

A New Troodontid Theropod Dinosaur from the Lower Cretaceous of Utah

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Abstract

Background: The theropod dinosaur family Troodontidae is known from the Upper Jurassic, Lower Cretaceous, and Upper Cretaceous of Asia and from the Upper Jurassic and Upper Cretaceous of North America. Before now no undisputed troodontids from North America have been reported from the Early Cretaceous.

Methodology/Principal Findings: Herein we describe a theropod maxilla from the Lower Cretaceous Cedar Mountain Formation of Utah and perform a phylogenetic analysis to determine its phylogenetic position. The specimen is distinctive enough to assign to a new genus and species, *Geminiraptor suarezarum*. Phylogenetic analysis places *G. suarezarum* within Troodontidae in an unresolved polytomy with *Mei*, *Byronosaurus*, *Sinornithoides*, *Sinusoanaxus*, and *Troodon* + (*Saurornithoides* + *Zanabazar*). *Geminiraptor suarezarum* uniquely exhibits extreme pneumatic inflation of the maxilla internal to the antorbital fossa such that the anterior maxilla has a triangular cross-section. Unlike troodontids more closely related to *Troodon*, *G. suarezarum* exhibits bony septa between the dental alveoli and a promaxillary foramen that is visible in lateral view.

Conclusions/Significance: This is the first report of a North American troodontid from the Lower Cretaceous. It therefore contributes to a fuller understanding of troodontid biogeography through time. It also adds to the known dinosaurian fauna of the Cedar Mountain Formation.

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Introduction

The family Troodontidae and its sister family Dromaeosauridae make up the clade Deinonychosauria [1]. Deinonychosauria, the sister taxon to Avialae, is a member of the theropod clade Coelurosauria [1]. Members of Troodontidae are gracile bipeds with an enlarged ungual on the second toe of each foot. They have been reported from the Upper Jurassic and Lower Cretaceous of China [2–5], the Lower and Upper Cretaceous of Mongolia [6–9], and the Upper Cretaceous of North America [10]. A tooth from the Upper Jurassic Morrison Formation of Utah has been referred to Troodontidae [11], but this assignment has been questioned [1]. A coelurosaurian skeleton from the Morrison Formation of Wyoming is possibly troodontid [12], but to date a description has not been published. Before now, no description has been published of an undisputed troodontid from North American sediments that predate the Late Cretaceous. Here we report the discovery of a troodontid maxilla from the basal Cedar Mountain Formation (Lower Cretaceous, Barremian?) of Utah.

Methods

Phylogenetic Analysis

We entered data from the new specimen into a phylogenetic data matrix of Coelurosauria from a recent study [13] (Appendix

S1). All characters were left unordered. The non-coelurosaurian theropods *Dilophosaurus*, *Allosaurus*, and *Sinovenator* were used as outgroups. The matrix from that study [13] was based on one published previously [14] but included updates and corrections that are delineated and justified elsewhere [13]. Phylogenetic analysis was performed with PAUP 4.0 for Windows [15]. A heuristic search with 1000 random addition-sequence replicates was performed, with no limit to “maxtrees.”

Results

Systematic Paleontology

Systematic hierarchy:

Dinosauria Owen, 1841 [16]

Saurischia Seeley, 1887 [17]

Theropoda Marsh, 1881 [18]

Coelurosauria von Huene, 1914 [19]

Troodontidae Gilmore, 1924 [20]

Geminiraptor gen. nov.

urn:lsid:zoobank.org:act:57057FD5-AB25-43F1-A9AA-C3C2E51B0C9F

Geminiraptor suarezarum sp. nov.

urn:lsid:zoobank.org:act:4B950765-6016-4FC8-96ED-2219112C6E48

Holotype. The holotype specimen is CEUM (College of Eastern Utah Prehistoric Museum, Price Utah) 7319, a maxilla (Fig. 1).

Etymology. The species name refers to Drs. Celina and Marina Suarez, the twin geologists who discovered the Suarez site. The genus name is from the Latin *gemmae* (“twins,” in honor of the Suarez sisters) and *raptor* (“one who seizes or takes by force,” a common part of deinonychosaurian genus names).

Locality and horizon. The specimen is from the Suarez site [21], a dinosaur bonebed (dominated by the therizinosaurid *Falcarius*) in the lower Yellow Cat Member (Lower Cretaceous: Barremian?) [22] of the Cedar Mountain Formation (Fig. 2). The site is in western Grand County, Utah.

Diagnosis. Troodontid possessing a maxilla with extensive pneumatization internal to the antorbital fossa, inflating the bone so that it has a triangular cross-section; a large, craniocaudally elongate maxillary fenestra; a promaxillary fenestra that is visible in lateral view; craniocaudally narrow promaxillary strut and interfenestral strut; small, square dental alveoli with bony septa between them.

Specimen Description

The maxilla is craniocaudally long and dorsoventrally low. The process dorsal to the external antorbital fenestra is horizontal, as in

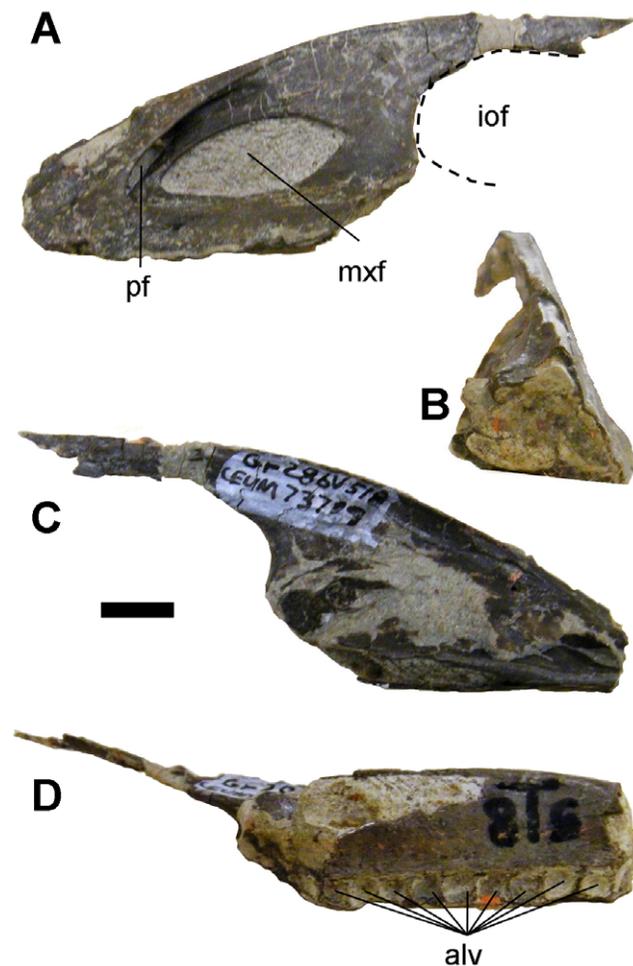


Figure 1. Maxilla of *Geminiraptor suarezarum*. (A)—Lateral view. (B)—Cranial view. (C)—Medial view. (D)—Ventral view. Scale bar = 10 mm. alv = dental alveoli, iof = internal antorbital fenestra, mx = maxillary fenestra, pf = promaxillary fenestra. doi:10.1371/journal.pone.0014329.g001

CEDAR MOUNTAIN FM. Yellow Cat Mbr. (In part)

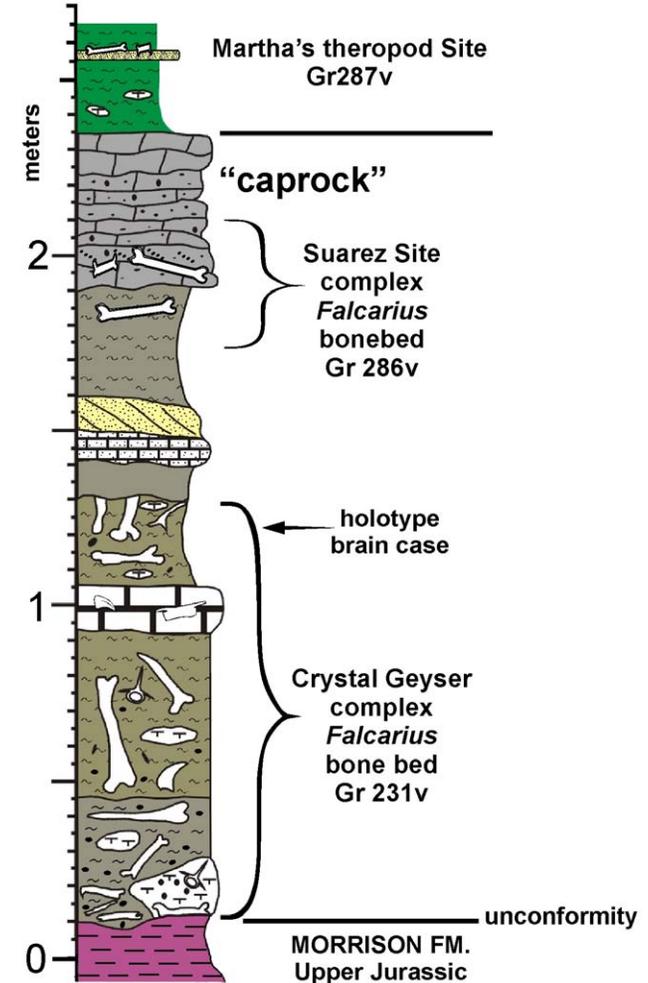


Figure 2. Stratigraphic setting of *Geminiraptor suarezarum*. doi:10.1371/journal.pone.0014329.g002

the troodontids *Byronosaurus* [8], *Sauromithoides* [9], and *Zanabazar* [9] (Fig. 3). The cranial tip of the maxilla is missing, as is the portion of the bone ventral to the internal antorbital fenestra. The preserved portion of the maxilla is 95 mm long, 30 mm tall, and 20 mm wide at the sixth preserved alveolus. Due to preservation, it is not possible to determine whether the maxilla participated in the border of the external naris.

The antorbital fossa occupies a large portion of the lateral surface of the maxilla cranial to the internal antorbital fenestra, as in other troodontids [2,4,8,9], dromaeosaurids [23–26], and the basal bird *Archaeopteryx* [27]. The promaxillary fenestra is visible in lateral view, as in *Archaeopteryx* [27], dromaeosaurids [23–26], the basal troodontid *Sinovenator* [2], and the troodontid *Sinusoanax* [4]. In contrast, the promaxillary fenestra has been lost or has become confluent with the maxillary fenestra in the troodontids *Sauromithoides* and *Zanabazar* [9]. In *Geminiraptor* the promaxillary fenestra is situated at the cranial end of the antorbital fossa. Infilling by matrix prevents determination of its exact dimensions, but the height of the opening is 8 mm or less. The maxillary fenestra of *Geminiraptor* is a large, craniocaudally elongate oval, as

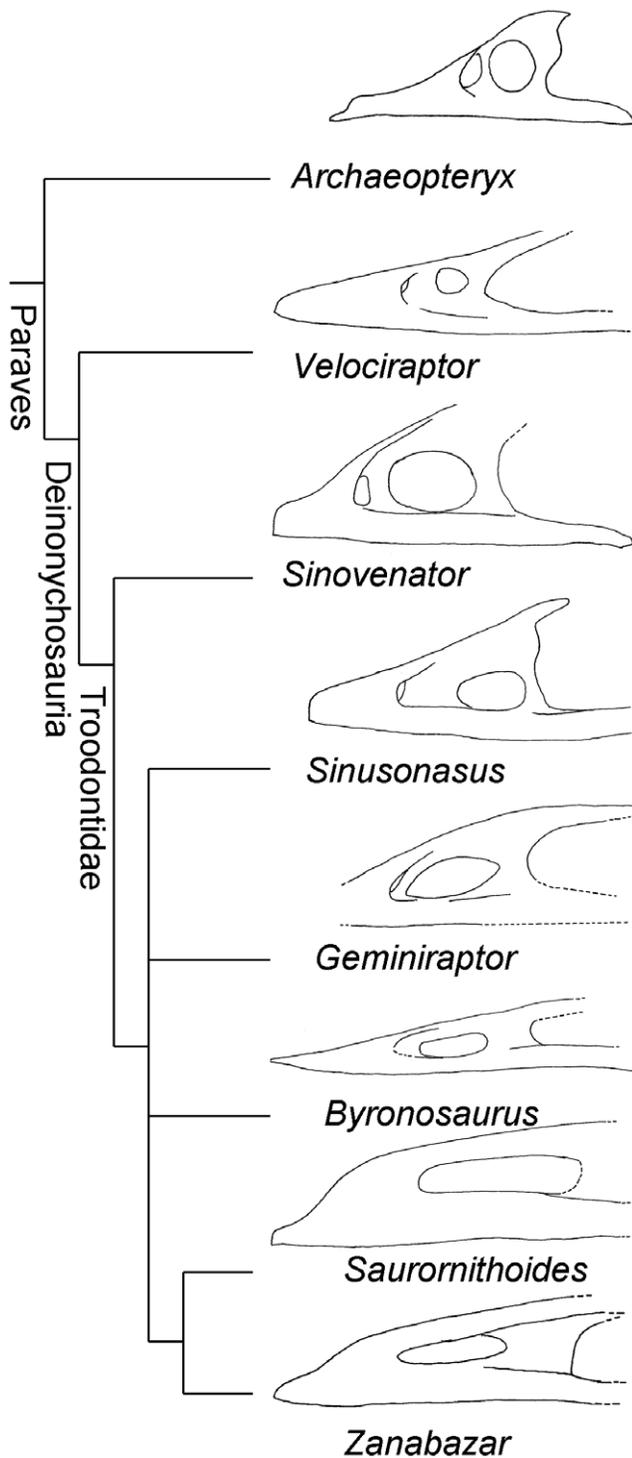


Figure 3. Comparison of the maxilla of *Geminiraptor suarezarum* to those of other paravians. Maxillae are drawn from photos by P.S. of AMNH (American Museum of Natural History, New York City, New York) FR 6515 (*Velociraptor*), IVPP V 12615 (*Sinovenator*), IVPP V 11527 (*Sinusonasus*), CEUM 7319 (*Geminiraptor*), IGM (Mongolian Institute of Geology, Ulaan Baatar, Mongolia) 100/983 (*Byronosaurus*), AMNH FR 6516 (*Saurornithoides*), and IGM 100/1 (*Zanabazar*); and reference 18 (*Archaeopteryx*).

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in *Troodon*, *Saurornithoides*, and *Zanabazar* [9,10]. It is 27 mm long and 10.4 mm high. As in most other deinonychosaurs [2,3,4,23–26] the fenestra does not reach the cranial margin of the antorbital fossa. In this respect *Geminiraptor* differs from *Troodon*, *Saurornithoides*, and *Zanabazar*, in which the maxillary fenestra reaches the cranial margin of the antorbital fossa [9,10]. The promaxillary strut, the vertical bar of bone between the promaxillary fenestra and the maxillary fenestra, is craniocaudally narrow in *Geminiraptor*, as in *Sinovenator* [2] and unlike the craniocaudally wide promaxillary strut of *Sinusonasus* [4]. In *Geminiraptor* the interfenestral strut, the vertical bar of bone between the maxillary fenestra and the internal antorbital fenestra, is not recessed inward from the lateral surface of the maxilla. The strut is craniocaudally narrow as in *Sinovenator* [2] and *Sinusonasus* [4] and unlike the craniocaudally wide interfenestral strut in *Byronosaurus*, *Saurornithoides*, and *Zanabazar* [8,9].

The maxilla of *Geminiraptor suarezarum* is remarkable in that it is inflated medially by a large pneumatic chamber that gives the maxilla a triangular cross-section such that there is a broad, ventrally convex shelf lingual to the tooth row. The bone surrounding this cavity is only ~2 mm thick. Such extensive pneumatization of this part of the maxilla is unreported in any other theropod except *Byronosaurus*. In *Byronosaurus* the medial wall of the inflated portion is vertical, so a triangular cross-section is absent [8]. In other theropods the maxillary antrum (the space within the inflated area) communicates with the maxillary fenestra [28], although obscuration by matrix prevents confirmation of this in *Geminiraptor*. In *Geminiraptor* the maxillary antrum appears to be closed off from the nasal cavity by a thin medial wall, as is the case in other coelurosaurs [28], including other troodontids [8,9].

The preserved portion of the maxilla includes alveoli for nine small teeth, dorsal to which is a row of neurovascular foramina on the lateral surface of the maxilla. After comparison with the maxillae of other deinonychosaurs, we estimate that the complete maxilla held at least three more teeth in the missing cranial part and at least seven more in the missing caudal part. The alveoli are square in occlusal view. No tooth crowns or roots are preserved. The alveoli are closely spaced but separated by complete septa. This is significant because in most other troodontids complete septa are absent [10,29–31], although P.S. has observed that they are present in the basal troodontid *Sinovenator changii*, IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China)V 12615. There is no break between the septa and the labial surface of the maxilla and therefore no discrete interdental plates.

Phylogenetic Analysis

The phylogenetic analysis found 1944 trees of 1285 steps. For these trees the consistency index is 0.3416, the homoplasy index is 0.6537, the retention index is 0.7711, and the rescaled consistency index is 0.2670. The strict consensus tree places *G. suarezarum* within Troodontidae in an unresolved polytomy with *Mei*, *Byronosaurus*, *Saurornithoides*, *Sinusonasus*, and the clade *Troodon* + (*Saurornithoides* + *Zanabazar*) (Fig. 4). Successive outgroups to this polytomy are the troodontid *Sinovenator*, the troodontid *Anchiornis*, Dromaeosauridae, and Avialae. Outside Troodontidae the topology of the tree is identical to that found by the latest study that used the present data matrix [13], as is the decay index (Bremer support) at all nodes but one. As in the latest analysis [13], the decay index is a robust 8 for Paraves, a robust 4 for Deinonychosauria, 1 for Troodontidae, and 1 for *Troodon* + (*Saurornithoides* + *Zanabazar*). The decay index dropped from 3 in the previous analysis [13] to 1 in the current analysis, at the node

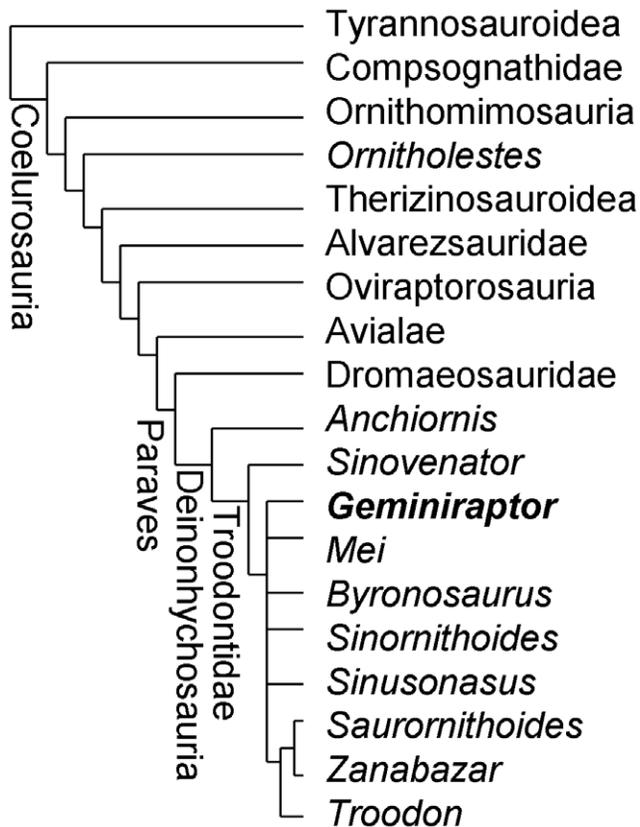


Figure 4. Phylogeny of coelurosaurian theropod dinosaurs, showing phylogenetic position of *Geminiraptor suarezarum*. See text for details of phylogenetic analysis.
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uniting *Sinovenator* with troodontids other than *Anchiornis*. This drop likely reflects the huge amount of missing data for *Geminiraptor*.

Geminiraptor is united with troodontids other than *Anchiornis* by presence of a large number of small teeth (character 85, state 1); the plesiomorphic condition, present in *Anchiornis* and most other theropods, is a small number of larger teeth (state 0). *Geminiraptor* is united with troodontids other than *Anchiornis* and *Sinovenator* by the presence of a maxillary fenestra in the form of a large, cranio-caudally elongate oblong (character 240, state 1); in *Anchiornis*, *Sinovenator*, and most other theropods the maxillary fenestra is large and round (state 0) (Fig. 3). A maxillary fenestra in the form of a large, cranio-caudally elongate oblong is unknown outside Troodontidae. Also, the general shape of the maxilla, with its long, low profile, is similar to that of advanced troodontids (Fig. 3), and the bone exhibits no morphology that is inconsistent with troodontid affinity. The presence of interdental septa is shared with *Sinovenator* and non-troodontid theropods and is consistent with a relatively basal position within the family.

Discussion

The discovery of *G. suarezarum* adds to the known diversity of the dinosaur fauna of the Cedar Mountain Formation. As the only Lower Cretaceous troodontid reported from North America it also increases the known temporal distribution of the family on the

continent. It was already known that troodontids were present in Asia and North America during the Late Jurassic [5,12] and the Late Cretaceous [8–10], and we now know that they were present on both continents during the Early Cretaceous as well. This indicates that the family underwent multiple transcontinental dispersal events through its history. However, there are not yet enough data to determine the direction of dispersal or the family's continent of origin.

Geminiraptor is considerably larger than other Early Cretaceous troodontids [2–4,6] and Jurassic troodontids [5] and is similar in size to the Late Cretaceous troodontids *Byronosaurus* [8], *Troodon* [10], *Sauromithoides* [9], and *Zanabazar* [9]. Its presence in the Early Cretaceous therefore demonstrates that the larger body size characteristic of Late Cretaceous troodontids had already appeared in the Early Cretaceous.

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Supporting Information

Appendix S1

Found at: doi:10.1371/journal.pone.0014329.s001 (0.16 MB DOC)

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Author Contributions

Analyzed the data: PS. Wrote the paper: PS, JK. Performed field work: JK. Performed lab work: JB, JAB.

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