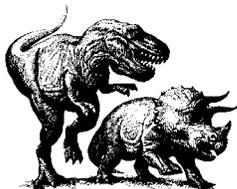


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CONTRIBUTIONS IN SCIENCE

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LATE CRETACEOUS WITH A DISCUSSION OF
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A NEW SPECIMEN OF *SHUVUUIA DESERTI* CHIAPPE ET AL., 1998, FROM THE MONGOLIAN LATE CRETACEOUS WITH A DISCUSSION OF THE RELATIONSHIPS OF ALVAREZSAURIDS TO OTHER THEROPOD DINOSAURS

SHIGERU SUZUKI,¹ LUIS M. CHIAPPE,²
GARETH J. DYKE,³ MAHITO WATABE,¹
RINCHEN BARSBOLD,⁴ AND
KHISIGJAW TSOGTBAATAR⁴

ABSTRACT. A partial skeleton of an immature individual of the alvarezsaurid mononykine theropod *Shuvuuia deserti* from the Late Cretaceous (Campanian) Tögrögiin Shiree locality of southern Mongolia exhibits a number of features, most importantly in the manus, pes, and caudal series, previously unknown for this taxon and all other alvarezsaurids. The well-preserved and articulated right hand of this new specimen confirms the presence of manual digits II and III among alvarezsaurids. The nearly complete tail of the new specimen indicates that previous calculations for the number of caudal vertebrae in mononykines (i.e., 25 or 26 vertebrae) underestimated this number by at least 10 elements. Complete and articulated pedal digits I (hallux) provide additional morphological information, which when added to new data from other skeletal regions strengthens the diagnosis of *Shuvuuia deserti*. Competing hypotheses for alvarezsaurid phylogenetic relationships have depicted these taxa either within Aves, or as nonavian theropods. These hypotheses are briefly summarized, and in particular, a critical evaluation of the character evidence in support of the ornithomimid affiliation of this theropod clade is provided. We demonstrate that the evidence in support of this latter hypothesis is largely unsubstantiated.

INTRODUCTION

Alvarezsaurids are one of the most bizarre groups of Mesozoic theropods, exhibiting unique osteological features in several parts of their skeleton, especially their abbreviated and stout forelimbs. These theropods were first recognized as a monospecific taxon by Bonaparte (1991) in his description of the Late Cretaceous *Alvarezsaurus calvoi* Bonaparte, 1991, from northwestern Patagonia. Novas (1996, 1997) expanded Alvarezsauridae to include the Late Cretaceous *Mononykus olecranus*

Perle et al., 1993a (see Perle et al. [1993b] for nomenclatural correction), and *Patagonykus puertai* Novas, 1997, from Mongolia and Patagonia, respectively, and Chiappe et al. (1998) added the Mongolian Late Cretaceous *Shuvuuia deserti* Chiappe et al., 1998, and *Parvicursor remotus* Karkhu and Rautian, 1996. Chiappe et al. (1998) also recognized a clade of Asian taxa nested within Alvarezsauridae (i.e., *Mononykus olecranus*, *Shuvuuia deserti*, and *Parvicursor remotus*), which they named Mononykinae.

Since *Mononykus olecranus* was first identified as a bird (Perle et al., 1993a), slightly more derived than the Late Jurassic *Archaeopteryx lithographica* Meyer, 1861, the phylogenetic placement of Alvarezsauridae has become one of the most controversial issues within theropod systematics. Although early dissenters (e.g., Wellnhofer, 1994; Zhou, 1995; Feduccia and Martin, 1996) did not frame their objections to this hypothesis in a cladistic context (see discussion in Chiappe et al. [1995, 1996, 1997]), recent phylogenetic analyses have raised similar questions (Serenó, 1997, 1999, 2001;

1. Hayashibara Museum of Natural Sciences, 2-3, Shimoishii-1, Okayama 700-0907, Japan.

2. Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA (correspondence).

3. Division of Vertebrate Zoology (Ornithology), American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA.

4. Mongolian Paleontological Center, Mongolian Academy of Sciences, Enkh Taivan Street-63, Ulaanbaatar-21035, Mongolia.

Chiappe, 2001; Norell et al., 2001; Chiappe et al., 2002; Novas and Pol, 2002). However, while these studies have not reached consensus regarding the placement of alvarezsaurids within the nonavian portion of the theropod tree, other hypotheses remain supportive of an avian relationship (e.g., Forster et al., 1998; Holtz, 1998, 2001).

In this paper, we report on a new specimen (MPD 100/120; Fig. 1) of the alvarezsaurid *Shuvuuia deserti*, discovered by an expedition of the Hayashibara Museum of Natural Sciences–Mongolian Paleontological Center in the Late Cretaceous sandstones of Tögrögiin Shiree (our usage of Mongolian names follows the transliteration of Benton et al., 2000) (Fig. 2) in the Mongolian Gobi Desert (Suzuki et al., 2000). MPD 100/120 comprises the articulated skeleton of an immature individual, with most skeletal elements preserved. Previous osteological evidence about *Shuvuuia deserti* was based on several partial skeletons collected from Ukhaa Tolgod and Tögrögiin Shiree in the collections of the Mongolian Paleontological Center (formerly, Mongolian Geological Institute, Ulaanbaatar). MPD 100/120 adds important anatomical information in a number of areas of the skeleton missing from all other specimens, in particular in the skull, tail, hand, and foot. We present this additional information and discuss the phylogenetic relationships of Alvarezsauridae.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York; MGI, Mongolian Geological Institute, Ulaanbaatar; MPD, Mongolian Paleontological Center, Ulaanbaatar; MUCPv, Museo de Geología, Neuquén; PVPH, Museo Carmen Funes, Plaza Huincul; USNM, National Museum of Natural History, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881

Alvarezsauridae Bonaparte, 1991

Mononykinae Chiappe et al., 1998

Shuvuuia deserti Chiappe et al., 1998

Figures 1, 3–9

DIAGNOSIS. Autapomorphic characters of *Shuvuuia deserti* include an articulation between the quadrate and postorbital, elongated basipterygoid processes, hypertrophied prefrontal/ectethmoid, and the presence of a sharp ridge on the medial margin of the distal tibiotarsus (Chiappe et al., 1998). This taxon is differentiated from the closely related mononykine *Mononykus olecranus* because it has less compressed cervical centra that bear large pneumatic foramina, a humeral head that is continuous with the deltopectoral crest, a pubis of subcircular section, femoral and tibiotarsal shafts that are bowed lateromedially, and a medial margin of the ascending process of the astragalus that is less excavated (Chiappe et al., 1998). The pes of

Shuvuuia deserti also has a much longer proximal phalanx of the hallux than that of *Mononykus olecranus*, an intermediate phalanx of digit II subequal in length to its ungual phalanx (instead of much shorter as in *Mononykus olecranus*), and longer and more slender intermediate phalanges of digit IV. *Shuvuuia deserti* is differentiated from the poorly known mononykine *Parvicursor remotus* because pedal digit IV in *Shuvuuia deserti* is longer than half the length of metatarsal IV (in *Parvicursor remotus*, digit IV is less than half of metatarsal IV) and this digit is shorter than digit II (without counting ungual phalanges). *Shuvuuia deserti* also lacks the ventral keel in the most rostrally located synsacral vertebra and has less coossification between the proximal tarsals and the tibia (Chiappe et al., 1998).

HOLOTYPE. MGI 100/975. Partial skeleton (Chiappe et al., 1998).

PUBLISHED REFERRED MATERIAL. MGI N 100/99, MGI 100/1001, MGI 100/977. Partial skeletons, some of them (MGI 100/1001, MGI 100/977) including nearly complete skulls (Chiappe et al., 1998).

NEWLY REFERRED SPECIMEN. MPD 100/120, a partial skeleton preserving a portion of the skull including nearly complete mandibular rami; most cervical, dorsal, and caudal vertebrae; portions of scapula, coracoid, and ilium; fragments of forelimb elements and a complete manus; distal ends of femora; and most of the remaining hindlimb bones (Fig. 1).

LOCALITY AND HORIZON. Tögrögiin Shiree (MPD 100/120, MGI 100/99) and Ukhaa Tolgod (MGI 100/975, MGI 100/977), South Gobi Aimak, Mongolia (Fig. 2). Djadokhta Formation (Late Cretaceous, Campanian) (Jerzykiewicz and Russell, 1991; Gao and Norell, 2000).

ANATOMICAL DESCRIPTION

Skull. The cranium and mandible of MPD 100/120 are exposed in ventrolateral view. The incomplete skull agrees in its preserved morphology with the described specimens of *Shuvuuia deserti* (Chiappe et al., 2002). Noteworthy among the already described features of the palate of this alvarezsaurid (Chiappe et al., 2002) is the presence of an extensive secondary palate formed by medial projections of the maxillae. MPD 100/120 demonstrates that the bone identified by Sereno (2001:fig. 10) as the rostral portion of the palatine of MGI 100/977 (visible through the antorbital fenestra) is part of this maxillary secondary palate, as described by Chiappe et al. (1998). Although the sutures between palatine and maxillary are not visible in MPD 100/120, the expected contact of these bones defines the rostral end of a lateral opening that is caudally bordered by a forked, dorsolateral flange of the palatine (Fig. 3). The precise homology of this opening remains unclear.

The mandible of MPD 100/120 also contributes

to our knowledge of the cranial anatomy of *Shuvuuia deserti*. The new specimen shows that the rostral ends of the two mandibular rami were not fused to one another in a coossified symphysis but contacted along a straight suture (Fig. 3). It also shows that the mandibular symphysis of *Shuvuuia deserti* was abbreviated, extending for less than 7% of the estimated length of the lower jaw.

Tail. The alvarezsaurid tail is poorly known. Although large portions of the tail are known for *Alvarezsaurus calvoi* Bonaparte, 1991, and *Shuvuuia deserti* (Chiappe et al., 2002), no more than 13 and 20 vertebrae, respectively, are preserved for these taxa. Previously discovered specimens of *Shuvuuia deserti* provided data on the proximal and middle portions of the mononykine tail, but absence of specimens preserving the distal portion of the caudal series led to underestimation of the tail length and vertebral count, which Chiappe et al. (1996) estimated to be some 25 or 26 elements. In MPD 100/120, the tail is nearly complete and provides a much better estimate of the number of caudal vertebrae. Although a definitive vertebral count cannot be obtained because of the incomplete preservation of the very distal and proximal portions, some 35 caudal vertebrae appear to fit the preserved segment of the tail. However, additional remnants distal to this series suggest that the true number was even higher.

The most informative portion of the tail of MPD 100/120 is the distal half (Fig. 4), where the vertebrae are exposed in both dorsal and left lateral views. In this section, the length of each vertebra, roughly three times its height, continually decreases toward the distal end of the tail (Fig. 4). This shortening is gradual; the lengths of the vertebrae decrease only 20% over a span of 12 elements. The sides of the vertebrae are parallel in dorsal view. No spinous processes are present; instead there is only a small ridge on the center of the dorsal surface of each vertebra (Fig. 4). Distal to this ridge, a subtriangular surface fans out. The distal apices of this surface form the postzygapophyses and their lateral borders define a shallow, central furrow. Like the postzygapophyses, the prezygapophyses are short in contrast to the long caudal prezygapophyses typical for nonavian theropods. The vertebral canal of the distal caudals is small. Its rostral margin is offset from the cranial end of the mid and distal vertebrae. However, the rostral margin of the vertebral canal shifts forward (becoming closer to the cranial edges of the vertebrae) toward the distal tip of the tail. The vertebral canal disappears at least 10 elements before the end of the tail. In lateral view, the ventral margin of the centrum has a slightly concave outline. A shallow groove runs longitudinally along the mid-height of the lateral surface; this groove becomes shallower toward the distal end of the tail. A few distal chevrons are articulated with their corresponding vertebrae (Figs. 1, 4). They have the inverted T-shape described for the

middle portions of the tail of *Shuvuuia deserti* (Chiappe et al., 2002).

Manus. The mononykine hand is characterized by the presence of a stout carpometacarpus with an hypertrophied first digit (Perle et al., 1994), a condition shared by *Patagonykus puertai* Novas, 1997, and perhaps all other alvarezsaurids. Although Perle et al. (1993a) emphasized the preeminence of the first digit when naming *Mononykus* (“single-clawed”) *olecranus*, they also pointed out minute distal articulations of metacarpals II and III as indicators of the existence, albeit highly reduced, of corresponding digits (see also Perle et al., 1994). The existence of these small digits was further supported by the discovery, years later, of a small intermediate phalanx lying close to the carpometacarpus of a specimen of *Shuvuuia deserti* (i.e., MGI 100/975) from Ukhaa Tolgod (Chiappe et al., 2002). MPD 100/120 is the only known alvarezsaurid to preserve a complete set of manual digits (Figs. 5, 6). These digits are complete and articulated in the right hand, confirming the presence of digits II and III in the mononykine hand. As predicted by the size of the distal articulations of the carpometacarpus (Perle et al., 1994; Chiappe et al., 2002), these digits are much smaller than digit I (Fig. 6). Digit II bears three phalanges, the typical number of the theropod hand. The proximal phalanx is more robust and somewhat longer than the intermediate phalanx. Even so, these two phalanges are relatively short, with lengths that are slightly more than twice their minimum widths (see Table 1). The intermediate phalanx of digit II shows a well-developed ginglymus on its distal end. The claw of this digit is nearly identical to the claw of digit III (Fig. 6). These claws gradually taper toward the tip. Their dorsal margins are only slightly convex and both claws are almost straight. Their lateral surfaces are excavated by deep grooves that are deeper proximally. The remaining phalanges of digit III are poorly preserved. Although it is clear that this digit has at least two phalanges in addition to its claw, the existence of a fourth phalanx (as typical of theropods) is unclear.

Pes. The general morphology of the pes of MPD 100/120 is similar to that described for *Mononykus olecranus* (Perle et al., 1994). Nonetheless, the preservation of a complete hallux, only slightly offset from its natural articulation (Fig. 7), allows us to add some additional points to existing descriptions. Metatarsal I of MPD 100/120 is short, proximally tapering, and laterally compressed (Fig. 8). Its shaft is slightly curved, resulting in a moderate concavity of its medial surface. The caudal surface slants laterally, and the medio-caudal margin is caudally projected (Fig. 8). The distal articulation is not ginglymous; instead it is a rounded, caudocranially extended facet. The surface medial to the distal articulation is excavated by a round fossa, presumably for the insertion of collateral ligaments. MPD 100/120 differs from *Mononykus olecranus* in the relative length of the proximal phalanx of the hallux,

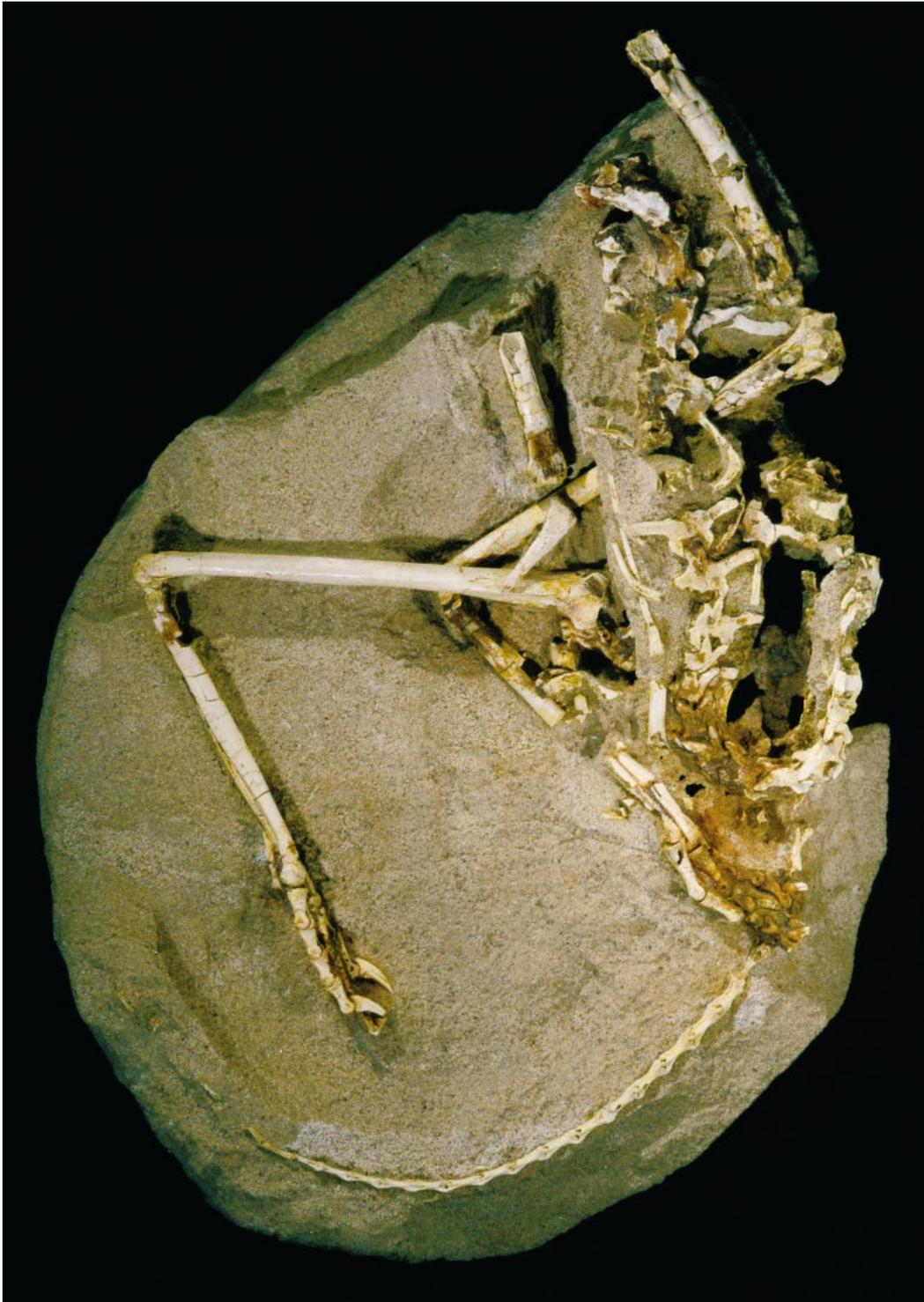


Figure 1 Photograph and interpretive drawing of MPD 100/120 after removal of articulated right manus (see Fig. 5). Abbreviations: cv, caudal vertebrae; cve, cervical vertebrae; fem (l), left femur; fem (r), right femur; fib (r), right fibula; ili, ilium; mtt (l), left metatarsus; mtt(r), right metatarsus; ph2I, phalanx 2 of manual digit I; r, thoracic rib; sc, scapula; sk, skull; tib (l), left tibia; tib (r), right tibia; tv, thoracic vertebrae; I-IV, pedal digits I-IV

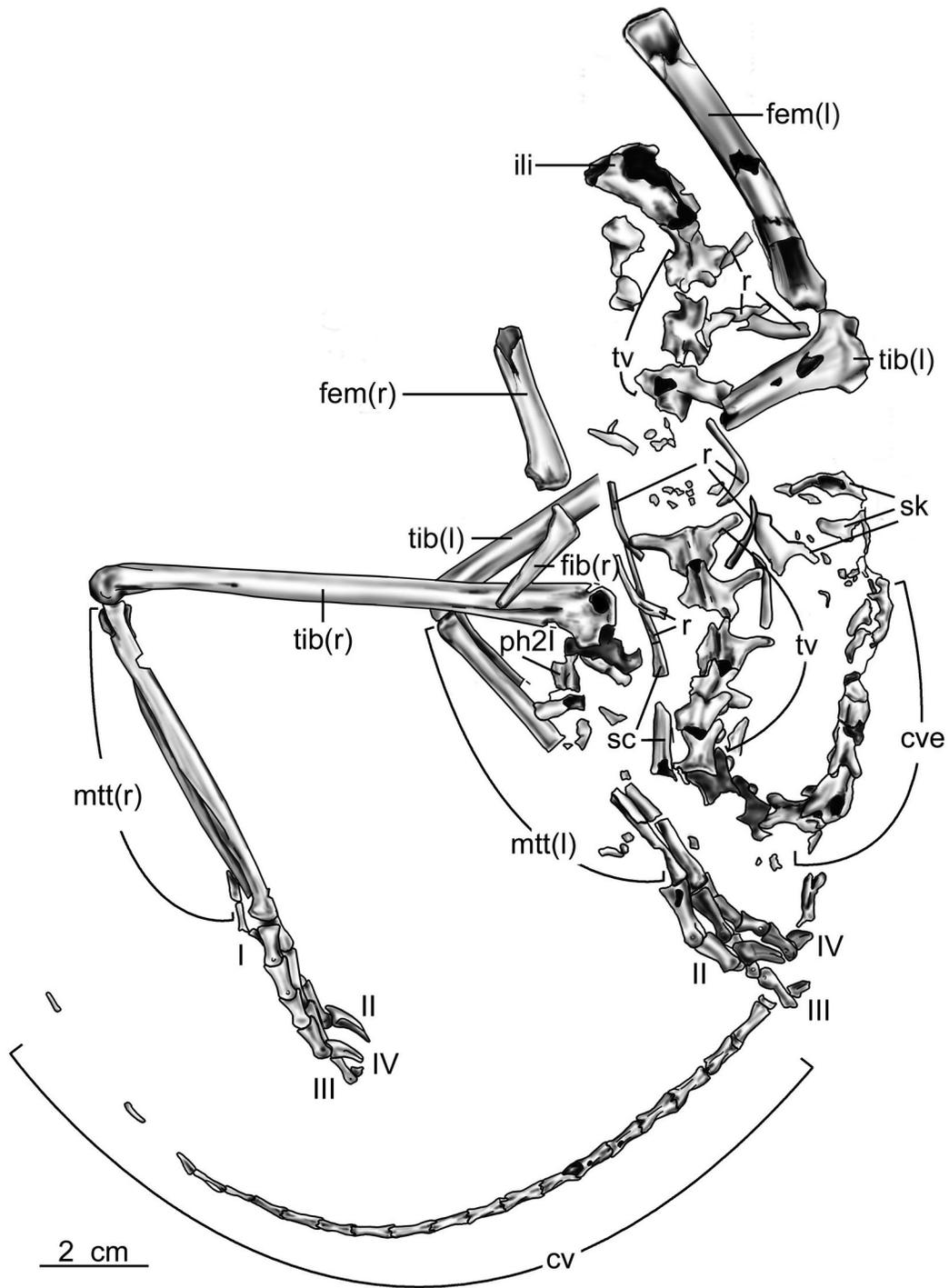


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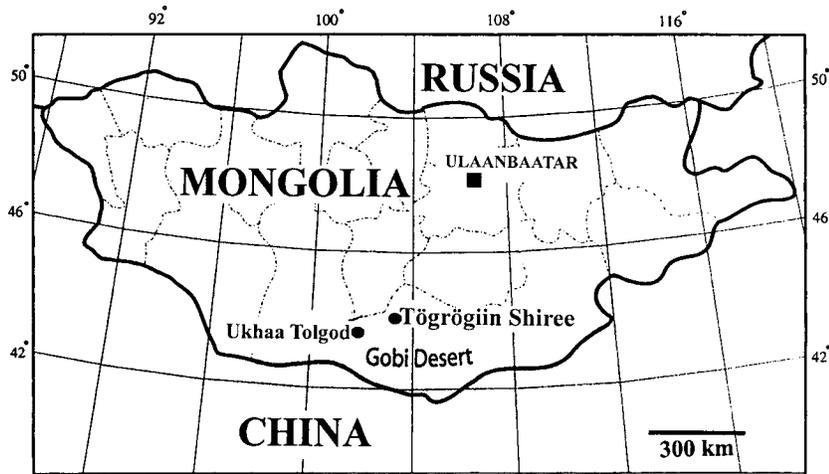


Figure 2 Map indicating Tögrögiin Shiree, the locality where MPD 100/120 was found

and has a much longer shaft than in the latter species (Fig. 8). MPD 100/120 also differs from *Mononykus olecranus* by having an intermediate phalanx of digit II subequal in length to the ungual phalanx; in *Mononykus olecranus* the intermediate phalanx of this digit is much shorter than its claw (Perle et al., 1994). An additional difference be-

tween the pedal morphology of *Shuvuuia deserti* and *Mononykus olecranus* is expressed in the relative robustness of digit IV. In MPD 100/120 and other specimens of *Shuvuuia deserti*, the intermediate phalanges of this digit are longer and more slender than the corresponding phalanges in *Mononykus olecranus*. Detection of these differences in

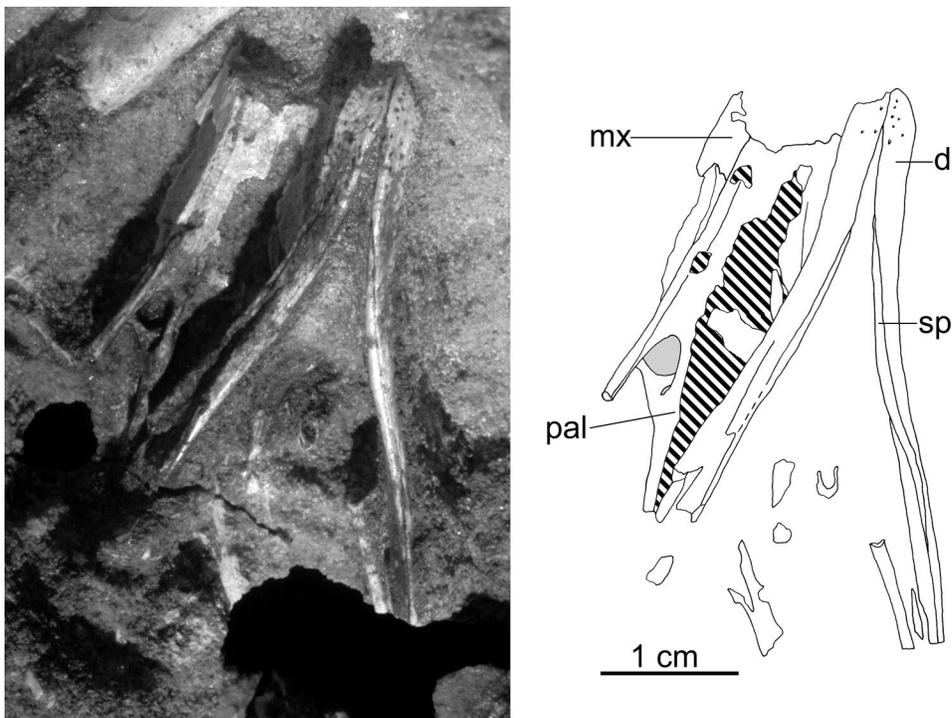


Figure 3 Photograph and interpretative drawing of the skull and mandible of MPD 100/120. Abbreviations: d, dentary; mx, maxilla; pal, palatine; sp, splenial

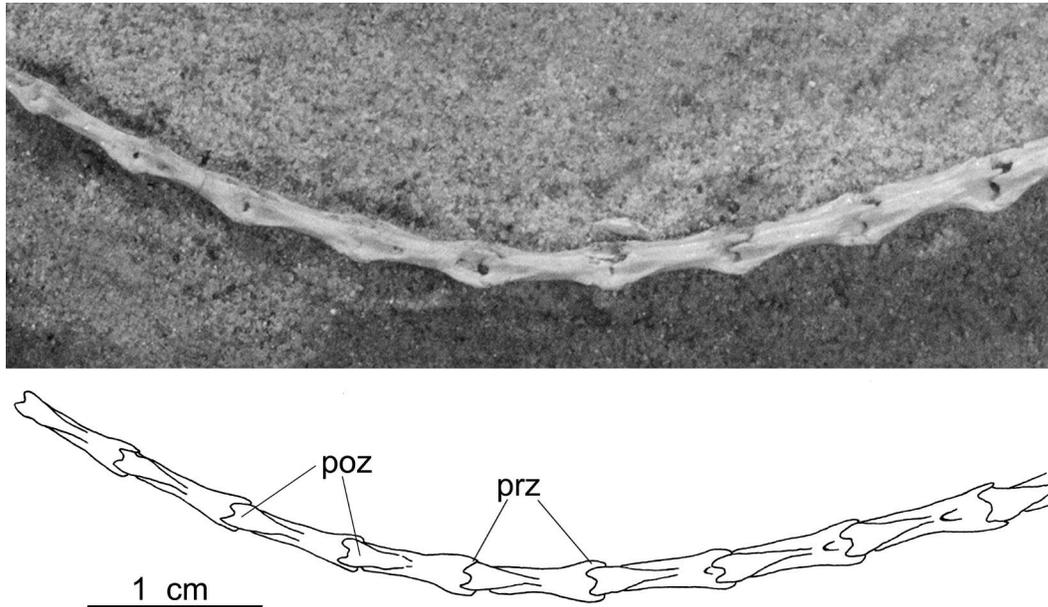


Figure 4 Photograph and interpretive drawing of distal caudal vertebrae. Abbreviations: poz, postzygapophyses; prz, prezygapophyses

MPD 100/120 and other specimens of *Shuvuuia deserti* strengthen the taxonomic discrimination provided by Chiappe et al. (1998) between this alvarezsaurid and *Mononykus olecranus*.

TAXONOMIC IDENTIFICATION OF MPD 100/120

Several synapomorphies of mononykines (Chiappe et al., 2002) are present in MPD 100/120: medial border of tibiotarsus strongly projected proximally, greatly reduced fibula not reaching the proximal tarsals, and reduced proximal end of metatarsal III (i.e., arctometatarsalian pes of Holtz, 1994a). MPD 100/120 also shows derived characters that have been proposed to group *Alvarezsaurus calvoi* and *Patagonykus puertai* with mononykines (Novas, 1996, 1997; Chiappe et al., 2002): laterally compressed synsacral vertebrae, hypertrophied and strongly depressed metacarpal I, and robust digit I with a claw bearing two proximoventral foramina or notches. Thus, several derived characters identify MPD 100/120 as a mononykine alvarezsaurid. Within mononykines, MPD 100/120 shares several derived characters with the holotype and referred specimens of *Shuvuuia deserti*: laterally compressed cervical centra with large pneumatic foramina, lateromedially bowed tibiotarsal shaft, less excavated medial margin of the ascending process of the astragalus, and presence of a crest on the mediocranial edge of the distal end of the tibia. Furthermore, MPD 100/120 is indistinguishable from the holotype and referred specimens of *Shuvuuia deserti*

with respect to all overlapping elements. Although Chiappe et al. (1998) regarded the lesser degree of coossification of the tibiotarsus and carpometacarpus of *Shuvuuia deserti* as derived with respect to other mononykines, the poor degree of coossification of these compound bones in MPD 100/120 may also be due to immaturity. Based on comparative measurements of the metatarsals, MPD 100/120 is approximately 60% of the size of the holotype of *Shuvuuia deserti* (MGI 100/975).

PHYLOGENETIC POSITION OF ALVAREZSAURIDAE

The phylogenetic position of Alvarezsauridae has raised a great deal of controversy in recent years. This has stemmed from the fact that in their initial description of *Mononykus olecranus*, Perle et al. (1993a) placed this bizarre animal closer to neornithine birds than to *Archaeopteryx lithographica*. Early criticisms of this hypothesis were based on noncladistic considerations (Martin and Rinaldi, 1994; Wellnhofer, 1994; Zhou, 1995; see Chiappe et al., 1995, 1996, 1997, for discussion). These disagreements emphasized the overall nonavian appearance of *Mononykus olecranus* and in most cases failed to propose alternative hypotheses of relationships. Over the years, however, a number of independent cladistic analyses (e.g., Chatterjee, 1995; Chiappe et al., 1996, 1998; Forster et al., 1996, 1998; Novas, 1996; Holtz, 1998, 2001; Ji et al., 1998; Chiappe, 2001, 2002) have continued to advocate for a close relationship between alvarez-

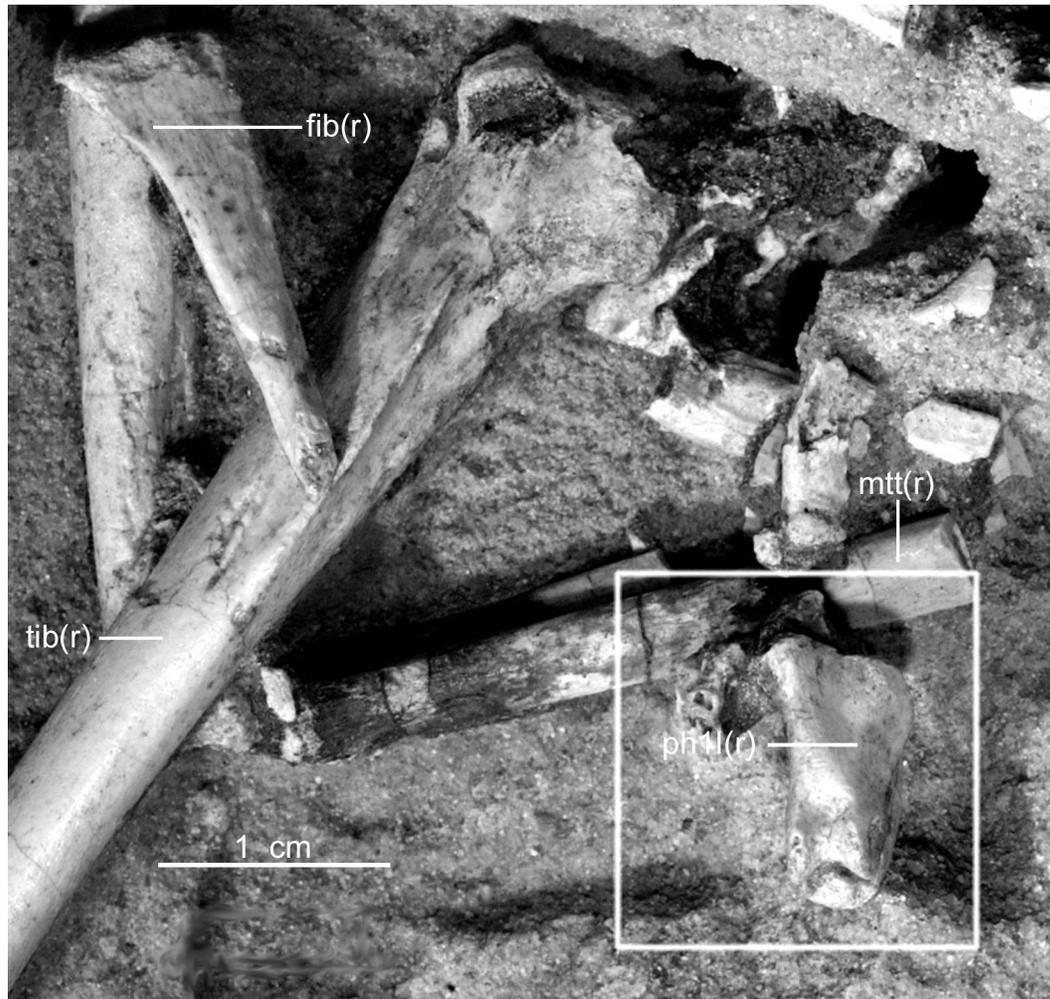


Figure 5 Location of right manus of MPD 100/120 before its removal for preparation. Abbreviations: fib(r), right fibula; phII(r), right proximal phalanx of manual digit I; tib(r), right tibia; mtt(r), right metatarsus

saurids and birds, either by placing alvarezsaurids closer to Neornithes than to *Archaeopteryx lithographica* or as the sister-group of Aves (Fig. 10). A radical departure from this nearly consensual view was presented by Sereno (1997, 1999, 2001), who placed alvarezsaurids as the sister-group of ornithomimids (Fig. 10), nonavian theropod dinosaurs typically regarded as far removed from the origin of birds (Gauthier, 1986; Holtz, 1994b, 1998, 2001; Currie and Padian, 1997; Sereno, 1999). A reanalysis of all characters and taxa used in the many cladistic analyses of alvarezsaurid relationships to other theropod taxa is beyond the scope of this paper. However, given the departure of Sereno's (1999, 2001) cladistic hypothesis from all others and the fact that MPD 100/120 provides new information on anatomical portions crucial to this hypothesis (i.e., skull, hand, and tail), we provide

a cursory examination of his data, which are available on the Internet (Sereno, 1999).

THE ORNITHOMIMOID HYPOTHESIS: A DISCUSSION OF THE EVIDENCE

Sereno's (1999, 2001) hypothesis of alvarezsaurid-ornithomimid relationships is based on the presence of 19 putative synapomorphies of Ornithomimoidae (the postulated clade encompassing these two groups) (Table 2). In this section, we comment on the distribution and validity of 15 of the 19 characters hypothesized to be shared between alvarezsaurids and ornithomimids, while finding no objections to the synapomorphic nature of the remaining four characters. Two basic facts about Sereno's (1999) cladistic analysis should be highlighted—Sereno (2001) summarized the results from the

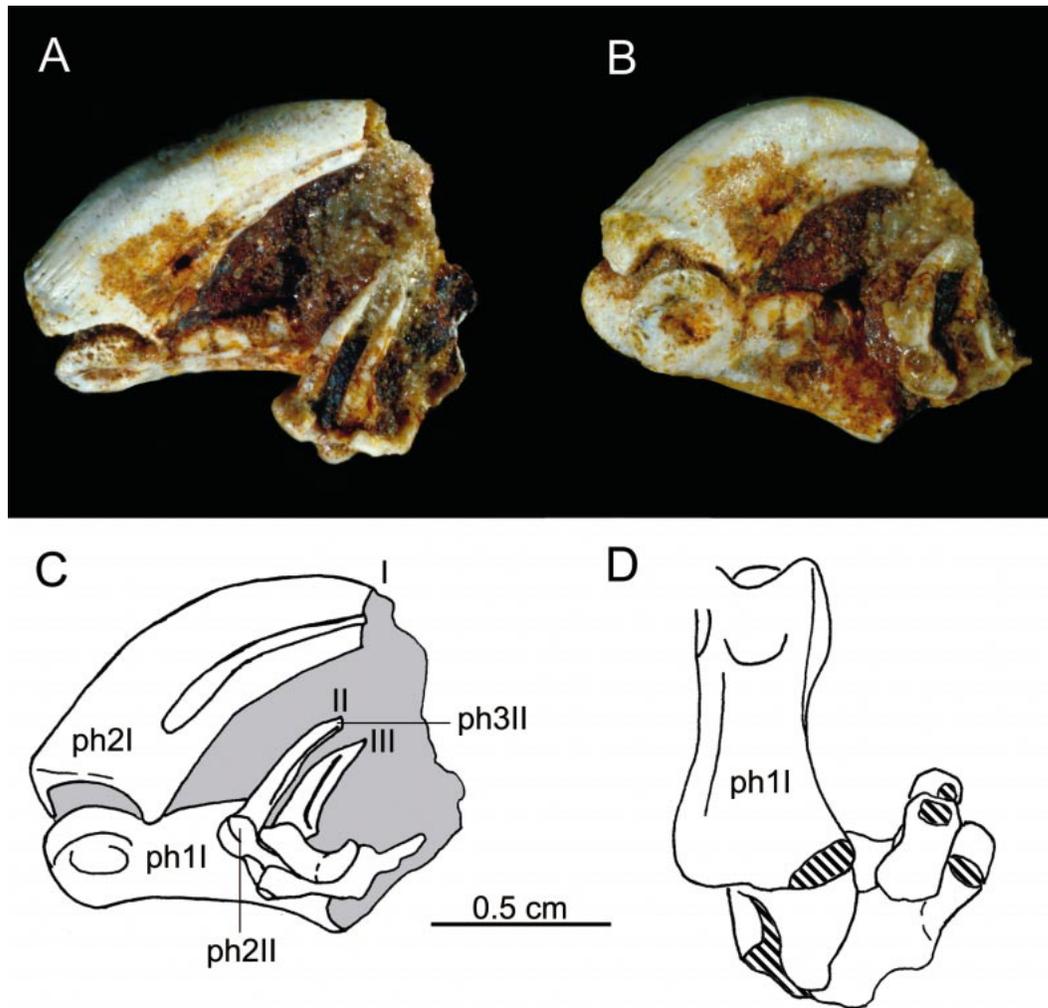


Figure 6 Detail of the right manus of MPD 100/120 in proximalateral (A), lateral (B, C), and dorsal (D) views. Abbreviations: ph1I, proximal phalanx of digit I; ph2I, second phalanx (claw) of digit I; ph2II, second phalanx of digit II; ph3II, third phalanx (claw) of digit II; I-III, digits I-III

1999 cladistic analysis. First, because this data set included both Alvarezsauridae and Ornithomimidae as terminal taxa, it is not explicit whether codings were based on basal taxa of each group—most likely representing character-states of these groups' common ancestors—or not. However, in the case of Alvarezsauridae, it is evident that much of the coding was not based on the most basal taxa *Alvarezsaurus calvoi* and *Patagonykus puertai* but on the more derived mononykine *Shuvuuia deserti* (Chiappe et al., 1998), the only alvarezsaurid for which Sereno's eight skull characters are observable (Table 3). The second important caveat of Sereno's (1999) cladistic analysis is his reliance on scoring Aves as a terminal taxon, thus disregarding *a priori* any hypothesis for the avian relationships of alvarezsaurids—the relationship that has been more

prominently featured by other cladistic analyses—instead of testing it with additional data.

1. Internarial process of the premaxilla dorsoventrally flattened (as opposed to transversely flattened; character 138, Sereno [1999]). Sereno's (1999) coding of this character indicates that the internarial bar is wider than it is tall (i.e., dorsoventrally flattened) in cross-section in both alvarezsaurids and ornithomimids. While this is certainly the case in *Shuvuuia deserti* (the only alvarezsaurid taxon for which skulls are known) and some ornithomimids (e.g., *Struthiomimus altus* Lambe, 1902; AMNH 5339), a derived state for this character is also seen in troodontids (e.g., *Byronosaurus jaffei* Norell et al., 2000, and *Saurornithoides mongoliensis* Osborn, 1924) (*contra* Sereno [1999]). Although some (e.g., Holtz, 1994b) have regarded

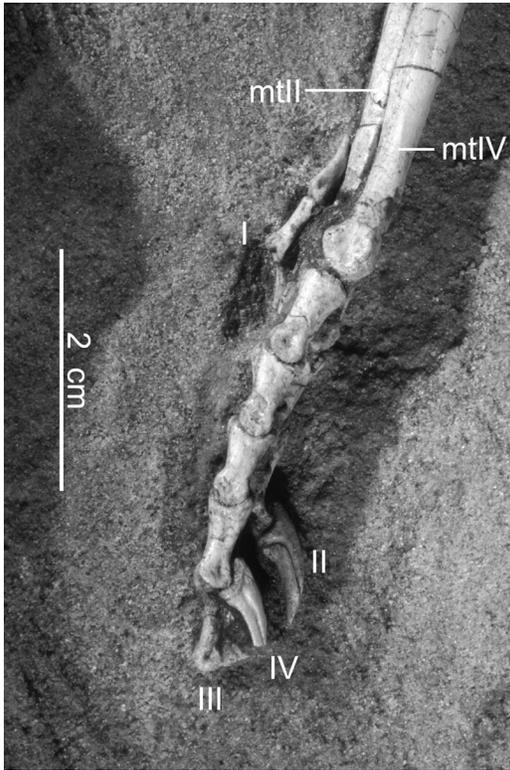


Figure 7 Right pes of MPD 100/120. Abbreviations: I-IV, digits I-IV; mtII, metatarsal II; mt IV, metatarsal IV

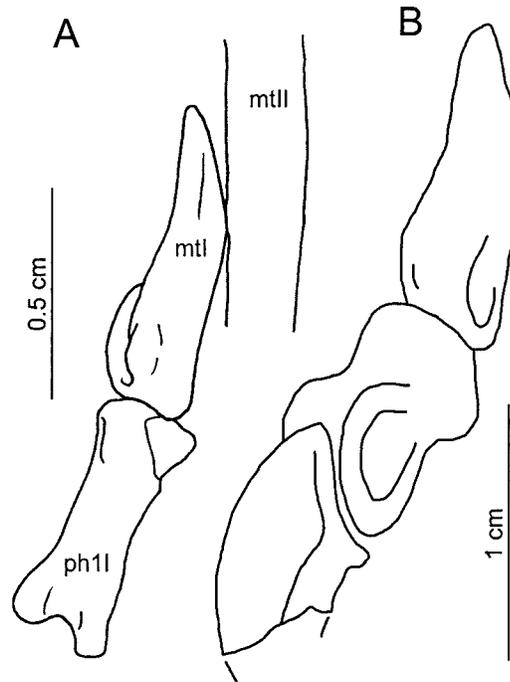


Figure 8 Pedal digit I of MPD 100/120 (A) in medioplantar view, as compared to pedal digit I of *Mononykus olecranus* in dorsolateral view (B; modified from Perle et al. [1994]). Note the proportionally shorter proximal phalanx of *Mononykus olecranus*. Abbreviations: mtI, metatarsal I; mtII, metatarsal II; ph1I, phalanx 1 of digit I

troodontids as closely related to ornithomimids, others (e.g., Forster et al., 1998) have considered them to be much more closely allied to birds (indeed, Holtz [1998] found both alternatives to be equally parsimonious). Thus, if the dorsoventrally flattened internarial bar is not a unique condition of alvarezsaurids and ornithomimids, as is shown by its presence in troodontids, the proposed homology of Sereno is weakened. After all, this condition could be considered equally synapomorphic of a troodontid–alvarezsaurid clade and troodontids could well be closely related to birds (Forster et al., 1998; Holtz, 1998). Further, the extent of this character within ornithomimids and alvarezsaurids cannot be precisely determined because the majority of described ornithomimid skulls are crushed (Barsbold and Osmólska, 1990) and skulls of basal alvarezsaurids are unknown.

2. Prefrontal exposed on the dorsal skull roof more than the lacrimal (as opposed to less exposed than the lacrimal; character 139, Sereno [1999]). The area immediately rostral to the orbit is well preserved in two skulls of *Shuvuuia deserti* (i.e., MGI 100/977 and MGI 100/1001). This region is characterized by the existence of a large ossification, broadly exposed on the dorsal surface of the snout (Chiappe et al., 1998). This large ossification

sends a ventromedial flange that forms the rostral wall of the orbit and contacts its counterpart in the midline, leaving a gap between the dorsal margin of these processes and the ventral surface of the frontals (Chiappe et al., 1998, 2002). As discussed by Chiappe et al. (1998, 2002), the homology of this element is controversial. Although Sereno (1999, 2001) has interpreted it as a prefrontal, Chiappe et al. (1998) argued that it could correspond to the avian ectethmoid (as opposed to the “composite” prefrontal–ectethmoid cited by Sereno [2001]), thus casting doubt on Sereno’s character. Even if one were to assume that this bone is a prefrontal, its large dorsal exposure, unprecedented within Theropoda, would clearly be autapomorphic for Alvarezsauridae (or of some subclade therein). In ornithomimids, the dorsal exposure of the lacrimal and prefrontal is approximately the same. This subequal exposure is also present in basal tetanurans such as *Acrocanthosaurus atokensis* Stovall and Langston, 1950 (Currie and Carpenter, 2000), *Allosaurus fragilis* Marsh, 1877 (Madsen, 1976), and *Sinraptor dongi* Currie and Zhao, 1993, thus rendering the ornithomimid condition primitive. Consequently, if the large ossification at the base of the snout of *Shuvuuia deserti* was to be interpreted as a uniquely overgrown prefrontal, the

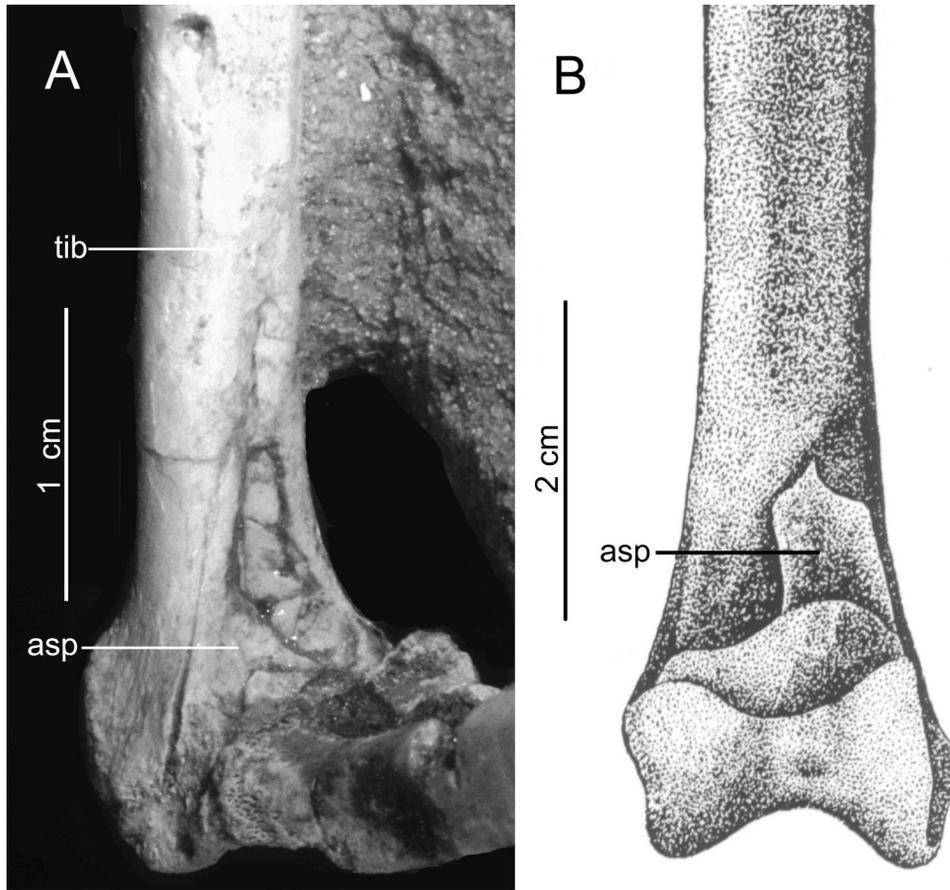


Figure 9 Laterocranial view of right tibia and proximal tarsals of MPD 100/120 (A) as compared to the left ones of *Mononykus olecranus* (B; after Perle et al. [1994]). Note the more prominent medial notch of the ascending process of *Mononykus olecranus*. Abbreviations: asp, ascending process; tib, tibia

retention of the tetanurine subequal dorsal exposure of prefrontals and lacrimals in ornithomimids would render Sereno's character irrelevant for understanding the phylogenetic position of *Shuvuuia deserti*.

3. Presence of a prefrontal orbital flange (character 140, Sereno [1999]). The controversy surrounding the homology of the bone Sereno (1999, 2001) called the prefrontal of alvarezsaurids (only known for *Shuvuuia deserti*) was discussed above. As pointed out in this discussion, this ossification forms the rostral wall of the orbit in *Shuvuuia deserti* (Chiappe et al., 1998). To the best of our knowledge, the prefrontal of ornithomimids (e.g., *Struthiomimus altus*; AMNH 5339) does not bear any significant ventral flange enclosing the orbit rostrally. The proposed primary homology of this character in Alvarezsauridae and Ornithomimidae appears unsubstantiated.

4. Dentary length up to 80% of lower jaw length (character 141, Sereno [1999]). The mandibular rami are incomplete in all specimens of *Shuvuuia*

deserti for which cranial remains are known; MGI 100/1001 and MGI 100/977 lack the rostral portion, and in MPD 100/120 the rami are caudally incomplete (Fig. 3). Although Sereno (1999) claimed the length of the alvarezsaurid dentary to be greater than 80% of the length of the mandible, our estimates of *Shuvuuia deserti*'s dentary do not exceed 77%. While dentary lengths in ornithomimids range between 70 and 80% of the mandible (Horum, 2001), the value for the basal *Garudimimus brevipes* Barsbold, 1981, is only 70%. Further, this and some other values for ornithomimid dentaries (e.g., *Gallimimus bullatus* Osmólska et al., 1972, and *Ornithomimus edmontonensis* Sternberg, 1933) (Horum, 2001) fall within the upper range of dentary lengths seen in other tetanurans. *Acrocantiosaurus atokensis* (Currie and Carpenter, 2000), *Simraptor dongi* (Currie and Zhao, 1993), *Caenagnathus collinsi* Sternberg, 1940 (Currie et al., 1993), *Allosaurus fragilis* (Madsen, 1976), *Deinonychus antirrhopus* Ostrom, 1969 (Ostrom, 1969b), *Dromaeosaurus albertensis* Matthew and

Table 1. Selected measurements of MPD 100/120 (right elements in mm).

Madibular ramus: maximum preserved length	37.3
Dentary symphysis: maximum length	3.4
Tibiotarsus: maximum length	97.7
Tibiotarsus midshaft: craniocaudal width	5.4
Tibiotarsus proximal end: craniocaudal width	12.9
Tibiotarsus lateral condyle: craniocaudal width	7.1
Tarsometatarsus: maximum length	81.2
Metatarsal I: maximum length	7.0
Metatarsal II: maximum length	67.9
Metatarsal III: maximum length	24.3
Metatarsal IV: maximum length	68.7
Digit I: maximum length	11.4
Digit II: maximum length	31.6
Digit IV: maximum length	35.2
Phalanx 1, manual digit II: maximum length	3.2
Phalanx 1, manual digit II: midshaft width	1.4
Phalanx 2, manual digit II: maximum length	2.9
Phalanx 2, manual digit II: midshaft width	1.2
Phalanx 3, manual digit II: maximum length	5.0
Claw, manual digit III: maximum length	5.0
Penultimate phalanx, manual digit III: maximum length	2.2
Estimated tail length	358.0

Brown, 1922 (Colbert and Russell, 1969), *Daspletosaurus torosus* Russell, 1970 (Carr, 1999), *Alber-tosaurus libratus* Lambe, 1914 (Carr, 1999), and *Tyrannosaurus rex* Osborn, 1905 (Carr, 1999), all had dentary lengths between 52 and 72% of the length of the mandible. Hence, the absence of two distinct states for this character makes its scoring problematic and undermines the strength of Sereno's purported synapomorphy.

5. **Maxillary and dentary teeth implanted in a groove (as opposed to in separate alveoli; character 142, Sereno [1999]).** Although dentary teeth are definitively implanted on a groove in *Shuvuuia deserti* (Chiappe et al., 1998), the implantation of maxillary teeth is not as clear in the only specimen preserving maxillary teeth (MGI 100/977). Of the described ornithomimid taxa, only *Pelecanimimus polyodon* Pérez-Moreno et al., 1994, has both maxillary and dentary teeth, which are indeed set in a groove (J. Sanz, pers. comm.). All of the other known ornithomimid taxa either have edentulous jaws (e.g., *Struthiomimus altus*, *Gallimimus bullatus*, and *Garudimimus brevipes* Barsbold, 1981; see Barsbold and Osmólska [1990]), or are simply not well enough preserved for this character-state to be coded (e.g., *Harpymimus okladnikovi* Barsbold and Perle, 1984). Further, although Sereno (2001) argued that this condition is unique to alvarezsaurids and ornithomimids, groove-like implantation of the maxillary and dentary teeth is also seen in troodontids (e.g., *Byronosaurus jaffei*) and hesperornithiform birds (Marsh, 1880).

6. **Teeth along maxillary and dentary rows uni-**

form in size (as opposed to larger anteriorly; character 144, Sereno [1999]). Maxillary and dentary teeth of uniform size along the tooth rows are seen in *Shuvuuia deserti* specimens MGI 100/1001 and MGI 100/977. This condition is also present in a variety of basal birds (e.g., *Archaeopteryx lithographica* [Wellnhofer, 1974] and Enantiornithes [Sanz et al., 1997; Chiappe and Walker, 2002]). Most important for the present discussion, this condition is not present in ornithomimids. In *Pelecanimimus polyodon*, the only ornithomimid for which this character-state is observable, the maxillary teeth become rostrally smaller (Pérez-Moreno et al., 1994). Thus, Sereno's (1999) proposed homology for this character does not conform to the similarity test required for primary homology statements (de Pinna, 1991).

7. **Chevron height four to five times height of corresponding neural spine (as opposed to approximately twice neural spine height (character 146, Sereno [1999]).** Like in all other theropods, the morphology of the chevrons of alvarezsaurids and ornithomimids varies along the caudal series. Consequently, this character is unclear as defined. We assume that Sereno (1999) is referring to the height of the proximal chevrons. Incomplete caudal vertebrae are known for all alvarezsaurids, but nearly complete proximal chevrons and their corresponding neural spines are only known for *Shuvuuia deserti*. Although the preserved proximal chevrons of this taxon are clearly longer than the heights of the neural spines of its corresponding proximal caudals, the chevrons appear to be only three times longer (MGI 100/99). In ornithomimids, the height of the proximal chevrons is also greater than that of the neural spines; yet our estimates for *Gallimimus bullatus* (Osmólska et al., 1972) and *Struthiomimus altus* (AMNH 5339) indicate that these do not exceed twice the height of the corresponding neural spines. This proportion approaches the condition seen in basal tetanurans (e.g., *Allosaurus fragilis* [Madsen, 1976] and *Compsognathus longipes* Wagner, 1861 [Ostrom, 1978]), in which the proximal neural spines exceed half the length of their corresponding chevrons. Sereno's (1999) character is ambiguous as defined and if interpreted as in this paper, the presence of the primitive tetanurine condition in ornithomimids renders this character irrelevant for understanding the phylogenetic relationships of Alvarezsauridae.

8. **Presence of a marked flexor depression proximal to the distal condyles on the manual proximal phalanges (character 148, Sereno [1999]).** Before the discovery of MPD 100/120, the only digits for which this condition could have been scored in alvarezsaurids is digit I seen in *Patagonykus puertai*, *Mononykus olecranus*, and *Shuvuuia deserti*. This character cannot be scored for digits II and III of MPD 100/120 (Fig. 6) because their ventral surfaces are not exposed (given the uniqueness of the articulated right hand of MPD 100/120, the specimen was not compromised by preparation of its ventral

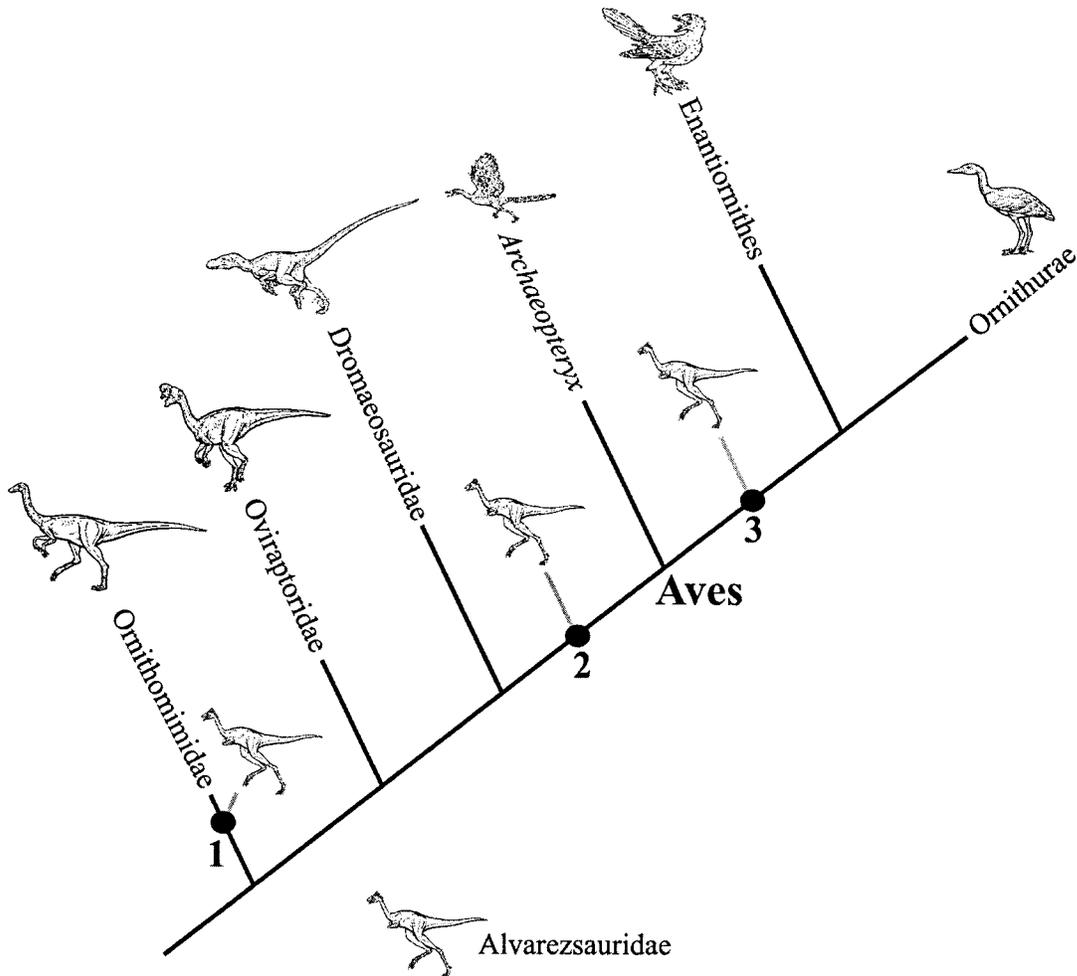


Figure 10 Three main hypotheses of relationships of Alvarezsauridae to other theropod dinosaurs: 1, Alvarezsauridae as the sister-taxon of Ornithomimidae (Serenó, 1999); 2, Alvarezsauridae as the sister-taxon of Aves (Chiappe, 2002); and 3, Alvarezsauridae as the sister-taxon of all birds except for *Archaeopteryx lithographica* (Perle et al., 1993a; Chiappe et al., 1996; Forster et al., 1998; Ji et al., 1998)

surface). Novas (1997) noted a ventral depression proximal to the distal articulation of the proximal phalanx of digit I of *Patagonykus puertai* and referred to this as the flexor ligament pit. A small depression is also present in this area of the proximal phalanx of digit I of both *Shuvuuia deserti* and *Mononykus olecranus* (Chiappe et al., 2002). It is also distinct in ornithomimids, for example *Archaeornithomimus asiaticus* Gilmore, 1933 (AMNH 6576). Although the presence of this flexor depression on the proximal phalanges of digit I of some alvarezsaurids and ornithomimids constitutes a statement of primary homology, presently, Sereno's (1999) character definition must be restricted to digit I.

9. Presence of paired flexor processes of manual proximal phalanges (character 149, Sereno [1999]).

As pointed out in our discussion of the previous character, this condition in Alvarezsauridae can only be assessed for the proximal phalanx of digit I of *Patagonykus puertai*, *Mononykus olecranus*, and *Shuvuuia deserti*. In mononykine alvarezsaurids, the proximoventral borders of this phalanx form distinct ridges delimiting a broad axial furrow (Perle et al., 1994) (Fig. 11). A more prominent ridge is present on the lateral side of the first phalanx of the right digit I of *Patagonykus puertai*; Novas (1997) correctly inferred the presence of a corresponding medial ridge from the development of an axial furrow on the ventral surface of this phalanx. However, the extent of this inferred ridge remains unknown. This specialized condition is quite dissimilar to that present in ornithomimids. As seen in *Struthiomimus altus* (Nicholls and Rus-

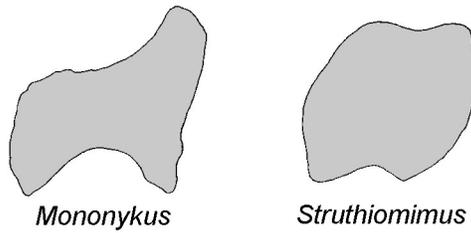


Figure 11 Proximal view of the right proximal phalanx of digit I of *Mononykus olecranus* and *Struthiomimus alatus* (modified from Perle et al. [1994] and Nicholls and Russell [1985], respectively). Figures not to scale

These are transversely narrow and the ventral border of at least the ungual of digit III is relatively round. While the ungual of digit I of the manus of *Mononykus olecranus* and *Shuvuuia deserti* is broad and ventrally flattened, a small fragment corresponding to the ungual phalanx of digit I of *Patagonykus puertai* (Novas, 1997) shows a ventrally convex surface. Sereno's (1999) character cannot be confidently assessed in the poorly preserved ungual of this digit of *Alvarezsaurus calvoi*. Thus, while we see some correspondence between the shapes of the ventral surfaces of the manual unguals in mononykines and ornithomimids, this character should be circumscribed to the ungual of the first digit. It should be further noted that the condition in the most basal alvarezsaurid—*Alvarezsaurus calvoi*—is unclear and that the scant evidence available for *Patagonykus puertai* suggests the presence of the primitive character-state.

12. Flexor tubercles on manual unguals displaced distally (as opposed to proximally; character 152, Sereno [1999]). While the flexor tubercle of the manual unguals of ornithomimids is indeed displaced distally (e.g., *Archaeornithomimus asiaticus*; AMNH 6576), it could be argued that the flexor tubercle is at best weakly developed in alvarezsaurids. Novas (1996) showed how the ventral surface of the ungual phalanx of digit I is flat with poor development of a flexor tubercle in *Alvarezsaurus calvoi*. The only fragment of a manual ungual for *Patagonykus puertai* that corresponds to digit I does not preserve any evidence of a flexor tubercle. Among mononykines, there is a distinct central area in the ventral surface of the unguals of *Mononykus olecranus* and *Shuvuuia deserti* to which the flexor ligaments of digit I presumably attached. However, this area does not resemble the bulbous flexor tubercle seen in all ornithomimids. Flexor tubercles appear to be equally undeveloped in the ungual phalanges of digits II and III of MPD 100/120. The absence of a prominent flexor tubercle in basal alvarezsaurids and the great dissimilarity of the ventral surface of the ungual phalanges of mononykines and ornithomimids renders Sereno's (1999) proposals for this character dubious.

13. Iliac blades deflected toward midline and

having partial contact along their dorsal margin (as opposed to erect and separated; character 153, Sereno [1999]). Although some deflection can be seen between the preserved iliac blades of mononykines (Chiappe et al., 2002), *Gallimimus bullatus* (Osmólska et al., 1972), and *Ornithomimus sedens* Marsh, 1892 (i.e., USNM 4736), this character-state is likely not present in *Alvarezsaurus calvoi*. Before the disarticulation of this specimen, the sagittally straight ilium of the only known specimen (MUCPv-54) was oriented vertically and parallel to the sacrum (Bonaparte, 1991; L.M. Chiappe, pers. obs.), showing no evidence of medial deflection. Further, this condition cannot be determined in the incomplete ilia of *Patagonykus puertai* (Novas, 1997). Although the iliac blades do show some medial deflection in mononykines and at least some ornithomimids, this character-state is either absent or unknown in the most basal Alvarezsauridae. Consequently, the optimization of Sereno's proposed synapomorphy is at best ambiguous.

14. Metacarpal-phalangeal joint with approximately 15° maximum extension (character 18, Sereno [2001]). Functional characters such as this are difficult to interpret because predictions of specific organismal functions based on morphology often have been shown to be unwarranted (Lauder, 1995). Evaluation of this character is even more difficult since Sereno (2001) did not include this condition in a cladistic analysis (the alleged primitive condition also was not specified and the scoring for other taxa was not provided). If one were to assume that the maximum extension of the metacarpal-phalangeal joint (presumably of digit I, although something Sereno [2001] did not specify) of alvarezsaurids and ornithomimids were to be 15°, this condition would have to be equally scored for all birds given the apparent limitations of their metacarpal-phalangeal joint. This functional assumption is supported by the fact that to the best of our knowledge, no basal bird shows any significant extension at this joint—in specimens of *Archaeopteryx*, *Confuciusornis*, and Enantiornithes, the main axes of metacarpal I and of its proximal phalanx are approximately aligned. Thus, even if Sereno's (2001) apomorphic condition were to be accepted, in spite of the intrinsic problems related to functional characters in extinct organisms (Lauder, 1995), there would be no *a priori* reason why to interpret this condition as a synapomorphy of Ornithomimoidea.

15. Metacarpal III midshaft width 75% or more that of metacarpal II (character 20, Sereno [2001]). Like the previous character, Sereno (2001) did not include this apomorphic condition in a cladistic analysis, thus leaving the primitive condition and the distribution of this character among other taxa unspecified. In spite that the midshaft of metacarpal III does approach that of metacarpal II in both mononykines (these metacarpals remain unknown in more basal alvarezsaurids) and ornithomimids, similar ratios are found in *Archaeopteryx* (e.g.,

80% in the Berlin specimen [Wellnhofer, 1974]), Enantiornithes (e.g., Chiappe and Calvo, 1994; Kurochkin, 1996), *Patagopteryx* (Chiappe, 1996), and some other basal birds. Thus, as with the previous character, we see no *a priori* reason why interpretation of this apomorphic condition as a synapomorphy of Ornithomimoidae should take precedence over interpretation of it as a shared apomorphy with (or within) Aves.

CONCLUSIONS

The discovery of MPD 100/120 adds significant data to the known skeletal morphology of the derived alvarezsaurid *Shuvuuia deserti* and strengthens its taxonomic diagnosis. Although the majority of cladistic analyses have placed Alvarezsauridae within, or close to, Aves, Sereno's (1999, 2001) recent hypothesis supporting a sister-group relationship between Alvarezsauridae and Ornithomimidae presents a significant departure from original proposals (Fig. 10). However, our examination of the distributions of the 19 characters used by Sereno (1999, 2001) in support of this hypothesis of alvarezsaurid relationships casts doubt on most of them as valid synapomorphies. Likely, the relationships of alvarezsaurids will continue to be at the center of the debate on theropod systematics (Chiappe and Witmer, 2002). More complete remains of basal alvarezsaurids combined with a better understanding of the major lineages of theropods will provide the basis for a better understanding of the phylogenetic relationships of this spectacular group of dinosaurs. Although in the end, Sereno's (1999, 2001) proposal may be substantiated by further data, existing support for a close relationship between ornithomimids and alvarezsaurids is weak.

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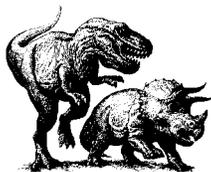
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900 Exposition Boulevard
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