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A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah

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Therizinosauroids are an enigmatic group of dinosaurs known mostly from the Cretaceous period of Asia, whose derived members are characterized by elongate necks, laterally expanded pelves, small, leaf-shaped teeth, edentulous rostra and mandibular symphyses that probably bore keratinized beaks^{1,2}. Although more than a dozen therizinosauroid taxa are known, their relationships within Dinosauria have remained controversial because of fragmentary remains and an unusual suite of characters. The recently discovered 'feathered' therizinosauroid *Beipiaosaurus* from the Early Cretaceous of China helped to clarify the theropod affinities of the group³. However, *Beipiaosaurus* is also poorly represented. Here we describe a new, primitive therizinosauroid from an extensive paucispecific bonebed at the base of the Cedar Mountain Formation (Early Cretaceous) of east-central Utah^{4,5}. This new taxon represents the most complete and most basal therizinosauroid yet discovered. Phylogenetic analysis of coelurosaurian theropods incorporating this taxon places it at the base of the clade Therizinosauroiden, indicating that this species documents the earliest known stage in the poorly understood transition from carnivory to herbivory within Therizinosauroida. The taxon provides the first documentation, to our knowledge, of therizinosauroids in North America during the Early Cretaceous.

Theropoda Marsh 1881

Coelurosauria von Huene 1914

Therizinosauroida Maleev 1954

Falcarius utahensis gen. et sp. nov.

Etymology. From *Falcarius* (Latin, a sickle-maker) and *utahensis* (refers to Utah as its place of origin).

Holotype. Utah Museum of Natural History; UMNH VP 15000 partial braincase (Fig. 1b, c).

Referred specimens (paratypes). Utah Museum of Natural History; UMNH VP 12279–12443, 14524–14999, 15001–15149.

Horizon and locality. The Crystal Geyser Quarry, Grand County, Utah, lies at the base of the Cedar Mountain Formation, directly but disconformably overlying the Upper Jurassic Morrison Formation (UMNH VP locality no. 157). The basal Yellow Cat Member is estimated to be Barremian in age on the basis of the preserved dinosaur fauna (the polacanthine ankylosaur *Gastonia*, the ornithomimid *Iguanodon*, three species of sauropods, and large and small theropods such as *Utahraptor* and *Nedcolbertia*^{4,5}), charophytes⁴ and palynomorphs (D. Eberth and B. Britt, personal communication 2004).

Diagnosis. *Falcarius* is a maniraptoran theropod diagnosed by the following suite of unique characters from holotype braincase: expansive, open pneumatic cavities in basioccipital and basisphenoid with the basisphenoidal recess directed ventrally; and extensive subcondylar pneumatic recesses lateral to the occipital condyle. From paratype elements: presence of one enlarged tooth at anterior-most end of dentary; laterally deflected and biconcave apex of the deltopectoral crest; posterior tuberosity on the distal end of the humerus opposite the radial condyle; flexor tubercle of phalanx I–II with well-defined collateral pits on the distal aspect; and the unique combination of the following features: dentary lacking lateral shelf found in other therizinosauroids; mid-caudal vertebrae elongate with zygapophyses less than one-third the length of centrum as opposed to shortened vertebrae in other therizinosauroids and oviraptorosaurs.

Description. *Falcarius* is a gracile, small- to medium-sized theropod, approximately 1 m in height at hips and 4 m in length. The specimens referred to this taxon account for approximately 90% of the skeleton (Figs 1 and 2).

Skull material is underrepresented and currently includes a left maxilla, right postorbital, paired frontals, two braincases, isolated juvenile basiocciput, left and right quadrates, one left and two right dentaries, and a right splenial. As in *Erlikosaurus*⁶, the number of maxillary neurovascular foramina is reduced to approximately one slit-like foramen for every three alveoli. The quadrates are anteriorly arched with large pneumatic fossae. The frontals are subrectangular, as in dromaeosaurids and oviraptorosaurs, with similarly inflated cerebral fossa (Fig. 1). The fossa for the olfactory bulb is approximately two-thirds as wide as the cerebral fossa. The paroccipital processes are more slender and elongate than in derived therizinosauroids and are pneumatized via caudal tympanic recesses (Fig. 1). The basioccipital is pocketed ventrolaterally by extensive subcondylar recesses that encompass two openings for cranial nerves X–XI and a single opening for XII. *Falcarius* lacks a dorsoventral expansion of the paroccipital process and a ventral pneumatic inflation of the basisphenoid, the derived condition found in both *Erlikosaurus*⁶ and *Nothronychus*⁷.

The dentary deepens posteriorly, but lacks the lateral shelf and down-turned symphyseal region possessed by all other known therizinosauroids^{2,3,6} (Fig. 2). The dentary is medially curved anteriorly, indicating the presence of a U-shaped snout as in other therizinosauroids^{2,6} and oviraptorosaurs⁸.

The dentary teeth share several features with the teeth of other therizinosauroids (Fig. 2). Similarities include posteriorly small, lanceolate and basally constricted crowns that become taller anteriorly, as well as the presence of inflated, circular roots. Also, in contrast to other therizinosauroids, conical teeth are present in the anteriormost portion of the dentary in *Falcarius*. The first alveolus of the dentary is hypertrophied and apparently housed a tooth with twice the cross-sectional area of more posterior tooth positions. This condition is comparable to the enlarged premaxillary teeth of the primitive oviraptorosaur *Incisivosaurus* (= *Protoarchaeopteryx*⁹), although its anterior dentary is

edentulous¹⁰. The preserved teeth of the fragmentary maxilla have lower tooth crowns that decrease in size posteriorly (Fig. 2). The denticles on all teeth are small (7–10 mm⁻¹), unlike other therizinosauroids (Fig. 2).

The vertebral column is well represented with the exception of the axis. Anterior cervical centra are amphicoelous, elongate (length four times height) and highly pneumatized, with multiple, small pneumatic foramina. As in derived therizinosauroids^{2,11–13} and oviraptorosaurs¹⁴, cervical neural arches are low and elongate and zygapophyses become more widely spaced posteriorly (giving the neural arch an X-shape in dorsal view). Dorsal neural arches have large transverse processes supported by multiple laminae, short neural spines that thicken dorsally, and thick hyposphenohypantrum articulations. There are five sacral vertebrae as in *Alxasaurus*¹², in contrast to six preserved in *Neimongosaurus*¹⁵ and *Segnosaurus*¹⁶, with the intermediate three possessing pneumatic fossae. Medial to distal caudals are more than four times as long as high. All caudal vertebrae seem to be apneumatic with loss of caudal ribs and neural spines distal to caudals 11–13 (Fig. 1), in contrast to

the condition in derived oviraptorosaurs¹³ and derived therizinosauroids^{2,13}.

The coracoids are strongly recurved with a pronounced ventral tubercle. As in more derived therizinosauroids, the humeri have an angular internal tuberosity, cranially positioned distal condyles and a hypertrophied entepicondyle^{1,2}. The humeral shaft lacks both the posterior tuberosity of more derived therizinosauroids^{1,2,16–19} and the anterior tuberosity proximal to the entepicondyle of *Neimongosaurus*¹⁵ and *Erliaosaurus*²⁰. The ulna is bowed with a robust olecranon process. The radius is straight and lacks the biceps tubercle seen on *Neimongosaurus*¹⁵. The manus is relatively gracile and elongate, as in *Beipiaosaurus*³ and many oviraptorosaurs¹⁴ (Fig. 1). Distal carpals are preserved in two morphs: one fused into a semilunate that caps metacarpals I and II, and the other as unfused pairs of distal carpals as in other therizinosauroids². Metacarpal I exhibits a rectangular buttress on its proximoventral surface, similar to that of *Alxasaurus*¹².

The pelvis is primitive in that the ilium is relatively elongate anteroposteriorly, with a parasagittal dorsal margin lateral to the

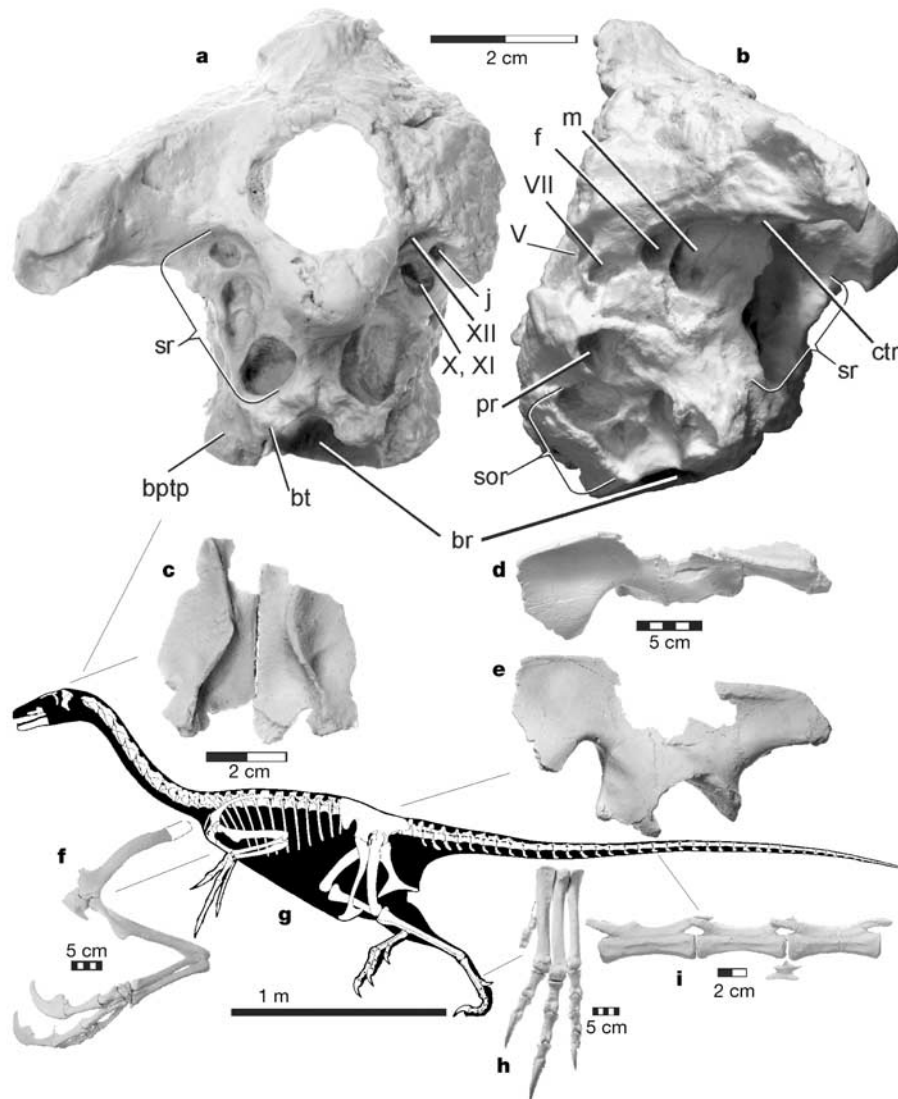


Figure 1 Skeletal elements of *Falcarius utahensis*. **a, b**, Holotype braincase UMNH-VP 15000 in posterior (**a**) and lateral (**b**) views; **c**, paired frontals UMNH VP 14524, 14525 in ventral view; **d, e**, left ilium UMNH VP12368 in dorsal (**d**) and lateral (**e**) views; **f**, reconstructed right pectoral girdle UMNH VP 12279, 12281 and forelimb UMNH VP 12284, 12287, 12289, 12291, 12294–12296, 12298, 12300, 12302, 12314, 12304, 12306, 12308, 12310, 12312, 12316, 12320 in lateral view; **g**, *Falcarius* skeletal

reconstruction; **h**, reconstructed left foot UMNH-VP 12330–12342, 12352–12356 in anterioposterior view; **i**, medial caudal vertebrae UMNH VP 12405, 12407, 12409 with chevron UMNH VP12391 in lateral view. bptp, basipterygoid process; br, basisphenoidal recess; bt, basitubera; ctr, caudal tympanic recess; f, fenestra ovalis and fenestra pseudorotunda; j, jugular foramina; m, metotic fissure; pr, prootic recess; sor, subotic recess; sr, subcondylar recess; roman numerals represent cranial nerves.

sacral transverse processes (Fig. 1), the pubis has not rotated to an opisthpubic condition, and the obturator process does not contact the pubis. The pubic peduncle is also primitive, being wide and dorsoventrally shallow. Derived therizinosauroid characters of the pelvis include a deep, strongly hooked and laterally flaring preacetabular process, and a dorsoventrally shortened postacetabular process of the ilium². The acetabulum of *Falcarius* is anteriomedially directed, a condition also present in *Neimongosaurus*¹⁵.

As with the forelimb, the hindlimb of *Falcarius* is relatively elongate and slender, with an anteriorly bowed femur estimated at approximately 85% tibial length. The lesser trochanter is alar, separated from the greater trochanter by a deep, narrow cleft. The tibia is gracile with a pronounced fibular crest. As in other therizinosauroids^{2,3,12,13}, the proximal fibula lacks the medial fossa found on most maniraptorans. The distal tibia is surrounded by the astragalus, unlike the reduced condition in other therizinosauroids². The ascending process of the astragalus is tall and nearly symmetrical, unlike the shortened, asymmetrical morphology of *Therizinosaurus*²¹. The functionally tridactyl pes is similar to that of *Beipiaosaurus*³ and oviraptorosaurs¹⁴ and unlike the functionally tetradactyl pes of all other known therizinosauroids^{1,2} (Fig. 1).

A phylogenetic analysis (Fig. 3) provides strong support for the hypothesis that *Falcarius* is the basalmost therizinosauroid known. *Falcarius* possesses several maniraptoran synapomorphies not previously documented in basal therizinosauroids, including hypapophyses on the presacral vertebral column, bowed ulna, presence of a semilunate comprised of fused distal carpals one and two, ischium less than two-thirds pubis length, and distally positioned obturator process of the ischium^{22–25}.

Therizinosauroids are here proposed as shifting their dietary habit from predation to herbivory on the basis of the development of a number of features that seem convergent with clades of other herbivorous dinosaurs. The most significant of these features include small, leaf-shaped teeth, an edentulous beak, posterior displacement of the pubis and lateral expansion of the pelvis associated with greatly increased intestinal volume^{1,26}, and shortening of the tibia relative to the femur and an increased number of weight-supporting pedal digits—the latter two being specific reversals of the cursorial

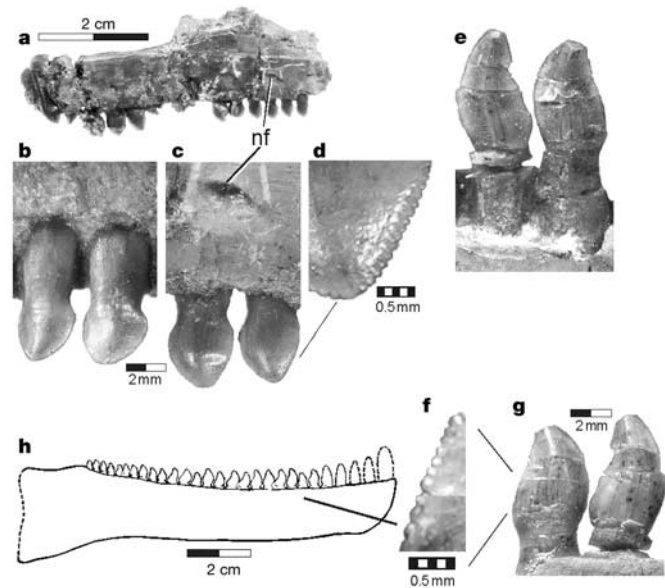


Figure 2 Jaws and teeth of *Falcarius utahensis*. **a**, Partial left maxilla UMNH VP 14526 in lateral view; **b**, **c**, close-up of maxillary teeth in lingual (**b**) and labial (**c**) views; **d**, detail of maxillary tooth denticles in labial view; **e**, dentary teeth UMNH VP 14527 in lingual view; **f**, detail of dentary tooth denticles in labial view; **g**, same dentary teeth in labial view; **h**, composite reconstruction of the dentary of *Falcarius* based on UMNH VP 14527, UMNH VP 14528 and UMNH VP 14529. nf, nutritive foramina.

condition. *Falcarius* demonstrates the mosaic nature of this evolutionary transition, indicating that the dentition and pelvis were among the first hard-tissue structures to undergo modification. These changes probably coincided with modifications in food acquisition and digestion during the early stages of therizinosauroid

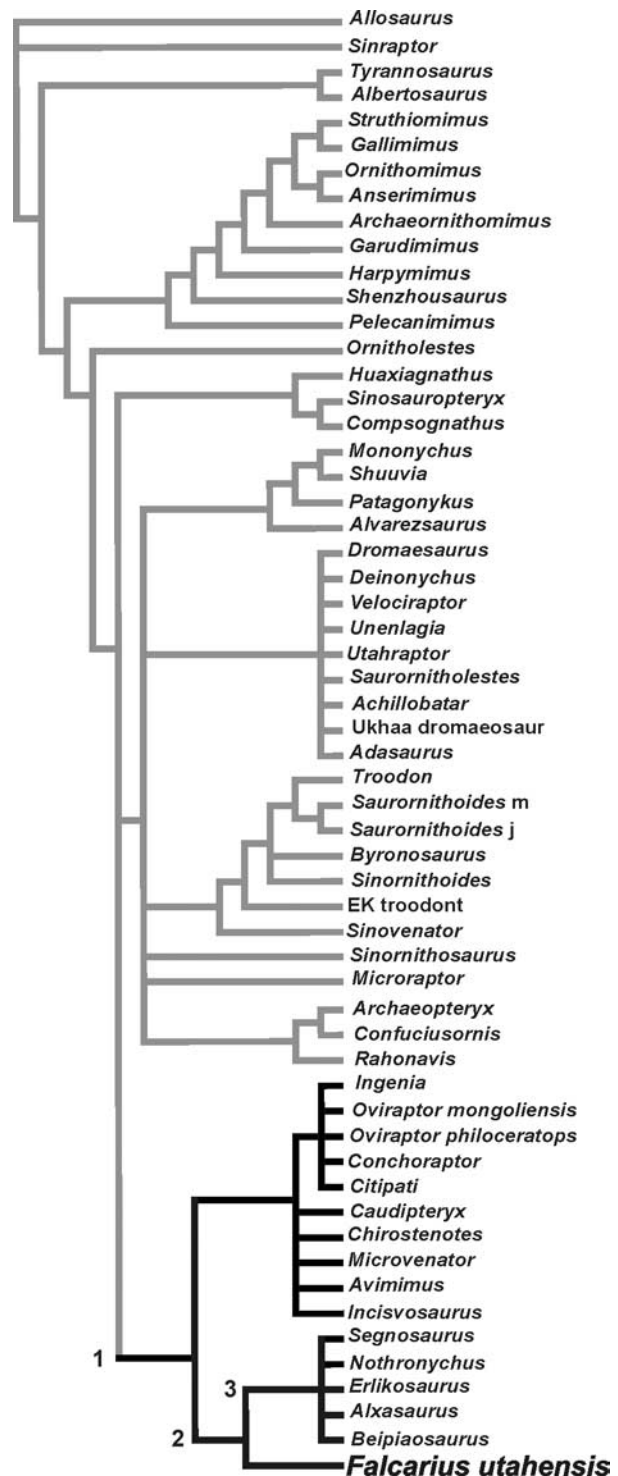


Figure 3 Phylogenetic relationships of *Falcarius* among the Coelurosauria. Strict consensus of 5,000 trees with the following statistics: treelength 679; Consistency Index, 0.41; Retention Index, 0.74; Rescaled Consistency Index, 0.31. Therizinosauroidae + Oviraptorosauria (node 1), Therizinosauroidae (node 2): Therizinosauroidae more derived than *Falcarius* (node 3). Character states defining these nodes are discussed in Methods. Advent of dietary shift from carnivory to herbivory is postulated to occur at base clade 1 (shaded black).

evolution. Moreover, similarities between the dentition of the basal therizinosaur *Falcarius* and the basal oviraptorosaur *Incisivosaurus*, in combination with their proposed sister relationship (Fig. 3), raises the possibility that the common ancestor of these clades had already undertaken the initial steps in this transition.

The Early Jurassic Chinese jaw from the Lufeng Series in southern China described tentatively as the basal therizinosaurid *Eshanosaurus*²⁷ is more derived in having a lateral shelf and down-turned symphysis, which are absent in *Falcarius*. Its therizinosaurid identification have been considered problematic by some authors^{13,25}. *Falcarius* casts further doubt on the affinities of *Eshanosaurus* by increasing its stratigraphic and phylogenetic inconsistency. Given the discovery of North American members of the therizinosaurid clade, together with the poor record of Middle Cretaceous dinosaurs, it seems that the generally accepted hypothesis of an Asian origin and radiation for Therizinosauridae^{1,2} requires additional testing. □

Methods

Collections from the Crystal Geyser Quarry made so far preserve a minimum of ten individuals based on prepared femora, but the quarry size indicates that perhaps hundreds of disarticulated individuals remain interred, representing multiple growth stages as well as robust and gracile morphotypes. The locality spans about 8,000 m² and the bone-bearing stratum is, on average, 1 m thick, with bone densities in some areas exceeding 100 elements per cubic metre. There is no evidence of another small theropod taxon, so all of the therizinosaurid materials are here referred to *Falcarius*. In addition to the therizinosaurid elements, the quarry contains rare remains of an unidentified ankylosaur. About 99% of all identified bones from the type locality (about 2,000 identifiable bones) represent *Falcarius*.

Several features of these fossils, including neurocentral fusion and fusion of cervical ribs to the vertebrae, indicate that the largest elements represent adult or near-adult individuals. Dorsal ribs and gastralia are the most poorly represented with only two dorsal ribs and one gastralia identified, although many bone fragments in the quarry are thought to be unidentifiable pieces of rib. There are multiple examples of nearly all bones, although much excavation and preparation remains before a detailed taphonomic analysis can be attempted. Overlapping examples of the largest elements are close to the same size, indicating that mature animals had restricted growth. Additionally, associated elements (particularly appendicular elements) indicate the relative proportions of skeletal elements in some individuals. The skeletal reconstruction of *Falcarius* in Fig. 1 was based on the largest preserved elements in the quarry, with vertebral numbers estimated on changing proportions of the vertebrae and comparisons with other maniraptoran theropods.

Phylogenetic relationships were analysed with the use of data from published sources supplemented with novel information (see Supplementary Information). Parsimony analysis of 57 taxa and 231 characters was performed with PAUP 4.0b10 (ref. 28), with all characters weighted equally and a single character ordered, using *Allosaurus* and *Sinraptor* as outgroups (Fig. 3).

Five unambiguous synapomorphies support Therizinosauridae: teeth serrated (reversal); ventral surface of dentary descends strongly posteriorly; ventral edge of anterior ala of ilium hooked anteriorly; distal humerus with large medial condyle, centred on distal end; and preacetabular portion of ilium laterally flaring. The basal position of *Falcarius* is supported by the absence of the following characters: labial face of dentary with lateral ridge and inset tooth row; interdental plates on dentary; obturator process of ischium does not contact pubis; metatarsal I without proximal articulating surface. Therizinosauridae + Oviraptorosauria characterized by basiptyergoid processes abbreviated or absent; suborbital fenestra reduced in size or absent; basiptyergoid processes hollow; symphyseal region of dentary strongly recurved; maxillary and dentary teeth lanceolate and subsymmetrical.

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Discovery of the first Asian plethodontid salamander

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Nearly 70% of the 535 species of salamanders in the world are members of a single family, the Plethodontidae, or lungless salamanders¹. The centre of diversity for this clade is North and Middle America, where the vast majority (99%) of species are found. We report the discovery of the first Asian plethodontid