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Therian femora from the Late Cretaceous of Uzbekistan

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Femora referable to metatherians and eutherians recovered from the Bissekty Formation, Dzharakuduk, Kyzylkum Desert, Uzbekistan (90 Mya), are described. Fourteen isolated specimens were sorted based on size and morphology into groups that likely correspond to the species level or higher. Groups were then tentatively assigned to taxa known from teeth, petrosals, and/or other postcrania at these localities. One distal femur of a small arboreal metatherian, and several eutherian distal femora that probably represent zhelestids and/or zalambdalestids were identified. With the exception of one proximal femur that is similar in some aspects to the zalambdalestid *Barunlestes*, and a previously described multituberculate specimen, all other proximal femora from the Bissekty Formation exhibit a metatherian-like morphology. The dental record currently suggests the presence of twelve eutherian species and only one metatherian at Dzharakuduk, whereas the humeral and crurotarsal evidence supports the presence of at least two or four metatherian species, respectively. Given the sample size of the proximal femora, the morphological diversity present, and the overwhelming presence of eutherians at these localities, it is highly unlikely that the overwhelming majority of proximal femora actually represent metatherians. Therefore, this sample may suggest that the metatherian proximal femoral condition is primitive for Theria and that some eutherian taxa (probably including Zhelestidae, which are dentally most abundant at these localities) retain this condition.

Key words: Theria, Metatheria, Eutheria, Zhelestidae, Zalambdalestidae, femur, Cretaceous, Uzbekistan.

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Introduction

Our understanding of the postcranial morphology of Cretaceous therian mammals has improved greatly in recent years with discoveries of fairly complete skeletons, such as those of *Eomaia* (Ji et al. 2002) and *Sinodelphys* (Luo et al. 2003), yet therian fossil skeletons or even three-dimensional preservation of isolated postcranial elements from the Mesozoic remain quite rare. Paleontological fieldwork in the Dzharakuduk area of the central Kyzylkum Desert in Uzbekistan has yielded thousands of Cretaceous mammal fossils, including hundreds of isolated postcranial elements (e.g., Szalay and Sargis 2006; Chester et al. 2010). These specimens were collected from 15 fossil localities in the fluvially deposited Bissekty Formation (90 Mya; late Turonian), and represent one of the oldest eutherian-dominated faunas (Archibald and Averianov 2005). The Bissekty local fauna (l.f.) provides the opportunity to assess the diversity of therian postcranial morphology present in a Late Cretaceous fauna, as well as hypotheses of postcranial character polarity for Theria.

Craniodental and postcranial specimens have been analyzed to assess the taxonomic diversity present in the Bissekty l.f. (Ekdale et al. 2004; Archibald and Averianov 2005; Szalay and Sargis 2006; Chester et al. 2010). The dental record suggests twelve species of eutherians, including five zhelestids, two zalambdalestids, four asioryctitheres, and *Paranyctoides* (Eutheria incertae sedis), and only one species each of Metatheria, Multituberculata, and Symmetrodonta (Archibald and Averianov 2005). Approximately 52% of dental specimens collected from these localities have been attributed to the family Zhelestidae. The taxonomic diversity estimated from petrosal bones recovered from these localities is in accord with estimations based on the dental record. Twenty petrosals have been attributed to zhelestids and zalambdalestids (Ekdale et al.

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2004), and one petrosal has been attributed to the metatherian *Sulestes* (Averianov et al. 2010). Postcranial evidence also suggests that a majority of the taxa in the Bissekty l.f. are eutherians, and that most of these taxa are probably zhelestids, but differs in suggesting the presence of more than one metatherian at Dzharakuduk (Szalay and Sargis 2006; Chester et al. 2010). Szalay and Sargis (2006) analyzed crurotarsal remains from the Bissekty l.f., which support the presence of at least four metatherian species. Chester et al. (2010) evaluated taxonomic diversity using distal humeri, and concluded that at least two metatherians were present at Dzharakuduk.

Here we describe Cretaceous therian femora from the Kyzylkum Desert, Uzbekistan. The femoral sample was used to estimate functional and taxonomic diversity present at Dzharakuduk. This represents an independent test of taxonomic diversity that can be compared to previous estimates based on dental, petrosal, crurotarsal, and humeral remains. Hypotheses have been put forth about the primitive condition of the distal femur for Theria (e.g., Szalay 1994; Muizon 1998; Szalay and Sargis 2001), but little has been stated about the proximal femoral morphology of the ancestral therian. Comparisons to other Late Cretaceous mammalian femora were made, and new insights on the primitive condition of the therian proximal femur are discussed.

Institutional abbreviations.—URBAC, Uzbek-Russian-British-American-Canadian Joint Paleontological Expedition (specimens currently housed at San Diego State University, San Diego, USA); ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Other abbreviations.—FDED, femoral distal end depth or maximum condylar depth; FDEW; femoral distal end width; FHL, femoral head length; FPEW, femoral proximal end width; l.f., local fauna.

Material and methods

Fourteen of thirty-two isolated femoral specimens preserved enough relevant morphology to be assessed in a comparative and functional context. Specimens were measured with digital calipers under an Olympus SZX10 microscope in order to evaluate their relative size. The following four measurements (Table 1) were taken: FPEW: femoral proximal end width (medial edge of femoral head to lateral edge of greater trochanter in anterior view), FHL: femoral head length (proximal edge of femoral head to distal edge in anterior view; measurement 10 from Sargis 2002), FDEW: femoral distal end width (medial edge of medial condyle to lateral edge of lateral condyle in anterior view; measurement 19 from Sargis 2002), and FDED: femoral distal end depth or maximum condylar depth (most posterior edge of condyles to most anterior edge of patellar ridges in distal view; combined measurements 20 and 21 from Sargis 2002). The isolated femora were sorted into groups based on size and overall morphology. These groups likely correspond to species or genera based on previous evaluations of ontogenetic and individual variation in extant mammals (Szalay and Sargis 2001, 2006; Sargis 2002; Salton and Sargis 2009; Chester et al. 2010). Groups were then allocated to taxa known from the dentition, petrosals, and/or other postcrania at these localities. All specimens described here were considered to represent adults, based on complete fusion of the epiphysis to the diaphysis. Descriptions of these specimens concentrated on osteological features that are known to be functionally significant (Fig. 1). All of the femora analyzed are incomplete and none is associated with any other elements. Mid-shaft diameter of isolated proximal and distal femora was not quantified because only a few specimens in the sample preserve this portion of the diaphysis. Comparisons were made to more complete fossils and extant therian mammals.

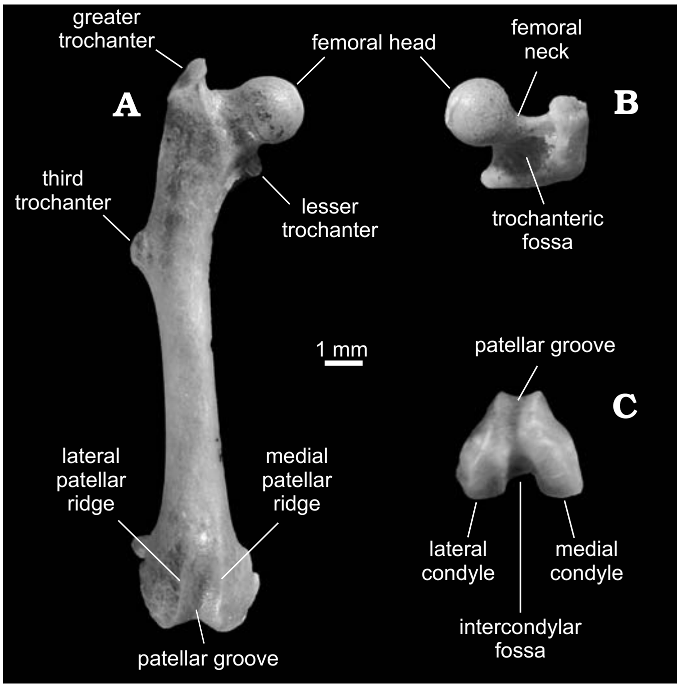

Fig. 1. Right femur of extant tenrec *Microgale cowani* Thomas, 1882, in anterior (**A**), proximal (**B**), and distal (**C**) views, to illustrate femoral features discussed in text (modified from Salton and Sargis 2009).

Descriptions

Metatherian distal femur

The metatherian distal femur (Fig. 2; URBAC 03-096) represents the smallest taxon in the sample (Table 1). It appears to represent an individual similar in size to that represented by an unassociated metatherian distal humerus with features related to climbing, possibly indicative of arboreality (see Chester et al. 2010: fig. 3A). The femur lacks a distinct patellar groove, which indicates the lack of a patella in the quadriceps femoris tendon. A very slight groove is present, representing the placement of the quadriceps femoris tendon

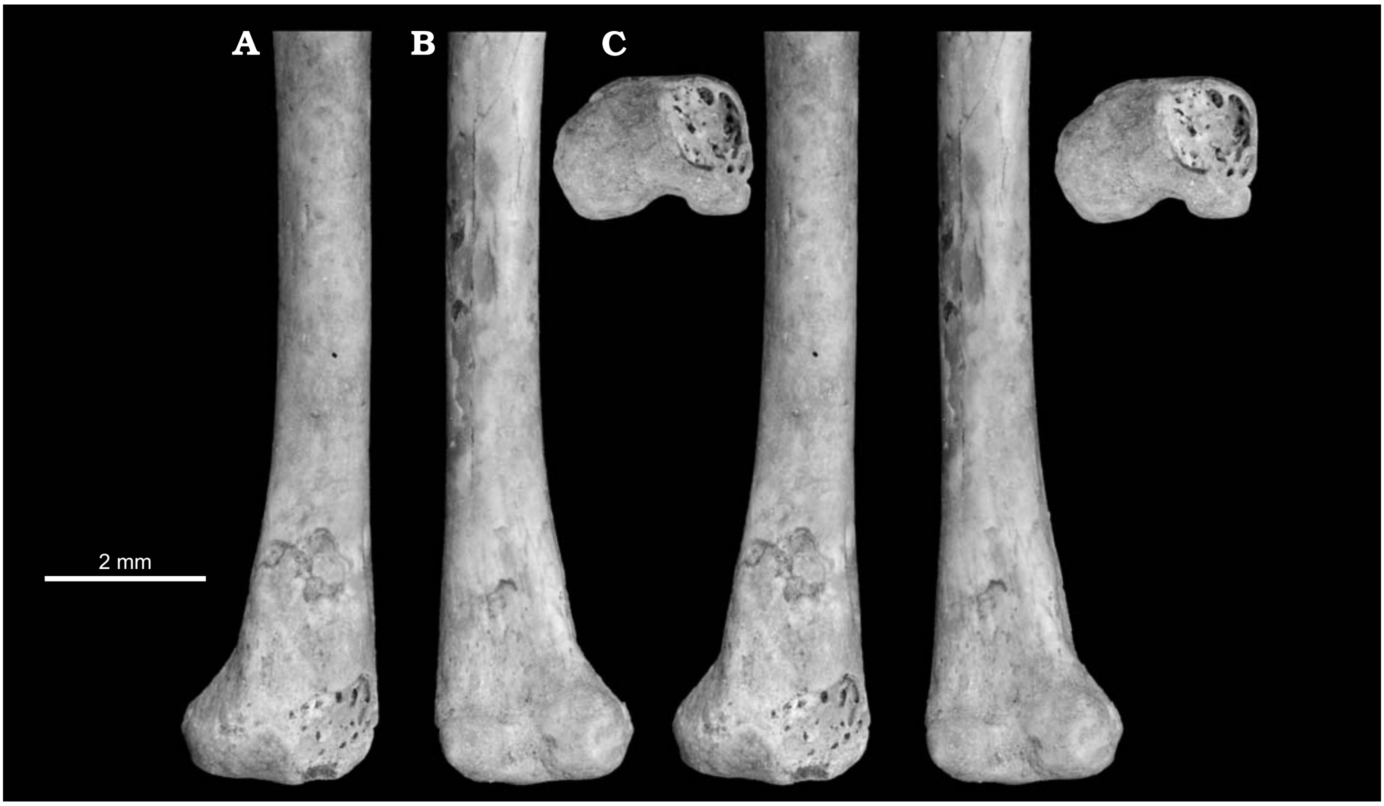

Fig. 2. Stereopairs of right distal femur of an unidentified metatherian (URBAC 03-096, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and distal (**C**) views.

as it crosses the knee (Szalay and Sargis 2001; Argot 2002). The femoral condyles are shallow anteroposteriorly, and quite asymmetrical due to their relative widths. Although the medial condyle is slightly broken, it is clear that the lateral condyle is much wider, which contributes to the lateral side flaring laterally. The discrepancy in the widths of the condyles combined with the lack of a patellar groove was used to differentiate this specimen from the eutherians.

Table 1. Measurements of femora from Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan. Abbreviations: FDED, femoral distal end depth; FDEW, femoral distal end width; FHL, femoral head length; FPEW, femoral proximal end width. All measurements in millimeters.

Specimen number	Distal femora	FDED	FDEW
URBAC 03-096	Metatherian	1.33	2.04
URBAC 00-018	Eutherian Group 1	3.05	4.06
ZIN C 85327	Eutherian Group 2	4.74	6.13
URBAC 04-095	Eutherian Group 3	4.26	6.47
URBAC 00-13	Eutherian Group 3	–	6.42
Specimen number	Proximal femora	FHL	FPEW
URBAC 02-052	Group 1	1.51	3.37
ZIN C 85321	Group 2	1.95	4.88
ZIN C 85324	Group 3	2.42	5.87
URBAC 04-052	Group 4	2.40	6.44
ZIN C 97885	Group 4	2.61	6.84
ZIN C 85322	Group 5	2.19	6.61
URBAC 03-051	Group 5	–	–
ZIN C 85325	Group 6	4.14	9.72
ZIN C 97886	Group 6	4.04	8.96

Eutherian distal femora

The eutherian distal femora have been assigned to three different groups. All of these femora possess a patellar groove, which indicates the presence of a patella in the quadriceps femoris tendon. The femoral condyles are subequal in width in all three eutherian groups, and the condyles are relatively deep anteroposteriorly compared to those of the metatherian.

Eutherian distal femur group 1.—This group is represented by the smallest eutherian distal femur (Fig. 3, Table 1; URBAC 00-018). It appears to represent an individual similar in size to that represented by proximal femur group 3 (see below). The femoral condyles are quite even in width, the patellar groove is fairly shallow, and the condyles are relatively deep compared to those of the metatherian distal femur.

Eutherian distal femur group 2.—This distal femur (Fig. 4; ZIN C 85327) is significantly larger than eutherian distal femur group 1 (Table 1). A considerable amount of the diaphysis is preserved, yet it is unclear whether the third trochanter is absent or was proximal to the break. This specimen has subequal condyles, a pronounced patellar groove, and the

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Fig. 3. Stereopairs of right distal femur of eutherian distal femur group 1 (URBAC 00-018, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and distal (**C**) views.

deepest condyles relative to the other distal femora. In these ways, this distal femur resembles that of the zalambdalestid cf. *Zalambdalestes* (see Novacek et al. 1997: fig. 3).

Eutherian distal femur group 3.—These femora (Fig. 5; URBAC 04-095, URBAC 00-13) are slightly larger than eutherian distal femur group 2 (Table 1). They differ from the other eutherians in possessing somewhat shallow and asymmetrical condyles, although these features are not as pronounced as in the metatherian distal femur.

Proximal femora

Other than a previously described fragmentary femur that was attributed to Multituberculata (see Kielan-Jaworowska and Nessov 1992), and one specimen that is similar in some aspects to the zalambdalestid *Barunlestes* (see below), all of the proximal femora in this sample exhibit a metatherian-like morphology. These specimens possess a rounded femoral head, with lateral and posterior extension of the articular surface onto the neck. They have a short greater trochanter that is lower than or even with the femoral head, and a lesser trochanter that projects medially or posteromedially. These specimens either possess a very small third trochanter or this trochanter is absent.

Proximal femur group 1.—This group is represented by the smallest proximal femur (Fig. 6; URBAC 02-052), which represents an individual that was much larger than that represented by the metatherian distal femur (Table 1). This specimen has a fairly spherical head, with lateral and posterior expansion of the articular surface. The greater trochanter is roughly at the height of the head and the lesser trochanter projects posteromedially. The third trochanter appears to be absent or very small, but it may not be preserved.

Proximal femur group 2.—This specimen (Fig. 7; ZIN C 85321) is the second smallest proximal femur (Table 1). It is the most complete specimen in the sample, with a fairly complete proximal end, diaphysis, and a fragmentary distal end. The head is rounded, although not as spherical as that of proximal femur group 1, and has lateral and posterior expansion of the articular surface. The greater trochanter is worn, but it appears as though it was roughly as high as the head. The lesser trochanter is abraded and only slightly developed on the posterior side. The third trochanter is absent. Like the proximal end, the proportions of the distal femur seem to indicate that this is a metatherian. Although the distal end is broken, it is clear that the lateral side flares laterally. This specimen also appears to lack a patellar groove. It is consid-

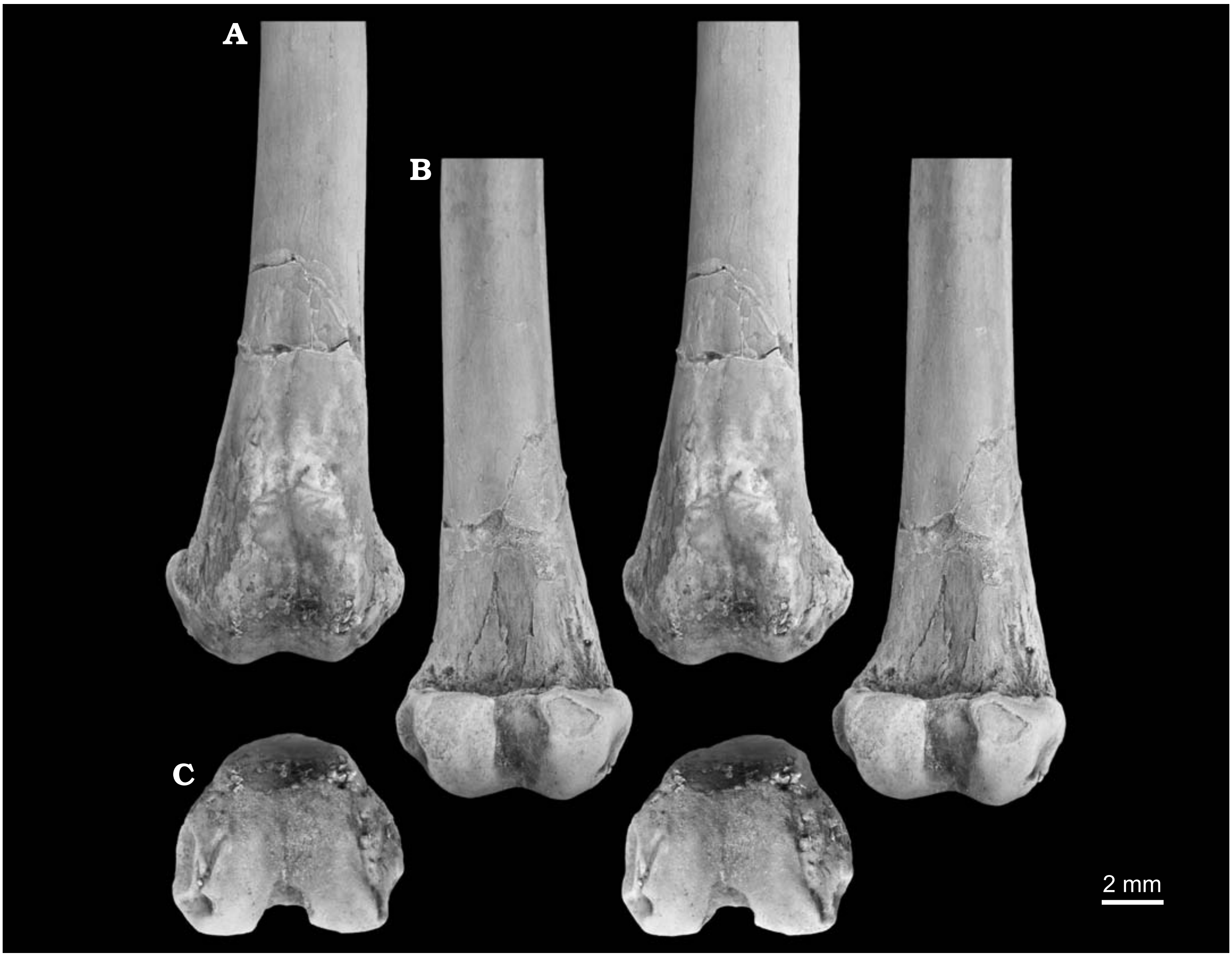

Fig. 4. Stereopairs of right distal femur of eutherian distal femur group 2 (ZIN C 85327, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and distal (**C**) views.

erably larger than the metatherian distal femur (Table 1), and represents the second likely metatherian in the sample.

Proximal femur group 3.—This specimen (Fig. 8; ZIN C 85324) represents an individual similar in size to that represented by the smallest eutherian distal femur (eutherian distal femur group 1; Table 1). The head appears to be fairly spherical, although it is abraded laterally and the articular surface originally may have been slightly more laterally extended. In this way, this proximal femur resembles that of the zalambdalestid *Barunlestes butleri* (see Kielan-Jaworowska 1978: fig. 14A, pl. 7.1a–c, pl. 11.2a–d). The neck is short and the greater trochanter is broken. The lesser trochanter projects medially and the third trochanter is represented by a pronounced proximal ridge, both of which are different from the condition in *Barunlestes*.

Proximal femur group 4.—These femora (Fig. 9; URBAC 04-052, ZIN C 97885) are slightly larger than that of proximal femur group 3 (Table 1). They have a rounded head with lateral and posterior extension of the articular surface onto the neck, and a worn greater trochanter that appears to be about the same height as the head. The lesser trochanter is broken but clearly projects posteromedially. The third trochanter is absent in one specimen and very small in the other. The trochanteric fossa is quite pronounced in both specimens.

Proximal femur group 5.—This group (Fig. 10; ZIN C 85322, URBAC 03-051) is approximately the same size as proximal femur group 4 (Table 1). These femora have a long, narrow, rounded head, and the articular surface extends laterally. The posterior side is flat with a shallow trochanteric fossa. The greater trochanter is worn, but it is slightly lower than the head. The lesser trochanter is pronounced, flares medially, and extends distally. The third trochanter appears to be absent but may not be preserved.

Proximal femur group 6.—These two proximal femora (Fig. 11; ZIN C 85325, ZIN C 97886) are the largest specimens in

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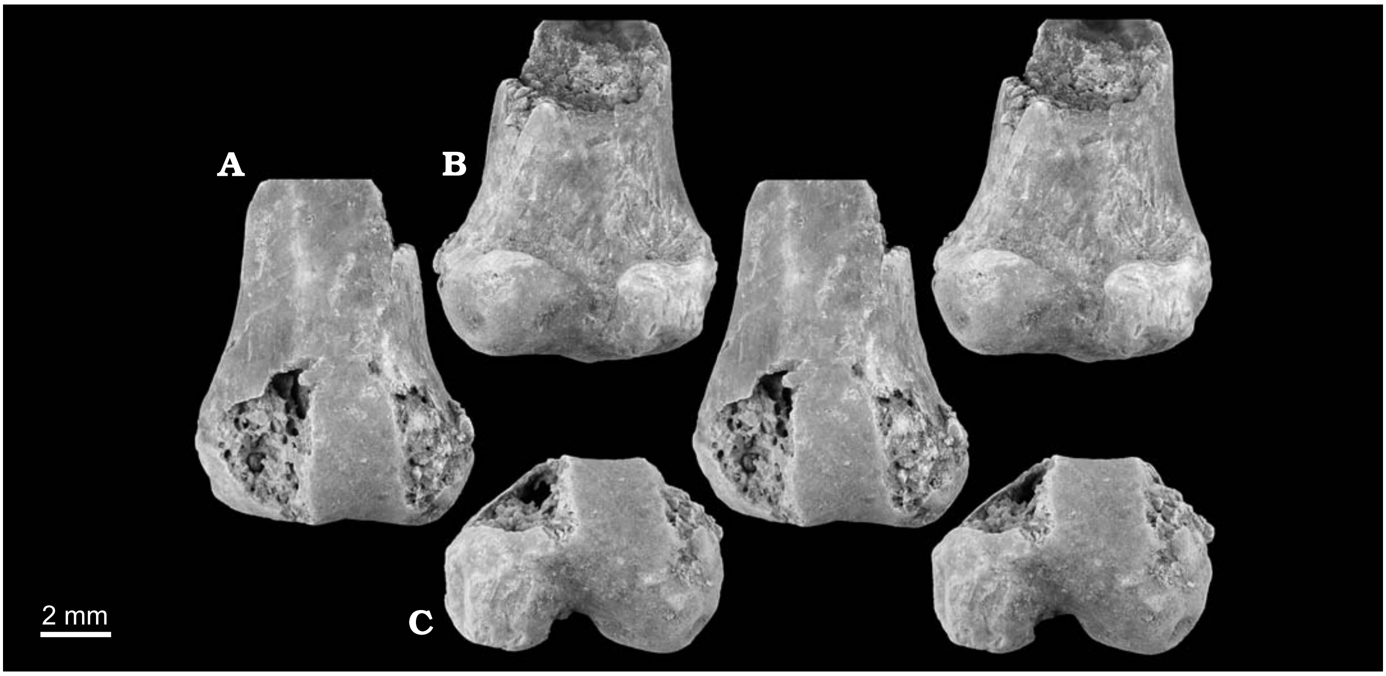

Fig. 5. Stereopairs of left distal femur of eutherian distal femur group 3 (URBAC 04-095, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and distal (**C**) views.

the sample (Table 1). ZIN C 85325 is noticeably larger than ZIN C 97886 in all dimensions (Table 1), but they are grouped together based on overall morphological similarity and size relative to the other groups. They have a somewhat spherical, rounded head, and the articular surface clearly extends laterally and posteriorly. The greater trochanter is about as high as the femoral head. The lesser trochanter projects posteromedially and does not extend as far distally as in proximal femur group 5. The third trochanter appears to be absent but may not be preserved.

Discussion and conclusions

Metatherian distal femur.—The relative width of the femoral condyles reflects the kind of motions that can be achieved between the femur and crus, and the type of loading in the distal femur and knee joint (Szalay and Sargis 2001). The metatherian distal femur from Dzharakuduk has a lateral condyle that is much wider than the medial condyle (Fig. 2). This suggests a laterally displaced load, and may be related to the abducted position of the femur in locomotion (Jenkins 1971). Femoral condyles that are not equal reflect the locomotor repertoire of arboreal marsupials, or of marsupials that likely have an arboreal ancestry (Szalay and Sargis 2001; Argot 2004). The lack of a patellar groove (and patella) also indicates this arboreal ancestry; the patella is absent in didelphids and the arboreal *Dromiciops*, but present in terrestrial caenolestids and peramelids (Szalay and Sargis 2001; Argot 2002). The distal femoral morphology of this specimen, and the distal and proximal femoral morphology of proximal femur group 2 (Fig. 7) suggest that these taxa were climbing mammals, similar to extant arboreal marsupials.

The two femora from the Bissekty l.f. that have been attributed to Metatheria are generally similar to other fossil metatherians from the Cretaceous and Paleocene in lacking a patellar groove and possessing an asymmetrical distal end with a wider lateral condyle. *Sinodelphys szalayi*, the oldest known putative metatherian from the Early Cretaceous (Luo et al. 2003), is represented by a fairly complete, yet flattened, skeleton. The femur of *Sinodelphys* has been interpreted to have an asymmetrical, laterally flared distal end (see Luo et al. 2003: SOM fig. 1), but presence or absence of a patellar groove could not be determined based on the character codings of Luo et al. (2003). The distal femur of *Asiatherium reshetovi* from the Late Cretaceous of Mongolia is damaged, but enough morphology is preserved to show that a patellar groove was not present and that the distal end was probably asymmetrical with a larger lateral condyle (Szalay and Trominov 1996).

The fossil didelphimorphs from the early Paleocene of Tiupampa, Bolivia, have a mosaic of arboreal and terrestrial features in their postcranial skeletons (Muizon 1998; Szalay and Sargis 2001; Muizon and Argot 2003). *Pucadelphys andinus* has many postcranial features that suggest that it was primarily terrestrial, whereas *Mayulestes ferox* and *Andinodelphys cochabambensis* have some features suggesting terrestriality and others related to adept climbing abilities (Muizon and Argot 2003). *Pucadelphys* has an anteroposteriorly deep distal femur, with a lateral femoral condyle that is only slightly wider than the medial one (Muizon 1998; Szalay and Sargis 2001), whereas *Mayulestes* has more unequal proportions of the femoral condyles. Such differences likely reflect the rela-

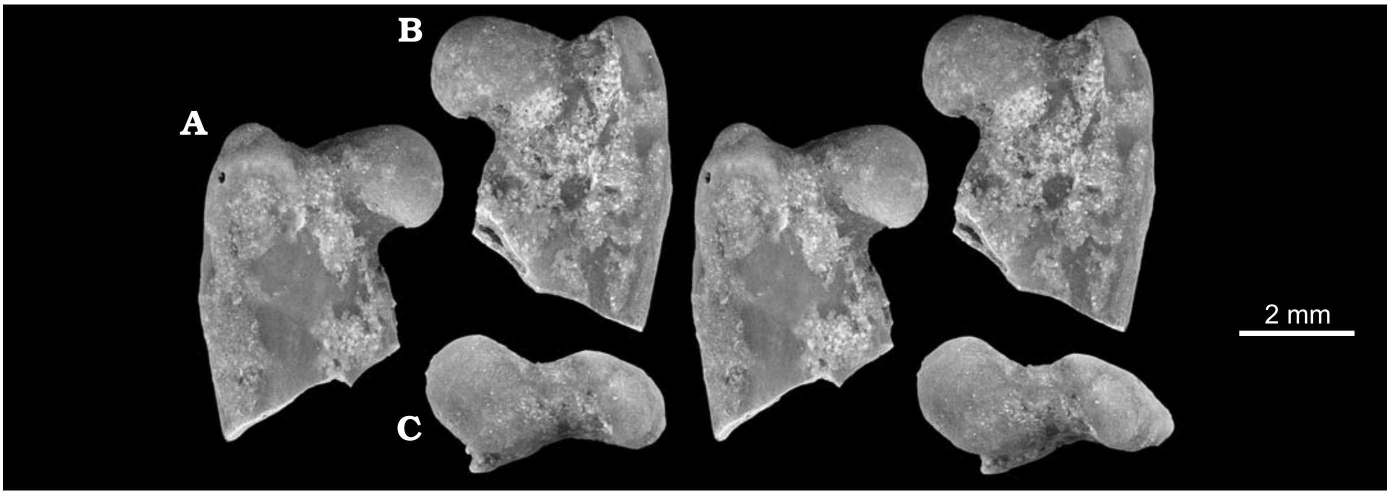

Fig. 6. Stereopairs of right proximal femur of proximal femur group 1 (URBAC 02-052, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and proximal (**C**) views.

Fig. 7. Stereopairs of right proximal femur of proximal femur group 2 (ZIN C 85321, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and proximal (**C**) views.

tively more terrestrial habitus of *Pucadelphys*. Muizon and Argot (2003) suggested that these taxa may retain the plesiomorphic condition for marsupials, which would not be arboreal as hypothesized by Szalay (1994) and Muizon (1998), but terrestrial with secondary specializations for climbing. These early Paleocene didelphimorph taxa are certainly informative because they are represented by fairly complete skeletal material, but earlier Cretaceous stem taxa such as *Sinodelphys*, *Asiatherium*, and material from the Bissekty l.f. may be more informative for assessing polarity of metatherian postcranial characters. Similarly, *Herpetotherium* cf. *fugax* from the Early Oligocene of Wyoming is known from femora and other

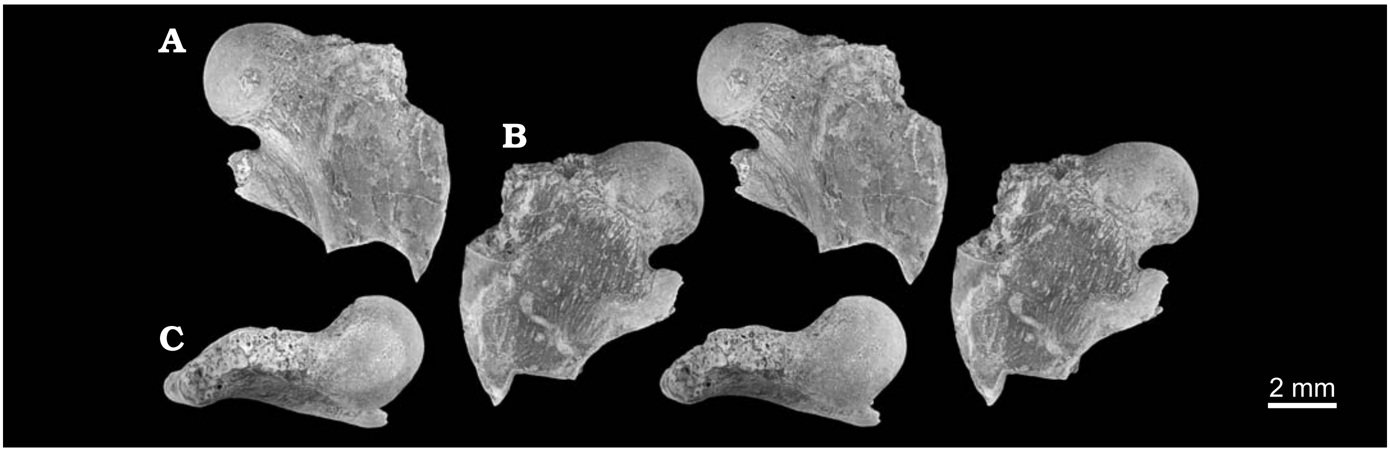

Fig. 8. Stereopairs of left proximal femur of proximal femur group 3 (ZIN C 85324, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and proximal (**C**) views.

postcrania with features suggesting a more terrestrial habitus, although this younger taxon is not as basal as the didelphimorphs from Tiupampa (Horovitz et al. 2008).

Eutherian distal femora.—The subequal width of femoral condyles in eutherians is caused by the narrowing of the lateral condyle (Szalay 1984, 1994). This modification of the knee in the ancestral eutherian was likely related to terrestrial locomotion, with the crus more in line with the femur during parasagittal movements of the hind limb (Szalay 1984, 1994; Szalay and Sargis 2001; Sargis 2002). The subequal proportions of the femoral condyles are fairly fixed in placentals, and therefore not particularly indicative of substrate preference (Szalay and Sargis 2001; Sargis 2002), instead reflecting their terrestrial ancestry (Szalay 1984, 1994). The presence of a patella in eutherians (and terrestrial marsupials) deepens the knee and increases the leverage of the quadriceps femoris muscle in extending the knee (Szalay and Sargis 2001, Sargis 2002). The ubiquitous presence of a patella in placentals likely reflects their terrestrial ancestry (Szalay 1984, 1994; Szalay and Sargis 2001; Sargis 2002). The condyles are relatively deeper in the eutherians from the Bissekty l.f. (e.g., Fig. 4) than in the metatherian (Fig. 2). Deep condyles increase the leverage of the quadriceps femoris muscle, and are another indicator of terrestrial locomotion and ancestry (Szalay 1984, 1994; Kappelman 1988; Szalay and Sargis 2001; Sargis 2002).

Partial skeletons of the zalambdalestids *Barunlestes butleri* and cf. *Zalambdalestes* from the Gobi Desert in Mongolia preserve distal femora (see Kielan-Jaworowska 1978: pl. 7.1d–h; Novacek et al. 1997: fig. 3). Like the distal femora from Dzharakuduk (see Figs. 3–5), these zalambdalestids have femoral condyles that are subequal in width. The femur of *Barunlestes* appears to differ from specimens from the Bissekty Formation in having a more pronounced patellar groove, intercondylar fossa, and a more pronounced medial patellar ridge. Eutherian distal femur group 2 (ZIN C 85327) is most similar to *Barunlestes* in its condylar depth, but differs from *Barunlestes* in having a mediolaterally wider distal end relative to the shaft. ZIN C 85327 also resembles cf. *Zalambdalestes*, particularly in condylar width and length (see Fig. 4). The pronounced condylar depth could be related to the proposed saltatory habits of zalambdalestids (Kielan-Jaworowska 1978). This specimen appears to represent an individual that was considerably larger than that represented by the previously identified zalambdalestid humerus from the Bissekty Formation (see Chester et al. 2010: fig. 7), and may represent a second zalambdalestid postcranial group. Dental remains suggest the presence of two zalambdalestids at Dzharakuduk, and similarities between ZIN C 85327 and the distal femoral morphology of zalambdalestids suggest that this specimen may represent Zalambdalestidae.

Based on the relative abundance of eutherian taxa known from other elements at Dzharakuduk, most of the eutherian femoral groups listed above probably represent zhelestids. Although substrate preference and limb posture are difficult to assess with isolated and fragmentary material, the eutherian distal femora suggest that these taxa may have been terrestrial. This is in accord with the previous functional interpretations of other postcrania from Dzharakuduk (Szalay and Sargis 2006; Chester et al. 2010).

Proximal femora.—The size, shape, and orientation of the femoral head, and the extent of the articular facet, reflect habitual contact with the acetabulum. The lateral and posterior extension of the articular surface in the proximal femora from the Bissekty Formation (except proximal femora group 3; see Figs. 6, 7, 9–11) indicates an extreme capability for abduction of the thigh when it is extended posteriorly (Szalay and Sargis 2001). This expanded articular surface allows for more mobility and is associated with arboreality, whereas a more restricted articular surface is associated with terrestriality (e.g., Gebo and Sargis 1994). The lateral and posterior extension of the proximal femoral articular surface and the low greater trochanter could be related to the lack of a parasagittal posture in these Cretaceous mammals, although these taxa are considered crown therians here and are not hypothesized to have a sprawling posture.

The gluteus medius muscle inserts on the greater tro-

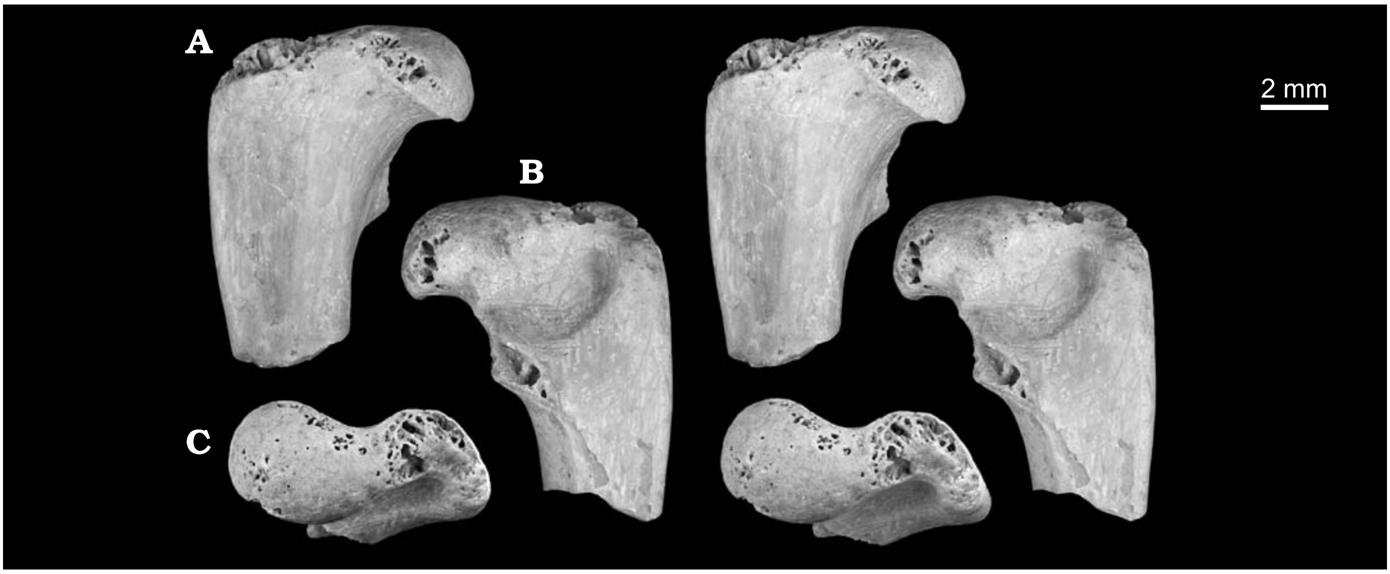

Fig. 9. Stereopairs of right proximal femur of proximal femur group 4 (URBAC 04-052, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and proximal (**C**) views.

Fig. 10. Stereopairs of right proximal femur of proximal femur group 5 (ZIN C 85322, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (**A**), posterior (**B**), and proximal (**C**) views.

chanter and is an extensor of the thigh. A less proximally projecting greater trochanter, as present in these specimens, would have allowed for greater mobility in the hip joint (Sargis 2002). The placement and size of the lesser trochanter varies among the specimens in this sample. A larger, more medially projecting lesser trochanter is correlated with greater climbing ability, whereas a more posteriorly placed lesser trochanter indicates no marked rotation of the femur (Taylor 1976). For example, the latter condition is seen in terrestrial mammals with hind limbs restricted to the parasagittal plane during propulsion (Taylor 1976; Szalay and Sargis 2001; Salton and Sargis 2009). The gluteus superficialis muscle inserts on the third trochanter and is an extensor of the thigh. The third trochanter appears to be absent in several specimens in this study, which is also the case for many extant therians, such as didelphid and australidelphian marsupials (Szalay and Sargis 2001), anthropoid primates (Gebo and Sargis 1994), and viverrids (Taylor 1976). The third trochanter is generally small when present in the specimens from Dzharakuduk, which may indicate a more habitually flexed hind limb (Sargis 2002). In summary, all of the proximal femora possess at least one characteristic that is commonly associated with hip joint mobility and possibly arboreality, in contrast to the terrestrial features present in the eutherian distal femora.

Primitive condition of the therian proximal femur

The dental record documents the presence of twelve eutherian species and only one metatherian at Dzharakuduk (Archibald and Averianov 2005; Averianov et al. 2010), whereas the crurotarsal (Szalay and Sargis 2006) and humeral (Chester et

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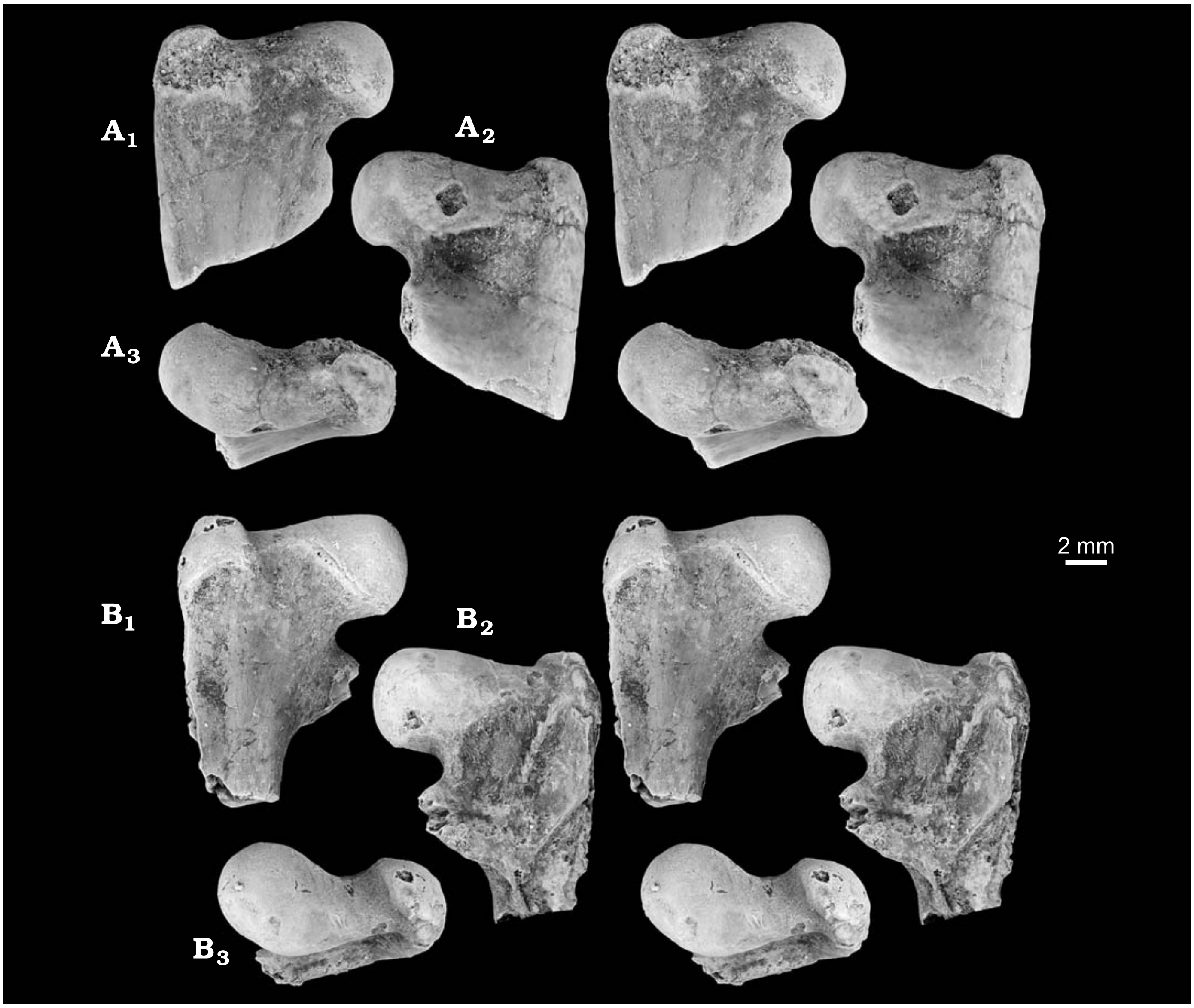

Fig. 11. Stereopairs of proximal femora of proximal femur group 6 from Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan. **A**. ZIN C 85325, right femur, in anterior (A_1), posterior (A_2), and proximal (A_3) views. **B**. ZIN C 97886, right femur, in anterior (B_1), posterior (B_2), and proximal (B_3) views.

al. 2010) evidence support the presence of at least two to four metatherian species. The femora from the Bissekty l.f. have allowed us to independently test the taxonomic diversity present at these localities. As reflected by all other previously studied elements, the distal femora mainly belong to eutherians. Based on dental abundance, most of the femora attributed to eutherians probably represent zhelestids. Similar to the previous study of humeri, the femora suggest the presence of at least two metatherians in the sample. This further demonstrates that postcrania are important for understanding the taxonomic diversity present at these Late Cretaceous localities.

When considering the sample size of the proximal femora from the Bissekty l.f. (which were classified into six different groups), and the overwhelming presence of eutherians at these localities (including three distal femoral groups), it is possible, yet unlikely, that the majority of proximal femora belong to metatherians as the result of sampling bias. Therefore, it is worth investigating why almost all of the proximal femora have a laterally and posteriorly expanded articular surface of the femoral head and a greater trochanter about the same height as the head. If many of the proximal femora represent zhelestids and/or other eutherians, the sample suggests that this condition is primitive for Theria and these Cretaceous eutherians retain it, or that zhelestids and/or other eutherians are convergent with metatherians in this regard. If the former scenario is correct, the distal end of the eutherian femur was modified from the condition of the ancestral therian before the proximal end, and several of these proximal femora may represent terrestrial eutherian mammals that retain the plesiomorphic condition of the ancestral therian.

In order to test this hypothesis, comparisons must be made to the femora of the oldest known therian mammals, as well as femora of non-therian outgroups. The proximal femoral morphology of several basal eutherians, two early metatherians, and several non-therian Mesozoic mammals is discussed below. Comparisons were made to eutherians that possess craniodental features that place them within this clade, but retain some plesiomorphic postcranial conditions, such as the presence of epipubic bones (e.g., Kielan-Jaworowska 1975; Novacek et al. 1997; Ji et al. 2002).

Early Cretaceous *Eomaia scansoria*, the oldest known eutherian (Ji et al. 2002), is represented by a fairly complete, yet flattened, skeleton. This early eutherian mammal has been reconstructed as scansorial based on aspects of the hindlimb (Ji et al. 2002). Unfortunately, the hip joint of this skeleton has not been described or figured in detail, and the proximal femur is difficult to interpret based on published figures. The original illustrations suggest an incomplete proximal femur with a broken greater trochanter. Based on the character codings of Ji et al. (2002), *Eomaia* has a femoral neck and a spherical head inflected medially, a greater trochanter directed dorsally, and a small lesser trochanter on the ventromedial or ventral side of the femoral shaft.

Partial skeletons of Late Cretaceous eutherian mammals that preserve a proximal femur include those of the asioryctithere *Ukhaatherium nessovi* and the zalambdalestid *Barunlestes butleri*. *Ukhaatherium* appears to have a spherical femoral head (see Novacek et al. 1997: fig. 2), although it is only partially exposed (Horovitz 2003). The greater trochanter is positioned lateral to the head, and extends proximally about to the height of the head (Horovitz 2003). The lesser trochanter is laminar and positioned medially. There is no evidence for the presence of a third trochanter (Horovitz 2003). As mentioned above, the proximal femur of the zalambdalestid *Barunlestes* (see Kielan-Jaworowska 1978: fig. 14A, pl. 7.1a–c, pl. 11.2a–d) has a fairly spherical head with an articular surface that does not appear to extend as far laterally and posteriorly onto the neck as all but one of the femora from the Bissekty l.f. The greater trochanter is approximately at the height of the femoral head, and the lesser trochanter is small and directed posteromedially. The third trochanter is not preserved, but has been suggested to be present based on a ridge on the lateral surface (Kielan-Jaworowska 1978).

The hip joint of *Sinodelphys szalayi* has not been described or figured in detail, although the character codings of Luo et al. (2003) suggest that most of the proximal femur is difficult to interpret. *Sinodelphys* is coded as having a femoral neck and a spherical head inflected medially, but the orientation of the greater trochanter and the position and size of the lesser trochanter could not be determined. *Asiatherium reshetovi* is a Late Cretaceous metatherian known from a partial skeleton that preserves femora. *Asiatherium* has a round femoral head that projects more proximally than the greater trochanter, and a lesser trochanter that projects medially (see Szalay and Trofimov 1996: fig. 20). The proximal ends of the femora are broken, but do not appear to have a laterally expanded articular surface.

In order to assess the distribution of proximal femoral morphology outside of crown Theria, several non-therian mammals were taken into consideration. The femoral head of the dryolestoid *Henkelotherium* is spherical from medial view (Krebs 1991), however other aspects of the proximal femur, such as the lateral extent of the articular surface, are difficult to interpret based on published illustrations. The spalacotheroid *Zhangheotherium* has a spherical head but does not have an articular surface that is laterally and posteriorly extended onto the neck, and it has a distinct greater trochanter that is as tall as or taller than the femoral head (Hu et al. 1997; Luo and Ji 2005). The spalacotheroids *Akidolestes* (Li and Luo 2006) and *Maotherium* (Rougier et al. 2003) have either been proposed and/or illustrated to have a similar condition, although this is difficult to assess based on published photographs. Therefore, outgroups to Theria suggest that the ancestral therian possessed a spherical femoral head lacking lateral or posterior expansion of the articular surface onto the neck, as well as a relatively tall greater trochanter.

In summary, the majority of Mesozoic mammals most relevant to determining the ancestral condition of the therian proximal femur are poorly preserved and/or not described or figured in detail. Outgroup comparisons seem to suggest that the condition of a spherical femoral head without lateral or posterior expansion of the articular surface onto the neck is plesiomorphic for Theria. Though it is possible that most of the proximal femora in our sample, those with lateral and posterior expansion of the femoral head articular surface onto the neck, are metatherians, this is not supported based on our present understanding of the taxonomic diversity present at Dzharakuduk. Therefore, it seems most likely that many of the metatherian-like proximal femora in our sample belong to eutherian mammals. If this is the case, then it is possible that an expanded articular surface of the femoral head is plesiomorphic for Theria (though not supported by non-therian outgroup comparisons; see above), and that eutherians in this fauna retain this condition, or that most eutherians in this sample have converged on the metatherian condition of this feature. The proximal femora of zalambdalestids appear to lack an expanded articular surface of the femoral head, so if many of the proximal femora in our sample represent eutherians as the dental evidence suggests, it seems likely that they represent zhelestids or other eutherians rather than zalambdalestids. Given that most putative zhelestids in the sample have been reconstructed as being more terrestrial than the more arboreal metatherians (Szalay and Sargis 2006; Chester et al. 2010), this would not support the hypothesis of convergence in the femoral head articular surface morphology between these two taxa. Because of the equivocal nature of each hypothesis regarding the proximal femora (i.e., nearly all metatherian despite dental evidence, eutherian but convergent with metatherians despite tarsal and humeral evidence, or eutherian but retain the primitive condition despite outgroup evidence) we are unable to confi-

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dently place these specimens in eutherian or metatherian groups, as we have with the distal femora. More complete and associated fossil material is needed before we can confidently assess whether most eutherians in this fauna retain the plesiomorphic therian condition of the proximal femur, or whether they are convergent with some metatherians in this regard.

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