

A monodactyl nonavian dinosaur and the complex evolution of the alvarezsauroid hand

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Digital reduction is a striking evolutionary phenomenon that is clearly exemplified in theropod dinosaurs by the functionally didactyl manus of tyrannosaurids, the flight-adapted manus of birds (Aves), and the tridactyl but digit II-dominated manus of alvarezsauroids. The enlargement of manual digit II in alvarezsauroids and the concurrent reduction of the lateral digits have been interpreted as adaptations for digging, although no detailed biomechanical analysis of hand function has so far been carried out for this group. In the derived alvarezsauroid clade Parvicursorinae, the lateral digits are so small as to be presumably vestigial. Here we report a new alvarezsauroid, *Linhenykus monodactylus* gen. et sp. nov., based on a specimen from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China. Cladistic analysis identifies *Linhenykus* as the most basal parvicursorine, and digit II of the manus retains a slender morphology and other primitive features. However, *Linhenykus* is also highly apomorphic in exhibiting the most extreme reduction of the lateral manual digits seen in any alvarezsauroid. Phalanges are retained only on the most medial digit (digit II), making *Linhenykus* the only known functionally monodactyl nonavian dinosaur. Other parvicursorines are more primitive in retaining a tridactyl manus but more derived in that digit II is highly robust and shows other apomorphic features in both of its phalanges. The unexpected combination of features seen in the hand of *Linhenykus* points to a complex mosaic pattern of manual evolution in alvarezsauroids, with loss of the presumably vestigial outer digits being decoupled from change in the form of digit II.

mosaic evolution | Theropoda | Late Cretaceous | biogeography

Modifications of the hand were commonplace in the evolution of theropod dinosaurs. Primitive theropods had five metacarpals, although the lateralmost of these lacked phalanges and therefore was not a functional digit. A reduced count of three manual digits is typically present in members of the derived theropod clade Tetanurae, which includes the birds, and several tetanuran subgroups underwent further modification of the manus. Tyrannosaurids present a widely known example of reduction to two functional digits, and in Aves the phalanges of the three digits are reduced in number and partially fused to strengthen the distal part of the wing. Another striking example of digital reduction in theropods occurred in the Alvarezsauroida, within which the manus became reduced to one functional medial digit and two very small, and presumably vestigial, lateral digits.

Alvarezsauroids were originally considered to be a group of flightless birds, but it is now widely accepted that they are not nested within Aves (1–3) and instead represent a basal maniraptoran lineage. Three functional digits are present in the basalmost known alvarezsauroid, the Asian Jurassic taxon *Haplocheirus* (1). In other members of the group, however, the outer digits are reduced to at least some degree (1, 4, 5). Derived members of the Alvarezsauroida form a monophyletic group known as the Parvicursorinae (here defined as the most inclusive

group including *Parvicursor* but not *Patagonykus*). The most distinctive part of the parvicursorine skeleton is perhaps the manus, in which digits III and IV are drastically reduced and digit II is normally widened and lengthened relative to the other forelimb elements. [We refer to the digits of the tetanuran hand as II–IV in this article (6, 7), although we recognize that some evidence favors identifying them as I–III (8–12). This issue of homology is immaterial to the present study.]

Here we report a new parvicursorine based on a specimen (Figs. 1 and 2) from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China. Unlike other parvicursorines, this taxon retains phalanges only on digit II, the phalanges of the other manual digits having been entirely lost. As a functionally monodactyl nonavian dinosaur, the new parvicursorine provides important information on the phenomenon of digit reduction in the evolution of the alvarezsauroid hand.

Systematic Paleontology

The specimen described in this article is referable to the following nested clades: Theropoda Marsh, 1881; Coelurosauria Huene, 1914; Alvarezsauroida Bonaparte, 1991; Parvicursorinae Karhu and Rautian, 1996; *Linhenykus monodactylus* gen. et sp. nov.

Etymology

The generic name is a combination of Linhe (a city in Inner Mongolia near the area where the specimen was found), and onyx (Greek, “claw”); the specific name refers to the presence of a single finger in this animal.

Holotype

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V17608, a partial postcranial skeleton including cervical, dorsal, sacral, and caudal vertebrae, the left scapulocoracoid, a nearly complete sternum, much of the forelimbs, a partial pelvis, nearly complete hindlimbs, and some unidentified fragments.

Locality

Fine-grained nodular sandstone layer above bioturbated strata in the “Gate area” at Bayan Mandahu, north of the city of Linhe, Inner Mongolia, China (detailed locality information is available from the authors upon request); Wulansuhai Formation, Campanian, Upper Cretaceous (13).

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Fig. 3. Suggested systematic position of *Linhenykus monodactylus* among the alvarezsauroids, based on a numerical cladistic analysis (SI Appendix). Continental distributions are listed after taxon names. Arrows indicate the directions of episodes of dispersal. The geographical distribution of alvarezsauroids is best explained by a dispersal hypothesis.

vertebrae, large pneumatic foramina in the middorsal vertebrae, and anteriormost caudal vertebrae whose centra are amphiplatyan and whose neural spines are located completely posterior to the neural pedicles.

Description and Comparisons

All preserved vertebrae of *Linhenykus* have completely closed neurocentral sutures. However, intercentral sutures are present between successive sacral vertebrae, metacarpal III is not fused to metacarpal II, and the proximal tarsals are not completely coossified with the tibiae. Although neurocentral fusion is not an infallible indicator of ontogenetic stage (14), this combination of vertebral and appendicular features suggests a relatively late, probably subadult, ontogenetic stage for *Linhenykus*.

The holotype specimen is small, in that the estimated femoral length of ≈ 70 mm would imply a body mass of ≈ 450 g (15). Thus, *Linhenykus* was smaller and lighter than *Mononykus olecranus* (16, 17) but larger and heavier than *Parvicursor remotus* (18) (SI Appendix).

The axial skeleton more closely resembles those of other parvicursorines than those of more basal alvarezsauroids in the following characteristics (Fig. 1): cervical centra strongly opisthocoelous and each bearing a longitudinal ventral furrow (19, 20); dorsal vertebrae opisthocoelous, lacking hyposphene-hypantrum articulations; dorsal parapophyses elevated to level of diapophyses, and dorsal postzygapophyseal articular facets oriented medially; posteriormost dorsal centrum biconvex; and anterior caudal vertebrae with transverse processes anteriorly displaced. In contrast, however, to both other parvicursorines and more basal alvarezsauroids (19), some dorsal centra have pneumatic foramina, and the anteriormost caudal centra are amphiplatyan. The small sternum generally resembles those of other parvicursorines but differs from them in numerous details, including much greater proportional transverse width, convexity of the anterior margin, medial displacement of the articular facet for the coracoid, and a much weaker carina that bears a proportionally longer medial groove (Fig. 1F).

Uniquely among alvarezsauroids (19), the scapula and coracoid of *Linhenykus* are fused together. The scapulocoracoid bears a weakly developed glenoid lip (Fig. 2A), a feature present in basal alvarezsauroids (1) but lost in other parvicursorines. The posterior surface of the distal end of the humerus is slightly concave, representing a condition intermediate between other Asian alvarezsauroids and *Patagonykus* (19).

The *Linhenykus* holotype includes a small, rounded radiale (Fig. 2B and C), a bone previously only known in *Haplocheirus* among alvarezsauroids (1). The manus has a general similarity to those of other parvicursorines (19, 21), reflected in such features as hypertrophied manual digit II subequal to humerus in thickness, metacarpal II dorsoventrally compressed, transversely broad, and with highly modified proximal end, and metacarpal III

much smaller than metacarpal II (Fig. 2B and C). However, *Linhenykus* differs from other parvicursorines in many other manual features (19). Digit II of *Linhenykus* is conspicuously more primitive than those of other parvicursorines in being more slender, in that the proximal phalanx is less dorsoventrally compressed and bears a less developed laterodorsal process, and in that manual phalanx II-2 is less hypertrophied, less dorsoventrally compressed, and characterized by lateral grooves that are only partly enclosed in bone. By contrast, the more lateral part of the manus of *Linhenykus* is highly derived relative to the condition in other parvicursorines. Digit III bears no phalanges, as indicated by the fact that metacarpal III is a very small element whose distal end is strongly compressed in the transverse direction and lacks a distal articular surface (Fig. 2B and C). Metacarpal IV is not preserved in the *Linhenykus* holotype. Given that digit III is a reduced structure lacking phalanges, it is probable that metacarpal IV is entirely absent in *Linhenykus*. Even if metacarpal IV is present, it is highly unlikely to bear phalanges given the prevailing patterns of digital reduction in tetrapods. Consequently, digit II clearly represents the only phalanx-bearing digit in the manus.

The preacetabular process of the ilium is nearly vertical in orientation, but the lateral surface of the iliac blade above the pubic peduncle faces somewhat dorsally as in other parvicursorines (19). The supracetabular crest is more prominent anteriorly than posteriorly (Fig. 2D), as in *Mononykus* (17). Unlike in other parvicursorines (19, 22), the pubis lacks a preacetabular tubercle, the proximal articular surface is subtriangular in outline rather than kidney-shaped, and the lateral margin of the proximal surface is not concave (Fig. 2E).

The femur is more primitive in general morphology than those of most other parvicursorines. Unlike in *Mononykus* (17), but resembling the condition seen in *Parvicursor* (18) and *Patagonykus* (5), the popliteal fossa is widely open distally (Fig. 2F). The medial condyle is transversely narrow in distal view and subtriangular in posterior view (Fig. 2F). The tibiotarsus is nearly identical in general morphology to those of other parvicursorines (Fig. 2G and H). As in other parvicursorines (2, 23), the metatarsus is longer than the femur and exhibits a specialized arctometatarsalian condition in which metatarsal III terminates well short of the proximal end of the metatarsus (Fig. 2I). The pedal phalanges are relatively long and slender compared with those of *Mononykus* (17).

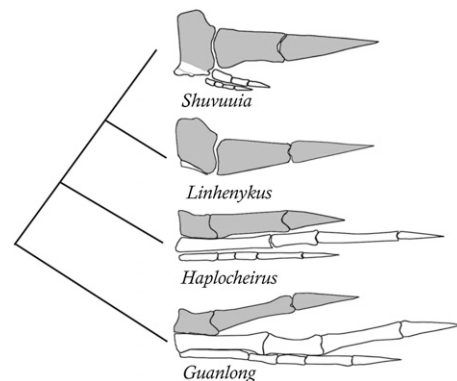


Fig. 4. Simplified alvarezsauroid phylogeny showing enlargement of manual digit II (in gray) and reduction of manual digits III and IV. *Linhenykus* has a less specialized digit II but much more reduced lateral digits compared with other derived alvarezsauroids. The basal tyrannosauroid *Guanlong* is used to illustrate the typical tetenan manus. Mani are not to scale.

Discussion

A cladistic analysis of alvarezsauroid relationships (*SI Appendix*) produced five most parsimonious trees, the strict consensus of which is shown in Fig. 3. *Linhenykus* is recovered at the base of the Parvicursorinae in all of the most parsimonious trees. Within the framework of the phylogeny proposed in Fig. 3, the biogeographic distribution of alvarezsauroids is best explained by a dispersal hypothesis (*SI Appendix*). Under this interpretation, the Alvarezsauridae originated in Asia, and at least three dispersal events subsequently occurred: one from Asia to Gondwana, one from Gondwana to Asia, and finally one from Asia to North America. This dispersal hypothesis is consistent with faunal interchanges between Gondwana and other continents that have been suggested on the basis of the distributions of abelisauroid dinosaurs and some other reptilian groups (24). However, the hypothesis is inconsistent with the distributions of certain other theropod groups, which are better explained by vicariance (25, 26). Unfortunately, the Jurassic fossil record of alvarezsauroids is scant, and this group is currently unknown from the Lower Cretaceous. A more stringent test of the biogeographic hypothesis awaits further data from these poorly represented time periods and from additional geographic regions.

As a basal parvicursorine, *Linhenykus* provides important data on the evolution of the highly modified alvarezsauroid hand. In the evolution of theropod dinosaurs, digital reduction has occurred independently multiple times in different ways. In most cases, reduction of a given metacarpal has been accompanied by loss of the phalanges of the same digit, as best exemplified by the didactyl manus of tyrannosaurids (27). By contrast, the two lateral manual digits of derived alvarezsaurids have reduced metacarpals but still at least approximate a normal phalangeal formula even though the individual phalanges are relatively small (19, 28). *Linhenykus* bears phalanges on only one metacarpal, documenting an extreme degree of digital reduction within this group (Fig. 4). Furthermore, the single phalanx-bearing manual digit of *Linhenykus* (digit II) is more primitive than the corresponding digit in more derived parvicursorines (see above), suggesting that *Linhenykus* was less derived in having a relatively less hypertrophied digit II but more derived with respect to the loss of phalanges on digits III and IV (Fig. 4). This documents a decoupling, representing mosaic evolution on a small scale, between two different types of specialization in the parvicursorine hand: functional refinement of digit II and reduction of digits III and IV. Mosaic evolution on various scales has also been suggested in other dinosaur groups, such as the Tyrannosauridae (29, 30) and the Sauropoda (31). The classic exemplar of mosaic evolution is the avian dinosaur *Archaeopteryx*, which is bird-like in some details of the skeleton and in having asymmetric flight feathers but more typically reptilian in retaining such features as a long bony tail and unfused metapodial elements (32). Although the transition from nonavian dinosaurs to birds is now understood in far more detail (33), current evidence confirms that asymmetric feathers of modern aspect were in place long before many other aspects of derived avian morphology. The discovery of *Linhenykus* further extends the known distribution of the phenomenon of mosaic evolution within dinosaurs.

Adaptation to a specialized function can lead to hypertrophy of some digits and reduction or loss of others (34). The highly

modified manus of derived alvarezsauroids, in which digit II significantly widens and lengthens and acquires a large trenchant unguis whereas digits III and IV are reduced, has been suggested to reflect adaptation for digging (23, 35, 36). These manual features are accompanied by a suite of other forelimb characters, including a distally located deltopectoral crest of the humerus, a large olecranon process of the ulna, and a short forearm and manus, that collectively resemble the biomechanical tool kit of extant mammalian diggers in hard substrates, such as the giant armadillo *Priodontes* (23, 37). In this context, the robustness and derived morphology of digit II in typical parvicursorines are most straightforwardly interpreted as additional digging adaptations.

However, the combination in *Linhenykus* of a less specialized manual digit II and total absence of phalanges on more lateral digits demonstrates that manual evolution in alvarezsauroids did not follow a simple linear trend (Fig. 4). The presence of lateral digits with phalanges in derived parvicursorines and their absence in *Linhenykus* can potentially be explained by the likelihood that the tiny lateral digits of the typical parvicursorine manus are vestigial, as postulated for various other structures in dinosaurs (38). Because vestigial structures have little or no functional significance by definition and are typically small and biologically inexpensive to build and maintain, they experience low levels of stabilizing selection and tend to show high morphological variability. This phenomenon is most amenable to quantitative study at the intraspecific level (39, 40), but examples at higher taxonomic levels are also known. Amphisbaenians or “worm lizards,” a group of squamates uniformly lacking external hindlimbs, vary significantly at the interspecific and intergeneric levels with respect to the form of the vestigial pelvic skeleton (41, 42). A slender, degenerate ilium is present but varies from boomerang-shaped in *Amphisbaena fuliginosa* to splint-like in *Amphisbaena ewerbecki* and hatchet-like in *Blanus cinereus* (Fig. 9 in ref. 41). *Blanus* is apparently unique in retaining an additional calcified (although not ossified) pelvic element. Furthermore, *Blanus* and *Bipes* both retain internal rudiments of the hindlimb skeleton, whereas these are lacking in other amphisbaenians (41, 43). The presence of similar variability in the apparently vestigial lateral digits of alvarezsaurid dinosaurs is thus not surprising.

Materials and Methods

We investigated the systematic position of *Linhenykus monodactylus* using a dataset specifically designed to illuminate alvarezsaurid interrelationships (23), adding three taxa including *Linhenykus monodactylus*. The data matrix was analyzed using the NONA (version 2.0, S. M. de Túcuman, Argentina) software package, and matrix formatting and character exploration were performed in WinClada (Nixon, KC, Ithaca, NY). The analysis was run with the following search parameters: 1,000 replications, 15 starting trees per replication, and Multiple TBR+TBR (mult*max*) search strategy.

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Supporting Information Appendix to

The first known monodactyl non-avian dinosaur and the complex evolution of the alvarezsauroid hand

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1. Selected measurements of *Linhenykus monodactylus* holotype
2. Length comparisons of selected elements in *Mononykus*, *Parvicursor*, *Shuvuuia*, and *Linhenykus*
3. Cladistic analysis
4. Biogeography of the Alvarezsauroidea
5. References

1. Selected measurements of *Linhenykus monodactylus* holotype (in mm; *estimated value)

Middle cervical centrum length	9.0
Middle dorsal centrum length	8.2
Posterior dorsal centrum length	7.6
Middle sacral centrum length	7.3
Caudal 1 centrum length	7.3
Caudal 2 centrum length	8.3
Caudal 3 centrum length	8.7
Caudal 4 centrum length	8.7
Caudal 5 centrum length	7.7
Caudal 6 centrum length	7.6
Caudal 7 centrum length	7.6
Caudal 8 centrum length	7.1
Caudal 9 centrum length	6.4
Sternum length	7.7
Sternum width	7.2
Metacarpal II length	7.1
Metacarpal II width	7.7
Metacarpal III length	5.1
Manual phalanx II-1 length	11.9
Manual phalanx II-1 width	6.0
Manual phalanx II-2 length	15.9
Femur length	70*
Tibia length	97.5
Metatarsal II length	68.0
Metatarsal III length	31.0
Metatarsal IV length	68.5*
Pedal phalanx II-1 length	11.3
Pedal phalanx III-2 length	6.9
Pedal phalanx IV-1 length	7.6
Pedal phalanx IV-3 length	4.0
Pedal phalanx IV-4 length	3.8*
Pedal phalanx IV-5 length	8.0

2. Length comparisons of selected elements in *Mononykus*, *Parvicursor*, *Shuvuuia*, and *Linhenykus*

	<i>Mononykus</i>	<i>Parvicursor</i>	<i>Shuvuuia</i>	<i>Linhenykus</i>
Middle cervical centrum	16.9	?	?	9.0
Middle dorsal centrum	14.2	?	?	8.2
Posterior dorsal centrum	?	5.4*	?	7.6
Middle sacral centrum	14.1	?	?	7.3
Anterior caudal centrum	?	5.8*	?	7.3
Sternum length	25.3	?	?	7.7
Sternum width	13.1	?	?	7.2
Metacarpal II length	11.9	?	?	7.1
Metacarpal II width	16.5	?	?	7.7
Manual phalanx II-1 length	21.3	?	?	11.9
Manual phalanx II-1 width	16.0	?	?	6.0
Femur length	138.6	51.0*	?	70*
Tibia length	170*	70.0*	97.0*	97.5
Metatarsal II length	?	52.0*	67.9	68.0
Metatarsal III length	?	14.0*	24.3	31.0
Metatarsal IV length	?	54.0*	68.7	68.5*

Data source: *Mononykus olecranus* holotype (1), *Parvicursor remotus* (2), and *Shuvuuia deserti* (3)

4. Biogeography of the Alvarezsauoidea

The most basal known alvarezsauroid is *Haplocheirus* from the Oxfordian of western China (7). Three alvarezsauroid taxa are known from Argentina: the Campanian *Alvarezsaurus* (8), the Coniacian-Santonian *Patagonykus* (9), and the Santonian *Achillesaurus* (10). These South American taxa are all relatively basal members of the group, but there is no phylogenetic evidence that they form a clade exclusive of other alvarezsauroids (7, 10, 11). Several Asian alvarezsauroids, including the Maastrichtian *Mononykus* (12), the Campanian *Shuvuuia* (13), the Campanian *Parvicursor* (2), the Coniacian-Santonian *Xixiyanus* (14), and possibly the Santonian *Ceratonykus* (15), form a monophyletic group that represents a highly specialized clade within the Alvarezsauoidea. The Maastrichtian *Albertonykus* is from North America and phylogenetically basal to the specialized Asian clade (4). The Campanian Asian taxa *Linhenyus* and *Kol* are phylogenetically intermediate between most other taxa from the northern continents and *Patagonykus* (16), the most derived of the Argentine alvarezsauroids. A probable derived alvarezsauroid is the Maastrichtian *Heptasteornis* from Romania (17, 18), which shares some derived femoral features with the specialized Asian taxa.

Although the Alvarezsauoidea was previously suggested to be of Gondwanan origin (8, 18), the discoveries of *Haplocheirus* suggests that the group originates in Asia and complicates the explanation of the distribution pattern of other alvarezsauroids (7). Given the phylogenetic and temporal positions of the known alvarezsauroids, it is likely that the group originated in Asia no later than the Oxfordian, dispersed to Gondwana no later than the Coniacian-Santonian, dispersed back to Asia from Gondwana no later than the Coniacian-Santonian, and finally dispersed from Asia to North America no later than the Maastrichtian. This complex pattern could be tested further by conducting a more taxonomically comprehensive phylogenetic analysis of alvarezsauroids, and by collecting more data on their distribution.

5. References

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