LETTERS

A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers

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Recent coelurosaurian discoveries have greatly enriched our knowledge of the transition from dinosaurs to birds, but all reported taxa close to this transition are from relatively well known coelurosaurian groups[1–3]. Here we report a new basal avialan, *Epidexipteryx hui* gen. et sp. nov., from the Middle to Late Jurassic of Inner Mongolia, China. This new species is characterized by an unexpected combination of characters seen in several different theropod groups, particularly the Oviraptorosauria. Phylogenetic analysis shows it to be the sister taxon to *Epidendrosaurus*[4,5], forming a new clade at the base of Avialae[6]. *Epidexipteryx* also possesses two pairs of elongate ribbon-like tail feathers, and its limbs lack contour feathers for flight. This finding shows that a member of the avialan lineage experimented with integumentary ornamentation as early as the Middle to Late Jurassic, and provides further evidence relating to this aspect of the transition from non-avian theropods to birds.

Theropoda Marsh 1881
Coelurosauria Huene 1914
Maniraptora Gauthier 1986
Avialae Gauthier 1986 (Padian, 2004)
Scansoriopterygidae Czerkas et Yuan 2002
Epidexipteryx hui gen. et sp. nov.

Etymology. *Epidexi* (Greek): display; *pteryx* (Greek): wing, feather; *hui*, in honour of the late young palaeontologist Yaoming Hu, who

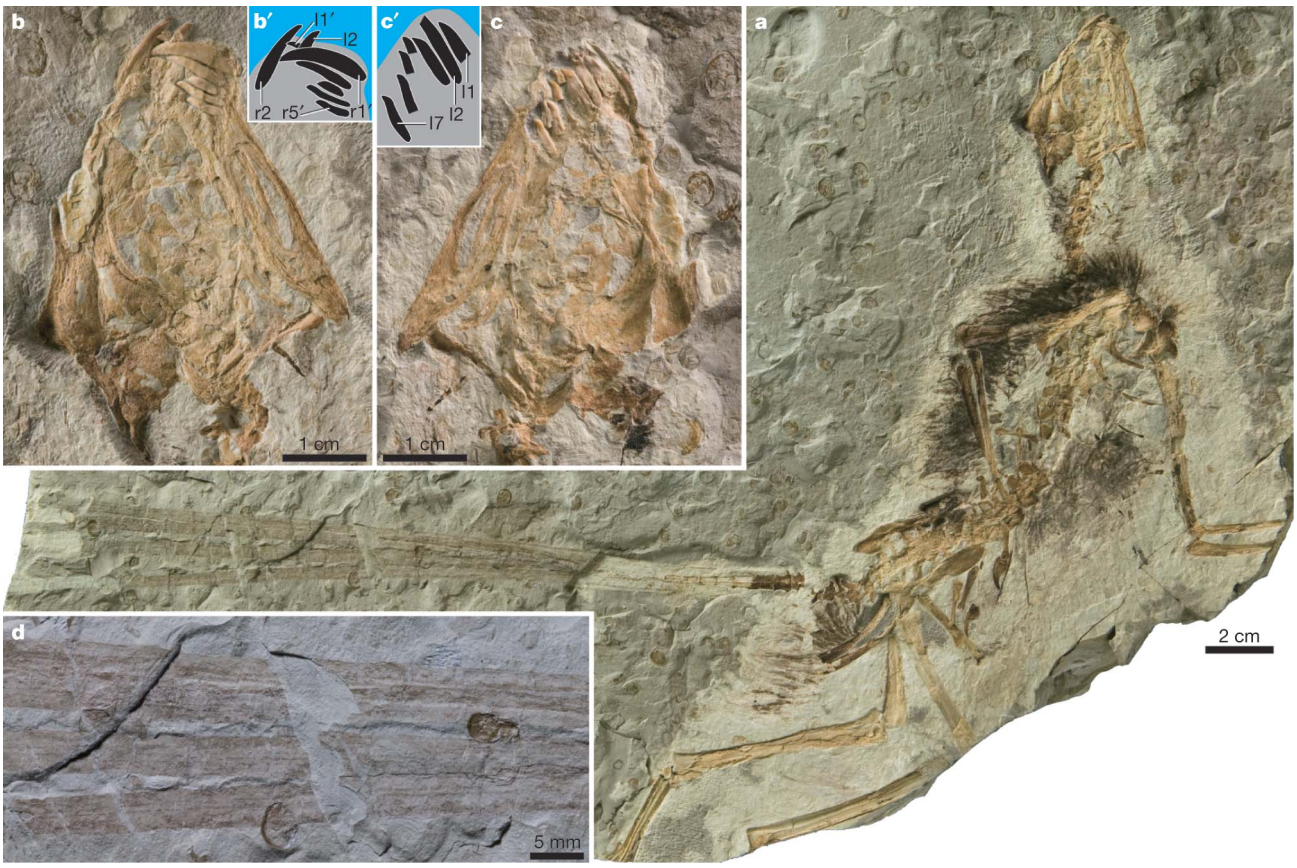

Figure 1 | *Epidexipteryx hui* gen. et sp. nov., IVPP V15471, main slab and close-up photos. **a**, Main slab; **b**, **c**, skull in main slab (**b**) and counterslab (**c**); **d**, four elongate ribbon-like tail feathers; **b′**, **c′**, line drawings of **b** and **c**, respectively. Abbreviations: l1, l2 and l7, 1st, 2nd and 7th left teeth of upper jaw; l1′, r1′ and r5′, 1st left, 1st right and 5th right teeth of lower jaw; l2 and r2, 2nd left and right teeth of upper jaw.

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contributed significantly to the study of Mesozoic mammals from China. Generic name pronounced 'ep-id-ecks-IP-ter-icks'.

Holotype. A feathered pigeon-sized skeleton, preserved on part and counterpart slabs, and housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, collection number IVPP V15471 (Fig. 1; see Supplementary Information).

Locality and horizon. Daohugou, Ningcheng County, Inner Mongolia, north China. The age of the Daohugou sediments is contentious, with possible dates ranging from Middle Jurassic[7] to Early Cretaceous. However, published radioisotopic dating results span a narrower range from 152 to 168 Myr (Middle to Late Jurassic)[8–10].

Diagnosis. Medium-sized avialan with four elongate ribbon-like tail feathers (ETFs), highly procumbent and significantly enlarged anterior teeth, and a distally tapering pygostyle-like structure formed by ten unfused caudals at the end of the tail (Figs 1 and 2; see Supplementary Information). Differs significantly from *Epidendrosaurus*, the only other known scansoriopterygid, in caudal morphology (tail 70% of trunk length in *Epidexipteryx*, compared with more than 300% in *Epidendrosaurus*; 16 caudal vertebrae in *Epidexipteryx*, compared with more than 40 in *Epidendrosaurus*; caudal prezygapophyses reduced in *Epidexipteryx* but significantly elongated in *Epidendrosaurus*).

Description and comparisons. *Epidexipteryx* is estimated to be 164 g in body mass (see Supplementary Information), smaller than most other basal avialans[3,11]. The holotype probably represents a subadult individual, because the ends of some of the long bones seem imperfectly ossified.

As in oviraptorosaurs[12], the skull is high in lateral view (height about 60% of length), the external naris is positioned high on the snout, and the parietal is proportionally long. The teeth of both the upper and lower jaws are highly procumbent, a feature previously known only in the ceratosaurian *Masiakasaurus* among theropods[13]. Furthermore, the anterior teeth are much larger than the posterior ones, as in basal oviraptorosaurs[12], basal therizinosaurs[14] and probably *Epidendrosaurus*[4,5]. There are probably 9 cervicals and 14 thoracic vertebrae, and the synsacrum is composed of 7 vertebrae. The caudal series is much shorter than in non-avian theropods or in other basal avialans. The anterior six caudal vertebrae are proportionally short and wide. The posterior ten caudals bear no transverse

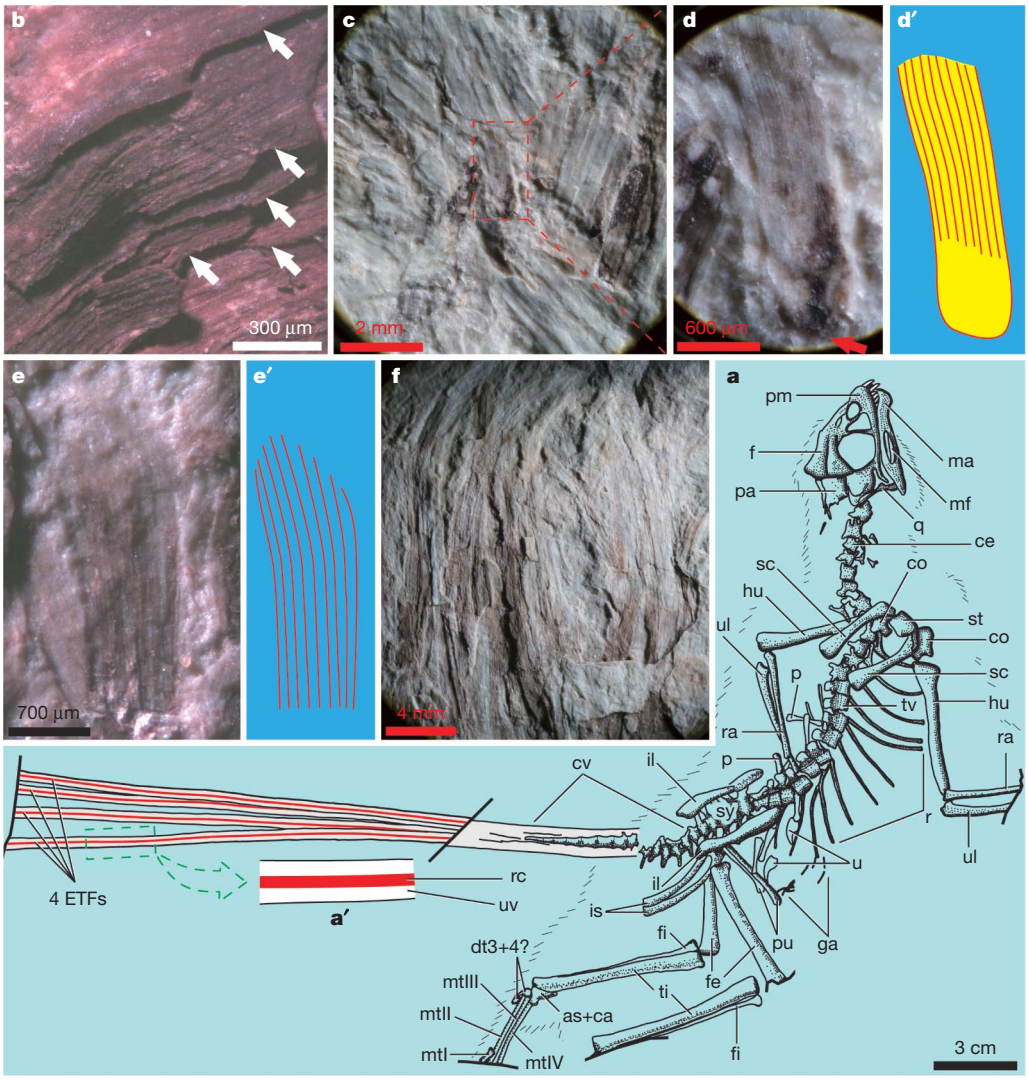

Figure 2 | Line drawings and close-up photographs of *Epidexipteryx hui* gen. et sp. nov. **a**, Skeleton and feather outline, based on both main slab and counterslab, showing that each shafted feather is formed by central rachis and two unbranched vanes (**a′**). **b**, **d**, **d′**, Proximal regions of non-shafted feathers; barbs are parallel and closely united as an unbranched membranous structure (**d**, **d′**), vanes are either layered, indicated by white arrows (**b**), or arranged irregularly (**c**). The red arrow indicates the proximal end of the feather (**d**). **e**, **e′**, **f**, Distal regions of non-shafted feathers, in which barbs appear loosely parallel. Abbreviations: as+ca, astragalus and calcaneum; ce, cervical vertebrae; co, coracoid; cv, caudal vertebrae; dt3+4, distal tarsals 3 and 4; f, frontal; fe, femur; fi, fibula; ga, gastralia; hu, humerus; il, ilium; is, ischium; ma, mandible; mtI–IV, metatarsals I–IV; p, phalanges or metacarpals; pa, parietal; pm, premaxilla; pu, pubis; q, quadrate; r, ribs; ra, radius; rc, rachis; sc, scapula; st, sternum; ti, tibia; tv, thoracic vertebrae; u, ungual phalanges; ul, ulna; uv, unbranched vane.

processes. They form a structure similar to the elongated, incipient pygostyle in some basal birds[15,16] but are not fused to each other (Figs 1a and 2a; see Supplementary Information).

The partly preserved sternum is small and convex anteriorly, and seems to comprise two incompletely fused sternal plates, as in the primitive bird *Jeholornis*[17]. The scapula is significantly shorter than the humerus, as in some derived maniraptorans, and the coracoid is sub-rectangular. The pelvis has an unexpected combination of features among theropods, as in *Epidendrosaurus*[4,5]. The ilium is bird-like in having a long preacetabular process with a strongly convex anterior margin, but differs from the ilia of most non-avian theropods in having a small pubic peduncle. Unusually among theropods, the straight pubis is shorter than the ischium and is significantly shorter than the femur. It is anteroventrally oriented and lacks a pubic boot. The posteriorly curved ischium is laterally compressed, gradually widens towards the distal end, and lacks an obturator process. The humerus is about same length as the femur, proportionally longer than in most other basal avialans. The ulna is posteriorly bowed and the manus is significantly elongated (see Supplementary Information) as in birds and other derived theropods[18–22]. The curvature of the manual claws falls within the range known for the pedal claws of ground-based foraging birds (see Supplementary Information). The femur is about 160% the length of the metatarsus, and 80% the length of the tibia (Figs 1a and 2a; see Supplementary Information).

Phylogeny and affinity. Phylogenetic analysis indicates that *Epidexipteryx* and *Epidendrosaurus* form a monophyletic Scansoriopterygidae (see Supplementary Information), representing a bizarre lineage at the base of the Avialae[6] (Fig. 3; see Supplementary Information).

Although possessing many derived features seen in birds, including a humerus as long as the femur, a long preacetabular process of the ilium with a strongly convex margin, and many other features, *Epidexipteryx* and *Epidendrosaurus* also show some striking similarities to oviraptorosaurs[12] and to a lesser degree therizinosauroids[14,21], including a short and high skull, an external naris positioned high on the snout, an anteriorly downturned and strongly dorsally convex mandible, a large external mandibular fenestra, and enlarged anterior teeth. Furthermore, some pelvic features, such as a proportionally very short pubis and a distally widening ischium, are not known in any other theropod. The bizarre appearance of scansoriopterygids indicates that morphological disparity among maniraptorans close to the origin of birds is higher than has previously been assumed, and underscores the importance of Jurassic theropods for understanding avian origins.

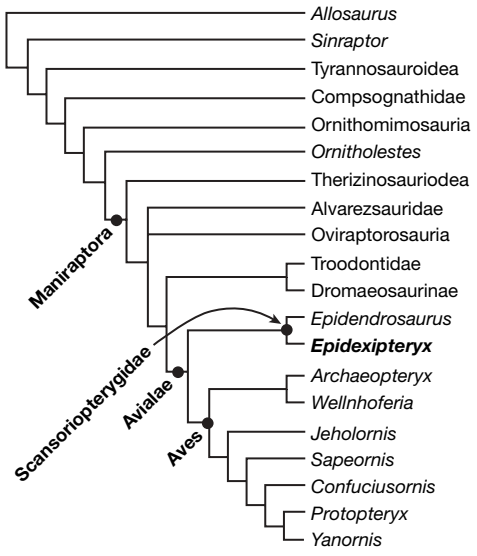

Figure 3 | Phylogenetic relationships of *Epidexipteryx hui* gen. et sp. nov. The cladogram is simplified from the strict consensus of nine most parsimonious trees (tree length 1,255; consistency index 0.35; retention index 0.75; see Supplementary Information). Scansoriopterygidae is defined as the least inclusive clade including *Epidendrosaurus* and *Epidexipteryx*, Avialae as the most inclusive clade including *Vultur gryphus* but not *Deinonychus antirrhopus*, and Aves as the least inclusive clade including *Archaeopteryx* and *Vultur gryphus*.

Integument. The integument bears feather-like structures of two types, ETFs and non-ETFs, which are roughly comparable to shafted and non-shafted feathers, respectively[23]. The distal part of each non-ETF is composed of filamentous parallel barbs (Fig. 2e, e′, f), similar to the condition seen in the non-shafted feathers of other feathered dinosaurs and primitive birds[18,22–25]. However, the free distal barbs of *Epidexipteryx* arise from the edge of a membranous structure (Fig. 2b, c, d, d′), an arrangement that has never previously been reported.

The four ETFs are tightly attached to the last ten caudal segments (Figs 1a and 2a). These feathers are incomplete distally, but the preserved part of each ETF is identical to the corresponding structure in some primitive birds[16,26–28], for example in having a similar central rachis and unbranched vanes (Fig. 1a, d and 2a, a′; see Supplementary Information). Elongate tail feathers are a normal component of the ornamental plumage in extant birds. In contrast to other feather types, ornamental plumage is used to send visual signals that are essential to a wide range of avian behaviour patterns, particularly relating to courtship[29]. For example, experiments have shown that, in some species, males with long tail plumage attract more mates than their short-tailed counterparts[30]. It is highly probable that the ETFs of *Epidexipteryx* similarly had display as their primary function, rather than serving other purposes such as flight or insulation[29]. Indeed, pennaceous feathers suitable for flight are not present in *Epidexipteryx*, even though the bones and integument are well preserved. Because pennaceous feathers are commonly encountered in other feathered maniraptorans[2,21,22,25], their absence constitutes another highly unusual feature of *Epidexipteryx*, as well as strongly implying that this taxon was non-volant. *Epidexipteryx* is the oldest and most phylogenetically basal theropod known to possess display feathers, indicating that basal avialans experimented with integumentary ornament as early as the Middle to Late Jurassic. Unless *Epidexipteryx* is interpreted as secondarily flightless, the absence of pennaceous limb feathers in this taxon suggests that display feathers appeared before airfoil feathers and flight ability in basal avialan evolution.

Received 14 June; accepted 19 September 2008.

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

Acknowledgements We thank F. Jin for discussion, Y. Li for specimen preparation, W. Gao for photography, and J. Choiniere for the use of his laptop computer. This research was funded by the National Natural Science Foundation of China, the Chinese Academy of Sciences, and Major Basic Research Projects of the Ministry of Science and Technology, China.

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