The taxonomy of a new parvicursorine alvarezsauroid specimen IVPP V20341 (Dinosauria: Theropoda) from the Upper Cretaceous Wulansuhai Formation of Bayan Mandahu, Inner Mongolia, China

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Abstract

A new parvicursorine alvarezsauroid theropod specimen IVPP V20341 from the Upper Cretaceous Wulansuhai Formation of Bayan Mandahu, Inner Mongolia, China is described. IVPP V20341 appears to be distinguishable amongst alvarezsauroids by cervical proceoly and relatively larger semi-circular neural canals, but these features are not proposed as autapomorphies because current knowledge of alvarezsauroid necks and tails remains sparse. IVPP V20341 is distinguishable from *Linhenykus* - the sole parvicursorine at Bayan Mandahu - by 13 anatomical features that mostly relate to cervical and caudal vertebrae. However, it is unclear how these vertebral elements compare positionally along the spine, so more complete future finds could revise the observed differences. Thus, there are still seven parvicursorine species from the Cretaceous Gobi Basin after the discovery of IVPP V20341.

Keywords

Parvicursorine, Alvarezsauroid, Theropod, Campanian, Upper Cretaceous, Inner Mongolia

Introduction

The Campanian-aged rocks of the Gobi basin of China and Mongolia have yielded alvarezsauroid theropods with impressive specialised body plans including the uniquely monodactyl parvicursorine *Linhenykus monodactylus* [1]. The latter is the only parvicursorine species from the Chinese Gobi Basin and was discovered in Bayan Mandahu, Inner Mongolia. Six parvicursorine species are known from the Mongolia Gobi Basin: *Albinykus* [2], *Ceratonykus* [3], *Kol* [4], *Mononykus* [5,6], *Parvicursor* [7,8] and *Shuvuuia* [9,10] (Table S1). Dinosaur discoveries at Bayan Mandahu have been important in demonstrating that distinct faunas existed across the Cretaceous Gobi basin [1,8,11-16], which has provided valuable insight into how dinosaurs behaved and coped over expansive semi-arid environments. Here we report IVPP V20341 a fragmentary disarticulated parvicursorine specimen that was discovered in Bayan Mandahu during the 2013 field season of the Inner Mongolia Research Project (IMRP). IVPP V20341 appears to have two autapomorphies (cervical proceoly and relatively larger semi-circular neural canals), but these cannot be confidently assigned because anatomical variation along the spine cannot be ruled out as an explanation for these observed differences, given the large amounts of missing data from known parvicursorine neck and tail specimens. IVPP V20341 is therefore an important parvicursorine specimen as comparative studies with future finds may either provide new information about anatomical variation in these animals or justify the erection of a new taxon, the second and seventh parvicursorine of Bayan Mandahu and the Gobi Basin respectively.

Systematic Palaeontology

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Alvarezsauridae Bonaparte, 1991
Parvicursorinae Karhu & Rautian 1996

Material

IVPP V20341, A highly fragmentary postcranial skeleton comprising of an articulated series of: 4 partial cervical vertebrae, an isolated anterior portion of a cervical vertebra; 4 isolated broken caudal vertebrae; a potential broken left scapula; various suspected pedal phalanges, including unknown digit II/III and IV phalanges, a right II-1, II-2, and IV, as well as a potential left III-2 and III-3.

Locality and horizon

IVPP V20341 was found at Bayan Mandahu, Inner Mongolia, China which is part of the Campanian-aged Wulansuhai Formation [17]. On July 2nd 2013, a team member (JS) discovered isolated alvarezsauroid bones weathering out of a cliff top exposure of a fine-grained, red structureless aeolian quartz arenite, ~3km SE of 'The Gate' locality (41°43'15.3"N, 106°44'43.3"E; Figure 1), close to the location of Eberth's [17] '7/12/90/2' stratigraphic section but not as far North as his '7/12/90/1' section [17]. The locality lies within an larger area that Jerzykiewicz *et al*. called the 'South Escarpment' locality, but the specific locality of IVPP V20341 is referred to as the 'eagle's nest' because a large predatory bird nest was found ~3 metres from the find. On July 3rd 2013, another team member (MP) further explored the sublocality and recovered several additional bones within 1m of the original material. Following the depositional environments and facies transitions identified by Eberth [17] at Bayan Mandahu, the specimen was deposited in the zone 1 palaeographic zone which consists of alluvial, lacustrine and aeolian sediments deposited in a distal alluvial fan or braid-plain environment adjacent to an aeolian dune field. Given the sandy depositional environment of the specimen IVPP V20341 was nicknamed 'Xiaoshalong', which is Chinese for 'little sand dragon'.

Description and comparison

IVPP V20341 appears to belong to a more ontogenetically mature individual (e.g. subadult or adult) because the neurocentral sutures on the vertebrae preserved appear to be completely closed [18,19]. However, this inference should be treated as tentative in the absence of other ontogenetically-informative fusion in the appendicular skeleton as well as relevant histological data. The skeletal elements common to both the IVPP V20341 and to *Linhenykus* are generally smaller in the former than in the latter. This suggests that IVPP V20341 was probably lighter in weight than *Linhenykus*, which itself weighed around 450g [1,20]. IVPP V20341 lacks a femur and skull so a more accurate proxy-based estimate of body mass was not possible [21,22]. The incomplete vertebral column and the missing skull also prohibited a meaningful measurement of body length. However, given the relative size of IVPP V20341 to *Linhenykus*, the former was probably lighter than other Asian parvicursorines, with the exception of *Shuvuuia* and *Parvicursor* (See Table S2).

Axial Skeleton

An articulated series of 4 partial cervical vertebrae (A-D) (Figure 2A), an isolated anterior portion of a cervical vertebra (Figure 2B) and 4 isolated broken caudal vertebrae (A-D) represent the axial skeleton (Figure 3).

Cervical vertebrae

The first of four articulated partial cervicals (cervical A) is broken and fragmentary whereas the second cervical in the series (cervical B) is almost completely preserved save for a small degree of dorsal crushing and abrasion. The third cervical in the preserved series (cervical C) is partially complete and is best represented on its left lateral side. The most posterior cervical preserved (cervical D) is also broken and fragmentary, like cervical A. An isolated cervical centra resembling the anteroventral portion of a smaller version of cervical B is preserved. However, the dorsal surface - including most of the neural arch - is missing. Linear measurements of the cervical vertebrae are given in Table 2.

Cervicals A and B in IVPP V20341 – a cervical fragment and a dorsally crushed complete cervical respectively – meet via a procoelous articular joint that is identified by the shape of the ventral rims of the articular faces: in cervical A, the posterior articular face has a convex ventral rim, whereas in cervical B, the anterior articular face has a concave ventral rim (Figure 2A). This joint is unlike the strongly opisthocoelous ones found in *Linhenykus*, *Shuvuuia* and *Mononykus* [1,5,20,23]. Cervical opisthocoely has also been proposed - albeit tentatively - for *Patagonykus* [23-25]. These articular joint morphologies contrast to the amphi- to platyceolous condition in the basalmost alvarezsauroid *Haplocheirus* [26] and the amphiplatyan condition proposed in *Alvarezsaurus* (MUCPv 54 [23,27]). Despite the prevalence of opisthocoely amongst alvarezsauroid cervicals, the paucity of complete alvarezsauroid cervical series (one complete neck for the basal alvarezsauroid *Haplocheirus solers* (IVPP V15988) and two near complete ones for *Mononykus* (MPC 107/6, [5]) and *Shuvuuia* (MPC 100/975, [23]) warrants caution in considering cervical proceoly as a potential autapomorphic characteristic of IVPP V20341, particularly given the array of articular face geometries that are preserved in the dorsal and caudal vertebral series of other alvarezsauroids e.g. the opisthocoloeus proximal and mid-dorsals and biconvex distal dorsals of *Mononykus* (MPC 107/6, [5]) and the procoelous, amphicoelous and opisthocoeolous/biconvex proximal caudals of *Achillesaurus* (MACN-PV-RN 1116, [28]). Thus, cervical procoely is considered as an *equivocal* autapomorphy of IVPP V20341 that cannot be used to erect a new taxon on its own for the aforementioned reasons. Like in other alvarezsauroids the condyles of the cervical centrum preserved appear smaller than their corresponding articular surfaces [20]. In ventral view, the rims of the anterior articular surfaces are concave whilst the posterior ones are convex.

In lateral view, the cervical centra of IVPP V20341 are long and low, as in other alvarezsauroids [23]. They are not as strongly laterally compressed as the posterior cervicals of *Linhenykus* (IVPP 17608, [20]) as only the ventral portion is compressed in IVPP V20341. Thus, the lateral surfaces of IVPP V20341 are more vertical in the middle portion of the centrum than in *Linhenykus*. Nevertheless, this qualified the specimen as an alvarezsaurid alvarezsauroid (cervical centra bearing deep lateral depressions is an alvarezsaurid synapomorphy [20] (character state 8.1 of Longrich & Currie [8]). The ventral surfaces of these cervicals are rounded and slightly pinched along their mid-length whereas they are grooved (longitudinal ventral furrow) and pinched along their mid-length in the posterior cervicals of *Linhenykus*, IVPP V17608 [20]. *Shuvuuia* appears to share the same morphology in its posterior cervical vertebrae (MPC 100/975, [23]) and potentially *Ceratonykus* as well (MPC 100/124, [3]; a furrow is present in the cranioventral and midventral postions of a posterior cervical, but the distoventral portion is broken). In the most proximal cervicals the ventral furrow of *Shuvuuia* does not span the entire centra, because the mid-line of the centra is interrupted by a rounded surface (MPC 100/975 [23]), like in *Mononykus* (MPC 107/6 [5]). The cranioventral furrows in *Shuvuuia* and *Mononykus* are bordered by prominences [23] and are the only furrows present in the most proximally preserved cervicals of *Shuvuuia.* The presence of a full length ventral furrow in posterior centra of *Shuvuuia* and *Ceratonykus* suggests that this feature is probably not a valid autapomorphy of the *Linhenykus*, unless future data can demonstrate that only *Linhenykus* has this furrow on all of its cervicals. The lack of a prominence-bordered cranioventral furrow in cervical B of IVPP V20341 appears unique to Asian parvicursorines, but it is known in South American forms. MCF-PVPH 38, a fragmentary 5th? cervical of a suspected indeterminate Argentine alvarezsauroid (? Alvarezsauridae indet.), has a straight, narrow and rounded ventral surface - much wider than a keel - with a 'veiny' surface texture [25]. The smooth cranioventral surface of the cervical could be a valuable character for distinguishing parvicursorines, but the absence of more complete neck specimens, the questionable taxonomy of MCF-PVPH 38 and the presence of this feature in the basal alvarezsauroid *Alvarezsaurus* [23] makes the taxonomic value of this feature ambiguous.

Dorsal to the left lateral postzygapophysis of cervicals B and C there is no evidence of an epipophysis, indicating that IVPP V20341 is an alvarezsauroid theropod (character state 6.1 of Longrich & Currie [8] is an alvarezsauroid synapopmorphy [20]). In IVPP V20341, the diapophysial ridge has a convex profile in the area around the small nubbin-like diapophysis (similar diapophysis in the posterior cervicals of *Linhenykus*, IVPP V17608 [20]) but shallows gradually towards the posteroventral corner of the centrum. This differs from the condition in *Linhenykus* - another autapomorphy of this taxon - where the diapophyseal ridges extend to the posterodorsal rim of the centrum [20]. However, the former may not be a valid autapomorphy owing to the presence of the same feature in *Shuvuuia* (MPC 100/975, [23]). In IVPP V20341 the diapophysial ridge's anteroventral surface is excavated and houses a broad shallow fossa. This feature is difficult to appraise in *Linhenykus* as the ridge and the anteroventral surface are not preserved in the same cervical. However, across two posterior caudals large collateral pneumatic foramina are present [20] instead of broad shallow fossa. Cervical B lacks a carotid process unlike in *Linhenykus* (where it is confluent with the anterior ends of the ventral ridges in the posterior cervicals [20]); also known in *Shuvuuia* [23] and *Mononykus* [5] as well as other theropods including some ornithomimosaurs, oviraptorosaurs and paravians [20]. Cervicals B and C of IVPP V20341 both lack pneumatic foramina as in *Mononykus* [5], but the lateral surfaces of their centra appear to be less compressed mediolaterally than in *Mononykus* (mediolaterally compressed cervical centra that lack pneumatic foramina are given in the diagnosis of *Mononykus* [23]). In *Linhenykus* - like *Alvarezsaurus* and *Shuvuuia* - pneumatic foramina occupy the area immediately posterior to the parapophyses [20,23,27]. As in *Linhenykus*, the neural pedicles are mediolaterally broad and dorsoventrally low and it appears that the anterior edge of each pedicle is also flush with the anterior articular surface of the centrum, whereas the posterior edge is anterior to the posterior articular surface (excluding the condyle) [20]. The parapophyses are also low, laterally projecting eminences like in *Linhenykus* [20]. The process is dorsolaterally orientated.

The zygapophyseal articular facets in cervicals B-D of IVPP V20341 have a low-angle (~78˚ and ~61˚ from the vertical [in anterior view] for the prezygapophyses of cervicals C and D respectively and ~50˚ and ~40˚ from the vertical [in posterior view] for the postzygapophyses of cervicals B and C respectively) suggesting a greater range of motion in the horizontal plane than the vertical one. This is because the prezygapophyses show the latter, whilst the postzygapophyses are complimentary to this pattern since they indicate that the range of motion was similar in either plane. The prezygapophyses are anteroposteriorly short and extend over approximately one third of the preceding centra. The postzygapophyseal processes of cervical B of IVPP V20341 are separated by a wider angle (~136˚ in cervical B) in comparison to the posterior cervicals preserved in *Linhenykus* (~105˚). However, this difference may simply reflect differences in anatomical position so should be treated with caution. The postzygapophyses (left one on cervical B) appear to be dorsally orientated, as in *Linhenykus* [20]. In dorsal view this postzygapophysis has a nearly straight medial edge and a convex lateral edge like in other Asian alvarezsauroids [20,23]. This contrasts with the postzygapophyses of *Alvarezsaurus* which have convex medial and lateral edges that create a paddle-like shape in dorsal view [27]. Epipophyses are absent from the postzygapophyses as evident from cervicals B and C (the left lateral sides) unlike the mid-cervicals of *Linhenykus* which have weakly developed ridge-like ones that are an autapomorphy of this taxon [20]. In IVPP V20341 the prezygapophyses are more widely separated laterally and have larger articular surfaces in comparison to the postzygapophyses - this pattern is not observed in *Linhenykus* which has laterally narrower prezygapophyses than postzygapophyses in the posterior caudals that are preserved [20]. In *Shuvuuia* (MPC 100/975) the prezyapophyses are laterally wider than the postzygapophyses in the anterior proportion of the cervical series, have a similar lateral width in the mid-series (at a currently undefined transition point due to the incompleteness of the cervical series), whilst in the distal portion of the series the prezygapophyses are laterally narrower the postzygapophyses [23] (as in *Linhenykus* [20]). If this pattern of zygapophyseal width is similar in other parvicursorines it suggests that cervicals A-D are anterior ones. This also compliments the observed partially damaged neural spine in cervical B that rises from a well-defined dorsal ridge - that spans the whole anterior dorsal surface of the vertebra - at the approximate position of the postzygapophyseal facets. Taking into account the damage to this neural spine it appears to be dorsoposteriorly directed but it would be speculative to comment on both its dorsoventral height and anteroposterior length in relative terms. This is at odds with identification of cervicals A-D as posterior ones based on the similarity of their rounded ventral surfaces to the cervicodorsals of *Mononykus* (MPC 107/6, [5]). However, the new zygapophyseal and neural spine information and the absence of rounded ventral surfaces in the cervicals of other known parvicursorine cervicals suggests that the presence of the latter is *potentially* a unique characteristic of IVPP V20341 amongst parvicursorines. However, a more complete understanding of cervical variation in parvicursorines is needed before this characteristic can be judged to be unique.

One suspected cervical rib is preserved in association with the posterior portion of cervical A. This element is identified as such because of its long, thin shape and its association with a cervical. However, breakage in this element - especially proximally - means that this identification is equivocal. Even so, there is no evidence that seems to support the fusion of the cervical ribs with their associated vertebrae, unlike in *Shuvuuia* (IGM 100/977, [23]).

The partial isolated cervical vertebra resembles a smaller version of cervical B based on the anterior portion that is preserved. Therefore like cervical B, this cervical was probably proceolous (posterior articular surface is missing) and from the small portion that is preserved it seems to have a smooth ventral surface that is pinched away from the anterior edge of the centrum. The smaller size of the isolated cervical relative to cervical B potentially suggests a more distal position along the series compared to the latter.

The neural canal is poorly exposed in cervicals A-D but the anterior portion of the canal is fully exposed in the isolated cervical, owing to its largely missing neural arch. The neural canal in the latter is proportionally larger in the cervical centra compared to other vertebra, as in most alvarezsauroids [23]. It appears to slope downwards in a posteroventral direction and has a mid-line ridge along its ventral surface.

Caudal vertebrae

IVPP V20341 includes four isolated caudal vertebrae, one well-preserved and the others poorly preserved (Figure 3). These are referred to as caudals A-D in order of their anteroposterior position along the tail, as determined using the anteroposterior position of the neural arch pedicle and transverse processes and the relative development of the furrows and ridges along the ventral surfaces of the centra. The dimensions of the caudal vertebrae given in Table 2 do not appear to unequivocally support the proposed ordering, nor any other ones. This probably reflects the large amount of missing data, particularly in caudals C and D (Table 2), and variability in vertebral geometry changes along the tail, as has been measured in a wide range of theropods [29].

The anterior placement of the neural arch pedicle along the anteroposterior length of the centrum suggests that caudals A-C are anterior ones as this characteristic is found in parvicursorine alvarezsauroids including *Alvarezsaurus* (MUCPv 54, [23,27]), *Achillesaurus* (MACN-PV-RN 1116, [28]), *Linhenykus* (IVPP V17608, [1,20]), *Parvicursor* (PIN 4487/25, [7]), *Shuvuuia* (MPC 100/975, [23]) and *Xixianykus* (XMDFEC V0011, [30]). In lateral view the distal margin of the narrowest portion of caudal A's neural arch (the neck) is approximately three-thirds along the anteroposterior length of the centrum, whereas in the first free caudal of *Parvicursor* (PIN 4487/25, [7]) and the proximal caudals of *Alvarezsaurus* (MUCPv 54, [23,27]) this is less than half way along the same length. However, the position of the neural arch pedicle in IVPP V20341 is comparable to the middle and distal caudals of *Alvarezsaurus* [23,27] and the first caudals of *Xixianykus* (XMDFEC V0011, [30]) and *Patagonykus* (the supposed first caudal of MCF-PVPH 37, [25]).

In the preserved series, caudals A to D show a posterior migration of the transverse processes (only the distal ridge of the process is visible on the left lateral side of caudal D), but these are all still situated anteriorly on the centrum which identifies IVPP V20341 as a parvicursorine alvarezsaurid [20]. These form a broad subhorizontal ridge that originate from the dorsoanterior corner of the centra (caudals A and B) rather than the posterior end of the prezygapophyses as in the middle and distal caudals of *Linhenykus* (best examples in caudals 7 and 8 of IVPP V17608 [20]) and in *Shuvuuia* (MPC 100/975, [23]). However, the ridge does deflect posteriorly towards the dorsal edge of the posterior articular face in both IVPP V20341 and *Linhenykus* [20], although this appears to deflect more ventrally in the former specimen. The caudals become anteroposteriorly shorter from caudal A to B (caudals C and D are not anteroposteriorly complete) but this pattern is not emphasised here given that the middle caudals are anteroposteriorly longer than the proximalmost ones in *Linhenykus* (IVPP V17608, [20]). Caudals A and B possess a longitudinal furrow along the centrum's entire ventral surface and this is bordered laterally by two ventral keels. This feature is also observed in *Linhenykus* [20], *Parvicursor* (PIN 4487/25, [7,23]), *Patagonykus* (supposed 20th caudal, MCF-PVPH 37 [25]) and *Shuvuuia* (MPC 100/975 [23]). However, this feature is less developed in caudal B and is barely visible in caudal C, where the ridges are low and the furrow is broad and shallow. The ventral surface of caudal D has been eroded down to the cortical bone. The ventral surfaces of caudals A, B and C therefore support their proposed positional ordering.

Caudals A-D are all laterally pinched and are procoelous, although the latter cannot be confirmed in caudals C and D owing to a missing posterior articular face in the former, and a missing anterior articular face in the latter. In caudals A and B, the concave anterior articular face is deep, whilst the posterior condyle is well-developed and hemi-spherical in shape. Procoely in caudal vertebrae is also observed in *Haplocheirus* (IVPP V15988, [26]), *Shuvuuia* (MPC 100/975, [23]), *Mononykus* (MPC N107/6, [5]), *Xixianykus* (XMDFEC V0011, [30]), *Alvarezsaurus* (MUCPv 54, [23,27]) and potentially in *Patagonykus* (MCF-PVPH 37), as only the posterior articular surfaces are preserved [25]. However, the first caudal of *Linhenykus* is amphiplatyan [20] whilst a proximal caudal of *Achillesaurus* - tentatively assigned as the fourth in the series - is amphicoelous (biconcave) [28].

Caudals A-D lack the sharp ventral keel that has been associated with the anteriormost caudals of many parvicursorines. In *Shuvuuia* and *Achillesaurus*, the first two caudals have a sharp ventral keel (caudals identified as the first two of *Shuvuuia* by Chiappe *et al.* [23]; the keel is assumed to have been present in life on the first caudal of *Achillesaurus* because - despite being damaged - this feature is preserved in the last sacral and second caudal [28]) whilst the same feature is present in the first caudal of *Xixianykus* [30] and in an anterior caudal of *Alvarezsaurus* [27], *Mononykus* [5] and, supposedly, of *Parvicursor* [7]. *Patagonykus* has a seemingly unique ventral surface as the assumed first caudal has a ventral surface that is transversely narrow and slightly flat [24]. No evidence of chevron articulation facets were found on the centra of caudals A, B and D - the only ones that preserve the posterior ventral surface. However, these facets are well-developed on the posteroventral surface of a distal caudal - supposedly the 20th caudal - of *P. puertai* (MCF-PVPH 37, [25]). In *Linhenykus* (IVPP V17608) chevron articulation facets are weakly developed on the posteroventral surface of the proximal caudals (caudal 4 and 5) and strongly developed on the anteroventral surface of a middle caudal (caudal 13) [20]. The absence of chevron articulation facets in IVPP V20341 appears to be a distinguishing feature between this taxon and *Linhenykus*.

On the anterior portions of the right and left lateral surfaces of caudal centra A and B respectively, there is a weakly developed foramen, but this is absent on the opposing side of the centrum. The lateral surfaces of caudals A-D lack both large, oval-shaped and small, subcircular fossa - unlike the first and second caudals of *Patagonykus* (MCF-PVPH 37, [24]) and *Achillesaurus* (MACN-PV-RN 1116, [28]) respectively. Foramen are absent from the caudals of *Linhenykus* but IVPP V20341 and *Linhenykus* (IVPP V17608) both have broad, shallow fossa on the lateral surfaces of their centra (e.g. caudal 5 and caudals A-D respectively).

The neural spine of caudal A is partially preserved and is missing its dorsoposterior portion. However, with what is present it is evident that the neural spine is rod-like, quite tall dorsoventrally, anteroposteriorly short and dorsoposteriorly directed. This suggests that caudal A is a more proximal caudal as this neural spine morphology is found in the proximal caudals of *Linhenykus* (caudal two of IVPP V17608 [20]), *Parvicursor* (the neural spine of the first caudal in PIN 4487/25 is dorsoventrally tall and dorsoposteriorly directed overall but its rounded tip protrudes by a relatively small height beyond the dorsal margin of the postzygapophyseal facets and is dorsally directed [7]), *Patagonykus* (the first caudal of MCF-PVPH 37 is dorsoventrally tall and weakly dorsoposteriorly directed [25]) and *Shuvuuia* (MPC 100/975, [23]). In contrast, the proximal neural spines of *Alvarezsaurus* (MUCPv 54) are dorsally directed and have a subtriangular lateral profile [23]. The anterior margin of the damaged neural spine on caudal A lies above the neural pedicle, whereas the whole neural spine is located posterior to the pedicle in the anterior caudals of *Linhenykus* [20]. However, this could be an artifact of the differing position of the caudals compared along the vertebral column.

The shape of the neural canals in caudals A-C are laterally wider and more semi-circular compared to the laterally narrower and more oval-shaped ones of *Linhenykus* (observable in caudals 2, 7 and 13 of IVPP V17608 [20]), *Patagonykus* (MCF-PVPH-37, the supposed first caudal [25]) and *Parvicursor* (PIN 4487/25, the supposed first caudal [7]). This feature represents a *potential* autapomorphy of IVPP V20341 because it is plausible that laterally wider and more semi-circular neural canals might actually be present in as yet unknown portions of other parvicursorine vertebral columns, since neural canal size and shape changes along the vertebral column of theropods (and other vertebrates). The ventral surface of the neural canal of caudal D bears a longitudinal ridge. However, the distribution of this characteristic amongst parvicursorine alvarezsauroids is unclear owing to a paucity of appropriate specimens.

Appendicular skeleton

The appendicular skeleton comprises of a potential left scapular shaft (Figure 4) and a range of suspected pedal phalanges (Figure 5), including an unknown digit II/III and IV phalanges, a right II-1, II-2 and IV, as well as a potential left III-2 and III-3.

Forelimb

Left scapula

In the same small block of sediment that contains cervicals A-D there is a broken, straplike piece of bone (Figure 4). The most complete margin of this bone is deflected and at one end of the bone (distal end?) the margins are subparallel. At the suspected distal end of this bone the generally flat surface sinks into two shallow grooves that traverse towards the midline to create a flattened triangular eminence. The bone superficially resembles an alvarezsauroid scapula shaft (preserved in *Haplocheirus* (IVPP V15988, [26]), *Bonapartenykus* (MPCA 1290, [31]), *Alvarezsaurus* (MUCPv 54, [23]), *Mononykus* (MPC 107/6, [5])) and *Shuvuuia* (MPC 100/977); Table S1) but it does not preserve enough information to help differentiate it amongst alvarezsauroids save for the triangular eminence. However, the latter feature has not been reported in the aforementioned alvarezsauroids so this could be a distinguishing feature of IVPP V20341 if this bone fragment is indeed part of a scapula, probably from the left side of the body.

Hind limb

Speculative right pedal phalanx II-1

The distal end of a digital element is preserved (Figure 5A). This has distinct condyles that are separated by an intercondylar groove, but the latter is narrower and less developed than in preserved phalangeal elements of *Linhenykus* (IVPP V17608 [20]: right manual phalanx II-1; left pedal phalanges I-1, I-2, II-1 and IV-1, ?right pedal phalanges II-1 to II-3 and IV-4, ?left pedal phalanges IV-3 to IV-5; IVPP V18190 [32]: left pedal phalanges III-1, IV-1 and IV-2), *Mononykus* (MPC 107/6 [5]: complete set of left pedal phalanges), *Kol* (MPC 100/2001 [4]: left pedal phalanx III-2) and *Albinkyus* (MPC 100/3004 [2]: right pedal phalanx IV-3). A similarly narrow and less developed intercondylar groove is found on the distal end of the left pedal phalanx II-1 of the *Linhenykus* paratype specimen (IVPP V18190 [32]), but a wider and more developed groove is found in the holotype specimen (IVPP V17608 [20]). This degree of variability implies that the element in question might be impossible to identify based on this characteristic alone. Alternatively, this morphological difference might be of taxonomic importance, although differentiating between this scenario and the former one is beyond the scope of this paper. A similarly developed narrow intercondylar groove appears to be present on the distal end of the right pedal phalanges II-1 and IV-1 of *Albinykus* (MPC 100/3004 [2]), but which of these the element most closely resembles overall is unclear. There is a well-developed, anteriorly-marginated, triangular-shaped ligamental fossa on the lateral surface of the lateral condyle of this IVPP V20341 element, but this area is poorly preserved in the aforementioned phalanges of *Albinykus*. In lateral view, the ventral surface of the lateral condyle of the element is deeper and more steeply inclined than its dorsal surface. Neither of the right pedal phalanges II-1 and IV-1 of *Albinykus* have this feature, although a more weakly developed version is present in the former. Therefore, the digital element in question is speculatively identified as a pedal phalanx II-1. This phalanx is potentially from the right foot because the largest condyle is the lateral rather than medial one in the left pedal phalanx II-1 of *Linhenykus* (IVPP V17608 [20]; IVPP V18190 [32]). However, the opposite can also be inferred as the reversed pattern is observable in the left pedal phalanx II-1 of *Mononkyus* (MPC 107/6, [5]). The shaft of the IVPP V20341 element is broken and incomplete, but it does appear to be relatively straight. This feature would appear to rule it out as a metatarsal III, because the only taxon where the distal articulation surface of MTIII has distinct condyles separated by a narrow intercondylar groove is *Alnashetri* (MPCA 477), but this has a shaft with an anteriorly convex curvature. *Albertonykus* (TMP 2001.45.52) and

Linhenykus (IVPP V17608) have a similar shaft curvature, but the intercondylar groove is weakly developed in *Albertonykus* (TMP 2000.45.12, [8]) and absent in *Linhenykus* (IVPP V17608, IVPP V18190, [20]).

Potential right pedal digit II-2 phalanx

A potential right pedal phalanx is preserved (Figure 5B). Its anterior articular surface has a simple concave morphology that indicates a more anteriorly-located phalange, like the right pedal phalanx II-1 of *Albertonykus* (TMP 2000.45.61 [8]). However, the narrow width of the phalanx is seemingly at odds with this inference. The thicker and more robust medial side of the anterior articulator surface rim suggests that it belongs to a right phalanx, like the right pedal phalanx II-1 of *Albertonykus* (TMP 2000.45.61 [8]). The broken dorsal surface of the phalangeal shaft rise up to the dorsal rim of the anterior articular surface more steeply than the lateral surface of the shaft rises up to the lateral rim of the anterior articular surface. As a right pedal phalanx II-1 has been suggested already (Figure 5A), this element could be from the II-2 position instead.

Possible pedal phalanx from the second or third digit

A reasonably anteroposteriorly long but dorsoventrally low phalanx is preserved with a shallowly sinking ventral surface and a dorsal surface with a broad ridge that traverses it diagonally. This potentially identifies this element as a pedal phalanx from the second or third digit (Figure 5C), although this element might be too small to fit this identification.

Suspected left pedal digit III-2/3

Based on how the suspected pedal phalanx II-1 was assigned to the right side of the body, it follows that the larger of two concavities that are separated by the vertical ridge on the anterior articulation surface corresponds to the lateral side of this surface (Figure 5D). This suggests that this element belongs to the left side of the body. However, as mentioned, this characteristic varies between taxa (*Linhenykus* (IVPP V17608 [20]; IVPP V18190 [32]) compared to *Mononkyus* (MPC 107/6, [5])) and seeming along a single digit as well (along left pedal digits III and IV of *Mononykus* (MPC 107/6 [5])). The concave articular facets of the anterior articular surface do not extend across the entire dorsoventral height of the articulation surface, but meet a flat facet approximately two-thirds down this surface. The dorsal portion of the vertical ridge extends slightly anteriorly to overhang the anterior articulation surface. However, this is far less extensive than in phalanx IV-4 of *Linhenykus* (IVPP V17608, [20]) where this happens for the dorsal and ventral portions of the ridge, dividing the entire dorsoventral height of the anterior articulation surface. These aforementioned features indicate a more posteriorly positioned phalanx from perhaps the second or third positions. The shaft of the phalangeal element is broken, but it appears to have a rounded ventral surface. The lateral condyle of the posterior articulation surface is missing, but the medial condyle is well-developed and is bound laterally by a well-formed intercondylar groove. This condyle has a strongly asymmetric lateral profile with a rounded dorsal surface and an elongated sloping ventral surface, as in many theropod pedal phalanges including those of *Deinonychus* (YPM 5205, [33]). This feature is present in a much less developed condition in phalanx IV-4 of *Linhenykus* (IVPP V17608 [20]), but this phalanx has a stouter profile than IVPP V20341 (in comparison, the latter phalanx is much longer anteroposteriorly than tall dorsoventrally compared to the former phalanx) [20]. A well-developed ligamental fossa occurs slightly below the mid-point of the condyle's lateral surface. The relative slenderness of the preserved phalange suggests that it belongs to the third rather than fourth digit. Thus, the phalanx concerned is suspected as the second or third position of a left pedal digit III (?left III-2/3).

Potential left pedal phalanx III-3

A fragment of the anterior portion of a pedal phalange is preserved (Figure 5E). This shares a similar asymmetrical anterior articular surface morphology as the suspected left pedal III-2/3 phalange, potentially indicating that it shares a similar position along the digit and belong to the same side of the body. However, the taller dorsoventral height of the articular surface and the more subtriangular outline of its dorsal edge, suggests that it is more anteriorly-located than the left pedal III-2/3 phalanx. This is also indicated by the prominently projecting ventrolateral corners of the left pedal phalanx's anterior articulation surface, instead of the rounded ventral surface of the anterior articulation surface of the left pedal phalanx III-2/3. Thus, this element could correspond to a left pedal phalanx III-3 whereas the previous phalanx could be a left pedal phalanx III-2 instead.

Possible right pedal phalanx possibly from digit IV

An anteroposteriorly long phalangeal element with a broad ridge along the dorsal surface of its shaft and an expanded anterior corner on its right lateral side (Figure 5F). Its anterior articular surface is similar in form to the suspected left III-2 and III-3 phalanges which also has unequally-sized concavities. However, following the logic used and discussed above, the position of the larger concavity on the right lateral side of the element - even though this facet is partly damaged - indicates that this phalanx is from the right side of the body. The anterodorsal portion of the phalange is laterally pinched (subtriangular outline) whilst the posterior end of the phalange is dorsoventrally depressed which could identify it as an element from digit IV, but this is speculative.

Suspected pedal phalanx from digit IV

A potential pedal phalanx from digit IV is identified based on its seemingly short anteroposterior length, its apparently asymmetrical condyle in lateral view (like the suspected left pedal phalange III-2 described above) and a shaft with a steeply lowering ventral surface (Figure 5G). These features resemble those of the ?right pedal phalanx IV-4 of *Linhenykus* (IVPP V17608 [20]), but the element in question is too poorly preserved for its position along the digit and its side of the body to be suggested.

Discussion

IVPP V20341 is referable to Alvarezsauroidea because of the absence of cervical epipophyses (absent above the left lateral postzygapophysis of cervicals B and C (Figure 1); character state 6.1 of Longrich & Currie [8] is an alvarezsauroid synapomorphy [20]). The specimen is an alvarezsaurid alvarezsauroid owing to the presence of cervical centra bearing deep lateral depressions [20] (centra of cervicals A-C and the isolated cervical (Figures 1 and 2); character state 8.1 of Longrich & Currie [8]). This placement is also supported by the presence of caudal procoely (Figure 3; character state 21.1 of Longrich & Currie [8]). Owing to the incomplete preservation of the pedal digits in IVPP V20341, it is unclear if pedal digit III is more slender than digits II or IV, so this alvarezsaurid synapomorphy [20] cannot be confirmed in this specimen. IVPP V20341 is further identified as a parvicursorine alvarezsauroid based on the presence of anterior caudal vertebrae with anteriorly displaced transverse processes [20] (Figure 3; character state 22.1 of Longrich & Currie [8]).

Currently, only one parvicursorine - *Linhenykus monodactylus* Xu *et al*. 2011 - is known from the same locality in Bayan Mandahu, Inner Mongolia, China as well as from the formation it belongs to, the Upper Cretaceous - possibly Campanian - Wulansuhai Formation [1,17,34]. However, six other parvicursorines are known from more northerly localities within the Santonian to Maastrichtian-aged Upper Cretaceous rocks [3,7,35-38] of the Mongolian Gobi Basin: *Albinykus* [2], *Ceratonykus* [3], *Mononykus* [5], *Parvicursor* [7], *Shuvuuia* [9] and *Kol* [4] (Table 1). Agnolin *et al.* [31] argue that *Kol* has stronger oviraptorosaurian affinities than alvarezsaurid ones, but having not studied the specimen yet first-hand, we adopt the original identification here. IVPP V20341 does not have any known autapomorphies of any other parvicursorine and its unique features (proceolous cervicals and laterally wider and more semi-circular neural canals) are insufficient to assign it to a new species because they can potentially be explained as anatomical variations along the vertebral column, particularly as this is poorly understood amongst parvicursorines. A better understanding of anatomical variation in *Linhenykus* in the future might led to IVPP V20341 being referred to this taxon, but current evidence does not permit such a referral.

Parvicursorines at Bayan Mandahu

The length of deposition represented at Bayan Mandahu is not known accurately, but some lithologies like the structureless sandstones seem to have been rapidly deposited by sandstorm events, whilst others like the carbonates (caliche) were probably deposited more slowly over thousands of years [34]. This suggests that deposition probably happened over thousands of years at Bayan Mandahu, although this cannot be determined unequivocally until absolute dating work is able to constrain the depositional period. Given this estimate, the locations of IVPP V20341 and *Linhenykus* specimens (IVPP V17608, IVPP V18190) at near the top and bottom of the local rock succession (Figure 1) suggests that the deposition of both taxa was probably separated by a similar magnitude of time. This time interval perhaps makes it more likely that IVPP V20341 belongs to *Linhenykus*, but it is possible that there were two or more distinct genera in the locality that had separate and/or overlapping temporal ranges. IVPP V20341 and *Linhenykus* were preserved under broadly similar semi-arid conditions – the former is preserved in a red structureless sandstone layer whilst the latter is preserved in a more resistant nodule-rich red sandstone layer (Table S1). This indicates that IVPP V20341 and *Linhenykus* lived in a similar environment within or close to a dune field, according to Eberth's [17] depositional model for Bayan Mandahu (alluvial material washed off the nearby palaeo-Lang Shan mountain range was fringed by a dune environment). The persistence of environmental conditions potentially favours the longevity of an existing genus, but this likelihood cannot be used to justify IVPP V20341's taxonomy. Thus, there are contextual arguments for the referral of IVPP V20341 to *Linhenykus* but these are seemingly weak ones. The study of the specimens themselves demonstrates that IVPP V20341 is distinguishable from *Linhenykus monodactylus* by 16 anatomical characteristics, including three tentative ones given in italics:

Axial skeleton:

Cervical vertebrae

1. The diapophyseal ridges extend to the posteroventral rim of the centrum rather than the posterodorsal one, as in *Linhenykus*.

2. Epipophyses are absent from the postzygapophyses unlike the weak ones observed in *Linhenykus*, but in IVPP V20341 the cervicals are interpreted as anterior rather than mid-series ones, as in *Linhenykus*.
3. The cervicals of IVPP V20341 have a rounded ventral surface (at least proximally) whereas the cervicals of *Linhenykus* have a shallow longitudinal furrow that runs along the entire length of the ventral surface that is bound laterally by two low ridges.
4. The cervical centra of IVPP V20341 are not mediolaterally compressed like the posterior cervicals of *Linhenykus* (IVPP 17608), as only the ventral portion is compressed in the former. Thus, the lateral surfaces of IVPP V20341 are more vertical in the middle portion of the centrum than in *Linhenykus*.
5. Cervicals lack a carotid process (cervical B) unlike in *Linhenykus*.
6. Absence of cervical pneumatic foramina (cervicals B and C and in *Mononykus* [5]), unlike in *Linhenykus* which has them in the area immediately posterior to the parapophyses (also in *Alvarezsaurus* [23,27] and *Shuvuuia* [23]).
7. *The prezygapophyses are set less lateral to the centra than in Linhenykus (this probably reflects the anterior vs. posterior position of the centra in the series).*
8. *Postzygapophyseal processes (cervical B, supposedly an anterior one) separated by a wider angle than the posterior cervicals of Linhenykus (~136˚ compared to 105˚) (this probably reflects the anterior vs. posterior position of the centra in the series).*
9. *In the supposed anterior cervicals, the prezygapophyses are more widely separated laterally than the postzygapophyses. This is the opposite of what is observed in the posterior caudals of Linhenykus. However, both patterns are found in the same locations in the cervical series of Shuvuuia (MPC 100/975) [23].*

Caudal vertebrae

10. Transverse processes originate from the dorsoanterior corner of the centra (caudals A and B) rather than the posterior end of the prezygapophyses, as in the middle and distal caudals of *Linhenykus* (e.g. caudals 7 and 8 and in *Shuvuuia*, MPC 100/975 [23]).
11. Transverse processes deflect posteriorly more ventrally away from the dorsal edge of the posterior articular face than in *Linhenykus*.
12. Chevron articulation facets are absent but in *Linhenykus* these are weakly developed on the posteroventral surface of the proximal caudals (caudals 4 and 5) and strongly developed on the anteroventral surface of a middle caudal (caudal 13).
13. Anterior portions of caudal centra A and B have a weakly developed foramen on their right and left lateral surfaces respectively, whereas no foramen are observable in the caudals of *Linhenykus*.

Appendicular skeleton:

Owing to the uncertainty in the identification of elements from the appendicular skeleton, their differences with *Linhenykus* are not included here.

IVPP V20341 compared to other Asian parvicursorines

~350km separates Bayan Mandahu and the closet Mongolian parvicursorine locality

(*Mononykus olecranus* at Bayan Dzak [39]). During the Late Cretaceous the mountain ranges within the Gobi basin (composed of Palaeozoic and Mesozoic rocks) were being subjected to extensional tectonism [34] that presumably promoted sediment deposition through the creation of accommodation space. This geological setting divided the Gobi basin and created obstacles to faunal interaction which probably promoted vicariance. The latter would help to explain why the Bayan Mandahu fauna seems to be distinct from Djadokhtan ones. If common Bayan Mandahu and Djadokhtan parvicursorines were found, this would suggest that at least some elements of the faunas are similar, which would advocate a complex scenario of selective isolation to explain the pattern of animals observed. Fortunately, for the skeletal elements that they share in common, IVPP V20341 lacks the autapomorphies of any Mongolian parvicursorine, so this provides limited support for the distinctiveness of the Bayan Mandahu fauna (see Table 3), as its status as a distinct taxon or specimen of *Linhenykus* remains unclear. *Parvicursor* and *Ceratonykus* are both known from the Upper Cretaceous (Lower Santonian, [3]; Middle Campanian; [7]) Barun Goyot Formation (Table S1) and appear to have shared their living environment. Niche partitioning by these taxa - if at all - probably relates to their body size differences as *Parvicursor* is smaller than *Ceratonykus* (75.6mm long tibiotarsus in *Parvicursor*, PIN 4487/25 [7]; 89mm long right and left tibiotarsus in *Ceratonykus*, MPC 100/124 [3]). If IVPP V20341 is demonstrated to be a valid taxon at a later date, the sharing of a relatively harsh semi-arid environment with *Linhenykus* might support niche partitioning too e.g. if IVPP V20341 actually has a more conventional hand morphology than *Linhenykus*.

IVPP V20341 compared to other alvarezsauroids

IVPP V20341 is seemingly distinct amongst alvarezsauroids because of the presence of cervical proceoly and caudal neural canals (caudals A-C) that are laterally wider and more semi-circular compared to the laterally narrower and more oval-shaped ones of *Linhenykus* (caudals 2, 7 and 13) and of the supposed first caudals of *Patagonykus* (MCF-PVPH 37, [25]) and *Parvicursor* [7]. However, these potential autapomorphies have caveats that need to be considered. Cervical proceoly is unknown in alvarezsauroids, but only one complete neck specimen is known and this belongs to the basalmost taxon *Haplocheirus solers* [26]. If the eleven cervical vertebrae of the latter is similar amongst all alvarezsauroids - an assumption that is speculative based on current fossil evidence - then the 8 and 9 cervical vertebrae preserved in *Mononykus* (MPC 107/6, [5]) and *Shuvuuia* (MPC 100/975, [23]) respectively may actual represent near complete series. These three neck specimens provide an indication of the basal alvarezsauroid and derived parvicursorine cervical conditions which should resemble that of IVPP V20341, so the absence of proceoly in all three is significant. However, *Haplocheirus* lacks the strong opisthocoelous condition of *Mononykus* (MPC 107/6, [5]) and *Shuvuuia* (MPC 100/975, [23]) which shows that there is significant variation in articular surface morphology within the clade, although it is impossible to say if such variation might include multiple taxa with a proceolous condition. The morphology of the alvarezsauroid tail is better understood than the neck because more material representing a broader phylogenetic sample is known. The most complete caudal series are found in *Haplocheirus* (IVPP V15988, 15? caudals [26]), *Alvarezsaurus* (MUCPv 54, 13 caudals [23,27]), *Linhenykus* (IVPP 17608, 13 caudals [20]) and *Shuvuuia* (MPC 100/975, 19 caudals [23]; MPC 100/120; 22? caudals [10]). The most complete alvarezsauroid tail is represented by specimen MPC 100/120 of *Shuvuuia* which preserve direct evidence of approximately 22 caudals [10]. However, the gaps in the caudal series suggest a caudal count upwards of 35 caudals [10]. The relatively large semi-circular caudal neural canals of IVPP V20341 are absent in *Linhenykus*, *Patagonykus* and *Parvicursor* – the only taxa that had specimens where the shape of the caudal neural canal could be determined from firsthand study or from the literature. This represents a small sample size and given the neural canal varies in size and shape along the vertebral column of theropods (and other vertebrates), this potential autapomorphy cannot be supported unequivocally. In the case of both of the tentative autapomorphies in IVPP V20341, future fossil specimens are needed to test their validity.

Potentially informative features for alvarezsauroid phylogeny

The currently unique proceolous cervicals of IVPP V20341 amongst alvarezsauroids requires character 3 of Longrich & Currie [8] to be edited. Cervical proceoly is probably a derived alvarezsauroid condition since the majority of alvarezsauroids have opisthoceolous cervicals and the basal condition seems to be amphiceolous, amphiplatyan or platyceolous (amphi-platyceolous in *Haplocheirus* (IVPP V15988 [26]) and amphiplatyan in *Alvarezsaurus* (MUCPv 54 [23,27]). However, given the unknown combinations of these vertebral types in alvarezsauroid necks and their changes through time, this character is not ordered here:

Cervical centra: amphiceolous, amphiplatyan or platyceolous (0), opisthocoelous (1), proceolous (2), amphiceolous, amphiplatyan or platyceolous AND opisthocoelous or proceolous (3), amphiceolous, amphiplatyan or platyceolous AND opisthocoelous AND proceolous (after Perle et al. [5])

At a qualitative level, we observed noticeable changes in the ventral surface width of parvicursorine cervicals along their series. This suggests that further quantitative study is needed to maximize the phylogenetic utility of this feature and build upon the ordered character 7 of Longrich & Currie [8].

As mentioned, the lateral sides of the cervicals of IVPP V20341 are less depressed than those of *Linhenykus* (IVPP 17608, [20]), and this depression is limited to the ventrolateral portion of the centra. To accommodate this difference as well as variability in the degree of lateral surface depression along the neck of parvicursorines - pending more in-depth quantitative studies - character 8 of Longrich & Currie [8] was edited slightly:

Lateral surfaces of cervical centra: convex or flat (0), strongly to mildly depressed across part of or the entire surface (1).

Comparisons made between the preserved cervical and caudal vertebrae of IVPP V20341 and all other parvicursorines has highlighted variation in the ventral surface along each series, including the relative development of furrows (partly or fully) and keels (absent, small or large in caudals) as well as the distribution of rounded and/or flat smooth ventral surfaces. To reflect these observations, character 9 of Longrich & Currie [8] has been reworded:

Ventral surfaces of cervical centra: smooth and flat and/or smooth and rounded (0), longitudinal furrow partly or fully spanning the length of the centrum (1), both conditions *are present (2) (after Novas, 1996).*

Character state 2 is added because current evidence cannot rule out the possibility that states 0 and 1 are present in the same cervical series. However, the character remains unordered in the absence of evidence regarding how this trait evolved across Alvarezsauroidea.

In consideration of the amphiplatyan first caudal of *Linhenykus* (IVPP 17608, [20]) and the amphiceolous (biconcave) proximal (4?) caudal of *Achillesaurus* (MACN-PV-RN 1116, [28]), character 21 of Longrich & Currie [8] is expanded to:

Caudal vertebrae: amphiplatyan or amphicoelous (0), or procoelous (1) (after Novas, 1996)

To utilise the potential of the caudal ventral keel towards reconstructing alvarezsauroid phylogeny whilst considering their poorly known extent along the tail, a new character limited to the first caudal is proposed:

Ventral surface of the first caudal vertebrae: not transversely narrow (0), 'pseudo-keel' present - the ventral surface is transversely narrow and slightly flat (1), sharp keel present (2).

Bayan Mandahu as a distinct fauna within the Late Cretaceous Gobi Basin

The Wulansuhai Formation rocks of Bayan Mandahu, Inner Mongolia comprise of lithologies that are similar to the Djadokhta Formation rocks of Bayan Dzak, Mongolia [17,34]. These lithologies indicate that both formations were deposited mostly under semi-arid conditions as alluvial and aeolian sediments, but the presence of some mudrocks shows that some deposition occurred under wetter climatic conditions [17,34]. Many Bayan Mandahu fossils have been referred to taxa known from the Djadokhta Formation [34,40,41] which both share a vertebrate fauna of dinosaurs, lizards, turtles, mammals and birds. The Wulansuhai Formation was assigned a Campanian age based on its lithological and faunal similarities [34] with the Campanian-aged Djadokhta Formation, which itself was dated based on faunal and magnetostratigraphic data (See Xu *et al*. [15] and references therein). The absolute age of the Wulansuhai Formation is still wanting so the stratigraphic correlation of these formations remains equivocal. However, an increasing body of evidence suggests that the two faunas represented in both formations are actually distinct [42]: several previous referrals of Bayan Mandahu specimens to Djadokhta taxa have been rejected [13,43] whilst several taxa unique to Bayan Mandahu have been described [1,12-14,16,20]. Unfortunately, the uncertain taxonomic status of IVPP V20341 does not contribute strong support towards the hypothesis that Bayan Mandahu is faunally distinct from the Djadokhta Formation.

Conclusions

A new parvicursorine alvarezsauroid theropod specimen IVPP V20341 from the Campanian-aged rocks of Bayan Mandahu, Inner Mongolia, China is described. This specimen shows 13 anatomical differences with the only other parvicursorine from this locality - *Linhenkyus* - and lacks any of the known autapomorphies of other Asian parvicursorines. IVPP V20341 is seemingly unique amongst alvarezsauroids because of the presence of cervical proceoly and its relatively larger semi-circular neural canals.

However, these features can plausibly be explained as anatomical variations of the parvicursorine cervical series because similar degrees of variation are actually observed in the dorsal and cervical series of parvicursorines. Thus, eering on the side of caution, IVPP V20341 is not identified as a new taxon here, although more complete knowledge of the parvicursorine vertebral column arising from future discoveries may warrant a taxonomic revision. As a parvicursorine specimen without any autapomorphies, IVPP V20341 does not contribute strong evidence that the Bayan Mandahu fauna is unique compared to other localities within the Cretaceous Gobi Basin.

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Tables

A

	Vertebral element								
Dimension in mm	Cv A	Cv B	Cv C	Cv D	Isolated cervical	Cd A	Cd B	Cd C	Cd D
Anteroposterior length between the dorsal rim of the anterior and posterior articular surfaces	-	6.89 (b)	-	-	-	6.70 (l)	5.26 (b,l)	-	-
Anteroposterior length between the dorsal rim of the anterior articular surface and the distalmost tip of the posterior articular condyle	-	-	-	-	-	7.53 (l)	7.29 (l)	-	-
Lateral width of the anterior articular face	-	4.20	-	-	3.79	3.87 (b)	4.12 (b)	4.34 (b)	-
Lateral width of the posterior articular face (at the rim of the articular surface	4.88(b)	-	-	-	-	3.86	4.05	-	3.84
Centrum height (dorsoventral height between the ventral and dorsal rims of the posterior articular surface)	-	1.87(b)	-	-	3.13 (a)	3.26 (l)	3.13 (l)	3.53 (a)	3.21 (l)
Prezygapophyseal angle from the vertical in ˚ (anterior view)	-	-	78 (l)	64 (l)	-	26 (l)	-	26 (l)	-

Postzygapophyseal angle from the vertical (posterior view)	-	50 (l)	40 (b,l)	-	-	76 (b,r)	-	-	-
Neural spine height (dorsoventral height between the dorsal rim of posterior articular surface and the neural spine tip	-	5.89 (b,l)	-	-	-	4.79 (l)	-	-	-

Key: b, broken/damaged/matrix obscured feature resulting in underestimated dimensions and approximate angles; l, left lateral side; r, right lateral side; a = anterior portion available only.

B

	Vertebral element			
	MTIII (right)	**II-1 (right)**	**III-2 (right)**	**III-3 (left)**
Maximum anterior articular surface dorsoventral height	-	2.92	-	2.33
Maximum anterior articular surface lateral width	-	2.72	-	2.45
Maximum posterior articular surface dorsoventral height	3.54(b)	-	3.07	-
Maximum posterior articular surface lateral width	3.56(b)	-	2.71	-
Maximum anteroposterior length	-	-	-	6.07(b)

Key: b, broken/damaged resulting in underestimated dimensions.

Table 1: A, dimensions of the cervical and caudal vertebrae preserved. B, dimensions of elements from the appendicular skeleton, including estimated ones.

Taxon	**Diagnosis**
Albinykus [2]	Possesses a unique character state combination amongst alvarezsaurids (from Nesbitt *et al*. [2]): • Short metatarsal I with a rounded proximal tip (unknown in both *Alvarezsaurus* and *Patagonykus*). • Well-pronounced and knob-like crest on fibula (attachment site for the M. iliofibularis) proportionally larger than other alvarezsaurids. • **Phalanx IV-4 longer than both phalanges IV-2 and IV-3.** o *Not equivocal in IVPP V20341 as phalange IV-2 is missing.* • Deep groove present on the anterior face of the ascending process of the astragalus. • A small flange on the lateral side of the distal end of metatarsal IV shared with *Parvicursor*, *Shuvuuia*, and *Mononykus* only.
Ceratonykus [3]	From Alifanov & Barsbold [3]: • Preorbital skull region long. • Upper temporal fenestrae ovate, 0.4 as long as frontals. • Length of one frontal almost four times greater than its width. • Frontals narrowing rostrally in narrow wedge. • Prefrontals adjoining each other medially. • Basipterygoid processes two-thirds as high as quadrates. • Labiooccipitally, dentaries forming deep and rostrally tapering depression. • Mandibular fenestrae extensive. • **Centra of cervical and anterior caudal vertebrae narrow.** o *No relative measure of narrowness is provided so this characteristic is difficult to confirm in IVPP V20341, especially when the latter lacks a suitable body proxy at present.*

- Deltopectoral crest separated from humeral head by notch.
- Basal phalanx of major digit of manus extended, its flanks moderately wide, and distal condyle narrow, symmetrical.
- Postacetabular plate of ilia with relatively small longitudinal craniomedial crest.
- Femora strongly curved, nearly half as long as tibiotarsus.
- Fourth trochanter distinct.
- Cnemial crest of tibiae undeveloped.
- Ascending process of astragali high and wide.
- Tarsometatarsals 1.33 as long as femora.
- Second and fourth metatarsals tightly adjoining each over entire extent; their dorsal and palmar surfaces ridge-like, deep grooves formed between these bones. Deep notch formed proximodorsally between these metatarsals.
- Distally, second metatarsals shorter than fourth.
- Tarsometatarsals 3.5 times as long as third metatarsals.
- **Basal phalanx of fourth digit of hind feet only slightly shorter than basal phalanx of second digit.**
  - *Basal phalanges of the second and fourth digits are missing in IVPP V20341.*

Linhenykus [1] Distinguished from other parvicursorines by (from [20]):

- Transversely compressed metacarpal III without a distal articular surface.
- **Longitudinal ventral furrow along the entire length of each cervical centrum.**
  - Rounded ventral surface in IVPP V20341, at least proximally.
- **Diapophyseal ridges on each cervical vertebra that extend to the posterodorsal rim of the centrum.**
  - Extend to the posteroventral rim in IVPP V20341.
- **Extremely weak, ridge-like epipophyses on the postzygapophyses of the middle cervical vertebrae.**
  - Epipophyses are absent in IVPP V20341 but the cervicals are anterior ones.
- Large pneumatic foramina in the mid-dorsal vertebrae.
- **Anteriormost caudal vertebrae whose centra are amphiplatyan and whose neural spines are located completely posterior to the neural pedicles.**
  - All preserved caudals in IVPP V20341 are proceolous and the anteriormost caudal (caudal A) has a broken neural spine whose anterior margin appears to lie above the neural pedicle.

Mononykus [6] From Chiappe *et al*. [23]:

- **Cervical centra strongly compressed laterally, lacking pneumatic foramina.**
  - IVPP V20341 also lack pneumatic foramina in their cervical centra, but these appear to be less strongly compressed mediolaterally.
- Cranialmost thoracic vertebrae strongly compressed.
- Fused ilium and ischium.
- Pillar-like deltopectoral crest of humerus.
- Supracetabular crest developed only in the cranial portion of acetabulum.
- Subtriangular cross-section of pubis.
- Two cnemial crest in tibiotarsus.

	• Medial indentation of ascending process with deeply excavated base. • Ascending process arises from medial margin of astragalar condyle instead of from lateral margin.
Parvicursor [7]	From Chiappe *et al*. [23]: • Similar to *Mononykus* but smaller. • Opisthocoelous caudal thoracic vertebrae. • No bi-convex thoracic vertebra. • Convex cranial margin of synsacrum.
Shuvuuia [9]	Autapomorphies from Suzuki *et al.* [10]: • An articulation between the quadrate and postorbital • Elongated basipterygoid processes • Hypertrophied prefrontal/ectethmoid • The presence of a sharp ridge on the medial margin of the distal tibiotarsus (Chiappe *et al*. [9]).

Table 2: Diagnoses of Asian parvicursorines. None of the listed osteological features are present in IVPP V20341. Features belonging to skeletal elements that are also preserved in IVPP V20341 are in bold font. See Table S1 for additional taxon information.

Figures

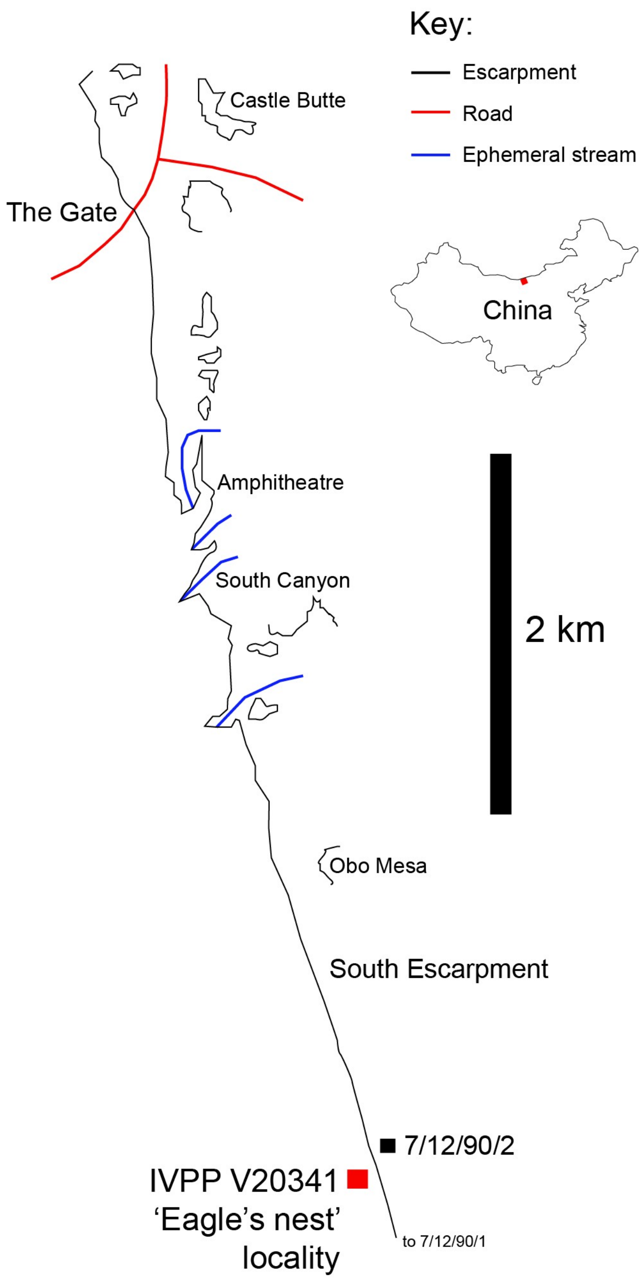
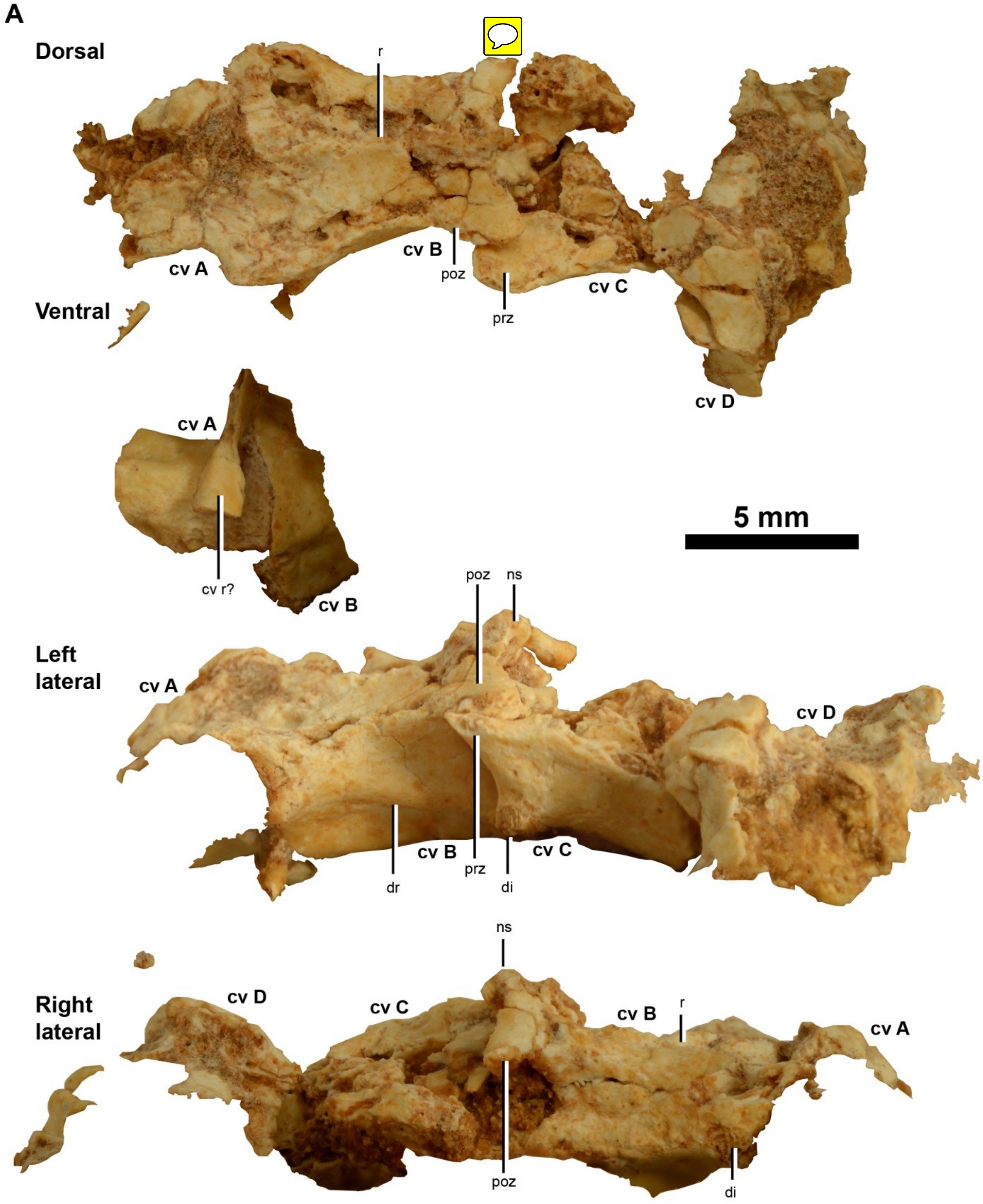


Figure 1: Place of discovery for IVPP V20341 (41°43'15.3"N, 106°44'43.3"E), ~3km SE of 'The Gate' locality and close to the location of Eberth's '7/12/90/2' stratigraphic section [17] (After Jerzykiewicz *et al.* and Eberth [17]).


A
Dorsal
Ventral
r
cv A
cv B
poz
prz
cv C
cv D
cv r?
5 mm
Left
lateral
ns
dr
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Right
lateral

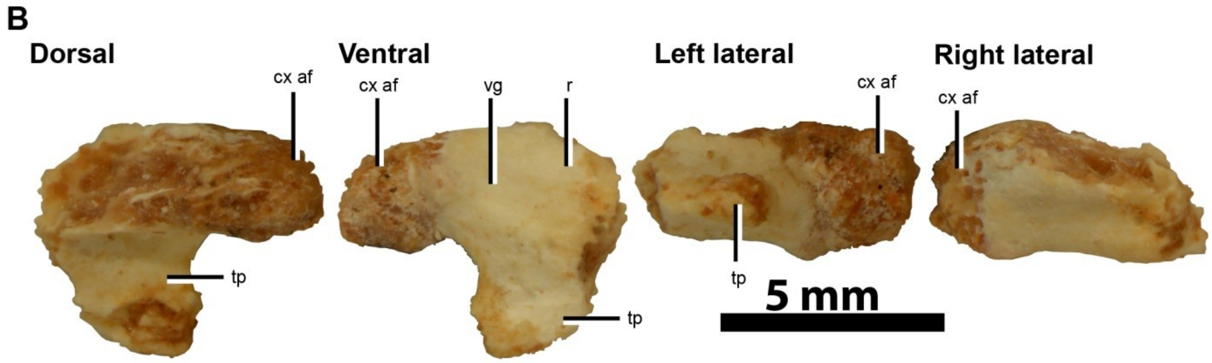


Figure 2: A, dorsal, ventral, left lateral and right lateral views of an articulated series of four partial cervical vertebrae (cervicals A-D). B, dorsal, ventral, left lateral and right lateral views of an isolated anterior portion of a cervical vertebra. Abbreviations: cv, cervical vertebra; cv r?, cervical vertebra rib?; cx af, convex articular face; di, diapophysis; dr, diapophysial ridge; ns, neural spine; poz, postzygapophysis; prz, prezygapophyses; r, ridge; tp, transverse process; vg, ventral groove. Scale = 5 mm.

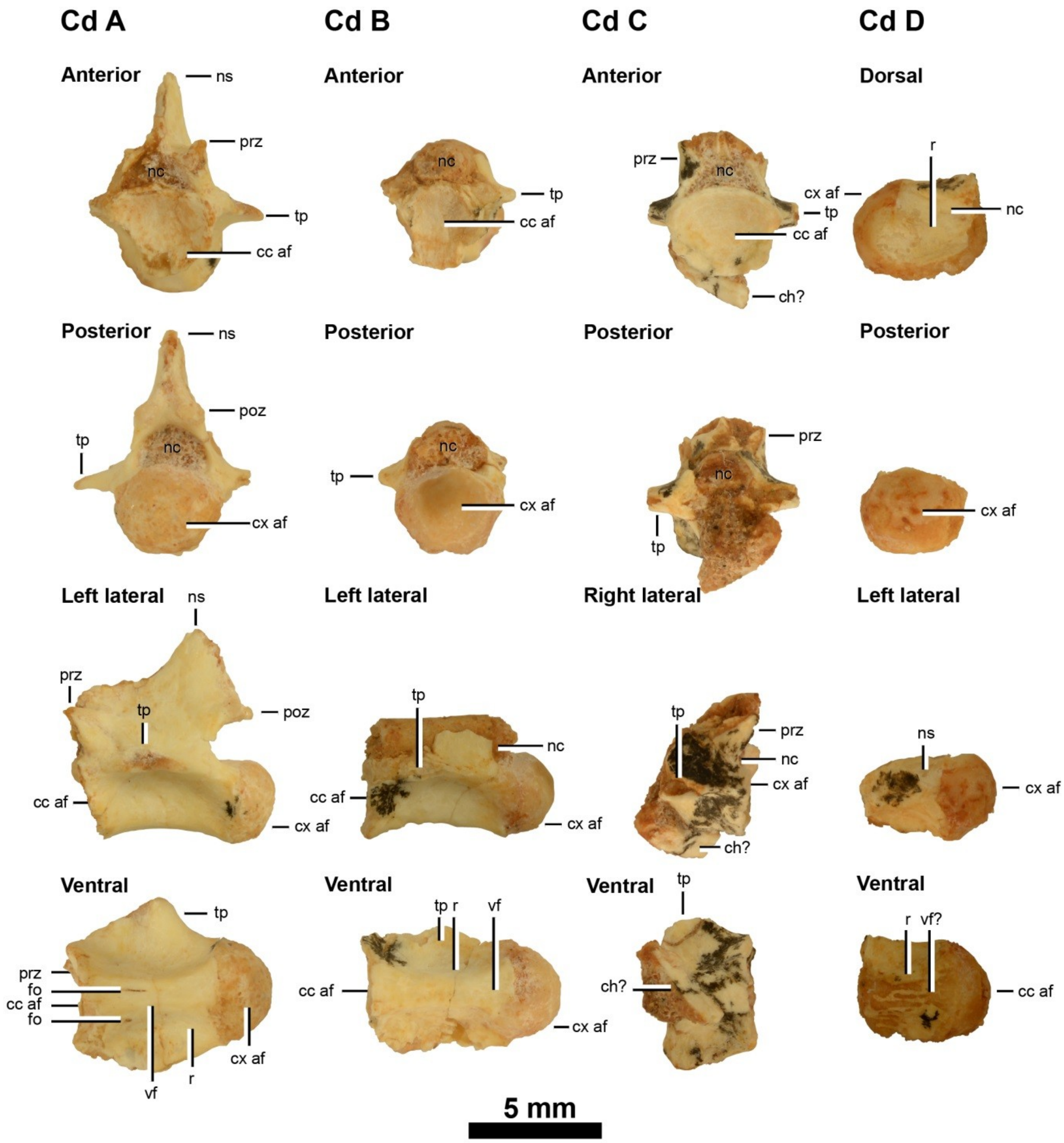
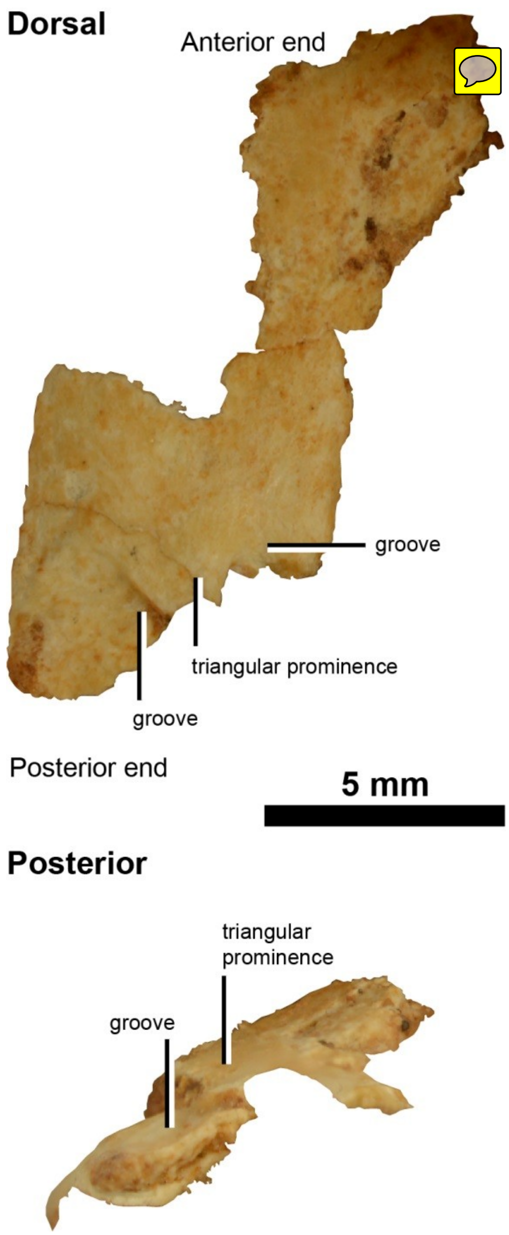
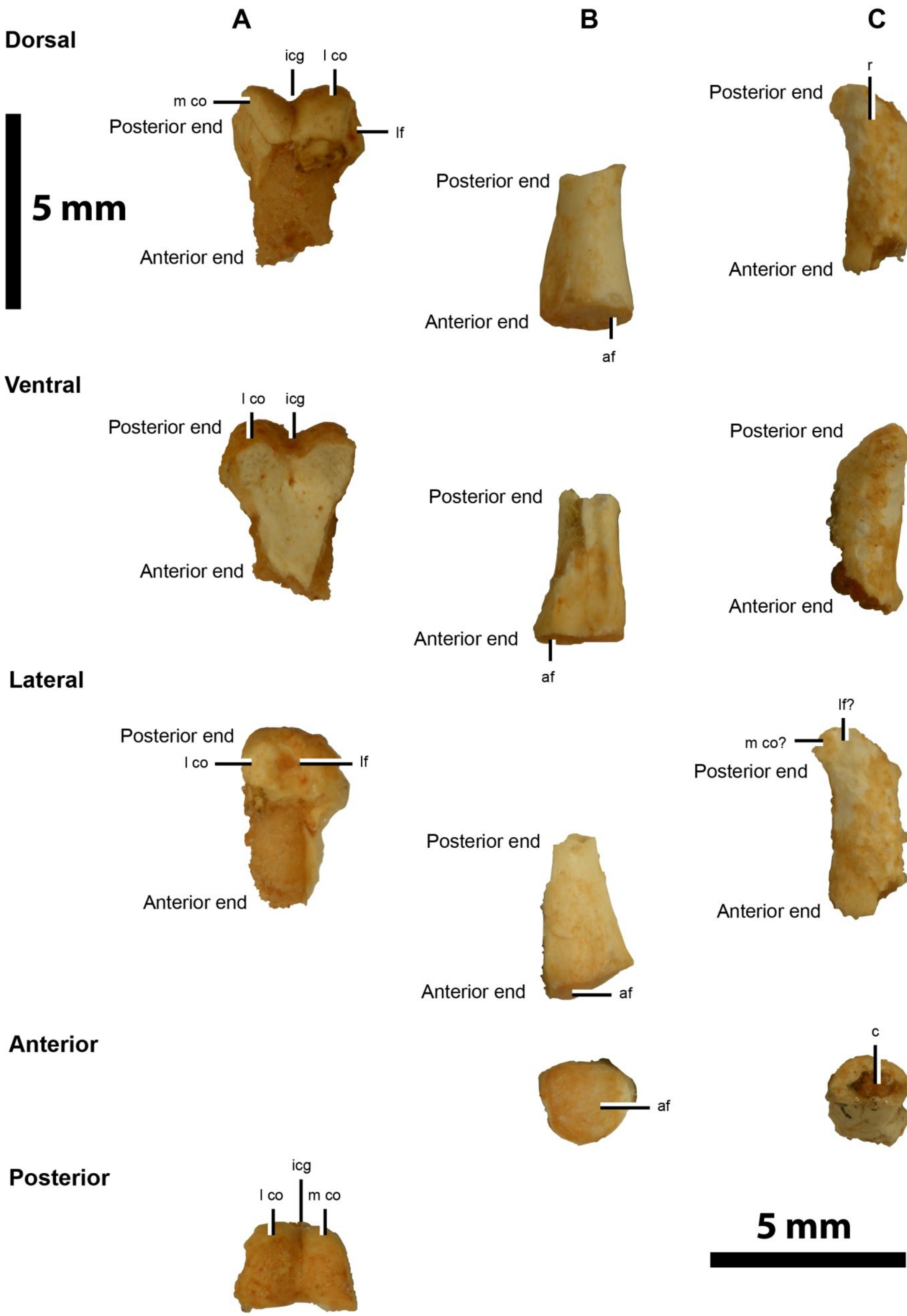


Figure 3: Caudal vertebrae A-D in anterior, posterior, lateral and ventral views (caudal D is damaged in anterior view so its dorsal view is shown instead). Abbreviations: cc af, concave articular face; ch?, chevron; cx af, convex articular face; fo, foramina; ns, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; r, ridge; tp, transverse process; vf(?), ventral furrow(?). Scale = 5 mm.



774 Figure 4: Scapular blade in dorsal and posterior views. Scale = 5 mm.


A
B
C
Dorsal
Ventral
Lateral
Anterior
Posterior
icg
l co
m co
lf
Posterior end
Anterior end
5 mm
af
r
lf?
m co?
c
5 mm

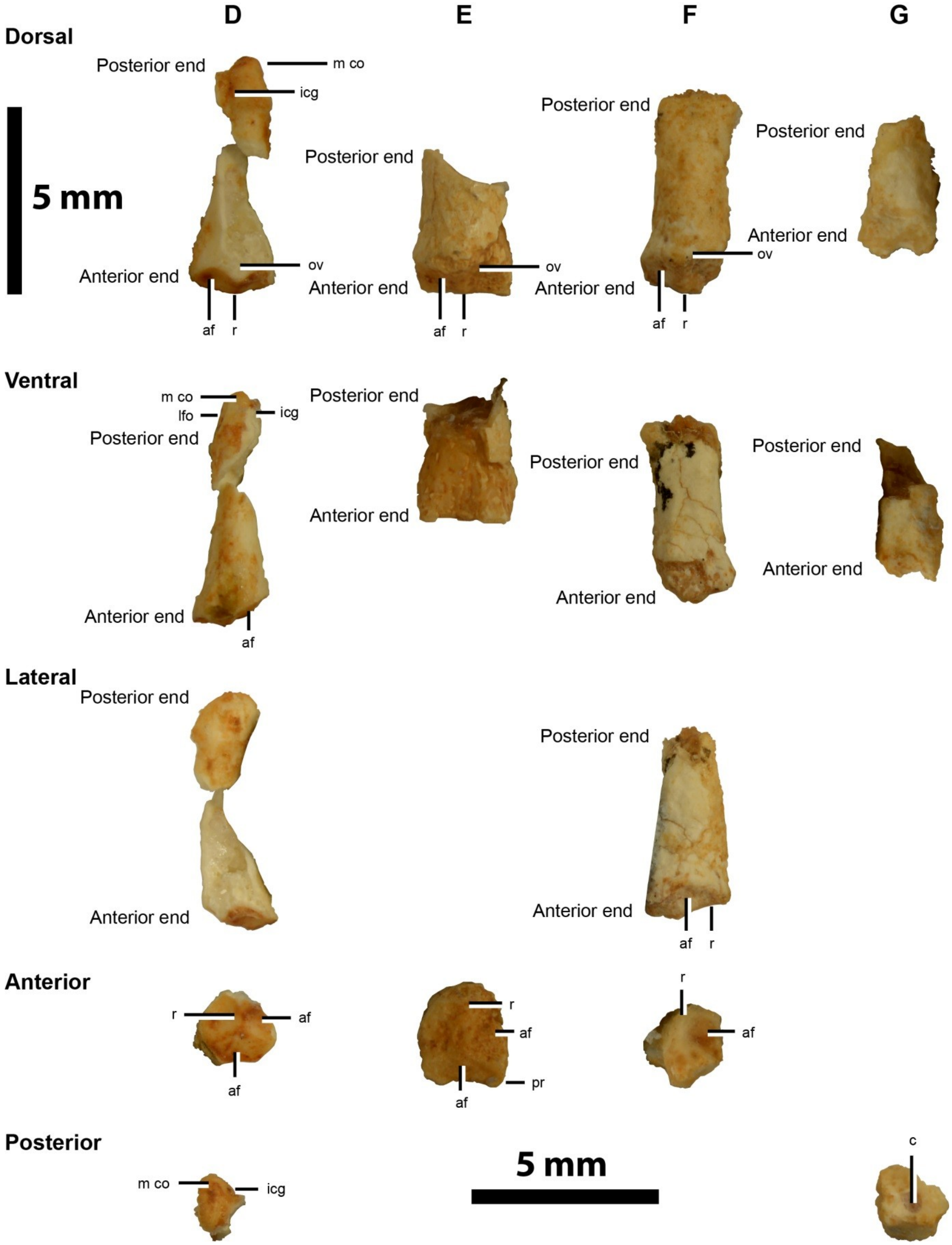


Figure 5: Hindlimb elements of IVPP V20341. Pedal phalanges possibly with the identities: A, ?right II-1, B, ?right II-2, C, II/III, D, ?left III-2, E, ?left III-3, F, ?right IV, and G, ?IV. Abbreviations: af, articular facet; c, cavity; icg, intercondylar groove; lfo, ligamental fossae; m co, medial condyle; ov, overhang; p, prominence; r, ridge. Scale = 5 mm.

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Supplementary Information

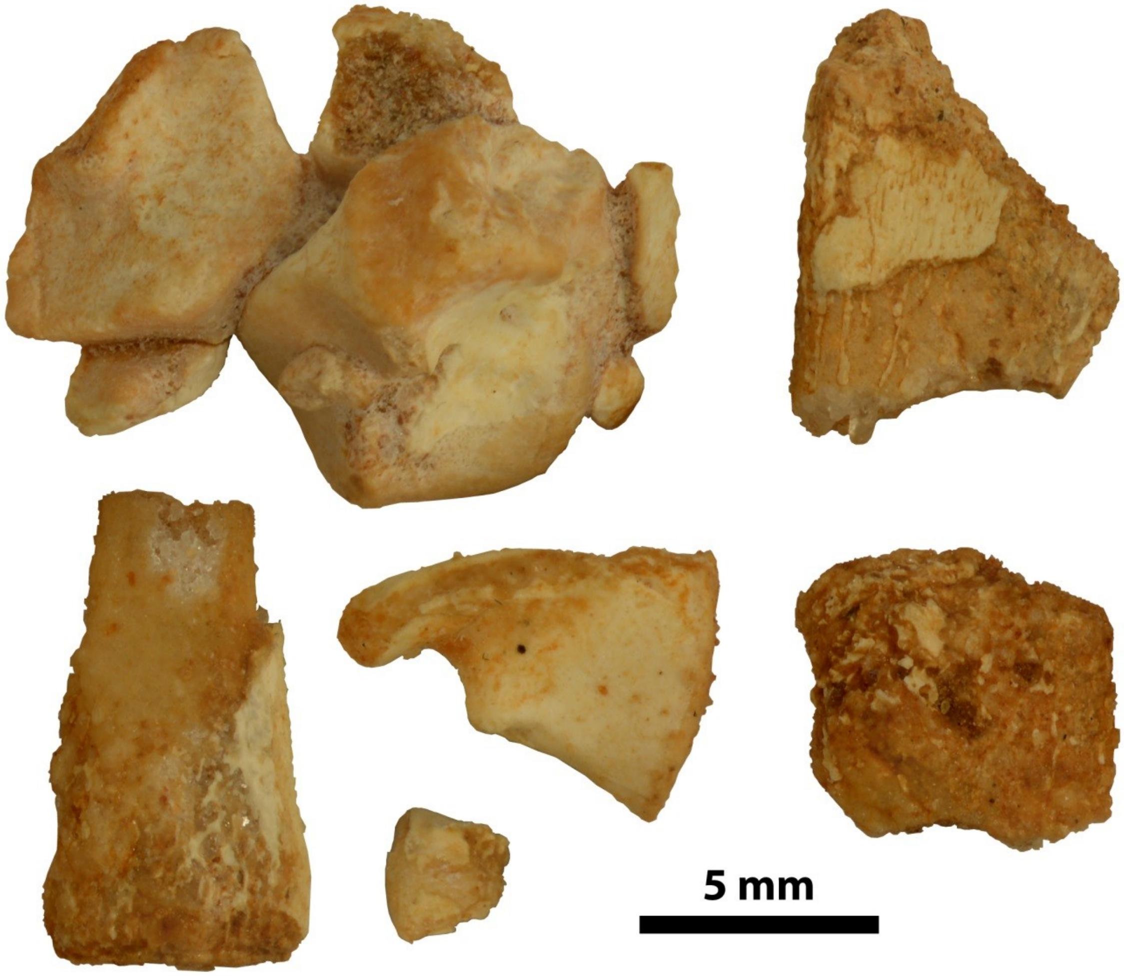

Figure S1: Unidentifiable bone fragments from the IVPP V20341 locality, including a probably partial centrum and potential mammalian tarsal bones.

Table S1: Taxon data for known alvarezsauroids

Table S2: Alvarezsauroid body size estimates and their associated measurements.