Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Jaw biomechanics of Troodontidae and their implications for the palaeobiology of this lineage of bird-like theropod dinosaurs

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LETHAIA

Troodontids are small-bodied paravian theropod dinosaurs that are conspicuous for their close evolutionary relationship with modern birds and unique bauplan among Mesozoic non-avian theropods, part of which has been interpreted as suggestive of a distinctive ecological niche as highly cursorial predators who primarily hunted small prey items or of an increased portion of plant material in their diet compared to other theropods. Despite the increased interest in paleobiology of bird-like dinosaurs more recently, however, feeding biomechanics of troodontids remains largely uninvestigated. Here, the feeding and predatory behaviours of five troodontids are investigated, using beam theory on their mandibles. Mandibular strength profiles reveal that the anterior extremity of the jaws in troodontids, even in early-diverging forms, is better adapted to endure mediolateral and torsional loads compared to most other theropods such as dromaeosaurids. In later-diverging, relatively large-bodied taxa, the anterior half of the dentary is strengthened in terms of its mediolateral bending rigidity. Such unique profiles suggest the anterior part of the lower jaw played an important role in the life habits of troodontids. These results could be interpreted that the anterior region of the troodontid dentary was used to crop off plant material, or assisted in prey capture when the prey was subdued by the pes of an animal. □ *Dinosauria, Theropoda, Paraves, Troodontidae, Mandible, Biomechanics, Ecology.*

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The Troodontidae is a clade of bird-like maniraptoran theropods that inhabited the terrestrial ecosystems of Laurasia through the Late Jurassic to the end Cretaceous (e.g. Makovicky & Norell 2004; Hartman *et al.* 2019; Wills *et al.* 2023), and a few fragmentary records from the Gondwanan region could potentially belong to this group as well (e.g. Goswami *et al.* 2013; Ding *et al.* 2020). Typically, this group is considered as very closely related to Avialae (=birds), but its exact phylogenetic position within Paraves is still uncertain: traditionally, Troodontidae has been considered a sister taxon of Dromaeosauridae, together forming Deinonychosauria within Paraves (e.g. Senter 2007; Holtz 2012; Turner *et al.* 2012; Currie & Evans 2020; Jasinski *et al.* 2020, 2023) but a number of recent studies have questioned such a relationship, instead recovered troodontids as more closely related to avialans than to dromaeosaurids (e.g. Godefroit *et al.* 2013a; Hendrickx *et al.* 2015; Cau *et al.* 2017; Agnolin *et al.* 2019). Furthermore, it is possible that the currently-established concept of Troodontidae is not monophyletic, since some taxa (e.g. *Eosinopteryx brevipenna*, *Xiaotingia zhengi*) that were usually considered as early-diverging members of this lineage (e.g. Godefroit *et al.* 2013b; Shen *et al.* 2017), may have closer phylogenetic affinities with other paravian clades such as Avialae (e.g. Godefroit *et al.* 2013a; Guo *et al.* 2018; Agnolin *et al.* 2019; Hartman *et al.* 2019). Nevertheless, it is certain that troodontids represent one of the closest extinct relatives of Avialae, and therefore studies about this group are crucial for our understandings on the origin of birds, as well as the palaeobiology of non-avian theropods that are on the line to modern avians.

A number of unique osteological features distinguish troodontids from the 'typical' bauplan seen in the majority of non-avian theropods, including enlarged brains with high encephalization quotients for Mesozoic dinosaurs, gracile snouts possessing many small, narrow teeth that are constricted between the crown and the root, elongated hindlimbs with asymmetrical arctometatarsus, and sickle-like claw on pedal digit II resembling those of dromaeosaurids (e.g. Russell 1969; Makovicky & Norell 2004; Holtz 2012; Hendrickx *et al.* 2015; Varricchio *et al.* 2021). Such peculiarities in skeletal anatomy of troodontids have long been speculated as adaptations for a lifestyle as fast-moving predators that preyed on a

https://doi.org/10.18261/let.58.1.3

variety of small animals (e.g. Russell 1969; Makovicky & Norell 2004; Fowler *et al.* 2011; Torices *et al.* 2018; Varricchio *et al.* 2021), although some degree of omnivorous to herbivorous habits have been suggested for derived taxa based on tooth denticle morphometrics and examination of element ratios in the tooth enamel (e.g. Holtz *et al.* 1998; Cullen & Cousens 2024). Such observations have been corroborated by bite marks left on herbivorous dinosaur bones which have been attributed to troodontids (e.g. Jacobsen 1997; Jacobsen & Bromley 2009; but see Brown *et al.* 2021 for an alternative opinion on the latter), regurgitalites containing small mammalian bones which are most likely produced by troodontids (e.g. Freimuth *et al.* 2021; Varricchio *et al.* 2021), and abundance of shed troodontid teeth associated with bones and nesting sites of ornithopods (e.g. Horner 1994; Ryan *et al.* 1998; Varricchio *et al.* 2021).

Besides these examples, however, much is still unknown about the palaeoecology of troodontids, which is partly owing to their rarity in the fossil record (e.g. Makovicky & Norell 2004; Averianov & Sues 2007; Wang *et al.* 2022). In particular, despite being actively used in recent studies in dinosaur palaeobiology (e.g. Alexander 2006), few biomechanical modelling approach has been made to investigate feeding or hunting behaviour of troodontids. A study of Monfroy (2017) investigated the correlation between bite force and the size, shape and position of the teeth in non-avian theropods, and one skull cast of '*Troodon*' sp. (TMP 82.53.4) was incorporated in the analyses, but the main focus of that work is about the general trend among Theropoda on a broad scale. Torices *et al.* (2018) performed finite element analyses on paravian teeth found in Upper Cretaceous strata of Alberta, Canada, and found teeth of troodontids were more likely to fail at non-optimal bite angles than other theropods like dromaeosaurids, and interpreted these results as suggesting troodontids were most likely preyed on small, soft prey items that did not require high bite forces to capture and kill. Using mechanical advantage and finite element analyses, Tse *et al.* (2024) found the troodontid *Gobivenator mongoliensis* had higher jaw mechanical advantage but lower resistance to bite force in the skull compared to dromaeosaurids, but this taxon was examined for only comparative purposes. Nabavizadeh & Weishampel (2023) noted the bending strength of the lower jaw in '*Troodon*' is relatively higher at the anterior portion than the rest of the mandible, presumably based on a medially-expanded dentary symphysis seen in later-diverging troodontids (Currie 1987) but no quantitative evidence was provided for this claim.

In this work, mandibular strength properties of various troodontid taxa are derived through employing the biomechanical modelling technique using the principles of beam theory (Therrien *et al.* 2005), which has been used on a variety of non-avian theropods (Therrien *et al.* 2005, 2021; Jasinski 2011; Monfroy 2017; Yun 2024), to determine the patterns of resisting loads from vertical and horizontal directions along the lower jaw in these dinosaurs. Since the external dimensions of various points along the mandible reflect adaptation of the jaw to specific loads, they are likely related to the hunting and feeding methods of the animal, and can be used to infer behaviours of extinct taxa (Therrien *et al.* 2005). Additionally, the results are compared with those of the previous biomechanical studies on other theropods, to test the likelihood that the ecology of troodontids differed from similarly-sized theropods (e.g. dromaeosaurids) at least to some degree, as previously suggested (Holtz *et al.* 1998; Cullen & Cousens 2024).

Material and methods

Measurements from the various parts of the dentary were made from specimens of *Byronosaurus jaffei* (MPC-D 100/983), *Latenivenatrix mcmasterae* (TMP 92.36.575), '*Polyodontosaurus grandis*' (CMN 8540), *Urbacodon itemirensis* (ZIN PH 944/16) and *Zanabazar junior* (MPC-D 100/1) from published images in dorsal/ventral and lateral views (Currie 1987, fig. 2; Makovicky *et al.* 2003, fig. 3; Averianov & Sues 2007, fig. 2; Norell *et al.* 2009, fig. 29; van der Reest & Currie 2017, fig. 8). It has been demonstrated that using measurements taken from images to derive mandibular strength profiles is a valid method, that yields a result that is akin to studies using measurements from real specimens (Brannick & Wilson 2020; Yun 2024) and therefore, this approach is considered as an appropriate alternative in this work. Of note, *Latenivenatrix mcmasterae* may represent a junior synonym of *Stenonychosaurus inequalis* (Cullen *et al.* 2021) and '*Polyodontosaurus grandis*' is a dubious taxon which may be synonymous with *Latenivenatrix mcmasterae* or *Stenonychosaurus inequalis* (van der Reest & Currie 2017; Cullen *et al.* 2021). Reassessment of troodontid taxonomy is beyond the scope of this work, and the usage of the names *Latenivenatrix mcmasterae* and '*Polyodontosaurus grandis*' is simply for the sake of pragmatism.

Based on the protocols of Therrien *et al.* (2005), the following measurements were taken using the program ImageJ (Schneider *et al.* 2012): (1) depth of the

dentary at 2nd alveolus; (2) width between the lateral margin of the 2nd alveolus and the most posterior point of the mandibular symphysis; (3) depth of the dentary at the middle of the tooth row; (4) width of the dentary at the middle of the tooth row; (5) depth of the dentary at the posteriormost alveolus; and, (6) width of the dentary at the posteriormost alveolus (Fig. 1). It should be noted that the portions of the examined specimens were sometimes incomplete, and as such some measurements had to be taken from the most adjacent region or estimated based on the preserved contour of the bone, but such uncertainties are quite minimal and would not affect the results dramatically.

These measurements were subjected to data processing via Microsoft Excel, following the protocols of Therrien *et al.* (2005, 2021) to derive biomechanical properties of the mandible along the tooth row, and components of the dataset are as follows: (1) Zx = π*(dentary width/2)*(dentary depth/2)^2/4, a vertical bending strength (=rigidity) of the bone; (2) Zy = π*(dentary depth/2)*(dentary width/2)^2/4, a horizontal bending strength of the bone; and (3) Zx/Zy, a relative strength of the bone that is proportional to the ratio of the vertical and horizontal radii of the cross-section of the dentary. Due to its nature, Zx/Zy reflects an adaptation to resist the major loads applied at a particular region of the jaw: that is, a ratio >1 (deeper than wide) represents an adaptation toward dorsoventral loads, a ratio <1 (wider than deep) represents an adaptation toward labiolingual loads, and a ratio of 1 represents equal adaptation toward dorsoventral and labiolingual loads (Therrien 2005a, b; Therrien *et al.* 2005, 2021). The complete dataset used in this work is provided as Supplementary Table 1.

Institutional abbreviations: CMN, Canadian Museum of Nature, Aylmer, Ottawa, Canada; MPC (=IGM), Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UCM, The Fossil Vertebrate Collection at the University of Colorado Boulder Museum of Natrual History, Boulder, Colorado, USA; ZIN PH, Paleoherpetological collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Results

In *Byronosaurus jaffei* (MPC-D 100/983), a small-bodied, early-diverging troodontid (e.g. Shen *et al.* 2017; van der Reest & Currie 2017; Hartman *et al.* 2019), the dorsoventral strength (Zx) decreases slightly from the symphyseal region (0.013) to the mid-dentary (0.009), then increases significantly to the posterior region of the dentary (0.019), making the overall profile of dorsoventral rigidity as a concave curve (Fig. 2A). This is due to the fact that the mandible is relatively deeper at the symphyseal and posterior regions than at the mid-dentary (Makovicky *et al.* 2003: fig. 3). The mediolateral strength (Zy) profile is largely similar to that of the Zx profile (Fig. 2A), excepting that the value at the posterior region (0.0081) is found to be similar to that (0.0086) at the

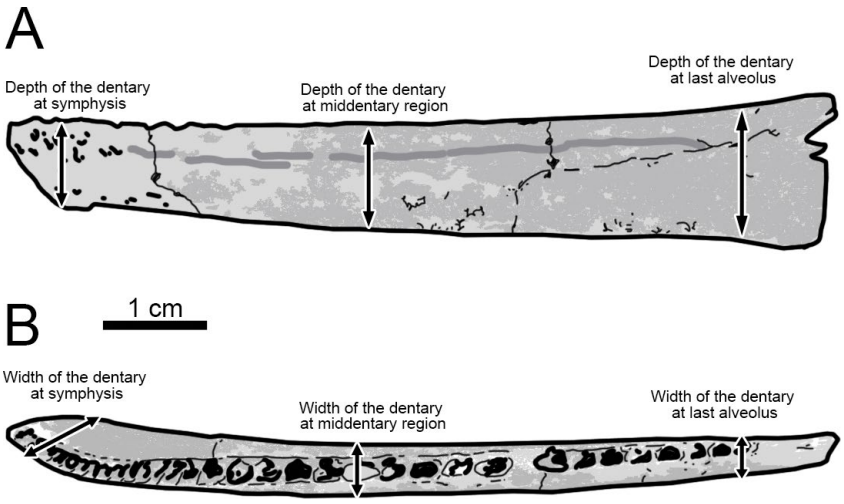

Fig. 1. Measurement parameters used in this study, with the dentary of *Urbacodon itemirensis* (ZIN PH 944/16) in lateral and dorsal views as an example. A, depths measured at the symphyseal region, mid-dentary region and last alveolus. B, widths measured at the symphyseal region, mid-dentary region and last alveolus. Illustration of the mandible is after Averianov & Sues (2007, fig. 2).

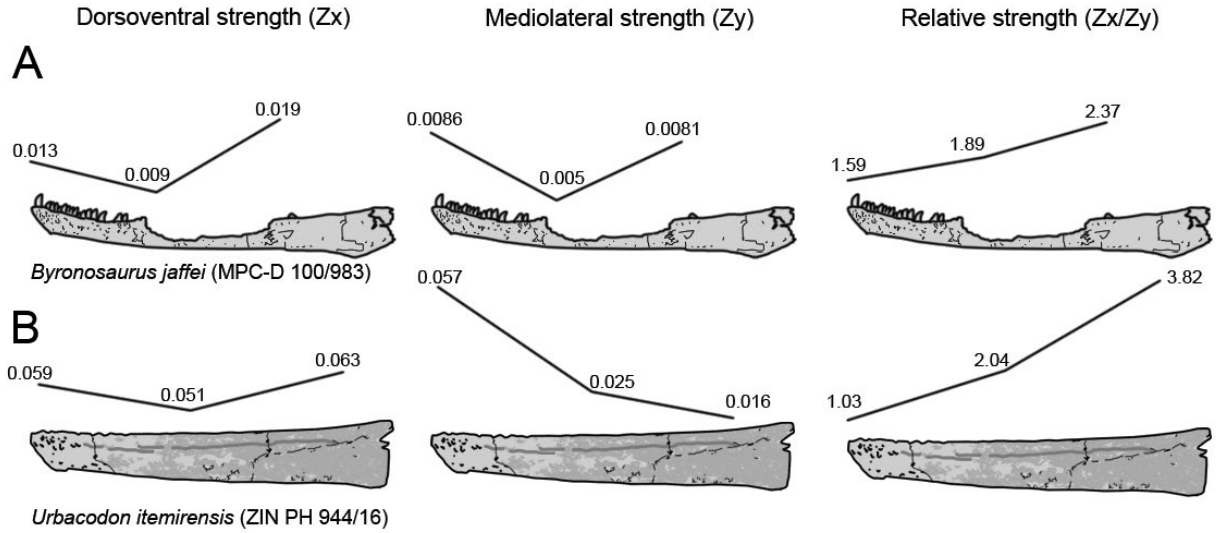

Fig. 2. Lower jaw strength profiles of small- to medium-sized troodontids. A, mandibular properties of *Byronosaurus jaffei* (MPC-D 100/983), B, mandibular properties of *Urbacodon itemirensis* (ZIN PH 944/16). Illustrations of the dentaries are after Makovicky *et al.* (2003, fig. 30) for *Byronosaurus jaffei*, and Averianov & Sues (2007, fig. 2) for *Urbacodon itemirensis*.

symphysis. In terms of relative strength of the mandible (Zx/Zy, overall shape of the lower jaw), the values range between 1.59 at the symphyseal region, 1.89 at the mid-dentary and 2.37 at the posterior region (Fig. 2A). This indicates that the dentary is only about 1.59 times deeper than wide at the anterior end, then becomes more dorsoventrally-buttressed posteriorly.

In *Urbacodon itemirensis* (ZIN PH 944/16), a medium-sized taxon which may be a later-diverging troodontid (Wang *et al.* 2024), the dorsoventral strength profile is largely similar to that of *Byronosaurus jaffei* excepting differences in absolute values (Fig. 2B), suggesting the anterior and posterior regions of the dentary are better adapted to withstand vertical loads (Zx values 0.059 and 0.063 respectively) than the mid-dentary is (Zx=0.051). Intriguingly, the mediolateral strength (Zy) is found to decrease sharply from the symphyseal region to the posterior part of the dentary, with values ranging from 0.057 at the symphysis, 0.025 at mid-dentary and 0.016 at the most posterior part of the tooth row (Fig. 2B). Such a profile indicates the symphyseal region of the mandible is much more resistant to mediolateral bending than the rest of the dentary in *Urbacodon itemirensis*. The Zx/Zy profile of the *Urbacodon itemirensis* dentary, reveals that the value at the symphyseal region is very close to 1.0 (1.03), then rapidly increases through the mid-dentary (2.03) and the posterior region (3.82). This implies the cross-section of the mandible of this taxon is strongly dorsoventrally buttressed at the most posterior alveolus, then becomes significantly rounder anteriorly (Fig. 2B).

In *Zanabazar junior* (MPC-D 100/1), a later-diverging, large-bodied Asian troodontid (e.g. Norell *et al.* 2009; Tsuihiji *et al.* 2014; van der Reest & Currie 2017; Hartman *et al.* 2019; Wang *et al.* 2024), Zx values are found to increase posteriorly along the tooth row, ranging from 0.093 at the symphyseal region, 0.167 at the mid-dentary and 0.271 at the posterior-most alveolus (Fig. 3A). In contrast, the Zy profile of this taxon reveals that the value at the mid-dentary (0.093) is higher than those at the symphysis and the posterior region, which both are approximately 0.082 (Fig. 3A). The Zx/Zy profile demonstrates a rapid decrease along the tooth row in an anterior direction, from a value of 3.31 at the most posterior alveolus, a value of 1.79 at mid-dentary to a value of 1.13 at the symphysis, suggesting that while being dorsoventrally-buttressed at the posterior region, the dentary of *Zanabazar junior* becomes nearly round anteriorly in cross-section (Fig. 3A).

The Zx profile of North American '*Polyodontosaurus grandis*' (CMN 8540) is roughly similar to that of *Zanabazar junior* (Fig. 3B), with the main difference is that the Zx value at the mid-dentary is only slightly higher (0.234) than that at the symphyseal region (0.229), suggesting both regions are similarly adapted to resist against vertical loads. The Zx value at the most posterior alveolus is about 0.300. Similarly, the Zy values at the symphyseal region and the mid-dentary are nearly identical in this taxon (0.169 and 0.168 respectively), whereas that at the posterior region is significantly lower (0.074). As expected, Zx/Zy values at the symphyseal region and the mid-dentary are broadly

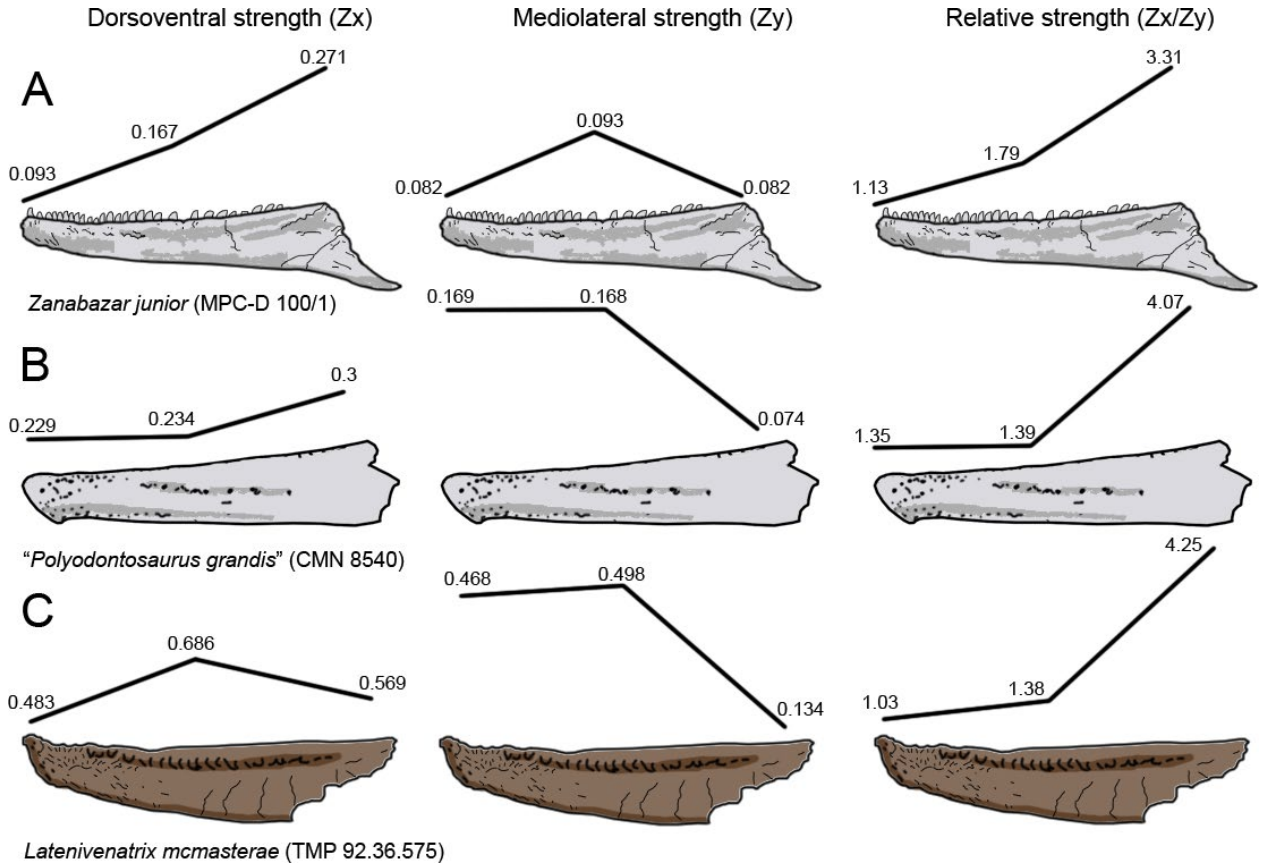

Fig. 3. Lower jaw strength profiles of large-bodied troodontids. A, mandibular properties of *Zanabazar junior* (MPC-D 100/1), B, mandibular properties of '*Polyodontosaurus grandis*' (CMN 8540), C, mandibular properties of *Latenivenatrix mcmasterae* (TMP 92.36.575). Illustrations of the dentaries are after Norell *et al.* (2009, fig. 29) for *Zanabazar junior*, Currie (1987, fig. 2) for '*Polyodontosaurus grandis*' and van der Reest & Currie (2017, fig. 8) for *Latenivenatrix mcmasterae*.

similar in this taxon (1.35 and 1.39, respectively), while that at the last alveolus is much higher (4.07). Such a profile indicates that while being strongly dorsoventrally buttressed in the posterior region, the anterior half of the dentary is relatively rounded in cross-section in '*Polyodontosaurus grandis*', being only 1.35–1.39 times deeper than wide (Fig. 3B).

In the North American *Latenivenatrix mcmasterae* (TMP 92.36.575), possibly the largest troodontid (van der Reest & Currie 2017), Zx values increase from the symphysis (0.483) to the mid-dentary (0.686), then slightly decrease at the last alveolus (0.569). In the case of Zy values, a slight increase occurs from the symphyseal region (0.468) to the mid-dentary (0.498), then it sharply decreases at the posterior region (0.134). The dentary of *Latenivenatrix mcmasterae* has Zx/Zy values that moderately increase from 1.03 at the symphyseal region to 1.38 at mid-dentary, then sharply increase to 4.25 at the last alveolus (Fig. 3C). Such a profile suggests the anterior region is nearly rounded in cross-section, slightly deepened at the mid-dentary, then was strongly dorsoventrally-buttressed in the posterior region (Fig. 3C).

Discussion

Previous studies regarding mandibular force profiles of non-avian theropods have found lower jaws of small-bodied theropods in general, behaved as a simple lever like those of varanid lizards: that is, the strength properties decrease constantly towards the anterior end (Therrien *et al.* 2005; Jasinski 2011). Additionally, Therrien *et al.* (2005) found that the lower jaws of dromaeosaurid theropods, which are phylogenetically close to troodontids and share a similar bauplan (e.g. Makovicky & Norell 2004; Fowler *et al.* 2011; Hendrickx *et al.* 2015), not only functioned as a simple lever, but also that the mandibles are strongly dorsoventrally-buttressed at all regions (i.e. high Zx/Zy values) and, thus, are mainly suitable for delivering rapid, slashing bites on prey rather than holding onto it. However, the results of this study indicate that, given the strong correlation between the strength properties of the mandible and the feeding or predatory behaviour of an animal (Therrien *et al.* 2005, 2021), the lower jaws of troodontids were not just simply suited for quick, slashing bites and instead,

different areas of their jaws were specialized for various functions. In all analysed troodontids, only the posterior region of the dentary is dorsoventrally-buttressed (Zx/Zy > 2.0), which may indicate this region of the lower jaw was used to slice or shear food items, as inferred for some other theropods (Therrien *et al.* 2005; Jasinski 2011).

In *Byronosaurus jaffei*, a small-bodied, longirostrine, early-diverging troodontid (e.g. Makovicky *et al.* 2003; Shen *et al.* 2017; van der Reest & Currie 2017), both Zx and Zy values of the mandibular symphysis are higher than those at the mid-dentary, unlike most other small theropods including dromaeosaurids (Therrien *et al.* 2005; Jasinski 2011). Additionally, the Zx/Zy value at the symphyseal region of this taxon is only 1.59, implying the cross-section at this region is relatively rounded, and is only 1.59 times deeper than wide. This differs strikingly from the condition in dromaeosaurids, in which the Zx/Zy values at the symphyseal region exceed 2.0 (Therrien *et al.* 2005). According to Therrien *et al.* (2005), high Zx/Zy values (>2) at the anterior part of the lower jaw suggest this region is mainly adapted for enduring vertical loads and therefore, are indicative of quick, slashing bites in life. The relatively low value in *Byronosaurus jaffei*, however, suggests the mandibular symphysis of this taxon is better suited for resisting mediolateral loads, and the behaviours of this taxon likely involved more frequent activities that induce torsional stresses at the anterior end of the jaw than dromaeosaurids. Therefore, rather than simply delivering slashing bites, the anterior end of the snout in *Byronosaurus jaffei* likely played more important roles in its lifestyle, such as seizing or manipulating prey items or objects. A number of craniodental features of this taxon support such interpretation: 1) the premaxillary and dentary teeth are closely packed anteriorly, 2) rounded cross-sections of the anteriorly positioned teeth that differ from elliptical to subrectangular teeth in more posterior positions, and 3) a 'chin'-like eminence at the anteroventral corner of the dentary (e.g. Makovicky *et al.* 2003). These are largely shared with other troodontids as well (e.g. Xu *et al.* 2002; Makovicky & Norell 2004; Wang *et al.* 2024). Nevertheless, the fact that the symphysis of the dentary is 1.59 times as deep as it is wide in *Byronosaurus jaffei* (Zx/Zy=1.59) indicates dorsoventral loads were still more important in this region, as in other typical non-avian theropods (Therrien *et al.* 2005), whereas mediolateral loads occurring at the anterior end of the jaw were relatively low.

Collectively, these observations suggest that, although *Byronosaurus jaffei* may have used the anterior end of the snout in lifestyle more frequently than dromaeosaurids, the mandible of this taxon was still suitable for slicing. Due to reasons such as the fossils being fragmentary or the mandible being preserved in occlusion with the skull, which made it difficult to obtain necessary dimensions and thus not directly included in the analyses of this work, it is predicted that other early-diverging, small-bodied troodontids (e.g. *Almas ukhaa*, *Sinovenator changii*) likely had mandibular strength profiles similar to those observed in *Byronosaurus jaffei*, as they also have a chin-like eminence at the anteroventral corner of the dentary, but lack a medially-expanded symphysis seen in later-diverging taxa (Averianov & Sues 2016; Pei *et al.* 2017; Yu *et al.* 2024, fig. 1).

In *Urbacodon itemirensis*, a medium-sized taxon which is either a later-diverging troodontid (Wang *et al.* 2024) or phylogenetically-intermediate taxon between the grade of early-diverging, small-bodied taxa (e.g. *Byronosaurus jaffei*) and large-bodied, derived taxa such as *Zanabazar junior* (e.g. Averianov & Sues 2016; van der Reest & Currie 2017), both Zx and Zy values at the symphyseal region are higher than those at mid-dentary as in *Byronosaurus jaffei*, but the main difference is that the Zx/Zy value at the mandibular symphysis is nearly 1.0 in *Urbacodon itemirensis* (1.03), suggesting the dentary is as wide as deep in this region. This reflects a more medially-curved nature of the anterior end of the dentary (= medially expanded symphysis) in this taxon (Wang *et al.* 2024; contra Averianov & Sues 2007), and this region is equally adapted to both dorsoventral and mediolateral loads in *Urbacodon itemirensis*. Therefore, the anterior extremity of the lower jaw of *Urbacodon itemirensis* is unsuited to deliver rapid, slashing bites in a manner similar to varanids or dromaeosaurids (Therrien *et al.* 2005), and likely involved in more complex behaviours like manipulating, or holding on objects.

The strength profiles of the lower jaws of large-bodied, derived troodontids (Troodontinae *sensu* van der Reest & Currie 2017), are more complex: Zx/Zy values of the mandibular symphysis of the three taxa examined (*Latenivenatrix mcmasterae*, '*Polyodontosaurus grandis*' and *Zanabazar junior*) are close to 1.0 (1.03–1.35), suggesting this region is equally adapted to both dorsoventral and mediolateral loads as in *Urbacodon itemirensis*. Intriguingly, Zy values at the mid-dentary in these taxa are equivalent (*Latenivenatrix mcmasterae*, '*Polyodontosaurus grandis*') or even higher than those at the symphysis (*Zanabazar junior*), suggesting this region is well-suited for enduring mediolateral or torsional loads as well. In *Latenivenatrix mcmasterae*, the Zx value at the mid-dentary also exceeds that of the symphyseal region, and at least two taxa (*Latenivenatrix mcmasterae*, '*Polyodontosaurus*

grandis') share fairly low Zx/Zy values (1.38–1.39) at the mid-dentary region, indicating the dentary is mediolaterally-buttressed to a similar degree as it is dorsoventrally. Such results reflect a robust nature of mandibles of these taxa, in which the middle portion of the dentary is mediolaterally-thickened (van der Reest & Currie 2017). Additionally, these suggest an anterior end, and perhaps the anterior half, of the jaws of these troodontids played key roles in their life habits. Given that the mediolaterally-expanded symphysis and mid-dentary region are also seen in mandibles of other later-diverging, large troodontid taxa (e.g. *Albertavenator curriei*, *Saurornithoides mongoliensis*, *Stenonychosaurus inequalis*) that were not available for the analyses of this work, it is probable that the unique lower jaw strength profiles observed in analysed large-bodied taxa are broadly present among enlarged, derived troodontids (e.g. Norell *et al.* 2009, fig. 3C; Evans *et al.* 2017, fig. 6; van der Reest & Currie 2017, fig. 8; Wang *et al.* 2024).

Collectively, these observations indicate the anterior end of the mandible was already suited to resist against mediolateral loads to some degree in early-diverging troodontids like *Byronosaurus jaffei*, relatively more so than in dromaeosaurids (Therrien *et al.* 2005), and the relative width of this portion increased farther during the course of troodontid evolution. And, eventually, the relative width of the mid-dentary region increased in later-diverging, large-bodied taxa, suggesting the whole anterior half of the dentary was suited to resist mediolateral stresses. Indeed, the anteriorly rounder nature of troodontid mandibles over other theropods like dromaeosaurids (Norell *et al.* 2006: fig. 4) is further corroborated by published figures of their coronal cross-sections (Currie 1987, fig. 1; Makovicky *et al.* 2003, fig. 9; Wang *et al.* 2024, fig. 3). It is also noteworthy that the orientation of the dentary symphysis in medial view, is inclined posteroventrally (Fig. 4A) in later-diverging troodontids (Currie 1987, fig. 2; Averianov & Sues 2007; Lü *et al.* 2010, fig. 3; Evans *et al.* 2017, fig. 6), and the anterodorsally-sloping nature of the anterior margin of the dentary seen in early-diverging taxa, suggests their symphyseal orientation is likely similar as well (e.g. Makovicky *et al.* 2003, fig. 5; Pei *et al.* 2017, fig. 2; Yu *et al.* 2024, fig. 1). Such morphology is different from the subvertical condition seen in most other non-avian theropods (Fig. 4B) but reminiscent to that of tyrannosaurids (Therrien *et al.* 2005, 2021). The peculiar orientation of the mandibular symphysis of tyrannosaurids, has been interpreted as an adaptation to sustain torsional stresses (Therrien *et al.* 2005, 2021), and the diagonally oriented nature of troodontid mandibular symphysis may be another indicator that their symphysis went through greater torsional stresses than other small-bodied, non-avian theropods such as dromaeosaurids.

Although troodontids were diminutive for non-avian theropods and phylogenetically close to dromaeosaurids (e.g. Senter 2007; Holtz 2012; Turner *et al.* 2012), the fact that an anterior part of their mandible was notably more resistant to mediolateral and torsional forces suggests they primarily used an anterior part of the snout for handling and

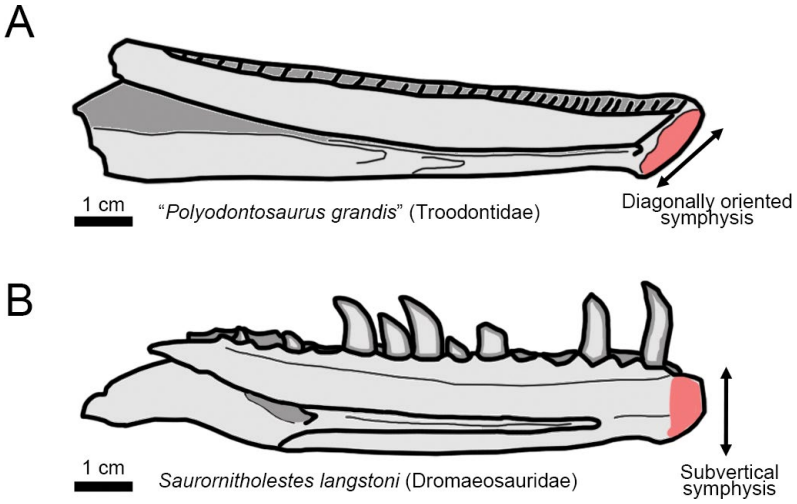

Fig. 4. Differences in orientation of the mandibular symphysis (marked in light red) between troodontid and dromaeosaurid theropods, using A) '*Polyodontosaurus grandis*' (CMN 8540) and B) *Saurornitholestes langstoni* (TMP 88.121.39) as examples. Notice the differences between the diagonally-oriented troodontid symphysis and the subvertical symphysis of dromaeosaurids. Illustrations of dentaries are after Brown *et al.* (2021, fig. 4).

grasping rather than for quick biting. It is unlikely that the increased mediolateral-bending rigidity of troodontid jaws is related to resisting loads induced by hunting large prey items or bone crushing as suggested for tyrannosaurids (Therrien *et al.* 2005, 2021), simply because troodontids were small-bodied theropods and their teeth are diminutive, closely spaced, narrow in width and, thus, are unsuited for enduring stresses caused through such behaviours (e.g. Makovicky & Norell 2004; Hendrickx *et al.* 2015, 2019). Additionally, the results of biomechanical analyses on troodontid teeth are consistent with such interpretations (Torices *et al.* 2018). Instead, the following hypotheses can be considered for why the anterior region of troodontid mandibles was better adapted to withstand torsional stresses than other small-sized theropods. First, tooth denticle morphometrics as well as analyses of element ratios (Sr/Ca, Ba/Ca) on shed teeth suggest the later-diverging troodontids were not strictly carnivores, but plant matter occupied a significant portion of their diet (Holtz *et al.* 1998; Makovicky & Norell 2004; Cullen & Cousens 2024). While the non-serrated teeth seen in early-diverging troodontids (e.g. *Byronosaurus jaffei*) could have been used to spear into flesh or deeply injure prey items (Xing *et al.* 2013; Hendrickx *et al.* 2019), such morphology could also indicate a higher degree of herbivory, considering its obviously less efficient nature in slicing through animal flesh (Lü *et al.* 2010; Hendrickx *et al.* 2015, 2019). Additional lines of evidence that argue against strictly hypercarnivorous diet of troodontids come from the microanatomy of their teeth: a study of Brink *et al.* (2015) found the teeth of derived troodontid ('*Troodon*') lacked deep interdental folds and narrow spacing between denticles that are usually seen in carnivorous theropod teeth. Strengthening the anterior region of the jaw would obviously be beneficial for cropping tough, fibrous plant materials using the tip of the snout, and convergent trends of acquiring mandibular adaptations to endure biting and feeding-induced stresses at the anterior tip have been noted for various clades of herbivorous dinosaurs (e.g. Lautenschlager *et al.* 2013; Button *et al.* 2016; Lautenschlager 2017; MacLaren *et al.* 2017; Ma *et al.* 2022). It is even probable that the increased usage of the anterior tip of the snout in feeding, represents a prerequisite for the evolution of rhamphotheca in numerous herbivorous dinosaurs (Lautenschlager *et al.* 2013). Perhaps, the increased mediolateral-bending rigidity of the anterior part of troodontid jaws also represents an adaptation to resist torsional stresses induced through feeding on tough plant matter as well, and the more rounded nature of the mandibles of later-diverging taxa could indicate an increased portion of herbivory in their diet.

Second, while the ungual on pedal digit II of troodontids is enlarged and strongly recurved like those of dromaeosaurids (e.g. Makovicky & Norell 2004; Hendrickx *et al.* 2015), it is not as hypertrophied as those of eudromaeosaurian dromaeosaurids, and distal articular surfaces of the metatarsals and pedal phalanges are either not or only weakly ginglymoid unlike the strongly ginglymoid surfaces seen in later-diverging dromaeosaurids (Fowler *et al.* 2011; Oswald *et al.* 2023; Kubota *et al.* 2024). The hypertrophied ungual of pedal digit II, as well as relatively short, strongly ginglymoid metatarsals and pedal phalanges, in dromaeosaurids are well-suited for grasping an object, and it is probable that the foot of eudromaeosaurian dromaeosaurids is used for immobilizing prey and served as the main organ in their predatory behaviour (Fowler *et al.* 2011). In contrast, only weakly-hypertrophied pedal digit II unguals, as well as elongated, often non-ginglymoid metatarsals and phalanges, in the troodontid pes indicate it was significantly less efficient in grasping compared to dromaeosaurids, and the pedal anatomy became more adapted to cursoriality rather than gripping through the course of evolution in this clade (Fowler *et al.* 2011; Oswald *et al.* 2023; Kubota *et al.* 2024). Therefore, the pedes of troodontids would have been less lethal than those of dromaeosaurids, and their efficiency in predation would have been lower as well. Other potential pieces of evidence for the less efficient nature of hunting through grasping prey with the pes in troodontids comes from their forelimb proportions and tail anatomy. Modern birds that grip prey with their hypertrophied pedal claws (e.g. Accipitridae) often flap their wings to stabilize their body and to assist in preventing prey escape during grasping, and the presence of elongated, feathered forelimbs in dromaeosaurids suggests the similar behaviour was likely present as well (Fowler *et al.* 2011). However, while it is probable that pennaceous feathers were likely present on forelimbs of later-diverging troodontids like their ancestors (Xu *et al.* 2017), it is recognized that significant shortening of the relative length of the forelimb occurred during the course of troodontid evolution, which would obviously decrease the efficiency of flapping (Xu *et al.* 2011). Of note, it is also possible that dromaeosaurids occasionally seized their prey with the manus (e.g. Therrien *et al.* 2005; Jasinski *et al.* 2020, 2023), but the shortened forelimbs in later-diverging troodontids would have been disadvantageous to do so. In dromaeosaurids, the prezygapophyses of the caudal vertebrae and the anterior end of the chevrons are

extremely elongated, and they would have increased tail stiffness (Ostrom 1969; Persons & Currie 2012; Senter *et al.* 2012) and it is hypothesized that such a stiff, beam-like nature of the tail is functionally related to the use of it as a balance stabilizer during gripping prey (Fowler *et al.* 2011). In troodontid tails, however, no peculiar features that are linked with increased stiffness have been reported (Fowler *et al.* 2011; Persons & Currie 2012). If such was the case, while troodontids may have gripped their prey with their pedes as inferred for dromaeosaurids (Fowler *et al.* 2011), they may have to use the anterior of their jaws in order to completely immobilize and kill it. If this was the case, the mediolaterally-wide nature of the anterior region of troodontid dentaries may represent an adaptation to resist the torsional and mediolateral loads induced by holding on struggling prey items or shaking the head in order to kill them.

At present, it is unclear which hypothesis better explains the unique morphology of troodontid mandibles and their strength profiles. Currently, both hypotheses are at odds with the previously suggested, strictly carnivorous diet for some Asian troodontids (*Byronosaurus jaffei*, *Zanabazar junior*) inferred through minimal number of confirmed skeletal traits that are correlated with herbivory (Zanno & Makovicky 2011) or mechanically weak nature of troodontid teeth (Torices *et al.* 2018). Indeed, a work of Fiorillo (2008) found microwear patterns on troodontid teeth lack the pitting that is indicative of hard food items but instead show only fine wear patterns, which is obviously inconsistent with the model of consuming tough plant matters. Therefore, more in-depth verification of these hypotheses will require procedures such as element ratio analyses of Asian troodontid teeth like the ones performed for some North American taxa (Cullen & Cousens 2024), or examination of cranial performance of troodontids with more specialized techniques such as Finite Element Analysis, which was recently done for dromaeosaurids (Tse *et al.* 2024).

In fact, the most parsimonious explanation for the diet of troodontids, is that it was neither strictly herbivorous nor hypercarnivorous, but rather omnivorous especially given that their skeletal anatomy possesses mixture of features that can be attributed to 'carnivorous' and 'herbivorous' habits (e.g. Holtz *et al.* 1998; Currie & Dong 2001; Brink *et al.* 2015; Torices *et al.* 2018; Cullen & Cousens 2024; contra Zanno & Makovicky 2011). Therefore, it is possible that both behaviours outlined above, may have been employed by troodontids. Perhaps, troodontids used their front of the jaw to crop off plants (albeit may have preferred relatively soft ones such as shoots or fruits; cf. Fiorillo 2008) and immobilize struggling prey, and sliced or sheared the food items with the posterior portion of the mandible that is strongly buttressed against dorsoventral loads (i.e. high Zx/Zy values).

Carpenter (1982) described a partial dentary (UCM 41666) of a hatchling troodontid (potentially referable to *Pectinodon bakkeri*) from the Lance Formation (Maastrichtian) of Wyoming, and found that it differs from adult troodontids (e.g. CMN 8540) by its weakly developed symphysis and lack of 'chin' at the anteroventral corner. Considering that the medial extent of the symphysis and the presence of a 'chin' are closely associated with mediolateral- and dorsoventral-bending strengths of the mandible, respectively (e.g. Therrien *et al.* 2005), the morphology of UCM 41666 may indicate the anterior end of the jaws in young troodontids was relatively weaker than that of mature individuals, and likely less efficient in foraging or predatory behaviours. Changes in mandibular strength properties during growth, could be an indicator of the presence of parental care or ontogenetic niche changes (Therrien *et al.* 2005, 2021). The presence of extended parental care in troodontids is indirectly indicated by their brooding biology (e.g. Varricchio *et al.* 1997, 1999, 2002, 2013, 2018, 2021), including probable communal nesting and nest reusing behaviours (e.g. Varricchio *et al.* 2015; Tagliavento *et al.* 2023). The occurrences of such complex, advanced social and reproductive behaviours could have been achieved through learning from older generations (e.g. Royle *et al.* 2012). Perhaps the presumed ontogenetic changes that occurred in troodontid mandibular anatomy might be another indicator for the extended parental care within this clade of theropods, in which youngsters lacked sufficient hunting abilities and had to be fed by adults, but such interpretation is obviously, largely hypothetical at the current status. Indeed, the observation that the lower jaws of young troodontids are mechanically weaker compared to adults could also suggest, similarly to what was previously proposed in *Coelophysis bauri* (Jasinski 2011), that juvenile individuals simply hunted smaller prey or consumed softer plants, rather than indicating that they could not obtain food on their own. Therefore, it may not necessarily be related to the presence or absence of parental care. Additionally, the well-ossified nature of the hindlimb of young troodontids indicates they were precocial (Currie & Peng 1993), which may suggest that they were able to move nimbly enough to find food themselves. To determine whether troodontid dinosaurs cared for their young, it seems necessary to conduct more thorough research on

their nests, eggs, and juveniles found at sites such as Egg Mountain site in Montana (e.g. Varricchio *et al.* 2021), in order to reveal more about their reproduction and growth.

Acknowledgements.– I thank two anonymous reviewers and the editor Peter Doyle for their efforts, which have greatly improved the quality of this manuscript.

SUPPLEMENTARY TABLE

Supplementary Table 1. Mandibular dimensions and strength properties for troodontids used in this work.

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