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A Mesozoic gliding mammal from northeastern China

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Gliding flight has independently evolved many times in vertebrates. Direct evidence of gliding is rare in fossil records and is unknown in mammals from the Mesozoic era. Here we report a new Mesozoic mammal from Inner Mongolia, China, that represents a previously unknown group characterized by a highly specialized insectivorous dentition and a sizable patagium (flying membrane) for gliding flight. The patagium is covered with dense hair and supported by an elongated tail and limbs; the latter also bear many features adapted for arboreal life. This discovery extends the earliest record of gliding flight for mammals to at least 70 million years earlier in geological history, and demonstrates that early mammals were diverse in their locomotor strategies and lifestyles; they had experimented with an aerial habit at about the same time as, if not earlier than, when birds endeavoured to exploit the sky.

Systematic palaeontology

Mammalia Linnaeus, 1758
Volaticotheria ord. nov.
Volaticotheriidae fam. nov.
Volaticotherium antiquus gen. et sp. nov.

Etymology. *Volaticus* (Latin): winged, flying; *theri* (Greek): beast; *antiquus* (Latin): ancient.

Holotype. A squashed skeleton preserved in the part and counterpart of a split slab that also contains numerous carapace valves of small conchostracans (*Euestheria*)[1] (Fig. 1). Some parts of the counterpart are missing. The specimen is housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP V14739; see Supplementary Information).

Horizon and locality. Daohugou, Ningcheng County, Inner Mongolia, China. Age estimates of the Daohugou beds are controversial, ranging from Middle Jurassic[2], through Late Jurassic[3], to Late Jurassic/Early Cretaceous[4,5]. However, the Daohugou fauna is older than the Jehol Biota that dates back to 125 Myr ago[6] (see Supplementary Information).

Diagnosis. A small squirrel-sized mammal that differs from all known Mesozoic mammals in having the following features: presence of a sizable furry patagium; elongated limb bones; femur with a small, ovoid-shaped head that lacks a neck; hallux diverging medially; proximal phalanges with pronounced flexor-sheath ridges; long tail with elongated and dorsoventrally flat caudal vertebrae and haemal arches; a highly differentiated dentition with a dental formula of I^3-C^1-P^4-M^3/I_2-C_1-P_4-M_2; incisors small and conical; canines long and sharp; molariforms with tall, sharp and posteriorly recumbent cusps that are aligned in line but are deeply separated; cusps of lower molariforms are more posteriorly recumbent and tightly packed than the uppers; cusp d of M_1 labially overlapping cusp b of M_2 (see Supplementary Information for a detailed description).

Comparison and affinity

In addition to its unique patagium and related skeletal features, the cheek teeth of *Volaticotherium antiquus* (Fig. 1) differ from those of any known Mesozoic mammals except that they resemble, and are probably derivable from, those of triconodonts because the tooth cusps align anteroposteriorly. The teeth are, however, more specialized and differentiated than those of any known triconodont. In addition to the high, posteriorly recumbent cusps on molariforms, the cheek teeth of *V. antiquus* differ from triconodont teeth in having cusp d of M_1 labially overlapping cusp b of M_2, and in lacking both an anterior accessory cuspate on the lower premolariforms and the interlock relationship of molariforms. Moreover, the presence of a posteriorly positioned angular process on the dentary further distinguishes *V. antiquus* from triconodonts.

The upper molariforms of *V. antiquus* are most comparable with two isolated teeth, identified as lower molars, of *Ichthyoconodon* from the Early Cretaceous littoral sediments, Morocco[7]. *Ichthyoconodon* is currently treated as a eutriconodontan, but its affinities are problematic[8,9]. If the known teeth of *Ichthyoconodon* are actually upper ones, they differ from those of *V. antiquus* by having lower cusps that are less recumbent posteriorly and more trenchant than those of *V. antiquus*. The lower molariforms of *V. antiquus* differ from those of any known triconodonts.

V. antiquus has body hair and a single-boned mandible, which are conventionally regarded as typical mammalian features. A single-boned mandible and the presence of paired sesamoid bones between the metatarsus and phalange further differentiate *Volaticotherium* from *Sinoconodon, Morganucodon* and docodontans[9,10]. The presence of an internasal process of the premaxilla is a primitive feature in Mammalia, but in *V. antiquus* the process does not extend posteriorly to contact the nasals, thus differing from the condition in *Sinoconodon, Morganucodon* and non-mammalian cynodonts. In addition, the naris is proportionally larger than those of *Sinoconodon, Morganucodon* and non-mammalian cynodonts.

A phylogenetic analysis of selected Mesozoic mammals based on a data set consisting of 58 taxa and 435 characters identifies *Volaticotherium* as an independent clade in Mammalia, defined either as the crown group[11] or as a more inclusive group[9] (Fig. 2; Supplementary Information). Within Mammalia, *Volaticotherium* forms the sister taxon to the clade containing eutriconodontans, multituberculates and trechnotherians. The phylogenetic position and numerous unique features indicate that *Volaticotherium* represents a previously unknown and highly specialized mammalian clade that

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was probably derived from a stock with triconodont-like dentitions. We recognize this clade as a new mammalian Order.

Patagium and supporting structures

The most prominent feature of *Volaticotherium antiquus* is the patagium that is covered with dense hair. The soft structures are preserved as impressions (Figs 1a, 3a; Supplementary Information). The patagium impression is not completely exposed but is sufficient to indicate its large size, certainly larger than that of the Oligocene gliding rodent[12]. In some areas, perpendicular orientations of the hair on different layers of impressions suggest folding of the patagium in preservation (Fig. 3a). The patagium impression continues with skin

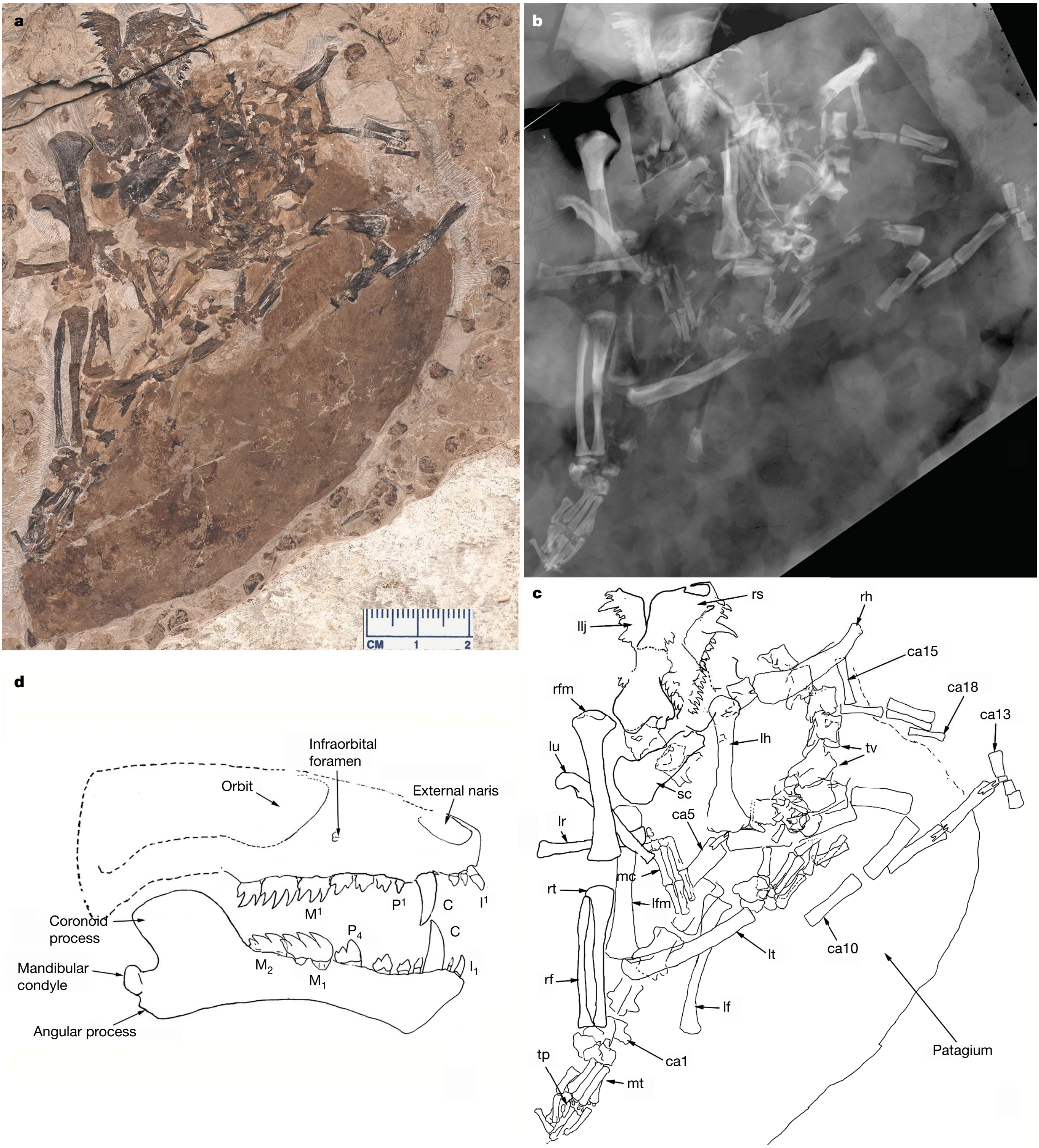

Figure 1 | *Volaticotherium antiquus* gen. et sp. nov. a, **b**, The specimen of *V. antiquus* (**a**) and its X-radiographic image (**b**; holotype, IVPP V14739). **c**, Line drawing illustrating major skeletal elements in **a** and **b**. ca1, 5, 10, 13, 15, 18 are the 1st, 5th, 10th, 13th, 15th and 18th preserved caudal vertebrate, respectively; lf, left fibula; lfm, left femur; lh, left humerus; llj, left lower jaw; lr, left radius; lt, left tibia; lu, left ulna; mc, metacarpals; mt, metatarsals; rf, right fibula; rfm, right femur; rh, right humerus; rs, rostrum of the skull; rt, right tibia; sc, scapula; tp, terminal phalange; tv, thoracic vertebrae. **a**–**c** are the same scale. **d**, Reconstructed skull and lower jaws of *V. antiquus*.

and hair impressions surrounding the area where the skeletal elements are concentrated; it stretches to the phalange area of the foot and sandwiches the tarsal region. These suggest that the limbs, probably including the pes and manus, had participated in supporting the patagium. The hair on the patagium and surrounding the body is fine and even, but that along several proximal caudal vertebrae is relatively thick. The parallel orientations of hair along some caudal vertebrae are indicative of the original anatomical relationships of the hair, skin and bones.

The furry patagium of *Volaticotherium antiquus* is direct evidence of its adaptation to gliding flight. Animal flight requires a high degree of morphological adaptation, of which the most important feature is the development of a sufficient surface area to form an airfoil that supports the weight of the animal and generates lift for the animal to travel horizontally in air. For mammals, such a surface area is obtained by the development of the patagium, a fold of skin membrane from the body, which usually stretches between the fore and hind legs[13–15] and is controlled by complex muscles[16]. To support an increased area of patagium, limbs of extant gliding mammals are commonly elongated[17,18].

Mesozoic mammals generally have relatively short limbs, whether they were terrestrial, such as *Jeholodens*[19] and *Zhangheotherium*[20], or tree climbers, such as *Eomaia*[21] and *Sinodelphys*[22]. In contrast, all limb elements of *V. antiquus* are significantly longer than the corresponding elements in other Mesozoic mammals (see Supplementary Information). Given its phylogenetic relationship, *V. antiquus* was probably derived from a short-limbed ancestor. The ratio of limb lengths of *V. antiquus* to those of other Mesozoic mammals is similar to that between living gliding and non-gliding mammals. In addition to limb elongation, the caudal vertebrae of *V. antiquus* are long, broad and dorsoventrally flat with a low, dorsal, longitudinal ridge (Fig. 3c). The haemal arch that ventrally bridges two adjacent caudal vertebrae is also long and flat. Several caudal vertebrae are also sandwiched by the impressions of the patagium. These structures and their relationships with the patagium suggest the participation of the proximal caudal vertebrae in supporting the patagium and thus

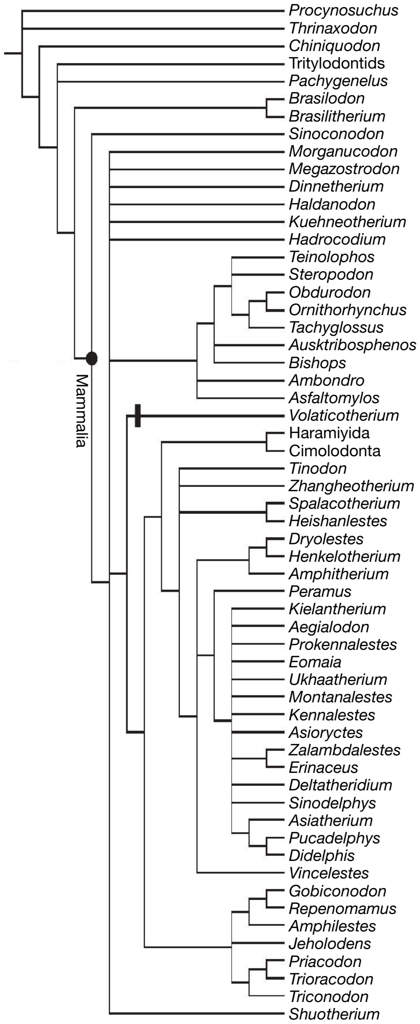

Figure 2 | Phylogenetic relationships of major Mesozoic mammalian groups, including *Volaticotherium antiquus*. The cladogram (tree length = 1,520; consistency index (CI) = 0.408; retention index (RI) = 0.609) is the strict consensus of 72 equally most parsimonious trees (tree length =1,354; CI = 0.458; RI = 0.749) obtained from 1,000 replications of random heuristic searches using PAUP 4.0b10 (Mac version)[43] with a parsimony principle assumed and all characters unordered. The data matrix consists of 58 taxa and 435 characters (see Supplementary Information); it was constructed using Mesquite (v. 1.06)[44] (http://mesquiteproject.org) and converted into the final data matrix using MacClade 4.08 for Mac OS X[45].

Figure 3 | Detailed features related to gliding and arboreal locomotion of *Volaticotherium antiquus*. a, Close-up view of the patagium impression of *V. antiquus* (IVPP V14739), with white arrows indicating nearly perpendicular orientations of hair on two layers of impressions. **b**, Ventral views of two long, flat, caudal vertebrae with white arrows pointing to two long, flat, haemal arches. **c**, Dorsal (anterior) and proximal views of the right femur, showing the small, ovoid-shaped head that lacks a neck. **d**, Comparison of the femoral head of *V. antiquus* (labelled) with that of a morganucodontid (modified from ref. 25). fh, femoral head, gt, greater trochanter; lt, lesser trochanter.

presence of uropatagia between the tail and hind limbs. The morphologies of caudal vertebrae and haemal arches also indicate a stiff tail that had limited lateral and dorsoventral movements, and could act as a stabilizer when the animal was gliding, consistent with the hypothesis that longitudinal control and stability of a glider are achieved more easily with a long, dorsoventrally flattened tail[14,15,23].

Other gliding and arboreal features

Two hind limbs are preserved with all elements nearly in original articulations (Fig. 1; Supplementary Information). The femur has a small, oval-shaped head and lacks a femoral neck (Fig. 3c, d), which is unique among mammals[9]. Although the hip structure was not preserved, the shape of the femoral head alone reveals that the acetabulum is probably shallow and open, perhaps similar to those of arboreal didelphids[24]. Unlike the ball-and-socket hip joint that provides ample excursion for legs in other mammals[25], the peculiar femoral head of *Volaticotherium* must have restricted flexibility of the leg in rotational movements, but could have allowed the leg to be extended laterally and remain steady during a glide.

Many other limb features of *V. antiquus* are related to arboreal locomotion (Fig. 1; Supplementary Information), which is essential for *V. antiquus* to obtain altitude to a launch point for a glide. The hallucal metatarsal diverges medially at a 35° angle from the second metatarsal. A sesamoid bone is at the distal phalange joint of the hallux. Pedal metatarsals and proximal phalanges are dorsally arched with paired sesamoid bones between them. The proximal phalange is relatively long compared to the metatarsal and has pronounced flexor sheath ridges that flare outward to confine a longitudinal groove on the ventral surface of the element. The proximal end of the intermediate phalange is dorsoventrally deep, corresponding to a robust and well-trochleated distal end of the proximal phalange. The terminal hallucal phalange, the only preserved terminal phalange, is large and mediolaterally compressed, indicating a large, deep claw. Only four digits of the manus are partially preserved; they are structurally similar to those of the pes. These features are significantly different from those that have a more generalized locomotion adaptation, such as morganucodontids[25], eutriconodontans[19,26] and symmetrodontans[20], but are similar to various arboreal and gliding mammals, such as didelphids, *Carpolestes*, paromomyids, *Cynocephalus* and gliding squirrels, as a result of adaptation for vertical postures, climbing and other arboreal behaviours[24,27–31]. The pedal and manual morphologies of *V. antiquus* show that both the hind and fore feet are relatively long, and could have a strong ability to flex the digits to secure grips around branches that are large relative to the size of the animal. When not committing its distal limbs to the patagial lifting surface, the hands and feet of *V. antiquus* could be used for surface transport and stable quadrupedal landing, as in some living, gliding mammals[32]. Coupled with the unique joint between the femur and hip, these morphologies indicate an extreme arboreal animal, a tree dweller that could forage on trees, similarly to some extant gliding mammals[33].

Life style

Extant gliding mammals have a body mass range of 10 g–1.5 kg, broadly similar to that of bats[13,18,23,34]. Given its 28.3 mm jaw length, the skull length of *V. antiquus* is estimated to be about 35 mm and the combined head and body length around 120–140 mm with a body mass of around 70 g, similar to that of the flying squirrel *Glaucomys volans*[18]. *Volaticotherium antiquus* was most probably nocturnal, not only because small Mesozoic mammals are generally thought to be nocturnal[9,35], but also because gliding mammals are predominantly arboreal and nocturnal[13,18,23,36]. *Volaticotherium antiquus* could have been an agile glider because of its low patagial load, resulting from its small body mass and relatively large patagium, but it probably did not have the ability to habitually capture airborne prey, as many insectivorous bats do. The patagium of *V. antiquus* has a low aspect ratio, as indicated by its limb lengths, which would have restricted it to gliding flight for transport and meant it was not manoeuvrable enough for aerial foraging.

Gliding flight is thought to be ancestral to bats[33,37–40] and arose up to seven times independently within three other mammalian groups: Marsupialia, Dermoptera and Rodentia[13,14,17,23,36,41]. Gliding as a locomotor strategy has its advantages, such as being energetically economic, allowing a wider foraging area and enabling evasion from predators in arboreal environments[15,23,33,42], but fossils of gliding mammals are extremely rare. The earliest confirmed record of bats dates from the Early Eocene about 51 Myr ago[40]; whereas the earliest confirmed gliding mammal with a small patagium is a Late Oligocene eomyid rodent[12]. There was no convincing evidence of flight adaptation in mammals before 51 Myr ago. The morphological evidence for the earliest gliding locomotion from *V. antiquus* shows that mammals had experimented with aerial life much earlier than previously expected: probably at the same time as, if not earlier than, when birds exploited the sky. The absence of identifiable gliding mammals in the fossil record during a period of at least 70 million years is probably due to poor preservation of these small animals, particularly their characteristic gliding structures, such as the patagium.

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

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