Comments on rodents from the Chinese Neogene

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Rodents from the Chinese Neogene indicate latitudinal changes in taxonomic composition. Lufeng is apparently more closely related to Siwalik faunas of about 8 Ma than to Chinese faunas further north. The more northerly faunas are Holarctic in composition with greater similarity to Europe than to North America. Definition of faunal sequences in China can be applied to resolving questions of correlations between Holarctic and Oriental regions.

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Introduction

The great land-mass of Asia was the centre of evolution for many groups of mammals during the Tertiary. Indeed, palaeontologists have long looked to Asia as the hypothetical homeland for diverse mammalian groups that appear abruptly in the European and North American record (see, for example, Osborn, 1910). The idea of Mother Asia in this context is probably correct, but the concept has one practical difficulty: knowledge of the fossil record in much of Asia is only now becoming as well documented as it is in Europe and North America.

Neogene and Pleistocene rodents are particularly interesting in this regard. The potential for migration between northern Asia and Europe, North America, and the Indian subcontinent and Africa existed at many times since the beginning of the

Table 1. Major groups of Neogene rodents found in China and their geographic relationships with other areas.

	Endemic	Also in Europe and/or Southwestern Asia	Also in North America	Also in Indian Subcontinent
Aplodontinae			x	
Sciuridae		x	x	x
Gliridae		x		x
Castoridae		x	x	
Eomyidae		x	x	
Cricetodontinae		x	x	x
Cricetinae		x		
Cricetinae *incertae sedis*		x		
Microtinae		x	x	
Gerbillinae		x		x
Myospalacinae	x			
Rhizomyidae				x
Muridae		x		x
Zapodidae		x	x	?
Dipodidae		x		
Hystricidae		x		x
TOTAL (N=16)	1	13	7	7 or 8

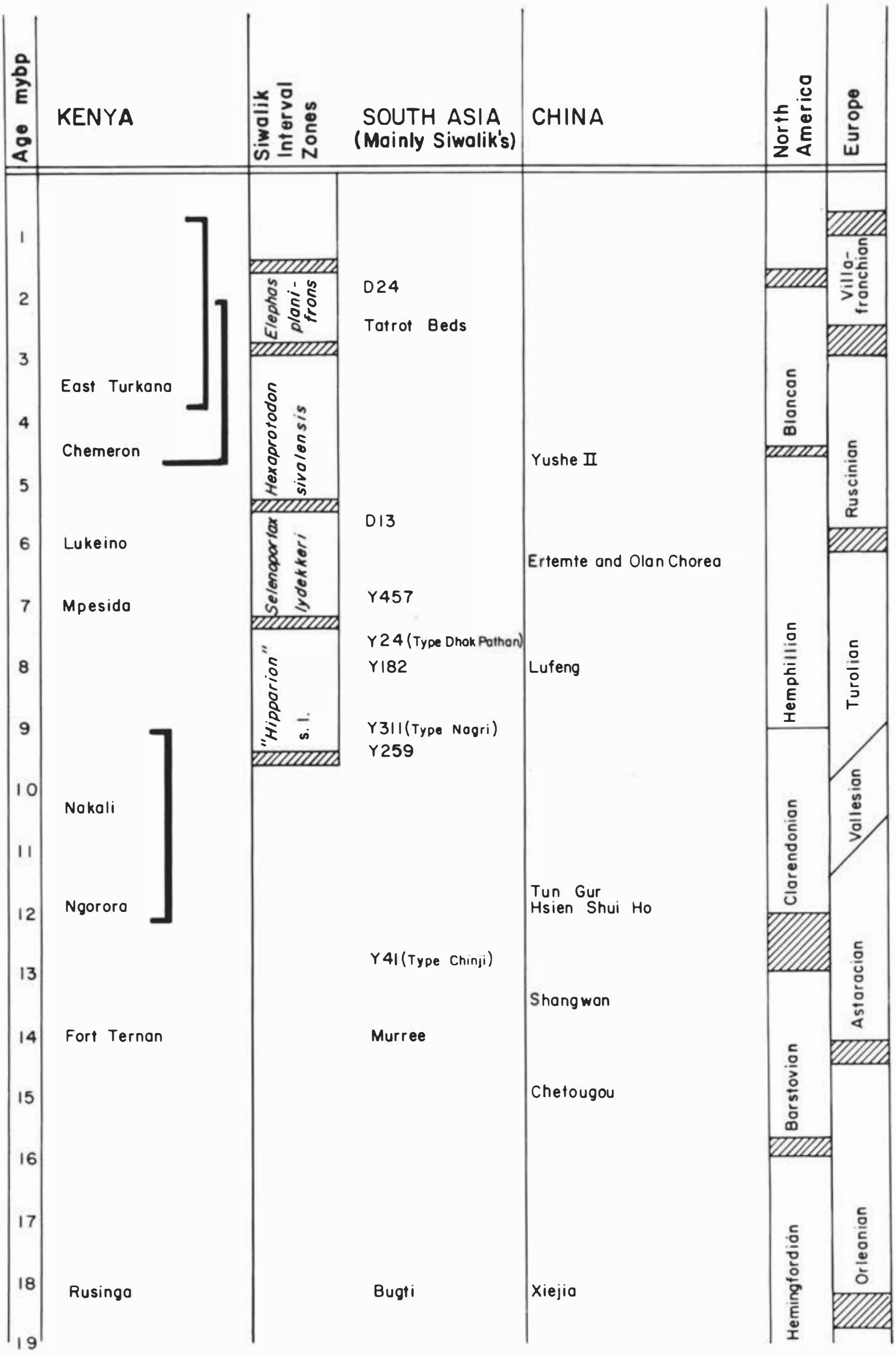

Fig. 1. Preliminary correlation chart of China with other areas. Evidence provided by Dr. John Barry (pers. comm. 1982) shows that locality Y24 lies in the *Selenoportax lydekkeri* interval zone.

Neogene. Exploitation of this potential by some (but not all) groups of mammals and the timing of dispersal events have important implications for palaeoecological reconstructions and biochronology. Never before has the prognosis for discovery and understanding been more cheery. This is due in large measure to the expansion of the data base relevant to small mammal studies by colleagues in many countries, but perhaps most importantly by those at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing. Because of advances being made in China, we take this opportunity to comment briefly on the Neogene rodents of the Lagrelius Collection of Uppsala, which for a long time formed the nucleus, indeed the bulk, of specimens from China and Mongolia available for study. This brief review is a series of comments and illustrations intended to enhance the usefulness of the Lagrelius Collection to emphasize the zoogeographic significance of the Chinese fauna. We are pleased to dedicate this effort to Birger Bohlin, Otto Zdansky, J. Gunnar Anderson, and Carl Wiman, for whose works we have great respect.

We are dealing only with rodents in this paper. Simpson (1947) and Repenning (1967) made significant reviews, broader in scope. Table 1 lists the major groups of fossil rodents found in China with their geographical relationships, and Figure 1, a correlation chart, serves as a framework for evaluating these faunas. The correlation chart is based on many sources, but mainly Chiu, Li, and Chiu (1979), Li, Qiu, and Wang (1981), Barry, Lindsay, and Jacobs (1982), Flynn and Qi (1982), Flynn (1982a, b), Jacobs (in press), and references therein.

Many of the correlations in Figure 1 are preliminary. For Africa, we have included a sequence of Kenyan localities because we have more first hand knowledge of Kenya than other African fossiliferous deposits. However, we do recognize that there are other extremely important East African sequences such as the Awash Valley, Ethiopia (Kalb, *et al.*, 1982). In the first column of Figure 1, the Ngorora Formation is shown as 12–9 Ma, the Chemeron Formation about 4,5–2 Ma, and East Turkana roughly 3,5–1 Ma. Sedimentation was not continuous during those periods, but fossil localities in these rocks occur sporadically throughout those time ranges.

Siwalik interval zones are more confidently placed than the older poorly delimited South Asian faunal assemblages. Brunet, Heintz, and Sen (1981) discussed a sequence of faunas from Afghanistan which complements that of the Siwaliks and indicates the likelihood of faunal provinciality between the two areas (see also Sen, 1983, Sen *et al*, 1979, Heintz and Brunet, 1982).

Much remains to be done on Chinese chronology, but obviously, refinement of the Chinese sequence based on detailed study of long sections will contribute significantly to Cenozoic chronology, especially with regard to Europe where many localities are isolated and dates are sparse. More is to be gained by establishing a well dated chronostratigraphic sequence in China than by correlating numerous isolated Chinese faunas to the European biochronological sequence.

The best known suite of rodents in the Lagrelius Collection is from the late Neogene of Ertemte and Olan Chorea. Less well known, but still highly significant, is the collection from Hsien Shui Ho.These collections were studied by Schlosser (1924), Young (1927), Schaub (1934, 1938), Miller (1927), and Stehlin and Schaub (1951, see also Teilhard and Leroy, 1942). Both Ertemte and Olan Chorea have been recollected by joint expeditions from the IVPP and the Federal Republic of Germany. They have greatly improved the sample of smaller taxa represented in the Lagrelius Collection, and their studies and conclusions will certainly be of great interest relative to our comments here.

In addition, C. A. Repenning of the United States and Oldrich Fejfar of Czechoslovakia are reviewing the faunal and chronological relationships of Holarctic voles, which are important elements in many Chinese small mammal faunas, including Ertemte and Olan Chorea. Their detailed studies are particularly important for Holarctic intercontinental correlations. This study was essentially completed in 1982 when LLJ was at the National Museums of Kenya and LJF was at Universite de Paris VI. In the intervening time, our views have been modified, and this is reflected somewhat in Jacobs and Lindsay (1984) and Flynn et al. (in press).

Major Groups of Chinese Neogene Rodents

Only one group shown in Table 1, the Myospalacinae, is endemic to the great land mass of northeastern Asia. All other groups have relationships to (1) Europe and southwestern Asia, (2) North America, (3) the Indian subcontinent, (4) Africa, or to a combination of these areas. Thirteen of the 16 groups listed in Table 1 show affinity with Europe and southwestern Asia, seven with North America, and seven or eight with the Indian subcontinent. All of those with North American representatives are also found in Europe, except for aplodontines. Squirrels and cricetodontines are also present in the Indian subcontinent. One family, the Rhizomyidae, shows relationships only with the Indian subcontinent (and Africa). Dipodids now live on the Indian subcontinent, but they did not occur there in the late Neogene (see Flynn and Jacobs, 1982), and they are probably late arrivals. Microtines are now peripheral inhabitants of the Indian subcontinent, and there is no evidence that they have ever been more than that.

Some rodent groups, particularly those with species of small body-size such as Gliridae, are at best poorly represented in Chinese localities. Gliridae are known from the Neogene of Europe and the Indian subcontinent and occur at Ertemte (Fahlbusch, Qiu, and Storch, 1983) and at Hsiatsaowan. Some North American families, such as Mylagaulidae, Erithizontidae, and perhaps Heteromyidae and Geomyidae (unless *Diatomys* described by Li, 1974, is truly a geomyoid), did not reach China, probably because they were filtered out by the rigors of the Bering Land Bridge. Thryonomyidae, unrepresented in China, are characteristic of Africa and occur as far eastward as the Indian subcontinent during the middle Miocene. Ctenodactylidae decline in China in the early Neogene, but persist longer in India and southwestern Asia, and to the Recent in Africa.

Eomyidae

The eomyid *Leptodontomys is* known from the Hemphillian of North America and similar species occur in equivalent age faunas of Europe. *Leptodontomys gansus* has recently been described from the Songshan fauna, Tianzhu, Gansu (Zheng, 1982a,b; Zheng and Li, 1982) and Ertemte (Fahlbusch, Qiu, and Storch, 1983). Eomyids are not represented in the Lagrelius Collection.

Cricetodontinae, Cricetinae, and Cricetinae *incertae sedis*

Li (1977) described the cricetodontine *Spanocricetodon ningensis* from Fang-shan near Nanjing. More recently, de Bruijn, Hussain, and Leinders (1981) recognized the same genus from the Murree Formation, which underlies the Siwalik Group in Pakistan. *Megacricetodon* is known from Nanjing, the lower Siwaliks, and Europe. Cricetodontines are represented in the Lagrelius Collection by *Paracricetulus schaubi* (Pl. 1, fig. 1) from Hsien Shui Ho, and possibly *Neocricetodon grangeri*. All of these taxa are relevant to understanding the relationships of *Copemys, Democricetodon, Spanocricetodon, Megacricetodon,* and their dispersal throughout the northern hemisphere (see also Qiu, Li, and Wang, 1981).

Cricetines are represented in the Lagrelius Collection by *Sinocricetus zdanskyi* (Pl. 1, figs. 3, 4) and *Nannocricetus mongolicus* (P. 1, fig. 5), both from Ertemte. Certainly much hamster evolution took place in Asia. From there they spread to Europe, but apparently not to North America, nor to the Indian subcontinent. The oldest certain cricetine is *Kowalskia* from the late Vallesian of Europe. *Kowalskia* is now reported from Songshan, Tianzhu, Gansu (Zheng, 1982a, b; Zheng and Li, 1982).

Several taxa in the Lagrelius Collection were referred to Cricetinae *incertae sedis* by Simpson (1945). These include *Anatolomys teilhardi* (Pl. II, fig. 3), *Lophocricetus grabaui* (Pl. 1, figs. 6, 7, 8), *Lophocricetus pusillus* (Pl. 1, fig. 2), and *Microtodon atavus* (Pl. 2, figs. 5, 6, 7 and Pl. III, fig. 1), all from Ertemte. Lower dentitions of *Lophocricetus* resemble cricetines by convergence and both species have been transferred to the Dipodoidea by Fahlbusch, Qiu, and Storch (1983). *A. teilhardi, M. atavus,* and *Plesiodipus leei* (Pl. 2, figs. 1, 2) from Hsien Shui Ho, are similar in that they are all relatively high-crowned. It is clear, however, that advanced height of crown is not a shared derived character uniting all these forms because increased hypsodonty characterizes numerous rodent lineages during the late Neogene in Europe and North America. Hypsodonty also becomes pronounced in the African otomyines, but slightly later. For now, it seems reasonable that the high-crowned cricetid (and dipodid) fauna of Ertemte represents a late Miocene radiation of grazing rodents. Some elements of this radiation also occur in Europe (e.g., *Microtodon,* Pl. 2, figs. 5, 6, 7 and Pl. 3, figs 1, 3; see also Repenning, 1968).

Plesiodipus leei (equals *Plesiocricetodon* of Schaub, 1934) is part of the Miocene radiation; however, it is older than Ertemte by several million years. Qiu, Li, and Wang (1981) noted that *Plesiodipus leei* from Hsien Shui Ho is quite similar to, or synonymous with, *Prosiphneus lupinus* from Tun Gur, and that this morphological similarity may indicate that *Plesiodipus* is close to the ancestry of miospalacines.

In addition, the morphology of *Plesiodipus* is similar to high-crowned rodents in both Europe and North America (see for example Li and Chi, 1981). Of particular importance is similarity to certain New World cricetids, for which Repenning (1967) suggested an Asian ancestry "because no possible ancestor is known in North America and all resemble earlier Old-World cricetine rodents." He was followed in this by Jacobs (1977). More recent improvement of the late Miocene and Pliocene record of North American rodents over the past few years (Baskin, 1978, 1979; Jacobs and Lindsay, 1981) presents a sequence that can be reasonably interpreted as evolution from the sigmodontine *Bensonomys,* through *Prosigmodon,* to *Sigmodon* in North America. Baskin (1978) suggested *Bensonomys* is best considered a subgenus of *Calomys* and that it was derived from North American *Copemys* (see also Jacobs and Lindsay, 1981). *Plesiodipus* from China is too hypsodont to have given rise to these sigmodontines, but it strongly resembles other more derived New World forms (see Stehlin and Schaub, 1951).

B. Slaughter and J. Ubelaker (1984) have most recently challenged the idea of a North American origin for all late Neogene New World cricetids, based on studies of internal parasites. They suggest that the pattern of sigmodontine origin and evolution is more complex than that advanced by Baskin (1978) and Jacobs and Lindsay (1981). *Plesiodipus* and the Ertemte "Cricetinae, *incertae sedis*" can be conveniently, but tentatively, grouped into higher categories that are characterized by differences in the last lower molar and the masseteric crest (C.A. Repenning, pers. comm.). These groups are recognizable in the New World cricetids by the same characters. Thus late Neogene New World cricetids are almost certainly of multiple origin.

Plesiodipus itself bears a strong resemblance to the latest Miocene *Pliotomodon primitivus* of California, except that it lacks most of the ectolophal closure of the reentrant valleys. *Plesiodipus* also resembles *Neotoma* and *Peromyscus,* but less strongly. Morphological resemblance of *Plesiodipus* to other high crowned Neogene rodents of both North America and Europe probably involves convergence or parallelism in some characters. Superficially similar "grazers" include *Peromyscus pliocaenicus, Galushamys,* and *Repomys* of North America and *Byzantinia* of Europe.

If our correlations are correct, the age of Hsien Shui Ho is close to or slightly older than early Clarendonian in North America. Small rodents are less well known in the Clarendonian than in the preceding Barstovian or succeeding Hemphillian North American land mammal ages. Concentrated field work during this and later time intervals (6–10 Ma) in both China and North America may help to clear up some of the uncertainty of the relationships of living New World cricetids, as well as improve understanding of the evolution and dispersal of other high-crowned cricetids (see also May, 1981; Slaughter and Ubelaker, 1984, and Jacobs and Lindsay, 1984.).

Gerbillinae

A fine skull in the Lagrelius Collection may be referrable to *Pseudomeriones abbreviatus* (holotype from Gansu). The species is known from the eastern Mediterranean, Afghanistan, and zone 1, Yushe Basin, China (Li, 1981). Sen (1983) has shown that the genus includes several forms at various stages of evolution. This, plus the widespread distribution of *P. abbreviatus,* suggests its value in correlation.

Rhizomyidae

Rhizomyid rodents, a group well represented in the Siwaliks of Pakistan and India, are becoming increasingly well known in eastern Asia, mainly by the work of Chinese palaeontologists. Most east Asian rhizomyids belong to the subfamily Rhizomyinae and exhibit burrowing adaptations. The early rhizomyine *Brachyrhizomys* is known from the *Selenoportax lydekkeri* and *"Hipparion"* s. l. interval zones of the Siwaliks (Barry *et al.*, 1982), and beds of similar age and probably younger age in China. Chinese rhizomyids from Lufeng, Yunnan, are closely comparable to those of the Siwaliks. Lufeng has yielded *Brachyrhizomys nagrii, B. tetracharax* and cf. *B. pilgrimi,* three species which occur together at about 8 Ma in Pakistan (Flynn and Qi, 1982; Pl. 4, figs. 1–3). *B. shansius* from the more northern locality Yushe, Shanxi, is the most advanced species known of *Brachyrhizomys,* and could be derived from a species close to those of about 7 Ma in Pakistan.

Brachyrhizomys hehoensis from the Bulong Basin, Xizang Plateau (Tibet; Zheng, 1980) is unlike any rhizomyid from Pakistan and may be congeneric with *Pararhizomys hipparionum* (Teilhard and Young, 1931). Flynn (1982a) proposed that *Pararhizomys* was a spalacid, which would constitute a great, eastward extension in range for that family. Discovery of unworn dentitions and cranial material of *B. hehoensis* will help to clarify its systematic position.

Rhizomyines became extinct in Pakistan during the *Selenoportax lydekkeri* interval zone, but persisted in China. A number of Pliocene and Pleistocene localities have yielded species of *Rhizomys,* for example, *R. schlosseri, R. troglodytes,* and *R. sinensis* (Colbert and Hooijer, 1953; Young, 1927, 1929). *Rhizomys troglodytes* in the Lagrelius Collection should be more closely compared with both *Brachyrhizomys* and living species of *Rhizomys.* The presence in China of rhizomyines from the late Neogene to the present offers the opportunity to document the evolution of living species of *Rhizomys* from *Brachyrhizomys*.

Among the many undescribed rhizomyids discovered in China is a new advanced form from near the northern border of Gansu. This species, in addition to *Pararhizomys hipparionum,* represents the northernmost occurrence of the family and possibly also the easternmost occurrence of the Tachyoryctinae, a subfamily that lives today only in Africa, although it is known from fossils in the Siwaliks.

Muridae

For many years, two specimens of murids from Ertemte, both lower jaws with M 1–2 were assigned to *?Progonomys orientalis* (Pl. 3, fig. 6) and *Parapodemus hipparionum* (Pl. 3, fig. 7), both European genera (Schaub, 1938). De Bruijn (1976) has suggested a possible synonymy of *?P. orientalis* with *Occitanomys? neutrum* and *P. hipparionum* with *O.? provacator* from Pikermi.

Jacobs and Li (1982) described the murid *Chardinomys yusheensis* from Yushe and possibly the slighly younger locality of Weinan. *Chardinomys* is most similar to *Orientalomys* from China (Zheng, 1981) and from Turkey and the eastern Mediterranean area (Sen, 1977). It does not appear to be closely related to the murids of the Indian subcontinent (Jacobs, 1978). However, cf. *Rattus* from Weinan may indicate south Asian affinities (Jacobs and Li, 1982).

Zapodidae and Dipodidae

Wessels *et al.* (1982) have recently reported an indeterminate zapodid from the Chinji Formation in the Siwalik Group of Pakistan. Aside from this doubtful occurrence, zapodids are not known from Siwalik faunas. The Ertemte fauna includes *Sminthoides fraudator* (Pl. 3, fig 8).

Dipodids have a long record in the Chinese Neogene, including *Protalactaga grabaui* from Hsien Shui Ho (Fig. 2) and at least three genera from Ertemte (Fahlbusch, Qiu and Storch, 1983). They will become more useful in establishing a comprehensive Chinese chronology, but will probably be less useful for correlations with the Indian subcontinent than southwestern Asia.

Hystricidae

Hystricid porcupines enter China relatively late. When they appear, they are fully developed hystricids and give no clue as to their immediate ancestry. That pattern is the same as in Europe and southwestern Asia, the Indian subcontinent, and Africa.

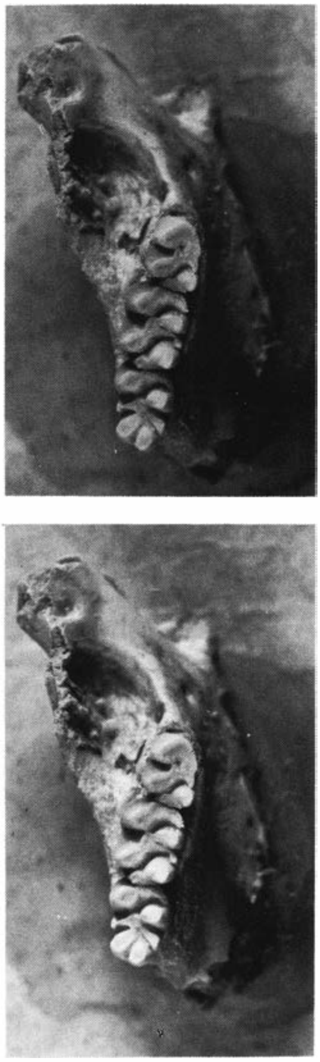

Fig. 2. *Protolactaga grabaui.* Specimen M.3427.162. Right dentary with M_{1-3}. M_{1-3} length = 6.4 mm. Young, 1927. Stereographs.

So where did hystricids evolve? Older faunas in Europe, Africa, and China do not contain any obviously ancestral elements. Neither do those from the Indian subcontinent. But the Indian subcontinent did have an endemic rodent fauna in the early Miocene (Flynn, Jacobs, and Cheema in preparation; Jacobs, Cheema, and Shah, 1982), and hystricids might have originated in an endemic south or southeast Asian fauna, spreading outward from there in the late Miocene. Colbert (1933) described the primitive hystricid *Sivacanthion complicatus* from the lower Siwaliks; additional specimens of *Sivacanthion* have not yet been recovered from Pakistan.

Conclusions

From the above comments it is obvious that the Lagrelius Collection contains a diverse suite of Neogene rodents, and this collection will continue to hold a critical and central position in understanding the systematic and zoogeographic relationships of rodents in China and elsewhere. The diversity of the Chinese rodent fauna is the result of both provinciality and latitudinal ecological variation reflected in the geographic distribution of fossil localities. Apparently, throughout the Neogene the northerly Chinese localities are more Holarctic in character, while those to the south are Oriental.

At the family and subfamily level, Holarctic Chinese rodent faunas are more similar to those of Europe than to North America. This is because the Bering Land Bridge acted as a filter to dispersal between Asia and North America. The rodent groups that were best able to withstand the rigors of the Bering Land Bridge are the Sciuridae, Castoridae, Zapodidae, Microtinae and Cricetidae.

The fossil record in China documents a radiation of high-crowned rodents during the late Miocene and Pliocene. Such an adaptation, allowing for a relatively more abrasive diet, appears to have evolved at approximately the same time in Europe and North America, probably as a response to changes in vegetation, possibly due to a Holarctic trend toward aridity (see also Wilson, 1937).

We have stressed above the similarity of Siwalik and Chinese rhizomyids. The Rhizomyidae appear to have emigrated from the Indian subcontinent by an eastern route to China. Northern Chinese rhizomyids, however, differ from those of the Upper Siwaliks, suggesting that a late Neogene chapter in the evolution of this group took place at higher latitudes. This late phase of evolution includes the origin of *Rhizomys.* Although present in late Miocene and later deposits in Africa (Flynn and Sabatier, 1984), rhizomyids never entered Anatolia or Europe.

Other faunal elements besides rodents, notably tree shrews and to some extent lorisine primates (Jacobs, 1980, 1981) seem to link the environment of the Siwaliks of seven million years ago (and older) more closely to that of present day southeast Asia than one would expect from the current more xeric environmental conditions in Pakistan (see also Flynn and Jacobs, 1982). This has important implications for faunal correlations, particularly because of the North-South Holarctic to Oriental faunal gradient in China. Southern Chinese faunas, notably Lufeng, can be related to Siwalik faunas of India and Pakistan, and probably to the Irrawaddy fauna of Burma. To the southwest, Siwalik fossils can be related to Africa. The Holarctic-Oriental connection can be studied best in China and then synthesized with other regions.

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REFERENCES

Barry, J.C., Lindsay, E.H., and Jacobs, L.L. 1982. A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeogr., Palaeoclimatol., Palaeoecol. 37,* 95–130. Amsterdam.

Baskin, J.A. 1978. *Bensonomys, Calomys,* and the origin of the phyllotine group of neotropical cricetines (Rodentia: Cricetidae). *J. Mammal. 59 (1),* 125–135. Baltimore.

Baskin, J.A. 1979. Small mammals of the Hemphillian age White Cone local fauna, northeastern Arizona. *J. Paleontol. 53 (3),* 695–708.

Bruijn, H. de 1976: Vallesian and Turolian rodents from Biota, Attica and Rhodes (Greece). *K. Nederl. Akad. van Wetenschappen, Proc., Ser. B* 79, 361–384. Amsterdam.

Bruijn, H. de, Hussain, S.T., and Leinders, J.J.M. 1981. Fossil rodents from the Murree formation near Banda Daud Shah, Kohat, Pakistan. *K. Nederl. Akad. van Wetenschappen, Proc., Ser. B 84 (1),* 71–99. Amsterdam.

Brunet, M., Heintz, E., and Sen, S. 1981: Datations paléontologiques et séquence biochronologique dans le Néogène continental d'Afghanistan. *C. R. séances Acad. Sci. Paris, Sér. II 293,* 473–476. Paris.

Chiu Chan-Siang, Li Chuan-kuei, and Chiu Chiu-Ting 1979: The Chinese Neogene. A preliminary review of the mammalian localities and faunas. *Ann. Geol. Pays. Hellen. 1,* 263–272. Athens.

Colbert, E.H. 1933: Two new rodents from the lower Siwalik beds of India. *Amer. Mus. Novitates 633,* 1–6. New York.

Colbert, E.H. and Hooijer, D.A. 1953. Pleistocene mammals from the limestone fissures of Szechuan, China. *Bull. Am. Mus. Nat. Hist. 102 (1),* 1–134. New York.

Fahlbusch, V., Qiu Zhuding, and Storch, G. 1983. Neogene mammalian fauna of Ertemte and Harr Obo in Nei Monggol, China. *Scientia Sinica (Ser. B) 26,* 205–224. Beijing.

Flynn, L.J. 1982a: Systematic revision of Siwalik Rhizomyidae (Rodentia). *Géobios 15 (4),* 327–389. Lyon.

Flynn, L.J. 1982b: A revision of fossil rhizomyid rodents from northern India and their correlation to a rhizomyid biochronology of Pakistan. *Géobios 15(4),* 583–588. Lyon.

Flynn, L.J. and Jacobs, L.L. 1982. Effects of changing environments on Siwalik rodent faunas of northern Pakistan. *Palaeogeogr., Palaeoclimatol., Palaeoecol. 38,* 129–138. Amsterdam.

Flynn, L.J., Jacobs, L.L., and Cheema, I.U. in preparation. (Fossil rodents from the Bugti beds, Baluchistan).

Flynn, L.J., Jacobs, L.L., and Lindsay, E.H. In press: Problems in muroid phylogeny: relationship to other rodents and origin of major groups. *In:* W.P. Luckett and J.-L. Hartenberger (Editors), *Evolutionary Analysis of Rodents.* Plenum, New York. In press.

Jacobs, L.L. and Lindsay, E.H. 1984. Holarctic radiation of Neogene muroid rodents and the origin of South American cricetids. *J. Vertebr. Paleontol. 4,* 265–272. Los Angeles.

Slaughter, B.H. and Ubelaker, J.E. 1984. Relationship of South American cricetines to rodents of North America and the Old World. *J. Vertebr. Paleontol. 4,* 225–264. Los Angeles.

Flynn, L.J. and Qi Guo-quin 1982. Age of the Lufeng, China, hominoid locality. *Nature 298 (5876),* 746–747. London.

Flynn, L.J. and Sabatier, M. 1984. A muroid rodent of Asian affinity from the Miocene of Kenya. *J. Vertebr. Paleontol. 3 (3),* 160–165. Norman.

Heintz, E. and Brunet, M. 1982. Une barrière géographique entre le souscontinent indien et l'Eurasie occidentale pour les faunes continentales du Miocène supérieure. *C.R. séances Acad. Sci.* Paris *Sér. II 294,* 477–480. Paris.

Jacobs, L.L. 1977. Rodents of the Hemphillian age Redington local fauna, San Pedro Valley, Arizona. *J. Paleontol. 51 (3),* 505–519. Tulsa.

Jacobs, L.L. 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Mus. North. Arizona, Bull. Ser.* 52, 1–103. Flagstaff.

Jacobs, L.L. 1980. Siwalik fossil tree shrews. *In:* W.P. Luckett (Editor), *Comparative Biology and Evolutionary Relationships of Tree Shrews.* Plenum, New York, pp. 205–216.

Jacobs, L.L. 1981. Miocene lorisid primates from the Pakistan Siwaliks. *Nature 289 (5798),* 585–587. London.

Jacobs, L.L. (in press). The beginning of the Age of Murids in Africa. *Acta Zoologica Fennica.* Helsinki.

Jacobs, L.L., Cheema, I.U., and Shah, S.M.I. 1981. Zoogeographic implications of early Miocene rodents from the Bugti beds, Baluchistan, Pakistan. *Géobios 15,* 101–103. Lyon.

Jacobs, L.L. and Lindsay, E.H. 1984. Holarctic radiation of Neogene muroid rodents and the origin of South American cricetids. *J. Vertebr. Paleontol. 4 (2),* 265–272. Los Angeles.

Jacobs, L.L. and Li Chuan-Kuei 1982. A new genus *(Chardinomys)* of murid rodent (Mammalia, Rodentia) from the Neogene of China, and comments on its biogeography. *Géobios 15,* 255–259. Lyon.

Jacobs, L.L. and Lindsay, E.H. 1981. *Prosigmodon oroscoi,* a new sigmodont rodent from the late Tertiary of Mexico. *J. Paleontol. 55,* 425–430. Tulsa.

Kalb, J.E., Oswald, E.B., Tebedge, S., Mebrate, A., Tola, E., and Peak, D. 1982. Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. *Nature 298 (5869),* 17–25. London.

Li Chuan-Kuei 1974. A probable geomyoid rodent from the middle Miocene of Linchu, Shantung. *Vertebr. Palasiatica 12 (1),* 43–53. Peking.

Li Chuan-Kuei 1977. A new Miocene cricetodont rodent of Fanshan, Nanking. *Vertebr. PalAsiatica 15,* 67–76. Peking.

Li Chuan-Kuei 1981. Pontian sand-rat from Yushe Basin, Shansi. *Vertebr. PalAsiatica 19,* 321–326. Beijing.

Li Chuan-Kuei and Chi Hungxiang 1981. Two new rodents from Neogene of Chilong Basin, Tibet. *Vertebr. PalAsiatica 19 (3),* 246–255. Beijing.

Li Chuan-Kuei, Qiu Zhuding, and Wang Shijie 1981. Discussion on Miocene stratigraphy and mammals from Xining Basin, Qinghai. *Vertebr. PalAsiatica 19,* 313–320. Beijing.

May, S.R. 1981. *Repomys* (Mammalia: Rodentia gen. nov.) from the late Neogene of California and Nevada. *J. Vertebr. Paleontol. 1,* 219–230. Norman.

Miller, G.S. 1927. Revised determinations of some Tertiary mammals from Mongolia. *Palaentol. Sin., Ser. C, 5 (2),* 1–20. Peking.

Osborn, H.F. 1910. *The Age of Mammals in Europe, Asia and North America.* The MacMillan Company, New York, 635 pp.

Qiu Zhuding, Li Chuan-Kuei, and Wang Shijie 1981. Miocene mammalian fossils from Xining Basin, Qinghai. *Vertebr. PalAsiatica 19,* 156–173. Beijing.

Repenning, C.A. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic. *In:* D.M. Hopkins (Editor), *The Bering Land Bridge,* Stanford Univ. Press, Stanford, California, pp. 288–311.

Repenning, C.A. 1968. Mandibular musculature and the origin of the subfamily Arvicolinae (Rodentia). *Acta Zool. Cracoviensia 13,* 29–72. Krakow.

Schaub, S. 1934. Über einige fossile Simplicidentaten aus China und der Mongolei. *Abh. Schweiz. Paläontol. Ges. 54,* 1–40. Zürich.

Schaub, S. 1938. Tertiäre und Quartäre Murinae. *Abh. Schweiz. Paläontol. Ges. 61,* 1–38. Zürich.

Schlosser, M. 1924. Tertiary vertebrates from Mongolia. *Palaeontol. Sin., Ser. C 1,* 1–119. Peking.

Sen, S. 1977. La faune de Rongeurs pliocènes de Calta (Ankara, Turquie). *Bull. Mus. Natl. Hist. Nat. Sci. Terre 61,* 89–171. Paris.

Sen, S. 1983. Rongeurs et Lagomorphes du gisement pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. *Bull. Mus. Natl. Hist. Nat. Paris, 5ᵉ sér. 5, sect. C,* 33–74, Paris.

Sen, S., Brunet, H., and Heintz, E. 1979. Découverte de Rongeurs "africains" dans le Pliocène d'Afghanistan (bassin de Sarobi). Implications paléobiogéographiques et stratigraphiques. *Bull. Mus. Natl. Hist. Nat. Paris, 4ᵉ sér. 1, sect. C,* 65–75. Paris.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Amer. Mus. Nat. Hist., Bull, 85,* 1–350. New York.

Simpson, G.G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. *Geol. Soc. Am., Bull. 58,* 613–688. Boulder.

Slaughtèr, B.H., and Ubelaker, J.E. 1984. Relationship of South American ericetines to rodentz of North America and the Old World. *J. Vertebr. Paleontol. 4,* 255–264. Los Angeles.

Stehlin, H.G. and Schaub, S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweiz. Palaontol. Abh., Basel 67,* 1–385. Basel.

Teilhard de Chardin, P. and Leroy P. 1942. Chinese fossil mammals. A complete bibliography analyzed, tabulated, annotated, and indexed. *Instut. de Geo-Biologie. Pékin 8,* 1–142. Peking.

Teilhard de Chardin, P. and Young, C.C. 1931. Fossil mammals from the late Cenozoic of northern China. *Palaeontol. Sin. Ser. C 9,* 1–66. Beijing.

Wessels, W., Bruijn, H. de, Hussain, S.T., and Leinders, J.J.M. 1982. Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *K. Nederl. Akad. van Wetenschappen, Proc., Ser. B. 85,* 337–364. Amsterdam.

Wilson, R.W. 1937. Pliocene rodents of western North America. *Carnegie Inst. Wash. Publ. 487,* 21–73. Washington, D.C.

Young, C.C. 1927. Fossile Nagetiere aus Nord-China. *Palaentol. Sin., Ser. C 5 (3),* 1–82. Peking.

Young, C.C. 1929. Notes on the mammalian remains from Kwangsi. *Bull. Geol. Soc. China 8 (2),* 125–130. Peiping.

Zheng Shaohua 1980. The *Hipparion* fauna of Bulong Basin, Biru, Xizang. Qinghai-Xizang Scientific Expedition Series *1,* 33–47. Beijing.

Zheng Shaohua 1981. New discovered small mammals in the Nihowan Bed. *Vertebr. PalAsiatica 19,* 348–358. Beijing.

Zheng Shaohua 1982a. Middle Pliocene micromammals from the Tianzhu loc. 80007 (Gansu Province). *Vertebr. PalAsiatica 20,* 138–147. Beijing.

Zheng Shaohua 1982b. Some Pliocene mammalian fossils from Songshan-2 and -3 (Tianzhu, Gansu) and the Songshan fauna. *Vertebr. PalAsiatica 20,* 216–227. Beijing.

Zheng Shaohua and Li Yi 1982. Some Pliocene lagomorphs and rodents from Loc. 1 of Songshan, Tianzu Xian, Gansu Province. *Vertebr. PalAsiatica 20,* 35–44. Beijing.

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PLATES

[All specimens are figured as stereographic pairs.]

Plate 1

Fig. 1. *Paracricetulus schaubi,* Specimen M.3419.361. Left maxilla with M^{1-3}. Young, 1927.

Fig. 2. *Lophocricetus pusillus*. Specimen M.3365.68. Left dentary with M_{1-2}. Schlosser, 1924.

Fig. 3. *Sinocricetus zdanskyi*. Specimen M.3415. Left dentary with M_{1-2}. Schlosser, 1924.

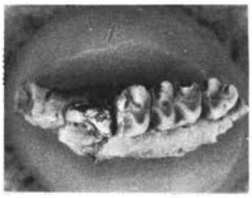
Fig. 4. *Sinocricetus zdanskyi*. Specimen M.3415. Right dentary with M_{1-2}. Schlosser, 1924.

Fig. 5. *Nanocricetus mongolicus*. Specimen M.375. Left dentary with M_{1-2}. Schlosser, 1924.

Fig. 6. *Lophocricetus grabaui*. Specimen M.3372.65. Right dentary with M_{1-3}. Schlosser, 1924.

Fig. 7. *Lophocricetus grabaui*. Specimen M.3372.65. Left dentary with M_{1-2}. Schlosser, 1924.

Fig. 8. *Lophocricetus grabaui*. Specimen M. 101.116.66. Right dentary with M_{1-2}. Schlosser, 1924.



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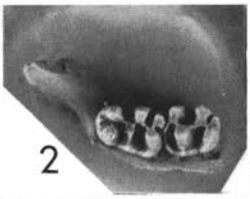

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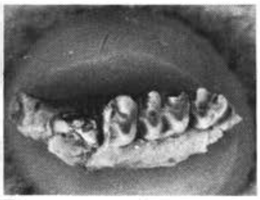

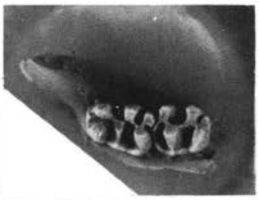

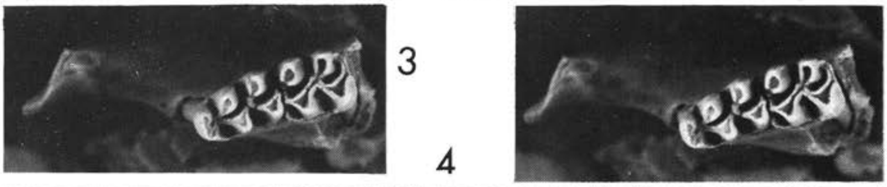

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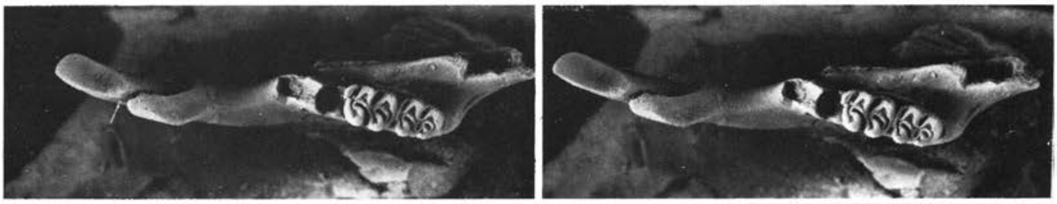

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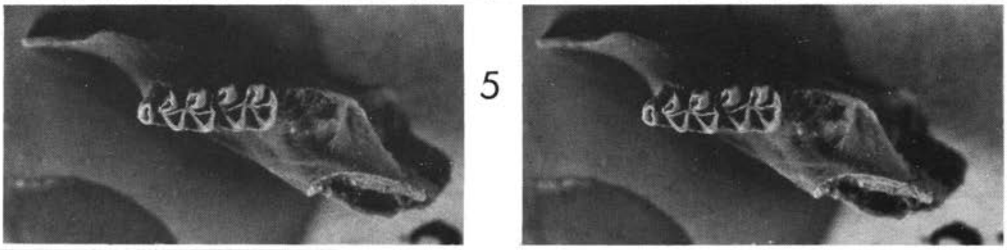

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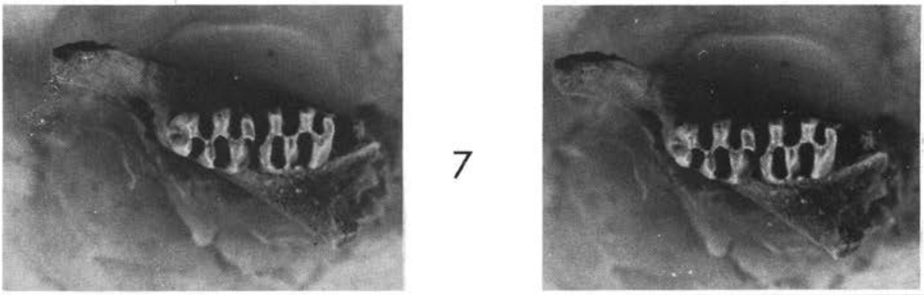

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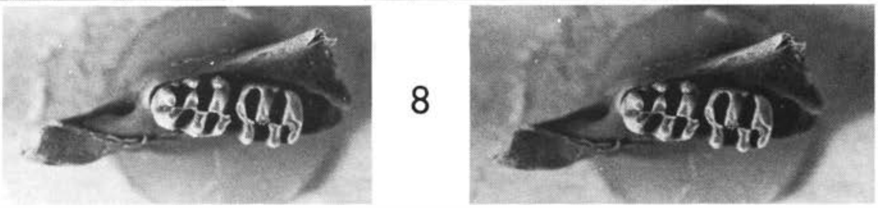

Plate 2

Fig. 1. *Plesiodipus leei.* Specimen M.3417.167. Right maxilla with M^{1-3}. Young, 1927.

Fig. 2. *Plesiodipus leei.* Specimen M.3417.167. Right dentary with M_{2-3}. Young, 1927.

Fig. 3. *Anatolomys teilhardi.* Specimen M.3374.74. Left dentary with M_{1-3}. Schlosser, 1924.

Fig. 4. *Lophocricetus pusillus.* Specimen M.3373.67. Right dentary with M_{1-2}. Schlosser, 1924.

Fig. 5. *Microtodon atavus.* Specimen M.101.116.71. Left dentary with M_{1-2}. Schlosser, 1924.

Fig. 6. *Microtodon atavus.* Specimen M.101.116.71. Left dentary with M_{1-2}, buccal view. Schlosser, 1924.

Fig. 7. *Microtodon atavus.* Specimen M.101.116.71. Left dentary with M_2, buccal view. Schlosser, 1924.

Plate 2

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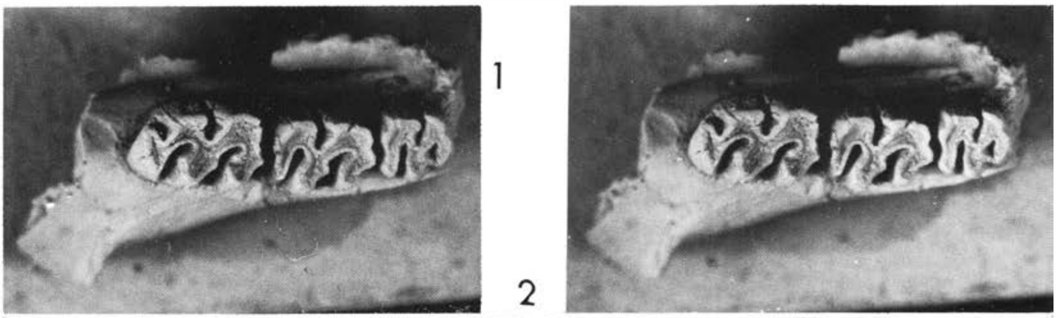

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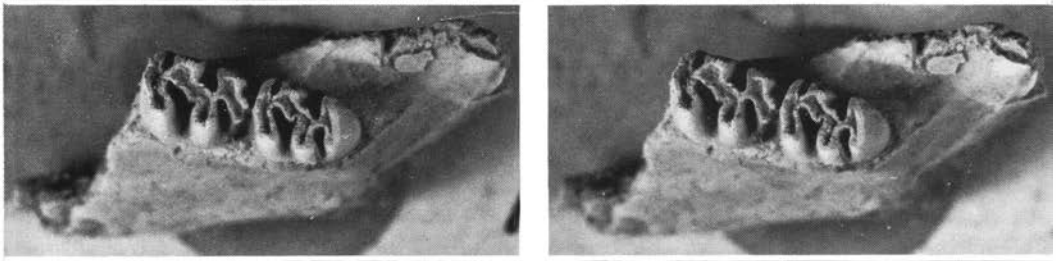

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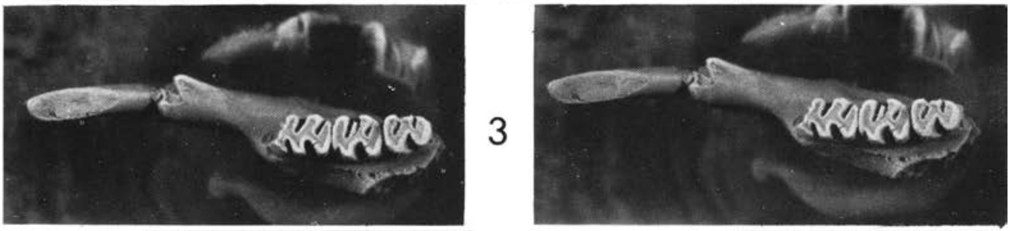

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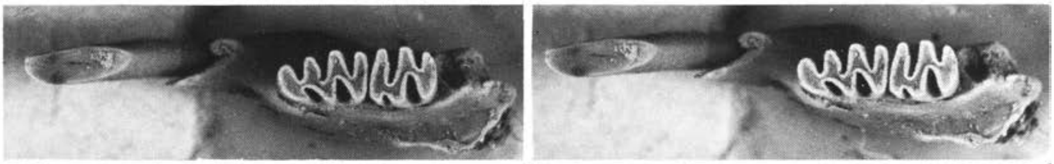

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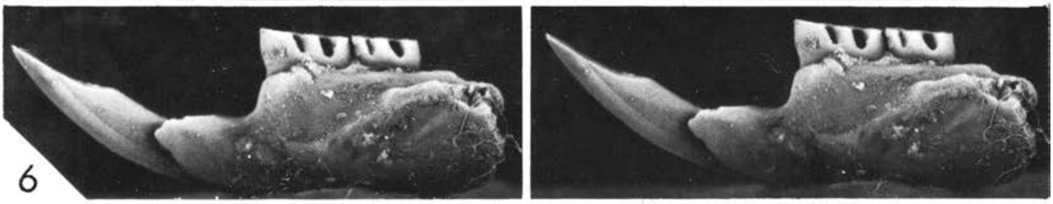

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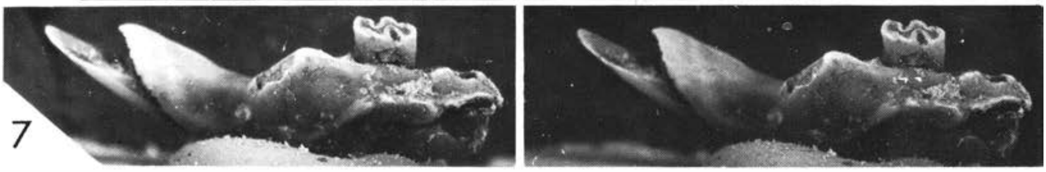


Plate 3

Fig. 1. *Microtodon atavus*. Specimen M.101.116.71. Left dentary with M_2. Schlosser, 1924.

Fig. 2. *Microtoscoptes praetermissus*. Specimen M.100. 288.38. Left M_1. Schlosser, 1924.

Fig. 3. *Microtodon atavus*. Specimen M.101.116.71. Right M_{2-3}. Schlosser, 1924.

Fig. 4. *Microtoscoptes praetermissus*. Specimen M.100. 288.38. Left M_1, buccal view. Schlosser, 1924.

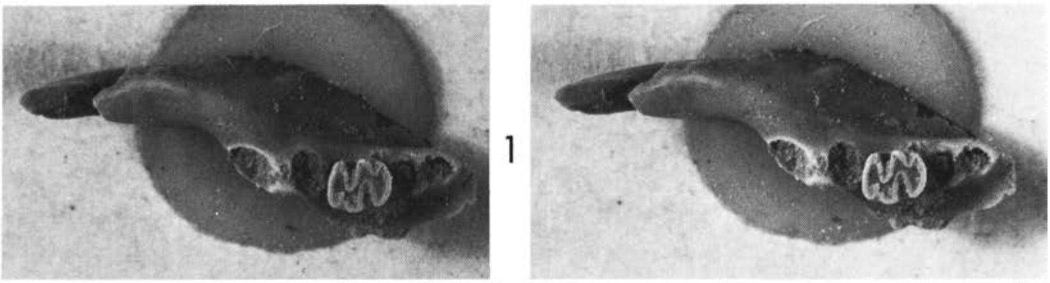
Fig. 5. *Microtoscoptes praetermissus*. Specimen M.100. 288.38. Left M_1, lingual view. Schlosser, 1924.

Fig. 6. *?Progonomys orientalis*. Specimen M.371. Right dentary with M_{1-2}. Schlosser, 1924.

Fig. 7. *?Parapodemus hipparionum*. Specimen M.3431. Left dentary with M_{1-2}. Schlosser, 1924.

Fig. 8. *Sminthoides fraudator*. Specimen M.3364.25. Left maxilla with M^{1-2}. Schlosser, 1924.

Plate 3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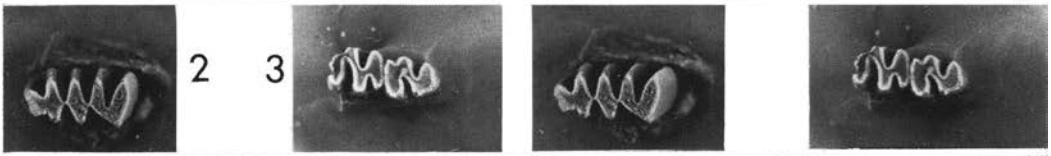
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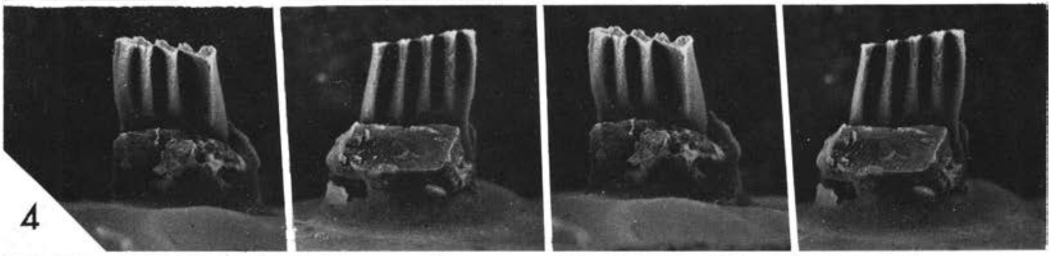
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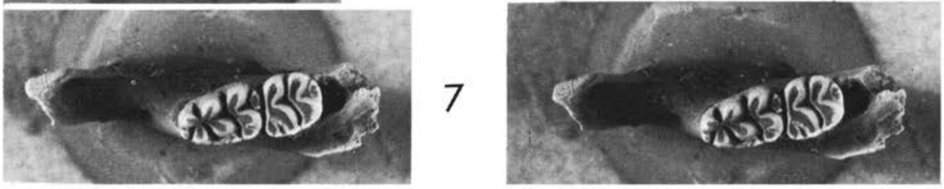
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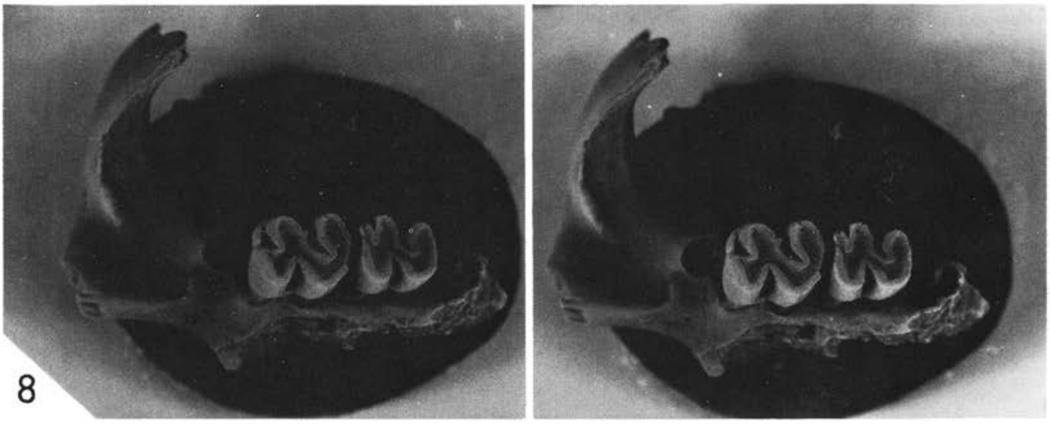
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Plate 4

Fig. 1. *Brachyrhizomys nagrii* from the Siwaliks of Pakistan. Specimen Yale-Geological Survey of Pakistan (YGSP) 8362. Skull. Bar equals 5 mm. After Flynn (1982a).

Fig. 2. *Brachyrhizomys nagrii* from the Siwaliks of Pakistan. Specimen YGSP 8364. Mandible. Bar equals 5 mm. After Flynn, 1982a.

Fig. 3. *Brachyrhizomys tetracharax* from the Siwaliks of Pakistan. Specimen YGSP 4810. Right dentary with M_{2-3}. Bar equals 5 mm. After Flynn (1982a).

Plate 4