 59 cm (Paul, 1988, 2016). The holotype UCMP 37,302 is smaller (283 kg weight, 6 m length and 52 cm length for the skull; Paul, 1988) (Table 4). A recent approach by Therrien and Henderson (2007) calculates 269 kg and 5 m for *D. wetherilli*, whereas Molina-Pérez and Larramendi (2019) propose 380 kg and 6.3 m (Table 4).

*Ceratosaurus* (Infraorder Neotheropoda, Superfamily Ceratosauria, Family Ceratosauridae) was a large predator that lived during the Late Jurassic (Kimmeridgian and Tithonian) of North America and Europe (Madsen and Welles, 2000; Mateus et al., 2006; Foster, 2007). *Ceratosaurus nasicornis* Marsh 1884 is characterized by a large head with respect to the rest of its body, with a narrow and rectangular section (Fig. 5). The skull length of the holotype USNM 4735 is 62.5 cm (Therrien and Henderson, 2007) and that of the specimen MWC 1 is 60 cm (Madsen and Welles, 2000). The jaw is deep and presents large bladed teeth (Fig. 5). A characteristic feature in the skull is a short horn (13 cm in specimen USNM 4735) located on the skull midline (Fig. 5). The tail is thick and heavy due to the presence of high neural spines and elongated chevrons, and constitutes about half

**Table 3** Volume, body-mass and surface of different theropod taxa according to the body-size of Therrien and Henderson (2007) applied to the 3D models. Note that body-mass was calculated using the density values proposed by Molina-Pérez and Larramendi (2019) being

0.9 g/cm<sup>3</sup> for small theropods such as *Coelophysis*, 0.925 g/cm<sup>3</sup> for medium size theropods such as *Dilophosaurus*, and 0.95 g/cm<sup>3</sup> for large theropods (*Ceratosaurus*, *Carnotaurus*, *Baryonyx*, *Allosaurus*, *Giganotosaurus* and *Tyrannosaurus*)

Species	Model	Estimated from scaled model			Model	Estimated from scaled model
		Volume (cm <sup>3</sup> )	Volume (m <sup>3</sup> )	Density (kg/m <sup>3</sup> )		
<i>Coelophysis bauri</i>	19.26	0.04	900.00	36.90	86.98	1.44
<i>Dilophosaurus wetherelli</i>	14.81	0.30	925.00	275.90	68.52	5.07
<i>Ceratosaurus nasicornis</i>	79.86	1.41	950.00	1336.52	197.84	13.39
<i>Carnotaurus sastrei</i>	119.12	2.22	950.00	2112.85	261.61	18.41
<i>Baryonyx walkeri</i>	22.02	1.50	950.00	1429.34	95.10	15.90
<i>Allosaurus fragilis</i>	122.75	1.14	950.00	1085.94	310.54	13.75
<i>Giganotosaurus carolinii</i>	186.70	7.57	950.00	7192.71	361.37	42.66
<i>Tyrannosaurus rex</i>	374.44	10.50	950.00	9979.24	577.32	53.30



**Fig. 3** *Coelophysis bauri*. **A** Skeletal reconstruction (redraw from Hendrikx et al., 2015 and Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

of the animal total length. The forelimbs are short and the manus retained four digits in contrast to more derived theropods, which only present three or two digits on each manus. Taking into account the body proportions, the hindlimbs are comparatively not as long as those of *Coelophysidae* and *Dilophosauridae* (Figs. 3, 4). The pes has three weight-bearing digits and an additional dewclaw.

The estimated length of *Ceratosaurus nasicornis* by different researchers ranges from 5.5 m (Molina-Pérez and Larramendi, 2019) to 6 m (Paul, 2016). The different proposed weight for this species also varies from 418 kg (Seebacher, 2001) to 670 kg (Anderson et al., 1985) (Table 4).

*Carnotaurus* (Infraorder Ceratosauria, Superfamily Abelisauroidea, Family Abelisauridae) is a large light theropod recorded in the Upper Cretaceous (Campanian

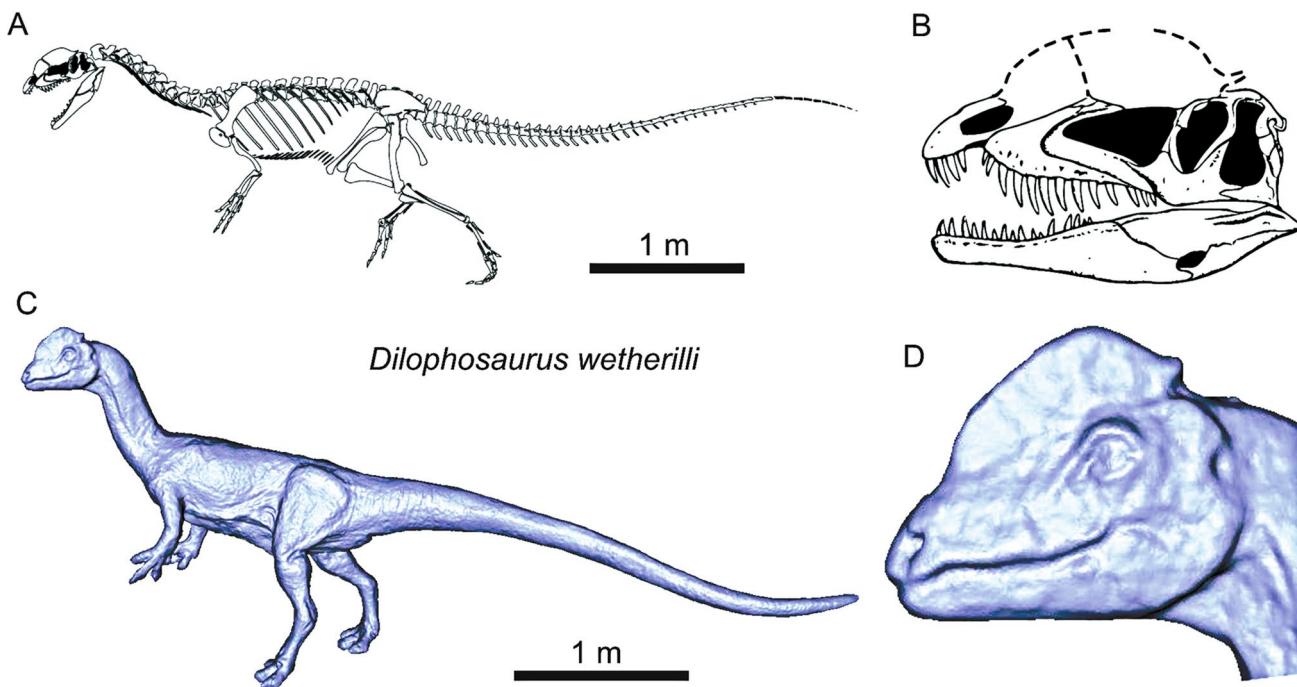
**Table 4** Length and body-mass of the eight selected theropods species compiled from the literature. In the body-mass is also included the estimation of this work based on 3D models

Length (m)	<i>Coelophysis bauri</i>	<i>Dilophosaurus wetherilli</i>	<i>Ceratosaurus nasicornis</i>	<i>Carnotaurus sastrei</i>	<i>Baryonyx walkeri</i>	<i>Allosaurus fragilis</i>	<i>Gigantosaurus carolinii</i>	<i>Tyrannosaurus rex</i>
Bates et al. (2012)						7.57		
Bonaparte et al. (1990)				7.6				
Charing and Milner (1997)					8.5			
Coria and Sal- gado (1995)							12.5	
Gilmore (1920)						7.4		
Grillo and Del- court (2017)				7.75				
Molina-Perez and Larra- mendi (2019)	2.75	6.3	5.5	7.7	9.7	10.4*	13.2	12.3
Paul (1988)		6			9.5	7.9		
Paul (2016)	3	7	6	7.5	7.5	8.5	13.5	12
Schwartz and Gillette (1994)	3							
Therrien and Henderson (2007)	2.86	5.07	5.9		8.19	6.36	13	11.71
Average	2.9	6.09	5.8	7.63	8.68	8.02	13.05	12
Body-mass (kg)	<i>Coelophysis bauri</i>	<i>Dilophosaurus wetherilli</i>	<i>Ceratosaurus nasicornis</i>	<i>Carnotaurus sastrei</i>	<i>Baryonyx walkeri</i>	<i>Allosaurus fragilis</i>	<i>Gigantosaurus carolinii</i>	<i>Tyrannosaurus rex</i>
Alexander (1989)						1400		7400
Anderson et al. (1985)			670					4500
Bates et al. (2009a)						1500.91		
Bates et al. (2009b)								6071–7654
Campione et al. (2014)				1743		2681	6349	6688
Campione and Evans (2020)							5508–6130	6845–7685
Christiansen and Fariña (2004)						1620		
Colbert (1962)						2090–2300		6890–7600
Coria and Sal- gado (1995)							6000	
Farlow et al. (1995)								5400–7300
Farlow (1990)								5700
Henderson (1999)								7224
Hutchinson et al. (2014)								9500
Mazzetta et al. (2004)				1488–2626			6510	

**Table 4** (continued)

Body-mass (kg)	<i>Coelophysis bauri</i>	<i>Dilophosaurus wetherilli</i>	<i>Ceratosaurus nasicornis</i>	<i>Carnotaurus sastrei</i>	<i>Baryonyx walkeri</i>	<i>Allosaurus fragilis</i>	<i>Gigantosaurus carolinii</i>	<i>Tyrannosaurus rex</i>
Molina-Perez and Larra-mendi (2019)	32	380	550	1850	2000	2900	8500	8500
Paul (1988)	15.3	283	524		1700	1700		5700
Paul (2016)	25	400	600	2000	1200	1700	7500	6000
Seebacher (2001)	16		418–472			952	6594.8	6650
Snively et al. (2019)								9131
Therrien and Henderson (2007)	24.23	269.38	511.81		1980.96	700.88		9110.74
Average	22.56	333.09	506.54	1912.5	1720.24	1734	6753.14	6978.64
This work	37	276	1337	2113	1429	1086	7193	9979

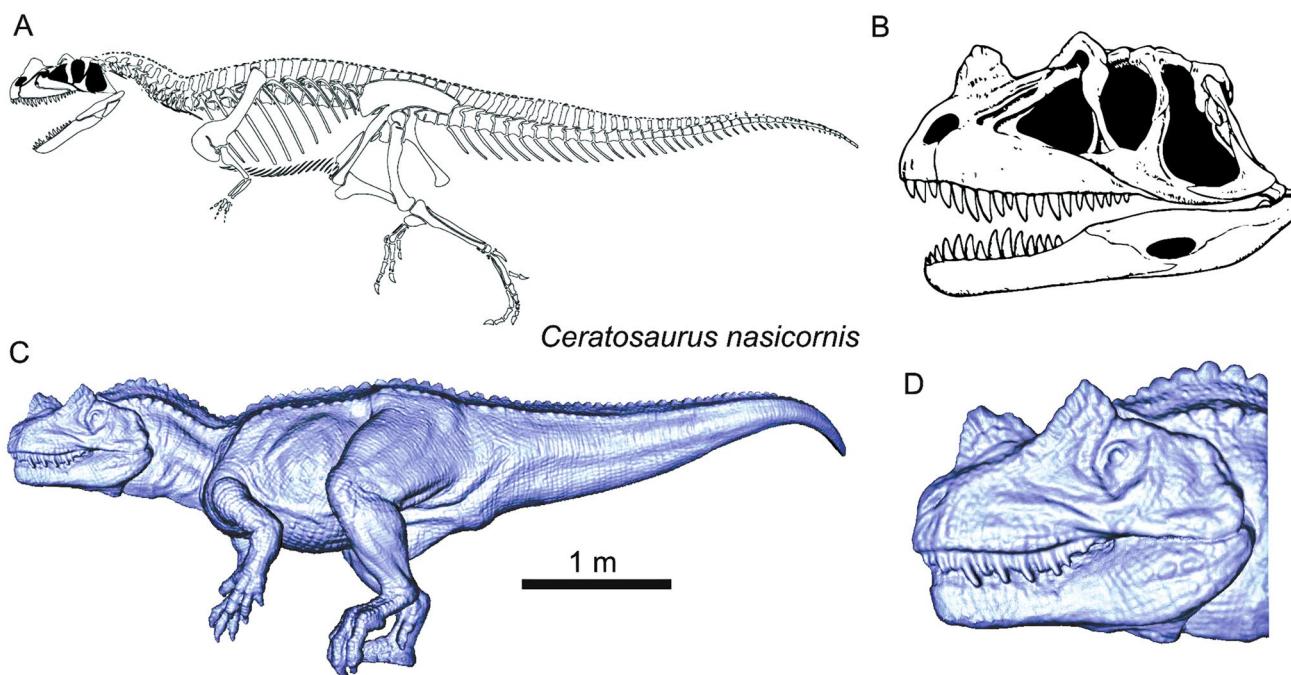
\*means that the length was estimated from only a femur



**Fig. 4** *Dilophosaurus wetherilli*. **A** Skeletal reconstruction (redraw from Hendrikx et al., 2015 and Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

to Maastrichtian) of Argentina (Bonaparte et al., 1990). It is characterized by a very flat and short skull (Fig. 6), compared with other theropods (52 cm in the holotype MACN-CH 894; Bonaparte et al., 1990). Its name refers to two stout-brow horns located over the eyes and directed sideways. According to Bonaparte et al. (1990) and Cerroni et al. (2020), the horns supported keratinous sheaths. The lower jaw is slender and the teeth are short and stout. The neck is unusually wide and nearly straight and not forming

the S-curve recorded in other theropods (e.g. *Allosaurus* and *Tyrannosaurus*). *Carnotaurus sastrei* Bonaparte 1985 presents short atrophied forelimbs with four digits as occur in other abelisaurids (Fig. 6). The body is elongated and the tail has high neural spines and elongated chevrons. Contrarily to *Ceratosaurus*, the hindlimbs of *Carnotaurus* are long and adapted for running. The femur is 103 cm in length, but shows an average diameter of only 11 cm in the holotype MACN-CH 894.



**Fig. 5** *Ceratosaurus nasicornis*. **A** Skeletal reconstruction (redraw from Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

Bonaparte et al. (1990) estimates a body length of the holotype as 7.6 m. Other proposals range from 7.5 m of Paul (2016) to 7.75 m of Grillo and Delcourt (2017). With respect to the weight, there are very different proposals; Mazzetta et al. (2004) published a body mass ranging from 1488 to 2626 kg; Campione et al. (2014) proposed a weight of 1743 kg; Paul (2016) proposed 2000 kg; and finally, Molina-Perez and Larramendi (2019) calculated 1850 kg.

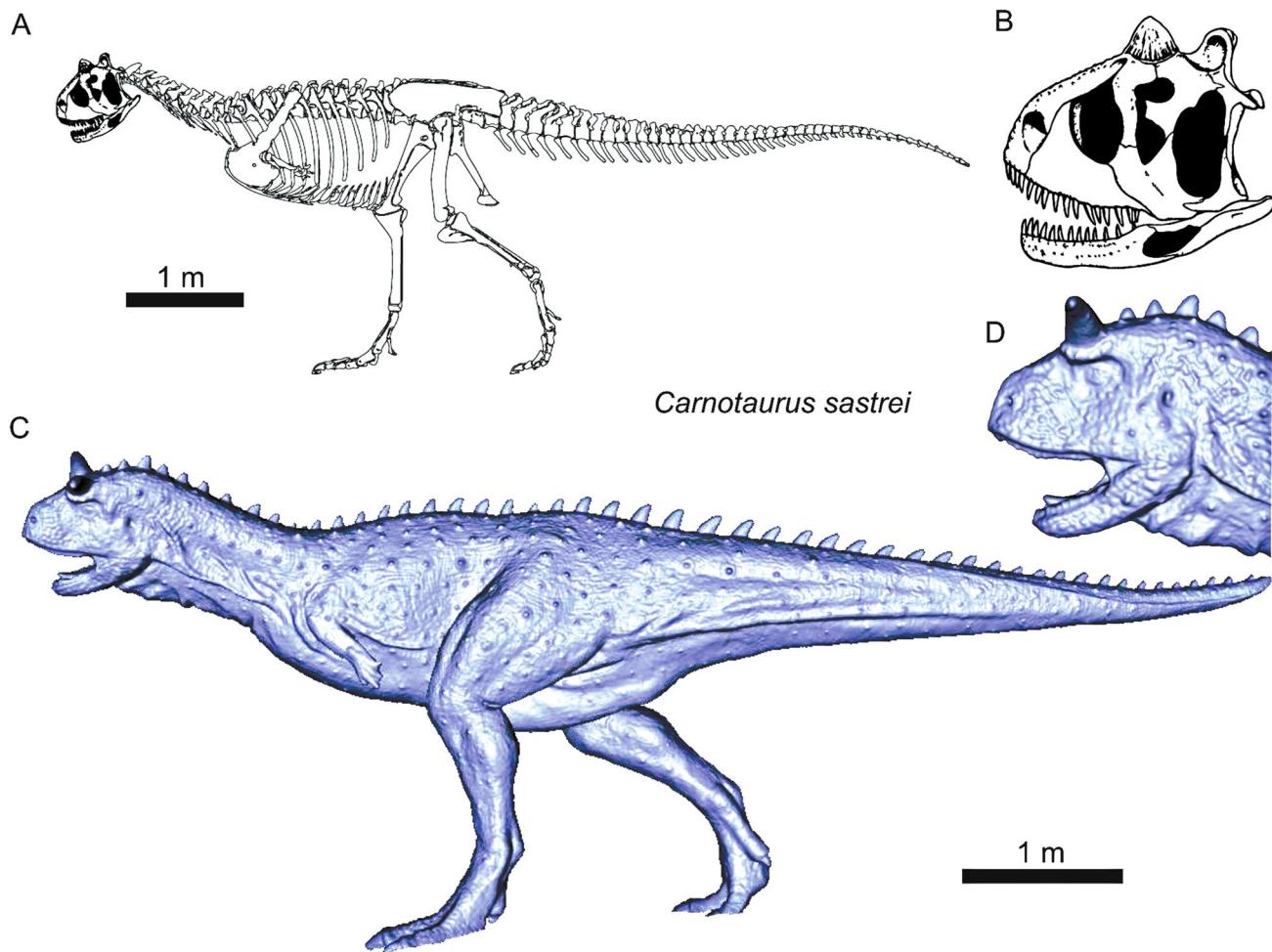
*Baryonyx* (Superfamily Megalosauroidea, Family Spinosauridae) is a large theropod of the Early Cretaceous (Aptian) of South England, Portugal, and Spain (Charig and Milner, 1986, 1997; Buffetaut, 2007). *Baryonyx walkeri* Charig and Milner 1987 is characterized by an elongated body and a head very long and shallow, as well as an elongated and narrow snout (Fig. 7). The full length of the skull is estimated to have been 91–95 cm, based on comparison with that of the related genus *Suchomimus* (Charig and Milner, 1997; Munt et al., 2017). *Baryonyx* has a large number of finely-serrated, conical teeth. It has an S shape neck, straighter than in other theropods. The neural spines of its dorsal vertebrae increase in height from front to back. *Baryonyx* has robust forelimbs, the manus had three digits with a very large claw on the first finger measuring about 31 cm long in the holotype specimen NHM R9951.

The body-length estimations for *B. walkeri* vary from 7.5 m (Paul, 2016) to 9.7 m (Molina-Perez and Larramendi, 2019). Charig and Milner (1997) proposed 8.5 m length whereas Therrien and Henderson (2007) calculated 8.19 m

for *Baryonyx*. With respect to the body-mass, different estimations ranges from 1200 kg (Paul, 2016) to 1980.96 kg (Therrien and Henderson, 2007) or 2000 kg (Molina-Perez and Larramendi, 2019) (Table 4).

*Allosaurus* (Infraorder Carnosauria, Superfamily Allosauroidea, Family Allosauridae) is a large theropod that habited in North America and Iberian Peninsula during the Late Jurassic (Oxfordian to Tithonian; Pérez-Moreno et al., 1999; Turner and Peterson, 1999; Mateus et al., 2006; Carpenter, 2010). *Allosaurus fragilis* Marsh 1877 is the best-known specie. Its body is slender and balanced by a long tail (Fig. 8). The head is short, light but robust, armed with sharp serrated teeth. The neck presents a S-shaped curve like in other carnosaurians. The forelimbs are large compared with other large theropods and are equipped with three digits (Fig. 8). The hindlimbs are relatively large and the pedes are equipped with three weight-bearing digits. According to Paul (1988), the skull length was around 84.5 cm for a specimen of 7.9 m length (UUVP 6000), and 68.2 cm for a specimen of 7.4 m length (YPM 1930).

According to different authors, the body-length of *Allosaurus fragilis* ranged from 6.36 m (Therrien and Henderson, 2007) to 10.4 m (Molina-Pérez and Larramendi, 2019). This variability is related to the different studied specimens, therefore some estimations are 6.36 m for YPM 1930 (Therrien and Henderson, 2007), 7.4 m for USNM 4734 (Gilmore, 1920), 7.57 m for MOR 693 (Bates et al., 2012), 7.9 m for



**Fig. 6** *Carnotaurus sastrei*. **A** Skeletal reconstruction (redraw from Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

UUVP 6000 (Paul, 1988; Madsen, 1993), and 9.7 m for AMNH 680 (Campione et al., 2014).

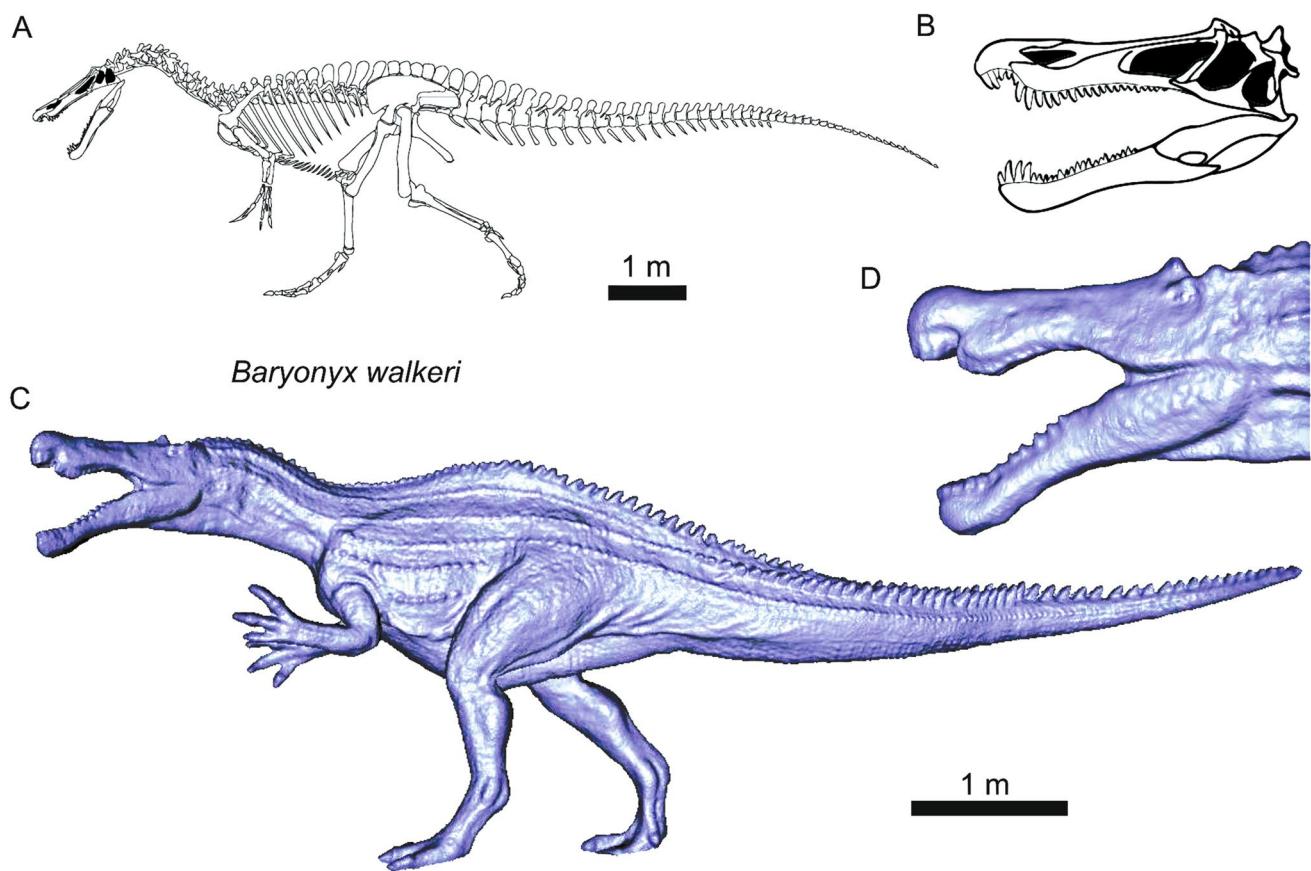
The body-mass of *A. fragilis* has been estimated with very variable values (Table 4). The lowest estimations correspond to Therrien and Henderson (2007) with 700 kg and Seebacher (2001) with 952 kg. An intermediate range of values for body-mass among 1400–1700 kg were proposed by Paul (1988, 2016), Alexander (1989), Christiansen and Fariña (2004), Bates et al. (2009a), and Snively et al. (2019). The highest estimations of body-mass for *A. fragilis* ranges from 2090 to 2900 kg as proposed by Colbert (1962), Campione et al. (2014), and Molina-Perez and Larramendi (2019).

*Giganotosaurus* (Infraorder Carnosauria, Superfamily Allosauroidae, Family Carcharodontosauridae) is one of the largest theropods. This carnosaur lived in South America during the early Late Cretaceous (Cenomanian) (Coria and Salgado, 1995). The skull of *Giganotosaurus carolinii* is low and deep, and the lower jaw is flattened (Fig. 9). The total length of the skull for the specimen MUCPv-CH-1 was

estimated in 1.53 m by Coria and Salgado (1995), 1.60 m by Coria and Currie (2002), and 1.56 m by Therrien and Henderson (2007). The neck is strong and almost straight. The pectoral girdle is comparatively short and the boot of the pubis further enlarged. The forelimbs are reduced and have three digits. The hindlimbs are large and robust compared with other large theropods.

The estimations of the body-length ranges from 12.5 m (Coria and Salgado, 1995) to 13.5 m (Paul, 2016) and then constitutes one of the biggest theropods ever. With respect to the body-mass, the lowest values proposed ranges from 5508 to 6600 kg (see Coria and Salgado, 1995; Seebacher, 2001; Mazzetta et al., 2004; Campione and Evans, 2020) (Table 4). Other estimations calculate a body-mass between 7.00 kg (Paul, 2016) and 8500 kg (Molina-Perez and Larramendi, 2019).

*Tyrannosaurus* (Infraorder Coelurosauria, Superfamily Tyrannosauroidea, Family Tyrannosauridae) is a giant theropod that lived during the end of the Cretaceous

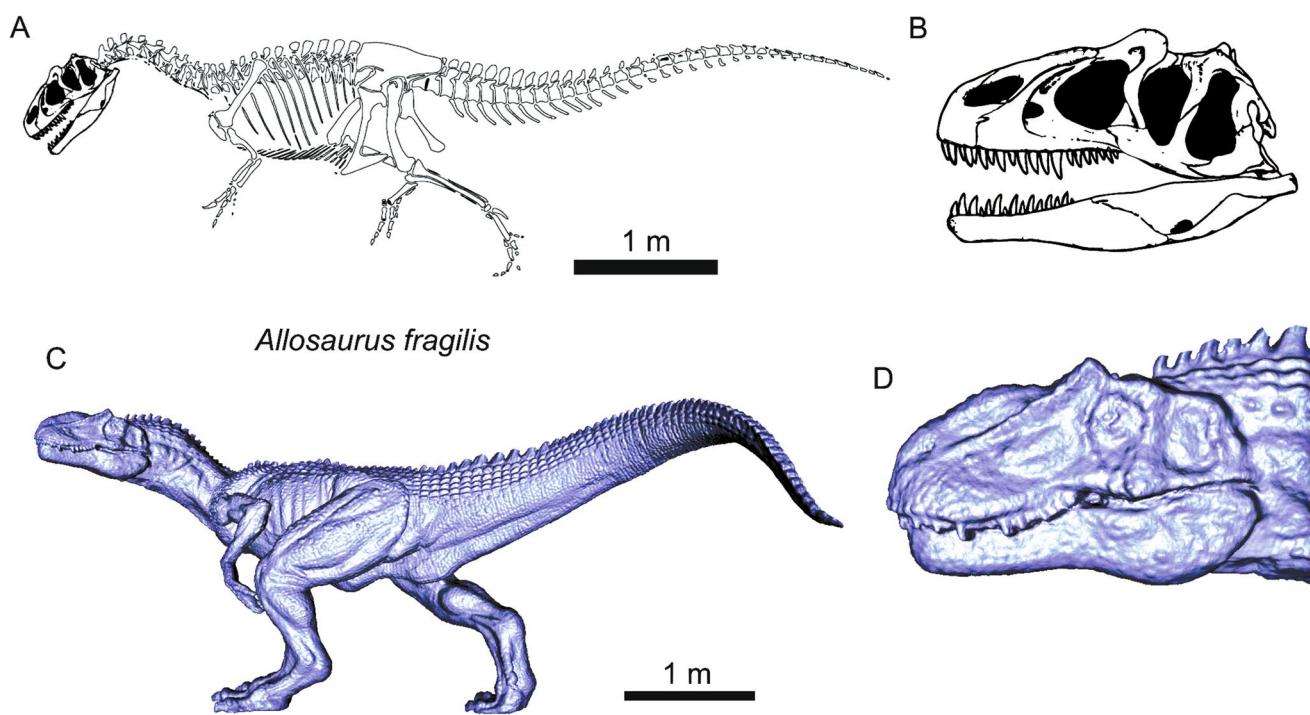


**Fig. 7** *Baryonyx walkeri*. **A** Skeletal reconstruction (redraw from Hendrikx et al., 2015). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

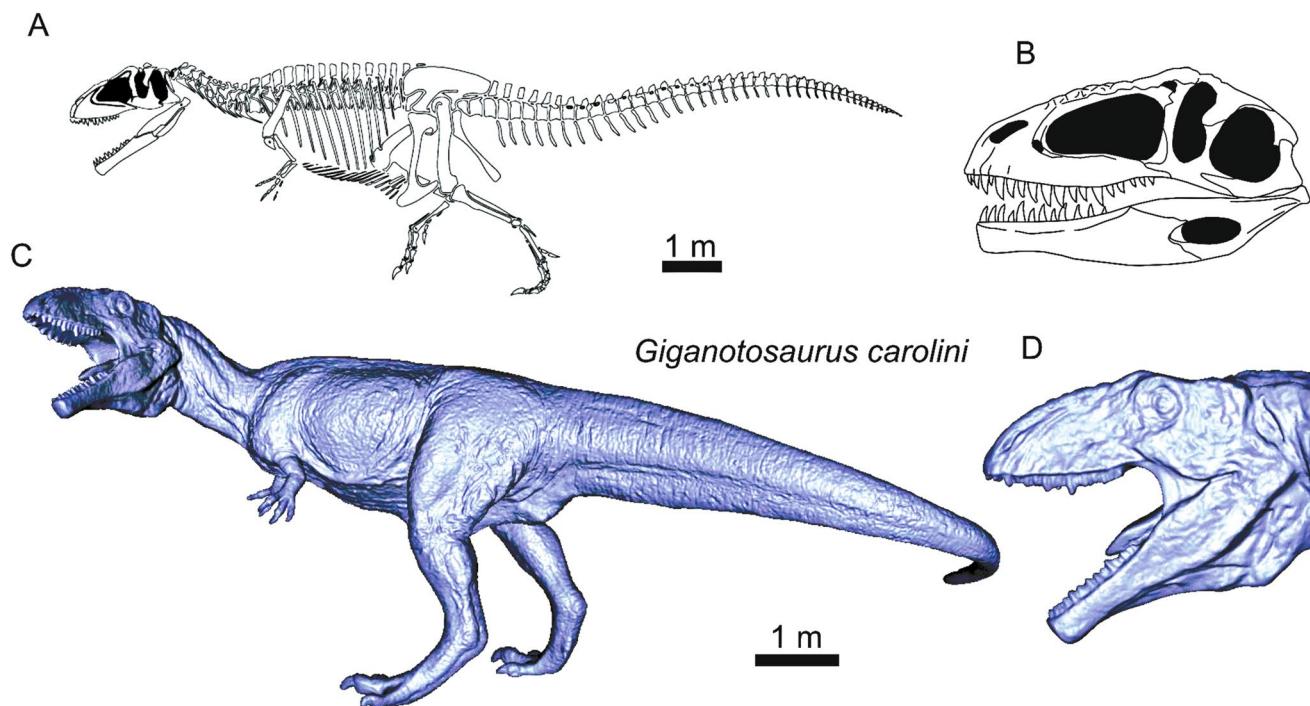
(Maastrichtian) in North America (e.g. Lockley and Hunt, 1994; Carr and Williamson, 2004). The main characteristic of the *Tyrannosaurus rex* Osborn 1905 is the large and long head that is robustly built with a powerful jaw muscles (e.g. Brusatte et al., 2010b). The skull is very wide at the rear. The total length of the skull is 1.39 m for specimen FMNH PR2081 and 1.36 m for AMNH 5027 (Therrien and Henderson, 2007). The teeth are large, reaching 30 cm including root (sample MOR 1125, Molina-Pérez and Larramendi, 2019). The neck for supporting this heavy head is robust and powerfully muscled and presents an S-shaped curve (Fig. 10). The trunk is short and the forelimbs reduced and with only two digits. The tail is heavy but proportionally shorter than in other theropods (Fig. 10). The pelvis and hindlimbs are large and the pedes are long and narrow. The reduction of tail and arms as well as the enlarged and elongated forelimbs indicates greater speed than other predators such as *Dilophosaurus* or *Carnotaurus* according to Dececchi et al. (2020). However, biomechanical studies show that *T. rex* could not run rapidly (see Brusatte et al., 2010b).

Estimations of the size of adult specimens of *Tyrannosaurus rex* range between 11.71 and 12.3 m (see Therrien and Henderson, 2007; Molina-Pérez and Larramendi, 2019; Table 4). The largest specimen FMNH PR2081 was 12.3 m (Hutchinson et al., 2011). Other large specimens are the holotype CM 9380 (11.9 m), BHI 3033 (11.8 m), MOR 555 (11.6 m), and AMNH 5027 (11.5 m) (see Therrien and Henderson, 2007; Hutchinson et al., 2011). Molina-Pérez and Larramendi (2019) inferred 12.3 m length based on the specimen UCMP 137,538 which is just a phalanx of the toe IV-2.

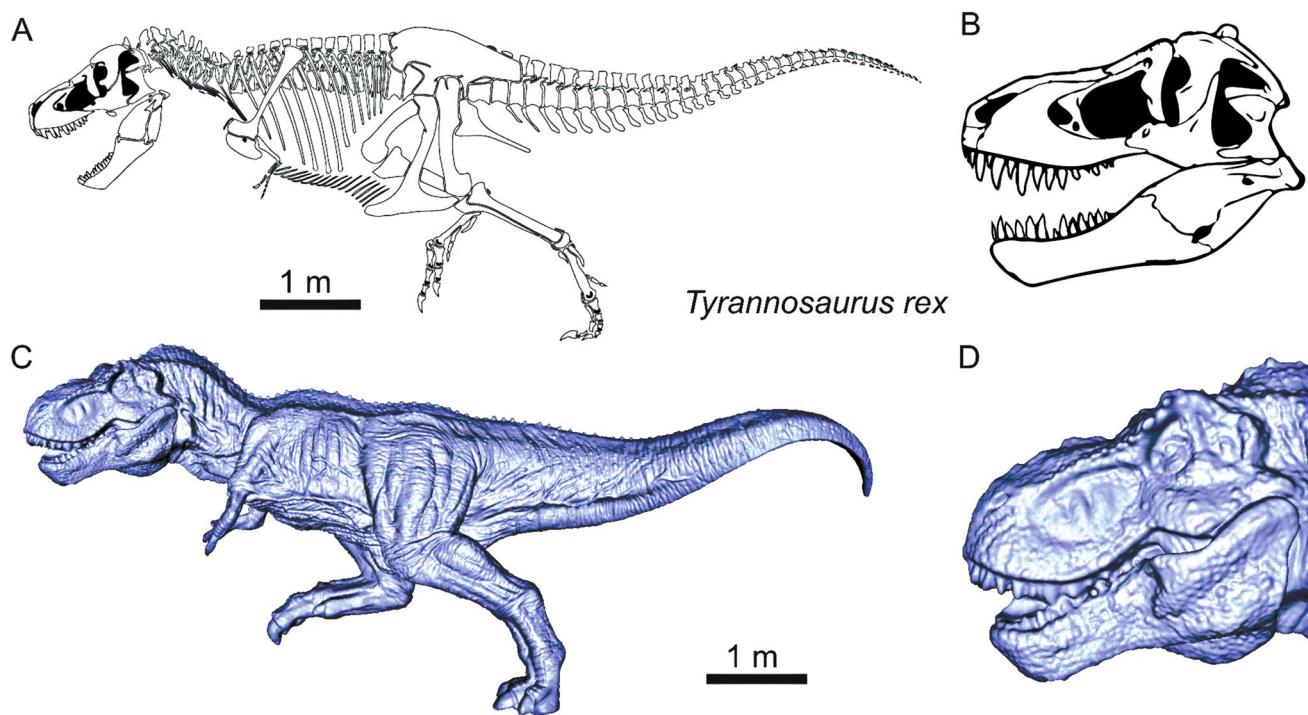
With respect to the body-mass, the lowest estimations for *T. rex* was 4500 kg (Anderson et al., 1985). Most of the estimations of body-mass ranges from 5400 to 7654 kg (Colbert, 1962; Paul, 1988; Alexander, 1989; Farlow et al., 1995; Henderson, 1999; Seebacher, 2001; Bates et al., 2009b; Campione et al., 2014; Campione and Evans, 2020). Largest estimations for FMNH PR2081 are 9110 kg by Therrien and Henderson (2007), 9131 kg by Snively et al. (2019), and 9500 kg by Hutchinson et al. (2011) (Table 4).



**Fig. 8** *Allosaurus fragilis*. **A** Skeletal reconstruction (redraw from Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model



**Fig. 9** *Giganotosaurus carolinii*. **A** Skeletal reconstruction (based on Hendrikx et al., 2015 and Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model



**Fig. 10** *Tyrannosaurus rex*. **A** Skeletal reconstruction (redraw from Hendrikx et al., 2015 and Paul, 2016). **B** Skull reconstruction. **C** The 3D model from scanned figure. **D** Detail of the head from 3D model

### 3 Results

#### 3.1 Coelophysis

According to the length proposed by Therrien and Henderson (2007) for the specimen AMNH 7223 with 2.86 m, the estimated body-mass for *Coelophysis bauri* is 37 kg, which is similar to that of Molina-Pérez and Larramendi (2019) with 32 kg and over the proposed body-mass of Paul (2016) with 25 kg, and Therrien and Henderson (2007) with 24.23 kg. The surface estimated according to the scaled model is 1.44 m<sup>2</sup> for a volume of 0.041 m<sup>3</sup>.

When applying this approach to other specimens described in the literature (Table 5), the *Coelophysis* body-mass ranges from 21 kg (specimen AMNH 7224, 2.38 m; Therrien and Henderson, 2007) to 33 kg ((UCMP 129,618, 2.75 m; Molina-Pérez and Larramendi, 2019).

#### 3.2 Dilophosaurus

According to the body-size of the specimen UCMP 37,302 (Therrien and Henderson, 2007) with 5.07 m the calculated body-mass for *Dilophosaurus wetherilli* is 389 kg. This values is very close to the proposals of Molina-Pérez and Larramendi (2019) with 380 kg and Paul (2016) with 400 kg. However, other proposals are clearly lighter as Therrien and Henderson (2007) with 269 kg. According to the model,

the volume of *Dilophosaurus* was 0.298 m<sup>3</sup> and the surface was 5.07 m<sup>2</sup>.

The body-mass estimation according to the specimen UCMP 77,270 are larger due to its body-size is 7 m according to Welles and Pickering (1995) and 6.3 m according to Molina-Pérez and Larramendi (2019), ranging from 529 to 726 kg (Table 5).

#### 3.3 Ceratosaurus

The specimen USNM 4735 of *Ceratosaurus nasicornis* is 5.9 m according to Therrien and Henderson (2007) and the resulting body-mass based in the model would be 1337 kg. Molina-Pérez and Larramendi (2019) proposed 5.50 m and 550 kg for USNM 4735, whereas Anderson et al. (1985) calculated a body-mass for *Ceratosaurus nasicornis* of 670 kg. This means that the model used is more robust than the estimated reconstructions from fossil skeletons, and then this is not a well-accurate model. For this model, the volume reaches 1.407 m<sup>3</sup> with a surface of 13.39 m<sup>2</sup>, probably both values being higher than real ones.

#### 3.4 Carnotaurus

The body-size based on *Carnotaurus sastrei* (MACN-CH894) is 7.75 m according to Grillo and Delcourt (2017) and our calculated body-size is 2113 kg (Table 3). The

**Table 5** Body-size published of the selected taxa by different authors with indication of the specimen used for the estimation. For these specimens and proposed length is calculated the body-mass, surface and volume

Species	Specimen	Body-size (m) and authors	Estimated values according body-size			
			Body-mass (kg)	Surface (m <sup>2</sup> )	Volume (m <sup>3</sup> )	Surface/volume
<i>Coelophysis bauri</i>	AMNH 7223	2.86 (Therrien and Henderson, 2007)	37	1.44	0.04	36.00
	AMNH 7224	2.38 (Therrien and Henderson, 2007)	21	1	0.024	41.67
	UCMP 129,618	2.75 (Molina-Perez and Larra-mendi, 2019)	33	1.33	0.036	36.94
<i>Dilophosaurus wetherilli</i>	UCMP 37,302	5.07 (Therrien and Henderson, 2007)	276	5.07	0.298	17.01
		6.03 (Paul, 1988)	464	7.17	0.52	13.79
	UCMP 77,270	6.30 (Molina-Perez and Larra-mendi, 2019)	529	7.83	0.572	13.69
		7.00 (Welles and Pickering, 1995)	726	13.39	0.785	17.06
<i>Ceratosaurus nasicornis</i>	USNM 4735	5.90 (Therrien and Henderson, 2007)	1337	13.39	1.407	9.52
		5.69 (Paul, 1988)	1199	12.46	1.262	9.87
		5.50 (Molina-Perez and Larra-mendi, 2019)	1083	11.64	1.14	10.21
<i>Carnotaurus sastrei</i>	MACN-CH894	7.75 (Grillo and Delcourt, 2017)	2113	18.41	2.22	8.29
		7.60 (Bonaparte et al., 1990)	1993	17.71	2.09	8.47
<i>Baryonyx walkeri</i>	BMNH R 9951	8.50 (Charig and Milner, 1997)	1598	17.12	1.68	10.19
		8.19 (Therrien and Henderson, 2007)	1429	15.9	1.5	10.60
<i>Allosaurus fragilis</i>	YPM 1930	7.40 (Paul, 1988)	1711	18.61	1.8	10.34
		6.36 (Therrien and Henderson, 2007)	1086	13.75	1.14	12.06
	UUPV 6000	7.90 (Madsen, 1993)	2081	21.21	2.19	9.68
	USNM 4734	7.40 (Gilmore, 1920)	1711	18.61	1.8	10.34
	MOR 693	7.57 (Bates et al., 2012)	1831	19.47	1.93	10.09
	AMNH 680	9.70 (Campione et al., 2014)	3853	31.97	4.05	7.89
	MUCPv-CH-1	12.50 (Coria and Salgado, 1995)	6394	39.44	6.73	5.86
<i>Giganotosaurus carolinii</i>		13.00 (Therrien and Henderson, 2007)	7193	42.66	7.57	5.64
<i>Tyrannosaurus rex</i>	FMNH RP2081	11.71 (Therrien and Henderson, 2007)	9979	53.3	10.5	5.08
		12.00 (Brochu, 2003)	10,739	55.98	11.3	4.95
		12.30 (Hutchinson et al., 2011)	11,565	58.81	12.17	4.83
	AMNH 5027	11.49 (Hutchinson et al., 2011)	9427	51.32	9.92	5.17
	CM 9380	11.90 (Hutchinson et al., 2011)	10,473	55.05	11.02	5.00
	BHI 3033	11.80 (Hutchinson et al., 2011)	10,211	54.12	10.75	5.03
	MOR 555	11.60 (Hutchinson et al., 2011)	9701	52.3	10.21	5.12

body-mass is also within the published estimations that ranges from 1488 to 2626 kg (Mazzetta et al., 2004; Paul, 2016). For this estimated length the volume of *Carnotaurus* is 2.22 m<sup>3</sup> and the body-surface is 18.41 m<sup>2</sup>.

### 3.5 Baryonyx

*Baryonyx walkeri* is estimated according to body-size proposed by Therrien and Henderson (2007) for the specimen

BMNH R9951 with 8.19 m. However, the body-size calculated by Therrien and Henderson (2007) is lower than proposed values by Paul (1988, 9.5 m), Charig and Milner (1997, 8.5 m), and Molina-Perez and Larramendi (2019, 9.7 m) (Table 4). For a body-size of 8.19 m, the calculated body-mass for the studied model is 1429 kg, which is closed to value proposed by Paul (2016) with 1200 kg and lower than values proposed by Therrien and Henderson (2007, 1980 kg) and Molina-Perez and Larramendi (2019, 2000 kg). Considering a body-size of 8.19 m, the 3D model represents 1.50 m<sup>3</sup> and a surface of 15.9 m<sup>2</sup>.

### 3.6 Allosaurus

In the case of *Allosaurus fragilis*, the estimation is obtained scaling the model to body-size proposed by Therrien and Henderson (2007) which is 6.36 m for specimen YPM 1930 (note that his specimen was 7.4 m for Paul, 1988, Table 5). The body-mass for this length is 1086 kg which is close to the proposed values of Alexander (1989) and Seebacher (2001, 952 kg), but very far of body-mass proposed by Colbert (1962, 2090–2300 kg), Campione et al., (2014, 2681 kg) and Paul (2016, 1700 kg). However, Therrien and Henderson (2007) proposed a body-mass comparatively low with 700 kg. For our model, the volume is 1.14 m<sup>3</sup> and the surface 13.75 m<sup>2</sup>.

If applying this approach to other specimens described in the literature (Table 5), the *Allosaurus* body-mass ranges from 1711 to 3853 kg. Therefore, YPM 1930 and USNM 4734 which are 7.4 m for Paul (1988) and Gilmore (1920) respectively, are estimated to 1711 kg. Other specimens such as MOR 693 (7.57 m for Bates et al., 2012) is 1831 kg, UUVP 6000 (7.9 m for Madsen, 1993 and Paul, 1988) is 2081 kg, and AMNH 680 (9.7 m for Campione et al., 2014) is 3853 kg. Other parameters such as volume and surface also increase when considered other specimens, with a maximum volume of 4.05 m<sup>3</sup> and maximum surface of 31.97 m<sup>2</sup> for the largest specimen AMNH 680.

### 3.7 Giganotosaurus

When scaling with the body-size proposed by Therrien and Henderson (2007) of 13 m for specimen MUCPv-CH-1 of *Giganotosaurus carolinii*, the resulting body-mass is 7193 kg. This value gives a body-mass for *Giganotosaurus* that fit fine within the proposed values of previous authors that ranges from 5508 kg of Campione et al. (2014) to 8500 kg of Molina-Perez and Larramendi (2019) (Table 4). All these estimations are based on the specimen MUCPv-CH-1. Taking into account the proposed body-size by Therrien and Henderson (2007) for the studied model, the volume of *G. carolinii* was 7.57 m<sup>3</sup> and a surface of 42.66 m<sup>2</sup>.

### 3.8 Tyrannosaurus

The model of *Tyrannosaurus rex* was scaled taking into account the dimensions of the specimen FMNH PR2081 proposed by Therrien and Henderson (2007) with 11.71 m and reaching a body-mass of 9979 kg. This approach based on the selected model gives a body-mass overestimated with respect to the values proposed by other works that shows a wide variability ranging from 4500 kg (Anderson et al., 1985) to 9500 kg (Hutchinson et al., 2011) (Table 4). This is meaning that the model used in our study is more robust than real specimens of *Tyrannosaurus rex*.

In this case, we have calculated the body-size scaling with the skull-body average factor and results 10.70 m and 7607 kg. is more accurate than scaled to body-length. For this body-mass, the estimated volume is 8.01 m<sup>3</sup> and the surface is 44.48 m<sup>2</sup>.

According to Hutchinson et al. (2011) the body-size of the specimen FMNH PR2081 was 12.3 m and not 11.71 m as indicated by Therrien and Henderson (2007). With this length the body-mass estimation based on the 3D model is 11,165 kg for FMNH PR2081. If applying this approach to the length of other fossil specimens compiled by Hutchinson et al. (2011), the *Tyrannosaurus* body-mass is 9,427 kg for AMNH 5027 (11.5 m), 9,701 kg for MOR 555 (11.6 m), 10,211 kg for BHI 3033 (11.8 m) and 10,473 kg for CM 9380 (11.9 m). The volume and surface taking into account the length values proposed by Hutchinson et al. (2011) ranges from 9.9 to 12.2 m<sup>3</sup> of volume and 51.3–58.8 m<sup>2</sup> for body-surface.

## 4 Interpretation

### 4.1 Morphometric parameter and theropod evolution

The convergent evolution between large theropods (Abelisauroidea, Allosauridae, Carcharodontidae, Ceratosauridae, and Tyrannosauridae) includes features such as proportionately large heads, and a tendency to shorter arms. As widely known from the fossil record and illustrated by the 3D models, theropod heads tended to be proportionately large from more primitive and small forms of the Late Triassic and Early Jurassic such as *Coelophysis* and *Dilophosaurus* to largest theropods of Cretaceous such as *Giganotosaurus* and *Tyrannosaurus* (Therrien and Henderson, 2007). In the case of the biggest, the head could reach 1.75 m in length (case of the *Tyrannosaurus rex* FMNH PR2081). The 3D analysis of these representative theropods confirm the different morphotypes from the slender primitive forms of the Early Jurassic to the robust large theropods developed during the Cretaceous.

## 4.2 Skull size and feeding strategies

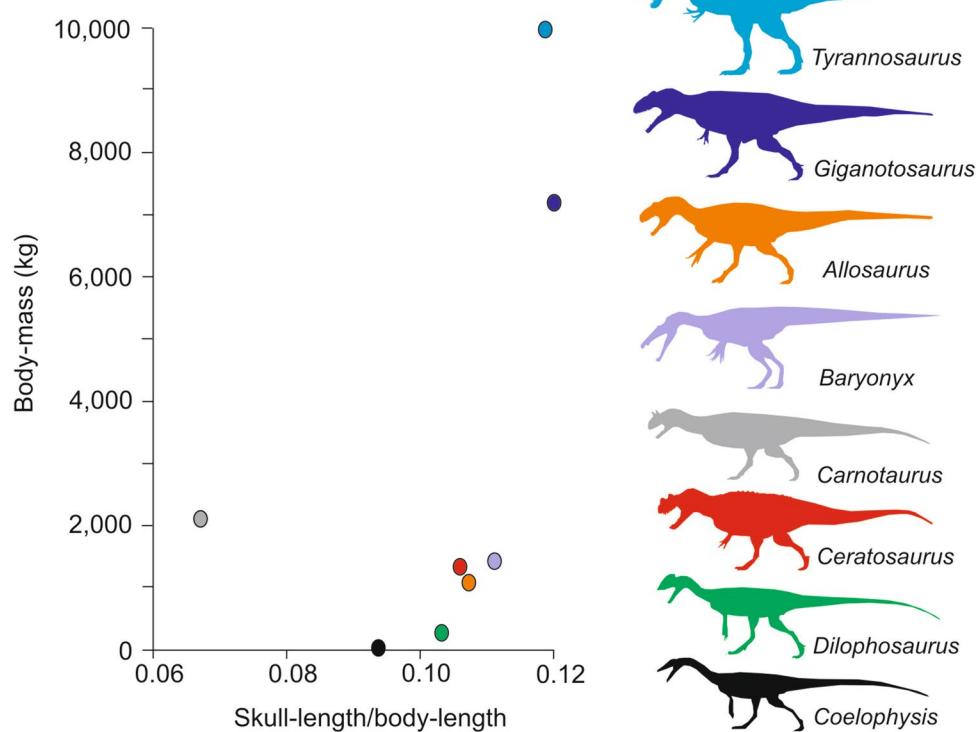
The skull length/body length in the studied genera increases according with the size of the body, therefore, this ratio is 0.093 for *Coelophysis*, 0.103 to 0.105 for *Dilophosaurus* and *Ceratosaurus*, 0.107 for *Allosaurus*, 0.113 for *Baryonyx*, and 0.119–0.120 for *Tyrannosaurus* and *Giganotosaurus* (Fig. 11). Only *Carnotaurus*, with a ratio of 0.067 (Fig. 11) is out of this trend due to the especially short skull (Fig. 6). Larger heads correspond to progressively larger and deeper jaws that correlates with increased body-mass and the enhanced demand of energy (Kane et al., 2016) (Fig. 11).

The skull length/body length ratio of *Coelophysis* (0.093) is the lowest of the studied genera. The teeth of *Coelophysis* were blade-like, curved and sharp, finely serrated, being larger in the upper jaw. Due to these features, *Coelophysis* probably preyed on small vertebrates and probably was also a fisher (Paul, 2016). *Dilophosaurus* is other primitive theropod of the Early Jurassic that was larger and more robust than *Coelophysis* with 5.68 m and 389 kg according to the estimations on the 3D model. However, *Dilophosaurus* was a slender theropod with a large elongated head (the skull length/body length ratio is 0.103). However, despite of the larger body-size than *Coelophysis*, the feeding habit of *Dilophosaurus* could be similar. The biomechanical study of Therrien et al. (2005) indicates that the bite force of the delicate skull

of *Dilophosaurus* rapidly decreased in the mandible hindwards in the tooth-throw. The large, but thin teeth confirm that *Dilophosaurus* probably feed small to medium size vertebrates.

According to our estimations, *Ceratosaurus nasicornis* was a medium-sized theropod around 5.06 m length with a body-mass around 843 kg, but as indicated before, probably the model used for calculation is more robust than the animal originally was. This Late Jurassic ceratosaurid was an ambush predator with large bladed teeth indicating that it hunted large preys, including sauropods and heavy ornithopods (Paul, 2016). The head was a much more important weapon (skull length/body length ratio 0.105) than in *Coelophysis* and *Dilophosaurus*, probably because his hunting strategy focused on the bite force and the muscled neck. *Ceratosaurus* shared habitat with *Allosaurus* being potential competitors for the same preys and probably developed different strategies for avoiding competition (Henderson, 1998; Foster and Chure, 2006). Some authors have discussed the potential adaptations of *Ceratosaurus* to hunt aquatic preys such as fishes, turtles, and crocodiles (Bakker and Bir, 2004; Yun, 2019). *Allosaurus*, in contrast, was an active predator that feed on large preys such as sauropods and ornithopods (Bakker, 1998; Rayfield et al., 2001; Carpenter et al., 2005; Paul, 2016), and its main weapon was the skull as could be deduced from its skull length/body length ratio ranging between 0.092 to 0.107.

**Fig. 11** Scatter plot showing the relation between body-mass and the skull-length/body-length ratio for the studied species calculated on the 3D models based on data body-size of Therrien and Henderson (2007)



*Carnotaurus sastrei* has proportionally the shorter skull of the studied theropods (the skull length/body length ratio is 0.067; Fig. 6). Different analyses of the jaw structure and other adaptations of the skull points to *Carnotaurus* fed upon large prey (Bakker, 1998; Therrien et al., 2005), however other works suggest that *Carnotaurus* was capable of quick but not strong bites which are adequate for capturing small preys (Mazzetta et al., 2009). The spinosaurid *Baryonyx*, in contrast have one of the most elongated and narrow heads among the studied theropods, with a skull length/body length ratio of 0.113, which is among the highest values of the studied genera with *Giganotosaurus* and *Tyrannosaurus* (Fig. 11). According to Charig and Milner (1986, 1997) the elongated and narrow snout armed with finely serrated teeth point to piscivorous feeding strategy, but some authors have recently suggested that *Baryonyx* was not exclusively piscivorous (Buffetaut et al., 2004; Therrien et al., 2005; Cuff and Rayfield, 2013; Sales and Schultz, 2017).

The largest heads and greater skull length/body length ratios are recorded in the largest theropods of the Late Cretaceous. *Giganotosaurus* was an apex predator sited in the top of the trophic chain and probably fed on large South American sauropods according to Paul (2016) based on the large size and the large head (the skull length/body length ratio is 0.12). However, Therrien et al. (2005) interpreted that neck muscles and jaws of *G. carolinii* were adapted to capture and bring down preys by delivering powerful bites. These authors proposed that *G. carolinii* may have been generalized predators that fed on a wide spectrum of prey smaller than themselves, such as ornithopods and juvenile sauropods. The apex predator in North America during the Late Cretaceous was *Tyrannosaurus rex* with a skull length/body length ratio of 0.119 (Fig. 11). The deep-jawed skull with bulbous large teeth and a heavily built skull are consistent with a powerful biter able to crush bones (Bates and Falkingham, 2012; Gignac and Erickson, 2017; Lautenschlager, 2015). Despite on the similar skull length/body length ratios, the trophic habits may be different between *T. rex* and *G. carolinii* due to length of the teeth and the bite force of the *T. rex* (5832 kg; Bates and Falkingham, 2012) were higher than in *G. carolinii* (1353 kg; Mazzetta et al., 2004). In addition, the flattened lower jaw of *Giganotosaurus* was useful for manipulate preys but not adapted to crush bones like in Tyrannosauridae.

#### 4.2.1 Body design and locomotion

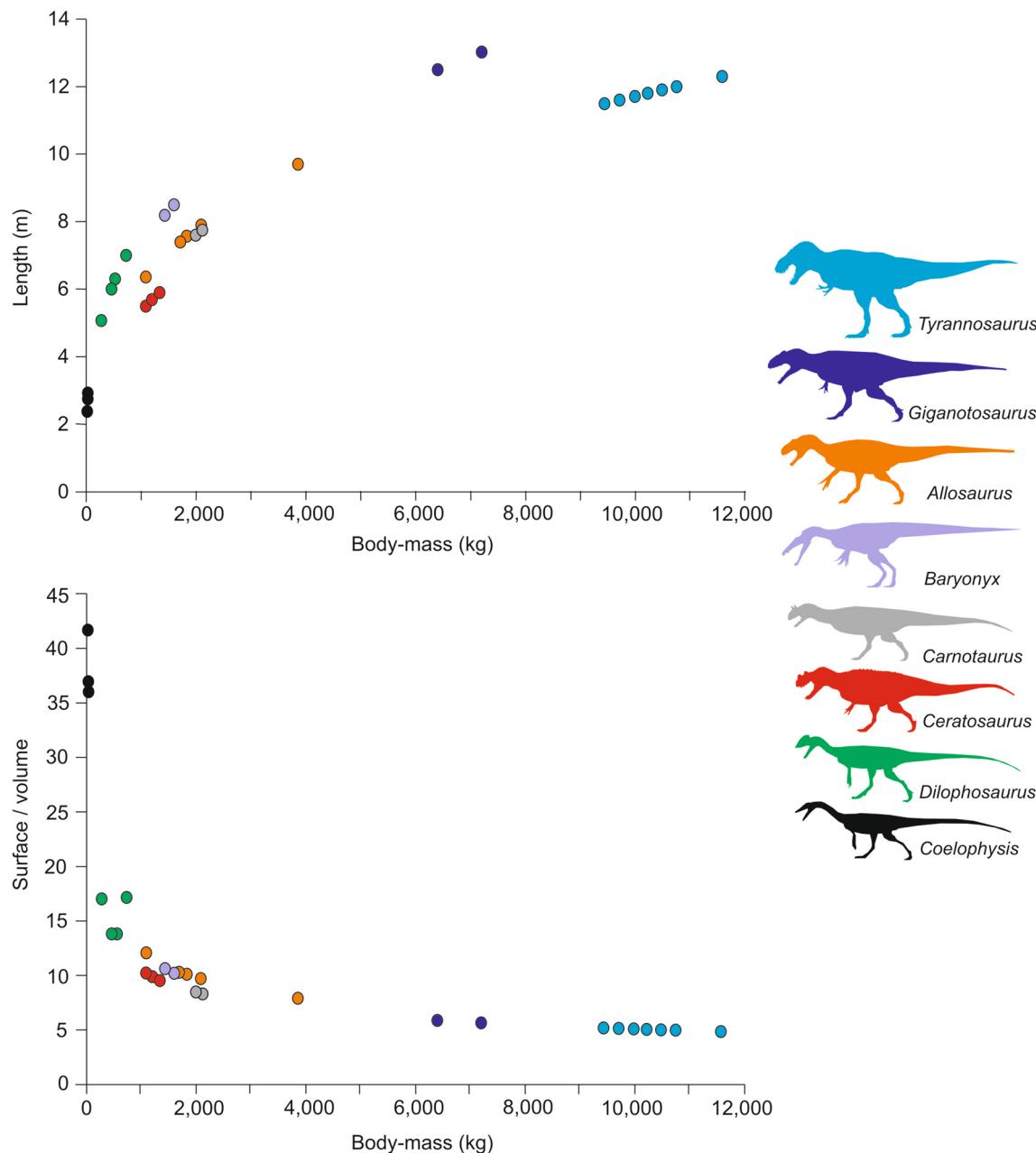
In order to increase body-size and skull-size yet maintaining reasonable agility as bipeds and predators, arms were progressively shortened in some taxonomic groups such as abelisaurids (*Abelisaurus*, *Carnotaurus*, *Majungasaurus*, and *Rajasaurus*) and tyrannosaurids (*Albertosaurus*, *Tarbosaurus*, and *Tyrannosaurus*) that present atrophied

forelimbs. However, despite their superficially convergent morphology among large theropods, they were different with derived characters mainly related to cranial distribution of bones and the vertebrae, but also manus and pedes among others.

Beginning with the oldest, *Coelophysis* was a light theropod (2.86 m and 37 kg), that probably was a fast-pursuit predator due to its slender body with narrow pelvis, large hindlimbs, and a semirigid tail working as counterweight. The forelimbs were adapted to catch small preys (Rinehart et al., 2009). The presence of outcrops such as Ghost Ranch Quarry (New Mexico) with numerous specimens has suggested that *Coelophysis* was gregarious (Schwartz and Gillette, 1994). *Dilophosaurus* also had large limbs, and probably was a good runner. Paul (2016) proposed that prey of *Dilophosaurus* included also early ornithischians and prosauropods. If that, *Dilophosaurus* had to employ the large claws for attacking large prey. In contrast, *Ceratosaurus* had shorter forelimbs than *Coelophysis* and *Dilophosaurus* and depended exclusively on the bite force and the muscled neck.

According to our analysis on 3D models, *Carnotaurus* was a medium size theropod with 7.75 m and 2113 kg. Its hindlimbs were long and adapted to fast running (Mazzetta and Farina, 1999; Persons IV and Currie, 2011a) whereas the forelimbs were atrophied as occurs in other abelisaurids such as *Abelisaurus*, *Majungasaurus*, and *Rajasaurus*. The body plan of *Carnotaurus* significantly differ from that of the spinosaurids as *Baryonyx*. *Baryonyx* was characterized by an elongated (and laterally flattened) body (8.19 m and 1429 kg). If compared with shorter body-size of *Carnotaurus* (7.75 m), the body-mass of *Baryonyx* is lower than in *Carnotaurus* (2.113 kg), and the volume according to 3D model is lower in *Baryonyx* (1.5 m<sup>3</sup>) than in *Carnotaurus* (2.2 m<sup>3</sup>). *Baryonyx* was not as good runner as *Carnotaurus*. This is supported by its robust forelimbs and a distinctive large claw in the first digits that may help it in capturing fish. This feeding habit was also interpreted for other spinosaurids (Taquet, 1984). Based on the δ<sup>18</sup>O composition of spinosaurid teeth, Amiot et al. (2010) proposed a semiaquatic life style for this family.

The 3D models of the largest analyzed theropods (*Allosaurus*, *Giganotosaurus*, and *Tyrannosaurus*), can also shed light on their locomotion styles. According to the digital model and using the length proposed by Therrien and Henderson (2007) for the specimen YPM 1930, *Allosaurus fragilis* was 6.36 m and 1086 kg. However, the weight estimated taking into account other body-sizes proposed by other authors and specimens reaches a maximum of 3853 kg for the specimen AMNH 680 (9.7 m for Campione et al., 2014) (Table 5, Fig. 12A). *Allosaurus* was a medium-size carnosaurian moderately robustly built. The slender body and the long tail indicate that this was an ambush and pursuit predator. The forelimbs, proportionally larger than in



**Fig. 12** **A** Scatter plot comparing length of different specimens proposed by some authors (Table 5) with the estimated body-mass based on the 3D models. **B** Scatter plot comparing surface/volume ratio

with the body-mass, both calculated on the 3D models using the body-length published by different fossil specimens in the literature (see Table 5)

other large theropods such as abelisaurids and tyrannosauroids, were probably used to handle and control preys, but the main hunter weapon was the skull.

*Tyrannosaurus rex* had a maximum body-mass ranging between 9979 kg and 11,565 kg if scaling the 3D model to 11.71 m (Therrien and Henderson, 2007) and 12.30 m (Hutchinson et al., 2011) respectively (Table 5, Fig. 12A). These maximum body-mass values result higher than previously reported in the literature (e.g. Anderson et al., 1985;

Alexander, 1989; Farlow et al., 1995; Seebacher, 2001; Therrien and Henderson, 2007; Hutchinson et al., 2011; Campione and Evans, 2020, Table 4). The weight overestimations in *Tyrannosaurus rex* in this work might be related to its accurate tail-reconstruction without lateral flattening as suggested by Persons IV and Currie (2011b). These authors suggest that such reconstructions may underestimate the actual weight of theropods. Nevertheless, both this model and the literature confirm that *T. rex* was heavier than *G. carolinii*.

*Giganotosaurus carolinii* was 13 m in length and 7193 kg when scaling it to Therrien and Henderson (2007), whereas it could be 12.5 m and 6394 kg when scaled based on Coria and Salgado (1995) (Table 5, Fig. 12A). This means that *G. carolinii* was larger than *Tyrannosaurus rex* but less robustly built. The maximum body-mass estimation for *G. carolinii* is by Molina-Perez and Larramendi (2019) with 8500 kg, whereas the maximum body-mass estimation for *T. rex* is 9500 kg by Hutchinson et al. (2011) (Table 4). However, the largest theropod recorded is *Spinosaurus aegyptiacus* with 16 to 18 m according to Dal Sasso et al. (2005) and 14.34 m according to Therrien and Henderson (2007).

Finally, when speaking about the locomotion of the large theropods, the controversy related to maximum running speed and trophic behavior of *Tyrannosaurus rex* should be addressed. Some works have interpreted that *Tyrannosaurus rex* was not a fast runner (Hutchinson and García, 2002; Hutchinson, 2004; Hirt et al., 2017; van Bijlert et al., 2021) but were exceptionally efficient walkers (Dececchi et al., 2020) and probably more agile than other large theropods (Snively et al., 2019). However, Sellers et al. (2017) interpreted that an adult *Tyrannosaurus rex* was unqualified for running due to high skeletal loads which these authors applied to other large theropods like Carcharodontosauridae. With respect to the trophic behaviour, and taking into account the different estimations about locomotion possibilities and bite force, the controversy is concerning to primarily a predator (e.g. Happ and Carpenter, 2008; Carbone et al., 2011; DePalma et al., 2013; Peterson and Daus, 2019) or a pure scavenger (Horner and Lessem, 1993; Horner, 1994; Carpenter, 1998; Stevens, 2006; Hone and Watabe, 2010), or both (Kane et al., 2016).

#### 4.3 Theropod volume and metabolism

The observed increase in size and mass through the theropod evolution of some clades also included potential metabolic problems due to the ratio of surface area to volume decreases as body size increases (e.g. Henderson, 2013), so smaller theropods had relatively more surface to exchange heat with the environment. Metabolic activity results in the production of body heat, and for large terrestrial tetrapods, elimination of excess body heat is an important factor (e.g. O'Connor and Dodson, 1999; Lucas, 2007; Henderson, 2013; Lovelace et al., 2020; Porter and Witmer, 2020). As some dinosaur lineages got progressively bigger (both in herbivores and carnivores) during the Late Jurassic and Cretaceous, the ratio of their surface area to their volume fell and they became less efficient at dissipating metabolic heat. According to Gillooly et al. (2006), efficiency for losing metabolic heat fall when they surpassed 600 kg. Lucas (2007) indicates that surface/volume ratio (S/V) fall sensible in dinosaurs over 1000 kg affecting the efficiency for dissipating metabolic heat.

However, the rate of body-heat loss is not only related to surface/volume ratio (S/V), but also the shape, the colour of the skin, the layer of fat beneath the skin, the presence of a feather entanglement, and the environmental temperature. Nevertheless, the main parameter is the S/V ratio. For the studied theropod genera according to our digital 3D models (scaling with the values proposed by Therrien and Henderson, 2007; Table 5) the S/V is 36.00 for *Coelophysis*, 17.01 for *Dilophosaurus*, 12.06 for *Allosaurus*, 10.60 for *Baryonyx*, 8.29 for *Carnotaurus*, 5.64 for *Giganotosaurus*, and 5.08 for *Tyrannosaurus*. The Fig. 12B shows the relation S/V and body-mass applying the size estimations of other authors and specimens to our 3D model compiled in Table 5. Taking into account the S/V ratio, *Coelophysis* lost heat at a higher rate than the other studied theropods, and thus had higher mass-specific metabolic rates. In the opposite side, *Giganotosaurus* and *Tyrannosaurus* had the lowest values of S/V (Fig. 12B), which is meaning that they lost heat at a low rate, the expected mass-specific metabolic rate would be low, and probably they spent long time resting after feeding if ectotherms. This can be relevant in the interpretation of the hunter or scavenger feeding behaviour of large theropods. However, uncertainty is surrounding the ectotherm and endotherm character of dinosaurs, which is important for understanding the physiology and gigantism developed in many groups (Barrick et al., 1996; O'Connor and Dodson, 1999; Amiot et al., 2006; Gillooly et al., 2006; Lucas, 2007; Eagle et al., 2011), due to for the same size endotherms needs more energy than ectotherms.

In the classic work of Spotila et al. (1973) an equation was developed to describe the effect of size on the response of body heat to environmental temperature. Authors indicated that gigantism of some dinosaurs would be a very useful strategy for providing a constant internal temperature without a high metabolic rate. Barrick and Showers (1999) recorded very similar  $\delta^{18}\text{O}$  patterns between bones of *Giganotosaurus carolinii* and *Tyrannosaurus rex*, and inferred a similar heat distribution in the body. These authors proposed a thermoregulatory pattern and a metabolism intermediate to that of reptiles and mammals, and were therefore homeothermic. Gillooly et al. (2006) studied the relation between body-mass and body temperature for extant crocodiles and proposed that dinosaur body temperatures increased with body-mass regarding that dinosaurs showed inertial homeothermy and stable core body-temperature. Lucas (2007) proposed that inertial homeothermy was probably for large herbivores such as sauropods (gigantothermia, Paladino et al., 1990) but with a slow ectothermic metabolism. In the opposite, Barrick et al. (1996) interpreted homeothermy for some Cretaceous ornithischians from  $\delta^{18}\text{O}$  but suggested that they had elevated metabolic rates. In the case of *Tyrannosaurus rex*, Barrick and Showers (1994) proposed that maintenance of homeothermy, interpreted from

$\delta^{18}\text{O}$  of bones, and implies a relatively high metabolic rate similar to that of endotherms. This homeothermy could be inferred also for other large theropods here studied such as *Carnotaurus*, *Baryonyx*, *Allosaurus* and *Giganotosaurus*. Other works propose directly endothermy for some dinosaur groups (e.g. Bakker, 1972; Seebacher, 2003; Amiot et al., 2006; Eagle et al., 2011).

It is not the aim of this work to solve the current discussion about the metabolism of the theropods, but to show how this 3D techniques, when applied to proper dinosaur models, provides an extent and accurate data set that may help in diverse study areas within the dinosaur palaeontology from ecology and feeding behaviour to locomotion or metabolic rates.

## 5 Conclusions

This work analysed diverse morphometric data obtained from photogrammetric 3D models of scientifically accurate palaeoreconstructions of theropods from eight representative families. The analysed PVC models belong to the genera *Coelophysis*, *Dilophosaurus*, *Ceratosaurus*, *Allosaurus*, *Baryonyx*, *Carnotaurus*, *Giganotosaurus*, and *Tyrannosaurus* and are based on some of the most recent and scientifically accurate palaeoreconstructions. These genera were selected as representatives of the main clades of the Order Theropoda. The figures were selected without feather entanglement in order to avoid overestimation of the body mass based on the volume. The scanned 3D models were scaled considering the body-size and body-mass estimations of other authors, different scaling was applied to the different species based on the skull length/body length ratio.

The 3D analysis of these genera confirms the, widely known from the fossil record, evolutionary trend of the different theropod morphotypes from the slender primitive forms of the Early Jurassic (i.e. *Coelophysis* and *Dilophosaurus*) to the robust large theropods developed during the Cretaceous (i.e. *Giganotosaurus* and *Tyrannosaurus*). The skull-length/body-length in the studied genera increases according with the size of the body, therefore, this ratio is 0.093 for *Coelophysis*, 0.103 to 0.105 for *Dilophosaurus* and *Ceratosaurus*, 0.107 for *Allosaurus*, 0.113 for *Baryonyx*, and 0.119 to 0.120 for *Tyrannosaurus* and *Giganotosaurus*. Only *Carnotaurus* with a ratio of 0.067 is out of this trend due to the especially short skull. Larger heads correspond to progressively larger and deeper jaws that correlates with increased body-mass and the enhanced demand of energy.

Together with the specific measurements on the skull length and body length that allows for recognition of major evolutionary trends, the study of photogrammetric 3D models provides morphometric information that cannot be obtained from the study of bones alone. That is the case of

the surface/volume ratio(S/V), a parameter closely related to the heat dissipation that help in the characterization of the metabolism of extinct taxa. For the studied theropod genera, according to our digital 3D models, S/V ratio is 35.21 for *Coelophysis*, 15.19 for *Dilophosaurus*, 12.03 for *Allosaurus*, 10.56 for *Baryonyx*, 8.27 for *Carnotaurus*, 5.63 for *Giganotosaurus*, and 5.55 for *Tyrannosaurus*. According to these S/V ratios, *Coelophysis* lose heat at a higher rate than the other studied theropods, and thus has higher mass-specific metabolic rates. In the opposite side, *Giganotosaurus* and *Tyrannosaurus* have the lowest values of S/V, which indicates that they lose heat at a low rate, the expected mass-specific metabolic rate would be low. This can be relevant in the interpretation of the hunter or scavenger feeding behaviour of large theropods. However, to elucidate the ectothermic or endothermic character of the theropods is not the aim of this study. This work shows how digitization techniques, when applied to proper dinosaur models, provide an extent and accurate data set that may help in diverse study areas within the dinosaur palaeontology from ecology and feeding behaviour to the analysis of their locomotion or metabolic rates.

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