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Baluchimyinae, A New Ctenodactyloid Rodent Subfamily from the Miocene of Baluchistan

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ABSTRACT

Rodents from early Miocene deposits near Dera Bugti, Baluchistan, Pakistan, represent an endemic radiation of ctenodactylids in the Indian subcontinent. The Bugti small mammal fauna contrasts sharply with other known middle Cenozoic faunas, but most taxa can be referred to the Chapattimyidae, a family known previously from Eocene deposits of the Indian subcontinent. Four new genera, *Baluchimys*, *Lindsaya*, *Lophibaluchia*, and *Hodsahibia* are placed in the new subfamily Baluchimyinae. The Baluchimyinae and the new genus *Fallomus* are placed in the redefined Chapattimyidae. An additional, rare element in the Bugti fauna, *Downsimys margolisi* new genus and species, is named without referral to family, but affinities may lie with chapattimyids or cylindrodontids. A single large tooth resembles specimens from Qujing, Yunnan, China, that are referred to the yuomyid *Dianomys*. The Bugti fauna must be considered in formulating hypotheses of relationships of higher rodent taxa and in biogeographic reconstructions. The fauna indicates that the Chapattimyidae are a diverse South Asian clade

that is closely related to the northern Yuomyidae and Ctenodactylidae. All three families are classified in the superfamily Ctenodactyloidea and are derived in their hystricomorphy with respect to the early Asiatic rodent *Cocomys*. Some evidence supports relationship of Baluchimyinae with African Thryonomyoidea.

Evolution of Chapattimyidae and other ctenodactylids is characterized by vicariant events in which different groups radiated to the south and to the north of the Tethys/Himalayas. If Chapattimyidae are close to Thryonomyoidea, then this establishes a record of Eocene rodents in the northern hemisphere of the Old World that could lie near the origin of African hystricognaths on the one hand and South American Caviomorpha on the other. This scenario then implies monophyly of most African, Asian, and South American hystricomorphous rodents. However, unless baluchimyines or late Paleogene Asiatic relatives prove to have hystricognathous jaws, this interpretation requires that hystricognathy arose independently in Oligocene African and South American groups.

INTRODUCTION

New taxa described in this paper represent a group of rodents apparently endemic to the Indian subcontinent during the middle Cenozoic. Work by the Geological Survey of

Pakistan has produced the oldest known Neogene rodent assemblage from the early Miocene of the subcontinent, but the previous 25 million years remain completely un-

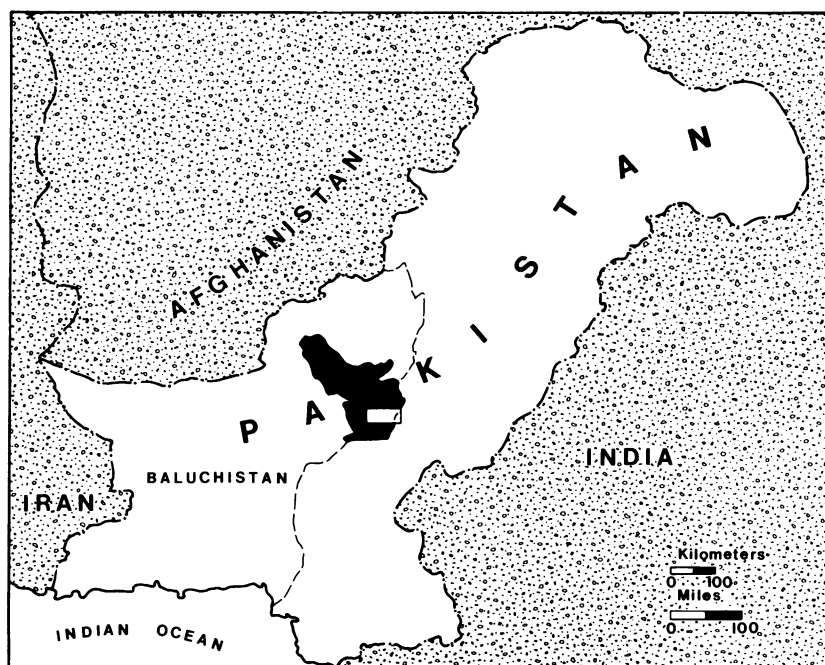


FIG. 1. Location map of Pakistan. Fossils are found in the Marri Bugti area of Baluchistan, shown as a white rectangle (see fig. 2).

documented by continental vertebrate fossils. As members of a new subfamily, these rodents supply knowledge of trends in small mammal evolution in south Asia during the Cenozoic and shed light on relationships of higher rodent categories that originated in Asia and Africa.

One of the richest early Miocene (Burdigalian equivalent) land vertebrate faunas in Asia comes from Baluchistan Province, Pakistan, near Dera Bugti (Savage, 1967; Raza and Meyer, 1984; see figs. 1, 2). The "Bugti Bone Beds" yield a classic fauna of large mammals unique in its mixture of Asian and African elements and its high diversity of rhinocerotids and anthracotheres. Most specimens derive from the lower fossiliferous Bugti Member (apparently about 100 m thick) of the Chitarwata Formation. In 1978, I. U. Cheema discovered a concentration of small mammal teeth in these deposits. This concentration occurs to the east of, but in the same strata as the megafauna reported by Raza and Meyer (1984). The exact superpositional relationships of this locality to local ranges of large mammal taxa are being documented by Mahmood Raza and others

affiliated with the Pakistan Museum of Natural History and the Geological Survey of Pakistan.

This assemblage represents the only documentation of small mammal evolution in the Indian subcontinent between the middle Eocene and early or middle Miocene. Rodents of about 16 Ma (Ma = megannum = 10^6 years; Berggren et al., 1978) and younger from Siwalik deposits are relatively well known (Jacobs, 1978; Munthe, 1980; Flynn and Jacobs, 1982; Flynn, 1982; Wessels et al., 1982; Barry et al., 1985). A fauna is also known from the Murree formation (de Bruijn et al., 1981), which lies under other Siwalik Group rocks. Siwalik and Murree rodents are of modern aspect and have Asian, African, and to a lesser degree, European components. Other than the Bugti assemblage, the next oldest small mammals known from India or Pakistan are middle Eocene in age (Sahni and Khare, 1973; Sahni and Srivastava, 1976, 1977; Hussain et al., 1978) and are completely different in character. Middle Eocene and earlier rodents (de Bruijn et al., 1982) are primitive ctenodactyloids that seem closely related to northern Asian forms of similar

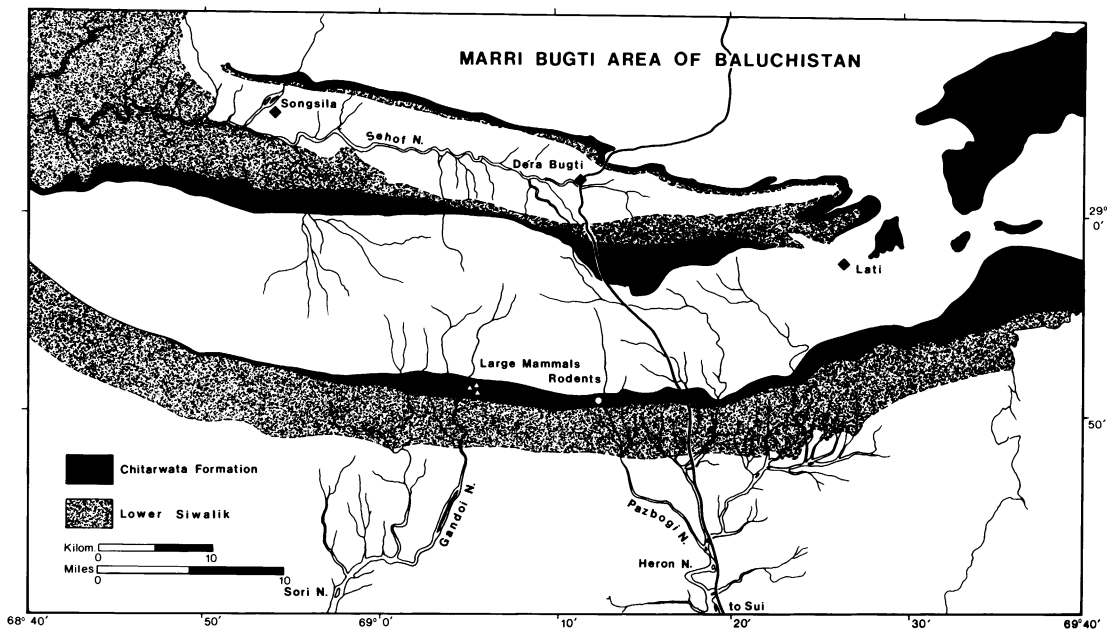


FIG. 2. Location map of the Marri Bugti area of Baluchistan, showing outcrop pattern of the Chitarwata Formation and lower Siwalik Group (after Pilgrim, 1912). The rodent locality (Y-GSP 417) is shown as a circle in the Chitarwata Formation. Triangles indicate the area of collection of large vertebrates, but are not meant to indicate specific sites.

age. The Dera Bugti fauna, although closer in age to the Murree fauna, has stronger affinity with and is readily derived from the Eocene fauna. It is endemic so far as known (Jacobs et al., 1981; see Discussion).

Dr. Albert E. Wood (1977) recognized the similarity of Eocene Indo-Pakistan rodents to primitive Asian ctenodactylids. Later, Hussain et al. (1978) proposed the new family Chapattimyidae to include the Indo-Pakistan forms, plus *Saykanomys calchis*, and questionably *Petrokoslovia*, the latter two taxa being known from elsewhere in Asia (Shevyreva, 1972). Other workers consider *Saykanomys* and other late Eocene to early Oligocene Russian, Mongolian, and Chinese genera to be ancestral to later Ctenodactylidae (see Wood, 1977) and feel that these should be included in that family. Hussain et al. (1978) referred some Pakistani and Indian samples to *Saykanomys*, but Hartenberger (1982a) places them in the distinct genus *Birbalomys* Sahni and Khare (1973), thus separating them systematically from more northern Asian ctenodactylids. Hartenberger (1982a) includes *Metkamys blacki* in *Bir-*

balomys woodi, and recognizes two subgenera and at least three other species within *Birbalomys*. Dawson et al. (1984) suggest the possibility of synonymy of *Saykanomys* with *Advenimus* Dawson (1964), which they place in the ctenodactyloid family Yuomyidae.

According to Hartenberger (1982a), the Indo-Pakistan species constitute a horizontal, primitive subfamily Chapattimyinae within the Ctenodactylidae, including *Chapattimys*, *Birbalomys*, and presumably *Gumbatomys*. Without more data, the taxonomic rank of the chapattimyids could be debated without resolution and remain a question of taste or preference. Addition of the Bugti fauna to the known array of forms permits recognition of the direction of evolution in features of these south Asian rodents, especially with reference to Miocene ctenodactylids, and sheds light on character polarities. Below, the Chapattimyidae are redefined, a new subfamily Baluchimyinae is established, and relationships with Ctenodactylidae and other higher rodent categories that originated during the Eocene are discussed.

GEOLOGY AND AGE

The geology and paleontology of the Bugti Hills, Baluchistan, Pakistan, have been most recently reviewed by Raza and Meyer (1984). The Bugti Bone Beds are a classic site in vertebrate paleontology, with a diverse suite of large mammals (see, for example, Osborn, 1924, 1932; Pilgrim, 1907, 1908, 1912; Savage, 1967; and Cooper, 1913, 1915, 1920, 1922, 1923, 1924a, 1924b, 1924c, 1934), usually considered to be early Miocene (Burdigalian) in age (Berggren and Van Couvering, 1974; Madden and Van Couvering, 1976; Van Couvering, 1972). However, the precise age of the fauna is difficult to determine considering the general dearth of continental terrestrial deposits on the Indian subcontinent between the Eocene Epoch and the Miocene represented at Dera Bugti.

The Bugti Bone Beds are assigned to the Bugti Member (Raza and Meyer, 1984), which is the lower fossiliferous portion of the Chitarwata Formation (Hemphill and Kidwai, 1973). The matrix containing rodent fossils is a friable yellow sand approximately 10 m above the base of the formation. The only fossils besides rodents found by screening the sands at locality Y-GSP 417 are shark teeth and fragments of bony fish.

Near shore or marine invertebrate fossils occur occasionally in the Bugti Member, including four species of the oyster genus *Ostrea* (Eames, 1950). These taxa are consistent with, but not proof of, an early Miocene age for Bugti. Nevertheless, large mammal fossils provide the best indicators of age for the Bugti Member. Analysis by Raza and Meyer (1984) suggests that the Bugti fauna is most similar to that from Rusinga Island, Kenya. Localities on Rusinga Island represent a range of ages, and dates span the time between 21 to 18 Ma (Van Couvering and Van Couvering, 1976; Pickford, 1985). Raza and Meyer (1984) concluded that the Chitarwata Formation may be correlative with the Orleanian Mammal Age of Europe, and the Bugti Member was correlated with the sequence of formations on Rusinga. The absolute age, by inference, was considered to be greater than 18 Ma.

Dera Bugti lies some 500 km to the southwest of Murree and Siwalik localities of the

Potwar Plateau. Pre-Siwalik sedimentation was discontinuous between these two areas, which constituted basins separated by a structural high at that time (Raza and Meyer, 1984). During the late Oligocene and early Miocene, fluvial systems probably carried sediment from the north, west of the Potwar, through the Bugti area to the Karachi Synclorium (Raza and Meyer, 1984; see also Sahni and Mitra, 1980a, 1980b). We see no reason to postulate faunal provincialism with contemporaneous high-level taxonomic differences between these areas, although we cannot confidently dismiss the possibility. We consider Bugti and Murree faunal differences, which for rodents are mainly at the family level, to reflect temporal dischroneity (Bugti being older) rather than distributional effects. Raza et al. (1984) list eight genera of large mammals in common between Bugti and the lower Siwalik Chinji fauna. The total large mammal fauna indicates an older age for Bugti, but the degree of generic similarity between the two is consistent with the interpretation that the age difference is not necessarily great, perhaps on the order of 3 million years.

All of the rodent species from the Bugti Member are endemic, and therefore are poor indicators for correlative biochronological age determination. There is no apparent reason why they could not be consistent with an early Miocene (or Oligocene) age, but they are constrained by the middle and late Miocene Murree Formation and Siwalik Group. As noted above, the Bugti fauna contrasts sharply with and probably antedates the Murree, Kamlial, and younger faunas. The Murree rodent fauna was studied by de Bruijn et al. (1981), but its absolute age is unknown.

Fatmi (1973) recognizes the Rawalpindi Group and Siwalik Group for Neogene molassic sediments in the Potwar area. The Rawalpindi Group is composed of the Kamlial Formation and the Murree Formation. The Siwalik Group (sensu Fatmi, 1973) includes the Chinji, Nagri, Dhok Pathan, and younger formations. We suspect that the recognition of two lithostratigraphic units of group magnitude is a distinction without a difference; therefore, we find it convenient to recognize only the Siwalik Group and include in it all the above-named formations.

TABLE 1
**Rodent Genera Represented at Bugti and in the
 Murree and Kamliyal Formations**
 (de Bruijn et al., 1981; Flynn et al., 1983; Lindsay,
 personal commun.)

Bugti	Murree plus Kamliyal
Chapattimyidae	Ctenodactylidae
<i>Fallomus</i>	<i>Sayimys</i>
Baluchimyinae	Thryonomyidae
<i>Baluchimys</i>	<i>Paraulacodus</i>
<i>Lindsaya</i>	Genera 1, 2
<i>Lophibaluchia</i>	Chapattimyidae
<i>Hodsahibia</i>	cf. <i>Fallomus</i>
New genus 1	Cricetidae
New genus 2	<i>Primus</i>
Chapattimyidae or Yuomyidae	cf. <i>Dakkamys</i>
cf. <i>Dianomys</i> or	<i>Spanocricetodon</i>
<i>Lophibaluchia</i>	<i>Megacricetodon</i>
Family indet.	<i>Democricetodon</i>
<i>Downsimys</i>	Genera 1, 2
	Rhizomyidae
	<i>Prokanisamys</i>
	<i>Kanisamys</i>
	Gliridae
	Sciuridae
	Rodentia indet.

The status of the Murree and Kamliyal strata as separate formations is open to question, but in any case we know of no evidence to suggest that they together encompass more than a few million years. These strata are deposited on a regional unconformity (John C. Barry, personal commun.). The base of the Kamliyal-Murree in the Chita Parwala-Gabhir section near Chinji village is dated at 18.3 Ma by magnetic polarity stratigraphy (Johnson et al., 1985). The oldest rodent-producing localities (Y-GSP 591, 592) in the Chita Parwala-Gabhir section are in the upper Kamliyal at about 16.1 Ma. The rodent fauna from these sites is distinct from that of Bugti (table 1), with a more modern, Siwalik aspect. A large anthracothere and a deinother were collected at the base of the Chita Parwala-Gabhir section, suggesting similar age with Bugti (Barry et al., 1985). No rodents are currently known from the base of that section.

The Murree rodent fauna from Kohat, Pakistan, occurs just above the regional uncon-

formity, dated near Chinji at 18.3 Ma. Illustrations in de Bruijn et al. (1981) document the presence of a rodent similar to *Fallomus razae* (from Bugti and described herein) in the Murree fauna, along with typical lower Siwalik taxa such as *Sayimys*, cricetids, sciurids, a rhizomyid, and a possible thryonomyid.

The correlation of Bugti with Rusinga by Raza and Meyer (1984), the dating of the initiation of Siwalik Group sedimentation at 18.3 Ma, the stratigraphic position of the known Murree rodent fauna just above the basal unconformity, the full development of the Siwalik rodent fauna by 16.1 Ma, and the somewhat transitional nature of both the rodent and large mammal faunas as known from just above the unconformity, suggest to us: (1) the Bugti fauna is older than 18.3 Ma, (2) the Bugti fauna is not likely to be older than about 21 Ma, but could be younger, (3) a major change in the rodent fauna of the Indian subcontinent occurred between Bugti and Murree time, and it involved extinction, decline in relative abundance of survivors, introduction from Africa (Thryonomyoidea), introduction from Asia (*Sayimys*, Cricetidae), and cladogenesis of new arrivals (Rhizomyidae). Between 18.3 Ma and 16.1 Ma the rodent fauna began to develop characteristics typical of the lower Siwaliks, viz., baluchimyines absent, cricetids, rhizomyids, ctenodactylids, and thryonomyoids present. By about 13 Ma, murids became a major part of the Siwalik fauna, probably through autochthonous evolution, and were dominant among rodents in Pakistan until relatively recent aridification and the spread of gerbils (Jacobs and Flynn, 1981; Flynn and Jacobs, 1982).

METHODS

The rodents described below were retrieved by screening fossiliferous sediments of the lower Bugti Member, about 10 m above its base. The locality Y-GSP 417 (Yale-Geological Survey of Pakistan) is about 16 km south of the village Dera Bugti in Pazbogi Nala (fig. 2). Preliminary dry screening in 1978 showed the locality to be productive, so in 1979 a large sample of matrix was processed by soaking in kerosene, followed by

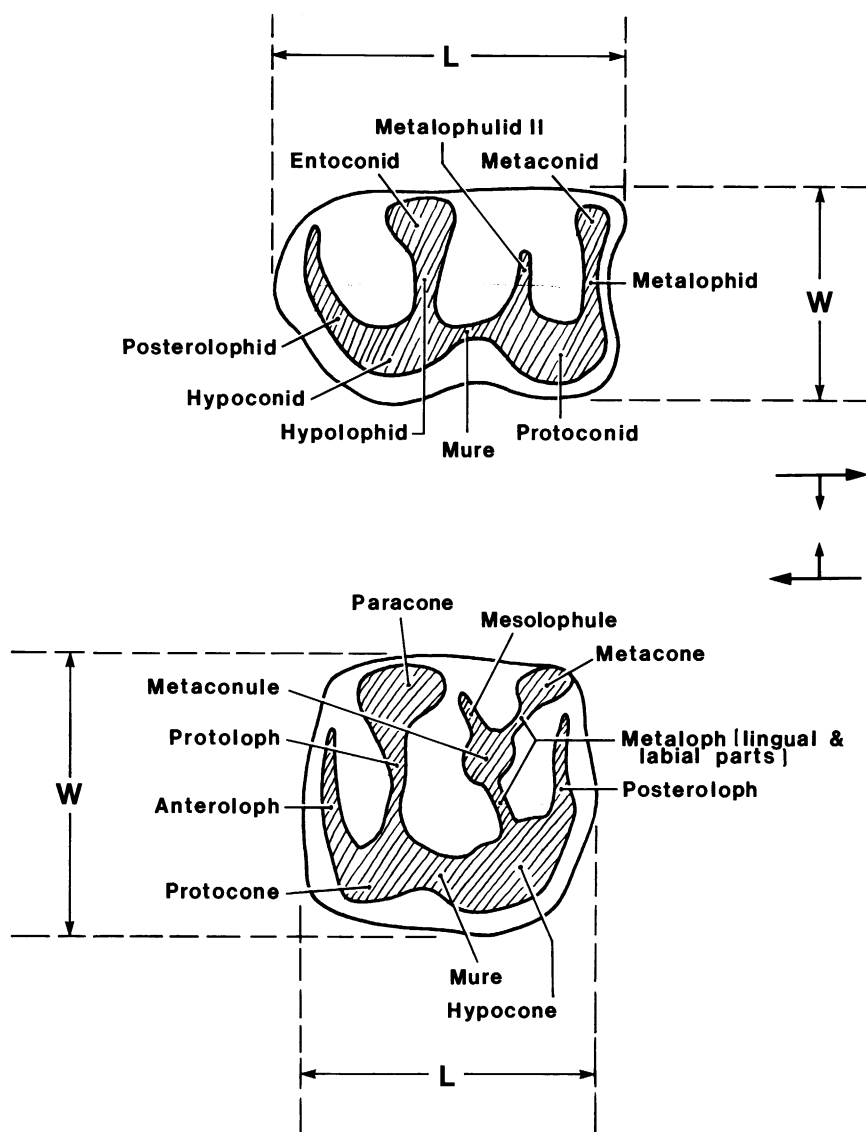


FIG. 3. Diagram of idealized chapattimyid upper and lower molars, showing terminology of cusps and lophs and method of measurement.

agitation in water. Tandem boxes with 1 mm outer mesh screen (diagonal dimension) were employed. Over 350 cheek teeth plus numerous fragments and incisors were recovered from the washed concentrate, but only two teeth occurred in association. No other jaw fragments were identified. No insectivores were retrieved, but shark teeth were present. All specimens bear GSP numbers and are the property of Pakistan. Plastic casts are housed at the American Museum of Nat-

ural History and at Southern Methodist University. All specimens were measured with a Wild microscope to the nearest 0.02 mm. Length (L) and width (W) were determined as in figure 3.

The interpretations of lophs used in this study are based on morphological similarities of occlusal patterns among Eocene chapattimyids (especially *Birbalomys*) and the various baluchimyine taxa. The rationale for our interpretations is presented in the Discus-

sion. We consider the loph directed anteriorly from the posteroloph (fig. 3) to be a modified metaloph, rather than the neoloph proposed for South American caviomorphs with a similar pattern (Patterson and Wood, 1982). This interpretation is more consistent with the dental terminology used by Lavocat (1976). Butler (1985) also questions that this crest is a new element because Patterson and Wood's (1982) homologies require that the paracone and metacone be closer together than the protocone and hypocone, which is unusual from a functional point of view.

We consider the loph directed labiad from the hypocone, through the metaconule, to be a mesolophule, although its lingual portion (i.e., between the hypocone and metaconule) is probably homologous with a portion of the primitive metaloph. Lavocat (1976) called a similar crest in caviomorphs a mesoloph, but the mesoloph of muroids is different in origin and our term mesolophule is designed to acknowledge this. Figure 3 illustrates loph geography and cusp nomenclature adapted from Wood and Wilson (1936).

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SYSTEMATICS

SUPERFAMILY CTENODACTYLOIDEA

TULLBERG, 1899

FAMILY CHAPATTIMYIDAE HUSSAIN,

DE BRUIJN, AND LEINDERS, 1978

EMENDED DIAGNOSIS: Hystricomorphous and sciurognathous rodents primitively with dental formula 1023/1013; premolars large, submolariform to molariform, with P⁴ retaining four or five major cusps (paracone, metacone, protocone, metaconule, usually hypocone); hypocone lingually placed and apparently developed from posterolingual cingulum shelf on P⁴ M¹⁻² and small on M³; metaconule inflated as a major cusp or else modified (incorporated in a loph or lost); P₄ oval in outline, length over 20 percent greater than width; lower molars with low anterior cingulum; hypoconulid always well developed on P₄ M₁₋₂; metalophulid II present; incisor enamel pauciserial in early forms, multiserial with thin lamellae (3 to 5 prisms wide) in later forms.

DISCUSSION: To discuss the significance of each of the traits included in our diagnosis, we consider the late Paleocene eurymylid *Heomys orientalis* Li (1977) in outgroup relationship to Rodentia and therefore assume characters shared with rodents are primitive conditions. The early Eocene Chinese rodent *Cocomys lingchaensis* (see Dawson et al., 1984; Hartenberger, 1985) indicates plesiomorphies for ctenodactyloids. Occurrences of these and other Glires discussed below are summarized in table 2. *Heomys* and *Cocomys* are both protrogomorphous and sciurognathous. Hystricomorphy is inferred for the Eocene Indian *Birbalomys* and other Chapattimyidae from similar ctenodactyloids of the Paleogene of Kazakhstan (Shevyreva, 1972) and China (Dawson et al., 1984). Figures and casts of *Birbalomys* avail-

TABLE 2
Geographic Distribution of Asiatic Genera Discussed in Text of Late Paleocene to Early Miocene Age

	Pakistan-India	Kazakhstan	Outer Mongolia	Inner Mongolia	China
Miocene	<i>Sayimys</i> (Ct) <i>Fallomys</i> (Ch) Baluchimyinae (Ch)				<i>Sayimys</i> , <i>Tataromys</i> (Ct)
Oligocene		<i>Woodomys</i> (?Y) <i>Terraboreus</i> (Y) <i>Ardynomys</i> (Cy)	<i>Tataromys</i> , <i>Karakaromys</i> (Ct) <i>Woodomys</i> (Y) <i>Morosomys</i> (Cy) <i>Petrokoslovina</i> (Y)	<i>Sayimys</i> , <i>Tataromys</i> , <i>Karakaromys</i> , <i>Yindertomys</i> , <i>Leptotataromys</i> (Ct) <i>Ardynomys</i> (Cy) <i>Hulgana</i> (Cy) <i>Yuomys</i> (Y)	<i>Sayimys</i> , <i>Tataromys</i> , <i>Karakaromys</i> , <i>Yindertomys</i> , <i>Leptotataromys</i> (Ct) <i>Dianomys</i> (Y) <i>Yuomys</i> (Y) <i>Tsinlingomys</i> (Ct)
Eocene	<i>Birbalomys</i> , <i>Chapatimys</i> , <i>Gumbatomys</i> (Ch) <i>?Petrokoslovina</i> (Y) Ch. indet. Cy, indet.	<i>Saykanomys</i> (Y) <i>Tamquammys</i> (Ct)	<i>Saykanomys</i> (Y)	<i>Advenimus</i> (Y) <i>Tamquammys</i> (Ct)	<i>Advenimus</i> (Y) <i>Cocomys</i> (Co) <i>Heomys</i> (E)
Paleocene			<i>Eurymylus</i> (E)		

Data from: Dawson et al., 1984; Wood, 1977; Wang, 1984; Savage and Russell, 1983; this paper.
Abbreviations: Ch, Chapattimyidae; Co, Cocomyidae; Ct, Ctenodactylidae; Cy, Cylindrodontidae; E, Eurymylidae; Y, Yuomyidae.

able to us suggest hystricomorphy but do not reveal details of this structure; all early ctenodactylids in which the zygomatic structure is definitely known are hystricomorphous. Casts of the dentary of *Birbalomys* and other known early Asian rodents indicate sciurognathy.

As a primitive character *Birbalomys* retained a small peglike P^3 , and the presence of P^3 is evidenced by an interdental pressure facet on the anterior side of P^4 in most other Chapattimyidae. Inflated metaconules and hypoconulids are synapomorphies of the family.

Hartenberger (1982a) and Wood (1977) consider that chapattimyids and *Saykanomys calchis* have small P^4 , but the fourth premolars of *Saykanomys* (or *Advenimus*) are not derived in size; they are nearly as large as the first molars. *Birbalomys woodi* also has unreduced premolars. Unfortunately, other Eocene chapattimyids are represented only by unassociated teeth. *Heomys* and *Cocomys* demonstrate the primitive premolar condition of ctenodactylids and probably for all rodents (see Dawson et al., 1984): P^4 small, with two major cusps (paracone and protocone) and (?variably) a minute hypocone and metacone; P_4 small with the talonid nearly as wide as the trigonid and lacking a cusped hypoconid or hypoconulid. This, plus occurrence of a nonmolariform premolar in the late early Eocene of Pakistan led de Bruijn et al. (1982) to postulate that the characteristically small premolar of ctenodactylids is plesiomorphous and not secondarily reduced, as had been assumed. However, the degree of premolar reduction seen in the family Ctenodactylidae, specifically narrowing and shortening of the talonid on P_4 , is a derived condition. Also derived are the large, molarized premolars of Chapattimyidae and Yuomyidae (see below). The overall evolutionary trend among chapattimyids is increase in size and complication of premolars.

Incisor enamel microstructure has been examined in sagittal sections of incisors from deposits yielding Eocene ctenodactylids (Hussain et al., 1978; Sahni, 1980; de Bruijn et al., 1982). These incisors probably are ctenodactylid, but identity is not certain. All of them exhibit pauciserial microstructure (Sahni, 1980; Hartenberger, 1982a; Dashze-

veg et al., in press), not multiserial as suggested by Hussain et al. (1978) and de Bruijn et al. (1982). They are characterized by vertical inner enamel bands of irregular width that are one to four prisms wide. These Eocene incisors show diversity in relative thickness of the outer layer of enamel and in regularity of inner enamel bands. In the diagnosis of Baluchimyinae, new subfamily, multiserial enamel with narrow, regular, inclined inner enamel bands is shown to occur in later chapattimyids.

TEMPORAL AND GEOGRAPHIC RANGE: Chapattimyids are first encountered in the early Eocene Mami Khel Clay near Banda Daud Shah, Pakistan (the molars illustrated by de Bruijn et al., 1982). They are known from several middle Eocene localities in Pakistan and India (Hussain et al., 1978; Hartenberger, 1982a; Sahni and Khare, 1973; Sahni and Srivastava, 1976, 1977) and probably from the late Eocene of Algeria (see below, p. 51). They occur in the early Miocene Bugti fauna of Baluchistan, Pakistan, and survive into the early or middle Miocene Murree Formation near Banda Daud Shah, northern Pakistan (see discussion of *Fallomus razae*).

SUBFAMILIAL CLASSIFICATION: Hartenberger (1982a) grouped *Chapattimys*, *Birbalomys*, and questionably *Gumbatomys* as a subfamily (Chapattimyinae) of Ctenodactylidae. These forms represent an Eocene radiation of ctenodactylids in the Indian subcontinent, separate from the diversification of true ctenodactylids and yuomyids elsewhere in Asia. In reestablishing the family Chapattimyidae, *Chapattimys*, *Birbalomys*, and *Gumbatomys* are removed from the Ctenodactylidae and united with the diverse early Miocene Bugti fauna, including *Fallomus* and the subfamily Baluchimyinae, which are described below. A suite of synapomorphies define the Baluchimyinae, but none are recognized that unite the remaining chapattimyid genera at the subfamilial level. Because "chapattimyines" comprise a primitive grade, we do not consider as particularly useful the formal recognition of a subfamily Chapattimyinae. Further, while no species is known to present a suitable primitive morphotype for the Baluchimyinae, that subfamily probably evolved from an undiscovered or unrecognized Eocene chapattimyid. Thus

the Eocene forms as a whole constitute a paraphyletic group. In addition, the diversity of known non-baluchimyine chapattimyids suggests that they might be divisible into more than one group when more data are available; e.g., *Chapattimys* and *Fallomys* are derived in different characters.

OTHER CTENODACTYLOID FAMILIES

Derived characters uniting the Chapattimyidae are development of large molarized premolars, presence of large hypoconulids on lower teeth, and inflation of the metaconule (see Wang, 1984). Additional traits seen in chapattimyids are shared with some other early ctenodactyloids, and thus define the superfamily Ctenodactyloidea (see Dawson et al., 1984). These include hystricomorphy, presence of a hypolophid that usually crosses the talonid, and occurrence of a mesoconid. Early ctenodactyloids retain plesiomorphic traits present in *Heomys*: increase in tooth size from P_4 to M_3 , conules and a hypocone on upper molars, a hypoconulid and a metalophulid II on lower molars. Early ctenodactyloids are bunodont and lack mesolophids and mesolophids. The superfamily Ctenodactyloidea Tullberg, 1899, is a valid taxon as used by Chaline and Mein (1979) and includes Chapattimyidae and Ctenodactylidae, as well as Yuomyidae Dawson, Li, and Qi (1984; see below). The latter authors include *Cocomys* in the Ctenodactyloidea, a preference with which we do not take issue. *Cocomys* embodies the primitive morphotype for Ctenodactyloidea with the added inconvenience that it is protrogomorphous and lacks hypolophids (Dawson et al., 1984). Dawson et al. (1984) name the family Cocomyidae for *Cocomys* plus *Tsinlingomys* and *Tamquammys* (see table 2). In this paper we refer the latter two genera to Ctenodactylidae because they have P_4 with reduced talonids and because *Tamquammys* is known to be hystricomorphous (see Dawson et al., 1984, and below). Although we exclude *Cocomys* from Ctenodactyloidea in figure 4, alternatively it could be included in the superfamily as the monotypic Cocomyidae and without reference to other groups (incertae sedis).

Ctenodactylidae are here defined by the structure of P_4 : the talonid is short and significantly narrower than the trigonid, con-

ditions derived with respect to *Cocomys* and *Heomys*. Ctenodactylidae develop many other autapomorphies after their appearance: loss of the mesoconid, submergence of the metaconule in a crest joining metacone and hypocone, loss of metalophulid II, development of a heavy and horizontal masseteric crest that progrades to below P_4 , lophodonty and hypsodonty, and multiserial enamel. True ctenodactylids appear by the middle Eocene (*Tamquammys*) and by the late Oligocene all of these transformations are developed (Wood, 1977; Dawson et al., 1984).

Yuomyidae Dawson et al. (1984) are a ctenodactyloid group also distinguished by premolar structure. These hystricomorphous rodents have molariform premolars with P_4 further derived in having a broad talonid that in width nearly equals P_4 length. On this character, *Advenimus hupeiensis* can be included in Yuomyidae, as Dawson et al. (1984) tentatively proposed. However, *A. burkei* Dawson (1964) has a slender P_4 . Wang (1984) pointed out that yuomyids lack a metaloph lingual to the metaconule and this apparently holds for *Saykanomys* Shevyreva (1972), which Dawson et al. (1984) suggest as synonymous with *Advenimus*. Wang (1984) showed that later yuomyids (*Yuomys*, *Dianomys*, *Petrokoslovia*) have P_4 larger than M_1 and are lophodont and high crowned; she includes *Terrarboreus* Shevyreva (1971) in Yuomyidae. Dawson et al. (1984) note the Eocene occurrences of yuomyids in Kazakhstan, Mongolia, and Inner Mongolia, China. Probably the Pakistani middle Eocene "*Petrokoslovia*" of Hussain et al. (1978) can be included in the family. Represented by *Terrarboreus* from Kazakhstan and *Dianomys* from Yunnan, China, the family persisted at least into the Oligocene of Asia.

P_4 size and outline is useful, but insufficient to recognize Yuomyidae. Non-ctenodactyloid cylindrodontids (e.g., *Ardynomys*) also have a large P_4 with broad talonid. Cylindrodontids, however, usually lack a strong metalophulid II and hypolophid. More distinctive is the lack of a hypocone in upper molars, unlike ctenodactyloids. Two other important differences are that cylindrodontids are protrogomorphous and have uniserial or pauciserial enamel. Cylindrodontids occur in the late Paleogene of Asia and are

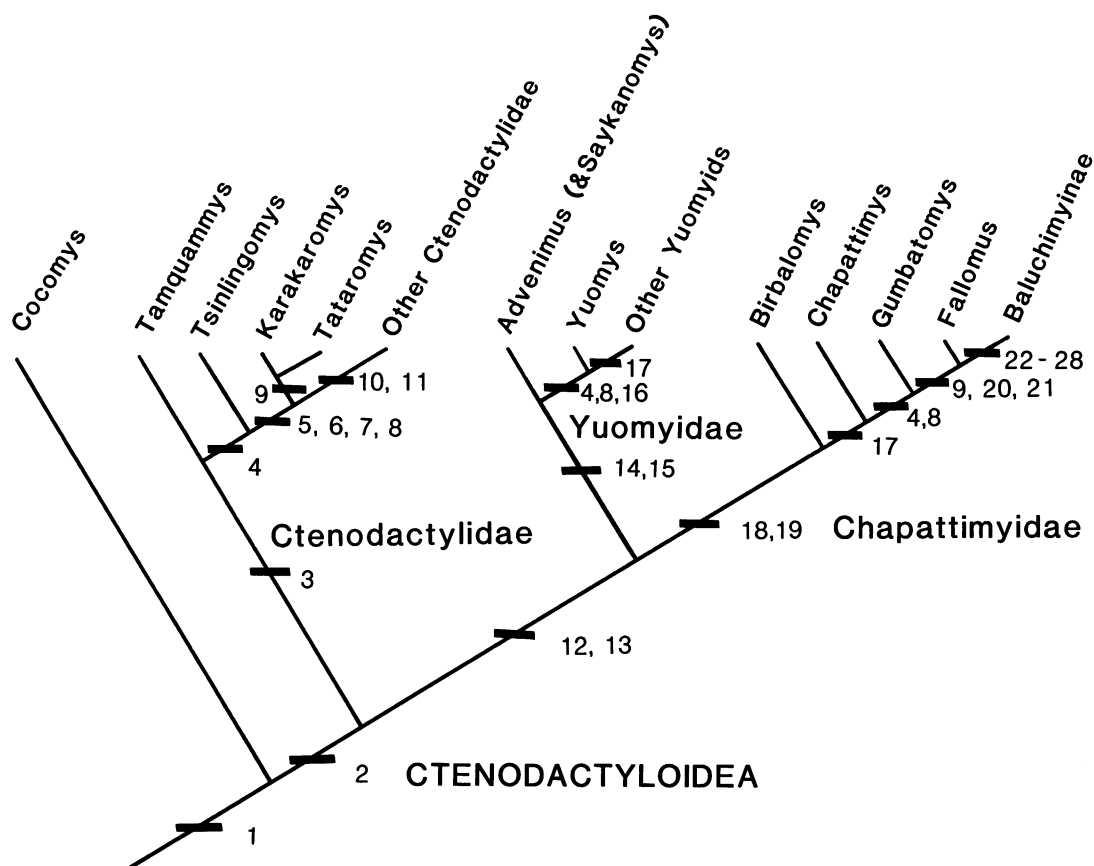


FIG. 4. Diagram of relationships among early ctenodactyloids with *Cocomys* used in outgroup comparison. Numbers correspond to derived traits listed in table 3.

similar to yuomyids. The early Oligocene *Hulgana* Dawson (1968) of Inner Mongolia should be placed in Cylindrodontidae. The family may have appeared in the Eocene of Pakistan. Perhaps the ischyromyoid P_4 of de Bruijn et al. (1982, their fig. 6) and the geologically somewhat younger tooth figured by Hussain et al. (1978, their plate 4, fig. 10) are early cylindrodontids.

Early ctenodactyloids are difficult to place in families because advanced traits are in some cases only moderately transformed. Thus *Advenimus* resembles *Birbalomys* and this led Wang (1984) to place both in the Chapattimyidae; but the P_4 talonid of *Advenimus* is broader than in *Birbalomys* and the latter has stronger hypoconulids. These derived states are the basis for their separation. On the other hand the P_4 of *Tamquammys* is less reduced than in later Ctenodactylidae.

Distributional data are coincident with the morphological basis for assigning early ctenodactyloids to family. *Birbalomys* and other chapattimyids are restricted to southern Asia, while *Advenimus* (and *Saykanomys*), *Tamquammys* and *Tsinlingomys* occur from Kazakhstan to Mongolia and China. We interpret the origin of the Chapattimyidae as a vicariant event in which a broad pan-Asian ctenodactyloid distribution was divided by a geographic barrier, the Paratethys-Himalayas. South of this barrier, chapattimyids radiated after splitting from other ctenodactyloids, specifically yuomyids. This event took place by the middle Eocene, probably after the origin of Ctenodactylidae (see also Flynn et al., 1985, and Jaeger et al., 1985).

Figure 4 summarizes relationships among early Eocene ctenodactyloids. Hystricomorphy (character 2 in table 3) is considered a

derived condition that appeared within the Rodentia, although Eastman (1982) has introduced the interesting hypothesis that hystricomorphy could be primitive for rodents. For the purpose of analyzing fossils, expansion of the infraorbital foramen is a derived condition and can be used as the operational definition of typical hystricomorphy.

The late Paleocene eurymyid *Heomys* is used for outgroup comparison (fig. 4) and three ctenodactyloid families, Ctenodactylidae, Yuomyidae, and Chapattimyidae are recognized. *Cocomys* is excluded from Ctenodactyloidea because it lacks hystricomorphy, a synapomorphy of the superfamily. Other researchers may elect to extend the Ctenodactyloidea to accommodate *Cocomys* based on dental characters or *Cocomys* could be considered as a monotypic family Cocomyidae Dawson et al. (1984). Those authors included *Tamquammys* and *Tsinlingomys* in Cocomyidae, but we consider these genera to be Ctenodactylidae. As Wang (1984) recognized, Yuomyidae and Chapattimyidae are united by their molariform premolars. *Birbalomys* is considered the least derived chapattimyid, but the relationships among *Chapattimys*, *Gumbatomys*, and *Fallomus* are considered poorly resolved at present. Family synapomorphies are detailed in table 3, where numbered traits correspond to derived conditions on figure 4.

CHAPATTIMYIDAE INCERTAE SEDIS

Fallomus, New Genus

TYPE SPECIES: *Fallomus razae*, new and only known species.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Latin, masculine for "false mouse."

DIAGNOSIS: Chapattimyid with cheek teeth transversely bilophodont, lacking well-developed longitudinal crests; high, inclined cusps; upper cheek teeth with four major cusps, lacking both metaconule and paraconule; lower teeth with five major cusps including hypoconulid; enterostyle and ectostylid present in high frequency; second molars are largest cheek teeth; M^{1-3} and M_2 with four roots.

TABLE 3
Derived Characters for Ctenodactyloid Cladogram (Fig. 4)

1. Mesoconid present on lower molars.
2. Hystricomorphy.
3. Talonid of P_4 short and significantly narrower than talonid.
4. Mesoconid absent.
5. Metaconule absent.
6. Posterolophids project posterolingually.
7. Masseteric crest heavy and extends to below M_1 .
8. Cusps joined by continuous crests.
9. Anterior cingulum present on lower molars.
10. Metalophulid II absent.
11. Masseteric crest horizontal and extends anteriorly to below P_4 .
12. Molariform P_4^1 , with large hypoconid on P_4 and metacone on P_4^1 .
13. Anteroconid variably present on P_4 .
14. P_4 waisted with wide talonid, nearly as wide as P_4 is long.
15. Metaloph incomplete.
16. Premolars larger than first molars.
17. Hypocone on P_4^1 .
18. Oval lower premolar.
19. Inflated metaconule.
20. Hypocone as large as protocone on P_4^1 .
21. P_4 anteroconid fixed as constant trait.
22. Strong metalophulid II.
23. Paraconule absent.
24. Metaconule joins hypocone.
25. Hypolophid in anterior position.
26. DP_4 bearing multiple, oblique lophs.
27. Mesolophule neomorph extends anterolabially from metacone.
28. Multiserial enamel with band width 3 to 5 rods wide.

Fallomus razae, new species

Figures 5, 6, tables 4, 5

HOLOTYPE: GSP 21218, left M^2 .

HYPODIGM: GSP 21200, DP_4^1 ; 21201–21207, P_4^1 ; 21208–21217, M^1 ; 21218–21225, M^2 ; 21226–21228, M^3 ; 21229–21230, DP_4^1 ; 21231–21234, P_4^1 ; 21235–21245, M_1 ; 21246–21256, M_2 ; 21257–21260, M_3 .

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for geologist and paleontologist, Dr. Mahmood Raza.

DIAGNOSIS: As for genus.

DESCRIPTION: A small P^3 is evidenced in at least some individuals by a minute facet on P^4 . DP^4 is represented by one unworn, chipped tooth. Cusps incline posteriorly as in all up-

TABLE 4
Tooth Dimensions in Millimeters for Cheek Teeth
of Sample Size Less Than Ten for *Fallomus razae*,
New Genus and Species

Specimen	Number	Length	Width
DP ⁴	21200	1.44	1.28
P ⁴	21201	1.40	1.24
P ⁴	21202	1.36	1.24
P ⁴	21203	1.32	1.24
P ⁴	21204	1.30	1.24
P ⁴	21205	1.30	1.24
P ⁴	21206	1.40	1.20
P ⁴	21207	1.40	1.24
M ¹	21208	1.26	1.28
M ¹	21209	1.48	1.44
M ¹	21210	1.40	1.44
M ¹	21211	1.68	1.58
M ¹	21212	1.52	1.50
M ¹	21213	1.48	1.40
M ¹	21214	1.48	1.46
M ¹	21215	1.48	1.48
M ¹	21216	1.64	1.54
M ¹	21217	1.46	—
M ²	21218	1.66	1.66
M ²	21219	1.54	1.62
M ²	21220	1.58	1.54
M ²	21221	1.54	1.60
M ²	21222	1.40	1.62
M ²	21223	1.50	1.60
M ²	21224	1.58	1.62
M ²	21225	1.52	1.60
M ³	21226	1.58	1.42
M ³	21227	1.56	1.52
M ³	21228	1.60	1.58
DP ₄	21229	1.36	1.04
DP ₄	21230	1.44	1.00
P ₄	21231	1.44	1.12
P ₄	21232	1.40	0.96
P ₄	21233	1.38	1.02
M ₃	21257	1.54	1.38
M ₃	21258	1.46	1.34
M ₃	21259	1.70	1.32
M ₃	21260	1.68	1.46

per cheek teeth, but are higher and connected by sharper crests than in P⁴. The hypocone and metacone, the largest cusps, are antero-posteriorly compressed and connected posteriorly by a high crest. A posterior cingulum sweeps labially, toward the base of the crown, from the middle of this crest. A shorter transverse crest joins the middle of the protocone to the middle of the smaller paracone. The base of the protocone touches the base of the

hypocone, but the paracone and metacone are separated by a broad valley. An anterior cingulum bearing an elevated ridge spans the anterolabial half of DP⁴. Swelling from the anterolingual side of the hypocone is a large enterostyle. A minute but well-defined, round mesostyle lies midway between metacone and paracone. DP⁴ is broad, expanding anterolingually and bearing an additional cusplule lingual to the protocone.

The seven P⁴ are slightly smaller (table 4) and relatively narrower anteriorly than DP⁴, and lack the anterolingual expansion and cusplule. The anterior cingulum is shorter and its crest is lower. The posterior cingulum is a poorly defined ridge. The metacone is the largest cusp. The enterostyle is well developed in five specimens, indistinct in two. A small mesostyle occurs in three P⁴; it is a swelling from the metacone in one and absent in the other three. P⁴ bears a large, laterally compressed lingual root and two smaller labial roots.

Average dimensions of M¹ are somewhat longer than wide and slightly narrower anteriorly than posteriorly. Cusps are antero-posteriorly compressed. The protocone and hypocone are the largest cusps and their bases converge. A transverse crest joins the centers of the protocone and paracone. A longer, gently curving crest joins the hypocone and metacone posteriorly, and a weak posterior cingulum extends from the middle of this crest toward the posterolabial corner of the base of the crown. From the anterior slope of the protocone, a ridge or anterior cingulum extends toward the anterolabial corner of M¹. In two of ten specimens the ridge is well developed and continues around the protocone as a swollen cingulum. The enterostyle is present in all ten specimens at the anterolingual base of the hypocone and is a large cusp in six. Paracone and metacone are separated by a valley in which a mesostyle occurs in two specimens. Four roots are present on M¹⁻².

M² resembles M¹, but is larger and nearly square in outline. On M² the anterior cingulum is stronger; the posterior cingulum is weaker. Protocone and paracone are as far apart as are hypocone and metacone. The enterostyle is less distinct than in M¹ and is a continuation of the curved crest that joins

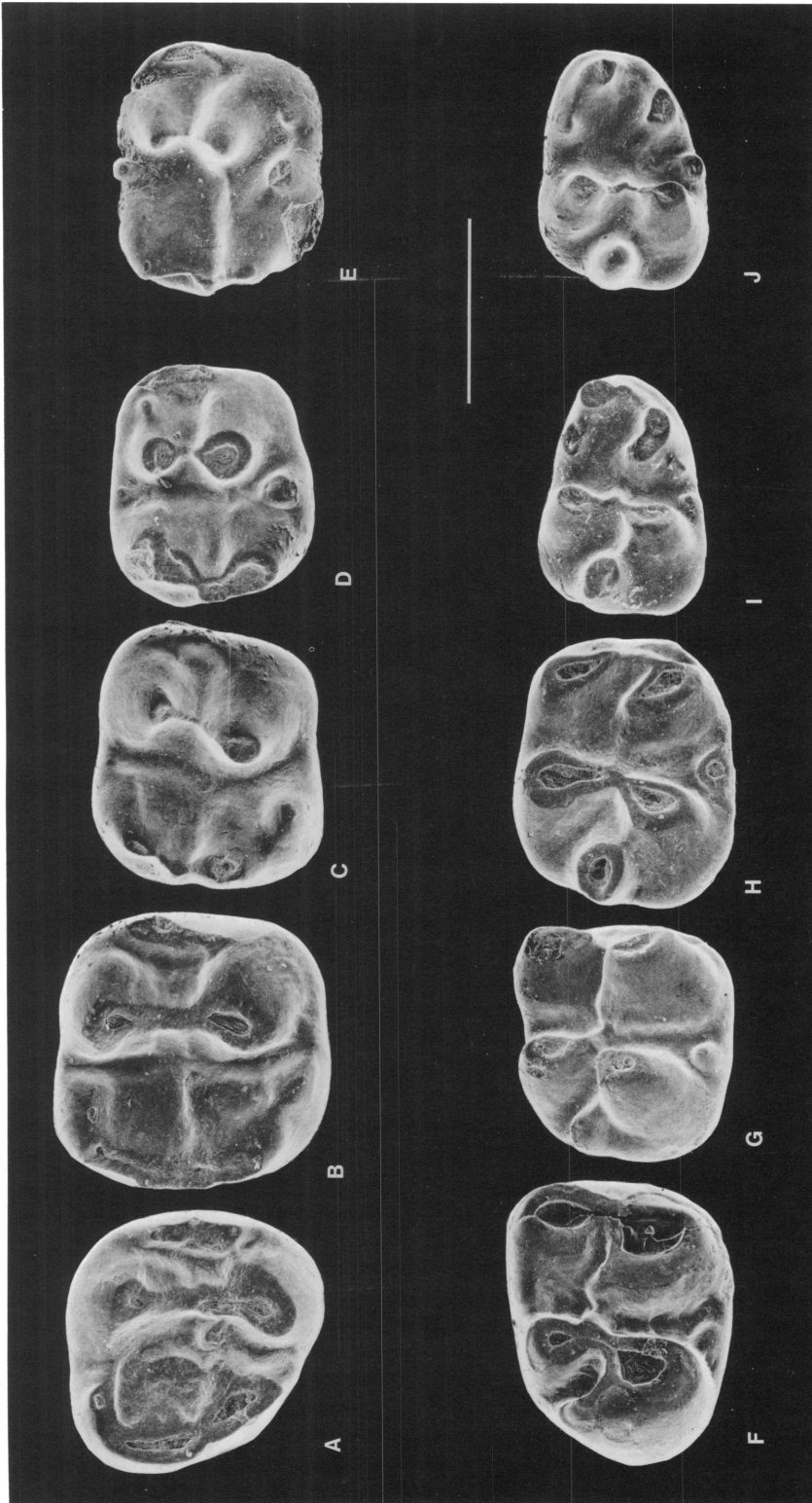


FIG. 5. Scanning electron photomicrographs of cheek teeth of *Fallomus razae*. Scale = 1 mm. A, GSP 21227, right M³; B, GSP 21221, right M²; C, GSP 21209, right M¹; D, GSP 21201, right P⁴; E, GSP 21200, right DP⁴; F, GSP 21260, right M₃; G, GSP 21252, right M₂; H, GSP 21236, right M₁; I, GSP 21233, right P₄; J, GSP 21229, right DP₄.

TABLE 5

Statistics for M_1 and M_2 of *Fallomus razae*, New Genus and New Species

Standard error given for mean (\bar{x}), standard deviation (S), and coefficient of variation (V). Other abbreviations: N (sample size); O.R. (observed range).

	N	O.R.	$\bar{x} \pm S_x$	$S \pm S_s$	$V \pm S_v$
			Length		
M_1	11	1.40–1.68	1.527 ± 0.024	0.080 ± 0.017	5.2 ± 1.1
M_2	10	1.52–1.66	1.582 ± 0.012	0.037 ± 0.008	2.3 ± 0.5
			Width		
M_1	11	1.20–1.46	1.331 ± 0.024	0.079 ± 0.004	5.9 ± 1.3
M_2	10	1.44–1.62	1.498 ± 0.017	0.053 ± 0.003	3.5 ± 0.8

hypocone and metacone. One of eight M^2 bears a mesostyle.

M^3 is asymmetrical, being longer labially than lingually. The protocone, paracone, and strong anterior cingulum resemble those of M^2 and form the anterior wall of a basin that expands posterolabially. The reduced hypocone and an indistinct metacone are incorporated into a posterior wall around the basin. This wall joins the paracone low on its posterior side. The basin contains irregular crenulations. The enterostyle is small in one M^3 and in two M^3 it is represented only by a ridge on the anterolingual side of the hypocone. M^3 has four roots and the root under the hypocone is displaced anterolabially.

Cusps of lower cheek teeth incline anteriorly. GSP 21229 and 21230 are provisionally identified as DP_4 , but may prove to be variant P_4 when better samples become available. DP_4 resemble P_4 but their cusps and crests are narrower and sharper. The hypoconid and entoconid are the largest cusps and are slightly compressed anteroposteriorly. The large, round hypoconulid lies closer to the hypoconid than the entoconid and projects beyond the posterior border of DP_4 . A transverse hypolophid joins the anterior part of the hypoconid to the middle of the entoconid. DP_4 is narrower anteriorly than posteriorly and the protoconid is anterolingual to the hypoconid. Lying at the anterior end of DP_4 , the metaconid is higher than the protoconid and is lingual to the midline of the tooth (fig. 6). A sharp, semicircular crest runs from the protoconid through the metaconid and extends posterolingually to a point opposite the posterior wall of the protoconid. This termination is marked by a cusplike swelling in

one of two DP_4 . The crest of this DP_4 bends sharply at the metaconid. A small cusp lies labial to and between the hypoconid and protoconid. Because it lies on the labial wall of the tooth, we call this cusp an ectostylid. There is a low ridge joining the protoconid to the labial end of the entoconid.

P_4 resembles DP_4 , but is narrower anteriorly, with the protoconid more lingual in position. The metaconid is less anterior in position and closer to the protoconid. Their connecting crest is low; its posterolingual end is short in one of three P_4 and slightly inflated in the other two. In two specimens, the ectostylid is strong; in the other it is small and accompanied by twin cusplike labial to the protoconid. A low ridge joins the protoconid to the entoconid on one P_4 . There are two roots: the anterior root is smaller and round, the posterior is anteroposteriorly compressed.

The protoconid and hypoconid are the largest cusps in lower molars. These and the metaconid and entoconid are anteroposteriorly compressed. M_1 is narrower anteriorly than posteriorly and bears a low anterior cingulum that varies in strength between teeth. Transverse crests join the protoconid to the metaconid and the middle of the entoconid to the front of the hypoconid. The hypoconulid is a round cusp close to the posterolingual side of the hypoconid. A short, low ridge joins the posterolingual corner of the protoconid to the labial side of the entoconid. Oblique valleys drain posterolingually from between the protoconid and the metaconid and between the hypoconid-hypoconulid and the entoconid. The ectostylid is small, but well developed in all 11 M_1 , and is located

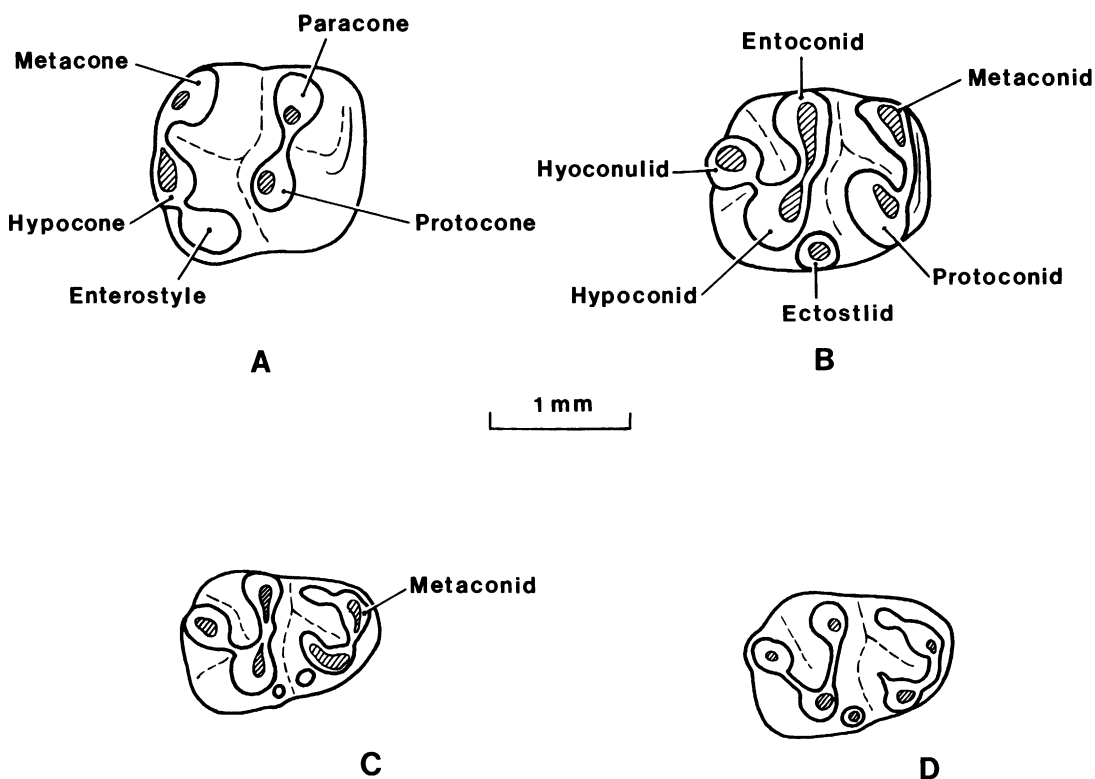


FIG. 6. Schematic drawing of cheek teeth of *Fallomus razae*, showing cusp terminology and deciduous and permanent lower premolar morphology. A, right M_1 ; B, right M_2 ; C, right P_4 ; D, right DP_4 .

in a transverse valley between the protoconid and hypoconid. M_1 has two posterior roots and an anteroposteriorly compressed anterior root with a vertical anterior sulcus.

M_2 is larger than M_1 and is almost as wide as long. M_2 is broad anteriorly unlike M_1 , so that the protoconid and metaconid are relatively larger. The hypoconulid is relatively smaller and closer to the hypoconid. Of 11 M_2 , the small ectostylid is well defined in 5, reduced in 5 and twinned in 1. The anterior root bifurcates so that M_2 has four roots.

M_3 is about the size of M_1 , narrow posteriorly, and lacks a hypoconulid. The hypoconid has a short, arcuate posterior arm. The ectostylid is present in three specimens and weak in one. M_3 appears to have one large anterior root and a posterior root.

DISCUSSION: *Fallomus razae* differs from other Bugti chapattimyids at the subfamily level, based in large part on our interpretation of DP_4 . If our assignment of specimens to DP_4 of *Fallomus* is correct, its lower decid-

uous premolar is not strongly modified as it is in Baluchimyinae. As in primitive Chapattimyidae from the Eocene Kuldana fauna, DP_4 of *Fallomus* resemble P_4 , but are distinguished by their sharper crests and somewhat different cusp arrangements. However, *F. razae* shares a number of derived features with Baluchimyinae. Premolars are large and molariform, paraconules are lost, and metacones join large hypocones. Absence of conules, autapomorphic loss of metalophulid II and longitudinal connections, and joining of the metacones with the hypocones, result in the strong transverse bilophodonty of this taxon. For the present, *Fallomus razae* is not classified as a baluchimyine, and we recognize that future fossil discoveries may expedite its subfamilial assignment.

Fallomus razae is highly derived with respect to all other chapattimyids. Cheek teeth are transversely bilophodont with strongly inclined cusps. Transverse wear surfaces are also inclined and on different levels in the

same tooth. In upper teeth, wear surfaces slope posteriorly and the posterior loph is higher; in lower teeth, surfaces slope anteriorly and the anterior loph is higher. Chewing in this taxon was unlike that of other chapattimyids, which were bunodont or had planar, lophodont teeth. Perhaps this unique dentition, distinct from that of contemporaneous baluchimyines, indicates a lifestyle that permitted the *Fallomys* lineage to persist after other early genera disappeared. *Fallomys* is also advanced in multiplication of roots and development of the enterostyle. The ectostylid is probably a neomorph counterpart to the enterostyle rather than a derivative of the mesoconid that is present in early ctenodactyloids like *Birbalomys* or *Advenimus*. One M¹ (GSP 21208; L = 1.26, W = 1.28; see table 4) of *Fallomys razae* is considerably smaller than the others, but for the present, we consider the sample to represent a single species.

Some Eocene cheek teeth from Pakistan resemble those of *Fallomys razae* in their partial isolation of cusps and reduction of the mure and metalophulid II (cf. plate 1, fig. 13 of Hartenberger, 1982a). *F. razae* is in turn similar to and perhaps near the ancestry of a chapattimyid from the Murree Formation, Pakistan. This species is a poorly represented element of a fauna that is older than faunas from the Chinji Formation; we estimate its age as early middle Miocene, or about 18 Ma. De Bruijn et al. (1981) correctly recognized the chapattimyid affinity of a lower cheek tooth of this taxon (their plate 3, fig. 7). It strongly resembles a left lower premolar of *F. razae*, but is much larger, the hypoconulid is more compressed and isolated, and the protoconid-entoconid ridge is absent. The configuration of the anterior end of the tooth resembles that of teeth assigned here as DP₄ of *F. razae*. This specimen has two posterior roots. While P₄ of *F. razae* has a single, broad posterior root, the root configuration of its deciduous counterpart is unknown. The Murree sample apparently includes lower and upper molar fragments. It appears that a *Fallomys*-like chapattimyid survived into the middle Miocene at a time when modern Asian and African elements had replaced most of the endemic fauna.

Fallomys razae also resembles the younger

Diatomys shantungensis from China (Li, 1974; Li et al., 1983). *Diatomys* upper and lower teeth are strongly bilophodont and four-rooted, but they lack styles and the lower molars lack hypoconulids. *Diatomys* has been referred with question to Geomyoidea, but its affinities lie possibly with Pedetidae. Sen (1977) described *Megapedetes aegaeus* from the middle Miocene locality of Bayraktepe, Anatolia, but he hesitated to allocate *Diatomys* to Pedetidae, mainly because *Diatomys* is a brachydont quadruped, while pedetids are saltatorial and more hypsodont. In our opinion the dentition of *Diatomys* resembles some chapattimyids (e.g., *Fallomys*) and is similar to hypothetical primitive pedetids. A pedetid-ctenodactyloid relationship is consistent with shared primitive fetal membranes (Luckett, 1971) and congruent occurrence of multiseriate enamel, sciurognath, and hystricomorphy in both families (see Wood, 1975; Fischer and Mossman, 1969). Certainly, more fossils are needed to substantiate and test hypotheses of ctenodactyloid-pedetid relationship.

BALUCHIMYINAE, NEW SUBFAMILY

DIAGNOSIS: Lophodont cheek teeth, moderately high crowned, slightly unilaterally hypsodont, and more lophodont than in chapattimyines; uppers may be secondarily bunodont; permanent premolars molariform and large, with lengths usually approximately 85 percent of molar lengths; P₄ with hypocone; DP₄ bears multiple oblique lophs; hypocone large, independent of protocone and lingual in position; mesolophule extends anterolabially from metaconule; paraconule absent; metaconule large, often incorporated in mesolophule; metaconule joins hypocone or is isolated from all cusps; hypolophid, from entoconid, intersects mure anterior to hypoconid; metalophulid II usually well developed; mesoconid absent; lower cheek tooth mure central; apices of protocone and hypocone labially placed; incisor enamel multiseriate, with bands only 3 to 5 prisms wide.

TYPE GENUS: *Baluchimys*, new.

INCLUDED GENERA: *Baluchimys*, *Lindsaya* (new), *Lophibaluchia* (new), *Hodsahibia* (new), two unnamed new genera.

DISTRIBUTION: All certainly known balu-

BUGTI

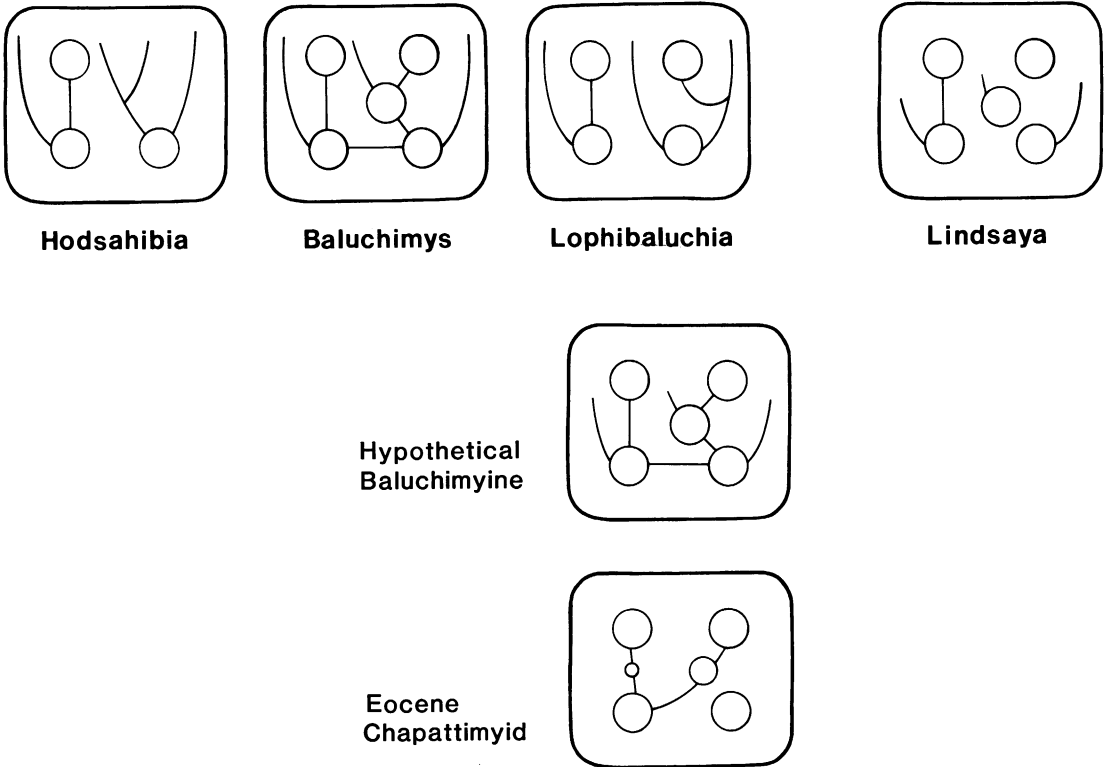


FIG. 7. Hypothetical path of transformation of the baluchimyine upper molar from that of the primitive chapattimyid morphotype. Note the mesolophule, mure, and hypocone-metacone connection in the hypothetical primitive baluchimyine. *Lindsaya* is derived in loss of cusp connections, while other baluchimyines become more lophodont. *Lophibaluchia* displays the derived connection of the metacone to the posteroloph, while *Hodsahibia* is fully pentalophodont.

chimyines occur in the early Miocene Bugti Member of the Chitarwata Formation of Baluchistan near Dera Bugti. The Baluchimyinae may have persisted into the middle Miocene. A poorly known taxon identified as a "thryonomyid" in the Murree fauna by de Bruijn et al. (1981; their plate 1, figs. 11, 12, 12a) may be a late baluchimyine.

DISCUSSION: At present the Baluchimyinae are the only formally recognized, defined subfamily of Chapattimyidae and all of the above diagnostic characters are derived with respect to other chapattimyids. The Baluchimyinae are a monophyletic clade probably derived from Eocene Chapattimyidae by autochthonous evolution, but at present we recognize no ancestor to Baluchimyinae among known species. Some apparently derived traits

are shared with *Gumbatomys*, but the single M^2 attributed to this genus is not baluchimyine because it lacks a mesolophule. Of the suite of derived traits, one of the most striking features is modification of the lower deciduous premolars, which bear four or five oblique lophs. In other chapattimyids the DP_4 resembles the permanent premolar. Permanent premolars are relatively large; those of other chapattimyids are about 75 percent of the length of their first molars. P^4 always bears a hypocone; the hypocone is small or lacking in P^4 of *Birbalomys* and *Chapattimys*.

Baluchimyines are also unified by increase in lophodonty, unilateral hypsodonty, and greater crown height. One unnamed new genus is markedly high crowned. *Lindsaya* ap-

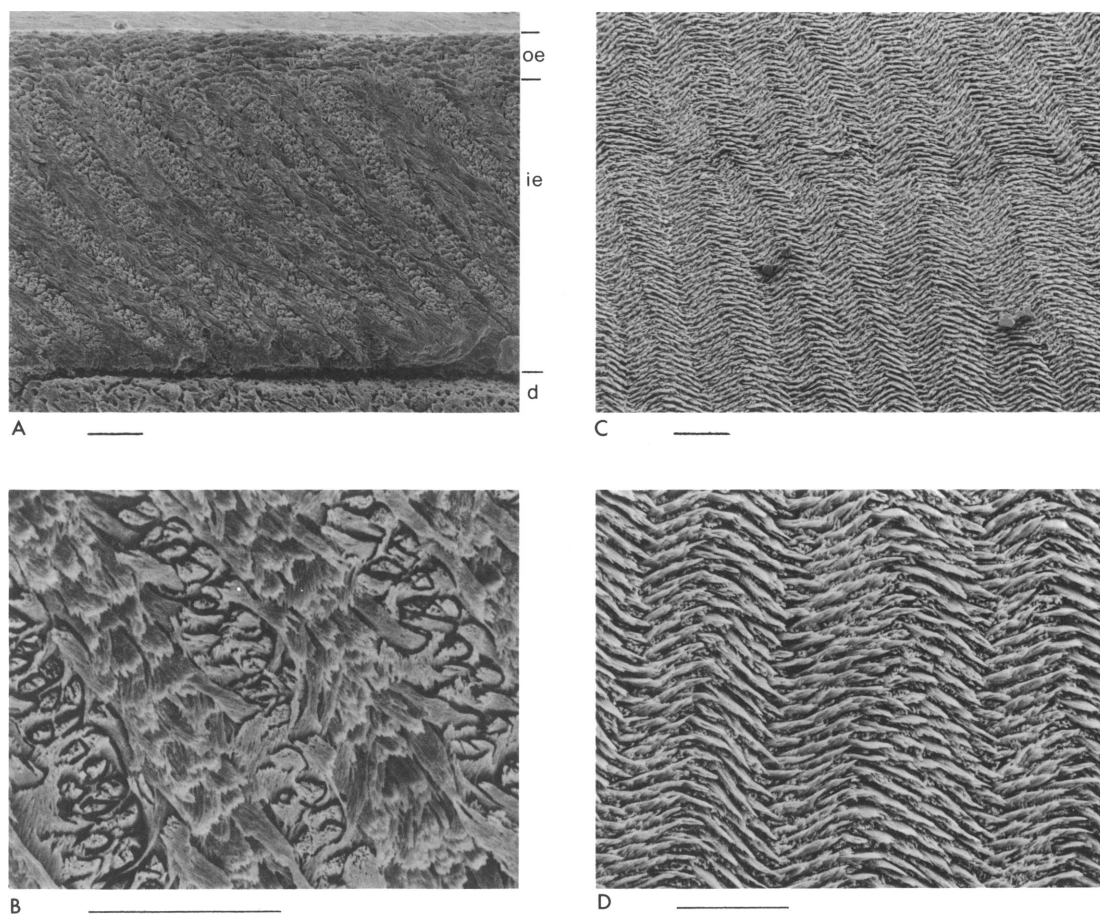


FIG. 8. Scanning electron photomicrographs of Bugti lower incisors showing multiseriate enamel microstructure. **A**, enamel of GSP 21558 in sagittal section: **d**, dentine; **ie**, inner enamel; **oe**, outer enamel. Note the thin outer enamel and multiprismatic, but narrow inclined bands of the inner enamel, both characteristic of ctenodactylids. **B**, sagittal section through inner enamel of GSP 21557 at higher magnification than in **A**. Prisms in neighboring bands differ in orientation, but those at the margins bend from one band and enter another. **C** and **D**, frontal section at two magnifications of GSP 21297 showing bands of the inner enamel. **D** shows that prisms at the margins of bands have intermediate orientations, resulting in a wavelike pattern as discussed by Wahlert (1984). All specimens photographed at 10 kilovolts; bar scales indicate 20 microns.

pears to have lost cusp connections in upper molars secondarily. The hypocone is stronger and more lingual in all Baluchimyinae than in molars of *Birbalomys*, but not *Chapattimys*. From the metacone, the metaloph bends posteriorly at the metaconule to join the hypocone, unlike early chapattimyids, which preserve a protocone-metaloph connection (fig. 7). The neomorphic mesolophule unites all Baluchimyinae. It continues anterolabially from the metaconule in the direction of the lingual portion of the metaloph; the labial

portion of the metaloph may be weak (*Lindsaya*) or turned posteriorly (*Lophibaluchia*). Yuomyids lack the lingual portion of the metaloph.

The hypolophid is always complete and intersects the mure anterior to the hypoconid; it is weaker and more posterior in *Birbalomys*, *Fallomus*, and *Chapattimys*. *Gumbatomys* resembles baluchimyines in this and in having a strong metalophulid II. The latter crest is short and low in all early ctenodactylids and in *Lindsaya*. The mure of lower

TABLE 6

Incisor Enamel Microstructure Measurements in Microns and Degrees (See Text)
Measurements marked with asterisk are in microns.

Specimen	TE*	EI (%)	II°	OI°	BW*
21297	130	19	44°	82°	9
21557	220	21	38°	83°	14
21558	250	19	38°	77°	15
21559	200	18	52°	90°	13

molars of all Baluchimyinae is more lingual and the protocone and hypocone have more sloping lingual walls than in other chapattimyids.

The enamel of four isolated incisor fragments was examined with a scanning electron microscope. All were apparently lower incisors, although some fragments were too short to be certain. All were determined to exhibit a multiserial microstructural organization of enamel rods. Incisor GSP 21297 (fig. 8C, D) in frontal view, shows the typical multiserial wavelike interlocking of rods from adjacent lamellae. In sagittal view of GSP 21558 (fig. 8A), the enamel comprises a thin outer layer with rods nearly parallel to the enamel surface, and an inner layer with inclined bands. Incisor fragments preserving tips show that inclination is toward the tip. Adjacent bands exhibit regular, alternating organization of rods and are usually three or four prisms wide. Rods bordering bands tend to be intermediate, in this case parallel to the section, and some can be seen to bend as they pass from one band to the next. This is typical in multiserial enamel (Wahlert, 1984).

Table 6 shows dimensions of the following characters for the four incisors (see Flynn and Wahlert, 1978): total enamel thickness (TE), external index (EI = OE/TE, where OE is outer enamel thickness), average band width (BW), the angle of outer enamel prism inclination (OI), and inner enamel band inclination (II). EI and BW are uniform among the four incisors. GSP 21297 stands out in having thinner enamel and GSP 21559 exhibits higher inclinations, with outer enamel rods lying parallel to the incisor surface. These incisors probably represent different species.

All of these incisors can be referred to the Chapattimyidae at a high level of probability,

TABLE 7

Dimensions in Millimeters for Cheek Teeth of Sample Size Less Than Ten for *Baluchimys barryi*, New Genus and Species

Specimen	Number	Length	Width
DP ⁴	21265	1.18	1.34
P ⁴	21266	1.16	1.36
P ⁴	21267	1.20	1.34
P ⁴	21268	1.22	1.34
P ⁴	21269	1.20	1.34
P ⁴	21270	1.20	1.30
P ⁴	21271	1.20	1.34
M ²	21281	1.36	1.68
M ²	21282	1.36	1.66
M ²	21283	1.40	1.62
M ²	21284	1.46	1.78
M ²	21285	1.42	1.76
M ²	21286	1.42	1.72
M ²	21287	1.40	1.62
M ²	21288	1.26	1.52
M ²	21289	1.38	1.48
M ³	21281	1.32	1.50
M ³	21290	1.34	1.54
M ³	21291	1.28	1.58
M ³	21292	1.26	1.46
M ³	21293	1.30	1.48
M ³	21294	1.32	1.42
M ³	21295	1.30	1.40
M ³	21296	1.34	1.48
P ₄	21298	1.36	1.08
P ₄	21299	1.36	1.08
P ₄	21300	1.40	1.10
M ₁	21301	1.58	1.44
M ₁	21302	1.58	1.32
M ₁	21303	1.68	1.46
M ₁	21304	1.60	1.34
M ₁	21305	1.48	1.32
M ₁	21306	1.64	1.40
M ₁	21307	1.64	1.34
M ₁	21308	1.58	1.38
M ₁	21309	1.60	1.44
M ₃	21321	1.30	1.28
M ₃	21322	1.34	1.42
M ₃	21323	1.38	1.32
M ₃	21324	1.38	1.28
M ₃	21325	1.34	1.30
M ₃	21326	1.38	1.28
M ₃	21327	1.40	1.38
M ₃	21328	1.24	1.38
M ₃	21329	1.44	1.44

because that is the only family represented by cheek teeth at Y-GSP locality 417, with the possible exception of the rare and minuscule *Downsimys margolisi*. The four inci-

TABLE 8
Statistics for M^1 and M_2 of *Baluchimys barryi*, New Species

	N	O.R.	$\bar{x} \pm S_x$	$S \pm S_s$	$V \pm S_v$
Length					
M^1	11	1.30–1.44	1.393 ± 0.012	0.041 ± 0.009	3.0 ± 0.6
M_2	11	1.48–1.68	1.616 ± 0.016	0.054 ± 0.011	3.3 ± 0.7
Width					
M^1	11	1.52–1.74	1.651 ± 0.022	0.074 ± 0.003	4.5 ± 1.0
M_2	11	1.28–1.52	1.440 ± 0.020	0.066 ± 0.003	4.6 ± 1.0

sors appear to be too large to pertain to *D. margolisi*. Probably most, if not all, of the four incisors pertain to Baluchimyinae. In the absence of association, however, *Fallomus razae* cannot be ruled out. In any case, Miocene chapattimyids differ from their pauciserial Eocene relatives in having multiserial enamel. Traditionally, multiserial enamel has been considered derived with respect to pauciserial enamel (but see von Koenigswald, 1980, 1985).

Among known multiserial rodents, Bugti rodents are unusual but not unique in having narrow bands. The observed range of inner enamel band width in multiserial rodents is 12 to 30 microns (Wahlert, 1968). Bugti incisor bands are narrow, only three to five rods wide (less than 16 microns on the average), and fall at the lower end of the multiserial range with ctenodactylids and several caviomorphs (Wahlert, personal commun.). Whether this condition is derived or not, narrow band width may be characteristic for Ctenodactyloidea. Note, however, that all known early ctenodactylids have pauciserial enamel and that baluchimyines and later ctenodactylids appear to have acquired multiserial enamel independently.

Baluchimys, New Genus

TYPE SPECIES: *Baluchimys barryi*, new species.

INCLUDED SPECIES: *B. barryi* and *B. ganeshapher*.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Baluchistan, plus *mys* (Greek) for mouse.

DIAGNOSIS: Moderately lophodont baluchimyine; metaloph joins large metacone

to hypocone and is weaker between metacone and metaconule; short mesolophule; DP_4 with four major oblique lophs, a fifth low loph, and an anterolabial shelf and cingulum; lower molars with narrow metalophulid II that usually fails to reach the lingual wall of molars, indistinct hypoconulids, and narrow, transversely elongated protoconids and hypoconids; straight anterior wall on M_2 ; on M_1 the anterior width approximately equals posterior width, M_3 short and narrow.

Baluchimys barryi, new species

Figure 9, tables 7, 8

HOLOTYPE: GSP 21281, left M^{2-3} .

HYPODGM: GSP 21281; 21265, DP^4 ; 21266–21271, P^4 ; 21272–21280, 21336, 21339, M^1 ; 21282–21289, M^2 ; 21290–21296, M^3 ; 21298–21300, P_4 ; 21301–21309, M_1 ; 21310–21320, M_2 ; 21321–21329, M_3 .

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Dr. John Barry who has advanced the knowledge of mammalian evolution in Asia and elsewhere.

DIAGNOSIS: Medium size *Baluchimys*, smaller than *B. ganeshapher*, M^2 and M^3 being the most distinctive teeth in size; they are 10 percent smaller relative to *B. ganeshapher*.

DESCRIPTION. Upper cheek teeth are rectangular in occlusal outline, wider than long. Protocones and hypocones have labial apices, slope lingually, and are pinched anteroposteriorly so that they wear as lobate lophs. The protocone spans about one-third molar width and is posterolingually directed. The hypocone is less oblique and shorter.

P^3 is evidenced by a small facet on only 2 of 13 P^4 of *Baluchimys*. Perhaps P^3 was not

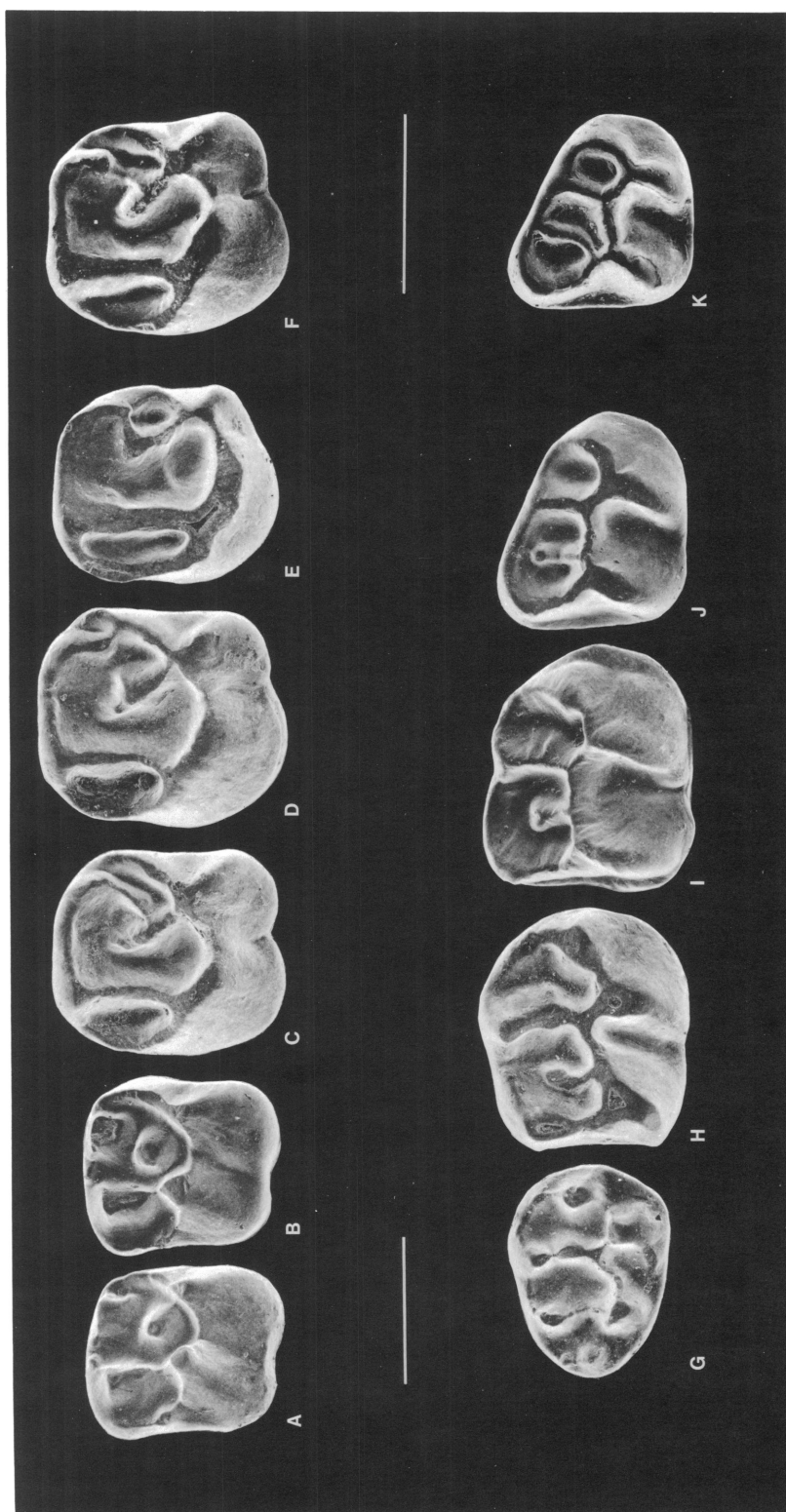


FIG. 9. Scanning electron photomicrographs of *Baluchimys barryi* (A-E, G-J) and *Baluchimys* sp. (F, K). Note that *Baluchimys* sp. has a different scale; both scales = 1 mm. A, GSP 21265, left DP⁴; B, GSP 21271, left P⁴; C, GSP 21275, left M¹; D, GSP 21286, left M²; E, GSP 21291, left M³; F, GSP 21300, left P⁴; G, GSP 21301, left M¹; H, GSP 21313, left M²; I, GSP 21326, left M³; J, GSP 21374, left M³; K, GSP 21374, left M³.

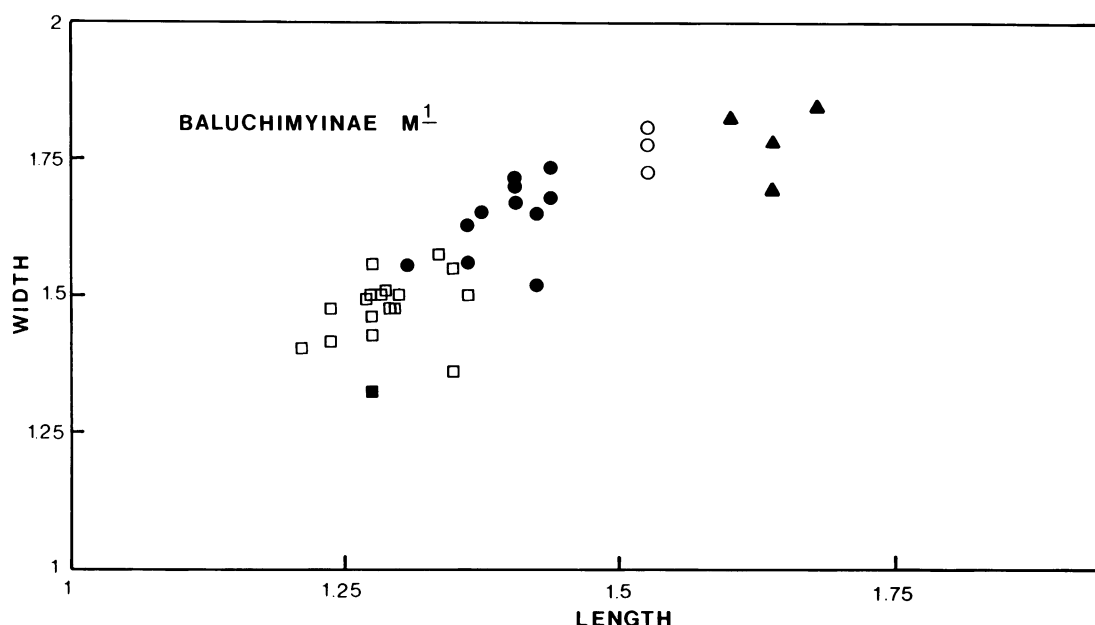


FIG. 10. Length-width scatter diagram of selected baluchimyine upper first molars. Measurements in millimeters. Solid circle, *Baluchimys barryi*; open circle, *Baluchimys ganeshapher*; solid square, *Baluchimys* sp.; open square, *Lindsaya derabugtiensis*; solid triangle, *Lophibaluchia pilbeami*.

present in all adults of *Baluchimys*. P⁴ of *B. barryi* is molariform except that the protocone is not pinched and is labial in position with respect to the hypocone and to the protocone in the molars. The conical protocone slopes strongly anterolingually. From its anterior wall, a low anteroloph traverses P⁴, ending next to the transversely elongated paracone. A narrow protoloph joins the paracone to the center of the protocone. There is no paraconule. The hypocone is pinched slightly and a low mure joins it to the protocone. The hypocone is continuous with a strong posteroloph that joins the conical metacone in advanced wear. The conical metaconule is as large as or larger than the metacone and remains isolated from the metacone and hypocone until advanced wear. A small mesostyle between and labial to the paracone and metacone is present in three P⁴, indistinct in three others. P⁴ has three roots, including a single large lingual root. Tentatively, GSP 21265 is considered a DP⁴ because cusps and ridges appear to be sharper and taller than in P⁴ and the mesostyle is doubled.

M¹ is more lophodont than P⁴ and the hy-

pocone is as lingual as the protocone. The walls of these cusps converge as a low lingual mure. The protocone lobe bifurcates as an anteroloph and a protoloph. The protoloph is transverse and continuous with the paracone and shows no hint of a paraconule. The strong anteroloph sweeps labially to end low on the paracone. The hypocone also bifurcates. Its metaloph joins a moderately inflated metaconule and turns posterolabially at an angle of 60 to 90°. The metaloph is narrower here and joins the metacone. From the metaconule a new crest here termed a mesolophule continues anterolabially in the direction of the lingual portion of the metaloph. Mesolophule strength and length vary between individuals. From the hypocone, the strong posteroloph descends and bends gently, terminating low on the posterior side of the metacone. A labial ectoloph joins the paracone and metacone. M¹ has a large, transversely compressed lingual root and two small labial roots. Size relationships of *Baluchimys barryi* M¹ compared to other baluchimyines is shown in figure 10.

M² is difficult to distinguish from M¹ but usually the hypocone is more labial in posi-

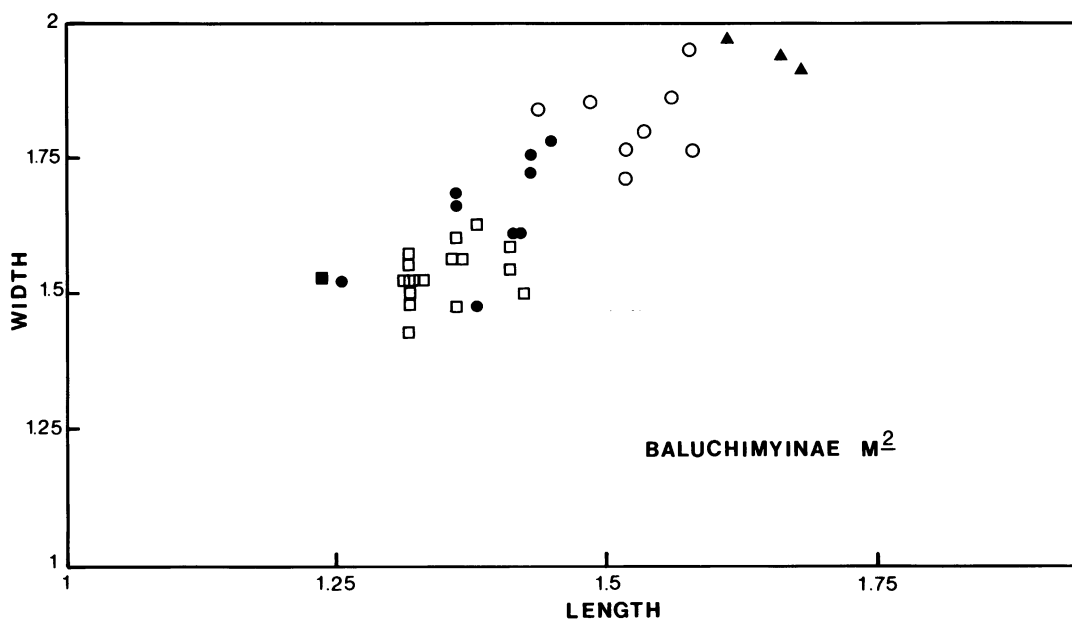


FIG. 11. Length-width scatter diagram of selected baluchimyine upper second molars. Symbols as in figure 10.

tion relative to the protocone than in M¹. Thus while M¹ and M² are about the same size, M² is relatively narrower posteriorly so that the tooth row tapers toward the smaller

M³. Size relationships of M² are shown in figure 11.

M³ is rounded in occlusal outline because the hypocone is displaced labially and re-

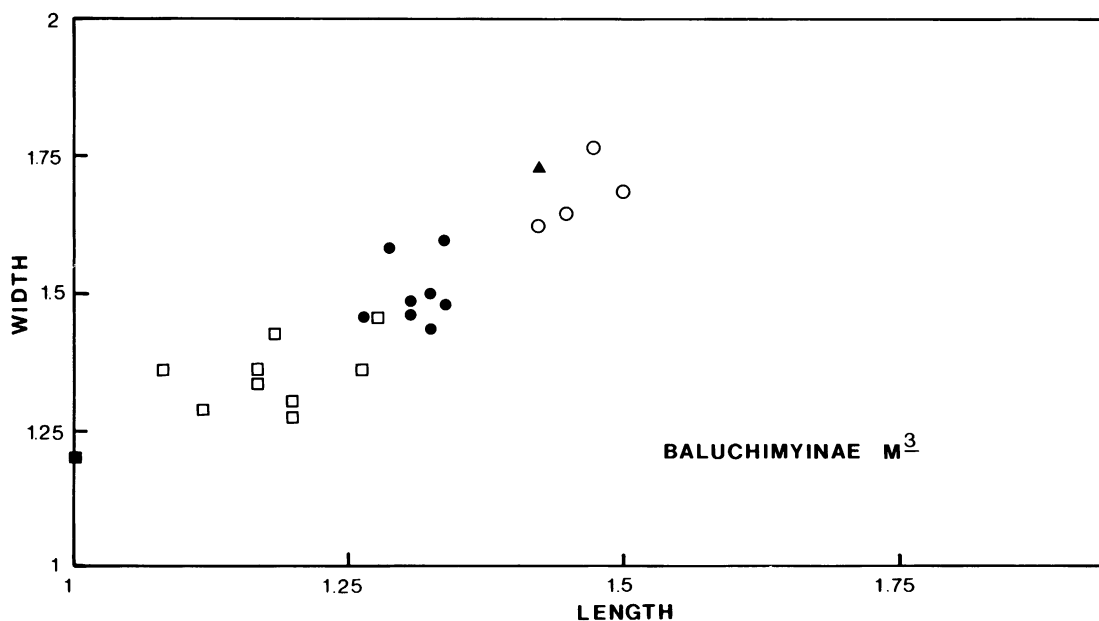


FIG. 12. Length-width scatter diagram of selected baluchimyine upper third molars. Symbols as in figure 10.

duced in size. The anteroloph and protoleph resemble those of M^2 , but the protocone lobe is longer, curves posteriorly and continues as a mure to the hypocone. The hypocone is somewhat elongated transversely in 3 of the 8 M^3 . The metaloph bends as in M^2 , but is shorter, and with the arcuate posteroloph encloses a basin. This posterior basin varies in size and in location from central to labial. The mesolophule is shorter than in M^2 and is well defined in only 3 of the 8 M^3 . A high ectoloph borders a large central basin. M^3 has three roots. Size relationships of M^3 are shown in figure 12.

P_4 is oval in occlusal outline and comprises six cusps joined by lophes. The protoconid and hypoconid are the largest of these and are joined by a mure that invaginates lingually at the hypolophid. The hypoconulid is nearly as large and lies on a strong posterolophid that continues to the lingual side of P_4 . The round hypoconulid is central in position and lies at the most posterior portion of P_4 . The metaconid is opposite to and somewhat smaller than the protoconid. These two cusps are connected posteriorly by a low crest probably homologous with metalophulid II. The entoconid is a small lingual cusp at the end of the hypolophid which intersects the mure closer to the hypoconid than the protoconid. A small cusp at the anterior end of P_4 is here termed an anteroconid. A low crest runs lingually from it. On one of the three P_4 the anteroconid is connected to the protoconid. There is one large posterior root and a smaller anterior root. Size relationships of P_4 are shown in figure 13.

The molars are more lophodont than P_4 and the protoconid and hypoconid are somewhat pinched anteroposteriorly so that they wear as short oblique lobes. M_1 and M_2 are rectangular, but some M_1 are narrower anteriorly than posteriorly, and the anterior wall of some M_1 is concave, conforming to the shape of the smaller P_4 . The anterior arm of the protoconid continues as a metalophulid I to the metaconid. Below this crest an anterior cingulum spans the tooth. The metalophulid II, of variable strength and length, continues from the posterior arm of the protoconid. It is usually lower than the other crests. A mure from the protoconid joins the anterior arm of the hypoconid at its junction with the hypolophid. The hypolophid ter-

minates at the slightly expanded entoconid anterolingual to the hypoconid. The posterolophid is a long arcuate extension of the posterior arm of the hypoconid. The posterolophid runs through an inflated hypoconulid that is central or somewhat labial to the midline of the tooth. A low lingual wall includes the posterolophid and joins the metaconid and entoconid. M_1 has a broad anteroposteriorly compressed posterior root and two small anterior roots. Size relationships of M_1 are shown in figure 14.

M_2 resemble M_1 closely but some are readily distinguished because they are narrower posteriorly than anteriorly. The anterior wall of M_2 is nearly straight and bears a cingulum. Size relationships of M_2 are shown in figure 15.

M_3 is shorter and narrower than the other molars and is triangular in outline. Its anterior wall is concave and bears a cingulum. The protoconid is more pinched and metalophulid II is higher than in other molars. The hypoconid lobe is relatively shorter and more lingual in position and the hypolophid and posterolophid are short. There is no hypoconulid. M_3 has three roots with the larger posterior root obliquely oriented. Size relationships of M_3 are shown in figure 16.

DISCUSSION: *Baluchimys barryi* is represented by a good sample including all of the dentition except DP_4 . It is higher crowned, more lophodont, and has a stronger metalophulid II than *Chapattimys* or *Birbalomys*. *Gumbatomys asifi* is poorly known and has not been compared directly with our samples, but may resemble *Baluchimys* in these characters. Lophes are higher in *Baluchimys* than in older chapattimyids. The metaloph of *Baluchimys* differs from that of Eocene chapattimyids in that it bends to join the hypocone rather than the protocone (fig. 9). The lingual portion of the metaloph, joining hypocone to metaconule, is stronger than the labial portion, joining metacone to metaconule. The metaconule is nearly submerged in the oblique crest comprising the lingual portion of the metaloph and the mesolophule. This crest, composed of two elements, appears to perform a single shearing function. We do not consider the mesolophule as homologous to the mesoloph of muroids because it originates at the metaconule and we interpret it as a neomorph resulting from increased loph-

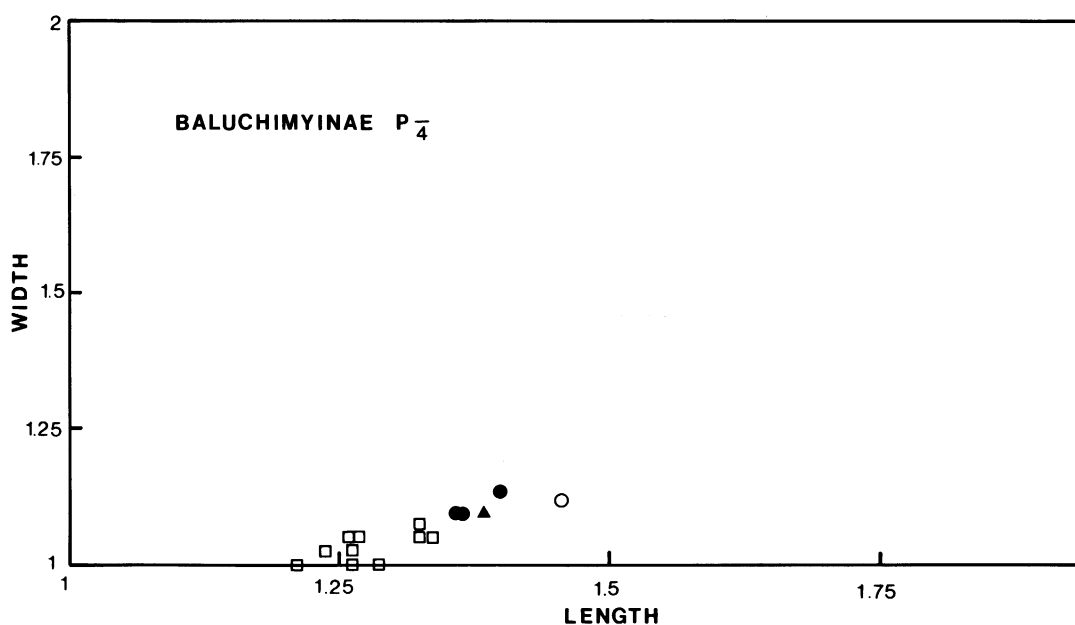


FIG. 13. Length-width scatter diagram of selected baluchimyine lower permanent fourth premolars. Symbols as in figure 10.

odonty. M^3 is variable in structure and in size. P_4^4 are less lophodont than the molars. Although we have named the anterior cusp of P_4 an anteroconid, as it is known in sciurids, we note that it is completely lacking

on the molars and is probably not homologous with the anteroconid of muroids. The anteroconid is present on most baluchimyine P_4 and occurs in some *Birbalomys* and phiomysid premolars considered to be deciduous.

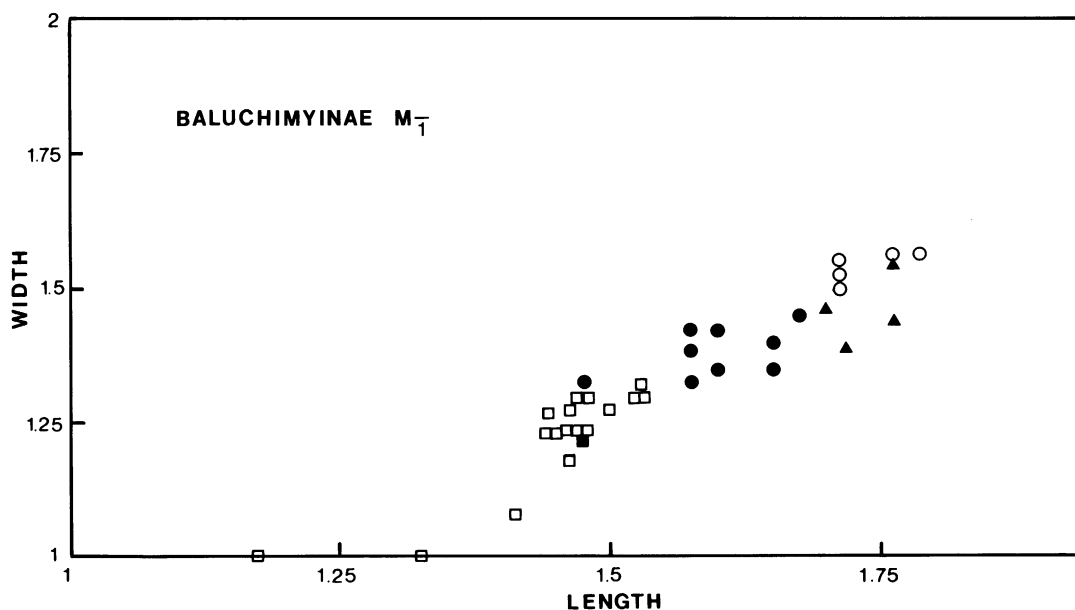


FIG. 14. Length-width scatter diagram of selected baluchimyine lower first molars. Symbols as in figure 10.

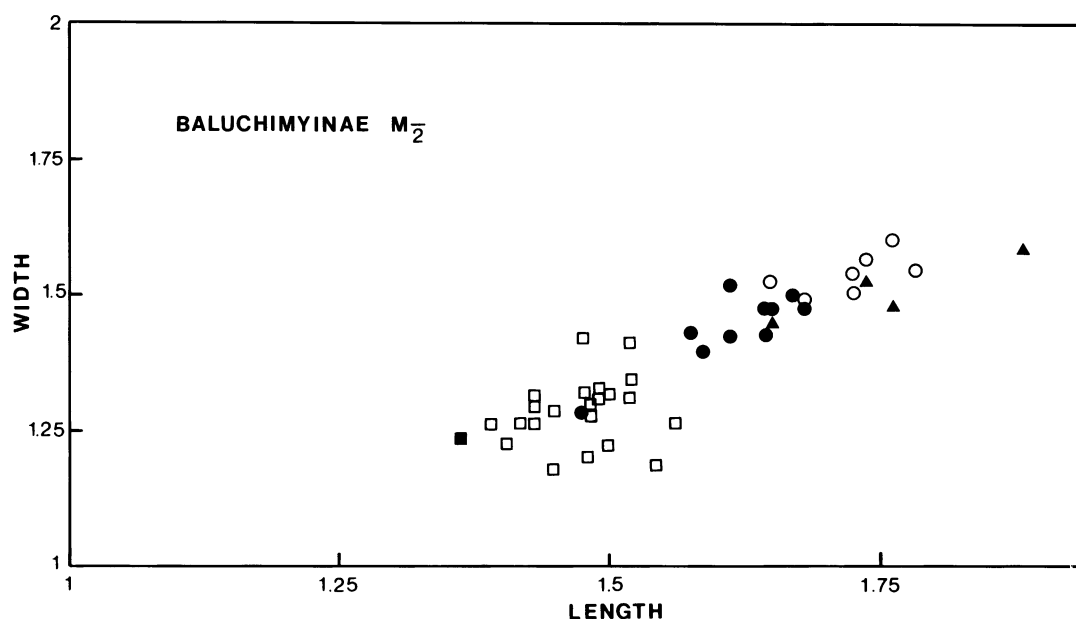


FIG. 15. Length-width scatter diagram of selected baluchimyine lower second molars. Symbols as in figure 10.

***Baluchimys ganeshapher*, new species**

Figure 17, table 9

HOLOTYPE: GSP 21342, left M^2 .

HYPODIGM: GSP 21330, DP^4 ; 21331–21335, P^4 ; 21337, 21338, 21340, M^1 ; 21341–

21347, M^2 ; 21348–21351, M^3 ; 21352, DP^4 ; 21353, P^4 ; 21354–21358, M^1 ; 21359–21365, M^2 ; 21366–21368, M^3 .

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

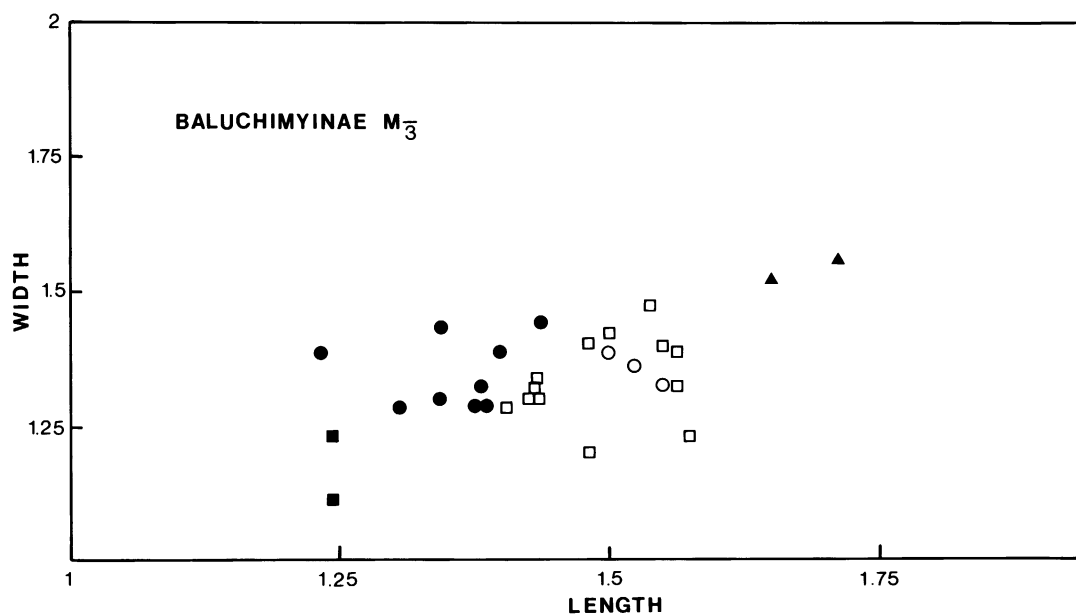


FIG. 16. Length-width scatter diagram of selected baluchimyine lower third molars. Symbols as in figure 10.

ETYMOLOGY: Named for the rodent that transports elephant-headed Ganesha on its back, in reference to the earliest known south Asian proboscideans found in Baluchistan.

DIAGNOSIS: Largest known species of the genus. M^2 and M^3 are relatively larger than the other teeth and are 10 percent larger than those of *B. barryi*.

DESCRIPTION: *B. ganeshapher* is represented by a smaller sample than *B. barryi*. DP^4 and P^4 are developed as in *B. barryi*. The posteroloph is the strongest crest, the protoloph is weak, and the anterior cingulum is low. The metaconule is large and isolated. The mesostyle is absent in two P^4 , present in two, and doubled in one P^4 and the single DP^4 . The molars are lophodont and M^2 has a relatively inflated metaconule. M^2 is the largest molar and M^3 is as large as M^1 . The mesolophule is well developed in one of four M^3 . The posterior basin is small in two, large in one, and a large, open valley draining labially in one M^3 .

One DP_4 is assigned to *B. ganeshapher*. It is lophodont and longer, but narrower than P_4 . DP_4 is narrow anteriorly and the posterolabial wall of the crown is high and sloping. From back to front the following transverse structures are developed: posterolophid, hypolophid, central ridge, metalophulid II, anterolophid, and anterior cingulum. The high posterolophid and hypolophid are the posterior and anterior arms of the hypoconid and define a large posterior valley that opens lingually. The hypolophid is straight and oblique; the posterolophid curves as it descends in height lingually. A short-basined labial valley is located between the hypoconid and protoconid. From the small protoconid, a short mure terminates low on the labial end of the hypolophid. An oblique, straight metalophulid II links the protoconid and metaconid. The metaconid and entoconid are slightly inflated and joined by a lingual wall. An obliquely oriented transverse ridge lies in the central basin bounded by the hypolophid, metalophulid II, mure, and lingual wall. This may be homologous to the mesolophid of *Hodsahibia* (see below). The oblique metalophulid II and parallel anterolophid border a basined valley. The anterolophid runs from a crescentic lingual cusp, through a smaller median cusp, and passes through a small, labial

TABLE 9
Cheek Tooth Dimensions in Millimeters for *Baluchimys ganeshapher*, New Species

Specimen	Number	Length	Width
DP^4	21330	1.18	1.36
P^4	21331	1.26	1.42
P^4	21332	1.24	1.44
P^4	21333	1.24	1.46
P^4	21334	1.20	1.40
P^4	21335	1.16	1.36
M^1	21337	1.52	1.82
M^1	21338	1.52	1.78
M^1	21340	1.52	1.72
M^2	21341	1.56	1.86
M^2	21342	1.54	1.82
M^2	21343	1.58	1.94
M^2	21344	1.42	1.54
M^2	21345	1.58	1.76
M^2	21346	1.48	1.84
M^2	21347	1.52	1.76
M^3	21348	1.42	1.64
M^3	21349	1.44	1.66
M^3	21350	1.48	1.76
M^3	21351	1.50	1.68
DP_4	21352	1.62	1.04
P_4	21353	1.46	1.12
M_1	21354	1.78	1.56
M_1	21355	1.76	1.56
M_1	21356	1.72	1.50
M_1	21357	1.72	1.52
M_1	21358	1.72	1.54
M_2	21359	1.64	1.52
M_2	21360	1.68	1.48
M_2	21361	1.72	1.54
M_2	21362	1.74	1.56
M_2	21363	1.72	1.50
M_2	21364	1.78	1.54
M_2	21365	1.76	1.60
M_3	21366	1.50	1.38
M_3	21367	1.52	1.36
M_3	21368	1.54	1.32

bial cusp to join the protoconid via a low ridge. Anterolabial to the anterolophid is a shelf bordered by a cingulum.

P_4 is more lophodont than P_4 of *B. barryi*. It is relatively narrower anteriorly and the anterior cusp lies on a stronger crest that joins the protoconid. Molars bear a low anterior cingulum. They are lophodont and the metalophulid II is usually short, but well developed.

DISCUSSION: *B. ganeshapher* is larger than *B. barryi* but M^2 and M^3 are proportionally even larger than the other cheek teeth. Av-

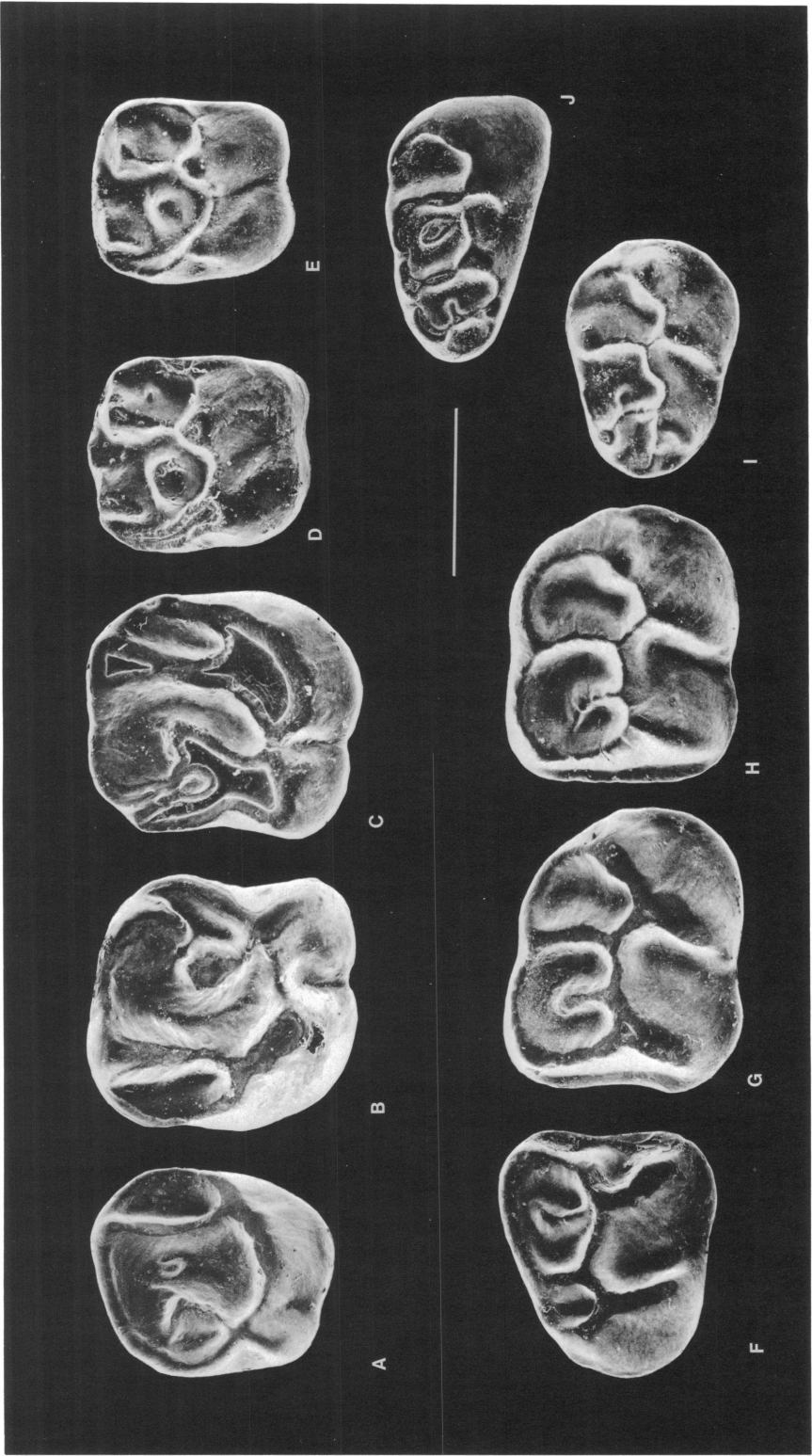


FIG. 17. Scanning electron photomicrographs of cheek teeth of *Baluchimys ganeshapher*. Scale = 1 mm. A, GSP 21350, right M³; B, GSP 21342, left M²; C, GSP 21338, right M¹; D, GSP 21333, right P⁴; E, GSP 21330, right DP⁴; F, GSP 21366, right M³; G, GSP 21361, left M²; H, GSP 21354, left M¹; I, GSP 21353, left P⁴; J, GSP 21352, left DP⁴.

erage dimensions of M^2 and M^3 are 10 percent greater than those of *B. barryi*. *B. ganesapher* appears to be somewhat more lophodont and its P_4 seems to be more derived as well. The DP_4 is assigned to this species on the basis of size and lophodonty, but could prove to pertain to *Lophibaluchia*.

Baluchimys sp.

Figure 9, table 10

REFERRED MATERIAL: GSP 21372–21378 from locality Y-GSP 417.

DISCUSSION: Seven teeth are set aside here on the basis of their small size. They may prove to be small individuals of *B. barryi* when larger samples are recovered. One upper molar (GSP 21375; $L = 1.24$, $W = 1.54$) has a strong but short mesolophule. A short M_3 (GSP 21374; $L = 1.24$, $W = 1.24$) has a well-developed metalophulid II (fig. 9).

Lindsaya, New Genus

TYPE SPECIES: *Lindsaya derabugtiensis*, new and only known species.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Everett Harold Lindsay, our mentor.

DIAGNOSIS: Bunodont baluchimyine with five cusps on upper cheek teeth, including inflated metaconule; metaloph and mesolophule poorly developed; hypocone large and lingual in position; DP_4 bears five oblique crests and lacks an anterior shelf and cingulum; metalophulid II reduced; hypoconulids strong and even evident on some M_3 ; M_3^3 are the most lophodont cheek teeth.

DISCUSSION: We consider loss of the metaloph to be a derived condition and therefore that bunodonty in this taxon is derived from a more lophodont ancestor. Thus, while most baluchimyines are lophodont, we consider *Lindsaya* to be secondarily bunodont. DP_4 differs from that of *Baluchimys* in lacking an anterior shelf and cingulum.

Lindsaya derabugtiensis, new species

Figure 18, tables 11, 12

HOLOTYPE: GSP 21427, left M^2 .

HYPODIGM: GSP 21392–21394, DP^4 ; 21395–21407, P^4 ; 21408–21424, M^1 ; 21425–

TABLE 10
Cheek Tooth Dimensions in Millimeters for *Baluchimys* sp.

Specimen	Number	Length	Width
M^1	21378	1.28	1.32
M^2	21375	1.24	1.54
M^3	21376	1.00	1.20
M_1	21373	1.48	1.22
M_2	21372	1.36	1.24
M_3	21374	1.24	1.24
M_3	21377	1.24	1.12

21442, M^2 ; 21443–21452, M^3 ; 21453, DP_4 ; 21454–21463, P_4 ; 21464–21482, M_1 ; 21483–21503, M_2 ; 21504–21515, M_3 .

TYPE LOCALITY: Y-417, Baluchistan, Pakistan.

ETYMOLOGY: For the village Dera Bugti.

DIAGNOSIS: Only known species of the genus.

DESCRIPTION: The cheek teeth of *Lindsaya* are relatively low crowned but do exhibit unilateral hypsodonty. There are five major cusps in the upper cheek teeth, and their arrangement is similar in all teeth except the third molars. The major cusps are distinct and rounded on DP^4 and P^4 M^{1-2} . DP^4 is similar in size and shape to the P^4 , but has higher, sharper crests. P^4 is narrower anteriorly than posteriorly. The anterior cingulum originates from the protocone. Protocone and paracone are joined by a weak protoloph. The protocone and hypocone are the largest cusps and are weakly connected at their midpoints. The metaconule is isolated from the metacone, but weakly connected to the hypocone in 5 of 12 specimens. The posterior cingulum is a loph extending from the posterolabial portion of the hypocone along the posterior margin of the tooth, to the labial border. P^4 has one broad lingual root and two labial roots, as do the molars.

M^1 is larger than the P^4 and slightly broader posteriorly than anteriorly. The metaconule is weakly connected to the metacone in 4 of 15 specimens. There is a weak but consistent connection between the metaconule and hypocone. The mesolophule is very short, variable in strength, and recognizable in only 8 of 15 M^1 .

M^2 is larger than M^1 , but essentially iden-

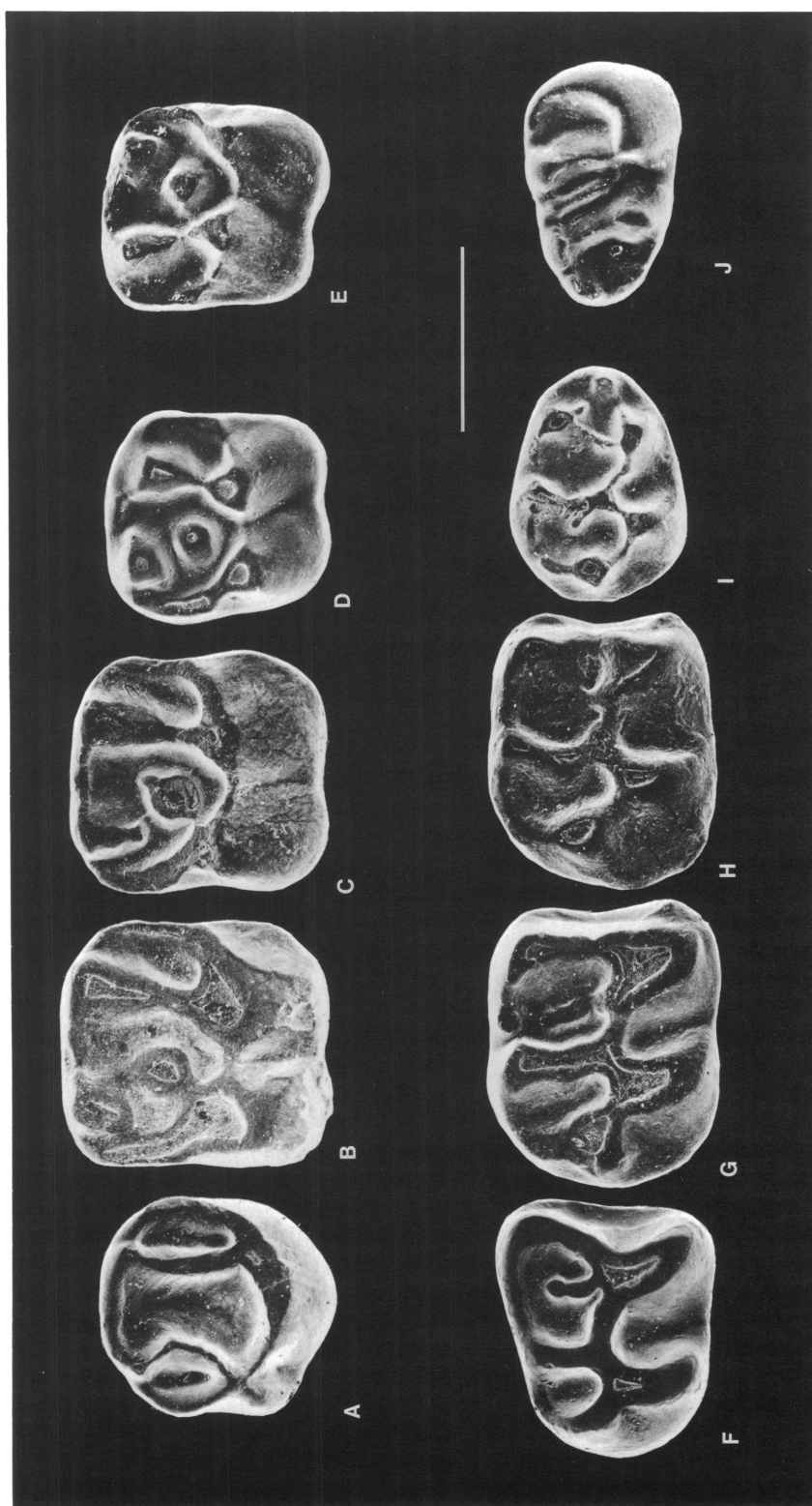


FIG. 18. Scanning electron photomicrographs of cheek teeth of *Lindsaya derbugiensis*. Scale = 1 mm. A, GSP 21450, right M²; B, GSP 21434, right M²; C, GSP 21415, right M¹; D, GSP 21392, left DP⁴; E, GSP 21400, right P⁴; F, GSP 21513, right M³; G, GSP 21494, right M²; H, GSP 21468, right M¹; I, GSP 21461, right P⁴; J, GSP 21453, left DP⁴.

TABLE 11
Dimensions in Millimeters for Cheek Teeth of
Sample Size Less Than Ten for *Lindsaya derabugtiensis*, New Genus and Species

Specimen	Number	Length	Width
DP ⁴	21392	1.12	1.24
DP ⁴	21393	1.08	1.24
DP ⁴	21394	1.12	1.32
M ³	21443	1.08	1.36
M ³	21444	1.16	1.36
M ³	21445	1.12	1.28
M ³	21446	1.20	1.32
M ³	21447	1.16	1.30
M ³	21448	1.18	1.40
M ³	21449	1.20	—
M ³	21450	1.26	1.36
M ³	21451	1.28	1.44
M ³	21452	1.18	1.30
DP ₄	21453	1.32	0.94

tical in morphology. The metaconule connects weakly to the metacone in 5 of 18 specimens. One of 18 specimens lacks a weak metaconule-hypocone connection. The mesolophule is developed in only 8 of 18 M².
The third molars are more round in occlusal outline and lophodont. Cusps are indistinct. The tooth is divided into closed basins by sharp lophs, the posterior basin being variably developed as in *Baluchimys*. M³ is smaller than M².

DP₄ is a long and narrow tooth, broader posteriorly. The protoconid is rounded, and the hypoconid slightly so. There are five distinct lophids: anterolophid curving along the anterior margin of the DP₄, metalophulid II joining protoconid and metaconid directly, low mesolophid, straight hypolophid, and high arcuate posterolophid. The mesolophid originates from the hypolophid near where it joins the hypoconid. There is no protoconid-hypoconid connection (mure).
P₄ is broader than DP₄, but of similar length. All of the major cusps are round and distinct and joined by low crests. A small anteroconid is developed in 9 of 10 specimens. It is weakly connected to the protoconid in six of the specimens. The protoconid and hypoconid are connected by a mure that is intersected by the hypolophid. There is a swelling on the hypolophid before it joins the entoconid. The hypoconulid is distinct and well developed. The metaconid is linked to the protoconid in 4 of 10 specimens by metalophulid II. P₄ typically has two roots, but in two specimens the roots are fused.
M₁ is larger and more lophodont than P₄. A low metalophulid II is present on 14 of 15 specimens and is variable in length and height, but never reaches the lingual wall of the molar. The protoconid and metaconid are joined by the anterolophid (metalophulid I). An an-

TABLE 12
Statistics for *Lindsaya derabugtiensis*, New Genus and Species

	N	O.R.	$\bar{x} \pm S_x$	$S \pm S_s$	$V \pm S_v$
Length					
P ⁴	12	1.14–1.20	1.170 ± 0.006	0.022 ± 0.004	1.9 ± 0.4
M ¹	17	1.22–1.36	1.289 ± 0.009	0.038 ± 0.006	2.9 ± 0.5
M ²	18	1.32–1.42	1.351 ± 0.008	0.034 ± 0.006	2.5 ± 0.4
P ₄	10	1.22–1.34	1.276 ± 0.012	0.039 ± 0.009	3.0 ± 0.7
M ₁	19	1.16–1.52	1.444 ± 0.019	0.084 ± 0.014	5.8 ± 0.9
M ₂	21	1.36–1.56	1.474 ± 0.010	0.047 ± 0.007	3.2 ± 0.5
M ₃	12	1.40–1.58	1.495 ± 0.019	0.065 ± 0.013	4.3 ± 0.9
Width					
P ⁴	12	1.20–1.36	1.312 ± 0.012	0.042 ± 0.002	3.2 ± 0.7
M ¹	17	1.32–1.58	1.481 ± 0.016	0.066 ± 0.002	4.5 ± 0.8
M ²	18	1.44–1.64	1.537 ± 0.012	0.051 ± 0.001	3.3 ± 0.6
P ₄	10	1.00–1.06	1.026 ± 0.007	0.021 ± 0.001	2.1 ± 0.5
M ₁	19	1.00–1.34	1.222 ± 0.022	0.095 ± 0.003	7.8 ± 1.3
M ₂	21	1.18–1.42	1.282 ± 0.012	0.057 ± 0.001	4.4 ± 0.7
M ₃	12	1.20–1.48	1.345 ± 0.023	0.080 ± 0.003	6.0 ± 1.2

TABLE 13
Cheek Tooth Dimensions in Millimeters for *Lophibaluchia pilbeami*, New Genus and Species

Specimen	Number	Length	Width
P ⁴	21518	1.24	1.50
P ⁴	21519	1.28	1.52
M ¹	21520	1.60	1.82
M ¹	21521	1.68	1.84
M ¹	21522	1.64	1.70
M ¹	21523	1.64	1.78
M ²	21524	1.68	1.90
M ²	21525	1.66	1.94
M ²	21526	1.60	1.98
M ³	21527	1.44	1.72
P ₄	21528	1.38	1.08
M ₁	21529	1.76	1.56
M ₁	21530	1.70	1.48
M ₁	21531	1.76	1.42
M ₁	21532	1.72	1.38
M ₂	21533	1.74	1.52
M ₂	21534	1.88	1.56
M ₂	21535	1.64	1.44
M ₂	21536	1.76	1.48
M ₃	21537	1.72	1.56
M ₃	21538	1.64	1.52

terior cingulum is poorly developed low on the straight anterior face of the tooth. M₁₋₃ bear two anterior roots and one posterior root.

The second and third molars are similar in size to M₁, but slightly larger. Otherwise, M₂ is arbitrarily separated from M₁. M₃ tapers posteriorly and has a strongly developed lingual wall. M₃ appears more lophodont than the other lower molars.

DISCUSSION: *Lindsaya* is relatively low crowned with fairly distinct and rounded cusps. The root pattern is basically simple. These characters are primitive. In addition, DP₄ is not so derived as that of *Baluchimys* in that it lacks an anterior shelf and cingulum. However, the loss of the metaloph is not primitive, and in this sense, at least part of the bunodonty seen in *Lindsaya* is secondarily derived. Whereas *Lindsaya* and *Baluchimys* shared a primitive baluchimyine ancestry, there is no evidence that *Lindsaya* is more closely related to other baluchimyines than is *Baluchimys*.

Lophibaluchia, New Genus

TYPE SPECIES: *Lophibaluchia pilbeami*, new species, only described species of the genus.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Greek, for lophodont baluchimyine.

DIAGNOSIS: Lophodont baluchimyine lacking distinct mure on upper cheek teeth; P⁴ small; mesolophule strong; metaloph joins posteroloph; M₁₋₂ with strong, long metalophulid II; lower molars with only four crests.

Lophibaluchia pilbeami, new species

Figure 19, table 13

HOLOTYPE: GSP 21524, right M².

HYPODIGM: GSP 21518–21519, P⁴; 21520–21523, M¹; 21524–21526, M²; 21527, M³; 21528, P₄; 21529–21532, M₁; 21533–21536, M₂; 21537–21538, M₃.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for David Pilbeam, who has contributed so much to the understanding of hominoid evolution and Miocene vertebrate history.

DIAGNOSIS: As for genus until other species are named.

DESCRIPTION: *Lophibaluchia* is a relatively high crowned, lophodont baluchimyine. Cheek teeth are unilaterally hypsodont. There is no distinct mure on upper cheek teeth, and the protocone and hypocone remain unconnected to each other. Cusps are submerged into lophs and the occlusal pattern is essentially similar for all upper cheek teeth. Relative to M¹, P⁴ is smaller than in most baluchimyines; M¹ is slightly smaller than M², and M² is larger than M³. The protocone and hypocone are compressed and aligned in a posterolingual to anterolabial direction. Two lophs extend from each of these cusps, the anterior cingulum and protoloph from the protocone, and the posterior cingulum and mesolophule from the hypocone. The metacone is indistinct in the mesolophule. The mesolophule curves posteriorly to join the metacone in P⁴ and in one of three specimens of M¹. It curves posteriorly but does not join the metacone in M² and M³. The posterolingual portion of the metacone joins the posterior cingulum near its termination to form a short loph, the fifth on the tooth. M³, the smallest molar, is modified in being more round in occlusal outline with strongly labi-

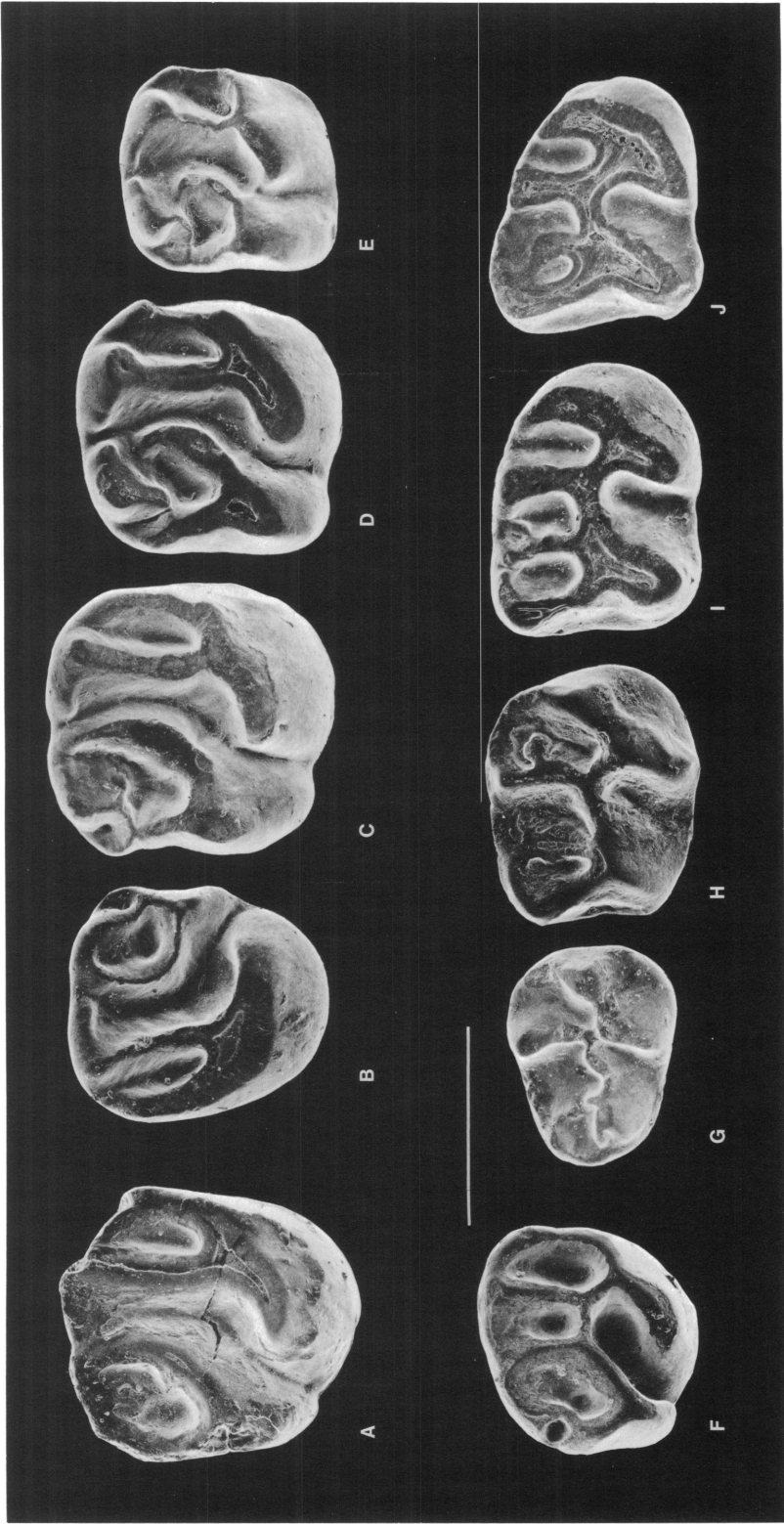


FIG. 19. Scanning electron photomicrographs of cheek teeth of *Lophibaluchia* cf. *L. pilbeami* (A), *Lophibaluchia pilbeami* (B-E, G-J), and new genus and species 1 (F). Scale = 1 mm. A, GSP 21539, right M³; B, GSP 21527, left M³; C, GSP 21524, right M²; D, GSP 21520, right M¹; E, GSP 21518, right P⁴; F, GSP 21540, right M³; G, GSP 21528, left P⁴; H, GSP 21529, left M¹; I, GSP 21534, left M²; J, GSP 21538, left M³.

ally displaced hypocone. Upper cheek teeth have two labial and one lingual root, so far as can be determined.

P₄ is molariform but relatively small, and individual cusps are more distinct than on molars. The anterior portion is narrower than the posterior and P₄ lacks an anteroconid. The protoconid and metaconid are joined by metalophulid II and a mure connects the protoconid with the hypoconid. The hypolophid joins the hypoconid and entoconid. The entoconid is well separated from the metaconid. A hypoconulid is distinct on the posterolophid.

The molars of *Lophibaluchia* are more lophodont than P₄. M₁ is smaller than M₂ and more narrow anteriorly. M₃ is slightly shorter than M₂ and more narrow posteriorly. The anterior face of all molars is concave and has a low cingulum. The lower molars have four strong transverse lophs. The protoconid and hypoconid are elongated in an anterolabial to slightly posterolingual direction and are connected by a mure. Metalophulid II is strong and long except in M₃. All lophs extend to the lingual margin of the teeth, except the metalophulid II of M₃. The anterolophid turns sharply posteriorly at the anterolingual corner of the tooth and approaches metalophulid II. One M₁ in four has a posterior spur off the hypolophid and another off metalophulid II. One M₂ in four has a posterior spur off metalophulid II. On M₃ the posterolophid is oriented transversely. The lower molars have two anterior roots and one posterior root.

DISCUSSION: *Lophibaluchia* is significantly derived relative to *Baluchimys* in a number of characters. The reduction of the mure in *Lophibaluchia* effectively divides the upper cheek teeth into two portions: the protocone with its two lophs, and the hypocone with its two. The upper cheek teeth of *Lophibaluchia* can be considered to have four major lophs plus a fifth short loph, but it is important to recall that the mesolophule, while occupying a position similar to a mesoloph, is formed in a completely different fashion. The mesolophule is an outgrowth from the metaconule, which is itself connected to the hypocone by what was originally the lingual portion of the metaloph. A true mesoloph is

derived from the mure or mesostyle or both. The labial portion of the metaloph is derived: instead of joining the metaconule it turns posteriorly to join the posteroloph. This short fifth loph is unlike the metaloph of any other known chapattimyid.

In the lower molars, the elongation of metalophulid II is particularly significant. There are, in effect, four transverse lophs on the lower molars. The orientation of the lophs may be indicative of a more efficient orientation of buccal and lingual chewing phases, perhaps associated with propalinal mastication (Rensberger, 1978). This, considered with the higher crowned teeth in *Lophibaluchia* relative to most other known baluchimyines, may suggest a distinct diet or lifestyle not utilized by other chapattimyids.

cf. *Lophibaluchia pilbeami*

Figure 19

REFERRED MATERIAL: GSP 21539, right M³ from locality Y-GSP 417.

DISCUSSION: One specimen of M³ (L = 1.82, W = 1.90) is lophodont and lacks a mure, and is therefore similar to *Lophibaluchia pilbeami*. However, the smaller M³ we have assigned to that species is more round in occlusal outline, and as a result, the hypocone is displaced more labially. GSP 21539 is almost as large as M² of *L. pilbeami*, which would agree better than GSP 21527 with the M₂/M₃ size ratio. We emphasize that our samples are fairly small and comprise only isolated teeth of *Lophibaluchia*. We do not know which, if either, or both of these third molars belong to the species *Lophibaluchia pilbeami*.

NEW GENUS AND SPECIES 1 (UNNAMED)

Figure 19

REFERRED MATERIAL: GSP 21540, right M³ from locality Y-GSP 417.

DISCUSSION: One M³ (L = 1.54, W = 1.58) resembles known *Lophibaluchia* in crest pattern including the posteriorly turned labial portion of the metaloph. However, this specimen has a mure connecting the protoloph and mesolophule. That suite of characters is distinct among currently available material,

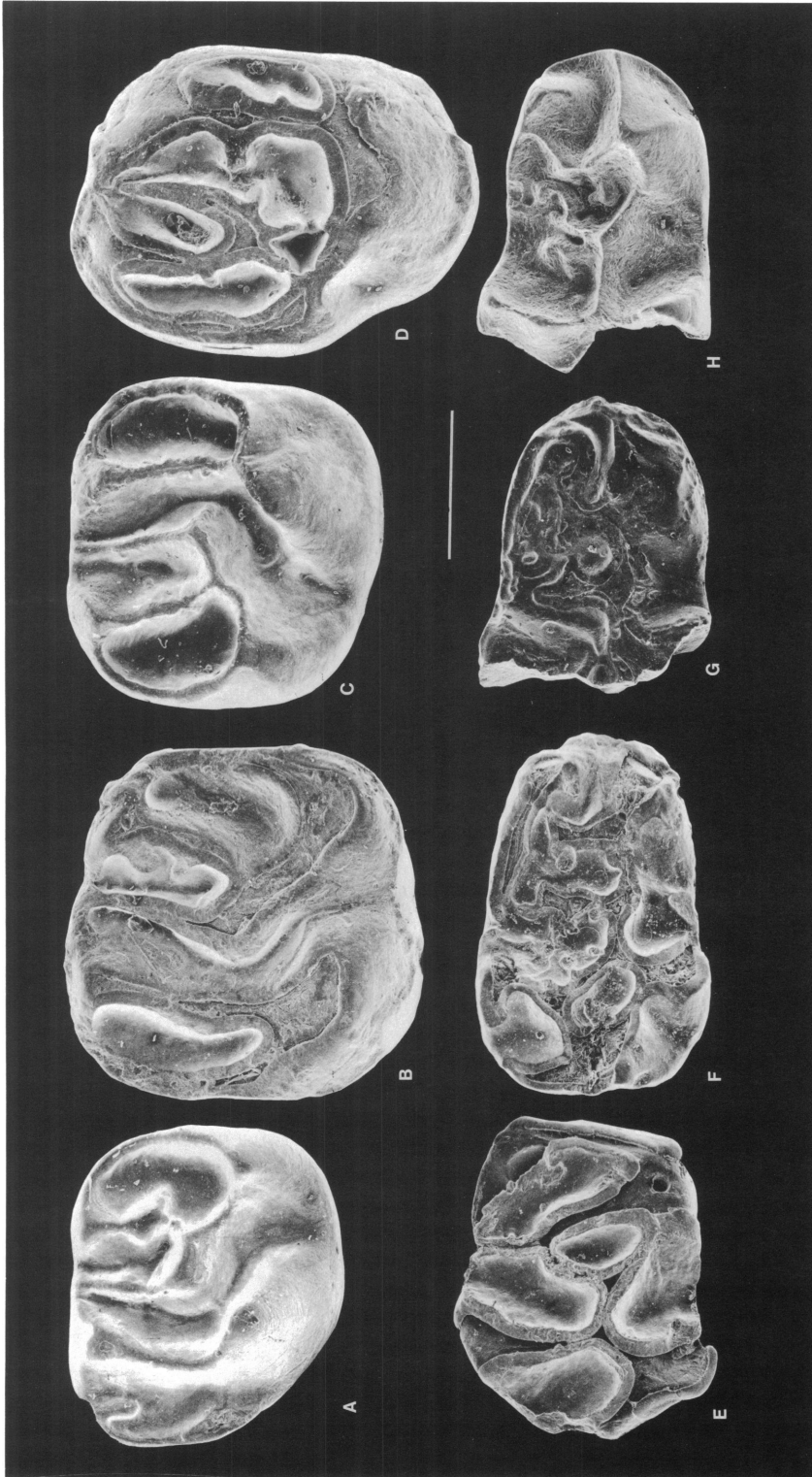


FIG. 20. Scanning electron photomicrographs of cheek teeth of *Hodsaahibia azrae*. Scale = 1 mm. A, GSP 21543, left DP⁴; B, GSP 21544, left M¹; C, GSP 21546, right M²; D, GSP 21548, right M³; E, GSP 21550, right P⁴; F, GSP 21549, right P⁴; G, GSP 21551, right P⁴; H, GSP 21552, right M¹⁻².

TABLE 14
Tooth Dimensions in Millimeters for *Hodsahibia*
azrae, New Genus and Species

Specimen	Number	Length	Width
DP ⁴	21543	2.20	1.92
M ¹	21544	2.36	2.52
M ²	21545	2.40	2.32
M ³	21546	2.20	2.28
P ³	21548	2.10	2.80
P ₄	21549	2.48	1.64
M ₁	21552	2.16	1.92

but we prefer not to name a new taxon until more specimens come to light.

Hodsahibia New Genus

TYPE SPECIES: *Hodsahibia azrae* new species, only known species.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Horace French, intrepid colleague.

DIAGNOSIS: Pentalophodont baluchimyine without distinct mures on upper molars; metacone joined to metaconule, which is submerged in a long mesolophule; lower molars with five crests, including a mesolophid that intersects a long metalophulid II.

Hodsahibia azrae, new species

Figure 20, table 14

HOLOTYPE: GSP 21544, left M¹.

HYPODIGM: GSP 21543, DP⁴; 21544–21547, M¹ or M²; 21548, M³; 21549–21551, P₄; 21552, M₁ or M₂.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Dr. Azra Sultana Ahmed of the Pakistan Science Foundation.

DIAGNOSIS: As for genus until other species are named.

DESCRIPTION: The dentition of *Hodsahibia* is moderately high crowned and unilaterally hypsodont and both upper and lower cheek teeth of this taxon have five crests. The mure in upper cheek teeth is incomplete, effectively separating the protocone and hypocone as in *Lophibaluchia*. DP⁴ has high, sharp crests and a low anterior cingulum with a low, rounded swelling near its origin from the protocone

and a sharp, short spur near the anterolabial corner of the tooth. The protocone is high, the largest cusp on the tooth, and well separated from the hypocone. A high, transverse crest joins the paracone to the protocone. The metaconule is an indistinct swelling, more strongly connected by the metaloph to the hypocone than the metacone. The narrow mesolophule extends transversely through the metaconule to the labial margin of the tooth. The posteroloph originates from the hypocone, forms the posterior boundary of the tooth, and joins the labial margin of the metacone, thereby enclosing a basin.

Three teeth are either M¹ or M². They are rounded squares in occlusal outline. The mesolophule is directed slightly posterolabially from the metaconule. Two of the three teeth have a weak, low connection between the protocone and hypocone, which appears to be a rather insignificant feature of the dental pattern. One of these teeth shows two labial and one lingual roots. The metaloph joins the metaconule.

One M³ is tentatively referred to this taxon. It is relatively large and lophodont, broader than long. The protocone and reduced hypocone are joined by a ridge that is continuous with the posteroloph. The metaconule is more strongly connected to the metacone than the hypocone and a narrow mesolophule trends somewhat anteriorly from the metaconule to the lingual margin of the tooth.

Three teeth are considered to represent P₄. Although DP₄ can not be ruled out, they differ from baluchimyine DP₄ in that transverse crests are not high and oblique. The P₄ are similar to the baluchimyine pattern previously described with the exception that a mesolophid is present. Protoconid and metaconid are high anterior cusps. The low, short anterior arm of the protoconid ends at the anterior midpoint of P₄ and lacks an anteroconid. The short posterior arm is a metalophulid II that ends low on the posterolabial side of the metaconid. A short mesolophid extends transversely from the mure. Low crenulations may occur anterior or posterior to it. Lophs join the hypoconid and entoconid at the mure. P₄ bears a strong posterolophid. Only one damaged lower molar is assigned to this taxon. A strong metalophulid II runs posterolingually past the metaconid to the

lingual side of the tooth. A narrow mesolophid runs lingually from the mure to intersect the metalophulid II.

DISCUSSION: *Hodsahibia* bears the characteristic baluchimyine mesolophule and shares the derived character of an unconnected protocone and hypocone with *Lophibaluchia*. It is distinct from *Lophibaluchia* in retaining a metaloph, an anterolingual connection between the metacone and metaconule, and is advanced over *Lophibaluchia* in having a mesolophid on lower molars.

NEW GENUS AND SPECIES 2 (UNNAMED)

Figure 21

REFERRED MATERIAL: GSP 21554, P₄; 21555, lower molar fragment; 21556, upper molar fragment, from loc. Y-GSP 417.

DESCRIPTION: These specimens are united by their moderate hypsodonty (greater than that of any other known chapattimyid) and large size. GSP 21556 resembles *Hodsahibia* in having a long, high mesolophule that extends transversely from the indistinct metaconule, in preserving a strong metaloph between metacone and metaconule, and in bearing a long, high posteroloph. Preserved anterior crown height is 1.4 mm. GSP 21555 has a relatively short, transverse metalophid, a long metalophulid II that joins the hypolophid, and lacks an anterior cingulum. P₄ (L = 2.28, W = 1.62) is corroded, but retains a transverse metalophid and hypolophid joined by a longitudinal median crest. It apparently had a large mesostylid.

DISCUSSION: This taxon is closely related to *Hodsahibia azrae*, but is more hypsodont and larger. It is about the size of GSP 21541, cf. *Lophibaluchia* n. sp., but GSP 21555, if indeed a lower molar fragment, differs from 21541 in that the metalophulid II joins the entoconid. The "thryonomyid" figured by de Bruijn et al. (1981; their plate 1, fig. 11) shares with *Hodsahibia* the presence of a short mesolophid and resembles GSP specimens 21554–21556 in hypsodonty. We suggest that the Murree specimen is not a thryonomyid but represents one of perhaps several baluchimyines that survived into the middle Miocene.

A high crowned pentalophodont baluchimyine like that represented by specimens

21554–21556 suggests that Ctenodactyloidea should be considered in the search for hystricid ancestors. *Sivacanthion*, a taxon from the younger middle Miocene Chinji Formation, is generally considered the oldest hystricid. While postdating the Bugti fauna, *Sivacanthion* is highly derived dentally and is hystricognathous. If hystricids evolved from ctenodactyloids, then hystricognathy would necessarily have evolved in Hystricidae independently of African thryonomyoids or have been shared by hystricids, certain post-Eocene ctenodactyloids and thryonomyoids.

CHAPATTIMYIDAE OR YUOMYIDAE

cf. *Lophibaluchia* or *Dianomys*,
new species (unnamed)

Figure 21

REFERRED MATERIAL: GSP 21541, right M₃ from locality Y-GSP 417.

DISCUSSION: GSP 21541, the largest tooth in the collection of teeth from Y-GSP 417, is about the size of small *Tataromys*, but is excluded from known true Ctenodactylidae by the presence of a strong Metalophulid II that reaches the lingual wall of M₃. Here, metalophulid II joins a posterior spur from the metalophid. M₃ is low crowned and has a low anterior cingulum. These traits, especially the long metalophulid II and low anterior cingulum, are shared with baluchimyinae and most closely with *Lophibaluchia*.

However, GSP 21541 also resembles the yuomyid *Dianomys qujingensis* in size (L = 3.24, W = 2.60) and dental pattern, but the metalophulid II is less oblique, while the posterolophid is directed more posterolingually than in *Dianomys*. Yuomyids are recognized mainly by their distinctive P₄ and upper molar morphology, so identification to family is not certain. The intriguing possible presence of a taxon in the Bugti rodent fauna that is similar to an Oligocene species from China raises interesting biogeographic questions. Regardless of the familial assignments of *Dianomys* and GSP 21541, it seems that some interchange of ctenodactyloids between Pakistan and China may have occurred during the Oligocene. Whether the age of the Bugti rodents should be reevaluated in light of this one tooth remains to be seen.

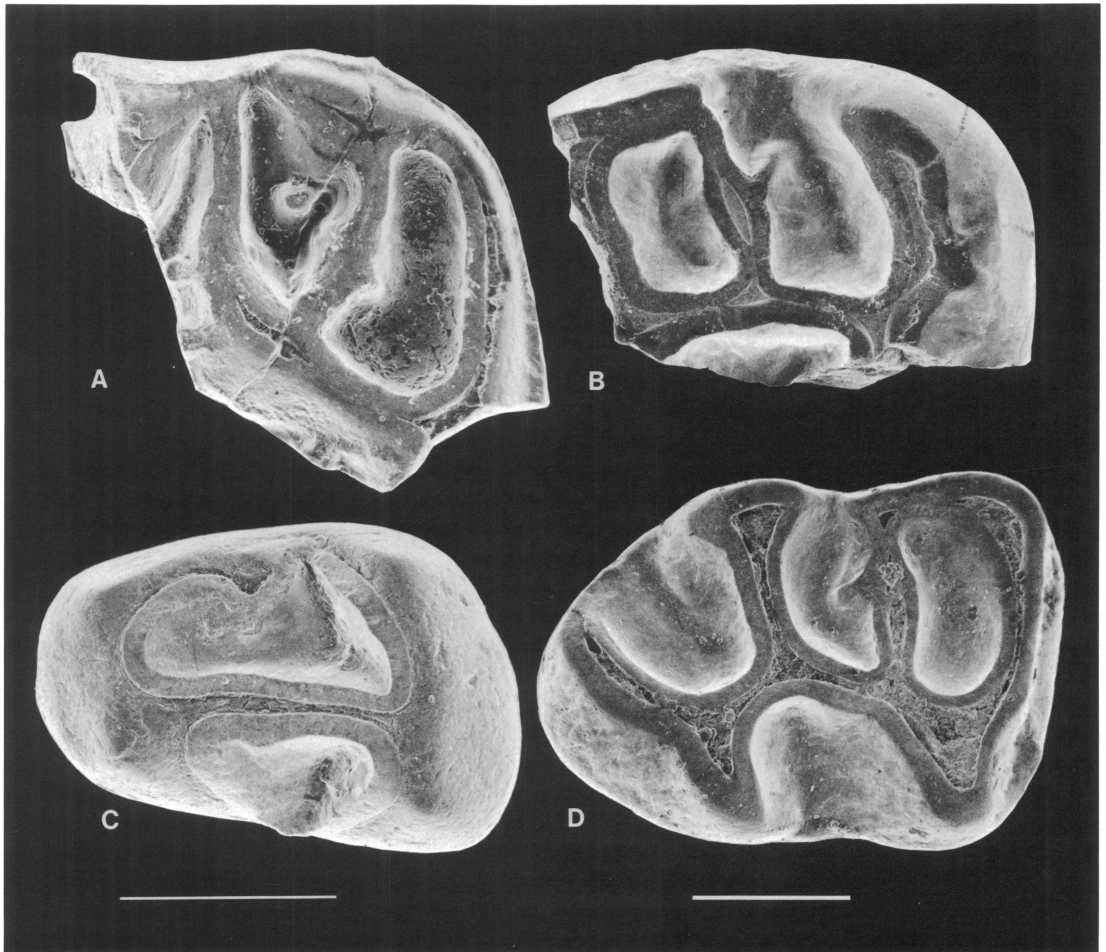


FIG. 21. New genus and species 2 (A–C, scale on left) and cf. *Lophibaluchia* or *Dianomys*, new species (D, scale on right). Scales = 1 mm. A, GSP 21555, left M^{1-2} ; B, GSP 21556, ?left M_{1-2} ; C, GSP 21554, ?left P_4 ; D, GSP 21541, right M_3 .

RODENTIA, FAMILY INDETERMINATE

***Downsimys*, New Genus**

TYPE SPECIES: *Downsimys margolisi*.

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named for Rosalind Downs in the recognition and appreciation of her efforts in the support of vertebrate paleontology; plus *mys*, Greek for mouse.

DIAGNOSIS: Small rodent with unilaterally hypsodont, cylindrical cheek teeth; high border with continuous ectoloph and wall joining lingual portions of protocone and hypocone; indistinct cusps incorporated into four transverse lophs.

***Downsimys margolisi*, new species**

Figure 22, table 15

HOLOTYPE: GSP 8407, left P^4 .

HYPODIGM: GSP 8411, left DP^4 ; 8407, left P^4 ; 8406 and 8409, right and left M^1 or M^2 ; 8408, left M^3 .

TYPE LOCALITY: Y-GSP 417, Baluchistan, Pakistan.

ETYMOLOGY: Named in appreciation for Henry Margolis, whose diverse efforts have contributed to the advancement of vertebrate paleontology.

DIAGNOSIS: Only known species of the genus.

DESCRIPTION: Five isolated cheek teeth represent a new genus and species of small

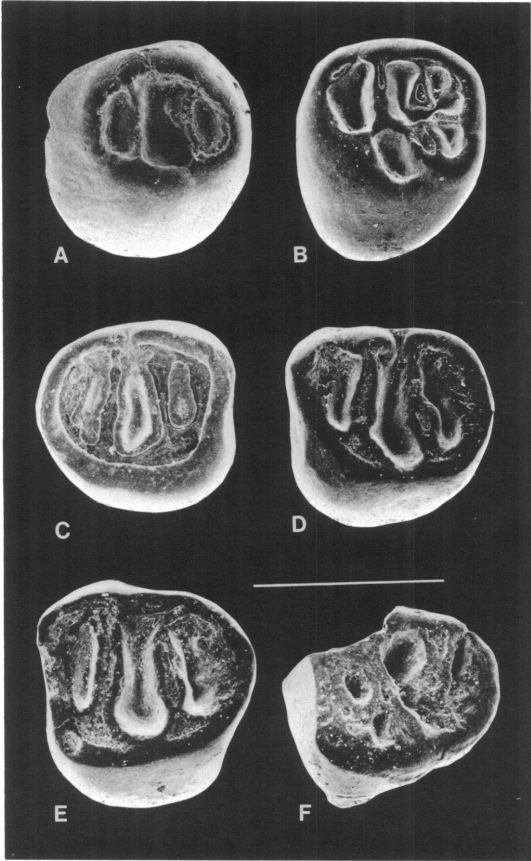


FIG. 22. Scanning electron photomicrographs of *Downsimys margolisi* (A–E) and *Downsimys* cf. *D. minutus* (F). Scale = 1 mm. A, GSP 8411, left DP⁴; B, GSP 8407, left P⁴; C, GSP 8406, right M¹⁻²; D, GSP 8409, left M¹⁻²; E, GSP 8408, left M³; F, GSP 8410, right M³.

rodent. Only upper teeth are represented in this sample. They are unilaterally hypsodont and bear four transverse lophs, anteroloph, protoloph, metaloph, and posteroloph. The small teeth are truly hypsodont, height (maximum observed is 1.36 mm for GSP 8409) being greater than length or width. Their cylindrical occlusal outline is formed by a high, relatively continuous border encircling each tooth. Cusps are nearly submerged into lophs. The high border includes a continuous ectoloph and a lingual wall not homologous with the mure. One specimen identified as M³ has three broken roots. One in five specimens (GSP 8407) retains a longitudinal mure, has a low lingual wall, and its metaconule connects with the posteroloph. These char-

TABLE 15
Tooth Dimensions in Millimeters for *Downsimys margolisi*, New Genus and Species, and cf. *Downsimys* sp.

Specimen	Number	Length	Width	Height
DP ⁴	8411	1.14	1.22	1.12
P ⁴	8407	1.10	1.28	1.28
M ¹	8406	1.12	1.20	—
M ²	8409	1.08	1.08	1.36
M ³	8408	1.16	1.24	—
M ³	8410	1.16	—	—

acters are reminiscent of less derived chapattimyids and we consider this tooth to be P⁴. Another specimen (8411) is molariform in crown pattern, but has a more distinct metaconule, and its base flares outward; this tooth is regarded as a deciduous premolar.

DISCUSSION: The relationships of this taxon are unclear. The loph pattern is somewhat similar to that of baluchimyines, especially the metaconule-posteroloph connection in GSP 8407. However, if baluchimyine, this taxon is divergent and indicates greater structural diversity in the subfamily. The hypsodonty, rounded occlusal outline, and relatively complete margins of the teeth recall *Cylindrodontidae* (e.g., *Mysops*, middle Eocene, North America), or even *Anomaluridae*, but those traits might easily be convergent, rather than indicative of any particular phylogenetic relationship. Finally, we cannot rule out the possibility of bathyergid affinities. If relationship proves to lie with cylindrodontids or with their possible relatives, *Tsaganomys* and *Cyclomytus* (see Patterson and Wood, 1982), then this would demonstrate that a second distinct group coexisted and survived in isolation with the Chapattimyidae in the Indian subcontinent, probably since the Eocene. A relationship between *Downsimys* and cylindrodontids would be interesting in light of Wood's (1984) comments on hystriognath and caviomorph origins.

There are intriguing similarities between *Downsimys margolisi* and the simple, cylindrical indeterminate rodent teeth reported by de Bruijn et al. (1981) from the Murree Formation (their plate 2, figs. 22, 23). This could represent yet another archaic lineage surviv-

ing from the Bugti fauna into the Murree fauna.

cf. *Downsimys* sp.

Figure 22, table 15

REFERRED MATERIAL: GSP 8410, (?) right M³ fragment from Y-GSP locality 417.

DESCRIPTION: GSP 8410 is probably an M³ with the lingual area broken away. There are four major lophs. The metaconule extends posterolaterally to connect with the posteroloph, a feature that may suggest baluchimyine affinities. This specimen is unique in having a longitudinal loph joining the protoloph and anteroloph, thus isolating an enamel lake between the lophs and the protocone. GSP 8410 and the specimens attributed to *Downsimys margolisi* may be indicative of further baluchimyine diversity. Alternatively, they may demonstrate that a second family of rodents contributed to the Bugti small mammal fauna.

DISCUSSION

This study is based on isolated teeth and therefore suffers from all the biases and inadequacies inherent in such a sample. Further, the Bugti rodent fauna is endemic and distinct from mid-Tertiary faunas elsewhere in the world. Nevertheless, most Bugti rodent taxa exhibit consistent characters, which in our judgment demonstrate affinity with known Asian ctenodactyloids. Many of these traits define a unique group that warrants subfamilial separation, and we have therefore erected the subfamily Baluchimyinae. We know of no rodents living today that show special relationship to Baluchimyinae, nor do we know of any fossil rodents outside of the Miocene of the Indian subcontinent that could be referred to the Baluchimyinae with certainty.

On the other hand, the baluchimyine occlusal pattern is easily derived from that of Eocene ctenodactyloids, specifically those from India and Pakistan studied by Hans de Bruijn, Jean-Louis Hartenberger, and their colleagues. There are no Oligocene rodents known from the Indian subcontinent, but the Bugti baluchimyines are sufficiently similar to Eocene Chapattimyidae to be considered a subfamily of them, and to suggest that the

chapattimyids did in fact have an independent radiation of significant proportions. In our opinion, this is justification enough for recognition of the Chapattimyidae as a ctenodactyloid family distinct from the Ctenodactylidae and Yuomyidae (see also previous discussion in the Introduction).

These relationships are portrayed in figure 4 and table 3. One main feature of the cladogram (fig. 4) is that hystricomorphy is used as a fundamental criterion for defining Ctenodactyloidea. The protrogomorphous *Cocomys* is thus excluded from the superfamily despite its great plesiomorphous (for rodents) similarity in dentition to early ctenodactyloids. Within Ctenodactyloidea, Yuomyidae are considered the sister group to Chapattimyidae based on possession of molariform (derived) premolars. Ctenodactylidae have premolars that are derived in a different direction, particularly in reduction of the talonid. Additional derived character states appear in late Eocene and younger genera of each family. Thus there is some likelihood that new fossil data could effect the familial allocation of early and middle Eocene ctenodactyloids because they show fewer derived character states.

The expanded talonid of the yuomyid P₄ is nearly as wide as the premolar is long and typically the outline of the tooth is pinched (waisted) between talonid and trigonid. The chapattimyid P₄ is oval in outline, elongated, and round posteriorly. The outline of some *Birbalomys* P₄ is slightly indented anterior to the hypoconid. All chapattimyids other than *Birbalomys* have a hypocone on P⁴. *Gumbatomys* is further derived (fig. 4) in absence of the mesoconid and possession of unbroken crests connecting cusps. The remaining chapattimyids of figure 4 occur in the Bugti fauna and a suite of characters distinguish most of them (including: DP₄ with multiple, oblique lophs, paraconule absent with metaloph joining hypocone, mesolophule on upper molars). This cluster of traits defines the Baluchimyinae. The remaining genus *Fallomys* does share some traits with baluchimyines, as here defined, but material currently available does not support particularly close affinity with the subfamily.

Four characters occur more than once on figure 4. Because rearrangement of the clado-

gram to reduce these appearances would result in many more instances of convergence or character reversal, these traits are believed to have evolved independently in the three families. Presence of a mesoconid (absent in eurymylids) is purported here to unite *Comys* with early ctenodactylids. This small cusp apparently disappears independently in each family, preceding or accompanying acquisition of lophodonty. The two traits may be linked. Lophodonty certainly has evolved independently in numerous rodent groups. Presence of an anterior cingulum on lower molars is characteristic for many chapattimyids and appears in the ctenodactylids *Karakaromys* and *Tataromys*. Finally, acquisition of a hypocone on P⁴, again characteristic for most chapattimyids, appears in the yuomyids *Dianomys* and *Petrokoslovia*.

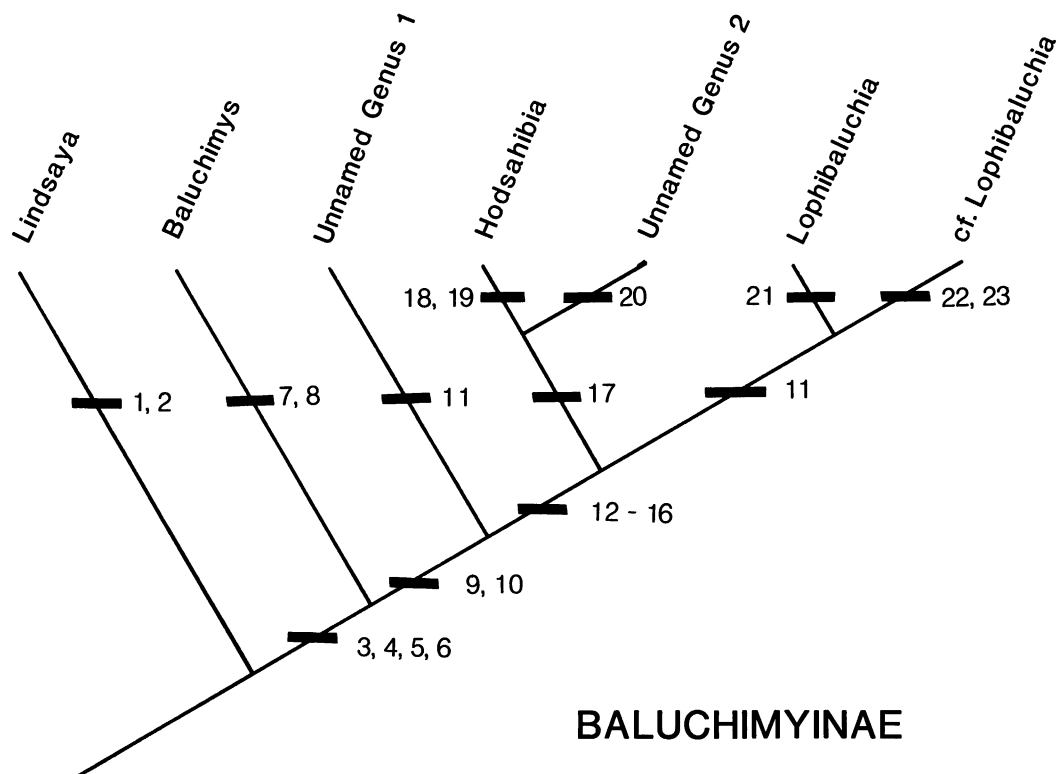
Figure 23 (table 16) is our interpretation of cladistic relationships among baluchimyine genera, and figure 7 is a diagrammatic representation of upper molars in baluchimyines and Eocene *Chapattimys*. One obvious character shared by baluchimyines and *Chapattimys* is inflation of the metaconule, with respect to other ctenodactylids. *Chapattimys* is distinct from Baluchimyines, and more primitive, in having the metaloph connected to the protocone, and in being more brachydont and bunodont.

Lindsaya appears to be the most primitive of the baluchimyines in being lower crowned (character 3, table 16; cladogram, fig. 23). However, it is unique among baluchimyines in lacking a well-developed metaloph; i.e., the metaconule is isolated. As we discussed above, we consider this a derived trait and hence, its bunodonty is secondary. We are convinced that the bunodonty is secondary because (1) most baluchimyines share a metacone-metaconule-hypocone connection, (2) the metacone and metaconule remain weakly connected in some specimens of *Lindsaya*, (3) most M¹ and M² retain a weak metaconule-hypocone connection, and (4) the primitive condition seen in *Chapattimys* (and other early rodents) is the presence of a metacone-metaconule-protocone connection. Thus, *Lindsaya* is derived relative to other baluchimyines in reduction of the metaloph and other crests, but primitive in height of crown. The alternative is that *Lind-*

saya is primitive in both characters and is therefore more primitive than *Chapattimys*. We accept the first interpretation and infer that *Lindsaya* and other baluchimyines share a common ancestor that is as yet unknown. Therefore we have included a hypothetical primitive baluchimyine molar occlusal pattern in figure 7 as a prediction of the common ancestral pattern. In addition, *Lindsaya* possesses a minute mesolophule that we interpret as reduced with respect to the longer one supposed in its hypothetical ancestor.

Baluchimys, *Hodsahibia*, and *Lophibaluchia* have five crests on upper molars, including the derived condition of having a long mesolophule; that is, a loph originating at the metaconule and directed labially. We have given it the name mesolophule because its origin demonstrates that it is not homologous with a mesoloph, even though it occupies an analogous position between protoloph and metaloph. It is tempting to postulate that lengthening and increase in height of crests on teeth was selectively advantageous for lophodont baluchimyines and that development of the mesolophule corresponded to strengthening of metalophulid II. *Hodsahibia* and *Lophibaluchia* are derived relative to *Baluchimys* in loss of the mure (character 14, table 16).

In both *Hodsahibia* and *Lophibaluchia* the metaconule and other cusps are submerged into lophs. In *Hodsahibia* the mesolophule is a continuation of the lingual portion of the metaloph, and the labial portion of the metaloph trends posterolabially from a point lingual to the metaconule. *Lophibaluchia* is different. The mesolophule and lingual portion of the metaloph form a continuous loph, as in *Hodsahibia*, but the labial portion of the metaloph arises from the metacone and projects posteriorly to join the posteroloph. The increased lophodonty from *Baluchimys* to *Hodsahibia* suggests that the mesolophule-metaloph arrangement in *Baluchimys* is the most primitive in these three genera. We consider it somewhat more probable that the mesolophule-metaloph arrangement in *Lophibaluchia* is derived from a pattern like that of *Baluchimys* rather than *Hodsahibia*, because *Hodsahibia* is derived with respect to the other genera in having longer crests and a mesolophid.



BALUCHIMYINAE

FIG. 23. Diagram of relationships among baluchimyine genera. This diagram is an extension of figure 4, where other chapattimyids demonstrate character polarity for the Baluchimyinae. Numbers refer to derived character states as listed in table 16.

The metaloph arrangement seen in *Lophibaluchia* is not unique to that genus. Some other rodents also exhibit the pattern, and some of them obviously derived the pattern in a different way from *Lophibaluchia*. For example, the rhizomyid (Muroidea) *Kanisamys* has a posteriorly directed metaloph that connects to the posteroloph (Jacobs, 1978; Flynn, 1982). However, the pattern in *Kanisamys*, which lacks a metaconule, derives from a posterolabial migration of the metaloph-hypocone juncture, not from a disconnection of the labial portion of the metaloph from the metaconule area as in *Lophibaluchia*.

At least two other baluchimyine genera are present in the Bugti fauna. Designated as "genus 1" is a lophodont form represented by one M^3 that is advanced in that the metaloph bends backward to join with the posterolophid, as in *Lophibaluchia*. It is placed as a

sister to *Hodsahibia* plus *Lophibaluchia* because it lacks characters 12–16 (table 16). "Genus 2" is like *Hodsahibia*, except that it is higher crowned. This hypsodont, pentalophodont form invites comparison with Hystricidae. A third new species is similar to *Lophibaluchia*, but presently cannot be differentiated from known Yuomyidae (*Dianomys*) in that it is represented by only one M_3 , the largest tooth in the entire Bugti collection.

The Baluchimyinae demonstrate how a pentalophodont pattern may be derived from a tetralophodont one. The terminology and our interpretation of homology appears to work equally well for hystricognaths, particularly thryonomyoids (see Flynn et al., 1983). Thus, our work on baluchimyine dentitions leads to conclusions of homology more similar to those of Lavocat (1976) and Butler (1985) than to those of Patterson and Wood (1982). Specifically, on upper molars we con-

sider the central crest as neomorphic (our mesolophule) and the crest posterior to it as the metaloph (Patterson and Wood's neoloph).

P4 or DP4?

As our samples consist of isolated teeth, we must acknowledge a degree of uncertainty in reconstruction of composite dentitions. We are reasonably certain of most associations, but for species of *Baluchimys* and *Lindsaya* M_1 and M_2 are difficult to differentiate. Also for these taxa, third molars seem to be under-represented and this may have led to some misidentifications. These sources of error probably have little effect on our conclusions. More significant is the difficulty of association of premolars. Premolars of *Fallomus* are recognizable as such, but whether they are permanent or deciduous is another question. We feel reasonably certain that we have correctly identified deciduous and permanent upper premolars of this genus, but all of the lower premolars of *Fallomus* are quite similar and it is possible that our sample includes no DP_4 .

As regards the baluchimyine premolars, we are struck by the occurrence of two different distinctive lower teeth that we feel must be deciduous by virtue of their lophodont crowns and constricted bases. These represent two genera. However, the other 18 lower premolars are homogeneous in structure, less lophodont than the molars, and are thought to be permanent teeth. We have designated some baluchimyine upper premolars as deciduous, but these are quite similar to their permanent counterparts. The possibility exists that future discoveries of associated dentitions will suggest different identifications. These could have important ramifications on higher-category relationships, particularly if baluchimyines were shown to possess only one premolar morphology; i.e., only permanent or only deciduous premolars. Since most phiomyid thryonomyoids retain DP_4^1 without replacement, demonstration that baluchimyines did not replace deciduous premolars by permanent premolars would constitute an impressive shared derived character state. At present we do not see evidence for this.

TABLE 16
Derived Characters for Cladogram of Baluchimyinae (Fig. 23)

1. Metacone-metaconule connection weak or absent.
2. Bunodonty; five main cusps on upper molars, including metaconule.
3. Greater crown height.
4. Hypoconulids submerged in posterolophids.
5. Pinched protoconids and hypoconids.
6. M_3 smaller than M_2 .
7. Anterior shelf on DP_4 .
8. M_2 with straight anterior wall.
9. Metaconule not distinct and other cusps submerged in crests.
10. Crests developed into lophs, crown height increased.
11. Metaloph turned posteriorly to join posteroloph.
12. Mesolophule reaches labial sides of upper molars.
13. Metalophulid II high and elongated in at least M_{1-2} .
14. Mure on upper molars absent.
15. Large size.
16. Loss of anteroconid on P_4 .
17. Pentalophodont cheek teeth, including mesolophids on lowers.
18. DP_4^1 with low anterior shelf.
19. P_4 longer than M_1 .
20. Teeth hypsodont.
21. P_4 small.
22. Increased size.
23. Posterolophid directed posterolingually on M_3 .

FAUNAL DIVERSITY

The Bugti micromammal fauna samples at least 10 and probably more species of rodents. This number is comparable to that retrieved at single sites in the Murree, Kamli, and Chinji Formations (de Bruijn et al., 1981; Wessels et al., 1982; work in progress). Moreover, diversity of the Bugti fauna encompasses the same range of dental specializations as is represented by cricetids, murids, ctenodactylids, and squirrels of Siwalik faunas. However most, if not all, of the Bugti rodents can be assigned to a single family, whereas typical Siwalik mammal faunas consist of representatives of seven or more families (see above references and Flynn and Jacobs, 1982). The Bugti fauna may be somewhat more diverse than Eocene faunas of Pakistan, which when combined comprise nine species, probably assignable to two families (see both Hussain et al., 1978, and Hartenberger, 1982a).

Chapattimyidae are rare in the Murree fau-

na and absent in Chinji faunas. Apparently elements of other rodent families perform the same roles as various genera of Bugti chapattimyids. Notable by its rarity is the occurrence of a species similar to *Fallomus raze* in the Murree fauna (de Bruijn et al., 1981). These authors also note a "thryonomyid" and an indeterminate rodent that may prove to be related to *Hodsahibia* (or our "Genus 2") and *Downsimys*, respectively. This remains to be investigated. The point is that the Chapattimyidae were the diverse, perhaps only, component of the Bugti rodent fauna and that faunas at most a few million years younger showed equal diversity and comprised several families almost to the exclusion of Chapattimyidae.

The foregoing invites speculation that these early Miocene small mammal faunas provide circumstantial evidence for competitive replacement of an endemic, monofamilial rodent fauna by elements of several modern families. Further, it seems probable that the Bugti fauna was representative of a small mammal fauna isolated on the Indian subcontinent throughout the late Eocene, the entire Oligocene, and the early Miocene, in part by the Paratethys and the Himalayas. This barrier to distribution broke down by the early middle Miocene and permitted numerous Asiatic and some African elements to out-compete the endemic rodent stock. At least one chapattimyid (*Fallomus*) persisted for some time into the middle Miocene, but by Chinji time all were replaced by rodents that we now consider as modern small mammals.

HYSTRICOMORPHY, HYSTRICOGNATHY, AND BIOGEOGRAPHY

Structure of the zygomatic arch/infraorbital foramen complex and of the dentary are traits taken to be important in rodent systematics. Hystricomorphy, in which a portion of the masseter muscle passes through an enlarged infraorbital foramen, occurs in many living rodents: *Hystrix*, *Thryonomys*, *Petromus*, Ctenodactylidae, Caviomorpha, Bathyergidae, Pedetidae, Anomaluridae, Myodonta, and arguably in Gliridae and Theridomyoidea (see Lindsay, 1977; Hartenberger, 1973; Wood, 1974, 1977; Flynn et

al., 1985; Luckett and Hartenberger, 1985; Vianey-Liaud, 1985). We follow Lavocat (1973) in considering hystricomorphy primitive for Bathyergidae, with later reduction of the infraorbital foramen in many species, although Patterson and Wood (1982) believe the opposite and consider inflation of the foramen a novelty in some bathyergids. As stipulated earlier, hystricomorphy can be recognized in fossils by an expanded infraorbital foramen.

Hystricognathy "in which the angular process of the lower jaw arises from the lateral surface of the alveolus of the lower incisor" (Patterson and Wood, 1982) is distributed more narrowly. Hystricognathy occurs in Hystricidae, Caviomorpha, Thryonomyoidea (including *Petromus*), Bathyergoidea, and apparently in a few Eocene North American forms. *Prolapsus*, *Protoptychus*, *Guanajuatomys*, and certain other North American rodents are considered by Wood (1974 and references therein) to show some degree of hystricognathy, but Korth (1984) disputes this for most of them. Wood (1984) sees hystricognathy among cylindrodontids, but they certainly do not possess all of the derived conditions of living hystricognaths. It is our opinion that at least *Prolapsus* is truly hystricognathous.

Woods (1972) considers the special assemblage of myological and osteological features of both hystricomorphy and hystricognathy to be derived conditions. Hystricomorphy may be a means of stabilizing the jaw during chewing and hystricognaths combine their jaw morphology with this condition to achieve simultaneous propalinal mastication on both sides of the mandible (Woods, 1972). It seems that hystricognaths may have added modification of the dentary to preexisting hystricomorphy and the fossil record is consistent with this. Eurymylidae (as represented by *Heomys*) and the earliest rodents (e.g., *Comomys* and *Paramys*) are protrogomorphous and sciurognathous (Li, 1977; Wood, 1962; Dawson et al., 1984; Dashzeveg et al., in press). Hystricomorphy appears first in ctenodactylids and a few North American Eocene forms (e.g., *Protoptychus*; Wahlert, 1973). Hystricognathy occurs in the later Eocene *Prolapsus* and in Oligocene rodents of Africa and South America (Wood, 1968;

Lavocat, 1976). Patterson and Wood (1982) reasserted their opinion that hystricognathy is unique and a defining character for a natural clade Hystricognathi. A major problem is finding a temporal and geographic link between early Oligocene hystricognaths of Africa and South America and with the Hystricidae whose earliest record is the middle Miocene of southern Asia. Wood feels that Eocene reithroparamyines of North America and presumably Asia (Wood, 1974) provide the linkage, while Lavocat (most recently, 1980) endorses direct transoceanic dispersal from Africa to South America.

Thus, hystricomorphy as recognized by an expanded infraorbital foramen, is a derived condition occurring in many rodents and hystricognathy occurs in a subset of those rodents. Whether hystricomorphy (or even hystricognathy) evolved more than once remains to be determined. Wood's (1984) statement that hystricomorphy *could* have evolved up to 10 independent times, while meant mainly as an illustration of possibility, seems overly pessimistic. Hypothesizing that hystricomorphy defines a monophyletic group, we see hystricognaths as the sister group to ctenodactyloids plus pedetids; these constitute a sister taxon to a group containing myomorphs (Flynn et al., 1985; see references therein).

This arrangement is portrayed diagrammatically in figure 24 and the accompanying table 17. Here we consider all major groups of rodents and use eurymylids in outgroup comparison. *Heomys orientalis* is taken as indicative of unspecialized Eurymylidae because it is relatively unmodified by eurymylid autapomorphies (table 17; but see Li, 1977, and Dashzeveg et al., in press, who review the possibility of eurymylid polyphyly). Higher-level systematic affinity of rodents and eurymylids lies with lagomorphs, as argued by Luckett (1977), Szalay (1977), Hartenberger (1980), and Novacek (1982) and reaffirmed by Novacek (in press; see also McKenna, 1975 and Dashzeveg et al., in press). These groups constitute the taxon Glires. In emending McKenna's (1975) Anagalida, Novacek (1986) associates Glires with *Anagale* and macroscelidids.

Macroscelidids, *Anagale*, lagomorphs, eurymylids, and most rodents have a hypocone

on upper molars. If the primitive rodent condition includes presence of hypocones on molars, then paramyine Ischyromyoidea, a protrogomorphous group, would be derived by their loss of the hypocone, an idea advanced by Korth (1984). The alternative is to consider rodents as diphyletic or to consider *Heomys* a rodent. Ischyromyoid relatives in this major rodent branch include squirrels, castoroids, aplodontoids, and cylindrodontids. Paramyines and squirrels have open talonid basins without crosscutting hypolophids, a derived state with respect to *Heomys* and ctenodactyloids, unless the opposite polarity suggested by Butler (1985) is correct. As regards the hypocone, some later ischyromyoids are traditionally thought to develop this cusp independently. Sciuravids may belong here, but it is more parsimonious to consider them to retain their hypocones from a *Heomys*-like ancestry, hence the dashed line in figure 24. Sciuravids may thus have originated close to the common ancestry of myomorphs and ctenodactyloids.

All other rodents are hystricomorphous. Among these are two major groups, one consisting of the Hystricognathi and their nearest relatives, the Ctenodactyloidea. In our discussion of *Fallomus*, we suggested the possibility that Pedetidae could be a ctenodactyloid derivative. This group is cohesive on various lines of evidence, including common occurrence of multiseriate enamel (see Flynn et al., 1985, and other papers in that volume). Multiseriate enamel microstructure has been considered derived relative to pauciseriate enamel mainly because all known early and middle Eocene rodents, including early ctenodactyloids, have pauciseriate enamel, while multiseriate enamel appears later. Although the temporal distribution of microstructural character states among fossils is consistent with this idea, von Koenigswald (1980, 1985) and Wahlert (1984) argue for the opposite relationship. Accepting for the moment that multiseriate enamel is advanced and appeared once, this would suggest a post-middle Eocene diversification of groups with multiseriate enamel.

The second hystricomorph group includes Myomorpha, glirids, anomalurids, and theridomyoids. This group is less easily defended (but see Klingener, 1964, Wahlert, 1978,

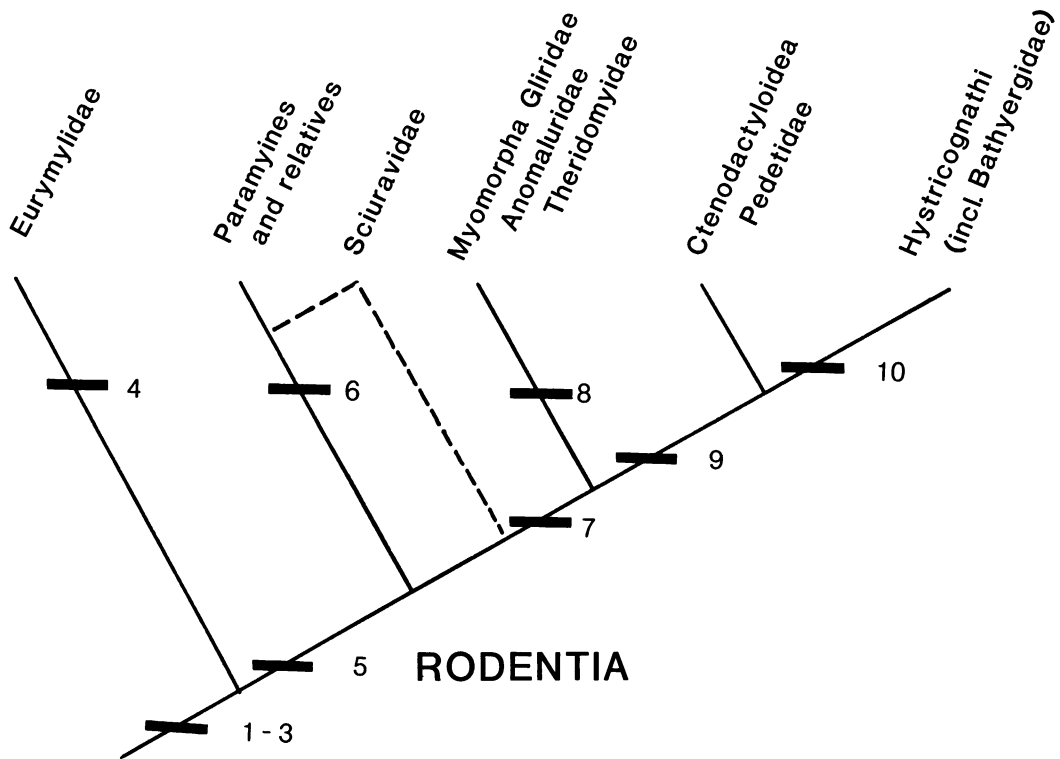


FIG. 24. Hypothetical relationships of major groups of rodents, with Eurymylidae (specifically *Heomys* and *Eurymylus*) as an outgroup. Dashed lines indicate alternative positions for the protrogomorphous Sciuravidae, which may have retained a hypocone from a *Heomys*-like ancestor or redeveloped it as did some paramyine relatives. Numbers refer to derived character states as listed in table 17.

and the attempt in Flynn et al., 1985) and includes the problematical geomorphs, which are sciuromorphic. One trait shared by these taxa (except several pauciserial theridomyoids) is uniserial enamel, a derived condition (Wahlert, 1968; von Koenigswald, 1980). Uniserial microstructure also occurs in squirrels, castoroids, some cylindrodontids, and apodontoids. Details of uniserial enamel are poorly surveyed across groups, but some evidence suggests that squirrels developed a distinctive variety of uniserial enamel independently of myomorphs (Boydé, 1978).

The cladogram in figure 24 is frankly unstable and is presented to stimulate analysis of character distributions. The cladogram of figure 4 may be more stable. When the two cladograms are compared, it is evident that if the protrogomorphous *Cocomys* is includ-

ed, then Hystricognathi should be represented on figure 4. Lack of appropriate fossil material makes placement of Hystricognathi uncertain. Early phiomyid thryonomyoids can be taken as relatively unmodified hystricognaths and some of their characteristics, with reference to ctenodactyloids, are listed in table 18. Figure 25 shows three positions where thryonomyoids might fall.

First, thryonomyoids may be linked to ctenodactyloids only by hystricomorphy and the usual presence of multiserial enamel. However, a number of dental features are shared by many ctenodactyloids and thryonomyoids, which led Hussain et al. (1978) to propose close phylogenetic relationship of Chapattimyidae to Thryonomyoidea and Caviomorpha. Hystricognaths possess molariform premolars (character 12, table 3, fig. 25), with hypoconids and hypoconulids on lower

premolars and metacones on upper premolars. Early thryonomyoids also possess trait 13 (table 3, fig. 25), usual presence of an anteroconid on P_4 , although Wood considers most of these premolars as deciduous. Whereas these two characters are shared by both yuomyids (Li, personal commun.) and chapattimyids, thryonomyoids are allied to the latter by shape of the P_4 (trait 18, table 3, fig. 25). However, the metaconule is indistinct in the studied upper molars of Fayum rodents (see Wood, 1968).

The lack of resolution at this point on the cladogram is offset by the fact that thryonomyoids display a number of traits that occur farther along the main axis of figure 25, and share them in particular with the Baluchimyinae. Thryonomyoids, like most chapattimyids, have a large hypocone on P^4 and a strong anterior cingulum on lower molars, are lophodont, and lack a mesoconid. However, the anteroconid is not a constant trait on lower premolars. Baluchimyine traits shared by thryonomyoids are: strong metalophulid II, loss of the paraconule, joining of the metacone to the hypocone, and anterior position of the hypolophid (characters 22–25, table 3, fig. 25). DP_4 is complex and lophodont in both groups, but the arrangement of the crests differs. At present it is not clear if the central loph of upper molars is a homologue to the mesolophule. Thryonomyoids, while multiserial, are poorly surveyed for this character and appear to have wider bands than baluchimyines.

In summary, dental evidence arguing that thryonomyoids may be the sister group to baluchimyines includes shared occurrence of molariform premolars, variable presence of an anteroconid on P_4 , oval shape of P_4 , large hypocone on P^4 , absence of mesoconid, lophodonty, anterior cingulum on lower molars, strong metalophulid II, absence of paraconule, metaloph joining hypocone, and hypolophid in an anterior position. However, in thryonomyoids, the anteroconid seems to occur only on DP_4 and the metaconule is not inflated, nor is there a mesolophule. For the present, it is not clear if these characters evolved independently in the two groups.

A simple parsimony test is not satisfactory because two features of Thryonomyoidea (table 18) are given great weight in defining the

TABLE 17

Derived Characters for Figure 24, Used to Depict Hypothetical Relationships of Eurymylidae and Major Groups of Rodents

1. Cheek teeth increase in size posteriorly.
2. Large, lingual hypocones present on upper molars.
3. Hypoconulids present on lower molars.
4. Unilaterally hypsodont, anteroposteriorly compressed molars.
5. P_3 absent, small P^3 .
6. Absence of hypocone on molars.
7. Hystricomorphous zygoma.
8. Uniserial enamel.
9. Multiserial enamel.
10. Hystricognathous dentary.

group: hystricognathy and retention of deciduous premolars (Wood, 1968). However, no dentaries of baluchimyines are known and we have previously mentioned the possibility that baluchimyines may have only one premolar morphology. The ramifications of a hystricognathous jaw from Dera Bugti, if one were ever found, are obvious.

As for Hystricognathi in general, many included taxa, e.g., Hystricidae are pentalophodont, a condition shared with *Hodsahibia*. Baluchimyinae demonstrate a pathway of transformation of a tetralophodont crown to a pentalophodont condition. Known cheek teeth of *Prolapsus* Wood (1973) and *Guana-juatomys* Black and Stephens (1973) are similar to those of early Ctenodactyloidea. Caviomorphs are characterized by strong lophodonty that could be derived from the chapattimyid cusp pattern just as some baluchimyines independently evolved similar crests.

If the relationship of chapattimyids to thryonomyoids and caviomorphs is plausible, a link is placed in the northern hemisphere that tends to support the arguments of Wood (1974, 1984) for terrestrial dispersion of early hystricognaths between North America and Asia. It also implies that diversification of these major groups began by the late Eocene. How these rodents migrated is a complex question, particularly as regards Afro-Indian plate tectonics. Waif dispersal directly between the two land masses may have been possible during the Paleocene, but by the Eocene this seems unlikely. Rather the

Indian plate was probably distant from Africa and Madagascar, but in contact at its northwest margin with Asia as evidenced by middle Eocene counterclockwise rotation of India (Patriat et al., 1982). Docking to the northwest could have begun during the later Cretaceous (Windley, 1983).

Rodents are not necessarily the only group of mammals to move between south Asia and Africa in the late Eocene. Wells and Gingerich (1983) erected the family Anthracobunidae, currently including five genera known from the early to middle Eocene of the Indian subcontinent. The anthracobunids have been referred to the Proboscidea, and according to Wells and Gingerich (1983), may be basal "tethytheres" (sensu McKenna, 1975). If this is the case, the late Eocene proboscidean *Moeritherium* from Africa may be derived from anthracobunids. *Moeritherium* and thryonomyoid rodents may have similar biogeographic histories involving south Asia and Africa.

Addendum. In figure 25 we have explored the possibility of close relationship between Baluchimyinae and Thryonomyoidea, specifically the primitive family Phiomyidae. If verified, this relationship would have the effect of deriving thryonomyoids (and perhaps all hystricognaths) from within the Ctenodactyloidea, as they are presently conceived (fig. 4). Thus Ctenodactyloidea and Chapattimyidae would be paraphyletic groups. While entertaining this hypothesis, we have not formally reclassified these rodents because the thryonomyoid autapomorphies, hystricognathy, and retained deciduous premolars cannot be evaluated for available baluchimyine material.

Recently, Jaeger et al. (1985) described an important rodent from Algerian rocks considered late Eocene in age. The few isolated teeth preserve mainly primitive ctenodactyloid traits, including a strong hypoconulid and metalophulid, a large M_3 , and a metaloph usually joining the protocone. All of the derived traits cited by Jaeger et al. (1985) occur in Chapattimyidae, and a few indicate baluchimyine affinity. Two such characters are the hypocone-metaconule connection and the short mesolophule of some specimens. Also the lower premolar, typically chapattimyid in shape and crown pattern, seems to have an

TABLE 18
Features Characterizing Early Thryonomyoids

1. Hystricomorphy.
2. Hystricognathy.
3. Most specimens have DP4; few have P4, which is less worn than M1.
4. Lower cheek teeth increase in size posteriorly.
5. Lower premolar oval in shape; may have small anteroconid.
6. Metalophulid II strong, often approaching lingual side of molar.
7. Low anterior cingulum present on M_{1-3} .
8. Hypolophid intersects more anterior to hypoconid.
9. Metalophulid II often with posterior spur.
10. Hypoconulid submerged in posterolophid.
11. P^3 present.
12. P^4 molariform, with hypocone.
13. Mesoloph present on upper cheek teeth.
14. Metaloph short, running between metacone and small metaconule.
15. Multiserial incisor enamel.

anteroconid. Furthermore, the isolated incisor reported by Coiffait et al. (1984) has narrow multiserial bands, despite the disclaimer in Jaeger et al. (1985).

Analysis of published descriptions and figures leads to several conclusions and a tentative scenario. *Protophiomys algeriensis* Jaeger et al. (1985) is apparently a chapattimyid of baluchimyine affinity, and it demonstrates widespread distribution of Chapattimyidae in the Eocene. Just as widespread ctenodactyloids diversified as Ctenodactylidae and Chapattimyidae in north and south Asia during the middle Eocene, a later vicariant event would have led to the flowering of Baluchimyinae in Pakistan and the origin of Phiomyidae in Africa.

This interpretation agrees in general with the Jaeger et al. (1985) conclusion that *Protophiomys algeriensis* presents a suitable structural ancestor for Thryonomyoidea; however, several features cited by these authors require comment, particularly since they assign the species to Phiomyidae. Most importantly, Jaeger et al. (1985) fail to demonstrate the presence of any phiomyid autapomorphy in *Protophiomys algeriensis*. There is no evidence for retained deciduous premolars: the figured lower premolar is identical to chapattimyid teeth identified here

as P₄; the figure 6 of Jaeger et al. (1985) could represent P₄; five teeth are insufficient to demonstrate deciduous premolar retention. Further, the phiomyid anterolabial cusp on lower molars is undeveloped, and hystricognathly cannot be assessed in this and other pertinent taxa. Finally, the central cusp on upper molars of *Protophiomys algeriensis* is clearly the homologue of the metacone in eurymylids and is not a neomorphic "mesocone."

Protophiomys algeriensis lends circumstantial support to the hypothesis that Thryonomyoidea originated from within the Ctenodactyloidea and are, perhaps, the sister group to Baluchimyinae. These important new fossils demonstrate more clearly the widespread Eocene distribution of ctenodactyloids and suggest that the origin of major ctenodactyloid groups proceeded by dissection of that broad area of distribution and subsequent vicariant evolution.

CONCLUSION

The samples described here represent the only known post-Eocene, pre-Siwalik Group small mammals from the Indian subcontinent. All species and probably all genera are new. Most, if not all, can be referred to the Chapattimyidae, heretofore known only from the Eocene of the Indian subcontinent. Most taxa present a suite of distinctive characters that we use to define a new subfamily, Baluchimyinae. Surprisingly, the small mammal fauna, estimated to be 18 to 21 million years old and little older than Siwalik faunas, lacks *all* of the higher-category Siwalik components, and consists of a diverse assemblage derived within the archaic family Chapattimyidae. This situation probably reflects an endemic radiation of rodents in isolation from communities of modern aspect elsewhere.

The origin and subsequent diversification of the Chapattimyidae is at least partially the result of vicariance. *Birbalomys*, *Advenimus*, *Tamquammys*, and other middle and early Eocene rodents of Asia resemble each other strongly, mainly in primitive characters, and apparently represent an early widespread ctenodactyloid radiation. This speaks for ease of dispersion of small mammals between the Indian subcontinent and Asia north of the

Himalayas and Tethys during the early Eocene (Hartenberger, 1982b). By the middle Eocene, rodents south and north of the Himalayas/Paratethys already differed; this indicates early development of a barrier to dispersal (Hartenberger, 1982b). Characters differentiating rodents south and north of the Himalayas became magnified in later species and are now chosen as definitions for major higher taxa. Thus Chapattimyidae, vicars of Yuomyidae and Ctenodactylidae, evolved when a geological barrier isolated two regions that had previously constituted a single faunal province.

Early ctenodactyloids may have been significantly more widespread. Chapattimyid-thryonomyoid similarities suggest that thryonomyoids could have evolved vicariantly following isolation of Eocene ctenodactyloids in Africa. This scenario assumes ctenodactyloid origin in Asia and dispersion westward by some means to Africa.

Hystricognath rodents have dental patterns similar to those seen in baluchimyines, including *Lophibaluchina*. As in baluchimyines, both tetralophodont and pentalophodont patterns are observed. We are struck by this similarity, and although we are unable to rule out homoplasy, we feel compelled to speculate further.

Hystricognath rodents are derived in having the angle of the lower jaw deflected. As this is a derived character, hystricognaths probably evolved from sciurognaths, and only once if hystricognaths are in fact monophyletic. The lower jaw of baluchimyines is unknown, but Eocene chapattimyids are apparently sciurognathus. As sciurognathly is primitive, this does not preclude chapattimyids from hystricognath ancestry. The fact that a number of derived dental traits are seen in both Baluchimyinae and Thryonomyoidea (see Discussion) leads us to look for other thryonomyoid traits in future fossil finds (hystricognathly, retention of deciduous premolars). Such a discovery would argue for placing the Hystricognathi next to Baluchimyinae (fig. 25) and would force dramatic reassessment of hystricomorph classification.

The dentition of known Miocene Baluchimyinae is probably too derived to be ancestral to primitive hystricognath molar patterns. However, there are similarities with

Phiomys and, in another instance, with Hystricidae. In addition, known baluchimyines occur much too late in time to be hystricognath ancestors. These arguments do not hold for early chapattimyids and because they do not we feel that the suggestions of Hussain et al. (1978) as to the pivotal position of the chapattimyids must be seriously considered.

On the other hand, should chapattimyids prove to have a special relationship to hystricognaths, that would place appropriate ancestors in the northern hemisphere, a hypothesis more in line with the biogeographic derivation of hystricognaths championed by Wood, as opposed to an African origin with subsequent rafting to South America of caviomorphs, as strongly supported by Lavocat. At the same time, this rationale agrees with Lavocat's arguments for close phylogenetic relationship between Africa and South American hystricognaths.

By the early Miocene, the Bugti fauna exhibited differential endemism. Small mammals there evolved apparently in isolation through the late Oligocene into the Miocene and the microfauna became distinct from that of Asia and Africa at the *family* level. However, the Bugti megafauna shared a number of elements with Asia and Africa at the *generic* or even specific level (Raza and Meyer, 1984). The Murree small mammal fauna resembles Asian and to some extent African small mammal faunas, while retaining a minor component derived from the older Bugti fauna. Elements, mainly from Asia and Africa, invaded the Indian subcontinent and apparently outcompeted and displaced the Baluchimyinae. Biogeographical factors allowing this long-term isolation followed by replacement remain to be studied.

LITERATURE CITED

- Barry, John C., N. M. Johnson, S. M. Raza, and L. L. Jacobs
1985. Neogene mammalian faunal change in southern Asia: correlation with climatic, tectonic, and eustatic events. *Geology*, vol. 13, pp. 637–640.
- Berggren, W. A., M. C. McKenna, J. Hardenbol, and J. D. Obradovich
1978. Revised Paleogene polarity time scale. *Jour. Geology*, vol. 86, pp. 67–81.
- Berggren, W. A., and J. A. Van Couvering
1974. The late Neogene: biostratigraphy, geochronology, and paleoclimatology of the last 15 million years in marine and continental sequences. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 16, nos. 1–2.
- Black, C. C., and J. J. Stephens III
1973. Rodents from the Paleogene of Guanajuato, Mexico. *Mus. Texas Tech Univ. Occas. Papers*, no. 14, pp. 1–10.
- Boyde, A.
1978. Development of the structure of the enamel of the incisor teeth in the three classical subordinal groups of the Rodentia. *In* P. M. Butler and K. A. Joysey (eds.), *Development, function and evolution of teeth*. London, Academic Press, pp. 43–58.
- Butler, P. M.
1980. Functional aspects of the evolution of rodent molars. *Palaeovertebrata*, Mem. Jubil. R. Lavocat, pp. 249–262.
1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. *In* W. P. Luckett and J. L. Hartenberger (eds.), *Evolutionary relationships among rodents: a multidisciplinary analysis*. New York, Plenum Press, pp. 381–422.
- Chaline, J., and P. Mein
1979. *Les rongeurs et l'évolution*. Paris, Doin Editeurs, 235 pp.
- Coiffait, P. E., B. Coiffait, J. J. Jaeger, and M. Mahboubi
1984. Un nouveau gisement à mammifères fossiles d'âge Eocène supérieur sur le versant sud des Nementcha (Algérie orientale): découverte des plus anciens rongeurs d'Afrique. *Compte Rendu Acad. Science Paris*, ser. 2, vol. 299, no. 13, pp. 893–898.
- Cooper, C. Forster
1913. New Anthracotheres and allied forms from Baluchistan—preliminary notice. *Ann. Mag. Nat. Hist.*, London, 8th ser., vol. 12, pp. 514–522.
1915. New genera and species of mammals from the Miocene deposits of Baluchistan—preliminary notice. *Ann. Mag. Nat. Hist.*, London, 8th ser., vol. 16, pp. 404–410.
1920. Chalicotheroidea from Baluchistan. *Proc. Zool. Soc. London*, pp. 357–366.
1922. Miocene Proboscidea from Baluchistan. *Proc. Zool. Soc. London*, pp. 609–626.
1923. Carnivora from the Dera Bugti deposits

- of Baluchistan. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 12, pp. 259–263.
- 1924a. The Anthracotheriidae of the Dera Bugti deposits of Baluchistan. *India Geol. Surv.*, Mem., Palaeontolog. Indica, n.s., vol. 8, no. 2, pp. 1–59.
- 1924b. *Baluchitherium osborni* (? syn. *Indricotherium turgaicum* Borriassah). *Phil. Trans. Royal Soc. London*, ser. B, vol. 212, pp. 35–66.
- 1924c. On the skull and dentition of *Paracerasitherium bugtiense*, a genus of aberrant rhinoceroses from the Lower Miocene deposits of Dera Bugti. *Phil. Trans. Roy. Soc. London*, ser. B, vol. 212, pp. 369–394.
1934. The extinct rhinoceroses of Baluchistan. *Phil. Trans. Roy. Soc. London*, ser. B, vol. 223, pp. 569–616.
- Dashzeveg, D., L. J. Flynn, and D. E. Russell
In press. New Glires (Mammalia) from the early Eocene of the People's Republic of Mongolia. *Palaeontology*.
- Dawson, Mary R.
1964. Late Eocene rodents (Mammalia) from Inner Mongolia. *Amer. Mus. Novitates*, no. 2191, pp. 1–15.
1968. Oligocene rodents (Mammalia) from East Mesa, Inner Mongolia. *Amer. Mus. Novitates*, no. 2324, pp. 1–12.
- Dawson, M. R., Li Chuan-kuei, and Qi Tao
1984. Eocene ctenodactyloid rodents (Mammalia) of eastern and central Asia. In R. M. Mengel (ed.), *Papers in vertebrate paleontology honoring Robert Warren Wilson*. Carnegie Mus. Nat. Hist., Special Publ. vol. 9, pp. 138–150.
- de Bruijn, H., S. T. Hussain, and J. J. M. Leinders
1981. Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Proc. Kon. Ned. Akad. Wetensch.*, ser. B, vol. 84, no. 1, pp. 71–99.
1982. On some early Eocene rodent remains from Barbara Banda, Kohat, Pakistan, and the early history of the order Rodentia. *Proc. Kon. Ned. Akad. Wetensch.*, ser. B, vol. 85, no. 3, pp. 249–258.
- Eames, F. E.
1950. On the age of the fauna of the Bugti Bone beds, Baluchistan. *Geol. Mag.*, vol. 87, no. 1, pp. 53–56.
- Eastman, C. B.
1982. Hystricomorphy as the primitive condition of the rodent masticatory apparatus. *Evol. Theory*, vol. 6, pp. 163–165.
- Fatmi, A. N. (ed.)
1973. Lithostratigraphic units of the Kohat-Potwar Province, Indus Basin, Pakistan. *Mem. Geol. Surv. Pak.*, vol. 10, pp. 1–80.
- Fischer, T. V., and H. W. Mossman
1969. The fetal membranes of *Pedetes capensis*, and their taxonomic significance. *Amer. J. Anat.*, vol. 124, pp. 89–116.
- Flynn, L. J.
1982. Systematic revision of Siwalik Rhizomyidae (Rodentia). *Géobios*, vol. 15, pp. 327–389.
- Flynn, L. J., and L. L. Jacobs
1982. Effects of changing environments on Siwalik rodent faunas of northern Pakistan. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 38, pp. 129–138.
- Flynn, L. J., L. L. Jacobs, and E. H. Lindsay
1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In W. P. Luckett and J. L. Hartenberger (eds.), *Evolutionary relationships among rodents: a multidisciplinary analysis*. New York, Plenum Press, pp. 589–616.
- Flynn, L. J., L. L. Jacobs, and S. Sen
1983. La diversité de *Paraulacodus* (Thryonomyidae, Rodentia) et des groupes apparentés pendant le Miocène. *Annales de Paléontologie*, vol. 69, no. 4, pp. 355–366.
- Flynn, L. J., and J. H. Wahlert
1978. Preparation and viewing of rodent incisors for SEM study. *Curator*, vol. 21, no. 4, pp. 303–310.
- Hartenberger, J. L.
1973. Etude systématique des Theridomyoidea (Rodentia) de l'Eocene supérieur. *Mém. Soc. Géol. France*, n.s., vol. 52, nos. 1–5, Mém. 117, 76 pp.
1980. Données et hypothèses sur la radiation initiale des rongeurs. *Palaeovertebrata*, Mém. Jubil. R. Lavocat, pp. 285–302.
1982a. A review of the Eocene rodents of Pakistan. *Univ. Mich., Contr. Mus. Paleont.*, vol. 26, no. 2, pp. 19–35.
1982b. Vertebrate faunal exchanges between Indian subcontinent and Central Asia in early Tertiary times. *Bull. Soc. Paleontol. Italiana*, vol. 21, nos. 2–3, pp. 283–288.
1985. The Order Rodentia: major questions on their evolutionary origin, relationships and suprafamilial systematics. In W. P. Luckett and J. L. Hartenberger (eds.), *Evolutionary relationships among*

- rodents: a multidisciplinary analysis. New York, Plenum Press, pp. 1-33.
- Hemphill, W. R., and A. H. Kidwai
1973. Stratigraphy of the Bannu and Dera Ismail Khan areas, Pakistan. U.S.G.S. Prof. Paper, no. 716-B, 36 pp.
- Hussain, S. T., H. de Bruijn, and J. J. M. Leinders
1978. Middle Eocene rodents from the Kala Chitta Range (Punjab Pakistan). Proc. Kon. Ned. Akad. Wetensch., ser. B, vol. 81, no. 1, pp. 101-112.
- Jacobs, L. L.
1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. Mus. Northern Arizona Press, Bull. ser. no. 52, 103 pp.
- Jacobs, L. L., I. U. Cheema, and S. M. I. Shah
1981. Zoogeographic implications of early Miocene rodents from the Bugti Beds, Baluchistan, Pakistan. Géobios, vol. 15, no. 1, pp. 101-103.
- Jacobs, L. L., and L. J. Flynn
1981. Development of the modern rodent fauna of the Potwar Plateau, Northern Pakistan. Neogene-Quaternary Field Conference, Chandigarh, India, Proceedings, pp. 79-82.
- Jaeger, J. J., C. Denys, and B. Coiffait
1985. New Phiomorpha and Anomaluridae from the late Eocene of north-west Africa: phylogenetic implications. In W. P. Luckett and J. L. Hartenberger (eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. New York, Plenum Press, pp. 567-588.
- Johnson, N. M., J. Stix, L. Tauxe, P. F. Cerveny, and R. A. K. Tahirkheli
1985. Paleomagnetic chronology, fluvial processes and tectonic implications of the Siwalik deposits near Chinji Village, Pakistan. Jour. Geology, vol. 93, pp. 27-40.
- Klingener, D.
1964. The comparative myology of four dipodoid rodents (genera *Zapus*, *Napeozapus*, *Sicista*, and *Jaculus*). Mus. Zool. Univ. Mich. Misc. Pub., no. 124, 100 pp.
- Korth, W. W.
1984. Earliest Tertiary evolution and radiation of rodents in North America. Bull. Carnegie Mus. Nat. Hist., vol. 24, pp. 1-71.
- Lavocat, R.
1973. Les rongeurs du Miocène d'Afrique Orientale. I. Miocene inférieur. Ecole Pratique des Hautes Etudes, Institut de Montpellier, Mém. 1, 284 pp.
1976. Rongeurs caviomorphes de l'Oligocène de Bolivie, II. Rongeurs du bassin Desadien de Salla-Luribay. Palaeovertebrata, vol. 7, pp. 15-90.
1980. The implications of rodent paleontology and biogeography to the geographical sources and origin of platyrrhine primates. In R. L. Ciochon and A. B. Chiarelli (eds.), Evolutionary biology of the New World monkeys and continental drift. New York, Plenum Press, pp. 93-102.
- Li Chuankuei
1974. A probable geomyoid rodent from middle Miocene of Linchu, Shantung. Vert. Palasiatica, vol. 12, no. 1, pp. 43-53.
1977. Paleocene eurymyloids (Anagalida, Mammalia) of Qianshan, Anhui. Vert. Palasiatica, vol. 17, no. 1, pp. 71-80.
- Li Chuankuei, Lin Yipu, Gu Yumin, Hou Lianhai, Wu Wenyu, and Qiu Zhuding
1983. The Aragonian vertebrate fauna of Xiaocowan, Jiangsu 1. A brief introduction to the fossil localities and preliminary report on the new material. Vert. Palasiatica, vol. 21, no. 4, pp. 313-327.
- Lindsay, E. H.
1977. *Simimys* and the origin of the Cricetidae (Rodentia: Muroidea). Géobios, vol. 10, pp. 597-623.
- Luckett, W. P.
1971. The development of the chorio-allantoic placenta of the African scaly-tailed squirrels (Family Anomaluridae). Amer. Jour. Anat., vol. 130, pp. 159-178.
1977. Ontogeny of amniote fetal membranes and their application to phylogeny. In M. K. Hecht, P. C. Hecht, and B. M. Hecht (eds.), Major patterns in vertebrate evolution. New York, Plenum Press, pp. 439-516.
- Luckett, W. P., and J. L. Hartenberger
1985. Evolutionary relationships among rodents: comments and conclusions. In W. P. Luckett and J. L. Hartenberger (eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. New York, Plenum Press, pp. 685-712.
- Madden, C. T., and J. A. Van Couvering
1976. The Proboscidean datum event. Early Miocene migration from Africa. Geol. Soc. Amer. Abstr. Programs, vol. 8, no. 6, pp. 992-993.
- McKenna, M. C.
1975. Toward a phylogenetic classification of the Mammalia. In W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Pri-

- mates. A multidisciplinary approach. New York, Plenum Press, pp. 21–46.
- Munthe, J.
1980. Rodents of the Miocene Daud Khel local fauna, Mianwali District, Pakistan. Part 1. Sciuridae, Gliridae, Ctenodactylidae, and Rhizomyidae. Milwaukee Publ. Mus., Contr. Biol. Geol., no. 38, pp. 1–17.
- Novacek, M. J.
1982. Information for molecular studies from anatomical and fossil evidence on higher eutherian phylogeny. In M. Goodman (ed.), *Macromolecular sequences in systematic and evolutionary biology*. New York, Plenum Press, pp. 3–41.
1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bull. Amer. Mus. Nat. Hist.*, vol. 183, art. 1, pp. 1–111.
- Osborn, H. F.
1924. *Serridentinus* and *Baluchitherium*, Loh Formation Mongolia. *Amer. Mus. Novitates*, no. 148, pp. 1–12.
1932. *Trilophodon cooperi*, sp. nov. of Dera Bugti, Baluchistan. *Amer. Mus. Novitates*, no. 585, pp. 1–6.
- Patriat, P., J. Segoufin, R. Schlich, J. Goslin, J. M. Auzende, P. Beuzart, J. Bonnin, and J. L. Olivet
1982. Les mouvements relatifs de l'Inde, de l'Afrique, et de l'Eurasie. *Bull. Soc. Géol. France*, vol. 24, no. 2, pp. 363–373.
- Patterson, B., and A. E. Wood
1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of Cavimorpha. *Bull. Mus. Comp. Zool.*, vol. 149, no. 7, pp. 371–543.
- Pickford, M.
1985. Kenya palaeontological gazetteer. Western Kenya. National Museums of Kenya.
- Pilgrim, G. E.
1907. Description of some new Suidae from the Bugti Hills, Baluchistan. *India Geol. Survey, Records*, vol. 36, pp. 45–56.
1908. The Tertiary and post-Tertiary freshwater deposits of Baluchistan and Sind, with notes on new vertebrates. *Records, India Geol. Survey*, vol. 37, pp. 139–166.
1912. The vertebrate fauna of the Gaj series in the Bugti Hills and the Punjab. *India Geol. Survey, Mem.* 2, Paleont. Indica, n.s., vol. 4, no. 1, pp. 1–83.
- Raza, S. M., J. C. Barry, G. E. Meyer, and L. Martin
1984. Preliminary report on the geology and vertebrate fauna of the Miocene Manchar Formation, Sind, Pakistan. *Jour. Vert. Paleontol.*, vol. 4, no. 4, pp. 584–599.
- Raza, S. M., and G. E. Meyer
1984. Early Miocene geology and paleontology of the Bugti Hills, Pakistan. *Geol. Surv. Pakistan, Mem.* no. 11, pp. 43–63.
- Rensberger, J. M.
1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In P. M. Butler and K. A. Joysey (eds.), *Development, function and evolution of teeth*. London, Academic Press, pp. 415–438.
- Sahni, A.
1980. SEM studies of Eocene and Siwalik rodent enamels. *Geoscience Jour.*, vol. 1, pp. 21–30.
- Sahni, A., and S. K. Khare
1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. *Jour. Paleontol. Soc. India*, vol. 17, pp. 31–49.
- Sahni, A., and H. C. Mitra
1980a. Neogene paleobiogeography of the Indian subcontinent with special reference to fossil vertebrates. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 31, pp. 39–62.
1980b. Lower Miocene (Aquitainian-Burdigalian) paleobiogeography of the Indian subcontinent. *Geologische Rundschau*, vol. 69, no. 3, pp. 824–848.
- Sahni, A., and M. C. Srivastava
1976. Eocene rodents and associated reptiles from the Subathu Formation of north-western India. *Jour. Paleontol.*, vol. 50, pp. 922–928.
1977. Eocene rodents of India: their palaeobiogeographic significance. *Geobios, Mem. Spec.* 1, pp. 87–95.
- Savage, D. E., and D. E. Russell
1983. *Mammalian paleofaunas of the world*. Reading, Addison-Wesley, 432 pp.
- Savage, R. J. G.
1967. Early Miocene mammal faunas of the Tethyan region. In C. G. Adams and D. V. Agar (eds.), *Aspects of Tethyan biogeography*. Systematic Assoc. Publ. no. 7, pp. 247–282.
- Sen, S.
1977. *Megapedetes aegaeus* n. sp. (Pedetidae) et à propos d'autres "rongeurs africains" dans le Miocène d'Anatolie. *Géobios*, vol. 10, no. 6, pp. 983–986.
- Shevyreva, N. S.
1971. New rodents from the middle Oligocene

- of Kazakhstan and Mongolia. Trans. Paleont. Inst. Acad. Sci. USSR, vol. 137, pp. 70–86.
1972. New rodents from the Paleogene of Mongolia and Kazakhstan. Paleontol. Jour., vol. 6, no. 3, pp. 399–408.
- Szalay, F. S.
1977. Phylogenetic relationships and a classification of the eutherian Mammalia. In M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major patterns in vertebrate evolution. New York, Plenum Press, pp. 315–374.
- Tullberg, T.
1899. Über das System der Nagethiere, eine phylogenetische Studie. Nova Acta Reg. Soc. Scient., Upsala, ser. 3, no. 18, pp. 1–514.
- Van Couvering, J. A.
1972. Radiometric calibration of the European Neogene. In W. W. Bishop and J. A. Miller (eds.), Calibration of hominoid evolution. Edinburgh, Scottish Academic Press, pp. 247–292.
- Van Couvering, J. A. H., and J. A. Van Couvering
1976. Early Miocene mammal fossils from East Africa; aspects of geology, faunistics and paleoecology. In G. L. I. Isaac and E. R. McCown (eds.), Human origins: Louis Leakey and the East African evidence. Menlo Park, Calif., W. A. Benjamin, pp. 155–207.
- Vianey-Liaud, M.
1985. Possible evolutionary relationships among Eocene and lower Oligocene rodents of Asia, Europe and North America. In W. P. Luckett and J. L. Hartenberger (eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. New York, Plenum Press, pp. 277–309.
- von Koenigswald, W.
1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. Senckenb. Naturforsch. Ges., no. 539, pp. 1–129.
1985. Evolutionary trends in the enamel of rodent incisors. In W. P. Luckett and J. L. Hartenberger (eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. New York, Plenum Press, pp. 403–422.
- Wahlert, J. H.
1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and Recent rodent groups. Mus. Comp. Zool. Breviora, no. 309, pp. 1–18.
1973. *Protoptychus*, a hystricomorphous rodent from the late Eocene of North America. Mus. Comp. Zool. Breviora, no. 419, pp. 1–14.
1978. Cranial foramina and relationships of the Eomyoidea (Rodentia, Geomorphina). Skull and upper teeth of *Kansasimys*. Amer. Mus. Novitates, no. 2645, pp. 1–16.
1984. Hystricomorphs, the oldest branch of the Rodentia. Ann. New York Acad. Sci., vol. 435, pp. 356–357.
- Wang Ban-Yue
1984. *Dianomys* gen. nov. (Rodentia, Mammalia) from the lower Oligocene of Qujing, Yunnan, China. Mainzer geowiss. Mitt., vol. 13, pp. 37–48.
- Wells, N. A., and P. D. Gingerich
1983. Review of the Eocene Anthracobunidae (Mammalia, Proboscidea) with a new genus and species, *Jozaria palustris*, from the Kuldana Formation of Kohat (Pakistan). Univ. Mich. Contr. Mus. Paleo., vol. 26, no. 7, pp. 117–139.
- Wessels, W., H. de Bruijn, S. T. Hussain, and J. J. M. Leinders
1982. Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. Proc. Kon. Ned. Akad. Wetensch., ser. B, vol. 85, no. 3, pp. 337–364.
- Windley, B. F.
1983. Metamorphism and tectonics of the Himalaya. Jour. Geol. Soc. London, vol. 140, pp. 849–865.
- Wood, A. E.
1962. The early Tertiary rodents of the Family Paramyidae. Trans. Amer. Phil. Soc. n.s., vol. 52, pp. 1–261.
1968. Early cenozoic mammalian faunas, Fayum Province, Egypt, Part II. The African Oligocene Rodentia. Bull. Peabody Mus. Nat. Hist., vol. 28, pp. 29–105.
1973. Eocene rodents, Pruett Formation, southwest Texas; their pertinence to the origin of the South American Caviomorpha. Texas Mem. Mus., Pearce-Selards ser., no. 20, pp. 1–40.
1974. The evolution of Old World and New World hystricomorphs. Symposia, Zool. Soc. London, no. 34, pp. 21–54; 55–60.
1975. The problem of the hystricognathous rodents. In G. E. Smith (ed.), Studies on Cenozoic paleontology and stratigraphy in honor of Claude W. Hibbard. Univ. Mich. Papers on Paleontology, no. 12, pp. 75–80.
1977. The evolution of the rodent family

- Ctenodactylidae. Jour. Palaeontol. Soc. India, vol. 20, pp. 120–137.
1984. Hystricognathy in the North American Oligocene rodent *Cylindrodon* and the origin of the Caviomorpha. In R. M. Mengel (ed.), Papers in vertebrate paleontology honoring Robert Warren Wilson. Carnegie Museum of Natural History, Special Publ. no. 9, pp. 151–160.
- Wood, A. E., and R. W. Wilson
1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Jour. Palaeontol., vol. 10, pp. 388–391.
- Woods, C. A.
1972. Comparative myology of jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull. Amer. Mus. Nat. Hist., vol. 147, art. 3, pp. 115–198.

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