

BEGINNING OF THE AGE OF
MAMMALS IN ASIA: THE
LATE PALEOCENE
GASHATO FAUNA,
MONGOLIA

FREDERICK S. SZALAY AND MALCOLM C. MCKENNA

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FAUNA, MONGOLIA

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INTRODUCTION

FOSSIL MAMMALS FROM THE CRETACEOUS and early Tertiary of the Mongolian People's Republic have long fascinated students of mammalian phylogeny and paleogeography, partly because of the strangeness of certain forms and partly because of the unexpected occurrence in Mongolia of families and genera known from other continents. These Cretaceous and early Tertiary Mongolian mammals were discovered mainly by the Central Asiatic Expeditions of the 1920's, but since World War II expeditions from the Academies of Sciences of the Union of Soviet Socialist Republics and Poland have visited Mongolia, participating in joint paleontological expeditions with the Mongolian Academy of Science, and Mongolian scientists themselves have begun paleontological work. As a result, important new collections from both new areas and old are now available for study. Meanwhile, the value of the original collections has been increased by the additional preparation of rare and delicate specimens and by the study of previously unreported fossils long dormant in the collections. The series of short descriptive papers published by the American Museum of Natural History in the 1920's and 1930's was never completed, nor was there a comprehensive review of all Mongolian fossil mammals or even of individual faunas. That work was postponed because of the deaths of Matthew, Osborn, and Granger; lack of funds; World War II; and competing research programs. Within the last two decades, however, there has been a revival of interest in late Mesozoic and early Tertiary mammals, and as the result of numerous new discoveries and interpretations it has become imperative to study anew the collections made in Mongolia by the Central Asiatic Expeditions. The present paper, therefore, attempts to bring into sharper focus the perplexing late Paleocene mammals of Southern Mongolia (fig. 1).

The original draft of the systematics section of this paper was prepared by Szalay. The other sections were prepared by McKenna. Both authors have modified each other's texts extensively, and the responsibility for the final draft is shared.

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R. H. Tedford, M. K. Hecht, M. Talwani, M. O. Woodburne, D. E. Savage, D. E. Russell, R. G. Zweifel, P. V. Rich, T. H. Rich, and W. C. Pitman, III, offered suggestions helpful in improving the manuscript.

The following abbreviation is used to designate an institutional collection:

A.M.N.H., the American Museum of Natural History, Department of Vertebrate Paleontology

THE GASHATO FAUNA

THE EARLIEST TERTIARY vertebrate fauna discovered in Asia was found in the Gashato Formation of southern Mongolia by F. K. Morris in 1923 while he was studying the stratigraphy of sediments overlying the Djadochta Formation. The latter formation is a Cretaceous unit famous for its excellently preserved dinosaurs, dinosaur eggs, and fossil mammal skulls. A preliminary paper on the Gashato fauna by Matthew and Granger was published in 1925, but while that paper was in press a second Gashato collection was made by the 1925 Central Asiatic Expedition. This permitted additional work on the Gashato fauna and modified the conclusions reached in the first paper. It is of interest to follow the development of our knowledge of the Gashato fauna and its significance.

In their first paper Matthew and Granger were rather cautious about both the affinities and the age of the Gashato fauna. The notoungulate *Palaeostylops* was known from one species stated to be ancestral to the American "Wasatch" genus *Arctostylops* and therefore believed to be indicative of Paleocene age.¹ The taeniolabidid multituberculate *Prionessus lucifer* was discussed as a possible ancestral form for the taeniolabidid

¹The Río Chico fauna of Patagonia was not yet known in 1925. Matthew and Granger (1925) and Matthew (1928) believed that the presence of a notoungulate at Gashato confirmed the theory that the South American Tertiary hoofed mammals were derived from the north. Patterson (1958, p. 12) and Patterson and Pascual (1968, p. 418) still accept a non-South American origin for notoungulates as such. Although this contention is logical and may be supported by other evidence, the molars of *Palaeostylops* are more advanced than any in the earliest South American notoungulates and probably indicate dispersal in the opposite direction after the origin of notoungulates in South America from condylarth stock of northern derivation. There is no physical evidence as yet that notoungulates were present prior to the late Paleocene on any continent, but the probability is far greater for South America where early and medial Paleocene deposits have yielded no mammal remains whatever than for North America. There is evidence, however, that notoungulates did not continue to flourish for very long after their initial appearances in North American and Asian Paleocene deposits. In North America this might be attributed to swamping by the Sparnacian faunal overturn. In Asia, however, many of the older endemics lingered, long past that time, yet notoungulates apparently did not. We regard notoungulates as unsuccessful Paleocene immigrants to Asia, not as ancient and ecologically entrenched inhabitants of either Asia or North America.

multituberculates and therefore indicative of Paleocene or Cretaceous age. Synonymy of the lagomorph-like genus *Baenomys* with *Eurymylus* was not yet discovered, and only the lower jaw ("*Baenomys*") was believed to have lagomorph affinities. The type maxilla of *Eurymylus laticeps* was compared favorably with Eocene tarsiods and plesiadapids, but was referred to the Menotyphla because of the complexity of the premolar pattern. *Phenacolophus* was compared with various ungulates, but no detailed comparisons with Pantodonta or Dinocerata were made. *Hyracolestes* and *Sarcodon* were described in the same paper, but Matthew and Granger's discussion of them was of necessity rather inconclusive.

Several years later Matthew, Granger, and Simpson (1928), on the basis of the 1925 collection, described the upper and lower molars of the multituberculate *Prionessus*, confirming its similarity to the American *Catopsalis* and *Taeniolabis*. They also described a new multituberculate genus and species, *Sphenopsalis nobilis*, which they regarded as a somewhat divergent taeniolabidid and which now is regarded as a cimolomyid (Van Valen and Sloan, 1966).

The bulk of the 1925 Gashato collection was discussed by Matthew, Granger, and Simpson in 1929. An additional species of *Palaeostylops* (*P. macrodon*) and four new genera and species of other mammals were named. The synonymy of "*Baenomys*" with *Eurymylus* was recognized and the distinctiveness of *Eurymylus* was emphasized by the creation of a monotypic family. The exact taxonomic position of the Eurymylidae was not fully determined, however, and several arguments against lagomorph affinities were briefly reviewed.

The four new genera named in 1929 were *Praolestes*, *Pseudictops*, *Opisthopsalis*, and *Prodinoceras*. *Praolestes* was based on a tiny lower jaw with three teeth mistakenly thought to be P_4-M_2 but actually P_3-M_1 . *Pseudictops* was based upon two specimens, the type consisting of a lower jaw with P_3-M_3 , and a maxillary fragment with two teeth.² Both *Pseudictops* and

²Several additional American Museum specimens of *Pseudictops* from Gashato have been identified recently in the course of additional preparation of the original collection.

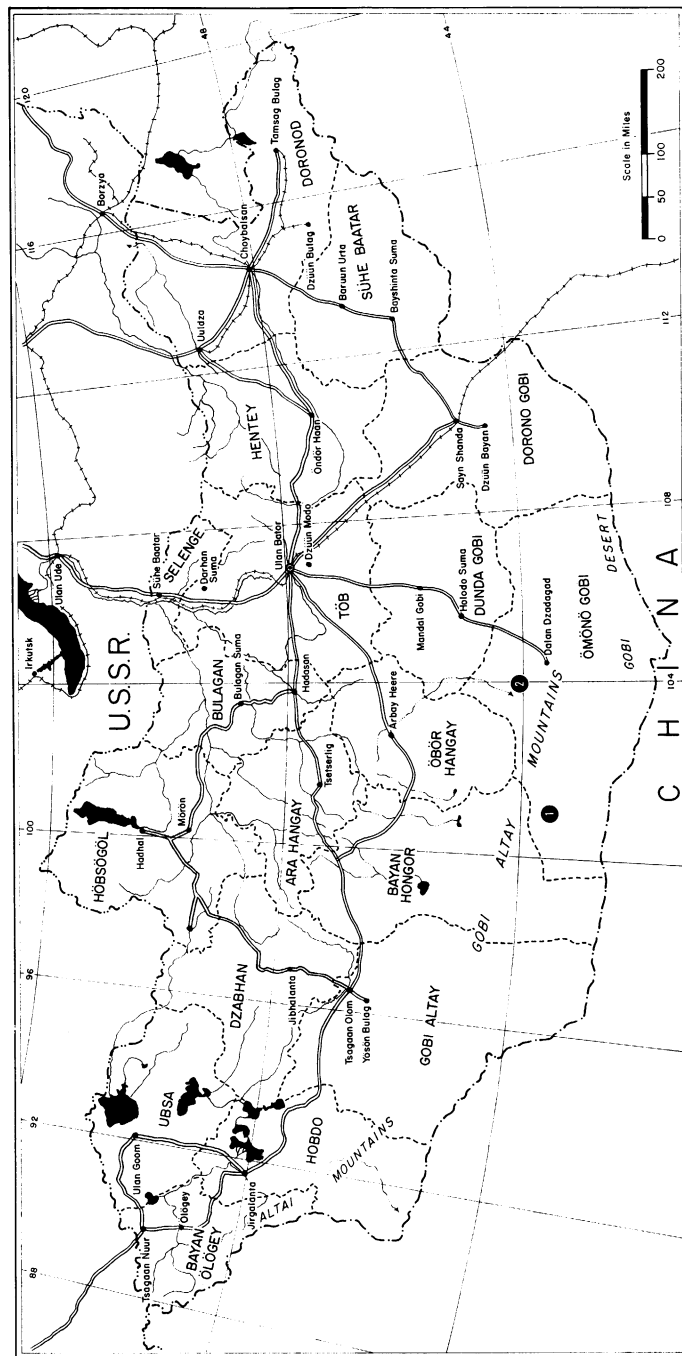


FIG. 1. Index map of Mongolian People's Republic, with Nemegt Valley shown with circled numeral 1 and Gashato with circled numeral 2.

Praolestes were placed in the Insectivora, *sensu lato*, but with doubt. *Opisthopsalis* was referred to the Hyaenodontidae with a query, mainly on the basis of resemblance to *Sinopa* (except P_4). In contrast to the previously discussed genera, the known remains of *Prodinoceras* proved to be similar, although differences were noted, to those of an American genus of primitive uintatheres, *Probathyopsis*, at that time the earliest known uintatheres. The angle of implantation and less distinct metacone of P^2 , complete molar cingula, relatively labial position of the molar hypocones, nature of the M_3 talonid, distinctive zygoria, and smaller size distinguish the American type specimen of *Probathyopsis praecursor* from that of the Mongolian *Prodinoceras martyr*. Presumably these differences are in themselves sufficient to merit maintenance of separate genera, and are now reinforced by differences in astragali not known in 1929, but the similarity of these two uintatheres was accepted as welcome

evidence of late Paleocene age of the Gashato fauna, bolstering the conclusions reached on the basis of comparison of *Palaeostylops* to the American earliest Eocene genus *Arctostylops*.¹

Continued research on New World Paleocene faunas has resulted in various minor advances in our understanding of the Asiatic Gashato fauna, notably as the result of discovery of late Paleocene faunas at Río Chico in Patagonia and Itaboraí, Brazil, and of uintatheres such as *Bathyopsoides* and *Prouintatherium* in various late Paleocene and early Eocene localities in the United States. The notoungulates of the South American faunas have a direct bearing on the *Palaeostylops* problem, and such South American genera as *Carodnia* and *Shecenia* conceivably could have a bearing, although we doubt it, on the problems of the affinities of uintatheres and *Phenacolophus*.

¹A late Paleocene *Arctostylops* from Wyoming has recently been reported (Jepsen and Woodburne, 1969, p. 544).

EXTENSION OF THE GASHATO FAUNA TO THE NEMEGT VALLEY SITES

Significant advances in understanding the earliest known Tertiary mammals of Mongolia have come from new studies of the previously described Gashato material, notably Wood's (1942; 1957) work on *Eurymylus*, and especially from renewed collecting by the Russians and Poles in cooperative expeditions with the Mongols at Gashato (=Khashiat, Khashaat, transliterated Russian and Polish equivalents, respectively, for the Mongolian *xauuam*, a corral) and at various localities at slightly different stratigraphic levels in the Nemegt Valley, Mongolia, about 250 kilometers west-southwest of Gashato (Novozhilov, 1954; Gradziński, Kaźmierczak, and Lefeld, 1969). Trofimov (1952) described new material of *Pseudictops lophiodon* Matthew, Granger, and Simpson, 1929 (= *P. arilophiodon* Trofimov, 1952), from both Gashato and Naran Bulak (presumably from the White Beds of Gradziński et al., 1969 = upper part of the white sandy-clayey series, bone-bearing series, Naran-Bulak Beds of Novozhilov, 1954, pp. 36, 37; Naranbulak Formation of Flerov, 1957b, p. 37, in the Nemegt Valley). Flerov (1952a) and Kielan-Jaworowska (1969a) described several specimens of the small barylambdid genus

Archaeolambda from the same deposits at Naran Bulak and Ulan Bulak in the Nemegt Valley, and Flerov (1957a) published on additional material of *Phenacolophus* (= *Procoryphodon* Flerov, 1957a; see Simons, 1960, p. 10) from Gashato.

The Soviet work in the Nemegt Valley resulted in acceptance by the Russians of two supposedly significantly different faunal levels, roughly equivalent to the American "Gray Bull" and "Wind River" according to Flerov (1957b), on the basis of *Mongolotherium efremovi* in the lower level and *M. plantigradum* in the upper, but this was clearly going beyond the evidence. Polish-Mongolian collections obtained by cooperative expeditions from the upper fossiliferous horizon at Naran Bulak, separated stratigraphically from the lower fossiliferous horizon by about 13 meters, contain *Pseudictops lophiodon*, *Eurymylus laticeps*, both species of *Palaeostylops*,² and an edentulous

²Simpson (1936, p. 8) appears to have been the first to suggest that the two species of *Palaeostylops* may represent two closely related genera. Gradziński, Kaźmierczak, and Lefeld (1969) listed only *Palaeostylops iturus* from their upper fossiliferous horizon in their White Beds. That both species are present is McKenna's conclusion based upon preliminary examination of both the Russian and Polish-Mongolian collections.

multituberculate jaw identified as *Prionessus* (Kielan-Jaworowska and Dovchin, 1969, p. 17; Gradziński et al., 1969) or ?*Prionessus* (Sulimski, 1969, p. 101). Flerov's two levels (at Naran Bulak) are said by him to be separated by only about 30 meters (K. K. Flerov, personal commun.), which would place both levels within the White Beds and suggests strongly that they are identical with the two horizons of the Polish geologists. It may not even be necessary to regard *Mongolotherium plantigradum* (upper level, Naran Bulak and Ulan Bulak) as the direct descendant of *M. efremovi* (lower level, both localities), especially because the Nemegt deposits were rapidly deposited (K. Kowalski, personal commun.). For convenience, it may suffice to regard the various Nemegt localities as essentially of a single age, either equivalent to, or only slightly younger than, the Gashato fauna. Although the assemblages at Gashato and the Nemegt Valley are poorly known and probably far from complete, they do share at least *Pseudictops*, *Eurymylus*, and *Palaeostylops*, all represented by identical species. A fourth genus, *Prionessus*, is also shared, but the species cannot yet be identified.

OTHER ASIAN PALEOCENE MAMMAL SITES

Paleocene localities also have been found in China; first in the Turfan Basin of Sinkiang (Chow, 1960) and later in the South China coastal province of Kwangtung (Young and Chow, 1962; Chow and Young, 1963; Young, 1964). *Prodinoceras turfanensis* Chow, 1960, is the only Paleocene mammal to be reported thus far from Sinkiang. The species is based upon a single individual, slightly smaller than the type specimen of *Prodinoceras martyr* from Gashato. Chow (*Ibid.*, p. 100) could find little reason for naming a new species distinct from *P. martyr*. The age of the Sinkiang deposits, reported to be "sandstones composed of clean white coarse grained sands probably of lacustrine origin," is therefore essentially the same as that of the Gashato fauna. The age of the Kwangtung locality is less certain. No descriptions of the mammals have been published. Chow and Young (1963) reported a mesonychid resembling *Dissacus*, a small primitive pantolambdid-like pantodont, turtle remains having earlier received the name *Anosteira lingnancia* Young and Chow, 1962, and three crocodilids: *Asiatosuchus nanlingensis* Young, 1964; *Eoalligator chunyi* Young, 1964; and *Eoto-*

mistoma multidentata Young, 1964 (emended from *Eotomiotoma*, a *lapsus*). Possibly the locality is earlier than late Paleocene, as Chow and Young speculated, but further comment is inappropriate until the mammalian evidence is fully published. The rocks from which these remains have been recovered are variously known as the Tanya group or Luofuzhai (=Luofucai) series.

Biryukov and Kostenko (1965) have indicated the presence of a Paleocene site in the Zaysan Depression of eastern Kazakhstan, but the evidence has not been presented.

THE AGE OF THE GASHATO FAUNA

The age of the Gashato fauna is clearly either latest Paleocene or early Eocene, but it is difficult at present to correlate continental deposits from Central Asia to either Europe or North America with sufficient resolution to settle the matter. We have attempted to date the basaltic lava mentioned by Berkey and Morris (1927, pp. 317, 358) by the Potassium/Argon method, but have been thwarted by the weathered nature and consequent geochemical unsuitability of the three samples collected by those authors. At our suggestion attempts to obtain adequate samples have been made by the Polish geologist Lefeld, but the lava has not yet been relocated in the field. It would be a service to paleontology if some future worker would collect and date an adequate unweathered sample of the 6-meter thick basalt occurring (*vide* Berkey and Morris, 1927) about 40 meters above the base of the Gashato Formation. An oriented sample should also be collected for the purpose of determining the virtual geomagnetic pole position at the time the flow cooled.

Paleontological arguments concerning both the Gashato occurrence and the Nemegt Valley occurrences must deal with problems of ecology (including paleolatitude, paleoclimate, and paleoaltitude), with evidence of widespread dispersal of Spornacian vertebrates between Europe and North America at the beginning of Eocene time, with evidence of dispersal between Asia and the Americas at about the same time, with current theories of global tectonics, and with problems of collecting bias. Not all of these can be dealt with satisfactorily at present. Table 1 attempts to assess each taxon of the complete faunal lists from Gashato and the Nemegt Valley from the standpoint of correlative usefulness at present.

TABLE 1
MAMMALIAN TAXA FROM GASHATO AND THE NEMEGT VALLEY, SOUTHERN MONGOLIA

| | Gashato | Nemegt | Correlation ^a |
|---|---------|--------|--------------------------|
| Multituberculata | | | |
| Taeniolabididae | | | |
| <i>Prionessus lucifer</i> | x | ? | ?P |
| Cimolomyidae | | | |
| <i>Sphenopsalis nobilis</i> | x | — | ?P |
| Insectivora | | | |
| Palaeoryctoidea | | | |
| Deltatheridiidae | | | |
| <i>Hyracolestes ermineus</i> | x | — | I/?E |
| <i>Sarcodon pygmaeus</i> (= <i>Opisthopsalis vetus</i>) | x | — | I |
| Anagalida, new order | | | |
| Zalambdalestidae | | | |
| <i>Praolestes nanus</i> | x | — | I |
| Eurymylidae | | | |
| <i>Eurymylus laticeps</i> | x | x | I |
| Pseudictopidae | | | |
| <i>Pseudictops lophiodon</i> (= <i>Pseudictops arilophiodon</i>) | x | x | I |
| Anagalidae | | | |
| <i>Khashanagale zofiae</i> , new genus, new species | x | — | I |
| ? <i>Khashanagale</i> , unnamed new species | x | — | I |
| Condylarthra | | | |
| Mesonychidae | | | |
| ? <i>Dissacus</i> sp. | x | — | I |
| <i>Pachyaena</i> sp. | — | x | I/?E |
| Unnamed new family ^b | | | |
| <i>Phenacolophus fallax</i> (= <i>Procoryphodon primaevus</i>) | x | — | I |
| Pantodonta | | | |
| Barylambdidae (including Archaeolambdidae) | | | |
| <i>Archaeolambda planicanina</i> | — | x | P |
| Dinocerata | | | |
| Uintatheriidae | | | |
| Prodinoceratinae, new rank | | | |
| <i>Prodinoceras martyr</i> | x | — | P |
| <i>Mongolotherium efremovi</i> | — | x | P |
| <i>Mongolotherium plantigradum</i> | — | x | P |
| Notoungulata | | | |
| Arctostylopidae | | | |
| <i>Palaeostylops iturus</i> | x | x | ?P |
| <i>Palaeostylops macrodon</i> | x | x | ?P |

^aP, Paleocene affinities; I, biostratigraphically indeterminate for intercontinental correlation at the resolution required; E, Eocene (Sparnacian) affinities.

^bOne of us (McKenna) is preparing for publication elsewhere a review of the genus *Phenacolophus*, based in part upon additional remains of the type and other specimens, collected by the Russians in 1948 at Gashato.

COMMENTS ON CORRELATIVE VALUE OF GASHATO AND NEMEGT MAMMALS

The mammalian assemblage from Gashato and the Nemegt Valley of Southern Mongolia can be subdivided into two major subgroups on the basis of paleogeographic origin. The first

subgroup, consisting of the Multituberculata, Insectivora, and Anagalida, represent endemic holdovers from Cretaceous times, historically isolated from Europe by the Turgai Straits (Schaffer, 1924, fig. 544; Kurtén, 1966; D. E. Russell, 1968), from India by the Tethys Ocean, and from North America by weak, roughly

concentric climatic belts centering around a rotational paleopole situated with respect to the continental masses relatively nearer northern Siberia than the present rotational pole (Irving, 1964; McElhinny and Wellman, 1969; Larsen, Mutschler, and Brinkworth, 1969). In late Paleocene time, limited high latitude dispersal westward to Asia of the second major subgroup, consisting of primitive uintatheres, barylambdids, notoungulates, and the ancestors of *Phenacolophus*, took place. These same animals were somehow apparently prevented from entering Europe at the same time, but the reasons for that are unknown and the question perplexing. Possibly the solution lies in an understanding of the altitude preferences of these early mammals: those with populations adapted to higher ground in lower latitudes may have been preadapted for early dispersal across the Bering area, but were prevented from reaching Europe westward by the Turgai Straits as well as by altitude and latitude preferences. If a land connection from the North American to the European crustal blocks existed at that time it was evidently a strong filter bridge, in contrast to Sparnacian time when little filter action is indicated, assuming a land connection was present. If such a land route existed in Sparnacian time it would also have existed in the Paleocene, but would at that time have been a strong filter bridge because of the relatively cooler and more varied Paleocene climate (Dorf, 1959; Wolfe and Hopkins, 1967). The Bering route would have been an even more effective filter in the Paleocene. Perhaps the North Atlantic and Bering routes simply filtered different genera in Paleocene time.

Gashato multituberculates are not useful for correlation beyond Mongolia because they are best interpreted as relicts, descended from the Cretaceous multituberculates of the same area. The same can be said for the insectivorans, which seem to be *in situ* differentiates.¹ The

order Anagalida, containing Zalambdalestidae, Pseudictopidae, Anagalidae, and Eurymylidae, constitutes a major radiation of several endemic families descended from an insectivoran stock but sharing some features with lagomorphs. Members of the order are unified by dental pattern and foot structure (where known), but in their various lineages have diverged from their common ancestry sufficiently to warrant creation of an order for the whole group. *Khashanagale*, though a primitive anagalid with important links with the zalambdalestids, eurymylids, and insectivorans, is not sufficiently known to be of correlative usefulness; its morphology is appropriate for either a late Paleocene or an early Eocene genus. *Praolestes*, *Eurymylus*, and *Pseudictops* are also of no use as yet in correlation beyond the boundaries of Mongolia.

Immigrants to the Mongolian area during the Paleocene were apparently few in number, suggesting a filter bridge. At least one mesonychid, another condylarth (arctocyonid or phenacodontid), a barylambdid pantodont, a prodinoceratine uintathere (or arctocyonine condylarth ancestor of the prodinoceratines), and an arctostyloid notoungulate all are interpreted here to have arrived prior to the Eocene, a majority and perhaps all immigrating to Asia from North America. Thus Asian endemism began to be broken down by sporadic arrivals of condylarths and condylarth derivatives from the northeast, across the Bering area, not by arrivals crossing the Turgai Straits from Europe. If any of the endemic Mongolian forms crossed the Bering area in the opposite direction, to colonize North America, we are forced to specify, *ad hoc*, that they would have been restricted to northern paleolatitudes and are therefore not known from American and southern Canadian Paleocene sites. The mesonychid, *Pachyaena* sp., from the "middle bone-bearing horizon" (Gromova, 1952, p. 71) of the Nemegt Valley, suggests early Eocene rather than late Paleocene age for one of the Nemegt levels, if one assumes significant age differences among the various Nemegt localities, but perhaps the animal is just an early occurrence in Asia of *Pachyaena*. Possibly *Pachyaena* arose in Asia from pre-existing mesonychids similar to *Dissacus*, such as were present at Gashato and in the Paleocene of South China (Young and Chow, 1963). In North America and Europe *Pachyaena* occurs only in the Eocene. *Phenacolophus*, on the other hand, represents

¹Van Valen (1966, p. 61) thought that *Sarcodon* weakly suggested early Eocene age, but this idea was based on incorrect views concerning the nature as well as the affinities of that genus. Van Valen (1967, p. 258 ff.) assigned a provisional early Eocene age to the Gashato insectivorans (and other taxa), referring apparently to figure 1 of Van Valen and Sloan (1966) but not to the text (pp. 271-272) or figures 4 and 5 of the same paper, which had indicated that in the authors' opinion Gashato was either late Paleocene or early Eocene in age. *Hyracolestes* or a close relative or descendant may have reached Europe by Sparnacian time (Rich, In press).

an endemic differentiation from some arctocyonid or phenacodontid condylarth, suggestive in several ways of Sirenia, Desmostylia, and Proboscidea. Presumably this differentiation had required time, but we have no evidence concerning the rate of evolution of *Phenacolophus*. The barylambdid pantodont, on the contrary, belongs to a family unknown before the late Paleocene in North America and unknown at any time in Europe. A peculiarity of the barylambdids is that they represent a number of closely related but distinct lineages at the generic level, yet intermediate steps in their phylogeny are unknown at present in the United States or Mexico where they are abundant in late Paleocene deposits (Simons, 1960; Morris, 1966). Presumably barylambdids originated in North America from *Pantolambda* or some closely related but still undescribed genus of Torrejonian pantodonts. Inasmuch as they must also have occupied at least western Canada and Alaska during at least some part of the late Paleocene, that area may well have been a true center of evolution, various offshoots from a central lineage similar to *Haplolambda* having proceeded from there to invade both Asia as far as Kwangtung¹ and also areas to the south of Canada in the United States and Mexico, but apparently the family never reached Europe.

The primitive Mongolian uintatheres *Prodinoceras* and *Mongolotherium* are closely related both to each other and to the American late Paleocene genus *Bathyopsoides*. The differences are minor and in part actually spurious; e.g., the plaster reconstructed horns of *Probathyopsis* (Patterson, 1939) accepted as fact by Flerov (1952b) when naming the essentially hornless *Mongolotherium* as a new genus. Such differences as do actually exist among members of these three genera, insofar as they indicate taxonomic differences rather than sexual dimorphism or growth-stage differences, may represent species differences only. If this is true, the Mongolian and Sinkiang occurrences of prodinoceratine uintatheres could all be Paleocene in age. Uintatheriine uintatheres were present in Asia by the early Eocene in the form of *?Probathyopsis* (Chow and Tung, 1965, p. 371), although whether descended from Asian Paleocene prodinoceratines or newly arrived from America we do not know.

¹We here assume that the undescribed Kwangtung pantodont is more likely to be a small barylambdid (including the "archaeolambdids") than a pantolambdid.

The arctostylopids need no longer indicate an Eocene age for the Asian localities inasmuch as *Arctostylops* is now known to have been present in the American late Paleocene. The original specimen of *Arctostylops steini* was collected from rocks no younger than early Wasatchian in any case.

SPARNACIAN FAUNAL REPLACEMENT

By early Eocene (Sparnacian) time climates warmed (Dorf, 1959; Wolfe and Hopkins, 1967) and a new wave of northern dispersal caused extensive faunal overturn in the Northern Hemisphere (Simpson, 1947; D. E. Russell, 1968). On the basis of paleontological evidence now in hand, this dispersal was apparently directly between Europe and North America prior to the final separation in the far north of those two land masses, but fossil mammal-bearing true early Eocene sediments are not yet known from Asia other than from coastal China, and the available sample from there is too poorly known to allow much speculation about dispersal to or from Europe of coastal forms across the Turgai Straits in Sparnacian time. The possible differences in faunal composition between Southern Mongolia and coastal China in early Eocene time are at present unfortunately unknown. The coastal early Eocene assemblage includes *Coryphodon*, *Homogalax*, and *Heptodon*, the last two genera being perissodactyls of American derivation potentially and probably actually ancestral to the Asian tapiroid² radiation of later deposits (Radinsky, 1965). Perissodactyls deployed easily throughout Asia by late Eocene time, and it is difficult to imagine any Eocene fauna in the Northern Hemisphere, especially an early Eocene one, lacking representatives of that order. *Coryphodon* is likewise ubiquitous in early Eocene faunas. We prefer to postulate that the Gashato

²Zdansky (1930) and Young (1944) have claimed that palaeotheres were present in Shantung and Kwangtung in the Eocene of China. Both occurrences have been referred to the otherwise European Lutetian genus *Propalaeotherium*, but that genus is now regarded as an hyracotheriine equid, not a palaeothere (Savage, Russell, and Louis, 1965, p. 1). We agree that the Chinese species are hyracotheriine differentiates, but question their reference to *Propalaeotherium*. The Chinese material is not yet well enough known to demonstrate special relationship to any European genus or to prove a crossing of the Turgai Straits. Chow (Tang and Chow, 1964; 1965, p. 1342) now regards the Kwangtung hyracotheriine occurrence as early Eocene in age.

and Nemegt assemblages were present before the advent of *Coryphodon* and perissodactyls in Asia rather than to attempt to claim ecological exclusion for which there is no independent evidence.

In summary, we believe that the Gashato fauna lived prior to an episode of increased dispersal that brought certain Sparnacian vertebrates to Asia via a northeastern, not a western route. We therefore regard the Gashato fauna as

latest Paleocene in age. Romer (1966, p. 335) has proposed but not defined a "Gashatan Asiatic Age" and an "Ulanbulakian Asiatic Age"; if the term "Gashatan Asiatic Age" is to be used, we suggest it be characterized by the joint overlapping time ranges of *Palaeostylops*, *Pseudictops*, *Prionessus*, and *Eurymylus*. We refer Romer's "Ulanbulakian Asiatic Age" to the "Gashatan."

PALEOGENE NORTHERN DISPERSAL ROUTES AND THE GEOLOGICAL EVIDENCE

A REVOLUTION in geophysical interpretation of our planet is currently sweeping geological thought and without question will also revolutionize and lend substance to paleogeographical interpretations by paleontologists. The three subjects of "continental drift," "polar wandering," and "sea floor spreading" have now been meshed with profound new insight by geophysicists. Interested readers are referred to recent issues of the *Journal of Geophysical Research* for some of the more important articles and lists of references. An excellent summary is provided by Heirtzler et al. (1968). We attempt here to assess the implications of some of this new geophysical work with regard to the calculated position of the rotational pole at the beginning of the Tertiary and with regard to the relative positions of possible intercontinental dispersal routes in relation to that calculated pole position. We accept for the purposes of argument that Earth's field is primarily a dipole and that averaged secular variation of individual virtual paleomagnetic pole positions should coincide with rotational pole positions (Irving, 1964, pp. 45, 105).

McElhinny and Wellman (1969, p. 203) have recently updated Irving's (1964) calculation of early Tertiary rotational pole positions by incorporation of additional data from Scottish Tertiary igneous rocks (Raja, 1964; Smith, 1966) and from Cretaceous and early Tertiary andesites from Bulgaria (Vollstädt, Rother, and Nozharov, 1968). A mean for 17 calculated positions for the Eocene and Oligocene lies close to the present position of the New Siberian Islands at latitude 77°N. , longitude 150°E. , with a 5-degree circle of 95 per cent confidence. This lies close to the previously calculated Mesozoic-Tertiary polar-wander path for Asia (Irving, 1964, p. 137) and is on the same side of the Arctic Ocean but 2000 kilometers east of three virtual geomagnetic pole positions determined recently by Larsen, Mutschler, and Brinkworth (1969) from North American Paleocene lavas in Colorado. We accept that the rotational pole was near the New Siberian Islands at the close of the Paleocene.

Funnell and Smith (1968) have calculated the rates of opening of various parts of the Atlantic Ocean and have arrived at a center of rotation of the North American continent away from Europe (or vice versa) at latitude 88°N. , longitude 28°E. This is a different center of rotation from those proposed by Carey (1958) and Wilson (1963, fig. 5), and is not the same as any of the centers of rotation of individual Atlantic plates. Funnell and Smith's calculations, based upon a steady rate of spreading for the last 200 million years, yield a figure of 67 per cent opening of the main part of the North Atlantic (south of Greenland or Norway) at the end of the Cretaceous. When extrapolated to late Paleocene time this requires North America to be rotated back toward Europe by only an 11-degree angle. But if the opening of the Atlantic has accelerated since the beginning of the Cretaceous (Reyment, 1969) or the Norwegian and Greenland seas did not begin to open until about 60 or 70 million years ago (Avery, Burton, and Heirtzler, 1968; Vogt, Ostenso, and Johnson, 1970), then a somewhat larger amount of movement per unit of time is necessary. If the opening of the Norwegian and Greenland seas took place mainly during the Tertiary, McElhinny and Wellman's (1969) early Tertiary rotational pole calculated from European data would more nearly coincide with the virtual geomagnetic poles of Larsen et al., calculated from North American data, but the data of Larsen et al. are only suggestive concerning the position of the Paleocene rotational pole with relation to North America because the sample of virtual poles is small.

By means of a globe and a hemispherical transparent plastic overlay we have attempted to plot the approximate positions of the northern continents at the beginning of the Eocene, oriented about a rotational pole in the vicinity of the New Siberian Islands. North America was first moved back toward Europe by the minimum amount required by Funnell and Smith (fig. 2), and then by the large amount suggested by Avery et al. (fig. 3). According to the Funnell and Smith scheme, southeastern (not north-

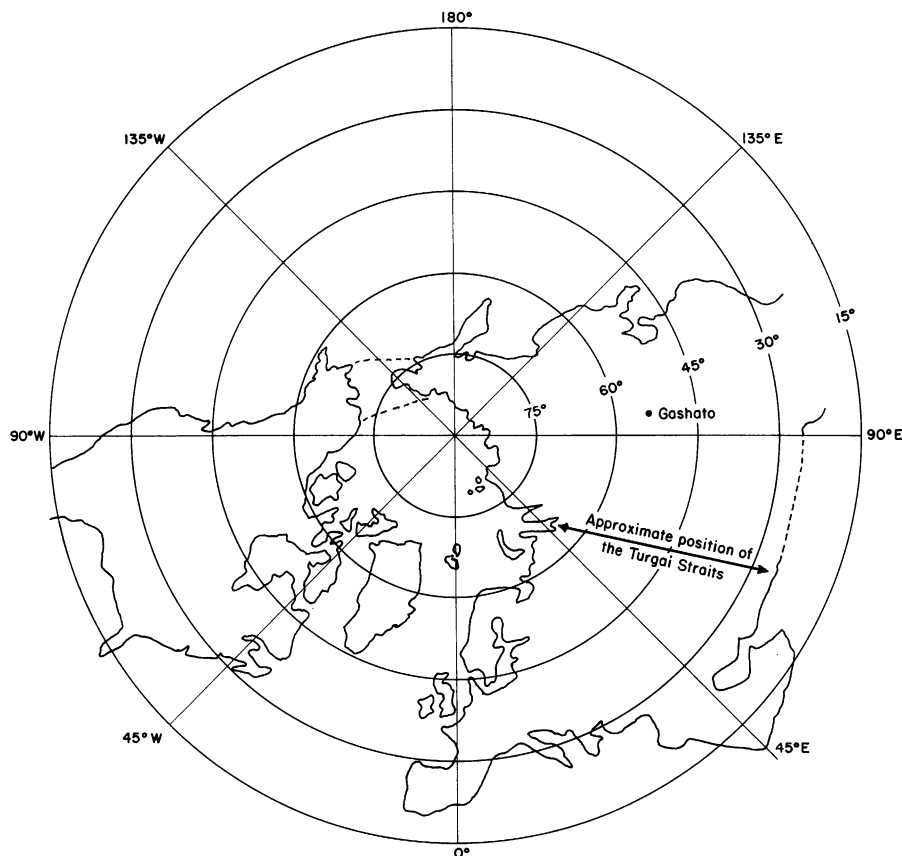


FIG. 2. Attempted paleopolar projection of Holarctica for approximately late Paleocene time, incorporating only the concepts of Funnell and Smith (1968) and McElhinny and Wellman (1969). North America has been rotated back toward Europe 11° about a center of rotation at 88°N , 28°E . The late Paleocene rotational pole has been placed at 77°N , 150°E , near the New Siberian Islands. No corrections are made for transform faults, fracture zones, or smaller crustal block movements in or north of the Norwegian and Greenland seas. A dry-land dispersal route across the Norwegian Sea is not suggested. Details of present coastlines are crudely depicted for ease of recognition. Iceland is omitted because it is not known to have existed in the Paleocene.

eastern) Greenland and western Norway would still have been about 1000 kilometers from each other during Sparnacian time, suggesting that if a North Atlantic dry-land dispersal route existed, it lay north of the Norwegian Sea, crossing the De Geer dextral transform fault zone (Spitsbergen fracture zone) (Harland, 1961, p. 127; Wilson, 1965, p. 344; Johnson and Heezen, 1967; Ostenso, 1968; Harland, 1969; Vogt et al., 1970) from Greenland to a juxtaposed Spitsbergen and from there to the rest of Europe via an elevated Barents shelf. Under the Funnell and Smith scheme about 200 kilometers of Tertiary dextral movement along the De Geer

transform fault zone (Spitsbergen fracture zone) is required. The Tertiary dextral movement along the same fracture zone under the rationale of Avery et al. would be close to 600 kilometers, but this requires no more than about 1 cm./year separation of Greenland from Norway and the Barents shelf, averaged over the last 55 million years. At the beginning of the Eocene Spitsbergen and the Barents shelf could have been juxtaposed to northern Greenland and Ellesmere Island if Avery et al. are correct. The European and North American crustal blocks would have been in contact, not separated by a spreading mid-ocean ridge. This is because the

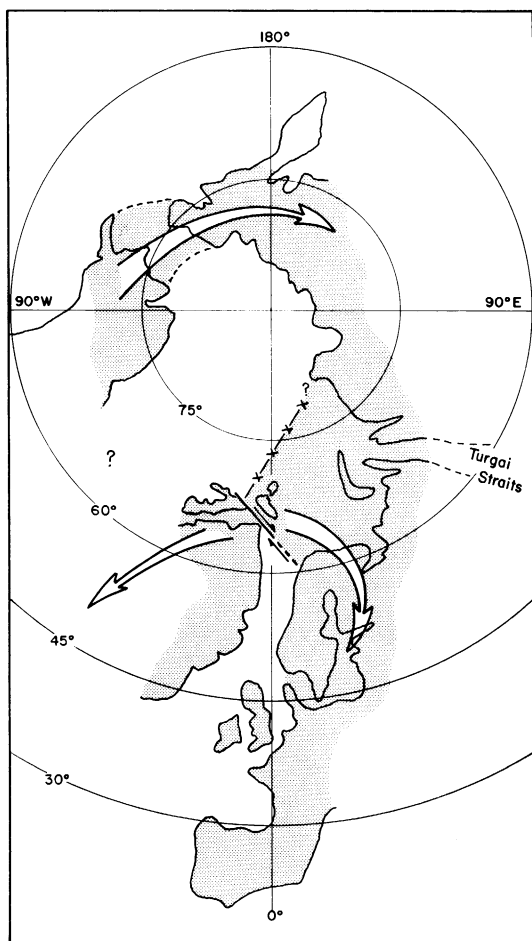


FIG. 3. Attempted Sparnacian reassembly of the North American and European crustal blocks at Spitsbergen, Greenland, and Ellesmere Island by subtracting subsequent motion along Wilson's (1965) De Geer transform fault zone (Spitsbergen fracture zone) and opening Norwegian and Greenland Seas at a rate suggested by Avery et al. (1968) and Vogt et al. (1970). Iceland is omitted because it is not known to have existed at that time. Latitudes are shown with respect to the rotational pole positions calculated by McElhinny and Wellmann (1969). The additional assumption is made that part of the Barents shelf was above sea level. The approximate edge of the Barents shelf is shown by a line -x-x-x-x. The epicontinental Turgai Straits would have extended to Tethys. Details of coastlines are crudely depicted for ease of recognition. Large arrows indicate postulated dry-land dispersal routes between European and North American crustal blocks, and from North America to Asia via the Bering route.

mid-ocean ridge itself was offset sinistrally by the De Geer transform fault zone (Spitsbergen fracture zone) (see Wilson, 1965, for geometrical explanation). The part of the fault zone lying between the now more widely offset mid-ocean ridges is still active (Heezen and Ewing, 1961, fig. 10), as would be expected. It seems to consist of several closely spaced transform faults (Vogt et al., 1970, fig. 10a). The final phase of opening of the Norwegian and Greenland seas, connecting the Atlantic permanently with the Arctic Ocean, could have occurred at the end of Sparnacian time in the early Eocene and would in that case be the cause of observed dissimilarities at the generic level between terrestrial Cuisian and later faunas of Europe and North America. Subsequent Tertiary faunal similarities between Europe and North America resulted from dispersal via the Bering Route.

A more southerly route for terrestrial organisms via Iceland and the Iceland-Faeroes aseismic ridge (Kurtén, 1966) would have involved island-hopping at best, even assuming Iceland was above sea level (Johnson and Heezen, 1967). Such a route would not suffice, however, for the large scale faunal transfer that took place in the Sparnacian. That the Atlantic was already connected with the Norwegian Sea, athwart this postulated route, has been demonstrated by Saito, Burckle, and Horn (1967), who reported a medial Paleocene foraminiferal assemblage northeast of Iceland at latitude 66°N. , longitude 0° .

Calculated paleolatitudes based upon a rotational pole near the New Siberian Islands show shifted latitudes for various localities (table 2). The Bering area would have been about 8 degrees farther north than the Greenland-Barents shelf route, and the latter would therefore have been more favorably situated from a climatic standpoint than it would have been had the rotational pole been where it is now. Although age determinations for Alaskan and Greenland early Tertiary floras are not precise, Paleocene and medial or late Eocene floras from Cook Inlet and the Gulf of Alaska (Wolfe, 1966; 1969) and ?Paleocene floras from east and western Greenland (Mathieson, 1932; Koch, 1963) consist of leaves and wood of abundant broad-leaved evergreens whose leaves had a high percentage of entire leaf margins. Such features are generally indicative of warm temperate to more tropical floras today. Clearly, by Sparnacian time, cli-

TABLE 2
PRESENT AND CALCULATED EARLY EOCENE
PALEOLATITUDES FOR SOME SIGNIFICANT LOCALITIES^a

| Locality | Present Latitude | Calculated | Displace- ment |
|--|---------------------|-----------------------------|-------------------|
| | | Early Eocene Latitude | |
| Gashato, Mongolia | 44° N. | 52° N. | 8° N. |
| Kwangtung, China | 23° N. | 34° N. | 11° N. |
| Bering Bridge | 65° N. | 74° N. | 9° N. |
| Katalla Dist., Alaska | 60° N. | 62° N. | 2° N. |
| Bighorn Basin, Wyoming | 44° N. | 38° N. | 6° S. |
| Big Bend, Texas | 30° N. | 22° N. | 8° S. |
| Punta Prieta, Baja California, Mexico | 29° N. | 25° N. | 4° S. |
| Spitsbergen | 80° N. | 66° N. | 14° S. |
| London | 51° N. | 38° N. | 13° S. |
| Paris | 49° N. | 36° N. | 13° S. |

^aBased primarily on the conclusions of McElhinny and Wellman (1969) and secondarily upon those of Funnell and Smith (1968).

mate had become favorable in both areas for the dispersal of terrestrial organisms, and Wolfe has even suggested that in the (correlated) medial Eocene, extended periods of darkness could not have existed and that therefore Earth's axis of rotation at that time may not have had so great an inclination as now. However, we know of no geophysical rationale for such a major axial change that does not involve postulation of unknown extraterrestrial forces.

If, during the Sparnacian, the Bering and Greenland-Barents shelf northern dispersal routes became about equally possible for the movement of terrestrial organisms from the standpoint of latitude and climate, and topography, narrow isthmuses, and other ecologically restrictive factors were at that time not of much greater importance in one area than in the other, then the early Eocene Sparnacian fauna, especially ungulates, should have reached Asia in sufficient strength to replace much of the endemic Asian fauna still present in late Paleocene time at Gashato and the Nemegt Valley in Mongolia.

SYSTEMATICS

WE DEAL HERE with only a part of the Gashato fauna, based mainly on specimens in the American Museum of Natural History. No attempt is made at this time to reevaluate multituberculates, pseudictopids, eurymylids, *Phenacolophus*, or the notoungulates, all of which are potential subjects of additional research, and some of which are currently under study by others.

ORDER INSECTIVORA

SUPERFAMILY PALAEORYCTOIDEA

FAMILY DELTATHERIDIIDAE

GREGORY AND SIMPSON, 1926

REVISED FAMILY DIAGNOSIS: Palaeoryctoids with $I^{?4}/\geq 2$ $C^1/1$ $P^4/4$ $M^2/2$. Last premolar somewhat molariform. P_4 and molar trigonids high and shearing. M_2 talonid elongate.

INCLUDED GENERA: *Deltatheridium*, *Sarcodon* (= *Opisthopsalis*), and *Hyracolestes*.

DISTRIBUTION: Cretaceous and Paleocene of southern Mongolia.

COMMENTS: It was recently recognized that the dental formula of *Deltatheridium* has been misinterpreted by previous investigators (McKenna, Mellett, and Szalay, In press). Van Valen (1966, p. 50) has made a case for four upper incisors and for reduction in the number of lower incisors, but with regard to the cheek teeth no one except Van Valen, to our knowledge, has gone on any other assumption than the original one, namely that three premolars and three molars were present in *Deltatheridium*. Van Valen (*ibid.*) apparently miscounted the number of lower premolars. It has been tacitly accepted by everyone else that $P^1/1$ were somehow lost, that the single-rooted $P^1/1$ were $P^2/2$, that the high penultimate premolars so characteristic of certain other Cretaceous therians were $P^4/4$, and that the $P^4/4$ were actually $M^1/1$. We have approached the matter from a different set of assumptions, of which the most important are the fundamental morphological similarity of the teeth themselves among *Deltatheridium*, *Hyracolestes*, and *Sarcodon*, the recognition that the same cheek teeth may be lost in all three genera, and that $M^3/3$ is the tooth most likely to have been lost in animals with prominent shearing modifications of $P^4/4$ – $M^2/2$.

SARCODON MATTHEW AND GRANGER, 1925

Sarcodon MATTHEW AND GRANGER, 1925, p. 11

Opisthopsalis MATTHEW, GRANGER, AND SIMPSON, 1929, p. 8.

TYPE SPECIES: *Sarcodon pygmaeus* Matthew and Granger, 1925.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Type locality only, late Paleocene of southern Mongolia.

DIAGNOSIS: In *Hyracolestes* and *Deltatheridium* the alveoli for P_1 and P_2 are constricted and small, characteristic of a short-faced animal, whereas in *Sarcodon* the alveoli for the premolars are well spaced, not constricted, somewhat like the spatial relationship of the premolars in miacid carnivorans. It appears that the talonid of the first lower molar (the only homologous molar preserved in all three genera) is relatively wider and has an entoconid in *Sarcodon*, whereas the narrower M_1 talonids of *Hyracolestes* and *Deltatheridium* seem to lack an entoconid.

Upper molars of *Sarcodon* are characterized by a long, shearing postmetacrista, closely compressed paracone and metacone, and a very large, posterolingually offset hypocone with a wide basin separating the apexes of the protocone and hypocone.

DISCUSSION: The genoholotype of *Hyracolestes* is clearly smaller than A.M.N.H. No. 21732 of *Sarcodon*, but small samples for each of these taxa suggest that this feature should be interpreted with caution.

The greatest similarities between *Sarcodon* on the one hand and *Hyracolestes* and *Deltatheridium* on the other lie in the construction of P_4 's and in the absence of the last lower molar. These are accepted by us as indicative of family relationships among these genera. Several differences, listed under the diagnosis, indicate that *Sarcodon pygmaeus* represents the more modified Paleocene genus and that *Hyracolestes ermineus* represents a more conservative, *Deltatheridium*-like lineage.

Van Valen (1966, p. 60) compared *Sarcodon* to *Pararyctes* in great detail and stated that "*Pararyctes* is the closest genus to *Sarcodon* yet discovered." On page 61 he noted that "except for *Micropternodus* (see below), the closest approach to *Sarcodon* among other genera is by

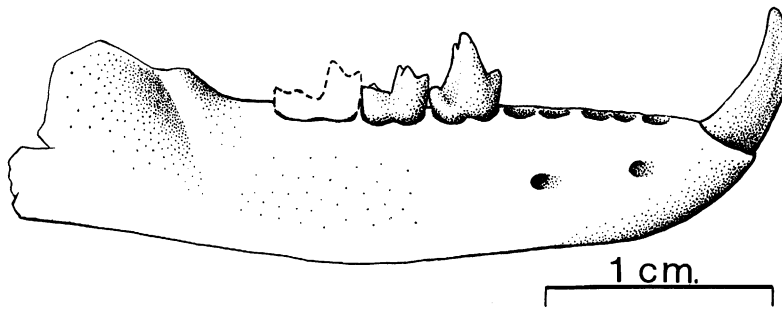


FIG. 4. *Sarcodon Pygmaeus*. Composite reconstruction of all available information concerning lower jaw (shown here as a right lower jaw).



FIG. 5. Fragmentary left lower jaw of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Occlusal view. Scale in mm. and 0.5 mm. intervals.

Gypsonictops. . . .” Under *Micropternodus* (*ibid.*, p. 61) Van Valen compared the North American genus to *Sarcodon*, suggesting strongly that the features cited by him as resemblances are indicators of close affinity between the genera. On page 68 he noted that “*Sarcodon* appears to be

intermediate between ordinary palaeoryctids and *Micropternodus*. . . .” In his classification of insectivorans, Van Valen (1967) placed *Sarcodon* with *Micropternodus* in the Micropternodontidae.

The similarity of the upper molars of *Sarcodon*, but not the lower molars, to those of *Micropter-*

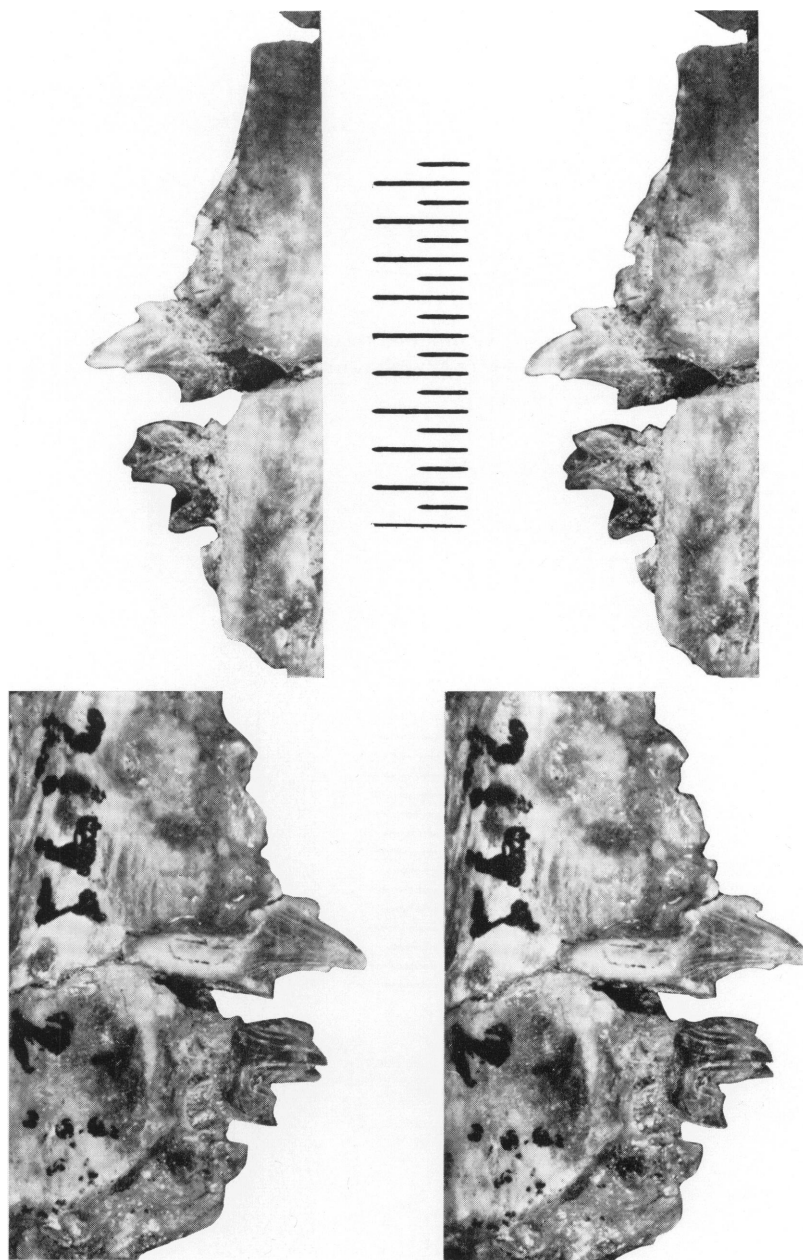


FIG. 6. Fragmentary left lower jaw of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Top, lingual view; bottom, buccal view. Scale in mm. and 0.5 mm. intervals.

nodus is the result of convergence. We agree with Robinson (1969, p. 129) that *Micropternodus* is probably a nyctitheriid insectivore, but we hold that *Sarcodon* is similar to *Micropternodus* partly because nyctitheres originated from Cretaceous palaeoryctoid stock via *Batodon*.

Sarcodon pygmaeus Matthew and Granger, 1925
Table 3, Figures 4–13

Sarcodon pygmaeus MATTHEW AND GRANGER, 1925,
p. 11.

Opisthopsalis vetus MATTHEW, GRANGER, AND SIMP-
SON, 1929, p. 8.

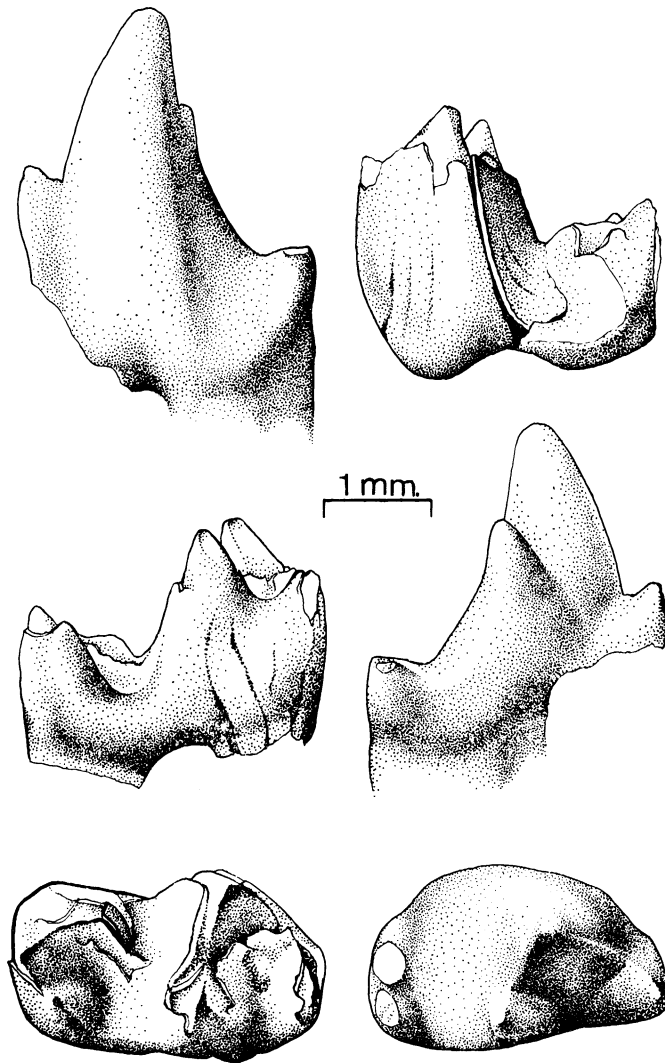


FIG. 7. Left P₄-M₁ of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Top, buccal view; middle, lingual view; bottom, occlusal view.

TYPE: A.M.N.H. No. 20427, left upper molar, probably M¹.

HYPODIGM: Type and A.M.N.H. No. 21732, badly crushed skull with premolars and molars, left horizontal ramus with P₄-M₁, and right horizontal ramus with canine and M₂ (originally crushed into the skull); both specimens were collected at Gashato.

SPECIFIC DIAGNOSIS: Only known species of genus.

DESCRIPTION: There is sufficient information from the two horizontal rami of the type of

"*Opisthopsalis vetus*" so that a relatively accurate reconstruction could be made (fig. 4), with at least the canine, the fourth premolar, and the two molars in place. It was possible to indicate the alveoli of the first three premolars in their correct positions.

No lower incisors are preserved. The canine, preserved on the right side only, is a slender, tall tooth. Judged from the alveoli, P₁ was single-rooted, P₂ and P₃ were double-rooted, and the roots of each of these were separated from those of the tooth anterior to it by a small diastema.

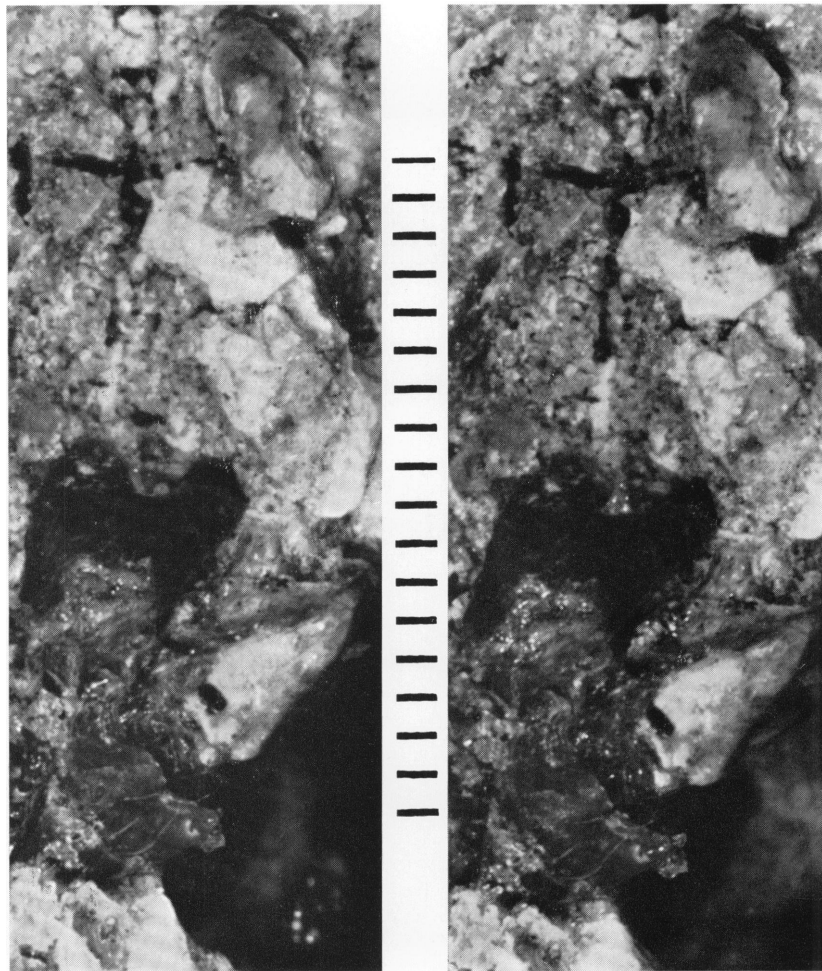


FIG. 8. A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*), left M_2 , in place before additional preparation. Upper tooth in contact with M_2 is probably M^2 . Scale in 0.5 mm. intervals.

There are two mental foramina; the larger, posterior foramen is under the anterior root of P_3 , whereas the smaller foramen is under the diastema between P_1 and P_2 . The posterior mental foramen is about halfway between the dorsal and ventral limits of the dentary, whereas the anterior one is slightly more dorsal.

The left P_4 is well preserved; it is a taller tooth than M_1 . The protoconid is the tallest cusp; the metaconid is taller than the paraconid in apparent (but perhaps not real because of possible breakage) contrast to P_4 of *Deltatheridium* (M_1 of authors). The angle between the planes of the protocristid and paracristid is approximately 85 degrees (see Szalay, 1969, pp. 198–203, for

nomenclature). The talonid is represented by a low shelf with two broken facets, probably representing the hypoconid (or hypoconulid) and the entoconid.

M_1 is considerably fractured but the broken enamel pieces are presumed to be retained in essentially their original positions. The trigonid is not very open lingually, and although the paraconid and metaconid might have been closer to each other, the three cusps are about equidistant. The angle between the protocristid and paracristid is about 50–55 degrees. The talonid is relatively wide transversely, and there is clear indication of an entoconid. The cristid obliqua joins the protocristid approximately

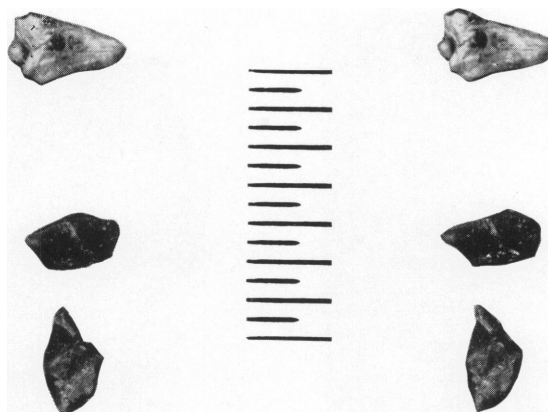


FIG. 9. Damaged left M_2 and $?M^2$ of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Top, occlusal view of $?M^2$; bottom, occlusal view of broken M_2 , with metaconid and most of protocristid missing. Scale in mm. and 0.5 mm. intervals.

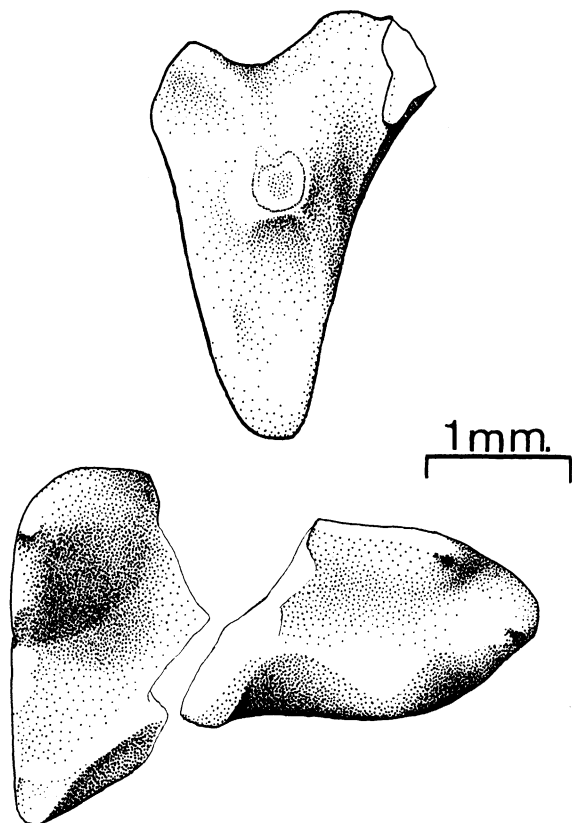


FIG. 10. Damaged left M_2 and $?M^2$ of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Top, occlusal view of $?M^2$; bottom, occlusal view of broken M_2 , with metaconid and most of protocristid missing.

halfway between the metaconid and protoconid. The hypoconulid appears to be in the middle of the posterior border of the talonid, but the exact position of the hypoconid cannot be determined.

The left M_2 is broken in half, and although great care was taken when it was excised from the mangled skull, the part bearing the metaconid was not found. The protoconid is slightly larger than the paraconid, and the paracristid forms a highly shearing V-shaped crest on a relatively straight, vertical plane. The trigonid fragment (figs. 9, 10) indicates a relatively large trigonid basin. The talonid, like the ultimate talonid in many mammals, is elongate. The hypoconid is nearly worn away, but the hypoconulid is tall and pointed, and the entoconid is clearly defined but shorter and smaller than the hypoconulid.

The right side of the muzzle of the crushed skull of "*Opisthopsalis vetus*," after it was cleaned, revealed remnants of the premolars and the first molar. Although the roots of P^1-3 are preserved, virtually nothing certain can be said of these teeth, with the possible exception that P^3 was three-rooted. The lingual half of the robust P^4 is of particular interest. In addition to the strong protocone there is a faint but recognizable remnant of a hypocone (fig. 11), smaller than, but similar to, the kind seen on the holotype of *Sarcodon pygmaeus* (figs. 12, 13). The buccal half of P^4 is somewhat puzzling. The dominant cusp is interpreted to be the paracone, but anterior

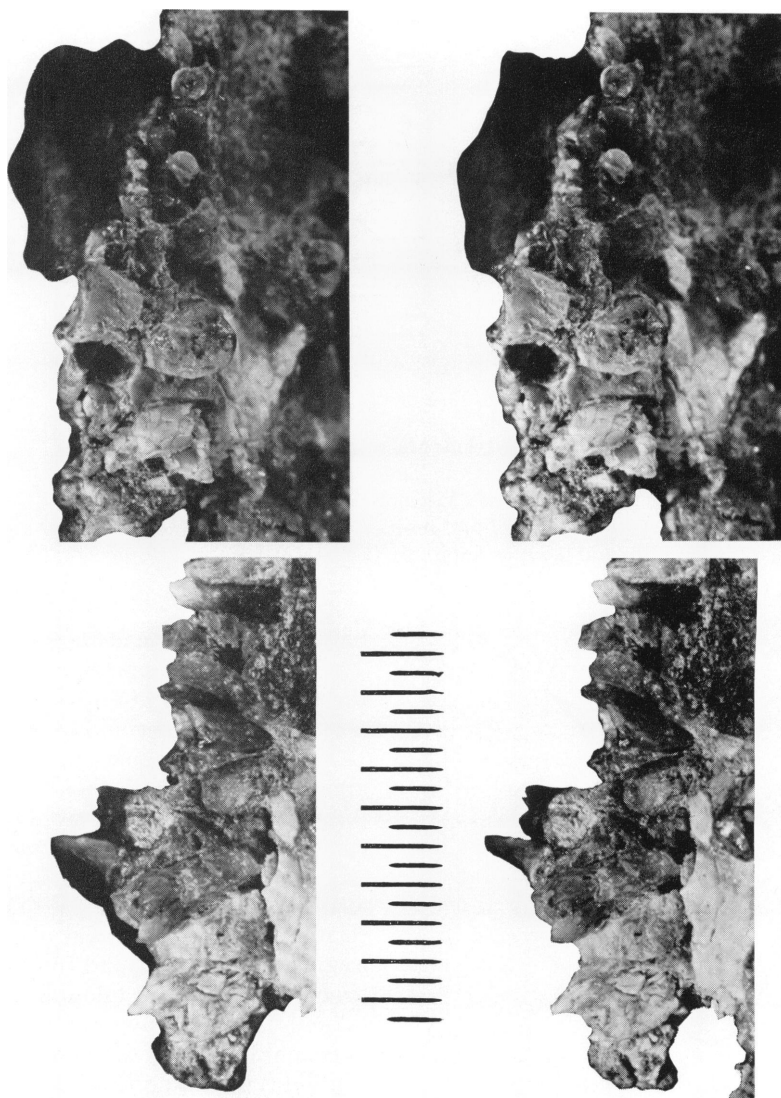


FIG. 11. Heavily damaged right maxillary dentition of A.M.N.H. No. 21732, *Sarcodon pygmaeus* (holotype of *Opisthopsalis vetus*). Top, approximately occlusal or ventral view; bottom, approximately lingual view. Scale in mm. and 0.5 mm. intervals.

and posterior to that cusp no elements can be homologized.

The badly eroded remains of the lingual half of a molar posterior to P^4 are the most conclusive proof for the synonymy of "*Opisthopsalis vetus*" with *Sarcodon pygmaeus*. Only the crumbling parts of the dentine remain, but it is quite clear that in addition to the apex of the protocone the hypocone was exactly like the characteristic structure seen on the type specimen of *Sarcodon pygmaeus*.

The upper cheek tooth in contact with the left M_2 prior to their excision was probably the ultimate left upper molar, M^2 (figs. 9, 10). The anterobuccal and posterobuccal parts of this tooth are broken off, and the single, centrally situated cusp (probably the paracone) is badly worn.

DISCUSSION: This taxon has been one of the most poorly prepared and studied of the Gashato mammals. New preparation of the



FIG. 12. A.M.N.H. No. 20427, damaged holotype of *Sarcodon pygmaeus*, left upper molar, probably M^1 , occlusal view. Scale in mm. and 0.5 mm. intervals.

holotype of "*Opisthopsalis vetus*" uncovered many important details previously not seen; when Matthew, Granger, and Simpson (1929, p. 8) diagnosed "*Opisthopsalis vetus*," they were deceived by the broken, separated right dentary posterior to the alveoli of P_4 and simply stated that there were three molars in addition to the four premolars. Restudy of the mandible fragments reveals that there were only two molars posterior to P_4 . P_4 and M_1 are present on the left side (figs. 5, 6), whereas only part of the trigonid and the talonid of M_2 are preserved. Prior to preparation (fig. 8) the remains of M_2 and the upper cheek tooth (figs. 9, 10) were in quasi-occlusion, or probably more correctly, in contact only.

Although the buccal half of the right upper molar on the holotype of "*Opisthopsalis vetus*" is poorly preserved, it is adequate to show that the construction of the hypocone is identical to that of the holotype of *Sarcodon pygmaeus* (figs. 12, 13). It should be added here that Matthew, Granger, and Simpson (1929, p. 9) already astutely noted that "*Opisthopsalis*" may be congeneric with *Sarcodon*, although they mistakenly concluded that "the interest of the present specimen [A.M.N.H. No. 21732] demands its separate diagnosis."

We cannot follow Van Valen (1966, p. 60) in endorsing the correctness of the figure of the holotype of *Sarcodon pygmaeus* published by Matthew and Granger (1925). We found the illustration to be inaccurate and had the type refigured (figs. 12, 13).

HYRACOLESTES MATTHEW AND GRANGER, 1925

Hyracolestes MATTHEW AND GRANGER, 1925, p. 10.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Type locality only, Gashato, late Paleocene, southern Mongolia.

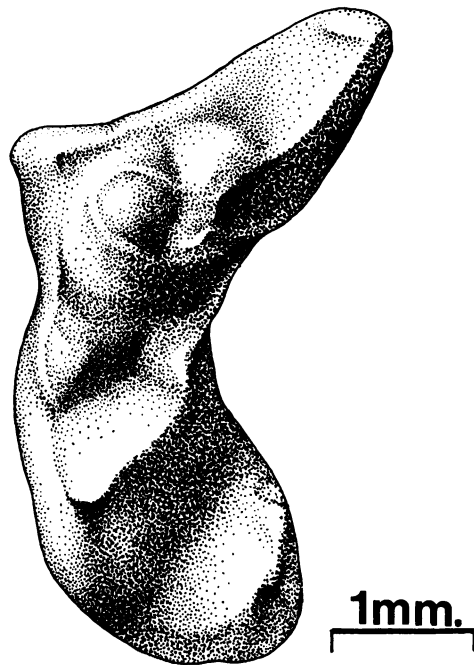


FIG. 13. A.M.N.H. No. 20427, left upper molar, probably M^1 , of holotype of *Sarcodon pygmaeus*. Occlusal view, damage restored.

TABLE 3

MEASUREMENTS^a (IN MILLIMETERS) OF LOWER TEETH OF VARIOUS PLACENTALS FROM THE GASHATO FORMATION

| | P ₃ | | | P ₄ | | | M ₁ | | | M ₂ | | | M ₃ | | |
|---|----------------|------|------|----------------|------|------------------|----------------|------------------|------|----------------|------|------|----------------|------|------|
| | L | PW | | L | AW | PW | L | AW | PW | L | AW | PW | L | AW | PW |
| <i>Hyracolestes ermineus</i> (A.M.N.H. No. 20425) | 1.80 | 0.95 | 2.35 | 1.30 | 1.35 | 2.40 | 1.35 | 1.20 | | — | | | | — | |
| <i>Praolestes nanus</i> (A.M.N.H. No. 21718) | 1.30 | 0.70 | 1.45 | — | 0.25 | 1.7 ^b | 1.35 | 1.2 ^b | | — | | | | — | |
| <i>Sarcodon pygmaeus</i> (A.M.N.H. No. 21732) | — | | 2.70 | 1.55 | — | 2.85 | 1.70 | 1.50 | | — | | | | — | |
| <i>Khashanagale zofiae</i> (A.M.N.H. No. 21751) | — | | | — | | 2.45 | 1.90 | 1.80 | 2.30 | 1.90 | 1.60 | 2.10 | 1.60 | 1.30 | |
| ? <i>Khashanagale</i> , new species (A.M.N.H. No. 21762) | — | | | — | | | — | | | — | | | — | 1.15 | 0.90 |

^aL, length; PW, posterior width; AW, anterior width.^bApproximately. Other values rounded to nearest 0.05 millimeter.

DIAGNOSIS: Palaeoryctoids with M₃/3 lost and morphology in several respects intermediate between that of *Deltatheridium* and *Sarcodon* (= *Opisthopsalis*), but more closely resembling the former. P₄ more elongate than in *Sarcodon*, but with metaconid apparently higher than in *Deltatheridium* (? due to wear). M₁ talonid with better formed basin than in *Deltatheridium* but without entoconid (in contrast to *Sarcodon*). Premolars anterior to P₃ evidently small and crowded and skull probably short-faced, as in *Deltatheridium*. Size about two-thirds that of *Sarcodon*.

DISCUSSION: Van Valen (1966, p. 86) referred to *Opisthopsalis*, *Hyracolestes*, and *Praolestes* as erinaceoids, under a common heading. His key statements, in addition to various comparisons, were: "As far as the single specimens known of *Opisthopsalis* and *Hyracolestes*, from the Gashato of Mongolia, are preserved, there are almost no generic distinctions between them," and "... provisional reference of *Opisthopsalis*, *Hyracolestes*, and *Praolestes* to the Erinaceoidea is indicated." Van Valen's fleeting survey misunderstood the significance as well as the relationships of these three distinct genera.

Insofar as the remains of *Hyracolestes* are known, they indicate a very unusual, puzzling mammal. It appears fairly certain to us that the teeth described are P₃-M₁, and the ultimate tooth, inferred from its alveoli only, was M₂ as in *Sarcodon*. Based on the simple, narrow talonid of M₁, and on the absence of M₃, it seems to us that *Sarcodon* and *Hyracolestes* represent two distinct lineages of a unique palaeoryctoid radiation,

which was apparently endemic in Asia until at least Paleocene and probably until Oligocene time. *Deltatheridium* constitutes the base of this radiation. Rich (In press) describes a tantalizing French Sparnacian tooth from Avenay which, except for larger size, is virtually identical with M₁ of *Hyracolestes*. Perhaps it is a European direct descendant of *Deltatheridium* or perhaps it is a descendant of *Hyracolestes* that somehow reached Europe, but we believe that reference to the Miacidae is also possible.

In terms of characteristic adaptations which set apart this interesting genus from almost all other placentals the structure of the trigonids is the most revealing. On P₄ it is slightly larger and more open lingually than on M₁. The gently curving prevallids support long carnassial edges and a well-developed carnassial notch is present. Although the upper teeth of *Hyracolestes* are not known, on the basis of the lower dentition we conclude that *Hyracolestes* was a small, carnivorous mammal, as suggested by its original describers, and that it was closely similar to *Deltatheridium* of the Cretaceous Djadochta Formation.

Hyracolestes ermineus Matthew and Granger, 1925

Table 3, Figures 14-18

Hyracolestes ermineus MATTHEW AND GRANGER, 1925 p. 10.

TYPE: A.M.N.H. No. 20425, right mandible fragment with P₃-M₁, and alveoli for the roots of C, P₁, P₂, and M₂.



FIG. 14. A.M.N.H. No. 20425, holotype of *Hyracolestes ermineus*, right P_3 - M_1 , and alveoli for the roots of C, P_1 , P_2 , and M_2 ; occlusal view. Scale in mm. and 0.5 mm. intervals.

HYPODIGM: Type specimen only.

SPECIFIC DIAGNOSIS: Only known species of the genus.

DESCRIPTION: For an appreciation of the unusual morphology and homologies of the teeth, the number and relative position of the alveoli are described. Only the posterior part of the canine alveolus is preserved; it is sufficient, however, to indicate that the canine was large. There are three discernible alveoli posterior to the canine alveolus. The most anterior preserved tooth is interpreted here to be the third premolar. The tiny, anterior alveolus (neither

recognized nor figured by the original describers) probably housed a very small, vestigial P_1 , whereas the remaining two alveoli probably held a double-rooted P_2 .

Our interpretation of the two alveoli posterior to the last preserved tooth (interpreted here as M_1) is that the anterior alveolus housed the root under the trigonid, whereas the posterior one held the long, laterally constricted root of the talonid of an ultimate lower molar, M_2 .

The most anterior preserved tooth, interpreted here as P_3 , is simple-crowned with a tall protoconid, an anterobasal nubbin in place of a



FIG. 15. A.M.N.H. No. 20425, holotype of *Hyracolestes ermineus*, right mandible fragment with P_3 - M_1 , and alveoli for the roots of C, P_1 , P_2 , and M_2 . Top, medial view; bottom, lateral view. Scale in mm. and 0.5 mm. intervals.

paraconid, and a single small cusp in the talonid position.

The tooth posterior to P_3 can be designated semimolariform (for definitions of premolari-form, semimolariform, etc., see Szalay, 1969a, p. 199) with a well-developed trigonid and a talonid that has not quite reached the basined

stage. The protoconid is the tallest of the trigonid cusps and the paraconid is the lowest. The angle between the planes of the protocristid and para-cristid is about 85 degrees and there is a deep trigonid notch between paraconid and protoconid. The talonid is only represented by a single, large cusp, structurally simpler than the

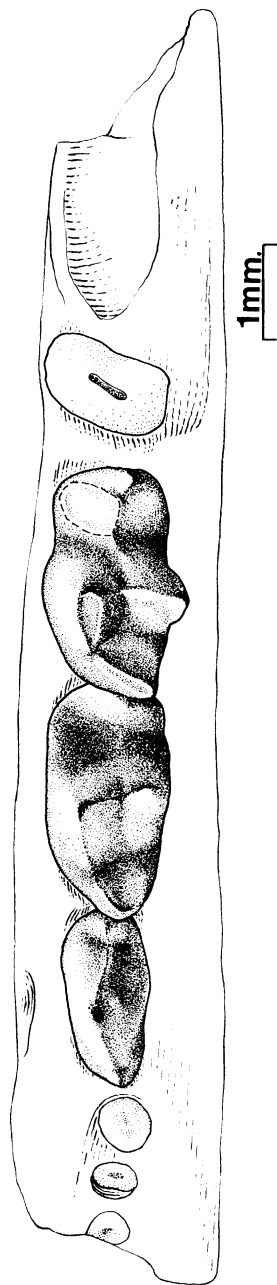


FIG. 16. A.M.N.H. No. 20425, holotype of *Hyracolestes ermineus*, right P_3 - M_1 , and alveoli for roots of C, P_1 , P_2 , and M_2 ; occlusal view.

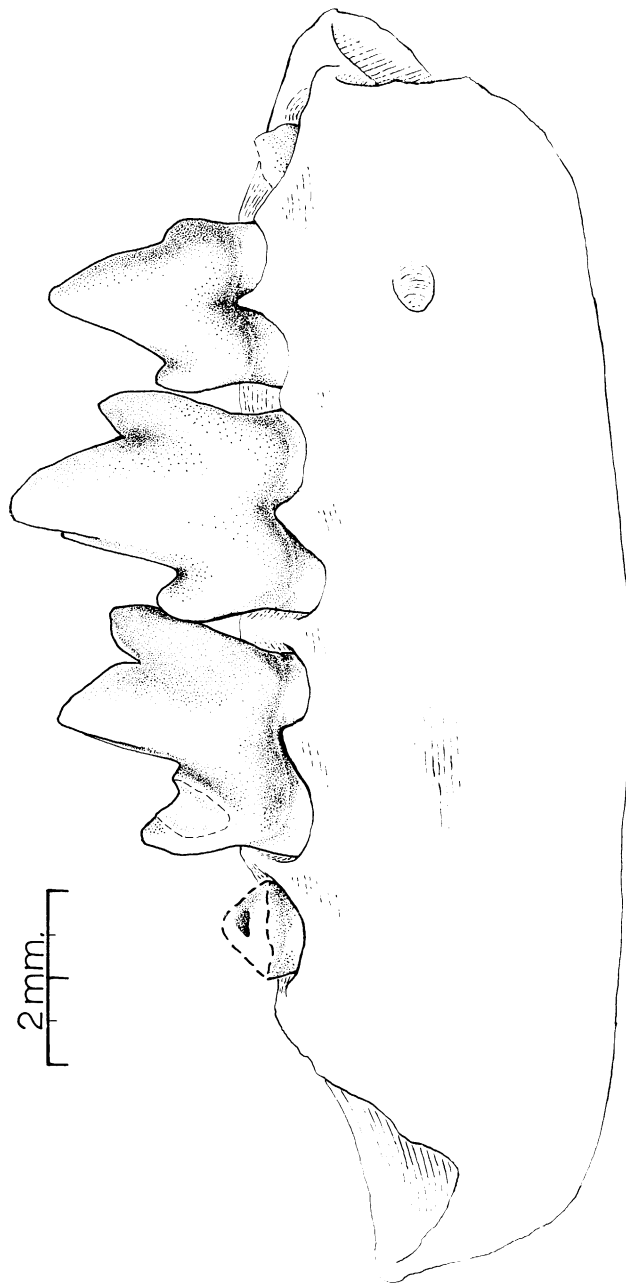


FIG. 17. A.M.N.H. No. 20425, holotype of *Hyracolestes ermineus*, right mandible fragment with P_3 - M_1 , and alveoli for roots of C, P_1 , P_2 , and M_2 ; lateral view.

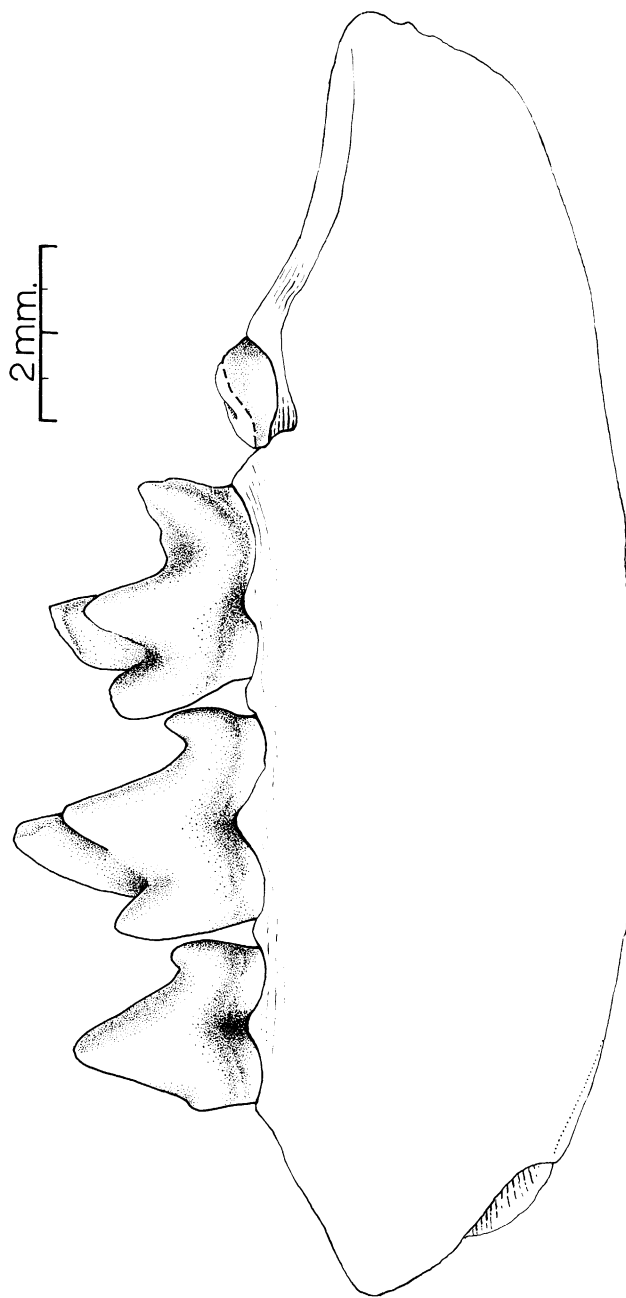


FIG. 18. A.M.N.H. No. 20425, holotype of *Hyracoolestes ermineus*, right mandible fragment with P₃-M₁, and alveoli for roots of C, P₁, P₂, and M₂; medial view.

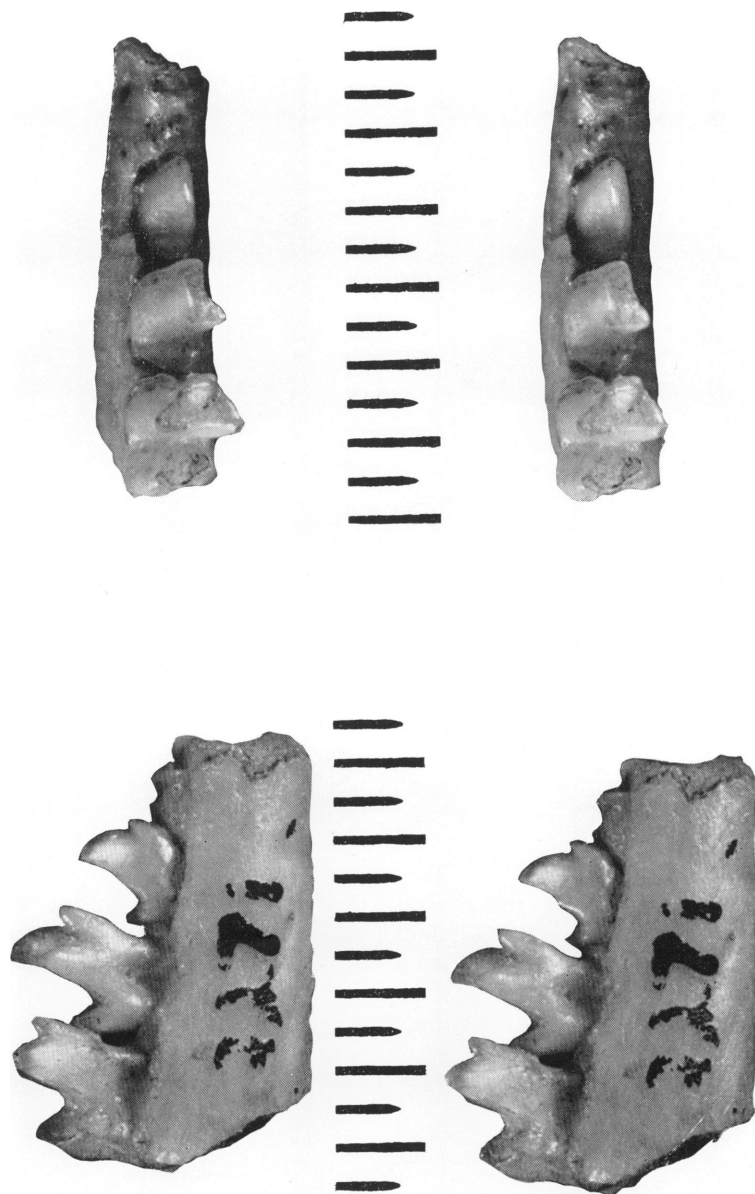


FIG. 19. A.M.N.H. No. 21718, holotype of *Praolestes nanus*, left mandible fragment with P_3 - M_1 , and alveoli for roots of P_2 . Top, occlusal view; bottom, medial view. Scale in mm. and 0.5 mm. intervals.

same region in *Sarcodon*. The hypoflexid is extensive and as a result the area anterobuccal to the talonid cusp is more extensive than the area on its opposite side which is homologous to the talonid basin of tribosphenic lower teeth.

On M_1 , as on P_4 , there is a deep notch on the curving surface of the prevallid. The metaconid

is large although it is smaller than the protoconid. The angle between the planes of the protocristid and paracristid is about 57 degrees. The anteroposteriorly elongate trigonid is wide open lingually. Although the posterolateral part of the talonid is chipped off, it is sufficiently well preserved to show that a large hypoconid was

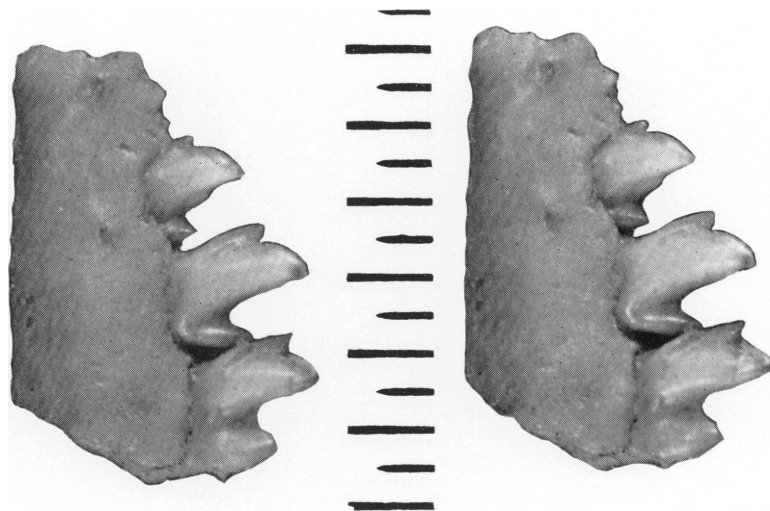


FIG. 20. A.M.N.H. No. 21718, holotype of *Praolestes nanus*, left mandible fragment with P_3 - M_1 , and alveoli for roots of P_2 ; lateral view. Scale in mm. and 0.5 mm. intervals.

present anterobuccal to the remaining talonid cusp. The hypoflexid is large, and the cristid obliqua joins the middle of the base of the trigonid. If one assumes the posterior talonid cusp to be the hypoconulid, there is no trace of an entoconid on the lingually wide-open talonid.

Under P_3 , on the ventrolingual aspect of the mandible fragment, there is a faint crest representing the posterior extension of the mandibular symphysis. There is a single, large mental foramen under the anterior root of P_3 .

DISCUSSION: We have elsewhere (McKenna,

Mellett, and Szalay, In press) suggested that *Deltatheridium*, *Sarcodon*, and *Hyracolestes* represent a natural group of palaeoryctoids and that the Eocene and Oligocene didymoconids may be (but see footnote p. 301) the only recognized descendants of the earlier group. Except for possibly a single tooth from the Sparnacian of France that is closely similar to M_1 of *Hyracolestes* but may represent merely an unrecognized miacid, no remains similar to those of any of these peculiar animals have been found outside of Asia. The viverravine miacids may be

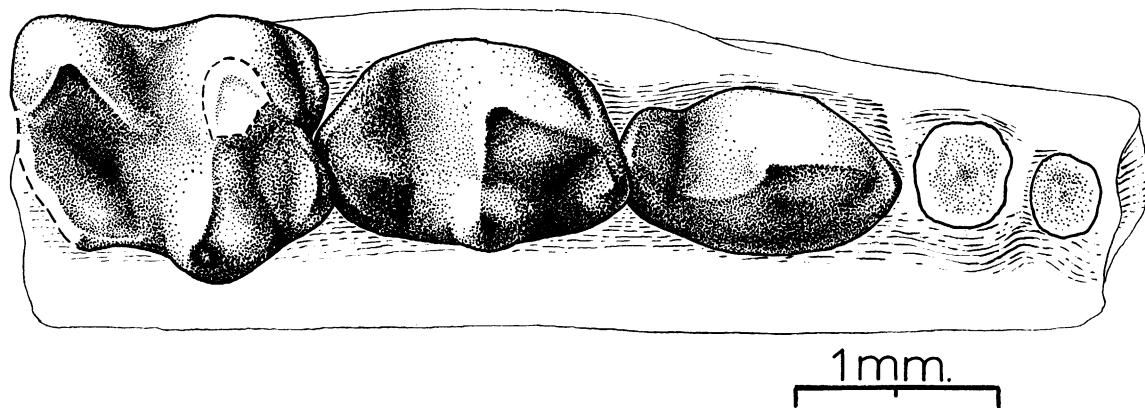


FIG. 21. A.M.N.H. No. 21718, holotype of *Praolestes nanus*, left mandible fragment with P_3 - M_1 , and alveoli for roots of P_2 ; occlusal view.

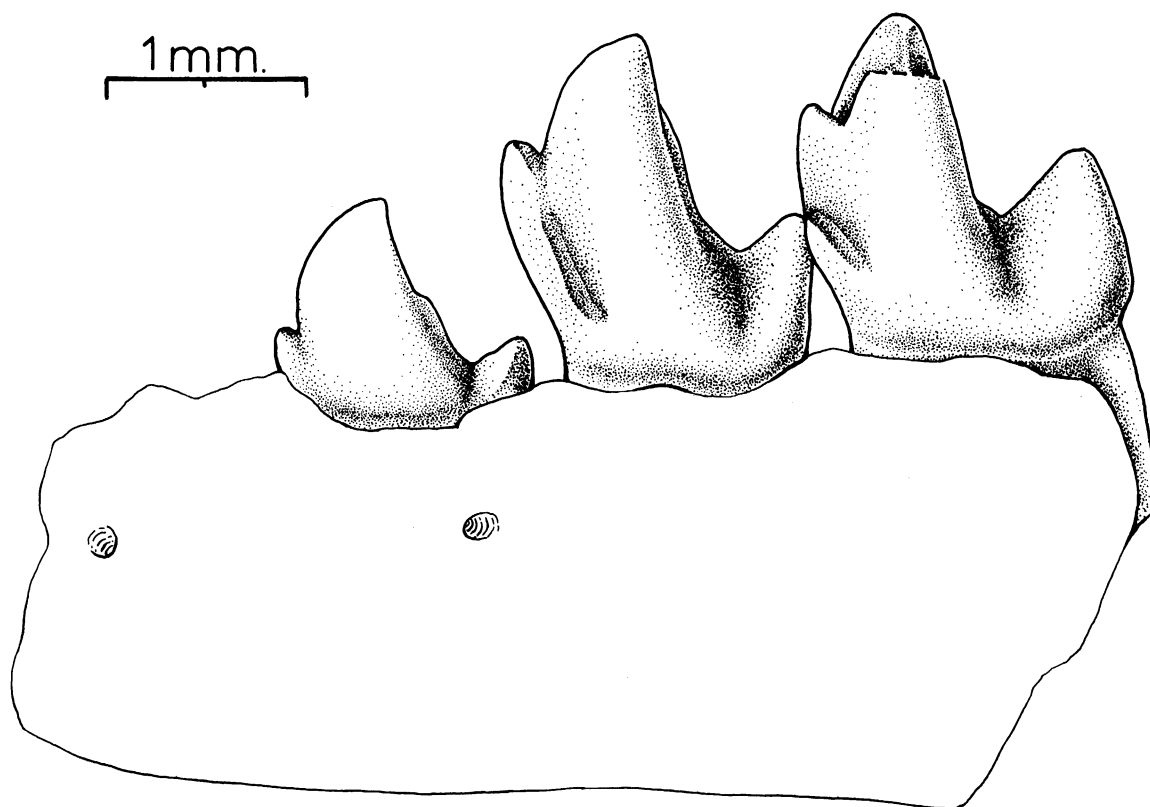


FIG. 22. A.M.N.H. No. 21718, holotype of *Praolestes nanus*, left mandible fragment with P_3 - M_1 ; lateral view.

distantly related, but, if so, then via a pre-Djadochta common ancestor.

ANAGALIDA, NEW ORDER

We regard the mammalian families Zalambdalestidae, Pseudictopidae, Anagalidae, and Eurymylidae as members of an endemic Cretaceous and early Tertiary Asian radiation, whose closest living relatives are the Lagomorpha.¹ The latter order also had an Asian origin, probably from the Anagalida, but ceased to be endemic to Asia in the Eocene. Among the principal characteristics of the order Anagalida are the possession of molariform posterior premolars, anteroposteriorly compressed trigonids,

a tendency toward prismatic or unilaterally hypsodont upper cheek teeth with crown pattern tending to be obliterated early in wear, a tendency toward procumbent incisors (variously expressed), and a skeleton (particularly the foot), where known, that is somewhat lagomorph-like.

FAMILY ZALAMBDALESTIDAE

GREGORY AND SIMPSON, 1926

PRAOLESTES MATTHEW, GRANGER, AND SIMPSON, 1929

Praolestes MATTHEW, GRANGER, AND SIMPSON, 1929, p. 3.

TYPE SPECIES: *Praolestes nanus*.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Type locality only, Gashato, late Paleocene, southern Mongolia.

DIAGNOSIS: Small zalambdalestids in which P_3 paraconid is no longer a basal cusp but has a more elevated position and a metaconid is begin-

¹Although we believe that the Didymoconidae may eventually prove to be a member of the Anagalida, possibly a descendant of the Zalambdalestidae, the phylogenetic and systematic position of this endemic Asian family should be decided on after the publication of J. S. Mellett's researches on didymoconids.

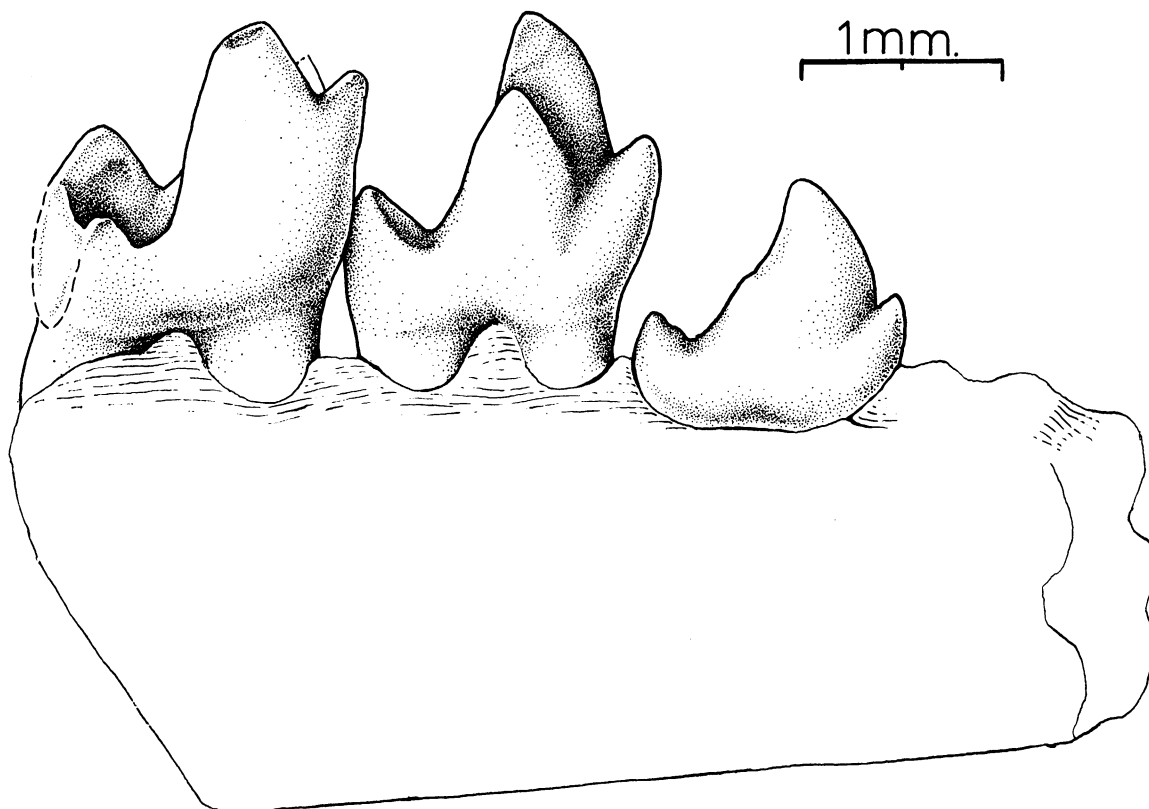


FIG. 23. A.M.N.H. No. 21718, holotype of *Praolestes nanus*, left mandible fragment with P_3 - M_1 ; medial view.

ning to form on the posterolingual corner of the protoconid; P_4 has a fully developed trigonid with high paraconid projecting anterolingually.

DISCUSSION: Van Valen (1967, p. 261) in his classification of insectivorans followed his earlier views (1966, pp. 86, 87), formally placing *Praolestes*, "*Opisthopsalis*," and *Hyracolestes* in the Geolabidinae without a query or a discussion of the problem. However, the premolars of geolabidines are not so advanced as those of zalambdalestids, especially in the development of the trigonid of P_4 . We ascribe the molar similarities to parallelism.

Kielan-Jaworowska (1969b) has now described unworn and undamaged lower dentitions of *Zalambdalestes* from the Cretaceous Djadochta Formation near Gashato, Mongolia, and meaningful comparisons with *Praolestes* can now be made. We regard *Praolestes* as a probable descendant of *Zalambdalestes* and the characteristics noted in the generic diagnosis are regarded as advances beyond the features demonstrated

by recently collected specimens of *Zalambdalestes*.

Praolestes nanus Matthew, Granger, and Simpson, 1929

Table 3, Figures 19-23

Praolestes nanus MATTHEW, GRANGER, AND SIMPSON, 1929, p. 3.

TYPE: A.M.N.H. No. 21718, left mandible fragment with P_3 - M_1 , and alveoli for P_2 .

HYPODIGM: Type specimen only.

SPECIFIC DIAGNOSIS: Only known species of the genus.

DESCRIPTION: Because the most anterior preserved tooth is P_3 , the two alveoli on the anterior part of the mandible fragment belonged to P_2 . P_3 is almost completely erupted; the protoconid, slightly curved posteriorly, is the dominant cusp. The paracristid, leading from the apex of the protoconid to the small but cusped paraconid is curved like the edge of a scimitar sword. An incipient metaconid is represented by a nubbin on the lingual side of the crest which extends



FIG. 24. Stereoscopic photographs of A.M.N.H. No. 21751, holotype of *Khashanagale zofiae*, new genus and new species, posterior half of right horizontal ramus with M_1-3 , with M_1 trigonid broken off; occlusal view. Scale in mm. and 0.5 mm. intervals.

posteroventrally from the apex of the protoconid. This lingual half of the protocristid meets the cristid obliqua of the tiny talonid, the latter represented by a single cusp.

P_4 has a well-developed trigonid with a precingulid and has a broad, shelllike talonid which has a tiny lingually shifted basin. The talonid occluded with an enlarged P^4 paracone as in *Lambdalestes* and many other mammals

with similar P^4 's. The protoconid is the tallest of the trigonid cusps; the metaconid is larger than the paraconid. The angle between the planes of the protocristid and paracristid of the trigonid is about 70 degrees.

M_1 has an anteroposteriorly constricted trigonid with a strong precingulid, and a talonid which is slightly broader than the trigonid. The hypoconulid and entoconid are broken off;



FIG. 25. Stereoscopic photographs of A.M.N.H. No. 21751, holotype of *Khashanagale zofiae*, new genus and new species, posterior half of right horizontal ramus with M_1 - $_3$, with M_1 trigonid broken off; lateral view. Scale as in figure 26.



FIG. 26. A.M.N.H. No. 21751, holotype of *Khashanagale zofiae*, new genus and new species, posterior half of right horizontal ramus with M_1 - $_3$, with M_1 trigonid broken off; scale in mm. and 0.5 mm. intervals.

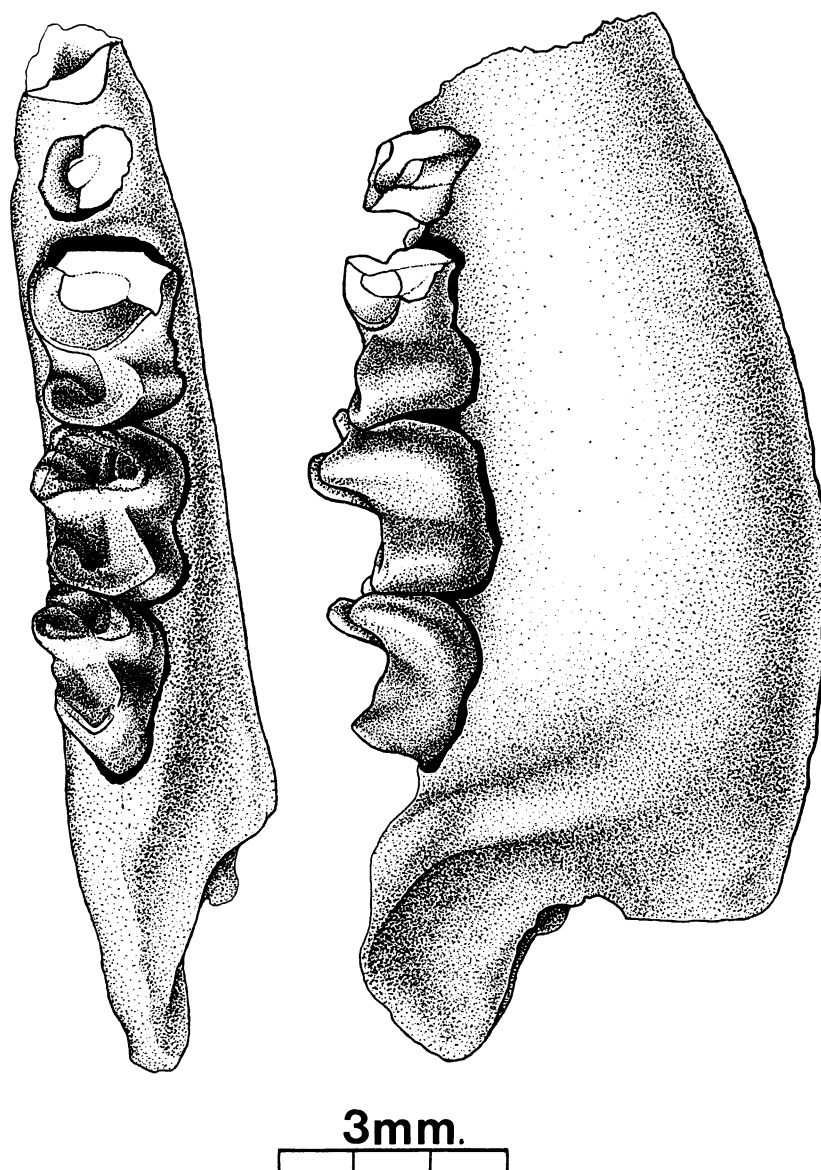


FIG. 27. A.M.N.H. No. 21751, holotype of *Khashanagale zofiae*, new genus and new species, posterior half of right horizontal ramus with M_{1-3} , with M_1 trigonid broken off. Left, occlusal and slightly buccal view of teeth; right, lateral view.

therefore, the crucial relations of the hypoconulid and entoconid to each other cannot be assessed. It is difficult to determine whether the protoconid or the metaconid was the tallest trigonid cusp, because the tip of the protoconid is not present. The angle between the planes of the protocristid and paracristid of the trigonid is approximately 40 degrees.

The mandible fragment, that of a relatively

young specimen, as indicated by the erupting P_3 , is moderately deep, with two mental foramina. The anterior one is under the anterior root of P_2 , whereas the posterior foramen is under the incipient talonid of P_3 .

FAMILY ANAGALIDAE SIMPSON, 1931

KHASHANAGALE, NEW GENUS

TYPE SPECIES: *Khashanagale zofiae*, new species.

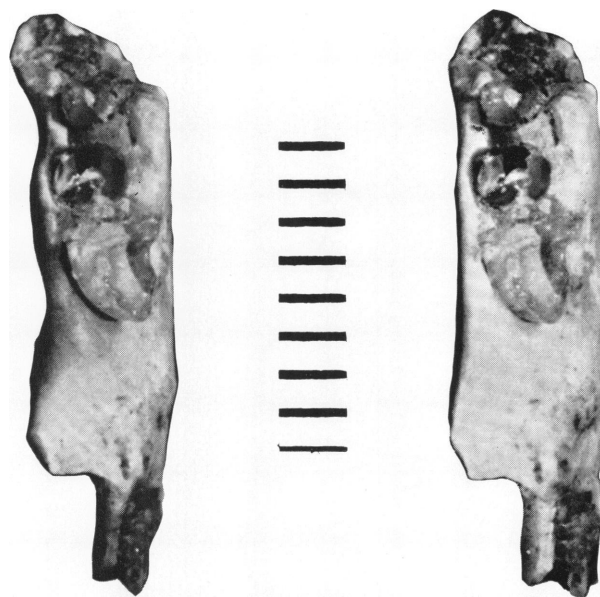


FIG. 28. A.M.N.H. No. 21762, ?*Khashanagale*, new unnamed species, left dentary fragment with talonid of M_3 ; occlusal view. Scale in 0.5 mm. intervals.

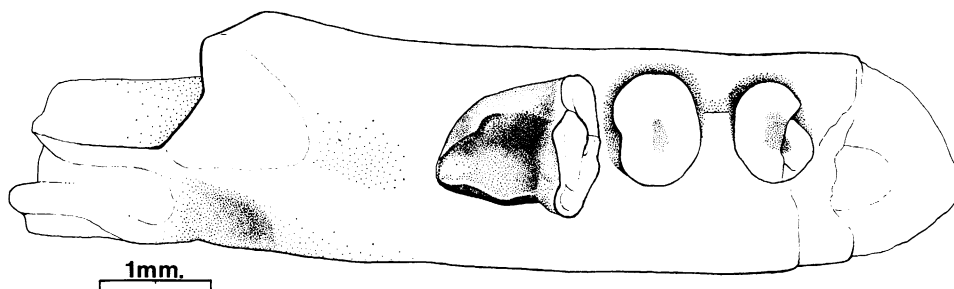


FIG. 29. A.M.N.H. No. 21762, ?*Khashanagale*, new unnamed species, left dentary fragment with talonid of M_3 ; occlusal view.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Type locality only, Gashato, late Paleocene, southern Mongolia.

ETYMOLOGY: Khashaat (*xauuaam*, i.e., Gashato) + *Anagale*.

DIAGNOSIS: Primitive anagalids, distinct from *Anagale* in having transversely narrower talonids, and slightly less bicolumnar molars. The cusps on the lower molars are more distinct than those of *Anagale*. The ratio of length to posterior width of the lower molars decreases from front to back. The numerical value of the ratios are 1.38, 1.43, and 1.63 for M_1 , M_2 , and M_3 respectively.

DISCUSSION: The anteroposteriorly narrow tri-

gonids, the incipiently bicolumnar molars, and the construction of M_3 suggest that *Khashanagale* is an early relative of *Anagale* (see McKenna, 1963, for a review of the Anagalidae). The talonids of *Khashanagale* are transversely narrower than those of *Anagale*; this seems to indicate that anagalids were differentiated from a stock of very primitive placentals with relatively narrow talonids (see also *Zalambdalestes*¹ and didymoconids).

¹We take this opportunity to present long-needed illustrations (figs. 31–35) of the original specimens of the important Asiatic Cretaceous mammal *Zalambdalestes*. Cleaning of the specimens reported by Gregory and Simpson

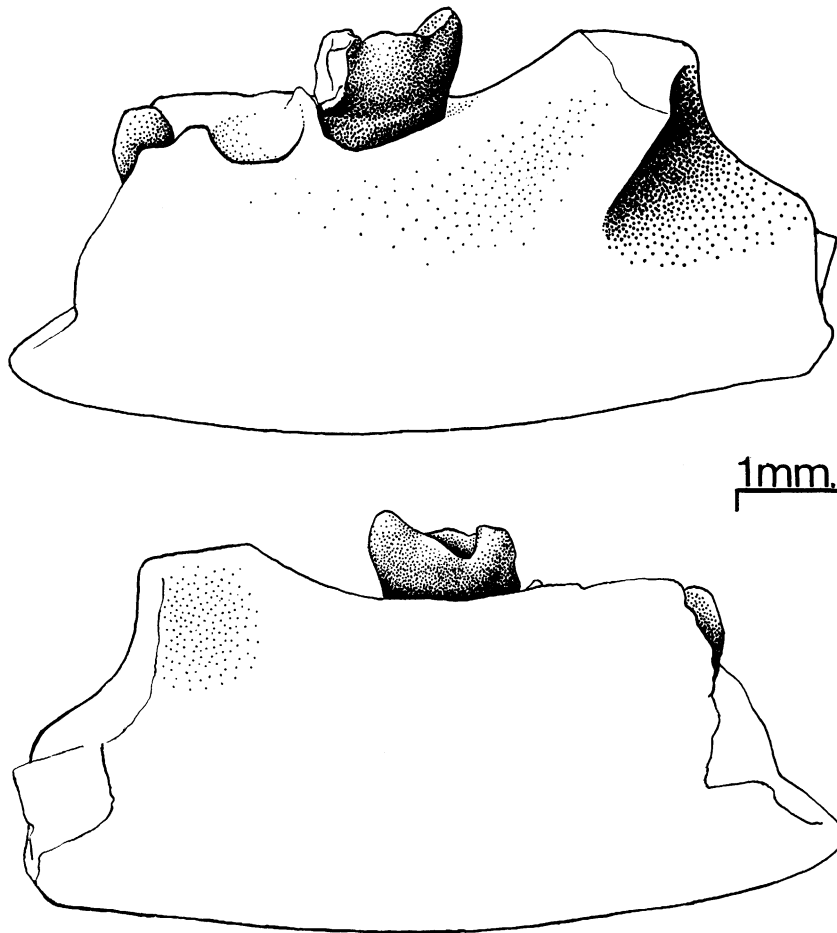


FIG. 30. Drawings of A.M.N.H. No. 21762, ?*Khashanagale*, new unnamed species, left dentary fragment with talonid of M_3 . Top, lateral view; bottom, medial view.

Van Valen (1966, p. 89) noted a number of similarities between *Ptolemaia* and *Anagale*. He clearly implied close, virtually family group taxonomic relationships between *Ptolemaia* and *Anagale*. At present, no special affinity between these genera appears probable to us, and we continue to regard *Ptolemaia* as a pantolestoid insectivoran.

(1926) has revealed many important new details of the dentition and the cranium. A.M.N.H. No. 21708, type of *Zalambdalestes lechei*, is an extremely aged individual with cheek-tooth crowns nearly worn away. P^1 and P^2 have dropped out and the alveoli have closed. The type of "*Z. grangeri*" is a somewhat younger individual of the same species, and the referred specimens in the Polish-Mongolian collections (Kielan-Jaworowska, 1969b) are younger still. All Djadochta *Zalambdalestes* can be regarded as a single species, *Z. lechei* Gregory and Simpson, 1926.

Derivation of *Pseudictops* of the Gashato and Nemegt assemblages from an ancestry similar to primitive anagalids, with anteroposteriorly constricted trigonids and narrow talonids, appears to be plausible at present (for similar views, see Van Valen, 1964).¹ The characteristically narrowed talonid of M_3 of *Pseudictops*, *Eurymylus*, anagalids, and lagomorphs appears to be a shared character, present probably in a common ancestor prior to the diversification of these groups.

One of the striking similarities of *Anagale* and *Eurymylus* is the manner in which the lower teeth wear. In both genera, as in lagomorphs, the

¹"Genus R" of Van Valen (1964, p. 486) appears to be a worn upper tooth of a leptictid near *Myrmecoboides*. Its relevance, in any way, to anagalid or lagomorph phylogeny is highly questionable.



FIG. 31. A.M.N.H. No. 21708, part of the holotype of *Zalambdalestes lechei*, almost complete cranium, Djadochta Formation, late Cretaceous. Top, ventral view; bottom, dorsal view. Scale in mm. and 0.5 mm. intervals.

anterior part of the trigonid and the talonid of the molar anterior to it form a basin into which the lingual half of the upper tooth occludes.

From a common ancestor which had certain characteristic predispositions of the masticatory apparatus, independent development of this



FIG. 32. A.M.N.H. No. 21708, part of the holotype of *Zalambdalestes lechei*, partial left and right mandibles, Djadochta Formation, late Cretaceous; occlusal view. Scale in mm. and 0.5 mm. intervals.

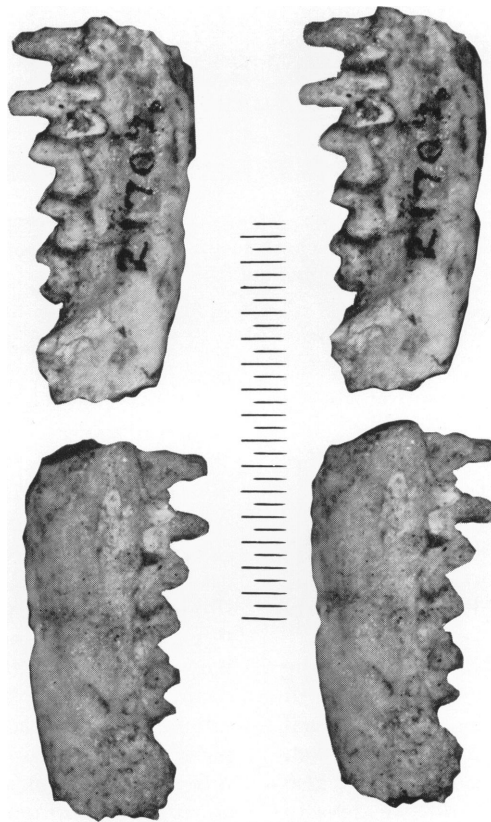


FIG. 33. A.M.N.H. No. 21707, *Zalambdalestes lechei*, part of right horizontal ramus with P_3 - M_3 , Djadochta Formation, late Cretaceous. Top, lateral, bottom, medial view. Scale in mm. and 0.5 mm. intervals.

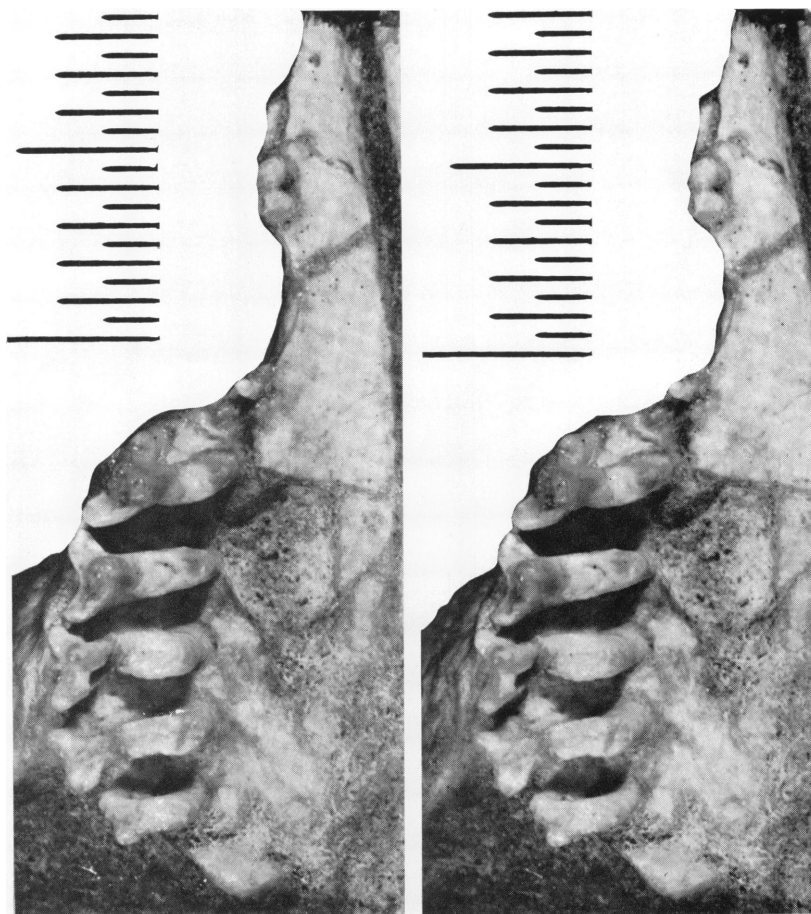


FIG. 34. A.M.N.H. No. 21709, *Zalambdalestes lechei* (holotype of "*Z. gran-geri*"), partial palate with right cheek teeth, Djadochta Formation, late Cretaceous, occlusal view. Scale in mm. and 0.5 mm. intervals.

specialized wear pattern is possible.

Khashanagale zofiae, new species

Table 3, Figures 24-27

TYPE: A.M.N.H. No. 21751, posterior half of right horizontal ramus with M_1 3.

HYPODGM: Type specimen only.

ETYMOLOGY: Named for our esteemed colleague, Dr. Zofia Kielan-Jaworowska.

SPECIFIC DIAGNOSIS: Only known species of the genus.

DESCRIPTION: A.M.N.H. No. 21751 is the posterior half of the horizontal ramus with broken remains of M_1 , and the relatively well preserved, but fractured M_2 and M_3 . Broken splinters of the posterior root of P_4 are also present. The surfaces of the teeth are densely

pock-marked as a result of somewhat poor preservation, possibly caused by etching by acidic ground water.

M_1 , or what is left of it, seems to have been the largest of the three molars. M_2 is slightly smaller than M_1 , and M_3 is distinctly smaller than M_2 . The molar trigonids, preserved only on M_2 and M_3 , are approximately twice the height of the talonids and are somewhat columnar. The highest cusp on the trigonids is the metaconid, but this may, at least in part, be caused by proportionally greater wear on the protoconid. The paraconids are shelflike and close to the metaconid; they form a functional unit with the talonid of the preceding tooth. A precingulid was present and extended farther buccally than in *Anagale*. The trigonid notch is V-shaped, making an angle of approximately 90 degrees between

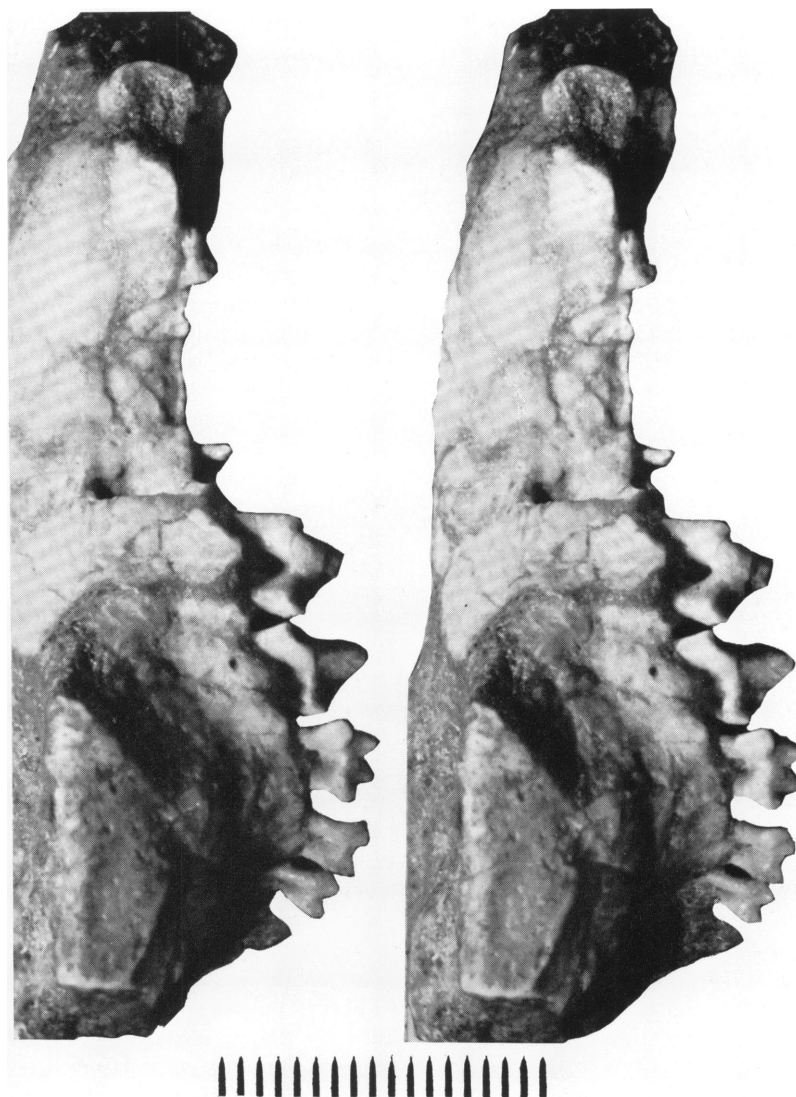


FIG. 35. A.M.N.H. No. 21709, *Zalambdalestes lechei* (holotype of "*Z. grangeri*"), partial palate with right cheek teeth, Djadochta Formation, late Cretaceous, lateral view. Scale in 0.5 mm. intervals.

the slopes of the protoconid and metaconid on M_2 . The talonid notch is deep and V-shaped, with a rounded bottom; it is the outlet for the small, lingually positioned remnant of the talonid basin. The talonid cusp apexes are obliterated by wear, but the cusps themselves were becoming subordinate components of what amounts to the enamel wall of the posterior column of the bicolumnar structure seen later in *Anagale*.

What remains of the dentary is deep and robust: the crista coronoidea arises from a very

thick base on the ascending ramus.

?Khashanagale, new unnamed species

Table 3, Figures 28–30

A.M.N.H. No. 21762 is a left dentary fragment with the talonid of M_3 . Comparison of this specimen with the type of *Khashanagale zofiae*, A.M.N.H. No. 21751, quickly reveals the great similarity of the talonids of the last molars. As in the genoholotype of *Khashanagale* the mandible of the unnamed species was relatively deep. The

crista condyloidea in front of the deep masseteric fossa is thick and well differentiated. This animal, judged by its teeth and jaw depth, was about one-half the size of *Khashanagale zofiae*. Although we consider it important to bring to light this new species from the Gashato Formation, we cannot justify naming it because of the inadequacy of the only known specimen.

ORDER CONDYLARTHRA

SUPERFAMILY MESONYCHOIDEA

FAMILY MESONYCHIDAE COPE, 1875

SUBFAMILY MESONYCHINAE COPE, 1875
(= Mesonychidae Cope, 1875, p. 444; Mesonychinae Wortman, 1901)
? *Dissacus* sp.

MATERIAL: A.M.N.H. No. 22145, fragmentary left P⁴.

COMMENTS: A small mesonychid similar to *Dissacus* is present at Gashato, but has not been identified by previous students. The specimen compares favorably with P⁴ of *Dissacus navajovius* or *D. saurognathus*. The styler area has been broken away, which is no doubt why this tooth has not been recognized previously. Elsewhere in Asia mesonychine mesonychids of comparable size are known only from the Paleocene of South China (Chow and Young, 1963), but that material still awaits description. *Dissacus*-like mesonychines are known in North America from medial Paleocene to early Wasatchian (Sparnacian) time and in Europe from the late Paleocene through medial Eocene time. Inasmuch as *Dissacus* was for a time a contemporary of *Pachyaena*, the presence of a *Dissacus*-like animal at Gashato is not evidence that the Gashato assemblage is earlier than the Nemegt Valley locality which has produced *Pachyaena*.

For additional comments and details on Asiatic mesonychids see Szalay and Gould

(1966) and Szalay (1969b; 1969c). We refrain from naming this species.

ORDER DINOCERATA

FAMILY UINTATHERIIDAE FLOWER, 1876
SUBFAMILY PRODINOCERATINAE FLEROV, 1952b, NEW RANK

We take this opportunity to make a minor adjustment in the taxonomy of uintatheres.

Flerov proposed a new family, Prodinoceratidae in his first paper (1952b) on *Mongolotherium* from the Nemegt Valley. The Prodinoceratidae, with *Prodinoceras* as its type genus, also included *Mongolotherium*, *Bathyopsoides*, and *Probathyopsis*. Of particular significance here is the fact that Flerov included the last genus. Later Wheeler (1961) employed a subfamily Bathyopsinae, a reduction in rank of Bathyopsidae Osborn, 1898, for the genera *Probathyopsis*, *Prodinoceras*, *Bathyopsoides*, *Bathyopsis*, and *Mongolotherium*, but such usage, if adopted, would make the uintathere subfamily Uintatheriinae diphyletic, as *Uintatherium* and *Prouintatherium* have been shown by Dorr (1958) to be derived from *Probathyopsis* prior to the origin from the latter genus of *Bathyopsis*. *Bathyopsis*, however, is the probable ancestor of *Tetheopsis* and *Eobasileus*. Therefore, in order to avoid diphyly, *Bathyopsis* and *Probathyopsis* are regarded here as primitive members of the subfamily Uintatheriinae, thus permitting use in modified form of Flerov's Prodinoceratidae for the mutually closely similar *Bathyopsoides*, *Prodinoceras*, and *Mongolotherium*. The Prodinoceratinae as thus visualized are unified by the possession of a sagittal crest rather than a flat skull roof. Horns were almost surely absent or rudimentary, in spite of Patterson's (1939, fig. 109) depiction of them in the plaster reconstruction of the skull of *Bathyopsoides*.

SUMMARY

THE EARLIEST TERTIARY MAMMALIAN FAUNA known from Asia occurs in southern Mongolia, where it is found in late Paleocene sediments approximately 55 million years old exposed at Gashato and in the Nemegt Basin. Romer (1966) has proposed, but not defined, a "Gashatan Asiatic Age" for the Gashato fauna and we propose that the term be extended to the occurrence of the same fauna, although to a different faunal facies, in the Nemegt Basin, subsuming Romer's (1966) "Ulanbulakian Asiatic Age." We supply a definition of the "Gashatan Asiatic Age": the joint overlapping time ranges of *Palaeostylops*, *Pseudictops*, *Prionessus*, and *Eurymylus*. Additional localities in Sinkiang and Kwangtung may also be Gashatan in age.

The Gashato fauna is made up of a mixture of endemic genera and a few genera that evidently reached Asia via the Bering route from North America and beyond. There is no special similarity to Paleocene faunas of Europe, but this could be because of a double filtering action. The most perplexing Gashatan mammals have been the notoungulates, but recently Paleocene notoungulates have been found in North America and there is no evidence that notoungulates as such originated in Asia. At the beginning of the Eocene (Sparnacian), increased northern dispersal brought about extensive, but still not complete, faunal replacement in eastern Asia.

Analysis of geophysical data, as well as the faunal data, suggests that there is strong evidence for a dry-land dispersal route between the North American and European crustal blocks via Greenland and the Barents shelf as late as Sparnacian time in the Eocene, but not thereafter. During Paleocene time, climate and other factors had a filtering effect on dispersal via both the Bering and Greenland-Barents shelf routes, but the former was closer to the rotational pole position in the Paleocene and was a more effective filter. During Sparnacian time, the Bering area still acted as a filter, but the Greenland-Barents shelf route now showed little filter

action. Presumably this was the result of a more equable climate. There is no evidence for a Greenland-Iceland-Faeroes dispersal route and some evidence against it.

No attempt is made in the present paper to reevaluate, except insofar as they bear on correlation, the Gashatan multituberculates, pseudictopids, eurymylids, *Phenacolophus*, or pantodonts, but the following taxonomic adjustments are made:

1. *Opisthopsalis* is synonymized with *Sarcodon*, and *Sarcodon* and *Hyracolestes* are added to the insectivoran family Deltatheridiidae.

2. A new order, Anagalida, is proposed. The Anagalida includes the families Zalambdales-tidae, Pseudictopidae, Anagalidae, and Eurymylidae. The Anagalidae are somewhat lagomorph-like and are believed to be related to lagomorphs.

3. *Praolestes* is referred to the Zalambdales-tidae.

4. The Cretaceous genus *Zalambdalestes* is known from a single species, *Z. lechei*. The type specimen of *Z. lechei* is an extremely aged individual with cheek-tooth crowns nearly worn away. P¹ and P² have dropped out and the alveoli have closed. The type specimen of "*Z. grangeri*" is a somewhat younger individual of the same species and the referred specimens in the Polish collections are younger still. New illustrations of American Museum specimens of *Zalambdalestes* are provided.

5. The Anagalidae are reported from the Paleocene for the first time and a new genus and species, *Khashanagale zofiae*, is named. A second species of *Khashanagale* or of a closely related form is present at Gashato, but is not named.

6. A small *Dissacus*-like mesonychid is present in the Gashato fauna at Gashato.

7. In the classification of uinatheres, utilization of Flerov's subfamily Prodinoceratinae is advocated in preference to Wheeler's subfamily Bathypsinae.

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