Chapter 13

Humeri of *Oligoscalops* (Proscalopidae, Mammalia) from the Oligocene of Mongolia

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ABSTRACT

Four humeri of *Oligoscalops* are described from the early Oligocene Hsanda Gol Formation of Central Mongolia, extending the known range of Proscalopidae from North America to Asia. Several characters support allocation of the humeri to Proscalopidae, including a prominent deltoid process that is situated on the middle of the humeral shaft and a partial fusion of the medial epicondyle and teres tubercle. Like those of North American *Oligoscalops*, the Mongolian humeri are small in size and have a partially, but not completely, fused teres tubercle and medial epicondyle. Several hypotheses to explain the occurrence of *Oligoscalops* in Asia are discussed. Although none of the hypotheses are convincingly supported by existing data, efforts to determine the sister-group of Proscalopidae may yield insights into its biogeographic history.

INTRODUCTION

Proscalopidae is a family of fossorial mammals that is known from the late Eocene (Chadronian) to middle Miocene (Early Barstovian) (Barnosky, 1981; Barnosky and Labar, 1989). Prior to the discovery described herein, proscalopids were known only from the following U.S. states: Colorado, Montana, Nebraska, North Dakota, and South Dakota (Barnosky, 1981). Initially, the humeri and skulls of proscalopids were described as different genera because no single specimen included both postcranial and cranial material. Matthew (1928) first suspected that the humeri described as *Arctoryctes* actually belonged to a proscalopid. Nearly 40 years later, Van Valen (1967) synonymized *Arctoryctes* with *Proscalops*, but this synonymy remained unconfirmed until Barnosky (1981) described a nearly complete skull and skeleton of the proscalopid *Mesoscalops*. This new material did not shed much light on the phylogenetic affinities of the group. Proscalopids were traditionally placed in the family Talpidae (e.g., Reed, 1961), although it was generally recognized that the evidence supporting this arrangement was weak. Barnosky (1981, 1982a) argued convincingly that many fossorial specializations evolved independently in talpids and proscalopids, and he concluded that these two lineages should be placed in separate families. Although the systematic position of Proscalopidae remained unresolved, the biogeography of Proscalopidae was seemingly straightforward because all taxa then known were from North America (Barnosky, 1981).

McKenna and Bell (1997: 279) reported the first proscalopid, *Oligoscalops*, from Asia, although the evidence for assigning the Asian material to this North American genus was not provided. In this paper, I describe the geographic and geologic setting of the proscalopid specimens from Mongolia, the evidence for referring them to *Oligoscalops*, and their biogeographic implications. During the 1990s the Mongolian Academy of Sciences and American Museum of Natural History joint expeditions collected fossils from early Oligocene localities in the Valley of the Lakes region in Mongolia. Among the thousands of fossils collected were four proscalopid humeri referred to the genus *Oligoscalops*: MAE-SG-91-10449, MAE-SG-91-

10450, MAE 9423, MAE 91-9418, which are the focus of the present study.

GEOLOGIC SETTING

The four *Oligoscalops* humeri were recovered from exposures in the Hsanda Gol Formation. Bryant and McKenna (1995) informally divided the Hsanda Gol Formation into three lithostratigraphic units, (1) the lower Tatal member, (2) a middle basalt referred to as the Mellet Lava, and (3) the upper Shand member. The Shand member is late early Oligocene in age as determined by the underlying Mellet Lava (31.5 Ma) and a basalt in the overlying Loh Formation (28 Ma) (Evernden et al., 1964; Daxner-Höck et al., 1997; Höck et al., 1999; McKenna et al., MS.). Based on the geomagnetic polarity scale of Cande and Kent (1995), the Mellet lava was formed in the reversed portion of Chron C12. A preliminary analysis of samples of the Mellet Lava indicates that it has a reversed characteristic magnetization, which is consistent with its radiometric age. The faunas from the lower part of the Shand member and the Tatal member are very similar (Bryant and McKenna, 1995; McKenna et al., MS.); therefore, the Tatal member is probably just slightly older than the Shand member. In addition, carnivorans from the Tatal member are most similar to those of Villebramar level (early Oligocene) in Europe (Dashzeveg, 1996). The Villebramar level immediately follows the Soumaille level (ca. 33 Ma), which is the oldest European mammal level in the Oligocene (Schmidt-Kittler, 1987). Therefore, radiometric ages of the basalts, biostratigraphy, and magnetostratigraphy all indicate that the entire Hsanda Gol Formation is early Oligocene in age, following the time scale of Berggren et al. (1995).

Bryant and McKenna (1995) informally named the Ulaan Khongil and Zavlia faunas of the Hsanda Gol Formation, with the division between the faunas occurring at a point 5–10 meters above the Mellet Lava (Bryant and McKenna, 1995). Despite intensive searching in both faunas, *Oligoscalops* appears to be restricted to the lower of the two, the Ulaan Khongil fauna. Although the MAE prospected numerous early Oligocene localities for fossils, proscalopid humeri were found at only two localities. Specimens MAE-SG-91-10449, SG-91-10450, and MAE 91-9418 were collected from a few meters below the Mellet Lava at Tatal Gol (also known as Ulaan Khongil; 45°17′16″N; 101°37′17″E) and specimen MAE 9423 was collected from Buylsteen Khuduk (45°24′09″N; 101°30′07″E). Although not as thoroughly prospected as Tatal Gol, previous expeditions have collected fossils from Buylsteen Khuduk (Russell and Zhai, 1987).

INSTITUTIONAL ABBREVIATIONS

AMNH-M   Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York

AMNH-VP   Division of Paleontology (vertebrate collection only), American Museum of Natural History, New York

MAE   Mongolian Academy of Sciences and American Museum of Natural History Expedition. Specimens with this prefix are currently housed in the American Museum of Natural History, but will be returned to the Institute of Geology, Mongolia

SDSM   South Dakota School of Mines and Technology

UWBM   University of Washington, Burke Memorial Washington State Museum

COMPOSITE MORPHOLOGICAL DESCRIPTION

Of the four humeri of *Oligoscalops* collected from Mongolia, MAE-SG-91-10449 (fig. 13.1A, B) and MAE-SG-91-10450 (fig. 13.1C, D) are right humeri, and MAE 9423 and MAE 91-9418 are left humeri. For each, most of the distal end and all of the deltoid process were preserved, but the humeral head, lesser and greater tuberosities, and most of the lateral epicondyle were not. The base of the lateral epicondyle and the accessory radial articular facet were preserved only in MAE-SG-91-10449. Features from all four humeri were combined to form a composite description. Individual specimens are cited for the measurements taken.

Proscalopid humeri are very different in morphology from those of most mammals. In general, I have followed Reed and Turnbull's
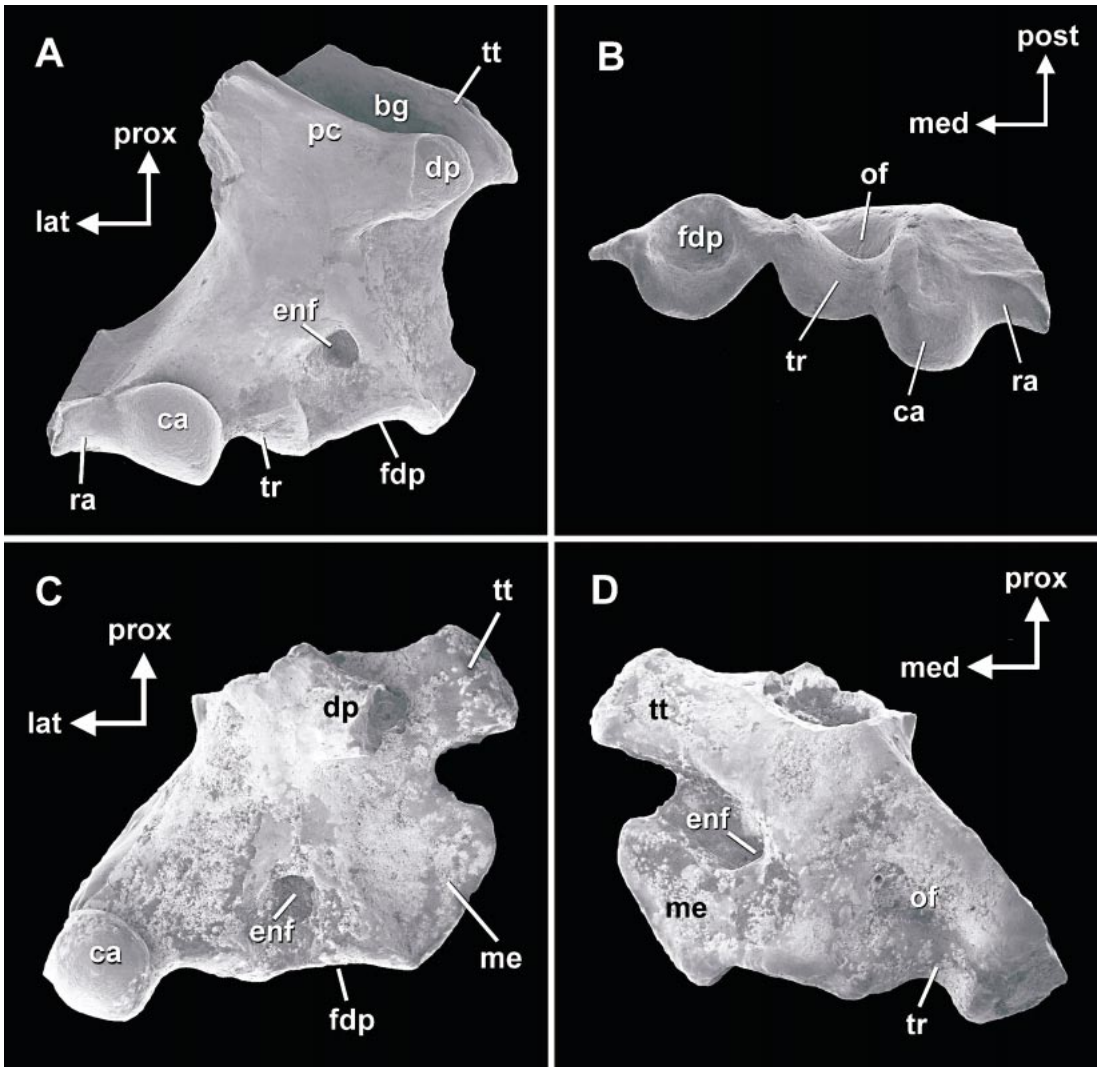
Fig. 13.1.   Views of two *Oligoscalops* right humeri from Mongolia. **A,** anterior view of MAE-SG-91-10449 (note that the extreme edge of the lateral epicondyle was cropped from the picture); **B,** distal view of the same specimen; **C,** anterior view of MAE-SG-91-10450; **D,** posterior view of the same specimen. Abbreviations: **bg,** bicipital groove; **ca,** capitulum; **dp,** deltoid process; **enf,** entepicondylar foramen; **fdp,** flexor digitorum profundus fossa; **lat,** lateral; **me,** medial epicondyle; **med,** medial; **of,** olecranon fossa; **pc,** pectoral crest; **prox,** proximal; **ra,** accessory radial articular facet; **tr,** trochlea; **tt,** teres tubercle.

(1965) nomenclature of proscalopid humeral morphology. One notable exception is the deltoid process, which Reed and Turnbull (1965) identified as the small ventral projection of the greater tuberosity. Following Barnosky (1981), I use deltoid process to refer to the projection on the distal end of the pectoral crest. In the following description, the distal end of the humerus is oriented so that the edge of the pit for the flexor digitorum profundus is parallel to the transverse plane. In this orientation, the trochlea is directed proximomedially to distolaterally.

The humeri are anteroposteriorly flat,

proximodistally short, and mediolaterally wide. In anterior view, the pectoral crest is oriented proximolaterally to distomedially. The pectoral crest is a sharp ridge, and its distal end bears a prominent deltoid process (fig. 13.1A: dp). Although the deltoid process projects medially, its distal end bears a smooth, oval-shaped, tip that faces anteriorly. A distinct lip encircling the tip, similar to the lip of a bottle cap, is present. The deltoid process is situated on the medial half of the humeral shaft. Proximal to the deltoid process is the bicipital groove, which is a deep trough between the deltoid process/crest and the shaft of the humerus (fig. 13.1A: bg). Presumably, this groove accommodated the tendon of the biceps brachii muscle (Reed and Turnbull, 1965). The bicipital groove deepens distally; its depth is less than 0.25 mm at its proximal end, but is 1.5 mm near its distal end (MAE-SG-91-10449). Like the pectoral crest, the bicipital groove is angled proximolaterally to distomedially across the anterior face of the humerus.

The teres tubercle forms a large, flattened, medially expanded flange (fig. 13.1A, C: tt). Its distal end is anteroposteriorly thickened: viewed medially, the thickened edge has a teardrop shape, with the narrow end proximal and the wide end distal. Like the teres tubercle, the medial epicondyle forms a flat and medially expanded flange (fig. 13.1D: me); however, unlike the teres tubercle, the medial epicondyle does not have a thickened edge. In anterior view, the medial epicondyle is nearly rectangular in shape. The lateral two thirds of the teres tubercle and medial epicondyle are fused, but their medial edges are separated by a distinct notch (fig. 13.1D). Although not perfectly preserved, it is clear that in anterior view the free edge of the medial epicondyle partially overlapped the teres tubercle. The epicondylar groove occurs on the posterior face of the humerus and courses proximomedially along the presumed line of fusion between the teres tubercle and the medial epicondyle. The groove is 1.2 mm wide, approximately 1 mm deep, and 1.6 mm in length (MAE-SG-91-10450). The medial end of the groove is adjacent to the notch between the teres tubercle and the medial epicondyle, and the lateral end of the groove leads into the entepicondylar canal, which

likely transmitted the median nerve and brachial artery. The entepicondylar canal is slightly less than 1 mm in length (MAE-SG-91-10449).

In anterior view, the most salient feature of the distal end of the humerus is the large ovoid capitulum, which juts distolaterally away from the rest of the humerus (fig. 13.1: ca). The capitulum is slightly ovoid and pointed distally. The anterior face of the capitulum also protrudes outward (anteriorly) away from adjacent parts of the humerus. Lateral to the capitulum is the base of a large lateral epicondyle; however, the exact size of this process could not be determined because it is damaged in all specimens. The articular surface for the radius extends beyond the capitulum onto the distal edge of the lateral epicondyle. This accessory radial articular facet is small and trochleated (fig. 13.1A: ra). The lateral edge of the facet is hooked distally; however, it does not extend as far as the capitulum distally.

In distal view, the humeral trochlea is oriented anterolateral to posteromedial (fig. 13.1B: tr). The lateral wall of the trochlea is much steeper than the medial wall. In anterior view, the medial half of the trochlea is visible as a small wedge that is pointing proximally. The concave and central part of the trochlea is visible only in distal and posterior views. The anterior portion of the trochlea wraps around onto the posterior face of the humerus, terminating in an oblong olecranon fossa. The olecranon fossa is shallow and its long axis is oriented transversely. Immediately medial to the trochlea is a huge pit for the origin of the flexor digitorum profundus muscle (fig. 13.1B: fdp). In distal view, the flexor digitorum pit is nearly circular with an average diameter of 2 mm and a maximum depth of about 0.6 mm (MAE-SG-91-10449). The anterior edge of the pit is formed by a thick lip, which is also partially visible in anterior view (fig. 13.1A: fdp). As a whole, the distal edge of the humerus is not straight when viewed anteriorly. Instead, the medial half of the trochlea and the pit for the flexor digitorum profundus form an angle of about 150°, while the lateral and medial halves of the trochlea form an angle of about 80°.

DISCUSSION

IDENTIFICATION AND COMPARISONS

The expanded distal ends of the four humeri are typical of fossorial mammals. To ensure that they were accurately identified, the Mongolian specimens were compared to the following fossorial mammals: Talpidae, Proscalopidae, *Notoryctes*, *Dasypus*, Chrysochloridae, and the palaeanodonts *Xenocranium* and *Epoicotherium* (table 13.1). Of these taxa, the Mongolian humeri are most similar to those of Talpidae and Proscalopidae. Like all talpid and proscalopid humeri considered in this study (table 13.1), the Mongolian humeri have a pectoral crest, a teres tubercle, and a bicipital groove. In addition, the Mongolian humeri share with talpids (except for *Uropsilus*) and proscalopids a distinct pit for the flexor digitorum profundus on the distal end of the humerus. In light of these similarities to talpids, the Mongolian humeri were also compared to other eulipotyphlans (table 13.1). They were very different from the humeri of soricids, erinaceids, *Solenodon*, and *Tenrec ecaudatus*.

While the Mongolian humeri are similar to those of talpids, they are nearly identical to those of advanced proscalopids. Several features support the allocation of the four humeri from Hsanda Gol to Proscalopidae, including a distinct deltoid process on the pectoral crest (fig. 13.1A: dp). A deltoid process occurs in the proscalopids *Proscalops* (AMNH-VP 12864; fig. 13.2A: dp), *Mesoscalops* (Barnosky, 1981: fig.17), and *Oligoscalops* (Reed, 1956: fig. 130) and is here interpreted as a proscalopid synapomorphy. By contrast, in talpids the deltoid process is not differentiated from the pectoral crest (fig. 13.2B: dp). Another apparent proscalopid synapomorphy present in the Mongolian humeri is a large gap between the end of the deltoid process and the lesser tuberosity. In talpids the gap is much narrower, and in some taxa (e.g., *Desmana*) the deltoid process and the lesser tuberosity are fused to form a bicipital tunnel. The humeri of proscalopids, including the Mongolian form, have a deltoid process that is located approximately midway along the humeral shaft. By contrast, the deltoid process of talpids is sit-

TABLE 13.1
Taxa Included in Study and Specimens Examined or References Consulted[a]

Taxa	Specimens	References
Proscalopidae		
Proscalops	12864[b]	(Barnosky, 1982b)
Cryptoryctes kayi		(Reed, 1956)
Mesoscalops montanensis		(Barnosky, 1981)
Oligoscalops		(Reed, 1956; Barnosky, 1981)
Talpidae		
Uropsilus gracilus	114564	
Desmana moschata	206	
Condylura cristata	48051	
Neurotrichus gibbsii	124312	
Parascalops breweri	140405	
Scalopus aquaticus	235615	
Scapanus latimanus	121212	
Talpa altaica	244223	
Talpa europaea	119495	
Other Eulipotyphlans		
Blarina carolinensis	217848	
Sorex arcticus	128686	
Solenodon paradoxus	35330	
Erinaceus europaeus	42563	
Echinosorex gymnurus	32640	
Tenrecidae		
Tenrec ecaudatus	170513	
Other Fossorial Mammals		
Chrysochloris stuhlmanni	236000	
Dasypus novemcinctus	266483	
Notoryctes typhlops	15015	
Xenocranium		(Rose and Emry, 1983)
Epoicotherium		(Rose and Emry, 1983)

[a]All specimens are located in the Division of Vertebrate Zoology (Mammalogy), AMNH, unless noted otherwise.
[b]Located in Division of Paleontology (Vertebrate), AMNH.

uated near the proximal end of the shaft (fig. 13.2B: dp).

The family Proscalopidae includes four genera: *Cryptoryctes*, *Oligoscalops*, *Proscalops*, and *Mesoscalops* (Barnosky, 1981). Of these four, the humeri from Mongolia most resemble the humeri of *Oligoscalops*. Like *Oligoscalops*, the Mongolian specimens have a teres tubercle and medial epicondyle that are partially, but not completely, fused (fig.
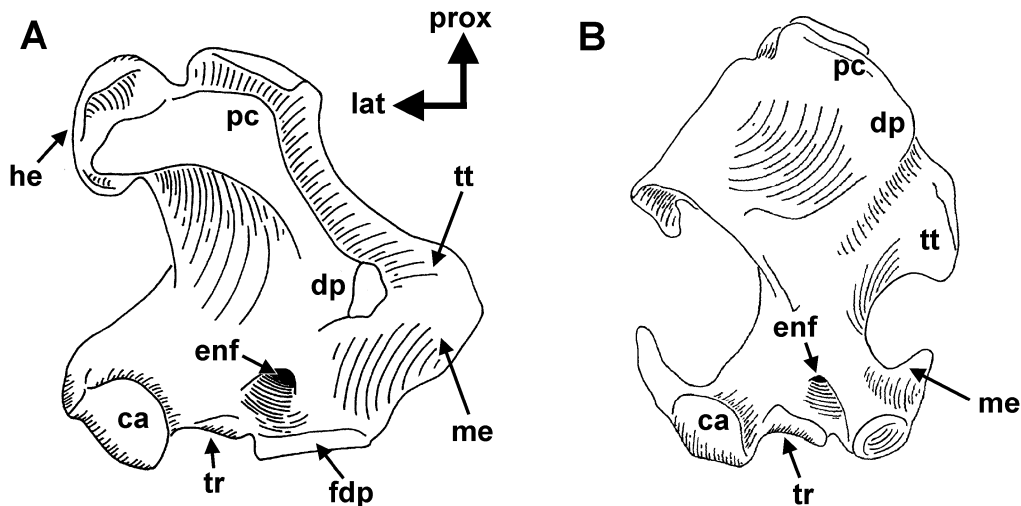
Fig. 13.2.   Anterior views of the humeri of a proscalopid and a talpid. **A,** left humerus of *Proscalops* (AMNH 12864), with image reversed to facilitate comparisons with figure 13.1; **B,** right humerus of *Talpa europaea* (AMNH 119495). See figure 13.1 for abbreviations. Note that in *Proscalops* the deltoid process is much more distinct and more distal than in *Talpa*.

13.1B). Partial fusion of the teres tubercle and medial epicondyle could be a synapomorphy of *Oligoscalops* if complete fusion of these features, such as in *Mesoscalops*, evolved from a taxon in which these features are unfused. However, if the completely fused state evolved from a taxon with partial fusion, then partial fusion is instead a synapomorphy of the clade including *Oligoscalops*, *Proscalops*, and *Mesoscalops*. In addition to a similar morphology, the small size of the Mongolian specimens is within the range of *Oligoscalops*, the smallest of the proscalopid genera (table 13.2).

The humeri from Mongolia are clearly different from those of *Proscalops* and *Mesoscalops*. Humeri of *Proscalops* differ from the Mongolian specimens in (1) being on average 1.5 times larger, (2) having a smaller notch between the teres tubercle and medial epicondyle, and (3) having the a flat edge for the flexor digitorum profundus fossa, in anterior view. *Mesoscalops* humeri are clearly different from the Mongolian humeri in hav-

TABLE 13.2
Measurements of Proscalopid Humeri
Note that *Oligoscalops galbrethi* is about the size of the four Mongolian specimens. All measurements are in millimeters. ''−'' means broken, not applicable, or unavailable. Measurements B, C, D, and E follow Reed and Turnbull (1965).

	B	C	D	E
MAE 9423	3.7	4.9	—	2.7
MAE 91-9418	3.5	4.6	5.5	2.1
MAE-SG-91-10449	3.7	4.8	5.9	2.0
MAE-SG-91-10450	3.5	4.9	6.0	2.0
Oligoscalops galbrethi[a]	4.0	4.2	6.9	1.6
Mesoscalops montanensis[b]	—	9.0	9.3	3.4
Proscalops evelynae[c]	—	7.6	8.4	—

[a]Measurements for *Oligoscalops galbrethi* are a mean of several specimens as reported by Reed and Turnbull (1965: 166).
[b]Measurements are for UWBM 54708 and are taken from Barnosky (1982b).
[c]Measurements are from SDSM 54250 and are taken from Barnosky (1982b).

ing complete or near complete fusion of the teres tubercle and medial epicondyle (Barnosky, 1981). The Mongolian humeri are easily distinguished from *Cryptoryctes*, the most primitive proscalopid, in having (1) partial fusion of the teres tubercle and the medial epicondyle and (2) a rounded medial edge of the trochlea, instead of a sharp ridge.

Although the four humeri from Mongolia are similar to those of the fossorial mammals *Notoryctes* (marsupial mole) and *Dasypus* (nine-banded armadillo) in having a pectoral crest, there are also major differences. The humeri of both *Notoryctes* and *Dasypus* lack the following characters of the Mongolian humeri: teres tubercle, distinct deltoid process, large medial epicondyle, and pit for the flexor digitorum profundus. *Notoryctes* also lacks a bicipital groove while that groove in *Dasypus* is restricted to the proximal end of the humerus. Based on these differences, it is clear that the Mongolian humeri are neither those of dasypodids nor of *Notoryctes*.

Chrysochloridae is a family of fossorial mammals that has traditionally been allied with talpids, soricids, erinaceids, tenrecids, and solenodontids (Butler, 1988; MacPhee and Novacek, 1993), but more recently has been allied with proboscideans, *Orycteropus*, sirenians, and hyracoids among others (Stanhope et al., 1996, 1998; Murphy et al., 2001; Madsen et al., 2001). The humerus of *Chrysochloris* (e.g. AMNH-M 236000) shares the following fossorial adaptations with the four humeri from the Mongolia: enlarged medial epicondyle, pectoral crest, and deltoid process. The last character is almost certainly convergent because the deltoid process of *Chrysochloris* is a small flange, whereas in proscalopids it is a robust process with an ovoid cross section. Despite these similarities, the preponderance of evidence strongly supports referral of the Mongolian humeri to Proscalopidae. The above-listed similarities between *Chrysochloris* and the Mongolian humeri also occur in proscalopids. In addition, the Mongolian humeri, like those of proscalopids but unlike chrysochlorids, have a teres tubercle and a pit for the flexor digitorum profundus.

The Mongolian humeri bear some resemblance to the Oligocene palaeaonodonts *Epoicotherium* and *Xenocranium*. As with the humeri of *Oligoscalops*, the humerus in advanced palaeanodonts has a pectoral crest, bicipital groove, and an enlarged medial epicondyle (Rose and Emry, 1983). *Xenocranium* also has a teres tubercle, although unlike those of the Mongolian humeri, the *Xenocranium* teres tubercle is small and clearly separated from the medial epicondyle. Palaeanodont humeri differ from those of *Oligoscalops* and other proscalopids in lacking a medially pointing deltoid process and a pit for the flexor digitorum profundus (Rose and Emry, 1983: fig. 8).

In summary, the anatomy of the Mongolian humeri clearly allies them with proscalopids and not with other fossorial mammals. Furthermore, the Mongolian specimens are referred to the proscalopid genus *Oligoscalops* based on their size and the occurrence of a possible synapomorphy of this genus. I consider the allocation to genus, but not to family, tentative until more complete material is recovered.

ORIGIN AND BIOGEOGRAPHY OF PROSCALOPIDAE

Prior to the discovery of proscalopids from Mongolia, Proscalopidae was considered an endemic North American family with little biogeographic significance. The discovery of proscalopids in Asia raises the question, how did they get there? Although the fossil record and our current knowledge of mammalian phylogeny are not sufficient to definitively answer this question, I will present three hypotheses: (1) Proscalopidae originated in Eurasia and dispersed to North America, (2) Proscalopidae originated in Africa and then dispersed to Asia and North America, and (3) Proscalopidae originated in North America and then dispersed to Asia. One caveat to the following biogeographic discussion is the bias in the fossil record. Thousands of fossils have been collected from the Hsanda Gol Formation, but only a handful of specimens are proscalopids. *Oligoscalops* may be present but undetected at localities that have not been thoroughly prospected.

One possible way to determine the place of origin of Proscalopidae is to ascertain the distribution of the oldest representatives of

its sister-group. Many authors have tentatively suggested that the sister-group to Proscalopidae is Talpidae (Matthew, 1928; Reed, 1961; Reed and Turnbull, 1965; McKenna and Bell, 1997). Although Barnosky (1981) was skeptical of a close relationship between talpids and proscalopids, he did list the following similarities between the groups: (1) simplified P4, (2) W-shaped ectoloph, and (3) torsion of forelimb such that the radius does not cross the ulna. Of the three, only the last is demonstrably derived as compared to other eulipotyphlans. Three previously unmentioned characters of the humerus that may also support a close relationship between Proscalopidae and Talpidae, are (1) center of humeral head lateral to lateral edge of humeral shaft (fig. 13.2A: he), (2) portion of bicipital groove proximal to the deltoid process is oriented distomedially (fig. 13.2: bg), and (3) long axis of humeral head oriented distolaterally, not parallel to the long axis of the humeral shaft. These characters occur in all talpids and proscalopids examined (table 13.1) or considered in this study with the exception that the third character does not occur in the primitive talpid *Uropsilus*. A relationship between talpids and proscalopids has been recognized in taxonomy by either having Proscalopinae a subfamily within Talpidae (Reed, 1961) or by placing Talpidae and Proscalopidae as the only families in the superfamily Talpoidea (Barnosky, 1981; McKenna and Bell, 1997). The oldest talpids are from the late Eocene of Europe (Sigé et al., 1977); therefore, the fossil record suggests this family originated in Europe. Talpids do not appear in North America for another 6 million years (ca. 29 Ma) (Tedford et al., 1987; Woodburne and Swisher, 1995). Further support for a Eurasian origin for Talpidae was published by Whidden (2000). Based on a cladogram developed from 58 myological characters, he found that it was most parsimonious to have talpids originate in Asia and then disperse to North America. If talpids arose in Eurasia and Proscalopidae and Talpidae are sister-taxa, then proscalopids likely have a Eurasian origin as well.

Matthew (1906) advocated that a humerus from South Dakota, which he later designated as the type of *Arctoryctes* (Matthew, 1907), belonged to a chrysochlorid. Matthew's hypothesis has important biogeographic implications because all extant and extinct chrysochlorids are restricted to the continent of Africa (McKenna and Bell, 1997). Although Matthew (1928) was less sure of a close relationship between chrysochlorids and proscalopids, other aspects of proscalopid anatomy are similar to chrysochlorids. Both Chrysochloridae and Proscalopidae have ridges on the lateral sides of the tip of the rostrum (Reed, 1961). Although the medial epicondyle of talpids is large, it is grossly enlarged in proscalopids and chrysochlorids. As in talpids and proscalopids, but unlike in most other mammals, the radius does not cross the ulna in chrysochlorids (Barnosky, 1981). Despite these similarities, more characters are shared between talpids and proscalopids, and the similarities between chrysochlorids and proscalopids have been attributed to convergence (Barnosky, 1981).

If Proscalopidae and Chrysochloridae are closely related, then it seems likely that either (1) both lineages originated in Asia with Chrysochloridae dispersing to Africa or (2) both lineages originated in Africa with Proscalopidae dispersing to Asia. Neither scenario receives support from the fossil record because proscalopids have not been found in Africa and chrysochlorids have not been found in Asia. However, recent molecular studies are consistent with the second hypothesis but not the first. Phylogenetic analyses of DNA sequence data (Stanhope et al., 1996, 1998; Murphy et al., 2001; Madsen et al., 2001), as well as an apparently unique nine-base-pair deletion (Madsen et al., 2001), support Afrotheria, a clade of endemic African mammals plus the aquatic Sirenia. The fact that all terrestrial members of the group (i.e., Proboscidea, Macroscelidea, Tubulidentata, Hyracoidea, Tenrecidae, and most importantly Chrysochloridae) are believed to have an African origin has been interpreted by Stanhope et al. (1998) to mean that Afrotheria evolved and diversified in Africa. Unfortunately there is no way to determine whether Proscalopidae is a member of Afrotheria because no dental or osteological synapomorphies have been identified for the group (Asher, 1999).

The oldest and most primitive proscalopid

is known from North America. Humeri of the proscalopid *Cryptoryctes* (Reed, 1954) have been found in the Chadronian Pipestone Springs local fauna of Montana, which is currently estimated to be 34 Ma (Prothero and Emry, 1996). Allocation of *Cryptoryctes* to Proscalopidae is supported by the following: a distinct deltoid process that is separated from the lesser tuberosity by a large gap, a large teres tubercle, a greatly enlarged medial epicondyle, a humeral head that is lateral to the humeral shaft, and a pit for the flexor digitorum profundus. Despite these similarities, *Cryptoryctes* is more primitive than all other proscalopids in having the teres tubercle in a more proximal position and separate from the medial epicondyle (Barnosky, 1981). Compared to the oldest North American proscalopids, the only known Asian proscalopids are 2 million years younger (ca. 32 Ma). Thus the geologic record suggests that Proscalopidae originated in North America and then immigrated to Asia.

The co-occurrence of *Oligoscalops* in North America and Asia, but not Europe, is unusual. Although several genera of carnivorous mammals from the Hsanda Gol Formation have a holarctic distribution (e.g. *Hyaenodon*, *Palaeogale*), only the rodent genus *Haplomys* occurs in the Oligocene of North America and Asia but not Europe (Matthew and Granger, 1924; McKenna and Bell, 1997; Daxner-Höck et al., 1997). This pattern is consistent with the findings of previous authors who noted that faunal exchange between North America and Asia was low during the early Oligocene (Woodburne and Swisher, 1995). The most notable biogeographic event during the Oligocene was the *Grande Coupure*, when Asian taxa immigrated to Europe at the beginning of the Oligocene. The absence of proscalopids in Europe would be consistent with the emigration of Proscalopidae from North America to Asia after the *Grande Coupure* (ca. 33 Ma), which occurred prior to or at the beginning of the deposition of the Hsanda Gol Formation (Dashzeveg, 1996; Meng and McKenna, 1998). Alternatively, if proscalopids immigrated to North America from Asia, then they must have done so in the late Eocene because of the Chadronian occurrence of *Cryptoryctes* in North America. The dispersal of *Oligoscalops* from North America into Asia, or vice versa, almost certainly occurred by means of Beringia, which at that time served as a filter (McKenna, 1973). The attributes that allowed *Oligoscalops*, but not most other mammals, to disperse via the Beringia filter will likely remain unknown.

One way to test competing hypotheses for the place of origin of Proscalopidae is to conduct a phylogenetic analysis with broad taxonomic scope, which would include proscalopids, micropternodontids, apternodontids, chrysochlorids, talpids and other extant eulipotyphlans, and putative members of Afrotheria. Although this is a large undertaking, a likely starting point would be to code Proscalopidae for the morphological characters in the matrix of Asher (1999), which includes 35 mammalian taxa scored for 71 characters. In addition to determining the most supported phylogenetic position for Proscalopidae, the inclusion of Proscalopidae into phylogenetic analyses may change our perceived relationships between other taxa. Although most of the anatomy of Proscalopidae is highly derived, this family does share some characters with talpids and chrysochlorids. Butler (1988) suggested that Talpidae and Chrysochloridae were sister-taxa, and this result was supported by some of the cladistic analyses of Asher (1999). Whether or not proscalopids are closely related to Chrysochloridae, Talpidae, or both remains to be seen, but the unique anatomy of Proscalopidae suggests that resolving their systematic position will have ramifications for eulipotyphlan, if not higher-level mammalian, phylogeny.

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