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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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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 procoelony 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.

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

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13 **Abstract**

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

25 **Keywords**

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

28 **Introduction**

29 The Campanian-aged rocks of the Gobi basin of China and Mongolia have yielded
30 alvarezsauroid theropods with impressive specialised body plans including the uniquely
31 monodactyl parvicursorine *Linhenykus monodactylus* [1]. The latter is the only
32 parvicursorine species from the Chinese Gobi Basin and was discovered in Bayan
33 Mandahu, Inner Mongolia. Six parvicursorine species are known from the Mongolia Gobi
34 Basin: *Albinykus* [2], *Ceratonykus* [3], *Kol* [4], *Mononykus* [5,6], *Parvicursor* [7,8] and
35 *Shuvuuia* [9,10] (Table S1). Dinosaur discoveries at Bayan Mandahu have been
36 important in demonstrating that distinct faunas existed across the Cretaceous Gobi
37 basin [1,8,11-16], which has provided valuable insight into how dinosaurs behaved and
38 coped over expansive semi-arid environments. Here we report IVPP V20341 a
39 fragmentary disarticulated parvicursorine specimen that was discovered in Bayan
40 Mandahu during the 2013 field season of the Inner Mongolia Research Project (IMRP).
41 IVPP V20341 appears to have two autapomorphies (cervical procoelony and relatively

42 larger semi-circular neural canals), but these cannot be confidently assigned because
43 anatomical variation along the spine cannot be ruled out as an explanation for these
44 observed differences, given the large amounts of missing data from known
45 parvicursorine neck and tail specimens. IVPP V20341 is therefore an important
46 parvicursorine specimen as comparative studies with future finds may either provide
47 new information about anatomical variation in these animals or justify the erection of a
48 new taxon, the second and seventh parvicursorine of Bayan Mandahu and the Gobi
49 Basin respectively.

50 **Systematic Palaeontology**

51 Dinosauria Owen, 1842

52 Theropoda Marsh, 1881

53 Alvarezsauridae Bonaparte, 1991

54 Parvicursorinae Karhu & Rautian 1996

55 **Material**

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

61 **Locality and horizon**

62 IVPP V20341 was found at Bayan Mandahu, Inner Mongolia, China which is part of the
63 Campanian-aged Wulansuhai Formation [17]. On July 2nd 2013, a team member (JS)
64 discovered isolated alvarezsauroid bones weathering out of a cliff top exposure of a fine-
65 grained, red structureless aeolian quartz arenite, ~3km SE of 'The Gate' locality
66 (41°43'15.3"N, 106°44'43.3"E; Figure 1), close to the location of Eberth's [17] '7/12/90/2'
67 stratigraphic section but not as far North as his '7/12/90/1' section [17]. The locality lies
68 within an larger area that Jerzykiewicz *et al.* called the 'South Escarpment' locality, but
69 the specific locality of IVPP V20341 is referred to as the 'eagle's nest' because a large
70 predatory bird nest was found ~3 metres from the find. On July 3rd 2013, another team
71 member (MP) further explored the sublocality and recovered several additional bones
72 within 1m of the original material. Following the depositional environments and facies
73 transitions identified by Eberth [17] at Bayan Mandahu, the specimen was deposited in
74 the zone 1 palaeographic zone which consists of alluvial, lacustrine and aeolian
75 sediments deposited in a distal alluvial fan or braid-plain environment adjacent to an
76 aeolian dune field. Given the sandy depositional environment of the specimen IVPP
77 V20341 was nicknamed 'Xiaoshalong', which is Chinese for 'little sand dragon'.

78 **Description and comparison**

79 IVPP V20341 appears to belong to a more ontogenetically mature individual (e.g.
80 subadult or adult) because the neurocentral sutures on the vertebrae preserved appear
81 to be completely closed [18,19]. However, this inference should be treated as tentative
82 in the absence of other ontogenetically-informative fusion in the appendicular skeleton
83 as well as relevant histological data. The skeletal elements common to both the IVPP
84 V20341 and to *Linhenykus* are generally smaller in the former than in the latter. This
85 suggests that IVPP V20341 was probably lighter in weight than *Linhenykus*, which itself
86 weighed around 450g [1,20]. IVPP V20341 lacks a femur and skull so a more accurate

87 proxy-based estimate of body mass was not possible [21,22]. The incomplete vertebral
88 column and the missing skull also prohibited a meaningful measurement of body length.
89 However, given the relative size of IVPP V20341 to *Linhenykus*, the former was probably
90 lighter than other Asian parvicursorines, with the exception of *Shuvuuia* and *Parvicursor*
91 (See Table S2).

92 Axial Skeleton

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

96

97 *Cervical vertebrae*

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

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

131 In lateral view, the cervical centra of IVPP V20341 are long and low, as in other
132 alvarezsauroids [23]. They are not as strongly laterally compressed as the posterior

133 cervicals of *Linhenykus* (IVPP 17608, [20]) as only the ventral portion is compressed in
134 IVPP V20341. Thus, the lateral surfaces of IVPP V20341 are more vertical in the middle
135 portion of the centrum than in *Linhenykus*. Nevertheless, this qualified the specimen as
136 an alvarezsaurid alvarezsauroid (cervical centra bearing deep lateral depressions is an
137 alvarezsaurid synapomorphy [20] (character state 8.1 of Longrich & Currie [8]). The
138 ventral surfaces of these cervicals are rounded and slightly pinched along their mid-
139 length whereas they are grooved (longitudinal ventral furrow) and pinched along their
140 mid-length in the posterior cervicals of *Linhenykus*, IVPP V17608 [20]. *Shuvuuia*
141 appears to share the same morphology in its posterior cervical vertebrae (MPC 100/975,
142 [23]) and potentially *Ceratonykus* as well (MPC 100/124, [3]; a furrow is present in the
143 cranioventral and midventral positions of a posterior cervical, but the distoventral portion
144 is broken). In the most proximal cervicals the ventral furrow of *Shuvuuia* does not span
145 the entire centra, because the mid-line of the centra is interrupted by a rounded surface
146 (MPC 100/975 [23]), like in *Mononykus* (MPC 107/6 [5]). The cranioventral furrows in
147 *Shuvuuia* and *Mononykus* are bordered by prominences [23] and are the only furrows
148 present in the most proximally preserved cervicals of *Shuvuuia*. The presence of a full
149 length ventral furrow in posterior centra of *Shuvuuia* and *Ceratonykus* suggests that this
150 feature is probably not a valid autapomorphy of the *Linhenykus*, unless future data can
151 demonstrate that only *Linhenykus* has this furrow on all of its cervicals. The lack of a
152 prominence-bordered cranioventral furrow in cervical B of IVPP V20341 appears unique
153 to Asian parvicursorines, but it is known in South American forms. MCF-PVPH 38, a
154 fragmentary 5th? cervical of a suspected indeterminate Argentine alvarezsauroid (?
155 Alvarezsauridae indet.), has a straight, narrow and rounded ventral surface - much wider
156 than a keel - with a 'veiny' surface texture [25]. The smooth cranioventral surface of the
157 cervical could be a valuable character for distinguishing parvicursorines, but the
158 absence of more complete neck specimens, the questionable taxonomy of MCF-PVPH
159 38 and the presence of this feature in the basal alvarezsauroid *Alvarezsaurus* [23]
160 makes the taxonomic value of this feature ambiguous.

161 Dorsal to the left lateral postzygapophysis of cervicals B and C there is no evidence of
162 an epiphysis, indicating that IVPP V20341 is an alvarezsauroid theropod (character
163 state 6.1 of Longrich & Currie [8] is an alvarezsauroid synapomorphy [20]). In IVPP
164 V20341, the diapophysial ridge has a convex profile in the area around the small
165 nubbin-like diapophysis (similar diapophysis in the posterior cervicals of *Linhenykus*,
166 IVPP V17608 [20]) but shallows gradually towards the posteroventral corner of the
167 centrum. This differs from the condition in *Linhenykus* - another autapomorphy of this
168 taxon - where the diapophyseal ridges extend to the posterodorsal rim of the centrum
169 [20]. However, the former may not be a valid autapomorphy owing to the presence of the
170 same feature in *Shuvuuia* (MPC 100/975, [23]). In IVPP V20341 the diapophysial ridge's
171 anteroventral surface is excavated and houses a broad shallow fossa. This feature is
172 difficult to appraise in *Linhenykus* as the ridge and the anteroventral surface are not
173 preserved in the same cervical. However, across two posterior caudals large collateral
174 pneumatic foramina are present [20] instead of broad shallow fossa. Cervical B lacks a
175 carotid process unlike in *Linhenykus* (where it is confluent with the anterior ends of the
176 ventral ridges in the posterior cervicals [20]); also known in *Shuvuuia* [23] and
177 *Mononykus* [5] as well as other theropods including some ornithomimosaurids,
178 oviraptorosaurs and paravians [20]. Cervicals B and C of IVPP V20341 both lack
179 pneumatic foramina as in *Mononykus* [5], but the lateral surfaces of their centra appear
180 to be less compressed mediolaterally than in *Mononykus* (mediolaterally compressed

181 cervical centra that lack pneumatic foramina are given in the diagnosis of *Mononykus*
182 [23]). In *Linhenykus* - like *Alvarezsaurus* and *Shuvuuia* - pneumatic foramina occupy the
183 area immediately posterior to the parapophyses [20,23,27]. As in *Linhenykus*, the neural
184 pedicles are mediolaterally broad and dorsoventrally low and it appears that the anterior
185 edge of each pedicle is also flush with the anterior articular surface of the centrum,
186 whereas the posterior edge is anterior to the posterior articular surface (excluding the
187 condyle) [20]. The parapophyses are also low, laterally projecting eminences like in
188 *Linhenykus* [20]. The process is dorsolaterally orientated.

189 The zygapophyseal articular facets in cervicals B-D of IVPP V20341 have a low-angle
190 (~78° and ~61° from the vertical [in anterior view] for the prezygapophyses of cervicals C
191 and D respectively and ~50° and ~40° from the vertical [in posterior view] for the
192 postzygapophyses of cervicals B and C respectively) suggesting a greater range of
193 motion in the horizontal plane than the vertical one. This is because the
194 prezygapophyses show the latter, whilst the postzygapophyses are complimentary to
195 this pattern since they indicate that the range of motion was similar in either plane. The
196 prezygapophyses are anteroposteriorly short and extend over approximately one third of
197 the preceding centra. The postzygapophyseal processes of cervical B of IVPP V20341
198 are separated by a wider angle (~136° in cervical B) in comparison to the posterior
199 cervicals preserved in *Linhenykus* (~105°). However, this difference may simply reflect
200 differences in anatomical position so should be treated with caution. The
201 postzygapophyses (left one on cervical B) appear to be dorsally orientated, as in
202 *Linhenykus* [20]. In dorsal view this postzygapophysis has a nearly straight medial edge
203 and a convex lateral edge like in other Asian alvarezsauroids [20,23]. This contrasts with
204 the postzygapophyses of *Alvarezsaurus* which have convex medial and lateral edges
205 that create a paddle-like shape in dorsal view [27]. Epiphyses are absent from the
206 postzygapophyses as evident from cervicals B and C (the left lateral sides) unlike the
207 mid-cervicals of *Linhenykus* which have weakly developed ridge-like ones that are an
208 autapomorphy of this taxon [20]. In IVPP V20341 the prezygapophyses are more widely
209 separated laterally and have larger articular surfaces in comparison to the
210 postzygapophyses - this pattern is not observed in *Linhenykus* which has laterally
211 narrower prezygapophyses than postzygapophyses in the posterior caudals that are
212 preserved [20]. In *Shuvuuia* (MPC 100/975) the prezygapophyses are laterally wider than
213 the postzygapophyses in the anterior proportion of the cervical series, have a similar
214 lateral width in the mid-series (at a currently undefined transition point due to the
215 incompleteness of the cervical series), whilst in the distal portion of the series the
216 prezygapophyses are laterally narrower the postzygapophyses [23] (as in *Linhenykus*
217 [20]). If this pattern of zygapophyseal width is similar in other parvicursorines it suggests
218 that cervicals A-D are anterior ones. This also compliments the observed partially
219 damaged neural spine in cervical B that rises from a well-defined dorsal ridge - that
220 spans the whole anterior dorsal surface of the vertebra - at the approximate position of
221 the postzygapophyseal facets. Taking into account the damage to this neural spine it
222 appears to be dorsoposteriorly directed but it would be speculative to comment on both
223 its dorsoventral height and anteroposterior length in relative terms. This is at odds with
224 identification of cervicals A-D as posterior ones based on the similarity of their rounded
225 ventral surfaces to the cervicodorsals of *Mononykus* (MPC 107/6, [5]). However, the new
226 zygapophyseal and neural spine information and the absence of rounded ventral
227 surfaces in the cervicals of other known parvicursorine cervicals suggests that the
228 presence of the latter is *potentially* a unique characteristic of IVPP V20341 amongst

229 parvicursorines. However, a more complete understanding of cervical variation in
230 parvicursorines is needed before this characteristic can be judged to be unique.

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

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

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

249 *Caudal vertebrae*

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

259 The anterior placement of the neural arch pedicle along the anteroposterior length of the
260 centrum suggests that caudals A-C are anterior ones as this characteristic is found in
261 parvicursorine alvarezsauroids including *Alvarezsaurus* (MUCPv 54, [23,27]),
262 *Achillesaurus* (MACN-PV-RN 1116, [28]), *Linhenykus* (IVPP V17608, [1,20]), *Parvicursor*
263 (PIN 4487/25, [7]), *Shuvuuia* (MPC 100/975, [23]) and *Xixianykus* (XMDFEC V0011,
264 [30]). In lateral view the distal margin of the narrowest portion of caudal A's neural arch
265 (the neck) is approximately three-thirds along the anteroposterior length of the centrum,
266 whereas in the first free caudal of *Parvicursor* (PIN 4487/25, [7]) and the proximal
267 caudals of *Alvarezsaurus* (MUCPv 54, [23,27]) this is less than half way along the same
268 length. However, the position of the neural arch pedicle in IVPP V20341 is comparable
269 to the middle and distal caudals of *Alvarezsaurus* [23,27] and the first caudals of
270 *Xixianykus* (XMDFEC V0011, [30]) and *Patagonykus* (the supposed first caudal of MCF-
271 VVPH 37, [25]).

272 In the preserved series, caudals A to D show a posterior migration of the transverse
273 processes (only the distal ridge of the process is visible on the left lateral side of caudal
274 D), but these are all still situated anteriorly on the centrum which identifies IVPP V20341
275 as a parvicursorine alvarezsauroid [20]. These form a broad subhorizontal ridge that
276 originate from the dorsoanterior corner of the centra (caudals A and B) rather than the
277 posterior end of the prezygapophyses as in the middle and distal caudals of *Linhenykus*
278 (best examples in caudals 7 and 8 of IVPP V17608 [20]) and in *Shuvuuia* (MPC
279 100/975, [23]). However, the ridge does deflect posteriorly towards the dorsal edge of
280 the posterior articular face in both IVPP V20341 and *Linhenykus* [20], although this
281 appears to deflect more ventrally in the former specimen. The caudals become
282 anteroposteriorly shorter from caudal A to B (caudals C and D are not anteroposteriorly
283 complete) but this pattern is not emphasised here given that the middle caudals are
284 anteroposteriorly longer than the proximalmost ones in *Linhenykus* (IVPP V17608, [20]).
285 Caudals A and B possess a longitudinal furrow along the centrum's entire ventral surface
286 and this is bordered laterally by two ventral keels. This feature is also observed in
287 *Linhenykus* [20], *Parvicursor* (PIN 4487/25, [7,23]), *Patagonykus* (supposed 20th caudal,
288 MCF-PVPH 37 [25]) and *Shuvuuia* (MPC 100/975 [23]). However, this feature is less
289 developed in caudal B and is barely visible in caudal C, where the ridges are low and
290 the furrow is broad and shallow. The ventral surface of caudal D has been eroded down
291 to the cortical bone. The ventral surfaces of caudals A, B and C therefore support their
292 proposed positional ordering.

293 Caudals A-D are all laterally pinched and are procoelous, although the latter cannot be
294 confirmed in caudals C and D owing to a missing posterior articular face in the former,
295 and a missing anterior articular face in the latter. In caudals A and B, the concave
296 anterior articular face is deep, whilst the posterior condyle is well-developed and hemi-
297 spherical in shape. Procoely in caudal vertebrae is also observed in *Haplocheirus* (IVPP
298 V15988, [26]), *Shuvuuia* (MPC 100/975, [23]), *Mononykus* (MPC N107/6, [5]),
299 *Xixianykus* (XMDFEC V0011, [30]), *Alvarezsaurus* (MUCPv 54, [23,27]) and potentially
300 in *Patagonykus* (MCF-PVPH 37), as only the posterior articular surfaces are preserved
301 [25]. However, the first caudal of *Linhenykus* is amphiplatyan [20] whilst a proximal
302 caudal of *Achillesaurus* - tentatively assigned as the fourth in the series - is
303 amphicoelous (biconcave) [28].

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

319 of a middle caudal (caudal 13) [20]. The absence of chevron articulation facets in IVPP
320 V20341 appears to be a distinguishing feature between this taxon and *Linhenykus*.

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

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

345 The shape of the neural canals in caudals A-C are laterally wider and more semi-circular
346 compared to the laterally narrower and more oval-shaped ones of *Linhenykus*
347 (observable in caudals 2, 7 and 13 of IVPP V17608 [20]), *Patagonykus* (MCF-PVPH-37,
348 the supposed first caudal [25]) and *Parvicursor* (PIN 4487/25, the supposed first caudal
349 [7]). This feature represents a *potential* autapomorphy of IVPP V20341 because it is
350 plausible that laterally wider and more semi-circular neural canals might actually be
351 present in as yet unknown portions of other parvicursorine vertebral columns, since
352 neural canal size and shape changes along the vertebral column of theropods (and
353 other vertebrates). The ventral surface of the neural canal of caudal D bears a
354 longitudinal ridge. However, the distribution of this characteristic amongst parvicursorine
355 alvarezsauroids is unclear owing to a paucity of appropriate specimens.

356 Appendicular skeleton

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

360 *Forelimb*

361 Left scapula

362 In the same small block of sediment that contains cervicals A-D there is a broken, strap-

363 like piece of bone (Figure 4). The most complete margin of this bone is deflected and at
364 one end of the bone (distal end?) the margins are subparallel. At the suspected distal
365 end of this bone the generally flat surface sinks into two shallow grooves that traverse
366 towards the midline to create a flattened triangular eminence. The bone superficially
367 resembles an alvarezsauroid scapula shaft (preserved in *Haplocheirus* (IVPP V15988,
368 [26]), *Bonapartenykus* (MPCA 1290, [31]), *Alvarezsaurus* (MUCPv 54, [23]), *Mononykus*
369 (MPC 107/6, [5])) and *Shuvuuia* (MPC 100/977); Table S1) but it does not preserve
370 enough information to help differentiate it amongst alvarezsauroids save for the
371 triangular eminence. However, the latter feature has not been reported in the
372 aforementioned alvarezsauroids so this could be a distinguishing feature of IVPP
373 V20341 if this bone fragment is indeed part of a scapula, probably from the left side of
374 the body.

375 *Hind limb*

376 Speculative right pedal phalanx II-1

377 The distal end of a digital element is preserved (Figure 5A). This has distinct condyles
378 that are separated by an intercondylar groove, but the latter is narrower and less
379 developed than in preserved phalangeal elements of *Linhenykus* (IVPP V17608 [20]:
380 right manual phalanx II-1; left pedal phalanges I-1, I-2, II-1 and IV-1, ?right pedal
381 phalanges II-1 to II-3 and IV-4, ?left pedal phalanges IV-3 to IV-5; IVPP V18190 [32]: left
382 pedal phalanges III-1, IV-1 and IV-2), *Mononykus* (MPC 107/6 [5]: complete set of left
383 pedal phalanges), *Koi* (MPC 100/2001 [4]: left pedal phalanx III-2) and *Albinykus* (MPC
384 100/3004 [2]: right pedal phalanx IV-3). A similarly narrow and less developed
385 intercondylar groove is found on the distal end of the left pedal phalanx II-1 of the
386 *Linhenykus* paratype specimen (IVPP V18190 [32]), but a wider and more developed
387 groove is found in the holotype specimen (IVPP V17608 [20]). This degree of variability
388 implies that the element in question might be impossible to identify based on this
389 characteristic alone. Alternatively, this morphological difference might be of taxonomic
390 importance, although differentiating between this scenario and the former one is beyond
391 the scope of this paper. A similarly developed narrow intercondylar groove appears to be
392 present on the distal end of the right pedal phalanges II-1 and IV-1 of *Albinykus* (MPC
393 100/3004 [2]), but which of these the element most closely resembles overall is unclear.
394 There is a well-developed, anteriorly-marginated, triangular-shaped ligamental fossa on
395 the lateral surface of the lateral condyle of this IVPP V20341 element, but this area is
396 poorly preserved in the aforementioned phalanges of *Albinykus*. In lateral view, the
397 ventral surface of the lateral condyle of the element is deeper and more steeply inclined
398 than its dorsal surface. Neither of the right pedal phalanges II-1 and IV-1 of *Albinykus*
399 have this feature, although a more weakly developed version is present in the former.
400 Therefore, the digital element in question is speculatively identified as a pedal phalanx
401 II-1. This phalanx is potentially from the right foot because the largest condyle is the
402 lateral rather than medial one in the left pedal phalanx II-1 of *Linhenykus* (IVPP V17608
403 [20]; IVPP V18190 [32]). However, the opposite can also be inferred as the reversed
404 pattern is observable in the left pedal phalanx II-1 of *Mononykus* (MPC 107/6, [5]). The
405 shaft of the IVPP V20341 element is broken and incomplete, but it does appear to be
406 relatively straight. This feature would appear to rule it out as a metatarsal III, because
407 the only taxon where the distal articulation surface of MTIII has distinct condyles
408 separated by a narrow intercondylar groove is *Alnashetri* (MPCA 477), but this has a
409 shaft with an anteriorly convex curvature. *Albertonykus* (TMP 2001.45.52) and

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

413 Potential right pedal digit II-2 phalanx

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

424 Possible pedal phalanx from the second or third digit

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

429 Suspected left pedal digit III-2/3

430 Based on how the suspected pedal phalanx II-1 was assigned to the right side of the
431 body, it follows that the larger of two concavities that are separated by the vertical ridge
432 on the anterior articulation surface corresponds to the lateral side of this surface (Figure
433 5D). This suggests that this element belongs to the left side of the body. However, as
434 mentioned, this characteristic varies between taxa (*Linhenykus* (IVPP V17608 [20]; IVPP
435 V18190 [32]) compared to *Mononykus* (MPC 107/6, [5])) and seeming along a single
436 digit as well (along left pedal digits III and IV of *Mononykus* (MPC 107/6 [5])). The
437 concave articular facets of the anterior articular surface do not extend across the entire
438 dorsoventral height of the articulation surface, but meet a flat facet approximately two-
439 thirds down this surface. The dorsal portion of the vertical ridge extends slightly
440 anteriorly to overhang the anterior articulation surface. However, this is far less
441 extensive than in phalanx IV-4 of *Linhenykus* (IVPP V17608, [20]) where this happens
442 for the dorsal and ventral portions of the ridge, dividing the entire dorsoventral height of
443 the anterior articulation surface. These aforementioned features indicate a more
444 posteriorly positioned phalanx from perhaps the second or third positions. The shaft of
445 the phalangeal element is broken, but it appears to have a rounded ventral surface. The
446 lateral condyle of the posterior articulation surface is missing, but the medial condyle is
447 well-developed and is bound laterally by a well-formed intercondylar groove. This
448 condyle has a strongly asymmetric lateral profile with a rounded dorsal surface and an
449 elongated sloping ventral surface, as in many theropod pedal phalanges including those
450 of *Deinonychus* (YPM 5205, [33]). This feature is present in a much less developed
451 condition in phalanx IV-4 of *Linhenykus* (IVPP V17608 [20]), but this phalanx has a
452 stouter profile than IVPP V20341 (in comparison, the latter phalanx is much longer
453 anteroposteriorly than tall dorsoventrally compared to the former phalanx) [20]. A well-
454 developed ligamental fossa occurs slightly below the mid-point of the condyle's lateral
455 surface. The relative slenderness of the preserved phalange suggests that it belongs to

456 the third rather than fourth digit. Thus, the phalanx concerned is suspected as the
457 second or third position of a left pedal digit III (?left III-2/3).

458 Potential left pedal phalanx III-3

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

470 Possible right pedal phalanx possibly from digit IV

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

480 Suspected pedal phalanx from digit IV

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

487 Discussion

488 IVPP V20341 is referable to Alvarezsauroidea because of the absence of cervical
489 epiphyses (absent above the left lateral postzygapophysis of cervicals B and C
490 (Figure 1); character state 6.1 of Longrich & Currie [8] is an alvarezsauroid
491 synapomorphy [20]). The specimen is an alvarezsaurid alvarezsauroid owing to the
492 presence of cervical centra bearing deep lateral depressions [20] (centra of cervicals A-
493 C and the isolated cervical (Figures 1 and 2); character state 8.1 of Longrich & Currie
494 [8]). This placement is also supported by the presence of caudal procoely (Figure 3;
495 character state 21.1 of Longrich & Currie [8]). Owing to the incomplete preservation of
496 the pedal digits in IVPP V20341, it is unclear if pedal digit III is more slender than digits II
497 or IV, so this alvarezsaurid synapomorphy [20] cannot be confirmed in this specimen.
498 IVPP V20341 is further identified as a parvicursorine alvarezsauroid based on the
499 presence of anterior caudal vertebrae with anteriorly displaced transverse processes
500 [20] (Figure 3; character state 22.1 of Longrich & Currie [8]).

501 Currently, only one parvicursorine - *Linhenykus monodactylus* Xu *et al.* 2011 - is known
502 from the same locality in Bayan Mandahu, Inner Mongolia, China as well as from the
503 formation it belongs to, the Upper Cretaceous - possibly Campanian - Wulansuhai
504 Formation [1,17,34]. However, six other parvicursorines are known from more northerly
505 localities within the Santonian to Maastrichtian-aged Upper Cretaceous rocks [3,7,35-38]
506 of the Mongolian Gobi Basin: *Albinykus* [2], *Ceratonykus* [3], *Mononykus* [5], *Parvicursor*
507 [7], *Shuvuuia* [9] and *Kol* [4] (Table 1). Agnolin *et al.* [31] argue that *Kol* has stronger
508 oviraptorosaurian affinities than alvarezsaurid ones, but having not studied the specimen
509 yet first-hand, we adopt the original identification here. IVPP V20341 does not have any
510 known autapomorphies of any other parvicursorine and its unique features (proceolous
511 cervicals and laterally wider and more semi-circular neural canals) are insufficient to
512 assign it to a new species because they can potentially be explained as anatomical
513 variations along the vertebral column, particularly as this is poorly understood amongst
514 parvicursorines. A better understanding of anatomical variation in *Linhenykus* in the
515 future might led to IVPP V20341 being referred to this taxon, but current evidence does
516 not permit such a referral.

517 *Parvicursorines at Bayan Mandahu*

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

542 Axial skeleton:

543 *Cervical vertebrae*

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

- 546 2. Epiphyses are absent from the postzygapophyses unlike the weak ones
 547 observed in *Linhenykus*, but in IVPP V20341 the cervicals are interpreted as
 548 anterior rather than mid-series ones, as in *Linhenykus*.
 549 3. The cervicals of IVPP V20341 have a rounded ventral surface (at least
 550 proximally) whereas the cervicals of *Linhenykus* have a shallow longitudinal
 551 furrow that runs along the entire length of the ventral surface that is bound
 552 laterally by two low ridges.
 553 4. The cervical centra of IVPP V20341 are not mediolaterally compressed like the
 554 posterior cervicals of *Linhenykus* (IVPP 17608), as only the ventral portion is
 555 compressed in the former. Thus, the lateral surfaces of IVPP V20341 are more
 556 vertical in the middle portion of the centrum than in *Linhenykus*.
 557 5. Cervicals lack a carotid process (cervical B) unlike in *Linhenykus*.
 558 6. Absence of cervical pneumatic foramina (cervicals B and C and in *Mononykus*
 559 [5]), unlike in *Linhenykus* which has them in the area immediately posterior to the
 560 parapophyses (also in *Alvarezsaurus* [23,27] and *Shuvuuia* [23]).
 561 7. *The prezygapophyses are set less lateral to the centra than in Linhenykus (this*
 562 *probably reflects the anterior vs. posterior position of the centra in the series).*
 563 8. *Postzygapophyseal processes (cervical B, supposedly an anterior one)*
 564 *separated by a wider angle than the posterior cervicals of Linhenykus (~136°*
 565 *compared to 105°) (this probably reflects the anterior vs. posterior position of the*
 566 *centra in the series).*
 567 9. *In the supposed anterior cervicals, the prezygapophyses are more widely*
 568 *separated laterally than the postzygapophyses. This is the opposite of what is*
 569 *observed in the posterior caudals of Linhenykus. However, both patterns are*
 570 *found in the same locations in the cervical series of Shuvuuia (MPC 100/975)*
 571 *[23].*

572 *Caudal vertebrae*

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

586 Appendicular skeleton:

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

589 *IVPP V20341 compared to other Asian parvicursorines*

590 ~350km separates Bayan Mandahu and the closet Mongolian parvicursorine locality

591 (*Mononykus olecranus* at Bayan Dzak [39]). During the Late Cretaceous the mountain
592 ranges within the Gobi basin (composed of Palaeozoic and Mesozoic rocks) were being
593 subjected to extensional tectonism [34] that presumably promoted sediment deposition
594 through the creation of accommodation space. This geological setting divided the Gobi
595 basin and created obstacles to faunal interaction which probably promoted vicariance.
596 The latter would help to explain why the Bayan Mandahu fauna seems to be distinct
597 from Djadokhtan ones. If common Bayan Mandahu and Djadokhtan parvicursorines
598 were found, this would suggest that at least some elements of the faunas are similar,
599 which would advocate a complex scenario of selective isolation to explain the pattern of
600 animals observed. Fortunately, for the skeletal elements that they share in common,
601 IVPP V20341 lacks the autapomorphies of any Mongolian parvicursorine, so this
602 provides limited support for the distinctiveness of the Bayan Mandahu fauna (see Table
603 3), as its status as a distinct taxon or specimen of *Linhenykus* remains unclear.
604 *Parvicursor* and *Ceratonykus* are both known from the Upper Cretaceous (Lower
605 Santonian, [3]; Middle Campanian; [7]) Barun Goyot Formation (Table S1) and appear to
606 have shared their living environment. Niche partitioning by these taxa - if at all - probably
607 relates to their body size differences as *Parvicursor* is smaller than *Ceratonykus*
608 (75.6mm long tibiotarsus in *Parvicursor*, PIN 4487/25 [7]; 89mm long right and left
609 tibiotarsus in *Ceratonykus*, MPC 100/124 [3]). If IVPP V20341 is demonstrated to be a
610 valid taxon at a later date, the sharing of a relatively harsh semi-arid environment with
611 *Linhenykus* might support niche partitioning too e.g. if IVPP V20341 actually has a more
612 conventional hand morphology than *Linhenykus*.

613 *IVPP V20341 compared to other alvarezsauroids*

614 IVPP V20341 is seemingly distinct amongst alvarezsauroids because of the presence of
615 cervical procoely and caudal neural canals (caudals A-C) that are laterally wider and
616 more semi-circular compared to the laterally narrower and more oval-shaped ones of
617 *Linhenykus* (caudals 2, 7 and 13) and of the supposed first caudals of *Patagonykus*
618 (MCF-PVPH 37, [25]) and *Parvicursor* [7]. However, these potential autapomorphies
619 have caveats that need to be considered. Cervical procoely is unknown in
620 alvarezsauroids, but only one complete neck specimen is known and this belongs to the
621 basalmost taxon *Haplocheirus solers* [26]. If the eleven cervical vertebrae of the latter is
622 similar amongst all alvarezsauroids - an assumption that is speculative based on current
623 fossil evidence - then the 8 and 9 cervical vertebrae preserved in *Mononykus* (MPC
624 107/6, [5]) and *Shuvuuia* (MPC 100/975, [23]) respectively may actually represent near
625 complete series. These three neck specimens provide an indication of the basal
626 alvarezsauroid and derived parvicursorine cervical conditions which should resemble
627 that of IVPP V20341, so the absence of procoely in all three is significant. However,
628 *Haplocheirus* lacks the strong opisthocoelous condition of *Mononykus* (MPC 107/6, [5])
629 and *Shuvuuia* (MPC 100/975, [23]) which shows that there is significant variation in
630 articular surface morphology within the clade, although it is impossible to say if such
631 variation might include multiple taxa with a procoelous condition. The morphology of the
632 alvarezsauroid tail is better understood than the neck because more material
633 representing a broader phylogenetic sample is known. The most complete caudal series
634 are found in *Haplocheirus* (IVPP V15988, 15? caudals [26]), *Alvarezsaurus* (MUCPv 54,
635 13 caudals [23,27]), *Linhenykus* (IVPP 17608, 13 caudals [20]) and *Shuvuuia* (MPC
636 100/975, 19 caudals [23]; MPC 100/120; 22? caudals [10]). The most complete
637 alvarezsauroid tail is represented by specimen MPC 100/120 of *Shuvuuia* which
638 preserve direct evidence of approximately 22 caudals [10]. However, the gaps in the

639 caudal series suggest a caudal count upwards of 35 caudals [10]. The relatively large
640 semi-circular caudal neural canals of IVPP V20341 are absent in *Linhenykus*,
641 *Patagonykus* and *Parvicursor* – the only taxa that had specimens where the shape of
642 the caudal neural canal could be determined from firsthand study or from the literature.
643 This represents a small sample size and given the neural canal varies in size and shape
644 along the vertebral column of theropods (and other vertebrates), this potential
645 autapomorphy cannot be supported unequivocally. In the case of both of the tentative
646 autapomorphies in IVPP V20341, future fossil specimens are needed to test their
647 validity.

648 *Potentially informative features for alvarezsauroid phylogeny*

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

657 *Cervical centra: amphiceolous, amphiplatyan or platyceolous (0), opisthoceolous (1),*
658 *proceolous (2), amphiceolous, amphiplatyan or platyceolous AND opisthoceolous or*
659 *proceolous (3), amphiceolous, amphiplatyan or platyceolous AND opisthoceolous AND*
660 *proceolous (after Perle et al. [5])*

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

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

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

673 Comparisons made between the preserved cervical and caudal vertebrae of IVPP
674 V20341 and all other parvicursorines has highlighted variation in the ventral surface
675 along each series, including the relative development of furrows (partly or fully) and
676 keels (absent, small or large in caudals) as well as the distribution of rounded and/or flat
677 smooth ventral surfaces. To reflect these observations, character 9 of Longrich & Currie
678 [8] has been reworded:

679 *Ventral surfaces of cervical centra: smooth and flat and/or smooth and rounded (0),*
680 *longitudinal furrow partly or fully spanning the length of the centrum (1), both conditions*

681 *are present (2) (after Novas, 1996).*

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

686 In consideration of the amphiplatyan first caudal of *Linhenykus* (IVPP 17608, [20]) and
687 the amphicoelous (biconcave) proximal (4?) caudal of *Achillesaurus* (MACN-PV-RN
688 1116, [28]), character 21 of Longrich & Currie [8] is expanded to:

689 *Caudal vertebrae: amphiplatyan or amphicoelous (0), or procoelous (1) (after Novas,*
690 *1996)*

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

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

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

698 The Wulansuhai Formation rocks of Bayan Mandahu, Inner Mongolia comprise of
699 lithologies that are similar to the Djadokhta Formation rocks of Bayan Dzak, Mongolia
700 [17,34]. These lithologies indicate that both formations were deposited mostly under
701 semi-arid conditions as alluvial and aeolian sediments, but the presence of some
702 mudrocks shows that some deposition occurred under wetter climatic conditions [17,34].
703 Many Bayan Mandahu fossils have been referred to taxa known from the Djadokhta
704 Formation [34,40,41] which both share a vertebrate fauna of dinosaurs, lizards, turtles,
705 mammals and birds. The Wulansuhai Formation was assigned a Campanian age based
706 on its lithological and faunal similarities [34] with the Campanian-aged Djadokhta
707 Formation, which itself was dated based on faunal and magnetostratigraphic data (See
708 Xu *et al.* [15] and references therein). The absolute age of the Wulansuhai Formation is
709 still wanting so the stratigraphic correlation of these formations remains equivocal.
710 However, an increasing body of evidence suggests that the two faunas represented in
711 both formations are actually distinct [42]: several previous referrals of Bayan Mandahu
712 specimens to Djadokhta taxa have been rejected [13,43] whilst several taxa unique to
713 Bayan Mandahu have been described [1,12-14,16,20]. Unfortunately, the uncertain
714 taxonomic status of IVPP V20341 does not contribute strong support towards the
715 hypothesis that Bayan Mandahu is faunally distinct from the Djadokhta Formation.

716 **Conclusions**

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

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

731 **Acknowledgements**

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 737 from our field site.

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 746 and Evolution (George Washington University).

747 **Tables**

748 A

| | Vertebral element | | | | | | | | |
|---|-------------------|----------|--------|--------|-------------------|----------|------------|----------|----------|
| | Cv A | Cv B | Cv C | Cv D | Isolated cervical | Cd A | Cd B | Cd C | Cd D |
| Dimension in mm | | | | | | | | | |
| 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) | - | - | - |

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

751 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) |

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

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

| Taxon | Diagnosis |
|------------------------|---|
| <i>Albinykus</i> [2] | <p>Possesses a unique character state combination amongst alvarezsaurids (from Nesbitt <i>et al.</i> [2]):</p> <ul style="list-style-type: none"> • Short metatarsal I with a rounded proximal tip (unknown in both <i>Alvarezsaurus</i> and <i>Patagonykus</i>). • 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. <ul style="list-style-type: none"> ◦ <i>Not equivocal in IVPP V20341 as phalange IV-2 is missing.</i> • 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 <i>Parvicursor</i>, <i>Shuvuuia</i>, and <i>Mononykus</i> only. |
| <i>Ceratonykus</i> [3] | <p>From Alifanov & Barsbold [3]:</p> <ul style="list-style-type: none"> • 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. <ul style="list-style-type: none"> ◦ <i>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.</i> |

- 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.
- **Antermost 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 procoelous and the antermost caudal (caudal A) has a broken neural spine whose anterior margin appears to lie above the neural pedicle.

Mononykus [6]

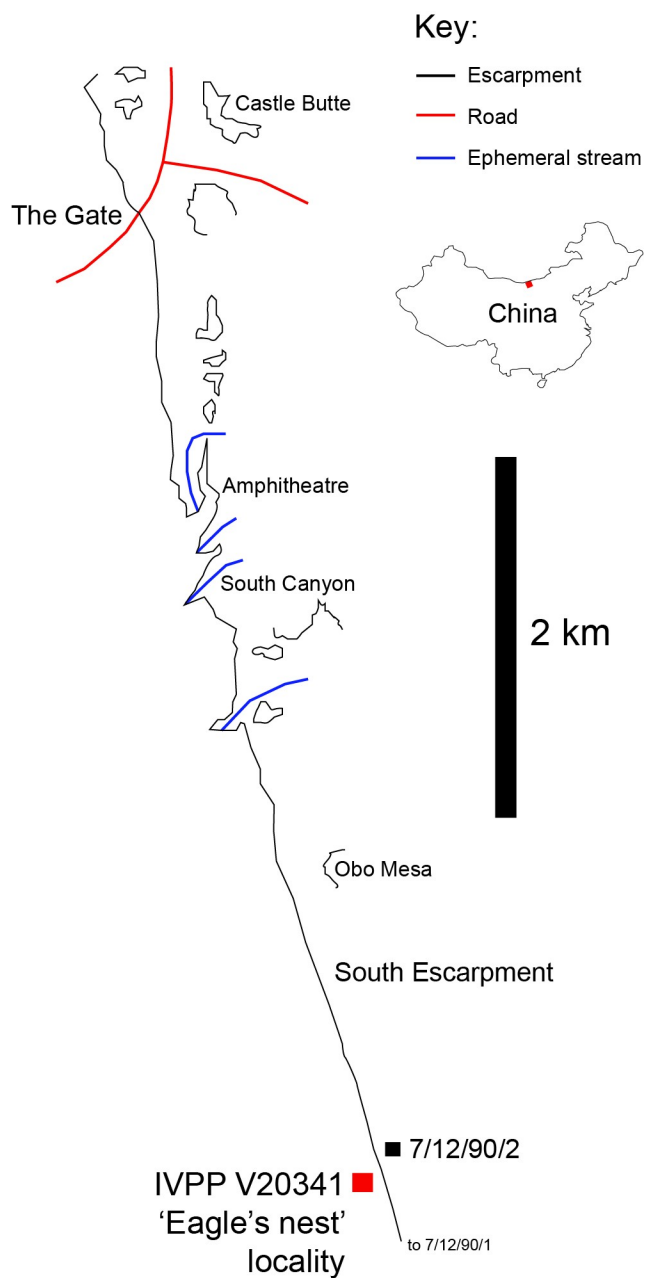
From Chiappe *et al.* [23]:

- **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.

| | |
|------------------------|---|
| <i>Parvicursor</i> [7] | <ul style="list-style-type: none"> • Medial indentation of ascending process with deeply excavated base. • Ascending process arises from medial margin of astragalar condyle instead of from lateral margin. From Chiappe <i>et al.</i> [23]: <ul style="list-style-type: none"> • Similar to <i>Mononykus</i> but smaller. • Opisthocoelous caudal thoracic vertebrae. • No bi-convex thoracic vertebra. • Convex cranial margin of synsacrum. |
| <i>Shuvuuia</i> [9] | Autapomorphies from Suzuki <i>et al.</i> [10]: <ul style="list-style-type: none"> • 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 <i>et al.</i> [9]). |

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

759 Figures



760 Figure 1: Place of discovery for IVPP V20341 ($41^{\circ}43'15.3''N$, $106^{\circ}44'43.3''E$), ~3km SE
 761 of 'The Gate' locality and close to the location of Eberth's '7/12/90/2' stratigraphic section
 762 [17] (After Jerzykiewicz *et al.* and Eberth [17]).

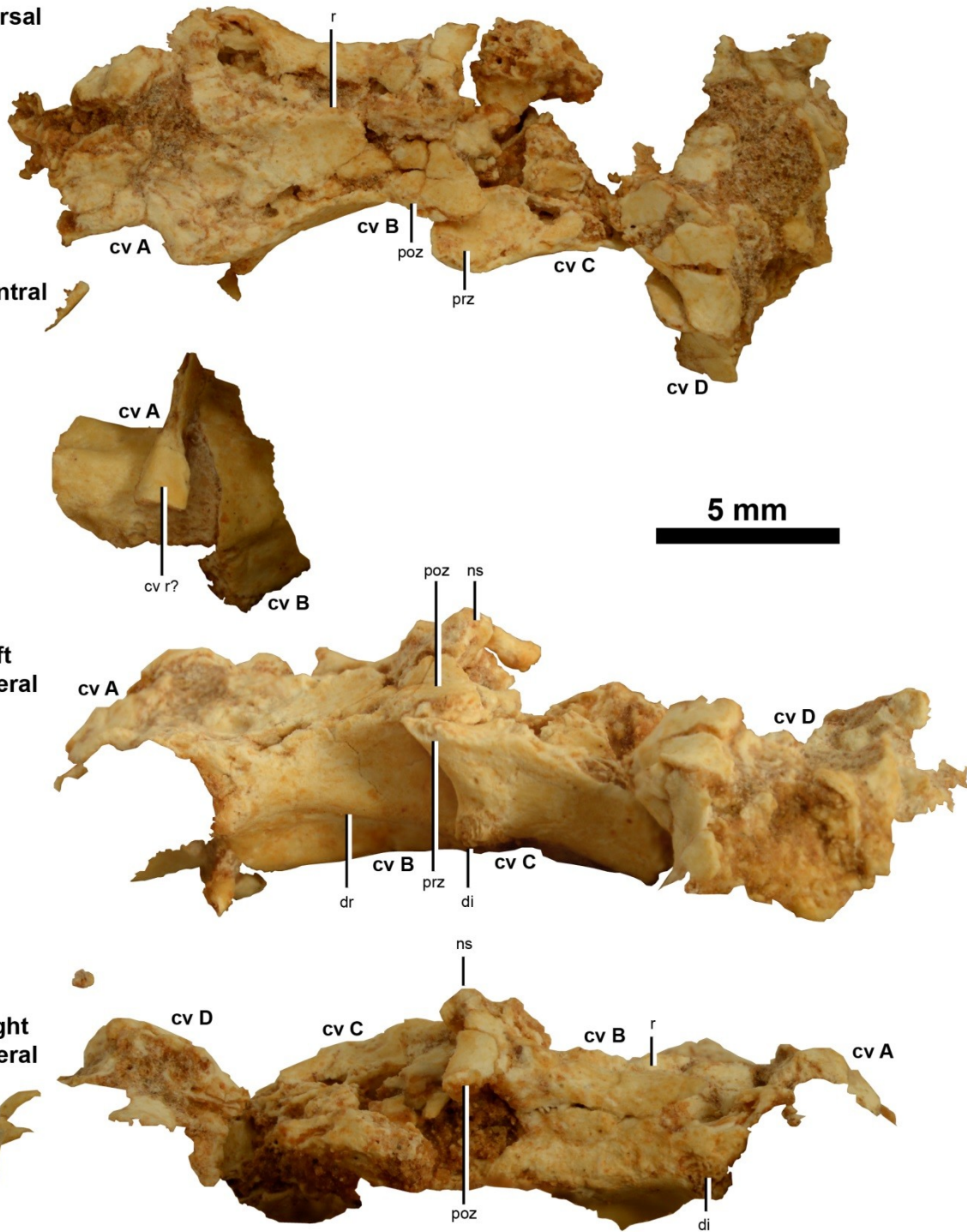
A

Dorsal

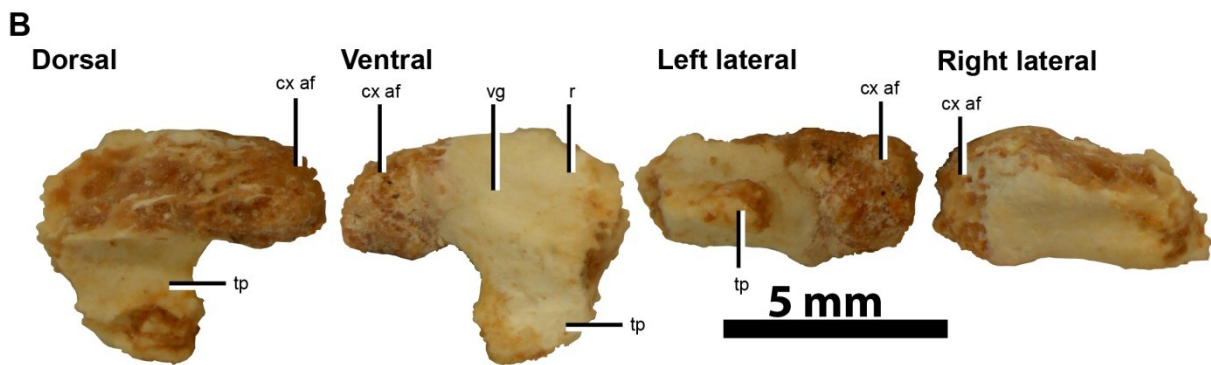
Ventral

Left lateral

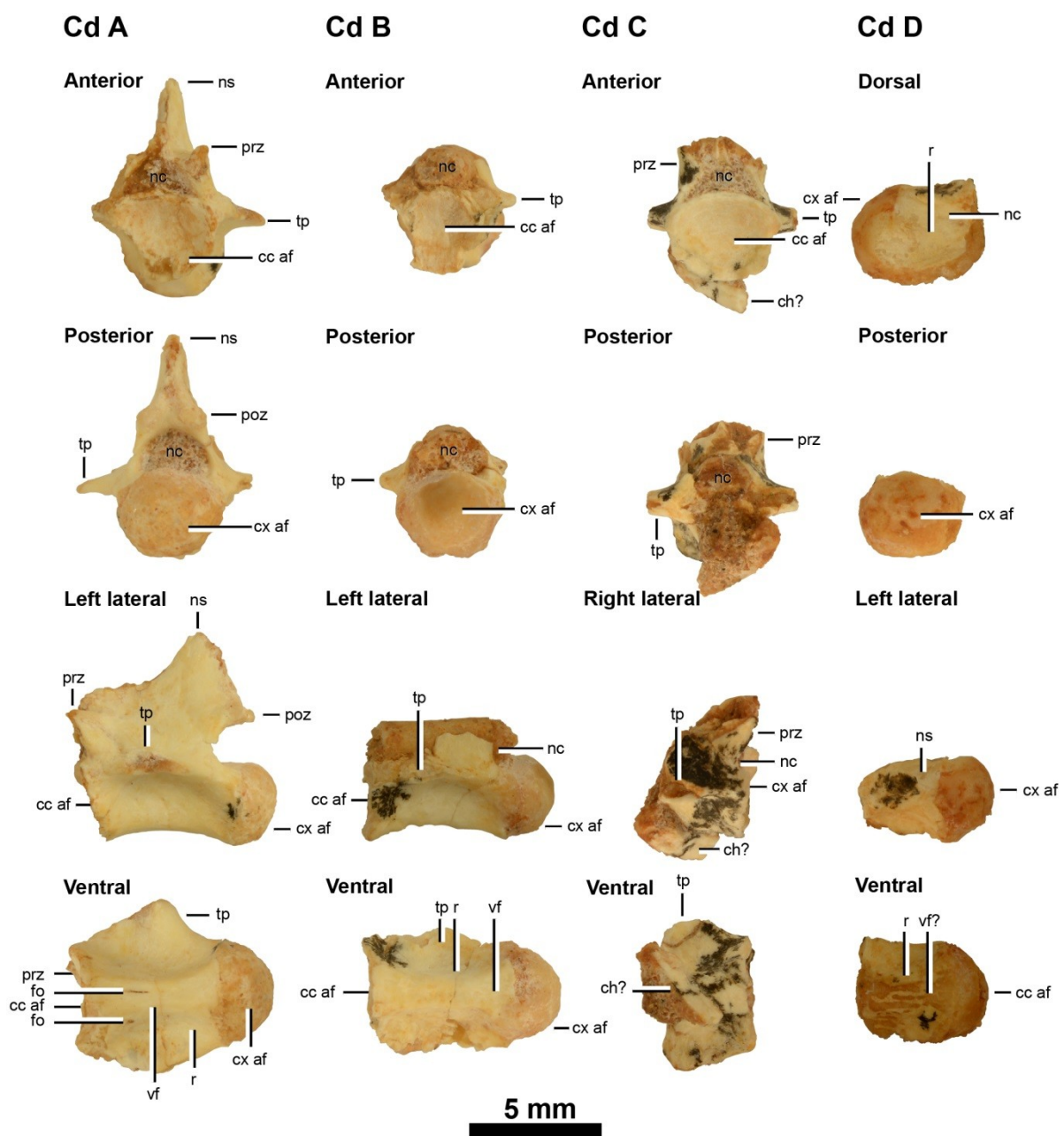
Right lateral



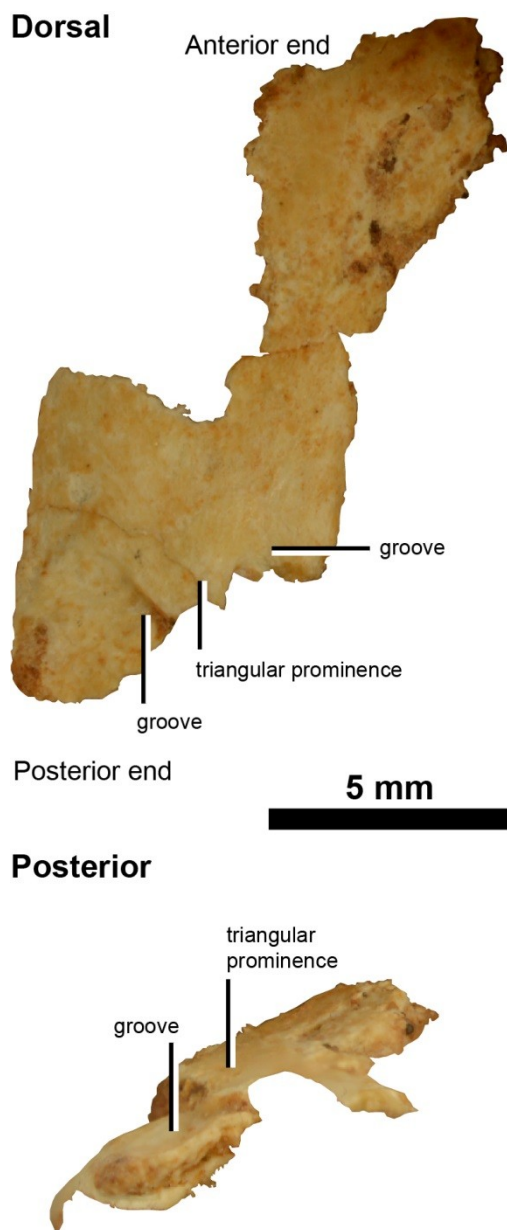
5 mm



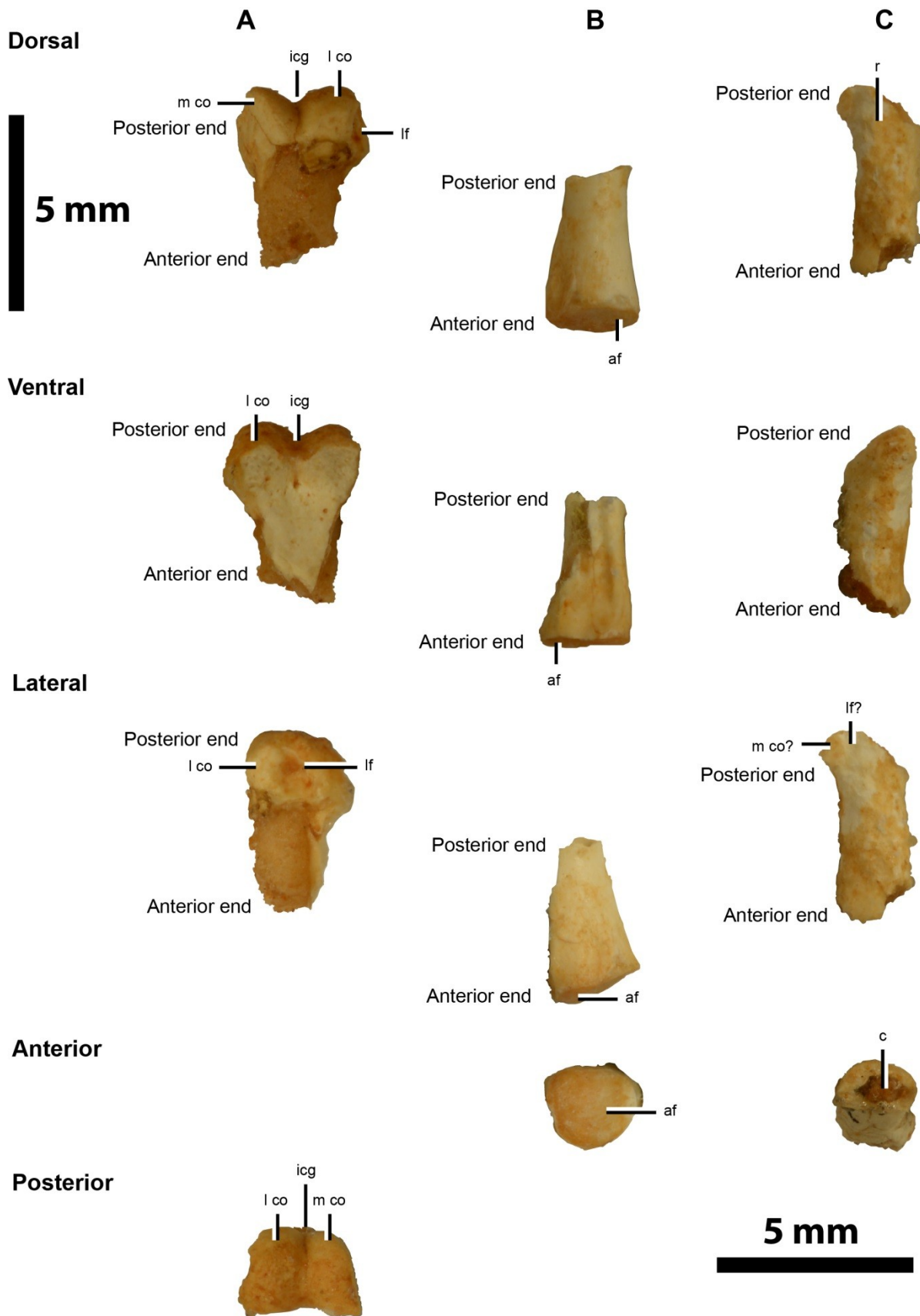
763 Figure 2: A, dorsal, ventral, left lateral and right lateral views of an articulated series of
 764 four partial cervical vertebrae (cervicals A-D). B, dorsal, ventral, left lateral and right
 765 lateral views of an isolated anterior portion of a cervical vertebra. Abbreviations: cv,
 766 cervical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

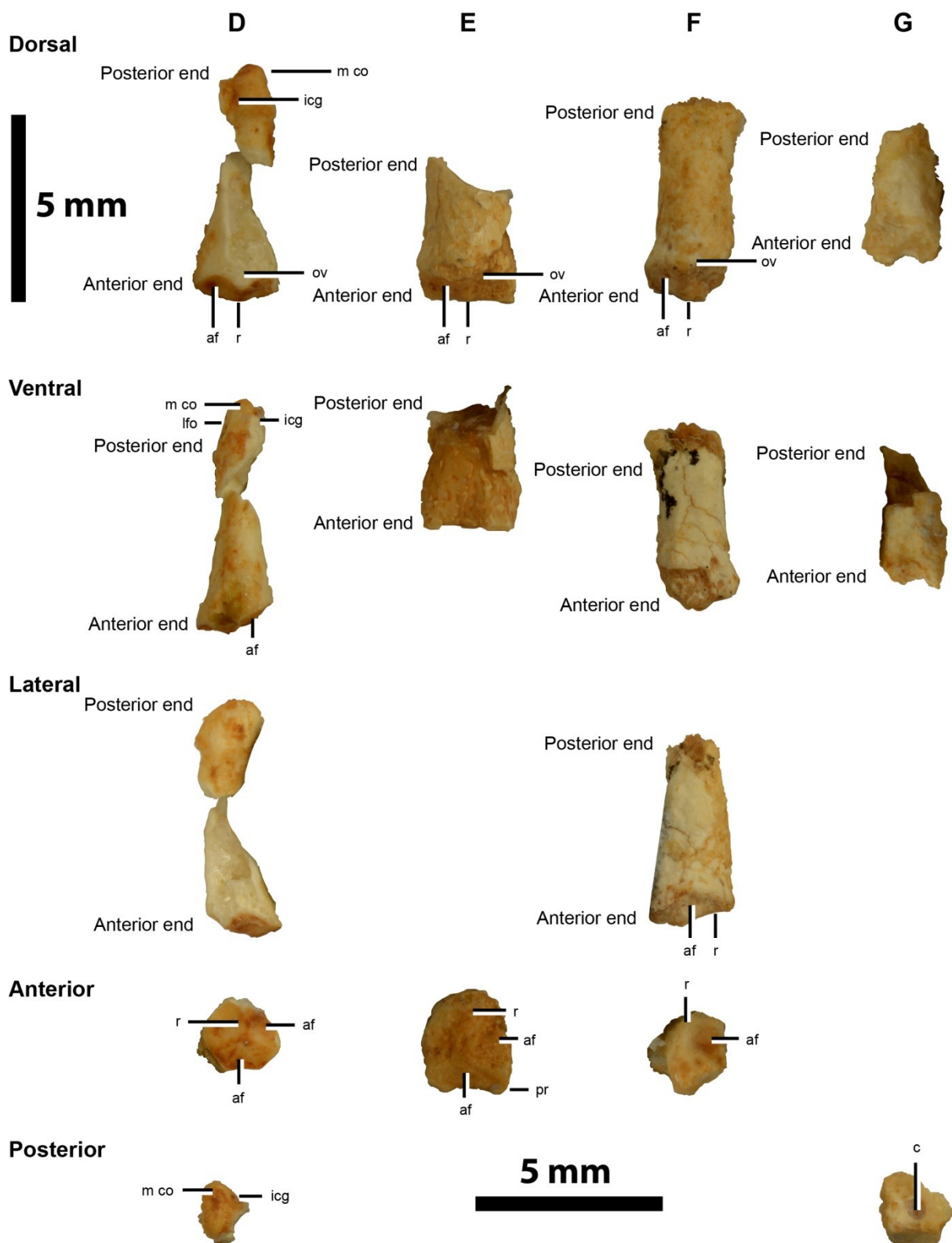


769 Figure 3: Caudal vertebrae A-D in anterior, posterior, lateral and ventral views (caudal D
 770 is damaged in anterior view so its dorsal view is shown instead). Abbreviations: cc af,
 771 concave articular face; ch?, chevron; cx af, convex articular face; fo, foramina; ns,
 772 neural canal; ns,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



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





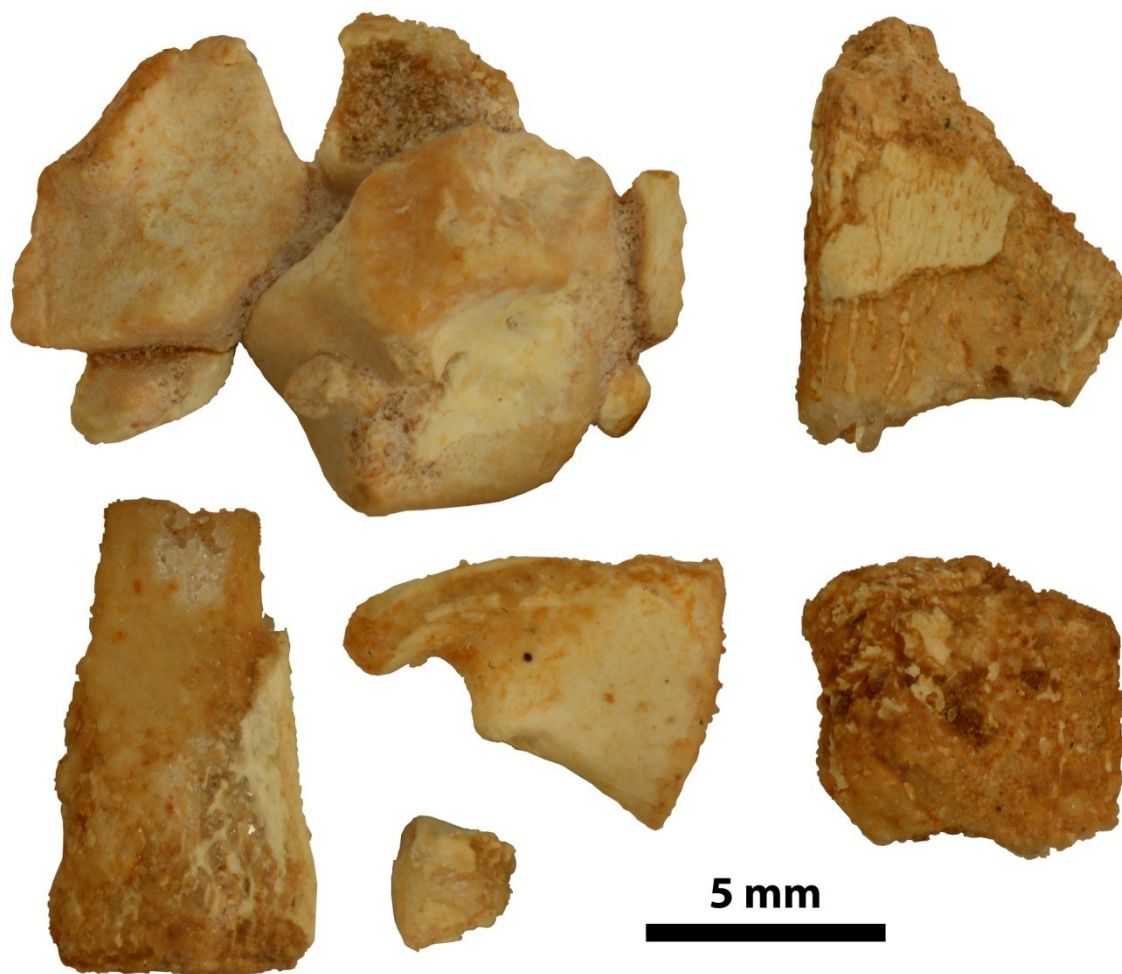
775 Figure 5: Hindlimb elements of IVPP V20341. Pedal phalanges possibly with the
 776 identities: A, ?right II-1, B, ?right II-2, C, II/III, D, ?left III-2, E, ?left III-3, F, ?right IV, and
 777 G, ?IV. Abbreviations: af, articular facet; c, cavity; icg, intercondylar groove; lfo,
 778 ligamental fossae; m co, medial condyle; ov, overhang; p, prominence; r, ridge. Scale =
 779 5 mm.

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

914 Table S1: Taxon data for known alvarezsauroids

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