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A Generic Review of the Stenomyline Camels

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INTRODUCTION

The unusual Miocene stenomylines have a number of unique characters and are the most aberrant members of the Camelidae. They are characterized most strongly by extreme dental specialization not observed in any other camelids. On the basis of their peculiar dentition, the stenomylines might well be considered as a separate family, but their other features are typically camelid. Added to the enigma of their morphologic adaptation is the enigma of their origin, for no real clue to stenomyline ancestry has yet been found. Although the present report does not solve the problem of stenomyline origin, it presents in detail the relationships and generic diversity of the members of the Stenomylinae from the earliest occurrences to the latest.

The subfamily Stenomylinae includes three genera, *Stenomylus* Peterson (1906), *Rakomylus* Frick (1937), and *Blickomylus,* new genus, and one new subgenus, *Stenomylus* (*Pegomylus*). *Stenomylus* (*Pegomylus*), distinguished by extremely large premolars, represents an ancient lineage, whereas *Blickomylus,* more advanced than *S.* (*Stenomylus*), is characterized by further reduction of the premolars and an anteroposterior expansion of the third molars. In the latter feature *Blickomylus* goes beyond the condition in the geologically youngest genus, *Rakomylus.*

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The Stenomylinae are known only from Miocene sediments, specifically in deposits of middle Arikareean to early Barstovian age. Geographically the subfamily ranged from California east to Arizona, New Mexico, and Texas, and north to Nebraska, Wyoming, and Montana.

The identification, grouping, and classification of the Stenomylinae are the work of the late Childs Frick and formed part of an extensive revision of the Camelidae at the time of his death in 1965. It was the privilege of the junior author to have assisted him in this preliminary work. Because the manuscript on the Camelidae was unfinished at the time of Frick's death, the junior author furnished the present text on the subfamily Stenomylinae.

Acknowledgments

This study has benefited greatly from discussions concerning taxonomic and geologic problems with Messrs. Ted Galusha and Morris F. Skinner. These gentlemen and Drs. Malcolm C. McKenna and Richard H. Tedford read the manuscript and made many helpful suggestions. Mrs. Shirley M. Skinner assisted in the preparation of the manuscript. We also thank all other members of the Frick Laboratory for their help, especially Messrs. George Krochak and Otto Simonis. Mr. Raymond J. Gooris and Miss Hazel De Berard prepared the illustrations, and Mrs. Marian Galusha and Miss Harriett Meek typed the manuscript. We are grateful to Dr. Craig C. Black and Dr. Mary R. Dawson of the Carnegie Museum for the loan of type material and field data.

The following abbreviations are used:

alv., alveolus
br., broken
C.M., Carnegie Museum, Pittsburgh, Pennsylvania
d., deciduous
F:A.M., Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

FAMILY CAMELIDAE GRAY, 1821

SUBFAMILY STENOMYLINAE MATTHEW, 1910

Included Genera: *Stenomylus* Peterson, 1906; *Rakomylus* Frick, 1937;

and *Blickomylus,* new genus.

DISTRIBUTION: From medial Arikareean to early Barstovian in the western United States.

REVISED DIAGNOSIS: Small camelids with unusual posterior production of nasal process of premaxilla; compression of muzzle by two maxillary pits; deep maxilla for extremely hypsodont molars; relatively short cranium; horizontal part of palatine bone absent; pterygoids completely united at their origin; incisiform lower canine; P_2 (lost in *Rakomylus*) separated from P_3 by a diastema similar to that of otherwise very different

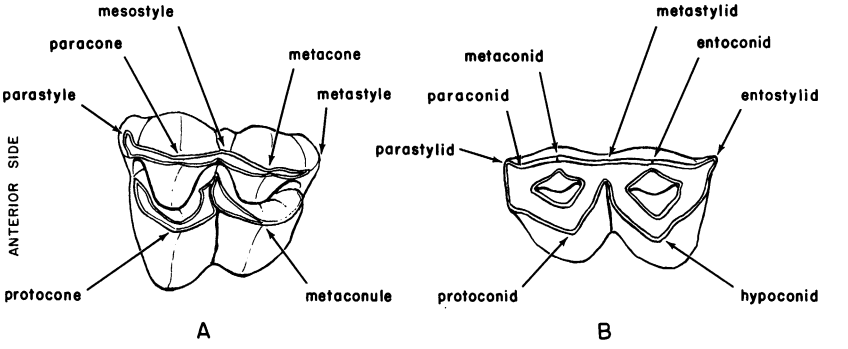

FIG. 1. *Poebrotherium.* A, B. F:A.M. No. 47077. A. Left M^3. B. Left M_2. ×2. Diagrammatic occlusal views to illustrate the cusp terminology used in this paper. All names are standard, and the application of these names is a consensus of the work of Gazin (1955), Arambourg (1947), and Singer (1960). Gazin (1955) is followed in the use of metaconule for the posterior lingual cusp which is referred to as the hypocone by Singer (1960) and Arambourg (1947). The use of the word "metaconule" is preferred for the Camelidae, because in ancestral artiodactyls the hypocone disappears and its position is occupied by the enlargement of the metaconule.

Floridatragulus; extremely narrow and hypsodont molars without mesostyles above and metastylids below, and buccal surface above and lingual surface below almost smooth; anteroposterior elongation of M_3^3; and only a slight projection on mandibular angle below condyle in place of characteristic camelid hook.

DISCUSSION: When Peterson described *Stenomylus* in 1906, he considered it a unique taxon of the Camelidae. In (1908, p. 300) he stated that it "should be regarded as the type of a new subfamily." The subfamily name Stenomylinae was first used by Matthew (1910, p. 42) in a classification of the Leptotragulinae in which he placed *Hypisodus* with "affinities to Stenomylinae." Matthew gave no diagnosis for the

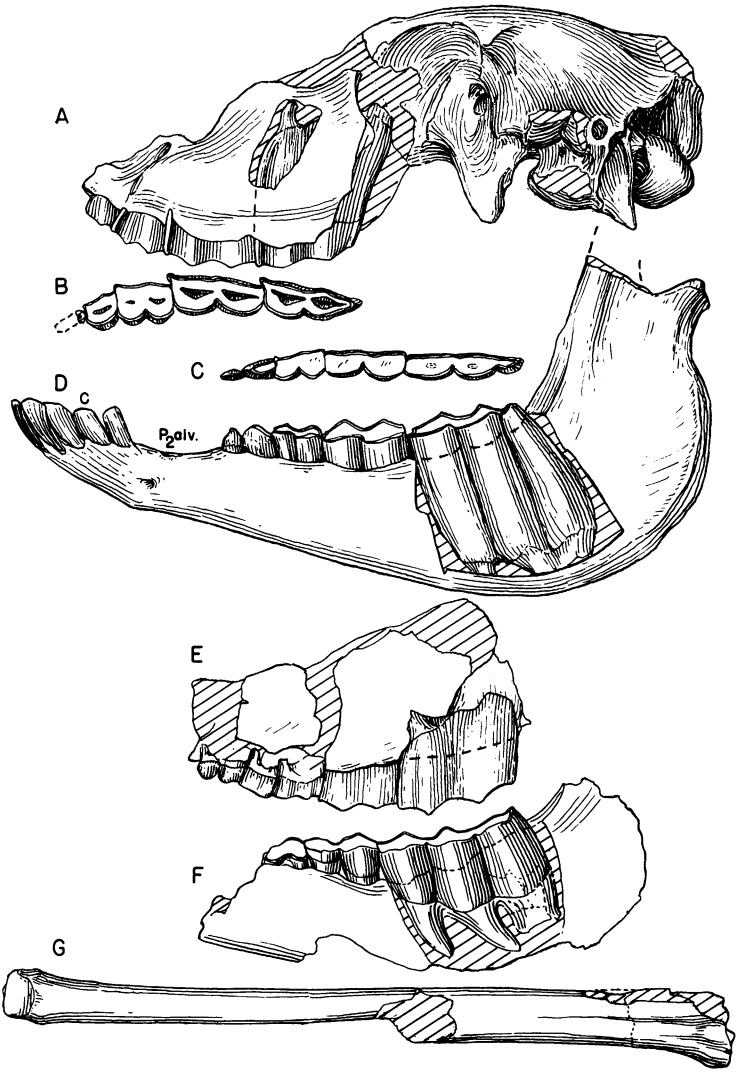

FIG. 2. *Stenomylus* (*Stenomylus*) *gracilis*. A–D. Type, C.M. No. 1610; from along the Niobrara River, Sioux County, Nebraska. A. Lateral view. B. Left P^3 root–M^3, occlusal view. C. Left P_3–M_3, occlusal view. D. Lateral view. (For limbs, see fig. 3.) E–G. Referred, F:A.M. No. 39635; from Hay Springs Creek, Dawes County, Nebraska. E, F. P^2–M^3. E. Lateral view. F. Lateral view, reversed. G. Left metatarsus, anterior view. All $\times 0.5$.

subfamily, but he accepted Peterson's recommendation for erecting the Stenomylinae. In essence, Peterson's description of the genus *Stenomylus* served as a diagnosis for the subfamily, which was monotypic at that time. Later Frick (1937, p. 656) elevated the Stenomylinae to "divisional rank" (Stenomylini). Frick's division was intermediate between the family and the subfamily, and his use of the "ini" ending does not conform with Simpson's usage (1945, p. 15) nor is it in accordance with the recommendations in the International Code (Stoll and others, 1961, Article 29A). Simpson (1945, p. 150) overlooked Matthew's (1910) initial mention of the Stenomylinae and credited the subfamily to Frick.

STENOMYLUS PETERSON, 1906

TYPE: *Stenomylus* (*Stenomylus*) *gracilis* Peterson, 1906.

DISTRIBUTION: Medial Arikareean to medial Hemingfordian of North America.

INCLUDED SUBGENERA: *Stenomylus* (*Stenomylus*) Peterson, 1906, new rank; and *S.* (*Pegomylus*), new subgenus.

DIAGNOSIS: *Stenomylus* differs from *Blickomylus* in having smaller incisors; larger, more elongate, and slightly more complex P^2 versus a diminutive, conical P^2 which is sometimes lost in *Blickomylus;* relatively larger P^3 and P^4; less caniniform and usually double-rooted P_2; relatively larger and double-rooted P_3 versus a smaller, single-rooted, peglike P_3 in *Blickomylus* which is occasionally lost; less hypsodont molars, with the root of M_3 fully formed when the talonid is only beginning to wear (C.M. No. 1610; fig. 2C,D). In *Blickomylus* the molars are more hypsodont, with the M_3 root unformed and still depositing enamel at the base while the M_3 talonid is in wear (F:A.M. No. 50863; fig. 10E); the molars have stronger parastyles above and stronger parastylids below, with more rounded buccal surfaces and deeper ectoflexids; M_1^1 are relatively larger, and there is a shallower horizontal ramus and less coossified metapodials.

Stenomylus differs from *Rakomylus* in the following characters: shorter muzzle; shorter and less posteriorly extended nasal process of the premaxilla; longer nasals; less recessed anteromaxillary fossa ("subnasal pit" of Loomis, 1910); shallower maxilla; relatively smaller and anteroposteriorly shorter glenoid fossa; less laterally compressed bullae; smaller I^{1-2}; less caniniform I^3; $P^{1-\frac{2}{2}}$ present; P_1 and P_3 strong versus a vestigial P_1 and P_3; relatively larger P_4^4; less hypsodont molars; and relatively longer and less coossified metapodials.

DISCUSSION: Peterson (1906, p. 41) established *Stenomylus gracilis* on a partial skeleton from the Harrison Formation along the Niobrara River, Sioux County, Nebraska. In 1906, he observed that certain cranial char-

acters were suggestive of *Hypisodus* from the Oligocene, but that the limb and foot structures were camelid-like. Two years later, Peterson (1908, pp. 286–300) gave a more detailed description of the type of *Stenomylus gracilis,* comparing it with the type of *Oxydactylus longipes* and the Recent camels. Peterson concluded that *Stenomylus* branched off from the early tylopod stem, possibly in the late Eocene, and exhibited "the most curious combination of characters" of any taxon in the Camelidae.

The first suggestion that *Stenomylus* was derived from a known taxon of the Camelidae was made by Loomis (1910, p. 321) when he compared *Stenomylus* with *Hypisodus* and *Poebrotherium.* Loomis concluded that the dentition of *Stenomylus* approximated *Hypisodus* but that other skeletal features indicated a close relationship to the Tylopoda. Loomis (*ibid.,* p. 323) stated that *Stenomylus* "must have had its beginning in the later part of the Oligocene, being derived from *Poebrotherium.*" Peterson (1911, p. 271) contended, however, that "the peculiar structure . . . at the sphenoid bones, the backward-sloped coronoid process of the lower jaw, caused by the higher position of the orbit, and also the development and position of the dentition of *Stenomylus* are such deep-seated characters and so different from those in *Poebrotherium* that one must hesitate before seriously regarding the former genus [*Stenomylus*] as directly derived from the latter [*Poebrotherium*]."

McKenna (1966, p. 4) stated, "Because *Stenomylus* is such a distinctive genus, it is usually given a hypothetical separate ancestral line leading back to the early Oligocene or even into the Eocene, but it may be pointed out here that there are a number of dental similarities to *Dyseotylopus migrans* of the upper Sespe Formation of California and to certain other specimens from the Gering or Monroe Creek formations similar to *Dyseotylopus* and *Pseudolabis.*"

The skull of *Stenomylus* differs from that of *Poebrotherium* in the posterior production of the nasal process of the premaxilla, the possession of a deep anteromaxillary fossa and a relatively short postorbital cranium, the unification of the pterygoids at their origin, the absence of the horizontal part of the palatine bone, and the forward position of the posterior nares, with their anterior edge bordering the palatine process of the maxilla, instead of the horizontal part of the palatine bone. Furthermore, the dentition of *Stenomylus* differs from that of *Poebrotherium* in the incisor-like C/C, the forward position of P_1, the separation of P_2 and P_3 by a diastema, and in having smaller premolars and specialized narrow, hypsodont molars. The numerous foregoing differences are so great that it would require a more rapid rate of evolution for *Stenomylus* to be derived from *Poebrotherium* between Whitneyan and medial Arika-

reean time than is known to occur elsewhere in the Camelidae. Instead, *Poebrotherium* and *Stenomylus* appear to represent diverging lines of camelid specialization in the Oligocene and Miocene, respectively. As Peterson surmised (1908, p. 300), the progenitor of *Stenomylus* is most likely an unknown late Eocene member of the Tylopoda.

STENOMYLUS (STENOMYLUS) PETERSON, 1906, NEW RANK

Stenomylus PETERSON, 1906, p. 41.

TYPE: *Stenomylus* (*Stenomylus*) *gracilis* Peterson, 1906.

DISTRIBUTION: Medial Arikareean to medial Hemingfordian, North America.[1]

RECOGNIZED SPECIES AND UNDESCRIBED MATERIAL: 1. *Stenomylus* (*Stenomylus*) *gracilis* Peterson (1906, p. 41) from "Lower Harrison beds on the Niobrara (Running Water) River, Sioux County, Nebraska, in 1901" and the Marsland Formation in Nebraska and Wyoming. 2. *Stenomylus* (*Stenomylus*) *hitchcocki* Loomis (1910, p. 297) from "the *Stenomylus* Quarry . . . five miles southeast of Agate Spring postoffice, and about one and a half miles up the 'draw' south of the upper Harris place, and about the same distance a little east of south from the famous Agate Springs Quarry of the Carnegie Museum . . . [from the] Lower Harrison beds about 75 feet from their upper boundary," Sioux County, Nebraska. 3. *Stenomylus* (*Stenomylus*) *crassipes* Loomis (1910, p. 319) from "seven miles northeast of Agate, Sioux Co., Neb., in the uppermost sandstones of the Lower Harrison beds." 4. Undescribed material in the Frick Collection of the American Museum of Natural History from (a) Monroe Creek Formation, eastern Wyoming; (b) deposits temporally equivalent to the Harrison Formation, eastern Wyoming; (c) deposits temporally equivalent to the Harrison Formation, western Montana; (d) deposits of Arikareean age,[2] southwestern Arizona; and (e) Piedra Parada Member and the Chamisa Mesa Member of the Zia Sand Formation, central New Mexico. 5. Undescribed material in other institutions: (a) Tick Canyon Formation, Soledad Basin, southern California (Los Angeles County Museum); (b) unnamed rocks of late Arikareean age, Hector Local Fauna, Mojave Desert, California (University of California, Riverside); and (c) unnamed rocks of Arikareean age, Big Bend National Park, Texas (Wilson, 1967, p. 158; University of Texas, Austin).

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[1] An isolated M_3 reported to be from sediments of the Brown's Park Formation, Moffat County, Colorado, described by Peterson (1924, p. 301, fig. 3) as a camelid closely allied to *Stenomylus* is here considered to belong to an indeterminate antilocaprine.

[2] Lance and Wood (1958, p. 1694) recorded the occurrence of *Stenomylus* 6 miles northeast of Wellton, Arizona, and assigned it as Arikareean(?) in age.

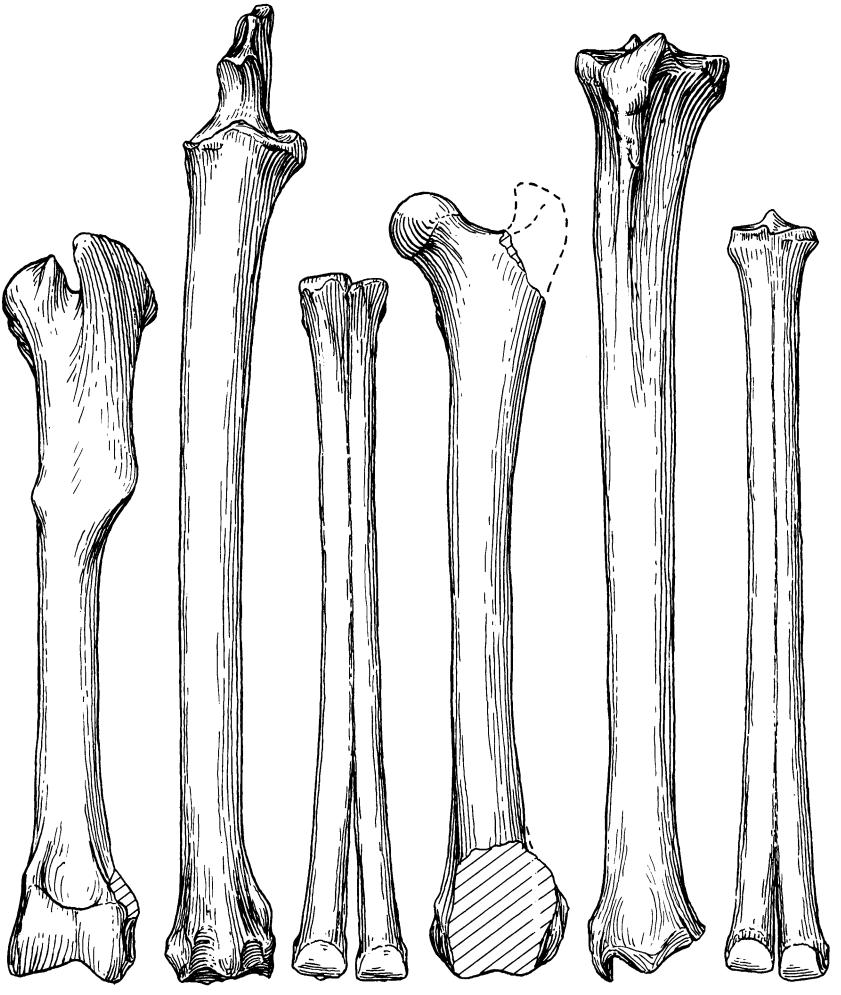

FIG. 3. *Stenomylus* (*Stenomylus*) *gracilis*. A–F. Type, C.M. No. 1610; from along the Niobrara River, Sioux County, Nebraska. A. Humerus, reversed. B. Radius. C. Metacarpus. D. Femur, reversed. E. Tibia, reversed. F. Metatarsus, reversed. All anterior views. (For partial skull and mandible, see fig. 2.) ×0.5.

DIAGNOSIS: *Stenomylus* (*Stenomylus*) differs from *S.* (*Pegomylus*) (fig. 15A, B) in having a slightly more incisiform lower canine; shorter P_2–P_3 diastema; smaller P_2; and much smaller P_3–P_4 of which the combined length is approximately 30 per cent less than in the type of *S.* (*Stenomylus*) *gracilis*.

DISCUSSION: The reasons for separating *S.* (*Stenomylus*) and *S.* (*Pegomylus*) are given in the foregoing diagnosis. Although distinguishing characters separate both subgenera, the basic characters indicate a relationship that is not considered generically distinct.

Stenomylus (*Stenomylus*) *gracilis* Peterson, 1906

Figures 2, 3, 4A, B, 5, 6A–D

Stenomylus gracilis PETERSON, 1906, pp. 35, 41, fig. 9, pl. 12; 1908, p. 286, figs. 1–12.

TYPE: C.M. No. 1610, partial skull with P^4–M^3, right and left rami with I_1–M_3 (P_1 alveolus), cervical vertebrae 3–7, humerus, both radii, left carpals, metacarpus, right articulated femur through metatarsus, left tarsals and partial metatarsus, and two first phalanges. The type[1] was collected by O. A. Peterson in the Harrison Formation on the Niobrara (Running Water) River, Sioux County, Nebraska, in 1901. (For illustrations, see Peterson, 1906, fig. 9, pl. 12; 1908, figs. 1–12; this report, figs. 2A–D, 3, 15B).

DISTRIBUTION: Harrison Formation, Sioux County, Nebraska; Marsland Formation (=Upper Harrison Formation), Dawes County, Nebraska; Marsland Formation, Niobrara, Goshen, and Platte counties, Wyoming. (See discussion, p. 19.)

HYPODIGM: 1. Harrison Formation, Niobrara River, Sioux County, Nebraska: type and F:A.M. No. 31178,[2] right and left partial rami (Frick, 1937, fig. 68). 2. Marsland Formation, Dawes County, Nebraska: F:A.M. No. 39635, palate, right and left partial rami (fig. 2E–G), partial femur, tibia, tarsals, metatarsus; F:A.M. No. 39636, partial tibia, tarsals, metatarsus, and broken first phalanx, Hay Springs Creek. 3. Deposits temporally equivalent to the Marsland Formation,[3] Niobrara, Goshen,

[1] Mary Dawson (personal communication) states: "There are three field labels for the . . . [type, C.M. No. 1610. The information on two of the labels is] Harrison beds, Running Water, Sioux Co., Neb. The third label, which may be the actual label written in the field, since it is in pencil states 'skeleton in block' whereas the others describe parts of the skeleton present." The third label states, "Loup Fork = Cork Screw beds at top, Running Water, Sioux County, Nebraska." The type of *S.* (*Stenomylus*) *gracilis* is similar to specimens from the Marsland (=Upper Harrison) Formation of Nebraska and presumably equivalent deposits in Wyoming.

[2] This fragmentary specimen, with badly worn dentition, was collected by Paul Miller in 1927 and referred by Frick (1937, p. 660) to *Stenomylus gracilis.* Frick recorded F:A.M. No. 31178 from the Lower Harrison Beds, but the matrix adhering to the specimen is similar to that from the Marsland (=Upper Harrison) Formation.

[3] These deposits in Wyoming were regarded as Marsland Formation by Schultz and Falkenbach (see discussion in this report, p. 19).

and Platte counties, Wyoming: F:A.M. No. 43578, partial skull and mandible (fig. 5A), 7 miles southeast of Lusk, Niobrara County; F:A.M. No. 32842, ramus, F:A.M. No. 32843, partial mandible, F:A.M. No. 32841 (fig. 5B), partial skull and ramus, east side of road to Jay-Em; F:A.M. No. 43583, mandible, north side of road 1½ miles west of Jay-Em; F:A.M. No. 36789, partial humerus, partial radii, carpals, metacarpus, and phalanges, Jay-Em, very high[1]; F:A.M. No. 43580, right and left partial rami; F:A.M. No. 43581, partial mandible, 20 Mile District, 20 miles southeast of Lusk; F:A.M. No. 43582, radius and metacarpus, 20 Mile District, 20 miles southeast of Lusk, middle of beds; F:A.M. No. 43586, fragmentary skull, 16 Mile District, 16 miles southeast of Lusk, west end, low white sand; F:A.M. No. 43577, right partial ramus, 16 Mile District, 16 miles southeast of Lusk, low brown sand; F:A.M. No. 43596, right ramus, 16 Mile District, 16 miles southeast of Lusk, light sand; F:A.M. No. 43595, right and left partial rami (fig. 6B), 16 Mile District, 16 miles southeast of Lusk, low light sand; F:A.M. No. 36719, partial femur, tibia, astragalus, calcaneum, tarsals, partial metapodial, first and second phalanges, 16 Mile District, 16 miles southeast of Lusk, high; F:A.M. No. 43608, scapula, partial radius, femur, partial tibia, two partial metatarsi, and calcaneum, 16 Mile District, 16 miles southeast of Lusk, north of fault; F:A.M. No. 43576, partial ramus and phalanges, 18 Mile District, 18 miles southeast of Lusk, middle brown sand; F:A.M. No. 43594, mandible (fig. 5C), partial radius, partial metacarpus, partial tibia, calcaneum, astragalus, first and second phalanges, 18 Mile District, 18 miles southeast of Lusk, high; F:A.M. No. 43587, partial skull, ramal fragment, and phalanges, 18 Mile District, 18 miles southeast of Lusk, middle brown sand; F:A.M. No. 43607, partial femur to partial metatarsus, 18 Mile District, 18 miles southeast of Lusk, high; F:A.M. No. 43579, immature maxilla, 17–20 miles southeast of Lusk; F:A.M. No. 43588, partial skull, 21 miles southeast of Lusk; F:A.M. No. 43600, immature mandible, 12–15 miles south of Lusk; F:A.M. No. 43591, partial immature skull, Sand Gulch, 18 miles south of Lusk, high sand; F:A.M. No. 36792, metacarpus (fig. 6C) and first phalanx, Spoon Buttes, high, Goshen County; F:A.M. No. 43610, partial ramus, 3 miles southeast of Guernsey; F:A.M. No. 43611, right and left partial maxillae, partial humerus, radius, partial tibia, and first phalanx, 2 miles south of Guernsey, low; F:A.M. No. 43609, immature mandible (fig. 6A), partial humerus, radius, partial femur, partial tibia, calcaneum, astragalus, phalanges, 4 miles southwest

[1] This is the only available geological datum.

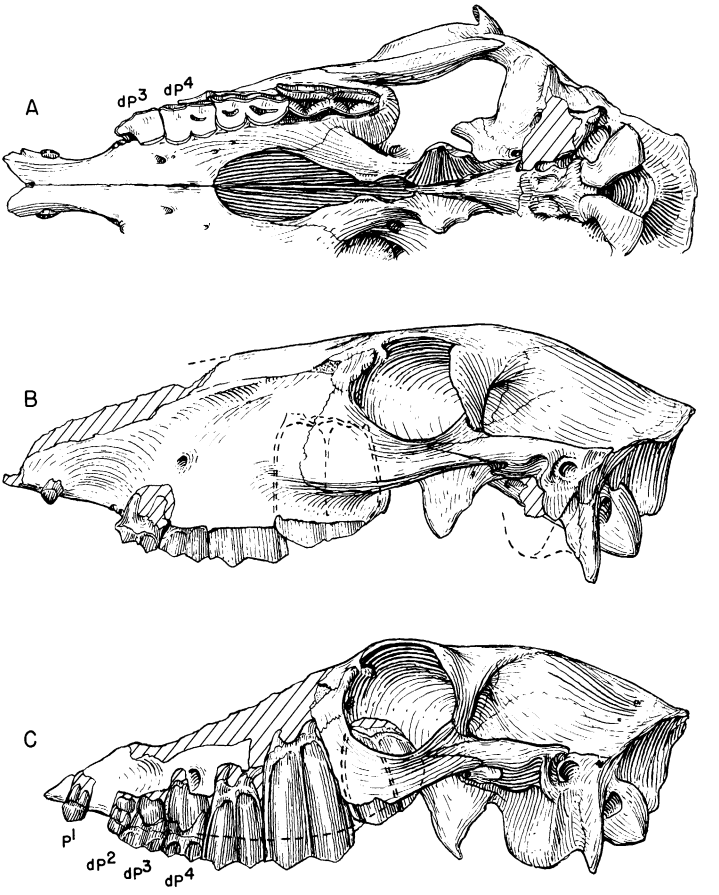

FIG. 4. *Stenomylus (Stenomylus) gracilis* and *Stenomylus (Stenomylus) hitchcocki.* A, B. *Stenomylus (Stenomylus) gracilis,* F:A.M. No. 43614; from 7 miles southeast of Chugwater water hole, Platte County, Wyoming. A. Ventral view. B. Lateral view. C. *Stenomylus (Stenomylus) hitchcocki,* partial skull with P^1, dP^2–dP^4, M^1–M^3 (M^3 erupting), and P^2–P^4 germs exposed, F:A.M. No. 47827, from the Galusha Stenomylus Quarry, Harrison Formation, Sioux County, Nebraska. Lateral view. All ×0.5.

of Guernsey, high; F:A.M. No. 36811, metacarpus, 6 miles southwest of Guernsey, very high; F:A.M. No. 43621, partial ramus and radius, F:A.M. No. 43616, partial maxilla and detached teeth, 5 miles southeast of Chugwater, low; F:A.M. No. 43635, astragalus, calcaneum, tarsals, and partial metatarsus, 5 miles southeast of Chugwater, high; F:A.M. No. 43615, palate, partial ramus, partial femur; F:A.M. No. 43622, im-

TABLE 1

WEAR AND MEASUREMENTS (IN MILLIMETERS) OF THE DENTITION AND DIASTEMATA OF *Stenomylus (Pegomylus) keelinensis,* NEW SPECIES, AND *Stenomylus (Stenomylus) gracilis* PETERSON

	F:A.M. No. 43668[a]	C.M. No. 1610[b]	F:A.M. No. 39635	F:A.M. No. 32841	F:A.M. No. 43615	F:A.M. No. 43609
Wear	—	W[c]	W3	W7	W3	I
Length						
Upper dentition[d]						
P^2	—	—	6.1	—	4.3	—
P^3	—	—	7.5	—	7.6	—
P^4	—	10.3	(10[e])	—	10.0	—
M^1	—	17.0	(13.5)	—	(12.5)	—
M^2	—	26.0	(22)	—	(25.5)	—
M^3	—	31.5	34.0	—	35.5	—
M^3 height	—	(43)	—	—	—	—
Lower dentition						
/C	6.7	8.5	—	8.5	—	—
/C–P_1diastema	(2.2)	(0.5)	—	1.7	—	—
P_1	(5)	5.3	—	5.1	—	5.5
P_1–P_2 diastema	8.0	(6)	—	7.5	—	12.5
P_2	7.8	—	—	5.7	—	*f*
P_2–P_3 diastema	14.5	(10.7)	—	8.0	—	(8.3)
P_3	(10)	6.0	—	6.2	—	4.8
P_4	11.7	8.8	—	(8.8)	9.0	9.8
M_1	(14.5)	(12.5)	—	(10)	(11)	(19.5)
M_2	19.5	22.5	(20)	(21.5)	(21.5)	(27)
M_3	31.0	38.0	41.0	35.0	—	39.5
Height						
M_3	—	—	—	—	—	(43)

[a] F:A.M. No. 43668 is the type of *S. (Pegomylus) keelinensis,* new species.

[b] C.M. No. 1610 is the type of *S. (Stenomylus) gracilis* Peterson. F:A.M. Nos. 39635, 32841, 43615, and 43609 are referred to *S. (Stenomylus) gracilis.*

[c] Wear, modified after Skinner (1942, p. 189); I, milk premolars present; M, milk premolars just shed, permanent premolars well erupted, M_3 unworn; W, premolars starting to wear, first molar retains anterior fossette; W1, anterior fossette of first molar worn away and posterior fossette wearing smaller. The articulated skulls and mandibles of the stenomylines show that in the superior dentition the wear count is different by as many as four stages fewer than the inferior, because the fossettes in the lower molars are shallower and disappear more rapidly than in the upper molars. W2, posterior fossette of the first molar gone and anterior fossette of second molar wearing smaller; W3–W7, successive loss of fossettes in molars with wear.

[d] I^1–P^1 are missing.

[e] Measurements enclosed in parentheses are approximate.

[f] dP_2.

mature ramus (fig. 5D, E), 7 miles southeast of Chugwater, low; F:A.M. No. 43614, immature skull (fig. 4A, B), radius and vertebrae, 7 miles southeast of Chugwater Water Hole, high; F:A.M. No. 36488, partial humerus, partial radius, partial tibiae, astragalus, calcanea, tarsal, and metatarsus, 7 miles southeast of Chugwater, 15 feet above water hole; F:A.M. No. 43619, immature mandible, humeri, radii, metacarpi, femur, and phalanges; F:A.M. No. 43636, limb fragments, 7 miles southeast of Chugwater, 10 feet above water hole; F:A.M. No. 36815, carpals, metacarpus (fig. 6D), and second phalanx, 8 miles southeast of Chugwater, high, Platte County.

MEASUREMENTS: See table 1.

SUPPLEMENTARY DESCRIPTION

SKULL: Peterson (1906, p. 42, pl. 12) described and illustrated the incomplete type skull of *S.* (*Stenomylus*) *gracilis.* In 1908, Peterson (p. 286, fig. 1) gave a more detailed description of the skull and described the skeletal elements. A partial immature skull (F:A.M. No. 43614, fig. 4A, B) from Platte County, Wyoming, is here referred to *S.* (*S.*) *gracilis.* This immature skull is more complete than the type of *S.* (*S.*) *gracilis,* and a supplementary description follows for areas missing in the type.

Anterior to the orbit, the face is depressed by two maxillary pits. The first, the anteromaxillary fossa (the "subnasal pit" of Loomis, 1910), is deeply excavated and extends from above P^1 to above dP^3. The second fossa is a deep, gutter-like depression (the "preorbital pit" of Loomis, 1910) that is situated high on the maxilla and parallels the nasal process of the premaxilla. Loomis observed in the description of *S.* (*S.*) *hitchcocki* that the preorbital pit is deep and "must nearly close the olfactory space within the muzzle." In F:A.M. No. 43614, the subnasal pit joins the preorbital pit and tends to be one large continuous fossa. The lacrimal bone is large, and a small facial vacuity is present. This vacuity is bordered by the lacrimal, maxilla, nasal, and frontal bones. The frontals are exceptionally wide between the orbits. Peterson (1906, p. 42) observed that the transverse expansion of the frontals results in an oblique outward position of the orbit. A small supraorbital foramen is situated between the orbital rim and the median frontal suture but is nearer the suture. The orbit is closed posteriorly by the downward production of the supraorbital process, which meets a strongly developed zygomatic process of the malar bone. A large malar borders the front and lower half of the orbit. The zygomatic process of the temporal is light in comparison with the strong zygomatic

process of the malar. Compared with the length of the skull, the cranium is relatively short and wide; weak parietal ridges extend posteriorly from the supraorbital processes to the lambdoidal crests. In the specimen used to supplement the type description (F:A.M. No. 43614), the failure of the parietal ridges to join and form a sagittal crest is probably due to immaturity. In mature specimens, the occiput is low, and the lambdoidal crests are prominent.

As observed by Peterson (1906, p. 42), the basicranial axis is strongly angled, and the tympanic bullae are less compressed than in *Blickomylus* and are coosified with the paroccipital processes. The pterygoids are thick and completely united at their origin, and the posterior nares are large and situated anteriorly. The horizontal part of the palatine bone is absent, and the anterior edge of the posterior nares borders the palatine process of the maxilla and not the horizontal part of the palatine bone as in the non-stenomyline Camelidae.

DENTITION: Peterson (1906, p. 42) described the dentition in the type of *S.* (*S.*) *gracilis*. A more complete description of the dentition of *S.* (*S.*) *gracilis* is given here, based on referred dentitions from Nebraska and Wyoming.

In F:A.M. No. 43578 (fig. 5A), I^2 is adjacent to I^1 and slightly in front of I^3. An incisiform upper canine is slightly smaller than I^3 and separated from it by a short diastema and from P^1 by a longer diastema. In F:A.M. No. 43614 (fig. 4A, B), P^1 (or perhaps, better, dP^1, because dP^1_1 are not replaced in the Camelidae), is small, laterally compressed, and double-rooted. P^1 has a simple crown which culminates midway in an apex. Behind P^1 is a long diastema that separates it from the alveolus of dP^2 (F:A.M. No. 43614). Two palates, F:A.M. Nos. 43615 and 39635 (fig. 2E), have P^2 preserved. P^2 is laterally compressed, has a simple crown, with the paracone rising to a point similar to that of P^1, and a double root that tends to unite. P^3 is elongate and narrow, with a simple crown and two roots. P^4 is a single-lobed tooth, with the inner and outer cusps separated by a deep fossette. Except for a weak parastyle, the buccal surface of P^4 is smooth.

The upper molars are transversely narrow, extremely hypsodont, and become progressively larger from M^1 to M^3. Each molar is bilobed, with deep fossettes separating the inner and outer cusps. The parastyle and metastyle are weak (F:A.M. No. 43614, fig. 4A, B) and disappear with wear. The mesostyle is absent, resulting in a slightly depressed surface between the paracone and metacone. There are no median vertical ribs on the paracone and metacone. M^1 is the smallest tooth, narrowing anteroposteriorly toward the root, and in aged individuals (such as

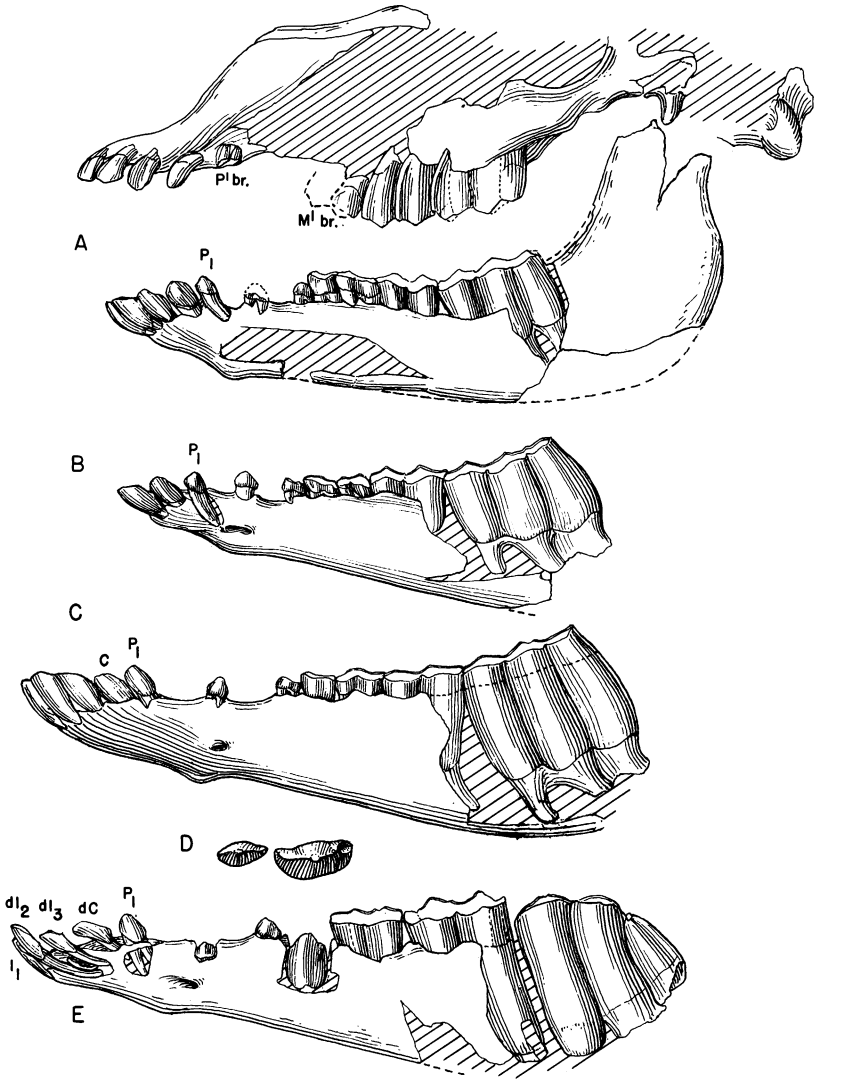

FIG. 5. *Stenomylus* (*Stenomylus*) *gracilis,* partial skulls and mandibles. A. F:A.M. No. 43578; from 7 miles southeast of Lusk, Niobrara County, Wyoming; lateral view (left side of mandible reconstructed from the right). ×0.5. B. F:A.M. No. 32841; from east side of road to Jay-Em, Goshen County, Wyoming; lateral view. ×0.5. C. F:A.M. No. 43594; from 18 Mile District, 18 miles southeast of Lusk, Goshen County, Wyoming; lateral view. ×0.5. D, E. F:A.M. No. 43622; from 7 miles southeast of Chugwater, Platte County, Wyoming. D. P_3–P_4, occlusal view. ×1. E. Lateral view. ×0.5.

F:A.M. No. 39635) M^1 is very small compared with M^{2-3}. M^2 is similar to M^1, but it is larger and narrows less toward the root. On M^2 the parastyle tends to be stronger than on M^1. In the type (C.M. No. 1610, fig. 2A), M^3 is extremely hypsodont, with the height of the crown exceeding the anteroposterior length by approximately 30 per cent. M^3 is proportionally longer than M^2, because of the expansion of the second lobe and the addition of a short heel as in F:A.M. No. 43615. The second lobe of M^3 is longest near the base, with the result that the grinding surface becomes progressively longer with wear.

The lower incisors are best illustrated in the type, C.M. No. 1610 (fig. 2D), and a referred mandible, F:A.M. No. 43594 (fig. 5C). They are large and spatulate, with I_2–I_3 strongly overlapping the preceding incisor. A laterally compressed and incisiform lower canine overlaps I_3. Immediately posterior to the canine is a single-rooted P_1. There is no diastema between the canine and P_1, but the tooth crowns are slightly separated because of the more erect position of P_1. P_1 is laterally compressed and more caniniform than the canine. The diastema between P_1 and P_2 is highly variable. In F:A.M. No. 32841 (fig. 5B), the P_1–P_2 diastema is 7.5 mm. versus 13.0 mm. in F:A.M. No. 43594 (fig. 5C). Unfortunately, P_2 is missing from the type specimen, but it is present in several referred mandibular rami from Wyoming (F:A.M. Nos. 43609, 43622, and 43594). P_2 is reduced, double-rooted, laterally compressed, and almost functionless, showing no wear in mature individuals (F:A.M. No. 43594, fig. 5C). P_2 has a protoconid that rises to a point and is the most trenchant tooth in the series. Behind P_2 is a diastema that is also variable, measuring 8.0 mm. in F:A.M. No. 32841 (fig. 5B) versus 12.6 mm. in F:A.M. No. 43594 (fig. 5C). P_3 is a small, laterally compressed, double-rooted, trenchant tooth and resembles P_2 except that it is more elongate and more functional, because it shows wear in older individuals. P_4 is tall-crowned and anteroposteriorly long in contrast to the other premolars: the protoconid is elevated to a blunt peak; the paraconid (or, more appropriately, the paralophid) is short, compressed, and slightly inflected; no metaconid is present.

The lower molars have narrow, hypsodont crowns and become progressively larger from front to back. All the molars lack the metastylid and median ribs on the metaconid and entoconid. The lingual surface of the molars is smooth except for a weak parastylid and a faint entostylid, which disappear rapidly with wear. Except for the talonid on M_3, the lower molars are bilobed, with the inner and outer cusps separated by fossettes which disappear rapidly with wear. M_3 is anteroposteriorly expanded and extremely hypsodont, with the crown height

exceeding the length by approximately 10 per cent (F:A.M. No. 43609, fig. 6A). The first molar is well worn when the third molar erupts. Both M_1 and M_2 narrow toward the roots in contrast to M_3, which expands anteroposteriorly toward the base. Therefore, as M_1 and M_2 wear and shorten anteroposteriorly, the resulting space is occupied by M_3, which becomes larger with wear so that the combined molar length tends to remain constant.

MANDIBLE: The horizontal ramus is deep beneath the molars and gradually narrows anteriorly. A long, gutter-like symphysis (F:A.M. No. 43594, fig. 5C) extends posteriorly to beneath P_2. Situated beneath P_2 and above the posterior border of the symphysis is a large mental foramen. The mandibular angle is rounded except for a slight projection just below the condyle in the place of the strong hooklike projection so characteristic of the non-stenomyline camelids. The coronoid process is slender and slopes slightly backward.

METAPODIALS: Peterson (1908) described the limbs of the type of *S.* (*S.*) *gracilis* in detail. The proximal halves of the third and fourth metacarpals are coossified, but the distal halves are unfused. Both the third and fourth metacarpals have small articular facets for rudiments of the second and fifth metacarpals. In the type (C.M. No. 1610) the maximum length of the metacarpals measures 183 mm. versus 195 mm. for the metatarsals. When the mandibular ramus of the type is articulated with the skull, the length of the metacarpals is equal to the distance from the incisive border to the glenoid fossa.

The proximal two-thirds of the third and fourth metatarsals are coossified. Peterson observed that in the type the second metatarsal is represented by a small, bony nodule and that the presence of a rudimentary fifth metatarsal is indicated by a minute articular surface on the cuboid and a corresponding articular surface on the posterofibular face of the fourth metatarsal. The length of the metatarsals is greater than that of the metacarpals, and in the type the metatarsal length is only slightly less than the distance from the incisive border to the foramen magnum.

DISCUSSION: The type of *S.* (*Stenomylus*) *gracilis* was reported by Peterson (1906, p. 41) as occurring "in the Lower Harrison beds on the Niobrara (Running Water) River, Sioux County, Nebraska, in 1901." Loomis (1910, p. 297) reported the type of *S.* (*Stenomylus*) *hitchcocki* from Stenomylus Quarry about 5 miles southeast of Agate, Sioux County, Nebraska, also from the "Lower Harrison beds about 75 feet from their upper boundary."

Although both *S.* (*S.*) *gracilis* and *S.* (*S.*) *hitchcocki* are reported from the Harrison Formation, *S.* (*S.*) *gracilis* is the more advanced, differing

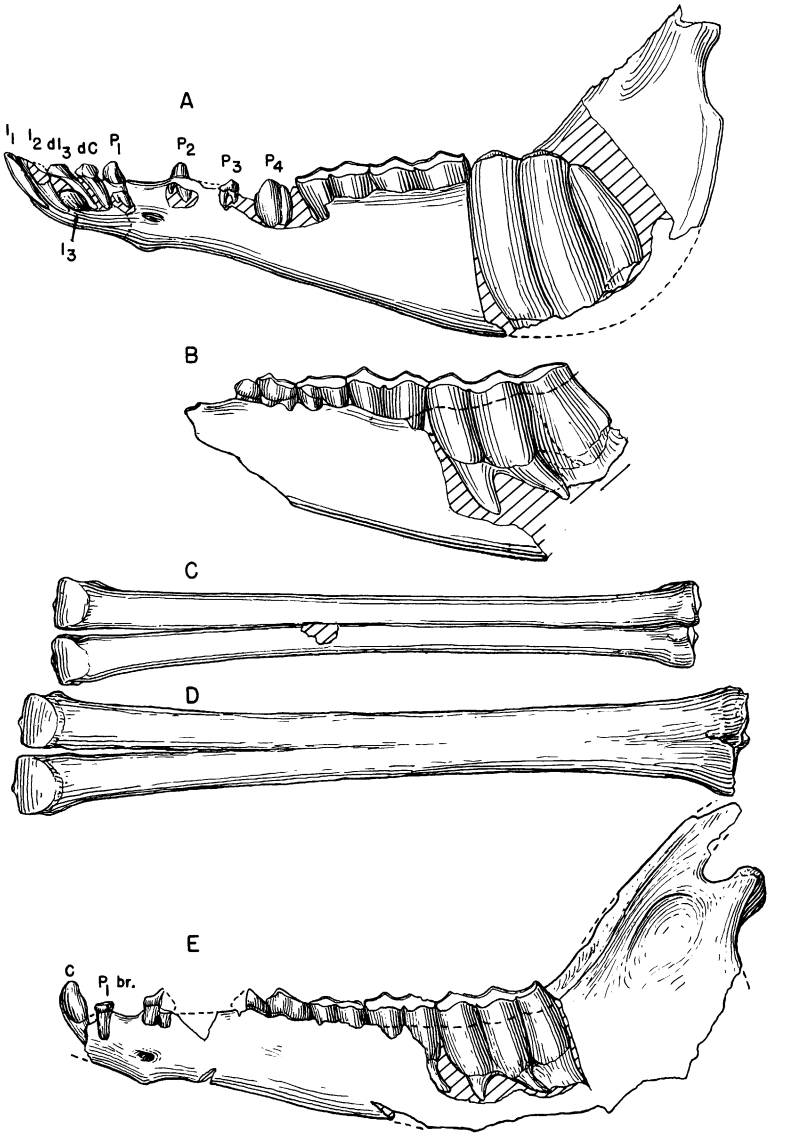

FIG. 6. A–D. *Stenomylus* (*Stenomylus*) *gracilis.* A. F:A.M. No. 43609; from 4 miles southeast of Guernsey, Platte County, Wyoming; lateral view (left side of mandible reconstructed from the right). B. F:A.M. No. 43595; from 16 Mile District, 16 miles southeast of Lusk, Goshen County, Wyoming; lateral view, reversed. C. Metacarpus, F:A.M. No. 36792; from Spoon Buttes, Goshen County, Wyoming; anterior view. D. Metacarpus, F:A.M. No. 36815; from 8 miles southeast of Chugwater, Platte County, Wyoming; anterior view, reversed. E. *Stenomylus* (*Pegomylus*) *keelinensis,* new subgenus, new species, type, F:A.M. No. 43668; from north of Keeline, Niobrara County, Wyoming; lateral view. All ×0.5.

from *S.* (*S.*) *hitchcocki* in its larger size, relatively smaller premolars, larger and taller-crowned molars, and the coossification of the proximal halves of the third and fourth metacarpals.

One individual, consisting of a partial palate, jaws, and limb elements (F:A.M. No. 39635, fig. 2E–G) from the Marsland Formation, Dawes County, Nebraska, is referred to *S.* (*S.*) *gracilis.* The dentition is larger than that of the type (C.M. No. 1610) of *S.* (*S.*) *gracilis,* but well within the size range of the population sample from the deposits in Wyoming that are considered biostratigraphically equivalent to the Marsland Formation by Schultz and Falkenbach.

Specimens similar to the type of *S.* (*S.*) *gracilis* are listed in the hypodigm from Marsland deposits in Niobrara, Goshen, and Platte counties, Wyoming. From these same deposits Schultz and Falkenbach (1940, pp. 289–291) identified *Merycochoerus matthewi* from the "Lower part of the Marsland Formation"; in 1947, (pp. 204, 208–221) they referred specimens to *Merychyus minimus* from the "lower Marsland"; and in 1950 (pp. 107, 109–110) they described *Phenacocoelus stouti* from the "lower Marsland formation."

Specimens listed in the hypodigm from the Marsland Formation in Nebraska and from deposits in Wyoming, which were called either Marsland or Lower Marsland on the basis of the oreodonts by Schultz and Falkenbach, are similar to the type of *S.* (*S.*) *gracilis* reported to be from the Harrison Formation. *Stenomylus* (*S.*) *gracilis,* however, is distinctly different from *S.* (*S.*) *hitchcocki* from the Harrison Formation in Sioux County, Nebraska, and may actually be restricted to the Marsland (=Upper Harrison) Formation.

STENOMYLUS (PEGOMYLUS),[1] NEW SUBGENUS

TYPE: *Steonomylus* (*Pegomylus*) *keelinensis,* new species.

DISTRIBUTION: From deposits temporally equivalent to the Harrison Formation, Niobrara County, Wyoming.

INCLUDED SPECIES: Type only.

DIAGNOSIS: *Stenomylus* (*Pegomylus*) differs from *S.* (*Stenomylus*) in having a slightly more caniniform lower canine; longer P_2–P_3 diastema; larger P_2; and much larger P_3–P_4. The combined length of P_3 and P_4 is approximately 30 per cent greater than in the type of *S.* (*Stenomylus*) *gracilis.*

DISCUSSION: Extremely large premolars are the primary reason for separating S. (*Pegomylus*) from *S.* (*Stenomylus*). In the stenomylines large

[1] From the Greek *pegos* (strong) and *myle* (grinder).

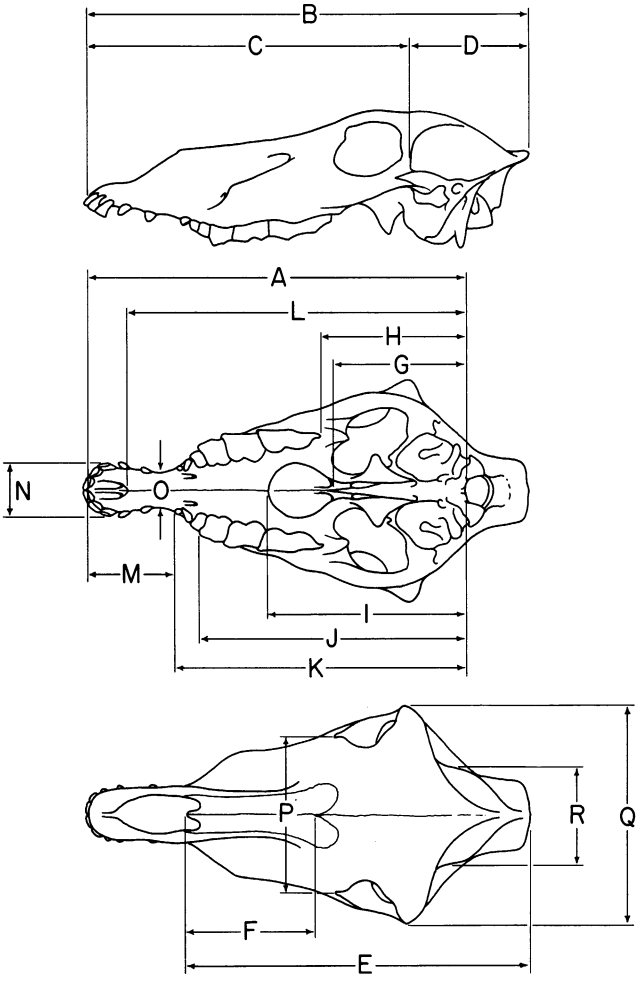

FIG. 7. Key to skull measurements of *Stenomylus*. A, foramen magnum to incisive border (basilar); B, occipital crest to anterior incisive border (vertex); C, postorbit to anterior incisive border (facial); D, postorbit to occipital crest (cranial); E, occipital crest to tip of nasals; F, nasofrontal suture to tip of nasals; G, anterior border of foramen magnum to vomer; H, anterior border of foramen magnum to posterior of M^3; I, anterior border of foramen magnum to anterior border of posterior nares; J, anterior border of foramen magnum to posterior of P^4; K, anterior border of foramen magnum to anterior of P^2; L, anterior border of foramen magnum to postpalatine fissure; M, anterior of P^2 to incisive border; N, I^3–I^3 (width of muzzle); O, narrowest part of rostrum on palatal side; P, anterior orbital width at narrowest point; Q, postorbital width, widest point at supraorbital processes; R, cranium, maximum width.

premolars are considered a primitive character. In both *S.* (*Stenomylus*) and *Blickomylus,* the premolars become relatively smaller in species from successively later deposits. Because of the presence of both *S.* (*Pegomylus*) *keelinensis* and *S.* (*Stenomylus*) *hitchcocki* in contemporaneous deposits in Wyoming, *S.* (*Pegomylus*), with large premolars, probably represents a separate lineage that is closer to the ancestral stem of *Stenomylus* and evolved separately.

Stenomylus (Pegomylus) keelinensis, new species

Figures 6E, 15A

TYPE: F:A.M. No. 43668, left ramus with C–M_3 (P_1–P_3) broken (figs. 6E, 15A). The type was collected by Charles Falkenbach in 1931.

DISTRIBUTION: From deposits temporally equivalent to the Harrison Formation north of Keeline, Niobrara County, Wyoming.

DIAGNOSIS: Only known species of the subgenus.

MEASUREMENTS: See table 1.

DESCRIPTION: A left ramus (F:A.M. No. 43668) is the type and only known specimen. Anterior to the canine the symphysis is missing. The canine is large and slightly more caniniform than in the type of *S.* (*Stenomylus*) *gracilis* (C.M. No. 1610). A short diastema separates the canine from P_1. Although P_1 is broken near the base of the crown, enough remains to indicate that it is about the size of P_1 in the type of *S.* (*S.*) *gracilis.* Behind P_1 is a diastema of moderate length (8.0 mm.) similar to that in *S.* (*S.*) *gracilis.* The posterior half of P_2 is missing, but, nevertheless, the root shows that it was large; the tooth has an estimated length of 7.8 mm. A long diastema (about 14.5 mm.) separates P_2 and P_3. This diastema is longer than in any species of *S.* (*Stenomylus*). The anterior half of P_3 is missing, but the alveolar border shows the anteroposterior length to be about 10 mm. and therefore larger than in any species of *S.* (*Stenomylus*). P_4 is extremely long, laterally compressed, and its anteroposterior length is 11.7 mm., compared with 8.5 mm. in the type of *S.* (*S.*) *gracilis.* The molars are well worn but are comparable in size and crown height with those of *S.* (*S.*) *gracilis* except that M_1 tends to be relatively larger.

Although the subgenotypic species is known only from the type ramus, the long P_2–P_3 diastema and the elongate premolar region indicate that the skull had a correspondingly long muzzle. In the type of *S.* (*Pegomylus*) *keelinensis,* the distance (60.5 mm.) from the canine to M_1 is approximately one-third longer than in the type of *S.* (*S.*) *gracilis.*

DISCUSSION: *Stenomylus* (*Pegomylus*), the most primitive member of the Stenomylinae, has very little in common with *Poebrotherium.* In *S.* (*Pego-*

mylus) the P_2 is more anteriorly situated than that of *Poebrotherium* and above the posterior border of the symphysis. Furthermore, in *S.* (*Pegomylus*) a diastema separates P_2 and P_3 (not present in *Poebrotherium*), P_4 is more laterally compressed, with a smaller uninflected paraconid, and the premolars are smaller compared with M_3 than in *Poebrotherium.* The molars in *S.* (*Pegomylus*) are extremely tall-crowned, with nearly smooth lingual surfaces in contrast to the low-crowned molars of *Poebrotherium* which have weak vertical ribs on the metaconid and entoconid.

BLICKOMYLUS,[1] NEW GENUS

TYPE: *Blickomylus galushai,*[2] new species.

DISTRIBUTION: Chamisa Mesa Member of the Zia Sand Formation and in deposits equivalent to the lower part of the Santa Fe Group, Sandoval County, New Mexico.

INCLUDED SPECIES: Type only.

DIAGNOSIS: *Blickomylus* differs from *Stenomylus* in having larger incisors; a smaller, more vestigial, conical P^2 which, in some aged individuals, is lost; a relatively smaller P^3 and P^4; smaller, more caniniform and single-rooted P_2; diminutive, vestigial, and single-rooted P_3 which in some cases is lost (F:A.M. Nos. 50841A, fig. 9C, and 50862); more hypsodont molars, with the crown height of M_3 still increasing and the root unformed when the talonid is worn (F:A.M. No. 50863, fig. 10E) in contrast to the less hyposodont molars in *S.* (*Stenomylus*) in which the full crown height of M_3 is attained and the root fully formed when the talonid is only beginning to wear (C.M. No. 1610, fig. 2D); molars with weaker parastyles above and weaker parastylids below; relatively smaller M_1^1 which narrow more sharply toward the root and become extremely reduced in aged individuals; relatively larger M_{2-3}^{2-3}, with flatter buccal surfaces and shallower ectoflexids below; more anteroposteriorly expanded M_3^3; deeper horizontal ramus beneath M_2 and M_3; and completely fused metapodials.

Blickomylus differs from *Rakomylus* in having a shorter and less posteriorly extended nasal process of the premaxilla; longer nasals; less-recessed anteromaxillary fossa ("subnasal pit" of Loomis, 1910); smaller I^1 and I^2; more incisiform I^3; P^1 and P^2 present; larger P^3 and P^4; strong P_1 versus a ?vestigial P_1 as indicated by the alveolus in *Rakomylus* (F:A.M. No. 50838, fig. 13B); P_2 present; relatively larger P_4; more

[1] Named for the late Mr. John C. Blick, collector for the Frick Laboratory.

[2] For Mr. Ted Galusha, who collected most of the stenomyline material from New Mexico.

anteroposteriorly expanded M_3^3; and metapodials that are approximately 30 per cent longer.

DISCUSSION: A nearly complete skull with worn dentition (F:A.M. No. 50840, fig. 8A–C), from Blick Quarry, Arroyo Pueblo drainage, Sandoval County, New Mexico, is the type of *Blickomylus galushai,* new genus, new species. The reduction of the premolars, the anteroposterior expansion of the second and third molars, and the increased hypsodonty of the molars in *Blickomylus* continue trends observed in the most advanced species of *S.* (*Stenomylus*).

The only occurrence of *S.* (*Stenomylus*) contemporaneous with *Blickomylus* is one palate (F:A.M. No. 50858) from Blick Quarry, Sandoval County, New Mexico, of an advanced and as yet undescribed species of *S.* (*Stenomylus*). This occurrence is also the latest known of *S.* (*Stenomylus*). The palate (F:A.M. No. 50858) has smaller and less anteroposteriorly expanded molars than those of *Blickomylus,* and the premolars are also greatly reduced and foreshadow the extreme reduction and loss of P_2 and P_3 in some individuals of *Blickomylus.* Thus, *S.* (*Stenomylus*) is the ideal structural ancestor for the more specialized *Blickomylus.*

The youngest known stenomyline, *Rakomylus,* also was probably derived from *S.* (*Stenomylus*), not from the stratigraphically intermediate *Blickomylus.* Distinguishing morphologic characters of *Rakomylus* that reflect the principal evolutionary changes in *S.* (*Stenomylus*) and *Blickomylus* are (1) the reduction in the size and number of the premolars, (2) the increased hypsodonty of the molars, and (3) the shorter and more coossified metapodials. The temporally intermediate *Blickomylus* has more anteroposteriorly expanded third molars than the earlier *S.* (*Stenomylus*) or the later *Rakomylus.* Derivation of *Rakomylus* from *Blickomylus* would require a reversal of the trend toward the anteroposterior expansion of the third molar that can be observed from *S.* (*Stenomylus*) to *Blickomylus. Rakomylus* and *Blickomylus* were probably independently derived from the more primitive *S.* (*Stenomylus*).

Blickomylus galushai, new species

Figures 8–11

TYPE: F:A.M. No. 50840, almost complete, crushed skull with I^1–M^3 (fig. 8A–C). The type is from Blick Quarry in the Arroyo Pueblo drainage, NW. ¼, SW. ¼, sect. 25, T. 16 N., R. 2 E., Sandoval County, New Mexico. A recent section published by Galusha (1966, fig. 5) indicates that Blick Quarry is near the middle of the Chamisa Mesa Member of the Zia Sand Formation and 355 feet below the top of the type section of the Chamisa Mesa Member. The type was collected by

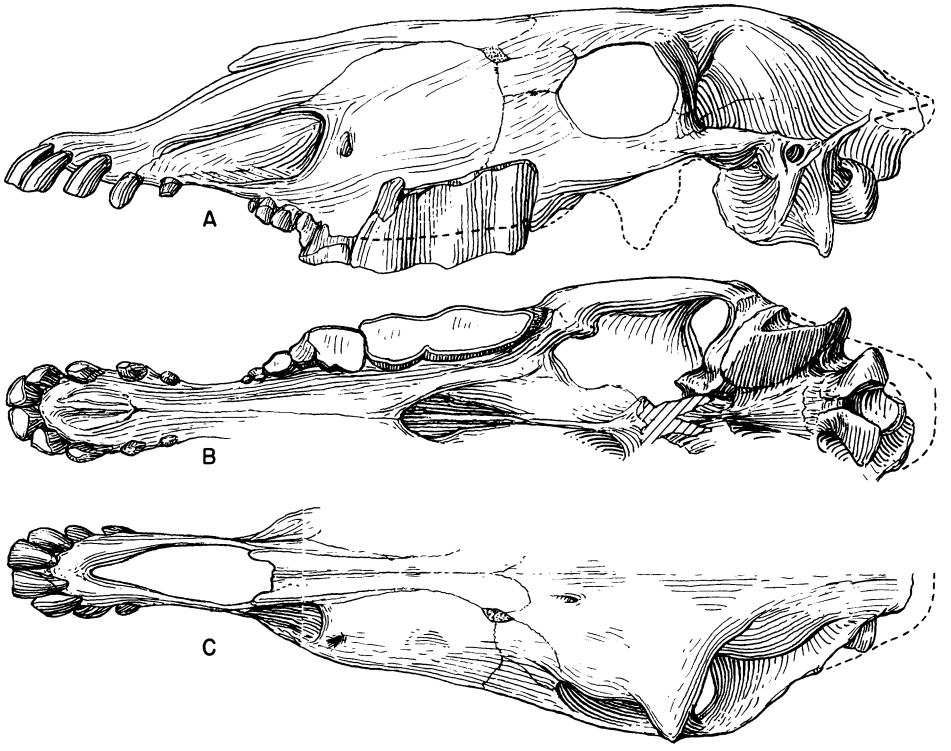

FIG. 8. *Blickomylus galushai,* new genus, new species, type, F:A.M. No. 50840, with suggested restoration; from Blick Quarry, middle part of the Chamisa Mesa Member of the Zia Sand Formation, Sandoval County, New Mexico. A. Lateral view. B. Palatal view. C. Dorsal view. All ×0.5.

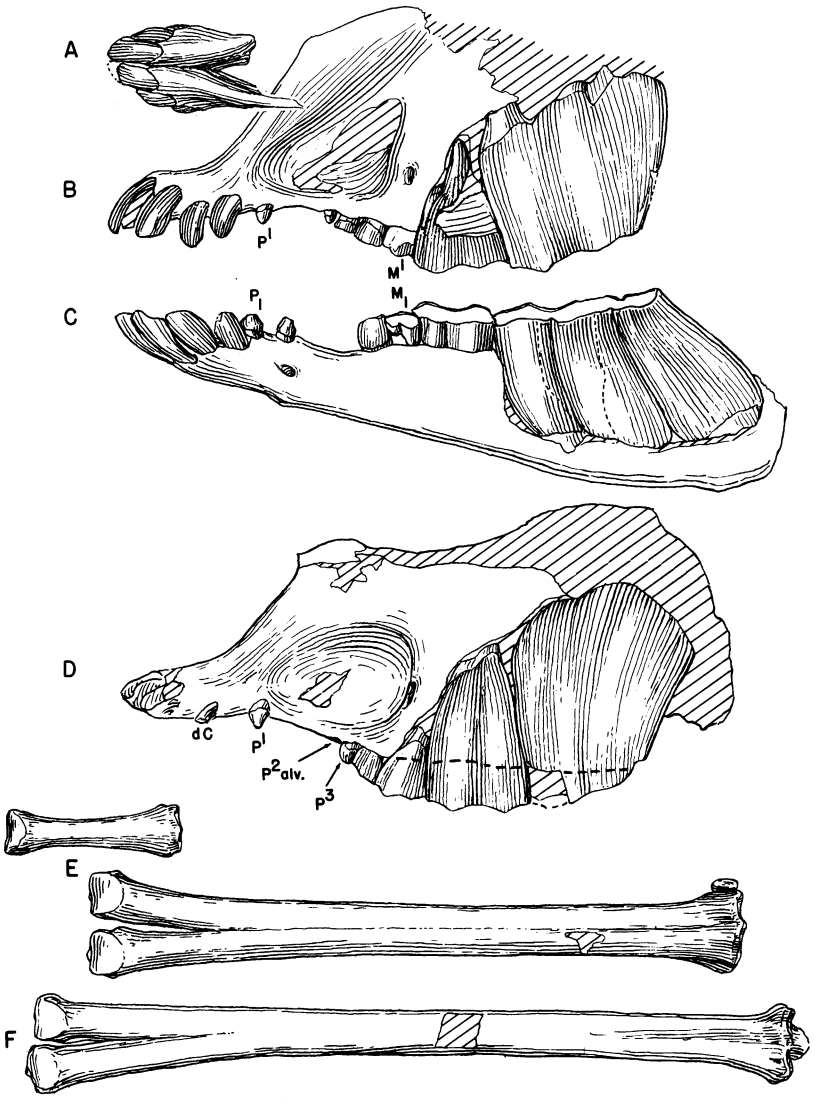

FIG. 9. *Blickomylus galushai,* from Blick Quarry, middle part of the Chamisa Mesa Member of the Zia Sand Formation, Sandoval County, New Mexico. A, B. F:A.M. No. 50841. A. Premaxilla, dorsal view. B. Partial skull, lateral view. C. F:A.M. No. 50841A (possibly the same individual as F:A.M. No. 50841), lateral view. D. F:A.M. No. 50846, lateral view (M^1–M^3 drawn from the right side). E. Right metacarpus and first phalanx, reversed, F:A.M. No. 68644, anterior view. F. Left metatarsus, F:A.M. No. 68645, anterior view. All ×0.5.

John C. Blick and Ted Galusha in 1949.

DISTRIBUTION: Chamisa Mesa Member of the Zia Sand Formation in the Arroyo Pueblo drainage and the Northern Ceja del Rio Puerco area and the equivalent of the lower part of the Santa Fe Group in the Arroyo Chamiso drainage as mapped by Galusha (1966, fig. 5), Sandoval County, New Mexico.

HYPODIGM: All from Sandoval County, New Mexico.

Blick Quarry, near the middle of the Chamisa Mesa Member of the Zia Sand Formation, Arroyo Pueblo drainage: Type and F:A.M. No. 50849, skull and mandible; F:A.M. Nos. 50842, 50843, 50845, 50846 (fig. 9D), 50847, 50850, 50856, 50857, skulls and partial skulls; F:A.M. Nos. 50841 (fig. 9A, B), 50844, 50848, 50859, maxillae; F:A.M. Nos. 50860, 50863 (fig. 10E), 50867, 50872, 50874, 68631, mandibles; F:A.M. Nos. 50841A (fig. 9C) (possibly the same individual as F:A.M. No. 50841), 50861, 50862, 50864 (fig. 10G), 50865 (figs. 10F, 15C), 50868, 50869 (fig. 10A, B), 50870, 50871, 50873, 50875, 68628–68630, 68632, rami; F:A.M. No. 50959, associated partial maxilla, partial ramus, and limb fragments; F:A.M. No. 50866, associated ramus (fig. 10C, D) and limb fragments; F:A.M. Nos. 50891, 50892, 50895, metacarpi; F:A.M. Nos. 50893, 50894, 68645 (fig. 9F), metatarsi; F:A.M. Nos. 50888, 50889, 50897, 50899, radii; F:A.M. No. 50890, associated partial humerus, partial radius, metacarpus, and first phalanx; F:A.M. No. 50896, associated humerus, proximal part of radius; F:A.M. No. 50898, associated partial metatarsus, calcaneum, and broken astragalus; F:A.M. No. 68644, associated distal part of radius, metacarpus, and first phalanx (metacarpus and first phalanx, fig. 9E); F:A.M. No. 68646, associated partial scapula, partial metatarsus, calcaneum, astragalus, and broken first phalanx; F:A.M. Nos. 50851, 50852–50855, 50884, 50887, 68633–68639, immature skulls and partial skulls; F:A.M. Nos. 50876–50883, 50885, 50886, 68640–68643, 68647, immature rami.

Cynarctoides Quarry, near the middle of the Chamisa Mesa Member of the Zia Sand Formation and the same level as Blick Quarry, Arroyo Pueblo drainage: F:A.M. Nos. 68620, 68621, mandibles; F:A.M. No. 68624, associated partial radius, partial metacarpus, partial tibia, broken calcaneum, astragalus, and tarsals; F:A.M. No. 68622, radius; F:A.M. No. 68623, distal part of metapodial.

Arroyo del Camello, northeast corner of Blick Hill, Zia Sand Formation, east of Arroyo Pueblo fault: F:A.M. No. 50957, partial skull, ramus, and skeletal elements (metacarpus and metatarsus, fig. 10H, I).

Jeep Quarry and Jeep Quarry horizon, upper part of the Chamisa Mesa Member of the Zia Sand Formation, Arroyo Pueblo drainage:

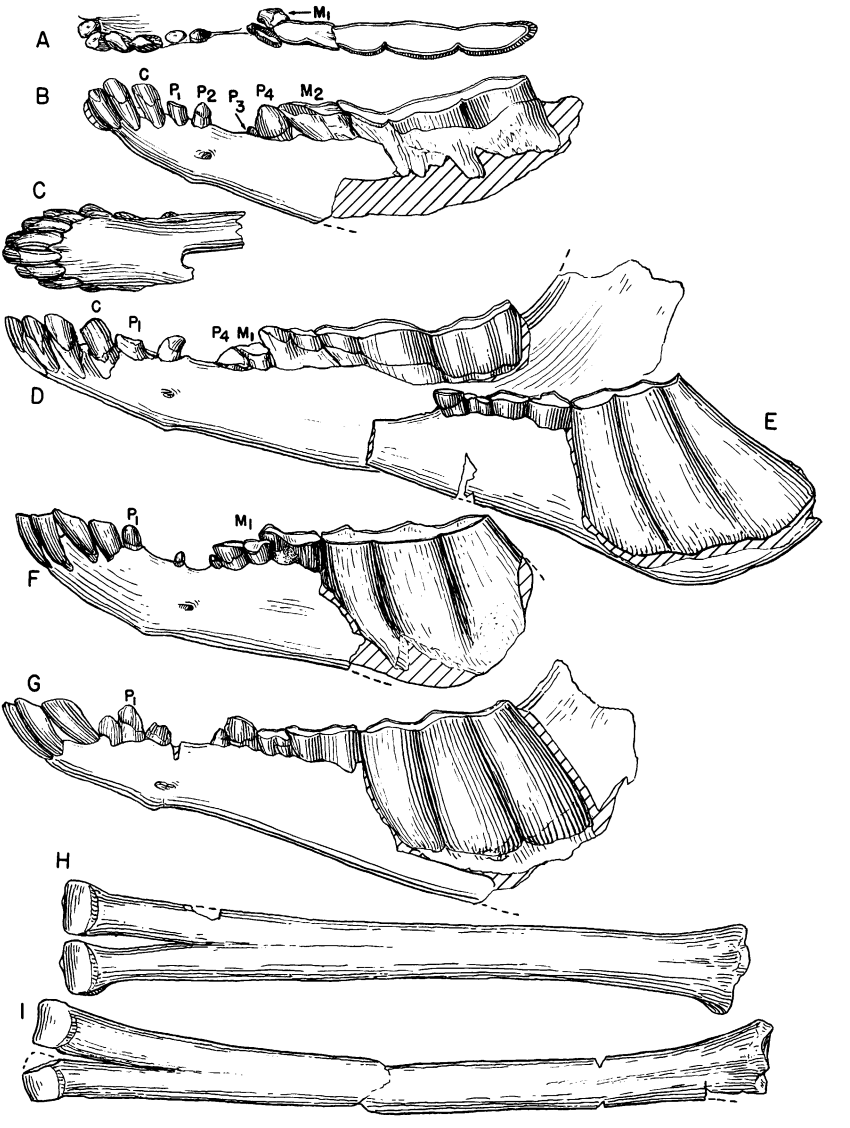

FIG. 10. *Blickomylus galushai.* A–F. From Blick Quarry, middle part of the Chamisa Mesa Member of the Zia Sand Formation, Sandoval County, New Mexico. A, B. F:A.M. No. 50869. A. Occlusal view, reversed. B. Lateral view, reversed. C, D. F:A.M. No. 50866. C. Symphysis, ventral view. D. Lateral view. E. F:A.M. No. 50863, lateral view (restored from the right side). F. F:A.M. No. 50865, lateral view, reversed. G. F:A.M. No. 50864, lateral view. H, I. F:A.M. No. 50957; from Arroyo del Camelo, Zia Sand Formation, east of Arroyo Pueblo fault, Sandoval County. H. Right metacarpus, reversed, anterior view. I. Right metatarsus, reversed, anterior view. All ×0.5.

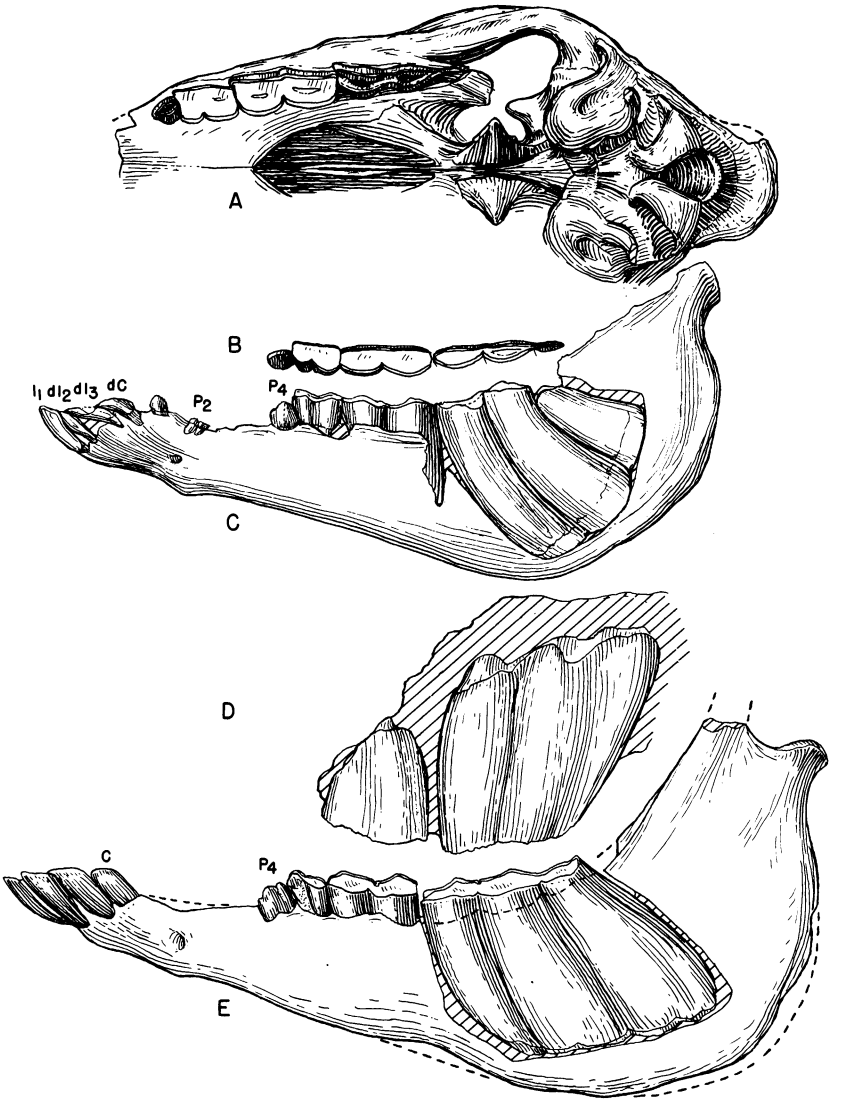

FIG. 11. *Blickomylus galushai,* from Straight Cliff Fork, Chamisa Mesa Member of the Zia Sand Formation, Canyada Pilares, Sandoval County, New Mexico. A–C. F:A.M. No. 50802, from top of the yellow sand cliffs, underlying the Red Band. A. Palatal view. B. Left P_4–M_3, occlusal view. C. Lateral view. D, E. F:A.M. No. 50803, from above the middle of the Red Band and 65 feet stratigraphically above F:A.M. No. 50802. D. Left M^2–M^3, lateral buccal view. E. Lateral view. All ×0.5.

F:A.M. No. 68618, partial skull; F:A.M. Nos. 68613, 68613A, partial maxillae; F:A.M. Nos. 68617, 68614, rami; F:A.M. No. 68614A, fragments of a metapodial and astragalus; F:A.M. No. 68615, fragments of pelvis, partial tibia, calcaneum, astragalus, tarsals, and partial metatarsus; F:A.M. No. 68616, partial metacarpus, from 20 feet below Jeep Quarry horizon.

Canyada Pilares, a part of the Northern Ceja del Rio Puerco area, Chamisa Mesa Member,[1] Zia Sand Formation: F:A.M. No. 50802, partial skull, ramus (fig. 11A–C) and vertebrae, Straight Cliff Fork, top of the yellow sand cliffs, underlying the Red Band; F:A.M. No. 50803, partial skull and mandible (M^2–M^3 and mandible, fig. 11D, E) and limb fragments, Straight Cliff Fork, above the middle of the Red Band, 20 feet below Straight Cliff Prospect (150–200 yards east of and 65 feet above F:A.M. No. 50802); F:A.M. No. 50804, partial ramus, lower one-third of the Zia Sand Formation as exposed in the Canyada Pilares area: F:A.M. No. 50813, immature skull and ramus, yellowish sand phase of the Zia Sand, 10 feet below the base of the Red Band; F:A.M. No. 50812, immature partial skull and limb fragments, tributary in which the Straight Cliff Quarry is situated, west of Pilares Fault, top of the yellowish sand below the Red Band; F:A.M. No. 50807, immature ramus, east of the Pilares Fault, north of wash, Red Band horizon; F:A.M. No. 50808, immature partial skull, Straight Cliff Prospect; F:A.M. No. 50809, immature skull, east of Pilares Fault, north of wash at the top of the pink beds, just below the distinctive Red Band; F:A.M. No. 68362, immature partial palate, partial ramus, and limb fragments; F:A.M. No. 68361, distal end of metapodial; F:A.M. Nos. 68364 and 68365, limb fragments, Red Band; F:A.M. No. 68366, partial metatarsus and tarsals, yellowish sand portion of the Zia Sand Formation, immediately below the Red Band.

Canyada Moquino, a part of the Northern Ceja del Rio Puerco area, Chamisa Member of the Zia Sand Formation: F:A.M. No. 50810, distal part of metapodial and phalanges; F:A.M. No. 50811, partial radius, partial metacarpus, calcaneum, astragalus, and tarsals, Red Band Prospect, green zone in Red Band.

Arroyo Chamiso drainage basin; these deposits are shown in a section published by Galusha (1966, fig. 5) as above the Chamisa Mesa Member of the Zia Sand Formation and in the equivalent of the lower part of the Santa Fe Group equivalent: F:A.M. Nos. 50829, 50833, 50834,

[1] These deposits are correlated with the Chamisa Mesa Member, but their exact stratigraphic position has not been determined (oral communication, Ted Galusha, 1967).

partial maxillae; F:A.M. No. 50821, partial mandible; F:A.M. Nos. 50814–50819, 50821–50828, partial rami; F:A.M. No. 50830, partial humerus and partial radius, all from Arroyo Chamiso Prospect, left fork; F:A.M. No. 50820, partial ramus; F:A.M. Nos. 50828A and 50828B, partial ramus and associated partial humerus, partial radius, partial metatarsus, and fragments, from Arroyo Chamiso, west fork; F:A.M. No. 50831, partial maxilla, partial radius, carpals, tarsals, astragalus, and phalanges, from Arroyo Chamiso, east fork.

DIAGNOSIS: Only known species of the genus.

MEASUREMENTS: See tables 2, 3, and 4.

TABLE 2

MAXIMUM LENGTH (IN MILLIMETERS) OF THE MOLARS OF *Blickomylus galushai*, NEW SPECIES, AND THE LENGTH OF EACH MOLAR COMPARED WITH THE COMBINED LENGTH OF ALL THE MOLARS IN THREE DIFFERENT STAGES OF WEAR

	F:A.M. No. 68269	F:A.M. No. 50841A	F:A.M. No. 50865
Wear	Worn	Well worn	Greatly worn
Length of M_1	16.5	(10.5)	(7.5)
Length of M_2	27	(22)	(16)
Length of M_3	44	62	(51)
M_1/M_1-M_3	16.5/87.5 (18.9%)	10.5/94.5 (11.1%)	7.5/74.5 (10.1%)
M_2/M_1-M_3	27/87.5 (30.8%)	22/94.5 (23.3%)	16/74.5 (21.5%)
M_3/M_1-M_3	44/87.5 (50.4%)	62/94.5 (65.6%)	51/74.5 (68.6%)

DESCRIPTION

SKULL: The type of *Blickomylus galushai* is a crushed skull (F:A.M. No. 50840, fig. 8A–C) with part of the occiput missing. Unique dental characters immediately distinguish it from *S.* (*Stenomylus*), but the general features of the skull are those of *Stenomylus.* Because of the similarity of skull characters between *Blickomylus* and *S.* (*Stenomylus*), the description of the skull is limited to the morphological differences observed between the two taxa.

Compared with examples of *S.* (*Stenomylus*), the type skull of *Blickomylus* (F:A.M. No. 50840) is larger and the muzzle averages longer. The anteromaxillary fossa above the premolars is larger and more depressed and, unlike that in *S.* (*Stenomylus*), is slightly recessed. In F:A.M. No. 50849, the malar is larger and the zygomatic process of the malar is heavier than in *S.* (*Stenomylus*). The glenoid fossa in F:A.M. No. 50850 is more anteroposteriorly expanded than in *S.* (*Stenomylus*). In the type of *Blickomylus galushai,* the tympanic bulla is extremely compressed laterally

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF *Blickomylus galushai*, NEW SPECIES

(The measurements are orthogonal projections; see fig. 7.)

	F:A.M No. 50840[a]	F:A.M. No. 50849	F:A.M. No. 50850
Median length			
Foramen magnum to incisive border (basilar)	208.0	(200)	206.0
Occipital crest to anterior incisive border (vertex)	(227)[b]	—	(232)
Postorbit to anterior incisive border (facial)	163.0	146.0	(165)
Postorbit to occipital crest (cranial)	(64)	—	(65)
Occipital crest to tip of nasals	(177)	—	(180)
Nasofrontal suture to tip of nasals	(65)	—	—
Anterior border of foramen magnum to vomer	54.0	—	52.0
Anterior border of foramen magnum to posterior of M^3	(80)	(63)	(65)
Anterior border of foramen magnum to anterior border of posterior nares	112.0	—	112.0
Anterior border of foramen magnum to posterior of P^4	139.0	(132)	(139)
Anterior border of foramen magnum to anterior of P^2	153.0	—	—
Anterior border of foramen magnum to postpalatine fissure	183.0	(175)	181.0
Anterior of P^2 to incisive border	55.0		
Width			
I^3–I^3 (width of muzzle)	24.5	21.0	26.0
Narrowest part of rostrum on palatal side	13.6	12.0	15.4
Anterior orbital width at narrowest point	(60)	(59)	—
Postorbital width, widest point at supraorbital processes	(94)	(88)	(82)
Cranium, maximum width	—	—	—

[a] Type of *Blickomylus galushai*, new species.

[b] Measurements enclosed in parentheses are approximate.

and is transversely narrower than in all known species of *S.* (*Stenomylus*). The posterior nares are large as in *S.* (*Stenomylus*) but, probably because of the forward expansion of M^3, the anterior border of the posterior nares is opposite the front lobe of M^3, whereas it is opposite the posterior lobe of M^2 in *S.* (*Stenomylus*).

UPPER DENTITION: The upper incisors are large and elongate. I^2 closely adjoins and overlaps I^1, whereas I^3 is slightly separated from I^2. Slightly behind I^3 is a semi-incisiform canine, which is more laterally compressed and tends to be smaller than I^3. A short diastema separates

TABLE 4

WEAR AND MEASUREMENTS (IN MILLIMETERS) OF THE LENGTH OF UPPER AND LOWER TEETH OF *Blickomylus galushai*, NEW SPECIES

	F:A.M. No. 50840[a]	F:A.M. No. 50849	F:A.M. No. 50850	F:A.M. No. 50845	F:A.M. No. 50841-A[b]	F:A.M. No. 50865	F:A.M. No. 50802[c]	F:A.M. No. 50803
Wear	W7	W5	W5	W5	W5	W7	M	W7
Upper dentition								
I^3	7.3	7.0	7.0	6.7	7.3	—	—	—
I^3–C diastema	4.2	2.0	3.2	3.0	2.4	—	—	—
C	6.2	5.5	6.2	6.7	6.3	—	—	—
C–P^1 diastema	4.5	5.2	3.0	1.5	4.6	—	—	—
P^1	5.0	3.9	4.8	4.9	3.8	—	—	—
P^1–P^2 diastema	18.1	—	—	—	14.2	—	—	—
P^2	2.0	—	—	3.0	2.8	—	—	—
P^3	5.2	—	6.2	6.7	6.9	—	—	—
P^4	(8.5)[d]	(9)	8.3	(8.5)	(8)	—	7.8	—
M^1	—	(10)	(10.5)	(12)	(10.5)	—	17.5	—
M^2	(16)	(20.5)	(22.5)	(23)	(24.5)	—	29.0	(29+)
M^3	46.0	49.0	50.0	47.0	48.0	—	(36)	48.0

TABLE 4—(*Continued*)

	F:A.M. No. 50840	F:A.M. No. 50849	F:A.M. No. 50850	F:A.M. No. 50845	F:A.M. No. 50841-A	F:A.M. No. 50865	F:A.M. No. 50802	F:A.M. No. 50803
Lower dentition								
C	—	7.0	—	—	7.0	7.2	—	8.0
C–P_1 diastema	—	1.3	—	—	0.8	0.6	—	—
P_1	—	4.0	—	—	4.3	5.0	4.1	—
P_1–P_2 diastema	—	7.5	—	—	3.6	9.0	6.8	—
P_2	—	3.3	—	—	4.5	3.0	—	—
P_2–P_3 diastema	—	9.3	—	—	—	6.6	—	—
P_3	—	2.8	—	—	Absent	2.5	—	—
P_4	—	8.3	—	—	7.6	8.3	7.3	7.8
M_1	—	(7)	—	—	(10.5)	(7.5)	(13)	(10.5)
M_2	—	(20)	—	—	(22)	(16)	24.5	(24)
M_3	—	54.0	—	—	62.0	51.0	47.5	60.0

[a] Type (F:A.M. No. 50840) of *Blickomylus galushai,* new species, and referred, F:A.M. Nos. 50849, 50850, 50845, 50841-A, and 50865 are from Blick Quarry, near the middle of the Chamisa Mesa Member of the Zia Sand Formation.

[b] F:A.M. No. 50841, skull, and F:A.M. No. 50841-A, mandible, are possibly one individual.

[c] F:A.M. Nos. 50802 and 50803 are from Straight Cliff Fork, from deposits which are correlated with the Chamisa Mesa Member, but their exact stratigraphic position has not been determined.

[d] Measurements enclosed in parentheses are approximate.

the canine from P^1, which is small and laterally compressed, with the paracone rising to a peak. P^1 is commonly single-rooted but it also may be double-rooted (F:A.M. No. 50849). Behind P^1 there is a long diastema separating it from a minute P^2. This second premolar is vestigial, single-rooted, conical, and apparently functionless for it is unworn in mature individuals (F:A.M. No. 50859). P^3 is relatively small and narrow, with the paracone rising to a point. Despite its reduction in size, P^3 is functional and shows wear by the time M^3 is well worn. There is a single-lobed P^4, with the inner and outer cusps separated by a fossette. P^4 is relatively smaller than that of *S.* (*Stenomylus*), and the fossette is shallower and disappears quickly with wear.

The molars are narrow and extremely hypsodont. Except for a heel on M^3, the molars are bilobed, with shallow fossettes separating the inner and outer cusps. The molars lack mesostyles and metastyles, and the buccal surfaces are smooth on each tooth except for a faint parastyle. From front to back, the molars become progressively larger and taller-crowned. Both M^1 and M^2 narrow anteroposteriorly toward the root, in contrast to M^3 which expands toward the base. M^3 is greatly expanded anteroposteriorly, the first lobe is large, and the second lobe is greatly expanded and to this a small heel is added. As both the upper and lower molars wear, the anteroposterior diameter of the first and second molars decreases, and this lost space is occupied by the forward movement of the third molar which enlarges with wear toward the base. Thus, the over-all length of the molars diminishes only slightly with wear, and the third molar tends to supplant the anterior molars, much as in the mammoth.

Lower Dentition: The incisors are large and crowded, with each incisor overlapping the preceding one. Commonly the large incisiform canine is separated slightly from I_3, but in some specimens it is adjacent to I_3 (F:A.M. No. 50865, fig. 10F). The spacing of P_1 is also variable. In most cases P_1 is directly behind the canine, but in others these two teeth are separated by a short diastema (F:A.M. No. 50860). The single-rooted P_1 is compressed laterally and is smaller and more caniniform than the canine. P_2 is also single-rooted and caniniform and highly variable in size and position. In F:A.M. No. 50865 (fig. 10F), P_2 is 8.5 mm. behind P_1 and thus closer to P_3, whereas in F:A.M. No. 50841A (fig. 9C) P_2 is more anterior and only 3.6 mm. behind P_1. P_2 varies in size from small, delicate, and only 3.3 mm. in length (F:A.M. No. 50865), to large and 6.0 mm. in length (F:A.M. No. 50866, fig. 10D). P_3 is tiny, single-rooted, and vestigial, too small to be functional, and remains unworn in mature individuals. In some very old individuals

(F:A.M. No. 68631) P_3 is missing from both sides of the mandible, and there are no alveoli. P_4 is small relative to the molars and is the only premolar that functions as a grinding tooth. It is a simple, laterally compressed, bladelike tooth without a metaconid; the paraconid is short, compressed, and uninflected. When the P_4 is unworn (F:A.M. No. 50872), the protoconid is elevated and trenchant.

The lower molars are narrow and much more hypsodont than those of *S.* (*Stenomylus*). From M_1 to M_3 they become progressively larger and taller-crowned. The lingual surface of the molars lacks the vertical ribs on the crescents, metastylids, and entostylids and is therefore smooth except for an occasional faint trace of the parastylid on little-worn examples. Except for a talonid on M_3, the lower molars are bilobed, with the lingual and buccal cusps separated by very shallow fossettes which disappear even more rapidly with wear than those of *S.* (*Stenomylus*). Compared with the teeth of *S.* (*Stenomylus*), M_1 is relatively smaller and M_2 and M_3 are larger and more hypsodont, with flatter buccal surfaces and deeper ectoflexids. M_1 is small and narrows toward the root, becoming increasingly smaller with wear. The second molar is larger and narrows toward the root as in M_1. M_3 is greatly expanded anteroposteriorly and is extremely hypsodont. The maximum crown height of M_3 can never be determined precisely because all three lobes of M_3 are in wear while enamel is still forming at the base of the tooth and the root is yet unformed (F:A.M. No. 50863, fig. 10E). The talonid of M_3 is greatly enlarged, with the anteroposterior diameter toward the base (F:A.M. No. 50803, fig. 11E), in some cases exceeding that of the second lobe. Unlike M_1 and M_2, which narrow toward the root, M_3 expands anteroposteriorly toward the base. Thus, as M_1 and M_2 wear and shorten anteroposteriorly, this space is occupied by the forward shifting of M_3, which becomes larger with wear toward the base. A comparison of the anteroposterior length of each molar with the combined length of the molars at three different stages of wear is shown in table 2.

MANDIBLE: The mandible is similar to the type of *S.* (*Stenomylus*) *gracilis* except that the horizontal ramus is even deeper beneath M_2 and M_3 and narrows more rapidly toward the symphysis.

METAPODIALS: In *Blickomylus galushai* both the third and fourth metacarpals and the third and fourth metatarsals (F:A.M. No. 50957, figs. 10H, I) are completely coossified compared with the type of *S.* (*Stenomylus*) *gracilis,* in which the proximal halves of the third and fourth metacarpals and the proximal two-thirds of the third and fourth metatarsals are fused. A rudimentary second metacarpal is indicated

by a small articular facet on the posteroradial side of the third metacarpal (F:A.M. No. 50957) and a small bony nodule which appears to be a rudimentary second metacarpal adheres slightly out of place on F:A.M. No. 68644. Both F:A.M. Nos. 50957 and 68644 have a second articular facet on the postero-ulnar side of the fourth metacarpal for a rudiment of the fifth metacarpal. The articular facets in *Blickomylus galushai* for both the second and fifth metacarpals are smaller than those in the type of *S. (S.) gracilis.* The second metatarsal in F:A.M. No. 50957 is represented by a small bony nodule that is coossified in place. In two unassociated referred metatarsi (F:A.M. Nos. 50893 and 50894), the rudimentary second metatarsals are present but not coossified, as in F:A.M. No. 50957. Peterson (1908), in his description of the type of *S. (S.) gracilis,* observed that a small facet on the posterofibular face of the fourth metatarsal would seem to indicate the presence of a rudimentary fifth metatarsal. In *Blickomylus galushai* the presence of a rudiment of the fifth metatarsal is indicated by a small but definite articular facet in F:A.M. No. 50894.

Discussion: The large sample of dentition of *Blickomylus galushai* from Blick Quarry must certainly represent one local population. Within this population, however, there are great differences: (1) in the size of the premolars; (2) the tendency to lose P^2 and P_3; (3) the wide variation in the spacing of P_1 and P_2 (described on p. 34 and recorded in measurement, table 4). In addition, the anteroposterior length of M_3 ranges from 43.5 mm. (F:A.M. No. 68628) to 62 mm. (F:A.M. No. 50841A), and the anteroposterior expansion of the third lobe of M_3 varies from moderate to extremely large. All these differences may be attributed to the range of individual, age, and sexual variation in a large, local population.

Rakomylus raki and *Blickomylus galushai* have never been found contemporaneously (fig. 14). The type (F:A.M. No. 30990) of *R. raki* and referred specimens from the Skull Ridge locality listed in the hypodigm occur in the type area of the Santa Fe Group, whereas *Blickomylus galushai* occurs in deposits in the Jemez Creek area that are earlier than any beds of the Santa Fe Group in the type area. The stratigraphic range of *Blickomylus,* however, is sufficiently great for it to have extended into beds that were correlated with the Santa Fe Group by Galusha (1966, fig. 5).

RAKOMYLUS FRICK, 1937

Type: *Rakomylus raki* Frick, 1937.

Distribution: From the lower part of the Santa Fe Group, Santa Fe County, New Mexico.

INCLUDED SPECIES: Type only.

DIAGNOSIS: *Rakomylus* differs from *Stenomylus* in having a longer muzzle; longer and more posteriorly extended nasal process of premaxilla; shorter nasals; deeper and more posteriorly pocketed anteromaxillary fossa and smaller and shallower preorbital fossa; relatively deeper maxilla for extremely hyspodont molars; larger malar; relatively larger and, especially anteroposteriorly, longer glenoid fossa; more laterally compressed bullae; larger incisors, more caniniform I^3; P^1 and P^2 absent; smaller P^4 and M^1; ?vestigial P_1; P_2 lost; vestigial P_3 (as indicated by minute alveoli in F:A.M. No. 50838, fig. 13A, B); relatively smaller P_4; more hypsodont molars; and relatively shorter and fully fused metapodials.

Rakomylus differs from *Blickomylus* in having a longer and more posteriorly extended nasal process of premaxilla; shorter nasals; more recessed anteromaxillary fossa; larger I^1–I^2; more caniniform I^3; P^1 and P^2 lost; smaller P^3 and P^4; ?vestigial P_1 as indicated by a broken alveolus (F:A.M. No. 50838, fig. 13B); P_2 lost; smaller P_4; less anteroposteriorly expanded M_3^3; and metapodials that are about 30 per cent shorter.

DISCUSSION: When Frick (1937, p. 657) described *Rakomylus raki,* the lower premolars were unknown. Since 1937 a partial mandible (F:A.M. No. 50838, fig. 13A, B) has been collected that shows these teeth. This specimen has lost P_2, has a ?vestigial P_1 indicated by a broken alveolus, and minute alveoli for right and left P_3.

The latest occurring stenomyline, *Rakomylus,* resembles *Blickomylus* in the reduction and partial loss of the premolars and in the extremely hypsodont molars. *Rakomylus,* however, has completely lost P^1, P^2, and P_2 and, moreover, has an even greater reduction of the premolars, less anteroposteriorly expanded molars, a more recessed anteromaxillary fossa, and relatively shorter metapodials than *Blickomylus.*

In the Camelidae, the correlation of the reduction and loss of premolars with time has been a widely accepted evolutionary trend. The greater reduction in both size and number of the premolars in *Rakomylus* could be the basis for suggesting the descent of *Rakomylus* from *Blickomylus.* In *Blickomylus,* however, the third molars are more expanded anteroposteriorly than in the earlier *S.* (*Stenomylus*) or the later *Rakomylus.* To derive *Rakomylus* from *Blickomylus* would require a reversal of the trend of the anteroposterior expansion of the third molars seen from *S.* (*Stenomylus*) to *Blickomylus.* It seems more likely that *Rakomylus* was derived from *S.* (*Stenomylus*). Apparently *Rakomylus* and *Blickomylus* are separate lineages that were derived from *S.* (*Stenomylus*), and the reduction of the premolars and the extreme hypsodont molars are parallel characters.

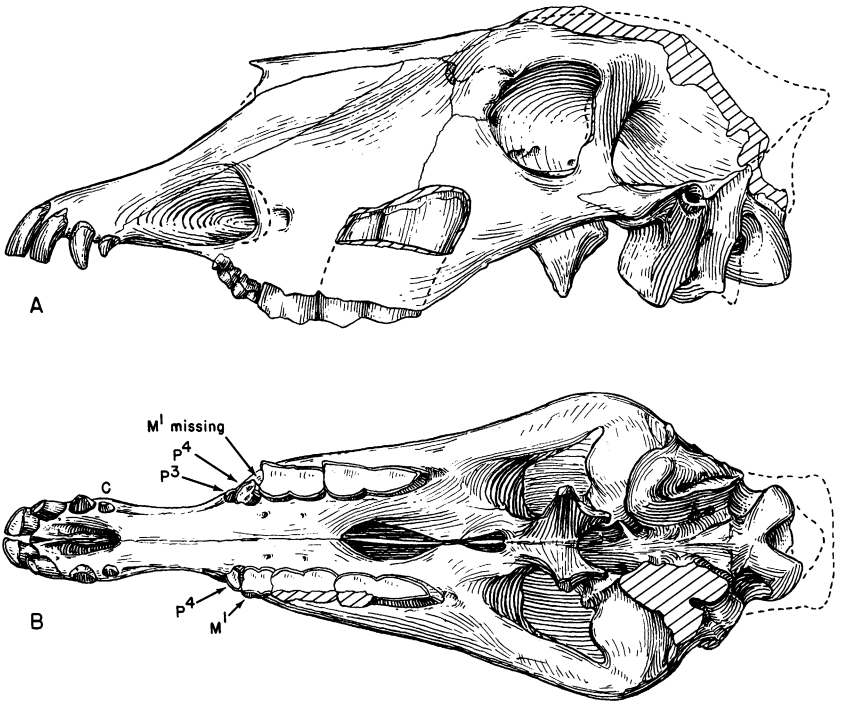

FIG. 12. *Rakomylus raki,* type, F:A.M. No. 30990, with suggested restoration, from the lower part of the Santa Fe Group, Sante Fe County, New Mexico. A. Lateral view. B. Palatal view. Both approximately ×0.5.

Rakomylus raki Frick, 1937

Figures 12, 13, 15D

TYPE: F:A.M. No. 30990, an almost complete skull except for the rear of the cranium, with I^1–C and P^3–M^3 represented. The left M^1 is missing, but the right M^1 is present (Frick, 1937, fig. 67; the present report, fig. 12A, B). The type was collected by the late John C. Blick in 1936 between Ash D and No. 4 White Ash stratum, lower part of the Santa Fe Group, from a point 1 mile north of White Operation Quarry, Santa Fe County, New Mexico.

DISTRIBUTION: From the lower part of the Santa Fe Group, Santa Fe County, New Mexico. The type and specimens listed in the hypodigm (with the exception of F:A.M. Nos. 30995 and 30997, for which there are no stratigraphic data) occurred between No. 3 and No. 4 White Ash strata. The stratigraphic position of these ashes in the Santa Fe Group

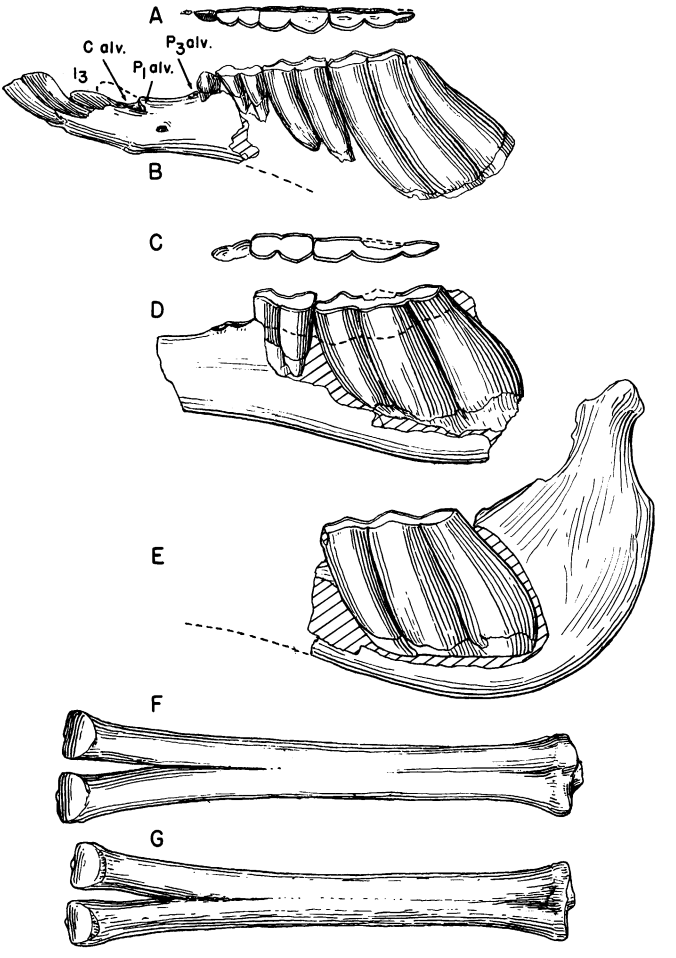

FIG. 13. *Rakomylus raki,* from the lower part of the Santa Fe group, Santa Fe County, New Mexico (see distribution, p. 38). A, B. F:A.M. No. 50838; from 50 feet above No. 3 White Ash stratum, Joe Rak Wash system. A. Right P_4–M_3, reversed, occlusal view. B. Lateral view, reversed. C, D. F:A.M. No. 30995; from north of Santa Fe. C. M_2–M_3, occlusal view, reversed. D. Lateral view, reversed (figured by Frick, 1937, figs. 67, 68). E. F:A.M. No. 30997; from Cuyamunque, lateral view, reversed. F. Left metatarsus, F:A.M. No. 30984; from Skull Ridge, anterior view. G. Right metacarpus, F:A.M. No. 50837; from East Cuyamunque, southeast side of wash, above No. 3 White Ash stratum, anterior view, reversed. All ×0.5.

will be given in a forthcoming report by Ted Galusha and John C. Blick.

HYPODIGM: Lower part of the Santa Fe Group, Santa Fe County, New Mexico: type, and F:A.M. No. 50838, partial mandible (figs. 13A, B, 15D), South Skull Ridge, 50 feet above No. 3 White Ash stratum, Joe Rak Wash system; F:A.M. No. 50836, partial ramus, Santa Fe area;

TABLE 5

SKULL MEASUREMENTS (IN MILLIMETERS) OF *Rakomylus raki* FRICK

(The measurements are orthogonal projections; see fig. 7.)

	F:A.M. No. 30990 Type
Median length	
Foramen magnum to incisive border (basilar)	196.0
Occipital crest to anterior incisive border (vertex)	—
Postorbit to anterior incisive border (facial)	170.0
Postorbit to occipital crest (cranial)	—
Occipital crest to tip of nasals	—
Nasofrontal suture to tip of nasals	—
Anterior border, foramen magnum to vomer	64.0
Anterior border, foramen magnum to posterior of M^3	86.0
Anterior border, foramen magnum to anterior border of posterior nares	110.0
Anterior border, foramen magnum to posterior of P^4	139.0
Anterior border, foramen magnum to anterior of P^2	—
Anterior border, foramen magnum to postpalatine fissure	169.0
Width	
I^3 to I^3 (width of muzzle)	22.8
Narrowest part of rostrum on palatal side	16.3
Anterior orbital width at narrowest point	—
Postorbital width, widest point of supraorbital process	78.0

F:A.M. No. 30995, partial ramus (Frick, 1937, figs. 67, 68; the present report, fig. 13C, D), north of Santa Fe; F:A.M. No. 30996, partial ramus, Santa Fe area; F:A.M. No. 30997, partial ramus (fig. 13E), Cuyamunque; F:A.M. No. 30998, immature partial ramus (Frick, 1937, fig. 68), Santa Fe area; F:A.M. No. 50837, metacarpus (fig. 13G), East Cuyamunque, southeast side of wash, above No. 3 White Ash stratum; F:A.M. No. 30999, metacarpus, Santa Fe area; F:A.M. No. 30984, metatarsus (fig. 13F), Skull Ridge.

DIAGNOSIS: Only known species of the genus.

MEASUREMENTS: See tables 5 and 6.

REDESCRIPTION

SKULL (SEE FIG. 12A, B): The premaxilla is much longer and slopes upward more gradually than does that of *Stenomylus.* The length of the muzzle is accentuated by the long, posteriorly sloping nasal process of the premaxilla which extends almost the full length of the nasals. Although

TABLE 6

WEAR AND MEASUREMENTS (IN MILLIMETERS) OF THE LENGTH OF THE UPPER AND LOWER TEETH AND DIASTEMATA OF *Rakomylus raki*

	F:A.M. No. 30990[a]	F:A.M. No. 50838
Wear	W7+	W
Upper dentition		
I^3	7.0	—
I^3–C diastema	2.0	—
C	5.0	—
C–P^3 diastema	30.0	—
P^3	4.8	—
P^4	7.8	—
M^1	9.3	—
M^2	18.5	—
M^3	35.5	—
Lower dentition		
Diastema from C alveolus to P_3 alveolus	—	14.5
P_3 alveolus	—	(3.5)[b]
P_4	—	7.0
M_1	—	11.5
M_2	—	18.4
M_3	—	(34)

[a] Type of *Rakomylus raki* Frick.

[b] Measurements enclosed in parentheses are approximate.

the nasal tips are missing, it is evident that there was extreme nasal retraction and that the nasal tips probably terminated above M^1. Anterior to the orbit, the face is high and, as in *Stenomylus,* the maxilla is depressed by two fossae. First, the anteromaxillary fossa, which corresponds to the "subnasal pit" of Loomis (1910), is a deeply excavated cavity, which extends from the canine to M^1. The anterior part of the fossa below the nasal process of the premaxilla and between the canine and P^4 is pinched inward deeply and forms a narrow shelf along the inferior border of the snout. Posteriorly, the fossa forms a deep pocket in the maxilla, unlike that of *S.* (*Stenomylus*) which is unpocketed. Frick

(1937, p. 657) stated that the "depth of the anteromaxillary fossae . . . [is] suggestive of a proboscis-like development of the upper lip." The second fossa ("preorbital pit" of Loomis, 1910) is a shallow depression on the upper part of the maxilla above the molars. This shallow fossa is less depressed than that in *S.* (*Stenomylus*). An infraorbital foramen is above the anterior lobe of M^2 and is higher on the maxilla than in *S.* (*Stenomylus*). A minute vacuity is present on the lacrimofrontal border. A large malar borders the lacrimal and forms the antero-inferior part of the orbit. The zygomatic process of the malar is very large, and the orbit is closed posteriorly by a well-developed supraorbital process. In the type (F:A.M. No. 30990), the orbit is situated more posteriorly than in *Stenomylus,* with the anterior rim of the orbit about 18.0 mm. behind M^3. The frontals are crushed, and most of the posterior part of the cranium and the occiput are missing.

The palatine fissure is large, with the posterior border opposite the back of the canine. The palatine process of the maxilla is narrow and shortened posteriorly by the anterior extension of the posterior nares, which are large in comparison with the palate; the anterior border of the nares is opposite the anterior part of M^3. As in *Stenomylus,* the pterygoids are strong and completely united at their origin. The large surface of the lateral pterygoid plate indicates a strong, lateral, pterygoid muscle. According to Gill and Grant (1966, p. 272), the medial pterygoids are responsible for the elevation of the mandible, but the "contraction of the right lateral pterygoid and the left zygomaticomadibular muscles pull the mandible to the left-hand side." Thus, strong lateral pterygoid muscles indicate a strong lateral movement of the mandible. Gill and Grant (1966, p. 272) stated, "Such lateral movements can be readily observed in sheep and goats during mastication." A similar lateral motion of the mandible in the stenomylines could be correlated with the rapid wear of the extremely hypsodont molars. Unlike that in *Stenomylus,* the glenoid fossa is long anteroposteriorly and its length is almost equal to the transverse diameter. The anteroposteriorly longer glenoid fossa in *Rakomylus* permits considerable fore-and-aft movement of the mandible in addition to the strong lateral movement. A low glenoid process is united with the bulla. The bulla is more laterally compressed than in *Stenomylus,* and it is coossified with the parocciptal process.

Upper Dentition: I^1 and I^2 are larger and more elongate than in *Blickomylus.* A large caniniform I^3 is separated from I^2 by a short space (2.0 mm.). Slightly behind I^3 is a small canine that is less than half the size of I^3. Frick (1937, p. 657) believed that the smallness of the canine indicated a female. The large I^3 appears, however, to function as the

canine and may be the sex-linked tooth. Neither P^1 nor P^2 was ever present; therefore a long diastema (30.0 mm.) separates the canine from P^3, which is relatively small and single-rooted, with a simple, conical crown that rises to a blunt peak. In the type (F:A.M. No. 30990), P^3 is unworn despite a well-worn P^4–M^3. Because of wear, little can be determined about P^4 in the type except that it is relatively smaller and transversely narrower than that of *Stenomylus.*

The upper molars are narrow, bilobed, and extremely hypsodont, becoming progressively larger from M^1 to M^3. The parastyle, mesostyle, and metastyle are absent from the worn molars of the type, and the buccal surface is smooth except for a slight depression between the paracone and metacone of M^3. Relative to the other molars, M^1 is small and M^2 is intermediate between M^1 and M^3 in anteroposterior diameter and crown height. With allowance for wear, M^3 in the type was extremely tall-crowned, similar to that of *Blickomylus,* but is less anteroposteriorly expanded.

Lower Dentition: The incisors and premolars are known only in one young mandibular ramus (F:A.M. No. 50838, fig. 13A, B) that was collected after Frick (1937, p. 657) had described *Rakomylus raki.* The lower incisors are large, procumbent, and spatulate. In F:A.M. No. 50838, I_1 is worn, I_2 slightly worn, and I_3 just erupting, even though M_3 is in wear. No lower canine is known, but a broken alveolus for the canine is adjacent to erupting I_3. The presence of vestigial P_1 is indicated by the posterior border of a small alveolus slightly behind the broken area for the canine. From the foregoing evidence, the presence of P_1 in a mature ramus is rather dubious, added to the fact that the first upper premolar in the type skull is also missing. The absence of P_2 seems conclusive because M_3 is already in wear and in *Stenomylus* P_2 erupts before the last molar. No P_3 is known, but small alveoli for a vestigial P_3 are present on both the right and left sides of F:A.M. No. 50838. The unworn P_4 is smaller than that of *Blickomylus,* laterally compressed, with the protoconid elevated to a peak and a paraconid that is extremely short, compressed, and uninflected; there is no metaconid.

The lower molars are narrow and hypsodont and become progressively larger and taller-crowned from front to back. Despite little wear on M_3 (F:A.M. No. 50838), all the molars lack the parastylid, metastylid, and the entostylid, thus presenting an almost smooth lingual surface. Both M_1 and M_2 narrow toward the root and become anteroposteriorly shorter with wear. M_3 is three-lobed, very hypsodont, anteroposteriorly expanded, and, unlike the first two molars, becomes increasingly larger toward the base, and anteroposteriorly longer with wear. In F:A.M. Nos. 30995

TABLE 7

SUMMARY OF DIAGNOSTIC CHARACTERS OF THE STENOMYLINAE

	S. (Pegomylus)	*S. (Stenomylus)*	*Blickomylus*	*Rakomylus*
Length of nasals	—	Moderate	Relatively shorter	Short
Anteromaxillary fossa	—	Unrecessed	Slightly recessed	Deeply recessed
I^1–I^2	—	Size small to moderate	Larger	Largest
I^3	—	Incisiform, approximate in size to upper canine	Incisiform, tending to be larger than upper canine	Caniniform, larger than upper canine
Upper canine	—	Incisiform	Incisiform	Caniniform
P^1	—	Small	Relatively smaller	Lost
P^2	—	Small	Minute, lost in some old individuals	Lost
Lower canine	Tending to caniniform	Incisiform	Incisiform	—
P_1	Moderate	Moderate	Tending to be smaller than in *S. (Stenomylus)*	?Vestigial
P_2	Large, double-rooted	Small, double-rooted	More caniniform, single-rooted	Lost
P_3	Large, double-rooted	Moderate in size, double-rooted	Diminutive, single-rooted, lost in some	Vestigial

TABLE 7—(*Continued*)

	S. (*Pegomylus*)	*S.* (*Stenomylus*)	*Blickomylus*	*Rakomylus*
M_3^3, anteroposterior expansion	Moderate	Moderate	Extreme	Intermediate between *S.* (*Stenomylus*) and *Blickomylus*
M_3^3, crown height	Tall	Tall	Extremely tall[a]	As in *Blickomylus*
Length of metacarpals relative to length of skull	—	Equivalent to distance from incisive border of skull to glenoid fossa	Incomplete associated evidence suggests metacarpals tend to be relatively shorter than in *S.* (*Stenomylus*)	Equivalent to distance from incisive border of skull to anterior part of orbit
Coossification of third and fourth metacarpals	—	Proximal halves fused	Completely fused	Completely fused

[a] The maximum height of M_3^3 is not measurable, because the tooth is worn before enamel ceases to form at the base.

(fig. 13D) and 30997 (fig. 13E) the M_3 talonid is large, increasing in anteroposterior length toward the base. The anteroposterior length of the talonid toward the base is equal to that of the second lobe, and greater than that of the first lobe. In F:A.M. Nos. 30995 and 30997, the buccal surface of M_3 is almost flat as in *Blickomylus,* whereas in F:A.M. No. 50838 it tends to be more rounded. M_3 is more hypsodont than that of *S.* (*Stenomylus*) and similar in crown height to that of *Blickomylus* but is less anteroposteriorly expanded.

MANDIBLE: The horizontal ramus is deep in the area of the last two molars (F:A.M. No. 30997, fig. 13E) and sharply decreases in depth toward the symphysis in F:A.M. No. 50838 (fig. 13B). The symphysis in the young mandible (F:A.M. No. 50838) is less depressed and shorter than that in *S.* (*Stenomylus*) *gracilis* and *Blickomylus galushai.* In both these latter species the symphysis extends posteriorly to beneath P_2, whereas in *Rakomylus raki* it terminates just behind the base of the canine alveolus. The mental foramen is situated more posteriorly (about midway between the canine and P_4) than its location above the posterior border of the symphysis in *S.* (*Stenomylus*) *gracilis* and *Blickomylus galushai.* As in *Stenomylus* and *Blickomylus,* the mandibular angle is rounded, and there is only a slight trace of the characteristic camelid projection of the mandibular angle below the condyle.

METAPODIALS: Unassociated, referred metacarpi (F:A.M. No. 50837, fig. 13G, and No. 30999) are completely fused and relatively shorter than those in *Stenomylus* and *Blickomylus.* The length of the referred metacarpus (F:A.M. No. 30999) is 132.0 mm. and approximately one-third less than the basilar length (196.0) of the type skull of *Rakomylus raki.* In contrast, associated remains of *S.* (*Stenomylus*) have only the proximal halves of the third and fourth metacarpals fused, and their length is equivalent to the distance from the incisive border of the skull to the glenoid fossa.

As in *Stenomylus,* a rudimentary second metacarpal is indicated (F:A.M. Nos. 30999 and 50837) by a small articular facet on the posteroradial side of the fused third metacarpal. A second, small, articular facet is present on the postero-ulnar side of the fused fourth metacarpal (F:A.M. No. 50837) for a rudimentary metacarpal, whereas in F:A.M. No. 30999 a small bony rudiment of a fifth metacarpal is actually coossified in place.

An unassociated, referred metatarsus (F:A.M. No. 30984, fig. 13F) is slightly longer (135 mm.) than the two metacarpi mentioned above and is completely fused and relatively shorter than that in *Stenomylus* or that in *Blickomylus.* There are small articular facets on the posterior side of

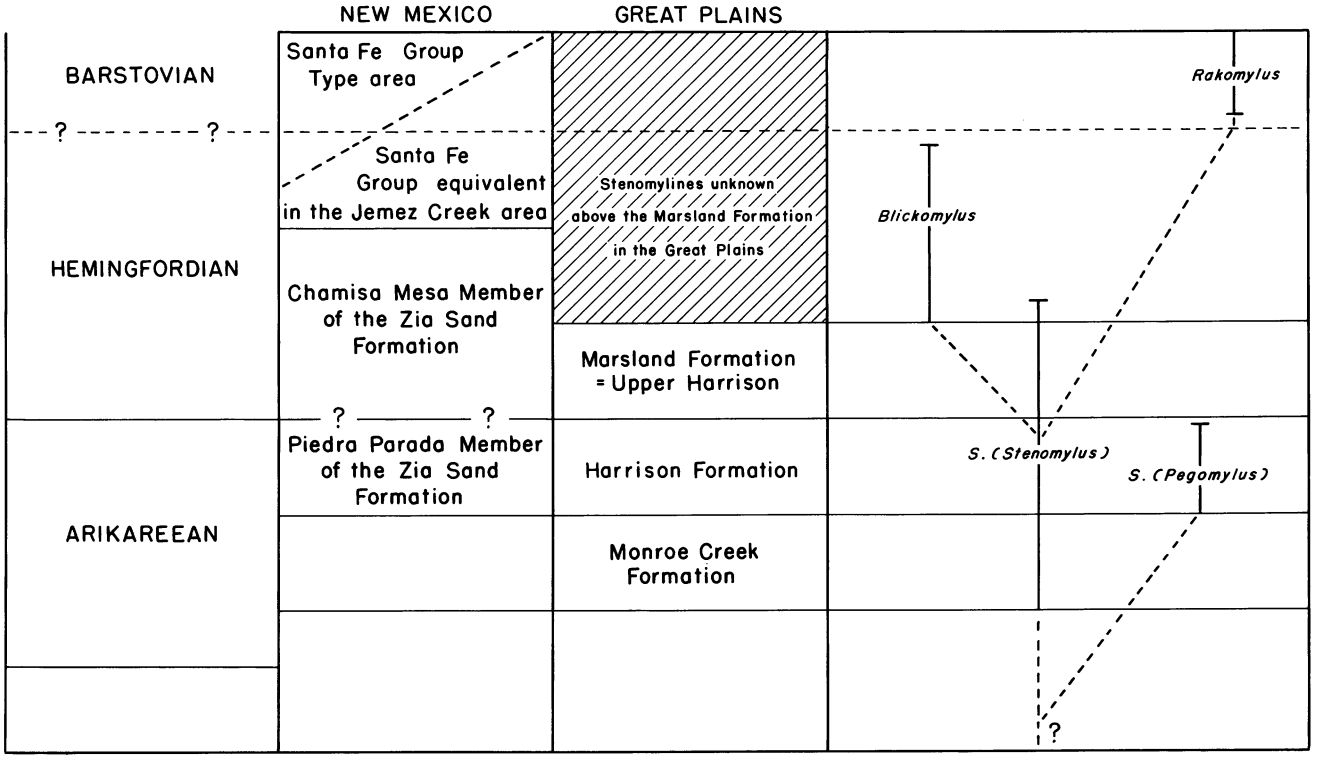

FIG. 14. Suggested phylogeny of the Stenomylinae. The time scale is expressed in geochrons of the Great Plains and New Mexico rock units. No fossils are known from the lower part of the Chamisa Mesa Member, and it may be temporally equivalent to the Marsland Formation.

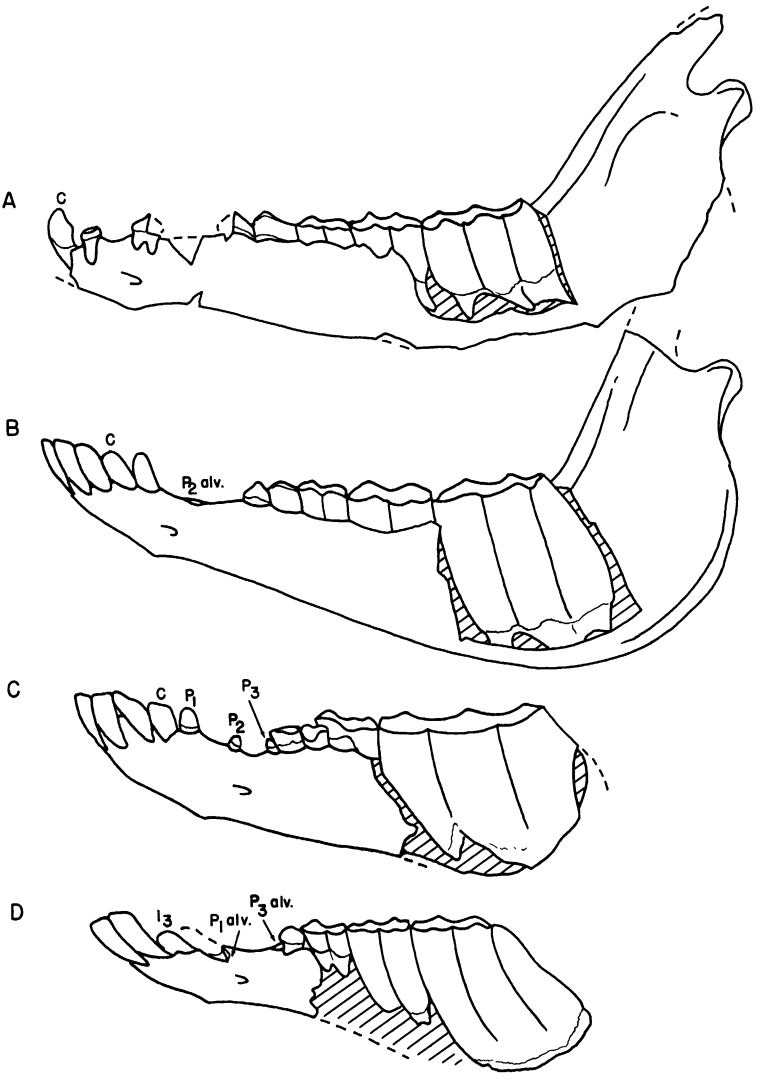

FIG. 15. Comparative outline drawings. A. *Stenomylus (Pegomylus) keelinensis,* new subgenus, new species, type, F:A.M. No. 43668, lateral view (see fig. 6E). B. *Stenomylus (Stenomylus) gracilis,* type, C.M. No. 1610, lateral view (see fig. 2C, D). C. *Blickomylus galushai,* F:A.M. No. 50865, lateral view, reversed (see fig. 10F). D. *Rakomylus raki,* F:A.M. No. 50838, lateral view, reversed (see fig. 13A, B). All ×0.5.

the fused third and fourth metatarsals for rudiments of the second and fifth metatarsals. Contrary to what one would expect, the articular facet for the fifth metatarsal is slightly larger in this advanced and late-occurring taxon, *Rakomylus,* than it is in *S.* (*Stenomylus*) and *Blickomylus.*

PHYLOGENY

Figure 14

The genus *Stenomylus,* of unknown ancestry, first appeared in the early Miocene in middle Arikareean time. Peterson (1908, p. 300) postulated that *Stenomylus* probably branched off the tylopod stem in the late Eocene, and the present writers accept this hypothesis as the most tenable. The earliest known occurrence of *S.* (*Stenomylus*) is in the Monroe Creek Formation[1] from Muddy Creek, Wyoming.

During Arikareean time, the evolutionary changes observed in *S.* (*Stenomylus*) species are (1) increased size, (2) decrease in size of premolars, (3) anteroposterior expansion of the third molars, (4) increased hypsodonty of the molars, and (5) partial coossification of the metacarpals. *Stenomylus* (*Pegomylus*), a contemporary of *S.* (*Stenomylus*) in the Harrison Formation, is characterized by large premolars which, on the basis of evolutionary changes observed in the other Stenomylinae, is considered a primitive character. Hence, *S.* (*Pegomylus*) is treated as an aberrant and separate lineage which is close to the ancestral stem of *Stenomylus.*

Blickomylus, also a contemporary of *S.* (*Stenomylus*) in the Chamisa Mesa Member of the Zia Sand Formation in New Mexico, is presumably derived from an earlier species of *S.* (*Stenomylus*). The morphological characters in advanced species of *S.* (*Stenomylus*) foreshadow the specialized characters that distinguish *Blickomylus.* Compared with *S.* (*Stenomylus*), *Blickomylus* has relatively smaller premolars with P^2 and P^3 lost from some individuals, more hypsodont molars, more anteroposteriorly expanded third molars, and completely fused metapodials.

Although the youngest known stenomyline, *Rakomylus,* resembles *Blickomylus* in the reduction and partial loss of premolars, the third molars of *Rakomylus* lack the distinctive anteroposterior expansion of those of *Blickomylus. Rakomylus,* furthermore, differs from *Blickomylus* in the complete loss of P^1, P^2, and P_2, and in having relatively smaller premolars and relatively shorter metapodials. It is unlikely that the late Miocene *Rakomylus,* with the third molars only moderately expanded anteropos-

[1] On the basis of the oreodonts described by Schultz and Falkenbach (1954, pp. 168, 196) these particular Muddy Creek deposits are allocated to the Monroe Creek Formation.

teriorly, as in the ancestral stock, *S.* (*Stenomylus*), was derived from *Blickomylus* with its greatly expanded third molars. *Blickomylus* and *Rakomylus* probably were derived from *S.* (*Stenomylus*) and thereafter paralleled each other in the reduction and loss of premolars.

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