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# Evaluating the palaeoecology of the Megaraptora (Dinosauria: Theropoda) through biomechanical approaches

## Evaluación de la paleoecología de Megaraptora (Dinosauria: Theropoda) mediante enfoques biomecánicos

Chan-gyu YUN

**Abstract:** Megaraptoran theropods represent an enigmatic and unusual lineage of theropod dinosaurs that are characterized by their unique bauplan including a low, elongated skull and robust forelimbs with enlarged claws. Such an unusual morphology has led to speculations that these theropods primarily used forelimbs instead of jaws in prey capture or feeding, but biomechanical studies regarding in-depth evaluations of the functions of their claws or jaws have been scarce. In this work, mandibular force profiles of Australian megaraptoran *Australovenator wintonensis* are constructed through the principle of beam theory, and mechanical advantages of first manual unguals of various megaraptoran taxa are evaluated using third-class lever model. Mandibular force profiles reveal that the lower jaw of *Australovenator wintonensis* behaved as a simple lever, suitable for delivering slashing bites, and likely unable to produce a high bite force. Biomechanical modeling of the first manual unguals of megaraptorans suggests a decrease in Mechanical Advantage in derived taxa, which indicates the claws became more adapted to hook-and-pull function during the course of evolution in this clade. Such results imply megaraptorans like *Australovenator wintonensis* mainly preyed on relatively small-sized animals, or relied more on their forelimbs to hunt large prey items through hooking the claws onto the victim and pulling them, tearing or slicing the flesh.

**Resumen:** Los terópodos megaraptores representan un linaje enigmático e inusual de dinosaurios terópodos que se caracterizan por su bauplan único que incluye un cráneo bajo y alargado y extremidades anteriores robustas con garras agrandadas. Una morfología tan inusual ha llevado a especulaciones de que estos terópodos usaban principalmente las extremidades anteriores en lugar de las mandíbulas para capturar o alimentarse de sus presas. Sin embargo, los estudios biomecánicos sobre evaluaciones en profundidad de las funciones de sus garras o mandíbulas son escasos. En este trabajo, los perfiles de fuerza mandibular del megaraptor australiano *Australovenator wintonensis* se construyen mediante el principio de la teoría del haz, y las ventajas mecánicas de los primeros unguales manuales de varios taxones de megaraptores se evalúan utilizando un modelo de palanca de tercera clase. Los perfiles de fuerza mandibular revelan que la mandíbula inferior de *Australovenator wintonensis* se comportó como una palanca simple, adecuada para realizar mordidas cortantes y probablemente incapaz de producir una fuerza de mordida alta. El modelado biomecánico de los primeros unguales manuales de megaraptores sugiere una disminución en la Ventaja Mecánica en los taxones derivados, lo que indica que las garras se adaptaron más a la función de gancho y tracción durante el curso de la evolución en este clado. Tales resultados implican que los megaraptores como *Australovenator wintonensis* se alimentaban principalmente de animales de tamaño relativamente pequeño, o dependían más de sus extremidades anteriores para cazar presas grandes enganchando con las garras a la víctima y tirando de ellas, desgarrando o cortando la carne.

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## INTRODUCTION

Megaraptora is a clade of medium-sized to large theropod dinosaurs that inhabited terrestrial ecosystems of Asia, Australia and South America from the Barremian through Maastrichtian (*e.g.*, Novas *et al.*, 2013; Samathi *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022a, 2022b). Despite their broad geographic and temporal distribution, the fossil record of megaraptorans is mainly composed of relatively fragmentary materials, which makes it difficult to establish their phylogenetic position within Theropoda or infer their ecology and behavior (*e.g.*, Novas *et al.*, 2013; Bell *et al.*, 2015; Lamanna *et al.*, 2020). The exact phylogenetic placement of this group is still uncertain and controversial: initially, megaraptorans were interpreted to be either close to megalosauroid (=spinosauroid) tetanurans (Smith *et al.*, 2008) or represent carcharodontosaurian allosauroids within a clade Neovenatoridae (Benson *et al.*, 2010; Carrano *et al.*, 2012; Zanno & Makovicky, 2013). Nowadays, megaraptorans are usually considered members of Coelurosauria (*e.g.*, Novas *et al.*, 2013; Porfiri *et al.*, 2014; Aranciaga-Rolando *et al.*, 2019, 2022a, 2022b). Within Coelurosauria, megaraptorans are usually considered as a subclade nested in, or a sister taxon, of Tyrannosauroidea (*e.g.,* Novas *et al.*, 2013; Porfiri *et al.*, 2014; Cau, 2018; Aranciaga-Rolando *et al.*, 2019, 2022a, 2022b; Naish & Cau, 2022; Kotevski *et al.*, 2024), but several studies have recovered them as a basal coelurosaurian clade that diverged earlier than Tyrannosauroidea within the lineage towards Neornithes (*e.g.*, Apesteguía *et al.*, 2016; Delcourt & Grillo, 2018; Porfiri *et al.*, 2018; Samathi *et al.*, 2019). Despite such unclear phylogenetic relationships as well as a sparse fossil record, megaraptorans have enjoyed a recent flurry of descriptions of new taxa (*e.g.*, Porfiri *et al.*, 2018; Samathi *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022b) as well as recovery of more materials or redescriptions of previously-erected taxa (*e.g.*, White *et al.*, 2012, 2013, 2015a, 2015b; Porfiri *et al.*, 2014; Novas *et al.*, 2016; Aranciaga-Rolando *et al.*, 2019, 2022a). Such new information has indicated that the bauplan of megaraptorans is rather different from other non-avian theropods in several features, including an elongated, shallow skull possessing apicobasally short, strongly recurved teeth, a robust forelimb with enlarged manus that possesses hypertrophied unguals, and a highly pneumatized axial skeleton (*e.g.*, White *et al.*, 2012, 2015a, 2015b; Novas *et al.*, 2013, 2016; Porfiri *et al.*, 2014; Aranciaga-Rolando *et al.*, 2022a, 2023).

Among these, a unique forelimb anatomy has received a particular attention, and based on enlarged, raptorial manual unguals, as well as well-developed muscle attachment sites, various authors have suggested the forelimb of megaraptorans was important to the palaeobiology of these theropods, and may played a key role in prey capture or feeding (*e.g.*, White *et al.*, 2012, 2015a; Aranciaga-Rolando *et al.*, 2023).

Although these are plausible claims, studies that examined the likely functions of the hypertrophied manual unguals of megaraptorans have been scarce, such as the biomechanical modeling of the manual ungual bones like that performed for other non-avian theropods (*e.g.*, Lautenschlager, 2014; Qin *et al.*, 2023). Additionally, the skulls and jaws of megaraptorans, which would also have been important for hunting and feeding, have received less attention than their forelimbs. This is likely due to a paucity of cranial remains of this clade (*e.g.*, Porfiri *et al.*, 2014; White *et al.*, 2015b; Coria & Currie, 2016; Kotevski *et al.*, 2024). So far, relatively complete bones that comprise the snout or anterior half of the mandible, which would have been used in hunting and feeding, are only known in *Australovenator wintonensis* and *Megaraptor namunhuaiquii* among derived megaraptorans (Hocknull *et al.*, 2009; Porfiri *et al.*, 2014; White *et al.*, 2015b). For this reason, biomechanical analyses on craniomandibular bones, which are important for assessing feeding function or hunting behavior and were frequently performed in other theropods (*e.g.*, Rayfield, 2005; Therrien *et al.*, 2005, 2021; Rowe & Snively, 2021; Johnson-Ransom *et al.*, 2024), have not been performed in megaraptorans.

Since the ungual bone generally operates as a third-class lever, the ratio of in-lever length to out-lever length (Mechanical Advantage) can be used as a proxy for structural strength of the claw (*e.g.*, Ostrom, 1966; Tsogtbaatar *et al.*, 2018; Kobayashi *et al.*, 2022; Kubota *et al.*, 2024). Despite being relatively simple in nature, biomechanical modeling of the theropod manual unguals through the principle of third-class lever (Kobayashi *et al.*, 2022) has recently proven to be yield results congruent with those produced through more complex finite element analyses (Qin *et al.*, 2023). Additionally, Mechanical Advantage of the ungual is correlated with the degree of development of the flexor tubercle, as the size of the tubercle affects the length of the in-lever of the claw. Considering that the flexor tubercle serves as an attachment point of the flexor digitorum longus, the values of Mechanical Advantage (=proxy for the size of the tubercle) can be used as indicators of the output force applied on the tip of the ungual (*e.g.*, Tsogtbaatar *et al.*, 2018; Kobayashi *et al.*, 2022; Kubota *et al.*, 2024).

The principles of beam theory, which requires only external dimensions on some aspects of the mandible, can be used to derive mandibular force profiles from the complete lower jaw, or even from the isolated dentary of a theropod (Therrien *et al.*, 2005, 2021; Jasinski, 2011; Monfroy, 2017; Yun, 2024). This technique is relatively simple, less time-consuming, does not require expensive, complex computer analysis programs, and has been shown to yield results compatible with the more complex Finite Element Analysis (**FEA**) (*e.g.*, Therrien *et al.*, 2005, 2016, 2021). A medium-sized megaraptoran dinosaur from Australia, *Australovenator wintonensis*, provides an optimal opportunity to study mandibular biomechanic profiles in order to infer feeding and hunting behavior, as well as bite force of this lineage. This is because the holotype of this taxon, AODF 604, is relatively well-preserved among known megaraptoran skeletons and, most importantly, preserves complete dentaries (Hocknull *et al.*, 2009; White *et al.*, 2015b).

In this work, a construction of a beam model for the *Australovenator wintonensis* mandible is provided, in order to evaluate its ability to resist bending loads generated during biting. Additionally, the results are compared to previously published results for extant *Varanus komodoensis* and various non-avian theropods (Therrien *et al.*, 2005, 2021) so that hunting techniques or feeding mechanisms employed by this taxon, or potentially other megaraptorans, can be gleaned. Additionally, Mechanical Advantages of known megaraptoran manual ungual I are derived, in order to investigate possible functions of this element as well as to infer evolutionary changes in ungual shape and role occurred in this clade.

### Institutional abbreviations

**AODF,** Australian Age of Dinosaurs Fossil, Winton, Australia; **BYU,** Brigham Young University, Utah, USA; **FPMN,** Fukui Prefectural Museum, Fukui, Japan; **MCF-PVPH,** Museo Carmen Funes, Paleontologia de Vertebrados, Plaza Huincul, Neuquén, Argentina; **MPCN,** Museo Patagónico de Ciencias Naturales, General Roca, Argentina; **MUCPv,** Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **NHMUK,** Natural History Museum, London, United Kingdom; **NMV,** Museums Victoria (formerly National Museum of Victoria), Melbourne, Australia; **SM,** Sirindhorn Museum, Department of Mineral Resources, Kalasin, Thailand; **TMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UNPSJB-PV,** Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

## MATERIAL AND METHODS

Measurements were made of the dentary of AODF 604 from the published figure 2 of White *et al.* (2015b), using the program ImageJ (Schneider *et al.*, 2012). While the postdentary region of the mandible in AODF 604 is missing, Aranciaga-Rolando *et al.* (2019, fig. 1) provided a composite reconstruction of a complete megaraptoran mandible, using the dentary of AODF 604 and postdentary bones of *Murusraptor barrosaensis* (MCF-PVPH-411), and this was scaled after the holotype of *Australovenator wintonensis*.

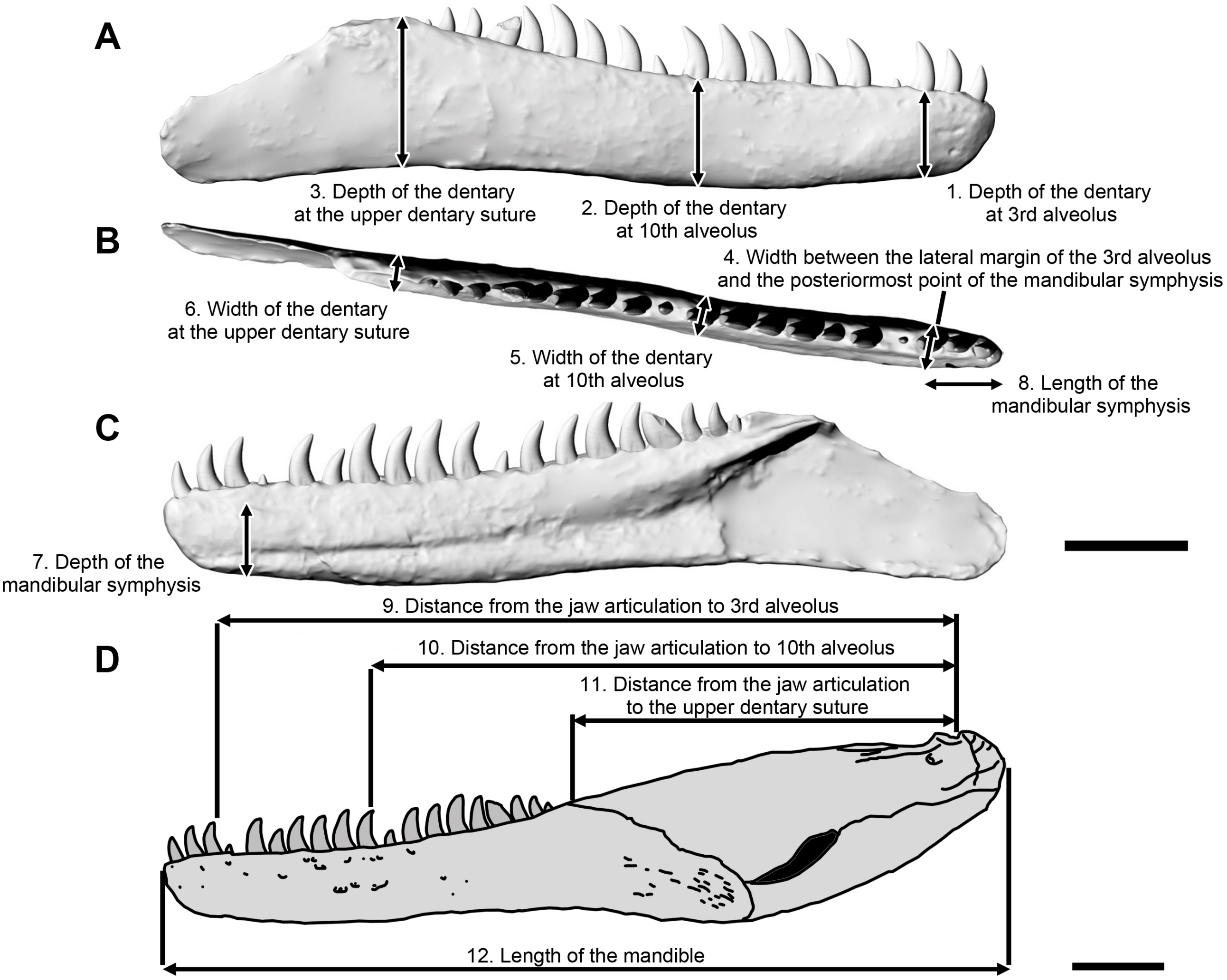

**Figure 1. A**–**D,** Measurement parameters used in this study, with mandible of *Australovenator wintonensis* (AODF 604) as an example; **A,** dimensions measured at the lateral surface; **B,** dimensions measured at the dorsal surface; **C,** depth of the mandibular symphysis measured at the medial surface; **D,** dimensions measured after the reconstructed, complete mandible. **A**–**C** are modified from figure 2 of White *et al.* (2015b), and **D** is after figure 1 of Aranciaga-Rolando *et al.* (2019); scale bars = 50 mm.

The fact that reconstruction was used suggests that some property values (*e.g.*, Zx/L, Zy/L) derived in this study are preliminary and, therefore, in such cases the results should be used as predictions when more complete materials are recovered. Use of images to derive mandibular force profiles is a valid method that produces congruent results with those using measurements directly taken from actual specimens (Brannick & Wilson, 2020).

Various measurements (Fig. 1) were taken following the protocols of Therrien *et al.* (2005, 2021), and are as follows: 1) depth of the dentary at 3rd alveolus; 2) depth of the dentary at 10th alveolus; 3) depth of the dentary at the upper dentary suture with the surangular; 4) width between the lateral margin of the 3rd alveolus and the posteriormost point of the mandibular symphysis; 5) width of the dentary at 10th alveolus; 6) width of the dentary at the upper dentary suture; 7) depth of the mandibular symphysis; 8) length of the mandibular symphysis; 9) distance from jaw articulation to 3rd alveolus; 10) distance from jaw articulation to 10th alveolus; 11) distance from jaw articulation to upper dentary suture; and 12) length of the mandible. Of note, the mandibular symphysis of *Australovenator wintonensis* is not clearly defined (White *et al.*, 2015b), but figure 2 of White *et al.* (2015b) provides an extent which both dentaries meet at their anterior portion, and this was used as a proxy to take measurements. From these measurements, a set of biomechanical properties is derived following protocols of Therrien *et al.* (2005, 2021), and each component are as follows: 1) Zx (a bending strength in the dorsoventral plane) = $\pi$*(dentary width/2)*(dentary depth/2)$^2$/4; 2) Zy (a bending strength in the labiolingual plane) = $\pi$*(dentary depth/2)*(dentary width/2)$^2$ /4; 3) Zx/Zy (a relative strength of the mandible); 4) Zx/L (a dorsoventral mandibular strength), in which L is the distance between the landmark and the jaw articulation; and 5) Zy/L (a mediolateral mandibular strength). This dataset was produced using Microsoft Excel. For comparative purposes, mandibular measurements, and lower jaw force profiles of various non-avian theropods are obtained and derived after the dataset of Therrien *et al.* (2021), and subjected to exponential regressions to investigate the correlations between mandibular length and the bite force among theropods, and how *Australovenator wintonensis* fits such trends.

The Mechanical Advantage (**MA**) of the theropod ungual can be derived from the following calculation: MA = $\sin(\theta + \delta)\, d / a$, when the flexor force is hypothesized to be applied perpendicular to the articulation surface (Tsogtbaatar *et al.*, 2018; Kobayashi *et al.*, 2022; Kubota *et al.*, 2024; Fig. 2). In this calculation, $a$ is the out-lever length measured from the most concave point of the articular surface to the tip of the ungual, $d$ is the in-lever length from the concave point of the articulation surface to the most convex point of the flexor tubercle, $\theta$ is the angle of the input force vector to the line of out-lever, and $\delta$ is the angle between the in-lever and the out-lever. Therefore, MA values represent efficiency of the output force that exerted at the tip of the ungual relative to the input force at the flexor tubercle (*e.g.*, Tsogtbaatar *et al.*, 2018; Kobayashi *et al.*, 2022; Kubota *et al.*, 2024). In addition, they are partly correlated with the degree of the development of the flexor tubercle: that is, unguals with well-developed flexor tubercle are likely to have high MA values as well (Tsogtbaatar *et al.*, 2018).

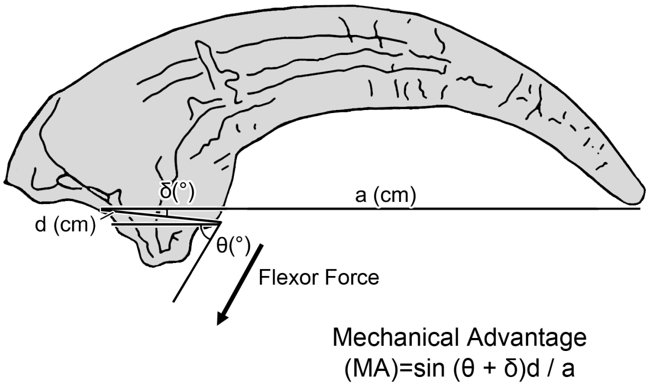

**Figure 2.** Biomechanical modeling of the theropod manual ungual, using third-class lever model (after Tsogtbaatar *et al.*, 2018). Explanations: $a$ is the out-lever measured from the articular surface to the tip of the ungual, $d$ is the in-lever from the articulation surface to the flexor tubercle, $\theta$ is the angle of the input force vector to the out-lever, and $\delta$ is the angle between the in-lever and the out-lever. Illustration of the ungual is after Lamanna *et al.* (2020).

Measurements of manual unguals I of megaraptorans were taken from the published figure 6 of Lamanna *et al.* (2020), using ImageJ (Schneider *et al.*, 2012), and the Mechanical Advantage values were derived through Microsoft Excel. Given that the ungual of the first digit is the most hypertrophied one within the manus of Megaraptora, it is reasonable to assume that this element played the most important role in the manual function (*e.g.*, White *et al.*, 2015a). To infer the possible evolutionary changes of this element in the clade, obtained Mechanical Advantage values were regressed against the out-lever length (a proxy for the size of an ungual), since previous studies have noted significant body size increase during the later course of megaraptoran evolution (*e.g.*, Lamanna *et al.*, 2020; Aranciaga-Rolando *et al.*, 2022a, 2022b). A total of 10 megaraptoran manual unguals were used to derive the Mechanical Advantage values, and same values for three non-megaraptoran theropods (*Allosaurus* sp. – NHMUK R10868 (cast), *Suchomimus tenerensis* – NHMUK R16013 (cast), *Torvosaurus tanneri* – BYU 2020) that might have used their forelimbs in predation (*e.g.*, Holtz, 2003, 2008) were also calculated for the comparative purposes, using the same method (Gasca *et al.*, 2018, fig. 1). A full list of analyzed ungual specimens, are provided in Table 1.

**Table 1.** Mechanical Advantage values of manual ungual I-2 of megaraptoran theropods and three non-megaraptoran theropods, derived from a variety of measurements.

| Clade | Taxon/Specimen | a (cm) | d (cm) | δ(°) | θ(°) | δ(rad) | θ(rad) | MA | Note | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| Megaraptora | *Australovenator wintonensis* AODF 604 | 15.87 | 3.26 | 4.61 | 65.91 | 0.080 | 1.150 | 0.194 | Moderately restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | cf. *Australovenator wintonensis* NMV P239464 | 14.37 | 2.93 | 20.68 | 60.81 | 0.361 | 1.061 | 0.202 | - | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | *Fukuiraptor kitadaniensis* FPMN 9712211 | 10.7 | 3.76 | 38.52 | 32.62 | 0.672 | 0.569 | 0.333 | - | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | *Gualicho shinyae* MPCN PV 0001 | 6.69 | 2.14 | 24.41 | 55.79 | 0.426 | 0.974 | 0.315 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | *Megaraptor namunhuaiquii* MCF-PVPH 79 | 26.65 | 4.63 | 21.82 | 62.28 | 0.381 | 1.087 | 0.173 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | *Megaraptor namunhuaiquii* MUCPv 341 | 25.91 | 5.26 | 11.05 | 70.95 | 0.193 | 1.238 | 0.201 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | *Phuwiangvenator yaemniyomi* SM-PW9B-19 | 6.73 | 2.37 | 23.96 | 39.5 | 0.418 | 0.689 | 0.315 | Moderately restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | UNPSJB-PV 958 | 24.43 | 4.8 | 26.61 | 63.72 | 0.464 | 1.112 | 0.196 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | UNPSJB-PV 1046 | 21.35 | 5.53 | 19.14 | 58.04 | 0.334 | 1.013 | 0.253 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Megaraptora | UNPSJB-PV 1102 | 20.15 | 4.82 | 12.58 | 61.38 | 0.220 | 1.071 | 0.230 | Slightly restored | Lamanna *et al.* (2020): fig. 6 |
| Non-Megaraptora (Allosauridae) | *Allosaurus* sp. NHMUK R10868 (cast) | 18.16 | 6.62 | 10.34 | 60.95 | 0.180 | 1.064 | 0.345 | - | Gasca *et al.* (2018): fig. 1 |
| Non-Megaraptora (Spinosauridae) | *Suchomimus tenerensis* NHMUK R16013 (cast) | 21.16 | 7.11 | 21.42 | 51.52 | 0.374 | 0.899 | 0.321 | - | Gasca *et al.* (2018): fig. 1 |
| Non-Megaraptora (Megalosauridae) | *Torvosaurus tanneri* BYU 2020 | 20 | 5.87 | 11.16 | 67.96 | 0.195 | 1.186 | 0.288 | - | Gasca *et al.* (2018): fig. 1 |

## RESULTS

Mandibular force profiles: The bending strength about the mediolateral axis (Zx) of the holotype (AODF 604) dentary of *Australovenator wintonensis* increases posteriorly (Tab. S1). The Zx value at the 3rd alveolus of AODF 604 is approximately 2.27, whereas that at the middentary is about 1.36 times higher (about 3.10). The Zx value at the upper dentary suture with the surangular is highest, being about 5.36. The bending strength about the dorsoventral axis (Zy) shows a slightly different trend (Tab. S1), as Zy values at the 3rd alveolus and middentary are found to be nearly identical (about 1.16). The Zy value at the upper suture region is slightly higher, being about 1.25.

In the case of the relative mandibular force (Zx/Zy), the Zx/Zy value is lowest at the 3rd alveolus (about 1.96), whereas those at the middentary and the upper dentary suture are significantly higher, being about 2.68 and 4.29, respectively (Fig. 3A). These values suggest that the lower jaw of *Australovenator wintonensis* is slightly more rounded in cross-section near the symphysis, but is still close to twice the width (*versus* depth), and becomes deeper posteriorly, reaching more than four times the width (Tab. S1).

The bending force in the dorsoventral plane (Zx/L) increases posteriorly (Fig. 3A): the Zx/L value at the 3rd alveolus of AODF 604 is estimated to be about 0.053, whereas those of the middentary and the upper suture region are estimated to be about 0.090 and 0.236, respectively (Tab. S1). The bending force in the mediolateral plane (Zy/L) shows a similar trend of increasing posteriorly like Zx/L (Fig. 3A): the Zy/L value at the 3rd alveolus is 0.027, and those at the middentary and upper dentary suture are about 0.034 and 0.055, respectively. These values, of course, also suggest that Zy/L does not increase as much posteriorly as the bending force in the dorsoventral plane (Tab. S1). Recent studies have demonstrated that Zx/L value at the middentary is a valid proxy for bite force in theropods (Therrien *et al.*, 2005, 2021), as this region is close to the most prominent upper jaw tooth where the bite force is usually estimated or compared in crocodylians and non-avian theropods (*e.g.*, Erickson *et al.*, 2003, 2004, 2012; Rayfield, 2004; Gignac & Erickson, 2015, 2017). The middentary Zx/L value (0.090) of *Australovenator wintonensis* is nearly identical to that of TMP 2016.14.1 (0.091; Tab. S1), an immature individual of the tyrannosaurid *Gorgosaurus libratus* with a mandibular length of 46.45 cm (Therrien *et al.*, 2021; Voris *et al.*, 2019, 2022; Fig. 3B). An estimated complete mandibular length of AODF 604 is approximately 48.69 cm (after White *et al.*, 2015b, fig. 2; Aranciaga-Rolando *et al.*, 2019, fig. 1), making both of similar lengths as well.

In terms of the proportion of the mandibular symphysis, it appears that *Australovenator wintonensis* has a symphysis length that is subequal to the depth with a ratio of 1.06 (Tab. S1). In this respect, the mandibular symphysis of this taxon is more similar to that of tyrannosaurids than to other non-avian theropods, in that an anteroposterior extent of the symphyseal region is nearly equal to the dorsoventral extent (Therrien *et al.*, 2005, 2021). In most other non-avian theropods, the depth of the symphysis is usually much higher than the length of the region, mostly because of its subvertical nature (Therrien *et al.*, 2005, 2021).

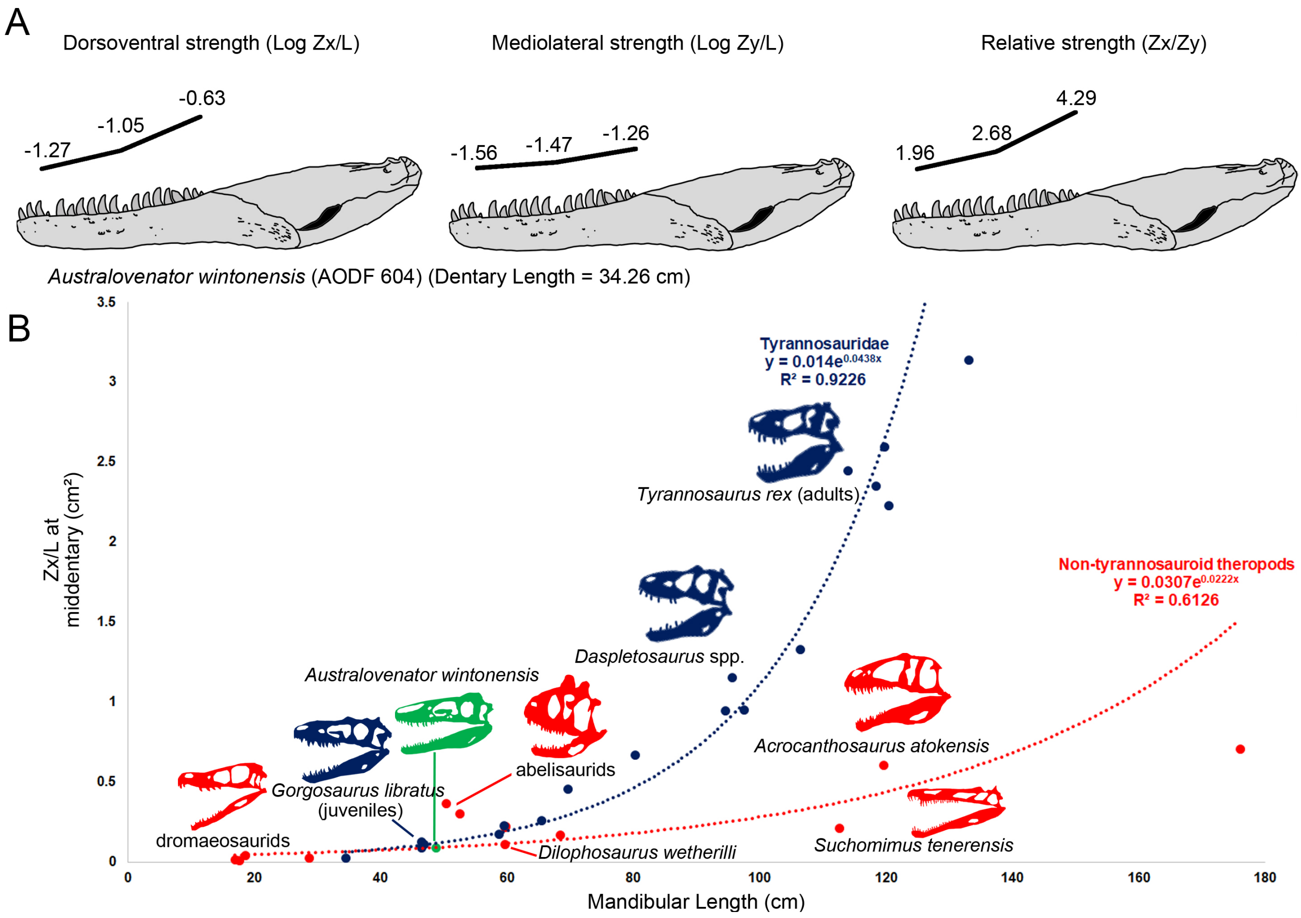

**Figure 3. A**–**B,** Mandibular force profiles of *Australovenator wintonensis* and other non-avian theropods; **A,** mandibular properties of *Australovenator wintonensis* (AODF 604); **B,** comparison of bite force estimates between *Australovenator wintonensis* and other non-avian theropods, using Zx/L at the middentary as a proxy. Illustrations are after Aranciaga-Rolando *et al.* (2019), Voris *et al.* (2019) and Therrien *et al.* (2021).

Mechanical Advantage of the first manual ungual: Among the analyzed manual ungual I specimens (Fig. 4), that of the early-diverging megaraptoran *Fukuiraptor kitadaniensis* (FPMN 9712211) is found to have the highest Mechanical Advantage value (0.333), followed by *Gualicho shinyae* (MPCN PV 0001), another putative early-diverging member of the clade (0.315). Another basal megaraptoran, *Phuwiangvenator yaemniyomi* (SM-PW9B-19), is also found to have nearly identical Mechanical Advantage value (0.315). It is notable that, the Mechanical Advantage values of non-megaraptoran theropods with raptorial manual ungual I, are found to be largely similar to those of early-diverging megaraptorans. *Allosaurus* sp. (NHMUK R10868 - cast) is found to have the value of 0.345, and those of *Suchomimus tenerensis* (NHMUK R16013 - cast), and *Torvosaurus tanneri* (BYU 2020) are estimated to be about 0.321 and 0.288 respectively.

In contrast, those of the later-diverging taxa tend to have lower values (Fig. 4). For example, unguals of *Megaraptor namunhuaiquii* (MCF-PVPH 79, MUCPv 341) are found to have values lower than 0.2 (0.173–0.201), and similarly lower values are found in those (AODF 604, NMV P239464) referred to *Australovenator wintonensis* (0.194–0.202).

## DISCUSSION

The results of biomechanical modeling of the dentary preserved in AODF 604 provide insights into hunting and feeding behavior in *Australovenator wintonensis*, and potentially other megaraptoran theropods. While the cranial anatomy of megaraptorans is still very poorly understood, a juvenile specimen (MUCPv 595) that is referred to *Megaraptor namunhuaiquii* indicates megaraptorans possessed an elongated skull with a shallow snout bearing small teeth (Porfiri *et al.*, 2014), and a gracile, elongated morphology of the dentary of *Australovenator wintonensis* appears to be consistent with such cranial form (Hocknull *et al.*, 2009; White *et al.*, 2015b). Additionally, despite the potential differences in the presence of mesial denticles between early-diverging members and derived forms (*e.g.*, Aranciaga-Rolando *et al.*, 2022b; Kotevski *et al.*, 2024), almost all known megaraptorid teeth share a unique combination of features such as short apicobasal length, a strongly recurved nature, and 8-shaped basal cross-section (*e.g.*, Novas *et al.*, 2008; Porfiri *et al.*, 2014; White *et al.*, 2015b; Hendrickx *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022b; Kotevski *et al.*, 2024). Although preliminary, these observations suggest craniodental anatomy of

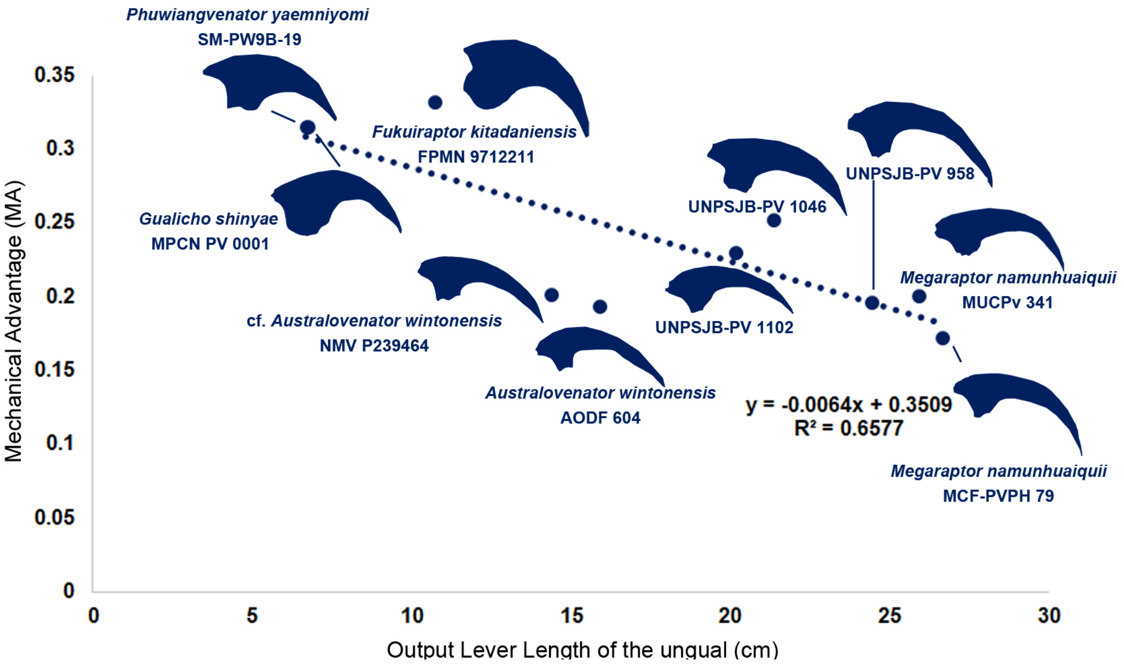

**Figure 4.** Comparison of the length of the first manual ungual and the mechanical advantage among megaraptoran theropods.

megaraptorans is broadly similar to each other, and the inferred feeding or hunting behavior of *Australovenator wintonensis* might also can be applied to a variety of other members of the lineage, if not all of them.

Both dorsoventral and mediolateral strengths along the dentary in *Australovenator wintonensis* increase towards rear of the bone, potentially suggesting the symphyseal region of this taxon is mechanically weaker than the post-symphyseal regions. Such results are broadly congruent with the simple-lever model of varanid lizards and most non-avian theropods, but different from a strengthened symphysis of tyrannosaurids (Therrien *et al.*, 2005, 2021), despite having a similar symphyseal proportion. It is assumed that tyrannosaurids, which have a mechanically strong symphyseal region, held their prey with the anterior part of their jaws, but other non-avian theropod dinosaurs that lacked a strong symphyseal region are likely to have hunted by delivering rapid, slashing bites like varanids (Therrien *et al.*, 2005, 2021). Results of this work strongly indicate *Australovenator wintonensis* and, possibly, other megaraptorans hunted in a manner that is more similar to other non-avian theropods and varanids, rather than tyrannosaurids. Considering that megaraptorans are often considered as tyrannosauroids that diverged earlier than Eutyrannosauria (*e.g.*, Novas *et al.*, 2013; Porfiri *et al.*, 2014; Cau, 2018; Naish & Cau, 2022; Kotevski *et al.*, 2024) or form a sister clade of Tyrannosauroidea (Aranciaga-Rolando *et al.*, 2022b), it appears that unique hunting and feeding behaviors of using the front of jaws to bite, capture and dismember prey that are assumed to be employed by derived tyrannosauroids (*e.g.*, Tyrannosauridae) likely occurred later in the course of the evolution in this clade. Indeed, Brusatte and Carr (2016) noted that the development of the mandibular symphysis into a bony brace that prevents dislocation between the complementary lower jaws first appeared in a grade of taxa on the line to Tyrannosauridae (*Appalachiosaurus montgomeriensis* + Tyrannosauridae), and cranial biomechanic studies using finite element analysis also showed that early-diverging tyrannosauroids have mechanically weaker skulls and lower bite forces compared to tyrannosaurids (Rowe & Snively, 2021; Johnson-Ransom *et al.*, 2024). Of course, the fact that the Zx/Zy value (1.96) of the anterior region is lower than those of the rear parts suggests that the front of the lower jaw of *Australovenator wintonensis* has a slightly rounded cross-section, which means it is slightly more resistant to torsional load. The fact that the first tooth of the lower jaw of *Australovenator wintonensis* may be smaller than the other teeth that are ziphodont, recurved and blade-like, but has a conical shape may also tentatively support this (White *et al.*, 2015b). In any case, the fact that the Zx/Zy value at the front of the jaw is high in absolute terms (close to 2.0), suggests the ability to withstand the dorsoventral load was still almost twice as important as the mediolateral load in this region. The fact that a similar phenomenon occurs in varanids and many non-tyrannosaurid theropods (Therrien *et al.*, 2005), suggests that although *Australovenator wintonensis* may have occasionally caught, held, or dismembered prey with the front of its snout, it did so to a similar extent as these animals and much less often than tyrannosaurids did.

Of note, the Zx/Zy value at the anterior region of the lower jaw (1.96) of *Australovenator wintonensis*, is close to those of captive individuals of *Varanus komodoensis* (2.00) and *Ceratosaurus nasicornis* USNM 4735 (2.01) examined by Therrien *et al.* (2005). Therrien *et al.* (2005) pointed out that *Varanus komodoensis* individuals in captivity do not experience high torsional loads at the front of the jaw since they are supplied with prey that is small or already dead and, therefore, are not required to be adapted to such loads. Based on this, Therrien *et al.* (2005) interpreted high Zx/Zy values at the symphyseal region of *Ceratosaurus nasicornis* as indicating that this taxon hunted small prey. Applying the same logic, *Australovenator wintonensis* may also have hunted primarily relatively smaller animals. This interpretation is reasonable, given that *Australovenator wintonensis* was a medium-sized theropod: while the ontogenetic status of the holotype is not clear, when the femur length (578 mm) of AODF 604 (Hocknull *et al.*, 2009) is introduced into an equation proposed by Christiansen and Fariña (2004) for estimating body mass using the corresponding measurement (log body mass (kg) = 3.22 log femur length (mm) – 6.288), the body mass of the holotype individual of *Australovenator wintonensis* is estimated to be about 403.1 kg.

The bite force (Zx/L at middentary) of *Australovenator wintonensis* is found to be close to that of other non-avian theropods with similar mandibular length (*Gorgosaurus libratus* TMP 2016.14.1) but it is unclear whether the same trend would have existed in later-diverging megaraptorans, which had significantly larger body sizes than *Australovenator wintonensis* (*e.g.*, Lamanna *et al.*, 2020; Aranciaga-Rolando *et al.*, 2022a, 2022b) and, presumably, longer mandibular length. It has been revealed that another large-bodied theropod (spinosaurid *Suchomimus tenerensis*) with a gracile, longirostrine skull had relatively and absolutely lower bite force for a theropod of its size (Therrien *et al.*, 2005, 2021) and, if large-bodied, derived megaraptorans had an elongated skull with a shallow snout that is provisionally suggested by an incomplete cranium of juvenile *Megaraptor namunhuaiquii* and the dentary of *Australovenator wintonensis* (Porfiri *et al.*, 2014; White *et al.*, 2015b), they also might have had somewhat low bite forces. Indeed, based on the features of the nasal and the contour of nasofrontal suture of known megaraptoran specimens, Kotevski *et al.* (2024) suggested the snouts of megaraptorans may have become more elongated over time, and the highly ziphodont, apicobasally short nature of known megaraptoran teeth, including those of later-diverging ones, imply they were probably incapable of withstanding high vertical or torsional loads (*e.g.*, Novas *et al.*, 2008; Porfiri *et al.*, 2014; White *et al.*, 2015b; Hendrickx *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022b; Kotevski *et al.*, 2024). Of note, the area of the dorsotemporal fossa in the frontal bone of megaraptorans is relatively large (Porfiri *et al.*, 2014; Paulina-Carabajal & Currie, 2017), and the fact that the width and depth of this bone scaled positively in this lineage (Porfiri *et al.*, 2014; Paulina-Carabajal & Coria, 2015; Coria & Currie, 2016; Paulina-Carabajal & Currie, 2017; Yun *et al.*, 2022) suggests a considerable amount of the jaw adductor musculature covered the dorsal surface of the skull in megaraptorans. However, other than this, there seems to be no clear evidence that megaraptorans had particularly strong bite forces. Based on these facts, it is assumed here that the bite force of the large, later-diverging megaraptorans may also have been similar to that of similarly-sized non-avian theropods (possibly lower), and much lower than that of tyrannosaurids. Of note, the fact that the Zx/Zy value of the anterior part of the lower jaw of *Australovenator wintonensis* revealed in this study is close to that of *Varanus komodonensis* individuals in captivity, may suggest that the mandible of megaraptorans played a minor role in prey capture. A similar idea was suggested for dromaeosaurid theropods by Therrien *et al.* (2005), based on similar values of the sampled mandibles.

However, although megaraptorans like *Australovenator wintonensis* may have had a relatively weak bite, they may have used their strong forelimbs equipped with large claws to take down larger prey. Analyses on unguals of the first manual digit indicate a decrease in Mechanical Advantage in derived megaraptorans such as *Australovenator wintonensis* and *Megaraptor namunhuaiquii* (*e.g.*, Porfiri *et al.*, 2014; Naish & Cau, 2022), compared to early diverging members like *Fukuiraptor kitadaniensis* and *Phuwiangvenator yaemniyomi* (*e.g.*, Samathi *et al.*, 2019; Aranciaga-Rolando *et al.*, 2019, 2022b). This is potentially corroborated by a high Mechanical Advantage value in *Gualicho shinyae*, another putative basal megaraptoran (*e.g.*, Apesteguía *et al.*, 2016). Indeed, low Mechanical Advantage values are also found in isolated ungual phalanges (UNPSJB-PV 958, 1046, 1102) from the Upper Cretaceous of Argentina, and their large sizes are indicative of later-diverging phylogenetic positions (*e.g.*, Lamanna *et al.*, 2020). Considering that Mechanical Advantage value is closely associated with the out-lever length and the degree of development of the flexor tubercle (Tsogtbaatar *et al.*, 2018), low values in later-diverging, large megaraptoran taxa reflect an elongated out-lever length and weakly developed flexor tubercle of their manual unguals and presumably, relatively low output force. A study of Kobayashi *et al.* (2022) found a trend of decreases in Mechanical Advantage and flexor tubercle size during evolution of therizinosaurian theropods, in which the results were corroborated by finite-element and functional-space analyses (Qin *et al.*, 2023). In that work, compact, short unguals with high Mechanical Advantage values found in early members were interpreted to be used in a generalist function, whereas elongated unguals with low Mechanical Advantage values of derived taxa represent adaptations for behaviors that are less prone to higher stresses, such as hook-and-pulling (Kobayashi *et al.*, 2022). Additionally, three large-bodied, non-megaraptoran predatory theropod taxa (*Allosaurus* sp., *Suchomimus tenerensis*, *Torvosaurus tanneri*) are found to have high MA values (0.288–0.345) in manual ungual I-2, suggesting they could have been used in a generalist fashion as well. In fact, the strongly recurved nature as well as the presence of the well-developed flexor tubercle in manual unguals of these taxa (*e.g.*, Gasca *et al.*, 2018, fig. 1) strongly recall the plesiomorphic theropod ungual morphology that is designed to withstand high forces (Senter & Parrish, 2005; Lautenschlager, 2014), which suggest their functions were not significantly deviated from grasping prey items.

The results of this work, provisionally indicate that manual ungual I-2 of the early-diverging megaraptorans were not specialized in any specific function and likely used in a generalist fashion, whereas elongate claws in later forms like *Australovenator wintonensis* and *Megaraptor namunhuaiquii* were functionally adapted for actions that involve hook-and-pull motions. Indeed, manual unguals of derived megaraptorans (*i.e.*, Megaraptoridae) greatly differ from the generalized theropod condition in being transversely narrow and bearing a sharp, longitudinal keel at the ventral surface as well as relatively small flexor tubercle, making the overall morphology of the claw sickle- or blade-like (*e.g.*, Novas *et al.*, 2013, 2016; Bell *et al.*, 2015; White *et al.*, 2015a, 2015b). Manual unguals of other theropods, including early-diverging megaraptorans such as *Fukuiraptor kitadaniensis*, do not possess a ventral keel and the ventral surface is transversely expanded and rounded (Novas *et al.*, 2016). Such unusual morphology seen in manual unguals of derived megaraptorans, could be another indicator that they were more specialized in specific functions compared to those in other theropods.

Indeed, a unique combination of features seen in megaraptoran forelimbs, provides additional evidence that they were adapted to hook-and-pull movements. The manus of megaraptorans is huge, and the unguals of the two medialmost manual digits (especially the first one) are enlarged and relatively narrow in width (*e.g.*, Benson *et al.*, 2010; White *et al.*, 2012; Novas *et al.*, 2013, 2016; Aranciaga-Rolando *et al.*, 2023). Additionally, the estimated range of motions of the forelimb bones suggest the arms of megaraptorans were very flexible, and their manual unguals were capable of hyperextension (White *et al.*, 2015a; Aranciaga-Rolando *et al.*, 2023). This suggests megaraptorans had strong forelimbs capable of complex movements, and such ability further developed over time (Aranciaga-Rolando *et al.*, 2023). Based on such observations, it has been suggested the forelimbs of megaraptorans played a key role in predation, by grasping prey and pulling it close to the chest to make it easy to dismember with their jaws (White *et al.*, 2015a; Aranciaga-Rolando *et al.*, 2023). Furthermore, the humerus of megaraptorans is robust and bowed laterally (White *et al.*, 2012), and the ulna has a well-developed large olecranon process that is transversely compressed and bladelike (Hocknull *et al.*, 2009; Novas *et al.*, 2013, 2016). In these respects, they are similar to those in spinosaurids like *Baryonyx walkeri* and *Suchomimus tenerensis* (Smith *et al.*, 2008). The radius of megaraptorans is short and robust, and bears an expanded triangular cranial process in the proximal part that is similar to spinosaurids as well (Smith *et al.*, 2008). The manual unguals of megaraptorans, especially the one in the first digit, were hypertrophied and flexible as aforementioned (White *et al.*, 2012, 2015a; Novas *et al.*, 2013, 2016; Bell *et al.*, 2015; Aranciaga-Rolando *et al.*, 2023). This suite of characters that is partly converged with spinosaurids (Smith *et al.*, 2008), is reminiscent to animals that engage in hook-and-pull movements of the forelimbs (*e.g.*, Hildebrand, 1985; Senter, 2005; Hone & Holtz, 2017; Gasca *et al.*, 2018). Indeed, the spinosaurid theropods, which are known to have similar forelimb anatomy with megaraptorans (Smith *et al.*, 2008), were recently suggested to have had a similar function of the forelimbs (Hone & Holtz, 2017; Gasca *et al.*, 2018). Hook-and-pull movements of the forelimbs could have been involved in a variety of situations, such as lifting prey from the ground, breaking up carcasses, or grasping and pulling prey items (Gasca *et al.*, 2018). The enlarged manual unguals of megaraptorans are transversely compressed (Smith *et al.*, 2008; Novas *et al.*, 2013), and by hooking such claws into a live animal and pulling them, they may have been able to cause fatal injuries through tearing. Indeed, a blade-like, sharp ventral margin formed by a ventral keel of megaraptorid manual unguals (*e.g.*, Novas *et al.*, 2013, 2016) may have been advantageous in tearing or slicing through a flesh of an animal. In such ways, megaraptorans may have been able to prey on large animals, despite having relatively weak jaws. It should be noted, however, that at least one study suggested that the ventral surface of the keratin sheath of the claw may not correspond to the morphology of that of the ungual bone (Manning *et al.*, 2006; but see Fowler *et al.*, 2011 for an alternative opinion), so the possibility that the ventral surface of the megaraptoran manual claw was not that sharp, cannot be dismissed. Therefore, these potential paleobiological interpretations are largely hypothetical and should be tested through more detailed biomechanical analyses such as Finite Element Analysis or robotic experiment on a flesh substrate, similar to those performed for other theropod manual unguals (*e.g.*, Manning *et al.*, 2006; Lautenschlager, 2014; Qin *et al.*, 2023). Such analyses may shed further light on the functional capabilities of the unusual forelimb anatomy of megaraptorans, and what that implies about hunting or feeding behavior of this theropod lineage.

## CONCLUSIONS

Mandibular force profiles of an Australian megaraptoran taxon *Australovenator wintonensis* suggest the lower jaw of this theropod behaved as a simple lever, and bending strengths in both dorsoventral and mediolateral planes decrease towards the front. Such mandibular morphology is broadly congruent with those of modern varanids and other non-avian theropods excepting tyrannosaurids, and suggests *Australovenator wintonensis* was unlikely able to produce a high bite force, and the lower jaw of this taxon was suited for delivering quick, slashing bites. Biomechanical modeling of the manual unguals I-2 suggests a decrease in Mechanical Advantage in later-diverging megaraptorans, which indicates the claws became more adapted to hook-and-pull function among derived taxa. Perhaps, derived megaraptorans were capable of hunt down large-bodied animals through causing fatal injuries by hooking claws into a live prey and pulling them, tearing through a flesh.

Supplementary Material. Table S1 is available at the Spanish Journal of Palaeontology website (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution.

**Table S1.** Mandibular dimensions and properties of *Australovenator wintonensis* (AODF 604) and other non-avian theropods used in this work. Data of other non-avian theropods are from and after Therrien *et al.* (2021).

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