

ing, is not well constrained by the present work. It is possible that anisotropy in these regions is caused by shape-preferred orientation involving aligned melt pockets.)

Our results show that slabs are characterized by high stress, resulting in deformation dominated by dislocation creep within a mantle otherwise dominated by diffusion creep. We find complicated strain fields associated with deformation due to dislocation creep, but one consistent feature appears to be a large degree of laterally directed strain directly above the CMB. When examined in the context of mineral-physics experiments, we predict that this strain field results in significant seismic anisotropy, with $V_{SH} > V_{SV}$. This work shows that LPO of (Mg, Fe)O is a likely candidate for the seismic anisotropy observed near the CMB in slab regions. Although other processes may contribute to the formation of anisotropy⁵, they are not required, and solid-state processes within a homogeneous material may suffice. □

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A ceratopsian dinosaur from China and the early evolution of Ceratopsia

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Ceratopsians (horned dinosaurs) represent one of the last and the most diverse radiations of non-avian dinosaurs^{1–4}. Although recent systematic work unanimously supports a basal division of Ceratopsia into parrot-like psittacosaurids and frilled neoceratopsians, the early evolution of the group remains poorly understood, mainly owing to its incomplete early fossil record. Here we describe a primitive ceratopsian from China. Cladistic analysis posits this new species as the most basal neoceratopsian. This new taxon demonstrates that some neoceratopsian characters evolved in a more incremental fashion than previously known and also implies mosaic evolution of characters early in ceratopsian history.

The lacustrine lower part of the Yixian Formation of western Liaoning, China, has produced many spectacular fossil remains, including feathered dinosaurs⁵. Recently a number of important three-dimensionally preserved vertebrate fossils, including specimens of a new ceratopsian, have been collected from the fluvial facies that form the lowest part of the Yixian Formation⁶. Some radiometric analyses suggest these deposits are older than 128 Myr and younger than 139 Myr (ref. 5) (Early Cretaceous period) but others imply they are older than 145 Myr (ref. 7) (Late Jurassic period).

Ceratopsia Marsh, 1890

Neoceratopsia Sereno, 1986

Liaoceratops yanzigouensis gen. et sp. nov.

Etymology. The generic name is derived from the provincial name 'Liaoning', and the suffix 'ceratops', commonly used for horned dinosaur names. The specific name 'yanzigou' refers to the village near which the holotype was found.

Diagnosis. Neoceratopsian characterized by sutures between premaxilla, maxilla, nasal and prefrontal intersecting at a common point high on the side of the snout, possession of several tubercles on the ventra margin of the angular, a foramen on the posterior face of the quadrate near the articulation with the quadratojugal, a small tubercle on the dorsal border of the foramen magnum, and a thick posterior border of the parietal frill.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V12738, an almost complete skull (Fig. 1).

Referred specimen. IVPP V12633, a juvenile skull (Fig. 2).

Locality and horizon. Yanzigou and Lujiatun, Shangyuan, western Liaoning, China; the lowest part of the Yixian Formation, probably Early Cretaceous.

Description. The holotype skull of *Liaoceratops* is comparable in size to other basal ceratopsians such as *Psittacosaurus* and *Chaoyangsaurus*. Progressive, but incomplete, sutural closures between skull elements suggest that it derives from a subadult individual. The rostral appears unkeeled as in *Psittacosaurus*. As in many neoceratopsians, the rostral bears lateral processes along the buccal margin. The premaxilla forms much of the side of the snout and extends posterodorsally to reach the prefrontal, as in psittacosaurids and basal ornithomimids. Three cylindrical premaxillary teeth are present as in the primitive neoceratopsian *Archaeoceratops*⁸. The snout is relatively wide in dorsal view, and tapers abruptly, being intermediate in form between that of psitta-

cosaurs and neoceratopsians. A large triangular antorbital fossa is present as in *Archaeoceratops*⁸. The jugal bears a low, lateral horn, which is positioned anterior to the quadrate rather than posterior to it as in higher neoceratopsians. A separate epijugal is apparently absent in *Liaoceratops*. A long posterodorsal process of the jugal reaches the squamosal and forms most of the anterior and dorsal border of the infratemporal fenestra. The quadratojugal is exposed in lateral view as in psittacosaur, but unlike in neoceratopsians—in which it is covered by the posteriorly expanded jugal horn. The skull roof is flat, and the fused parietals bear a tall sagittal crest as in *Protoceratops*⁹. *Liaoceratops* possesses a short parietal frill, which has a rounded posterior border as in *Leptoceratops*. The squamosal contributes to the lateral part of the frill. Irregular, asymmetric openings are present on each side of the frill midline, but these are, at least in part, preservational artefacts and presence or absence of frill fenestration cannot be established with certainty. The parietal is very thin rostral to the posterior margin, which is exceptionally robust. The rostral face of this thick bar is densely pitted indicating muscular insertion.

The buccal cavity is expanded at the level of the premaxillary palate, and the buccal margin of the maxilla–premaxilla forms a sinuous curve in ventral view. The tooth row is short, and not expanded behind the orbit as in higher neoceratopsians. The postpalatal part of the pterygoid is long and bears a large posterior process as in some psittacosaur and several basal neoceratopsian taxa such as *Leptoceratops*¹⁰. The paired pterygoid processes cover most of the basicranium from view. The ectopterygoid is large and extends from its contact with the jugal to the tip of the elongate mandibular process of the pterygoid. The occipital condyle is spherical, but the basioccipital may participate in the foramen magnum. A narrow ridge extends along the basioccipital midline, ventral to the occipital condyle as in *Archaeoceratops*⁸ and *Microceratops*¹¹.

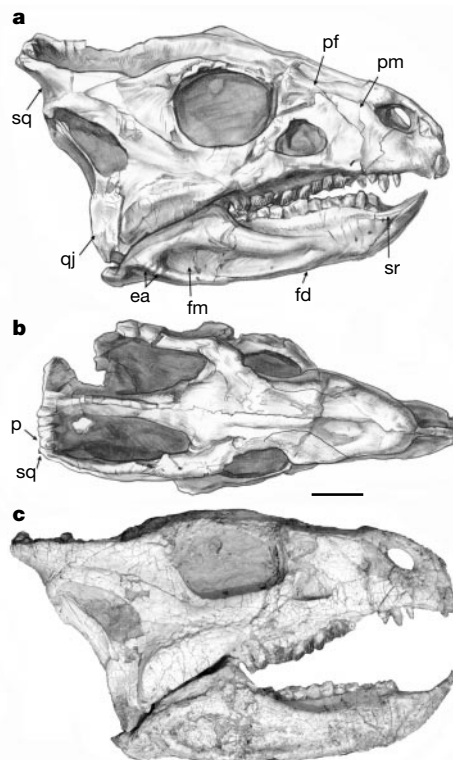


Figure 2 Skull of the juvenile specimen referred to *Liaoceratops yanzigouensis* (IVPP V12633) in lateral (a, c) and dorsal (b) views. Scale bar, 1 cm. Abbreviations as in Fig. 1, except for Sr, sharp ridge.

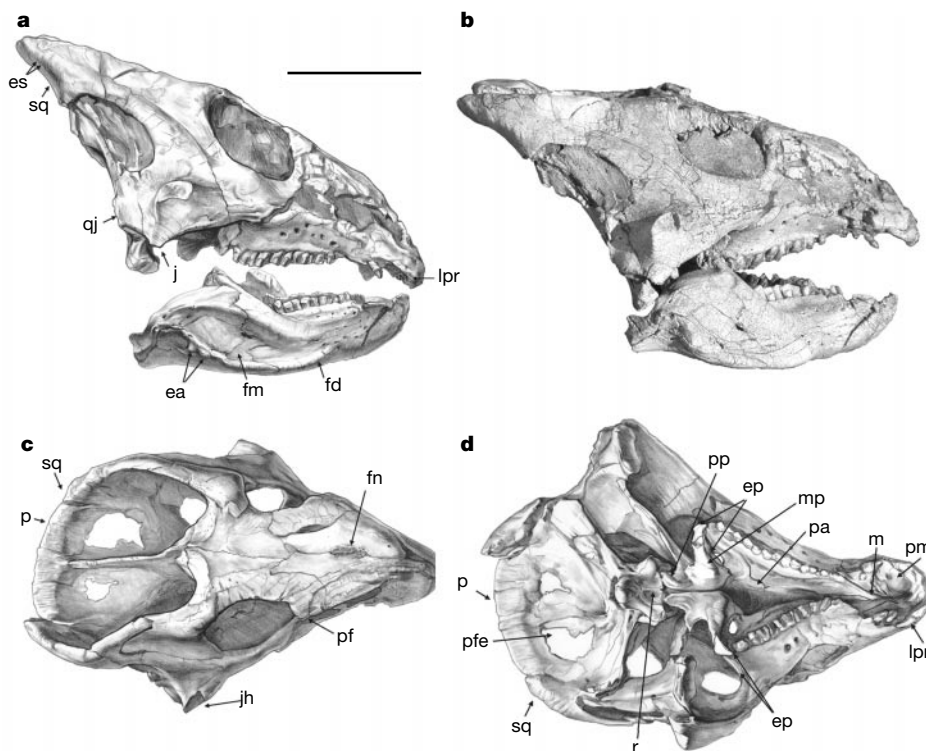


Figure 1 Holotype skull of the ceratopsian *Liaoceratops yanzigouensis* (IVPP V12738) in lateral (a, b), dorsal (c) and ventral (d) views. Scale bar, 4.5 cm. Abbreviations: ea, eminences on angular; ep, ectopterygoid; es, eminences on squamosal; fd, flange on dentary; fm, fossa on external surface of the mandible; fn, fossa on nasals; j, jugal; jh,

jugal horn; lpr, lateral process of jugal; m, maxilla; mp, mandibular process of pterygoid; p, parietal; pa, palatine; pf, prefrontal; pm, premaxilla; pp, posterior process of pterygoid; r, ridge; pfe, parietal fenestra; qj, quadratojugal; sq, squamosal.

The prementary is hooked dorsally and has a bevelled edge as in basal neoceratopsians. The dentary is massive and bears a small ventral flange. As in neoceratopsians, the surangular bulges laterally, but it lacks the lateral wall to the glenoid present in other members of the group. The retroarticular process is short.

Weak, incipient primary ridges are present on the cheek teeth of the holotype, and are less pronounced in the referred juvenile specimen. Where visible, the roots appear to lack lateral grooves, and the eruption pattern in the dentary is not as rigidly determinate as in neoceratopsians although more ordered than in psittacosaurids and *Chaoyangsaurus*¹². Cingula are not developed near the crown bases, and worn teeth display oblique wear facets as in primitive ornithischians.

The referred juvenile skull is about half as long as the holotype. It differs from the holotype of *Liaoceratops* in features characteristic of juvenile ceratopsians^{9,13,14}, including fewer teeth, vaulted frontals, a weaker jugal horn and a proportionately shorter and narrower frill. Similar differences are observed in the growth series of other basal ceratopsians such as *Psittacosaurus*¹⁵ and *Protoceratops*⁹. Comparison between the juvenile and holotype specimens shows that the squamosal contribution to the frill margin increases allometrically with growth and the squamosals form half the frill margin in the adult. This contrasts with *Protoceratops*, in which the squamosal contribution to the frill decreases proportionately throughout ontogeny.

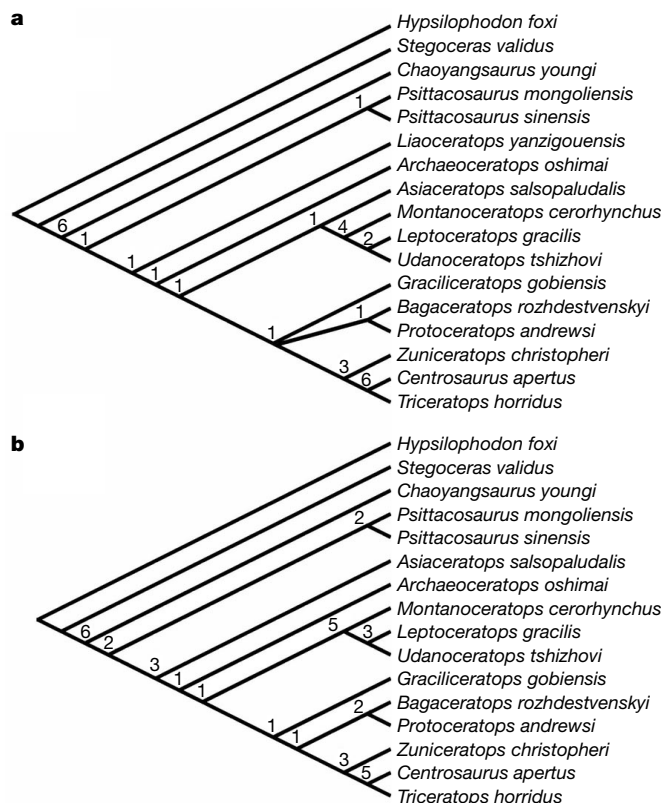


Figure 3 Phylogenetic relationships among ceratopsians. **a**, A strict consensus cladogram of two most-parsimonious trees (200 steps; consistency index, 0.69; retention index, 0.78) derived from analysis of our data set (based in part on refs 4, 17, 18) placing *Liaoceratops* as the most basal neoceratopsian. Integers above internodes are decay indices. The strict and Adam's consensus trees have identical topologies. **b**, Single most-parsimonious cladogram (190 steps; consistency index, 0.73; retention index, 0.81) based on phylogenetic analysis of the same data set with *Liaoceratops yanzigouensis* excluded. We note the different phylogenetic positions of *Archaeoceratops* and *Asiaceratops* and higher decay indices relative to **a** after exclusion of *Liaoceratops yanzigouensis*.

Discussion. Cladistic analysis (see Supplementary Information) posits *Liaoceratops* as the most basal neoceratopsian (Fig. 3a). Derived characters shared with other neoceratopsians include the lateral processes of the rostral, an expanded frill with squamosal participation, a spherical occipital condyle, a deep temporal bar, a triangular postorbital and laterally convex surangular. *Liaoceratops* still retains a number of primitive ceratopsian characters, however. For example, the quadratojugal is flat rather than transversely expanded, the rostral is unkeeled, an epijugal is absent, and the maxillary teeth have weakly developed primary ridges and oblique occlusion angles. Indeed, some character states in *Liaoceratops* are intermediate between those of psittacosaurids and higher neoceratopsians, documenting an incremental evolution for certain neoceratopsian diagnostic characters.

We note that *Liaoceratops* also exhibits characters traditionally used to diagnose either psittacosaurids or more exclusive clades within Neoceratopsia. For example, *Liaoceratops* bears a weak ventral flange on the dentary and has an infratemporal fenestra that is wider ventrally, as in some, but not all, *Psittacosaurus* species¹⁶. Analysis of the data set with *Liaoceratops* excluded results in a decrease in tree length of ten steps, and a concomitant increase in the support for nodes near the base of Ceratopsia, including Psittacosauridae, Neoceratopsia and the clade that unites them (Fig. 3b). The mosaic character distribution in *Liaoceratops* introduces homoplasy to the data, which strips away some traditional psittacosaurid synapomorphies, and repolarizes certain characters within Neoceratopsia, causing a reversal in the phylogenetic order between *Asiaceratops* and *Archaeoceratops*.

Liaoceratops is the oldest known neoceratopsian, and represents a significant stratigraphic range extension for this clade, whose other members are Albian⁸ or younger. *Liaoceratops* co-occurs with specimens of *Psittacosaurus* in the lowermost part of the Yixian Formation, whereas *Chaoyangsaurus* is known from the underlying, probably Late Jurassic¹² Tuchengzi Formation. The basal ceratopsian split between psittacosaurids and neoceratopsians occurred no later than the earliest part of the Cretaceous, and both lineages appear to have acquired some of their diagnostic features rapidly within the latest part of the Jurassic and possibly the earliest part of the Cretaceous. The combination of these temporal constraints with the previously unsuspected mosaic evolution introduced by *Liaoceratops* indicates a more rapid rate of character evolution at the base of Ceratopsia and its major subclades than was hitherto recognized⁴. □

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Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia

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The genesis, evolution and fate of *Homo erectus* have been explored palaeontologically since the taxon's recognition in the late nineteenth century. Current debate¹ is focused on whether early representatives from Kenya and Georgia should be classified as a separate ancestral species (*H. ergaster*)^{2–4}, and whether *H. erectus* was an exclusively Asian species lineage that went extinct^{5,6}. Lack of resolution of these issues has obscured the place of *H. erectus* in human evolution. A hominid calvaria and postcranial remains recently recovered from the Dakanihylo Member of the Bouri Formation, Middle Awash, Ethiopia, bear directly on these issues. These ~1.0-million-year (Myr)-old Pleistocene sediments contain abundant early Acheulean stone tools and a diverse vertebrate fauna that indicates a predominantly savannah environment. Here we report that the 'Daka' calvaria's metric and morphological attributes centre it firmly within *H. erectus*. Daka's resemblance to Asian counterparts indicates that the early African and Eurasian fossil hominids represent demes of a widespread palaeospecies. Daka's anatomical intermediacy between earlier and later African fossils provides

evidence of evolutionary change. Its temporal and geographic position indicates that African *H. erectus* was the ancestor of *Homo sapiens*.

The Early Pleistocene Dakanihylo ('Daka') Member comprises 22 to ≤45 m of sediments unconformably atop the Pliocene Hatayae Member of the Bouri Formation⁷ (Fig. 1). These deposits contain abundant archaeological and palaeontological remains embedded in primarily alluvial deposits relating to lakeside beaches or shallow water deposits in distributary channels⁸. Initial interpretations identified Daka sediments as postdating hominid remains and Acheulean artefacts from Bodo⁹. However, the Daka artefacts clearly antedate those at Bodo, and single-crystal ⁴⁰Ar/³⁹Ar dating of a pumiceous unit at the base of the Member gave an age of 1.042 ± 0.009 Myr (ref. 8). The entire Dakanihylo Member is of reverse magnetic polarity, so the minimum age of its palaeoanthropological contents is ~0.8 Myr.

An extensive vertebrate fauna was recovered from the Daka Member. Faunas of this age are rare in Africa. Of 713 identified specimens (see Supplementary Information for faunal list), 377 are bovids, including three new species and two new genera¹⁰. The bovid assemblage is dominated by alcelaphine diversity and abundance not recorded at older African sites. Widespread open grassland habitats are thereby indicated. Adjacent water-margin habitats are evidenced by three *Kobus* species and abundant hippo fossils.

Daka Member archaeological sites are abundant. Bone modifications characteristic of the butchery of large mammals by hominids scar several equid, bovid and hippo postcrania. Lithic assemblages closely conform to African early Acheulean analogues. Handaxes and cleavers are ubiquitous elements, with invasive flake scars and fewer flake removals than later Acheulean counterparts⁸.

A hominid calvaria (BOU-VP-2/66) was discovered *in situ* in Daka Member silty sand by W.H.G. on 27 December 1997. The specimen was orientated base-down, without associated artefacts, encrusted by fossilized root casts. Surface detail is well preserved, with no sign of fluvial transport or surface weathering. Its vault and supraorbitals exhibit perimortem scraping damage; the frontal and parietals bear multiple sets of subparallel striae, each with internal striations. The patterning and morphology of these marks is unusual and inconsistent with cutmarks made by hominids engaged in defleshing activities. We tentatively attribute this damage to animal gnawing.

The calvaria preserves a largely intact base and is only slightly distorted (plastic deformation skews the vault slightly to the individual's left (Fig. 2)). Endocranial capacity is 995 cm³ (measured repeatedly with teff seed). The thick supraorbital tori are strongly arched, with markedly depressed glabellar and supraglabellar regions. Radiographs reveal an asymmetrical frontal sinus extending to the left midorbital level. The frontal squama is bossed at midline and there is weak sagittal keeling there and on the parietals. The mandibular fossa is deep and anteroposteriorly short. Suprameatal and supramastoid crests and angular tori are weak. The damaged mastoids are small. There is no true occipital torus demarcated superiorly by a supratoral sulcus. Rather, the occipital squama rises vertically and curves anteriorly. Viewed posteriorly, the undistorted parietal walls would have been vertical. The cranial vault is smaller and shorter than Olduvai hominid OH-9 and is phenetically similar to the partly described Buia cranium from Eritrea¹¹. Three isolated hominid femora and a proximal tibia were recovered from Daka deposits far removed from the calvaria (Fig. 1). No femur is complete, but all display the marked platymeria and extremely thick midshaft cortex characteristic of *H. erectus*.

The new 'Daka' hominid fossils afford unique insights into unresolved spatial and temporal relationships of *H. erectus*. Most fossils attributed to this taxon came to light in Java, China, Europe and Africa during the twentieth century. Additional genus and species names were proposed before the application of modern