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Mammalian distal humeri from the Late Cretaceous of Uzbekistan

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We describe mammalian distal humeri recovered from the Bissekty Formation, Dzharakuduk, Kyzylkum Desert, Uzbekistan (90 Ma). Isolated elements were sorted into groups that likely correspond to species (or genera). These groups were allocated to taxa known mostly from the dentition, petrosals, and/or tarsals at this site. We identified one humerus of a multituberculate and one of a zalambdalestid. Several eutherian humeri have been tentatively assigned to Zhelestidae based on their dissimilarity to zalambdalestids and the abundance of zhelestids in the dental record. The zalambdalestids and zhelestids were probably terrestrial. At least two metatherian taxa have also been identified, and both were likely arboreal. Although the dental record suggests twelve eutherian species and only one metatherian, crurotarsal evidence supports the presence of at least four metatherian species at Dzharakuduk. The humeri analyzed here also provide support for the presence of multiple metatherians in the fauna, further demonstrating that postcrania are critical to understanding the taxonomic diversity present at these Late Cretaceous localities.

Key words: Mammalia, Multituberculata, Metatheria, Zalambdalestidae, Zhelestidae, humerus, Cretaceous, Uzbekistan.

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Introduction

The Kyzylkum Desert in Uzbekistan (see Archibald and Averianov 2005: fig. 1) is an extremely important area for recovering Cretaceous mammals. Over the last decade, the joint Uzbek-Russian-British-American-Canadian expedition (URBAC) has carried out paleontological fieldwork on the Dzharakuduk assemblage from the Bissekty Formation (90 Ma; late Turonian). URBAC has concentrated on the Dzharakuduk area in the central Kyzylkum Desert, which has yielded thousands of mammalian specimens after intensive screen-washing.

Fifteen mammal-producing localities have been found in the fluviially deposited Bissekty Formation. Seventy meters separate the lowest and highest localities, but no faunal differences have been detected. These localities have been collectively termed the Bissekty local fauna (l.f.). The Bissekty l.f. is

unarguably the taxonomically richest eutherian fauna known for the Cretaceous and is also one of the oldest eutherian-dominated faunas (Archibald and Averianov 2005).

Taxonomic diversity

Based on craniodental remains the Bissekty l.f. consists of fifteen named and unnamed species of mammals. Twelve of these species are eutherians, and have been identified as the asioryctitheres *Uchkudukodon nessovi*, *Daulestes kulbeckensis*, *D. inobservabilis*, *Bulaklestes kezbe*; the zalambdalestids *Kulbeckia kulbecke* and *Kulbeckia* sp.; the zhelestids *Aspanlestes aptap*, *Parazhelestes mynbulakensis*, *P. robustus*, *Zhelestes temirkazyk*, *Eoungulatum kudukensis*; and the indeterminate eutherian *Paranyctoides*. Zhelestidae is the most common mammalian family in the Bissekty l.f. Approximately

52% of the mammalian dental specimens collected from these localities are attributed to five different species of zhelestids listed above (JDA and AOA unpublished data). Although three metatherians were originally identified from this dental material, further study resulted in the recognition of only one species, the deltatheroidan *Sulestes karakshi* (Archibald and Averianov 2005). One multituberculate, *Uzbekbaatar*, and one symmetrodont, *Shalbaatar*, have also been identified based on gnathic or dental remains (Archibald and Averianov 2005).

Two studies have focused on non-dental remains of mammals recovered from deposits in the Bissekty Formation. Ekdale et al. (2004) described twenty mammalian petrosal bones; nine of these specimens were assigned to Zhelestidae and eleven to the zalambdalestid *Kulbeckia kulbecke*. Based on petrosals, zhelestids are represented by three size classes and zalambdalestids are represented by four (Ekdale et al. 2004). Subsequently one petrosal assignable to *Sulestes* was identified (Averianov et al. in press). Szalay and Sargis (2006) described crurotarsal remains, which support the presence of at least four metatherian species at Dzharakuduk. Nine calcaneal specimens (45% of the well-preserved calcanea included in this study) were attributed to at least three species of zhelestids (Szalay and Sargis 2006). In the present study, we evaluated taxonomic and functional diversity using evidence from distal humeri. This represents an independent test of the taxonomic conclusions based on dental, petrosal, and tarsal remains.

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

Other abbreviation.—l.f., local fauna.

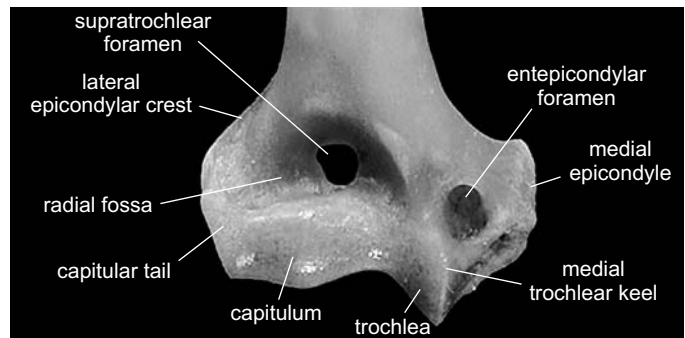


Fig. 1. Anterior view of right distal humerus of extant *Echinorex gymnurys* Raffles, 1822 to illustrate humeral features discussed in the text (modified from Salton and Sargis 2008).

Material and methods

Of the forty-two humeral specimens collected at Dzharakuduk, sixteen specimens preserved enough relevant features to be assessed in a comparative and functional context. After evaluating ontogenetic and intraspecific variation in extant mammals (Szalay and Sargis 2001, 2006; Sargis 2002; Salton and Sargis 2008), the isolated humeri were sorted into groups based primarily on size and overall morphology. These groups probably correspond to species or genera, and were allocated to taxa known mostly from the dentition, petrosals, and/or tarsals at this site. All specimens described here are considered to represent adults, based on complete fusion of the epiphysis to the diaphysis. Our descriptions of these specimens concentrate on particular osteological features that are known to be functionally significant (Fig. 1). All of the humeri in this study are incomplete and none is associated with any other elements, so comparisons were made to more complete fossils, as well as extant therians.



Fig. 2. Left distal humerus of multituberculate (URBAC 03-076, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.



Fig. 3. Distal humeri of metatherian group 1 from Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan. **A.** Right humerus (URBAC 02-075), in anterior (A_1), distal (A_2), and posterior (A_3) views. **B.** Left humerus (URBAC 04-002) in anterior (B_1), posterior (B_2), and distal (B_3) views.

Descriptions

Multituberculata.—There is one multituberculate distal humerus (URBAC 03-076), which is broken distolaterally (Fig. 2). Like other multituberculate humeri, it has a very

large medial epicondyle and an intercondylar groove separating a semispherical radial condyle from a narrow, deep, rounded ulnar condyle that spirals laterally from the anterior to the posterior side. It is also characterized by a short, laterally-flaring capitular tail and shallow olecranon fossa.

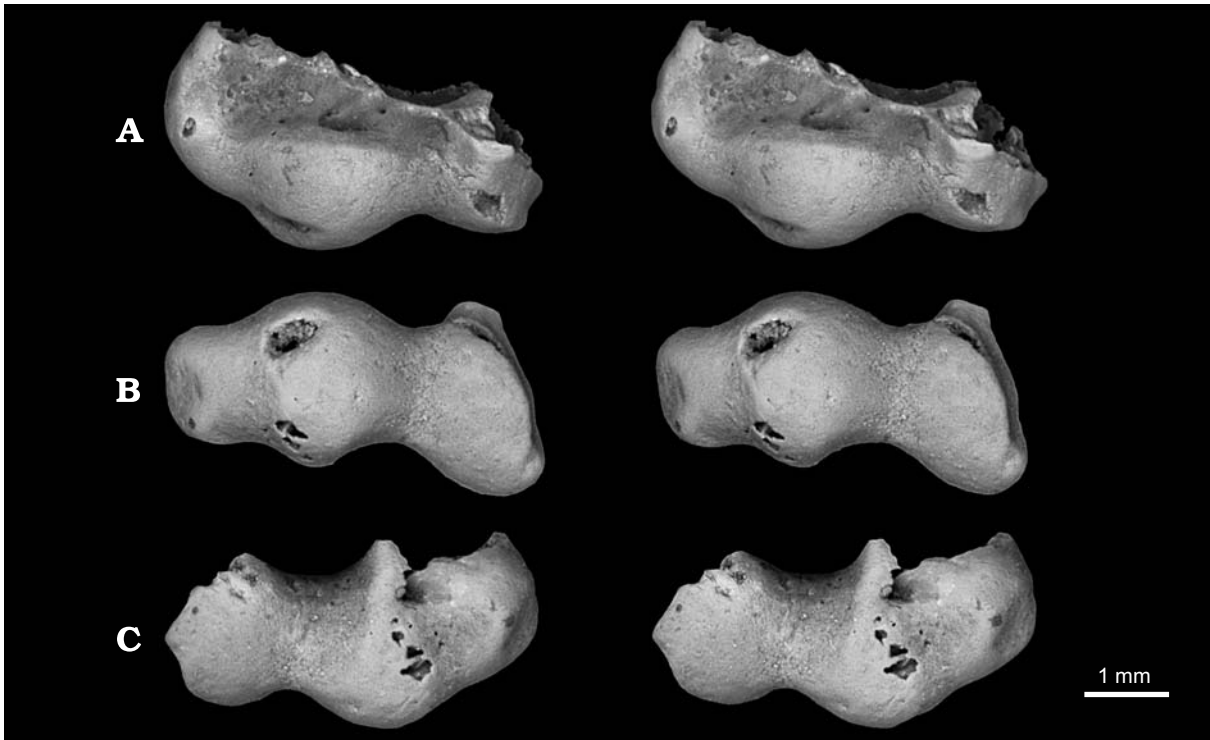


Fig. 4. Right distal humerus of metatherian group 2 (URBAC 06-103, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

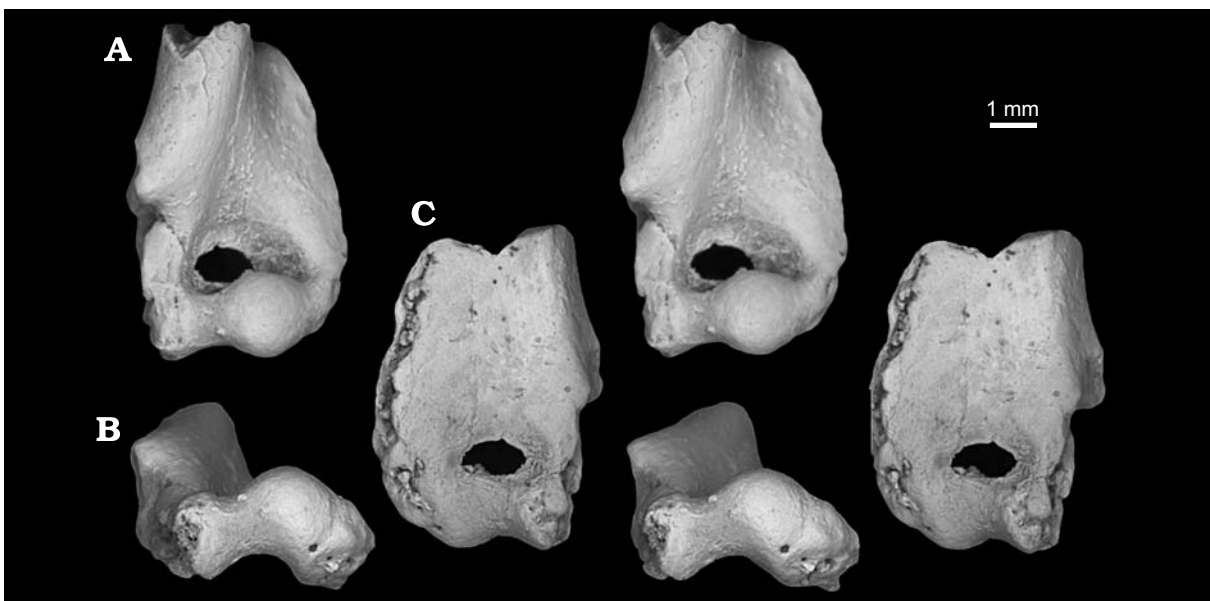


Fig. 5. Left distal humerus of metatherian group 3 (ZIN C 85305, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

It is similar in these features to the unidentified multi-tuberculate (AMNH 118267) from the early Paleocene Bug Creek Anthills site in Montana (see Kielan-Jaworowska and Gambaryan 1994: fig. 14B).

Metatheria.—Two metatherian taxa are represented in the sample, based on two well-preserved specimens. They have

been differentiated from eutherians by size and morphological characteristics (Szalay and Sargis 2001, 2006). Both specimens possess a spherical capitulum; a trochlea separated from the capitulum by a short groove; and a well-developed lateral epicondylar crest (see Argot 2001; Szalay and Sargis 2001). A specimen that is intermediate in size may represent a third metatherian group.

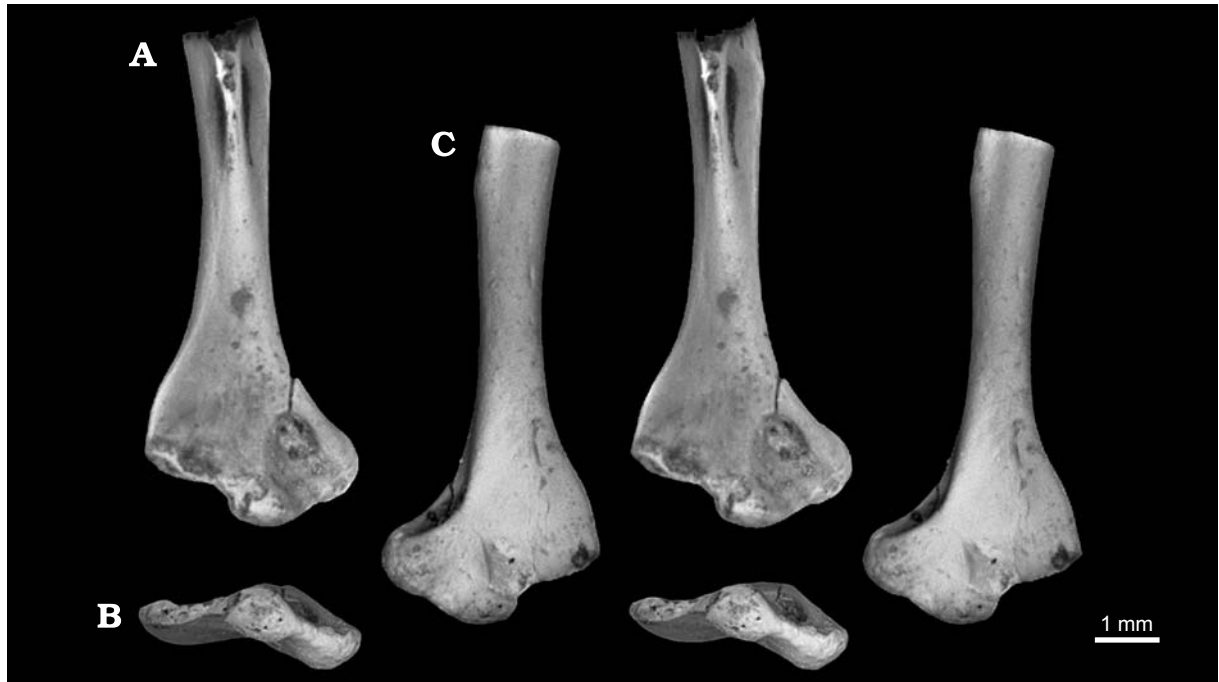


Fig. 6. Right distal humerus of eutherian group 1 (URBAC 06-062, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

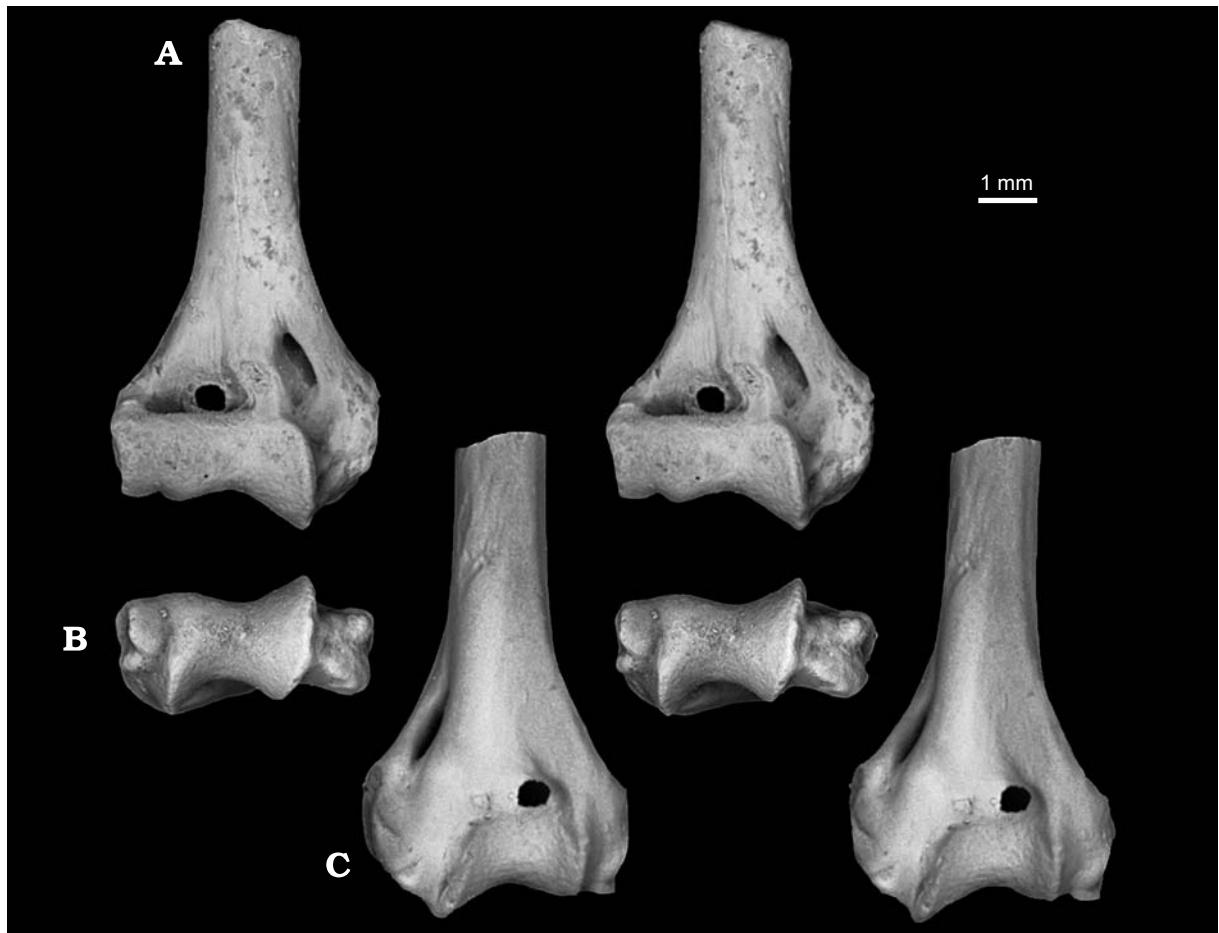


Fig. 7. Right distal humerus of zalambdalestid (ZIN C 85309, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.



Fig. 8. Right distal humerus of zhelestid group 1 (URBAC 06-057, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

Metatherian group 1.—The smallest metatherian (URBAC 02-075) has a short medial trochlear keel; a narrow, shallow trochlea; and a large medial epicondyle (Fig. 3A). The capitular tail is relatively large compared to that of the larger metatherian, but relatively short compared to that of the zalambdalestid (see below). Another small metatherian specimen (URBAC 04-002), which has a broken medial epicondyle, capitulum, and lateral epicondylar crest (Fig. 3B), may also belong to this group.

Metatherian group 2.—A distal fragment (URBAC 06-103) that is intermediate in size between metatherian groups 1 and 3 may represent a separate group. It exhibits a large, spherical capitulum and a relatively wide capitular tail (Fig. 4).

Metatherian group 3.—The medial side of the largest meta-

therian humerus (ZIN C 85305) is broken. The preserved lateral side exhibits a twisted distal articular area, a small capitular tail, and there is a supratrochlear foramen (perforation) between the relatively shallow olecranon fossa and the radial fossa (Fig. 5).

Eutheria.—The eutherian taxa have a trochlea that is continuous with the capitulum.

Eutherian group 1.—One eutherian humerus (URBAC 06-062) is similar to that attributed to the early Paleocene *Procerberus formicarum* from Bug Creek Anthills in Montana (see Szalay and Dagosto 1980: fig. 1). It has a large medial epicondyle, a well-developed lateral epicondylar crest, and a short trochlea (Fig. 6). The capitulum is broken off in this specimen, precluding its assignment to a lower taxonomic level.

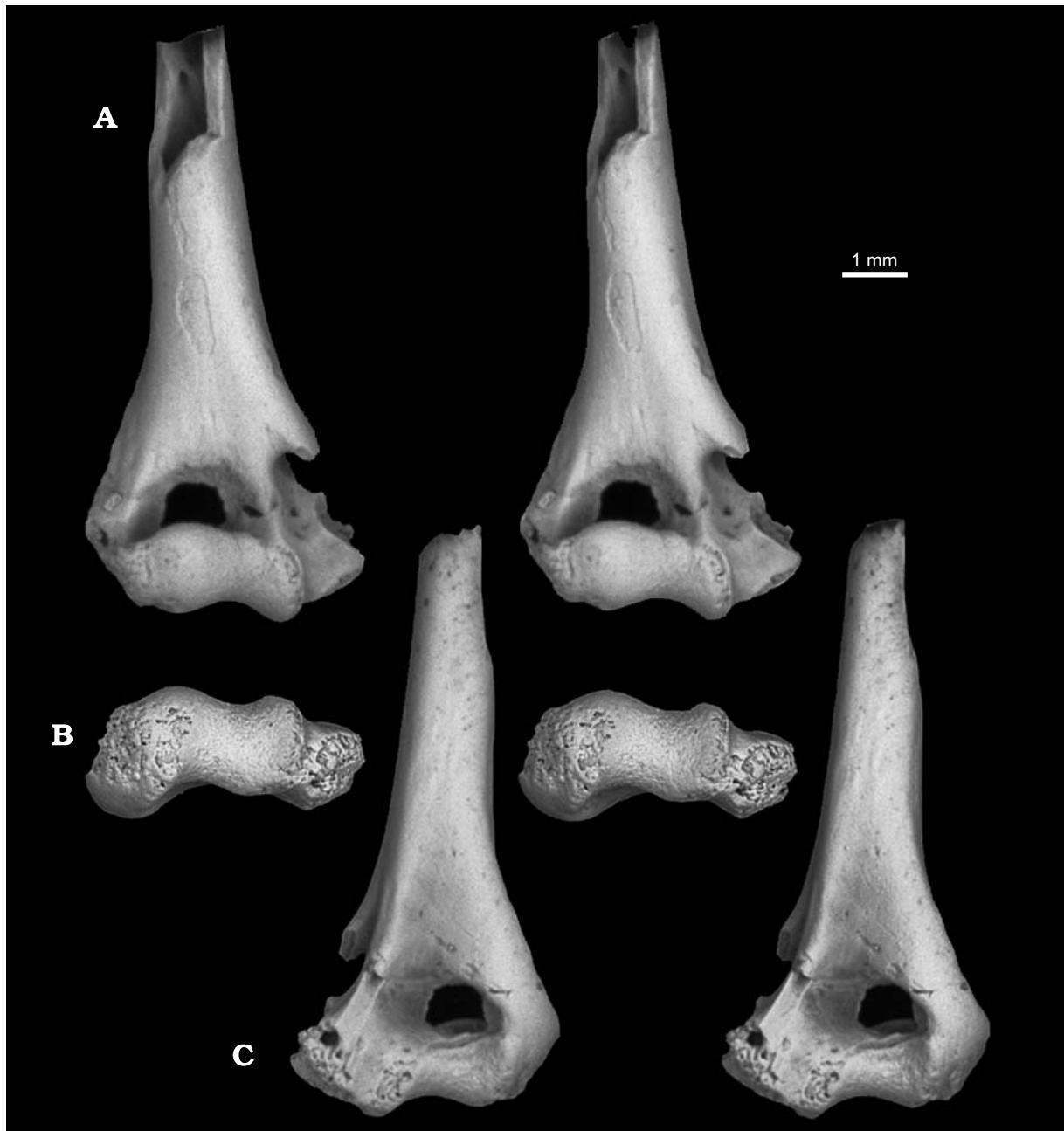


Fig. 9. Right distal humerus of zhelestid group 1 (URBAC 97-P04, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

Zalambdalestidae.—The zalambdalestid humerus (ZIN C 85309) is quite similar to that of the Late Cretaceous Mongolian zalambdalestid *Barunlestes butleri* (see Kielan-Jaworowska 1978: fig. 11A, pl. 9.2b) in possessing a large capitular tail separated from a cylindrical capitulum by a shallow groove, a large medial trochlear keel, and a deep trochlea (Fig. 7). However, the Bissekty zalambdalestid has a wider distal end, partially due to a larger medial epicondyle, and a shorter trochlea than *Barunlestes butleri*. The Bissekty zalambdalestid has a relatively larger medial epicondyle than that of zhelestid group 1 (Figs. 8–10), but smaller than that of metatherian group 1 (Fig. 3). The lateral epicondylar crest is

poorly developed, a groove between the trochlea and the capitulum is lacking, and there is a supratrochlear foramen between the radial and olecranon fossae (Fig. 7).

Zhelestid group 1.—Some eutherian humeri have been tentatively assigned to Zhelestidae based on their dissimilarity to zalambdalestids and the abundance of zhelestids in the dental record. Specimens placed in zhelestid group 1 (URBAC 06-057, URBAC 97-P04, URBAC 03-187) differ from those of zalambdalestids in having a more rounded capitulum (though less spherical than in the metatherians), a shorter capitular tail (that is relatively large compared to that of metatherian group 3), a smaller medial trochlear keel, and

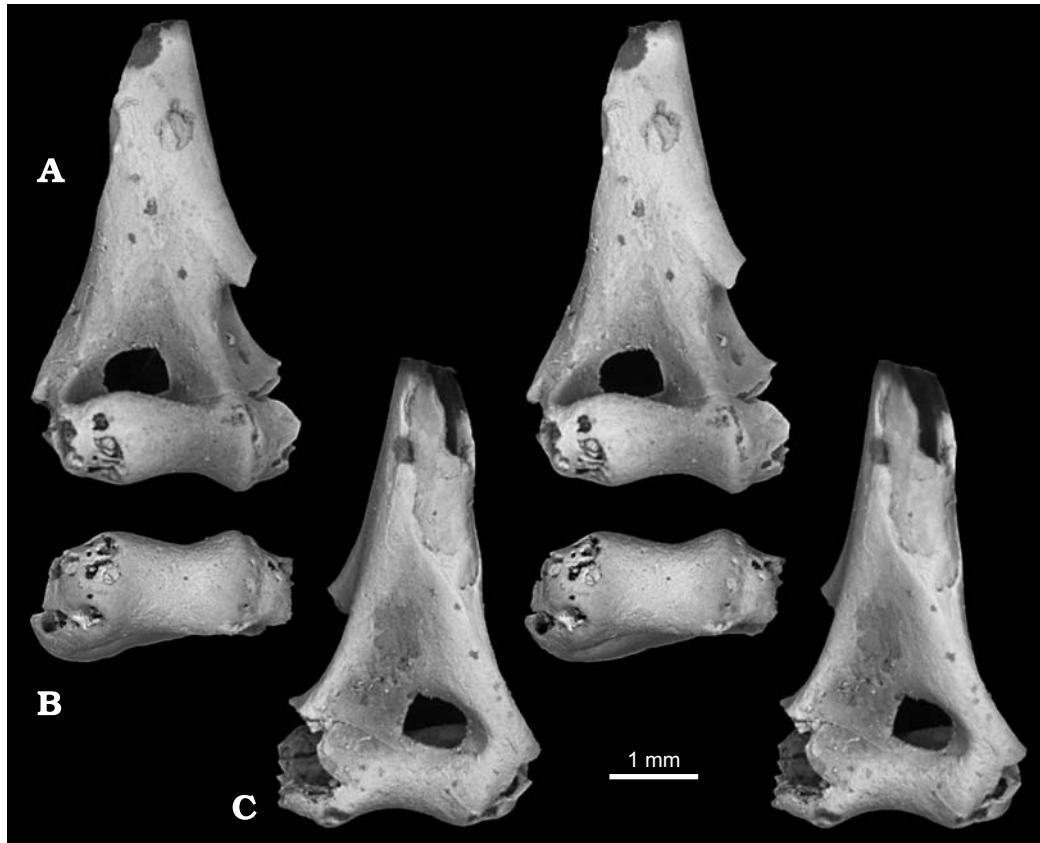


Fig. 10. Right distal humerus of zhelestid group 1 (URBAC 03-187, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

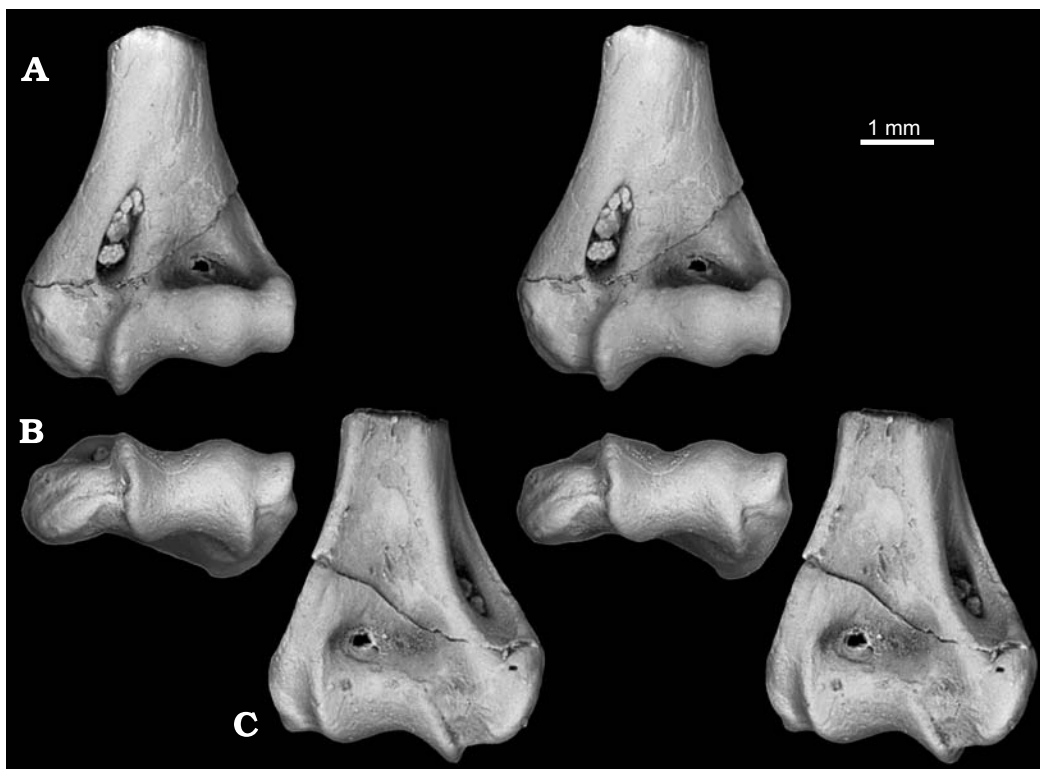


Fig. 11. Left distal humerus of zhelestid group 2 (URBAC 97-P07, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.



Fig. 12. Left distal humerus of zhelestid group 2 (URBAC 03-099, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.



Fig. 13. Right distal humerus of zhelestid group 3 (URBAC 06-072, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

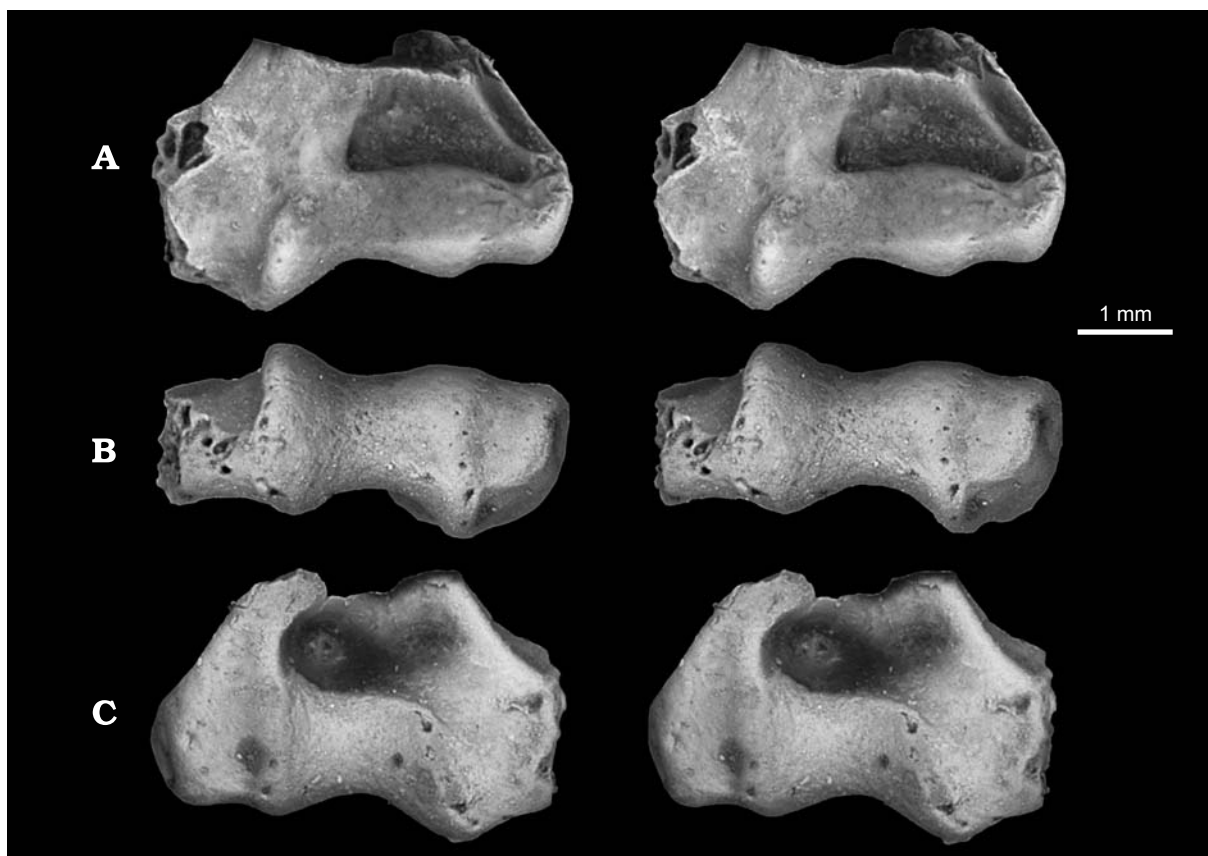


Fig. 14. Left distal humerus of zhelestid group 4 (URBAC 03-126, Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan), in anterior (A), distal (B), and posterior (C) views.

a shallower trochlea (Figs. 8–10). The medial epicondyle is relatively small, there is no groove separating the trochlea from the capitulum, there is a supratrochlear foramen between the radial and olecranon fossae, and the lateral epicondylar crest is not as well-developed as in metatherian group 3. There is also a groove medial to the trochlea. These are the smallest zhelestids in the sample.

Zhelestid group 2.—Two humeri (URBAC 97-P07, URBAC 03-099) are slightly larger than the humeri of zhelestid group 1. One (URBAC 97-P07) has a well-developed medial trochlear keel, deep trochlea, and large capitular tail separated from a cylindrical capitulum by a shallow groove (Fig. 11). Compared to the zalambdalestid, this specimen has a more rounded medial epicondyle; shorter, shallower trochlea; less prominent medial trochlear keel; and more globular capitulum (Figs. 7, 11). The other specimen (URBAC 03-099) has a broken medial epicondyle, abraded trochlea, and broken capitular tail (Fig. 12), but may belong to this group. These specimens also have a supratrochlear foramen between the radial and olecranon fossae.

Zhelestid group 3.—This humerus (URBAC 06-072) is slightly larger than the humeri of zhelestid group 2. It exhibits a more flaring lateral epicondylar crest. It also lacks a groove between the capitulum and capitular tail, has a relatively shallow trochlea, and has a supratrochlear foramen between the radial and olecranon fossae (Fig. 13).

Zhelestid group 4.—This humerus (URBAC 03-126) is similar in size to that of zhelestid group 3, and somewhat similar in trochlear morphology to that of group 2 in having a relatively deep trochlea (Fig. 14). The capitulum and capitular tail are somewhat compressed proximodistally and lack a groove between the two. The medial epicondyle is broken in this specimen.

Zhelestid group 5.—The largest humeri (URBAC 00-72, URBAC 98-P08) that may represent zhelestids are both distal fragments, so they were tentatively assigned to a separate group. These specimens have a relatively large medial epicondyle, shallow trochlea, and large capitular tail separated from a short capitulum by a shallow groove (Fig. 15). If better-preserved specimens are recovered in the future, it may be possible to better distinguish this group of larger individuals.

Discussion and conclusions

Multituberculata.—Most Asian multituberculates have been reconstructed as terrestrial runners (Kielan-Jaworowska and Gambaryan 1994), whereas Krause and Jenkins (1983) proposed that some North American forms were arboreal based on their pedal and tail morphology. Furthermore, Sereno and McKenna (1995) and Sereno (2006) have suggested that

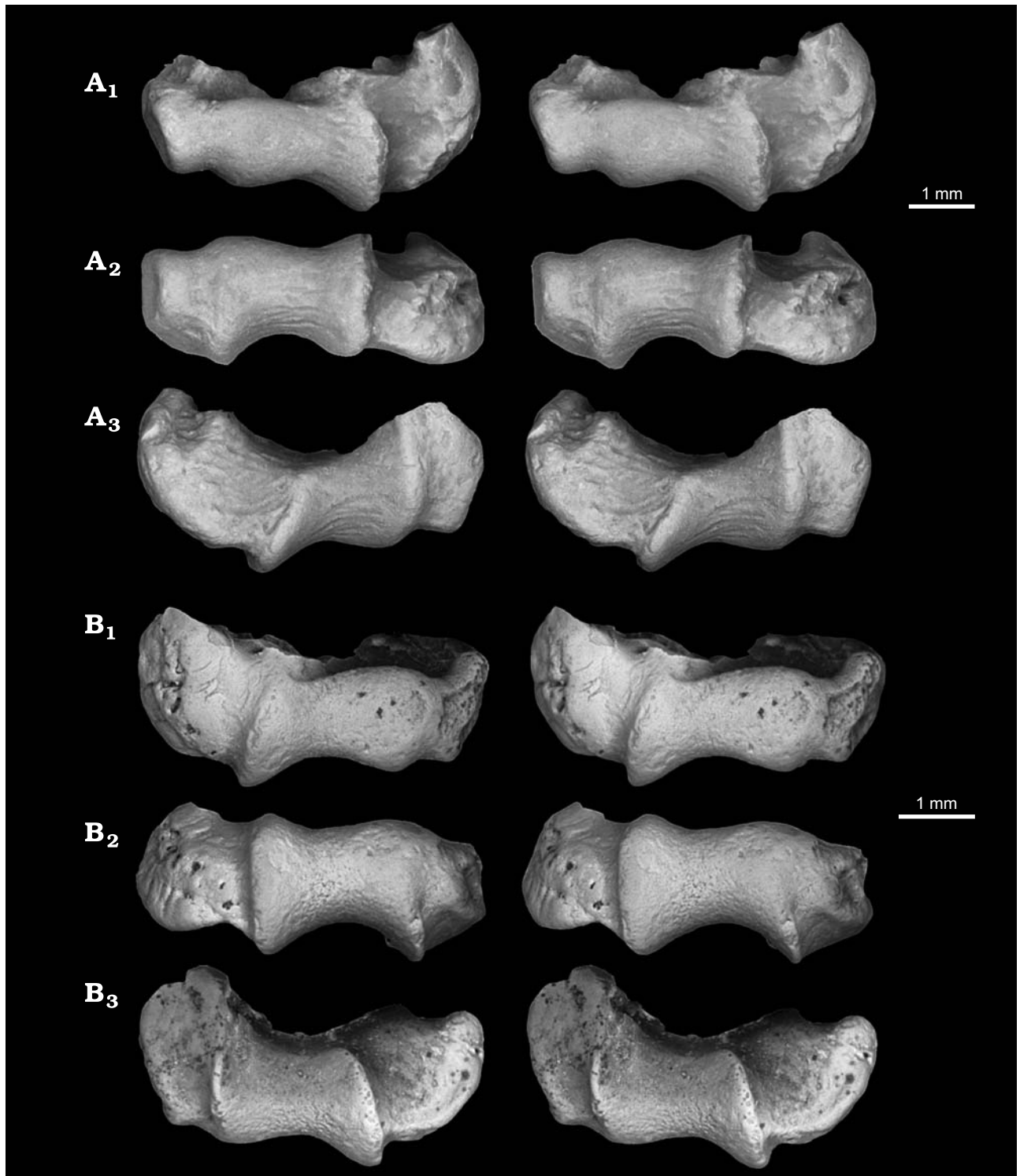


Fig. 15. Distal humeri of zhelestid group 5 from Bissekty Formation, Upper Cretaceous: Turonian, Kyzylkum Desert, Uzbekistan. **A.** URBAC 00-72, right humerus, in anterior (A_1), distal (A_2), and posterior (A_3) views. **B.** URBAC 98-P08, left humerus, in anterior (B_1), distal (B_2), and posterior (B_3) views.

multituberculates had a parasagittal limb posture, whereas Kielan-Jaworowska and co-authors (e.g., Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1997; Kielan-Jaworowska and Hurum 2006) have argued that multituberculates had a sprawling stance. Unfortunately, the incomplete distal humerus described above is one of the only

postcranial elements known for Multituberculata in this fauna, other than a fragmentary proximal humerus and proximal femur (Kielan-Jaworowska and Nesson 1992), and we are unable to infer the substrate preference or limb posture of the Bissekty multituberculate without better evidence from other regions of the postcranium.

Metatheria.—The metatherians have a spherical capitulum separated from the trochlea by a short groove (Figs. 3–5). The spherical shape of the capitulum increases joint mobility by enabling a greater degree of rotation between the radius and humerus (Szalay and Dagosto 1980; Gebo and Sargis 1994; Sargis 2002). The separation of the trochlea from the capitulum by a groove allows both the ulna and radius to move more freely (Gebo and Sargis 1994; Sargis 2002). The well-developed lateral epicondylar crest provides a large area of origin for the brachioradialis muscle, which is a flexor of the antebrachium. This muscle is particularly active when the manus is semi-prone and the forearm is flexed against resistance (Pauly et al. 1967), giving it an active role during climbing (Argot 2001). It may also be involved in supination of the antebrachium to bring the hands into semi-prone position so that the palms face medially toward the arboreal substrate (McEvoy 1982; Argot 2001). Szalay and Sargis (2001: 179) proposed that the lateral epicondylar crest was well-developed in the last common ancestor of metatherians, so it is not surprising to see this feature in these Late Cretaceous metatherians. The large medial epicondyle of metatherian group 1 provides a large area of origin for the wrist and digital flexors. This may indicate enlarged flexor muscles and the ability to grasp in this group, as these muscles are important for arboreal mammals (including marsupials) during grasping (Argot 2001; Szalay and Sargis 2001; Sargis 2002). In summary, the distal humeral morphology of the metatherians suggests that they were likely arboreal.

Eutheria.—The zalambdalestid and zhelestids have a trochlea that is continuous with the capitulum (Figs. 7–15). This continuity keeps the articulations of the proximal radius and ulna in closer proximity, thereby restricting joint mobility (Sargis 2002), particularly the range of motion of the humeroradial articulation. They likely had a limited degree of radial rotation, with movement at the elbow joint being limited to flexion and extension in the parasagittal plane (see Gebo and Sargis 1994; Sargis 2002). The restricted elbow joints of the zalambdalestid and zhelestids imply that they were probably terrestrial.

The zalambdalestid (Fig. 7) has a (proximodistally) long medial trochlear keel, a feature that is pronounced in cursors (Jenkins 1973), which resists torques produced in flexed and semi-flexed pronated postures (Jenkins 1973). This feature also further restricts humeroulnar movements to the parasagittal plane (Jenkins 1973). The humeroradial joint appears to be similarly restricted to this plane based on the presence of a shallow groove between the capitular tail and the capitulum, as well as the cylindrical shape of the capitulum (see Gebo and Sargis 1994; Sargis 2002). The deep, wedge-shaped trochlea creates greater articular contact between the trochlea and trochlear notch of the ulna, particularly in close-packed positions of the joint, and this stabilizes parasagittal movements during repetitive loading of the humeroulnar joint (Argot 2001; Szalay and Sargis 2001; Sargis 2002). All of these features are found in terres-

trial mammals, and the Bissekty zalambdalestid was likely terrestrial like *Barunlestes* (see Kielan-Jaworowska 1978).

Although zhelestid group 1 lacks the long medial trochlear keel, groove between the capitular tail and capitulum, and deep, wedge-shaped trochlea found in the zalambdalestid described above, group 2 does exhibit these features (to a lesser degree) and the other zhelestid groups exhibit one or more of these features to varying degrees. Based on the variable presence of these features and the continuity between the trochlea and capitulum, the zhelestids were probably terrestrial as well.

Taxonomic diversity.—The Bissekty l.f. humeri have allowed us to independently estimate the taxonomic diversity present at these localities. We have identified a multituberculate and a zalambdalestid by comparing these specimens to more complete postcranial fossils that are associated with dental taxa. We have also tentatively assigned five groups of humeri to the family Zhelestidae based on their dissimilarity to zalambdalestids and the abundance of zhelestids in the dental record. Like the relative abundances of Zhelestidae based on dental and tarsal specimens, the groups of humeri assigned to zhelestids represent approximately half of the humeral specimens that were collected. *Sulestes* is considered the only metatherian present in the Bissekty l.f. based on craniodental remains (Archibald and Averianov 2005). This taxon represents only 5.5% of dental remains. The tarsal evidence suggests that at least four groups of metatherians were present and that 30% of the mammalian calcanea from Bissekty belong to these groups (Szalay and Sargis 2006). The humeri analyzed here provide support for the presence of at least two (and perhaps three) metatherians in the fauna, further demonstrating that postcrania are critical to understanding the taxonomic diversity present at these Late Cretaceous localities.

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