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A giant dromaeosaurid theropod from the Upper Cretaceous (Turonian) Bissekty Formation of Uzbekistan and the status of *Ulughbegsaurus uzbekistanensis*

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Abstract

The Upper Cretaceous (Turonian) Bissekty Formation of Uzbekistan has yielded many isolated bones and teeth representing a variety of non-avian theropod dinosaurs. A pedal phalanx II-2 indicates the presence of a dromaeosaurid theropod that attained a larger body size than any previously known member of that clade. The same formation also yielded a large maxillary fragment that has recently been described as a neovenatorid carcharodontosaurian (*Ulughbegsaurus uzbekistanensis*). However, this specimen lacks unambiguously diagnostic features of that clade, and its purported carcharodontosaurian characters are either taphonomic artefacts or also shared by dromaeosaurids. Thus, the phylogenetic relationships of *Uleghbegsaurus uzbekistanensis* remain uncertain. A giant dromaeosaurid occurred together with the medium-sized tyrannosauroid *Timurlengia euotica* in the Bissekty assemblage.

1. Introduction

The Turonian-age Bissekty Formation in the central Kyzylkum Desert of Uzbekistan has yielded one of the most diverse assemblages of early Late Cretaceous terrestrial and freshwater vertebrates found to date. The dinosaurs from this assemblage include representatives of various clades of non-avian theropods: a tyrannosauroid (*Timurlengia euotica*, Brusatte *et al.* 2016); dromaeosaurids (*Itemirus medullaris* and a large-bodied form, Sues & Averianov, 2014); troodontids (*Urbacodon* sp., Averianov & Sues, 2007); alvarezsaurids (*Dzharaonyx etsi*, Averianov & Sues, 2022); an unnamed ornithomimid; at least two unnamed taxa of therizinosauroids; and a caenagnathid (*Caenagnathasia martinsoni*, Sues & Averianov, 2015). In addition, there are two form taxa for distinctive small theropod teeth, *Richardoestesia americana* and *Paronychodon asiaticus* (Sues & Averianov, 2013; Averianov & Sues, 2019). Recently, Tanaka *et al.* (2021) described what they considered a neovenatorid carcharodontosaurian, *Ulughbegsaurus uzbekistanensis*, which will be further discussed in this paper.

Although almost invariably dissociated, the bones and teeth of these dinosaurs are often exquisitely preserved and provide a wealth of anatomical information. At Dzharakuduk in the Navoi District of Uzbekistan, strata of the Bissekty Formation are widely exposed along an escarpment that extends from approximately 42° 06′ 22.60″ N, 62° 37′ 09.00″ E to 42° 05′ 44.22″ N, 62° 4′ 06.49″ E. The Bissekty Formation encompasses an up to 80 m thick succession of poorly lithified, medium-grained and cross-bedded fluvial sandstones and several laterally extensive, clast-supported intraformational conglomerates (Redman & Leighton, 2009). The Bissekty Formation is underlain by the Dzheirantui Formation and overlain by the Aitym Formation, both of which were deposited in marginal- or shallow-marine environments. Based on the fieldwork by the late Christopher King (pers. comm.), the Dzheirantui Formation can be dated as latest early Turonian based on the co-occurrence of two taxa of inoceramid bivalves, *Mytiloides* aff. *M. labiatus* and *Mytiloides subhercynicus*. The Meshekeli Member of the Aitym Formation is late Turonian primarily based on the presence of the inoceramid *Mytiloides incertus*. Thus, the age of the Bissekty Formation is middle Turonian (Averianov, 2010).

Most bones and teeth of non-avian dinosaurs from the Bissekty Formation have been recovered by surface collecting. As expected in a fluvial depositional setting, many skeletal remains show signs of postmortem transport. For some bones, preservation was further adversely affected by prolonged surface exposure in the harsh present-day desert climate.

Institutional abbreviations: BYU – Museum of Paleontology, Department of Geological Sciences, Brigham Young University, Provo, Utah, USA; CCMGE – Chernyshev's Central
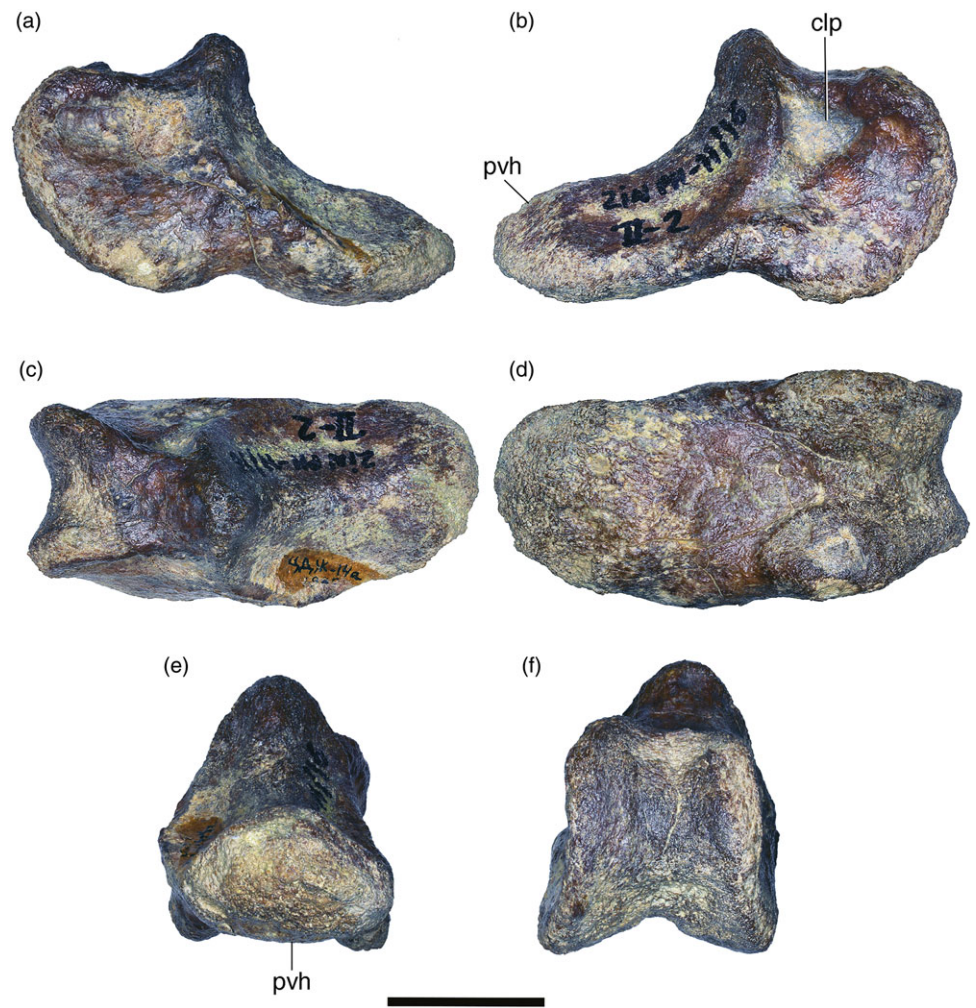
Fig. 1. (Colour online) Eudromaeosauria gen. et sp. indet., Bissekty Formation, left pedal phalanx II-2 (ZIN PH 11/16), in (a) lateral, (b) medial, (c) dorsal, (d) ventral, (e) proximal and (f) distal views. Scale bar = 3 cm. Abbreviations: clp, collateral ligament pit; pvh, posteroventral 'heel'.

Museum of Geological Exploration, Saint Petersburg, Russia; UALVP – University of Alberta Vertebrate Palaeontology Lab, Edmonton, Alberta, Canada; UzSGM – State Geological Museum of the State Committee of the Republic of Uzbekistan on Geology and Mineral Resources, Tashkent, Uzbekistan; YPM – Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; ZIN PH – Zoological Institute, Paleoherpetological Collection, Russian Academy of Sciences, Saint Petersburg, Russia.

2. Systematic palaeontology

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
PARAVES Sereno, 1997
DROMAEOSAURIDAE Matthew & Brown, 1922
EUDROMAEOSAURIA Longrich & Currie, 2009
Gen. et sp. indet.

Sues & Averianov (2014) tentatively assigned all dromaeosaurid bones and teeth to *Itemirus medullaris*, which was originally named on the basis of an excellently preserved partial braincase (Kurzanov, 1976). Further review suggests most of the material represents a small- to medium-sized dromaeosaurid (based on fully closed sutures between the bones of the holotypic braincase and the closed neurocentral sutures on the available vertebrae),

to which we apply the binomen *Itemirus medullaris*, and a very large dromaeosaurid that is the subject of the present study.

A complete left pedal phalanx II-2 ZIN PH 11/16 (Figs 1 and 2c) has a greatest length of 84.5 mm (correcting the measurement in Sues & Averianov, 2014). It was briefly described by Sues & Averianov (2014). The proximal width of this phalanx is 41.3 mm and its distal width is 39.8 mm. The phalanx is proportionately shorter anteroposteriorly and wider transversely than the homologous bones in most known dromaeosaurids except in *Achillobator giganticus* from the Upper Cretaceous (Cenomanian–Santonian) Bayn Shire Formation of Mongolia (Perle et al. 1999, pl. 13; length: 56.4 mm – PJ Currie, pers. comm.). By comparison, pedal phalanges II-2 of the up to 3 m long *Deinonychus antirrhopus*, from the Lower Cretaceous (Aptian–Albian) Cloverly Formation of Montana and Wyoming (Ostrom, 1969), have lengths of up to 49.9 mm (Brusatte et al. 2013), and two pedal phalanges II-2 of *Austroraptor cabazai* from the Upper Cretaceous (Maastrichtian) Formation of Argentina are 58.1 and 58.8 mm long, respectively (Currie & Paulina Carabajal, 2012). The phalanx ZIN PH 11/16 has a long, in dorsal/ventral view lobate proximoventral flange or 'heel' (Fig. 1c, d). The ventral surface of this heel is gently convex transversely rather than flat as in *Deinonychus antirrhopus* (YPM VP.005205). The presence of a well-developed proximoventral heel on pedal phalanx II-2 has been hypothesized as diagnostic for Eudromaeosauria (Longrich & Currie, 2009; Turner et al. 2012). The proximal articular facet extends onto the heel and is
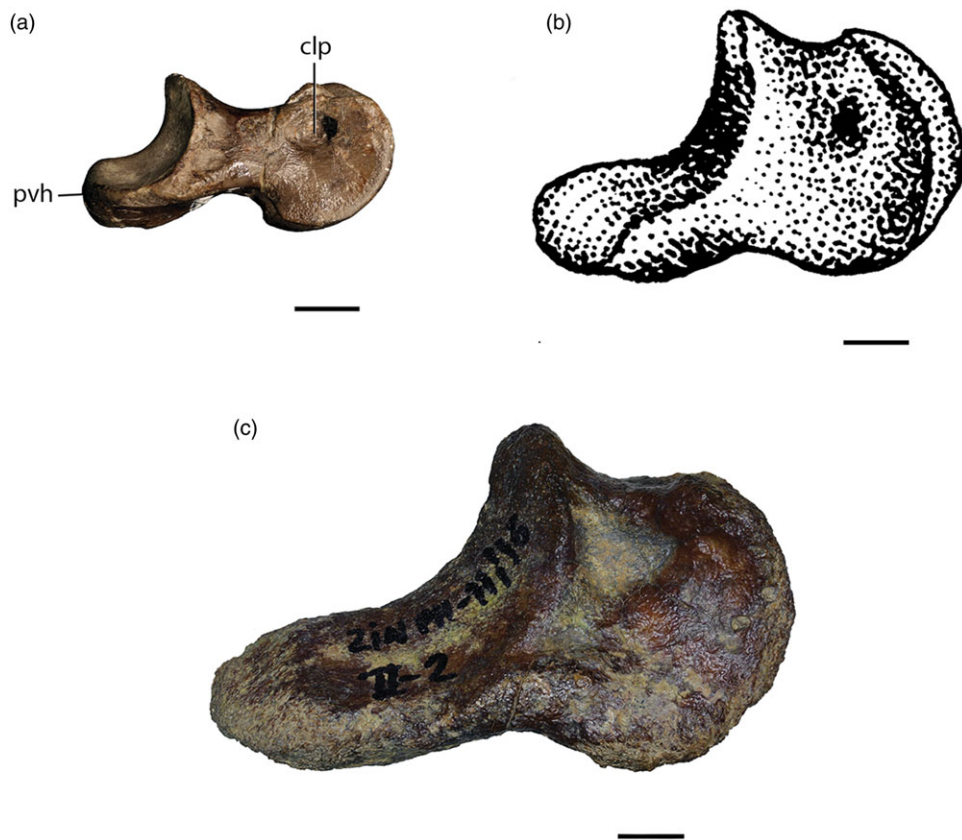
Fig. 2. (Colour online) Pedal phalanges II-2 of (a) *Deinonychus antirrhopus* (YPM VP.005205, reversed), (b) *Achillobator giganticus* and (c) ZIN PH 11/16, shown at the same scale for comparison. (a) Courtesy of DL Brinkman and (b) scanned and reversed from Perle *et al.* (1999, pl. 13). Scale bars each equal 1 cm. Abbreviations: clp, collateral ligament pit; pvh, posteroventral 'heel'.

asymmetrically divided by a median ridge into a lateral and a wider medial articular surface. Its dorsal margin forms a distinct median 'lip'. As in *Achillobator giganticus* (Perle *et al.* 1999; Fig. 2b), the body of the phalanx is only slightly constricted in side view. By contrast, the body has a clearly defined 'neck' between the two articular ends in most other dromaeosaurids such as *Deinonychus antirrhopus* (YPM VP.005205; Fig. 2a). The distal end of ZIN PH 11/16 forms a grooved ginglymoid articular facet, which is semicircular (~180°) in side view and narrower transversely than the proximal facet. As in other dromaeosaurids, its articular facet extends farther proximally onto the ventral surface than onto the dorsal surface of the bone. The lateral and medial surfaces of the distal end of the phalanx bear collateral ligament pits positioned posterodorsal to the geometrical centre of the ginglymus arc. The lateral pit is obscured by tightly adhering matrix whereas the medial pit is well-developed and visible even in dorsal view.

Sues & Averianov (2014) described two fragments of the posterior ends of large maxillae, which closely resemble the post-alveolar portions of the maxillae of *Dromaeosaurus albertensis* (Currie, 1995). The more complete and better-preserved fragment of the posterior portion of a left maxilla (CCMGE 600/12457) is *c.* 150 mm long and preserves the posterior four alveoli and parts of two preceding the former. The posterior ramus of the maxilla extends posteriorly well behind the tooth row, which closely resembles the condition in dromaeosaurids such as *Achillobator giganticus* (Turner *et al.* 2012) and *Dromaeosaurus albertensis* (Currie, 1995) but is also present in some carcharodontosaurians (e.g. *Acrocanthosaurus atokensis*, Currie & Carpenter, 2000).

3. Affinities of *Ulughbegsaurus uzbekistanensis*

Tanaka *et al.* (2021) reported a fragment of a left maxilla of a large theropod from the Bissekty Formation, which they designated as the holotype of a new taxon of neovenatorid carcharodontosaurian, *Ulughbegsaurus uzbekistanensis*. Based on this specimen, the authors argued that the non-avian theropod assemblage from the Bissekty Formation resembles that from the Cenomanian Mussentuchit Member of the Cedar Mountain Formation in Utah (USA), in which the large neovenatorid *Siats meekerorum* (Zanno & Makovicky, 2013) occurred together with the diminutive tyrannosauroid *Moros intrepidus* (Zanno *et al.* 2019). If the identification of *Ulughbegsaurus uzbekistanensis* as a neovenatorid were substantiated, the Bissekty material would represent the geologically youngest example of a non-avian theropod assemblage in which a large carcharodontosaurian co-occurred with a medium-sized tyrannosauroid.

The holotype of *Ulughbegsaurus uzbekistanensis* (UzSGM 11-01-02) is a fragment of a left maxilla without erupted teeth (Fig. 3a, b) from Dzharakuduk. Here we reassess the phylogenetic relationships of this taxon based on the description and figures published by Tanaka *et al.* (2021).

Tanaka *et al.* (2021) listed several purported synapomorphies in support of the referral of *U. uzbekistanensis* to neovenatorid carcharodontosaurians. Firstly, they cited the rugose lateral surface of the holotypic maxilla. Their excellent photographs (Tanaka *et al.* 2021, figs 1a, 2a; Fig. 3a) show that the lateral surface of UzSGM 11-01-02 is badly eroded. The lateral surface of the maxilla fragment presents a distinctly fibrous internal structure, which is
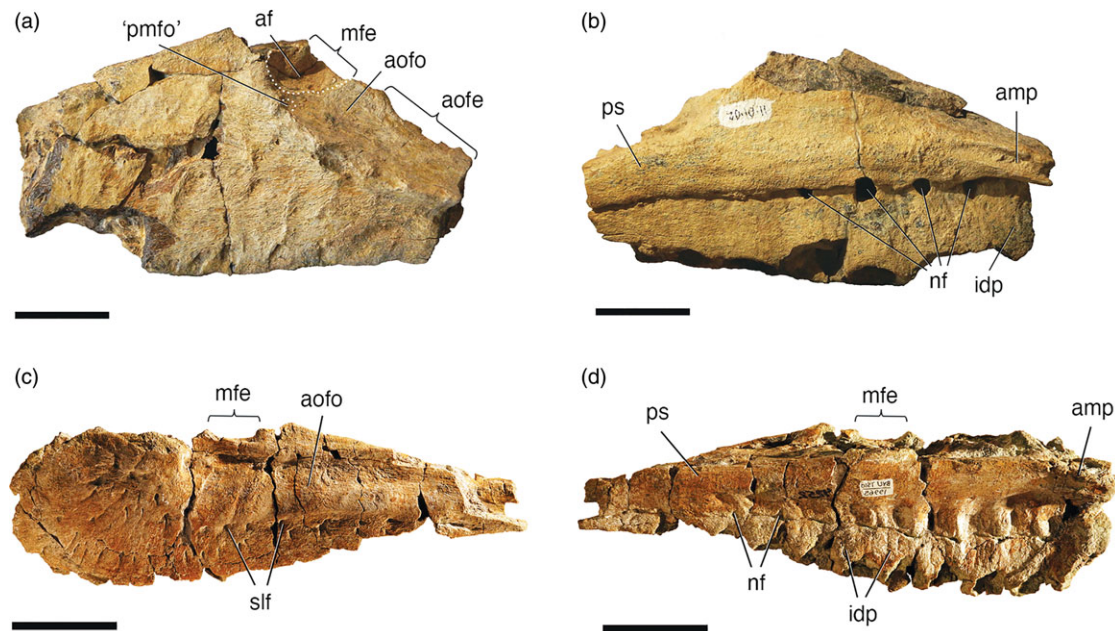
Fig. 3. (Colour online) Partial maxillae of *Ulughbegsaurus uzbekistanensis* (holotype, UzSGM 11-01-02; a, b) and *Utahraptor ostrommaysi* (BYU 19965, reversed; c, d), each in (a, c) lateral and (b, d) medial views. (a, b) From Tanaka *et al.* (2021) – CC BY 4.0. Scale bars each equal 5 cm. Abbreviations: amp, anteromedial process of maxilla; af, accessory fossa; aofe, margin of antorbital fenestra; aofo, antorbital fossa; idp, interdental plate; mfe, maxillary fenestra; nf, nutrient foramen; 'pmfo', 'promaxillary fossa'; ps, palatal shelf; slf, supralabial foramen.

commonly observed on vertebrate bones after prolonged abrasion by sediment-laden flowing water (Behrensmeyer, 1978). Some of the bony fibres cross the margins of eroded neurovascular canals, creating the appearance of 'ridging'. This pattern does not resemble the distinct ridging present on the lateral surface of the maxilla in undisputed carcharodontosaurians such as *Carcharodontosaurus* spp. (Brusatte & Sereno, 2007; Delcourt & Grillo, 2018; Ibrahim *et al.* 2020). Furthermore, we note that maxillae of various other theropods have rugose lateral surfaces with ridges and grooves extending from the neurovascular foramina, including Abelisauridae (Lamanna *et al.* 2002; Sampson & Witmer, 2007), Dromaeosauridae (e.g. *Dromaeosaurus albertensis*, *Utahraptor ostrommaysi*, Fig. 3c) and Tyrannosauridae (e.g. *Tarbosaurus bataar*, Hurum & Sabath, 2003). Thus, rugose lateral surfaces of the maxillae are not unique to carcharodontosaurians and, in the case of UzSGM 11-01-02, this feature is a taphonomic artefact.

Secondly, Tanaka *et al.* (2021) considered the position of what they identified as a 'promaxillary fossa' on the anterior rim of the antorbital fossa as comparable to the condition in allosauroids. Their illustration (reproduced here as Fig. 3a) shows a small, round pit with irregular edges on the rounded anteroventral rim of the antorbital fossa, but it is unclear whether this is a genuine morphological feature or merely taphonomic damage similar to another, larger pit on the margin of the antorbital fossa. A small maxillary foramen is present in this position in *Carcharodontosaurus* spp. (Brusatte & Sereno, 2007) and a large maxillary fenestra in *Neovenator salerii* (Brusatte *et al.* 2008). However, the carcharodontosaurid *Shaochilong moartuensis* lacks such a foramen (Brusatte *et al.* 2010). Given the variability in this feature even among carcharodontosaurians, its diagnostic value is questionable. Dromaeosaurids have promaxillary fenestrae of various sizes (Powers *et al.* 2022).

Thirdly, Tanaka *et al.* (2021) cited the presence of fused, slightly rugose interdental plates in *Ulughbegsaurus uzbekistanensis*. The absence of distinct interdental plates is not restricted to most

but not all allosauroids (Currie, 1995) but is shared by abelisaurids (Lamanna *et al.* 2002; Sampson & Witmer, 2007), the megalosauroid *Torvosaurus* spp. (Britt, 1991; Hendrickx & Mateus, 2014), dromaeosaurids (Currie, 1995; Turner *et al.* 2012) and troodontids (Currie, 1987). By contrast, the tyrannosauroid *Timurlengia euotica* from the Bissekty Formation has distinct interdental plates (Averianov & Sues, 2012). Rugose interdental plates also occur in other non-avian theropods (e.g. *Tarbosaurus bataar*, Hurum & Sabath, 2003).

Fourthly, Tanaka *et al.* (2021) cited the presence of alveoli that are labiolingually narrower than mesiodistally long in *Ulughbegsaurus uzbekistanensis* as a similarity to carcharodontosaurians. However, dromaeosaurids (e.g. *Saurornitholestes langstoni*, UALVP 12339) also have alveoli that are distinctly more narrow labiolingually than long mesiodistally with ratios of labiolingual width to mesiodistal length of *c.* 0.5, comparable to the ratios cited by Tanaka *et al.* (2021) for *Ulughbegsaurus uzbekistanensis*.

We could not identify a single feature that unambiguously supports referral of *Ulughbegsaurus uzbekistanensis* to neovenatorid carcharodontosaurians. Three of the purported synapomorphies cited by Tanaka *et al.* (2021) are also shared by dromaeosaurids. In addition, some features like the sub-vertical contact between the premaxilla and maxilla and the smooth junction between the ventral margin of the antorbital fossa and the lateral surface of the maxilla ventral to this margin (Powers *et al.* 2022) are present in both *Ulughbegsaurus uzbekistanensis* and some dromaeosaurids such as *Utahraptor ostrommaysi* (Fig. 3c,d).

Tanaka *et al.* (2021) presented a phylogenetic analysis that included only allosauroids and tyrannosauroids and excluded all other non-avian theropod clades. This selective taxon sampling assumed relationships a priori and did not allow a comprehensive assessment. Dromaeosaurids such as *Achillobator giganticus* from the Late Cretaceous (Cenomanian–Santonian) Bayn Shire

Formation of Mongolia (Perle *et al.* 1999; Turner *et al.* 2012) and *Utahraptor ostrommaysi* from the Lower Cretaceous (Barremian–Aptian) Upper Yellow Cat Member of the Cedar Mountain Formation of Utah (Kirkland *et al.* 1993) attained linear dimensions comparable to those of other large theropods. Indeed, Tanaka *et al.* (2021) even made reference to ZIN PH 11/16 discussed here.

Tanaka *et al.* (2021) referred the two fragments of maxillae described by Sues & Averianov (2014) to *Ulughbegsaurus uzbekistanensis*, even though there is no anatomical similarity or overlap between the three specimens. They then reconstructed a remarkably long maxilla by combining the holotype and CCMGE 600/12457 (Tanaka *et al.* 2021, fig. S7) and based a high estimate of body size on this reconstruction. However, this reconstruction cannot be justified since there are no anatomical landmarks to associate the two fragments and determine their relative positions.

Tanaka *et al.* (2021) referred CCMGE 600/12457 to *Ulughbegsaurus uzbekistanensis* based on the 'beading' along the ventral rim of the antorbital fossa. This 'beading' on the two jaw fragments is likely not an anatomical feature. For example, the ventral rim of the antorbital fossa on the lateral surface of the maxilla of the *Utahraptor ostrommaysi* is closely associated with a number of neurovascular foramina (Fig. 3c). Even slight surficial erosion would generate 'beads' from the slightly thickened bone around canals associated with these openings. This is clearly evident on the eroded lateral surface of the holotypic maxilla of *Ulughbegsaurus uzbekistanensis* (Tanaka *et al.* 2021, fig. 2b).

The structure of CCMGE 600/12457 resembles that in some carcharodontosaurians (e.g. *Acrocanthosaurus atokensis*, Currie & Carpenter, 2000) but also that in dromaeosaurids such as *Dromaeosaurus albertensis* (Currie, 1995). Tanaka *et al.* (2021) cited the 'approximately 20° ventral orientation at the jugal' as a carcharodontosaurian synapomorphy but their assessment is based only on the referred fragment CCMGE 600/12457. Furthermore, this character-state is also shared by dromaeosaurids such as *Achillobator giganticus* (Perle *et al.* 1999) and *Dromaeosaurus albertensis* (Currie, 1995).

The anteromedial process of the maxilla with a medial horizontal groove for contact with adjacent cranial elements in *Ulughbegsaurus uzbekistanensis* does not resemble the homologous feature in undisputed carcharodontosaurians (e.g. *Neovenator salerii*, Brusatte *et al.* 2008) but matches those in dromaeosaurids (*Dromaeosaurus albertensis*, Currie, 1995; *Utahraptor ostrommaysi*, Fig. 3d).

Among the hundreds of non-avian theropod remains from the Bissekty Formation personally examined by AA and H-DS, there were no bones that could definitively be assigned to carcharodontosaurians. Tanaka *et al.* (2021) surmised that some of the larger isolated teeth assigned to *Timurlengia euotica* (Averianov & Sues, 2012) might belong to carcharodontosaurians. While this cannot be ruled out, at least none of the numerous teeth referred to *Timurlengia euotica* and examined by AA and H-DS shows features inconsistent with attribution to tyrannosauroids.

4. Conclusions

A pedal phalanx II-2 demonstrates the presence of a dromaeosaurid in the Bissekty Formation that attained larger body size than any other known member of this clade. Among dromaeosaurids, several taxa are distinguished by large body size: *Utahraptor ostrommaysi* with a femur length of 56.5 cm (Turner *et al.* 2012); *Austroraptor cabazai*, from the Upper Cretaceous (Campanian–Maastrichtian) Allen Formation of Argentina, with a femur length

of 56 cm (Novas *et al.* 2009); the possibly chimaeric *Dakotaraptor steini*, from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of South Dakota, with a femur length of 55.8 cm (DePalma *et al.* 2015); and *Achillobator giganticus* with a femur length of 55 cm (Turner *et al.* 2012). In addition, isolated teeth from the Lower Cretaceous (Barremian) Wessex Formation of England (Sweetman, 2004) and the Upper Cretaceous (Campanian) Tar Heel Formation of North Carolina (Brownstein, 2018) record dromaeosaurids as large as or larger than *Deinonychus antirrhopus*. The dimensions of the pedal phalanx II-2 of the giant Bissekty dromaeosaurid considerably exceed those of the corresponding phalanges in *Achillobator giganticus* and *Austroraptor cabazai*, respectively. Turner *et al.* (2007) estimated the total length of *Achillobator giganticus* at 4.85 m, and Novas *et al.* (2009) provided an estimate of 5 m for the total length of *Austroraptor cabazai*. *Achillobator giganticus* and *Utahraptor ostrommaysi* are placed in Dromaeosaurinae (Turner *et al.* 2012; Powers *et al.* 2022). By contrast, *Austroraptor cabazai* is a representative of Unenlagiinae, a predominantly South American clade of Dromaeosauridae. Thus, evolution toward very large body-size occurred at least twice among Dromaeosauridae (Wang *et al.* 2022). Giant (>4 m long) dromaeosaurids clearly were apex predators in several Cretaceous terrestrial ecosystems.

The holotypic maxilla of *Ulughbegsaurus uzbekistanensis* presents several features that are found in both carcharodontosaurians and dromaeosaurids. In view of its highly fragmentary nature and the lack of unambiguous apomorphies linking it to any particular clade of non-avian theropods, the phylogenetic position of *Ulughbegsaurus uzbekistanensis* remains unresolved. It does not definitively establish the presence of carcharodontosaurian theropods in the Bissekty Formation. In the absence of autapomorphies or a diagnostic combination of character-states for *Ulughbegsaurus uzbekistanensis*, we also consider this binomen a nomen dubium.

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