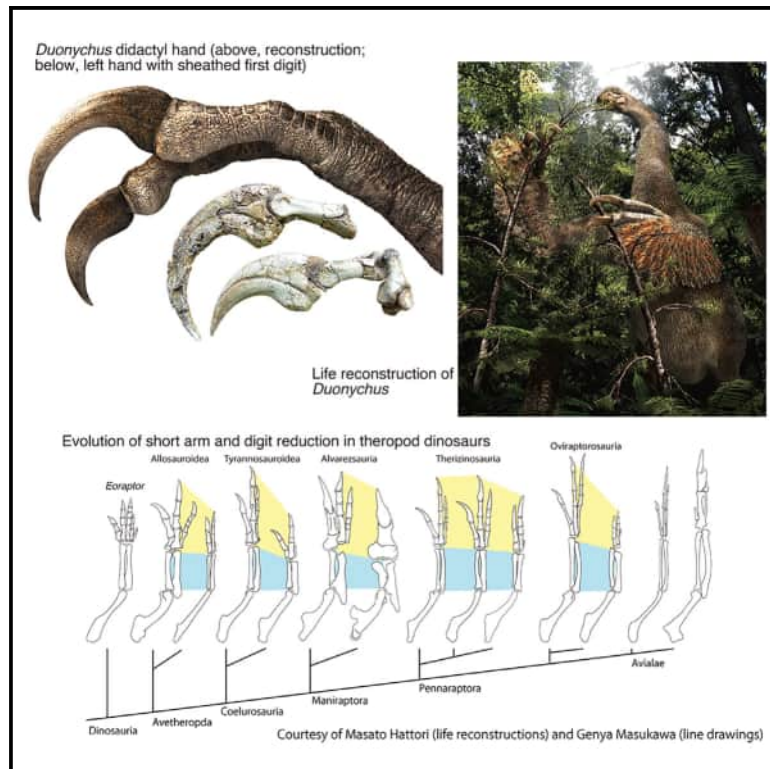


Didactyl therizinosaur with a preserved keratinous claw from the Late Cretaceous of Mongolia

Graphical abstract



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In brief

Earth sciences; Geology; Paleontology;
Paleobiology

Highlights

- *Duonychus tsogtbaatari* is described as another therizinosaur from Mongolia
- It is a didactyl therizinosaur, possessing only two manual digits
- A keratinous sheath on digit I provides rare insight into theropod claw structure
- *Duonychus* reveals convergent digit III loss in at least five theropod clades

Article

Didactyl therizinosaur with a preserved keratinous claw from the Late Cretaceous of Mongolia

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SUMMARY

Therizinosaurids were a group of herbivorous/omnivorous theropod dinosaurs that lived in Asia and North America during the Cretaceous Period. These theropods are notable for their three-fingered hands sporting large claw-like unguals. Here, we describe a new and unusual species of the therizinosaurid *Duonychus tsogtbaatar*, recovered from the lower Upper Cretaceous Bayanshiree Formation of the Gobi Desert of Mongolia. This species is different from other therizinosaurids in that the hand possesses only two fingers, rather than three fingers, the typical condition for Avetheropoda, providing further insight into forelimb/hand reduction among theropods. Phylogenetically, *Duonychus* reveals a broader but still limited appearance of didactyly among avetheropodans. The manual ungual of *Duonychus tsogtbaatar* also preserves a nearly complete three-dimensional structure covering the ungual of the left manual digit I, which represents a keratinous manual claw. The strong curvature of this large claw and high ungual flexion indicate that *Duonychus* was likely amplexorial (grasping) and an effective grasper of vegetation, despite having only two functional fingers.

INTRODUCTION

Therizinosauria is a clade of unusual herbivorous or omnivorous theropod dinosaurs known from Cretaceous deposits of Asia and North America. This clade is most recognizable for their tridactyl (three-fingered) hands sporting three large claw-like unguals, as exemplified by the large-bodied *Therizinosaurus* from the latest Cretaceous of Mongolia.^{1–3} More primitive members of the clade like *Falcarius*,⁴ *Beipiaosaurus*,⁵ and *Jianchangosaurus*⁶ had relatively smaller unguals compared to more derived forms, such as *Erliaosaurus*,⁷ *Nothronychus*,^{8,9} and especially *Therizinosaurus*.^{1,2} As herbivorous or omnivorous theropods with long necks^{5,8,10} and small leaf-shaped teeth,^{11–13} the evolution of their unusual hands likely played an important role in the feeding ecology of this clade.^{14,15}

Although the manus is quite distinct in therizinosaurids, specimens with relatively complete hands are not overly common in the fossil record.¹⁵ Of the known therizinosaur species where the manus is relatively well preserved (including *Falcarius*,⁴ *Beipiaosaurus*,⁵ *Jianchangosaurus*,⁶ *Erliaosaurus*,⁷ *Nothronychus*,⁸ and *Therizinosaurus*^{1,2}), they all possess three digits, which is the primitive and typical condition of avetheropods. In derived therizinosaurids, these digits and relatively large unguals (i.e., large relative to the preceding/penultimate phalanx) are considered to have performed a hook-and-pull function for grasping branches to bring to the mouth during feeding.^{14,15} The keratinous claws

covering the unguals in life also would have affected manus function, but these structures, which are much less prone to fossilization than the bony unguals, have yet to be reported in therizinosaurids.

Here, we describe a new therizinosaur taxon, *Duonychus tsogtbaatar*, based on a specimen that has exceptionally preserved and atypical hands, recovered from the Upper Cretaceous Bayanshiree Formation (Cenomanian to Santonian) in Ömnögovi Province, southeastern Mongolia (Figure 1). With respect to other therizinosaurids, this new taxon is unique in possessing a definitive didactyl (two-fingered) hand; the specimen also novelly (among non-paravian theropods) preserves a complete, three-dimensional sheath representing the keratinous claw. Consequently, *Duonychus tsogtbaatar* provides insight into the evolution of digit reduction among avetheropods and reveals feeding behavioral implications associated with the large claws in therizinosaurids.

RESULTS

Systematic Paleontology

Theropoda Marsh¹⁶

Coelurosauria von Huene¹⁷

Therizinosauria Russell¹⁸

Therizinosauridae Maleev¹

Duonychus tsogtbaatar gen. et sp. nov.



Figure 1. Localities of Late Cretaceous therizosaurs and excavation of *Duonychus tsogtbaatari* gen. et sp. nov.

(A) Map of the Gobi Desert near Mongolia-China border, showing localities of Late Cretaceous therizosaurs.

(B) Photo of excavation of *Duonychus*, showing manus with a keratinous sheath.

(C) Life reconstruction of *Duonychus* (Courtesy of Masato Hattori).

Etymology

The generic epithet is derived from *duo* for two in Greek in reference to the presence of a didactyl hand which is unusual in therizosaurs, and from *onyx* for claw in Greek. The species epithet honors Khishigjav Tsogtbaatar, a paleontologist and former director of the Institute of Paleontology, Mongolian Academy of Sciences in Ulaanbaatar, Mongolia.

Holotype

MPC-D 100/85 (Institute of Paleontology, Mongolian Academy of Sciences in Ulaanbaatar, Mongolia) consists of a partial skeleton, including: six articulated dorsal vertebrae, six articulated

sacral vertebrae with sacral ribs, the anterior-most caudal vertebra, some dorsal ribs, partial left scapula and coracoid, humeri, ulnae, radii, carpals, metacarpals, the left and right manus, the right ilium, both pubes, and the proximal end of the left ischium.

Horizon and locality

The holotype specimen was collected from the Uribe Khudak Locality (N43°27.092', E107°23.476') within the Bayanshiree Formation (Figure 1), which primarily consists of conglomerates, sandstones, and mudstones deposited in alluvial and fluvial settings,¹⁹ in the eastern Gobi Desert, Mongolia. This formation,

dated to the Late Cretaceous, spans the Cenomanian to Santonian stages, as indicated by radiometric dating and biostratigraphic data.^{20,21} Recent U–Pb dating of calcite from caliche layers at Khongil Tsav Locality, which represents only a portion of the formation, yielded ages of 95.9 ± 6.0 Ma and 89.6 ± 4.0 Ma, corresponding to the Cenomanian to earliest Coniacian stages, consistent with ages reported in previous studies.²²

Diagnosis

A derived therizinosaur exhibiting the following unique combination of characters: dorsal vertebrae with a long neural spine; a thick centrodiapophyseal lamina without additional laminae; dorsal vertebrae lacking pleurocoels; sacral vertebrae (2–4) with flat ventral surfaces; dorsal vertebrae possessing a weak ventral keel; pneumatic dorsal ribs; fused distal carpals 1 and 2; distal carpals 1 and 2 semilunate-shaped with a mediodorsal process; a small angle between the articular surfaces of the radiale for the semilunate carpal and the radius; a reduced metacarpal III forming a splint; absence of digit III; equally sized manual unguals I-2 and II-3; absence or reduction of the flexor fossa in manual phalanges; and a reduced dorsal process at the proximal end of manual phalanges. *Duonychus* can be distinguished from other therizosaurs of the Bayanshiree Formation by several features. Its humerus has a more proximally positioned deltopectoral crest compared to *Erlikosaurus*, and in *Duonychus*, the entepicondyle is reduced with a markedly narrow groove separating it from the ulnar condyle. Unlike *Enigmosaurus*, which has a fused pubic boot and coalesced sacral vertebrae, *Duonychus* has an unfused pubic boot and ventrally flat sacral vertebrae with a shorter second sacral. *Duonychus* has an anteriorly deflected humeral shaft and a nearly straight ventral border of the pubic boot, distinguishing it from the convex shape seen in *Segnosaurus*.

Description and comparisons

Most therizinosaur skeletons are incomplete and often lack the femur, leading this study to apply the body mass estimation method of Zanno and Makovicky^{23,24} for *Duonychus*. Our results indicate that *Duonychus* is a medium-sized therizinosaur, with an estimated body mass of approximately 260 kg (268 kg and 259 kg based on the ulna and metacarpal II, respectively). *Duonychus* appears comparable in size to *Erlikosaurus* (278 kg) but smaller than other therizosaurs from the Bayanshiree Formation, including *Enigmosaurus* (567 kg) and *Segnosaurus* (1469 kg). Open neurocentral sutures in all six dorsal vertebrae, two of six sacral vertebrae (1st and 6th), and the single caudal vertebra suggest the individual was not fully mature.

Duonychus preserves six articulated middle to posterior dorsal vertebrae (Figure 2D; Methods S1). The neural spines are long (>2 times centrum height), inclined posteriorly, and their length gradually increases posteriorly. This latter trend resembles that of *Jianchangosaurus* but differs from more derived forms like *Nanshiungosaurus*.²⁵ The neural spines are thickened dorsally and have a rounded tip. The series of transverse processes are rod-like, with convex diapophyses that project posterodorsally and become dorsolateral posteriorly, while maintaining a consistent length. The centrodiapophyseal lamina ridge is robust. The parapophysis of the first dorsal is large and oval-shaped,

although this feature shifts dorsally and decreases in size along the series posteriorly. The posterior dorsal vertebrae have a deep postzygapophyseal centrodiapophyseal fossa, a similar condition seen in *Suzhousaurus*. The neurocentral sutures remain unfused in all preserved dorsals, and the centra are amphiplatyan, and lack pleurocoels.

Duonychus has six sacral vertebrae, consistent with other therizosaurs, except *Jianchangosaurus* (Figures 2A and 2C; Methods S1). The first five sacral centra are completely fused, whereas the sixth remains partially unfused. The neurocentral sutures of the first and sixth centra remain unfused. The transverse processes are dorsally positioned. The first sacral displays infradiapophyseal and infrapostzygapophyseal fossae, whereas the second through fifth sacra have T-shaped transverse processes in lateral view, and the sixth sacral has an inverted L-shaped transverse process due to the lack of a posterior extension. The width of the anterior articular surface of the sacra remains relatively consistent up to the fifth sacral, but the last sacral is reduced by one-quarter.

Only the anteriormost caudal vertebra is preserved, while the neural spine and transverse processes are damaged (Figure 2A; Methods S1). The neurocentral suture remains open. The prezygapophyses are steeply inclined, and the transverse process exhibits an inverted “L” morphology similar to the last sacral vertebra. A shallow infraprezygapophyseal fossa is present. The centrum is amphiplatyan.

At least 26 pieces of dorsal ribs are preserved, mostly rib shafts (Methods S1). Two ribs from the right side retain their proximal ends with the tuberculum and capitulum preserved. The tuberculum is reduced, whereas the capitulum is elongated and slender. The medial surface of the rib shaft has a fossa with grooves containing minute foramina.

The right scapula and ventral half of the coracoid are preserved and are unfused (Figure 2E; Methods S1). The glenoid fossa is oriented caudoventrally as in *Falcarius*, *Suzhousaurus*, and *Therizinosaur*, but unlike in *Nothronychus* and *Neimongosaurus*. The proximal scapular blade has a prominent ridge on the medial surface. The coracoid exhibits moderate curvature, contrasting with the strong curvature in *Falcarius* and *Suzhousaurus*.

Both humeri are preserved (Figures 2F and 2G; Methods S1). As in *Suzhousaurus* and *Nothronychus*, the humerus in *Duonychus* is not robust and has expanded proximal and distal ends (typical of therizosaurs). The humeral head is more developed dorsally, with a limited articular surface on the ventral side. The internal tuberosity at the proximal end is hypertrophied. The deltopectoral crest is well-developed, projecting nearly 90° from the main axis of the proximal end. The overall shape of the humerus is similar to that of *Erlikosaurus*,²⁶ where the ulnar and radial condyles at the distal end are positioned close together on the anterior surface. In *Duonychus*, the entepicondyle is reduced, and the groove separating it from the ulnar condyle is markedly narrow. Additionally, the deltopectoral crest is positioned more proximally than in *Erlikosaurus*.

The ulna and radius from both sides are preserved but are incomplete (Figure 2H; Methods S1). The ulna is nearly straight, with a triangular proximal end and a semi-square distal end in cross-section. The radius shows a slight sigmoidal curvature

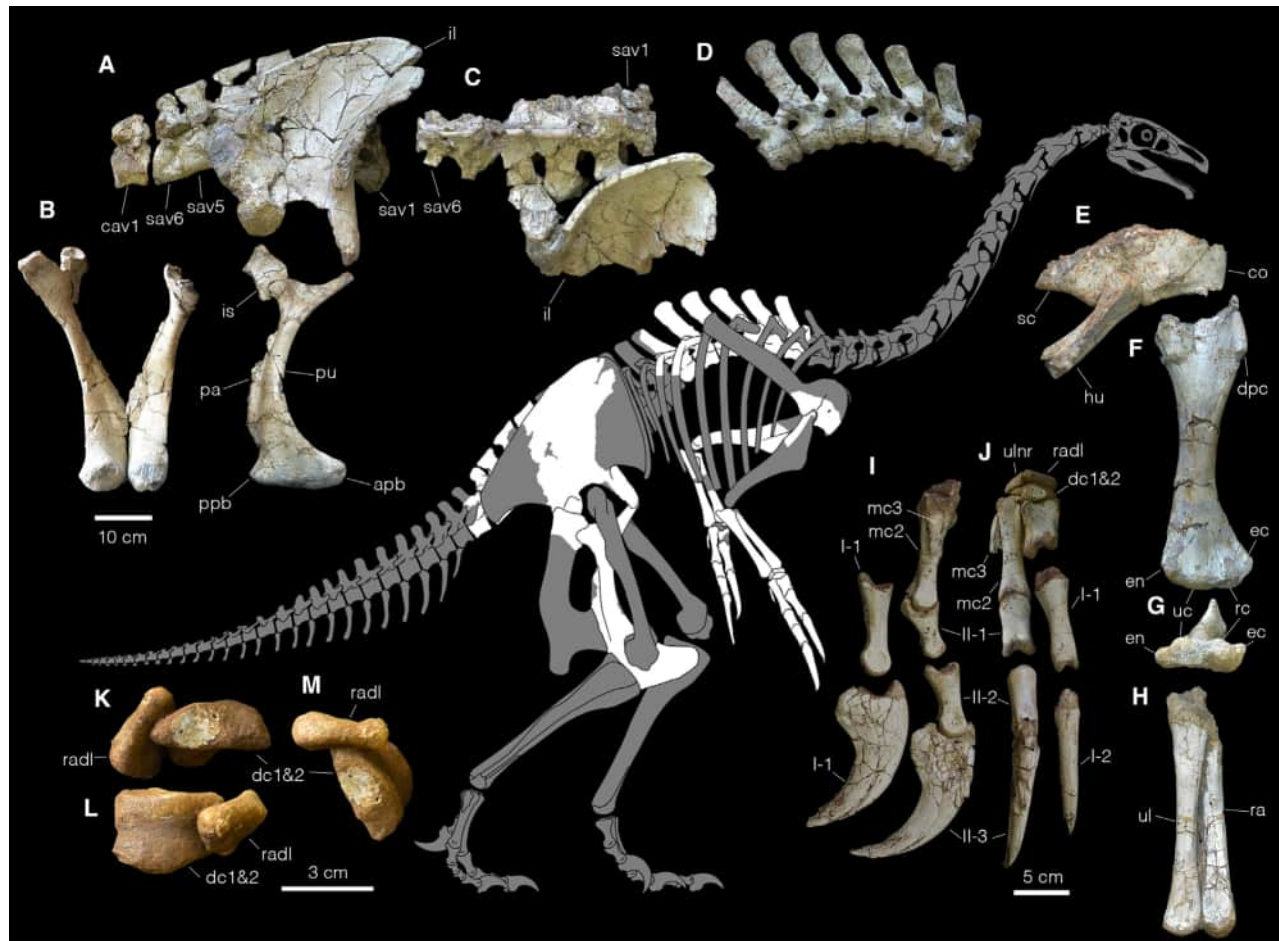


Figure 2. Reconstructed skeleton and selected elements of *Duonychus tsogtbaatari* gen. et sp. nov.

(A–M) Recovered elements are shown in white in the reconstructed skeleton (center) (Courtesy of Genya Masukawa). Pelvis (ilium, pubis, and partial ischium), sacral vertebrae, and the first caudal vertebra in right lateral (A) and dorsal (C) views; both pubes in anterior view (B); six articulated dorsal vertebrae in right lateral view (D); articulated partial right scapula, coracoid, and humerus in lateral view (E); left humerus in ventral (F) and distal (G) views; right ulna and radius in anterior view (H); right manus in lateral (I) and dorsal (J) views; left distal carpals 1 and 2 in dorsal (K) and proximal (L) views; left radiale in dorsal view (M). apb, anterior pubic boot; cav, caudal vertebra; co, coracoid; dc, distal carpal; dpc, deltopectoral crest; ec, ectepicondyle; en, entepicondyle; hu, humerus; il, ilium; is, ischium; mc, metacarpal; pa, pubic apron; ppb, posterior pubic boot; pu, pubis; radl, radiale; rc, radial condyle; sav, sacral vertebra; sc, scapula; uc, ulnar condyle; ul, ulna; ra, radius; ulnr, ulnare.

and is more robust than the ulna, with a proximal end that is flat and oval in proximal view.

Three left carpals (fused distal carpals 1 and 2, ulnare, and radiale) are preserved, and two right carpals (fused distal carpals 1 and 2, and radiale) are articulated (Figures 2J and 3A–3E; Methods S1). The semilunate carpal covers the entire proximal surface of metacarpal I and the medial half of metacarpal II. The angle between the articular surfaces of the flat radiale for the semilunate carpal and the radius is approximately 15°, much smaller than in *Alxasaurus* (39°).²⁷

Metacarpals are preserved in both hands (Figures 2J and 3; Methods S1). The right metacarpus is complete, whereas the left is missing the shaft of metacarpal I and the distal half of metacarpal II. Metacarpal I is robust and short (about 57% of the metacarpal II length) (Table S2). A concavity is present on the dorsal surface of metacarpal I as in *Falcarius*, *Beipiaosaurus*,

and *Alxasaurus*,^{4,28} but not in *Therizinosaurus*.³ The proximal end of metacarpal I is triangular and has three processes: the medial process projects proximally and contacts the dorsomedial process of the semilunate carpal; the dorsolateral process is strongly developed and partially covers the dorsal surface of metacarpal II; the ventrolateral process underlies the ventral surface of metacarpal II, as in other therizosaurs.²⁸ Metacarpal I has a straight medial border in dorsal view and is tightly appressed along the shaft of metacarpal II (Figure 3A). A ridge runs along the medial side between the proximally located medial process and the medial condyle at the distal end, a condition otherwise observed only in *Therizinosaurus*.² The shaft of metacarpal I is triangular in cross-section. The distal condyles are sub-equally developed and are well separated by a deep intercondylar groove, although the lateral condyle extends further. The medial condyle is larger of the two in *Falcarius*⁴ and

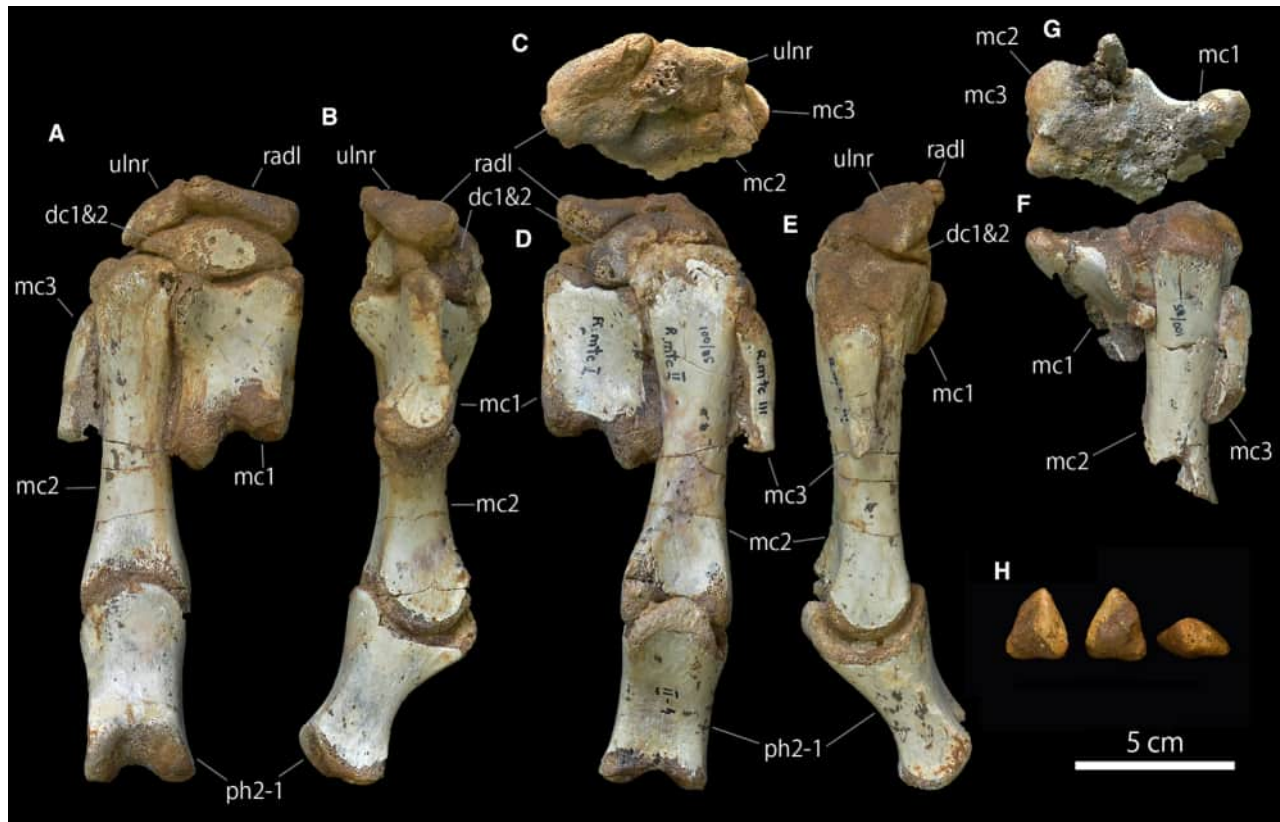


Figure 3. Distal carpals and metacarpals of *Duonychus tsogtbaatari* gen. et sp. nov.

(A–H) Right distal carpals and metacarpals in dorsal (A), medial (B), proximal (C), ventral (D), and lateral (E) views. Left partial metacarpals in dorsal (F) and proximal (G) views. Intermedium in proximal, distal, and dorsal views from left to right (H). dc, distal carpal; mc, metacarpal; ph, phalanx; radl, radiale; ulnr, ulnare. The scale bar below (H) applies to (A) to (H).

Erialsaurus.⁷ The distal condyles are essentially parallel to the main axis of the metacarpal, differing from the condition in *Falcarius*, where the distal end is twisted by 30°. Metacarpal I lacks an extensor pit and collateral ligament fossae as in *Falcarius*⁴ and *Therizinosaurus*.²

Metacarpal II is the longest in the metacarpus, and its proximal end is situated more proximally than those of metacarpals I and III (Figure 3A). The proximal end is sub-rectangular in the proximal view. The medial half of this surface is flat where it articulates with the semilunate carpal. Laterally, the surface recesses distally and is not involved in the proximal articulation. The lateral margin of the surface has dorsal and ventral processes, whereas this margin is straight in *Erialsaurus*.⁷ The shaft is circular in cross-section, which is quadrangular and dorsoventrally flattened in *Falcarius*.⁴ The distal end of metacarpal II has almost symmetrical, equally developed condyles, unlike *Falcarius*,⁴ *Jianchangosaurus*,⁶ and *Erialsaurus*.⁷ Metacarpal II lacks collateral ligament fossae, as in *Therizinosaurus*.² An extensor pit is faintly present.

As a therizinosaur, the most striking feature of *Duonychus* is the absence of digit III (digit formula, 2-3-0) along with a greatly reduced metacarpal III (Figures 2J and 3; Methods S1). In other therizosaurs, the third digit (digit formula, 2-3-4) is present, and metacarpal III has well-developed proximal and distal ends. In

Duonychus, metacarpal III is a laterally convex splint, which is situated more distally than metacarpals I and II, resting between the two lateral condyles near the proximal end of metacarpal II. The proximal end of metacarpal III is flat, lacks an articular surface, and is thus not part of the proximal articulation. Its shaft is rounded in cross-section and the distal articular surface is slightly damaged. A reduced metacarpal III is also present in *Tyrannosaurus*, although its proportion relative to metacarpal II (57%) is greater than that of *Duonychus* (<50%).

The proximal end of manual phalanx I-1 is as wide as it is high, unlike *Falcarius*⁷ (Figures 2I and 2J; Methods S1). The dorsal intercondylar process is short, similar to *Alxasaurus*,²⁰ but less pronounced than in *Falcarius*.⁴ The ventral intercondylar process extends further than the dorsal intercondylar process. The lateral fossa of the proximal articular surface is slightly larger than the medial fossa. The shaft is semi-circular with a flat ventral surface. A broad and shallow ventral flexor fossa is present to receive the ventral intercondylar process of the ungual. The dorsal extensor fossa is absent as in *Falcarius*,⁴ differing from a very deep extensor fossa found in *Therizinosaurus*.² The collateral ligament fossae are dorsally placed in *Duonychus*, but the lateral fossa is more distinct.

The manual ungual of digit I is strongly recurved, unlike in *Therizinosaurus*,² and laterally compressed (Figures 2I

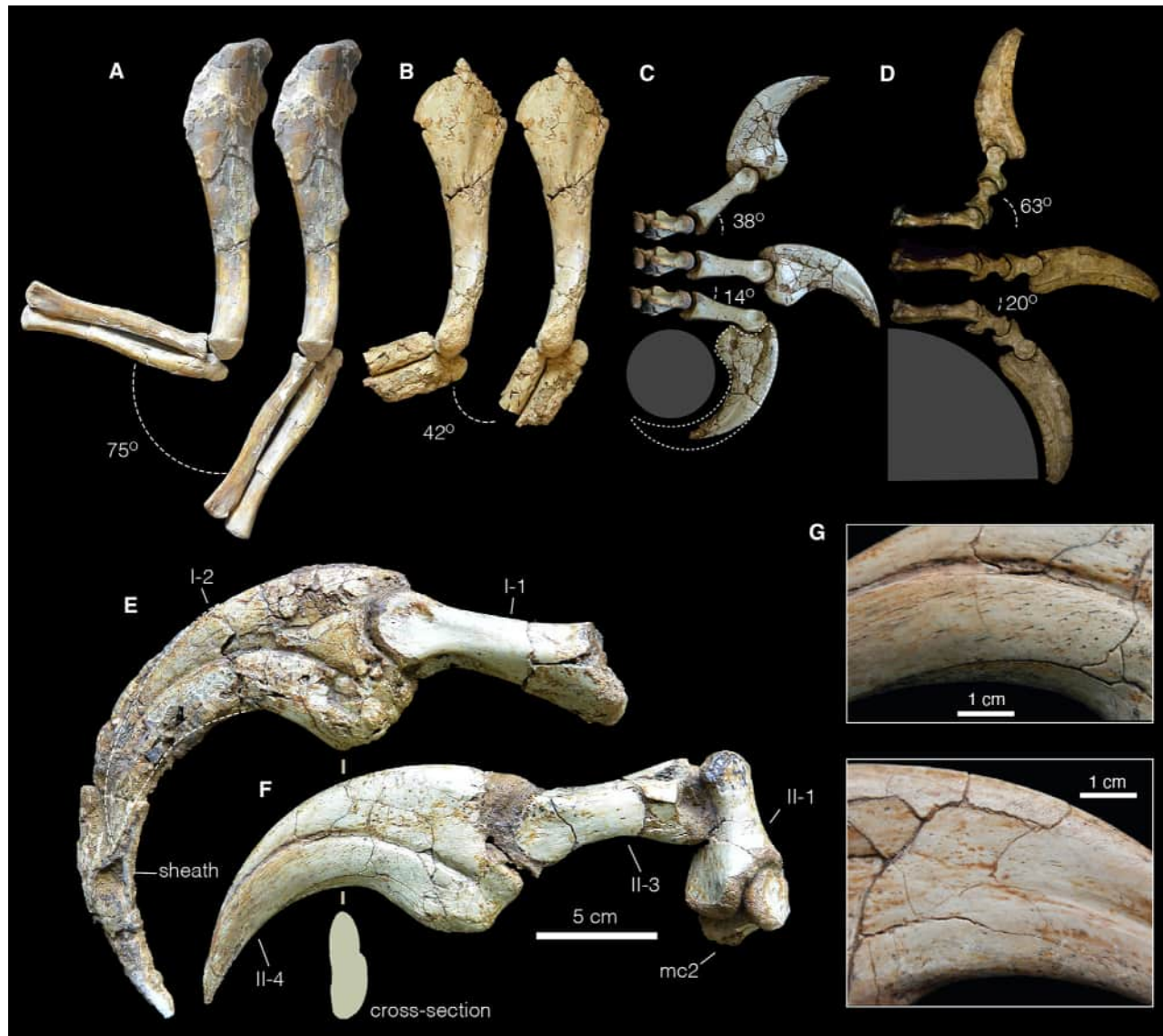


Figure 4. Forelimb and manual digit range of motion in therizosaurs

Range of motion of the elbow in *Segnosaurus* (A) and *Duonychus* (B). Range of motion of left manual digit I in *Duonychus* (C) and digit II in *Therizinosaurus* (D). The gray circle (C) and fan-shaped sector (D) represent the size of the object that can be grasped. Left digit I with a keratinous sheath (E) and digit II (F) in lateral view. (G) Close-up of lateral (above) and medial (below) surfaces of right ungual I-2. (A)–(D) are not to scale. A scale below (F) is for (E) and (F).

and 4E; Methods S1). It is much longer than the penultimate phalanx, similar to *Nothronychus* and *Therizinosaurus*. The dorsal intercondylar process does not form a “dorsal lip” as present in the unguals of digits I and II of *Falcarius*⁷ and of digit II in *Alxasaurus*.²⁰ A bulbous, rugose flexor tubercle lacks medial and lateral pits and is not separated from the ventral intercondylar process of the ungual by a groove. Both lateral and medial surfaces of the ungual have a groove. The medial groove remains on the medial surface, whereas the deeper and more defined lateral groove ends on the dorsal side of the ungual. The lateral surface of the ungual is convex with numerous minute foramina (more than 30), whereas the medial surface is flat with significantly smaller and fewer foramina (Figure 4G). The

left ungual is encapsulated by the preserved remnants of its keratinous sheath and is located ventrally in the sheath (Figures 4E and 4F). The measured curvature of the sheath is much longer than that of the ungual, revealing the keratinous claw was >40% longer than the ungual (Table S2). The ventral curvature of the keratinous sheath is approximately 120°, whereas the angle of attack is 59° (Figure 6A).

Although manual phalanx II-1 is generally similar to phalanx I-1, some morphological differences exist, including a sub-rectangular (wider than high) cross-section, a much shallower ventral flexor fossa, and poorly developed collateral ligament fossae and dorsal extensor pit. Manual phalanx II-1 is 40% shorter than manual phalanx I-1 in *Duonychus* (Table S2), whereas these

phalanges are subequal in length in the basal therizosaurs (e.g., *Falcarius*⁴ and *Jianchangosaurus*⁶) and phalanx II-2 is shorter in more derived forms (76% in *Erliaosaurus*⁷ and less than half in *Therizinosaurus*²). The sum of lengths of phalanges II-1 and II-2 is much shorter than the length of metacarpal II, unlike other therizinosaurids (*Alxasaurus*, *Erliaosaurus*, and *Therizinosaurus*), but similar to basal therizosaurs (*Falcarius* and *Beipiaosaurus*).

The ungual of digit II is similar to that of digit I in size and morphology, with the only clear difference being the presence of a shallow groove between the ventral intercondylar process and flexor tubercle in the former (Figures 2I and 4F; Methods S1). The ungual of digit I is the longest and the largest in *Falcarius*,⁴ *Erliaosaurus*,⁷ *Alxasaurus*,²⁸ and *Nothronychus*.^{8,29} The unguals of digits I and II are similar in length in *Therizinosaurus*.²

The right ilium is partially preserved, missing the postacetabular blade and part of the preacetabular blade (Figures 2A and 2C; Methods S1). The ilium is not fully fused with the first and second sacral ribs but is fused with the third sacral rib. The ilium flares laterally, with a dorsal margin of the preacetabular blade that is expanded dorsally but not everted as in *Segnosaurus*. The acetabulum is wide, and the pubic peduncle is significantly longer than the ischiadic peduncle. The ischiadic peduncle is robust and has a boss with a rugose surface.

The pubes are retroverted as in derived therizosaurs (Figures 2A and 2B; Methods S1). The iliac peduncle is missing on the left side but present on the right where it is narrow in lateral view. Its acetabular surface is wide narrowing toward the pubis-ischia contact, with no pronounced cranio-lateral tubercle, unlike *Nothronychus*.⁸ The iliac contact surface of the iliac peduncle is rugose and flat. In lateral view, the ischiadic peduncle is much taller than the iliac peduncle, as in *Suzhousaurus*³⁰ and *Segnosaurus*.³¹ The ventral half of the ischiadic peduncle has a posterior process that contacts the medial surface of the pubic peduncle of the ischia, forming a sigmoid pubis-ischia contact in lateral view. This posterior process may be unique to *Duonychus*. A shallow groove on the ventral border of the ischiadic peduncle seen in *Nothronychus* is absent, but there are two nutrient foramina. Ventral to these foramina is the beginning of the pubic apron, forming the anterior border of the obturator foramen. The pubic shaft is gently curved posteriorly, as in other therizosaurs except *Falcarius*,³² circular in cross-section unlike *Suzhousaurus*,³⁰ and lacks the lateral deflection as seen in *Suzhousaurus*³⁰ and the slight medial deflection observed in *Nothronychus*.⁸ The pubis is not fused to the obturator process of the ischium, unlike *Nothronychus*.⁸ The contact surface with the obturator process is tall, unlike *Enigmosaurus*³³ or *Nothronychus*,⁸ and is approximately two-thirds of the pubic boot length (Table S2). The contact surface is rugose and wide in the lower half. A groove between the contact surface with the obturator process and the pubic boot is absent, unlike *Nothronychus*.⁸ The pubic boots are not fused, unlike *Enigmosaurus*. The boot has a well-developed anterior process and an extremely short posterior process. The anterior process is massive, as in other derived therizosaurs, especially

similar to *Suzhousaurus*,³⁰ *Segnosaurus*,³¹ and *Nothronychus*.⁸ The posterior process is short, as in *Nothronychus*,⁸ whereas the process is absent in *Segnosaurus*² and *Suzhousaurus*.³⁰ The anterior and posterior processes are slender in *Enigmosaurus*.³³ In lateral view, the ventral border of the pubic boot is nearly straight. The border is slightly convex in other therizosaurs except *Enigmosaurus*.³³ The pubic boot is triangular in ventral view because it is transversely expanded anteriorly. The ventral surface of the pubic boot is rugose, as in *Nothronychus*.⁸

The pubic peduncle of the left ischium is preserved (Figure 2A; Methods S1). The transverse width of the pubic contact surface is nearly consistent and thins ventrally to form a ridge, covering the posterior process of the ischiadic process of the pubis laterally. A third of the proximal end of the ischium contributes to the acetabula, which is much less than that of the pubis. The remaining two-thirds forms a bowl-shaped socket that receives the ischiadic peduncle of the ilium.

Joint range of motion and ungual shape

The range of motion of the elbow and digits, using the barebones method, in *Duonychus* differs from other known therizosaurs (Figures 4A–4D). Unlike *Segnosaurus*, mobility at the elbow was limited as the forearm could not flex beyond a right angle relative to the humerus. Also, the range of motion of the manual phalanges of digit I in *Duonychus* was notably limited, 38° in extension and 14° in flexion, but comparable to those of other didactyl taxa, the tyrannosaurid *Tyrannosaurus* (35° in extension and 18° in flexion)³⁴ and the oviraptorid *Oksoko* (27° in extension and 13° in flexion).³⁵ *Therizinosaurus* had a greater degree of extension in the phalanges but was unable to flex its digits. At the ungual joint, *Duonychus* had significant flexion where the ungual could flex almost perpendicular to the preceding phalanx, a range of motion not known for *Therizinosaurus*, *Tyrannosaurus*, or *Oksoko*. With respect to ungual shape, the two unguals of *Duonychus*, in general, group with those of other therizosaurs, except *Therizinosaurus* based on a geometric morphometric analysis (Figure 6B; STAR Methods). The *Duonychus* unguals are similar to one another, but show slight shape differentiation where the ungual of digit I shows a dorsal shift of the ventral border and a distal shift of the tip relative to digit II. This pattern similarly occurs for digits I and II of the tridactyl therizosaurs, *Alxasaurus*, and *Falcarius*.

DISCUSSION

Phylogenetic analysis reveals *Duonychus* is nested in a derived clade within Therizinosauridae, where it and *Nanshiungosaurus* and the clade of *Suzhousaurus*, the Bissekty taxon, *Paralitherizinosaurus*, and *Therizinosaurus* form an unresolved polytomy (Figure 5; STAR Methods). *Duonychus* is thus recovered in a clade distinct from the three other known species of therizinosaur (i.e., *Enigmosaurus*, *Erliaosaurus*, and *Segnosaurus*) from the lower upper Cretaceous (Cenomanian to Santonian) Bayanshiree Formation of Mongolia. In addition to an unexpected morphological diversity of the therizinosaur manus (i.e., didactyl), *Duonychus* reveals a greater species richness

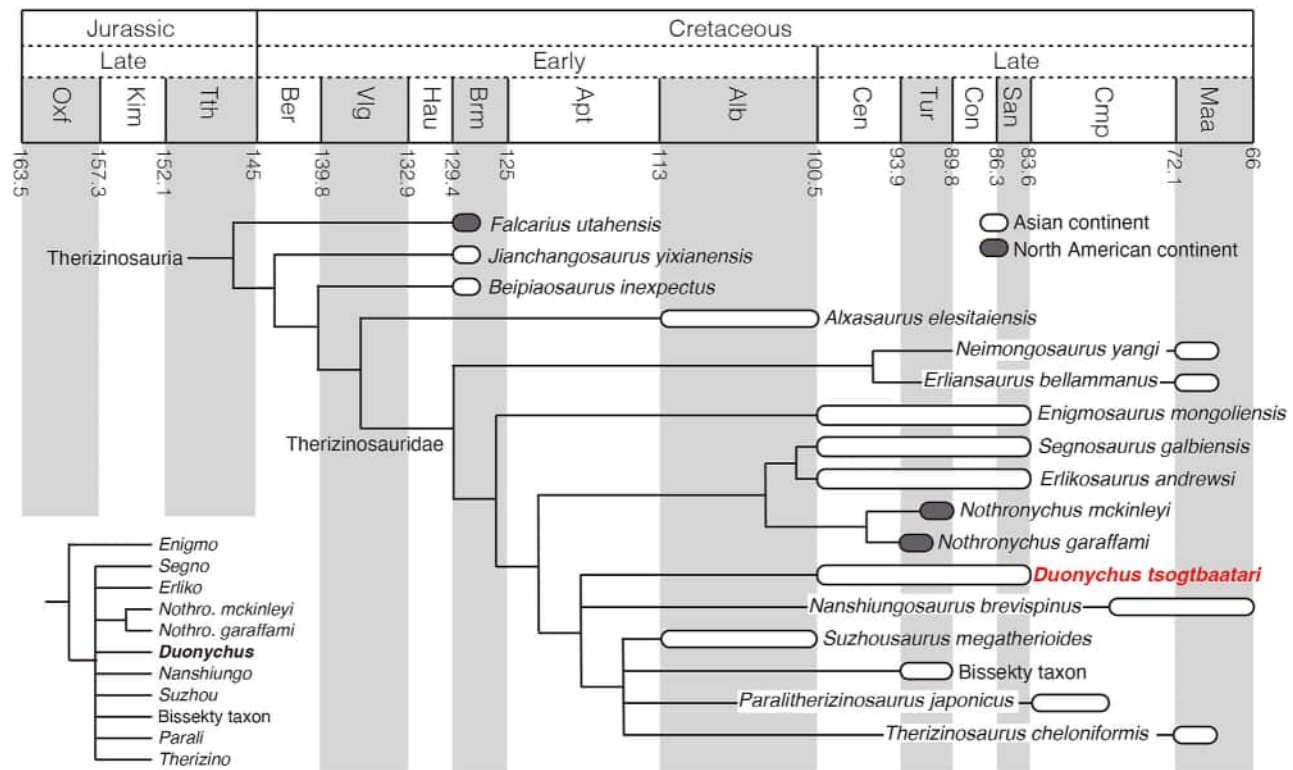


Figure 5. Phylogenetic relationships and temporal ranges of Therizinosauria

A time-scaled 50% majority-rule consensus tree of Therizinosauria from this study. The strict consensus tree of Therizinosauridae is shown in the lower left. The lengths of the ovals represent the potential temporal ranges of therizosaurs.

of therizosaurs in ecosystems of the Bayanshiree Formation than previously realized.

The well-preserved manus and three-dimensional claw of *Duonychus* (Figure 4E) provide insight into potential functional aspects of the hand. Based on ventral curvature and angle of attack parameters of the claw,³⁶ the preserved keratinous claw of *Duonychus* reveals functions within the range of scansorial (climbing), tenasorial (grappling) to amplexorial (grasping) (Figure 6A). Of these functions, the herbivorous or omnivorous diet and body size of *Duonychus*, as in other therizosaurids,⁸ would suggest an amplexorial usage where the claws serve to grasp branches as in chameleons and some mammals (e.g., southern tamandua, anteater), rather than to climb trees (e.g., squirrels), or to grasp, seize, or manipulate prey (e.g., birds of prey, felids)³⁶ (Figure 1). Despite having only two functional digits, *Duonychus* was likely an effective grasper, considering the extreme flexion (near 90°) at the ungual joint and the strong curvature of the keratinous claw, features unknown for other therizosaurs. Based on the shape of the ungual and the dimensions of the keratinous claw, *Duonychus* could have grasped branches or swaths of vegetation up to approximately 10 cm in diameter, which is less than the diameter of those grasped by *Therizinosaurus* (Figures 4C and 4D), suggesting that *Duonychus* may have been more selective in its foraging behavior. Although keratinous claws are not preserved in other therizosaur specimens, the bony un-

guals of *Duonychus* are of comparable morphology to those found in forms, such as *Falcarius*, *Erliansaurus*, and *Nothronychus* (although the degree of flexion of their ungual joints is uncertain) (Figure 6B). The manus of *Duonychus*, with its strong ungual flexion and claw curvature, further supports that the manus of derived therizosaurs likely served in a rake or hook-and-pull function to bring vegetation to the mouth during feeding as previously suggested.^{14,15} Although claws usually have a dominant function,³⁶ likely for hook-and-pull foraging in most derived therizosaurs, these structures could also have been utilized for other purposes, such as territoriality, defense, courtship, play, etc.

Duonychus also provides insight into evolutionary patterns of manual digit reduction/loss in theropods, particularly among Avetheropoda (*sensu* Hendrickx et al.³⁷) where the presence of three functional digits (I-III) represents the general or typical condition. The functionally didactyl (digits I and II) hand in *Duonychus* is unique among therizosaurs and relatively rare among theropod species. Our discovery reveals that the reduction/loss of a (functional) third digit has occurred five times (at least) in Theropoda, specifically within the subclade Avetheropoda (Figure 7). Such a reduction in the third digit appears to have occurred convergently in five clades, including Allosauroidae (assuming such a phylogenetic placement for *Gualicho*,³⁸ but see Porfiri et al.;³⁹), Tyrannosauridae, Alvarezsauridae, Therizinosauridae, and Oviraptorosauria. With respect to taxa within each

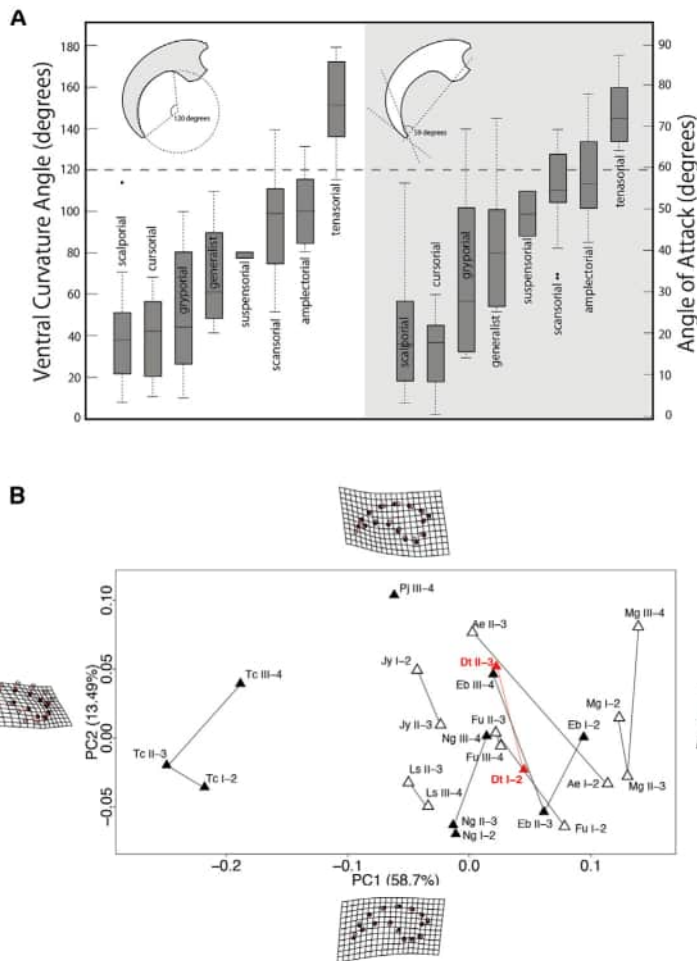


Figure 6. Morphometric analysis of forelimb functional morphology in therizinosauroids

(A) Boxplots for ventral curvatures and angle of attack among functional categories from Thomson and Motani,³⁶ showing the position of *Duonychus* (dashed line). Data are represented as median (central mark) and interquartile range (box), with whiskers indicating the most extreme data points not considered outliers.

(B) Scatterplot showing the PC1 and PC2 values obtained from the geometric morphometric analysis. The gray dots on the thin plate spline represent the “average” positions of the landmarks after deformation. The black dots represent the positions before deformation. Abbreviations: Ae, *Alxasaurus elesitaiensis*; Eb, *Erlansaurus bellamanus*; Pj, *Paralitherizinosaurus japonicus*; Fu, *Falcaurus utahensis*; Jy, *Jianchangosaurus yixianensis*; Ls, *Lingyuanosaurus sihedangensis*; Mg, *Martharaptor greenriverensis*; Ng, *Nothronychus graffami*; Tc, *Therizinosaurus cheloniformis*; Dt, *Duonychus tsogtbaatari*. These figures were created by using Adobe Photoshop 21.2.0 and Adobe Illustrator 24.2.1 (<https://www.adobe.com/>).

among both large-bodied dinosaur clades, such as Allosauroidea (*Gualicho*) and Tyrannosauroidae (Tyrannosauridae) and is likely due to a shift toward cranial-dominant predation strategies that rendered long forelimbs with tridactyl hands functionally redundant. *Gualicho* and tyrannosaurids completely lost the third digit, where the latter clade shows the most

of these clades, this reduction may be more exclusive in both Allosauroidea (*Gualicho*³⁸) and Therizinosauroidae (*Duonychus*), but more inclusive within Tyrannosauroidae (i.e., Tyrannosauridae⁴⁰), Oviraptorosauria (i.e., Heyuanninae³⁵), and Alvarezsauridae (i.e., Alvarezsauridae⁴¹).

Forelimb reduction is found in several theropod species or clades and often appears to be associated with digit modifications in the hand (e.g., abelisaurids,⁴² alvarezsaurids, *Gualicho*, *Limusaurus*, *Oksoko*, and tyrannosaurids). Within Avetheropoda, where tridactyly was the typical manus condition, a reduced forelimb and digit count (functional didactyly and even monodactyly) evolved independently among clades, regardless of the feeding ecology (herbivory, carnivory, or insectivory, etc.) (Figure 7). In some largely herbivorous/omnivorous clades, Therizinosauria (*Duonychus*) and Oviraptorosauria (*Oksoko* and possibly other Heyuanninae³⁵) independently evolved a reduced forelimb size along with functional didactyly, with a complete loss of digit III in *Duonychus*. In *Oksoko*, a size discrepancy between unguis I and II suggests a retained functional specialization for digit I, in contrast to *Duonychus* where comparable unguis I and II indicate similar functional roles. In some hyper-carnivorous clades, independent reduction in the forelimb/hand occurred

extreme reduction in *Tyrannosaurus*. The size discrepancy between unguis I and II of *Gualicho* indicates a potential retained functional specialization for digit I, in contrast to *Tyrannosaurus* where similar-sized unguis suggest similar functional roles. With a probable insectivorous diet, alvarezsaurids represent another avetheropodan clade that independently reduced forelimb size and the manus. Alvarezsaurids took reduction to an extreme by evolving a single, hypertrophied claw in some taxa,⁴³ uniquely adapted for digging into insect nests.⁴⁴ Among Avetheropoda, *Duonychus*, as the first-known didactyl therizinosaur, exemplifies further plasticity in digit three associated with various feeding ecologies and highlights the morphological/functional diversity in multiple instances of convergent evolution where the forelimb/manus are reduced.

Limitations of the study

The study is limited by the partial nature of the skeleton, a result of both the depositional environment and the circumstances of its discovery. The specimen was uncovered during the construction of a water pipeline near Khanbogd Town in Ömnögovi Province, southern Mongolia. Time constraints associated with the construction restricted the excavation,

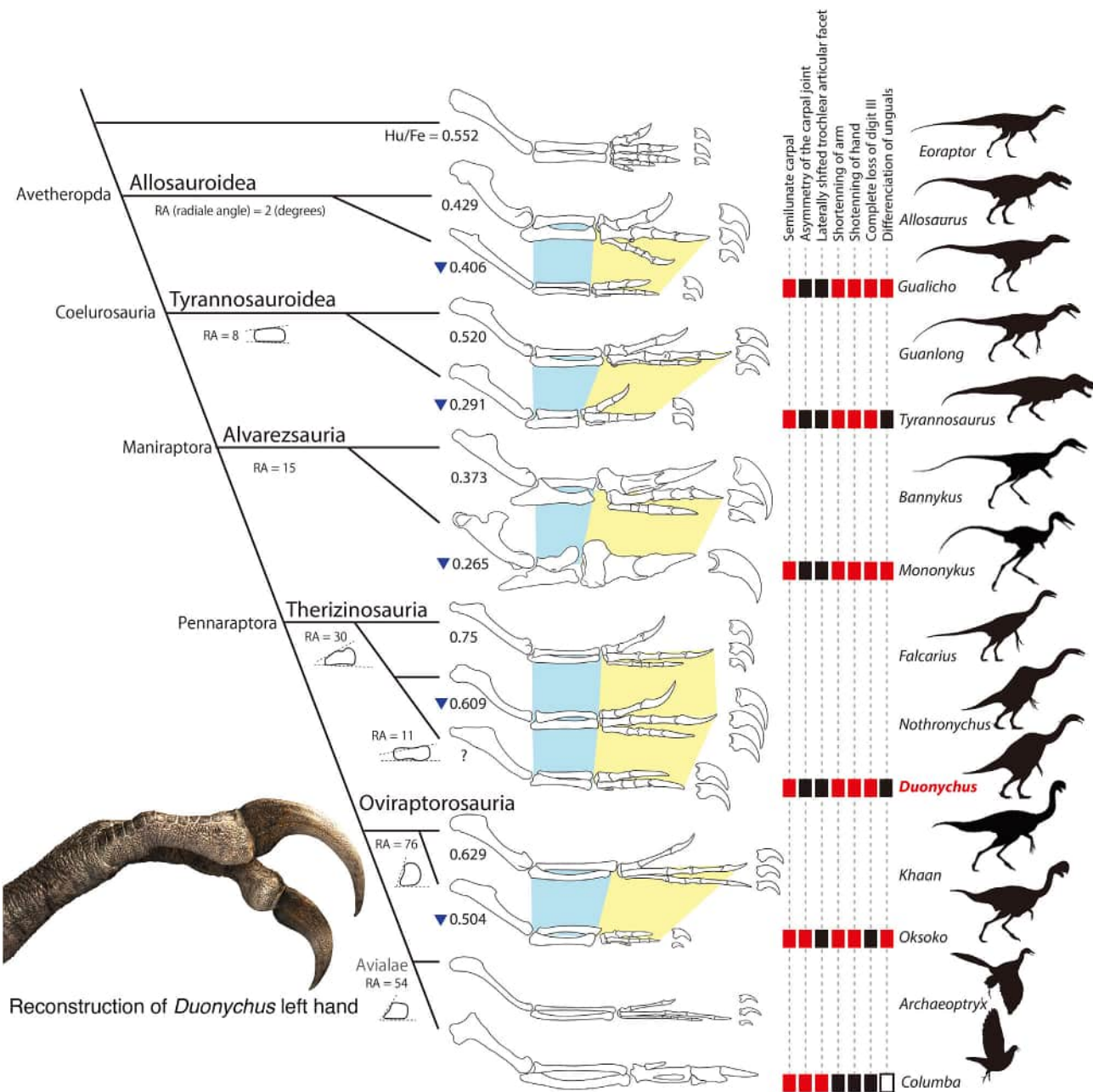


Figure 7. Cladogram of Avetheropoda highlighting forelimb shortening and digit III loss

A simplified clade of Avetheropoda, showing the shortening of the forelimb and loss of the functional third digit in Allosauroidea, Tyrannosauroidae, Alvarezsauria, Therizinosauria, and Oviraptorosauria. RA is the angle between the articular surfaces of the radiale for the semilunate carpal and the radius.²⁷ Hu/Fe is the length ratio of the humerus to the femur, and inverted blue triangles indicate a “decrease” in the ratio. The blue shading highlights changes in the length of the radius, while the yellow shading emphasizes comparisons of the second digit. Red boxes on the right side represent the presence of a semilunate carpal, asymmetry of the carpal joint (large RA values), a lateral shift in the position of the trochlear articular facet on the proximal surface of the carpometacarpus, shortening of the arm and hand, complete loss of digit III, and size differences of the unguals. Black boxes are absent, and the blank box is unknown. The arm line drawings and dinosaur silhouettes were illustrated by Genya Masukawa. The reconstruction of the left hand of *Duonychus tsogtbaatari*, depicting its didactyl configuration with a keratinous sheath, was illustrated by Masato Hattori (lower left).

limiting the search area and the extent of fossil recovery. Despite efforts to maximize recovery within the available time frame, only a partial skeleton was retrieved. The fossil

was deposited as part of a channel lag, thus the combination of rapid field excavation and the high-energy fluvial deposition contributed to the incomplete nature of the specimen. These

factors limited the availability of more comprehensive material, presenting a key limitation to the study.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to the lead contact, Yoshitsugu Kobayashi (ykobayashi@museum.hokudai.ac.jp).

Materials availability

The specimen reported in this paper (MPC-D 100/85) is accessioned at the public institute, Institute of Paleontology, Mongolian Academy of Sciences in Ulaanbaatar, Mongolia. The specimen is available for research.

Data and code availability

The dataset used in this study has been deposited at figshare (<https://figshare.com/>). DOI is listed in the [key resources table](#). This paper does not report the original code. Any additional information is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

Y.K. conceived the project and conducted comparative anatomical research, phylogenetic analysis, and statistical analysis. T.C. contributed geological context and interpretations. Y.K. drafted the initial version of the manuscript. Y.K. and D.K.Z. rewrote, revised, and refined the manuscript into its final form. A.R.F. and T.C. further improved the text, and all authors contributed to and approved the final manuscript for publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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REFERENCES

1. Maleev, E.A. (1954). New turtle-like reptile in Mongolia. *Priroda* 3, 106–108.
2. Zanno, L.E. (2010). A taxonomic and phylogenetic re-evaluation of Therizinosauria (Dinosauria: Maniraptora). *J. Syst. Palaeontol.* 8, 503–543. <https://doi.org/10.1080/14772019.2010.488045>.
3. Barsbold, R. (1976). New data on *Therizinosaurus* (Therizinosauridae, Theropoda). *Trans. Jt. Soviet–Mong. Palaeontol. Exped.* 3, 76–92.
4. Zanno, L.E. (2006). The pectoral girdle and forelimb of the primitive therizinosaurid *Falcarius utahensis* (Theropoda, Maniraptora): analyzing evolutionary trends within Therizinosaurioidea. *J. Vertebr. Paleontol.* 26, 636–650. <https://doi.org/10.1671/0272-4634>.
5. Xu, X., Tang, Z.L., and Wang, X.L. (1999). A therizinosaurid dinosaur with integumentary structures from China. *Nature* 399, 350–354. <https://doi.org/10.1038/20670>.
6. Pu, H., Kobayashi, Y., Lü, J., Xu, L., Wu, Y., Chang, H., Zhang, J., and Jia, S. (2013). An unusual basal therizinosaur dinosaur with an ornithischian dental arrangement from northeastern China. *PLoS One* 8, e63423. <https://doi.org/10.1371/journal.pone.0063423>.
7. Xu, X., Xiao-Hong, Z.H., Sereno, P., Xi-Jin, Z.H., Xue-Wen, K.U., Jun, H., and Lin, T. (2002). A new therizinosaurid (Dinosauria, Theropoda) from the Upper Cretaceous Iren Dabasu Formation of Nei Mongol. *Vertebr. Palaeontol.* 40, 228–240.
8. Hedrick, B.P., Zanno, L.E., Wolfe, D.G., and Dodson, P. (2015). The slothful claw: osteology and taphonomy of *Nothronychus mckinleyi* and *N. graffami* (Dinosauria: Theropoda) and anatomical considerations for derived therizinosaurids. *PLoS One* 10, e0129449. <https://doi.org/10.1371/journal.pone.0129449>.
9. Kirkland, J.I., and Wolfe, D.G. (2001). First definitive therizinosaurid (Dinosauria; Theropoda) from North America. *J. Vertebr. Paleontol.* 21, 410–414. [https://doi.org/10.1671/0272-4634\(2001\)021\[0410:Fdtatf\]2.0.Co;2](https://doi.org/10.1671/0272-4634(2001)021[0410:Fdtatf]2.0.Co;2).
10. Zanno, L.E., Gillette, D.D., Albright, L.B., and Titus, A.L. (2009). A new North American therizinosaurid and the role of herbivory in ‘predatory’ dinosaur evolution. *Proc. Biol. Sci.* 276, 3505–3511. <https://doi.org/10.1098/rspb.2009.1029>.
11. Hendrickx, C., Mateus, O., Araújo, R., and Choiniere, J. (2019). The distribution of dental features in non-avian theropod dinosaurs: taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontol. Electronica* 22, 1–110. <https://doi.org/10.26879/820>.
12. Clark, J.M., Perle, A., and Norell, M. (1994). The skull of *Erikosaurus andrewsi*, a Late Cretaceous “segosaur” (Theropoda: Therizinosauridae) from Mongolia. *Am. Mus. Novit.* 3115, 1–39.
13. Zanno, L.E., Tsogtbaatar, K., Chinzorig, T., and Gates, T.A. (2016). Specializations of the mandibular anatomy and dentition of *Segnosaurus galbinensis* (Theropoda: Therizinosauria). *PeerJ* 4, e1885. <https://doi.org/10.7717/peerj.1885>.
14. Lautenschlager, S. (2014). Morphological and functional diversity in therizinosaur claws and the implications for theropod claw evolution. *Proc. Biol. Sci.* 281, 20140497. <https://doi.org/10.1098/rspb.2014.0497>.
15. Kobayashi, Y., Takasaki, R., Fiorillo, A.R., Chinzorig, T., and Hikida, Y. (2022). New therizinosaurid dinosaur from the marine Osoushinai Formation (Upper Cretaceous, Japan) provides insight for function and evolution of therizinosaur claws. *Sci. Rep.* 12, 7207. <https://doi.org/10.1038/s41598-022-11063-5>.
16. Marsh, O.C. (1881). Principal characters of American Jurassic dinosaurs, Part V. *Am. J. Sci. Series* 3, 417–423.

17. von Huene, F. (1914). Das natürliche system der Saurischia. Zentralbl. Mineral. Geol. Paläontol. B 1914, 154–158.
18. Russell, D.A. (1997). In *Encyclopedia of Dinosaurs*, P.J. Currie and K. Padian, eds. (Academic Press), pp. 729–730.
19. Eberth, D.A., Badamgarav, D., and Currie, P.J. (2009). The Baruungoyot-Nemegt transition (Upper Cretaceous) at the Nemegt type area, Nemegt Basin, south central Mongolia. *J. Paleontol. Soc. Korea* 25, 1–15.
20. Shuvalov, V.F. (2000). In *The age of dinosaurs in Russia and Mongolia*, M.J. Benton, M.A. Shishkin, E.N. Kurochkin, and D.M. Unwin, eds. (Cambridge University Press), pp. 256–278.
21. Jerzykiewicz, T., and Russell, D.A. (1991). Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretac. Res.* 12, 345–377. [https://doi.org/10.1016/0195-6671\(91\)90015-5](https://doi.org/10.1016/0195-6671(91)90015-5).
22. Kurumada, Y., Aoki, S., Aoki, K., Kato, D., Saneyoshi, M., Tsogtbaatar, K., Windley, B.F., and Ishigaki, S. (2020). Calcite U–Pb age of the Cretaceous vertebrate-bearing Bayn Shire Formation in the Eastern Gobi Desert of Mongolia: usefulness of caliche for age determination. *Terra Nova* 32, 246–252. <https://doi.org/10.1111/ter.12456>.
23. Zanno, L.E., and Makovicky, P.J. (2013). No evidence for directional evolution of body mass in herbivorous theropod dinosaurs. *Proc. Biol. Sci.* 280, 20122526. <https://doi.org/10.1098/rspb.2012.2526>.
24. Christiansen, P., and Fariña, R.A. (2013). Mass prediction in theropod dinosaurs. *Hist. Biol.* 16, 85–92.
25. Dong, Z. (1979). In *Mesozoic and Cenozoic red beds of south China* (Science Press), pp. 342–350.
26. Perle, A. (1981). A new segnosaurid from the Upper Cretaceous of Mongolia. *Trans. Jt. Soviet–Mong. Palaeontol. Exped.* 8, 45–55.
27. Sullivan, C., Hone, D.W.E., Xu, X., and Zhang, F. (2010). The asymmetry of the carpal joint and the evolution of wing folding in maniraptoran theropod dinosaurs. *Proc. Biol. Sci.* 277, 2027–2033. <https://doi.org/10.1098/rspb.2009.2281>.
28. Russell, D.A., and Dong, Z.M. (1993). The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People’s Republic of China. *Can. J. Earth Sci.* 30, 2107–2127. <https://doi.org/10.1139/e93-183>.
29. Smith, D.K., and Gillette, D.D. (2024). Osteology of the derived therizinosaur *Nothronychus* with evidence for convergence in dinosaurian evolution. *Zool. J. Linn. Soc.* 203, zlad148. <https://doi.org/10.1093/zoolin-nean/zlad148>.
30. Li, D.Q., Cuo, P.E., Hailu, Y.O., Lamanna, M.C., Harris, J.D., Lacovara, K.J., and Jianping, Z.H. (2007). A large therizinosaurid (Dinosauria: Theropoda) from the Early Cretaceous of northwestern China. *Acta Geol. Sin.* 81, 539–549.
31. Perle, A. (1979). *Segnosauridae – a new family of theropods from the Late Cretaceous of Mongolia*. *Trans. Jt. Soviet–Mong. Palaeontol. Exped.* 15, 28–39.
32. Zanno, L.E. (2010). Osteology of *Falcarius utahensis* (Dinosauria: Theropoda): characterizing the anatomy of basal therizosaurs. *Zool. J. Linn. Soc.* 158, 196–230. <https://doi.org/10.1111/j.1096-3642.2009.00464.x>.
33. Barsbold, R. (1979). Opisthopubic pelvis in the carnivorous dinosaurs. *Nature* 279, 792–793. <https://doi.org/10.1038/279792a0>.
34. Senter, P., and Parrish, J.M. (2005). *Functional analysis of the hands of the theropod dinosaur Chirostenotes pergracilis: evidence for an unusual paleoecological role*. *PaleoBios* 25, 9–19.
35. Funston, G.F., Chinzorig, T., Tsogtbaatar, K., Kobayashi, Y., Sullivan, C., and Currie, P.J. (2020). A new two-fingered dinosaur sheds light on the radiation of Oviraptorosauria. *R. Soc. Open Sci.* 7, 201184. <https://doi.org/10.1098/rsos.201184>.
36. Thomson, T.J., and Motani, R. (2021). Functional morphology of vertebrate claws investigated using functionally based categories and multiple morphological metrics. *J. Morphol.* 282, 449–471. <https://doi.org/10.1002/jmor.21317>.
37. Hendrickx, C., Hartman, S.A., and Mateus, O. (2015). An overview of non-avian theropod discoveries and classification. *PalArch’s J. Vertebr. Palaeontol.* 12, 1–73.
38. Apesteguía, S., Smith, N.D., Juárez Valieri, R., and Makovicky, P.J. (2016). An unusual new theropod with a didactyl manus from the Upper Cretaceous of Patagonia, Argentina. *PLoS One* 11, e0157793. <https://doi.org/10.1371/journal.pone.0157793>.
39. Porfiri, J.D., Valieri, R.D.J., Santos, D.D.D., and Lamanna, M.C. (2018). A new megaraptoran theropod dinosaur from the Upper Cretaceous Bajo de la Carpa Formation of northwestern Patagonia. *Cretaceous Res.* 89, 302–319. <https://doi.org/10.1016/j.cretres.2018.03.014>.
40. Padian, K. (2022). Why tyrannosaurid forelimbs were so short: an integrative hypothesis. *Acta Palaeontol. Pol.* 67, 63–76.
41. Kubo, K., Kobayashi, Y., Chinzorig, T., and Tsogtbaatar, K. (2023). A new alvarezsaurid dinosaur (Theropoda, Alvarezsauria) from the Upper Cretaceous Baruungoyot Formation of Mongolia provides insights for bird-like sleeping behavior in non-avian dinosaurs. *PLoS One* 18, e0293801. <https://doi.org/10.1371/journal.pone.0293801>.
42. Burch, S.H. (2017). Myology of the forelimb of *Majungasaurus crenatissimus* (Theropoda, Abelisauridae) and the morphological consequences of extreme limb reduction. *J. Anat.* 231, 515–531. <https://doi.org/10.1111/joa.12660>.
43. Xu, X., Sullivan, C., Pittman, M., Choiniere, J.N., Hone, D., Upchurch, P., Tan, Q., Xiao, D., Tan, L., and Han, F. (2011). A monodactyl nonavian dinosaur and the complex evolution of the alvarezsaurid hand. *Proc. Natl. Acad. Sci. USA* 108, 2338–2342. <https://doi.org/10.1073/pnas.1011052108>.
44. Senter, P. (2005). *Function in the stunted forelimbs of Mononykus olecranus* (Theropoda), a dinosaurian anteater. *Paleobiology* 31, 373–381.
45. (2019). *Geomorph: Software for Geometric Morphometric Analyses. R package version 3.1.0*.
46. Xu, X., Xiao-Hong, Z.H., Sereno, P., Xi-Jin, Z.H., Xue-Wen, K.U., Jun, H., and Lin, T. (2002). A new therizinosaurid (Dinosauria, Theropoda) from the Upper Cretaceous Iren Dabas Formation of Nei Mongol. *Vertebr. Palaeasiat.* 40, 228–240.
47. Yao, X., Liao, C.C., Sullivan, C., and Xu, X. (2019). A new transitional therizinosaurian theropod from the Early Cretaceous Jehol Biota of China. *Sci. Rep.* 9, 5026. <https://doi.org/10.1038/s41598-019-41560-z>.
48. Sues, H.-D., and Averianov, A. (2016). Therizinosaurioidea (Dinosauria: Theropoda) from the Upper Cretaceous of Uzbekistan. *Cretac. Res.* 59, 155–178. <https://doi.org/10.1016/j.cretres.2015.11.003>.
49. Senter, P., Kirkland, J.I., and DeBlieux, D.D. (2012). *Martharaptor greenriverensis*, a new theropod dinosaur from the Lower Cretaceous of Utah. *PLoS One* 7, e43911. <https://doi.org/10.1371/journal.pone.0043911>.
50. Chinzorig, T., Kobayashi, Y., Tsogtbaatar, K., Currie, P.J., Takasaki, R., Tanaka, T., Iijima, M., and Barsbold, R. (2018). Ornithomimosaur from the Nemegt Formation of Mongolia: manus morphological variation and diversity. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 494, 91–100. <https://doi.org/10.1016/j.palaeo.2017.10.031>.
51. (2019). *R: A Language and Environment for Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing).

STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|--|---|---|
| Deposited data | | |
| Phylogenetic analysis character description | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Phylogenetic analysis data matrix | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Geometric morphometric analysis data taxa.csv | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Geometric morphometric analysis data therizinosaur unguual.tps | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Geometric morphometric analysis data curvslide.csv | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Geometric morphometric analysis data R script | figshare https://figshare.com/ | https://doi.org/10.6084/m9.figshare.27966855 |
| Software and algorithms | | |
| RStudio | RStudio Team https://www.rstudio.com/ | RStudio Version 2023.06.1 |
| TNT (Tree Analysis Using New Technology) | http://www.iillo.org.ar/phylogeny/tnt/ | TNT 1.6 |

METHOD DETAILS

Institutional abbreviations

MPC-D; Institute of Paleontology, Mongolian Academy of Sciences in Ulaanbaatar, Mongolia.

Geological setting

The fossil records of Therizinosauria are notably abundant in Cretaceous deposits across eastern Asia, particularly in Mongolia and China. Within Mongolia, the Late Cretaceous formations have yielded a plethora of therizinosaur taxa, including *Enigmosaurus*, *Erikkosaurus*, and *Segnosaurus* from the Bayanshiree Formation (Cenomanian to Santonian), as well as *Therizinosaurus* from the Nemegt Formation (early Maastrichtian) near the Sino-Mongolian border. Of these formations, the Bayanshiree Formation stands out for its exceptional diversity of therizosaurs. During the construction of a water pipe in 2012 near Khanbogd Town in Ömnögovi Province, southern Mongolia, a partial skeleton of a novel therizinosaur was discovered in a proxy of an area of 40 cm and 60 cm with pebbles at the bottom of a fluvial sandstone bed, indicating that the material was deposited as channel lag. This locality, referred to as the Urliibe Khudak Locality, lies close to other renowned sites within the Bayanshiree Formation, notably the Amtgai and Baishin Tsav localities. Since 2016, collaborative paleontological expeditions spearheaded by the Institute of Paleontology of the Mongolian Academy of Sciences and Hokkaido University Museum have systematically explored this region, unveiling a rich assemblage of dinosaurian taxa encompassing hadrosaurs, ankylosaurs, ceratopsians, ornithomimosaur, therizosaurs, oviraptorosaurs, and sauropods.

QUANTIFICATION AND STATISTICAL ANALYSIS

Phylogenetic analysis

A phylogenetic analysis was performed using TNT (Tree Analysis Using New Technology) v. 1.6 and the data matrix of Kobayashi et al.,¹⁴ which is based on the matrix of Zanno,² with the addition of *Duonychus* described here (key resources table). Most parsimonious trees were obtained by heuristic search methods on 1000 replicates of Wagner trees with random addition sequences and subject to tree bisection-reconnection swapping methods holding 10 trees per replicate. As noted by Zanno,² twenty characters (characters 27, 37, 40, 68, 76, 78, 97, 106, 113, 157, 163, 168, 253, 303, 308, 309, 310, 334, 342, and 345) were designated additive. This study follows Zanno,² Clark et al.,¹² and Kobayashi et al.¹⁴ for the definitions of Therizinosauria, Therizinosaurioidea, and Therizinosauridae, respectively. Therizinosauria is the most inclusive clade containing *Therizinosaurus cheloniformis* but not *Tyrannosaurus rex*, *Ornithomimus edmontonicus*, *Mononykus olecranus*, *Oviraptor philoceratops* or *Troodon formosus*. Therizinosaurioidea is defined as the least inclusive clade containing *Beipiaosaurus inexpectus* and *Therizinosaurus cheloniformis*. Therizinosauridae is the most inclusive clade containing *Therizinosaurus cheloniformis* but not *Alxasaurus elesitaiensis*.

Geometric morphometric analysis

To quantify two-dimensional ungual shape variations, geometric morphometric analysis was performed using R package geomorph version 3.3.1.⁴⁵ ([key resources table](#)). Ungual images other than of *Duonychus* and *Therizinosaurus* were obtained from the literature.^{4,6,8,28,46–49} Outlines of the unguals in the lateral view were digitized into four fixed landmarks and 12 sliding semi-landmarks, following Chinzorig et al.⁵⁰ The landmarks were subjected to the generalized Procrustes analysis to superimpose the specimens, followed by the principal component analysis (PCA) to reduce dimensionality. The statistical analyses were conducted on software R version 4.0.2.⁵¹ The analyses are conducted using the R script provided as a deposited file on figshare ([key resources table](#)).