Mesozoic 001 (4): 459–468
https://www.mapress.com/mz/

Article

ISSN 3021-1859 (print edition)
MESOZOIC
ISSN 3021-1867 (online edition)

https://doi.org/10.11646/mesozoic.1.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:95AC5962-CB0F-4AC9-885B-1A1851B989F4

Mandibular biomechanics of *Acheroraptor temertyorum* (Theropoda: Dromaeosauridae) with implications for the feeding ecology and behaviour

CHAN-GYU YUN
Independent Researcher, Incheon 21974, Republic of Korea
changyu1015@naver.com; https://orcid.org/0000-0002-2158-7918

Abstract

Acheroraptor temertyorum is a dromaeosaurid theropod, probably a saurornitholestine, found in the upper Maastrichtian Hell Creek Formation of Montana. This enigmatic dromaeosaurid is known from only a partial maxilla and dentary, as well as referred isolated teeth, making even the general aspects of its palaeobiology largely elusive. In this work, beam theory is applied to the lower jaw of *Acheroraptor temertyorum* to document the biomechanical properties of the mandible of this taxon and to infer the feeding mechanism of this dinosaur. This work suggests the lower jaw of *Acheroraptor temertyorum* is mainly adapted to produce rapid, slashing bites, as previously inferred for other dromaeosaurids. Intriguingly, despite having a closer phylogenetic affinity with *Saurornitholestes langstoni*, overall biomechanical properties of the lower jaw of *Acheroraptor temertyorum* are found to be weaker than the former taxon, but rather comparable to Asian velociraptorines. Such results may indicate *Acheroraptor temertyorum* preyed on smaller animals compared to other saurornitholestines, and suggest diets or predation methods of saurornitholestine dromaeosaurids might have been more diverse than previously assumed.

Keywords: Dinosauria, Theropoda, Dromaeosauridae, Saurornitholestinae, Velociraptorinae, beam theory, mandible

Introduction

In 2009, a group of private fossil collectors excavated an almost complete maxilla of a dromaeosaurid theropod from a fossil locality in Garfield County of Montana, USA that corresponds to the upper part of the Hell Creek Formation (uppermost Maastrichtian). Several years later, an isolated dentary which probably belongs to the same individual as the maxilla was recovered in the same region by one of the original collectors of the maxilla. These specimens were latterly purchased by Royal Ontario Museum, and the reference numbers ROM 63777 and ROM 63778 were given to the maxilla and dentary, respectively. In 2013, a new dromaeosaurid taxon, *Acheroraptor temertyorum* was erected based on these materials, and ROM 63777, the maxilla, was designated as the holotype of this taxon (Evans *et al*., 2013). Initially, *Acheroraptor temertyorum* was considered a member of Velociraptorinae, a group of Asian eudromaeosaurians mainly based on an elongated anterior ramus of the maxilla (Evans *et al*., 2013; Jasinski *et al*., 2020), but subsequent studies have recovered this taxon as North American saurornitholestine, and supposed similarities with velociraptorines were regarded as convergences (Powers *et al*., 2020, 2022; Jasinski *et al*., 2023). Nevertheless, being one of the geologically latest occurring dromaeosaurids in the world, the recognition of *Acheroraptor temertyorum* has contributed significantly to our understanding of dromaeosaurid theropods. For example, isolated dromaeosaurid teeth from the upper Maastrichtian Lance and Hell Creek formations were often referred to earlier-occurring North American taxa (*e.g.*, *Dromaeosaurus albertensis*, *Saurornitholestes langstoni*) but it turned out that most, if not all, of them probably belong to *Acheroraptor temertyorum* (Evans *et al*., 2013). Such reinterpretations may indicate the diversity of dromaeosaurids from the late Maastrichtian of western North America might have been lower than those of the earlier ages, such as the Campanian (Evans *et al*., 2013). Despite such scientific importance of this taxon, however, the general aspects of the paleobiology of *Acheroraptor temertyorum*, such as the paleoecology, are still poorly understood, which is owing to the fragmentary nature of the holotype individual. In fact, despite a recent increase in scientific interest (*e.g.*, Roach & Brinkman, 2007; Senter, 2009; Jasinski, 2015; Gianechini *et al*., 2020; King *et al*., 2020; Jasinski *et al*., 2023), much information regarding the predatory ecology and the

Submitted: 12 Jul. 2024; accepted by D.-Y. Huang: 14 Nov. 2024; published: 23 Dec. 2024

feeding behaviour of dromaeosaurids as a whole, is still largely unknown mainly because of the rarity of non-dental remains that is caused by size-related taphonomic or collecting bias (Evans *et al*., 2013; Longrich & Currie, 2009; Poust *et al*., 2020). This is an issue, especially given that dromaeosaurids were small-to-medium sized hypercarnivorous animals that are very closely related to modern birds and, therefore, are crucial for understanding the macroevolutionary history of the feathered dinosaurs, as well as terrestrial ecosystems of the Mesozoic area (*e.g*., Norell & Makovicky, 2004; Fowler *et al*., 2011; Turner *et al*., 2012; Bishop, 2019).

The principles of beam theory, which assume the mandible as a solid beam that undergoes loads during biting of food ingestion, are able to derive mandibular force profiles that can provide information related to the hunting and feeding behaviour of a predator (*e.g*., Therrien *et al*., 2005, 2021; Jasinski, 2011; Monfroy, 2017; Yun, 2024). The biomechanical modelling of the mandible through the principles of beam theory is advantageous in being relatively simple and efficient, as it requires only several external dimensions of the lower jaw and therefore, does not require complex, expensive and time-consuming computer programs that are used in other biomechanical methods such as finite element analyses (*e.g*., Therrien *et al*., 2021). Furthermore, the results of beam theory modelling are largely consistent with those of other more complex methods (*e.g*., FEA or finite element analysis) and potentially provide more accurate bite force estimates than those yielded from jaw muscle architecture measurements in some cases (Therrien *et al*., 2016, 2021). Based on such advantages, the beam theory method has been applied to a variety of theropod dinosaurs, including dromaeosaurids (*e.g*., Therrien *et al*., 2005, 2021; Jasinski, 2011; Monfroy, 2017; Yun, 2024). Therrien *et al*. (2005) derived mandibular force profiles of four dromaeosaurid taxa (*Deinonychus antirrhopus*—YPM 41147, *Dromaeosaurus albertensis*—AMNH 5356, *Saurornitholestes langstoni*—TMP 88.121.39, *Velociraptor mongoliensis*—Utah Geological Survey cast of privately owned specimen) and found, while they were only capable of delivering weak and fast slashing bites, the bite force of *Dromaeosaurus albertensis* was relatively, and absolutely, higher compared to others. Monfroy (2017) reached a largely similar conclusion, but only two dromaeosaurid taxa were examined in this work (*Dromaeosaurus albertensis*, *Saurornitholestes langstoni*).

In order to investigate feeding and predatory behaviour of this scientifically important but largely unknown dromaeosaurid taxon, mandibular force profiles of *Acheroraptor temertyorum* are derived in this work, through a beam theory technique utilized by Therrien *et al*. (2005). The results are compared with those of other non-avian theropods including dromaeosaurids, as well as modern *Varanus komodoensis*, so that the probable feeding and hunting behaviours for *Acheroraptor temertyorum* can be determined.

Institutional abbreviations: AMNH, American Museum of Natural History, New York City, New York, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Material and methods

Since the principles of beam theory are utilized to derive the mandibular strength profiles of *Acheroraptor temertyorum* in this work, a brief summary of this method is presented here. A mandible of an animal can be modelled as a solid beam undergoing bending loads during biting, and therefore the bite force applied at any given region along the lower jaw should be proportional to external dimensions at any location (Therrien, 2005; Therrien *et al*., 2005). Thus, the patterns of variation in external dimensions of the mandible reflect the adaptation of the jaw to habitual loads, which are related to the feeding and hunting behaviours (Therrien, 2005; Therrien *et al*., 2005, 2016). While the dentaries can be partly hollow in some cases, the solid mandible model has been demonstrated to accurately estimate the pattern of change in biomechanical properties along the lower jaw (Therrien *et al*., 2016, 2021).

Measurements were taken from a high-quality cast of ROM 63778 using a digital caliper. Of note, post-dentary bones of the mandible are not preserved in ROM 63778, but Powers *et al*., (2022, Fig. 20) provided rigorous reconstructions of the cranium and mandible of the holotype individual of *Acheroraptor temertyorum* using phylogenetically-close relatives like *Saurornitholestes langstoni*, and this figure was used as a basis for several measurements (*e.g*., length of the mandible, distance between the jaw articulation and each landmark) using the program ImageJ (Schneider *et al*., 2012). While the use of the reconstruction suggests that the results are somewhat preliminary, it remains the best option available. Given that the height/length ratio of the maxilla in *Acheroraptor temertyorum* closely resembles that of *Saurornitholestes langstoni* (Powers *et al*., 2020, 2022), it is likely that the proportion of the mandible also did not differ significantly, making this approach reasonably justified.

The measurements used in this work (Fig. 1, Table 1) follow the protocols of previous studies (*i.e*., Therrien *et al*., 2005, 2021), and are as follows: (1) depth of the dentary at 2nd alveolus; (2) depth of the dentary at 9th

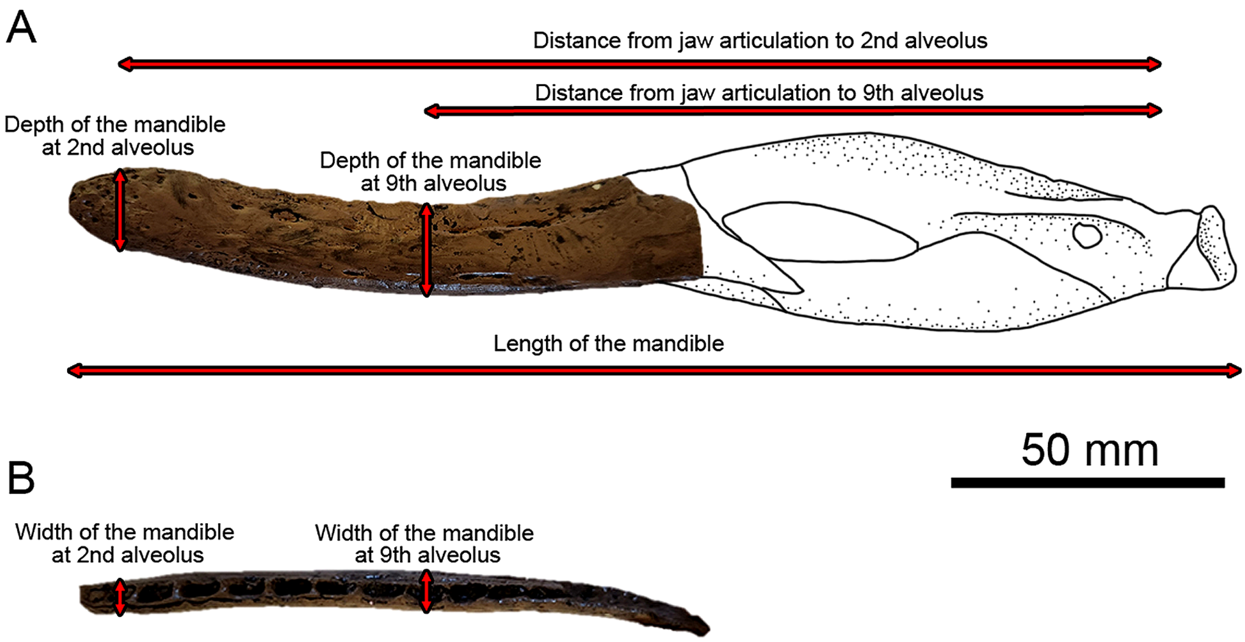

FIGURE 1. Measurement parameters used in this study, with the mandible of *Acheroraptor temertyorum* (cast of ROM 63778) as an example. **A**, Mandibular depths and distances measured on the lateral side of the bone. **B**, Mandibular widths measured on the dorsal side of the bone. Postdentary region is reconstructed after Powers *et al*. (2022, Fig. 20).

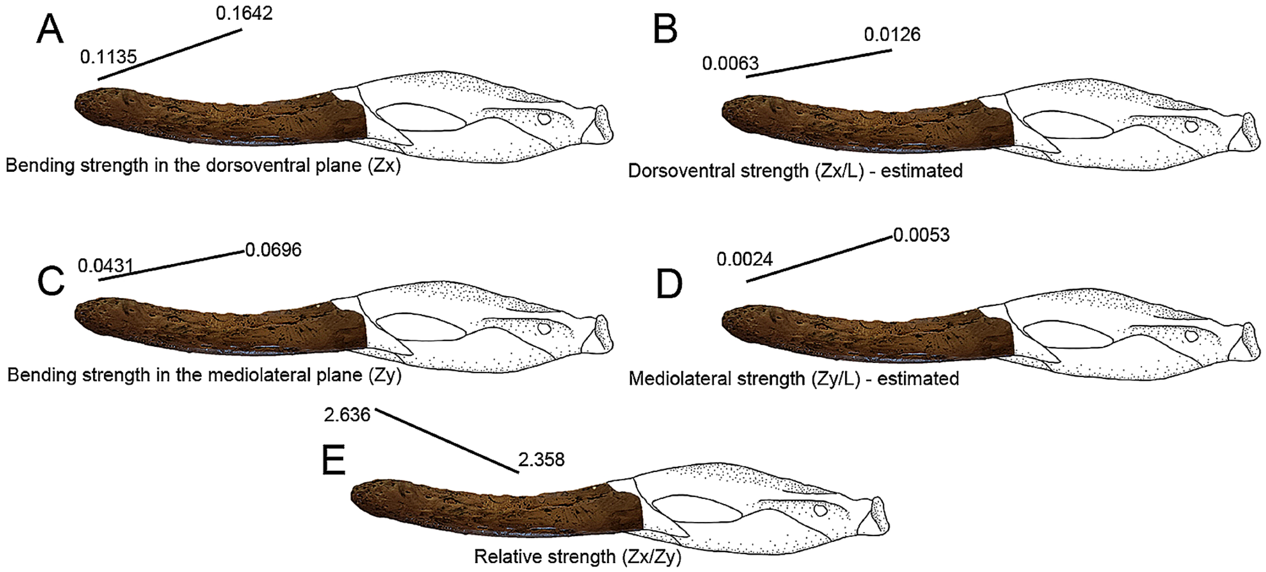

FIGURE 2. Mandibular force profiles of *Acheroraptor temertyorum* (cast of ROM 63778). Values are presented for the 2nd and 9th alveoli. **A**, Zx values of ROM 63778. **B**, Zx/L values of ROM 63778. **C**, Zy values of ROM 63778. **D**, Zy/L values of ROM 63778. **E**, Zx/Zy values of ROM 63778. Zx/L and Zy/L values are estimated after the reconstruction of Powers *et al*. (2022, fig. 20).

alveolus (middentary); (3) width between the lateral margin of the 2nd alveolus and the most posterior point of the mandibular symphysis; (4) width of the dentary at 9th alveolus; (5) distance from 2nd alveolus to the jaw articulation; (6) distance from 9th alveolus to the jaw articulation; and (7) total length of the mandible.

The aforementioned dimensions were used to generate a dataset of biomechanical properties using Microsoft Excel (Table 1), following protocols of Therrien *et al.* (2005, 2021). Each component of the biomechanical property dataset are as follows: (1) Zx = π*(dentary width/2)*(dentary depth/2)^2/4, a bending

TABLE 1. Mandibular dimensions and properties of *Acheroraptor temertyorum* (ROM 63778).

Depth at 2nd tooth (cm)	Width at 2nd tooth (cm)	Zx (2nd tooth)	Zy (2nd tooth)	Zx/L (2nd tooth)	Zy/L (2nd tooth)	Zx/Zy (2nd tooth)	Distance to articulation (cm)	Length of mandible (cm)
1.45	0.55	0.113527	0.043062	0.006349	0.002408	2.636364	17.882	20.533
Depth at middentary (cm)	Width at middentary (cm)	Zx (middentary)	Zy (middentary)	Zx/L (middentary)	Zy/L (middentary)	Zx/Zy (middentary)	Distance to articulation (cm)	
1.58	0.67	0.164206	0.069632	0.012583	0.005336	2.358209	13.05	

strength in the dorsoventral plane (=labiolingual axis); (2) $Zy = \pi*(\text{dentary depth}/2)*(\text{dentary width}/2)^2 /4$, a bending strength in the labiolingual plane (=dorsoventral axis); (3) Zx/Zy, a relative strength of the mandible; (4) Zx/L (L= a distance between the landmark and the jaw articulation), a dorsoventral strength of the mandible; and (5) Zy/L, a mediolateral strength of the mandible. These results are compared with those of Therrien *et al*. (2005, 2021). The mandibular dimensions and force properties of other theropods, including dromaeosaurids, are obtained and derived from the dataset of Therrien *et al*. (2021).

Results

Hypotheses

The following hypotheses are tested through the results of this work:

Hypothesis 1: A study of Therrien *et al*. (2005) found, excepting for absolute mandibular force values and variations in slope of mandibular properties, the mandibular force profiles of dromaeosaurid taxa they examined (*Deinonychus antirrhopus*, *Dromaeosaurus albertensis*, *Saurornitholestes langstoni*, *Velociraptor mongoliensis*) are largely similar to each other, and the mandible behaved as a simple lever exhibiting linear decrease in dorsoventral and labiolingual forces from the back to the front. As the overall anatomy of ROM 63778 is largely consistent with other dromaeosaurids such as *Velociraptor mongoliensis* (Evans *et al*., 2013), it is expected here that *Acheroraptor temertyorum* will show a similar pattern in its mandibular force profile.

Hypothesis 2: Therrien *et al*. (2005) demonstrated that the dorsoventral and labiolingual force profiles of *Dromaeosaurus albertensis* are highest among the four dromaeosaurid taxa they examined, in absolute terms. Such results indicate that *Dromaeosaurus albertensis* was capable of delivering a stronger bite than other dromaeosaurids, and the lower jaw of this taxon is more adapted to sustain greater stresses as well. The same study also found mandibular force profiles of *Saurornitholestes langstoni* are fairly lower compared to *Dromaeosaurus albertensis* (Therrien *et al*., 2005), in which the former has a less robust skull compared to the latter (*e.g*., Currie & Evans, 2020; Powers *et al*., 2020, 2022). Being a probable saurornitholestine (Powers *et al*., 2020, 2022), it is expected that the mandibular force properties of *Acheroraptor temertyorum* would be lower than those of *Dromaeosaurus albertensis* as well.

Hypothesis 3: Currie & Evans (2020) found the snout of *Saurornitholestes langstoni* is shorter and deeper compared to most Asian eudromaeosaurians such as *Velociraptor mongoliensis*, and such morphology may suggest that this taxon was able to withstand greater stresses during biting, and was more well-suited to prey on relatively larger animals compared to Asian velociraptorines (*e.g*., Hone *et al*., 2023; Tse *et al*., 2024). Indeed, Therrien *et al*. (2005) found the mandible of *Saurornitholestes langstoni* has slightly higher values in its force profiles in the anterior and middentary regions compared to *Velociraptor mongoliensis*. The height/length ratio of the maxilla (ROM 63777) of *Acheroraptor temertyorum* is largely similar to that of *Saurornitholestes langstoni* (Powers *et al*., 2020, 2022), suggesting the overall proportions of the snout of both taxa were similar as well. Therefore, it is expected here that the mandibular properties of *Acheroraptor temertyorum* will be similar to *Saurornitholestes langstoni*, and higher than *Velociraptor mongoliensis*.

In the case of the dorsoventral strength (Zx) profiles, the Zx value is higher at middentary (0.1642) than at the 2nd alveolus (0.1135) in *Acheroraptor temertyorum* (Fig. 2A). As such, the estimated bending force (Zx/L) value (Fig. 2B) is also higher at middentary (0.0126, Log Zx/L = -1.90) than in the 2nd alveolus region (0.0063, Log Zx/L = -2.20). When compared with other dromaeosaurids, the Zx value at the middentary (0.1642) of *Acheroraptor temertyorum* is fairly close to that of *Velociraptor mongoliensis* (0.1593), but significantly lower than *Deinonychus antirrhopus* (0.5447), *Dromaeosaurus albertensis* (0.5768), and *Saurornitholestes langstoni*

(0.2354). The bending strength profiles in the labiolingual plane (Zy) are found to have a similar trend (Fig. 2C), as the Zy value at the middentary (0.0696) is higher than at the 2nd alveolus (0.0431). As such, the estimated bending force (Zy/L, Fig. 2D) at the 2nd alveolus (0.0024, Log Zy/L = -2.62) is lower than at the middentary (0.0053, Log Zy/L = -2.27). When compared with other dromaeosaurids, the Zy value in the middentary region of *Acheroraptor temertyorum* (0.0696) is higher than that of *Velociraptor mongoliensis* (0.0483), but still far lower compared to *Deinonychus antirrhopus* (0.1844), *Dromaeosaurus albertensis* (0.2451), and *Saurornitholestes langstoni* (0.0968). In the case of the relative strength of the mandible (Zx/Zy), the Zx/Zy value at the 2nd alveolus (about 2.64) is slightly higher than at middentary (about 2.36), suggesting the dentary of *Acheroraptor temertyorum* is significantly deeper than wide (more than 2 times) in both regions (Fig. 2E). Such high values of Zx/Zy, are similar to those of modern varanids (*e.g.*, *Varanus komodoensis*) and consistent with conditions seen in other dromaeosaurids (Therrien *et al*., 2005).

Previous works have demonstrated that the Zx/L value at the middentary can be used as a proxy for bite force in theropods (Therrien *et al*., 2005, 2021), as this region is close to the position of the most pronounced maxillary tooth where the bite force is usually estimated in non-avian theropods and crocodylians (*e.g.*, Erickson *et al*., 2003, 2004, 2012; Rayfield, 2004; Gignac & Erickson, 2015, 2017). The estimated Zx/L value at the middentary (0.0126) of *Acheroraptor temertyorum* is significantly lower than those of non-dromaeosaurid theropods, which is expected given the relatively, and absolutely, small body size of dromaeosaurids (Fig. 3A). When compared with other dromaeosaurids, the value of *Acheroraptor temertyorum* is most similar to that of *Velociraptor mongoliensis* (0.0128), but significantly lower than other dromaeosaurids such as *Deinonychus antirrhopus* and *Saurornitholestes langstoni* (Fig. 3B). Indeed, the estimated Zx/L value at the middentary of *Acheroraptor temertyorum* is only 66% that of *Saurornitholestes langstoni* (0.0190), 50% that of *Deinonychus antirrhopus* (0.0251) and only 29% of *Dromaeosaurus albertensis* (0.0442).

Discussion

The results of this work suggest the lower jaw properties

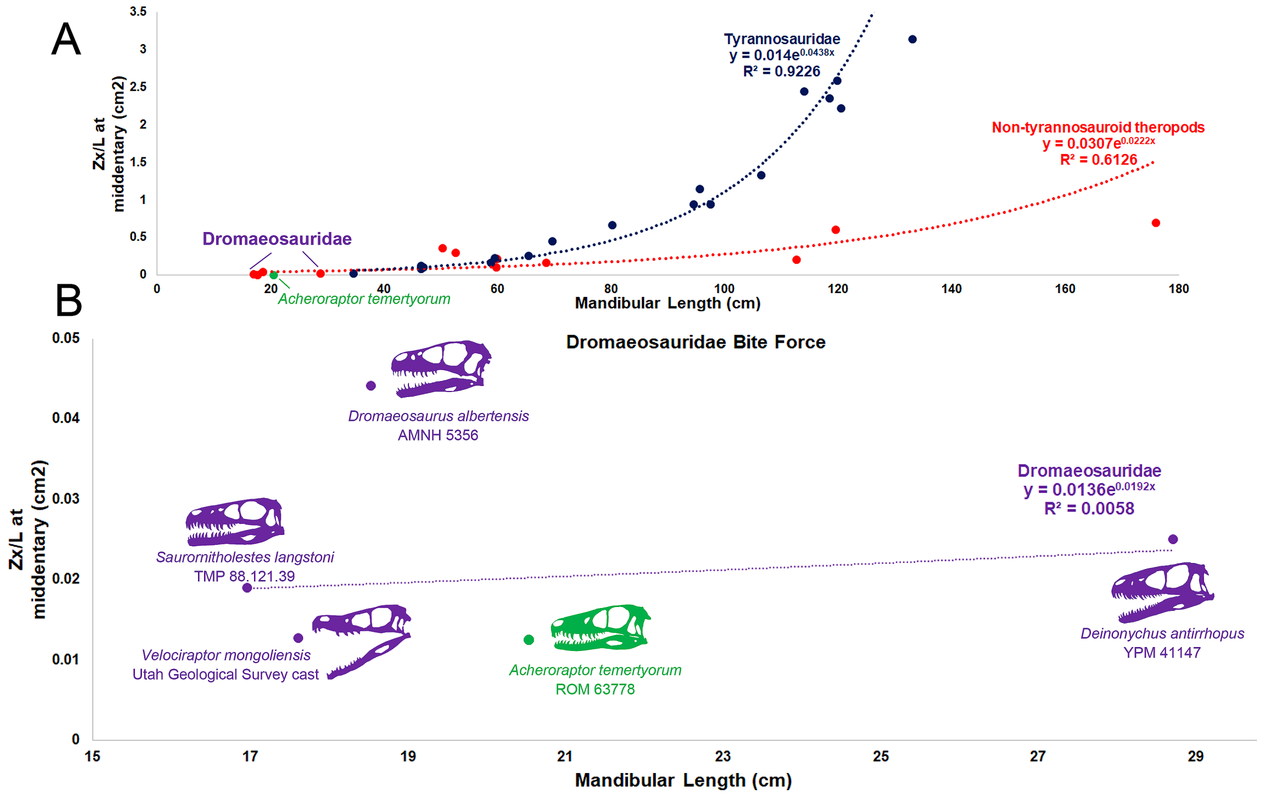

FIGURE 3. Bite force estimations in theropods. **A**, Comparison of middentary Zx/L values between non-avian theropods. Bite force estimations are considerably lower in dromaeosaurids than in other non-avian theropods. **B**, Bite force estimates in dromaeosaurid theropods, using Zx/L at the middentary region as a proxy. Data for taxa other than *Acheroraptor temertyorum* are derived from Therrien *et al*. (2021). Skull silhouettes are after Norell & Makovicky (2004), Currie & Evans (2020), Therrien *et al*. (2021) and Powers *et al*. (2022).

in *Acheroraptor temertyorum* decrease linearly toward the anterior part, indicating the mandible of this taxon behaved as a simple lever. Such results are broadly consistent with those of other dromaeosaurids (Therrien *et al*., 2005) and imply *Acheroraptor temertyorum* was also suited to deliver weak, but fast slashing bites like other dromaeosaurids in a manner similar to those of varanids or other small-bodied theropods such as *Coelophysis bauri* (Jasinski, 2011). Additionally, mechanically-weaker values of the anterior region of the dentary in *Acheroraptor temertyorum* indicate the front of the jaw in this taxon is unsuited to hold onto struggling prey items and likely was not used in such a manner, as inferred in other dromaeosaurids (Therrien *et al*., 2005). Therefore, Hypothesis 1 is supported by the results. It is notable, however, that simple-lever force profiles are prevalent among non-tyrannosaurid theropods (Therrien *et al*., 2005, 2021). Therrien *et al*. (2005) interpreted simple-lever force profiles of the lower jaw of dromaeosaurids, as well as a similar value of Zx/Zy at the anterior region with those of captive *Varanus komodoensis* individuals, as suggestive of these theropods delivering slashing bites to relatively small animals without holding onto them, and the mandible being used less frequently than the manus and pedes during prey capture. While no definitive postcranial material is currently known in *Acheroraptor temertyorum* (Evans *et al*., 2013), the force properties of the lower jaw suggest the predatory behaviour of this taxon would have been no different. Additionally, all of the derived force profiles for ROM 63778 are significantly lower than those of *Dromaeosaurus albertensis*, suggesting the lower jaw of *Acheroraptor temertyorum* is mechanically weaker compared to *Dromaeosaurus albertensis*. Therefore, Hypothesis 2 is supported as well. Therrien *et al*. (2005) interpreted the mechanically-stronger nature of the mandible in *Dromaeosaurus albertensis*, compared to other dromaeosaurids, as indicating this taxon was capable of delivering more powerful slashing bites and may have relied more on its jaws in hunting than its relatives, possibly allowing it to prey on larger animals. In contrast, the weaker nature of the mandible of *Acheroraptor temertyorum* would suggest the lower jaw of this taxon went through less bending force during biting compared to *Dromaeosaurus albertensis*, and probably less suited to hunt down relatively large prey items. Perhaps the jaws of *Acheroraptor temertyorum* were primarily used just for dismemberment after grasping and immobilizing prey through its pedes with hypertrophied sickle-claw on digit II or its forelimbs, as suggested for other dromaeosaurids (Therrien *et al*., 2005; Fowler *et al*., 2011).

Perhaps the most important conclusion arising from these results is that, despite having a relatively tall and short maxilla that is proportionally similar to that of *Saurornitholestes langstoni* (Powers *et al*., 2020, 2022), the mandibular biomechanical properties of *Acheroraptor temertyorum* are found to be lower than those of *Saurornitholestes langstoni* and, instead, rather comparable to those of *Velociraptor mongoliensis*. Indeed, the estimated Zx/L value at the middentary region of *Acheroraptor temertyorum* (0.0126) is nearly identical to that of *Velociraptor mongoliensis* (0.0128) but strikingly lower compared to other dromaeosaurids examined by Therrien *et al*. (2005, 2021), although this should be treated with caution as this value for *Acheroraptor temertyorum* is mainly based on a reconstruction (Powers *et al*., 2022, fig. 20). Such results, although preliminary, indicate *Acheroraptor temertyorum* and *Velociraptor mongoliensis* shared comparably lower bite forces among eudromaeosaurians. Additionally, it provisionally suggests the differences in overall morphology of the skull in eudromaeosaurians that are reflected by those in proportions of the maxilla (Powers *et al*., 2020, 2022), may not be solely related to bite force, but also could reflect phylogenetic differences or disparities in feeding behavior, as recently suggested for albertosaurine and tyrannosaurine theropods (Therrien *et al*., 2021). Of note, the Zy value at the middentary region of *Acheroraptor temertyorum* is found to be higher than *Velociraptor mongoliensis* but lower than *Saurornitholestes langstoni*, which may indicate the capability for withstanding torsional stresses and labiolingual loads at this region of the lower jaw in *Acheroraptor temertyorum* was intermediate between *Velociraptor mongoliensis* and *Saurornitholestes langstoni*.

Nevertheless, the results revealed here largely contradict Hypothesis 3, and the inferred mechanically-weak nature of the lower jaw of *Acheroraptor temertyorum* is likely to be real given that the absolute raw dimensions at the middentary of ROM 63778 are lower than those of *Deinonychus antirrhopus*, *Dromaeosaurus altertensis* and *Saurornitholestes langstoni*, especially the depth (after Therrien *et al*., 2021). Similar values of biomechanical properties between the lower jaws of *Acheroraptor temertyorum* and *Velociraptor mongoliensis* may indicate the feeding and hunting behaviours of the former could have been similar to velociraptorines rather than its phylogenetically-close relatives (*e.g*., *Sauornitholestes langstoni*). Additional lines of evidence that provisionally support such convergences come from the dental anatomy of *Acheroraptor temertyorum*: denticles on the distal carinae of the maxillary teeth of ROM 63777 are rounded and only very slightly apically oriented, differing from the strongly-hooked denticles of other saurornitholestines (*e.g*., *Atrociraptor marshalli*, *Saurornitholestes langstoni*) but rather similar to other eudromaeosaurians including velociraptorines (Evans *et al*., 2013; Hendrickx *et al*., 2019). According to Fowler *et al*. (2011), hooked denticles on the distal carina enhance the effectiveness of the jaws'

FIGURE 4. Life restoration of *Acheroraptor temertyorum*, depicted as employing the Raptorial Prey Restraint (RPR) hunting method on the smaller mammal *Didelphodon vorax*. The sculptures are made by Boban Filipović and currently housed at the Badlands Dinosaur Museum in Dickinson, North Dakota, USA with the commission of Dr Denver Fowler. The picture is taken by Boban Filipović (who retains the copyright on this image), used with permission.

grip on the prey, and the lack of such a feature, combined with the mechanically-weaker nature of the lower jaw, may indicate the jaws of *Acheroraptor temertyorum* were poorly suited for subduing prey items even for a dromaeosaurid, and the same likely applies to velociraptorines as well. Although dromaeosaurids may not have used their jaws very actively in hunting overall (Therrien *et al*., 2005), *Acheroraptor temertyorum* might have used its jaws even less compared to other saurornitholestines. Perhaps, this taxon frequently utilized the Raptor Prey Restraint (RPR) method by grasping a prey with pedes, bearing a hypertrophied claw on the second pedal digit (Fowler *et al*., 2011) to a degree similar to velociraptorines (Fig. 4). Based on the deep nature of the maxilla, Powers *et al*. (2020) suggested that saurornitholestines, such as *Atrociraptor marshalli* and *Saurornitholestes langstoni*, would have been able to hunt relatively large items more efficiently compared to velociraptorines, and might have had similar lifestyles with modern canids with short, deep snouts or moderately elongated ones (Slater *et al*., 2009). Indeed, *Acheroraptor temertyorum* possesses an elongated anterior ramus of the maxilla that superficially resembles those of velociraptorines, which may also suggest that the entire snout of this taxon was likely elongated as well (Evans *et al*., 2013; Powers *et al*., 2020, 2022). Such an elongated snout is suited for delivering fast, slashing bites that are advantageous in hunting small animals (*e.g*., Van Valkenburgh & Ruff, 1987; Henderson, 1998; Slater *et al*., 2009; Powers *et al*., 2020, 2022; Tse *et al*., 2024). Perhaps the ecology of *Acheroraptor temertyorum* might have been similar to those of some modern cerdocyonin canids such as maned wolf (*Chrysocyon brachyurus*), which dwells in tropical or subtropical environments (*e.g*., Juarez & Marinho-Filho, 2002), has an elongated snout, and primarily preys on small vertebrates (*e.g*., Slater *et al*., 2009; Segura *et al*., 2021).

If the aforementioned hypothesis that *Acheroraptor temertyorum* was more adapted to hunting different prey items or relied more on different hunting techniques from other saurornitholestines is true, exactly what factors have contributed to such diversification remains unclear. Perhaps it could have been related to niche partitioning given that multiple other carnivorous theropods with comparable body sizes to *Acheroraptor temertyorum* occur in the Hell Creek Formation (*e.g.*, juvenile tyrannosaurids, troodontids, *Richardoestesia* spp.) but the same is true for other saurornitholestines as well (*e.g.*, Longrich & Currie, 2009; Holtz, 2021). Perhaps, future discoveries of more complete cranial material of small-bodied theropods from the Campanian-Maastrichtian strata of North America and evaluating their mechanical differences through beam theory modeling or finite element analyses may shed additional light on this issue.

Acknowledgements

The author thanks Boban Filipović, who allowed to use the picture of his beautiful sculptures as a figure of this paper. Discussions regarding the palaeobiology of *Acheroraptor temertyorum* with Mark Powers were also helpful, and the author is grateful for that. This manuscript benefited from insightful comments from two anonymous reviewers, and from the editor Diying Huang (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China).

References

Bishop, P.J. (2019) Testing the function of dromaeosaurid (Dinosauria, Theropoda) 'sickle claws' through musculoskeletal modelling and optimization. *PeerJ*, 7, e7577. https://doi.org/10.7717/peerj.7577

Currie, P.J. & Evans, D.C. (2020) Cranial anatomy of new specimens of *Saurornitholestes langstoni* (Dinosauria, Theropoda, Dromaeosauridae) from the Dinosaur Park Formation (Campanian) of Alberta. *The Anatomical Record*, 303, 691–715. https://doi.org/10.1002/ar.24241

Erickson, G.M., Gignac, P.M., Steppan, S.J., Lappin, A.K., Vliet, K.A., Brueggen, J.D., Inouye, B.D., Kledzik, D. & Webb, G.J.W. (2012) Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. *PLoS ONE*, 7, e31781. https://doi.org/10.1371/journal.pone.0031781

Erickson, G.M., Lappin, A.K. & Vliet, K.A. (2003) The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology*, 260, 317–327. https://doi.org/10.1017/S0952836903003819

Erickson, G.M., Lappin, A.K., Parker, T. & Vliet, K.A. (2004) Comparison of bite-force performance between long-term captive and wild American alligators (*Alligator missippiensis*). *Journal of Zoology*, 262, 21–28. https://doi.org/10.1017/S0952836903004400

Evans, D.C., Larson, D.W. & Currie, P.J. (2013) A new dromaeosaurid (Dinosauria: Theropoda) with Asian affinities from the latest Cretaceous of North America. *Naturwissenschaften*, 100, 1041–1049. https://doi.org/10.1007/s00114-013-1107-5.

Fowler, D.W., Freedman, E.A., Scannella, J.B. & Kambic, R.E. (2011) The Predatory Ecology of *Deinonychus* and the Origin of Flapping in Birds. *PLoS ONE*, 6, e28964. https://doi.org/10.1371/journal.pone.0028964

Gianechini, F.A., Ercoli, M.D. & Díaz-MartDínez, I. (2020) Differential locomotor and predatory strategies of Gondwanan and derived Laurasian dromaeosaurids (Dinosauria, Theropoda, Paraves): inferences from morphometric and comparative anatomical studies. *Journal of Anatomy*, 236, 772–797. https://doi.org/10.1111/joa.13153

Gignac, P.M. & Erickson, G.M. (2015) Ontogenetic changes in dental form and tooth pressures facilitate developmental niche shifts in American alligators. *Journal of Zoology*, 295, 132–142. https://doi.org/10.1111/jzo.12187

Gignac, P.M. & Erickson, G.M. (2017) The biomechanics behind extreme osteophagy in *Tyrannosaurus rex*. *Scientific Reports*, 7, 2012. https://doi.org/10.1038/s41598-017-02161-w

Henderson, D.M. (1998) Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison Formation theropods. *Gaia*, 15, 219–226.

Hendrickx, C., Mateus, O., Araújo, R. & Choiniere, J. (2019) The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontologia Electronica*, 22, 1–110. https://doi.org/10.26879/820

Holtz Jr., T.R. (2021) Theropod guild structure and the Tyrannosaurid Niche Assimilation Hypothesis: Implications for predatory dinosaur macroecology and ontogeny in later Late Cretaceous Asiamerica. *Canadian Journal of Earth Sciences*, 58, 778–795. https://doi.org/10.1139/cjes-2020-0174

Hone, D.W.E., Dececchi, T.A., Sullivan, C., Xing, X. & Larsson, H.C.E. (2023) Generalist diet of *Microraptor zhaoianus* included mammals. *Journal of Vertebrate Paleontology*, 42, e2144337. https://doi.org/10.1080/02724634.2022.2144337

Jasinski, S.E. (2011) Biomechanical modeling of *Coelophysis bauri*: possible feeding methods and behavior of a Late Triassic theropod. *New Mexico Museum of Natural History and Science Bulletin*, 53, 195–201.

Jasinski, S.E. (2015) A new dromaeosaurid (Theropoda, Dromaeosauridae) from the Late Cretaceous of New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 67, 79–87.

Jasinski, S.E., Sullivan, R.M., Carter, A.M., Johnson, E.H., Dalman, S.G., Zariwala, J. & Currie, P.J. (2023) Osteology and reassessment of *Dineobellator notohesperus*, a southern eudromaeosaur (Theropoda: Dromaeosauridae: Eudromaeosauria) from the latest Cretaceous of New Mexico. *The Anatomical Record*, 306, 1712–1756. https://doi.org/10.1002/ar.25103

Jasinski, S.E., Sullivan, R.M. & Dodson, P. (2020) New dromaeosaurid dinosaur (Theropoda, Dromaeosauridae) from New Mexico and biodiversity of dromaeosaurids at the end of the Cretaceous. *Scientific Reports*, 10, 5105. https://doi.org/10.1038/s41598-020-61480-7

Juarez, K.M. & Marinho-Filho, J. (2002) Diet, habitat use, and home ranges of sympatric canids in central Brazil. *Journal of Mammalogy*, 83, 925–933. https://doi.org/10.1644/1545-1542(2002)083<0925:DHUAHR>2.0.CO;2

King, J.L., Sipla, J.S., Georgi, J.A., Balanoff, A.M. & Neenan, J.M. (2020) The endocranium and trophic ecology of *Velociraptor mongoliensis*. *Journal of Anatomy*, 237, 861–869. https://doi.org/10.1111/joa.13253

Longrich, N.R. & Currie, P.J. (2009) A microraptorine (Dinosauria—Dromaeosauridae) from the Late Cretaceous of North America. *Proceedings of the National Academy of Sciences*, 106, 5002–5007. https://doi.org/10.1073/pnas.0811664106

Monfroy, Q.T. (2017) Correlation between the size, shape and position of the teeth on the jaws and the bite force in Theropoda. *Historical Biology*, 29, 1089–1105. https://doi.org/10.1080/08912963.2017.1286652

Norell, M.A. & Makovicky, P.J. (2004) Dromaeosauridae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds), *The Dinosauria*: *Second Edition*. University of California Press, Buckley, California, 196–209. https://doi.org/10.1525/california/9780520242098.003.0012

Poust, A.W., Gao, C., Varricchio, D.J., Wu, J. & Zhang, F. (2020) A new microraptorine theropod from the Jehol Biota and growth in early dromaeosaurids. *The Anatomical Record*, 303, 963–987. https://doi.org/10.1002/ar.24343

Powers, M.J., Fabbri, M., Doschak, M.R., Bhullar, B.A.S., Evans, D.C., Norell, M.A. & Currie, P.J. (2022) A new hypothesis of eudromaeosaurian evolution: CT scans assist in testing and constructing morphological characters. *Journal of Vertebrate Paleontology*, 41, e2010087. https://doi.org/10.1080/02724634.2021.2010087

Powers, M.J., Sullivan, C. & Currie, P.J. (2020) Re-examining ratio based premaxillary and maxillary characters in Eudromaeosauria (Dinosauria: Theropoda): Divergent trends in snout morphology between Asian and North American taxa. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 547, 109704. https://doi.org/10.1016/j.palaeo.2020.109704

Rayfield, E.J. (2004) Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proceedings of the Royal Society of London Series B*, 271, 1451–1459. https://doi.org/10.1098/rspb.2004.2755

Roach, B.T. & Brinkman, D.L. (2007) A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History*, 48, 103–138. https://doi.org/10.3374/0079-032X(2007)48[103:AROCPH]2.0.CO;2

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675. https://doi.org/10.1038/nmeth.2089

Segura, V., Cassini, G.H. & Prevosti, F.J. (2021) Evolution of cranial ontogeny in south American canids (carnivora: Canidae). *Evolutionary Biology*, 48, 170–189. https://doi.org/10.1007/s11692-020-09529-3

Senter, P. (2009) Pedal function in deinonychosaurs (Dinosauria: Theropoda): a comparative study. *Bulletin of the Gunma Museum of Natural History*, 13, 1–14.

Slater, G.J., Dumont, E.R. & Van Valkenburgh, B. (2009) Implications of predatory specialization for cranial form and function in canids. *Journal of Zoology*, 278, 181–188. https://doi.org/10.1111/j.1469-7998.2009.00567.x

Therrien, F. (2005) Mandibular force profiles of extant carnivorans and implications for the feeding behaviour of extinct predators. *Journal of Zoology*, 267, 249–270. https://doi.org/10.1017/S0952836905007430

Therrien, F., Henderson, D. & Ruff, C.B. (2005) Bite me: biomechanical models of theropod mandibles and implications for feeding behavior. *In*: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington, 179−237.

Therrien, F., Quinney, A., Tanaka, K. & Zelenitsky, D.K. (2016) Accuracy of mandibular force profiles for bite force estimation and feeding behavior reconstruction in extant and extinct carnivorans. *The Journal of Experimental Biology*, 219, 3738–3749. https://doi.org/10.1242/jeb.143339

Therrien, F., Zelenitsky, D.K., Voris, J.T. & Tanaka, K. (2021) Mandibular force profiles and tooth morphology in growth series of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* (Tyrannosauridae: Albertosaurinae) provide evidence for an ontogenetic dietary shift in tyrannosaurids. *Canadian Journal of Earth Sciences*, 58, 812–828. https://doi.org/10.1139/cjes-2020-0177

Tse, Y.T., Miller, C.V. & Pittman, M. (2024) Morphological disparity and structural performance of the dromaeosaurid skull informs ecology and evolutionary history. *BMC Ecology and Evolution*, 24, 39. https://doi.org/10.1186/s12862-024-02222-5

Turner, A.H., Makovicky, P.J. & Norell, M.A. (2012) A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History*, 371, 1–206. https://doi.org/10.1206/748.1

Van Valkenburgh, B. & Ruff, C.B. (1987) Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology*, 212, 379–397. https://doi.org/10.1111/j.1469-7998.1987.tb02910.x

Yun, C.G. (2024) Mandibular force profiles of Alioramini (Theropoda: Tyrannosauridae) with implications for palaeoecology of this unique lineage of tyrannosaurid dinosaurs. *Lethaia*, 57, 1–12. https://doi.org/10.18261/let.57.2.6