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A new dromaeosaurid (Dinosauria: Theropoda) with Asian affinities from the latest Cretaceous of North America

David C. Evans · Derek W. Larson · Philip J. Currie

Abstract Dromaeosaurids from the Maastrichtian of North America have a poor fossil record and are known largely from isolated teeth, which have typically been referred to taxa based on more complete material from earlier Campanian strata. An almost complete maxilla with well-preserved dentition and an associated dentary from the Hell Creek Formation of Montana are used to establish a new dromaeosaurid taxon in the latest Maastrichtian, immediately prior to the end-Cretaceous extinction event. *Acheroraptor temertyorum* gen. et sp. nov. is differentiated from other dromaeosaurids on the basis of a hypertrophied postantral wall that projects posteriorly into the antorbital fenestra, a maxillary fenestra positioned low in the antorbital fossa and directly posterior to the promaxillary fenestra, and distinctive dentition with marked apicobasal ridges. The new material allows a dromaeosaurid from the Maastrichtian of North America to be placed within a phylogenetic framework for the first time. Phylogenetic analysis suggests *Acheroraptor* is a velociraptorine that is more closely related to Asian dromaeosaurids, including *Tsaagan* and *Velociraptor*, than it is to *Dromaeosaurus*, *Saurornitholestes*, or any other taxon from North America.

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As part of the Lancian *Tyrannosaurus–Triceratops* fauna, *A. temertyorum* is the latest occurring dromaeosaurid. Its relationships and occurrence suggest a complex historical biogeographic scenario that involved multiple, bi-directional faunal interchanges between Asia and North America during the Late Cretaceous.

Keywords Dromaeosauridae · Theropoda · Cretaceous · Biogeography

Introduction

Dromaeosaurids are a group of carnivorous theropods notable for their close phylogenetic relationship to Aves. Although dromaeosaurids can be inferred to have originated sometime prior to the Late Jurassic, their fossil record is largely restricted to the Cretaceous (Norell and Makovicky 2004; Turner et al. 2012). Dromaeosaurids had a global distribution during the Late Cretaceous, but their fossil record for this time is generally poor. Despite over a century of sustained collecting, dromaeosaurids from North America remain surprisingly poorly known; only eight species have been named, most of which are based on highly incomplete fossil remains. Two taxa are recorded from the Early Cretaceous. *Deinonychus antirrhopus* from the Lower Cretaceous Cloverly Formation of the western USA is the earliest dromaeosaurid from North America and is known from the most fossil material (Ostrom 1969; Maxwell and Ostrom 1995; Brinkman et al. 1998). *Utahraptor ostrommaysorum* is represented by fragmentary remains from Aptian sediments of the Cedar Mountain Formation of Utah (Kirkland et al. 1993). All other named dromaeosaurids from North America are based on holotype specimens that are Campanian in age. With the exception of *Bambiraptor* (Burnham et al. 2000), these taxa are known only from fragmentary specimens or isolated bones and teeth.

Dromaeosaurus albertensis (Matthew and Brown 1922; Currie 1995), *Hesperonychus elizabethae* (Longrich and Currie 2009), and *Saurornitholestes langstoni* (Sues 1978) are based on incomplete skeletons from the Belly River Group of Alberta. *Saurornitholestes robustus* is known from isolated bones from the Kirtland formation of New Mexico (Sullivan 2006) and may be a nomen dubium (Turner et al. 2012), and the hypodigm of *Atrociraptor marshalli* from the uppermost Campanian strata of the Horseshoe Canyon Formation, Alberta, consists of an associated snout and referred isolated teeth (Currie and Varricchio 2004).

Maastrichtian dromaeosaurids from North America are known only from teeth and isolated bones of limited diagnostic value at low taxonomic levels (Longrich 2008; Sankey 2008). Teeth referred to the genera *Dromaeosaurus*, *Saurornitholestes*, and *Velociraptor* have been reported from Maastrichtian-aged sediments throughout North America, including Alaska, but no associated skeletons or diagnostic cranial material has been reported to date (Sloan et al. 1986; White et al. 1998; Russell and Manabe 2002; Norell and Makovicky 2004; Weishampel et al. 2004; Longrich 2008; Sankey 2008; Horner et al. 2011; Lyson and Longrich 2011). Here, we report on a new dromaeosaurid based on an almost complete maxilla with teeth and an associated dentary that were recently recovered from the same mixed faunal bonebed in the Hell Creek Formation, MT, USA. The maxilla and dentition are variable within deinonychosaurs and preserve morphology considered diagnostic at low taxonomic levels (Currie and Varricchio 2004; Turner et al. 2007; Godefroit et al. 2008; Senter et al. 2010). The new taxon is the first dromaeosaurid named on material from the Maastrichtian of North America, and it adds significant new information on the diversity and biogeography of this group immediately prior to the end-Cretaceous extinction event.

Systematic paleontology

Dinosauria Owen 1842
    Saurischia Seeley 1888
    Theropoda Marsh 1881
    Dromaeosauridae Matthew and Brown 1922
    Velociraptorinae Barsbold 1983
    Acheroraptor temertyorum gen. et sp. nov.

Etymology

The generic name is derived from *Acheron*, the River of Pain in the underworld of ancient Greek mythology, in reference to the Hell Creek Formation, and Latin *raptor*, robber, a suffix used in previously named dromaeosaurids. The name *Acheron* has been deliberately shortened in the combination for euphony. The specific epithet honors James and Louise

Temerty for their outstanding service and contributions to the Royal Ontario Museum.

Holotype

ROM (Royal Ontario Museum) 63777, an almost complete right maxilla, missing only the posterior portion of the jugal ramus and an associated maxillary tooth complete with root.

Referred specimen

ROM 63778, an almost complete left dentary (missing only the teeth and a small posterior portion of the bone) that may pertain to the same individual as ROM 63777.

Horizon and locality

The holotype was found in strata of the Hell Creek Formation (Upper Maastrichtian, Upper Cretaceous), approximately 45 km southwest of the town of Jordan, Garfield County, MT, USA (Fig. S1). The specimen was recovered in situ from a reddish-colored, coarse-grained sandstone containing other small vertebrate fossils and invertebrate shell fragments. The referred dentary, ROM 63778, was found approximately 4 m from the holotype maxilla in the same sandstone-hosted bonebed. Detailed locality data are on file at the ROM.

Comments

The referred dentary (ROM 63778) can be assigned to Dromaeosauridae on the basis of fused interdental plates and the curved dentary ramus with parallel dorsal and ventral margins in lateral view. The corresponding size and close physical association of the holotype maxilla and the dentary in the same bonebed suggest that they may belong to the same individual animal. However, this assignment is inconclusive, and therefore, ROM 63778 is provisionally referred to *Acheroraptor*.

Diagnosis

Mid-sized dromaeosaurid that differs from other eudromaeosaurs in the following characters: relatively small anterior region of the antorbital fossa (defined as the region between the anterior borders of the antorbital fenestra and the antorbital fossa); maxillary fenestra that almost reaches the ventral margin of the antorbital fossa and is positioned directly posterior to the promaxillary fenestra; extensive, posteriorly projected postantral wall that is visible laterally through the antorbital fenestra (convergent in *Austroraptor*); maxillary dentition with unique configuration of prominent apicobasal ridges on both the labial and lingual surfaces of the tooth. *Acheroraptor* can be further differentiated from

Saurornitholestes in having a relatively longer anterior ramus of the maxilla, a much smaller anterior portion of the antorbital fossa, a more robust jugal ramus of the maxilla below the antorbital fossa, and dentition with posterior denticles that are not strongly hooked apically.

Description

Maxilla

ROM 63777 (Fig. 1) consists of an almost complete right maxilla, missing only the posterior portion of jugal ramus. The bone surface preserves excellent anatomical detail, although there is some minor crushing and a large horizontal crack extends through the main body of the specimen. The maxilla is roughly triangular in lateral aspect, with a slightly convex ventral margin of the tooth-bearing ramus, and a long ascending process that extends posterodorsally from the body of the bone. The incomplete alveolar ramus is 92 mm long as preserved and contains nine alveoli. The lateral surface is sculptured above the tooth row and is marked by a series of short, irregular, subvertical grooves that terminate in ventrolaterally directed neurovascular foramina. The anterior margin contacts the body of the premaxilla in a tall butt joint, which continues on the inclined anterodorsal surface of the maxilla as a groove for the subnarial process of the premaxilla. There is no indication that the maxilla contributed to the margin of the naris. The ascending (nasal-lacrimal) process extends posterodorsally from the main body of the bone above the antorbital fenestra. The distal end of this process is bifurcated into dorsal and ventromedial processes; the dorsal process extends between the lacrimal and nasal, and the ventromedial process is overlapped laterally by the lacrimal. The medial surface of the lacrimal-nasal process has a long contact surface for the nasal adjacent to its inclined anterodorsal margin.

The antorbital fossa occupies much of the posterolateral surface of the maxilla, but it is relatively small for a dromaeosaurid (Fig. S3). It is sharply delineated on all sides and has a horizontal ventral margin below the maxillary fenestra. This is unlike the condition in *Bambiraptor* and *Saurornitholestes*, where the ventral margin of the antorbital fossa slopes posteroventrally toward the maxillary tooth row in this region (Currie and Varricchio 2004). The anterior margin of the antorbital fossa is located above the fifth maxillary tooth position, as in *Atrociraptor*, *Saurornitholestes*, and *Velociraptor*. Anterior to the fossa, the anterior ramus of the maxilla (=rostral plate of Godefroit et al. (2008)) is large but shallow for a dromaeosaurid and closely resembles that of *Tsaagan mangas* in its proportions. The lateral lamina extends 42 mm in front of the antorbital fossa and is 37 mm high at the anterior end of the fossa, resulting in a length/height ratio of 1.14. This is similar to

the condition in *T. mangas* (1.13) and *Velociraptor* spp. (1.3–1.38) but contrasts with that of *Atrociraptor* (0.69), *Bambiraptor* (0.62–0.75), *Deinonychus* (0.9), and *Saurornitholestes* (0.8), which have proportionately deeper snouts (Godefroit et al. 2008). The distance between the posterior margin of the interfenestral strut and the anterior margin of the antorbital fossa is only 20 mm. The lateral lamina of the maxilla is approximately twice as long as the latter measurement (ratio=2.25), reflecting the relatively small size of the anterior region of the antorbital fossa. This condition is similar to *T. mangas* (2.1) but contrasts with the proportionately larger anterior region of the antorbital fossa of most Campanian dromaeosaurids from North America, including *Bambiraptor* (lamina length=26 mm, anterior portion of the antorbital fossa=20 mm, ratio=0.7) and *Saurornitholestes* (lamina length=27 mm, anterior portion of the antorbital fossa=26 mm, ratio=1.1).

The anterior portion of the antorbital fossa contains the promaxillary and maxillary fenestrae. The small maxillary fenestra is located in the anteroventral region of a deep, posterodorsally open accessory antorbital fossa, as in *Atrociraptor* and *Saurornitholestes*. The accessory antorbital fossa is separated from the antorbital fenestra proper by a narrow interfenestral strut. A similar combination of characters occurs in *Bambiraptor feinbergi*, *D. antirrhopus*, *S. langstoni*, and *Shanag ashile* (Currie and Varricchio 2004; Turner et al. 2007). The distance between the lower edge of the maxillary fenestra and the dentigerous margin is 23.5 mm, which when divided by the height of the largest maxillary tooth (13.2 mm) results in a ratio of 1.78. This proportion is similar to the condition observed in most dromaeosaurids, in which the height between the maxillary fenestra and the alveolar margin is less than twice that of the height of the largest tooth (1.5–1.6 in *Bambiraptor*, *Deinonychus*, and *Dromaeosaurus*, and 1.8 in *Saurornitholestes)* but contrasts (2.2) with the proportionately deeper maxilla in *Atrociraptor* (Currie and Varricchio 2004). The slit-like promaxillary fenestra is not visible in lateral view. It is located in an anterior pocket along the anterior margin of the antorbital fossa, deep to the lateral lamina of the maxilla. The promaxillary strut is a broad and plate-like sheet of bone, and the outlines of the accessory antorbital fenestrae do not overlap in the vertical plane in lateral view, as they do *A. marshalli*, *T. mangas*, and *Velociraptor osmolskae*. Conversely, the morphology of the promaxillary strut of ROM 63777 more closely resembles that of *B. feinbergi*, *D. antirrhopus*, and *S. langstoni* (Godefroit et al. 2008). ROM 63777 differs from all other known dromaeosaurids in that the ventral margin of the promaxillary fenestra is approximately level with that of the maxillary fenestra, with both situated immediately above the ventral margin of the antorbital fenestra in lateral view (Currie and Varricchio 2004).
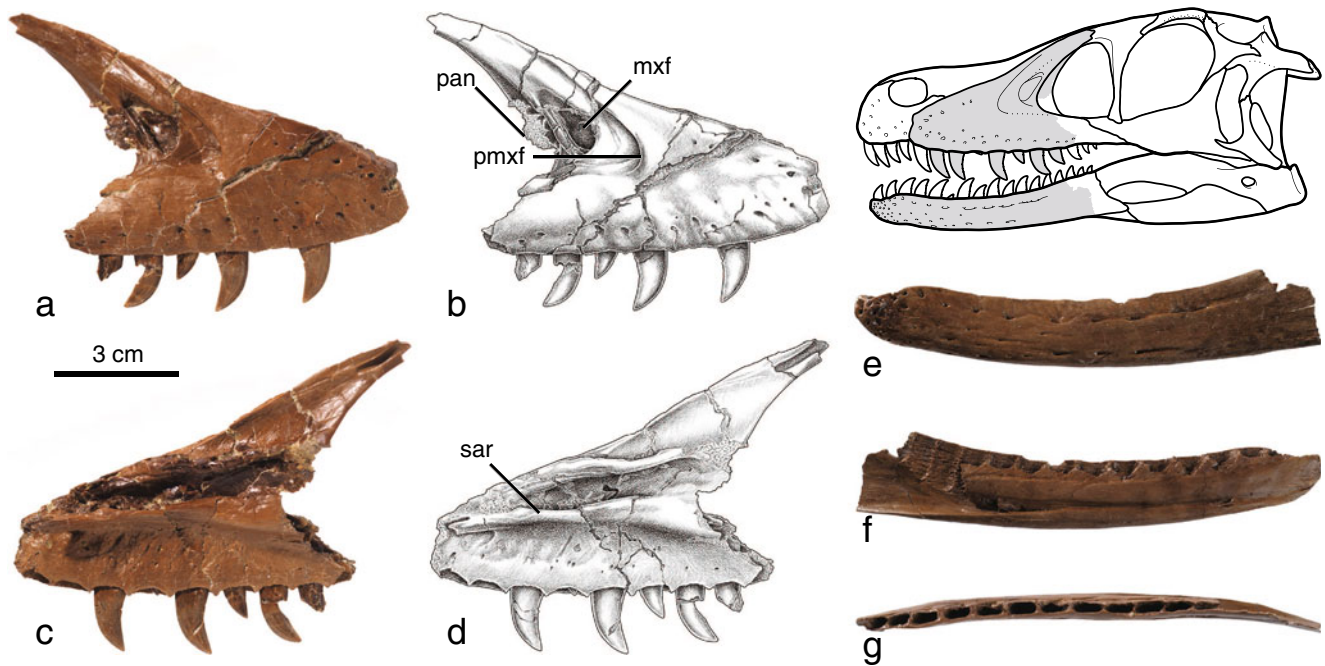
Fig. 1 *Acheroraptor temertyorum*, gen. et sp. nov., holotype maxilla, ROM 63777, in lateral (**a, b**) and medial (**c, d**) views. Referred dentary, ROM 63778 in lateral (**e**), medial (**f**), and dorsal (**g**) views. *mxf* maxillary fenestra, *pan* postantral wall, *pmxf* promaxillary fenestra, *sar* supraalveolar ridge

On the lingual surface of the maxilla, a medially directed horizontal ridge, or ledge (the supraalveolar ridge, Fig. 1), up to 10 mm wide, extends along the entire preserved length of the maxilla. The ridge projects anteriorly to form the base of a well-developed anteromedial process, the anterior end of which is broken, but suggestive that it would have extended well anterior to the main premaxillary–maxillary contact when complete, as in the isolated maxilla referred to *Saurornitholestes* (TMP 1994.012.0844, Currie and Varricchio 2004). The medial surface of the anteromedial process is grooved for contact with the vomer. Below the horizontal ridge, the interdental plates are fused to the maxilla, and each other, as in other dromaeosaurids (Currie and Varricchio 2004). The individual interdental plates can be discerned by subtle textural differences in the surfaces, the interdental plates being more highly vascularized (Currie 1987).

Above the supraalveolar ridge, the maxillary sinus system appears to be divided into a series of chambers that connect with the antorbital, maxillary, and promaxillary fenestrae. The postantral strut (sensu Witmer 1997), a thin sheet of bone, extends dorsally from the medial ridge to the ventromedial surface of the ascending process and encloses a chamber (the maxillary antrum) medial to the maxillary fenestra. The postantral strut forms the medial border of a pocket that extends deep to the interfenestral strut and posterodorsal to the maxillary sinus system. The posterior margin of the postantral strut is broken and fragmented but is complete dorsally, along the posteromedial margin of the ascending (nasal-lacrimal) process. Although broken, it is clear from the preserved morphology that the postantral strut expanded posteriorly as a large sheet of bone that projected into the

antorbital fenestra. This large apron would have been visible in the lateral view of the skull through the antorbital fenestra. A broad, posteriorly projected postantral wall is unusual in dromaeosaurids, where it is known only in *Austroraptor cabazai* (Novas et al. 2008) and *T. mangas* (Norell et al. 2006). Although incomplete, it appears that the posterior development of postantral wall in *Acheroraptor* is much greater than in *T. mangas* (Norell et al. 2006) but is likely not as extensive as in *A. cabazai* (Novas et al. 2008). The medial surface of the maxilla anterior to the postantral strut is crushed, reflecting the delicate nature of the thin sheet of bone that encloses the maxillary sinus system medially. As far as can be discerned, the maxillary sinus system in ROM 63777 is similar to that of *Saurornitholestes* (Currie and Varricchio 2004), *Velociraptor* (Barsbold and Osmólska 1999), and other theropods (Ostrom 1969; Witmer 1997).

Complete tooth crowns of the maxilla are preserved in the third, fifth, and seventh positions, and a complete tooth collected with the specimen probably originated in the second alveolus (Fig. 2; Table S1). The sixth and fourth teeth show successive stages of eruption, and the eighth tooth is present but probably missing at least half of the crown. Teeth show alternating waves of tooth eruption with the pattern of replacement beginning posteriorly and progressing anteriorly, although an X-ray of the specimen reveals little information about the tooth replacement (Fig. S2). This pattern is similar in *B. feinbergi* (Burnham 2004) and *Velociraptor mongoliensis* (Barsbold and Osmólska 1999) but differs from those in *A. marshalli* and *T. mangas* (Norell et al. 2006). The teeth exhibit a number of dromaeosaurid characteristics, including

smaller denticles on the anterior carina than on the posterior carina, strong curvature of the crowns, and lack of any constriction in diameter between the crown and the root. All maxillary teeth are labiolingually narrow, curved, and bladelike. The teeth are roughly perpendicular to the alveolar margin as in most known dromaeosaurids except *Atrociraptor* (TMP 1995.166.0001), *Bambiraptor* (AMNH 30556), and *Deinonychus* (YPM 5232), which have teeth that are posteroventrally inclined (Currie and Varricchio 2004). The third and fifth crowns are the largest and roughly equal in size. Alveolar lengths indicate, however, that the second through fifth teeth were approximately equivalent in size, that the first, sixth, and seventh teeth were slightly smaller, and the eighth and ninth teeth were smaller yet (Table S1). Distinct apicobasal ridges occur on the tooth crowns, and, while the mere presence of ridges is not believed to be of systematic use (Larson 2008), the consistent presence, locations, and prominence of these ridges on ROM 63777 are diagnostic at the species level. The ridges are less pronounced than those described on *Dromaeosaurus* Morphotype A (sensu Sankey et al. 2002; likely referable to *Zapsalis abradens* (Larson and Currie 2013)) and *Paronychodon lacustris*. The ridges are consistently close to the anterior margins of the labial and lingual sides of the crowns. There are two to three ridges on the lingual side and three to four ridges on the labial side, with fewer ridges present on more posterior teeth. The gumline is inclined at an angle of roughly 45° from a horizontal line drawn through the base of the posterior carina (Fig. 2). This is a higher angle than has been described in other dromaeosaurids (Currie et al. 1990).

The denticles on the anterior carinae are much smaller than those on the posterior carinae (Table S2), as in *V. mongoliensis* and all known North American dromaeosaurids other than *D. albertensis* and *U. ostrommaysorum* (Currie et al. 1990; Kirkland et al. 1993). The largest denticles range from 6.6 to 7.8 denticles per millimeter on the anterior carina, and 4.4 to 5.0 per millimeter posteriorly. Anterior denticles are low and rounded on partially erupted teeth but worn on erupted teeth (Fig. 2). As in most other dromaeosaurids, the anterior and posterior carinae lie on the midlines of the maxillary teeth, and the carinae do not twist onto the lingual side as in *Dromaeosaurus* (Currie et al. 1990). Posterior denticles are rounded but are very slightly asymmetrical and apically oriented (Fig. 2), unlike the strongly hooked denticles of *A. marshalli* and *S. langstoni*, but similar to those described in *T. mangas* (Norell et al. 2006). The largest posterior denticles are midway along the posterior carinae but become progressively smaller apically and basally, as is typical in dromaeosaurids. Additionally, the posterior denticles are largest on the second tooth (the first preserved tooth) and decrease in size on more posterior teeth. This pattern does not directly correlate with tooth size. A similar pattern may be present in *A. marshalli* but has not been reported in other dromaeosaurids.

Morphometric analyses (see Electronic Supplementary Information for more details) of tooth measurements from the specimen (Tables S1 and S2) indicate that the teeth are similar to previously collected isolated dromaeosaur teeth from the Hell Creek and Lance formations and that they are more similar to these teeth than any other North American dromaeosaur (Fig. S4).

Dentary

ROM 63778 has 15 alveoli in the preserved section of the almost complete ramus, with the possibility of an estimated one or two additional, missing tooth positions. The alveolar lengths are generally shorter than those in the maxilla (Table S1), which is consistent with the pattern in *Atrociraptor*, *Bambiraptor*, and *Dromaeosaurus* and is thus consistent with the possibility that it is from same individual animal as ROM 63777. Although it lacks preserved teeth, fused interdental plates and a more ventrally positioned Meckelian groove preclude identification of the specimen as pertaining to *Richardoestesia* or Troodontidae, also known from the Hell Creek Formation (Larson and Currie 2013).
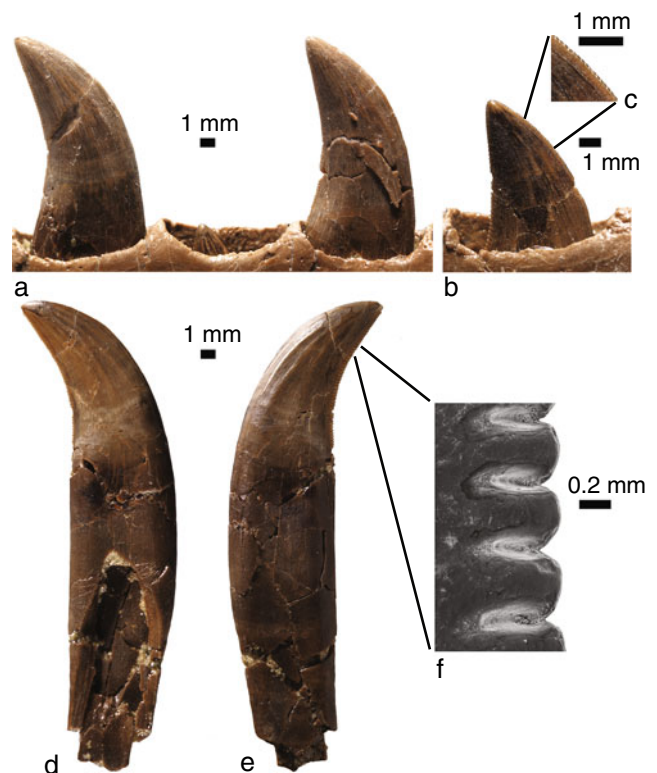
Fig. 2 Dentition of *Acheroraptor temertyorum*, gen. et sp. nov., ROM 63777. **a** Tooth positions 3, 4, and 5 in medial view. **b** Tooth position 6 in medial view, with an enlargement of the anterior denticles (**c**). Isolated tooth, probably from the second alveolus in medial (**d**), and lateral (**e**), views, with scanning electron microscopy enlargement of the posterior denticles (**f**)

The lateral surface of the dentary is perforated by a series of small, irregularly distributed foramina. In lateral view, the dentary is concave dorsally with subparallel dorsal and ventral margins. The anterior terminus of the dentary is deflected from the main ramus to form a slight "chin," unlike *Velociraptor*, in which this feature is strongly developed (e.g., AMNH 6515). The anterior end of the dentary is distinctive in being strongly tapered anterior to the third alveolus in lateral view, as in *Linheraptor exquisitus* and *V. mongoliensis*, but unlike the blunt termini of *Atrociraptor*, *Bambiraptor*, and *Saurornitholestes*, where tapering is less pronounced and restricted more anteriorly. In dorsal view (Fig. 1g), the dentary ramus is virtually straight and would have met the opposing dentary at an acute angle, as in other dromaeosaurids, including *Bambiraptor* and *Deinonychus*.

Phylogenetic analysis

In order to assess the systematic relationships of *Acheroraptor temertyorum*, both holotype and referred specimens were coded into a modified dromaeosaurid data matrix (Longrich and Currie 2009) (see Electronic Supplementary Information for details). Additionally, we tested this hypothesis of relationships by including *A. temertyorum* in the latest analysis of Turner et al. (2012), which constitutes a broader analysis of theropod phylogenetics.

The phylogenetic analysis based on Longrich and Currie (2009) resulted in 90 most parsimonious trees (MPTs), each with a tree length of 237 steps, a Consistency Index of 0.523, a Retention Index of 0.705, and Rescaled Consistency Index of 0.369 (Fig. 3). In the strict consensus topology (Fig. 3; Fig. S6), as in the original analysis (Longrich and Currie 2009), Unenlagiinae and Microraptorinae form successive sister taxa to Eudromaeosauria. *A. temertyorum* is recovered as a velociraptorine eudromaeosaur. An unnamed new taxon from the Senonian-aged Bayanshiree Formation (Turner et al. 2012) is recovered as the sister taxon to all other velociraptorines. Synapomorphies of Velociraptorinae (sensu Longrich and Currie 2009; all taxa more closely related to *V. mongoliensis* than to *D. albertensis*, *S. langstoni*, and *D. antirrhopus*) include a shortened premaxillary body that is at least as tall as long (4[0]) and has limited exposure of the narial fossa on its lateral surface (6[1]). Within this clade, *Acheroraptor* is posited to be the sister-taxon of a clade containing *Adasaurus*, *Tsaagan*, and the two species of *Velociraptor*. Synapomorphies of this clade that are present in *Acheroraptor* include maxillary fenestra positioned low in antorbital fossa (13[0]), an elongate anterior ramus of the maxilla that is longer than tall (16[0]), and anterior denticles smaller than posterior denticles (48[0]). Interestingly, *Velociraptor* is found to be paraphyletic in this analysis, with *V. osmolskae* being more closely related to *Tsaagan* than to

Velociraptor mongolienesis from Mongolia. Although the elongate shape of the maxilla in *V. oskmolskae* is similar to that of *V. mongoliensis*, *V. osmolskae* shares a number of features with *Linheraptor* (Xu et al. 2010a) (here synonymized with *T. mangas* following Turner et al. (2012)) from the same host formation, including a large, teardrop-shaped maxillary fenestra positioned anteriorly within the antorbital fossa (115[1]) and directly above the promaxillary fenestra. The composition of the unresolved Dromaeosaurinae is consistent with the original analysis, but Saurornitholestinae of Longrich and Currie (2009) is found to be paraphyletic, with a clade composed of *A. marshalli* and *D. antirrhopus* having a closer relationship to dromaeosaurines and velociraptorines, than to the sister taxa *Bambiraptor* and *Saurornitholestes*. Running the analysis with scorings from the holotype maxilla (ROM 63777) alone also resulted in 90 most parsimonious trees of 237 steps, with the same strict consensus topology (CI=0.523, RI=0.707, RCI=0.370). Phylogenetic analysis including the isolated dentary as a separate OTU confirms its identification as a eudromaeosaur and does not contradict its referral to *Acheroraptor*.

Inclusion of *Acheroraptor* within a broader analysis of coelurosaur relationships (Turner et al. 2012) produced 9600 MPTs of 2042 steps that resulted in a strict consensus tree where Eudromaeosauria is largely collapsed into a polytomy (Fig. S5). The results of this analysis are not inconsistent with the results presented above based on Longrich and Currie (2009), which provides greater resolution within the dromaeosaur in-group.

Discussion

The Hell Creek Formation and contemporaneous deposits that date from the late Maastrichtian of North America have been extensively sampled for more than a century, in part because these strata provide the only high-resolution record of terrestrial vertebrate faunas through the last several million years of the Cretaceous and into the Palaeocene. As such, they are important for understanding dinosaur diversity and ecology just prior to the end-Cretaceous extinction event. These intensive collecting efforts have yielded over 300 associated or articulated skeletons to date (Lyson and Longrich 2011). The large-bodied dinosaur fauna is well known (White et al. 1998; Russell and Manabe 2002; Lyson and Longrich 2011; Horner et al. 2011) and is represented by dozens of exquisitely preserved skulls and skeletons of *Edmontosaurus*, *Triceratops*, and *Tyrannosaurus*. Despite this intense sampling, phylogenetically informative remains of small-bodied taxa are scarce (White et al. 1998; Horner et al. 2011), which may be the result of strong taphonomic biases against the preservation of small skeletons (e.g., Brown et al. 2013; Evans et al. 2013). Associated skeletons of

Fig. 3 Time-calibrated strict consensus of 90 most parsimonious trees recovered in phylogenic analysis of Dromaeosauridae, showing only relationships of Eudromaeosauria. *Acheroraptor temertyorum*, gen. et sp. nov., is found to be more closely related to Asian velociraptorines than to any North American taxon. Silhouettes correspond to continental areas used in biogeographic optimizations (see text for discussion). For complete phylogenies, see Figs. S5 and S6
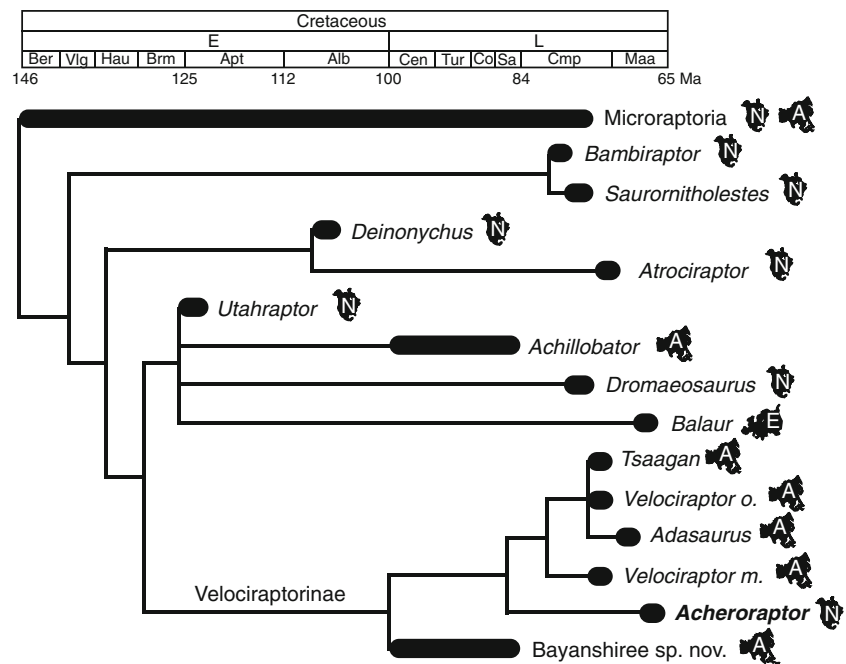
maniraptoran dinosaurs are completely unknown (Horner et al. 2011; Lyson and Longrich 2011), and by any count, dromaeosaurids represent less than 3 % of the total dinosaur fossil assemblage (White et al. 1998; Russell and Manabe 2002; Horner et al. 2011).

Prior to the discovery of ROM 63777, dromaeosaurids from the Maastrichtian deposits of North America were known predominantly from isolated teeth. Recent studies of small theropod teeth from the Upper Maastrichtian Lance and Hell Creek formations have predicted the presence of a new, unknown dromaeosaurid species on the basis of the unique morphology of isolated teeth that are identical to those of ROM 63777 (Longrich 2008; Larson and Currie 2013). Authors (Longrich 2008; Sankey 2008; Larson and Currie 2013) have differed in opinion on how many taxa are likely represented by isolated teeth from these units. Some isolated specimens with matching size and denticle morphology lack the distinct apicobasal ridges (Longrich 2008; Sankey 2008), and it is uncertain whether a lack of ridges indicates taxonomic or individual (including positional) variation. Canonical variate analyses indicate that the maxillary teeth preserved in ROM 63777 fall within the range of variation of a large sample of dromaeosaurid teeth from the Lance and Hell Creek formations; they are more similar to these isolated dromaeosaurid teeth than to any other small theropod tooth morphotypes from these formations (Fig. S4a), indicating that most of these isolated teeth likely belong to *Acheroraptor*. Similar analyses conducted on a larger sample of Campanian and Maastrichtian dromaeosaurid teeth (Larson and Currie 2013) suggest *Acheroraptor* teeth are closer morphologically to Lance and Hell Creek dromaeosaurid teeth than to any other

dromaeosaurid (Fig. S4b). However, Lance and Hell Creek teeth are dimensionally similar to teeth from the Dinosaur Park Formation referred to *S. langstoni*. We therefore concur with previous studies (Estes 1964; Longrich 2008) that there is little evidence for more than a single dromaeosaurid taxon, *A. temertyorum*, in the Hell Creek-Lance assemblages, suggesting a low diversity of this group just prior to the end-Cretaceous extinction event.

A. temertyorum is the last known dromaeosaurid in North America, and one of the latest occurring dromaeosaurids in the world, although the precise age of presumably slightly older Maastrichtian taxa from Europe, such as *Balaur bondoc* (Brusatte et al. 2013) and Asia, such as *Adasaurus mongoliensis*, are not established with certainty. As such, *Acheroraptor* extends our knowledge of dromaeosaurid morphological diversity in the latest Maastrichtian. The maxilla is a diagnostic bone in dromaeosaurids (Godefroit et al. 2008), and the unique morphology of ROM 63777 can be differentiated from other members of this clade on the basis of three autapomorphies: hypertrophied postantral wall that projects posteriorly into the antorbital fenestra, a maxillary fenestra located low in the antorbital fossa and directly posterior to the promaxillary fenestra, and distinctive dentition with rounded denticles and prominent apicobasal ridges. Unlike other North American dromaeosaurids, *Acheroraptor* has a relatively long anterior projection of the maxillary body anterior to the antorbital fossa, as in *Tsaagan* and *Velociraptor*, suggesting it also had a relatively long snout compared to other taxa from the Late Creteceous of North America.

This material allows a Maastrichtian dromaeosaur from North America to be put into a detailed phylogenetic context for the first time. Several features of the maxilla clearly set *Acheroraptor* apart from other North American taxa and suggest close affinities to Asian velociraptorines. *Acheroraptor* is posited as the sister-taxon to a clade of *Adasaurus*, *Tsaagan*, and *Velociraptor* and is nested within Velociraptorinae, which otherwise consists of only Asian forms. Although dromaeosaurid relationships remain controversial (Longrich and Currie 2009; Turner et al. 2012), within the context of this analysis, Velociraptorinae (sensu Longrich and Currie 2009) is inferred to have originated in Asia, and the lineage that includes *Acheroraptor* represents a dispersal event from Asia to North America, possibly during the Late Campanian. Fitch optimization of continental areas (Eurasia and North America) onto the resulting cladogram (Fig. 3) suggests a complex biogeographic scenario for Eudromaeosauria that involved several dispersal events in both directions across the Bering Strait in the Late Cretaceous: at least once from North America to Asia, and at least once in the opposite direction involving the *Acheroraptor* lineage. This is significant given that a predominant direction of dispersal from Asia to North America has been suggested for many other vertebrate groups prior to the Campanian (Russell 1993). However, recent phylogenies of ceratopsians (Xu et al. 2010b), pachycephalosaurs (Schott et al. 2009; Evans et al. 2013), tyrannosaurs (Brusatte et al. 2010), lambeosaurine hadrosaurids (Evans 2010), and saurolophine hadrosaurids (Prieto-Márquez 2010) show evidence of intercontinental dispersal back to Asia via Beringia within the Campanian (Sampson et al. 2011). This historical biogeographic analysis of dromaeosaurids provides new evidence for a more complex pattern of faunal interchange between North America and Asia than has been previously recognized in the latest Cretaceous. With its strong similarities to Asian velociraptorines, the occurrence of *Acheroraptor* suggests that immigration from Asia also played an important role in the assembly of North American Maastrichtian dinosaur communities.

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