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An unusual oviraptorosaurian dinosaur from China

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Oviraptorosaurians are an unusual group of theropod dinosaurs, with highly specialized skulls[1–6]. Here we report a new oviraptorosaurian, *Incisivosaurus gauthieri*, gen. et sp. nov., from the lowest part of the Lower Cretaceous Yixian Formation of China. This oviraptorosaurian displays a number of characters closer to more typical theropods, such as a low skull and toothed jaws, thus greatly reducing the morphological gap between oviraptorosaurs and other theropods[4–11]. *Incisivosaurus* has a pair of premaxillary teeth resembling rodent incisors and small, lanceolate cheek teeth with large wear facets. These dental features were previously unknown among theropods and suggest a herbivorous diet. The new discovery provides a case of convergent evolution and demonstrates that non-avian theropods were much more diverse ecologically than previously suspected.

Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Oviraptorosauria Barsbold, 1976
Incisivosaurus gauthieri gen. et sp. nov.

Holotype. IVPP V13326 (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing), an almost complete skull and a partial cervical vertebra (Fig. 1).
Etymology. The generic name refers to the presence of incisor-like premaxillary teeth; the specific name is in honour of J. Gauthier for his contributions to theropod systematics.
Locality and horizon. Lujiatun, Shangyuan, Beipiao City, Liaoning, China; lowest part of Yixian Formation, older than 128 Myr (ref. 12, Hauterivian).
Diagnosis. An oviraptorosaur displaying the following derived characters: a highly heterodont upper dentition (large incisciform first premaxillary tooth, much smaller, subconical second to fourth premaxillary teeth, and very small lanceolate maxillary teeth); large high-angled wear facets on the mesial margins of the teeth; longitudinal crest on the ventral surface of the basisphenoid; contact between the accessory ventral flanges of the pterygoids; subsidiary ectopterygoid fenestra present; triradiate palatine with very short maxillary process.

Incisivosaurus is a small oviraptorosaur, with a basal skull length of approximately 100 mm. The skull is relatively low, and the length of the snout constitutes 48% of the basal skull length (Fig. 1a). The large, subcircular external naris is positioned high on the snout. A prominent subnarial foramen is visible in lateral view. The oval antorbital fenestra is dorsoventrally tall and anteroposteriorly narrow and the triangular maxillary fenestra is located in the anterior corner of the antorbital fossa. The large orbit is approximately 133% of the antorbital fossa length. The large infratemporal fenestra is subtriangular in outline, and the supratemporal fenestra is long anteroposteriorly. In lateral view, the palate is mostly obscured by the maxilla and jugal; in ventral view, the ventral margins of the premaxillae and maxillae are straight (Fig. 1c), rather than sinuous as in oviraptorids.

The large premaxilla has a shallower main body than that of other oviraptorosaurs[1,2,5,6]. The maxilla forms the anterior border of the antorbital fossa, which contains a pneumatic fossa dorsally and a small opening ventrally between the large antorbital fenestra and the smaller maxillary fenestra. The posteriormost portion of the ventral margin of the maxilla is inset medially, a feature also seen in the troodontid *Sinovenator*[13]. The nasal is pneumatized as in oviraptorids[1], with a large pneumatic fossa immediately posterior to the external naris (Fig. 1a). Unlike other oviraptorosaurs, therizinosaurs, and basal birds[6,14], the nasal is longer than the frontal. The parietal is transversely narrow, and is much shorter than the frontal. The lacrimal is pneumatized, and 'T'-shaped as in dromaeosaurs and troodontids. The postorbital is 'T'-shaped, unlike the condition in other oviraptorosaurs. The quadrate is inclined posterodorsally, and has a pneumatic fossa on the caudal surface at midshaft length (Fig. 1b), as in troodontids[13]. The quadratojugal closely abuts the lateral surface of the quadrate, and is positioned relatively dorsally. The jugal is deep and straplike and is situated below the orbit.

The crescentic occiput has long, pendant paroccipital processes (Fig. 1b), as in oviraptorids[1,15] and a prominent supraoccipital crest. The occipital condyle is smaller than the foramen magnum, which is higher than it is wide. The shallow basisphenoid recess is divided by a longitudinal crest (Fig. 1c). The anteriorly oriented basipterygoid processes are reduced.

The pterygoid has an accessory ventral flange that contacts its fellow on the midline (Fig. 1c). The 'C'-shaped ectopterygoid, with its hooked jugal process, extends vertically. It has an extensive contact with the jugal and barely touches the lacrimal. A large palatine fenestra is present posterior to the palatine, and a second much smaller opening (subsidiary ectopterygoid fenestra) is present between the ectopterygoid and the ventral flange of the pterygoid. The triradiate palatine has a large pterygoid process, a moderately large vomeral process, and a very short maxillary process. The internal naris, usually bordered by the palatine, vomer and maxilla in other non-avian theropods, is absent here; instead, it might be confluent with the subsidiary palatine fenestra that is bordered by the vomer and the vomeral process of the palatine.

The mandible is shallow, with a large, anteroposteriorly long mandibular fenestra (Fig. 1d), as in Caenagnathidae[1–4,16]. The mandibular symphysis is fused, with a small symphyseal shelf. The anterior end of the mandible is toothless and forms a small beak. In side view, the dentary has a slightly convex dorsal margin and a concave ventral margin. The posterodorsal process of the dentary is short, in contrast to the condition seen in other oviraptorosaurs. However, the posteroventral process of the dentary is long and slender, and reaches the posterior limit of the mandibular fenestra, as in other oviraptorosaurs. The coronoid process is weakly developed and a straplike coronoid appears to be present (Fig. 1e). The surangular extends significantly anteriorly, as in other oviraptorosaurs, but its posterior end is missing. The angular is large, and makes the largest contribution to the posterior part of the mandible. The articular and prearticular are not preserved. The splenial is long and straplike, and its anterior end is expanded dorsoventrally.

The upper dentition is markedly heterodont (Fig. 1a, c). There are four premaxillary and nine maxillary teeth. The greatly enlarged, anteroposteriorly compressed, first premaxillary tooth projects anteriorly and has a large, slightly concave wear facet on the lingual surface that has a sharp enamel cutting edge. *Caudipteryx* also has a pair of long premaxillary teeth, but they are slender and curved[17,18]. The other three premaxillary teeth of *Incisivosaurus* are much smaller, slender, and are subconical. The maxillary teeth are very small relative to the first premaxillary tooth, are lanceolate (as in therizinosauroids), and lack serrations or denticles. Most teeth have prominent, obliquely inclined wear facets on their mesial margins. There are eight or nine dentary teeth, which are closely packed, and which are similar to the maxillary teeth in size and shape.

The oviraptorosaurian affinities of *Incisivosaurus* are established by the following derived features[1–6]: skull with short preorbital region; large premaxillary main body; dorsally positioned external naris; pendant paroccipital process; vertically oriented ectopterygoid; fused dentary symphysis; long and shallow posteroventral process of the dentary; strap-like splenial; large mandibular fenestra; and long retroarticular process. Unlike the short, deep, toothless skulls of most other oviraptorosaurs[1–6], *Incisivosaurus* has a relatively low skull and toothed jaws. The shallow mandible of *Incisivosaurus* lacks some of the specializations seen in Oviraptoridae or more inclusive clades within Oviraptorosauria[1–6]. *Incisivosaurus* displays an intermediate cranial morphology between the typical coelurosaurs and the unusual oviraptorids, and shortens the morphological distance between the two groups. Cladistic analysis places *Incisivosaurus* as the most basal oviraptorsaur (Fig. 2). Collected from sediments deposited more than 128 Myr ago[12], *Incisivosaurus* represents the oldest definitive oviraptorosaur found to date. This is consistent with its basal position in Oviraptorosauria.

Although most work suggests that oviraptorosaurs have a relatively distant relationship to avians[3,13–15,19], some recent work has suggested that oviraptorosaurs are close relatives of birds or are even secondarily flightless birds[6,11,20]. Many characters (including, toothless jaws, short nasals, long parietals, quadrate with a lateral cotyle for the quadratojugal, rodlike jugal bar, long maxillary process of the palatine, absence of a subsidiary palatine fenestra, ectopterygoid that articulates primarily with the lacrimal and maxilla laterally, and absence of a jugal hook on the ectopterygoid) have been used to support the avialan status of oviraptorosaurians[6,11,20]. We note that the basal oviraptorosaur *Incisivosaurus* lacks these birdlike features, which suggests that they have evolved independently in avialians and derived oviraptorosaurs. Within basal maniraptoran lineages, such as Oviraptorosauria and, possibly, Alvarezsauridae, the derived and stratigraphically younger members are more birdlike in a number of features than the basal taxa; in more derived maniraptoran lineages, including Dromaeosauridae and Troodontidae, the later, derived members become less birdlike by secondary

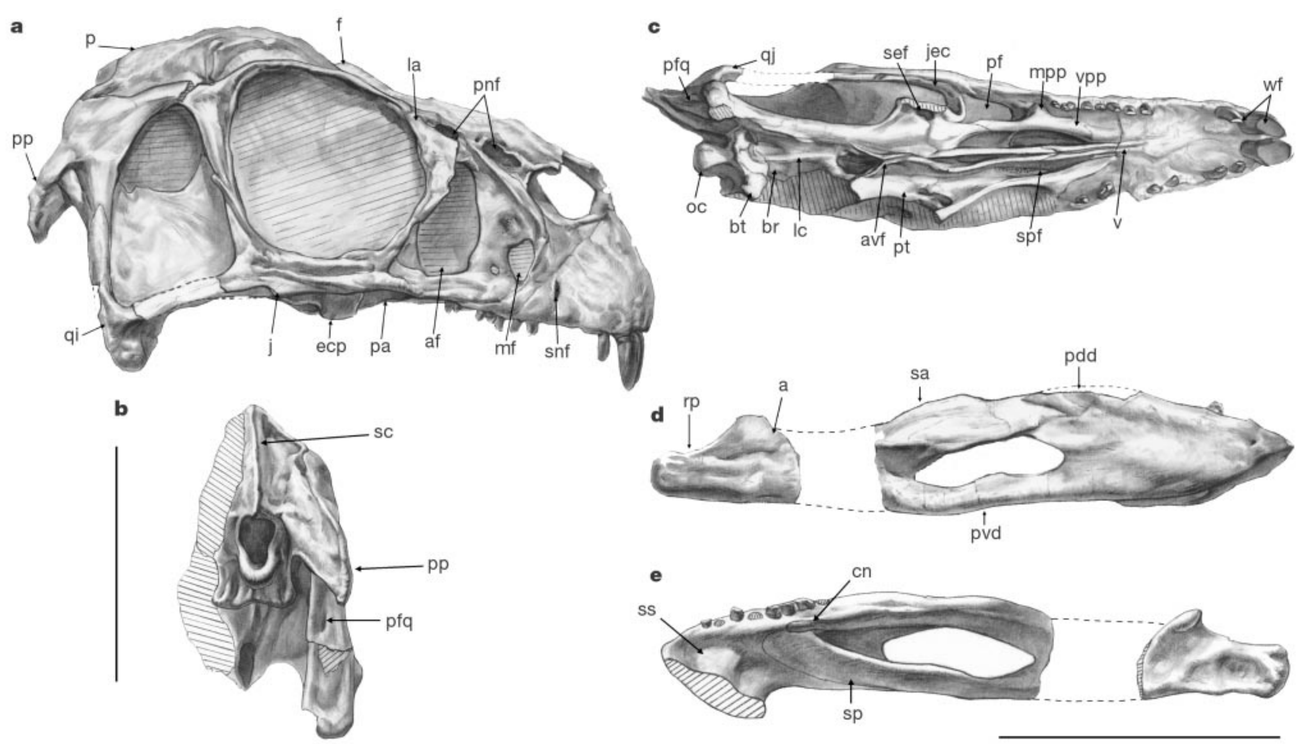

Figure 1 Holotype skull of the oviraptorosaurian *Incisivosaurus gauthieri* (IVPP V13326). **a**–**e**, Lateral (**a**), occipital (**b**), and ventral (**c**) views, and mandible in lateral (**d**) and medial (**e**) views. Scale bar, 4 cm. Abbreviations: a, angular; af, antorbital fenestra; avf, accessory ventral flange; br, basisphenoid recess; bt, basal tubera; cn, coronoid; ecp, ectopterygoid; f, frontal; j, jugal; jec, jugal process of ectopterygoid; la, lacrimal; lc, longitudinal crest; mf, maxillary fenestra; mpp, maxillary process of palatine; oc, occipital condyle; p, parietal; pa, palatine; pdd, posterodorsal process of dentary; pf, palatine fenestra; pfq, pneumatic fossa on quadrate; pnf, pneumatic fossa; pp, paroccipital; pt, pterygoid; pvd, posterodorsal process of dentary; qj, quadratojugal; rp, retroarticular process; sa, surangular; sc, supraoccipital crest; sef, subsidiary ectopterygoid fenestra; snf, subnarial foramen; sp, splenial; spf, subsidiary palatine fenestra; ss, symphyseal shelf; v,vomer; vpp,vomeral process of palatine; wf, wear facet.

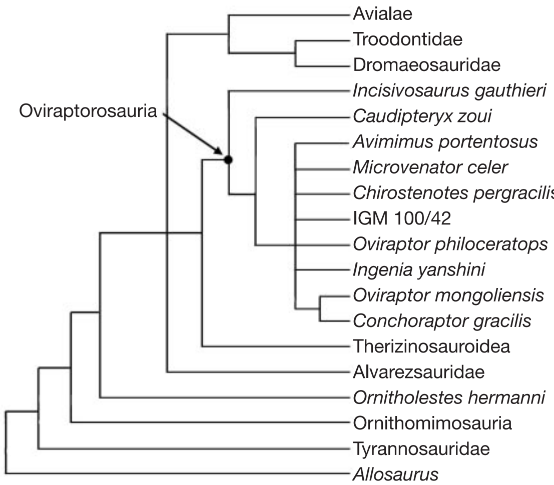

Figure 2 A simplified cladogram representing a strict consensus of 210 trees showing the phylogenetic position of *Incisivosaurus gauthieri*. For detailed information, see Supplementary Information.

reversal of many primitive maniraptoran features. This leads to conflicting results in the reconstruction of maniraptoran phylogeny, and reinforces the importance of including basal members of each group when attempting to reconstruct the phylogeny.

The most interesting features of *Incisivosaurus* are in its dentition. The paired first premaxillary teeth are very similar to the incisors found in a few specialized mammalian lineages, such as rodents, multituberculates and some primatomorphans, which use them for gnawing[21]. The peglike premaxillary teeth are comparable to the dentition of some herbivorous sauropod dinosaurs[22]; the lanceolate cheek teeth are similar to those of therizinosauroids, providing further evidence for the close relationship between Oviraptorosauria and Therizinosauroidea[3,13,15]. Although some theropods show a relatively high degree of heterodonty[13,23–25], the dental differentiation never reaches the degree seen in *Incisivosaurus* in terms of differences in tooth shape and size. The large wear facets on the teeth indicate tooth-to-tooth occlusion in *Incisivosaurus*. *Incisivosaurus* represents the first theropod displaying distinct dental adaptations for an herbivorous diet, although some other non-avian theropods have been suggested to be herbivorous on the basis of the presence of gastroliths[17,26] or of some ambiguous morphological evidence[27–29].

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Incremental training increases the plasticity of the auditory space map in adult barn owls

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The plasticity in the central nervous system that underlies learning is generally more restricted in adults than in young animals[1–4]. In one well-studied example, the auditory localization pathway has been shown to be far more limited in its capacity to adjust to abnormal experience in adult than in juvenile barn owls[5]. Plasticity in this pathway has been induced by exposing owls to prismatic spectacles that cause a large, horizontal shift of the visual field. With prisms, juveniles learn new associations between auditory cues, such as interaural time difference (ITD),

