

MIDDLE EOCENE RODENTS FROM THE SUBATHU GROUP, NORTHWEST HIMALAYA

by

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ABSTRACT

Extensive collecting in previously known and new Middle Eocene rodent localities in the Subathu Group of the Rajauri and Reasi districts, Jammu and Kashmir (northwest Himalaya, India) has yielded over 500 isolated cheek teeth, numerous incisor and cheek tooth fragments and two mandibular fragments with M/1-M/3. An analysis of this additional material and a restudy of that reported earlier from the Metka (Rajauri) area has revealed the presence of diverse Middle Eocene ctenodactyloid rodents in India. The assemblage comprises six genera and twelve species, viz., *Birbalomys woodi*, *B. ibrahimshahi*, *B. sondaari*, *Basalomys vandermeuleni*, *B. ijlsti*, *B. lavocati*, *Chapattimys wilsoni*, *C. debruijni*, *Gumbatomys asifi*, cf. *Advenimus bohlini*, cf. *Petrokoslovia* sp. indet. 1 and cf. *Petrokoslovia* sp. indet. 2. Most species of this assemblage are endemic to the Indian subcontinent and are referred to the Family Chapattimyidae. However, at least three taxa, viz., cf. *Advenimus bohlini*, cf. *Petrokoslovia* sp. indet. 1 and cf. *Petrokoslovia* sp. indet. 2 show close affinities with their Central and Eastern Asiatic contemporaries and are attributed to the Family Yuomyidae. The dentitions of most of the Middle Eocene rodents from India are described here in better detail thus providing more precise characterization than was available earlier. The taxonomic status of *Basalomys*, formerly a subgenus of *Birbalomys* has been raised to that of a genus. *Basalomys vandermeuleni* is here designated as the type species of *Basalomys* in place of *B. ijlsti*. The rodent assemblage from the Subathu Group is specifically similar to that from the coeval Kuldana Formation of Pakistan. The absence of *Birbalomys ibrahimshahi* and cf. *Advenimus bohlini* in Pakistan is related to sampling bias. The identifications of the Early Eocene rodents from Barbara Banda, Pakistan have been reexamined and the familial assignments of some of the Early and Middle Eocene rodents from Central and Eastern Asia have been discussed and reviewed in the light of recent discovery of early rodents in Mongolia.

INTRODUCTION

The Early-Middle Eocene sediments of India and Pakistan contain one of the earliest records of rodents and thus provide important clues not only for tracing the early evolutionary history of the mammalian Order Rodentia but also for the palaeogeographic reconstructions of the Indian subcontinent during that time. There are a number of localities in the Himalayan regions of India and Pakistan where continental Eocene strata are exposed (Fig. 1). In Pakistan, they are represented by the Mamikhel Clay (basal part of the Chharat Group) and the Kuldana Formation which yield Early and Middle Eocene rodents respectively at several localities (Hussain *et al.* 1978, Hartenberger 1982a, de Bruijn *et al.* 1982). In India, the Early Eocene continental beds equivalent to the Mamikhel Clay have not been sampled yet and are probably absent. However, the Middle Eocene sediments equivalent to the Kuldana Formation are present. They are represented by the Subathu Formation in its type area in Himachal Pradesh (H.P.) and lateral extension in Jammu and Kashmir (J & K) where its status has been raised to that of a 'group' (Singh 1980). The Middle Eocene rodents have been found in both areas but they are much more abundant in J & K localities than in H.P. (Sahni & Khare 1973, Sahni & Srivastava 1976, 1977, Kumar 1982, Loyal 1986, Srivastava 1993, Kumar *et al.* 1994, Kumar *et al.* 1997). This paper deals with the Middle Eocene rodents from the Subathu Group of the Rajauri and Reasi districts, J & K, India.

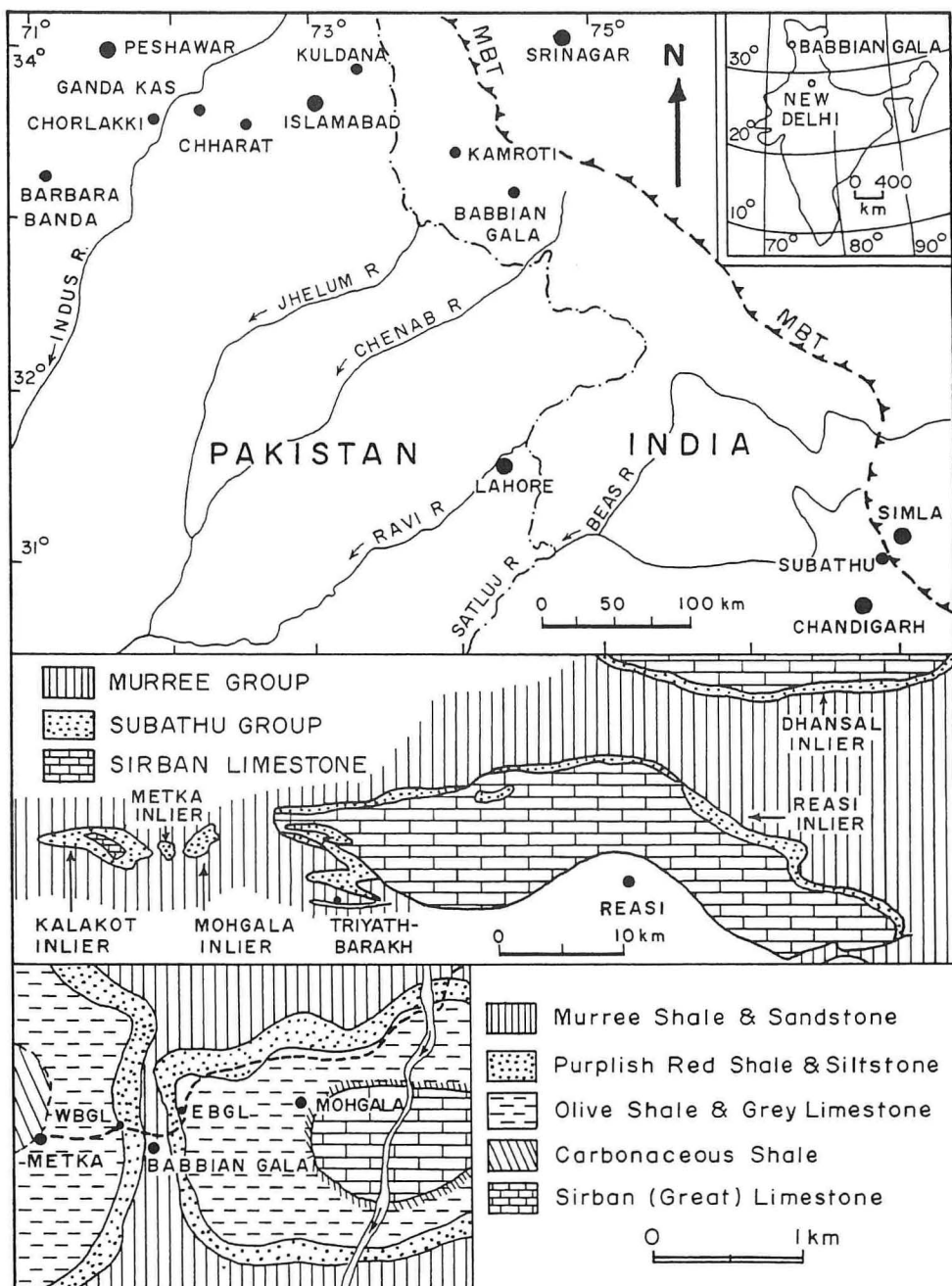


Fig. 1.— Maps showing Eocene rodent localities of the Indian subcontinent, the outcrops of the rodent-yielding Subathu Group in Jammu & Kashmir (J & K), India, and the main rodent locality of East Babbian Gala (EBGL) near Metka, J & K.

In J & K, the Subathu Group is exposed in a series of northwest-southeast trending inliers, viz., Kalakot, Metka, Mohgala (Rajauri District), Reasi (Reasi and Udhampur districts) and Dhansal. This sequence continues northwestwards in Pakistan where the easternmost inliers, situated about 45 km northwest of Kalakot, are known as

Dandili-Devigarh. The rodents have now been recovered from all of these except Dhansal which remains unexplored due to poor accessibility.

For this study, collections were made from six localities, viz., Sindkhatuti, Tattapani, Chenpur (all in the Kalakot Inlier), West Babbian Gala, East Babbian Gala (Metka Inlier) and Triyath-Barakh Road (Reasi Inlier), covering an area of about 50 square km between the latitude 33° 12' 35" N to 33° 15' 0" N and the longitude 74° 20' 40" E to 74° 29' 30" E (Fig. 1). Of these, East Babbian Gala locality (EBGL) is the richest followed by Triyath-Barakh Road (TBRL), Tattapani (TTPL), West Babbian Gala (WBGL), Chenpur (CPL) and Sindkhatuti (SKL). Chenpur is the type locality for the first Eocene rodent from the Indian subcontinent (Sahni & Khare, 1973). Tattapani, WBGL and TBRL are new localities. Sindkhatuti, one of the oldest and the richest locality for the continental Eocene vertebrates in the Indian subcontinent has for the first time produced rodent remains. The rodent-bearing lithologies of Chenpur and Tattapani are somewhat different from those of EBGL and WBGL. In Chenpur, the rodent-yielding rock is sea green claystone and in Tattapani it is purplish-red silty-claystone with occasional clay granules whereas in EBGL and WBGL it is purplish-red granulestone. The rodent horizon at TBRL consists of pale granulestone whereas at Sindkhatuti grey ashy siltstone yields rodents. The rodent remains in these localities are concentrated in under 20 cm thick beds that occur in the uppermost transitional part of the Subathu Group (Fig. 2). Besides rodents they yield other mammalian, reptilian and fish remains (Ranga Rao 1971a, 1971b, 1972, 1973, Ranga Rao & Obergfell 1973, Sahni & Khare 1972, 1973, Khan 1973, Khare 1976, Sahni *et al.* 1978, Kumar 1982, Kumar & Sahni 1985, Kumar & Jolly 1986, Kumar 1991, 1992). They are considered contemporaneous on the basis of contained rodent assemblage, associated vertebrates, sedimentary facies and their relative stratigraphic position in reference to the marker horizons (Srivastava & Kumar, 1996).

BACKGROUND

Sahni & Khare (1973) first recorded Eocene rodents from the Indian subcontinent. They described a nearly complete dentition of *Birbalomys woodi* SHANI & KHARE 1973 from Chenpur near Kalakot, Rajauri District, and assigned it to the Family Paramyidae MILLER & GIDLEY 1918. Later Sahni & Srivastava (1976, 1977) reported several isolated cheek teeth from Metka, about 07 km southeast of Chenpur and referred them to *Metkamys blacki* SHANI & SRIVASTAVA 1976, *B. woodi*, ?*Franimys* WOOD 1962 and ?*Microparamys* WOOD 1962.

Hussain *et al.* (1978) described a number of isolated teeth from the Middle Eocene Kuldana Formation of Kala Chitta and Ganda Kas areas in Pakistan, under a new Family Chapattimyidae and one RP4/ under the Ischyromyidae ALSTON 1876. They synonymized *Birbalomys* SAHNI & KHARE 1973 with *Saykanomys* SHEVYREVA 1972 and reported a diverse assemblage comprising *Saykanomys ijlsti* HUSSAIN *et al.* 1978, *S. vandermeuleni* HUSSAIN *et al.* 1978, *S. lavocati* HUSSAIN *et al.* 1978, *S. sondaari* HUSSAIN *et al.* 1978, *S. chalchae* SHEVYREVA 1972, *Chapattimys ibrahimshahi* HUSSAIN *et al.* 1978, *C. wilsoni* HUSSAIN *et al.* 1978, *Petrokoslovina* SHEVYREVA 1972 sp. and Ischyromyidae gen. et sp. indet. Hartenberger (1982a)

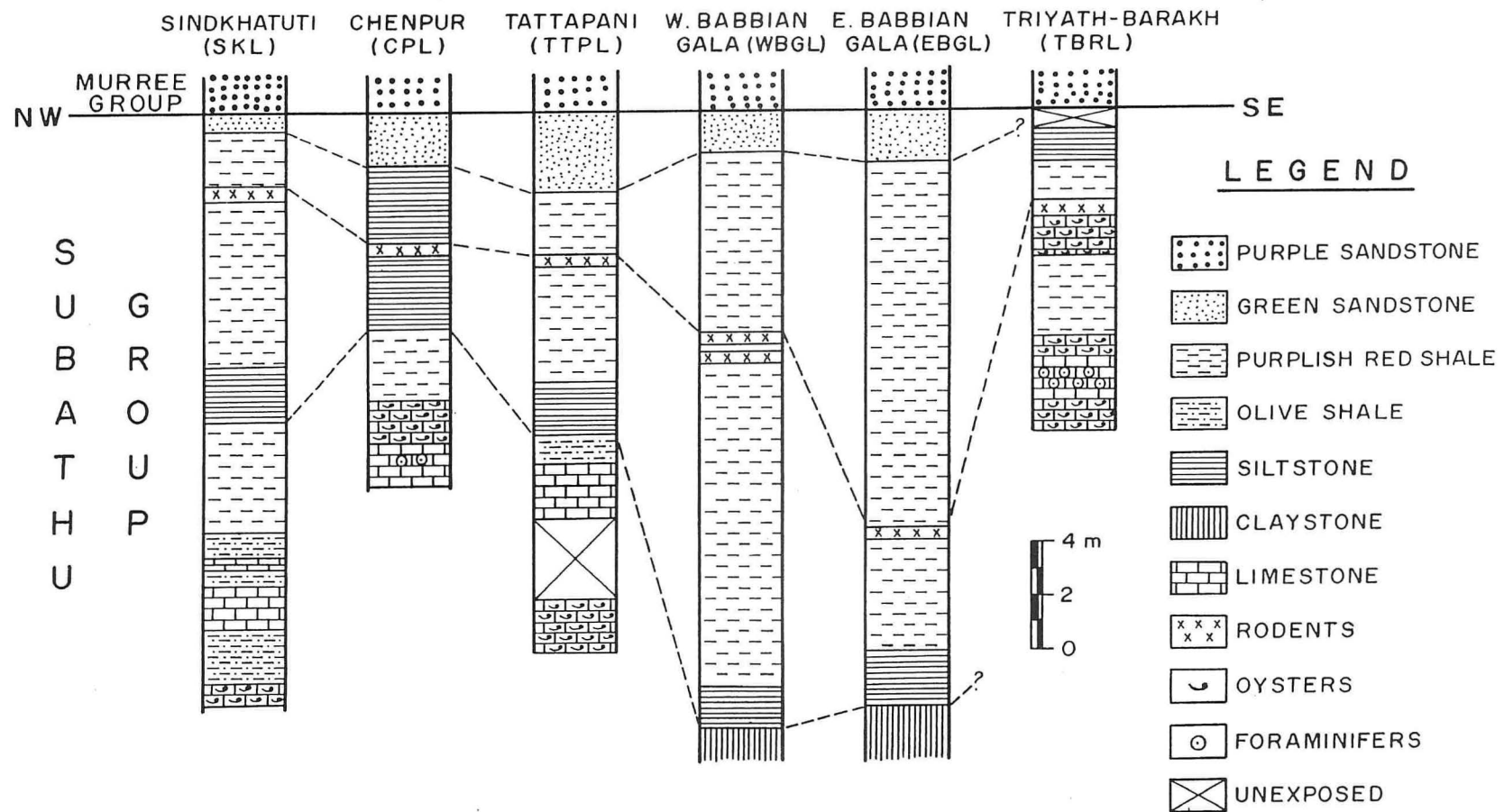


Fig. 2.— Lithologs showing the Middle Eocene rodent-yielding beds in relation to the Subathu-Murree contact, J & K, India.

rejected the synonymy of *Birbalomys* with *Saykanomys* and subdivided the former into the subgenera, *Birbalomys* proper and *Basalomys*. The author synonymized *Metkamys* with *Birbalomys*. Hartenberger (1982a) abandoned the Family Chapattimyidae and included all Indo-Pakistan Eocene rodents in Ctenodactylidae ZITTEL 1893. He opined that *Birbalomys* and *Chapattimys* and possibly also *Gumbatomys* HARTENBERGER 1982 might instead be considered as a subfamilial group, Chapattimyinae. Subsequently, Flynn *et al.* (1986) referred back all Eocene rodents from the Indian subcontinent in the Family Chapattimyidae and argued against reducing its status to that of a subfamily.

This study based on six cranial fragments (including holotype of *B. woodi* described by Sahni & Khare 1973) and numerous unassociated teeth has revealed the presence of a diverse assemblage of the Middle Eocene rodents in India. The assemblage comprises *Birbalomys woodi* SAHNI & KHARE 1973, *B. sondaari* (HUSSAIN *et al.* 1978), *B. ibrahimshahi* (HUSSAIN *et al.* 1978), *Basalomys vandermeuleni* (HUSSAIN *et al.* 1978), *B. ijlsti* (HUSSAIN *et al.* 1978), *B. lavocati* (HUSSAIN *et al.* 1978), cf. *Advenimus bohlini* DAWSON 1964, (= cf. *Saykanomys chalchae*), *Chapattimys wilsoni* HUSSAIN *et al.* 1978, *C. debruijini* HARTENBERGER 1982, *Gumbatomys asifi* HARTENBERGER 1982, cf. *Petrokoslovia* sp. indet. 1 HARTENBERGER 1982 and cf. *Petrokoslovia* sp. indet. 2 HARTENBERGER 1982. All these taxa except cf. *Advenimus* and cf. *Petrokoslovia* are referred to the redefined Indo-Pakistan Family Chapattimyidae HUSSAIN *et al.* 1978 (Ctenodactyloidea). The relative abundance of the Middle Eocene rodent taxa from J & K, India is depicted in figure 3 and their locality-wise distribution is shown in table 1.

The rodent assemblage described herein has provided sufficient and reliable data to correlate different rodent localities of India and Pakistan because the assemblages of the two regions are nearly identical (Srivastava & Kumar, 1996). The absence of *Birbalomys ibrahimshahi* and cf. *Advenimus bohlini* in Pakistan is attributed to sampling bias.

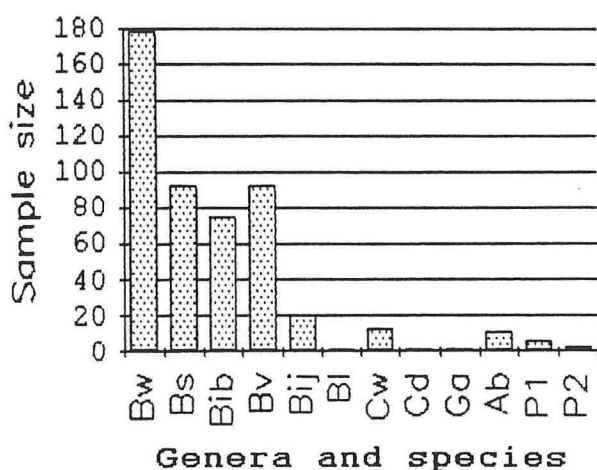


Fig. 3.— Relative abundance of the Middle Eocene rodent species in J & K, India (based on number of teeth).

Abbreviations : Bw, *Birbalomys woodi*; Bs, *B. sondaari*; Bib, *B. ibrahimshahi*; Bv, *Basalomys vandermeuleni*; Bij, *B. ijlsti*; Bl, *B. lavocati*; Cw, *Chapattimys wilsoni*; Cd, *C. debruijini*; Ga, *Gumbatomys asifi*; Ab, *Advenimus bohlini*; P1, *Petrokoslovia* sp. indet.1; P2, *Petrokoslovia* sp. indet.2.

MATERIALS AND METHODS

The rodent material included in this study comprises four mandibular and two maxillary fragments (collectively representing three individuals), over 500 complete isolated teeth, an even number of fragmentary cheek teeth, and numerous incisor fragments. The incisors are too fragmentary to be identified even up to the familial level. However, the micro and ultrastructural studies of their enamel indicate a pauciserial pattern.

A large number of isolated teeth and the two mandibular fragments referred herein were recovered by chipping the rock matrix into tiny pieces using fine chisels, a small hammer and a hand lens/binocular microscope. This technique was fairly productive and also fast, but it was good only for specimens of over 2 mm diameter and the chances of missing the smaller component were too great. Another disadvantage was that a considerable number of teeth broke during extraction and some developed weak planes. To avoid these, over 1000 Kg of rock matrix was disaggregated for fossil recovery by screen washing. For disaggregating the rock matrix of TBRL, EBGL, WBGL, Chenpur, and Tattapani localities, boiling of sample in a detergent, Quaternary 'O' was very effective. The matrix from Sindkhatuti was disaggregated using kerosene-to-water technique. The disaggregated rock matrix was later washed using ASTM sieves of 10, 20, and 30 mesh. These techniques were fairly successful for disaggregation of lithologies of all localities and produced a rich collection but mostly from EBGL. Chenpur, the type locality for *Birbalomys woodi* did not yield any rodent material during this work. WBGL was also not much productive as it yielded only about two dozen incisor fragments from over 100 kg of sample. From Tattapani, a mandibular fragment with M1/-M3/ and several incisor fragments were recovered. TBRL produced over a dozen well preserved cheek teeth and a few incisor pieces and SKL just a solitary molar. The method of measurements and the cusp and loph terminology adapted in this paper are depicted in figure 4, and the measurements for all teeth referred herein are summarized in tables 2 to 9.

REPOSITORY OF THE MATERIAL

The specimens referred in this work, are catalogued and stored in the museum repository of the Wadia Institute of Himalayan Geology, Dehradun (WIMF/A, collection of Dr. K. Kumar), in the Vertebrate Palaeontology Laboratory (VPL/RS) of the Panjab University, Chandigarh, and in collection of the Lucknow University (LUV), Lucknow, India.

ABBREVIATIONS

GSP-UM - Geological Survey of Pakistan - University of Michigan.

H-GSP - Howard University - Geological Survey of Pakistan.

LUV - Lucknow University Vertebrate Palaeontology, Department of Geology, Lucknow, India.

VPL/RS - Vertebrate Palaeontology Laboratory / Rahul Srivastava, Panjab University, Chandigarh, India.

WIMF/A - Wadia Institute Micro Fossil / A series, Wadia Institute of Himalayan Geology, Dehradun, India.

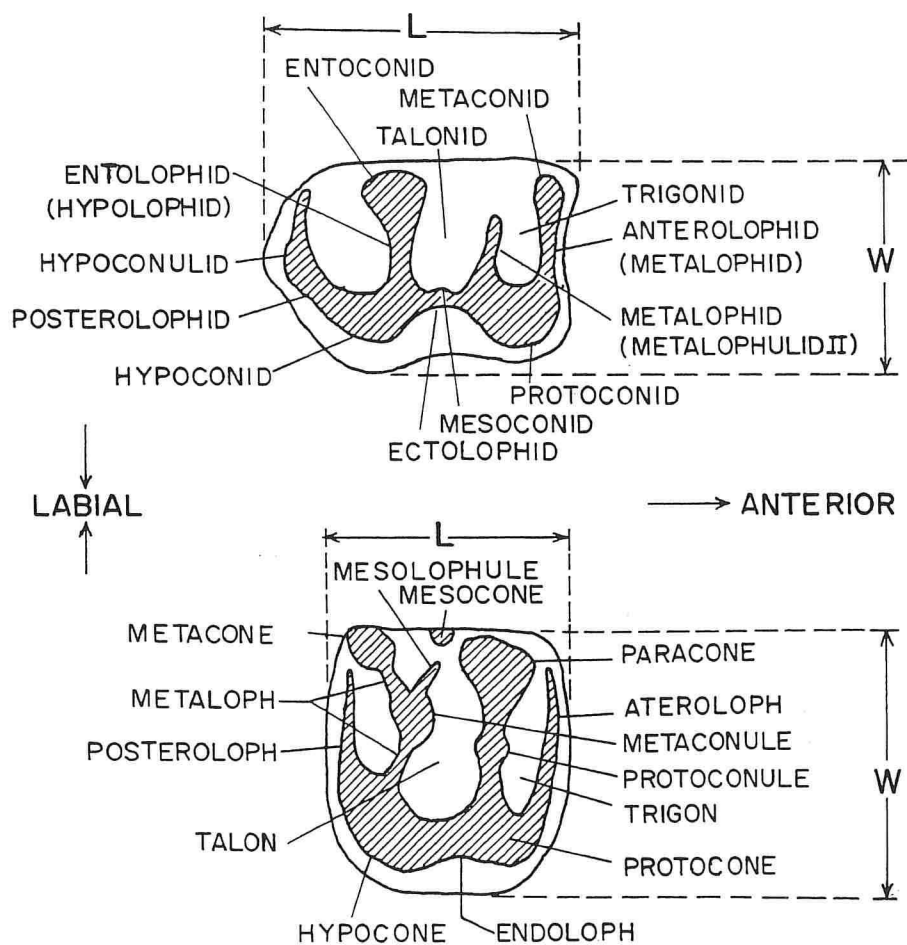


Fig. 4.— Idealized chapattimyid upper and lower molars depicting the dental terminology and method of measurements of teeth.

SYSTEMATIC PALAEONTOLOGY

Order **RODENTIA** BOWDICH, 1821

Suborder **HYSTRICOMORPHA** BRANDT, 1855

Superfamily **CTENODACTYLOIDEA** TULLBERG, 1899

Family **CHAPATTIMYIDAE** HUSSAIN, *et al.* 1978

Emended Diagnosis: Hystricomorphous and sciurognathous; dental formula 1023/1013; premolars large and molariform but smaller than molars; in M1/-M2/ protocone and hypocone subequal; in M3/ hypocone reduced, merged with protocone or absent; protoloph and metaloph converge towards protocone; metaconule and protoconule may be inflated as major cusps, incorporated in a loph, poorly developed or even absent; mesocone present or absent; P/4 generally oval with length up to 20 percent greater than width; P/4-M/2 with strongly developed hypoconulids and entolophids, the latter often reaches the ectolophid; metalophid present; anterolophid low; anteroconid absent in permanent teeth but may be present in deciduous premolars; incisor enamel pauciserial in early (Eocene) and multiserial in later forms.

Comparisons: In Chapattimyidae, P4/4 are smaller than M1/1 and P/4 is oval in comparison to a 'waisted' one (talonid significantly wider than trigonid) in yuomyids (Figs. 5-6, 7E-G). Also the metaconule is more inflated in chapattimyids. Differs from Ctenodactylidae in possessing molariform P4/4 and a P/4 with trigonid narrower than talonid. Differs from Cocomyidae in possessing molariform P4/4 and hystricomorphous skull.

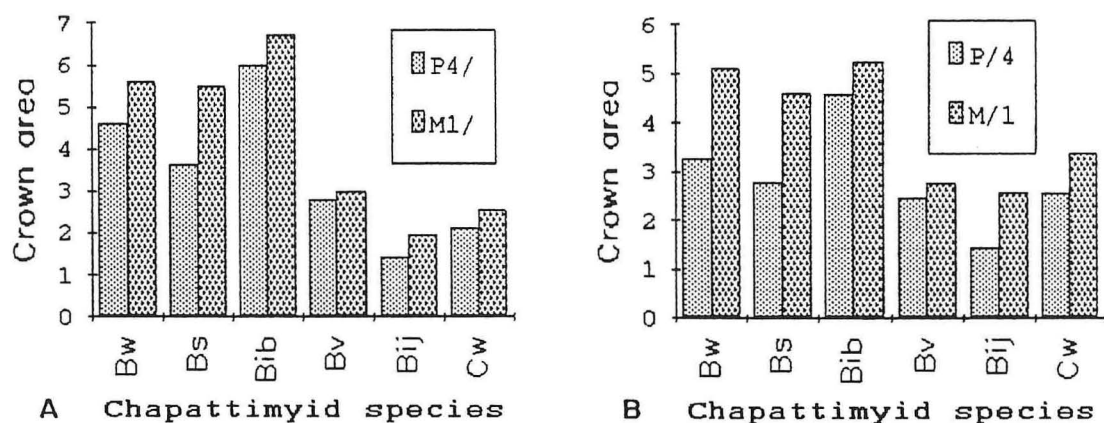


Fig. 5.— Relative size of P4/4 and M1/1 of various chapattimyids as indicated by crown areas (length x width in sq. mm). Abbreviations as in fig. 3.

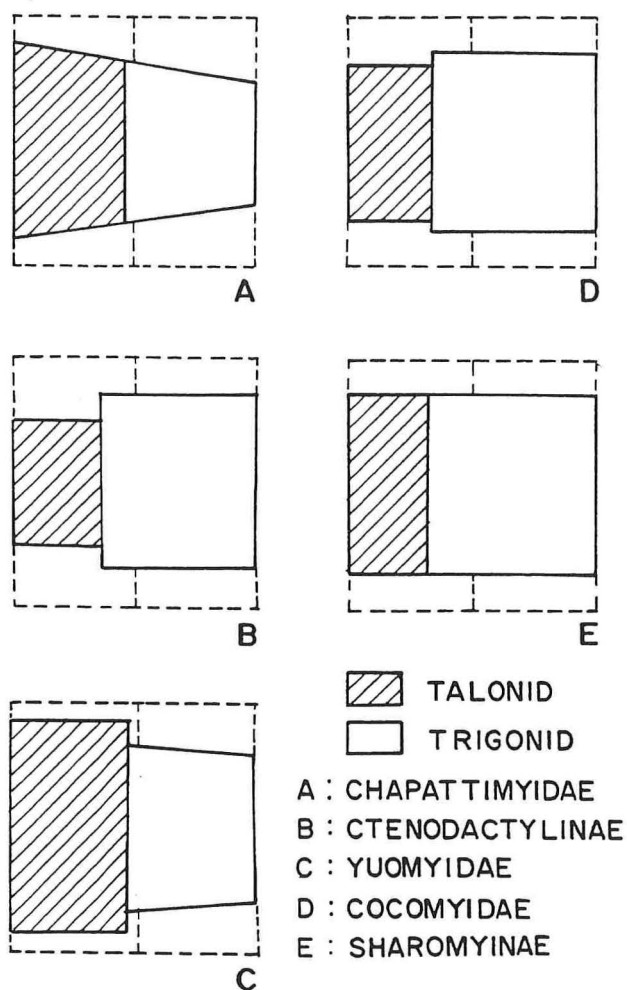


Fig. 6.— Schematic diagrams of fourth lower premolars of the early and Middle Eocene Asiatic rodents showing the relative dimensions of their talonids and trigonids.

BIRBALOMYS SAHNI & KHARE, 1973

Birbalomys SAHNI & KHARE, 1973, p. 34.

Metkamys SAHNI & SRIVASTAVA, 1976, p. 89.

Saykanomys (in part) HUSSAIN *et al.*, 1978, p. 81.

Birbalomys (*Birbalomys*) HARTENBERGER 1982a, p. 25.

Type Species : *Birbalomys woodi* SAHNI & KHARE, 1973.

Emended Diagnosis : Large chapattimyid, brachydont; lower jaw massive; P3/ much reduced; upper teeth with low and strong cusps; protoloph complete; mesocone present in M1/ and M2/; entolophid straight and connected to nearly complete ectolophid. Differs from *Basalomys* in over 30 percent larger size, from *Chapattimys* in narrower and less lophate lower teeth and in much less crenulated tooth basins, and from

Gumbatomys in lacking the posterior crest of protoconid.

***Birbalomys woodi* SAHNI & KHARE, 1973**

(Figs. 7A-D; Plate 1, Figs. 1-9; Table 2)

- *Birbalomys woodi* SAHNI & KHARE 1973, p. 34-37, Pl. 1: figs.3-6; SAHNI & SRIVASTAVA 1976, p. 922-923, figs. 1-2, Pl. 1: figs. 1-6; SAHNI & SRIVASTAVA 1977, p. 89-90, Pl. 1: figs. 1-8; DAWSON 1977, Pl. 1: figs. 1, 3.

- *Metkamys blacki* (in part), SAHNI & SRIVASTAVA 1976, p. 924-925, figs. 2A-2B, Pl. 1: figs. 8-9; SAHNI & 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.

- *Birbalomys* (*Birbalomys*) *woodi* HARTENBERGER 1982a, p. 25.

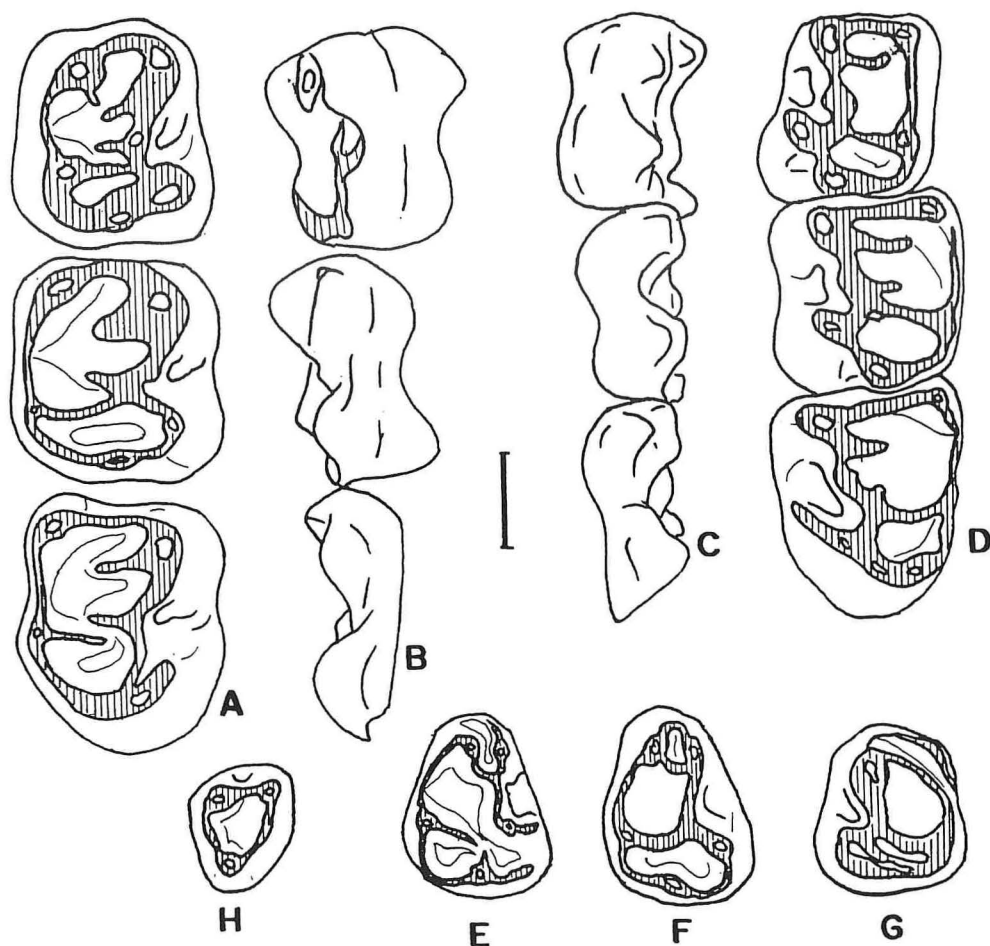


Fig. 7.— *Birbalomys woodi*. (A-B) WIMF/A 1158, right mandible with M/1-M/3 in occlusal and labial views; (C-D) WIMF/A 1159, left mandible with M/1-M/3 in labial and occlusal views; (E-G) P/4s of chapattimyids (E-F, *Birbalomys*) and yuomyids (G, *Petrokoslovia*) depicting differences in dimensions of their talonids and trigonids; (H) VPL/RS 10173, Rodentia indet. P4/. (Scale = 1 mm).

Differential Diagnosis : Smaller than *B. ibrahimshahi* and slightly larger or equal to *B. sondaari*; upper cheek teeth differ from those of other species in position and orientation of protoloph and metaloph; metaloph directed towards protocone, it weakens lingually after joining metaconule; ectolophid strong and complete and joins the protoconid and hypoconid; zygomatic arch anterior to P4/; pterygoid fossa extends posteriorly; angle of the pterygoid crests open.

Holotype : LUVF 15005/1a, left maxilla with P3/-M3/.

Paratypes : LUVF 15005/1b, right mandible with P4-M/3; 15005/1c, left mandible with P4-M/1; 15005/1d, right maxilla with M1-M/3/.

Hypodigm : WIMF/A 1158, right mandible with M1-M/3; WIMF/A 1159, left mandible with M1-M/3; VPL/RS 10131, 10168, 10181, LUVF 20027, WIMF/A 907, 1132, 1134-1135, DP4/; VPL/RS 1013, 10111, 10118, 10189, 10192, 10194, LUVF 17164, WIMF/A 897, 904, 906, 1103, 1123, 1163, 1186, 1252, P4/; VPL/RS 1016, 10123, 10142, 10145, 10152, 10193, 101121, LUVF 16061, 16073, 17023, 17129, 17215, WIMF/A 894, 923, 957, 966, 1107, 1112, 1137, 1224, M1/; VPL/RS 1018, 10110, 10117, 10134, 10150, 10166, 10198, 101111, 101113, LUVF 16008, 17008, 17012, 17025, 17116, 17141, 17154, WIMF/A 851, 881, 892, 895, 915, 955, 967-968, 994, 1105, 1164-1165, 1228-1229, 1248, M2/; VPL/RS 101102, 101107; LUVF 16043, 16069, 17011, 17113, 17176, WIMF/A 856, 870, 926, 953, 965, 1185, 1189, M3/; LUVF 16066, 17175, 20020, WIMF/A 860, 882, 918, 945, DP4/; VPL/RS 10167, 10180, 101106, LUVF 16010, 17006, 17103, 17144, WIMF/A 876, 889, 925, 962, 984, 1203, 1217, 1249, P4/; VPL/RS 10127, 10143, 10147, 10191, 101125, 101130-101131, LUVF 17108, 17131, 17162, 20022, WIMF/A 888, 931, 986, 1101, 1118, 1207, M1/; VPL/RS 1011, 10113, 10174, 10182, 10195, 101108, 101118, LUVF 16011-16012, 16055, 16058, 17020, 17102, 17130, 17172, 17208, WIMF/A 867, 879, 964, 974, 977-979, 981, 1128, 1154-1155, 1162, 1202, 1213-1215, M2/; VPL/RS 10129, 10151, 101124, LUVF 17017-17018, 17152, 17179, WIMF/A 890, 961, 973, 975, 990, 1152, 1254, M3/.

Horizon and Locality : Holotype and paratypes - green claystone, Upper Subathu Group, Chenpur, Rajauri District, J & K; WIMF/A 1158 - purplish-red silty claystone, Tattapani, Rajauri; WIMF/A 1254 - pale granulestone, TBRL, Reasi; all others - maroon granulestone, EBGL, Rajauri.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

Cranium: The holotype skull of *B. woodi* is so badly compressed and deformed that its cranial morphology could not be worked out in detail. Among the important features noted are : zygomatic arch is anterior to P4/, pterygoid fossa extends posteriorly farther behind the M3/, and the angle between the two crests of the pterygoid is quite open. Besides these, the lower jaws are fairly strong and heavy.

Upper Dentition : P3/ - highly reduced (one fourth of P4/) and peg like. DP4/ -

sharp and protruding conical cusps with prominent anteroloph and metaconule; protoconule small but distinct; mesocone distinct in most specimens; hypocone exceedingly lingually shifted and appear as an isolated cusp; metaconule shifted towards metacone in VPL/RS 10168 and closer to protocone in VPL/RS 10131. P4/ - anteroloph, posteroloph, protoloph and metaloph distinct; protoloph and metaloph extend to base of protocone; protoconule and metaconule distinct in unworn teeth; mesocone absent; in VPL/RS 10111 and 10192, hypocone poorly developed. M1/ - metaconule closer to metacone; protoloph straight; metaloph directed towards protocone, it weakens lingually after joining metaconule; posteroloph as high as metaloph, it is indistinct in holotype. M2/ - mesocone distinct; in holotype protoconule and metaconule merged into protoloph and metaloph respectively, separate in others; metaloph strong in holotype, in others strong only between metacone and metaconule; in LUV 17025, metaloph directed towards hypocone. M3/ - paracone prominent, hypocone merged with protocone; in WIMF/A 953 metaloph short and curved; anteroloph, posteroloph and protoloph straight; small parastyle present in LUV 17011.

Lower Dentition : DP4 - metaconid and protoconid closely appressed; anterolophid, metalophid and ectolophid present, the latter bears a small mesoconid; anteroconid absent; hypoconid separated from hypoconulid by a deep valley. P4 - hypoconulid closer to hypoconid than to entoconid; metalophid absent; anterolophid broad in LUV 17144; entolophid weak, extends to ectolophid which is weak in LUV 15005/1b, LUV 16010, and LUV 17144 and absent in VPL/RS 101106; talonid shallower and broader than trigonid. M1 - metaconid and protoconid connected by metalophid and anterolophid; entolophid strong but incomplete except in LUV 17108; ectolophid complete in VPL/RS 10127 but incomplete in LUV 17131; mesoconid weak; talonid deep and wider than trigonid. M2 - squarish with higher anterior cusps and complete entolophid; ectolophid complete in most specimens but incomplete and terminates into a small mesoconid in LUV 17130; metalophid extends to base of metaconid. M3 - posterior cusps reduced; mesoconid prominent; in LUV 15005/1b entoconid smaller and more anteriorly placed, entolophid absent; ectolophid originates from posterolophid and extends to protoconid; metalophid short and straight; talonid and trigonid equally deep, former is broader.

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

(Plate 2, Figs. 1-10; Table 3)

- *Saykanomys sondaari* HUSSAIN *et al.* 1978, p. 86, 92, Pl. 1: figs. 9-13; Pl. 2: figs. 8-12; Pl. 5: figs. 1-8; Pl. 6: figs. 7-9;

- *Birbalomys (Birbalomys) sondaari* HARTENBERGER 1982a, p. 25-26.

Differential Diagnosis : Smaller than *B. ibrahimshahi*, and nearly as large as *B. woodi*; differs from them in anteriorly shifted protoconule, in protoloph which is divided into lingual and labial parts with later terminating posterior to the protoconule,

in incomplete ectolophid that extends labially instead of going towards protoconid, and in posterocentrally placed hypoconulid.

Paratypes : WIMF/A 935, DP4/; 1182, P4/; 1187, M1/; 1188, M2/; 951, M3/; 1198, P/4; 1199, M/1; VPL/RS 1012, M/2.

Hypodigm : WIMF/A 940, 1133, 1239, VPL/RS 101123, DP4/; WIMF/A 861, 865, 921, 993, P4/; VPL/RS 101103, 101120, LUV 17014, 17133, WIMF/A 896, 949, 989, 1136, 1138, 1183, M1/; VPL/RS 10121, 10154, 101114, 101119, LUV 16305, 17028, WIMF/A 971, 991-992, 1125, 1179, 1184, 1220, M2/; WIMF/A 884, 950, 1240, LUV 17197, M3/; WIMF/A 873, DP4/; LUV 17001, 17201, WIMF/A 858, 1194, P/4; VPL/RS 1019, 10125, 10160, 101105, LUV 16030, 17106, 17109, 17126, 17140, 17166, 17180, 17205, WIMF/A 871, 874, 963, 1111, 1153, 1195, 1204, 1212, M/1; VPL/RS 10171, 101116, LUV 16052, 17022, 17148, 17183, WIMF/A 878, 919, 982-983, 985, 1117, 1119, 1130, 1196, 1200, 1205, 1208, 1216, 1247, M/2; WIMF/A 1120, 1197, 1201, 1223, M/3.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

Upper Dentition : DP4/ - low crowned with divergent roots; hypocone lingually shifted; paracone and metacone subequal; protoconule poorly developed and anteriorly shifted; protoloph weak labially; metaloph poorly developed but complete with strong metaconule; mesocone present; anteroloph lower at crown in comparison to posteroloph; talon deep and elongated. P4/ - anteroloph and posteroloph distinct; mesocone small; protoconule poorly developed and anteriorly shifted; parastyle and metastyle absent; metaloph and protoloph short, latter is weak. M1/ - protoloph incomplete; metaloph complete, directed towards protocone; mesocone and parastyle distinct; protoconule projected towards parastyle; metastyle absent. M2/ - metastyle, anteroloph and posteroloph distinct; protoconule poorly developed and anteriorly displaced; in VPL/RS 10121, an accessory loph originates from mesocone and terminates into talon. M3/ - metacone, protocone and hypocone highly reduced; parastyle distinct in WIMF/A 951 but weak in WIMF/A 950; metaconule small but distinct; protoconule indistinct; protoloph straight in most cases, slightly curved in WIMF/A 951; metaloph absent; anteroloph and posteroloph usually straight, latter is curved in WIMF/A 951.

Lower Dentition : DP/4 - anteroconid absent; protoconid and metaconid closely appressed, latter is anteriorly shifted; entoconid large; hypoconulid posterocentral; anterolophid, metalophid and entolophid present, latter is straight; ectolophid originates from between hypoconid and hypoconulid. P/4 - short with characteristically complete metalophid and anterolophid (WIMF/A 858); ectolophid complete, straight and high; it originates from between hypoconid and hypoconulid and joins metalophid near protoconid; entoconid as high as hypoconid; entolophid curved and complete, it joins ectolophid. M/1 - hypoconulid postero-centrally placed; metalophid reaches to base of metaconid, in VPL/RS 1019, LUV 17140 and 17126, it terminates into talonid; entolophid runs straight and deep into labial margin in LUV 17126, in others it

touches ectolophid at base of hypoconid; ectolophid incomplete, extends labially instead of joining protoconid; it is weak in VPL/RS 101105 and LUV 17140 and absent in LUV 17126. M/2 - squarish with incomplete entolophid and ectolophid; in VPL/RS 10171 metalophid complete and very prominent, ectolophid originates from hypoconid and terminates just before protoconid. M/3 - posteriorly reduced; hypoconid and hypoconulid merged in posterolophid; entoconid small but distinct; entolophid strong and complete, joins ectolophid; ectolophid curved with a distinct mesoconid; mesolophid absent; metalophid short; anterolophid indistinct; trigonid incomplete.

***Birbalomys ibrahimshahi* (HUSSAIN *et al.* 1978)**

(Plate 2, Figs. 11-20; Table 4)

- *Birbalomys woodi* (in part), SAHNI & KHARE, 1973

Differential Diagnosis : Larger than *B. woodi* and *B. sondaari* with tendency towards lophodonty; upper teeth possess typical 'V' shaped valley due to characteristic orientation of metaloph and protoleph; angle between metaloph and protocone-hypocone axis less than that in *B. woodi*; protoconule poorly developed. Lower teeth less lophate and less transverse unlike in *B. woodi* and *B. sondaari*; ectolophid incomplete; a strong metalophid gradually weakens and extends into talonid.

Paratypes : WIMF/A 1176, P4/; LUV 17125, M1/; VPL/RS 10164, M2/; WIMF/A 952, M3/; 912, DP4/; 1124, P4/; 980, M1/; 1109, M2/.

Hypodigm : VPL/RS 10196, WIMF/A 908, 1237, DP4/; 866, 885, 1166, 1172, 1236, 1238, P4/; VPL/RS 10161, 101100, LUV 16048-16049, 16074, 17024, 17174, 20024, WIMF/A 886, 928, 937, 1108, 1173, 1225, M1/; VPL/RS 10120, 10126, 10135, 10165, 10188, 101127, LUV 16016, 16022, 16040, WIMF/A 1106, 1116, 1131, 1174-1175, 1219, 1231, 1253, M2/; LUV 17009-17010, WIMF/A 926, 939, 1209, M3/; VPL/RS 10128, WIMF/A 863, 958, 1221, DP4/; VPL/RS 10136, 10149, 10169; WIMF/A 864, 922, P4/; 987, VPL/RS 10114, 10132, LUV 17124, 17160, 20021, M1/; 16060, 17115, 17168, WIMF/A 1121, M2/; 1127, 1226, LUV 17033, M3/.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India.

Description

Upper Dentition : DP4/ - broad with distinct anteroloph and posteroloph; hypocone anterolingually shifted; paracone high; metaconule larger than protoconule; metaloph weak; protoleph incomplete. P4/ - protoconule absent; anteroloph straight; posteroloph complete. M1/ - protoleph straight and complete; mesocone and metastyle absent; hypocone equal to protocone in VPL/RS 10161, smaller in LUV 17125; protoconule very small; metaconule closer to metacone; metaloph makes an acute angle with protocone; anteroloph and protoleph parallel, former terminates into an

indistinct parastyle; posterior cusps tend to become lophate. M2/ - metacone and protoconule poorly developed; mesocone present; metaloph directed towards massive protocone. M3/ - hypocone and metacone indistinct; protoloph straight with a tiny protoconule; metaloph curved and complete with a feeble metaconule; talon crenulated.

Lower Dentition : DP/4 - anteroconid present in 4 out of 5 teeth; protoconid and metaconid closely placed; anterolophid and metalophid present; entolophid sometimes posteriorly directed; ectolophid short. P/4 - anteriorly narrow; lacks anterolophid and mesoconid; hypoconid, entoconid and hypoconulid connected at their bases, last cusp posterocentrally placed; entolophid and ectolophid complete; in VPL/RS 10136 small mesolophid present. M/1 - anterolophid small; metalophid incomplete, directed towards metaconid; entolophid straight and incomplete, directed towards an incomplete ectolophid which terminates into a very small mesoconid; talonid crenulated, shallower and wider than trigonid. M/2 - entoconid smaller; ectolophid incomplete and curved; hypoconid and hypoconulid merged; trigonid indistinct due to poor development of metalophid. M/3 - entoconid small; entolophid well developed and complete; metaconid crested and larger than protoconid; hypoconid and hypoconulid merged, only former distinguishable; metalophid incomplete and straight; anterolophid and ectolophid complete, latter is very prominent; mesoconid well developed with a short mesolophid.

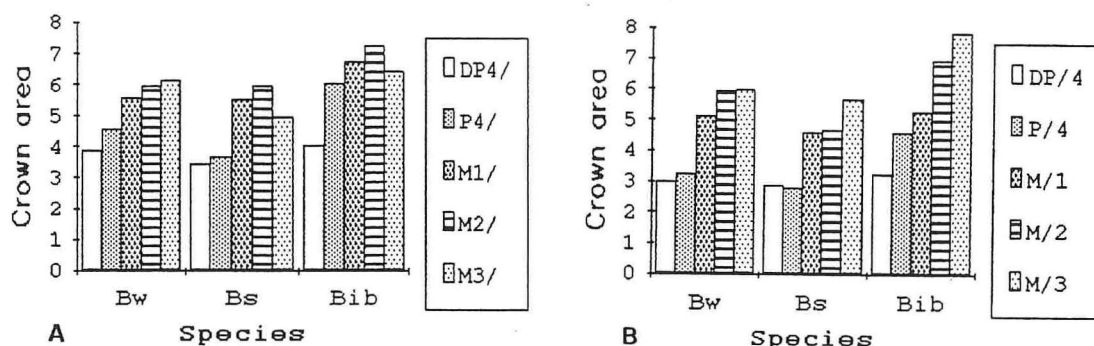


Fig. 8.— Relative size of the upper (A) and lower (B) cheek teeth of various species of *Birbalomys* as indicated by the average crown areas (in sq. mm). Abbreviations as in fig. 3.

Comparisons and Remarks

Among the Middle Eocene ctenodactyls from the Indian subcontinent, *Birbalomys* is the largest and most abundant taxon, and its type species, *B. woodi* is the most common Eocene rodent in J & K (Fig. 3). *B. ibrahimshahi* is the largest species of *Birbalomys* closely followed by *B. woodi* and *B. sondaari* (Fig. 8).

Besides the P3/ that is a part of the holotype of *B. woodi*, there is just one more P3/ (WIMF/A 875) in the collection but it is unassociated and difficult to identify. Its size is, however, the same as that of holotype of *B. woodi*.

DP4/ of *B. ibrahimshahi* differs from that of *B. woodi* in poorly developed protoconule and in lacking lophs. In *B. woodi*, the cusps are sharp and crested but in *B. ibrahimshahi* they are low and massive. The 'V' shaped valley in *B. ibrahimshahi* is sharper and encloses less space as compared to that in *B. woodi*. In *B. sondaari*, a protoconule is poorly developed and anteriorly shifted, protoloph is labially weak and metaloph poorly developed but complete. The posteroloph is better developed in *B. woodi*. In P4/ of *B. sondaari*, a tiny protoconule is displaced towards parastyle; in *B. woodi* it is situated on the protoloph but in *B. ibrahimshahi* it is absent. The hypocone is more lingually placed in *B. sondaari*. A mesocone is distinct only in *B. sondaari*. In *B. woodi*, protoloph and metaloph are complete; in *B. ibrahimshahi*, both are incomplete and in *B. sondaari*, protoloph is incomplete and metaloph is complete. P4/ of *B. sondaari* is less transverse and more elongated.

M1/ and M2/ of *B. ibrahimshahi* possess well developed protoloph and metaloph and poorly developed protoconule and metaconule. The protoconule is small in M1/ of *B. sondaari*, poorly developed in *B. woodi* and absent in *B. ibrahimshahi*. The protoloph and metaloph are complete in *B. woodi* but incomplete in *B. sondaari*. An anteroloph is thick in *B. ibrahimshahi* and thin but complete in *B. woodi*. The posteroloph is better developed in *B. ibrahimshahi* than in *B. woodi*. The holotype M2/ of *B. woodi* possesses a well developed mesocone and a faint protoconule; it lacks metaconule. A mesocone is also present in M1/ of *B. sondaari*. The metaconule is better developed than protoconule in M1/ and M2/ of *B. woodi* and in M1/ of *B. sondaari*. In M2/ of *B. sondaari*, both conules are well developed but protoloph is incomplete and metaloph weakens lingually after joining the metaconule. The anteroloph, in M1/ and M2/ of *B. sondaari*, is much lower at crown than protoloph and metaloph. A parastyle is distinct in M2/ of *B. sondaari* but indistinct in *B. woodi* and *B. ibrahimshahi*.

In M3/ of *B. woodi* and *B. sondaari*, protoconule is missing but in *B. ibrahimshahi*, a very feeble protoconule may be present. In *B. woodi*, the metaloph is short and curved and joins the metacone at the posterior margin, in *B. ibrahimshahi* it is complete and curved with a feeble metaconule, whereas in *B. sondaari* it is incipient or absent but a distinct metaconule exists.

DP/4s of *B. ibrahimshahi* are characterized by a small anteroconid which is missing in *B. woodi* and *B. sondaari*. In *B. sondaari*, a hypoconulid is posterocentrally placed. P/4 of *B. sondaari* and *B. ibrahimshahi* are shorter (average L/W = 1.14) than those of *B. woodi* (average L/W = 1.32). An anterolophid is prominent in *B. sondaari*, indistinct in *B. woodi* and absent in *B. ibrahimshahi*. The metalophid is connected to metaconid in *B. ibrahimshahi*, straight in *B. woodi* and typically curved reaching up to metaconid in *B. sondaari*. In *B. sondaari*, a straight ectolophid terminates between hypoconid and hypoconulid.

M/1 and M/2 of *B. woodi* differ from those of *B. sondaari* and *B. ibrahimshahi* in curved and complete ectolophid, and in the presence of a short but distinct mesolophid. In *B. sondaari*, a straight entolophid joins ectolophid which sometimes

bears a tiny mesoconid. A small mesoconid is also present in *B. ibrahimshahi*. In *B. ibrahimshahi*, a strong metalophid gradually weakens and merges into talonid. The trigonid is shallow and narrow in *B. ibrahimshahi*, deeper in *B. woodi*, and wide in *B. sondaari*. M/3 of *B. woodi* is elongated whereas those of *B. ibrahimshahi* and *B. sondaari* are shorter. The anterior cusps, in *B. ibrahimshahi*, are larger than in *B. woodi*; the posterior cusps are reduced in both, but they are even more so in *B. sondaari*. In *B. sondaari*, hypoconid and hypoconulid are merged in posterolophid and are hardly distinguishable. The entolophid is complete in *B. ibrahimshahi* and *B. sondaari* and incomplete in *B. woodi*. An ectolophid is curved but complete in *B. woodi* and *B. sondaari*. It bears a small mesoconid in *B. ibrahimshahi* and *B. sondaari*. The crenulations are more frequent in *B. ibrahimshahi*. A mesolophid is present only in *B. ibrahimshahi*.

***BASALOMYS* gen. nov. (HARTENBERGER, 1982)**

- *Birbalomys* (in part) SAHNI & SRIVASTAVA 1976, p. 922.
- *Birbalomys* (in part) SAHNI & SRIVASTAVA 1977, p. 89.
- *Birbalomys* (*Basalomys*) HARTENBERGER 1982a, p. 26.

Type Species : *B. vandermeuleni* (HUSSAIN *et al.* 1978)

Diagnosis : Brachydont with tendency towards reduction of P/4 and M/3; over 35 percent smaller than *Birbalomys*. Differs from *Chapattimys* in narrower and less lophate lower teeth with poorly developed entolophid and ectolophid, and from *Gumbatomys* in lacking the posterior crest of protoconid.

***Basalomys vandermeuleni* (HUSSAIN *et al.* 1978)**

(Plate 2, Figs. 21-24; Plate 3, Figs. 1-5; Table 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.
- *Birbalomys* (*Basalomys*) *vandermeuleni* HARTENBERGER 1982a, p. 26.

Differential Diagnosis : Differs from *B. ijlsti* in larger size and in possessing a small mesocone and a straight posteroloph.

Paratypes : WIMF/A 943, DP4/; VPL/RS 101110, P4/; WIMF/A 1168, M1/; 1169,

M2/; 1170, M3/; 1149, P/4; 1148, M/1; 1147, M/2; 1146, M/3.

Hypodigm : WIMF/A 1245, 1257, DP4/; VPL/RS 10141, WIMF/A 909, 917, 1122, 1144, 1167, 1171, P4/; LUVF 17107, 17150, 17196; WIMF/A 869, 1104, 1110, 1190, 1230, 1259, 1271, VPL/RS 10197, M1/; VPL/RS 10122, 10139, 10155, 10158, 10163, 10177, 10183, 10186, 101126, 101128-101129; LUVF 16019; WIMF/A 857, 891, 914, 916, 927, 969-970, 1227, 1250, M2/; VPL/RS 10112, 10162, 10187, LUVF 16017, WIMF/A 920, M3/; VPL/RS 10144, 10156, 10190, 101101, 101115; LUVF 17137, WIMF/A 902, 933, 1115, 1242-1243, P/4; VPL/RS 10124, 10176, 101122, 101132, WIMF/A 868, 877, 932, 944, 946, 960, 988, 1102, 1151, 1232, 1234, M/1; VPL/RS 10146, 10153, LUVF 16041, WIMF/A 853, 1222, M/2; 910, 941, VPL/RS 10130, 10148, 10175, LUVF 16037, M/3.

Horizon and Locality : WIMF/A 1257, 1259 - pale granulestone, Upper Subathu Group, TBRL, Reasi, J & K; WIMF/A 1271 - ash grey siltstone, SKL, Rajauri; all others - maroon granulestone, EBGL.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

Upper Dentition : DP4/ - differs from P4/ in better developed anteroloph, more lingually shifted hypocone, divergent roots, and in lacking a metaloph. P4/ - metaloph complete and curved and directed towards protocone; protoloph straight, joined with protocone; metaconule closer to protocone; protoconule absent. M1/-M2/ - protoconule poorly developed or absent; metaloph generally incomplete, absent in LUVF 17107; anteroloph straight; in M2/ anteroloph lower at crown and parallel to protoloph; metaloph directed towards protocone; posteroloph well developed; endoloph present in VPL/RS 10155. M1/ differs from M2/ in more lingually shifted hypocone and in lacking a mesocone. M3/ - most specimens considerably worn with merged hypocone and protocone and highly reduced metacone; metaloph poorly developed or absent; protoloph complete and straight; metaconule prominent but completely worn in some specimens; protoconule absent; anteroloph and posteroloph poorly developed, posteroloph absent in VPL/RS 10112; trigon frequently crenulated.

Lower Dentition : P/4 - entolophid straight and incomplete, it terminates in front of hypoconulid; ectolophid absent in VPL/RS 10156 and LUVF 17137 but present in VPL/RS 10144; hypoconulid and entoconid as large as hypoconid; anterolophid present in some specimens; metalophid absent. M/1 - metalophid and entolophid straight; ectolophid either interrupted by a small mesoconid or absent; mesoconid, if present, shifted labially (WIMF/A 868); hypoconulid large and posterocentrally placed. M/2 - in VPL/RS 10153 hypoconulid and hypoconid connected with each other but separated from entoconid; straight entolophid joins ectolophid. M/3 - metaconid larger than protoconid; in VPL/RS 10148, all posterior cusps merged, in others at least entoconid differentiable; ectolophid curved, terminates on posterolabial side of protoconid, it is absent in VPL/RS 10148; metalophid straight and incomplete; trigonid narrow and deep in all M/3's but absent in VPL/RS 10148; VPL/RS 10130 more elongated with very well developed mesoconid.

***Basalomys ijlsti* (HUSSAIN *et al.* 1978)**

(Plate 3, Figs. 6-13; Table 6)

- *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.
- *Birbalomys (Basalomys) ijlsti* HARTENBERGER 1982a, p. 26.

Differential Diagnosis : Over 25 percent smaller than *B. vandermeuleni*. Upper teeth lack mesocone and possess an arcuate posteroloph.

Paratypes : WIMF/A 1177, DP4/; 852, M1/; 1258, M2/; 954, M3/; 1241, P/4; 938, M/2; 901, M/3.

Hypodigm: WIMF/A 1260, DP4/; 1251, M1/; 913, 1178, M2/; 880, M3/; 1255, DP/4; 1261, P/4; 859, 872, 899, 942, M/2; 1139-1140, M/3.

Horizon and Locality : WIMF/A 1255, 1258, 1260-1261 - pale granulestone, Upper Subathu Group, TBRL, Reasi; all others - maroon granulestone, EBGL, Rajauri.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

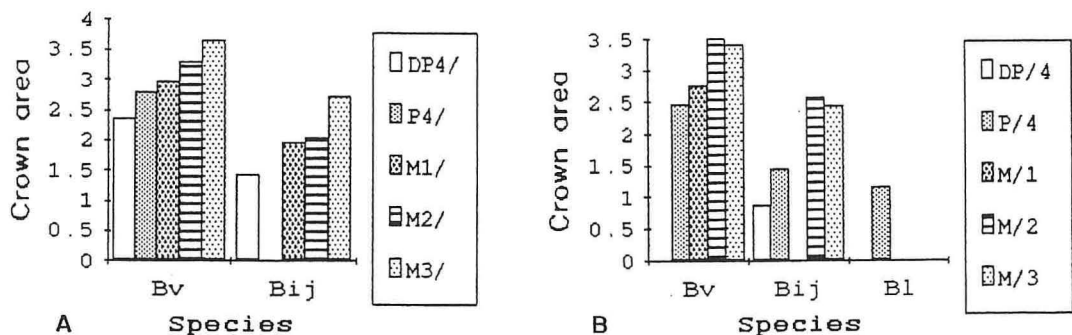


Fig. 9.— Relative size of the upper (A) and lower (B) cheek teeth of various species of *Basalomys* as indicated by the average crown areas (in sq. mm). Abbreviations as in fig. 3.

Description

Upper Dentition : DP4/ - WIMF/A 1260's reference to *B. ijlsti* is tentative and based on size as its posteroloph is partly broken and it has a small mesocone. Protocone high and massive; protoloph complete and strong; protoconule completely merged with protoloph or absent; metaloph strong but not connected to protocone; metaconule large, nearly merged with metacone along metaloph; anteroloph and posteroloph distinct with

partly broken wide shelves; hypocone broken. RM1/ - WIMF/A 852 is very similar to '*S. ijlsti*' specimen from locality H-GSP 144 in Pakistan (Hussain *et al.*, 1978, Plate 2, Fig. 2) but differs in lacking mesocone. Protoloph complete, metaloph incomplete and poorly developed; protoconule absent, metaconule and posteroloph well developed; anteroloph straight, posteroloph arcuate. M/2 - differs from M/1 in squarish outline, lower anteroloph and posteroloph and in hypocone which is connected to protocone; WIMF/A 913 is heavily worn with distinct metaloph bearing a small metaconule. M3/ - at least 20 percent larger than M2/; in WIMF/A 954, only paracone well developed, hypocone not differentiable; protoloph distinct, lacks protoconule; metaloph and metaconule rudimentary. WIMF/A 880 is much heavily worn with indiscernible conules and lophs.

Lower Dentition : DP/4 - WIMF/A 1255 is elongated with large anteriorly protruded metaconid; hypoconid massive; protoconid, entoconid and hypoconulid equally developed; hypoconulid somewhat transverse, posterocentrally placed and separated from entoconid by a valley; ectolophid nearly complete with a labially shifted mesoconid; anterolophid absent; posterolophid indistinct except behind hypoconid; entolophid indistinct; trigonid narrow and deep; talonid wide and shallow. P/4 - in WIMF/A 1241 cusps high and crested; posterior cusps placed in triangular fashion and equally high; hypoconulid centrally placed; short and weak entolophid terminates into talonid before hypoconulid; ectolophid straight and lacks a mesoconid; mesolophid absent; anterolophid complete; metalophid strong, curved and complete, trigonid and talonid well developed and deep. M/2 - ectolophid and entolophid complete, latter is curved; metalophid straight but incomplete; anterolophid present; ectolophid with a small labially shifted mesoconid; metaconid highest cusp; hypoconulid and hypoconid connected with each other. M/3 - hypoconulid absent or merged with hypoconid; metalophid strong and complete; entolophid complete and straight in WIMF/A 901 but short and slightly posteriorly directed in WIMF/A 1139; anterolophid and mesoconid present; ectolophid well developed, short in WIMF/A 1139.

***Basalomys lavocati* (HUSSAIN *et al.* 1978)**

(Plate 3, Fig. 14)

- ?*Saykanomys lavocati* (in part), HUSSAIN *et al.* 1978, p. 91.

Differential Diagnosis : P/4 differs from those of *B. ijlsti* and *B. vandermeuleni* in being anteroposteriorly shorter, in lacking an entolophid and in possessing an indistinct hypoconulid which is incorporated in posterolophid.

Paratype : WIMF/A 1113, P/4.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

P/4 is anteroposteriorly short (length, 1.15 mm; width, 1mm) with indistinct hypoconulid incorporated in posterolophid; entoconid strong but smaller than hypoconid; hypoconid separated from posterolophid and shifted posterolabially; entolophid absent; ectolophid straight and complete; mesoconid absent; metalophid directed towards metaconid which is larger than protoconid; anterolophid absent; trigonid deep and narrow; talonid deep and wide. The tooth is very similar with the P/4 described as '*Saykanomys lavocati*' from Pakistan by Hussain *et al.* (1978, Plate 5, Fig. 4) but it is slightly smaller.

Comparisons and Remarks

Basalomys differs from *Birbalomys* in at least 35 percent smaller size, and in an ectolophid which is incomplete and terminates into a small mesoconid. In M1/ and M2/ of *Basalomys*, metaloph and protoconule are either absent or very poorly developed. P/4 and M/3 of *Basalomys* are anteroposteriorly short which suggests that it is more derived than *Birbalomys*.

Basalomys ijlsti is over 25 percent smaller than *B. vandermeuleni*. *B. lavocati* is presently known only by a P/4 which is as small as DP4/ of *B. ijlsti* (Fig. 9). The upper cheek teeth of *B. vandermeuleni* possess a straight and broad posteroloph in comparison to an arcuate one in *B. ijlsti*. In *B. vandermeuleni*, a small mesocone is present between paracone and metacone; it is absent in *B. ijlsti*. In M3/ of *B. vandermeuleni*, protoloph and anteroloph are stronger and a small protoconule is also present; it is absent in *B. ijlsti*. P/4 of *B. ijlsti* has a complete entolophid and a distinct ectolophid; in *B. vandermeuleni* entolophid is incomplete and ectolophid is present in just one specimen. In *B. lavocati*, entolophid is absent but ectolophid is straight and complete. P/4 of *B. lavocati* is anteroposteriorly shorter than those of *B. ijlsti* and *B. vandermeuleni*. DP/4 of *B. vandermeuleni* and M/1 of *B. ijlsti* are not available for comparison. M/2 of *B. vandermeuleni* possesses protruding cusps, a straight entolophid and a weak ectolophid. In comparison to this, M/2 of *B. ijlsti* possesses smaller and heavy cusps and a curved entolophid. M/3s of *B. ijlsti* and *B. vandermeuleni* are comparable in size but that of former has a crenulated talonid. The metalophid is complete in *B. ijlsti* and incomplete in *B. vandermeuleni*.

Basalomys was earlier reported as a subgenus of *Birbalomys* by Hartenberger (1982a). However, in view of its fair abundance and common presence in India and Pakistan, its status is raised here to that of a genus. Hartenberger (1982a) designated *Basalomys ijlsti* as the type species of *Basalomys* but according to Article 30 of the 'International Code' a type species should be of common occurrence besides being a morphological representative of the group with known geographic and geologic ranges and an established taxonomic relationship. These conditions are better fulfilled by *B. vandermeuleni* which is much more abundant, being represented in India by about hundred specimens, whereas *B. ijlsti* is known by just twenty. Hence *B. vandermeuleni* is designated here as the type species of *Basalomys* in place of *B. ijlsti*.

CHAPATTIMYS HUSSAIN *et al.*, 1978

- *Chapattimys* HUSSAIN *et al.* 1978, p. 87

- *Chapattimys* HARTENBERGER 1982a, p. 26

Type Species : *Chapattimys wilsoni* HUSSAIN *et al.*, 1978.

Emended Diagnosis : Brachydont chapattimyid with irregularly crested lophodont and wider lower cheek teeth; M/2 slightly wider than long; M/3 with a peculiar arrangement of entolophid, ectolophid and metalophid; M3/ longer than anterior molars; protoconule and metaconule invariably present in M1/-M2/.

***Chapattimys wilsoni* HUSSAIN *et al.* 1978**

(Plate 3, Figs. 15-20; Table 7)

Chapattimys wilsoni HUSSAIN *et al.* 1978, p. 87, Pl. 3 : figs.1-3; Pl. 4 : figs. 1-4; HARTENBERGER 1982a, p. 26-27.

Differential Diagnosis : Over 30 percent smaller than *C. debruijini*. Metalophid curved and complete; ectolophid also complete; in M/3 metalophid posteriorly directed and connected to an anteriorly directed entolophid.

Paratypes : WIMF/A 911, P/4; 1180, M/2; 936, M/3.

Hypodigm : WIMF/A 1191, P/4; 1156, 1246, M1/; 1157, M2/; 855, 1206, 1244, P/4; LUVF 17173, M/2; WIMF/A 1114, 1277, M/3.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

Upper Dentition : P4/ - transverse with massive protocone, very small hypocone and well developed metaconule; protoloph complete; metaloph incomplete; protoconule indistinct; mesocone absent; posteroloph arcuate; anteroloph straight. WIMF/A 1191 is very similar to *C. wilsoni* P4/ described by Hussain *et al.* (1978, Plate 4, Fig. 1) from Pakistan. M1/-M2/ - high crowned with subequal protocone and hypocone and well developed metaconule and protoconule; protoloph and metaloph complete; labial half of protoloph posteriorly directed; mesocone present; anteroloph and posteroloph well developed. M2/ (WIMF/A 1157) is identical with *C. wilsoni* M2/ from locality 144 in Pakistan (Hussain *et al.*, 1978, Plate 4, Fig. 2). It is characterized by extension of labial part of protoloph into the middle of the tooth basin.

Lower Dentition : P/4 - ectolophid and entolophid straight and connected, latter is weak; anterolophid, posterolophid and mesoconid absent; hypoconulid equal to

hypoconid in WIMF/A 855 but smaller in WIMF/A 911; metalophid extends to base of metaconid in WIMF/A 911, it is indistinct in WIMF/A 855; trigonid higher at crown than talonid. M/2 - metaconid higher than protoconid; hypoconid and hypoconulid reduced, join to form posterolophid; hypoconulid very small in WIMF/A 1180; entolophid straight, strong and complete; ectolophid strong, sometimes labially directed with a strong mesoconid; metalophid complete and straight, slightly curved in WIMF/A 1180; trigonid deep but narrower than talonid; anterolophid present. M/3 - metaconid largest cusp; metalophid posteriorly directed and connected with a curved, crescentric and anteriorly directed entolophid; entoconid extremely reduced or absent; ectolophid complete but not straight; hypoconid and hypoconulid merged into posterolophid.

***Chapattimys debruijini* HARTENBERGER, 1982**
(Plate 3, Fig. 21)

- *Chapattimys debruijini* HARTENBERGER 1982a, p. 27, Pl. 2: fig. 1

Emended Diagnosis : Over 30 percent larger than *C. wilsoni*. Talonid frequently crenulated.

Paratype : WIMF/A 1126, M/3.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description

M/3 - 2.4 mm long and 2 mm wide; slightly reduced posteriorly with well developed lophs and frequent crenulations in basins that are deep and lower at crown; protoconid and metaconid equally high; anterolophid poorly developed; metalophid well developed, terminates at base of metaconid; hypoconid and hypoconulid distinct with their apices incorporated in posterolophid; entoconid better differentiated with complete and prominent entolophid terminating at a distinct mesoconid; mesolophid prominent; ectolophid curved and complete; an additional lophid originates from metalophid and joins mesolophid thus dividing the talonid into a wide and somewhat shallower lingual and a narrow and deep labial parts; trigonid as deep as talonid and well developed.

Comparisons and Remarks

Chapattimys differs from *Birbalomys*, *Basalomys* and *Advenimus* in more lophate lower teeth with irregular crests in basins. *C. wilsoni* is over 30 percent smaller than *C. debruijini* (Fig. 10). It also differs from the latter in poorly developed entoconid, posteriorly directed metalophid and larger metaconid. M/3 of *Chapattimys* is easily

recognisable because of a peculiar arrangement of entolophid, metalophid and ectolophid. Prior to this work, there was no report of *Chapattimys* from India. *Chapattimys* shows lophodont tendency which is a derived feature.

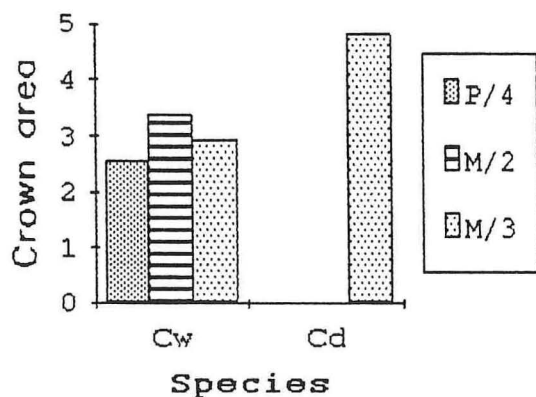


Fig. 10.— Relative size of the two species of *Chapattimys* as indicated by the average crown areas (in sq. mm) of their lower cheek teeth. Abbreviations as in fig. 3.

GUMBATOMYS HARTENBERGER, 1982

- *Gumbatomys* HARTENBERGER 1982a, p. 27

Type species : *Gumbatomys asifi* HARTENBERGER 1982

Emended Diagnosis : Brachydont teeth with hypsodont tendency. Lower cheek tooth pattern comparable to *Karakoromys* with development of a posterior crest of the protoconid (=pseudomesolophid). Anterior part of lower cheek tooth has U-shaped crests; posterior part shows ectolophid more lingually placed and connected with the middle part of pseudomesolophid. Talonid interrupted.

Gumbatomys asifi HARTENBERGER, 1982

(Plate 3, Fig. 22)

- *Gumbatomys asifi* HARTENBERGER 1982, P. 27, Pl. 1: fig. 12; Pl. 2: figs. 7, 9.

Hypodigm : WIMF/A 1233, M/3.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India and Pakistan.

Description and Remarks

M/3 is 2.1 mm long and 1.8 mm wide; hypoconid and hypoconulid closely placed and connected; entoconid placed more lingually; metalophid curved and complete; a posterior lophid (?pseudomesolophid of Hartenberger 1982a) originates from protoconid and joins entolophid; entolophid strong and complete, joins ectolophid as well as pseudomesolophid; ectolophid also strong and complete; additional conulids and lophulids present labial to ectolophid; trigonid deep and transverse; talonid interrupted. *Gumbatomys* is so far recognized only by its last lower molars which are distinct from those of all other Middle Eocene rodent species. A second upper molar and a deciduous premolar were tentatively referred to *G. asifi* by Hartenberger (1982a). Owing to the scanty material the genus remains poorly characterized.

Family **YUOMYIDAE** DAWSON *et al.* 1984

cf. *Advenimus bohlini* DAWSON 1964

(Plate 3, Figs. 23-28; Table 8)

Hypodigm : WIMF/A 1141, M1/; 1142, 1161, 1192, M2/; 1143, 1193, M3/; 854, 959, 1150, P/4; 947, M/2; 887, M/3.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India.

Description

Upper Dentition : M1/-M2/ - squarish with low and subequal cusps and shallow basins; metaloph and protoloph converge on protocone; metaloph weak lingually; metaconule better differentiated than protoconule; shelf between anteroloph and protoloph anteriorly prolonged; mesocone absent. M3/ - mesocone present; metaconule very prominent; protoloph complete; metaloph indistinct.

Lower Dentition : P/4 - metalophid and ectolophid incomplete; mesoconid indistinct; entolophid directed towards hypoconulid; entoconid and metaconid closer as compared to hypoconid and protoconid. M/2 - hypoconid closer to protoconid as compared to entoconid and metaconid; entolophid runs transversely and then turns to join hypoconulid; anterolophid and trigonid poorly developed. M/3 - hypoconid and hypoconulid merged together; entolophid short and posteriorly directed; an additional cuspid present between entoconid and metaconid; tiny mesoconid apparent.

Comparisons and Remarks

Cf. *Advenimus bohlini* is smaller than all species of *Birbalomys* but it is comparable with *Basalomys*. As in *Basalomys*, the lower teeth of cf. *A. bohlini* also possess an incomplete ectolophid. In *Basalomys*, a small mesoconid is always present

but in cf. *A. bohlini*, it is apparent only in M/3. Cf. *A. bohlini* differs from *Birbalomys*, *Basalomys*, *Chapattimys* and *Petrokoslovia* in entolophid which is directed towards hypoconulid instead of hypoconid. The upper molars of cf. *A. bohlini* are squarish with a prolonged shelf between protoloph and anteroloph. Its M3/ possesses a very prominent metaconule which lies on a faint metaloph. WIMF/A 1211, a RM/3 from EBGL shows all characters of cf. *A. bohlini* but it is twice as large.

cf. *Petrokoslovia* sp. indet. 1 HARTENBERGER, 1982
(Plate 3, Figs. 29-32; Table 9)

- Cf. *Petrokoslovia* sp. indet. 1 HARTENBERGER 1982a, p. 28, Pl. 2: fig. 6.

Hypodigm : WIMF/A 883, 1279, P4/; 1235, M1/; 1210, M2/; 1181, 1218, P/4.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian) of northwest India and Pakistan.

Description

Upper Dentition : P4/ - protoloph straight with indistinct protoconule; incomplete metaloph terminates at metaconule; anteroloph well developed and lower at crown; WIMF/A 883 is very similar to GSP-UM 236 from Panoba, Pakistan (Hartenberger, 1982a; Plate 2, Fig. 6). M1/ - WIMF/A 1235 is high crowned and more transverse; anteroloph absent; posteroloph well developed; paracone located slightly lingually; mesocone and endoloph present; protoloph straight and more anteriorly placed with a weak lingual half; protoconule and metaloph absent; metaconule large; talon deep and narrow. M2/ (WIMF/A 1210) - squarish with a weak endoloph, feeble protoconule, incomplete metaloph, and strong and complete anteroloph and posteroloph.

Lower Dentition : P/4 - WIMF/A 1218 has high and crested anterior and reduced posterior cusps; hypoconulid and anterolophid absent; hypoconid and entoconid small; posterolophid strong; entolophid strong and complete; it joins strong and complete ectolophid; metalophid small, curved and complete; talonid deep and wide.

cf. *Petrokoslovia* sp. indet. 2 HARTENBERGER, 1982
(Fig. 7G; Plate 3, Figs. 33-35)

- Cf. *Petrokoslovia* sp. indet. 2 HARTENBERGER 1982a, p. 28, Pl. 2: fig. 12.

Hypodigm : VPL/RS 101109, P4/; 10133, M2/; 10199, P/4.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri

District, J & K.

Age and Distribution : Middle Eocene (Lutetian) of northwest India and Pakistan.

Description

Upper Dentition : P4/ - 1.3 mm long and 1.7 mm wide; transverse and lophate with low noncrested protocone, indistinct hypocone, and small but distinct paracone and metacone; protoconule and metaconule absent; protoloph, metaloph and endoloph present; anteroloph as well developed as in *Petrokoslovia notos* SHEVYREVA 1972 but lower at crown. M2/ - 1.3 mm long and 1.5 mm wide; lophate but less transverse with very strong metacone, low anteroloph and small mesocone; hypocone and posteroloph form a ridge; VPL/RS 10133 similar to cf. *Petrokoslovia* sp. indet. 2 from Chorlakkhi, Pakistan (Hartenberger, 1982a; Plate 2, Fig. 12).

Lower Dentition : P/4 - 1.7 mm long and 1.6 mm wide; very similar to corresponding teeth of *P. notos* and *Petrokoslovia* sp. from Pakistan (Hussain *et al.* 1978, Plate 3, Fig. 11) but slightly smaller; VPL/RS 10199 is high crowned with narrow valley between entolophid and posterolophid; hypoconulid and metaconid indistinct; entolophid and ectolophid straight but incomplete; metalophid absent; crenulations common.

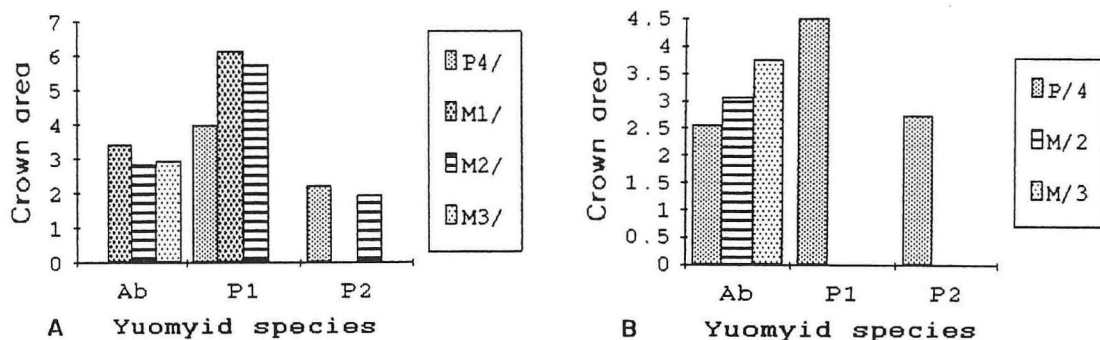


Fig. 11.— Relative size of the upper (A) and lower (B) cheek teeth of yuomyids from J & K India as indicated by their average crown areas (in sq mm). Abbreviations as in fig. 3.

Comparisons and Remarks

Cf. *Petrokoslovia* sp. indet. 1 is larger than *Basalomys*, *Chapattimys*, cf. *Advenimus* and cf. *Petrokoslovia* sp. indet. 2, but smaller than *Birbalomys* (Fig. 11). It differs from cf. *Petrokoslovia* sp. indet. 2. in possessing a protoconule, a distinct hypocone, an incomplete protoloph and a P4/ with larger cusps. Its P4/ differs from other species in being transverse and in possessing a straight protoloph, large metaconule and incomplete metaloph which terminates at metaconule.

Cf. *Petrokoslovia* sp. indet 2 is lophodont, much smaller than *Birbalomys* and cf. *Petrokoslovia* sp. indet. 1. Its size is comparable with *Basalomys vandermeuleni*. P/4 of cf. *Petrokoslovia* sp. indet. 2 is very similar to that of *Petrokoslovia* sp. described

from Pakistan by Hussain *et al.* (1978; Plate 3, Fig. 11) and also to that of *P. notos* but it is smaller than both. The general morphology of cf. *Petrokoslovia*. sp. indet. 1 and 2 is similar to *B. woodi* but the difference in size is diagnostic (Hartenberger, 1982a). The smaller size of cf. *Petrokoslovia*. sp. indet. 1 and 2 is a derived character.

RODENTIA indet.

(Fig. 7H; Plate 3, Fig. 36)

Hypodigm : VPL/RS 10173, LP4/.

Horizon and Locality : Maroon granulestone, Upper Subathu Group, EBGL, Rajauri District, J & K.

Age and Distribution : Middle Eocene (Lutetian), northwest India.

Description and Remarks

P4/ - triangular, high-crowned and considerably worn with wide and shallow tooth basin, paracone, protocone and metacone distinguishable, paracone highest cusp; hypocone indistinct; anteroloph and posteroloph absent. The tooth is smaller (1.1 mm long and 1.2 mm wide) and morphologically distinct from all other teeth from India and Pakistan. It can not be a P3/ as it has no resemblance with P3/ of *B. woodi* which is peg like.

DISCUSSION

Familial status of Indo-Pakistan Middle Eocene rodents :

The Eocene rodents from India were first referred to the Family Paramyidae (Ischyromyoidea) and later included in Chapattimyidae (Ctenodactyloidea) with closely similar coeval taxa from Pakistan (Sahni & Khare 1973, Sahni & Srivastava 1976, 1977, Hussain *et al.* 1978). Similarly, Eocene rodents from Kazakhstan, China and Inner Mongolia were originally referred to Paramyidae and Sciuravidae MILLER & GIDLEY 1918 (Li 1963, 1975, Dawson 1964, Shevyreva 1971, 1972, 1976). Later on Wood (1977) transferred all Eocene rodents from the Central and East Asia to the Family Ctenodactylidae (Ctenodactyloidea) but did not comment on those from the Indian subcontinent. Following Wood's (1977) proposition, Hartenberger (1982a) included all Indo-Pakistan Eocene rodents as primitive forms in Ctenodactylidae.

Dawson *et al.* (1984) noted that Indo-Pakistan ctenodactyls are distinct and that among their Central and East Asian contemporaries, *Advenimus* DAWSON 1964 and *Saykanomys* are closest to them. The authors stated that in Eocene rodents, the

morphological variations and lines of divergence are so remarkable that their inclusion in the single Family Ctenodactylidae is not fitting. They grouped the Central and East Asian Eocene ctenodactyls in two new families, Cocomyidae and Yuomyidae. Following this, Flynn *et al.* (1986) redefined Chapattimyidae with all known Eocene rodents from India and Pakistan. However, the authors excluded Cocomyidae from Ctenodactyloidea. Despite such frequent reshuffles in the familial status of Indo-Pakistan rodents, problems have persisted and inadequacy of data has been the main reason for this uncertainty. However, since the work of Hartenberger (1982a) and Dawson *et al.* (1984), more complete materials have been found and substantial new data gathered. This prompted us to review the familial assignments of Indo-Pakistan and certain Central and East Asiatic Eocene rodents (Table 10).

Presently three families, viz., Ctenodactylidae, Yuomyidae and Chapattimyidae are included in the superfamily Ctenodactyloidea. Ctenodactylidae, as diagnosed before Wood (1977), is characterized by hystricomorphous skull, sciurognathous jaw, and nonmolarised or submolarised premolars with talonid shorter and significantly narrower than trigonid (Fig. 6). Yuomyidae and Chapattimyidae are also hystricomorphous and sciurognathous but their premolars are distinctly molarised as in the Middle Eocene rodents of the Indian subcontinent.

Unfortunately, most Indo-Pakistan rodents are represented by unassociated dentitions and cranium is known only for *Birbalomys*. As such there is no way to ascertain if they were hystricomorphous. However, on the basis of hystricomorphy in *Birbalomys* and the allied taxa from Central Asia, viz., *Advenimus*, the same has been inferred for the whole assemblage.

The Indo-Pakistan ctenodactyls can not be grouped in the Family Ctenodactylidae because of remarkable dissimilarities in their premolar structure, and in this respect they are closer to yuomyids and chapattimyids. The diagnostic characters of Yuomyidae and Chapattimyidae are nearly identical, but as also demonstrated by Hartenberger (1982a) and Dawson *et al.* (1984), the similarities are mainly in the primitive characters and the two are distinct otherwise. Chapattimyids differ from yuomyids in P4/4 which is smaller or subequal to M1/1, P/4 oval (in yuomyids it is waisted, i.e., talonid is significantly wider than trigonid), inflated metaconule, complete metaloph etc. A comparative analysis of diagnostic dental characters indicates that most of the Indo-Pakistan rodent genera are endemic to the region and favours their attribution to the Family Chapattimyidae. At least three taxa, viz., cf. *Advenimus bohlini*, cf. *Petrokoslovia* sp. indet. 1 and cf. *Petrokoslovia* sp. indet. 2 show close affinities with the Central Asiatic forms and are, therefore, classified in the Family Yuomyidae. *Birbalomys*, *Basalomys*, *Chapattimys* and *Gumbatomys* are referred to Chapattimyidae whose diagnosis has been emended in this work after Hussain *et al.* (1978) and Flynn *et al.* (1986).

Flynn *et al.*'s (1986) report of Miocene chapattimyids (Subfamily Baluchimyinae) from Pakistan has further focussed on evolution in the South Asian rodents from Eocene to Miocene. The authors have convincingly demonstrated through a cladogram that the Eocene chapattimyines were ancestral to the Miocene baluchimyines. This has endorsed the validity of the Family Chapattimyidae and supports the attribution of the Middle Eocene rodents from India and Pakistan to this endemic family.

Comments on Eocene rodents from Pakistan :

Except for the absence of *Birbalomys ibrahimshahi* and cf. *Advenimus bohlini*, the Middle Eocene rodent assemblage from Pakistan is identical with that reported in this paper. In view of the specific similarities in the rodent assemblages of India and Pakistan, the absence of certain species in Pakistan may be logically attributed to sampling bias. In abundance and diversity of rodent taxa, the East Babbian Gala locality of J & K, India is closely comparable with Chorlakki in Pakistan. Hartenberger (1982a) opined that the P4/ described by Hussain *et al.* (1978, Plate 4, Fig. 10) as *Ischyromyidae* indet. should be referred to *Rodentia* indet. P3/. Although little can be said about the familial status of this tooth, it certainly looks more like a P4/.

De Bruijn *et al.* (1982) described three isolated cheek teeth from the Early Eocene Mamikhel Clay (basal part of the Chharat Group) of Barbara Banda, Kohat. Of these, one (LP4/, de Bruijn *et al.* 1982, Fig. 3) was referred to the *Cocomyidae* as genus A and species I, the other (RM1-2/, Fig. 4) to species II of the same genus and the third one (RP/4, Fig. 6) to the *Paramyidae*, genus and species indeterminate.

De Bruijn *et al.*'s (1982) identification of LP4/ as a *cocomyid* was logical but Flynn *et al.*'s (1986) review of *ctenodactylids* and recent reports of new Early Eocene rodents from Mongolia by Dashzeveg (1990b) necessitate its reexamination. The tooth in question is nonmolarised as its lingual and buccal aspects possess single cusps. In this respect, it differs from P4/'s of all known *ctenodactylids* and *Cocomys* DAWSON *et al.* 1984, and resembles that of *Alagomys inopinatus* DASHZEVEG 1990b (*Alagomyidae*), from the Lower Eocene of Mongolia (Dashzeveg 1990b). The P4/ of *A. inopinatus* is, however, at least 50 percent smaller. Besides this, it is bunodont and lacks lophs; its lingual and buccal cusps are separated from each other by a valley. In comparison to this, the P4/ from Pakistan is lophodont with distinct protoloph and metaloph, and a trigon which is higher than anteroloph and posteroloph. These features suggest that the P4/ from Pakistan is more derived. The antiquity of *A. inopinatus* is also evident from its upper molars which are triangular and lack hypocones. The P4/ of *Cocomys* is submolariform and not nonmolariform as it lacks just one of the buccal cusps and in this feature the LP4/ from Pakistan is more primitive than *Cocomys*. It is thus apparent that the LP4/ from Pakistan belongs to a taxon intermediate between *Alagomys* DASHZEVEG 1990b and *Cocomys*.

The RM1-2/, described by de Bruijn *et al.* (1982, Fig. 4) as *cocomyid* genus A and species II, is distinctly lophodont. It can not be associated with the LP4/ (genus A, species I) from the same locality as the latter is too robust (de Bruijn *et al.* 1982). Besides being robust, the LP4/ (length, 0.82 mm; width, 1.4 mm) is also about 7 percent wider than RM1-2/ (length, 1.17 mm; width, 1.3 mm). This corroborates the view that the two belong to different species. Although the available evidence is insufficient to ascertain if the two species are congeneric, the lophodont nature of both teeth support this possibility. de Bruijn *et al.* (1982) inferred that since RM1-2/ shows *ctenodactylid* characteristics it must have had nonmolariform P4/4. However, this may not necessarily be correct as the *ctenodactylids* described in this paper invariably possess molarised premolars.

RP/4 described by de Bruijn *et al.* (1982, Fig. 6) as a *paramyid* possesses a well developed entoconid, a distinct hypoconid, and an incipient hypoconulid. The peaks of

all the posterior cusps are connected by a transverse ridge which make it look molariform. de Bruijn *et al.* (1982) referred this tooth to Ischyromyoida on the basis of absence of metalophid and hypoconulid. It may be mentioned here that hypoconulid and metalophid are also indistinct in certain teeth referred in this paper. It is possible that the so called ischyromyoid tooth is deciduous as also indicated by its shape and increasingly brachydont nature. Dashzeveg (1990a) compared it with the corresponding tooth of *Tsagamys subitus* from the Lower Eocene Naran-Bulak Formation of Mongolia and opined that it belongs to Ctenodactyloidea.

Flynn *et al.* (1986) included all the Early Eocene rodent material (LP4/, RM1-2/ and RP/4) described by de Bruijn *et al.* (1982) from Pakistan in the Family Chapattimyidae. However, their reference of LP4/ (cocomyid genus A, species I of de Bruijn *et al.* 1982, Fig. 3), in particular, to the Chapattimyidae is mistaken. The available evidence is grossly insufficient to determine the familial status of this tooth and since it does not resemble the corresponding tooth of *Cocomys* and no other characters are known, it can not be retained in Cocomyidae either. Therefore, until the additional evidences are forthcoming it would be appropriate to refer it as Rodentia indet. Regarding the familial status of RM1-2/ (de Bruijn *et al.* 1982, Fig. 4), little can be said as it shows the diagnostic characters of all ctenodactyloid families and since no additional clues are available it is best to refer this tooth as Ctenodactyloidea indet. Likewise, the RP/4 described by de Bruijn *et al.* (1982, Fig. 6) as a paramyid and referred by Flynn *et al.* (1986) to Chapattimyidae should also be regarded as Ctenodactyloidea indet. as suggested by Dashzeveg (1990a). Thus the familial relationships of the Early Eocene rodents from Pakistan (de Bruijn *et al.* 1982) are unclear, but they do appear to be more primitive than *Cocomys* and are perhaps intermediate between alagomyids-orogomyids and the cocomyids.

Comments on Central and Eastern Asiatic Eocene rodents :

Dawson *et al.* (1984) classified the Eocene ctenodactyloids of Kazakhstan, China and Inner Mongolia in two new families, the Cocomyidae (with *Cocomys*, *Tamquammys* SHEVYREVA 1971 and *Tsinlingomys* LI 1963) and Yuomyidae (with *Yuomys* LI 1975, *Advenimus* and *Petrokoslovia*). On the basis of shorter and significantly narrower P/4 talonids in *Tamquammys* and *Tsinlingomys*, Flynn *et al.* (1986) preferred to classify these genera in the Ctenodactylidae. Further, the authors removed *Cocomys* from the Ctenodactyloidea because of its protrogomorphous skull. Flynn *et al.* (1986) suggested that Cocomyidae could alternatively be treated as a monotypic family under the Ctenodactyloidea. In view of the fact that hystricomorphy/protrogomorphy are superfamilial characters, the exclusion of *Cocomys* from Ctenodactyloidea and the transfer of *Tamquammys* and *Tsinlingomys* in Ctenodactylidae are supported here.

Seemingly unaware of Flynn *et al.*'s (1986) work Dashzeveg (1990a) divided the Cocomyidae into two subfamilies, Cocomyinae and Advenimurinae and referred several new Early Eocene rodents from Mongolia to the Cocomyinae. The author differentiated these subfamilies on the basis of buno-brachydonty of molars and the premolar structure which he showed molariform in Advenimurinae and nonmolariform (sometimes with molarised P/4) in Cocomyinae. The former subfamily was diagnosed

by brachydont molars with bunodont cusps, and the latter by slightly higher and lophodont teeth. Dashzeveg (1990a) also transferred *Advenimus* to Advenimurinae and synonymized *Saykanomys* with *Advenimus*. This study supports synonymy of *Saykanomys* with *Advenimus* and that of *Saykanomys chalchae* with *Advenimus bohlini* DAWSON 1964. However, the subdivision of the Family Cocomyidae by Dashzeveg (1990a) is unwarranted and so is the attribution of *Advenimus* to the Advenimurinae under the Family Cocomyidae. Since hystricomorphy/protrogomorphy are the superfamilial characters, it is illogical and inconvenient to club forms with these characters in a single family. Slight hypsodonty and lophodonty in molars, the main diagnostic characters of Advenimurinae, are inadequate to differentiate the new subfamily. Besides this, most advenimurine characters, viz., hystricomorphous skull and molariform P4/4 etc., are closer to Yuomyidae and not to Cocomyidae as has been assumed by Dashzeveg (1990a). The subdivision of Cocomyidae and reference of *Advenimus* etc. to Advenimurinae are, therefore, not supported here. In the present state of knowledge, *Advenimus* is best placed in the Yuomyidae. Among other genera referred to the Advenimurinae by Dashzeveg (1990a), *Boromys* DASHZEVEG 1990a and *Chkhikvadzomys* SHEVYREVA 1984 can easily be accommodated in the Yuomyidae and *Tsinlingomys* has already been assigned to the Ctenodactylidae by Flynn *et al.* (1986). Hence, the subfamily Advenimurinae is abandoned here and its contents are referred to the Family Yuomyidae.

Dashzeveg (1990a) described new rodents, *Sharomys singularis*, *S. parvus*, *Kharomys mirandus*, *K. gracilis*, *Tsagamys subitus* and *Ulanomys mirificus* from the Lower Eocene Bumban Member of the Naran-Bulak Formation of Mongolia and classified them under the subfamily Cocomyinae (Cocomyidae). Most of these taxa are characterized by a large hystricomorph type of infraorbital foramen. This implies that they possessed at least an incipiently hystricomorphous skull. Besides this, their P4/4's are submolariform and can not be described nonmolariform as has been done by Dashzeveg (1990a). This is because in P4's of most taxa only one of the labial or lingual cusps (i.e., metacone or hypocone) is missing or is rudimentary and rest of the cusps and even conules are distinct. It may be emphasized here that a nonmolariform P4/ has only one major cusp each on its labial (paracone) and lingual (protocone) aspects; P4's without or with a poorly developed hypocone or without a metacone are partially molarised and are, therefore, referred submolariform. Lower teeth or at least P/4 are not known for *S. parvus*, *K. mirandus*, *K. gracilis* and *U. mirificus* but, wherever known, the P/4 is either submolariform (*T. subitus*) or molariform (*S. singularis*). Its structure is characterized by the trigonid which is significantly longer but more or less as broad as the talonid. In this respect, it resembles *Cocomys* as well as ctenodactylids (Fig. 6). But these taxa do not fit into the Cocomyidae because the family is essentially protrogomorphous. Taking into account the aforementioned points, the familial characters of *Sharomys*, *Kharomys*, *Tsagamys* and *Ulanomys* come closest to the Ctenodactylidae and not to the Cocomyidae as has been shown by Dashzeveg (1990a). However, still these forms are distinct from the presently known ctenodactylids (except *Tamquammys* and *Tsinlingomys*) in at least two features. Firstly, in new forms, fourth premolars are submolariform in contrast to nonmolariform in ctenodactylids. Secondly, their lower premolars possess trigonids that are either slightly wider or slightly narrower than talonids; in ctenodactylids trigonids are

considerably wider than talonids (Fig. 6). A new subfamily Sharomyinae is, therefore, proposed here under the Family Ctenodactylidae to include forms with at least incipiently hystricomorphous skulls and submolariform premolars. Sharomyinae nov. includes *Sharomys*, *Kharomys*, *Tsagamys*, *Ulanomys*, *Tamquammys* and *Tsinlingomys*. It is differentiated from the Ctenodactylinae which includes all Oligocene-Recent ctenodactylids, on the basis of submolarised P4/4 (nonmolarised in Ctenodactylinae) and P/4 with talonid shorter but more or less as wide as trigonid. *Tamquammys*, also included in Cocomyinae by Dashzeveg (1990a) was earlier transferred in to Ctenodactylidae by Flynn *et al.* (1986). It has been included here in Sharomyinae nov. on the basis of submolariform P4/4. Likewise *Tsinlingomys* is also attributed here to Sharomyinae to vacate Ctenodactylinae exclusively for Oligocene-Recent forms. The Family Cocomyidae is thus left only with *Cocomys* and is presently monotypic. Consequently, its diagnosis stands emended and is now the same as of genus.

Dashzeveg (1990b) reported two additional new Lower Eocene rodents, *Alagomys inopinatus* and *Orogomys obscurus* from the Naran-Bulak Formation of Mongolia and referred them to new families, Alagomyidae and Orogomyidae respectively. Although uncertain about the relationships of these families, the author stated that they marked the beginning of the phylogenetic history of rodents. *Orogomys obscurus* DASHZEVEG 1990 is now considered as a junior synonym of *Ivanantonia* SHEVYREVA 1989 and its present status is enigmatic (J.-L. Hartenberger, pers. comm.). Recently another new primitive rodent, *Tribosphenomys minutus* MENG *et al.* 1994 has been reported from the transitional Palaeocene-Eocene sequence of Inner Mongolia, China (Meng *et al.* 1994). Size-wise and morphologically, *Tribosphenomys* MENG *et al.* 1994 is comparable with *Alagomys* DASHZEVEG 1990 but differs in possessing a molariform P4/, a pronounced labial shelf in upper cheek teeth, larger metaconule, stronger hypocone and having a paraconid on M/1. Little can be said about the affinities of Alagomyidae because firstly, it is still known by limited material and secondly, no cranial elements are yet known. However, it is amply evident that the alagomyids represent the basal rodents, for both *Alagomys* and *Tribosphenomys* are undoubtedly more pristine than *Cocomys* which was considered the most primitive prior to the discoveries by Dashzeveg (1990b). Dashzeveg's (1990b) conclusion that *Heomys* can not be considered as ancestral to rodents as suggested by various workers is convincing.

Evolution and radiation of early rodents in Asia :

In Asia, the most primitive rodents are represented by the Alagomyidae in the transitional Palaeocene-Eocene Ulan Bayan beds (Nomogen Formation) of Inner Mongolia, China (Meng *et al.* 1994) and in the Lower Eocene Bumban Member (Naran-Bulak Formation) of Mongolia (Dashzeveg 1990a). The orogomyids also occur associated with the alagomyids but they are somewhat derived in features like possessing a hypocone and better developed trigone on M1/ and M2/ (Dashzeveg 1990a). Besides this, the status of Orogomyidae is presently uncertain because of the synonymy of *Orogomys obscurus* with *Ivanantonia* (J.-L. Hartenberger, pers. comm.). The cocomyids which are perhaps even more derived than orogomyids (as indicated by their premolar structure) are known from the Early Eocene deposits in China. The

Baluchistan, Pakistan (Flynn *et al.* 1986). As also pointed out by Dawson *et al.* (1984) the similarities in the premolar structure of cocomyids and ctenodactylids indicate that the Ctenodactylidae may also have evolved from Cocomyidae. Sharomyines could have been a good link between cocomyids and the latter ctenodactyloids.

With the understanding that eurymyloids are the likely ancestors of rodents it has become obvious that rodents originated in central Asia because eurymyloids are so far known only from Palaeocene of China and Inner Mongolia (Li 1977; Vianey-Liaud 1985). From Central Asia first radiation of rodents during the late Palaeocene could have given rise to the Ischyromyidae (= Paramyidae) in the North Atlantic continents and the Alagomyidae in Asia. In the Lower Eocene, contemporaneous families Paramyidae and Alagomyidae-Orogomyidae-Cocomyidae evolved in North America and Central Asia, respectively. From North America Paramyidae spreaded and reached Europe. In Central Asia, Alagomyidae, Orogomyidae and Cocomyidae evolved forming an early stock of rodents. From Central Asia, these early rodents spreaded and reached the Indian subcontinent during the Lower Eocene (de Bruijn *et al.* 1982). In early Middle Eocene, Chapattimyidae descended from the ?cocomyids. They evolved, diversified and spreaded in whole of the northwestern part of the Indian subcontinent during the Middle Eocene. At about the same time, cocomyids gave rise to yuomyids in the Central and east Asia. The phylogenetic representation of the Early and Middle Eocene rodents is shown in figure 12.

The presence of Lower Eocene rodents in Pakistan indicates that a migration route existed between the Indian subcontinent and the Central Asia during that time. This strengthens the view that at least the northwestern part of the subcontinent was in contact with the Asian plate during the Lower Eocene and possibly even earlier (Hartenberger 1982b, Jaeger 1988, Jaeger *et al.* 1989, Kumar 1993).

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GENUS & SPECIES	I N D I A						P A K I S T A N					
	Sindk- khatuti	Chen- pur	Tatta- pani	West Babbian Gala	East Babbian Gala	Triyath Barakh	Kam- roti	H-GSP 57	H-GSP 144	Chor- lakki	Pan- oba	Shek- han
<i>Birbalomys woodi</i>	-	X	X	?	X	X	X	-	X	?	-	X
<i>B. sondaari</i>	-	-	-	-	X	-	-	X	X	X	-	-
<i>B. ibrahimshahi</i>	-	-	-	-	X	-	?	?	?	?	?	?
<i>Basalomys vandermeuleni</i>	X	-	-	-	X	X	-	X	X	?	-	-
<i>B. ijlsti</i>	-	-	-	-	X	X	-	X	X	X	-	X
<i>B. lavocati</i>	-	-	-	-	X	-	-	-	-	-	-	?
<i>Chapattimys wilsoni</i>	-	-	-	-	X	-	-	-	X	X	-	-
<i>C. debruijini</i>	-	-	-	-	X	-	-	-	-	X	-	-
<i>Gumbatomys asifi</i>	-	-	-	-	X	-	-	-	-	X	-	-
<i>Cf. Advenimus bohlini</i>	-	-	-	-	X	-	?	?	?	?	?	?
<i>Cf. Petrokoslovia sp. indet. 1</i>	-	-	-	-	X	-	-	X	-	-	X	-
<i>Cf. Petrokoslovia sp. indet. 2</i>	-	-	-	-	X	-	-	-	-	X	-	-

Table 1.— Locality-wise distribution of the Middle Eocene rodents in India and Pakistan (X, present; ?, presence uncertain; -, no data available).

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
DP4/	1.70 - 1.80	1.74	08	2.22	2.00 - 2.40	3.86
P4/	1.70 - 2.10	1.88	15	2.42	2.00 - 2.70	4.58
M1/	1.95 - 2.50	2.16	20	2.57	2.10 - 3.00	5.58
M2/	1.90 - 2.75	2.25	31	2.62	2.20 - 3.00	5.92
M3/	2.30 - 2.70	2.52	14	2.43	2.10 - 2.70	6.13
DP/4	1.86 - 2.10	1.98	07	1.51	1.33 - 1.70	3.00
P/4	1.80 - 2.40	2.05	15	1.57	1.30 - 2.20	3.25
M/1	2.00 - 2.60	2.39	19	2.13	1.80 - 2.30	5.11
M/2	2.10 - 2.80	2.49	34	2.37	1.90 - 2.80	5.93
M/3	2.10 - 3.00	2.61	16	2.28	1.90 - 2.60	5.98

Table 2.— Summary of measurements (in mm) of upper and lower teeth of *Birbalomys woodi*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
DP4/	1.60 - 1.70	1.68	05	2.05	2.00 - 2.20	3.44
P4/	1.60 - 1.80	1.72	05	2.11	2.00 - 2.30	3.63
M1/	1.80 - 2.40	2.16	11	2.53	2.20 - 2.80	5.50
M2/	2.00 - 2.50	2.28	14	2.60	2.20 - 2.90	5.95
M3/	2.00 - 2.50	2.23	05	2.20	2.00 - 2.40	4.92
DP4/	-	1.80	01	1.60	-	2.88
P4/	1.60 - 1.90	1.78	05	1.56	1.40 - 1.65	2.78
M1/	1.90 - 2.50	2.26	21	2.03	1.70 - 2.30	4.60
M2/	1.70 - 2.60	2.25	21	2.05	1.50 - 2.40	4.66
M3/	2.30 - 2.80	2.57	04	2.20	2.00 - 2.30	5.68

Table 3.— Summary of measurements (in mm) of upper and lower teeth of *Birbalomys sondaari*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
DP4/	1.65 - 2.00	1.78	03	2.23	2.10 - 2.40	4.00
P4/	1.80 - 2.45	2.12	07	2.81	2.50 - 3.10	5.99
M1/	2.05 - 2.60	2.34	15	2.86	2.50 - 3.30	6.72
M2/	2.25 - 2.95	2.48	18	2.89	2.53 - 3.45	7.22
M3/	2.20 - 2.85	2.55	06	2.50	2.20 - 2.70	6.40
DP4/	2.00 - 2.15	2.05	05	1.57	1.42 - 1.70	3.23
P4/	2.00 - 2.50	2.26	06	2.00	1.60 - 2.50	4.58
M1/	2.20 - 2.70	2.46	07	2.13	2.00 - 2.30	5.25
M2/	2.40 - 3.00	2.71	05	2.55	2.40 - 2.90	6.94
M3/	3.00 - 3.20	3.10	03	2.53	2.50 - 2.60	7.86

Table 4.— Summary of measurements (in mm) of upper and lower teeth of *Birbalomys ibrahimshahi*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
DP4/	1.20 - 1.40	1.33	03	1.77	1.60 - 1.90	2.35
P4/	1.26 - 1.55	1.48	08	1.88	1.68 - 2.00	2.79
M1/	1.20 - 1.80	1.55	12	1.90	1.40 - 2.20	2.97
M2/	1.30 - 2.00	1.67	22	1.94	1.30 - 2.30	3.28
M3/	1.60 - 1.90	1.84	06	1.98	1.89 - 1.90	3.64
P/4	1.55 - 1.90	1.75	12	1.41	1.20 - 1.60	2.46
M/1	1.50 - 2.10	1.79	16	1.53	1.10 - 1.80	2.76
M/2	1.90 - 2.05	1.96	06	1.78	1.56 - 2.00	3.50
M/3	1.80 - 2.30	2.01	07	1.69	1.50 - 1.83	3.40

Table 5.— Summary of measurements (in mm) of upper and lower teeth of *Basalomys vandermeuleni*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
DP4/	1.00 - 1.10	1.05	02	1.35	1.20 - 1.50	1.42
M1/	1.30 - 1.40	1.35	02	1.45	1.40 - 1.50	1.95
M2/	1.30 - 1.45	1.38	03	1.47	1.40 - 1.50	2.03
M3/	1.70 - 1.70	1.70	02	1.60	1.60 - 1.60	2.72
DP/4	-	1.10	01	0.80	-	0.88
P/4	1.20 - 1.50	1.35	02	1.05	0.90 - 1.20	1.44
M/2	1.60 - 1.80	1.66	05	1.54	1.50 - 1.70	2.56
M/3	1.50 - 1.80	1.63	03	1.48	1.35 - 1.70	2.44

Table 6.— Summary of measurements (in mm) of upper and lower teeth of *Basalomys ijlsti*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
P4/	-	1.30	01	1.60	-	2.08
M1/	1.30 - 1.50	1.40	02	1.80	1.70 - 1.90	2.53
M2/	-	1.50	01	1.90	-	2.85
P/4	1.40 - 1.90	1.70	04	1.47	1.20 - 1.70	2.54
M/2	1.80 - 1.85	1.82	02	1.85	1.80 - 1.90	3.38
M/3	1.65 - 2.00	1.82	03	1.60	1.40 - 1.80	2.93

Table 7.— Summary of measurements (in mm) of upper and lower teeth of *Chapattimys wilsoni*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
M1/	-	1.85	01	1.85	-	3.42
M2/	1.40 - 1.80	1.65	03	1.72	1.60 - 1.80	2.85
M3/	1.65 - 1.85	1.75	02	1.68	1.60 - 1.75	2.94
P/4	1.70 - 1.85	1.78	03	1.43	1.40 - 1.45	2.56
M/2	-	1.85	01	1.65	-	3.05
M/3	-	2.20	01	1.70	-	3.74

Table 8.— Summary of measurements (in mm) of upper and lower teeth of Cf. *Advenimus bohlini*.

Tooth	Length		Sample size	Width		Mean crown area (LXW)
	Observed range	Mean		Mean	Observed range	
P4/	1.60 - 1.90	1.75	02	2.25	1.90 - 2.60	3.99
M1/	-	2.20	01	2.80	-	6.16
M2/	-	2.30	01	2.50	-	5.75
P/4	2.20 - 2.30	2.25	02	2.00	1.90 - 2.10	4.50

Table 9.— Summary of measurements (in mm) of upper and lower teeth of Cf. *Petrokoslovia* sp. indet. 1.

Family/ Superfamily/ Order	Genera	Distribution			
		Paleocene- Eocene	Early Eocene	Middle Eocene	Late Eocene
Alagomyidae	<i>Tribosphenomys</i>	China	-	-	-
	<i>Alagomys</i>	-	Mongolia	-	-
Orogomyidae	<i>Orogomys</i>	-	Mongolia	-	-
Cocomyidae	<i>Cocomys</i>	-	China	-	-
Ctenodactylidae (Sharomyinae)	<i>Sharomys</i>	-	Mongolia	-	-
	<i>Kharomys</i>	-	Mongolia	-	-
	<i>Tsagamys</i>	-	Mongolia	-	-
	<i>Ulanomys</i>	-	Mongolia	-	-
	<i>Tamquamys</i>	-	-	Kirgiz, China, & Kazakhstan	-
	<i>Tsinlingomys</i>	-	-	China	-
	<i>Yuomys</i>	-	-	Mongolia & China	China
Yuomyidae	<i>Petrokoslovia</i>	-	-	Kirgiz, India, Kazakhstan, Pakistan & Mongolia	Kazakhstan
	<i>Advenimus</i>	-	China	China, India, & Kazakhstan	-
	<i>Boromys</i>	-	-	Mongolia	-
	<i>Chkhivadzomys</i>	-	-	Kazakhstan	-
Chapattimyidae	<i>Birbalomys</i>	-	-	Indo-Pakistan	-
	<i>Basalomys</i>	-	-	Indo-Pakistan	-
	<i>Chapattimys</i>	-	-	Indo-Pakistan	-
	<i>Gumbatomys</i>	-	-	Indo-Pakistan	-
Ctenodactyloidea	*indet. M1-2/	-	Pakistan	-	-
	*indet. P/4	-	Pakistan	-	-
Rodentia	*indet. P4/	-	Pakistan	-	-
	#indet. P4/	-	-	Pakistan	-

Table 10.— Distribution and the revised familial status of Eocene rodents from central, eastern and southeastern Asia.

* de Bruijn *et al.* 1982, p. 253, fig. 4 (M1-2/); p. 254, fig. 6 (P/4); p. 252, fig. 3 (P4/).

Hussain *et al.* 1978, p. 102; Hartenberger 1982, p. 28.

LEGENDS OF PLATES

PLATE 1

Figs. 1-9.- *Birbalomys woodi*, dentition in occlusal views. 1, LUV 15005/1a holotype, left maxilla with P3/-M3/; 2, 15005/1b paratype, right mandible with P4-M3/; 3, LUV 15005/1d paratype, right maxilla with M1/-M3/; 4, VPL/RS 10131, isolated RDP4/; 5, 17023, isolated LM1/ (reversed); 6, 17116, isolated RM2/; 7, 17011, isolated RM3/; 8, WIMF/A 1159, left mandible with M/1-M/3; 9, 1158, right mandible with M/1-M/3. (Scale = 1 mm).

PLATE 2

Figs. 1-10.- *Birbalomys sondaari* (all except 1 & 5 paratypes). 1, WIMF/A 873, RDP4/; 2, 1198, *LP4/; 3, 1199, *LM1/; 4, VPL/RS 1012, RM2/; 5, WIMF/A 1197, RM3/; 6, 935, LDP4/; 7, 1182, LP4/; 8, 1187, *RM1/; 9, 1188, *RM2/; 10, 951, LM3/.

Figs. 11-20.- *Birbalomys ibrahimshahi* (12-19 paratypes). 11, VPL/RS 10196, *LDP4/; 12, WIMF/A 1176, *LP4/; 13, LUV 17125, RM1/; 14, VPL/RS 10164, *LM2/; 15, WIMF/A 952, RM3/; 16, 912, RDP4/; 17, 1124 *LP4/; 18, 980, RM1/; 19, 1109, RM2/; 20, 1127 *LM3/.

Figs. 21-24.- *Basalomys vandermeuleni* (all paratypes). 21, VPL/RS 101110, RP4/; 22, WIMF/A 1168, RM1/; 23, 1169, RM2/; 24, 1170, RM3/.

All isolated teeth in occlusal views; * = Reversed; Scale=1 mm

PLATE 3

Figs. 1-5.- *Basalomys vandermeuleni* (all paratypes). 1, WIMF/A 1149, LP4/; 2, 1148, LM1/; 3, 1147, LM2/; 4, 1146, LM3/; 5, 943, *LDP4/.

Figs. 6-13.- *Basalomys ijlsti* (all except fig. 10 paratypes). 6, WIMF/A 1177, *LDP4/; 7, 852, RM1/; 8, 1258, RM2/; 9, 954, RM3/; 10, 1255, RDP4/; 11, 1241, *LP4/; 12, 938, RM2/; 13, 901, RM3/.

Fig. 14.- *Basalomys lavocati*, WIMF/A 1113, LP4/.

Figs. 15-20.- *Chapattimys wilsoni* (18-20 paratypes). 15, WIMF/A 1191, RP4/; 16, 1156, RM1/; 17, 1157, RM2/; 18, 911, LP4/; 19, 1180, LM2/; 20, 1277, *RM3/.

Fig. 21.- *C. debruijini*, paratype, WIMF/A 1126, LM3/.

Fig. 22.- *Gumbatomys asifi*, WIMF/A 1233, LM3/.

Figs. 23-28.- Cf. *Advenimus bohlini*. 23, WIMF/A 1141, RM1/; 24, 1142, RM2/; 25, 1143, RM3/; 26, 854, LP4/; 27, 947, LM2/; 28, 887, *RM3/.

Figs. 29-32.- *Petrokoslovia* sp. indet. 1. 29, WIMF/A 883, *RP4/; 30, 1235, LM/1; 31, 1210, LM2/; 32, 1218, LP/4.

Figs. 33-35.- *Petrokoslovia* sp. indet. 2. 33, VPL/RS 10199, LP/4; 34, 101109, LP4/; 35, 10133, LM2/.

Figs. 36.- Rodentia indet., VPL/RS 10173, LP4/.

All isolated teeth in occlusal views, * = Reversed; scale = 1 mm.

