

Chapter 23

Tedford's Gerbils from Afghanistan

LAWRENCE J. FLYNN,¹ ALISA J. WINKLER,² LOUIS L. JACOBS,³ AND
WILL DOWNS⁴

ABSTRACT

Thirty-five years ago Dick Tedford and Len Radinsky collected the remains of three individuals of a new gerbil in the hill country of Afghanistan. Tedford's gerbil is a new, large species of a widespread late Neogene genus, *Abudhabia*. The material is extraordinarily complete, including three crania and many of the postcrania. The extinct taxon is clearly a gerbil based on dental and cranial features, while it has a relatively underderived basicranium. The long hind limb proportions appear strongly derived. The bulla is enlarged and the mastoid is little inflated, not as inflated as in many gerbils. The fossil form is a primitive taterilline and suggests homoplasy in ear structure and dentition among modern taxa.

INTRODUCTION

“Another magnificent day, this one in the field—at last!” So opens the October 13, 1967, entry in the field book of the brand new curator from the American Museum of Natural History, Richard H. Tedford. Seeking a new field-based project to kick off his career in New York, Tedford had planned with Leonard Radinsky to open an investigation of early Tertiary deposits in Afghanistan along the border with Pakistan. They predicted that deltaic deposits along the southern margin of the Asian continental plate ought to include terrestrial facies and a hitherto unknown record of early Tertiary evolution in southern Asia—all of this hypothesized as plate tectonics was gelling into a coherent theory. Over 30 years later, the prediction that fossiliferous early Tertiary deposits exist along the border with Pakistan has proven true (Gingerich et al., 2001).

The intrepid paleontologists had planned for everything—except mountains of bureaucracy. To be fair, they had asked administra-

tors to facilitate a very difficult trip to a problematic tribal area, and this was no small feat. Yet they were stuck for days awaiting clearance. This led to the field excursion of October 13, a survey of the geologic setting of the late Neogene basins to the east of Kabul.

The American paleontologists were in contact with German researchers who, in addition to French geologists, had a long tradition of field study in Afghanistan. They set out to observe the field geology described in the published literature. East of Lataband Pass in the Sarobi Basin, the Kabul River valley has a thin veneer of late Cenozoic fill smoothing out the paleorelief of the late Precambrian bedrock. This is the Lataband Series of Mennessier (1961). Its thickness approximately equals the maximum paleorelief according to Tedford's field notes, as peaks of Precambrian poke through the fill. The Lataband Series is mainly conglomeratic, but includes lenses of finer grained buff and greenish micaceous sandstones and silt-

¹ Assistant Director, Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA 02138.

² Department of Geological Sciences, Southern Methodist University, Dallas, TX 75275.

³ Professor, Department of Geological Sciences, Southern Methodist University, Dallas, TX 75275.

⁴ Deceased. Formerly Bilby Research Center, Northern Arizona University, Flagstaff, AZ 86011.

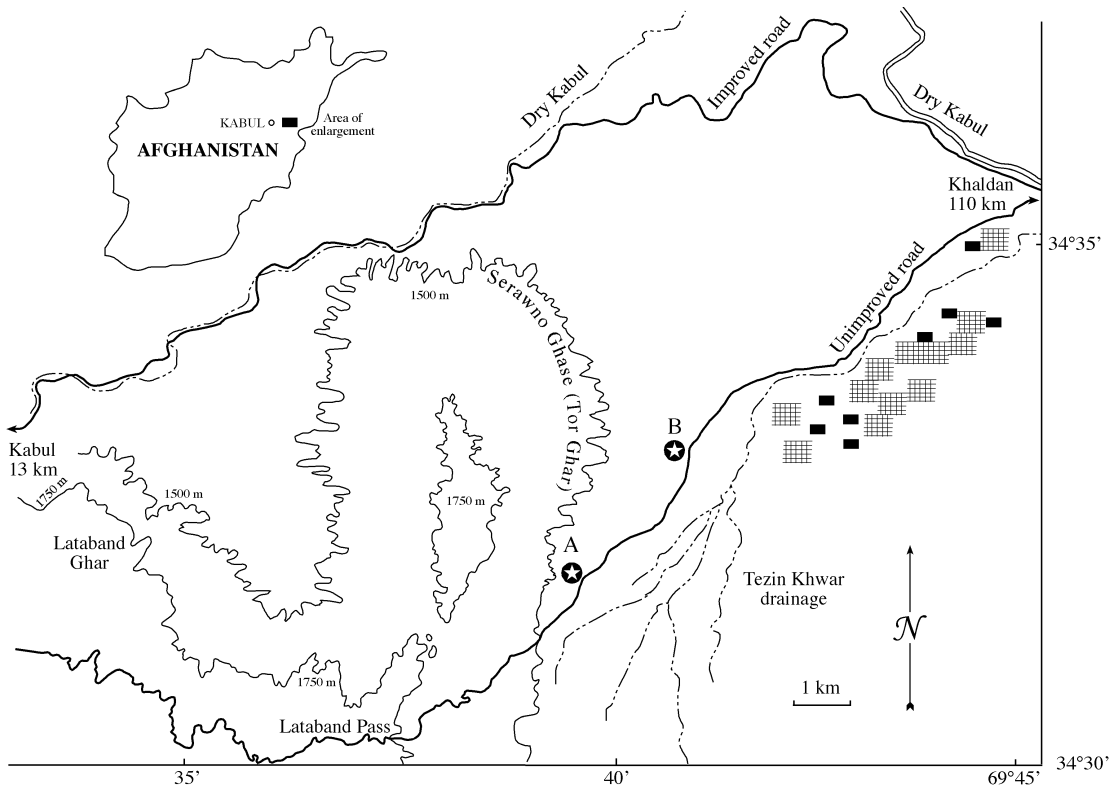


Fig. 23.1. Locality map adapted from the field map used by Tedford and Radinsky, Fairchild Aerial Surveys sheet 510 D1, original scale 1:50,000. The local hill, Tor Ghar, exceeding 1750 m is indicated. **A**, Locality of *Abudhabia*. **B**, Approximate location of fossils collected by the French team of Heintz et al. (1978; see also Flynn et al., 1983). Black rectangles are dwellings; hatching indicates fields.

stones. These finer deposits yield fossil vertebrates sporadically, and Tedford's gerbils are among the first ever recovered in the Sarobi region.

Traveling eastward from Kabul (fig. 23.1), and after the Lataband Pass on the way to Sarobi, Dick and Len descended into the valley of the large watercourse Tezin Khwar, and stopped their Land Rover at the promising exposures near the base of Tor Ghar (hill; fig. 23.1). The fine-grained deposits there yielded three skulls plus some postcrania of a fossil rodent that shares derived features with modern gerbils. The association of the specimens, the degree of articulation, and lack of other fossils nearby indicate peculiar taphonomic or behavioral circumstances contributing to fossilization, such as preservation in burrows (Tedford, personal commun.) They are extremely interesting in that they

illustrate most, but not all, autapomorphies expected in south Asian gerbils, and a new aspect of the Afghan fossil record.

Late Tertiary fossils are apparently fairly common in the basin fill of Afghanistan's mountainous terrain, but documentation has lagged due to civil unrest. Nonetheless, significant advances have been made by French and German teams. Early work resulted in recovery of a few rhizomyid rodent specimens from the Bamian region, 150 km west-northwest of Kabul (Lang and Lavocat, 1968; revised by Flynn, 1983). Raufi and Sickenberg (1973) reported on mammal remains from east of Sarobi (a town 50 km east of Kabul), including camel (Pliocene index fossil; see Flynn, 1997) and a heavily worn jaw of *Rhizomyides*, possibly *R. carbonelli* Brandy (1979), known from the early Pliocene of Kabul Basin. In the late 1970s

French colleagues had an active research program well underway in Afghanistan. Although the field work was cut short by war, publications continue (e.g., Sen, 2001), and several discuss the Sarobi Basin (e.g., Heintz et al., 1978; Sen et al., 1979). These studies show the Lataband Series to yield late Tertiary fossils. Miocene localities are known to the south, but all indications of age for Sarobi Basin deposits are Pliocene. Hadji Rona in the north of the basin appears to be later Pliocene based on presence of the arvicoline *Mimomys* and advanced murids (Sen et al., 1979). This age is consistent with remains of a reduncine antelope (Heintz et al., 1978) and a derived tachyoryctine rodent (Flynn et al., 1983) from near the area explored by Tedford and Radinsky.

Tedford and Radinsky recognized their Afghan fossils as gerbils, and the specimens were mentioned in Lay's (1972) study as *Tatera* cf. *T. indica*, a personal communication from Tedford. The specimens, with illustrations by Margaret Stevens, were turned over to the late Marie Lawrence for a study which, unfortunately, could not be completed.

Gerbils are a group of rodents adapted to arid conditions and currently distributed in southern, eastern, and northern Africa, the Middle East, and across Asia. Temporally they are best known from the late Miocene through the Recent, but some primitive species of early Miocene age are attributed to the group (Wessels, 1998). Their diversity is greatest in North Africa, but they are broadly characteristic of the Great Palaeartic Desert. They are noted for inflation of the bulla, a characteristic rodent adaptation for life in arid climates. This feature in gerbils is most thoroughly reviewed by Lay (1972). There is no comprehensive phylogenetic analysis of muroid rodents to guide hierarchical ranking, but Musser and Carleton (1993) utilize subfamily Gerbillinae, while Chaline et al. (1977) and Wessels (1998) recognize gerbils at the family rank (Gerbillidae) with three subfamilies (Gerbillinae, Taterillinae, and Myocricetodontinae). The classification of McKenna and Bell (1997) is more complex, recognizing Gerbillinae as a subfamily of Muridae, with four tribes (Myocricetodontini, Ammodillini, Gerbillini, and Taterillini).

Modern gerbils, for the most part, can be

distinguished at least at the generic level by dental characteristics and by derived features related to expansion of the cavities surrounding the middle and inner ear. The fossil record of gerbils is based primarily on isolated teeth, with very little cranial or postcranial material known or described. This presents problems in documenting the pattern and sequence of acquisition of derived features, in incorporating the fossil record into a testable pattern of phylogeny, and in evaluating the origin of the group. Our interest in gerbils derives from our work on muroid rodents from the Siwalik Group of Pakistan (Flynn and Jacobs, 1999) and in East Africa (Winkler, 2003). The gerbil samples previously available from these areas were isolated teeth and jaw fragments. The skulls and postcrania of Tedford's gerbil from Afghanistan provide a unique opportunity to evaluate a fossil gerbil more thoroughly than has been possible previously.

Our purposes in this paper are to provide a preliminary description and comparison of the gerbils found by Tedford and Radinsky and to place them in context by evaluating the derived characters that make them gerbils. They are compared dentally with other fossil gerbils, which helps to elucidate the pattern of acquisition of derived dental features in these rodents. This study is preliminary because there exists no comprehensive phylogenetic analysis for gerbils, nor have we reviewed all characters in all gerbil taxa. Moreover, additional preparation of the Afghan specimens to expose more of the postcrania and skull might reveal significant characters, such as those found inside the bulla in the middle ear.

The primary references for this work are the anatomical and functional review of living gerbils by Lay (1972), the review of the gerbil fossil record by Tong (1989), and the comparative studies of Pavlinov (1985, 1988). Tong's work was based on the sequence of Plio-Pleistocene fossils, mainly teeth, from the Maghreb region (Algeria, Morocco, and Tunisia) of North Africa. She also reviewed dental and cranial morphology of modern taxa, examined briefly some postcranial proportions, and compared her results to early molecular work. The inflation of the bulla in gerbils necessitates architectural

changes in the skull that affect the arrangement of foramina. Useful references include Bugge (1970), Hill (1935), Musser (1982), Musser and Newcomb (1983), and Wahlert (1985).

ABBREVIATIONS

- AMNH American Museum of Natural History, New York
 MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA

SYSTEMATIC PALEONTOLOGY

FAMILY MURIDAE ILLIGER, 1811

SUBFAMILY GERBILLINAE GRAY, 1825

TRIBE TATERILLINI CHALINE ET AL., 1977

Abudhabia de Bruijn and Whybrow, 1994

DIAGNOSIS AS EMENDED BY DE BRUIJN (1999: 188): "The m1 always has the posterior cingulum developed as an isolated cusp. The M2 and m2 have remnants of the anterior cingulum. Cusp pairs of the M1, M2, and m2 form transverse ridges. The m1 has alternating main cusps and an anteroconid with a posterolabially directed crest as in most cricetids. The upper incisor has one longitudinal groove."

COMMENTS: The cheek teeth of *Abudhabia* are characterized by suppression of longitudinal connections of transverse crests, and by emphasis of transverse valleys. The cusps of m1 are not directly opposed pairs, but staggered slightly; hence, the cross-valleys are oblique. Upper first and second molars show a remnant of a posterior cingulum, except in advanced wear. The cingulum is represented by a posterior bulge at the midline, near the hypocone. Lower first and second molars show a stronger posterior cingulum, which in some species can be manifested as a separate, low midline cusp. This is the case in the type species. This cusp is quickly fused by wear with the posterolingual arm of the hypoconid. In other species, the teeth show only a bulge in this area, not a distinct cusp. Third molars are small and simple, the uppers with a posterior cusp representing the reduced hypocone-metacone complex. There are no other accessory cusps on teeth; notably the enterocone is lacking on M1, and the anteroconid of m1 is simple (lacking protoconulid).

Information supplied by the Afghan fossil remains shows that *Abudhabia* had an auditory region less inflated than in most living gerbils, and that the limb proportions are designed for greater power in hind limb extension than in living forms. The mastoid is uninflated, unlike *Tatera*.

Abudhabia radinskyi, new species

HOLOTYPE: AMNH 133507, including an incomplete skull and lower jaws, plus a partial skeleton (consisting of vertebrae, ribs, scapula, clavicle, humerus, radius, ulna, distal tibia).

HYPODIGM: AMNH 133507–133510. AMNH 133508 includes the skull, lower jaws, and articulated cervical vertebrae. AMNH 133509 has an incomplete cranium (without lower jaws), and associated postcranial fragments (prepared elements include scapula, radius and humerus fragments, partial innominate, tibiae, proximal right femur, left pes). AMNH 133510 is blocks of matrix bearing scattered, unprepared bone.

ETYMOLOGY: After vertebrate paleontologist Leonard Radinsky, Tedford's field companion and cofinder of the gerbil remains, in accordance with Tedford's wish.

TYPE LOCALITY: East Base, Tor Ghar. Laband Series, in local gray micaceous sandstone immediately above green-gray silty sandstone with limonite-stained root casts (field notes of Tedford). One specimen (AMNH 133508) occurs as a concretion.

DIAGNOSIS: Largest known species of the genus (table 23.1). Molar dimensions at least 8% greater than in any known species of *Abudhabia*. Distinct from all other species except *A. sp.* from Kenya in lacking any trace of longitudinal crests (derived). Remnant of anterior cingulum on M2 reduced relative to *A. baynunensis*, *A. pakistanensis*, and *A. kabulense* (derived). Higher crowned than *A. pakistanensis*. Anteroconid of m1 with reduced labial arm (no protoconulid) and triangular in outline, compared to more rhomboid-shaped anteroconid of *A. baynunensis* and *A. kabulense*; anteroconid wider on *A. sp.* Transverse crests of m1 not so oblique (derived toward condition of *Tatera*); third loph of m1 relatively transverse compared to that of *A. baynunensis* and *A. sp.*, but within

TABLE 23.1

Occlusal Measurements (mm) for Taxa that Have Been Included in *Abudhabia*

Sources: *A. radinskyi* (described herein), *A. baynunensis* (de Bruijn and Whybrow, 1994; de Bruijn, 1999), *A. kabulense* (Sen, 1983), *A. cf. A. kabulense* (Patnaik, 1997), *Abudhabia* sp. (Winkler, 2003), *A. pakistanensis* (Flynn and Jacobs, 1999), *Protatera yardangi* (Munthe, 1987).

Tooth and measurement	Taxon						
	<i>Abudhabia radinskyi</i>	<i>Abudhabia baynunensis</i>	<i>Abudhabia kabulense</i>	<i>A. cf. A. kabulense</i>	<i>Abudhabia</i> sp.	<i>Abudhabia pakistanensis</i>	<i>Protatera yardangi</i>
M1 length							
<i>N</i>	4	1	3	—	—	1	2
Range	3.28–3.37	2.47	2.91–3.06	—	—	2.68	2.23–2.25
\bar{x}	3.30	2.47	2.98	—	—	2.68	2.24
M1 width							
<i>N</i>	3	1	3	—	—	1	4
Range	2.22–2.46	1.75	2.00–2.13	—	—	1.84	1.50–1.58
\bar{x}	2.31	1.75	2.08	—	—	1.84	1.54
M2 length							
<i>N</i>	4	4	7	2	—	1	—
Range	1.72–1.89	1.55–1.59	1.76–1.96	1.53–1.65	—	1.68	—
\bar{x}	1.81	1.58	1.85	1.59	—	1.68	—
M2 width							
<i>N</i>	4	4	8	2	—	1	—
Range	2.05–2.30	1.54–1.75	1.76–2.06	1.73–1.89	—	1.76	—
\bar{x}	2.22	1.60	1.93	1.81	—	1.76	—
M3 length							
<i>N</i>	4	3	3	—	—	—	—
Range	0.90–1.15	0.82–0.97	0.96–1.21	—	—	—	—
\bar{x}	1.05	0.88	1.10	—	—	—	—
M3 width							
<i>N</i>	4	3	3	—	—	—	—
Range	1.40–1.56	0.95–1.10	1.29–1.40	—	—	—	—
\bar{x}	1.48	1.02	1.36	—	—	—	—
m1 length							
<i>N</i>	2	4	7	—	1	—	2
Range	3.04	2.22–2.46	2.60–2.85	—	2.56	—	2.40–2.50
\bar{x}	3.04	2.34	2.73	—	2.56	—	2.45
m1 width							
<i>N</i>	2	4	7	—	1	—	3
Range	2.13–2.22	1.45–1.59	1.79–1.94	—	1.60	—	1.60
\bar{x}	2.18	1.52	1.89	—	1.60	—	1.60
m2 length							
<i>N</i>	2	3	8	—	—	—	2
Range	1.97	1.50–1.67	1.70–1.89	—	—	—	1.40–1.43 ^a
\bar{x}	1.97	1.59	1.84	—	—	—	1.42 ^a
m2 width							
<i>N</i>	2	3	7	—	—	—	1
Range	2.05–2.13	1.37–1.60	1.81–1.97	—	—	—	1.48
\bar{x}	2.09	1.52	1.89	—	—	—	1.48
m3 length							
<i>N</i>	1	6	5	—	—	—	—
Range	1.15	0.76–0.98	1.02–1.14	—	—	—	—
\bar{x}	1.15	0.87	1.09	—	—	—	—
m3 width							
<i>N</i>	1	6	5	—	—	—	—
Range	1.48	0.95–1.20	1.19–1.48	—	—	—	—
\bar{x}	1.48	1.05	1.32	—	—	—	—

^aEstimated.

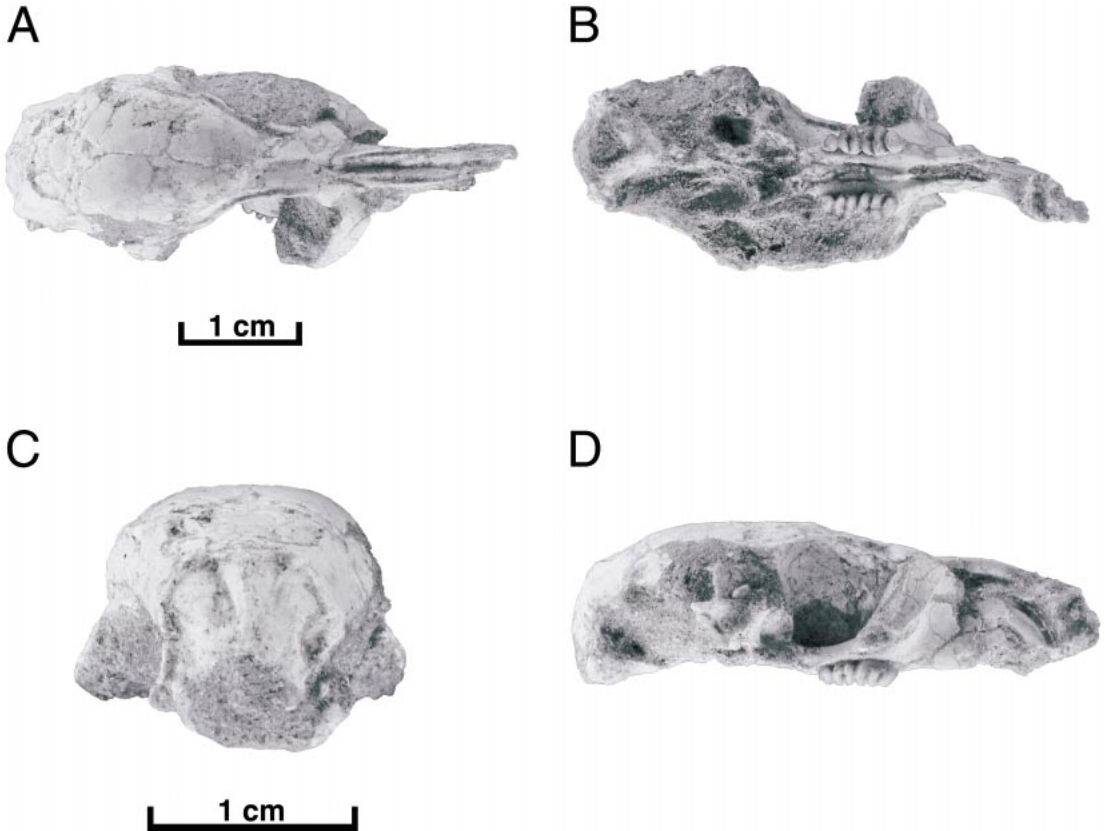


Fig. 23.2. *Abudhabia radinskyi*, AMNH 133509. Skull in (A) dorsal, (B) ventral, (C) posterior, and (D) lateral views. A, B, D at same scale, anterior to right.

the range of variation of *A. kabulense* (derived); second loph of m1 more oblique (not as derived) as that of *A. sp.*

DESCRIPTION OF SKULL

DORSAL VIEW (fig. 23.2A): The nasals are long and narrow, extending anteriorly beyond the incisors. Laterally, the nasals are bordered by the premaxillaries. The nasals and premaxillaries form a transverse suture with the frontals, posterior to the infraorbital foramen, at the level of the anterior extent of the orbit. The maxillaries in turn border the premaxillaries and constitute the anterior root of the zygomatic arch. The maxillaries flare laterally, then anteriorly, to form the zygomatic plate, which is more expanded than in *Rattus*. The lacrimals are large, typical for gerbils, but unclear in the specimens at hand. The frontals taper gently anteriorly, and are

little constricted at the orbits. The supraorbital ridge runs along the dorsal margin of the orbit, forming a narrow shelf. Unlike *Rattus*, the ridges are less convergent, lying only along the margin and then fading anteriorly near the suture with the premaxilla. The ridges do not extend onto the dorsomedial surface. The supraorbital ridge ends posteriorly in a small knob at the convergence of the frontal, parietal, and squamosal. The frontoparietal suture is concave anteriorly. A parasagittal crest runs posteriorly from the knob at the frontal-parietal-squamosal convergence, continuing the supraorbital ridge. The crest follows the parietal-squamosal suture until about the level of the squamosal root of the zygomatic arch, posterior to which the crest continues to the supraoccipital. The parietal-squamosal suture dips laterally and follows a secondary crest, which fades out as it

approaches the supraoccipital. A lambdoidal crest is formed in the region of the parietal-supraoccipital suture, more similar to that of *Tatera indica* than *Meriones*. The posterior portion of the parietal, ventral to the parasagittal crest and above the suture with the squamosal, is rectangular in shape. The large interparietal lies between the parietals and supraoccipital, tapering laterally. The anterior processes of the supraoccipital, which would truncate the interparietals laterally, appear to be absent.

VENTRAL VIEW (fig. 23.2B): The premaxillary-maxillary suture falls in the anterior middle portion of the anterior palatine foramen. The anterior palatine foramen extends posteriorly to about the anterior margin of M1. The posterior palatine foramen is elongate, about a third the length of the anterior palatine foramen, and much longer than in *Rattus*. The maxillo-palatine suture intersects the posterior palatine foramen. The pterygoid fossa is short and roundly triangular, but not deep, more similar to *Tatera indica* than *Meriones*. The mesopterygoid fossa is narrow. The foramen ovale lies at the posterolateral extent of the pterygoid fossa at the anterior limit of the tympanic bulla. The presence of an accessory foramen ovale cannot be determined. In *Tatera indica*, a bridge off the pterygoid is present, but quite delicate, and is associated with the accessory foramen ovale. If such a bridge was present in *Abudhabia*, it was also quite delicate. Wahlerl (1974, 1985) considered possession of an accessory foramen ovale to be a rodent synapomorphy that is lost in more advanced forms. In gerbils with the bulla more inflated than in *Tatera*, the accessory foramen ovale is lost. Posterolateral to the foramen ovale the medial lacerate foramen lies in the fissure anterior to the auditory bulla. A postglenoid foramen is present near the bulla, posterior to the glenoid fossa on the ventral surface of the squamosal root of the zygomatic arch. The basisphenoid and basioccipital are narrow. No complete, undistorted bullae are preserved and visible; however, the tympanic portion, while not appearing to be greatly inflated, is elongate anteroposteriorly. The mastoid portion does not appear to be inflated. Tong (1989) mentions a small foramen on the ventral surface of the maxilla anterior

to M1 as present in gerbils, but it is not present in these specimens.

LATERAL VIEW (fig. 23.2D): In lateral view, the nasals are shown to extend anterior to the incisors, and the incisors are strongly recurved. Opisthodonty is emphasized by an increase of the length of arc of the incisors, extending their apices rearward (see Landry, 1957). The zygomatic plate is developed on the maxillary root of the zygomatic arch and closes off the infraorbital foramen. While the anterior margin of the zygomatic plate is not preserved in any specimen, the remaining portions are consistent with an anteriorly expanded zygomatic plate. Preserved portions clearly extend anterior to the nasolacrimal foramen and conceal it from view. The sphenopalatine foramen is large, anteroposteriorly elongate, and sits approximately over the posterior half of M1, similar to *Tatera indica* and *Meriones*, but unlike *Rattus*. The frontal folds ventrally to form the dorsomedial wall of the orbit. A small ethmoid foramen is present in the frontal, anterodorsal to the optic foramen, and above the level of contact between M1 and M2.

Ventral to the frontal is the orbitosphenoid. The optic foramen in the orbitosphenoid is large, its anterior end at the level of the posterior border of M2. The ventral margin is straight while the dorsal border is convex. The large sphenoid fissure sits posteroventral to the optic foramen, separated from it by a thin process of the orbitosphenoid. Its posterior limit is in the alisphenoid. Its upper limit does not reach the level of the upper border of the optic foramen.

The alisphenoid is comparable to that of *Tatera indica*. The foramen ovale sits opposite the lateral process of the alisphenoid, which helps define the pterygoid fossa, separated by a thin piece of bone from the medial lacerate foramen.

The squamosal forms the lateral surface of the skull dorsal to the alisphenoid and tympanic bulla and ventral to the frontal and parietal. The glenoid fossa for the articulation of the dentary is a broad troughlike groove on the ventral surface of the squamosal root of the zygomatic arch. A postglenoid foramen may be present. The zygomatic root extends a short distance anteriorly along the skull as a crest that elongates the glenoid for-

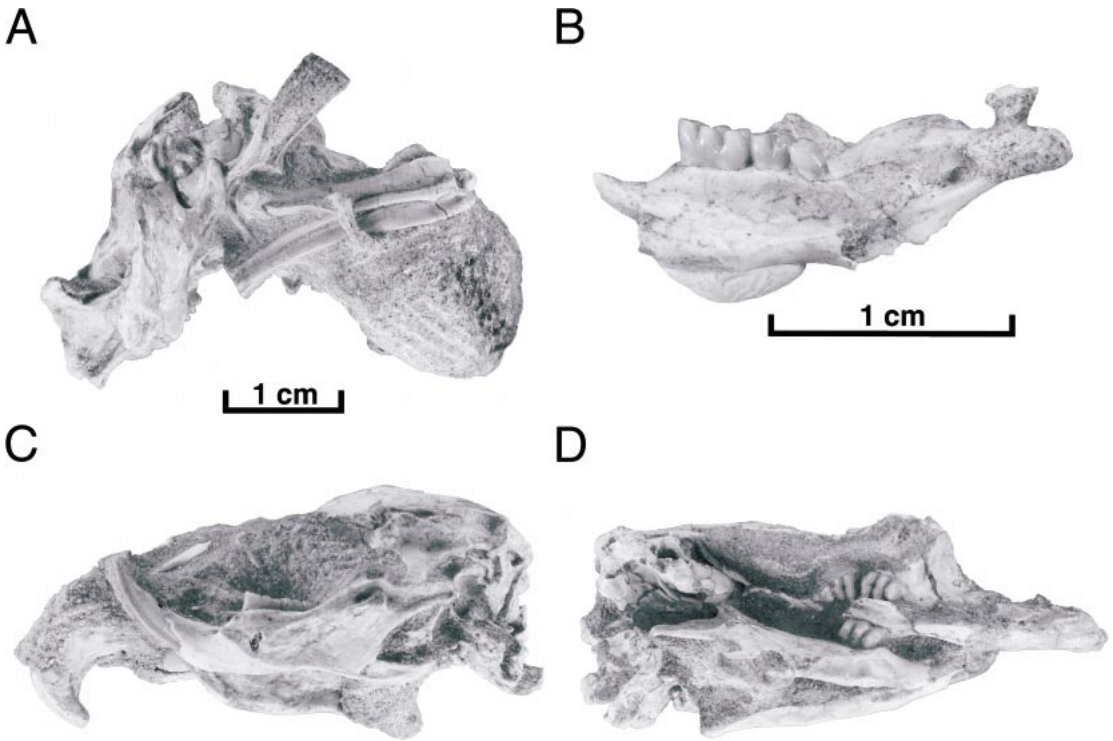


Fig. 23.3. *Abudhabia radinskyi*, AMNH 133507, holotype, (A, B) and 133508 (C, D). A, Partial skull obscured by broken left dentary, with scapula above, humerus and radius + ulna in articulation. B, Associated right dentary. C, D, Skull and associated mandible in left lateral and ventral views. A, C, D at same scale.

ward. The posterior margin of the zygomatic root extends posteriorly to the mastoid region. The posterior portion of the squamosal surrounds the squamosomastoid window. The ventral squamosal process terminates in a bony triangle that contacts the dorsal squamosal process to enclose the window. The mastoid apparently is not swollen. Structures inside the bulla cannot be seen because they are internal to other bones or because they require additional preparation to observe if they are present. The paroccipital process apparently does not protrude posteriorly beyond the occipital condyle.

MANDIBLE

The dentary of *Abudhabia radinskyi* (fig. 23.3B, C) has a reduced coronoid process. The incisor capsule is distinct. The mental foramen is anterior to m1 along the dorso-lateral margin of the diastema. The angular process reclines posteriorly. It is well devel-

oped and deflected only slightly laterally. In more derived gerbils, such as *Meriones*, the angular processes are deflected much more strongly to accommodate greatly inflated bullae. The inferior masseteric crest extends from the mental foramen to the ventral margin of the jaw towards the angle. The ventral margin at the angle folds medially to form a flat surface. The superior masseteric crest is distinct, but less developed than the inferior crest. It extends from the anterior margin of the coronoid process and converges with the inferior masseteric crest at the mental foramen. The mandibular foramen is high on the medial surface of the ascending ramus, posterior to the posterior border of the coronoid process, and near the posterior margin of the ascending ramus. Only the left mandible of AMNH 133508 is preserved sufficiently for measurement of the diastema: 6.08 mm to the anterior edge of m1 (5.8 mm to its alveolus). The dentary resembles that of *Tatera indica* in size and most details.

DENTAL DESCRIPTIONS

The dentitions of all specimens show moderate occlusal wear (fig. 23.4). Maximum upper tooth row lengths in millimeters (using a reticule fitted onto a Wild dissecting microscope) are: AMNH 133507, left = 6.17; AMNH 133509, right = 6.50 and left = 6.42. Maximum lower tooth row lengths are: AMNH 133507, right = 6.42; AMNH 133508, left = 6.25. Lower molar tooth row lengths are about 6% greater than diastema length. Occlusal measurements of the cheek teeth are given in table 23.1. Tooth terminology is illustrated in figure 23.5.

The upper and lower molars are low-crowned and broad, with rounded (exaenodont) sides. Lophes are separated by deep, transverse valleys. Longitudinal connections between the lophes are absent. Lophes of the M1 are inclined slightly posteriorly. Lophes of M2 are relatively vertical. The M3 is inclined somewhat anteriorly. Lophes of the lower molars are inclined slightly anteriorly.

UPPER DENTITION: The upper incisors are preserved in AMNH 133508 and 133509 (figs. 23.2, 23.3, 23.5). Cross-sectional dimensions (mm) are: 2.62 buccolingual length \times 1.07 mediolateral width, and 2.70 \times 1.15, respectively. The incisor enamel wraps well onto the lateral surface, covering about 45% of the tooth in lateral view. The single longitudinal groove is located just lateral to the midline of the major axis of the elliptical cross section. The groove is a sharp step with rounded margins, but not invaginated. The groove of *Tatera indica* is similar, although nearer the midline and slightly invaginated.

The M1 includes three transverse lophes. The anterior loph consists of a broad triangular anterocone extended labially as an inconspicuous short cingulum. A faint indentation along the anterior wall indicates derivation from a bilobed condition. The width of the anterocone is about three-fourths or more that of the second loph. An anterolingual inflection (sensu Flynn and Jacobs, 1999) is lacking. The posterior apex of the anterior loph is in contact with the midpoint of the second loph. The second loph is formed by the joined protocone and paracone. The protocone is slightly more bulbous, relative to a more transversely elongate

paracone. The posterior loph consists of the metacone and larger hypocone. This loph is slightly oblique (more anterior labially; AMNH 133507) or transverse (AMNH 133509 and AMNH 133508) to the long axis of the tooth. The cusps are confluent posteriorly, with a distinct posterior cingulum labial to the long axis of the tooth. The posterior cingulum represents an abbreviated posteroloph. There is a strong root under the anterocone; specifics of other roots cannot be determined.

The M2 includes two transverse lophes. The first has transversely elongated protocone and a smaller paracone. There is a small anterolabially directed anterior cingulum (faint on AMNH 133507) emerging from the longitudinal midline. The second loph has transversely elongated metacone and larger hypocone. The metacone is slightly anterior to the hypocone. This loph is continuous with the distinct posterior cingulum located near the midline of the tooth and confluent with the posterolabial border of the hypocone. Specifics of root morphology cannot be determined.

The M3 includes a single, wide anterior transverse cusp that represents coalesced protocone and paracone, and is fused posteriorly (via the paracone) with a prominent posterior cusp, which represents a reduced hypocone-metacone complex. The posterior cusp is located labial to the longitudinal midline of the tooth, and gives the tooth a hooklike appearance. There appears to be a single large root.

LOWER DENTITION: Lower incisors are preserved on AMNH 133507 and 133508. The lower incisor is gracile and lacks prominent ornamentation. This tooth can be measured readily on AMNH 133507. Cross-sectional dimensions are 2.13 buccolingual length, and 0.98 mediolateral width. The enamel is rounded and wraps 42% of the way onto the lateral side of the incisor.

The m1 has three lophes. The first is a triangular anteroconid, which (on AMNH 133507, fig. 23.5C; labial only on AMNH 133508) has gentle labial and lingual indentations suggesting derivation from a tripartite condition. The anteroconid is continuous labially as a cingulum, which is bulbous on AMNH 133507. The second loph includes a transverse protoconid and metaconid. The

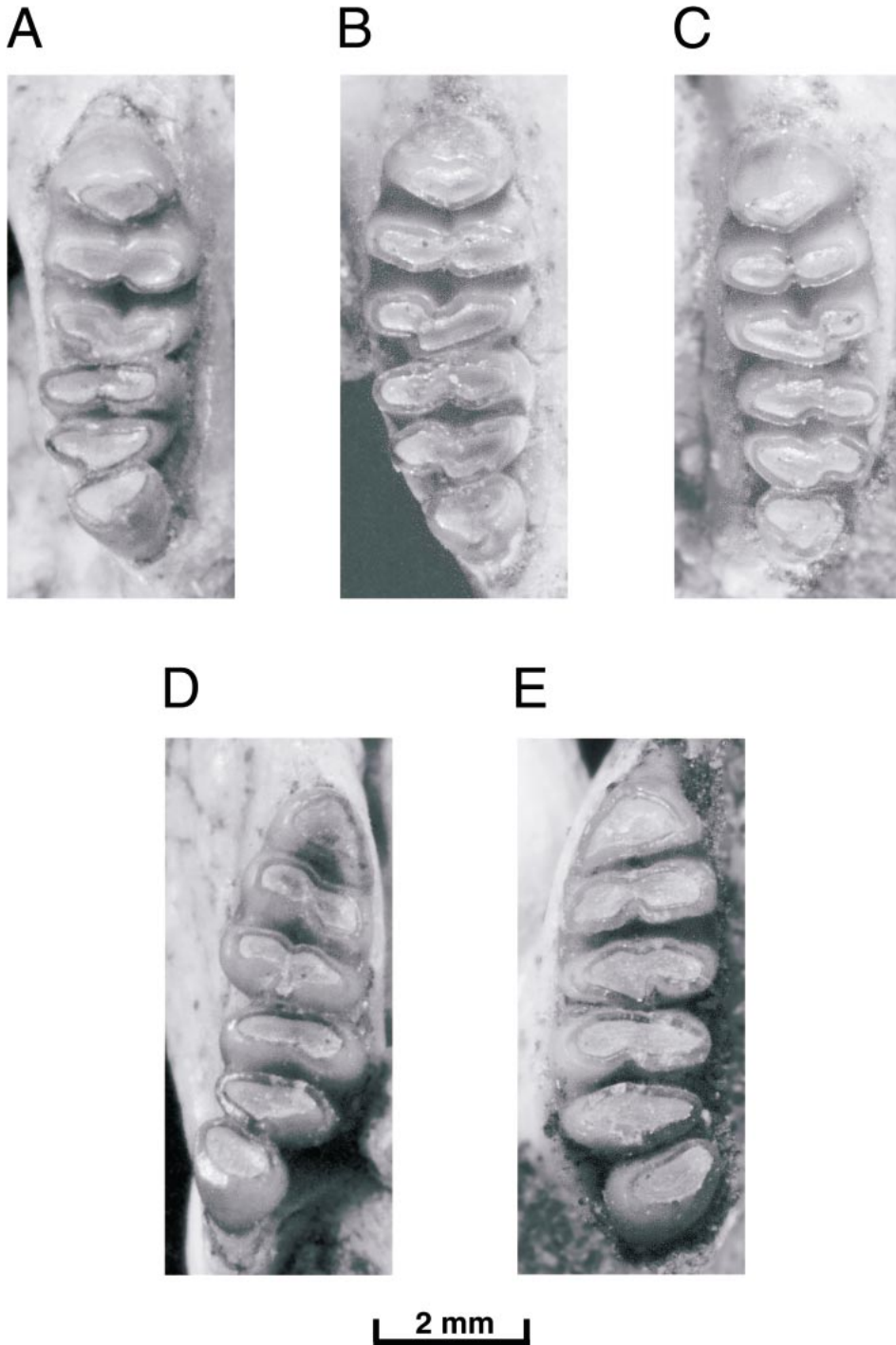


Fig. 23.4. Five dentitions of *Abudhabia radinskyi*. **A**, Right upper dentition of AMNH 133507, holotype. **B**, **C**, Right and left upper dentitions of AMNH 133509. **D**, Right lower dentition of AMNH 133507. **E**, Left lower dentition of AMNH 133508. Anterior is upward.

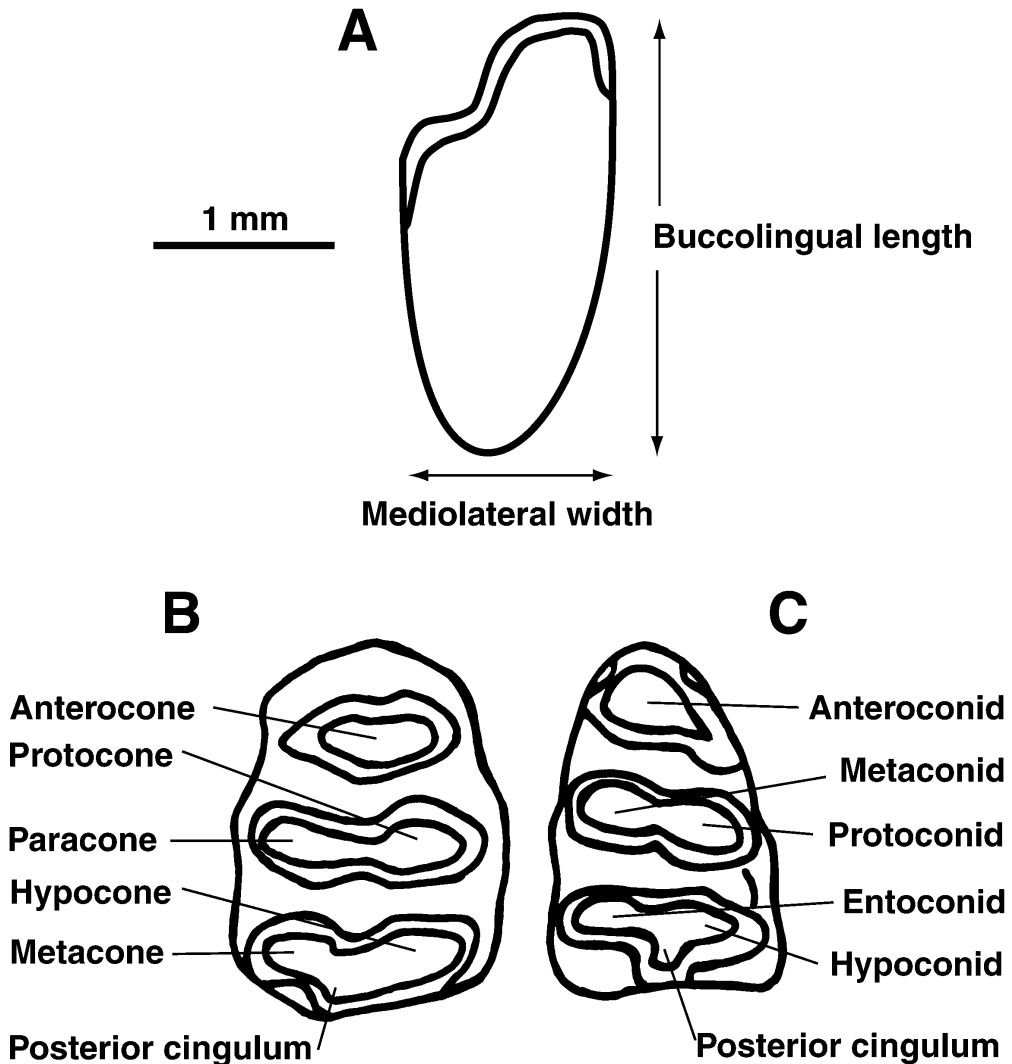


Fig. 23.5. Tooth terminology used in the text. A, Cross section of right upper incisor of AMNH 133509. B, C, Stylized upper and lower first molars.

metaconid is slightly larger than the protoconid. This loph is somewhat oblique, with the metaconid anterior. A low labial cingulum abutts the protoconid and hypoconid. Lingual cingula are absent. The third loph is transverse, and connects the entoconid with the larger hypoconid. This loph is continuous with the prominent conical posterior cusp, or cingulum, that fuses rapidly with the hypoconid. Root development is difficult to determine, but includes a very large anterior root plus one large or a double root under the posterior end of the tooth.

The m2 has two transverse lophes. The first has a broadly confluent protoconid and metaconid. The protoconid is bulbous relative to the more transversely elongate metaconid. There is a small anterolabial cingulum on AMNH 133508, which is more weakly developed on AMNH 133507. The second loph has a broadly confluent entoconid and slightly anteriorly located hypoconid. These cusps are continuous with a weak, somewhat lingually located, posterior cingulum on the right m2 of AMNH 133507. The posterior cingulum is greatly reduced to absent on the

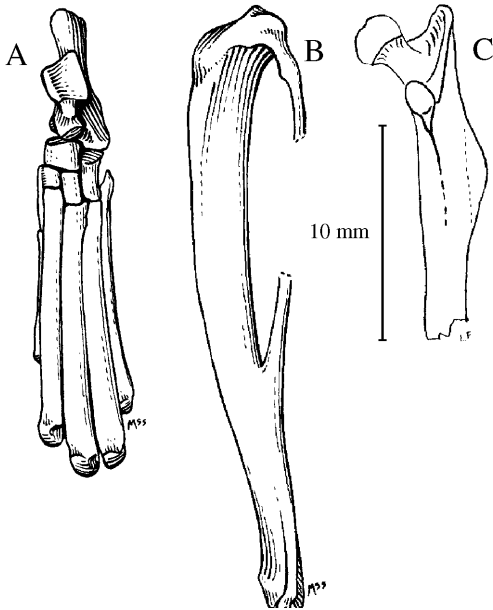


Fig. 23.6. Postcrania of *Abudhabia radinskyi*, AMNH 133509. **A**, **B**, Left pes and left tibia, drawn by Margaret Stevens. **C**, Femur, added for comparison. All to same scale.

other specimens. This tooth has anterior and posterior roots, but specifics are indeterminate.

The m3 consists of a single transversely elongated cusp, more rounded than that of *Tatera indica*. The tooth is positioned lingually in the tooth row with respect to the other molars. The roots are not exposed except for the posterior portion, which angles sharply posterolabially relative to the crown, suggesting that a separate anterior root may be present.

POSTCRANIA

Representation of the postcranial skeleton is indicated above in the hypodigm, but further preparation is required. Specimen AMNH 133509 includes both tibiae and the proximal two-thirds of one femur. The femur compares with *Meriones persicus* in size. Its third trochanter (fig. 23.6C) is an extended, long flange that reaches farther distally than in *Meriones* and would supply greater surface area for muscle attachment and a longer lever arm for the muscle fibers. Type specimen AMNH 133507 includes a left scapula,

TABLE 23.2
Limb Element Lengths (mm) for
Abudhabia radinskyi

Element	Length	Estimated length
Tibia	39.4	
Femur	>22	34, 31 ^a
Humerus	20.2	
Ulna	>20.5	23.5

^aThe two estimates for femur are based on comparisons with *Meriones persicus* and *Mesocricetus auratus*, respectively.

humerus, radius, and ulna in anatomical association (fig. 23.3A). The elbow joint is hyperflexed with olecranon dislocated from its fossa. The ulna is lacking most of its olecranon process, about 3 mm by comparison with modern gerbils. These fossils allow computation of limb element length ratios (table 23.2).

Tong (1989: 46) selected a number of gerbils to compute limb element ratios and judge relative degree of saltatorial adaptation. She measured the tibia/femur + tibia ratio (which differs from the crural index, tibia/femur), and the hind/forelimb ratio (femur + tibia/humerus + ulna; this differs from the intermembral index, which is humerus + radius/femur + tibia).

The posterior/anterior limb ratio of Tong (1989) did not sharply distinguish gerbils from other muroids, although African taterillines exceeded 1.5, a value greater than typical muroids. Our own measurements of a specimen of *Tatera indica* from Pakistan yield a ratio of 1.52. The unadjusted data for *Abudhabia radinskyi* yield a greatly underestimated ratio of 1.4, which is observed in some gerbils and is approached by *Rattus*. Estimating length of the incomplete femur (table 23.2) gives a ratio of >1.6, beyond any values computed by Tong. This indicates a long hind limb for *Abudhabia* relative to studied gerbils.

The second ratio discussed by Tong (1989) is the proportion of the tibia to the total hind limb length, which clearly distinguishes gerbils from other muroids. Gerbil tibiae are found to be quite long. Our measurements for one specimen of *Tatera indica* give a ratio of 54%. For *Abudhabia radinskyi*, the uncorrected values are $39.4/39.4 + 22 = 64\%$

TABLE 23.3

Miocene and Early Pliocene Gerbils Most Closely Comparable to *A. radinskyi* from Afghanistan

Taxon	Material	Locality	Geologic age	Reference
<i>Abudhabia baynunensis</i> ^a	29 isolated teeth	Shuwaihat sites S1, S4, Baynunah Fm., UAE	Late Miocene	de Bruijn and Whybrow (1994); de Bruijn (1999)
<i>A. kabulense</i>	Afghanistan: 41 isolated teeth	Pul-e Charkhi, Afghanistan	Afghanistan: Early Pliocene	Sen (1983, as <i>Protatera</i>)
<i>A. cf. A. kabulense</i>	India: 2 isolated teeth	Tatrot Fm., India	India: Pliocene	India: Patnaik (1997)
<i>A. pakistanensis</i>	M2; maxillary fragment with M1	Locality Y387, Pakistan	8.6 Ma	Flynn and Jacobs (1999)
<i>Abudhabia</i> sp.	m1	Lothagam, Kenya	5.23 Ma	Winkler (2003)
<i>Protatera algeriensis</i> ^a	Many isolated teeth	Amama 2, Algeria	Late Miocene	Jaeger (1977)
<i>P. almenarensis</i>	~26 isolated teeth	Casablanca—M, Spain	Late Miocene	Agustí (1990) and see Geraads (1998a)
Aff. <i>P. almenarensis</i>	3 m1	Lissasfa, Morocco	Miocene/Pliocene limit	Geraads (1998a)
<i>P. davidi</i>	~1000 isolated teeth	Lissasfa, Morocco	Miocene/Pliocene limit	Geraads (1998a)
<i>P. yardangi</i>	10 isolated teeth	Sahabi Fm., Libya	Late Miocene	Munthe (1987)
<i>Protatera</i> sp.	Many teeth	North Africa and Spain	Miocene/Pliocene limit	See Geraads (1998a, 1998b)
<i>Myocricetodon ultimus</i>	M1	Kendek-el-Ouaich, Morocco	Late Miocene	Jaeger (1977)
<i>Myocricetodon magnus</i>	M1, m1, m2	Pataniak 6, Morocco	Late middle Miocene	Jaeger (1977)

^aDenotes type species.

(beyond any observed values). Femur length must be corrected. Estimates based on *Meriones* and *Mesocricetus* (table 23.2) yield 56% and 54%, respectively, comparable to values seen in the most derived gerbils. The estimated ratios, albeit imprecise, are indicative of long tibia proportions for *Abudhabia*, and are conservative since they are ratios.

We conclude that *Abudhabia radinskyi* had a long hind limb, longer than typical gerbils. Its lengthened femoral crest and bladeli-like third trochanter would allow powerful extension. These observations are consistent with efficient hopping, at least as efficient as that seen in modern gerbils. The hind limb is not quite as long as in the truly saltatorial kangaroo rat, *Dipodomys merriami*. Measurements on one specimen of *D. merriami* yield

posterior limb ratio of $(34.2 + 24.5)/(12 + 19.7) = 1.85$. Tong (1986) hypothesized the Miocene fossil *Myocricetodon irhoudi* from North Africa as sister taxon to extant gerbils, but showed its limbs to be typically murine in proportions except for a slightly elongated tibia. *Abudhabia radinskyi* was clearly derived with respect to *M. irhoudi*.

COMPARISONS WITH OTHER EXTINCT GERBILS

New fossil gerbils from Afghanistan are significant not only in representing a new species of *Abudhabia*, but also in being the most completely known Neogene gerbil in terms of elements represented. Table 23.3 summarizes the record of Neogene gerbils most closely comparable to *A. radinskyi*.

Type species, *A. baynunensis*, is from the late Miocene of Abu Dhabi, United Arab Emirates. *Abudhabia kabulense* has been recognized in Afghanistan (Sen, 1983; de Bruijn and Whybrow, 1994) and possibly India (Gupta and Prasad, 2001), *A. pakistanensis* is reported from Pakistan (Flynn and Jacobs, 1999), and unnamed relatives occur in the Pliocene of Kenya (Winkler, 2003) and India (Patnaik, 1997).

The late Miocene of the Potwar Plateau, Pakistan, yielded two teeth named *A. pakistanensis* by Flynn and Jacobs (1999). This is a form less derived in having lower crown height and a stronger anterior cingulum on M2 than the Afghan *A. kabulense*, which is referred to the early Pliocene. The assignment of *A. pakistanensis* to *Abudhabia* was problematic, given the original diagnosis (de Bruijn and Whybrow, 1994) that included presence of a posterior cingulum on M1, especially since the single known M1 of *A. pakistanensis* is worn. This contradiction was removed with the revision of the diagnosis by de Bruijn (1999), and therefore *A. pakistanensis* matches the generic diagnosis. Nonetheless, consistent with its age, *A. pakistanensis* is the most primitive of the known populations of *Abudhabia*.

Protatera was erected by Jaeger (1977) based on isolated teeth of *P. algeriensis* from Algeria. This genus is now relatively well known, at least from isolated teeth from southern Europe and North Africa (table 23.3). *Protatera* was diagnosed as having cusps fused into transverse lophes on M1 and M2 and oblique lophes on m1, vestigial longitudinal crests, large anterocone of M1 with a smooth anterior wall, anterocone transversely elongate, anteroconid of m1 complex and including an anterior sinus, a central fovea and a labial tubercle, m3 reduced, and simple root pattern. The new gerbil from Afghanistan is distinct from *Protatera* (based on the diagnosis) because it has a complete lack of longitudinal crests (derived) and a simple anteroconid on m1 (derived).

The generic assignment of *Protatera yardangi* from Libya (Munthe, 1987) was questioned by Flynn and Jacobs (1999), and de Bruijn (1999) suggested referral to *Abudhabia*. The scant published material of *Protatera yardangi* would fit generic assignment

to *Abudhabia* based on M1 and m2 with transverse crests that are weakly joined longitudinally, and m1 with alternating cusps, posterior labial cusp, and anteroconid with posterolabially directed crest. De Bruijn and Whybrow (1994) consider *Protatera* to have stronger longitudinal ridges and prismatic cusps compared to *Abudhabia*. Flynn and Jacobs (1999) also mention *Protatera* having taller cusps than *Abudhabia*. Relative height of the cusps of *P. yardangi* is not discussed by Munthe (1987) and is indeterminate from illustrations. In our current view, cusp height differences between *P. algeriensis* and *Abudhabia* are minor, so we leave the status of *P. yardangi* unresolved until more material is described.

Among fossil gerbils, de Bruijn and Whybrow (1994) regard *Abudhabia* as similar to *Myocricetodon ultimus* (late Miocene of Kendek-el-Ouaich, Morocco; Jaeger, 1977) and *Myocricetodon magnus* (late middle Miocene of Pataniak 6, Morocco; Jaeger, 1977). The generic assignment of these extremely poorly known species is questioned by de Bruijn (1999) and Wessels (1996), but accepted by Tong (1989). *Myocricetodon ultimus* is known only from an isolated M1. The M1 of *A. radinskyi* is about 26% larger. *Myocricetodon ultimus* is primitive in having the middle row of cusps less transverse (more oblique) and having a longitudinal connection between the anterocone and protocone. Like *A. radinskyi*, *M. ultimus* has a posterior cingulum that is fused with the posterior row of cusps.

Myocricetodon magnus is known only from a maxillary fragment with M1, a mandibular fragment with m2, and an isolated m1. The cheek teeth of *A. radinskyi* average about 15% larger than those of *M. magnus*. The M1 of *M. magnus* is derived in lacking any trace of longitudinal crests, having transverse cusp pairs, and lacking a posterior cingulum. The m1 of *M. magnus* is derived relative to *Abudhabia* in lacking (from the description) or having an extremely reduced (Jaeger, 1977: plate II:11) posterior cingulum. However, the specimen has a short longitudinal crest between the anteroconid and protoconid, has a very strong anterolabial cingulum, and is primitive in possessing strongly oblique lophes. The m2 of *M. mag-*

nus has strong anterolabial and posterior cingula.

Mascaramys has two named species from the middle or late Pliocene of Tunisia and late Pliocene to middle Pleistocene of Algeria (Tong, 1986, 1989). It is dentally similar to *Meriones* but less derived in that longitudinal connections on molars are not as elevated. *Mascaramys* is clearly derived relative to *Abudhabia* in greater crown height and more prismatic cusps. It was considered the sister taxon to *Meriones* by Tong (1989).

Gerbil taxa based on isolated teeth sometimes lack clear distinction. For example, defining characters of *Mascaramys*, *Protatera davidi* from Morocco (Geraads, 1998a), and *Debruijnmys* from Spain (Castillo and Agusti, 1996) appear to overlap. Given the limited number of dental characters available, and the demonstrated homoplasy of increased crown height and prismatic cusps in rodents, it is not surprising that significant phylogenetic and taxonomic questions remain unresolved. Nevertheless, the dental characters of *A. radinskyi* fall well within the generic diagnosis of *Abudhabia*.

COMPARISONS WITH OTHER SPECIES OF *ABUDHABIA*: Comparisons are based on descriptions of *A. baynunensis* (de Bruijn and Whybrow, 1994; de Bruijn, 1999), *A. kabulense* (Sen, 1983), *A. cf. A. kabulense* (Patnaik, 1997; Gupta and Prasad, 2001), *A. pakistanensis* (Flynn and Jacobs, 1999), and *Abudhabia* sp. from Lothagam, Kenya (Winkler, 2003). The great reduction or absence of longitudinal crests is an important characteristic of *Abudhabia*. *Abudhabia baynunensis*, *A. pakistanensis*, and *A. kabulense* may have a low crest between the first and second lobes of M1, joining the protocone to the lingual anterocone. This connection may not be evident until later in wear of the tooth. With advanced wear of M1, *A. kabulense* also shows a low connection between the second and third lophs (see Sen, 1983). Like *A. baynunensis*, *A. kabulense* and *A. cf. A. kabulense* have a projection of the anteroconid toward the metaconid on the m1. In contrast, *A. radinskyi* and *A. sp.* are derived in lacking traces of longitudinal crests on any molars.

Upper M1: De Bruijn (1999) observes a variable posterior cingulum on M1 of *Abud-*

habia baynunensis. In *A. kabulense*, this feature is present as a bulge because the posterior cingulum fuses with the third loph (see Sen, 1983: figs. 49, 50). This is also the condition for *A. radinskyi*. The single M1 of *A. pakistanensis* is very worn and shows no indication of a posterior cingulum.

Upper M2: Like *A. baynunensis* and *A. kabulense*, the M2 of *A. radinskyi* shows the remnant of an anterior cingulum, but this structure is greatly reduced on *A. radinskyi*. The central anterior cingulum on M2 of *A. pakistanensis* remains strong. *Abudhabia kabulense* has an anteroconid cusp on lightly worn teeth. With wear, this forms an anterior projection from the midline, confluent with the protocone and paracone. Unlike other species, *A. baynunensis* shows a distinct anterolabial cingulum cusp.

Upper M3: All species of *Abudhabia* have a triangular M3 with an anterior loph formed by a protocone and a metacone that are fused transversely. The posterior part of the tooth varies among species. The single known M3 of *A. baynunensis* is described as having a short ridge formed by the fused hypocone and metacone. This ridge is slightly oblique with the labial end connected to the paracone. The three M3s of *A. kabulense* show two morphotypes. There is a single transverse anterior loph, and in two of three teeth, the posterior loph is separate (but reduced relative to *A. baynunensis* and not oblique) from the anterior loph. The third specimen is comparable to that of *A. radinskyi* in its hooklike appearance. However, in *A. kabulense* the posterior cusp of the tooth is attached to the protocone, while the posterior cusp of *A. radinskyi* is attached to the paracone.

Lower m1: The shape of the anteroconid of *A. radinskyi* is distinct from that of other known species of *Abudhabia*. The anteroconid of *A. radinskyi* is asymmetrically triangular in outline with a straight posterior border. On *A. baynunensis* and *A. kabulense* the outline of the anteroconid is more rhomboid shaped: The posterior border of the anteroconid projects toward the second loph as a spur. *Abudhabia* from India (Himachal Pradesh, Patnaik, 1997; Jammu District, Gupta and Prasad, 2001) is similar. The anteroconid of *A. sp.* from Kenya differs from *A. radin-*

skyi, *A. baynunensis*, and *A. kabulense*, in being wider, semicircular in outline, and having only a faint labial cingulum. The posterolabial crest from the anteroconid of *A. radinskyi* is reduced relative to other species; in *A. baynunensis* and *A. kabulense* it is developed sometimes as a distinct cusp (protoconulid).

The m1 of *Abudhabia* is characterized as having the main cusps alternating (fused cusp pairs being oblique versus transverse). There is variability, however, in the extent to which the cusps are offset. The second loph of *A. radinskyi* is oblique, but the third loph is more transverse. The third loph of *A. baynunensis* is oblique compared to that of *A. radinskyi*. The third loph of *A. kabulense* is more variable, ranging from transverse, similar to *A. radinskyi*, to oblique as in *A. baynunensis*. The second loph of *A. sp.* from Kenya is distinctive in being more transverse. The Jammu specimen differs from others in small size and nearly opposite location of cusps (Gupta and Prasad, 2001).

In addition to the anterolabial crest off the anteroconid of m1, *A. radinskyi* has a labial cingulum between the protoconid and hypoconid. This latter cingulum is also seen on illustrations of *A. baynunensis*, but not on *A. kabulense* or on *A. sp.* from Kenya.

All species of *Abudhabia* have a distinct conical posterior cingulum on m1 that fuses to the hypoconid with wear. De Bruijn and Whybrow (1994) consider the posterior cingulum of *A. baynunensis* to be stronger than that of *A. kabulense*, but the differences are subtle. The posterior cingulum of *A. radinskyi* may be a little weaker, but again, the differences are subtle.

Lower m2: The generic diagnosis for the m2 of *Abudhabia* stresses that the main cusps form transverse ridges, and that the tooth has remnants of an anterior cingulum. On all species, the first loph is transverse. The second loph is slightly oblique on *A. radinskyi* and *A. kabulense*, and more transverse on the one known m2 of *A. baynunensis*. An anterolabial cingulum or separate cusp is present on *A. baynunensis*, and may be present or absent on *A. radinskyi* and *A. kabulense*. A short anterolingually directed spur extending from the protoconid is also present on *A. baynunensis*.

There is a distinct small conical posterior cusp (posterior cingulum) slightly closer to the entoconid on the m2 of *A. baynunensis*. The m2 of *A. radinskyi* has a weak posterior cingulum, or the posterior cingulum is absent. The illustrations of *A. kabulense* may indicate a posterior cingular cusp that has fused with wear to the entoconid, but Sen (1983) considers a posterior cingulum to be lacking on m2. *Abudhabia* cf. *A. kabulense* from India (Patnaik, 1997) has a distinct posterior cingular cusp as in the type species of the genus.

Lower m3: The m3 of *Abudhabia* consists of a single ovoid cusp that is transversely elongated. De Bruijn and Whybrow (1994) assign two very different m3s to *A. baynunensis*. One tooth (AAM 570, plate I, fig. 5) consists of a single lobe. The other (AAM 569, plate I, fig. 4) is larger, with an additional small posterior cusp and is of uncertain affinity. All other known m3 of *Abudhabia* resemble the former morphology.

COMPARISONS WITH ASIAN *TATERA*

As noted in the Introduction, Tedford's Afghani gerbils were conferred to the extant, exclusively Asian *Tatera indica* by Lay (1972). Pavlinov (1985, 1988, 2001; Pavlinov et al., 1990) argues cogently that ear structure demonstrates *T. indica* to be the sole living species of the genus *Tatera*. *Tatera indica* ranges from Syria to India and Sri Lanka (Nowak, 1999). All other extant species occasionally referred to *Tatera* are restricted to Africa and assigned variously to *Gerbilliscus* and *Taterona*. Pavlinov's observations confirm the suspicion of Musser and Carleton (1993: 560) that "there are distinctive features separating the Asian from all the African species. . . ." Tong (1989), in her comprehensive review of the origin and evolution of North African gerbils, studied African species, but did not include *T. indica*.

Abudhabia radinskyi associates in morphology with other species of the genus, to the exclusion of *Tatera indica*. However, there is considerable resemblance, including size, so it is important to specify distinctive features. We compare *A. radinskyi* with specimens of *T. indica* collected from Pakistan and India. A major difference in the postcra-

nia is that *A. radinskyi* had proportionally longer hind limbs (see above). Similarities include elongate incisive foramina, large posterior palatine foramina, opisthodonty, and compact, parallel tooth rows with cross lophs. Differences in the skull relate principally to degree of inflation of the bulla. This single character complex includes a number of differences; coding these entails a judgment on how tightly they are interconstrained. Unlike *Tatera indica*, the mastoid of *Abudhabia* is not inflated. The bulla itself is inflated and expanded in *A. radinskyi*, but not to the degree seen in *Tatera*, where it constricts adjacent fissures and forces the auditory meatus posterodorsally. Because the ear region of *T. indica* is more greatly inflated, the whole back of the skull, including interparietal, is broader and more rounded (parasagittal and lambdoid crests less prominent). The occiput is more vertical and broader.

Skull measurements, following Musser (1970), illustrate the difference. Greatest length of skull/breadth of braincase in *A. radinskyi* is 44/13.5 mm; 44.5/18 in *Tatera indica* (MCZ 9065). Given approximately the same skull length in these rodents, the braincase is broader in *Tatera*. Bulla length also differs: approximately 8 mm in *Abudhabia*, 11 in *Tatera*. Further preparation would make this measurement more precise in *A. radinskyi*.

The mandible of *A. radinskyi* is similar to that of *T. indica*, but in *A. radinskyi* the angular process is narrower with a less superiorly projecting posterior portion, a character related to inflation of the bulla. Upper and lower incisor morphology is comparable. The position of the groove in the upper incisor is consistent, perhaps slightly deeper in *Tatera*. In contrast, living African species have more medial placement of the groove.

Proportions of elements of the cheek teeth are similar in *A. radinskyi* and *T. indica*, except that m3 is greatly reduced in size in the living gerbil. Both taxa also have the cusps located roughly opposite each other (but slightly offset on m1 of *A. radinskyi*). *Tatera indica* molars are slightly higher crowned with the cusps losing their distinctiveness at an earlier wear stage to form transverse lophs (MCZ 5370, for example). The crowns are

dominated by relatively broader, closer transverse lophs than in the fossil.

The M1 of both taxa show a fairly triangular anterocone. Three of four anterocones of *A. radinskyi* have a short labial cingulum off the anterocone, which is lacking on observed specimens of *T. indica*. Longitudinal connections between the rows of cusps are absent in *A. radinskyi*, but *T. indica* shows a weak connection on M1 between the anterocone and the next row of cusps (usually to the protocone). This connection is likely homologous to the posteriorly directed apex of the anterocone triangle in *Abudhabia*. These teeth also have the protocone and the hypocone closely appressed, such that in advanced wear they would join. The posterior cingulum is weaker in *T. indica*. The longitudinal connection of the first and second laminae is secondary in *T. indica*, and not developed in African species formerly placed in the genus.

Overall morphology of the M2 of the two taxa is similar, but on *T. indica* the protocone and the hypocone are close to each other and would join with heavy wear. These cusps are further apart on *A. radinskyi*. *Tatera indica* also lacks an anterior cingulum, but this feature could be present early and lost through occlusal wear in either species. The posterior cingulum on *T. indica* varies from absent to weakly developed, comparable to that of *A. radinskyi*.

The M3 of the two taxa are similar, although the wide anterior loph of *A. radinskyi* is more transverse (less rounded at its labial and lingual edges) than that of *T. indica*. The M3 of *T. indica* variably shows two small cusps at the posterior end of the tooth. Other specimens of *T. indica*, and all those of *A. radinskyi*, have one cusp in this position.

The lower dentitions of *T. indica* and *A. radinskyi* are comparable in relative length and width of the teeth (except m3), and in having fairly opposite to slightly offset (m1) cusps. There are, however, a number of differences. The anteroconid is distinctly triangular on *A. radinskyi*, and more horseshoe-shaped on *T. indica*. The anteroconid complex has labial and lingual wings, and a distinct posterior reentrant in *T. indica*. No connections or incipient connections between the rows of cusps are observed on the m1 of

A. radinskyi. They may occur on the anterior end of *T. indica* between the lingual side of the anteroconid and the metaconid. The other loph pairs on m1 are closely appressed and may join in advanced wear. Both taxa have a posterior cingulum on m1, but it is reduced on *T. indica*.

The m2 of *T. indica* lacks posterior and anterolabial cingula. These are variably developed in *A. radinskyi*, but never strong. With occlusal wear, a longitudinal connection may develop between the two rows of cusps on *T. indica* (absent on m2 of *A. radinskyi*). The m3 of *T. indica* is smaller, more lingually placed, and compressed antero-posteriorly compared to that of *A. radinskyi*. Among all species of *Abudhabia*, the average length to width ratio is 0.8 ($N = 12$ individual teeth), while that for *Tatera* is 0.6 ($N = 3$). These genera may also differ in root structure; *Tatera indica* has one root on m3, while *A. radinskyi* may have two roots.

DENTAL COMPARISONS OF *T. INDICA* AND SPECIES OF *ABUDHABIA*: Overall morphology of the cheek teeth is similar, including cusp pairs of M1, M2, and m2 forming transverse ridges, cusp pairs of m1 more offset, reduction of longitudinal connections between cusp pairs (relative to other gerbils such as *Meriones*), and presence of a posterior cingulum on M1, M2, and m1 (sometimes represented by just a bulge on the posterior end of the tooth). *Abudhabia* is distinct from *T. indica*, however, in *Abudhabia* having: (1) slightly lower crown height with cusps fusing into lophs at a later wear stage; (2) relatively weak (or absent) longitudinal connections; (3) an anteroconid on m1 that is rhomboid (*A. baynunensis*, *A. kabulense*), triangular (*A. radinskyi*), or semicircular (*A. sp.* from Kenya) in shape compared to a horseshoe shape on *T. indica*; (4) a less reduced m3; and (5) a more distinct posterior cingulum on m1.

Note that the M1 of *Tatera indica* consistently shows a tendency for the two anterior lophs to join at the midline early in wear. This would appear to be an autapomorphy in this lineage, in contrast to *Abudhabia*, or any African taterillines. *Tatera indica* also often exhibits the horseshoe anteroconid (see Pavlinov, 1985) in contrast to African taterillines. Pavlinov's hypothesis of anteroconid

evolution might predict a horseshoe predecessor in *Abudhabia*. Available fossils do not support this.

FOSSIL *TATERA* AND *ABUDHABIA*: One fossil species of Asian *Tatera* has been described, *T. pinjoricus* from the late Pliocene (circa 2 Ma) Ghaggar River Section, Pinjor Formation, India (Patnaik, 1997). We agree with the generic allocation, yet compare it to the Afghan gerbil because *T. pinjoricus* (M1 length about 2.8 mm) is nearly as large. This species is known from two maxillae, two mandibles, and five isolated molars. Unfortunately, the m1 is known only from one heavily worn tooth. *Tatera pinjoricus* is diagnosed (Patnaik, 1997) as having M1 with a relatively narrow anterocone and a longitudinal connection between the anterocone and the protocone, upper molars with alternately arranged labial and lingual cusps, and a prominent posterior cingulum on M1 and M2. It is considered most similar to *Tatera indica*, but differs in its smaller size, narrower anterocone, and more lingually placed longitudinal connection between the anterocone and protocone.

Patnaik (1997) noted similarities between the M1 of *T. pinjoricus* and *A. kabulense* including a longitudinal connection between the anterocone and protocone, alternate labial and lingual cusps, a connection between the second and third lophs, and a prominent posterior cingulum. Except on the m1, the cusp pairs of M1, M2, and m2 of *A. kabulense* (and *Abudhabia* in general) are diagnostically transverse. The cusp pairs of the M1, in particular, of *Abudhabia*, appear more transverse than those of *T. pinjoricus* (*Abudhabia* derived). Patnaik (1997) considered *A. kabulense* to differ from *T. pinjoricus* in having weakly connected cusps on unworn molars, M1 with a narrower anterocone, and m1 with a distinct posterior cingulum and labial cusp of the prelobe (anteroconid) reduced and weakly joined to the lingual cusp. However, the only m1 of *T. pinjoricus* is very heavily worn, and disposition of components of the anteroconid and the development of the posterior cingulum cannot be determined with confidence. Patnaik (1997) stated that unlike *T. pinjoricus*, *A. kabulense* has an m2 with a faint anterolabial cusp and a weak posterior cingulum, but these structures may be ob-

scured on a heavily worn m2 (his Plate 3q). Patnaik (1997) also noted that the M1 of *A. kabulense* has three roots and the m1 two roots, while the M1 and m1 of *T. pinjoricus* have four roots (*T. pinjoricus* derived). The m3 of *Tatera pinjoricus* and *T. indica* both have one root, but at least two species of *Abudhabia*, *A. radinskyi* and *A. kabulense*, show some evidence of two roots (*Abudhabia* primitive).

Patnaik (1997) suggests a close relationship between *A. kabulense* (primitive; and *A. cf. A. kabulense* from India), *T. pinjoricus* (derived), and *T. indica* (most derived). It is difficult to assess this based on the limited dental samples involved. Nevertheless, we agree that *T. pinjoricus* is dentally most closely allied with *T. indica* and that it is more primitive based on root structure at least.

SUMMARY AND CONCLUSIONS

Modern gerbils, as a group, can be recognized without much difficulty using dental and osteological characters. Some of the most derived features are related to exaggerated expansion of the bulla and associated accommodation of skull architecture. However, gerbils, as is the case with many rodent groups, have not been subjected to rigorous phylogenetic analysis. This is the next step in the study of *Abudhabia radinskyi* after preparation reveals more basicranial features.

Carleton and Musser (1984) provide a useful compilation of 17 diagnostic features for the Gerbillinae to which *A. radinskyi* conforms in observable characters. It has a supraorbital shelf, the zygomatic plate appears broad, the mesopterygoid fossa is narrow, the posterior palatine foramina are long, the optic foramen and sphenoidal fissure are large and comparable in size, sphenopalatine foramen is large, the angular process of the mandible is laterally deflected, the third molars are reduced with the posterior lamina (hypoconid and entoconid) of m3 absent, and the bulla is enlarged. These features appear to be gerbil synapomorphies that can be tracked among well-preserved fossils.

Tong (1989) provides a tree of relationships among living and most fossil genera of gerbils. Her tree is based on a total of 61 char-

acters: 22 of the middle ear, 12 cranial and 5 cranial foramina, 3 mandibular, 18 dental, and 1 long bone. She included *Rattus* sp. in her analysis, presumably as an outgroup, and *Myocricetodon irhoudi*, a fossil taxon known from incomplete material, including teeth, jaws, a partial skull, and some postcrania. Her tree shows a distribution of characters among the branches, but is not cladistic in the strict sense. It does not score characters consistently across taxa, and therefore cannot methodologically define monophyletic groups based on them. It is a graphic representation of an interpretation of gerbil evolution, rather than an objective hypothesis based on the parsimonious distribution of shared derived characters. The polarity of some of the characters appears to be interpreted based on choice of outgroup: *Rattus* features are taken as primitive for the gerbils and the gerbils are evidently considered derived murines. Consequently, for example, loss of lingual cusps in M1 is considered to characterize extant gerbils; an alternate view sees gerbils as primitive but *Rattus* (and *M. irhoudi*) as derived in this regard.

Myocricetodonts are the muroids in which Jaeger (1977) placed the ancestry of the gerbils. This has been accepted generally (e.g., Lavocat and Parent, 1985). There are at least two areas of uncertainty with respect to the placement of myocricetodonts as the sister taxon to all other gerbils. First, myocricetodonts are diverse dentally, some taxa being complicated with accessory cusps and other taxa much more simplified. The monophyly of this diverse group has not been clearly supported phylogenetically (see comments by de Bruijn, 1999). Second, most myocricetodonts are known only from teeth or jaw fragments. Nevertheless, Tong (1989) indicates 16 characters, which if accepted uncritically would unite *Myocricetodon irhoudi* as sister taxon to the crown group of living gerbils. If myocricetodonts are gerbils, we would agree that they are primitive among the group.

Accepting gerbils as a monophyletic group, the number of lower level groups and their detailed relationships are more problematic and would benefit from a thorough phylogenetic review. As Tong (1989) opined, the group is ripe for melding morphological and molecular approaches; phylogenetic

analysis will be enriched by evidence from fossils such as *Abudhabia*. Factors that complicate gerbil phylogeny include their adaptations to arid environments, most notably differentiation of the bulla, and their simplified dentitions. Their broad distribution in arid Africa and Asia would appear conducive to vicariance. Such a scenario of vicariance in desert regions seems prone to homoplasy, and homoplasy appears to be revealed in two character complexes by *Abudhabia*. If *Abudhabia* is closely related to *Tatera*, then likely the large degree of ear region inflation seen in *Tatera indica* arose independently to that of other more distantly related genera with inflated bullae. *Abudhabia* supports the hypothesis of independent bulla inflation for *Tatera* suggested by Pavlinov (2001). Further, the horseshoe type of anteroconid on m1, so characteristic of *Tatera indica* and other gerbils, is not evidenced by *Abudhabia* and likely appeared late in *Tatera* evolution.

Abudhabia radinskyi resembles *Tatera indica* in morphology and size, and we can speculate on ecological similarity. Roberts (1977) stressed the ecological adaptability of *T. indica* in Pakistan. It inhabits most areas and substrates except for high mountains and extensive dune fields, although it occurs in expansive desert areas and low mountainous regions. *Tatera indica* may be gregarious, but individuals are aggressive and usually live in pairs in separate burrows. *Tatera indica* is nocturnal and omnivorous. Nasal protrusion is common in gerbils, and is seen in both *Abudhabia* and *Tatera*. The effect is to extend incisor apices rearward to facilitate processing resistant food resources (Landry, 1957). The diet of *Tatera indica* is known to include significant amounts of insects (at least 25% by volume for half the year; Prakash, 1962). According to Roberts (1977), insects contribute a larger proportion to the diet than in other rodents in the same region. The success of *Abudhabia* in Asia could have been associated with increasingly open habitat and insectivory.

Abudhabia radinskyi is a remarkably well-preserved rodent from the late Neogene of Afghanistan. It illustrates the widespread distribution of this genus first recognized in the United Arab Emirates. The structures preserved in the Afghan fossils reveal an open-

habitat-adapted rodent that presents many modern gerbil features, except for those related to expansion of cavities in the middle and inner ear. While inflation of the bulla unites the crown group of gerbils, more derived conditions likely were subject to homoplasy. So, too, certain dental features likely arose in parallel in different lineages. Our present hypothesis is that *Abudhabia* is a taterilline related to *Taterillus*, *Gerbilliscus*, and *Taterona* in Africa, plus *Tatera* in Asia. This hypothesis is testable through a survey of osteological features across the group, a basis for phylogenetic analysis enriched by the fossil record.

ACKNOWLEDGMENTS

We thank Dick Tedford, whose abiding and polymathic interests promoted study of the Afghan gerbils. He encouraged collaborative work on them with Marie Lawrence, and we benefitted from many discussions with both Dick and Marie. In addition, Dick supplied field notes and map, references, and drawings produced by Margaret Stevens. Our discussions with Guy Musser and John Wahlerl helped us to develop our understanding of the systematic relevance of this gerbil species. We appreciate information on rodent incisors shared with us by Stuart Landry, and help with literature by Haiyan Tong. Michèle Morgan and John Barry advised on earlier drafts; we thank Sevet Sen for his review. Access to the mammal collections of the American Museum of Natural History, National Museum of Natural History, and Museum of Comparative Zoology was indispensable. Mike Polcyn and M. Morgan digitally photographed the specimens; Diana Vineyard prepared figs. 23.2–23.4. The Institute for the Study of Earth and Man, Dallas, and the Peabody Museum, Cambridge, provided support for this work. This is the final manuscript on which we (L.J.F., A.J.W., L.L.J.) collaborated with our friend Will Downs.

REFERENCES

- Agustí, J. 1990. The Miocene rodent succession in Eastern Spain: a zoogeographical appraisal. *In* E.H. Lindsay, V. Fahlbusch, and P. Mein (ed-

- itors), European Neogene mammal chronology: 375–404. New York: Plenum.
- Brandy, L.D. 1979. Rongeurs nouveaux du Néogène d'Afghanistan. *Comptes Rendus de l'Académie des Sciences, Paris, séries D*, 289: 81–83.
- Bugge, J. 1970. The contribution of the stapedia artery to the cephalic arterial supply in muroid rodents. *Acta Anatomica* 76: 313–336.
- Carleton, M.D., and G.G. Musser. 1984. Muroid rodents. *In* S. Anderson and J.K. Jones, Jr. (editors), *Orders and families of Recent mammals of the world*: 289–379. New York: Wiley.
- Castillo, C., and J. Agustí. 1996. Early Pliocene rodents (Mammalia) from Asta Regia (Jerez Basin, southwestern Spain). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 99: 25–43.
- Chaline, J., P. Mein, and F. Petter. 1977. Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia* 41: 245–252.
- de Bruijn, H. 1999. A late Miocene insectivore and rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. *In* P.J. Whybrow and A. Hill (editors), *Fossil vertebrates of Arabia*: 186–197. New Haven: Yale University Press.
- de Bruijn, H., and P.J. Whybrow. 1994. A late Miocene rodent fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 97: 407–422.
- Flynn, L.J. 1983. Sur l'âge de la faune de vertébrés du Bassin de Bamian, Afghanistan. *Comptes Rendus de l'Académie des Sciences, Paris, séries II*, 297: 687–690.
- Flynn, L.J. 1997. Late Neogene mammalian events in North China. *Actes du Congrès BiochroM'97. Mémoires et Travaux EPHE, Institut Montpellier* 21: 183–192.
- Flynn, L.J., E. Heintz, S. Sen, and M. Brunet. 1983. A new Pliocene tachyoryctine (Rhizomyidae, Rodentia) from Lataband, Sarobi Basin, Afghanistan. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* B86: 61–68.
- Flynn, L.J., and L.L. Jacobs. 1999. Late Miocene small-mammal faunal dynamics: the crossroads of the Arabian Peninsula. *In* P.J. Whybrow and A. Hill (editors), *Fossil vertebrates of Arabia*: 410–419. New Haven: Yale University Press.
- Geraads, D. 1998a. Rongeurs du Mio-Pliocène de Lissasfa (Casablanca, Maroc). *Géobios* 31: 229–245.
- Geraads, D. 1998b. Biogeography of circum-Mediterranean Miocene-Pliocene rodents; a revision using factor analysis and parsimony analysis of endemism. *Palaeogeography, Palaeoclimatology, Palaeoecology* 137: 273–288.
- Gingerich, P.D., M. Arif, I. Hussain Khan, M. Ul-Haq, J.I. Block, W.C. Clyde, and G.F. Gunnell. 2001. Gandhera Quarry, a unique mammalian faunal assemblage from the early Eocene of Baluchistan (Pakistan). *In* G.F. Gunnell (editor), *Eocene biodiversity: unusual occurrences and rarely sampled habitats*: 251–262. New York: Kluwer Academic/Plenum.
- Gupta, S.S., and G.V.R. Prasad. 2001. Micromammals from the Upper Siwalik subgroup of the Jammu Region, Jammu and Kashmir State, India: some constraints on age. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 220(2): 153–187.
- Heintz, E., L. Ginsburg, and J.-L. Hartenberger. 1978. Mammifères fossiles en Afghanistan: état des connaissances et résultats d'une prospection. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Séries 3(516), Sciences de la Terre* 69: 101–119.
- Hill, J.E. 1935. The cranial foramina in rodents. *Journal of Mammalogy* 16: 121–129.
- Jaeger, J.J. 1977. Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata* 8: 1–166.
- Landry, S.O. 1957. Factors affecting the procumbency of rodent upper incisors. *Journal of Mammalogy* 38: 223–234.
- Lang, J., and R. Lavocat. 1968. Première découverte d'une faune de vertébrés dans le tertiaire d'Afghanistan et datation de la série de Bamian. *Comptes Rendus de l'Académie des Sciences, Paris, séries D*, 266: 79–82.
- Lavocat, R., and J.-P. Parent. 1985. Phylogenetic analysis of middle ear features in fossil and living rodents. *In* W.P. Luckett and J.-L. Hartenberger (editors), *Evolutionary relationships among rodents: a multidisciplinary analysis*: 333–354. New York: Plenum.
- Lay, D.M. 1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. *Journal of Morphology* 138: 41–120.
- McKenna, M.C., and S.K. Bell. 1997. *Classification of mammals above the species level*. New York: Columbia University Press.
- Mennessier, G. 1961. Les caractères structuraux des montagnes de la région de Kaboul (Afghanistan). *Société Géologique de France, Bulletin Séries 3(7)*: 40–49.
- Munthe, J. 1987. Small-mammal fossils from the Pliocene Sahabi Formation of Libya. *In* N.T. Boaz et al. (editors), *Neogene paleontology and geology of Sahabi*: 135–144. New York: Alan R. Liss.
- Musser, G.G. 1970. Species limits of *Rattus brah-*

- ma*, a murid rodent of northeastern India and northern Burma. *American Museum Novitates* 2406: 1–27.
- Musser, G.G. 1982. Results of the Archbold Expeditions. No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. *American Museum Novitates* 2746: 1–43.
- Musser, G.G., and M.D. Carleton. 1993. Family Muridae. In D.E. Wilson and D.M. Reeder (editors), *Mammal species of the world. A taxonomic and geographic reference*: 501–756. Washington, DC: Smithsonian Institution Press.
- Musser, G.G., and C. Newcomb. 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* 174: 327–598.
- Nowak, R.M. 1999. *Walker's mammals of the world*. Baltimore: The Johns Hopkins University Press.
- Patnaik, R. 1997. New murids and gerbillids (Rodentia, Mammalia) from Pliocene Siwalik sediments of India. *Palaeovertebrata* 26: 129–165.
- Pavlinov, I.J. 1985. [Contributions to dental morphology and phylogeny of gerbils (Rodentia, Gerbillinae).] *Zoologicheskii Zhurnal* 64: 574–582.
- Pavlinov, I.J. 1988. [Evolution of mastoid part of the bulla tympani in specialized desert rodents.] *Zoologicheskii Zhurnal* 67: 739–750.
- Pavlinov, I.J. 2001. Current concepts of gerbillid phylogeny and classification. In C. Denys, L. Granjon, and A. Poulet (editors), *African small mammals*: 141–149. Paris: IRD Éditions. Institut de Recherche pour le Développement.
- Pavlinov, I.J., A.Y. Dubrovsky, E.G. Potapova, and O.L. Rossolimo. 1990. [Gerbillids of the world.] Moscow: Nauka Publication. [In Russian]
- Prakash, I. 1962. Ecology of the gerbils of the Rajasthan Desert, India. *Mammalia* 26: 311–331.
- Raufi, F., and O. Sickenberg. 1973. Zur Geologie und Paläontologie der Becken von Lagman und Jalalabad. *Geologische Jahrbuch* B3: 63–99.
- Roberts, T.J. 1977. *The mammals of Pakistan*. London: Ernest Benn Limited.
- Sen, S. 1983. Rongeurs et lagomorphes du gisement pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. *Bulletin du Museum National d'Histoire Naturelle, Paris, Séries 5C*: 33–74.
- Sen, S. 2001. Rodents and insectivores from the upper Miocene of Molayan, Afghanistan. *Palaeontology* 44: 913–932.
- Sen, S., M. Brunet, and E. Heintz. 1979. Découverte de rongeurs "africains" dans le Pliocène d'Afghanistan. Implications paléobiogéographiques et stratigraphiques. *Bulletin du Museum National d'Histoire Naturelle, Paris, Séries 4–1-C(1)*: 65–75.
- Tong, H. 1986. The Gerbillinae (Rodentia) from Tighennif (Pleistocene of Algeria) and their significance. *Modern Geology* 10: 197–214.
- Tong, H. 1989. Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. *Mémoires de la Société Géologique de France* 155: 1–120.
- Wahlert, J.H. 1974. The cranial anatomy of protrogomorphous rodents; an anatomical and phylogenetic study. *Bulletin of the Museum of Comparative Zoology* 146: 363–410.
- Wahlert, J.H. 1985. Cranial foramina of rodents. In W.P. Luckett and J.-L. Hartenberger (editors), *Evolutionary relationships among rodents*: 311–332. New York: Plenum.
- Wessels, W. 1996. Myocricetodontinae from the Miocene of Pakistan. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 99: 253–312.
- Wessels, W. 1998. Gerbillidae from the Miocene and Pliocene of Europe. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 38: 187–207.
- Winkler, A.J. 2003. Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, northern Kenya. In M.G. Leakey and J.M. Harris (editors), *Lothagam: dawn of humanity in eastern Africa*: 169–198. New York: Columbia University Press.