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A gigantic feathered dinosaur from the Lower Cretaceous of China

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Numerous feathered dinosaur specimens have recently been recovered from the Middle–Upper Jurassic and Lower Cretaceous deposits of northeastern China, but most of them represent small animals[1]. Here we report the discovery of a gigantic new basal tyrannosauroid, *Yutyrannus huali* gen. et sp. nov., based on three nearly complete skeletons representing two distinct ontogenetic stages from the Lower Cretaceous Yixian Formation of Liaoning Province, China. *Y. huali* shares some features, particularly of the cranium, with derived tyrannosauroids[2,3], but is similar to other basal tyrannosauroids[4–12] in possessing a three-fingered manus and a typical theropod pes. Morphometric analysis suggests that *Y. huali* differed from tyrannosaurids in its growth strategy[13,14]. Most significantly, *Y. huali* bears long filamentous feathers, thus providing direct evidence for the presence of extensively feathered gigantic dinosaurs and offering new insights into early feather evolution.

The Tyrannosauroidea was one of the longest-lived theropod subgroups, with a fossil record extending from the Middle Jurassic to the uppermost Cretaceous[2]. Basal tyrannosauroids are relatively small, and gigantic ones (adult body mass greater than 1,000 kg) are almost entirely restricted to the latest Cretaceous[2,15]. Four tyrannosauroid taxa have recently been reported from the Lower Cretaceous of China[6,8,9,15,16], although the provenance of one of them, *Raptorex kriegsteini*, has been seriously questioned[17]. These taxa range from 1.4 m to about 10 m in body length[6,8] and show considerable morphological disparity: some taxa closely resemble the highly specialized Tyrannosauridae[9,16], whereas others are more similar to generalized coelurosaurs[6,8]. Combined with discoveries from outside China, these morphologically and taxonomically diverse basal tyrannosauroid specimens document the occurrence of a significant radiation in the early history of the group.

Here we report the discovery of a new feathered tyrannosauroid (Figs 1 and 2 and Supplementary Figs 1–3) from the Lower Cretaceous of China that is close to some Late Cretaceous tyrannosauroids in adult size (Supplementary Information). Phylogenetic analyses using two different theropod matrices place this taxon among basal tyrannosauroids, but relatively close to the Tyrannosauridae (Fig. 3 and Supplementary Information). In combination with other recent discoveries, such as that of the similarly sized *Sinotyrannus* from the Lower Cretaceous of Liaoning[8], the new find demonstrates that tyrannosauroids were the dominant large predators in the middle Early Cretaceous ecosystems of northeastern China, suggesting that the ecological dominance of the group was achieved early in their evolution in some geographical regions at least.

Theropoda Marsh, 1881
Coelurosauria sensu Gauthier, 1986
Tyrannosauroidea Osborn, 1905
Yutyrannus huali gen. et sp. nov.

Etymology. The generic name is derived from 'yu' (Mandarin for 'feathers') + 'tyrannus' (Latin for 'king' or 'tyrant'). The specific name 'huali' means 'beautiful' in Mandarin, referring to the beauty of the plumage of this animal.
Holotype. ZCDM (Zhucheng Dinosaur Museum, Shandong) V5000, a semi-articulated, nearly complete skeleton. A cast of the specimen is housed at the Institute of Vertebrate Paleontology and Paleoanthropology as IVPP FV1960.
Paratypes. ZCDM V5001, a nearly complete, articulated skeleton; and ELDM (Erlianhaote Dinosaur Museum, Inner Mongolia) V1001, an articulated skeleton missing the tail. Casts of these specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology as IVPP FV1961 and IVPP FV1962, respectively.
Horizon and locality. Batuyingzi, Beipiao, Liaoning Province, China; Lower Cretaceous Yixian Formation[18].
Diagnosis. A gigantic tyrannosauroid distinguishable from other tyrannosauroids by the unique presence of a rugose, highly fenestrated midline crest formed by the premaxillae and nasals, an anteroventrally projecting orbital process in the area of the junction between the frontal and jugal processes of the postorbital, a large concavity on the lateral surface of the main body of the postorbital, and an external mandibular fenestra located mostly within the surangular. Also differs from *Sinotyrannus* in that the morphologically lateral surface of the maxillary process of the premaxilla faces dorsally, the maxilla lacks an anterior ramus, the maxillary fenestra is posteriorly positioned, the antorbital fossa has a posteroventrally sloping ventral margin, and the ilium has a straight dorsal margin and a postacetabular process whose ventral margin bears a lobe-like flange.
Description and comparisons. ZCDM V5000 probably represents an adult individual, given that the neurocentral sutures on all of the visible vertebrae are closed and the sacrals are fused together. With a femoral length of 85 cm, ZCDM V5000 even exceeds the adult sizes of some Late Cretaceous tyrannosauroids, such as *Dryptosaurus* (77 cm) and *Appalachiosaurus* (79 cm). ZCDM V5000 is estimated to have had a mass of about 1,414 kg as a living animal, on the basis of an empirical equation[19], and ZCDM V5001 and ELDM V1001 are estimated to have had respective masses of 596 kg and 493 kg. Both ZCDM V5001 and ELDM V1001 display fusion features, such as visible neurocentral sutures on all of the presacral vertebrae, suggesting an ontogenetic stage considerably earlier than that inferred for ZCDM V5000. On the basis of data on the growth of other large tyrannosauroids[13], ELDM V1001 is estimated to be at least 8 years younger than ZCDM V5000.

The most striking cranial feature of *Y. huali* is a highly pneumatic midline crest resembling those of *Guanlong*[7] and the carcharodontosaurian *Concavenator*[20], although in *Y. huali* the crest is formed by premaxillary and nasal portions that are only loosely articulated with each other. The dorsal margin of the crest bears a series of low prominences that are likely to be homologous to the rugosities seen in all Late Cretaceous tyrannosauroids[9]. The cranium of *Y. huali* also exhibits some features that occur consistently in basal, but not derived,

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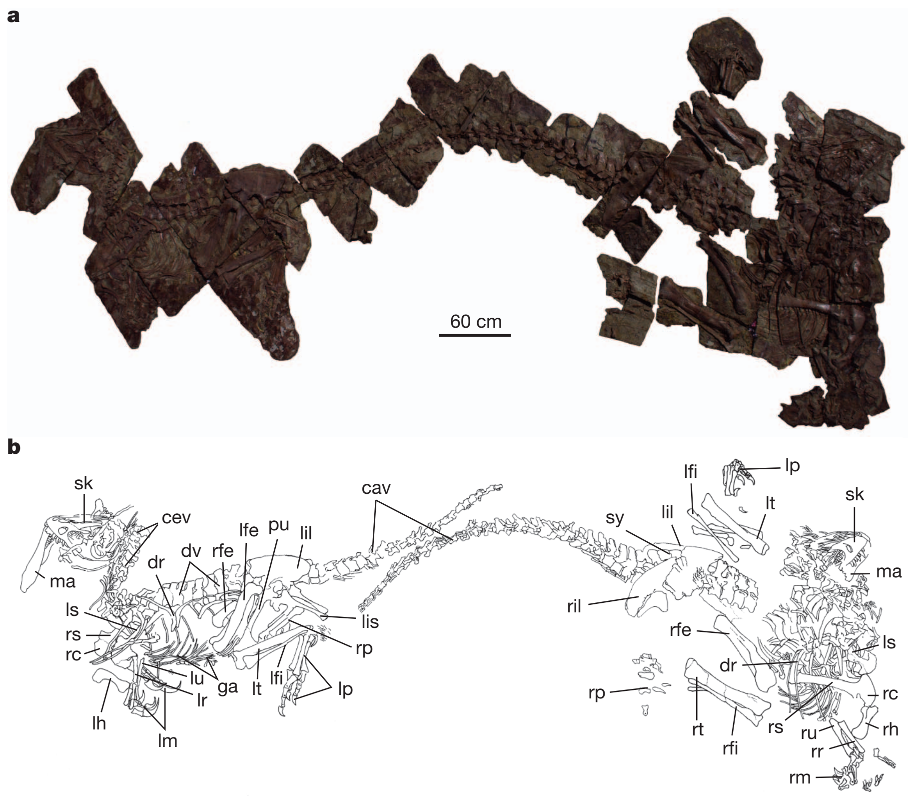

Figure 1 | ***Yutyrannus huali*** **(ZCDM V5000 and ZCDM V5001).** **a**, Photograph of the slab preserving ZCDM V5000 and ZCDM V5001. **b**, Line drawing of the slab. Abbreviations: cav, caudal vertebra; cev, cervical vertebra; dr, dorsal rib; dv, dorsal vertebra; ga, gastralia; lfe, left femur; lfi, left fibula; lh, left humerus; lil, left ilium; lis, left ischium; lm, left manus; lp left pes; lr, left radius; ls, left scapula; lt, left tibiotarsus; lu, left ulna; ma, mandible; pu, pubis; rc, right coracoid; rfe, right femur; rh, right humerus; ril, right ilium; rm, right manus; rp, right pes; rr, right radius; rs, right scapula; rt, right tibiotarsus; ru, right ulna; sk, skull; sy, synsacrum.

tyrannosauroids[2,3,15]. The elliptical external naris is large and posteriorly positioned; a sharp groove runs along the anterior margin of the premaxilla; the maxilla bears a sharp groove paralleling the ventral rim of the antorbital fossa; the jugal has a raised, anteroposteriorly orientated rim; and the surangular has a long anterior flange. Previous studies have suggested that some of these features are synapomorphies of the basal clade Proceratosauridae[4,15], but our phylogenetic analysis optimizes several of these features as synapomorphies of the Tyrannosauroidea.

However, many other cranial features of *Y. huali* are more similar to those of derived tyrannosauroids[2,3,21,22]. For example, the skull is large and deep; the premaxilla has a proportionally deep main body and a maxillary process whose morphologically lateral surface faces dorsally in adults; the maxilla has a markedly convex ventral margin and a posteriorly tapering main body; the lacrimal is in the shape of a '7'; the cornual process of the lacrimal is a large conical structure; the postorbital has a wide jugal process and a suborbital process extending into the orbit; the squamosal has an anteroposteriorly orientated quadratojugal process that intrudes into the infratemporal fenestra; the quadratojugal has a large posterior process that overlaps the posterior surface of the quadrate; the external mandibular fenestra is small; the dentary has a strongly concave dorsal margin and a posteriorly located inflection point between the anterior and ventral margins in lateral view; and the surangular has a prominent horizontal ridge.

The vertebrae are not pneumatized to the degree seen in the Tyrannosauridae, but they show initial development of some features that are characteristic of derived tyrannosauroids[2,21]. These features include prominent flanges for ligament attachment on the anterior and posterior margins of the neural spines of the cervical and dorsal vertebrae, tall neural spines on the posterior cervical vertebrae, laterally placed prezygapophyses on the middle cervical vertebrae, and anteroposteriorly shortened dorsal vertebrae with posteriorly placed neural spines.

The shoulder girdle is in general plesiomorphic, as indicated by the relative robustness of the scapular blade, the weakly expanded distal end of the scapula, and the large coracoid foramen. The forelimbs are also similar to those of basal tyrannosauroids in retaining a typical basal coelurosaurian design, including a three-fingered manus[15].

The pelvis displays several derived features[15]: the dorsal margin of the ilium is mostly straight, the ventral margin of the postacetabular process of the ilium bears a prominent lobe-like flange, the pubic boot is large and forms a distinct anterior expansion, and the ischium is much more slender than the pubis. The hindlimbs are generally similar to those of basal tyrannosauroids, and the distal segments are proportionally short, more similar to allosauroids and basal tyrannosauroids than to tyrannosaurids[2,14].

Filamentous integumentary structures are preserved in all three specimens. Those preserved in ZCDM V5000 are evidently associated with the posterior caudal vertebrae. As preserved, they are parallel to each other and form an angle of about 30° with the long axis of the tail. The filaments are at least 15 cm long. They are too densely packed for it to be possible to determine whether they are elongate broad filamentous feathers (EBFFs) like those seen in the therizinosauroid *Beipiaosaurus*, slender monofilaments, or compound filamentous structures. Those of ZCDM V5001 are near the pelvis and pes. They are filamentous structures, but morphological details are not preserved. In ELDM V1001, integumentary filaments are visible extending from the dorsal side of the neck, and near a limb bone that is tentatively identified as a humerus. Those extending from the neck measure more than 20 cm, and those along the humerus at least 16 cm. Although feather preservation is patchy in these specimens, as occurs even in some fossil birds from the Jehol Group that undoubtedly had plumage covering most of the body, the distribution of the preserved filamentous feathers in the three specimens of *Y. huali* implies that this taxon had an extensively

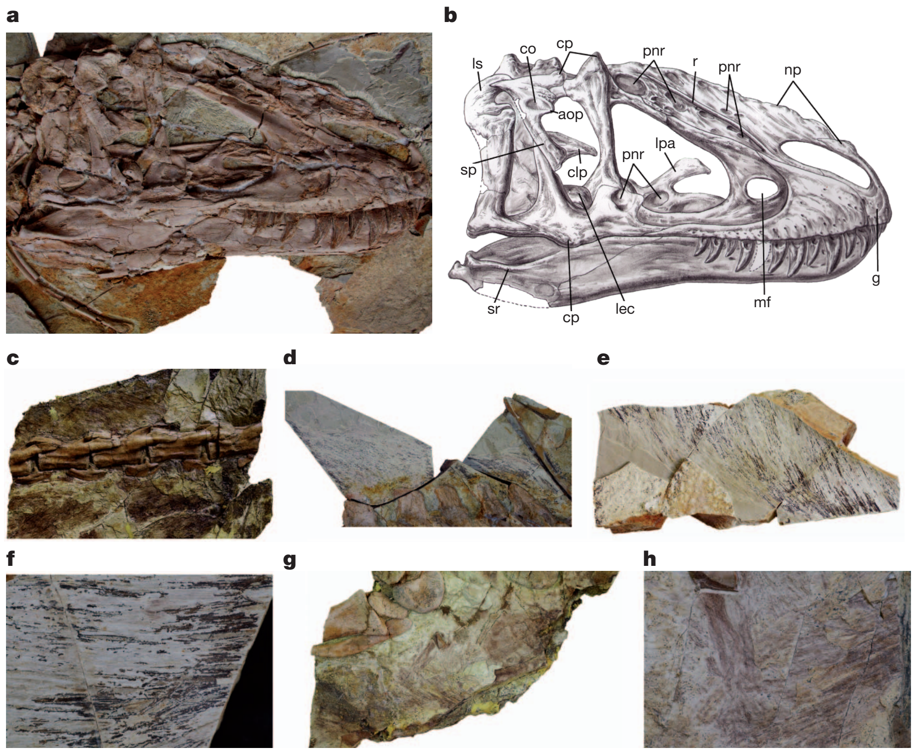

Figure 2 | Selected elements of *Y. huali* (ZCDM V5000, ZCDM V5001 and ELDM V1001). **a**, Photograph of the skull and mandible of ELDM V1001. **b**, Line drawing of the skull and mandible of ELDM V1001. **c–h**, filamentous integumentary structures preserved in the three specimens: **c**, along the posterior caudal vertebrae of ZCDM V5000; **d**, along the cervical vertebrae of ELDM V1001; **e**, **f**, along a limb bone of ELDM V1001; **g**, **h**, near the pes of ZCDM V5001 (**f** and **h** are close-up views). Abbreviations: aop, accessory orbital process; clp, cultriform process; co, concavity; cp, cornual process; g, groove; lec, left ectopterygoid; lpa, left palatine; ls, left squamosal; mf, maxillary fenestra; np, nasal prominences; pnr, pneumatic recesses; r, ridge; sp., suborbital process; sr, surangular ridge.

feathered integument in life. This has also been inferred for *Dilong*, and some other non-avian feathered dinosaurs[1].

Morphological variations. Some morphological differences between ZCDM V5000, ZCDM V5001 and ELDM V1001 may represent ontogenetic variations. With increasing maturity, for example, the skull becomes deeper and more robust, the premaxilla becomes narrower and taller, the anterior portion of the premaxilla becomes more medially orientated, the lateral surface of the maxillary process of the premaxilla rotates to face dorsally, and the maxillary fenestra becomes more anteriorly located. Several other morphological variations, such as the presence of a relatively straight dorsal margin of the ilium in ZCDM V5000 and ELDM V1001 and a convex one in ZCDM V5001, are more difficult to interpret in ontogenetic terms. They may reflect individual genetic variation or sexual dimorphism.

A morphometric analysis suggests that *Y. huali* differed in its growth pattern from the highly specialized tyrannosaurids (Supplementary Information). Using femur length as a standard proxy for overall size, the scapula and ilium display negative allometry in *Y. huali* (in contrast to positive allometry and near isometry, respectively, in tyrannosaurids[14]). The radius, metacarpus and distal hindlimb segments are negatively allometric in both *Y. huali* and the Tyrannosauridae, but the negative allometry of the metacarpus, tibia and metatarsus is much stronger in *Y. huali* than in tyrannosaurids[14].

This discovery has implications for early feather evolution. Although some gigantic dinosaurs are likely to have been feathered animals[23], the largest previously known non-avian dinosaur in which direct evidence for a feathery covering is available is *Beipiaosaurus*[24] (adult body mass about 1/40 that of ZCDM V5000). The discovery of *Y. huali* provides solid evidence for the existence of gigantic feathered dinosaurs and, more significantly, of a gigantic species with an extensive feathery covering.

Gigantism affects many aspects of animal structure and function. Extensive filamentous integumentary coverings such as feathers and hair are partly or even primarily insulative in function, but some large mammals have become almost entirely hairless because their low surface-to-volume ratios permit them to retain metabolic heat even without a pelage (although large mammals living in cold environments, such as the bovid *Bison bison*, retain substantial fur). Gigantic tyrannosauroids have been suggested to lack an extensive feathery covering for analogous reasons[6]. This interpretation derives some support from reported impressions of small patches of scaly skin[25,26], and there is certainly no direct fossil evidence for the presence of feathers in gigantic Late Cretaceous tyrannosauroids. The discovery of *Y. huali*, however, indicates that at least one gigantic dinosaur had an extensive insulative coat of feathers, showing in turn that drastic reduction of the plumage was not an inevitable consequence of very large body size. If Late Cretaceous tyrannosaurids such as *Tyrannosaurus rex* were similar to *Y. huali* in this respect, both basal and derived tyrannosauroid dinosaurs would differ from mammals in lacking a tendency to lose their integumentary covering as result of gigantism.

Alternatively, if scales were indeed the dominant integumentary structures in most Late Cretaceous tyrannosauroids, the presence of long feathers in the gigantic *Y. huali* could represent an adaptation to an unusually cold environment. *Y. huali* lived during a period (the Barremian–early Albian) that has been interpreted as considerably colder than the rest of the Cretaceous (a mean annual air temperature of about 10 °C in western Liaoning, in contrast with about 18 °C at a similar latitude in the Late Cretaceous)[27]. Most gigantic Late Cretaceous tyrannosauroids, by contrast, lived in a warm climate that was conducive to the loss of an extensive insulative feathery covering, although populations inhabiting cold environments such as the land that is now Alaska would have been a notable exception[28,29]. It is possible that the extent and nature of the integumentary covering changed over time in response to shifts in body size and the temperature of the environment throughout tyrannosauroid evolutionary history, as has clearly occurred in some mammalian taxa[30]. However, it must be noted that

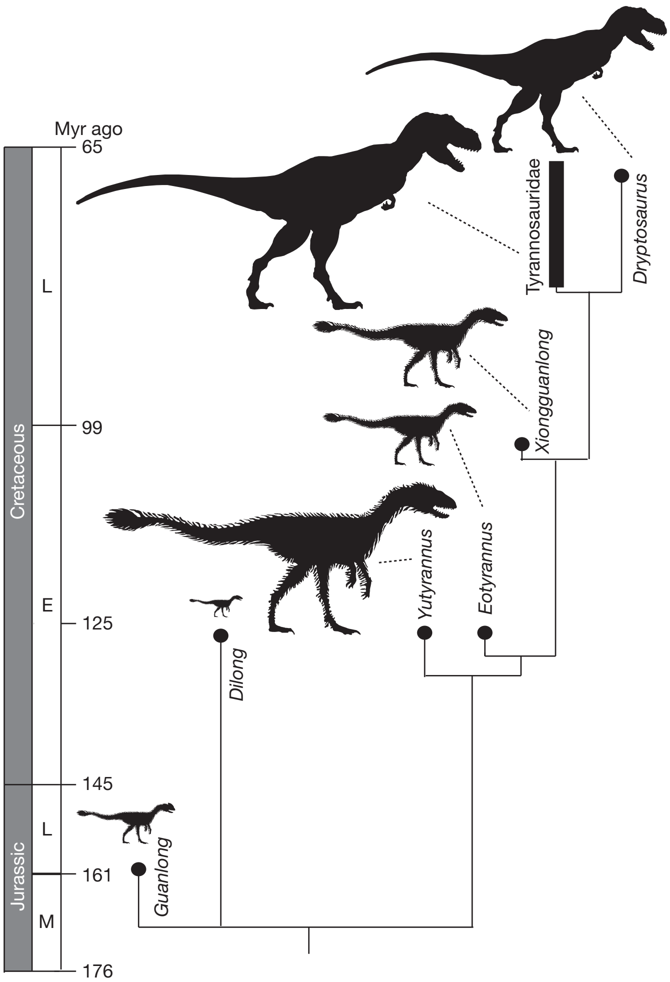

Figure 3 | A simplified cladogram showing the systematic position of *Y. huali* among the Tyrannosauroidea. Silhouettes indicate body size and possible extent of plumage. Different tyrannosauroids seem to have attained gigantic body size independently in the Early and Late Cretaceous, but only in the Early Cretaceous is there direct evidence of a gigantic form with an extensively feathered integument. This may reflect the relatively cold climate of the middle Early Cretaceous. See also Supplementary Information.

the plumage is only partly preserved in all three known specimens of *Y. huali*, and the possibility that the feathers had only a restricted distribution on the body cannot be completely excluded. If this was so, the feathers might have functioned primarily as display structures as in some other non-avian theropod groups[1].

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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