A gliding lizard from the Early Cretaceous of China

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Gliding is an energetically efficient mode of locomotion that has evolved independently, and in different ways, in several tetrapod groups. Here, we report on an acrodontan lizard from the Early Cretaceous Jehol Group of China showing an array of morphological traits associated with gliding. It represents the only known occurrence of this specialization in a fossil lizard and provides evidence of an Early Cretaceous ecological diversification into an aerial niche by crown-group squamates. The lizard has a dorsal-rib-supported patagium, a structure independently evolved in the Late Triassic basal lepidosauromorph kuehneosaurs and the extant agamid lizard *Draco*, revealing a surprising case of convergent evolution among lepidosauromorphans. A patagial character combination of much longer bilaterally than anteroposteriorly, significantly thicker along the leading edge than along the trailing edge, tapered laterally to form a wing tip, and secondarily supported by an array of linear collagen fibers is not common in gliders and enriches our knowledge of gliding adaptations among tetrapods.

Squamata | Acrodonta | gliding adaptation | Liaoning | patagium

Over the last decade, numerous exceptionally well preserved vertebrate fossils have been recovered from the Jehol Group of northeastern China, which have improved greatly our understanding of the evolution of various vertebrate clades, notably the birds and mammals (1). Here, we report on a new acrodontan lizard from the Barremian Zhuanchengzi Bed of the Yixian Formation of China (2), showing an array of morphological traits that suggest a gliding mechanism different from that of many other tetrapod gliders (3–5). This find not only sheds light on our understanding of the evolution of the squamates, a major vertebrate group relatively poorly represented by the fossil record in the Jehol Group, but also greatly enriches our knowledge of the gliding behavior among tetrapods.

Systematic Paleontology. Squamata Oppel, 1811. Iguania Cope, 1864. Acrodonta Cope, 1864. *Xianglong zhaoi* gen. et sp. nov.

Holotype. The holotype is a complete skeleton with fine skin impressions preserved on slab and counter slab, and the specimen is reposited at the Liaoning Paleontological Museum (specimen no.: LPM 000666).

Etymology. The generic name means flying dragon in Chinese; the specific epithet honors Zhao Dayu, one of the founders of the Liaoning Paleontological Museum.

Locality and horizon. The holotype was collected at the Zhuanchengzi locality, near Yizhou, Liaoning Province, China. The horizon of the find is the Lower Cretaceous Zhuanchengzi Bed of the Yixian Formation.

Diagnosis. An acrodontan distinguishable from other species in having eight elongate dorsal ribs, significant elongation of transverse processes of dorsal vertebrae, short and expanded transverse processes of anterior caudals, ulna and radius divergent distally, metacarpal IV shorter than other metacarpals, pedal digit V greatly elongated, first manual and pedal digits curved ventromedially, and the presence of secondary support of patagium by dense parallel collagen fibers.

Description and Comparison. The *Xianglong* holotype was probably at a young ontogenetic stage at the time of death as indicated by the absence of ossified carpals and poorly ossified tarsals. It is 155 mm long, including an extremely slender 95-mm-long tail (Fig. 1). The entire body including the skull is covered with small granular scales, which show little size variation (Fig. 2 *A–D*). No osteoderms are visible. The most striking feature of the specimen is its superbly preserved membranous patagium, which is in a half-open position, probably reflecting a postmortem relaxing of the folded "wing." The patagium is internally supported by eight greatly elongated dorsal ribs. The second of these is the longest and the most robust, with succeeding ribs becoming progressively shorter. Numerous collagen fibers run parallel to the ribs, and they are particularly well developed along the trailing edge (Fig. 2*E*). The leading edge of the patagium is supported mainly by the elongate second rib but is further strengthened by the abutting first rib. The trailing edge is thin and supported only by the collagen fibers, because the elongate dorsal ribs terminate before this level. When fully open, the patagium would be about three times as wide transversely as long anteroposteriorly, with a tapered lateral edge. Externally, the patagium is covered by scales along its leading edge (Fig. 2*B*), but the remainder appears naked. A large gular flap is present, internally supported by a posterolaterally oriented, rod-like second ceratobranchial process of the hyoid apparatus, and externally covered by scales (Figs. 1*B* and 2*A*).

Xianglong has a short snout and rounded temporal corners, but these are possibly juvenile features. As in other iguanians, the dorsal process of the maxilla is located anteriorly. Together with the jugal, it has a rectangular configuration, a feature seen in many nonchamaeleontid acrodontans (6). Premaxillary teeth appear to be considerably smaller than the maxillary teeth, the posterior of which have a wide tooth base and pointed tip giving a triangular outline in lateral view. However, some of these features need further confirmation by additional specimens because the skull of the only known specimen is extensively covered by scales, which partially obscure the sutures of the roofing elements.

There are 24 short procoelous presacral vertebrae, of which eight are cervicals. Slender, laterally extended transverse processes are present on the 5th through 21st presacral vertebrae, with those of the 12th through 19th presacrals being longer than the corresponding centra (Fig. 1*B*). The unicapitate dorsal ribs are proximally expanded and distally straight. Two sacral and ≈50 caudal vertebrae are present. No caudal vertebra shows intravertebral autotomy septa.

Of the shoulder girdle, the clavicle is slender, rod-like, and medially curved. As in many (but not all) other arboreal forms,

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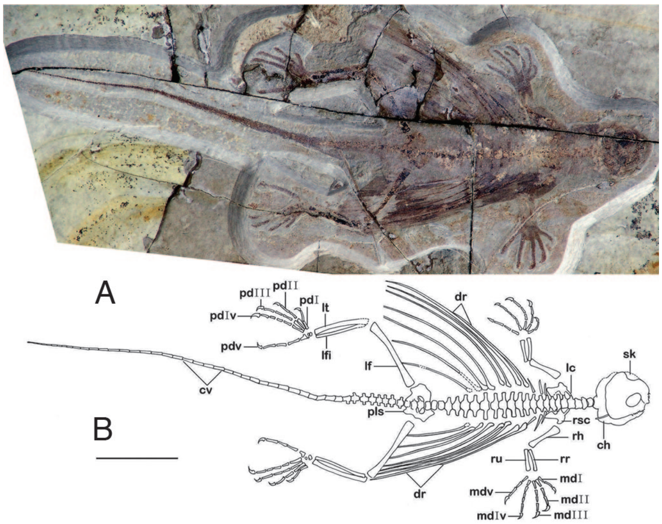

Fig. 1. *Xianglong zhaoi* holotype (LPM 000666). Photograph (*A*) and line drawing (*B*) of LPM 000666. Abbreviations: cv, caudal vertebrae; ch, ceratobranchial process of hyoid apparatus; dr, dorsal ribs; lc, left clavicle; lf, left femur; lfi, left fibula; lt, left tibia; md I–V, manual digits I–V; pd I–V, pedal digits I–V; pls, pelvis; rh, right humerus; rr, right radius; rsc, right scapulocoracoid; ru, right ulna; sk, skull. (Scale bar: 2 cm.)

the forelimb is proportionally short and slender, about half the hindlimb length, comparable with those of some facultatively bipedal lizards (7, 8). The ulna is slightly shorter than the radius, and the two bones are noticeably divergent distally. The metacarpals are divergent distally (Fig. 2*C*), with the fourth one the

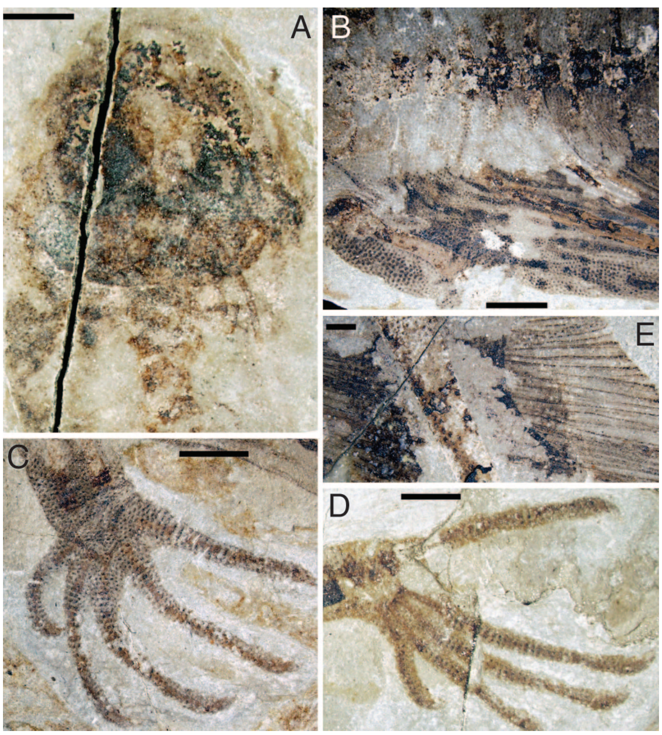

Fig. 2. Close-up of LPM 000666. (*A*) Cranial region showing skull roof scales and gular flap. (*B*) Anterior trunk region showing scales along dorsal series, left arm, and leading edge of the patagium (counterpart). (*C*) Left manus. (*D*) Left pes. (*E*) Collagen fibers along trailing edge of the patagium (counterpart). (Scale bars: *A*–*D*, 3 mm; *E*, 1 mm.)

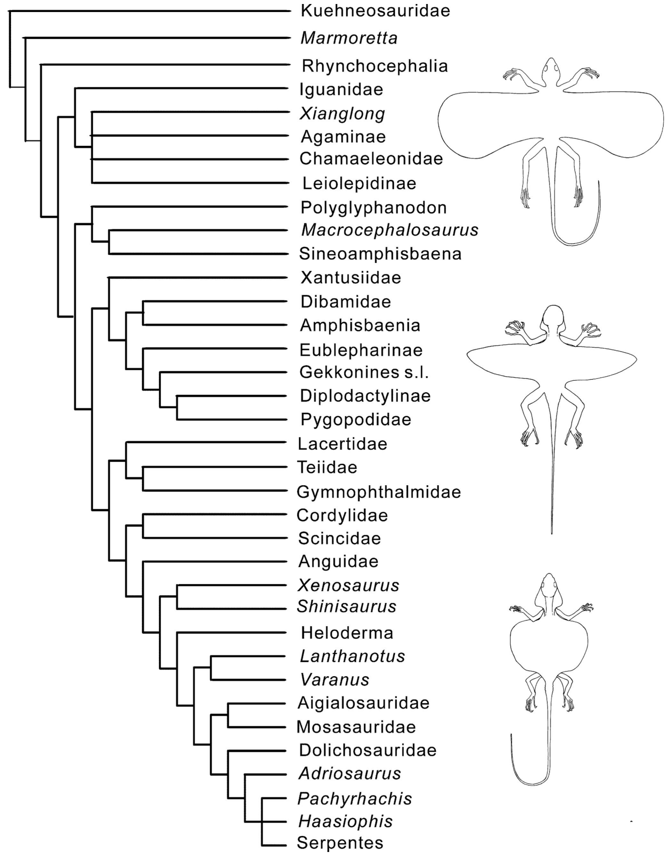

Fig. 3. Phylogenetic position of *Xianglong*. (*Left*) The tree presented here is a strict consensus of the four most parsimonious trees (tree length, 1,058; consistency index, 0.47; retention index, 0.69) produced by an analysis on squamate interrelationship (see SI Figs. 4 and 5) with the addition of several squamate outgroups, the systematic positions of which are generally agreed. (*Right*) Several taxa possessing a patagium supported by elongate dorsal ribs are illustrated to highlight the convergent evolution of this unusual structure within the Lepidosauromorpha and to show some salient differences between the patagium of these taxa: kuehneosaur *Icarosaurus* (*Top*), *Xianglong* (*Middle*), and agamid *Draco* (*Bottom*).

shortest (Fig. 1*B*). The phalangeal formula of the manus is 2-3-4-5-3.

The tibia is significantly shorter than the femur. The fibula is much thinner than the tibia and bows from the latter for much of its length. In the pes, the first pedal digit is curved, the fifth metatarsal is double-hooked, and the greatly elongated fifth digit diverges from the other digits (Figs. 1*B* and 2*D*). The pedal phalangeal formula is 2-3-4-5-4.

Discussion and Conclusions. The squamate affinities of *Xianglong* are indicated by the procoelous presacral vertebrae, loss of the gastralia, and the highly modified fifth metatarsal (6, 7, 9). A character combination of the smaller premaxillary teeth relative to maxillary ones, probably acrodont posterior maxillary teeth, and small granular scales with little size variation, suggests that *Xianglong* is probably an acrodontan (6, 7, 9), and this phylogenetic hypothesis is supported by a cladistic analysis [Fig. 3 and supporting information (SI) *Text*].

Different from the majority of the Squamata, which are ground living (7), *Xianglong* shows clear climbing adaptations suggestive of an arboreal habit, including the following: a curved manual and pedal digit I, elongate penultimate manual and pedal phalanges, a greatly elongated pedal digit V, and strongly curved manual and pedal claws (7, 10). Furthermore, it possesses a gliding capability, an adaptation only seen in few living species within the Squamata (10, 11). The discovery of *Xianglong*, therefore, provides unambiguous and the only known fossil evidence so far documenting the gliding behavior in the squamate evolution; and the discovery indicates that squamates had diversified into an aerial niche by Barremian time (2).

Xianglong possesses an unusual combination of morphological features associated with gliding. Like the Late Triassic basal lepidosauromorph kuehneosaurs and the extant agamid lizard *Draco* (12–15), *Xianglong* has a patagium supported by elongate dorsal ribs (Fig. 3). Noteworthy is that *Xianglong*'s patagium shares with the wings of powered fliers several features critical to flight performance according to aerodynamic theory (4, 16, 17), such as much greater transverse width compared with the anteroposterior length, a significantly thickened leading edge relative to a thin trailing one, and a tapered wing tip, which are sporadically distributed but not common in gliding tetrapods. Furthermore, *Xianglong*'s patagium is mostly naked and is strengthened by tough parallel collagen fibers, a feature otherwise known only in pterosaurs and the enigmatic reptile *Sharovipteryx* (18, 19). Of the wing shape parameters, wing loading, aspect ratio, and the outer area proportions (one-fifth of the wing) are the three important indicators of aerial performance (20). *Xianglong* is estimated to have a wing loading of 0.24 g/cm^2 (=23.5 N/m^2), an aspect ratio of 6.5, and an outer area proportion of 8% (see *SI Text*). These ratios are close to those in fast-flying birds with great maneuverability, such as passeriforms. It is remarkable that several lepidosauromorphan lineages independently evolved a dorsal-rib-supported patagium in the Late Triassic, Early Cretaceous, and modern time, respectively, although their patagia are different from each other in many details, including the overall shape, internal structure, and epidermal surface, among others (Fig. 3) (see SI Table 1). The discovery of *Xianglong* reveals a surprising case of convergent evolution among lepidosauromorphans and enriches our knowledge of gliding adaptations among tetrapods.

Methods. We coded *Xianglong* into a matrix that was published recently (21). The data matrix was analyzed by using the NONA (version 2.0) software package (22), and formatting and character exploration was performed in WinClada (23). The analysis protocol consisted of 1,000 Tree Bisection and Regrafting tree searches followed by branch swapping. Settings included collapsing unsupported branches and counting all states in polymorphic codings. Other settings including the character ordering follow the methods presented in ref. 21.

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1. Zhou Z-H, Barrett PM, Hilton J (2003) *Nature* 421:807–814.
2. Chen Y-X, Chen W-J, Zhou X-H, Li Q, Zhang G-H, Chen S-H (1997) *Mesozoic Volcanic Rocks in Western Liaoning and Its Adjacent Areas—Geochronology, Geochemistry and Tectonic Setting* (Seismic Press, Beijing).
3. Norberg UM (1985) *Functional Vertebrate Morphology*, ed Hildebrand M (Harvard Univ Press, Cambridge, MA), pp 129–158.
4. Norberg UM (1990) *Vertebrate Flight* (Springer, Berlin).
5. Frey E, Sues H-D, Munk W (1997) *Science* 275:1450–1452.
6. Estes R (1983) *Sauria terrestria, Amphisbaenia* (Gustav Fischer, Stuttgart).
7. Evans SE (2003) *Biol Rev* 78:513–551.
8. Berman DS, Reisz RR, Scott D, Henrici AC, Sumida SS, Martens ST (2000) *Science* 290:969–972.
9. Estes R, De Queiroz K, Gauthier J (1988) *Phylogenetic Relationships of the Lizard Families*, eds Estes R, Pregill G (Stanford Univ Press, Stanford, CA), pp 119–281.
10. Pianka ER, Vitt LJ (2003) *Lizards: Windows to the Evolution of Diversity* (University of California Press, Berkeley, CA).
11. Russell AP, Dijkstra LD (2001) *J Zool Lond* 253:457–471.
12. Robinson PL (1962) *Proc Geol Soc London* 1601:137–146.
13. McGuire JA (2003) *Am Nat* 161:337–349.
14. McGuire JA, Dudley R (2005) *Am Nat* 166:93–106.
15. Colbert EA (1970) *Bull Am Mus Nat Hist* 143:85–142.
16. Polhamus EC (1971) *J Aircraft* 8:193–199.
17. Rayner JMV (1988) *Curr Ornitho* 5:1–66.
18. Dyke GJ, Nudds RL, Rayner JMV (2006) *J Compilation* 19:1040–1043.
19. Padian K, Rayner JMV (1993) *Am J Sci* 293A:91–266.
20. Combes SA, Daniel TL (2001) *J Exp Biol* 204:2073–2085.
21. Lee MSY (2005) *Org Divers Evol* 5:25–45.
22. Goloboff PA (1993) NONA (Instituto Miguel Lillo, Tucumán, Argentina), Version 2.0.
23. Nixon KC (1999) Winclada (Ithaca, NY), Version 0.9.9 beta.