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A REVIEW OF THE EOCENE RODENTS OF PAKISTAN

BY

JEAN-LOUIS HARTENBERGER[1]

Abstract.—New specimens of rodents from Eocene localities of Pakistan (NW Frontier Province and Azad Kashmir) are described and compared to previous records from the Ganda Kas area. A total of nine species are recognized in collections made to date from the Eocene of Pakistan. All of these species belong to the family Ctenodactylidae. The most common lineages are known only from the Indian subcontinent; these include *Birbalomys* (with subgenus *Basalomys* n. subgen.), and *Chapattimys*. The new genus *Gumbatomys* could be related to younger Central Asiatic *Karakoromys*. A *Petrokoslovia*-like lineage is also present but rare (*Petrokoslovia* is a genus previously described from Mongolia). Conclusions about the biochronology of localities on the Indo-Pakistan subcontinent are necessarily tentative: all localities appear to be similar in age, but Kalakot and Mekta in India may be more recent than Ganda Kas and Chorlakki in Pakistan. The early history of this Asiatic group indicates that ctenodactylids had a Central Asiatic and Indo-Pakistan distribution by early Eocene times. No clear relationships of Eocene ctenodactylids to modern groups of Rodentia can be established.

INTRODUCTION

The first rodents from the Eocene of Pakistan were collected by P. Y. Sondaar and J. Van der Meulen in 1966 as a result of preliminary field work in the Kuldana Formation. This material was not described, probably because the sample collected consisted of only three isolated teeth. The enigmatic aspect of these teeth and the possible middle Eocene age of the horizon in which they were found resulted in their being mentioned in several articles. Sondaar and Van der Meulen showed them to numerous workers. For example, Lavocat (1974, 1975), based on the observations that he was able to make, thought they represented a rodent population from the Old World that could have given rise to the Phiomyidae of the Egyptian Oligocene (see Hoffstetter, 1975). These Pakistan rodents were therefore, for Lavocat, among the most important in the history of the Rodentia. It should be remembered that until recently the rodents of the early Paleogene of Asia were poorly known.

During the past decade several new forms have been discovered. Sahni and Khare (1973) described *Birbalomys woodi* from the Subathu Formation of India, an approximate equivalent of the Kuldana Formation in Pakistan. Shevyreva (1976) published a complete review of the

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rodents from the Paleogene of the Soviet Union, among which *Saykanomys* Shevyreva and *Tamquamys* Shevyreva were given particular attention. In China, Li (1975) described *Yuomys* from the late Eocene. However, the systematic position proposed by these authors for the new fossils was not completely satisfactory because they were included either in the Paramyidae or the Sciuravidae. In 1977, Wood analyzed one of the hypotheses proposed earlier by Dawson (1964, 1968) and showed that one could attribute these Eocene Asian forms to the family Ctenodactylidae because they possess, as early as the Eocene, all of the characteristics of this group. Moreover, a gradual series of intermediate forms connected the Eocene ancestral type *Saykanomys* to species previously described by Bohlin (1946) from the Mongolian Oligocene.

In recent years discoveries of Eocene rodents in Pakistan have multiplied. The successive expeditions organized by the University of Michigan and Howard University in collaboration with the Geological Survey of Pakistan have resulted in the collection of numerous specimens, principally from three localities. An initial paper by Hussain, de Bruijn, and Leinders (1978) demonstrated that rodent communities were diverse. Subsequently a number of taxonomic problems have become apparent, as have problems concerning biogeographic interpretation, and it seems necessary to reexamine the data. Close comparison of the Pakistan material with that from other regions of Asia is necessary, particularly material from Mekta and Kalakot (Jammu-Kashmir, India) and from Kazakhstan (U.S.S.R.).

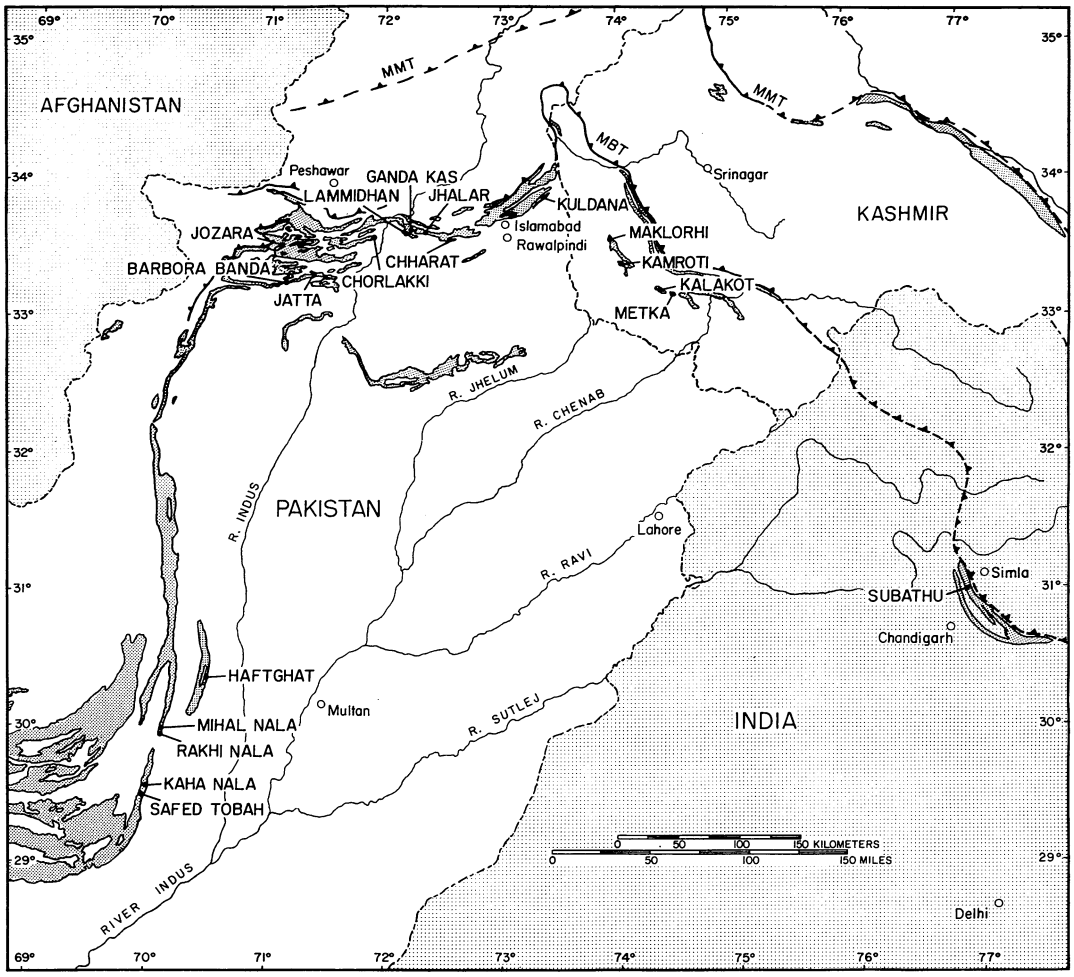
Fossil mammals are reasonably common in the Kuldana Formation of Pakistan, and in three localities careful collecting has resulted in the discovery of significant rodent remains. Two of these are Hussain-Geological Survey of Pakistan (H-GSP) localities 57 and 144 near Ganda Kas, studied by Hussain et al. (1978), from which 800 and 500 kg, respectively, of matrix were treated. The matrix at H-GSP localities 57 and 144 is argillaceous and it was washed and screened, yielding isolated teeth of rodents. Hussain et al. (1978) considered site 57 to be situated lower in the Kuldana Formation than 144. The third locality is at Chorlakki where, so far, about 200 kg of matrix have been dissolved in formic or acetic acid. Fossils here are found in a micro-conglomerate of reworked calcareous soil nodules that yields a diverse mammalian fauna including isolated teeth of rodents.

In 1980 the University of Michigan-Geological Survey of Pakistan expedition found new localities with rodent remains in sediments attributed to the "Chalpani Formation" at Kamroti in Azad Kashmir. Attempts to treat this matrix chemically have so far been unsuccessful. Consequently little material is known, but, due to its geographical situation, Kamroti is important for purposes of correlation. The "Chalpani Formation" is usually considered as an equivalent of the Subathu Formation of India.

The geographic positions of Eocene rodent-bearing localities discussed in this paper are shown in Text-figure 1. Specimen numbers prefaced by GSP-UM refer to specimens to be deposited in the Pakistan National Museum of Natural History, Islamabad, or with the Geological Survey of Pakistan (GSP), Islamabad and Quetta. Epoxy casts of these specimens are also being deposited permanently in the University of Michigan Museum of Paleontology (UM), Ann Arbor, and the Muséum National d'Histoire Naturelle, Paris. Specimens prefaced by LUVP are in the vertebrate paleontology collections of the Department of Geology, Lucknow University.

SYSTEMATIC PALEONTOLOGY

All of the rodents discovered to date from the Eocene of Pakistan can be attributed to the family Ctenodactylidae. As I have shown elsewhere, the same is probably also true for all rodents described from the early Paleogene of Asia (Hartenberger, 1980). Apparently unaware



TEXT-FIG. 1 — Eocene fossil vertebrate localities in the Indus Basin of Pakistan and western India. Heavy stippling shows the outcrop pattern of Eocene sedimentary rocks. MBT and MMT are the Main Boundary Thurst and Main Mantle Thrust, respectively, representing the tectonic suture between Indo-Pakistan and the Eurasian lithospheric plate. Eocene rodents have been found in the broad belt of localities from Barbora Banda in Pakistan to Subathu in India. Map redrawn, with additions, from Gingerich and Russell (1981).

of the publication on Asian rodents by Wood (1977), Hussain et al. (1978) created the new family Chapattimyidae. They included in this new family *Chapattimys* Hussain et al. itself and *Saykanomys* Shevyreva (to which they referred some Pakistan material). They suggested that perhaps *Petrokoslovia* Shevyreva could also belong to this family. The generic attributions made by Hussain et al. will be discussed below, and it will be shown in particular that *Saykanomys*, from the Eocene of Kazakhstan, is absent so far from the Pakistan fossil record, which has important biogeographic implications. As for the familial attribution used by these authors, it would seem better to abandon it in favor of Wood's proposition. *Saykanomys* (in so far as its cranial anatomy and dental morphology are known) should be regarded as a primitive ctenodactylid.

Saykanomys has all the characters diagnostic of Ctenodactylidae, and gradual evolutionary

progression can be demonstrated from these primitive Eocene forms to ctenodactylids of the Oligocene described by Bohlin (1946), involving, among other characteristics, the acquisition of hypsodonty. This interpretation takes into account the fact that, following recent discoveries made in the Paleocene and Eocene of China, the history of the initial radiation of rodents appears very different from that which was known several years ago. The North American and European fossil record yields what were long thought to be the oldest rodents, the Ischyromyidae or Paramyidae (Hartenberger, 1980), but these are not as primitive as early ctenodactylids now known from China.

Detailed analysis of the proposed family Chapattimyidae of Hussain et al. reveals that the type genus is known by less than 20 more or less well preserved, isolated teeth from the type locality. The original generic diagnosis of *Chapattimys* cites characters common to all primitive ctenodactylids, such as *Saykanomys*, *Birbalomys*, and other forms described here. The principal generic difference of *Chapattimys* from other forms is its more highly developed lophodonty.

In the absence of cranial remains of *Chapattimys*, Hussain et al. deduced the anatomical characters mentioned in the familial diagnosis of Chappatimyidae from what can be seen in *Saykanomys* and *Birbalomys*, which they consider (incorrectly) to be synonyms. Hystricomorphy and sciurognathy are characters found in the ctenodactylids. All the other morphological dental characters (such as the development of a large hypoconulid on the lower teeth and the very lingual position of the hypocone on the upper teeth) are characters which occur in all primitive ctenodactylids.

Hussain et al. (1978) present a study of the enamel microstructure of the incisors from material collected in the localities near Ganda Kas (H-GSP 57 and 144), even though great systematic importance is not attributed to it. According to them, the 15 specimens show a multiserial type of structure. The authors themselves are not in complete agreement as to the value of enamel microstructure in classification (op cit., p. 105), but it is one of the elements of the diagnosis of Chapattimyidae. Korvenkontio (1934) defined types of enamel in rodent incisors according to their aspect in sagittal view: pauciserial, multiserial, uniserial. Since then Walhert (1968) and Flynn and Walhert (1978) have proposed certain rules for systematizing these studies. Examination of the illustrations in Hussain et al. permits some doubt as to the presence of a multiserial state; the enamel observed by them appears to be pauciserial, as is the case in all primitive rodents. This impression is confirmed by the rigorous observations made by Sahni (1980) on material of a comparable age collected at Mekta (Jammu and Kashmir). Sahni clearly shows that Indian forms that are comparable at the generic and sometimes specific level are pauciserial.

In conclusion, I think that it would be preferable to abandon Chapattimyidae and follow Wood's proposition, whereby "Chapattimyidae" are included as primitive forms in the family Ctenodactylidae. It is generally unsatisfactory to subdivide a natural phylogenetic group into successive chronological taxa based on historical development. In an equivalent situation, the European family Theridomyidae has been subdivided into subfamilies, but each of these was established on phyletic rather than gradistic grounds (Hartenberger, 1971, p. 1919). The main argument, apart from phylogenetic considerations, is that it is unnecessary to assign family rank to small groups of genera of short duration. In this perspective, the genera *Chapattimys*, *Birbalomys*, and possibly *Gumbatomys* n. gen., might be considered as a subfamilial group, Chapattimyinae, of Indo-Pakistan forms. As I show below, these Indo-Pakistan forms are quite different from contemporaneous rodents in Central Asia like *Saykanomys*, *Advenimus*, *Tamquamys*, and another genus to be described by Dawson and Li. *Chapattimys*, *Birbalomys*, and *Gumbatomys* are primitive Ctenodactylidae with P^4 well developed and cheek teeth brachyodont, with rounded and bulbous cusps and frequent crenulations.

Family CTENODACTYLIDAE Zittel, 1893

Birbalomys Sahni and Khare, 1973

Birbalomys Sahni and Khare, 1973, p. 34.
Metkamys Sahni and Srivastava, 1976, p. 89.
Saykanomys (in part), Hussain et al., 1978, p. 81.

The material on which the genus *Metkamys* was based is heterogeneous and consists of only four isolated teeth. Since the type of *Metkamys blacki* is a dP^4 that can be attributed to *Birbalomys woodi* Sahni and Khare, it is necessary to synonymize *Metkamys blacki* with the latter. Hussain et al. (1978) proposed that *Birbalomys* be considered as a junior synonym of *Saykanomys*, but this synonymy is not acceptable, as will be shown below. As a working hypothesis one can consider *Tamquamys tantillus* Shevyreva to be the ancestral stock from which two lineages, represented by *Birbalomys* and *Saykanomys*, might be derived. It should also be borne in mind that *Saykanomys* Shevyreva may in future prove to be synonymous with *Advenimus* Dawson. *Birbalomys* and *Saykanomys* are compared in the following paragraphs.

Anatomy of the cranium.—*Birbalomys* and *Saykanomys* are very different in size: the first is as big as a rat, and the second is smaller than a house mouse. The anterior part of the cranium is known in each case, but it is quite difficult to compare the infraorbital area in detail. The zygomatic arch is anterior to P^4 in both. Comparison of the lower jaws is easier: that of *Birbalomys* is very strong and heavy, while the jaw of *Saykanomys* is very slender. The pterygoid fossa extends anteriorly beyond the position of M_3 in *Saykanomys*, while in *Birbalomys* it is situated more posteriorly. The angle of the two crests of the pterygoid is more open in *Birbalomys* than it is in *Saykanomys*. In *Tamquamys* this angle is larger; if *Tamquamys* is the most primitive form of the group, then it follows that *Birbalomys* is more primitive than *Saykanomys* in this characteristic.

Deciduous dentition.—The specimen LUVP 20020 was described as a left P_4 of *B. woodi* by Sahni and Srivastava (1976, text-fig. 1a), but it is clearly a deciduous tooth: the crests are sharp and low, and the tooth is elongated. Another undescribed specimen has widely divergent roots, a condition frequently seen in deciduous teeth. A short anteroconid is present on the anterior part of the tooth. The protoconid and metaconid are close together, and separated by a deep valley. The ectolophid is not complete and, in the posterior part of the tooth, the entoconid, hypoconid and hypoconulid are of equal size. This dP_4 is very similar to the P_4 of *Saykanomys*. Hussain et al. (1978, p. 85) have interpreted the P_4 of *Saykanomys* as a dP_4. But after studying the original specimen, I was able to determine that it really is a definitive premolar. The main differences that can be observed between the dP_4 of *B. woodi* and P_4 of *S. chalchae* are the absence of an anteroconid in *S. chalchae* and the fact that the three posterior cusps are aligned buccolingually—in *B. woodi*, on the other hand, these three cusps are disposed in a triangular fashion.

The dP_4 of *Birbalomys woodi* is very similar to P_4 of *Saykanomys chalchae* as observed on the type specimen of the latter. The anterior and posterior cingula are well developed and, especially, the hypocone occupies a position even more lingual than the protocone. In *S. chalchae* the hypocone is less developed and lower than the protocone, whereas in *B. woodi* it is as high as the protocone. The protoconule is not well developed and it is slightly forward with respect to the paracone-protocone alignment. The metaconule is isolated from the hypocone. The principal cusps are sharp, which is also a characteristic of milk teeth.

Sahni and Srivastava (1976) described *Metkamys blacki* as a new genus and species, based on a molariform upper tooth from Metka. A new interpretation of the holotype LUVP 20026 is given here: it is almost certainly a milk tooth, as is shown by the thin roots and the morphology

of the tooth. Other teeth of this kind have been found in Pakistan localities with *Birbalomys woodi* or *B. sondaari*. Comparisons made in the USSR on specimens from Kazakhstan support this interpretation. The size of the tooth indicates that most probably it is referable to *B. woodi*. The same can be said about LUVP 20027 (Sahni and Srivastava, 1976, text-fig. 2B, pl.2: fig. 9).

Permanent dentition.—P_4 is damaged on the holotype of *B. woodi*, but many isolated specimens from the same locality permit its description. The anterior part of P_4 has two cusps; the protoconid and metaconid are close together, separated by a shallow valley. This tooth is very different from that of *S. chalchae*, where the ectolophid joins the lower part of the protoconid, where the inner basin very often has crenulations, and where the entoconid, hypoconulid and hypoconid are separated by deep valleys. In *Birbalomys* the hypoconid has a crest joining the ectolophid and the cusps are strong and massive, not as in a milk tooth.

In *Birbalomys* the metaconid and protoconid on M_1 and M_2 are higher than the talonid. There is no hypolophid, and the ectolophid is always low and incomplete. The hypoconulid is a large cusp. It is always possible to distinguish M_2 from M_1, because the anterior and posterior widths are equal on M_2. The mesoconid is always well distinguished, but the mesolophid and metalophulid are less distinct. As in P_4, it should be noted that the main cusps are massive, differing from those of *S. chalchae*, which has sharp and high cusps, especially the internal ones. Also, in *S. chalchae* the metaconid is higher than the protoconid; in *B. woodi* the metaconid and protoconid are of equal height. M_3 is longer than M_1 and M_2, and this tooth has the hypoconulid and posterior cingulum united. The mesostylid is situated near the entoconid and on the external side the ectolophid is quite incomplete.

The hypocone on P^4 is little developed in *Birbalomys*, and this tooth is reduced with respect to the upper molars. There is a well developed anterior cingulum that ends at the base of the protocone. When wear is advanced, a protoloph appears, as does a nearly continuous metaloph. In *S. chalchae* the P^4 is triangular. The hypocone and protocone of M^1 are of equal size, but the protocone is a little higher than the hypocone. The anterior cingulum is well developed and on the buccal side it extends slightly below the protocone. The paracone is more developed than the metacone and between them there exists a mesostyle. The metaconule is on the metaloph and it is retained only on unworn teeth. In comparison with *S. chalchae*, the external cusps are lower. The metaconule of M^1 in *S. chalchae* is always well preserved and distinct, situated in the middle of the tooth. The hypocone and protocone of *S. chalchae* are very near to each other and an internal sinus is not well pronounced. The cheek teeth are triangular in *S. chalchae* but square in *B. woodi*. Isolated upper second molars in *Birbalomys* can be distinguished from M^1 because the metacone is less developed on M^2 and a mesostyle is almost always present. The paracone and metacone of M^3 are well separated and the hypocone is poorly developed. Crenulations are present in the basin of the tooth.

Revised diagnoses.—From this comparison it is possible to propose emended diagnoses for both *Birbalomys* and *Saykanomys*.

Emended diagnosis of *Birbalomys* (type species *B. woodi*): brachyodont ctenodactylid; lower jaw massive; reduced P^3; upper teeth with low and strong cusps; hypocone and protocone of same size; protoloph present; P_4 short; mesoconid present in the nearly complete ectolophid; metalophid and hypolophid with a transverse direction.

Emended diagnosis of *Saykanomys* (type species *S. chalchae*): brachyodont ctenodactylid; slender lower jaw; P^4 as large as M^1; cusps of the upper teeth high and sharp with an incomplete protoloph; hypocone smaller than protocone; P_4 very elongated; mesoconid of M_1 and M_2 nearly complete.

Birbalomys and *Saykanomys* are very different. In all the material I have seen from Pakistan or India no tooth can be referred to *Saykanomys* or *Tamquamys*, and biogeographical or

chronological (or both) reasons could be proposed to explain these systematic differences between otherwise similar rodents of Central Asia and Indo-Pakistan.

Proposal to subdivide the genus Birbalomys.—In this paper, at least four species are recognized as valid and referable to the genus *Birbalomys*, and a fifth is doubtful (*B. lavocati*). Material used to describe these species was mainly isolated teeth; only one specimen of *B. woodi* is represented by a jaw and a complete upper dentition. As proposed by Hussain et al. (1978), measurements are the main tool used to segregate the different species, but this is not completely satisfactory. I propose to distinguish two main subgroups of *Birbalomys* at the subgeneric level: one the subgenus *Birbalomys* proper, and the second a new subgenus *Basalomys*, whose species *B. ijlsti* and *B. vandermeuleni* have relatively shorter P_4 and M_3.

Birbalomys (*Birbalomys*)

Diagnosis.—Same as the genus (see above).
Referable species.—*B. woodi*, *B. sondaari.*

Birbalomys (*Birbalomys*) *woodi* Sahni and Khare, 1973

Birbalomys woodi Sahni and Khare, 1973, p. 34–37, Pl. 1: figs. 3–6. Sahni and Srivastava, 1976, p. 922–923, Figs. 1–2, Pl. 1: figs. 1–6. Sahni and Srivastava, 1977, p. 89–90, Pl. 1: figs. 1–8. Dawson, 1977, Pl. 1: figs. 1, 3.
Metkamys blacki (in part), Sahni and Srivastava, 1976, p. 924–925, Figs. 2A–2B, Pl. 1: figs. 8–9. Sahni and Srivastava, 1977, p. 90, Pl. 1: fig. 10.
Chapattimys ibrahimshahi (in part), Hussain et al., 1978, p. 88, Pl. 3: figs. 5–10, Pl. 4: figs. 5–8.

Holotype.—LUVP 15005/1a, left maxilla with P^3–M^3 and both left and right incisors.

Distribution.—Kalakot, Mekta (Jammu and Kashmir); Ganda Kas H-GSP loc. 144 (Punjab); Chorlakki, Shekhan (North-West Frontier Province); Kamroti (Azad Kashmir).

Emended diagnosis.—Large species; metaconule and protoconule apparent on upper teeth; mesostyle present on M^1 and M^2; incomplete metaloph. On lower teeth the entolophid is connected to the ectolophid; crenulations in the talonid basin are very frequent.

Discussion.—Abundant in Kalakot and Mekta among other rodents, this species is represented at Chorlakki by only three specimens. The total amount of material identified at Shekhan and Kamroti is insufficient to give any idea about the relative abundance of *B. woodi.*

Birbalomys (*Birbalomys*) *sondaari* (Hussain et al., 1978)

Pl. 1, figs. 1–6, 8; Pl. 2, figs. 2, 3

Saykanomys sondaari Hussain et al., 1978, p. 86 and 92, Pl. 1: figs. 9–13; Pl. 2: figs. 8–12; Pl. 5: figs. 1–8; Pl. 6: figs. 7–9.

Distribution.—Ganda Kas H-GSP loc. 144 and 57 (Punjab); Chorlakki (North-West Frontier Province).

Emended diagnosis.—Smaller species than *B. woodi*; protoconule is less apparent than in *B. woodi*; mesoconid is included in the ectoloph.

Discussion.—This species is the most abundant rodent in Chorlakki and Ganda Kas localities, where *B. woodi* is rare. On the contrary in Mekta and Kalakot, *B. woodi* is the most abundant form and only a few specimens are tentatively referred to *B. sondaari.*

Birbalomys (Basalomys), new subgenus

Type species.—Birbalomys (*Basalomys*) *ijlsti* (Hussain et al., 1978).

Other referred species.—B. vandermeuleni (Hussain et al., 1978).

Diagnosis.—Primitive ctenodactylid with brachyodont cheek teeth. Cusps of these teeth are as smooth as in other species of *Birbalomys* but differences exist: the ectolophid is incomplete and lacks a mesostylid; the hypoconulid is not well developed on M_3; P_4 is shorter than in other *Birbalomys*; M^3 is reduced anteroposteriorly.

Discussion.—Discovery of more complete lower and upper jaws of *Birbalomys* will probably demonstrate greater diversity in the *Birbalomys* group of Eocene rodents. At present, with only isolated teeth available for most species, *Birbalomys* can be subdivided into two groups: the first group (subgenus *Birbalomys*) has P_4 and M_3 as long as the other cheek teeth; the second group (subgenus *Basalomys*) clearly shows a tendency toward reduction of P_4 and M_3. This tendency is also well expressed in Oligocene ctenodactylids and in other modern forms.

Birbalomys (*Basalomys*) *ijlsti* (Hussain et al., 1978)

Pl. 1, figs. 7, 10, 11, 13; Pl. 2, figs. 8, 10, 11, 13

Saykanomys ijlsti Hussain et al., 1978, p. 81, Pl. 1: figs. 1–4; Pl. 2: figs. 1–3.
Saykanomys chalchae (in part), Hussain et al., 1978, p. 90.
?*Saykanomys lavocati* (in part), Hussain et al., 1978, p. 91.

Distribution.—Shekhan, Chorlakki (North-West Frontier Province); Ganda Kas H-GSP loc. 57 and 144 (Punjab).

Discussion.—Variation is difficult to evaluate in this species; I think that "*S. lavocati*" could be a synonym of *B. ijlsti*, but some specimens are probably referable to *B. vandermeuleni.*

Birbalomys (*Basalomys*) *vandermeuleni* (Hussain et al., 1978)

Pl. 2, figs. 4, 5

Saykanomys vandermeuleni Hussain et al., 1978, p. 84, Pl. 1: figs. 5–8, Pl. 2: figs. 4–7.
Saykanomys lavocati (in part), Hussain et al., 1978, p. 91.

Distribution.—Ganda Kas H-GSP loc. 57 and 144 (Punjab); Chorlakki (North-West Frontier Province).

Chapattimys Hussain et al., 1978

Chapattimys Hussain et al., 1978, p. 87.

Type species.—C. wilsoni

Emended diagnosis.—Brachyodont ctenodactylid with lophodont lower teeth; the M_2 is wider than long. Main cusps are low and lingually and buccally situated; crenulations are frequent.

Chapattimys wilsoni Hussain et al., 1978

Pl. 1, fig. 9

Chapattimys wilsoni Hussain et al., 1978, p. 87, Pl. 3: figs. 1–3, Pl. 4: figs. 1–4.

Distribution.—Ganda Kas, H-GSP loc. 144 (Punjab); Chorlakki, Shekhan (North-West Frontier Province).

Diagnosis.—"The protocone and the hypocone of M^1 and M^2 are sub-equal in size, but the hypocone protrudes further lingually than the protocone. The M^3 is longer than the M^1 or the M^2. The protoloph and metaloph of P^4, M^1 and M^2 converge toward the protocone. The protoconule and the metaconule are present in all M^{1-2}. The lower cheek teeth are relatively wide, as in *Phiomys* Osborn, 1908. M_1 and M_2 have hypoconulids which are of the same size and height as the hypoconid." (Hussain et al., 1978, p. 87).

Discussion.—Some characters mentioned in the original diagnosis of this genus and species are general characters, found in all primitive ctenodactylids. For example, "the hypocone protrudes further lingually than the protocone"—this is true for all dP^4 of ctenodactylids from Eocene to Oligocene. The size of hypoconulid was mentioned, but this characteristic also holds for *Saykanomys*, *Birbalomys*, and *Tamquamys*.

Chapattimys is an important form because of its tendency toward lophodonty and multiplication of crenulations. It is interesting to note that this kind of tooth pattern is found in several different families of rodents (Ischyromyidae, Sciuravidae, Theridomyidae) in middle Eocene times.

Chapattimys debruijni, new species

Pl. 2, fig. 1

Holotype.—GSP-UM 350, a right M_3 from Chorlakki.

Distribution.—Chorlakki (North-West Frontier Province); Mekta (Jammu and Kashmir).

Diagnosis.—Large *Chapattimys*, as large as *B. woodi*, with numerous crenulations in the talonid basin.

Derivatio nominis.—Named for Dr. Hans de Bruijn in appreciation of his work on glirid rodents.

Discussion.—This form is twice the size of *C. wilsoni*, and it is easily identifiable but rare: two specimens are known to date from Chorlakki and three more are known from Mekta.

Gumbatomys, new genus

Type species.—*G. asifi* n. sp.

Diagnosis.—Brachyodont ctenodactylid but with hypsodont tendency. Lower cheek tooth pattern comparable to *Karakoromys* with development of a posterior crest of the protoconid (psuedomesolophid of authors); the anterior part of the tooth has U shaped crests. Posterior part shows ectolophid connected with the middle part of pseudomesolophid. Posterior cingulum is crescentiform.

Derivatio nominis.—Named for the small village of Gumbat where the University of Michigan expedition established its headquarters while working at Chorlakki.

Gumbatomys asifi, new species

Pl. 1, fig. 12; Pl. 2, figs. 7, 9

Holotype.—GSP-UM 277, a right M_3 from Chorlakki.

Referred specimens.—One M_3 (GSP-UM 365), one M^2 (GSP-UM 293), one dP^4 (unnumbered).

Diagnosis.—As for the genus.

Derivatio nominis.—Named for Mr. Asif Jah, geologist of the Geological Survey of Pakistan.

Discussion.—M_3 is compressed anteroposteriorly and is quite as long as it is wide. Similarities to the crown pattern of *Karakoromys* (and *Sayimys*) are striking. A dP^4 and M^2 from the same

locality are tentatively referred to the same species because their size and hypsodonty compare well with the holotype M_3. M^2 occludes well with the anterior part of M_3. M^2 has a central protocone connected to the protoconule. The paracone is weakly joined to the metaconule, which is situated in the middle of the protocone-metacone crest. The hypocone, like that in primitive ctenodactylids, is well developed and more lingual than the protocone. The crown pattern of dP^4 is similar to *B. ijlsti* but with an individualized protoconule and a well developed cingulum. As in M^2 there is a crest joining the protocone, metaconule, and metacone.

Cf. *Petrokoslòvia* sp. indet. 1

Pl. 2, fig. 6

Localities.—Ganda Kas, H-GSP loc. 57 (Punjab); Panoba near Chorlakki (North-West Frontier Province).

Discussion.—One tooth from each locality is referred to cf. *Petrokoslovia*. Shevyreva (1972) described *P. notos* from the middle to upper Eocene locality of Khaitchinsk Oula II (Mongolia), a larger and more advanced species than that represented here. From Aksyr (Kazhakstan), Shevyreva (1976, Pl. 2, fig. 3a) has also illustrated a more primitive form which is probably a P^4 in the opinion of this author. The Pakistan form is morphologically similar to this tooth but the anterior cingulum is not as well developed as it is in the Central Asiatic form. Also the Pakistan form is smaller (length = 1.58, width = 1.95 for specimen from Panoba). There are similarities between these two P^4s and that of *Birbalomys woodi*, and one may presume that a *Petrokoslovia*-like lineage evolved in Indo-Pakistan.

Cf. *Petrokoslovia* sp. indet. 2

Pl. 2, fig. 12

Locality.—Chorlakki (North-West Frontier Province).

Discussion.—A small tooth (probably an M^1) is provisionally referred to *Petrokoslovia*. This second *Petrokoslovia* lineage is more similar to the Central Asiatic forms than that mentioned above.

Order RODENTIA indet.

Hussain et al. (1978, Pl. 4, fig. 10) interpreted a tooth identified as P^4 as an ischyromyid. It seems more likely that this tooth is a P^3, and nothing can be said about its family attribution.

DISCUSSION

Rodents are common faunal elements in the Eocene localities of Pakistan (Table 1). They are diverse at the generic and specific level, but all can be referred to a single family group. If one considers that the study of Eocene localities in Pakistan is only beginning and that extraction of fossils from these localities is difficult, it is remarkable that the richest locality, Chorlakki, has yielded six (maybe eight) different species of rodents. This species diversity is comparable to other contemporaneous localities from Europe or North America. All of the Pakistan Eocene rodents are small forms; the largest known to date represents a rodent weighing no more than 100 g and the most common forms probably weighed between 20 to 50 g. There is no genus or

Table 1—Distribution of Eocene ctenodactylid rodents of Pakistan according to locality.

Genus and species	Ganda Kas H-GSP Loc. 57	Ganda Kas H-GSP Loc. 144	Chorlakki	Panoba	Shekhan	Kamroti
Birbalomys (Birbalomys) woodi		+	?		+	+
Birbalomys (Birbalomys) sondaari	+	+	+			
Birbalomys (Basalomys) vandermeuleni	+	+	?			
Birbalomys (Basalomys) ijlsti	+	+	+		+	
Chapattimys wilsoni		+	+		?	
Chapattimys debruijni			+			
Gumbatomys asifi			+			
cf. *Petrokoslovia* sp. indet. 1	+			+		
cf. *Petrokosolvia* sp. indet. 2			+			

species comparable in size, for example, to *Plesiarctomys*. Forms of this large size have been found in the Eocene of North America and Europe, and in some localities they are common. Further study will be required to determine whether or not this size problem is related to local paleoecological conditions or to some general trend of peninsular faunas.

Biochronology of Pakistan localities.—On paleontological grounds, it is impossible to correlate the Eocene localities of Pakistan based on the rodent record. In Azad Kashmir the record is poor; only a few specimens are known and all of them are referrable to *Birbalomys woodi*, a species first described from Mekta and Kalakot (Jammu-Kashmir) and also recorded in H-GSP locality 144 near Ganda Kas (Punjab). A few specimens from Chorlakki are referred tentatively to *B. woodi*. Samples from other localities are insufficient at present to warrant a more precise comparative biometric study of this species.

All of the species recorded from Ganda Kas are also present at Chorlakki. Thus on present evidence one can assume that all of these localities are nearly contemporaneous. Based on stratigraphic observations, Hussain et al. (1978) think that H-GSP locality 144 is older than H-GSP locality 57. At Chorlakki the sequence is different, but further stratigraphic work may yield a better understanding of the correlation between Chorlakki and the Ganda Kas area (N. Wells, work in progress).

The *Chapattimys* and *Gumbatomys* lineages should provide more information about biochronology when they are better known, but at this time it is impossible to provide sound justification for any biochronological differences between various localities of the Kuldana Formation.

Affinities of primitive Ctenodactylidae. Ctenodactylids, which are first known in Asia, are probably the most primitive family of rodents. They show many similarities with Eurymylidae and with *Heomys orientalis* Li. A study by Dawson et al. (in prep.) considers this relationship in more detail. Individualization of the "*Microparamys* group" was the next important event of early rodent evolution, and a third event was the divergence of Ischyromyidae. *Microparamys* and Ischyromyidae are first known in North America and Europe but differentiation of ctenodactylids is recorded only in Asia. This sequence of radiations is a hypothesis tentatively drawn, based on current knowledge of the fossil record. Major problems remain with correlations between localities in different geographic areas where early rodents have been found. Undoubtedly further research in Central Asia will lead to better correlations and also new discoveries bearing on the early evolution of rodents.

In the middle Eocene, the following families of rodents can be identified on each continent:

North America:	Ischyromyidae
	Microparamys group
	Sciuravidae
	Cylindrodontidae
Europe:	Ischyromyidae
	Microparamys group
	Theridomyidae
	Gliridae
Central Asia:	Ctenodactylidae
Pakistan + India:	Ctenodactylidae
Southeast Asia:	Unknown
Africa:	Unknown

At first glance one might consider that the rodent faunas of Europe and North America are more diverse. Discoveries and systematic studies of early Asiatic rodents are only beginning, and, in fact, the history of Ctenodactylidae and relationships of this family to other families of rodents are not well understood. However, there are as many species of rodents at a locality like Chorlakki as there are in European faunas known from fluvial deposits of the same age.

Tamquamys and "*Microparamys*" *lingchaensis* from the early Eocene of Central Asia have sharp cusps and an unusual P_4, and these forms may be considered as possible ancestors of the *Saykanomys-Advenimus* group of rodents. These primitive forms may also have given rise in Pakistan and India to *Birbalomys* and *Chapattimys*, and tentatively I add *Gumbatomys* to this group. In addition, *Yuomys* and *Petrokoslovia* are distinctive. Thus a total of three groups can be distinguished on morphological and probably biogeographical grounds in the Eocene:

1. "*Microparamys*" *lingchaensis*, *Tamquamys*, *Advenimus*, *Saykanomys* (+ *Terrarboreus* and *Tsinlinomys*)
2. *Birbalomys*, *Chapattimys* (+ *Gumbatomys*?)
3. *Yuomys*, *Petrokoslovia.*

Ctenodactylids show clear similarities to ischyromyids and to the *Microparamys* group of rodents, but possible relationships with other more modern groups like Phiomorpha or Caviomorpha are very speculative and no characteristics clearly support this latter hypothesis. The gap between European *Microparamys* and theridomyids, for example, is probably less pronounced than that between primitive ctenodactylids and phiomorphs or any other modern group of late Eocene age.

Finally, it must be kept in mind that ctenodactylids evolved in Asia in faunas containing primitive Lagomorpha. This was not the case for other families of rodents in other areas before the early Oligocene. Some aspects of the early history of ctenodactylids, their lack of diversity and small body size for example, could be a consequence of their coevolution with lagomorphs.

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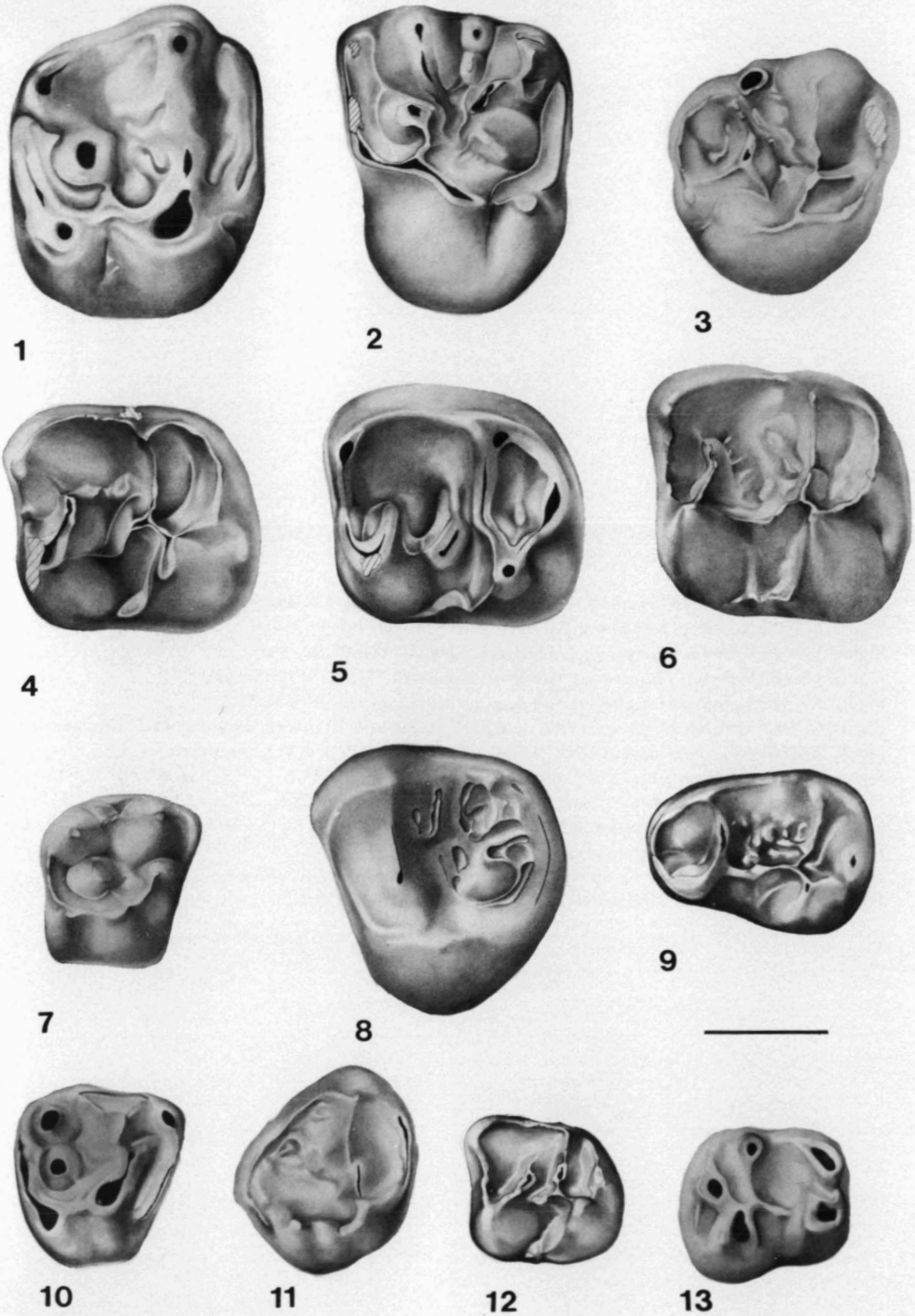
EXPLANATION OF PLATE 1

All drawings in occlusal view. Scale bar = 1 mm.
All specimens from Chorlakki, unless otherwise noted.

Figure 1 — *Birbalomys* (*Birbalomys*) *sondaari*, right M^2 (GSP-UM 361).
Figure 2 — *Birbalomys* (*Birbalomys*) *sondaari*, left M^2 (GSP-UM 360).
Figure 3 — *Birbalomys* (*Birbalomys*) *sondaari*, right M^3 (GSP-UM 363).
Figure 4 — *Birbalomys* (*Birbalomys*) *sondaari*, left M_2 (GSP-UM 354).
Figure 5 — *Birbalomys* (*Birbalomys*) *sondaari*, left M_2 (GSP-UM 353).
Figure 6 — *Birbalomys* (*Birbalomys*) *sondaari*, left M_2 (GSP-UM 398).
Figure 7 — *Birbalomys* (*Basalomys*) *ijlsti*, right dP^4 (GSP-UM 367).
Figure 8 — *Birbalomys* (*Birbalomys*) *sondaari*, left M^3 (GSP-UM 362).
Figure 9 — ?*Chapattimys* cf. *wilsoni*, left P^4 (GSP-UM 180) from Shekhan Nala.
Figure 10 — *Birbalomys* (*Basalomys*) *ijlsti*, left dP_4 (GSP-UM 295).
Figure 11 — *Birbalomys* (*Basalomys*) *ijlsti*, right M^3 (GSP-UM 231).
Figure 12 — *Gumbatomys asifi* n. gen., n. sp., left M_3 (GSP-UM 365).
Figure 13 — *Birbalomys* (*Basalomys*) *ijlsti*, right M_1 (GSP-UM 392).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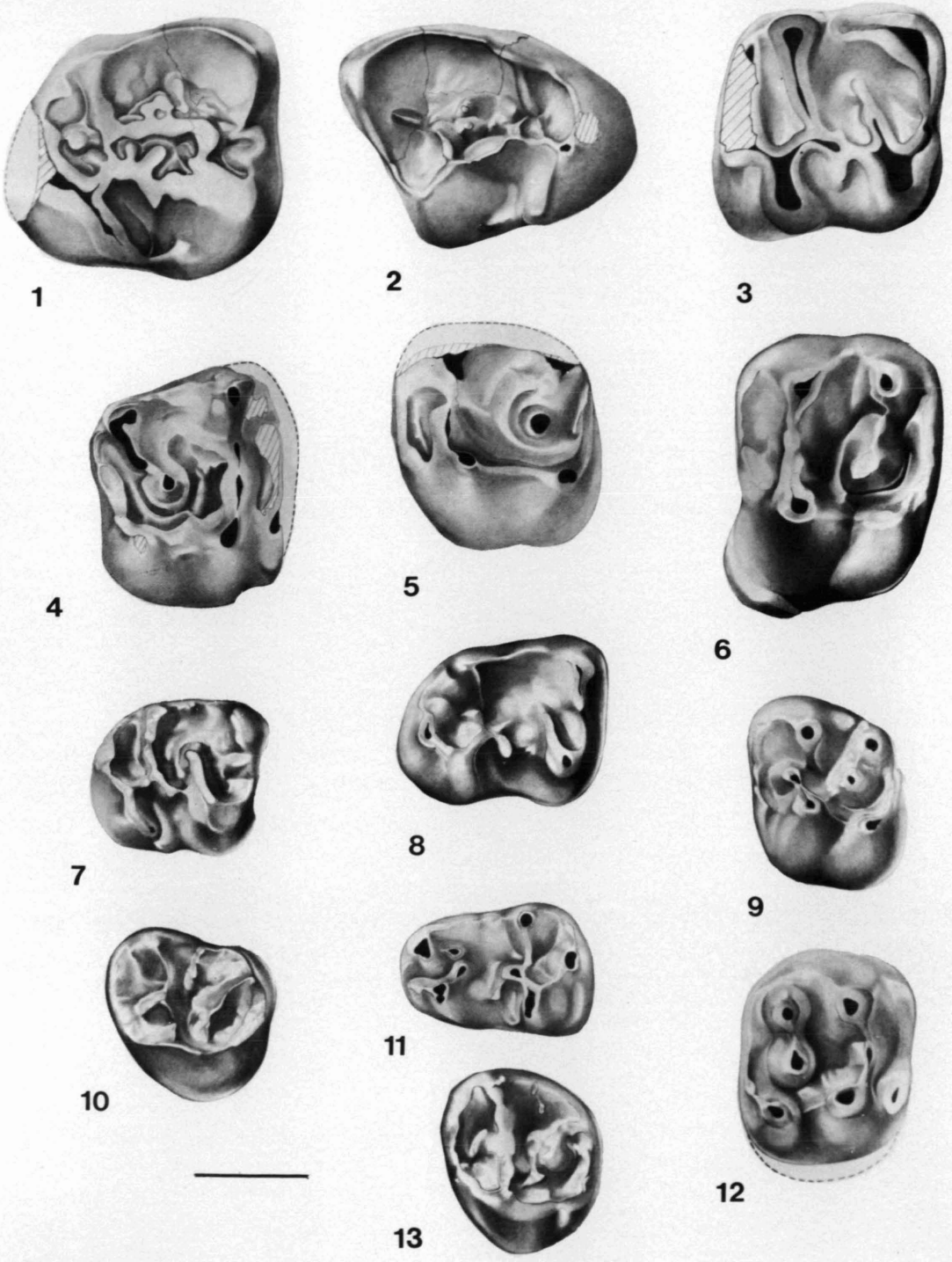
EXPLANATION OF PLATE 2

All drawings in occlusal view. Scale bar = 1 mm.
All specimens from Chorlakki, unless otherwise noted.

Figure 1 — *Chapattimys debruijni* n. sp., right M_3 (GSP-UM 350, holotype).
Figure 2 — *Birbalomys* (*Birbalomys*) *sondaari*, left M_3 (GSP-UM 352).
Figure 3 — *Birbalomys* (*Birbalomys*) *sondaari*, right M_2 (GSP-UM 397).
Figure 4 — *Birbalomys* (*Basalomys*) *vandermeuleni*, right M^2 (GSP-UM 369).
Figure 5 — *Birbalomys* (*Basalomys*) *vandermeuleni*, left M^1 (GSP-UM 370).
Figure 6 — Cf. *Petrokoslovia* sp. indet. 1, left P^4 (GSP-UM 236) from Panoba near Chorlakki.
Figure 7 — *Gumbatomys asifi* n. gen., n. sp., right M_3 (GSP-UM 277, holotype).
Figure 8 — *Birbalomys* (*Basalomys*) *ijlsti*, right M_3 (GSP-UM 183).
Figure 9 — *Gumbatomys asifi* n. gen., n. sp., left M^2 (GSP-UM 293).
Figure 10 — *Birbalomys* (*Basalomys*) *ijlsti*, left M^3 (GSP-UM 231).
Figure 11 — *Birbalomys* (*Basalomys*) *ijlsti*, left dP_4 (GSP-UM 368).
Figure 12 — Cf. *Petrokoslovia* sp. indet. 2, right $?M^1$ (GSP-UM 158).
Figure 13 — *Birbalomys* (*Basalomys*) *ijlsti*, left M^3 (GSP-UM 301).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