

V

A TERTIARY MAMMALIAN FAUNA  
FROM THE SAN ANTONIO MOUNTAINS  
NEAR TONOPAH, NEVADA

PAUL C. HENSHAW

With eleven plates and seven text figures

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INTRODUCTION

Discovery of fossil mammals near Tonopah, Nevada, affords opportunity not only to date significant geologic events in the west central part of the state, but also to describe the plains life of the region during Upper Miocene time. The fauna contains nineteen species, six of which are known from no other locality. Close association of the mammalian assemblage with remains of diatoms, mollusks, and fishes in the stratigraphic record establishes a definite correlation in time between these groups. The value of the discovery as a record of Upper Miocene life is greatly enhanced by the simultaneous occurrence in a limited area of these two entirely different and complementary facies of contemporary faunas, representing arid plains and inland lake. This association furnishes interesting and detailed information as to the paleogeography of the region. Abundance of individual mammals from a quarry of narrow horizontal and vertical limitations provides a large unmixed fauna on which to base paleoecological studies.

The fossil mammal occurrence in the San Antonio Mountains was discovered in 1922 by H. G. Ferguson, of the U. S. Geological Survey. A letter from Mr. Ferguson under date of March 9, 1940 gives the following interesting statement concerning the discovery and development of this fossil site:

I found the locality in the summer of 1922 during the course of reconnaissance mapping of the Tonopah Quadrangle. The discovery was purely accidental, and not the result of any systematic search. The fossils were abundantly exposed at the surface in a bed of greenish marl about two feet thick and traceable along the strike for something over 100 feet. Someone, probably a prospector, had been there before me, as there was a shallow hole cut with a pick. Evidently he was not interested. I made a small collection, chiefly of teeth, and these were later identified by Dr. Gidley. Later in the season another collection was made. . . . I later gave Dr. Stock a note as to the locality and still later showed the place to Mr. H. C. Clinton, a mineral collector at Manhattan, Nevada. Mr. Clinton collected at the site before Dr. Stock's party, and I believe exchanged fossils for minerals with different museums and universities. When I revisited the site in 1937 with Professor Muller of Stanford, I was astonished at the large-scale mining done by the California Tech. party.

In 1931 and 1932 field parties of the California Institute of Technology carried on quarrying operations in the most productive parts of the fossil-bearing horizon. In 1939, in the course of a brief geological reconnaissance of the area, A. B. Drescher relocated an invertebrate horizon near by which had been described by Spurr. In addition, Drescher discovered the fossil remains of fish at approximately the same horizon.

## ACKNOWLEDGMENTS

It is a pleasure to acknowledge the advice and counsel of Dr. Chester Stock, whose indispensable aid and critical reading of the manuscript have been a constant source of encouragement and inspiration. I am indebted to E. L. Furlong, who prepared much of the material and furnished many valuable suggestions. R. W. Wilson kindly contributed a statement regarding the fossil rodents and lagomorphs in the collection. For their courtesy, cooperation, and helpful suggestions I am obligated to the staff of the Museum of Paleontology, University of California. The illustrations were prepared by David P. Willoughby.

## LOCATION OF FOSSIL MATERIAL

The fossil material in the Tonopah collection was found at the California Institute of Technology Vertebrate Paleontology locality 172 (plate 1). The locality lies on the western flank of the San Antonio Mountains, approximately 9 miles north of Tonopah, Nevada. The area where the fossiliferous strata are exposed is located at a point 3.67 miles N. 39° W. of Mineral Monument No. 206, U.S.G.S. topographic map of the Tonopah Quadrangle, Nevada, edition of 1908, reprinted 1922 (see fig. 1).

## HISTORICAL REVIEW

In 1866 William P. Blake read before the California Academy of Sciences a short notice pointing out that "fossilized fish are found in a light colored clay shale in the mountains a few miles north of Silver Peak." He displayed a few of the specimens, but did not venture to identify them.

The first published notice of extensive fresh-water deposits in the Silver Peak region appears to be that of M. A. Knapp, a mining engineer. Knapp (1897) described particularly the coal deposits occurring in beds at the north end of the Silver Peak Range. Molluscan remains collected by Knapp near the coal beds were examined by J. C. Merriam, of the University of California, who identified *Campeloma* sp., *Unio* sp., *Planorbis* like *spectabilis* Meek, and *Ancylus* like *undulatus* Meek. He suggested that the shells were early Miocene or late Eocene in age.

H. W. Turner (1900a) named and briefly described the Esmeralda formation. In his more complete report published later in the year, Turner (1900b) described the stratigraphy and structure of the Esmeralda formation in detail. He estimated the total thickness of the beds at 14,800 feet.

F. H. Knowlton (1900) examined a florule collected by Turner at two localities in the Esmeralda formation. These fossil plants embraced fourteen forms, all but one regarded as new. Most of the new forms were found referable to well known living genera. Knowlton assigned no geological age to the florule.

F. A. Lucas (1900a, 1900b) described as a new species, *Leuciscus turneri*, a small fish obtained by Turner in the Esmeralda deposits of the Silver Peak

Quadrangle. In the title of one of the published notices (1900a), Lucas suggested that the species was Miocene in age.

J. E. Spurr (1905, pp. 51-55), in the study of the Tonopah mining district, defined the Siebert tuff (lake beds) as consisting of white stratified tuffs, beautifully and uniformly bedded, and composed of well sorted material. He

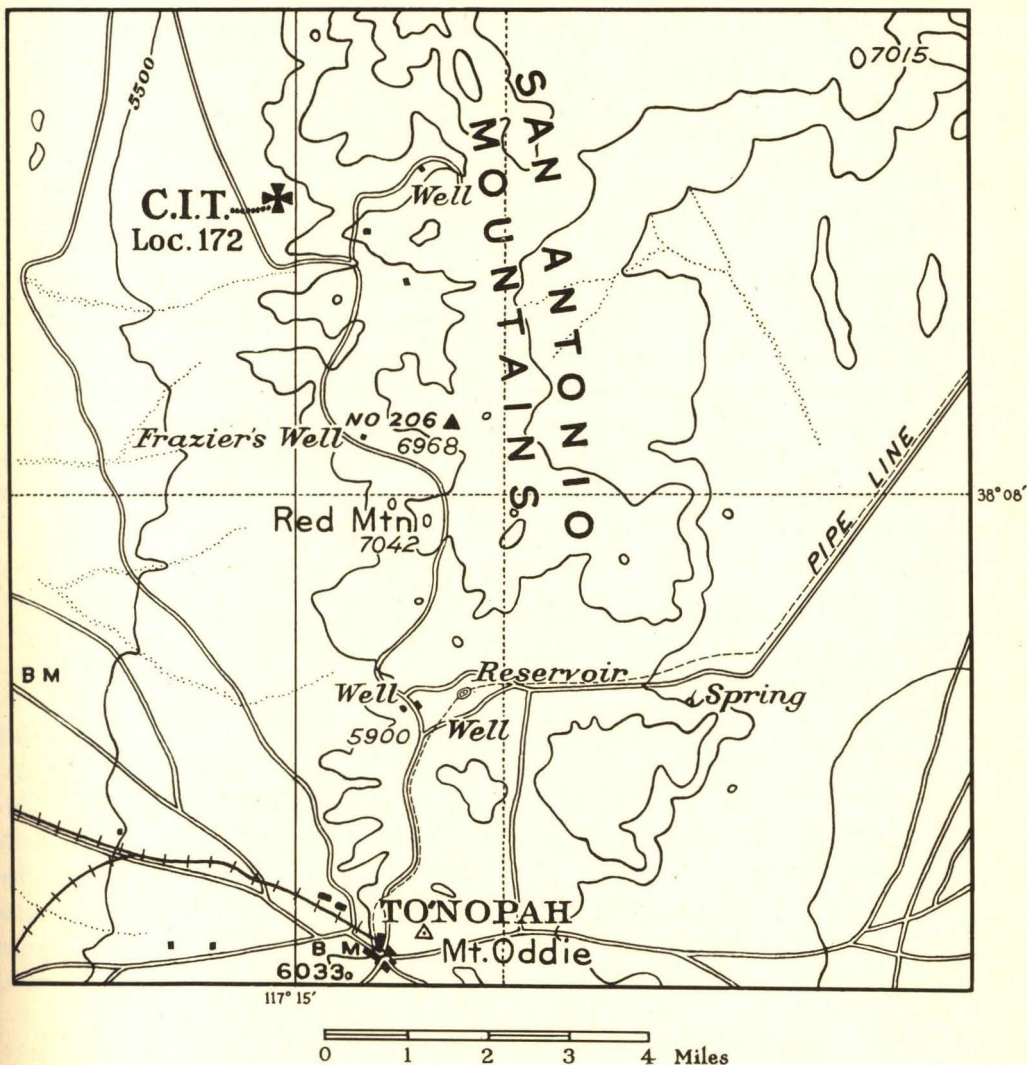


Fig. 1. Part of the southeastern quarter of the Tonopah Quadrangle, Nevada, showing location of Upper Miocene vertebrate fossil quarries (Calif. Inst. Tech. Vert. Pale. Loc. 172) in the San Antonio Mountains. Contour interval, 500 feet.

noted that where beds of conglomerate occur the pebbles are perfectly rounded. The principal deposits include several hundred feet of lake beds of consistent fine-grained character containing fresh-water infusoria. Sandy and cross-bedded sediments were considered to represent shore and delta facies. Spurr concluded that the lake must have been of considerable size from the fact that over 600 feet of lake beds are exposed on Siebert Mountain, with neither top nor bottom

present. He hypothesized that the lake basin originated from a crustal depression that followed volcanic activity and was perhaps coupled with a climatic change to increased rainfall. The sedimentary materials were derived mostly from glassy dacites and rhyolites. Limited deposits of volcanic ash and small lava flows indicate that mild vulcanism continued during deposition of the lake beds. Upper beds of river gravels, some of which contain petrified wood, indicate uplift and renewed erosion of the highlands and mark the conclusion of lacustrine deposition.

From some of the tuffs Spurr collected infusoria which were identified by R. M. Bagg, Jr., as *Gallionella granulata* Bailey, *Gallionella varians* Agardh, and *Coscinodiscus radiatus* Ehrenberg.

In the same publication, Spurr (1905, pp. 66-67) mentions a locality 8 miles north of Tonopah and 1 mile west of the little mining camp of Ray where there occurs a series of folded gravels, tuffs, lavas, and some white, thin limestones carrying numerous Eocene fossils. W. H. Dall noted that the fossils are like those from the Wasatch or Bear River Laramie Eocene of White and Meek. They are: *Vivipara* near *V. couesi*, *Planorbis utahensis* Meek, *Ancylus?* sp., and *Corbicula?* cf. *Sphaerium idahoense* Meek. Of *Corbicula* Dall remarked that "the specimens are merely internal casts, but if they are really *Corbicula* they may prove to be *C. occidentalis* Meek. Their condition is too imperfect to be certain even of the genus, but the form closely approaches that of the figures of *S. idahoense*." Spurr states further: "These [beds] overlie the Paleozoic limestones near Ray. Similar beds were noted at several places between Ray and Sodaville." He intimated that they are probably continuous with a part of the Tertiary deposits of the Silver Peak and Monte Cristo mountains.

Following Spurr's intensive study of the Tonopah region, S. H. Ball (1907), F. L. Ransome (1907, 1909), and later Adolph Knopf (1921) applied the term Siebert formation to a series of volcanics and lake beds in widely scattered localities throughout west central Nevada and eastern California. H. G. Ferguson (1924) has pointed out that all these authors failed to restrict the name Siebert formation to Spurr's definition. All of them extended the formation to include equivalents of Spurr's underlying Fraction breccia. Ferguson suggested that the Esmeralda formation of Turner is the approximate equivalent of the Fraction breccia and Siebert tuff combined.

Harold Hannibal (1912) summarized the Recent and Tertiary fresh-water Mollusca of the California province. He included a number of species recorded from the Truckee Lake beds, Nevada. For the new species which he described as *Viviparus turneri*, Hannibal cited several localities in the vicinity of Silver Peak.

Junius Henderson (1935, p. 225), in reviewing the fossil nonmarine Mollusca of North America, points out with regard to Hannibal's contribution of 1912 that "his synonymies and classification in this paper are notably erroneous." Henderson deleted all species of indefinite locality from Hannibal's list of forms

from the Truckee beds and combined the remainder with the molluscan fauna reported by Turner from the type Esmeralda. Following is his list of Mollusca (Henderson, 1935, p. 46): from the Esmeralda beds, Silver Peak region, Nevada, *Unio* sp., *Sphaerium catherinae* Hannibal, *Planorbis cordillerana* (Hannibal), *Lanx* like *undulatus* (Meek), *Viviparus turneri* Hannibal; from the Truckee beds, Hawthorne, Nevada, *Pisidium?* *meeki* Hannibal.

J. P. Buwalda (1914) described the Esmeralda formation in considerable detail as it occurs in Stewart and Ione valleys in the vicinity of Cedar Mountain, Nevada. He discussed the distribution, lithology, thickness, stratigraphic relations, and structure of the formation. Mammalian fossil material collected from the Esmeralda by Buwalda and Baker was studied by J. C. Merriam. The fossil mammalian remains, according to Buwalda (1914), "are most abundant in sandstones and in ashy deposits; a portion of a single connected skeleton was found in limestone. A few specimens were found in beds of coarse angular terrestrial material." The age of the fauna was determined as approximately Upper Miocene. Buwalda identified four species of fresh-water mollusks in the collections from the Esmeralda beds in Ione and Stewart valleys: *Heliosoma cordillerana* Hannibal, *Viviparus turneri* Hannibal, *Melania* near *sculptilis* Meek, *Corneocyclas meeki* Hannibal. Buwalda traced the beds in Ione Valley by continuous outcrops to the type Esmeralda locality, and found the first two of the molluscan species named above occurring in abundance in the type section.

Merriam (1916a) reported on the fauna of the Cedar Mountain region collected by Buwalda and Baker. The literature on the region was reviewed. Merriam drew largely on the published observations of Buwalda's geological reconnaissance for his information on the Cedar Mountain beds and the relation of the fauna to its environment. Mention was made of two fishes examined by J. O. Snyder, a salmonlike form and a cyprinoid; a testudinate, possibly *Clemmys*; and three ducks identified by L. H. Miller as *Nettion carolinense* (Gmelin), *Marila collaris* (Donovan), and *Querquedula cyanoptera* (Vieillot)?. In his discussion of the faunal relationships, Merriam noted that the mammals included elements of both primitive and advanced types, and suggested that more than one fauna might be represented. He compared the stage of the fauna to that of the Barstow and Santa Fe.

In 1924 S. H. Cathcart assembled a small collection of fossil plants from the Esmeralda. The fossils were taken from a coal prospect 4 miles southeast of Morgan Ranch and 15 miles west of Hawthorne, Mineral County, Nevada. E. W. Berry (1927) combined his findings with those of Knowlton and presented a revised floral list of the Esmeralda formation. Berry considered that the known "flora does not furnish conclusive evidence regarding the regional environment." He compared the Esmeralda flora with that of Florissant, Mascall, Latah, and Payette, and concluded that the Esmeralda is "not older than Middle Miocene and is almost certainly Upper Miocene."

Axelrod (1940) on the basis of recent collections of later Tertiary floras in the Great Basin province pointed out that the Esmeralda flora as described

by Knowlton is distinct from the Coal Valley flora reported by Berry. Axelrod revised and added to the Esmeralda flora. He demonstrated that the assemblage shows a close relation to the flora now living in southern Arizona and in the middle Kern River Canyon area. He ascribed a Lower Pliocene age to the Esmeralda flora and suggested that the Coal Valley flora is Uppermost Miocene.

Further collecting in the Cedar Mountain area and discovery of fossiliferous strata in Fish Lake Valley renewed interest in the faunas of the Esmeralda beds. Reports on various finds followed in quick succession (Matthew, 1929; Burt, 1929; Hall, 1929; Stirton, 1929; Hall, 1930b, 1930c). Stirton (1932) summarized the results of a study of the new material in conjunction with a re-study of the earlier University of California collections. He found that at no single locality does a mixed fauna occur. A lens of brown sandstone containing fossils of the older *Merychippus* fauna occurs at a locality distinct from those characterized by the younger *Plihippus*-*Hipparion* fauna. Stirton noted that the fossils of the older fauna give evidence of having been reworked. The older Cedar Mountain fauna was designated Middle Miocene in age. The Fish Lake Valley fauna was considered Lower Pliocene and equivalent to the Upper Snake Creek of Nebraska. A comparison of the Fish Lake Valley and late Cedar Mountain faunas indicates that these assemblages are of the same age or closely related.

In subsequent publications Stirton (1933, 1936; Teilhard and Stirton, 1934) used the old name Esmeralda to designate the Lower Pliocene mammalian remains from the Fish Lake Valley and Cedar Mountain areas. Stewart Spring was suggested as a name for the Middle Miocene fauna obtained at U.C. locality 2027 (Teilhard and Stirton, 1934, p. 285) in the Cedar Mountain area. At the same time, Stirton stated definitely that "*Merychippus* teeth clearly indicate that the Stewart Spring fauna is, approximately, equivalent to the Virgin Valley and not as advanced as the Santa Fe."

California Institute of Technology locality 172, which was discovered by Ferguson, has yielded an abundant fauna. Furlong (1934) briefly commented on the locality and described two new species of *Merycodus* in the fauna.

Bode (1934, pp. 56, 59) compared the crown heights of upper and lower merychippine cheek teeth obtained in faunas from the Mascall, *Merychippus* zone at Coalinga, Barstow, and Tonopah.

In a paper read before the Paleontological Society, Pacific Coast Branch, Stock (1934) described the skull and dentition of *Pseudaelurus intrepidus* from Tonopah. Stock (1935, p. 1067, fig. 2c) compared the lower deciduous molars of *Merychippus calamartus* (C.I.T. no. 1827) from Tonopah with those in a section of jaw of *Plihippus tehonensis* taken from a well core in the Chanac formation, California.

In the present study a description is given of the remaining species in the fauna as represented by the collections of the California Institute of Technology. An attempt is also made to demonstrate the relations of the fauna to other Tertiary mammalian assemblages of western North America.

## GEOLOGIC OCCURRENCE AND NOMENCLATURE OF FOSSIL BEDS

The deposits containing the mammalian fauna are those which Spurr visited and described (1905, pp. 66-67), 8 miles north of Tonopah (fig. 1) and 1 mile west of the mining camp of Ray (see above). Though Spurr did not find the vertebrate fossils, he collected shells from near-by Tertiary limestones.

*Stratigraphy*

Approximately 1 mile east of C.I.T. Vertebrate Paleontology locality 172 the Tertiary lake beds are found in fault contact with Paleozoic limestones. At several localities in the cores of anticlinal folds in the immediate vicinity of the mammalian fossil deposit, the beds can be seen to overlie pre-Esmeralda lavas.

The section at locality 172 was estimated from near-by exposures to be approximately 40 feet thick.

Thickness  
(feet)

2-3 . . . . .	Dendritic calcareous tufa
4-5 . . . . .	Gray-green silts, gravelly sandstone, occasional chert. Extremely abundant mammalian remains
25 . . . . .	Gray tuffaceous sediments
5 (est.) . . . . .	Conglomerate with pebbles of green and red volcanic rocks in green matrix
Base . . . . .	Unknown

The locality where Spurr collected fossil invertebrates is situated approximately  $\frac{3}{4}$  mile due east of C.I.T. locality 172. The section containing the invertebrates is somewhat thicker.

Thickness  
(feet)

1 . . . . .	Dendritic tufa tubes and pipes
30 . . . . .	Punky gray shale
20 . . . . .	Alternating thin layers of light gray tuffaceous sandstone, light gray punky shale, white coquina, fine angular gravel, light-colored calcareous sandstone. Very great abundance of invertebrate fossils
30 (est.) . . . . .	White to gray soft shale
Base . . . . .	Unknown

A third roughly measured section is located on the south side of the first important wash to the south of C.I.T. locality 172. It lies slightly more than  $\frac{1}{2}$  mile south of C.I.T. locality 172, and approximately  $\frac{3}{4}$  mile southwest of Spurr's invertebrate locality. The section here is even thicker than at the latter.

Thickness  
(feet)

4-6 . . . . .	Dendritic tufa domes and pipes
35 . . . . .	Light gray, poorly bedded shales
0.75 . . . . .	Resistant gray sandy tuff
15 . . . . .	Light gray shale
1 . . . . .	Dense, resistant, gray-white, tuffaceous shale. <i>Marker bed</i>
85 . . . . .	White, thin-bedded to laminated, diatom-bearing shale
Base . . . . .	Andesitic volcanics cut by breccia dikes

At about  $\frac{1}{4}$  mile northeast of the locality where the third section was measured, the basal shales show a gray-buff facies not so thinly bedded as the laminated shales of the measured section. Thirty feet below the resistant 1-foot *marker bed* these gray-buff shales contain abundant fish remains along with some fossil plant material.

At still another locality situated almost equidistant from the localities of the three measured sections, fish remains similar to those mentioned above occur intimately associated with invertebrates of the types which are found at Spurr's locality.

In the vicinity of all the fossil-bearing localities, the weather-resistant dendritic tufa beds form the highest remaining horizon. To the west of C.I.T. locality 172 lies a considerable thickness of gently tilted buff sandstones which are thought to be younger than the thin fossiliferous series.

### *Structure*

California Institute of Technology locality 172 lies near the north side of a basin, slightly over a mile wide and about 3 miles long, which reaches into the west flank of the San Antonio Mountains. Esmeralda sediments underlie most of the area within the basin. A few scattered outcrops of pre-Esmeralda lavas are exposed in the main wash where down-cutting and lateral planation have stripped away the overlying lake beds. The eastern end of the basin is bounded by a fault contact with the Paleozoic rocks. To the north of the basin the Esmeralda sediments are overlain with angular unconformity by Pliocene (?) andesite. On the south the narrow basin is bounded by rhyolite which Ferguson regards as post-Esmeralda Upper Miocene in age.

The fossil-bearing strata have been folded along east-west axes into two synclines and an anticline. The steepest dips are less than  $25^{\circ}$ . All the flexures plunge gently eastward toward the main front of the San Antonio Mountains.

Several minor transverse faults striking west of north have locally displaced the folded strata. A longitudinal fault along which the south side has moved east a few hundred feet lies almost on the axial plane of the anticline. This minor faulting probably occurred at the time of the folding of the sediments.

### *Molluscan and Piscine Faunas*

In addition to the mammalian remains, the fossils obtained from the Tertiary lake beds north of Tonopah comprise a considerable number of molds and casts of four species of fresh-water mollusks. The anterior part of one fossil fish and an abundance of fish bones and scales were also found.

The Mollusca have been tentatively identified. They represent the same four species which Spurr collected and Dall identified. Revised list: *Pisidium?* *meeki* Hannibal; *Planorbis* cf. *cordillerana* (Hannibal), small, diameter 16 mm.;

*Lanx* cf. *undulatus* (Meek), large, length 20 mm.; and *Viviparus turneri* Hannibal. All these species are apparently lacustrine in habitat (Hannibal, 1912).

These Mollusca are closely allied to, although not identical with, species in the molluscan fauna described by Buwalda (1914) from the Esmeralda of Ione and Stewart valleys. *Planorbis* cf. *cordillerana* differs from *Planorbis cordillerana* in its smaller size and more deeply umbilicate shell. There is a similar close relationship yet lack of identity between this San Antonio Mountain fauna and the molluscan fauna of the type Esmeralda which was examined by Merriam (Turner, 1900b, pp. 203-204).

A single fossil fish in the collection has been referred to *Leuciscus turneri* Lucas. Absence of the caudal and anal fins, and the poor preservation of the remaining skeletal parts, render impossible any detailed comparison with the type of the species from near Silver Peak.

On the basis of an extensive geological reconnaissance of the area, H. G. Ferguson (written communication) includes all these deposits in the Esmeralda formation. Ferguson remarks that "the beds have the same position relative to older and younger formations as in Turner's type locality, though, of course, there is not continuous outcrop between the two areas." The similarity of the molluscan and piscine fauna of the San Antonio Mountain Esmeralda beds to the corresponding assemblage of the type Esmeralda adds support to the correlation made by Ferguson.

## OCCURRENCE AND PRESERVATION OF FOSSIL MATERIAL

### *Local Correlation*

The mammalian fossil material was recovered from stratified beds of gray-green silt and sandy silt in which occur lenses of gravelly sandstone and occasional beds of chert. Although the fossil mammal horizon is limited in vertical extent to less than 10 feet, fossil float was found continuously along the weathered outcrop for more than  $\frac{1}{2}$  mile to the southwest and south of the producing quarries. This strict stratigraphic limitation of the fossil-bearing horizon proclaims the purity of the mammalian fauna. The invertebrates and fishes are likewise strictly limited as to stratigraphic horizon. The invertebrate-bearing marls and light gray shales total not more than 20 feet in thickness. All the fossiliferous localities, both vertebrate and invertebrate, occur stratigraphically beneath the dendritic tufa layer, and presumably lie not far above the local base of the Esmeralda sediments. It is believed that the faunas of all these San Antonio Mountain localities are essentially contemporaneous.

### *Lacustrine Facies*

The large extent of the sedimentary deposits and the thickness of the diatom-bearing beds indicate the existence of a lake of considerable size in Upper Miocene time. The light-colored shales and marls of the fish and invertebrate

localities must have been deposited out in the lake far enough from shore to escape admixture with coarser stream-borne sediments. Sporadic volcanic activity showered the lake and surrounding country with fine gray ash, much of which was incorporated in the offshore sediments of the lake. The marl, diatomite, and tufa of the lacustral beds were deposited by organic and chemical action.

#### *Salinity of the Miocene Lake*

The layer of dendritic tufa noted at the top of each measured section appears to be identical in character with similar deposits of Lake Lahontan, described in detail by Russell (1885). Tufa tubes, pipes, and hollow domes are extremely common in the horizon. For similar structures in Mono Lake and the Lahontan basin, Russell suggested two possible modes of origin: "First, by the direct precipitation of calcareous tufa about nuclei. Second, from the precipitation of the same material from springs rising in lakes that are highly charged with mineral matter in solution." From the presence of abundant normally developed molluscan shells embedded in the dendritic tufa, Russell concluded that the waters of Lake Lahontan were not strongly alkaline or saline when that deposit was laid down. By analogy, the Upper Miocene Esmeralda lake may have been somewhat saline but not greatly so when the dendritic tufa was formed.

The presence of the fresh-water mollusks and fish indicates that at least occasionally the waters were not too saline for animal life to exist. Under the heading "Syntonia" Hannibal (1912, pp. 114-116) discusses the effect of various salines on molluscan life. He notes that whereas magnesium compounds produce remarkable physiological effects and act as poisons, even high concentrations of sodium, potassium, and calcium salts have little effect. Hence, waters saline enough to form precipitates (e.g. dendritic tufa and chert) may still support normal or almost normal molluscan faunas.

Though *Leuciscus* is predominantly a fresh-water fish in both Europe and North America, many members of the genus are found in the brackish waters of the Baltic Sea and in bays of the eastern and western shores of the Atlantic. Accordingly, it is assumed that although *Leuciscus turneri* may be primarily a fresh-water type, this fish could persist for a time at least under conditions of increasing salinity.

#### *Delta Facies*

The gray-green silts, sands, gravels, and occasional cherts enclosing the mammalian fossils are indicative of a near-shore deposit, perhaps deltaic in character. The occasional layers of chert interbedded with the silts may provide significant evidence as to the nature of the environment at the time of deposition. According to Twenhofel (1939), the normal environment for chert

interbedded with clastic sediments, particularly clays and silts, is an area where fresh silica-bearing waters mingle with saline water. Ideal conditions for such a deposit would be found adjacent to an entrance of a stream into a saline lake.

#### *Preservation of the Fossils*

All the fossil material from C.I.T. locality 172 is highly silicified. Most of the unweathered specimens are tinted with the distinctive green color of the surrounding sedimentary formation.

A few of the teeth in the collection are definitely rounded as though they had been rolled and abraded either by stream transportation or by wave action near a lake shore. Most of the fossil material, however, shows no post-mortem wear whatsoever. In many cases, delicate tooth structures have been preserved with great fidelity.

The fossil material consists almost entirely of dentitions and limb bones. Out of a collection representing more than 225 individuals, only a single cat skull and a few antelope frontlets were preserved well enough to merit description. Equally noteworthy is the almost complete absence of vertebrae and ribs.

During the course of excavation at C.I.T. locality 172 two maps of the major quarry site were made on a scale of 1 inch to 1 foot. All fossil finds within the first 6 feet below the surface were plotted on one map, and finds from 6 to 10 feet below the surface were recorded on the second. These maps form an important record of the fossil occurrence. The productive part of the quarry covered an area of approximately 40 feet on the strike of the beds and 50 feet down the dip. Over 80 per cent of the fossils were derived from the upper horizon of the quarry, a 3-foot zone extending from 3 to 6 feet below the surface of the ground. The maps give no indication of any special orientation of the fossil bones, nor is there any suggestion of channels determining the localization of bones within the quarry. It must be remembered, however, that the entire quarry may represent a channel of concentration 40 feet wide in the half-mile outcrop of sparsely fossiliferous to barren beds.

The quarry maps do reveal the relatively high degree of association of the fossil bones. Dentitions and limb bones of the same individual were not found in association except in a few doubtful cases. Associations of maxillae and rami and of various bones of the same limb, however, are frequent. Invariably the lateral metapodials of the feet of horses are intimately associated with the medial metapodial. Furthermore, the metapodials are often closely associated with carpals and tarsals and occasionally with parts of the upper limb bones. The dentitions, though still associated, are more widely scattered. For example, the left maxilla and dentition of a rhinoceros was separated by a distance of 2 feet from the left ramus and dentition, and a tooth from the right ramus of the same individual was found 8 feet away in the same horizon.

Association and distribution of the kind noted appears to indicate that the osseous material arrived at the locality still held together by ligaments. Furthermore, burial must have been relatively rapid to prevent any wide scattering of the osseous material.

#### FAUNAL CENSUS AND ENVIRONMENT

Of the 225 individuals in all stages of growth represented in the collections of the California Institute of Technology, 195 are herbivores. Except for 1 insectivore and a number of uncounted rodents and lagomorphs, the remainder of the fauna consists of carnivores. Less than 20 of the individuals are young animals.

#### CENSUS OF TONOPAH MAMMALIAN FAUNA

Genus	No. individuals
Metechinus . . . . .	1
Tomarctus . . . . .	9
Leptocyon . . . . .	6
Aelurodon . . . . .	4
Amphicyon? . . . . .	2
Brachypsalis . . . . .	3
Pseudaelurus . . . . .	5
Hypohippus . . . . .	12
Merychippus . . . . .	110
Aphelops? . . . . .	3
Alticamelus? . . . . .	8
Merycodus . . . . .	62

(Rodentia and Lagomorpha not included)

This distribution of genera approaches the normal conditions which might be expected in a plains habitat. In contrast, attention may be directed to the faunas of Rancho La Brea (Stock, 1929) and McKittrick (Schultz, 1938), where an unnatural preponderance of carnivores occurs. The tar pools of Rancho La Brea most certainly functioned as baited traps for unwary carnivores. Though the McKittrick assemblage approaches more normal ecological conditions, the concentration of carnivores is still extremely high; hence, McKittrick likewise must have acted to some extent as a carnivore trap. The Tonopah fauna comes closer to furnishing a normal cross section of mammalian life as it existed at the stage when the deposits were laid down. The balance appears still to remain in favor of the predators, however, for there are 11 individuals in the fauna representing *Aelurodon*, *Amphicyon*, and *Pseudaelurus*.

In the attempt to reach an estimate of the number of herbivores which ought to be present in the assemblage on the basis of the carnivore population, certain assumptions are perhaps permissible. For example, at least one major kill had to be made each day to satisfy the hunger of the predatory group. We may assume also that the horses and antelopes, which

furnished most of the food, produced offspring but once a year. On this basis, a normal population for a given moment in time must contain more than 365 herbivores for every 11 large carnivores. Yet in the Tonopah fauna we find a ratio of only 195 to 11. It may be concluded, therefore, that in the collections from Tonopah the carnivore-herbivore ratio is still abnormally high. Probably the smallest representation occurs in the antelope family. This ordinarily prolific group is represented by only 60-odd individuals.

The abundance of grazing horses (*Merychippus*) and antelopes, coupled with the occurrence of camels and long-limbed rhinoceroses, indicates without question that the environment was one of grassy, perhaps shrub-covered plains. It has often been suggested that *Hypohippus* was a browser, not a grazer. The relative number of individuals of this genus is small. Perhaps the hypohippines foraged in stream bottoms or along the edges of the lake, where doubtless there flourished shrubs and trees to their liking.

#### CONDITIONS OF ACCUMULATION AND BURIAL

Summarizing the conclusions drawn from the geological and faunal evidence, we find that the fossils occur in delta deposits along the shores of a large saline lake. The mammals probably died near their burial place. The bones were quickly covered, before they could be scattered far. The species represented in the fauna are predominantly of a plains-dwelling type.

A saline lake and a plains fauna suggest aridity of climate. In an arid region, the occurrence of occasional droughts is extremely probable. During a severe drought the larger mammals are forced to congregate about the more permanent water holes. In this instance the lake, and perhaps the lower reaches of a stream entering the lake, furnished the last available sources of water in the district. Perhaps famine coupled with the depredations of the carnivores decimated the assembled multitude. With the coming of rain, stream-borne silts and sands buried the carcasses before the bones became widely scattered.

#### COMPOSITION AND STAGE OF EVOLUTION OF FAUNA

Representatives of the family Erinaceidae are rare in the later Tertiary record of western North America. Only two species have been described thus far, *Metechinus nevadensis* and *Meterix latidens* from the Fish Lake Valley Lower Pliocene of California. *Metechinus fergusoni* differs from all other erinaceids (Leche, 1902) except *M. nevadensis* in the extreme reduction of its tooth row. It parallels *M. nevadensis* in many details of the dentition and tooth structure. On the basis of the less complete reduction of the upper premolars in *M. fergusoni*, the latter is regarded as slightly more primitive than *M. nevadensis* from Fish Lake Valley.

In his introductory statement concerning the Tonopah Rodentia and Lagomorpha, Wilson states that this part of the fauna is late Miocene or early

Pliocene in age. The content and relationships of the faunule, namely, "*Mylogaulus*" sp., cf. *Eutamias ateles* Hall, cf. *Peromyscus longidens* Hall or possibly n. sp., and *Hypolaemus* sp., suggest that it is most closely related to the Barstow.

*Tomarctus paulus* from Tonopah differs from Matthew's *T. confertus*, and from material referred to that species by Matthew, in slightly larger size and in the more slender proportions of the teeth. It is doubtful whether C.I.T. no. 1229 is closely related to the Lower Snake Creek type. Even if close relation between the two species were established, it would still be difficult to determine the relative stage of advancement of each form.

*Tomarctus? kelloggii* of the Tonopah fauna agrees closely with the type specimen from Virgin Valley. The only possibility of determining the phylogenetic position of this species rests on the questionable assumption that the second lower molars U.C. no. 10651 and U.C. no. 12542, of the Virgin Valley and Thousand Creek mammal beds respectively, are correctly referred to *T. kelloggii*. Without the accompanying lower carnassials it is impossible to demonstrate that these teeth are "relatively large" and "extraordinarily developed." If Merriam was correct in referring both these teeth to *T. kelloggii*, the following argument may have a little weight.  $M_2$ , C.I.T. no. 789, is slightly smaller over all and is slightly more constricted between trigonid and heel than is U.C. no. 10651 from Virgin Valley.  $M_2$  from Thousand Creek, U.C. no. 12542, referred by Merriam to *T. near kelloggii*, shows even more constriction and is still smaller. If this crown constriction and diminution in size of  $M_2$  mark an evolutionary trend, the Tonopah form lies between *T. kelloggii* of Virgin Valley and *T. near kelloggii* of Thousand Creek.

*Tomarctus brevirostris*, represented in the Tonopah collection by a canine and a single lower carnassial tooth, conforms almost exactly to Pawnee Creek and Lower Snake Creek material which has been referred to Cope's species.

*Leptocyon vafer* shows no specific difference from Leidy's type, and agrees perfectly with Matthew's description of the Lower Snake Creek form. The Tonopah material is smaller than the referred specimen from Ricardo, which differs further in having an entoconid in  $M_1$ .

Evidence discussed in detail below indicates that the varietal form *Aelurodon wheelerianus asthenostylus* differs markedly from typical *Aelurodon*s of the Ricardo, Esmeralda, and Barstow faunas. The Tonopah variety appears to approximate an undescribed *Aelurodon* from Barstow, and to be closely allied to Cope's relatively primitive type *A. wheelerianus* from Santa Fe. *Aelurodon wheelerianus asthenostylus* is differentiated by extreme weakness of the parastyle on  $P^4$ .

The *Amphicyon?* metapodials are comparable with some undescribed material in the Pawnee Creek collection of the University of California. Since canid metapodials change relatively slowly in character, it is doubtful whether further light could be shed on the position of the Tonopah *Amphicyon?* even if similar material were present in other faunas.

*Brachypsalis pachycephalus* of the Tonopah represents an evolutionary stage close to that of *B. modicus* of Lower Snake Creek, and appears to be cospecific with Cope's type from the Loup Fork Upper Miocene. An undescribed specimen from the Barstow collection of the University of California (U.C. no. 35447) closely resembles C.I.T. no. 1231.

*Pseudaelurus intrepidus* is very closely allied to Leidy's type from Niobrara River. Referred specimens from Lower Snake Creek are similar. The Barstow material differs in being more massive. A lower jaw from the Avawatz Mountains is definitely more advanced.

*Hypohippus* near *affinis* may be slightly more primitive than referred material from the Burge of Gordon Creek, Nebraska, and more advanced than referred material in the University of California Niobrara River collection.

The relationships of *Merychippus calamartus* are discussed at length below. The form has close affinities with the same species from Barstow, but seems a little more advanced in its greater crown height and more complex enamel pattern. On the basis of its highly complex enamel pattern, the Santa Fe type may be more advanced in turn than the Tonopah form.

*Aphelops? cristatus*, n. sp., is apparently definitely more advanced than the Pawnee Creek *A. megalodus*, and considerably more primitive than *A. mutillus* from the Coffee Ranch and Higgins Quarry A.

The peculiar *Alticamelus? stocki*, n. sp., presents a difficult problem in phylogenetic position. It may correspond roughly in evolutionary stage to *A. leptocolon* in the Lower Snake Creek and the Pawnee Creek faunas.

The relationships of the unusual and primitive merycodonts, *Merycodus loxocerus* and *Merycodus hookwayi*, are likewise difficult to demonstrate. These species have no counterparts in either the Barstow or the Ricardo fauna. In fact, no similar forms have been reported from any part of the North American Tertiary. Since they are both characterized by primitive dentitions coupled with a previously unrecorded type of horn core, it appears that these forms represent an aberrant development from a primitive type which persisted locally.

## RELATIONSHIPS OF FAUNA

### Great Basin

The wealth of material in the Tonopah collection renders feasible detailed comparisons with other well represented faunas of southeastern California and western Nevada (fig. 2).

The Tonopah rodent and lagomorph faunule is close to the Barstow. *Tomarctus brevirostris* may be near the Barstow *T.* near *temerarius*. At least one of the Barstow Aelurodonts resembles closely the Tonopah *A. wheelerianus asthenostylus*. *Pseudaelurus* sp. of the Barstow differs somewhat in its more massive jaw from the Tonopah form. An undescribed *Brachypsalis* from Barstow has close affinities with the slightly smaller Tonopah specimen. *Hypohippus* near *affinis* occurs

in the Barstow fauna, but the fragmentary nature of the material precludes any conclusive determination of relationship. The most advanced merychippines of the Barstow are certainly very close to *Merychippus calamarius*

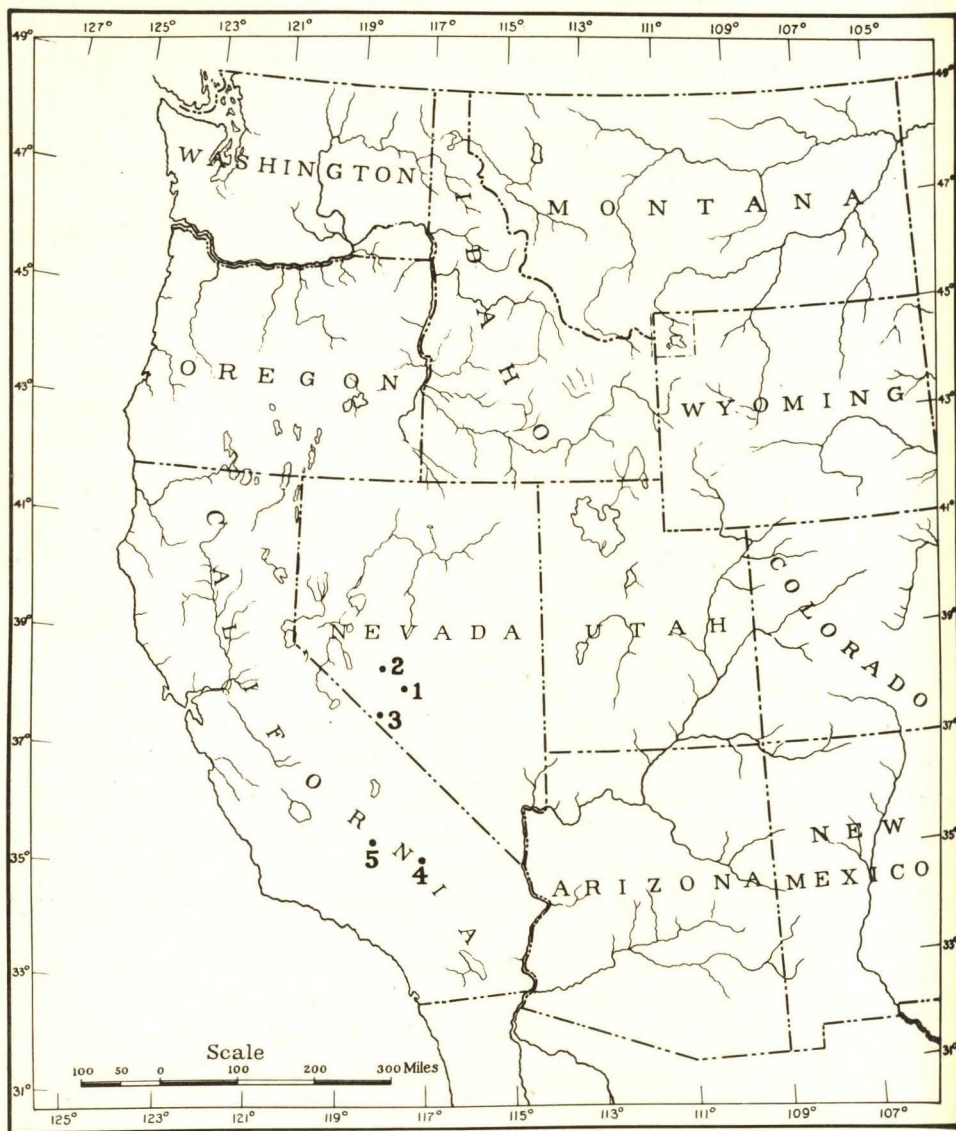


Fig. 2. Location of Upper Miocene and Lower Pliocene vertebrate fossil localities in the southern Great Basin province. 1, Tonopah; 2, Cedar Mountain; 3, Fish Lake Valley; 4, Barstow; 5, Ricardo.

from Tonopah. *Alticamelus alexandrae* seems more advanced than the primitive-appearing *A.?* *stocki* of Tonopah. The Tonopah merycodonts are likewise relatively primitive, more so perhaps than any of the Barstow forms except *Ramoceros* (*Merriamoceros*) *coronatus*.

In summary, the only demonstrable difference which may be indicative of the relative geologic ages of the Tonopah and Barstow faunas appears in the Equidae. *Merychippus calamarius* constitutes one of the most advanced merychippine forms to be recorded from the North American Tertiary, but the advance of this form beyond the stage represented by the Barstow species is very slight. It is interesting to note that an undescribed series of merychippine upper cheek teeth found in one of the uppermost horizons of the Barstow by Clair Steggall, of the University of California at Los Angeles, is as advanced as *M. calamarius* in crown height, although it lies in the *M. intermontanus* line.

Detailed comparison demonstrates clearly that the Fish Lake Valley fauna (Esmeralda of Stirton, 1932) represents a stage of evolution more advanced than that of the Tonopah. Interest centers in the occurrence of an insectivore in the Tonopah fauna, because this type appears to be closely related to *Metechinus nevadensis*. *Metechinus fergusoni* shows considerably less reduction of the premolar teeth and consequently seems definitely more primitive than *M. nevadensis*. The rodent and lagomorph faunule of Tonopah appears to be slightly more primitive than the Fish Lake Valley assemblage. *Aelurodon haydeni* from Fish Lake Valley shows larger size and perhaps more progressive characters than the Tonopah *Aelurodon*. *Hypohippus* near *affinis* shows characters in which it is assuredly more primitive than, if not directly ancestral to, *H.* near *nevadensis* of Fish Lake Valley. *Neohipparion* cf. *occidentale* and *Pliohippus* cf. *leidyani* of Fish Lake Valley are much more advanced than *Merychippus calamarius* from Tonopah. The primitive camel and merycodonts of the Tonopah fauna show no close affinities with the fragmentary Fish Lake Valley material.

Without exception, the members of the Ricardo mammalian assemblage clearly display an advance in evolutionary stage over comparable species from Tonopah. *Canis? vafer* of the Ricardo is larger than the Tonopah species. The Ricardo *Aelurodon*s typically bulk much larger than *A. wheelerianus asthenostylus*. One undescribed Ricardo *Aelurodon*, slightly larger than the Tonopah species, is unfortunately too fragmentary to permit a close comparison. The relatively large lower jaw of *Aphelops* sp. (Stock and Furlong, 1926) from the Ricardo represents a form probably more advanced than the Tonopah species. The Ricardo Equidae include several species of *Hipparion* and *Pliohippus* and typify a stage of evolution considerably later than that of *Merychippus calamarius* from Tonopah. Fragmentary camelid material from Ricardo affords no satisfactory comparison with *Alticamelus? stocki*. *Merycodus (Paracosoryx) furlongi* is much more advanced in its dentition than either of the Tonopah species.

*Tomarctus? kelloggii* from Tonopah may be roughly equivalent to *T.* near *kelloggii* from Stewart Spring (Stirton, 1932; Teilhard and Stirton, 1934, p. 285). The Stewart Spring Equidae, however, consist of *Hypohippus* near *osborni* and *Merychippus isonesus*, and are much more primitive than *H.* near *affinis* and *M. calamarius* respectively from Tonopah.

*Pacific Coast*

No known forms in the Mint Canyon fauna (Maxson, 1930; Stirton, 1933) are at all comparable with the Tonopah species. The Nevadan fauna is considered definitely younger than the Tick Canyon (Jahns, 1939), and it appears to be older than the Hipparion zone of the Upper Mint Canyon. Further finds in the Mint Canyon series may reveal a faunal zone comparable with that occurring near Tonopah.

The Quatal Canyon fauna (Gazin, 1930; VanderHoof, 1939) offers no comparable species.

The Chanac fauna (Merriam, 1915, 1916b; Stock, 1935) has been divided on the basis of its Equidae into an upper and lower part (Stirton, 1939a, p. 135). The Lower Tejon Hills (Drescher, 1941), characterized by *Nannippus tehonensis* and *Pliohippus tehonensis*, seems definitely more advanced than the Tonopah.

The Lower Pliocene fauna of the San Francisco Bay region (Merriam, 1913a, 1917; Stirton, 1935, 1939b) corresponds closely to that of the Tejon Hills and accordingly is definitely younger than the assemblage from Nevada.

*Great Plains*

In the absence of any revision of the Santa Fe fauna it is impossible to make a satisfactory comparison at this time. Frick (1933) states that the Santa Fe beds, as determined by mammalian fossils, range in age from Middle Miocene to Pleistocene. *Aeluroidon wheelerianus asthenostylus* is smaller than and not identical with the type *A. wheelerianus* of Santa Fe. *Aphelops meridianus* from New Mexico seems more primitive than the Tonopah *A. ? cristatus*. The Tonopah *Merychippus calamarius* appears almost identical with Cope's type from the Santa Fe. Out of the abundance of merycodont types reported by Frick from the Santa Fe, none belong to the subgenus *Merycodus* (*Paracosoryx*) into which both of the Tonopah species seem to fall. Future exploration in the valley of the Rio Grande will doubtless reveal a series of distinct faunas, some of which may well be contemporary with the Tonopah.

On the basis of the distinctly more primitive forms *Aphelops ceratorhinus* and *Merycodus agilis*, the Madison Valley fauna of Montana (Douglass, 1900) is regarded as pre-Tonopah in age.

Specimens from the Niobrara River, namely *Hypohippus* cf. *osborni*, *Merychippus republicanus*, *M. insignis*, and *M. perditus*, in the collections of the University of California are all more primitive than *H. near affinis* and *M. calamarius* from Tonopah.

The Burge fauna (McGrew, 1938) in the collections of the University of California includes *Hypohippus affinis*, *Neohipparion coloradense*, *Nannippus* cf. *retrusus*, and *Pliohippus* cf. *supremus*, and typifies an evolutionary stage more advanced than that of the Tonopah. Both the Niobrara River and the Burge faunas included members of the genus *Metechinus*. If future exploration yields more

diagnostic material representing the latter genus, it will be of some significance to determine in detail the relation of the Great Plains species to the Tonopah and the Fish Lake Valley material.

The relations between the Tonopah fauna and other Tertiary mammalian assemblages known from North America are shown in the accompanying chart.

RELATION OF THE TONOPAH FAUNA TO MIOCENE-PLIOCENE VERTEBRATE  
HORIZONS OF WESTERN NORTH AMERICA

Age	Nevada	California	New Mexico	Montana	Nebraska
Lower Pliocene		Ricardo			
	Esmeralda				Burge
Upper Miocene	Tonopah	Barstow	Santa Fe	Madison Valley	Niobrara River
	Stewart Springs				

For lists of the Tonopah and Barstow faunas see the following page.

## Faunal Lists

## TONOPAH FAUNA

*Metechinus fergusonii*, n. sp.

"*Mylogaulus*" sp.

Cf. *Eutamias ateles* Hall

Cf. *Peromyscus longidens* Hall or  
possibly n. sp.

*Hypolagus* sp.

*Tomarctus paulus*, n. sp.

*Tomarctus? kelloggi* (Merriam)

*Tomarctus brevirostris* Cope

*Leptocyon vafer* (Leidy)

*Aelurodon wheelerianus asthenostylus*, n. var.

*Amphicyon?* sp.

*Brachypsalis pachycephalus* Cope

*Pseudaelurus intrepidus* Leidy

*Hypohippus* near *affinis* (Leidy)

*Merychippus calamarius* (Cope)

*Aphelops? cristatus*, n. sp.

*Alticamelus? stocki*, n. sp.

*Merycodus loxocerus* Furlong

*Merycodus hookwayi* Furlong

## BARSTOW FAUNA

## Insectivora

*Limnoecus tricuspis* Stirton

## Rodentia

*Eutamias ateles* Hall

*Perognathoides cf. tertius* Hall

*Perognathoides* sp.

*Heteromyid* gen. and sp.

*Peromyscus longidens* Hall

*Peromyscus* sp.

*Peromyscus* sp.

## Lagomorpha

*Hypolagus cf. vetus* L. Kellogg

*Hypolagus* sp.

## Carnivora

*Tomarctus* near *temerarius* (Leidy)

Canid (*Canis?*) sp. small

*Aelurodon* near *wheelerianus* Cope

*Aelurodon*, *Dinocyon*, or *Amphicyon* sp.

*Brachypsalis* sp.

*Machaerodont* sp. a

*Machaerodont* sp. b

*Machaerodont* sp. c

Felid? indet.

*Pseudaelurus* sp.

## Proboscidea

*Tetrabelodon?* sp.

## Perissodactyla

*Hypohippus* near *affinis* (Leidy)

*Parahippus?* *mourningi* Merriam

*Merychippus intermontanus* Merriam

*Merychippus calamarius stylodontus* Merriam

*Merychippus sumani* Merriam

*Protohippus?* or *Pliohippus?* sp.

## Artiodactyla

## Tayassuidae

*Prosthennops?* sp.

## Merycoidodontidae

*Merycochoerus buwaldi* Merriam

## Camelidae

*Procamelus* sp. a

*Procamelus* sp. b

*Pliauchenia* sp.

*Alticamelus alexandrae* Davidson

## Cervidae

*Dromomeryx* or *Cervus?* sp.

## Antilocapridae

*Ramoceros* (*Paramoceros*) *brevicornis* Frick

*Ramoceros* (*Merriamoceros*) *coronatus* (Merriam)

*Merycodus* (*Paracosoryx*) *alticornis* (Frick)

*Meryceros joraki* Frick

## SYSTEMATIC DESCRIPTION

## ERINACEIDAE

Part of a shattered left maxillary with the anterior part of the zygomatic arch, and most of a left ramus of the same individual, comprise the insectivore material from Tonopah. The teeth which are present include C and P<sup>4</sup> and P<sub>4</sub>-M<sub>2</sub>. All these teeth are excellently preserved. The teeth show resemblance to those of a hedgehog and more particularly to those of the genus *Metechinus* from the Fish Lake Valley beds. On the basis of apparent differences in tooth structure, the material is described as belonging to a new species. It gives me great pleasure to name this species for Henry G. Ferguson, of the U. S. Geological Survey.

*Metechinus fergusoni*, n. sp.

(Plate 2, figures 1-2b)

*Type specimen.* A part of the left maxillary, C.I.T. no. 2817 (pl. 2, figs. 1, 1a, 1b), and a part of the left ramus bearing most of the tooth row, C.I.T. no. 2817 (pl. 2, figs. 2, 2a, 2b). The maxillary shows part of the alveoli for two incisors, C, the roots of P<sup>3</sup>?, P<sup>4</sup>, part of the alveolus of M<sup>1</sup>, and the anterior part of the zygomatic arch. The lower jaw shows three anterior alveoli, one of which is partially closed, P<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>, and part of the lower posterior portion of the ramus.

*Specific characters.* Small size. Upper canine with two distinct roots. P<sup>3</sup> present, not caducous. P<sup>4</sup> with very high, large metacone blade. P<sub>4</sub> well developed, with two distinct roots and slightly complex crown. M<sub>1</sub> with very long trigonid.

*Skull.* The infraorbital foramen lies just anterior to P<sup>4</sup>. The anterior part of the zygomatic arch arises from the maxillary at a point external to the anterior root of M<sup>1</sup>.

*Mandible.* The lower border of the mandible is almost flat beneath P<sub>4</sub>-M<sub>2</sub>, curving gently upward anteriorly and posteriorly. The part of the ramus posterior to M<sub>2</sub> is long, whereas that in front of this tooth is considerably shortened. The major part of the ascending ramus is missing; the ridge at the lower anterior edge of the part which is present makes a sharp anterior boundary for the masseteric fossa. The inferior boundary of this fossa is very weak. A large mental foramen lies below P<sub>4</sub>. The mandibular foramen lies in the almost smooth internal surface of the ramus. Depth of mandible below M<sub>1</sub>, 2.8 mm.; width of mandible below M<sub>1</sub>, 1.7 mm.

*Upper dentition.* A sharp-cusped tooth with small anterior basal cusp and strong basal heel cusp is tentatively regarded as a canine. Low cingula border the base of the tooth near these cusps. The tooth has two distinct roots.

P<sup>3</sup> is represented by two roots set diagonally in the jaw. The antero-external root is larger than the posterointernal.

In  $P^4$  the long metacone blade is almost as high as the backward-sloping sharp-pointed paracone, and is approximately equal to it in total bulk. The metacone blade is strongly developed and extends posteroexternally. Two inner cusps, of equal height, arise from a common internal platform and are further connected by a low internal cingulum. The posterior border of the cingulum curves well back, giving a large areal extent to the posterior part of the internal platform.

Two upper incisors appear to be represented by the internal borders of their alveoli. Of  $M^1$  only the alveolus of the anteroexternal root is present. Since  $M_2$  is present in the mandible, a second molar must have been present in the upper series, although no trace of it is preserved.

*Lower dentition.*  $P_4$ , supported by two separate roots, is set obliquely in the jaw. The principal cusp is moderately high and suggests that in its unworn state the tip was divided into two very small cuspules, the posterior one located slightly external to the anterior one. The cingulum, rising high and strong on the anterior and posterior borders of the crown, forms almost an anterior basal cusp and a cusp on the heel.

$M_1$  has a long trigonid and is relatively very large. The long, slender paraconid blade is curved gently inward, and is more anteroposterior than transverse in position. The protoconid is strong, high, and separated from the almost equally large metaconid by a very shallow valley. The low-set heel is basined and bears a hypoconid and entoconid of equal size. A moderately strong cingulum extends along the external side of the tooth from the anterior part of the protoconid to the middle of the base of the hypoconid.

$M_2$  is much smaller than  $M_1$  and bears a short paraconid with anteroposterior shear. The protoconid and metaconid cusps are of equal size. The small heel is narrower than the trigonid. The hypoconid equals the entoconid in size. A low cingulum lies along the external side of the tooth and extends from the anterior end of the tooth to the middle of the base of the hypoconid.

Of the three anterior alveoli, the very large, oval, almost horizontal one is considered to be for  $I_2$ ; the small, partially closed one contained a caducous  $I_3$ ; and the large, round one immediately anterior to  $P_4$  held the lower canine. These assumptions are open to question, but they are in accord with such information as is available on loss of teeth in the family Erinaceidae (Leche, 1902).  $M_3$  is absent.

*Comparative measurements (in millimeters) of dentition of Metechinus fergusoni*

Upper dentition:	C.I.T. no. 2817	U.C. no. 29600
C, anteroposterior diameter . . . . .	1.2	...
C, transverse diameter . . . . .	0.7	...
$P^4$ , anteroposterior diameter . . . . .	3.2	4.5
$P^4$ , transverse diameter . . . . .	2.3	4.2

## Comparative measurements - Continued

Lower dentition:	C.I.T. no. 2817	U.C. no. 29600
Length of series P <sub>4</sub> -M <sub>2</sub> . . . . .	6.2	10.1*
P <sub>4</sub> , anteroposterior diameter . . . . .	1.4	1.5
P <sub>4</sub> , transverse diameter . . . . .	1.1	...
M <sub>1</sub> , anteroposterior diameter . . . . .	3.0	5.3
M <sub>1</sub> , transverse diameter . . . . .	1.7	2.7
M <sub>2</sub> , anteroposterior diameter . . . . .	1.9	3.6
M <sub>2</sub> , transverse diameter . . . . .	1.2	2.2
M <sub>2</sub> , width of heel . . . . .	0.9	1.9

\*Composite.

*Relationships.* The position of *Metechinus fergusonii* from Tonopah is definitely within the family Erinaceidae. Detailed comparison with the modern *Erinaceus europaeus europaeus* from Germany and *Neotetracus sinensis* from Ho-mu-shu Pass, China, reveals many striking similarities and a few important differences in dentition.

*Meterix latidens* Hall (1929) from Fish Lake Valley bulks larger and has a much more nearly complete dental battery. It also differs in having two mental foramina and a strong ridge on the posterointernal face of the ramus.

*Metechinus nevadensis* Matthew (1929) from Fish Lake Valley shows a close similarity to the Tonopah form. The two species agree in the reduction of the premolars and the posterior molars, and in the corresponding enlargement and specialization of M<sub>1</sub>. The dental formulas are probably identical. That in specimen C.I.T. no. 2817 may be recorded as follows:

$$\frac{? \ 2 \ . \ 1 \ . \ 2 \ . \ ?}{2 \ . \ 1 \ . \ 1 \ . \ 2}$$

In both species M<sub>2</sub> is much smaller than M<sub>1</sub>, and M<sub>3</sub> is absent. All these points of agreement are in characters designated by Matthew as of generic rank. The forms differ in two generic characters given by Matthew: (1) P<sup>3</sup> of *M. nevadensis* is caducous, whereas it is less reduced in C.I.T. no. 2817; (2) P<sub>4</sub> of *M. nevadensis* is small and simple; in the Tonopah erinaceid it is larger and more complex.

Some of the minor differences between C.I.T. no. 2817 and *M. nevadensis* are as follows: In the Tonopah species the upper canine is less reduced and more complex in pattern; P<sup>4</sup> is relatively longer and narrower and has a relatively higher and larger metacone blade; and P<sub>4</sub> is much less reduced and slightly more complex. Except for the slightly longer paraconid blade and the external cingulum in M<sub>1</sub> from Tonopah, the two molars of both species are in close agreement. The most obvious difference between the two forms is that in size, C.I.T. no. 2817 being only about 60 per cent as large as *M. nevadensis*.

Perhaps none of these differences can be considered of generic rank. All but two of them lie in the same direction, that is, increase in total size accompanied by reduction of anterior premolars and posterior molars, perhaps indicative of an evolutionary trend from the Tonopah species to *Metechinus*

*nevadensis*. The two features in *M. fergusoni* which seem relatively more advanced than in *M. nevadensis* are really one and the same: the relatively greater anteroposterior length of  $P^4$  and of  $M_1$  in C.I.T. no. 2817.

Though the Tonopah form may later be given generic distinction, temporarily at least it is referred to Matthew's genus *Metechinus*.

#### RODENTIA AND LAGOMORPHA

By Robert W. Wilson

This small and fragmentary collection includes three rodents and a lagomorph. In age, the Tonopah assemblage is closest perhaps to the Barstow fauna, but identification of the several types is tentative. A late Miocene or early Pliocene age is suggested rather strongly by the collection. A provisional list of forms is as follows: "*Mylagaulus*" sp.; cf. *Eutamias ateles* Hall; cf. *Peromyscus longidens* Hall, or possibly n. sp.; *Hypolagus* sp.

#### "*Mylagaulus*" sp.

A mylagaulid is represented by a palate with  $P^4$ ,  $M^2-M^3$  of both sides, and several isolated cheek teeth. Until a thorough revision of the mylagaulids is undertaken, a more specific determination is hardly possible.

#### Cf. *Eutamias ateles* Hall

The presence of a small sciurid is recorded by several isolated cheek teeth, an incisor fragment, and two pieces of ramus each with a single cheek tooth. The Tonopah species apparently is closer to *Eutamias ateles* of the Barstow than to any other form, although it is not certain that the two are cospecific. Chipmunks are rare as fossils, and the present occurrence apparently is only the second record of these squirrels in the North American Tertiary. Perhaps it is open to question whether either of these forms can be referred to the living genus.

#### Cf. *Peromyscus longidens* Hall, or possibly n. sp.

A cricetid type, close to the Barstow *Peromyscus longidens*, but possibly representing a new species, is known by the following: skull fragment with incisor and  $M^1-M^3$ , maxillary fragment with  $M^1-M^2$ , two isolated molars, and several bits of rami with not more than a single cheek tooth in each.

#### *Hypolagus* sp.

A partial skull with dentition, a cheek-tooth series comprising right  $P^2-M^1$ , a left ramus with  $P_3-M_3$ , and various individual teeth are to be assigned to the very common later Tertiary leporid *Hypolagus*. In size,

the material indicates a species smaller than *H. vetus*, and more nearly agreeing with *H. limnetus* from the Hagerman and *H. cf. vetus* from the Fish Lake Valley beds. The Tonopah species probably represents an undescribed if not hitherto unknown form. In several characters of the dentition, such as relatively simple enamel folding of the upper cheek teeth, it apparently is somewhat more primitive than Middle Pliocene and later leporids. The species is no more primitive, however, than its stratigraphic position would suggest.

#### CANIDAE

Fossil remains of the Canidae in the Tonopah collection represent a surprisingly large variety of forms. The well preserved, almost complete dentition of a young adult described as the species *Tomarctus paulus* is the best specimen in the collection. Part of a lower jaw and a few lower teeth are referred to the species *Tomarctus? kelloggi*. *Tomarctus brevirostris* and *Leptocyon vafer* are represented by more or less fragmentary material. Two jaws, part of a palate, and a few separate teeth are designated as a new variety, *Aelurodon wheelerianus asthenostylus*. An interesting pair of large canid metacarpals and a phalanx are referred to *Amphicyon*. If properly assigned to this genus, they furnish the first real clue to the foot structure of that type.

#### *Tomarctus paulus*, n. sp.

(Plate 2, figures 3-4a)

*Type specimen.* A palate with well preserved, complete dentition; a complete lower jaw of the same individual with all teeth except  $I_1$ , C.I.T. no. 1229 (pl. 2, figs. 3, 4, 4a).

*Referred material.* A few separate upper teeth and a number of partial rami complete the collection. No skeletal parts have been referred to this species. A minimum population count based on rami totals five individuals.

*Specific characters.* Size of *Tomarctus confertus* (Matthew).  $P^4$  elongate with protocone set very far forward. Upper molars very wide transversely. Lower dentition differs from *T. confertus* type in narrower premolars with only moderately high cusps.  $M_1$  short, not compressed.  $M_2$  moderately long and narrow.

*Skull.* All that can be determined from the poorly preserved skull material is that the posterior part of the palate was relatively wide as compared with that of *Canis latrans* (47 mm. least over-all diameter across the palate immediately posterior to  $P^4$ ). The infraorbital foramen lies over the anterior end of  $P^4$ .

*Mandible.* The mandible is fairly well preserved except for the anterior part of the symphysis, the tip of the coronoid process of the right ramus, and the ascending left ramus. The ramus is slender, but not so slender as that of

a fox or coyote. The anterior mental foramen lies below  $P_1$ ; the posterior below the middle of  $P_3$ . In C.I.T. no. 1229, the length from condyle to alveolus for  $I_1$  is approx. 90 mm.; minimum over-all diameter from lower border of ramus to tip of coronoid process, approx. 35 mm. The depth of the ramus below  $M_1$  in this specimen is 14.7 mm., the width 7.3 mm.; in C.I.T. no. 1232 the corresponding measurements are 17.3 and 8.5 mm. Although the mandible of no. 1232 is of an older individual and is much more massive than that of no. 1229, the dentition is of the same size.

*Upper dentition.* The incisors are small. All these teeth, even  $I^3$ , characteristically bear accessory tubercles on either side of the principal cusp, and a cingulum behind. The canine is short and slightly stouter than that of *C. latrans*.

All the premolars have a slight backward cant to the principal cusp. The single-rooted  $P^1$  has a small posterior accessory cusp but no anterior one.  $P^2$  and  $P^3$  are both double-rooted and have small heel cusps as well as posterior accessory cusps.  $P^3$  bears a definite anterior accessory cusp on the internal side, but  $P^2$  has no such cusp.

The carnassial is long, but relatively not so narrow as in *C. latrans*. A small parastyle lies on the anterior border. The strong protocone is sharply set off from the rest of the tooth and stands well forward of the anteroexternal border.

$M^1$  and  $M^2$  are very similar to these teeth in *Canis*, with the exception that their heels are slightly larger.

*Lower dentition.* The small incisors resemble those of *Canis* in every way. The canine is proportionally shorter and stouter.

Single-rooted  $P_1$  has a simple conical cusp.  $P_2$ ,  $P_3$ , and  $P_4$  are all double-rooted. Each bears a posterior accessory cusp and a heel cusp;  $P_4$  has a slight suggestion of an anterior accessory cusp.

$M_1$  is doglike in almost every respect. The tooth is less elongate than in *Canis*, and the metaconid is proportionally slightly larger.  $M_2$  is proportionally larger than in *Canis*. It bears the distinguishing paraconid, and its entoconid is well developed.  $M_3$  bears an anterior paraconid crest, well marked protoconid and metaconid cusps, and a posterior hypoconid-entoconid crest. The roots of the tooth have coalesced to form a single root which is extremely elongate anteroposteriorly.

*Measurements (in millimeters) of dentition of Tomarctus paulus, C.I.T. no. 1229*

Upper dentition:

Length of series $I^1$ - $M^2$ . . . . .	60a
Length of series $P^1$ - $M^2$ . . . . .	45.5
C, anteroposterior diameter . . . . .	6.4
C, transverse diameter . . . . .	3.9
$P^1$ , anteroposterior diameter . . . . .	3.6
$P^1$ , transverse diameter . . . . .	2.2
$P^2$ , anteroposterior diameter . . . . .	6.0
$P^2$ , transverse diameter . . . . .	3.2

a, approximate.

## Measurements - Continued

## Upper dentition - continued:

P <sup>3</sup> , anteroposterior diameter . . . . .	7.5
P <sup>3</sup> , transverse diameter . . . . .	3.5
P <sup>4</sup> , anteroposterior diameter on external side . . .	13.0
P <sup>4</sup> , anteroposterior diameter on internal side . . .	14.9
P <sup>4</sup> , transverse diameter . . . . .	6.5
M <sup>1</sup> , anteroposterior diameter . . . . .	9.8
M <sup>1</sup> , transverse diameter . . . . .	13.2
M <sup>2</sup> , anteroposterior diameter . . . . .	6.0
M <sup>2</sup> , transverse diameter . . . . .	9.6

## Lower dentition:

Length of series I <sub>1</sub> -M <sub>3</sub> . . . . .	65a
Length of series P <sub>1</sub> -M <sub>3</sub> . . . . .	51a
C, anteroposterior diameter . . . . .	4.1
C, transverse diameter . . . . .	4.1
P <sub>1</sub> , anteroposterior diameter . . . . .	2.9
P <sub>1</sub> , transverse diameter . . . . .	2.0
P <sub>2</sub> , anteroposterior diameter . . . . .	5.4
P <sub>2</sub> , transverse diameter . . . . .	3.0
P <sub>3</sub> , anteroposterior diameter . . . . .	6.5
P <sub>3</sub> , transverse diameter . . . . .	3.5
P <sub>4</sub> , anteroposterior diameter . . . . .	7.7
P <sub>4</sub> , transverse diameter . . . . .	4.0
M <sub>1</sub> , anteroposterior diameter . . . . .	15.0
M <sub>1</sub> , transverse diameter . . . . .	6.0
M <sub>2</sub> , anteroposterior diameter . . . . .	7.6
M <sub>2</sub> , transverse diameter . . . . .	5.0
M <sub>3</sub> , anteroposterior diameter . . . . .	4.0
M <sub>3</sub> , transverse diameter . . . . .	3.0

a, approximate.

*Relationships.* Comparisons show that a close relation exists between *Tomarctus paulus* and *T. confertus* (Matthew, 1918, pp. 188-189, fig. 1) from the Snake Creek *Merychippus paniensis* zone. *Tomarctus confertus* has a slightly shorter tooth row and smaller teeth; its premolars are slightly shorter and wider, and M<sub>1</sub> is much more compressed. On the other hand, M<sub>2</sub> is slightly larger than the comparable tooth in C.I.T. no. 1229. In a skull referred to *T. confertus* by W. D. Matthew (1924, pp. 96-97) the upper dentition is slightly smaller than in C.I.T. no. 1229; P<sup>4</sup> is less elongate and the protocone does not stand so far forward. The upper molars of A.M.N.H. no. 18253, although of approximately the same anteroposterior diameter, are much shorter transversely than in C.I.T. no. 1229.

If the specimen shown in Leidy's figure (1869, pl. 1, fig. 12) were taken as the type of *T. temerarius* as Matthew suggests (1924, p. 98), then all material which corresponds to the large upper jaw fragment described but unfigured by Leidy would be excluded from the species. On the basis of page priority, however, it is deemed advisable to consider the larger unfigured upper jaw material as the type of Leidy's species *T. temerarius*. Hence, the relatively large jaw from Barstow referred by Merriam (1919) to *T. near temerarius* does not resemble the type and is certainly not conspecific with *Tomarctus paulus*.

On the other hand, C.I.T. no. 1229 agrees very closely in size and cusp

arrangement with Leidy's figure of  $M_1$ . Furthermore, the depth of ramus below  $M_1$  of Leidy's figure falls between the values recorded for *T. paulus*.

All other material referred to *Tomarctus* represents species of much larger size.

*Tomarctus? kelloggi* (Merriam)

(Plate 3, figures 1-2a)

A partial ramus bearing  $P_1$ - $M_1$ , C.I.T. no. 1235 (pl. 3, figs. 1, 1a), a ramal fragment with  $M_1$  and  $M_2$ , C.I.T. no. 789 (pl. 3, figs. 2, 2a), and separate  $M_1$  and  $M_2$  differ in several important respects from other canids of this group. At least three individuals are represented by this material.

*Mandible.* The ramus, deep beneath  $P_1$ , becomes still deeper below  $M_2$ . To some extent this depth is attributable to the advanced age of the individual. In spite of its depth, the mandible does not attain very great thickness. The symphyseal region appears to have been relatively small. The masseteric fossa does not reach as far forward as  $M_2$ . In C.I.T. no. 1230, the depth of the mandible below  $P_3$  is 22.0 mm.; depth of mandible below  $M_2$ , 26.0 mm.; thickness of mandible below  $M_2$ , 9.2 mm.

*Lower dentition.* The lower teeth are well spaced and uncrowded. The moderate-sized premolars have suffered little reduction.  $M_1$  appears relatively short, and  $M_2$  inordinately long.

$P_1$ , single-rooted and peglike, is nevertheless rather large.  $P_2$ ,  $P_3$ , and  $P_4$  are all two-rooted and progressively increase in size.  $P_2$  is simple.  $P_3$  bears a small heel cusp.  $P_4$  has a small posterior accessory cusp as well as a strong heel cusp.

$M_1$  in C.I.T. no. 1235 is much worn on its external side by a crushing and grinding action without much shear. A referred unworn specimen, C.I.T. no. 789, is of almost identical size. It bears a short, blunt paraconid, a blunt, heavy protoconid, and a relatively very large rounded metaconid high up on the protoconid cusp and closely appressed to it. On the heel the large entoconid, which closely resembles the hypoconid in size, occupies a more elevated position than the latter. A small tubercle lies between the base of the protoconid and the hypoconid. The external base of the heel is expanded, making the heel the widest part of the tooth.

The extremely large second lower molar is 80 per cent as long as  $M_1$ , but appears to be characteristically canid. A protoconid of moderate size, a paraconid almost as strong as the protoconid, and a very large and elevated metaconid constitute the trigonid. The long, basined heel bears the hypoconid and entoconid cusps, both well developed. A small tubercle lies in the valley between the protoconid and the hypoconid. The cingulum is developed into a prominent ridge on the anteroexternal side of the trigonid. Between trigonid and heel, the external wall is strongly indented and the internal wall is slightly indented, giving the tooth a pronounced "waist." The enamel of the posterior face of the tooth is abraded slightly owing to contact with a third molar.

Comparative measurements (in millimeters) of dentition of *Tomarctus? kelloggi*

	C.I.T. no. 1235	C.I.T. no. 789	U.C. no. 11562 Virgin Valley
Length of series P <sub>1</sub> -M <sub>1</sub> . . . . .	45.6	....	....
P <sub>1</sub> , anteroposterior diameter . . . . .	3.9	....	....
P <sub>1</sub> , transverse diameter . . . . .	2.5	....	....
P <sub>2</sub> , anteroposterior diameter . . . . .	6.5	....	6.0
P <sub>2</sub> , transverse diameter . . . . .	3.4	....	....
P <sub>3</sub> , anteroposterior diameter . . . . .	7.3	....	6.7
P <sub>3</sub> , transverse diameter . . . . .	3.6	....	....
P <sub>4</sub> , anteroposterior diameter . . . . .	8.4	....	8.4
P <sub>4</sub> , transverse diameter . . . . .	4.7	....	....
M <sub>1</sub> , anteroposterior diameter . . . . .	13.5	13.0	15.0
M <sub>1</sub> , transverse diameter . . . . .	6.9	6.6	7.0
M <sub>2</sub> , anteroposterior diameter . . . . .	....	10.5	10.5
M <sub>2</sub> , transverse diameter . . . . .	....	5.9	6.7

*Relationships.* The completely canid appearance of the lower dentition, combined with the presence of a well developed paraconid in M<sub>2</sub>, corresponds to the characteristic features of the genus *Tomarctus*. The most striking peculiarities are the depth of the ramus, the simplicity of the premolars, the anteroposterior shortness of M<sub>1</sub>, and the relatively great length of M<sub>2</sub>.

Although *Tomarctus temerarius* and *T. paulus* approach C.I.T. no. 1235 in size, they differ strikingly in the proportions of M<sub>1</sub> and M<sub>2</sub>. In fact, all but one of the species assigned to the genus *Tomarctus* have a large to very large lower carnassial and a small to very small M<sub>2</sub>. The one species *T.? kelloggi* (Merriam, 1911b) differs from all others in having an M<sub>2</sub> "relatively large and extraordinarily developed." Merriam's species from Virgin Valley agrees closely with the Tonopah material. The jaw is "relatively heavy in the posterior half." The jaw of C.I.T. no. 1235 is still heavier, but it has been mentioned already that the extreme depth of jaw (for a canid) of no. 1235 may be partly explained by the age of the individual. The premolars are slightly larger and more massive in C.I.T. no. 1235. M<sub>1</sub> and M<sub>2</sub> of C.I.T. nos. 1235 and 789 agree in almost every detail with the type of the species. The paraconid of M<sub>1</sub> is not quite so long as in U.C. no. 11562.

The posterior part of a lower carnassial, U.C. no. 19767, from Stewart Spring (Merriam, 1916a) is probably conspecific with the Tonopah material although slightly smaller.

Any comparison with referred M<sub>2</sub>'s U.C. no. 10561 from Virgin Valley and U.C. no. 12542 from Thousand Creek (Merriam, 1911b) would have limited value in view of the fact that such reference is far from indisputable.

On the basis of the extremely long and slender M<sub>2</sub>, and the low-crowned M<sub>1</sub> with pairs of subequal cusps, the species *T.? kelloggi* may be regarded as generically distinct from *Tomarctus*. Additional material, especially of the maxillary dentition, will undoubtedly throw further light on this question.

*Tomarctus brevirostris* Cope

(Plate 3, figures 3-4a)

A much worn M<sub>1</sub>, C.I.T. no. 774 (pl. 3, figs. 4, 4a), is like a coyote molar in size and resembles the comparable tooth in *Tomarctus brevirostris*.

The tooth is moderately large and differs from those of other members of the genus in its exceptionally long heel. Tooth wear has undoubtedly accentuated the heel length.

A long, slender upper canine tooth, C.I.T. no. 2853 (pl. 3, fig. 3), has also been referred to this species.

*Measurements (in millimeters) of dentition of Tomarctus brevirostris*

C.I.T. no. 2853

C, upper, anteroposterior diameter . . . . .	5
C, upper, transverse diameter . . . . .	2.5
C, upper, distance from tip of crown to end of root . . . . .	3.8

No. 774

M <sub>1</sub> , anteroposterior diameter . . . . .	19.5
M <sub>1</sub> , transverse diameter . . . . .	7.6
M <sub>1</sub> , anteroposterior diameter of heel . . . . .	6.8

*Relationships.* *Tomarctus rurestris* (Condon) is distinctly larger than this form from Tonopah. *Tomarctus kelloggi* is much smaller. *Tomarctus temerarius* has a considerably smaller M<sub>1</sub> with a shorter heel. Of the canids described from the Great Plains region, *Tomarctus brevirostris* Cope (1873; Matthew, 1924, pp. 88-96, figs. 11-16) is nearest to the specimen from Tonopah. In size, proportions, metaconid development, and heel length, a specimen from Barstow (U.C. no. 19402) shows very close resemblance. The Barstow specimen was referred by Merriam (1919, pp. 462-464) to *T.* near *temerarius*. Matthew remarks that the type upper jaw of *T. temerarius* belongs to an animal only slightly smaller than the small variant *T. brevirostris*. The M<sub>1</sub> C.I.T. no. 774, which is a little larger than U.C. no. 19402 from Barstow, agrees almost exactly with M<sub>1</sub> of *T. brevirostris* from the Pawnee Creek and Lower Snake Creek.

*Leptocyon vafer* (Leidy)

(Plate 3, figures 6, 6a)

Both rami of a lower jaw, C.I.T. no. 780 (pl. 3, figs. 6, 6a), with some teeth missing combine to provide a series from C to M<sub>2</sub> complete except for P<sub>4</sub>. Another lower jaw fragment, C.I.T. no. 2815, bears P<sub>4</sub>-M<sub>2</sub>. Additional lower jaw fragments, the posterior half of P<sub>4</sub>, and a few milk teeth (poorly preserved C-Dm<sub>4</sub>) make up the rest of the material representing this species. Five adults and one young individual are represented in the collection.

*Mandible.* The jaw is long, slender, shallow, and foxlike in appearance. The anterior mental foramen lies between P<sub>1</sub> and P<sub>2</sub>, the posterior below P<sub>3</sub>. Depth of mandible below middle of M<sub>1</sub>, 10.5 mm.; thickness of mandible below middle of M<sub>1</sub>, 5.2 mm.

*Lower dentition.* The long, slender canine is relatively larger than that in *Tomarctus paulus*. P<sub>1</sub> is single-rooted and simple-cusped. All the remaining premolars are double-rooted. P<sub>2</sub> has a simple cusp, P<sub>3</sub> a posterior accessory cusp, and P<sub>4</sub> a slight anterior basal cusp, a strong posterior accessory cusp, and a marked posterior basal cusp.

M<sub>1</sub> differs from this tooth in *T. paulus* in size and in presence of a low marginal entoconid crest rather than a strong entoconid cusp. This crest bears a very small entoconid. M<sub>2</sub> likewise differs strikingly from the corresponding tooth of *T. paulus*. It is characterized by an almost complete lack of paraconid and by a low entoconid crest bearing a minute entoconid. M<sub>2</sub> is followed by an alveolus for a single-rooted M<sub>3</sub>.

*Measurements (in millimeters) of dentition of Leptocyon vafer*

	C.I.T. no. 780	C.I.T. no. 2815
Length of series C-M <sub>2</sub> . . . . .	52.5	....
C, anteroposterior diameter . . . . .	4.3	....
C, transverse diameter . . . . .	3.0	....
P <sub>1</sub> , anteroposterior diameter . . . . .	2.2	....
P <sub>1</sub> , transverse diameter . . . . .	1.4	....
P <sub>2</sub> , anteroposterior diameter . . . . .	5.4	....
P <sub>2</sub> , transverse diameter . . . . .	1.8	....
P <sub>3</sub> , anteroposterior diameter . . . . .	6.6	....
P <sub>3</sub> , transverse diameter . . . . .	2.0	....
P <sub>4</sub> , anteroposterior diameter . . . . .	....	7.5
P <sub>4</sub> , transverse diameter . . . . .	....	3.0
M <sub>1</sub> , anteroposterior diameter . . . . .	10.5	10.8
M <sub>1</sub> , transverse diameter . . . . .	4.2	4.3
M <sub>2</sub> , anteroposterior diameter . . . . .	5.4	5.8
M <sub>2</sub> , transverse diameter . . . . .	3.5	3.4

*Relationships.* Although Leidy's type specimen *Leptocyon vafer* (1869, pl. 1, fig. 11) differs from the Tonopah form in having slightly larger proportions throughout, no apparent specific difference can be found to distinguish the two.

*Leptocyon vafer* from the Ricardo as described and figured by Merriam (1919, pp. 533-535, fig. 138a, b) is slightly larger and has an entoconid in M<sub>1</sub> which "is relatively small but prominent."

C.I.T. no. 780 is larger than Canid, indet., C.I.T. no. 2308, from the Avawatz Mountains (Henshaw, 1939, p. 17, pl. 2, figs. 2, 2a).

On the basis of the peculiar heel in M<sub>1</sub> of the Tonopah material, the author agrees with Matthew (1918, p. 190) that although the foxes parallel *L. vafer* in proportions of the jaw, they are "too closely related in dentition to *Canis* to be separately descended from *Leptocyon* instead of *Tephrocyon*" (*Tomarctus*), or from *Cynodesmus* (see McGrew, 1935, p. 310).

*Aelurodon wheelerianus asthenostylus*, n. var.

(Plate 4)

*Type specimen.* The posterior part of a palate with P<sup>4</sup>, M<sup>1</sup>, and M<sup>2</sup>, right and left, C.I.T. no. 781 (pl. 4, figs. 1, 1a); jaw of the same individual, C.I.T. no. 781 (pl. 4, figs. 2, 2a, 2b), lacking incisors, M<sub>3</sub>, ascending rami, right P<sub>1</sub>, and left M<sub>1</sub>.

*Referred material.* A fragment of maxillary with M<sup>1</sup> and part of P<sup>4</sup>, C.I.T. no. 775; milk upper carnassial, C.I.T. no. 790; moderately complete

rami with dentition, C.I.T. no. 776; loose canines and premolars; a fragment of a radius and part of a calcaneum. At least two adults and one young individual are recorded.

*Varietal character.* Parastyle of  $P^4$  very weak.

*Mandible.* The mandible is short, deep, and thick for a canid. Three mental foramina can be observed, the first a small one beneath  $I_3$ , the second and largest beneath the anterior part of  $P_2$ , and the third beneath the posterior part of  $P_3$ . The deep masseteric fossa extends forward to a point below the posterior root of  $M_3$ . Depth of mandible below middle of  $M_1$ , 32.0 mm.; thickness of mandible below middle of  $M_1$ , 12.9 mm.

*Upper dentition.* The upper carnassial tooth is relatively short and stout. It bears a parastyle in the form of a tiny tubercle which is not set off from the anterior part of the paracone. The strong protocone, located directly medial to the parastyle, does not project in front of the anteroexternal border of the tooth. A pronounced cingulum is present on the internal side of the heel.

$M^1$  is short anteroposteriorly and wide transversely. The heel is large, but there is no protoconule. The metaconule is relatively strong, being almost as well developed as the protocone. The hypocone crest is likewise well developed. A moderately strong cingulum traverses the anterior, external, and part of the posterior border of the tooth.

$M^2$  is relatively long anteroposteriorly and short transversely. All the cusps are small. In the heel only the protocone and hypocone are developed. A weak cingulum borders the anteroexternal part of the tooth.

A large, trenchant upper milk carnassial has the characteristic features of this tooth in canids. It bears only the faintest suggestion of a parastyle.

*Lower dentition.* The canine is short-crowned, stout, and heavy-rooted.

The lower premolar teeth are large and crowded. They tend to have a slight backward pitch. Individually these teeth show slight reduction in size, and are slightly compressed.  $P_1$  in C.I.T. no. 781 is small and single-rooted.  $P_2$  and  $P_3$  are moderately large, double-rooted, and subequal in size. They are characterized by a large, conical main cusp and a small heel cusp, between which lies a distinct and moderately large posterior accessory cusp. There is a very small anterior accessory cusp on each tooth.

$P_4$  resembles  $P_2$  and  $P_3$  in form but is larger. The anterior end is toed in very slightly, giving the tooth an orientation not quite parallel to the jaw. The heel of the tooth differs from that of  $P_2$  and  $P_3$  in slightly greater transverse diameter.

$M_1$ , though massive, has no unusual features.  $M_2$  has a small paraconid.  $M_3$  is not preserved, but one ramus bears two small alveoli for its roots.

All teeth, both upper and lower, are moderately worn. There is little evidence of a shearing wear on the carnassials.

## Comparative measurements (in millimeters) of dentition

	<i>A. wheelerianus</i> A.M.N.H. no. 8307*	C.I.T. no. 781	<i>A. saevus</i> A.M.N.H. no. 8305**
Upper dentition:			
P <sup>4</sup> , external anteroposterior diameter . . .	23.2	21.2	23.8
P <sup>4</sup> , greatest transverse diameter . . .	13a	12.6	12.5
M <sup>1</sup> , external anteroposterior diameter . . .	14.8	15.6	17.6
M <sup>1</sup> , greatest transverse diameter . . .	21.0	21.0	22.2
M <sup>2</sup> , external anteroposterior diameter . . .	7.4	8.1	6a
M <sup>2</sup> , greatest transverse diameter . . .	12.0	13.3	14.0
No. 790			
Dm <sup>3</sup> , anteroposterior diameter . . . . .	16.8		
Dm <sup>3</sup> , greatest transverse diameter . . . . .	9.0		
No. 781			
Lower dentition:			
Length of series C-M <sub>2</sub> . . . . .	96	100a	103
C, anteroposterior diameter at base of crown . . . . .	12a	11.0	10.1
C, transverse diameter at base of crown .	10a	8.8	8.5a
P <sub>1</sub> , anteroposterior diameter . . . . .	6.8	5.5	4.0
P <sub>1</sub> , transverse diameter . . . . .	4.6	3.9	3.3
P <sub>2</sub> , anteroposterior diameter . . . . .	10.8	9.2	9.1
P <sub>2</sub> , transverse diameter . . . . .	6.2	5.4	5.1
P <sub>3</sub> , anteroposterior diameter . . . . .	12.6	10.9	11.5
P <sub>3</sub> , transverse diameter . . . . .	7.4	6.5	6.5
P <sub>4</sub> , anteroposterior diameter . . . . .	16.4	14.2	16.1
P <sub>4</sub> , transverse diameter . . . . .	9.4	8.3	9.4
M <sub>1</sub> , anteroposterior diameter . . . . .	26.8	25.0	27.3
M <sub>1</sub> , transverse diameter . . . . .	12.4	10.2	11.5
M <sub>2</sub> , anteroposterior diameter . . . . .	11.0	11.8	12.8
M <sub>2</sub> , transverse diameter . . . . .	8.2	7.9	8.6

a, approximate.

\*Matthew, 1904, figs. 3, 4.

\*\*Cope and Matthew, 1915, pl. 118.

*Relationships.* *Aelurodon wheelerianus asthenostylus* of the Tonopah fauna falls apparently within the genus *Aelurodon* (see Matthew and Stirton, 1930, p. 182). Only in the fact that the parastyle in P<sup>4</sup> is very weak does *A. w. asthenostylus* differ from the strong-styled type.

A very close relation appears to exist between *A. wheelerianus asthenostylus* and the type *A. wheelerianus* Cope from Santa Fe (Cope, 1877, pl. 69, type figs. 2, 2a, 2b; Cope and Matthew, 1915, pl. 119a; refiguration, Matthew, 1904, figs. 3, 4). In a recent publication VanderHoof and Gregory (1940) referred the latter specimen from the Great Plains to *A. taxoides*, pointing out that the material from New Mexico is too poorly preserved to define the species *A. wheelerianus*. No. 781 C.I.T. approximates the referred specimens very closely in size. *Aelurodon w. asthenostylus* has slightly reduced premolars and slightly enlarged molars. The anterior accessory cusps in the lower premolars are a little weaker in C.I.T. no. 781 than they are in the referred material A.M.N.H. no. 8307. P<sup>4</sup> of the latter specimen bears a strong

parastyle, distinct from the anterior blade of the paracone. In *A. w. asthenostylus* the parastyle, no longer distinct, forms a weak anterior ridge on the paracone.

The ramus of the type *Aelurodon saevus* (Leidy, 1869, pl. 1, fig. 9; also Cope and Matthew, 1915, pls. 118-119; Matthew, 1904, figs. 3, 4) is longer and more slender, and its premolars are more widely spaced than in C.I.T. no. 781. The anterior mental foramen lies below the posterior root of  $P_2$  in *A. saevus*. The latter species has been regarded by Matthew and Stirton (1930, p. 188) as a progressive derivative of *A. wheelerianus*. It shows in its dentition the same evolutionary trends as *A. w. asthenostylus*, carried out to a greater extent; it likewise ranks close to *A. w. asthenostylus* in size. The premolars of *A. saevus* are still more reduced; the molars are further enlarged. Anterior accessory cusps have disappeared completely; posterior accessory cusps are weaker.  $P^4$ , however, does bear a parastyle. Thus *A. w. asthenostylus* with its weak parastyle seems to lie on a side branch near the primitive end of the direct line of evolution between *A. wheelerianus* and *A. saevus*.

Two rami from Barstow, U.C. nos. 19398 and 21231 (Merriam, 1919, p. 465, figs. 10, 11), have been referred to *Aelurodon* near *wheelerianus* Cope. Both are larger and more massive, but similar in proportions to *A. w. asthenostylus*.  $M_2$  and  $M_3$  of U.C. no. 19398 are proportionally very small;  $M_2$  of U.C. no. 21231 is large. An undescribed *Aelurodon* from Barstow, U.C. no. 35295, is represented by a jaw which, although closely comparable with C.I.T. no. 781, is slightly smaller and more slender, with teeth slightly smaller, more trenchant, and not so closely spaced. This ramus bears only one mental foramen.

*Aelurodon haydeni*, U.C. no. 29638, from the Esmeralda of Fish Lake Valley, close to Leidy's type (1869, pl. 1, fig. 10), is more than one-third larger than *A. w. asthenostylus*.

*Aelurodon aphobus* Merriam (1919) is much larger than *A. w. asthenostylus*. A single undescribed lower jaw, U.C. no. 22472, from the Ricardo, though slightly larger, approximates C.I.T. no. 781 in size. The comparison can be carried no further, as the dentition of U.C. no. 22472 has not been preserved.

#### *Amphicyon?* sp.

(Text figure 3)

Metacarpals III and IV, C.I.T. no. 767 (fig. 3a), the distal end of another metapodial, C.I.T. no. 783, and a phalanx, C.I.T. no. 777 (fig. 3b), are characterized by very large size, massive appearance, and rugose surfaces. These foot elements are canid in appearance. Although the proximal ends have large lateral articular facets, they do not have the extreme overlap which is characteristic of the Felidae.

The proximal articular surface of metacarpal III is smooth with a slight groove on the dorsal side, and slopes down toward metacarpal II, making an

angle of  $75^{\circ}$  with the long axis. Immediately distal to this articular surface, on the dorsal side, lies a deep pit for the insertion of a ligament. Another pit is located near the proximal end, distal to the volarad surface, for articulation with metacarpal II. The shaft is slightly convex dorsally in its long diameter. Near its distal end are two very large lateral eminences for attachment of ligaments, a catlike feature. The dorsal side of the distal articular surface presents a surface which is more nearly hemispherical than hemicylindrical, another catlike character. Although the distal keel is strong, it is not so long and narrow as it is in either *Felis* or *Canis*.

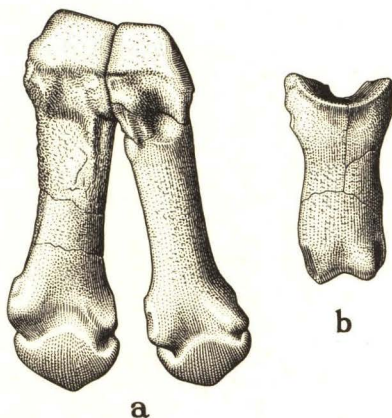


Fig. 3. *Amphicyon?* sp. a, metacarpals III and IV, no. 767, front view; b, phalanx, no. 777, front view.  $\times 0.5$ .

Calif. Inst. Tech. Vert. Pale. Coll.  
Upper Miocene, Tonopah, Nevada

In metacarpal IV the proximal articular surface is smooth and slopes toward metacarpal III. The dorsal articular facet for metacarpal III is flat, in contrast with the slight projection of the surface in *Canis* and the very strong projection in *Felis*. The entire proximal half of the volar side of metacarpal IV is covered by an upraised, wide, flat, rough area for attachment of a ligament. The shaft is straight, not curved as in *Felis*. The distal end resembles that of metacarpal III.

The proximal end of the phalanx presents a deep, smooth, hemispherical cup. The wide, flattened shaft is dorsally convex. Deep lateral pits for insertion of ligaments lie on either side of the broad distal end.

*Measurements (in millimeters) of foot elements of Amphicyon? sp.*

	AP, anteroposterior diameter		
	Tr, transverse diameter		
	Metacarpals, no. 767		Phalanx, no. 777
	III	IV	
Length . . . . .	97	98.5	54
Proximal end, AP . . . . .	36.5	32.5	28
Proximal end, Tr . . . . .	21.5	27.0	19.5
Distal end, AP . . . . .	22.7	23.5	14.3
Distal end, Tr . . . . .	25.8	26.5	21.8
Least dimension of shaft, AP . . .	13.9	14.5	9.8
Least dimension of shaft, Tr . . .	15.0	15.8	17.5

*Relationships.* Although the foot structure of *Amphicyon* is at present unknown (Matthew, 1924, p. 115), it is believed that these elements from Tonopah are of that genus. The material is not strictly comparable with the metapodials described by Schlosser (1899) as *Amphicyon*. The latter metapodials, from Eckington near Ulm, as Matthew has already noted, "belong to a much smaller animal, very different in foot proportions."

A series of metapodials found in definite association with skull and dentition of *Amphicyon* from Pawnee Creek is in the collections of the U.C. Museum of Paleontology. These Pawnee Creek metapodials are almost identical with C.I.T. no. 767.

## MUSTELIDAE

Part of an upper dentition, two mandibular fragments, and several individual teeth clearly belong to mustelids. The minimum mustelid population within the one species which occurs in the Tonopah fauna consists of three individuals, a young adult and two adults of more advanced age.

*Brachypsalis pachycephalus* Cope

(Plate 3, figures 5, 5a, 7, 7a)

An almost complete maxillary, C.I.T. no. 1231 (pl. 3, figs. 5, 5a), with P<sup>1</sup> to P<sup>4</sup> in place, a loose M<sup>1</sup>, two loose P<sup>4</sup>'s; a ramus, C.I.T. no. 1230 (pl. 3, figs. 7, 7a), with worn C, and P<sub>3</sub>-M<sub>2</sub>; another partially preserved ramus, C.I.T. no. 778, and individual canine teeth are believed to represent this species.

*Skull.* The maxillary is short and high. The anterior rim of the orbit lies above the anterior root of P<sup>4</sup>. The lachrymal foramen is large and round. The infraorbital foramen opens over the middle of P<sup>3</sup>. The malar forms a very massive zygomatic arch. In C.I.T. no. 1231, the least depth of malar below orbit is 13.0 mm.; least distance from rim of infraorbital foramen to orbital rim, 11.8 mm. Corresponding measurements in A.M.N.H. no. 8338, 11.8 and 12.7 mm.

*Mandible.* The short, heavy mandible deepens posteriorly. Three small mental foramina lie in a horizontal line below the region between P<sub>3</sub> and C. The masseteric fossa reaches forward to a point below the anterior end of M<sub>2</sub>.

*Upper dentition.* Alveoli show that the incisors were large. The upper canines are relatively very large, with short crown and very massive root. The crown is grooved anteriorly from wear against the lower canines.  $P^1$  is a small single-rooted, peglike tooth.

$P^2$  and  $P^3$  are fairly short and wide and are so worn that the original characters of their cusps are difficult to determine.  $P^2$  was set slightly diagonal.  $P^3$  may have had a small heel cusp.

$P^4$  is likewise short and wide. The very large protocone projects strongly forward and inward. A small parastyle is present. A low cingulum lies along the posterior internal base of the metacone. Although the shear of the unworn tooth appears high, the tooth wears to a low cutting edge.

$M^1$ , which has been referred to this species, is characterized by a small paracone, a still smaller metacone, a large ridgelike protocone, almost no sign of metaconule, perhaps because of wear, a parastyle crest, a metastyle crest, and, most important of all, a very strong anterointernal flange which makes the heel of the tooth wider than the outer edge. There is no indication in the specimens available of an alveolus for  $M^2$ .

*Lower dentition.* The canines are comparable in size with those in the upper dentition.  $P_1$  probably was present in the young animal. From its alveolus  $P_2$  appears to be single-rooted, although the two roots may have been closely appressed.

$P_3$  and  $P_4$  are rather short and wide like the upper premolars, and have lost all other characters because of wear. A shattered  $P_4$  in specimen C.I.T. no. 778 suggests that there was a posterior accessory cusp on the crown of this tooth.

$M_1$  is also short and wide, and is characterized by a very strong metaconid and a short heel with a small entoconid crest rather than an entoconid cusp; the surface is worn to a low angle of shear.  $M_2$  is small and almost round in outline, and has a very short basined heel.

*Comparative measurements (in millimeters) of dentition of Brachypsalis*

1a, b. *B. pachycephalus*, Tonopah. a, C.I.T. no. 1231; b, no. 1230.

2a. *B. ? hyaenoides*, Republican River, A.M.N.H. no. 8338. 2b, *B. pachycephalus*, Upper Miocene, Niobrara, A.M.N.H. no. 8544.

3a, b. *B. matutinus*, Lower Sheep Creek, A.M.N.H. no. 18921.

4a, b. *B. modicus*, Lower Snake Creek. a, A.M.N.H. no. 17210; b, no. 17209.

5a, b. *B. pristinus*, Upper Snake Creek. a, A.M.N.H. no. 18268; b, no. 18922.

	1a	2a	3a	4a	5a
Upper dentition:					
Length of series $P^2$ - $P^4$ . . . . .	35.0	32.7	....	....	....
C, anteroposterior diameter . . . . .	13.1	....	....	....	....
C, transverse diameter . . . . .	8.8	....	....	....	....
$P^1$ , anteroposterior diameter . . . . .	2.4	....	....	....	....
$P^1$ , transverse diameter . . . . .	2.3	....	....	....	....
$P^2$ , anteroposterior diameter . . . . .	7.3	7.0	....	....	....
$P^2$ , transverse diameter . . . . .	5.0	4.6	....	....	....
$P^3$ , anteroposterior diameter . . . . .	9.3	8.8	....	....	....
$P^3$ , transverse diameter . . . . .	6.5	5.8	....	....	....

*Continued on next page*

## Comparative measurements - Continued

Upper dentition - continued:	1a	2a	3a	4a	5a
P <sup>4</sup> , internal anteroposterior diameter . . .	15.4	14.1	13.9	15.5	16.7
P <sup>4</sup> , greatest transverse diameter . . . .	10.6	10.0	9.0	11.0	12.8a
M <sup>1</sup> , greatest transverse diameter . . . .	12.5	13.0	12.4	14.4	14.3
M <sup>1</sup> , width of heel . . . . .	8.0	7.8	6.5	8.0	10.0
Lower dentition:	1b	2b	3b	4b	5b
Depth of jaw at M <sub>2</sub> -M <sub>3</sub> . . . . .	23.2	25.3	....	20.0	18.9
Length of series C-M <sub>2</sub> . . . . .	64.0	....	....	62.4	....
C, anteroposterior diameter . . . . .	11.0	....	....	10.7	....
C, transverse diameter . . . . .	7.6	....	....	8.0	....
P <sub>3</sub> , anteroposterior diameter . . . . .	8.0	....	....	8.4	....
P <sub>3</sub> , transverse diameter . . . . .	5.0	....	....	5.8	....
P <sub>4</sub> , anteroposterior diameter . . . . .	11.0	....	8.3	10.2	9.6
P <sub>4</sub> , transverse diameter . . . . .	6.9	....	5.7	6.5	5.2
M <sub>1</sub> , anteroposterior diameter . . . . .	14.0	14.4a	12.7	15.7a	17.5
M <sub>1</sub> , transverse diameter . . . . .	7.5	7.8a	5.6	7.5	8.8
M <sub>2</sub> , anteroposterior diameter . . . . .	7.1	....	6.4	....	....
M <sub>2</sub> , transverse diameter . . . . .	6.2	....	4.6	....	....

a, approximate.

*Relationships.* The form and construction of the teeth, especially P<sup>4</sup> and M<sup>1</sup>, reveal the affinities of C.I.T. nos. 1230 and 1231 with the *Paroligobunis-Brachypsalis* group of mustelids (Matthew, 1924, p. 129).

*Brachypsalis modicus* Matthew (1918, figs. 4, 5) from the Lower Snake Creek approximates C.I.T. no. 1231 very closely in size. The protocone of P<sup>4</sup> in C.I.T. no. 1231 projects farther forward than in A.M.N.H. no. 17210. This projection is more apparent than real, however, because the parastyle in P<sup>4</sup> of C.I.T. no. 1231 is entirely worn away and this has shortened in appearance the anteroposterior diameter taken through the outer section of the tooth. M<sup>1</sup> of C.I.T. no. 1231 has a smaller paracone than A.M.N.H. 17210. The advanced age of C.I.T. no. 1230 partly accounts for such differences in the lower jaw as loss of P<sub>1</sub>, constriction of alveolus of P<sub>2</sub>, and increased heaviness and depth of jaw. For the most part the lower dentitions are similar.

*Brachypsalis pristinus* (Matthew, 1904, 1924) differs from C.I.T. no. 1231 in its much larger P<sup>4</sup> with no parastyle. M<sup>1</sup> is also much larger and bears a strong posterior heel crest. The lower jaw of this Upper Snake Creek species is not so deep as in C.I.T. no. 1230, but M<sub>1</sub> bulks larger, especially in the heel region. P<sub>4</sub> of A.M.N.H. no. 18922 is distinctly more slender than P<sub>4</sub> of the Tonopah form.

*Brachypsalis matutinus* Matthew (1924) of the Lower Sheep Creek is much smaller all around, and has a more elongate M<sub>2</sub>.

*Brachypsalis obliquidens* Sinclair (1915) from the Upper Snake Creek is characterized by large teeth, greatly crowded in the lower jaw so that P<sub>2</sub> and P<sub>3</sub> are set obliquely in the jaw.

*Brachypsalis marshalli* Martin (1928) from Edson, Kansas, differs in its larger size, and in its relatively shorter, wider teeth.

*Brachypsalis angustidens* Hall (1930a) from the Kern River Pliocene is much smaller than the Tonopah species.

The skull fragment with superior dentition, A.M.N.H. no. 8338, the type of *Aelurodon hyaenoides* Cope from Driftwood Creek, Nebraska (Cope, 1881, p. 388; 1883, p. 244, fig. 11c; Cope and Matthew, 1915, pl. 119a, fig. 5), was considered by Matthew (1918, pp. 195-196) to represent *B. pachycephalus*. This form, though slightly smaller than C.I.T. no. 1231, resembles it closely in character of the dentition. In both forms  $P^1$  is a peg,  $P^2$  is set slightly oblique, and the protocone of  $P^4$  projects rather far forward.  $M^1$ , though similarly constructed, is a little larger transversely in A.M.N.H. no. 8338.

The type of *B. pachycephalus* Cope (1890), A.M.N.H. no. 8544 from the Loup Fork Upper Miocene, resembles C.I.T. no. 1230 in length of tooth row and apparently in size of lower carnassial. Unfortunately, the type is fragmentary and the teeth are either absent or, as in the case of  $M_1$ , badly broken. The jaw of the type is slightly deeper and more massive.

Although the type material is poorly preserved, the referred specimen, A.M.N.H. no. 8338, still shows some distinguishing characteristics. If this reference by Matthew is correct, then the relationships of the Tonopah species are with *B. pachycephalus* Cope.

An undescribed maxillary dentition, U.C. no. 35447 from Barstow, closely resembles C.I.T. no. 1231, although  $P^2$ - $P^4$  are slightly more massive in the former than in the latter specimen.

#### FELIDAE

The cats appear to be represented in the Tonopah collection by remains of at least five individuals. The skull and lower jaw material was described in detail by Stock (1934). Though the specimens varied somewhat in size and slightly in characters, Stock referred all of them to *Pseudaelurus intrepidus* Leidy.

#### *Pseudaelurus intrepidus* Leidy

*Relationships.* Stock has pointed out that C.I.T. no. 791 is closely similar to the Old World *Pseudaelurus*, and differs from *Metailurus* Zdansky (1924) in premolar dental formula and in having an alisphenoid canal.

*Pseudaelurus marshi* Thorpe (1922) agrees closely with C.I.T. no. 1233 in size, but differs in a number of minor respects (see Stock, 1934). Except for the smaller size of the lower jaw material, the Tonopah felid agrees closely in all respects with the type *P. intrepidus*.

A part of a lower jaw without teeth, U.C. no. 21516, from the Barstow beds, is larger, deeper, and heavier than C.I.T. no. 1233. Fragmentary material from the Avawatz Mountains, C.I.T. no. 2309, represents a type larger than C.I.T. no. 1233 in all measurements, with more crowded teeth, and with a smaller heel cusp in  $M_1$ . Specimens from the Cedar Mountain region (Merriam, 1916a) and from Thousand Creek (Merriam and Stock, 1928) are too fragmentary to be of any diagnostic value.

## EQUIDAE

Remains of the Equidae comprise the bulk of the fossil collection from Tonopah. Isolated teeth and foot bones are preserved in greatest abundance. Maxillary and mandibular tooth rows make up a considerable part of the collection, but there are no complete skulls. Curiously, only a few poorly preserved vertebrae were found.

All the equid material may be divided into two distinct groups, the hypohippine and the merychippine. A population count based on astragali and teeth indicates a minimum of approximately 10 adult and 2 young hypohippine individuals, and 100 adult and 10 young of *Merychippus*.

All the specimens referable to *Hypohippus* appear to fall into a single species.

The merychippine material, although extremely abundant, shows surprisingly little variation. Hence, the specific and subspecific differentiation which was encountered in the Sheep Creek, Pawnee Creek, Snake Creek, and Barstow faunas contrasts with a stability of type in the Tonopah assemblage.

*Hypohippus* near *affinis* (Leidy)

(Plate 5; plate 6; plate 8, figures 1, 1a; plate 9, figures 1, 1a)

*Skull.* The infraorbital foramen in maxillary C.I.T. no. 685 lies directly above the anterior part of  $P^4$ . The diastema between  $I^3$  and C ranges from 12 to 15 mm. in length, and the diastema between C and  $P^1$  falls between 27 and 22 mm. in length.

*Mandible.* A single specimen representing the symphyseal region indicates that the diastema between C and  $P_2$  approximates 42 mm. in length. The mental foramen is located below the posterior part of the diastema. In C.I.T. no. 680, the anteroposterior diameter of the symphysis measured on inferior border from notch to base of crown of  $I_1$  is 65.6 mm.; least width of symphyseal region, 24.0 mm.; least depth of symphyseal region, 22.5 mm.; depth normal to alveolar border anterior to  $P_2$ , approx. 35 mm. In C.I.T. no. 1881, the depth normal to the alveolar border anterior to  $M_1$  is 46 mm.

*Upper permanent dentition.* The collections of the California Institute include two almost complete upper dental series, nos. 1404 and 1401 (pl. 5, figs. 1, 2), as well as a number of shorter series, nos. 1238, 1239, 1879, and 2860 (pl. 6, figs. 1, 1a).

The incisors are large, short-crowned, and deeply cupped, but uncemented. A strong break occurs between the thickly enameled crown and the root. The large, short canine has a rounded exterior surface, and a strong median ridge on the inner surface.

$P^1$  is a relatively large, short-crowned, double-rooted tooth. It appears to be cupped on the occlusal surface, and is suboval in outline.

In striking contrast with those of *Merychippus*, the molariform teeth are by no means subequal in size. The teeth of the premolar row increase steadily in

size from  $P^2$  to  $P^4$ , the latter being the largest of the cheek teeth. The molar teeth decrease rapidly in size from  $M^1$ , which is almost as large as  $P^4$ , to  $M^3$ , by far the smallest of all the cheek teeth.

The large protocone displays a characteristic subconical shape with anterior border flattened, and is larger than the hypocone. A strong cingulum anterior to the protocone usually disappears on the median border of the base of the protocone. In teeth of one premolar series, C.I.T. no. 1879, the cingulum continues across the median border of the base of the protocone. In  $P^3$ ,  $P^4$ , and  $M^3$  the internal basal border of the protocone lies lingual to that of the hypocone.

Normally the protoloph remains separate from the ectoloph. Generally speaking, the anterior premolars show greatest separation of protoloph from ectoloph. The extent of this separation decreases progressively toward the posterior molars. With increased wear the protoloph tends to become attached to the ectoloph. Such attachment has been observed in several specimens of  $M^1$ , but in only one example of  $P^4$ . In a few cases the protocone is separate from the protoconule, but the two cusps are usually joined together.

The hypocone is slightly smaller than the protocone and is not so perfectly conical in shape. A small cingulum may be present at the medial end of the valley between protocone and hypocone, usually on  $P^2$ , sometimes on  $P^3$ , never on the other teeth. In well worn teeth the hypocone and hypostyle are connected.

The metaloph is attached to the ectoloph in almost all permanent teeth of *Hypohippus* in the collection.  $P^2$  in C.I.T. no. 1239 forms a single exception. The transverse crest which makes the connection curves anteriorly from the hypocone, then swings back to join the ectoloph at a point opposite the mesostyle.

The large hypostyle is generally cupped posteriorly. With wear, the cup or infold disappears. The hypostyle generally remains discrete, though with wear it does become connected with the hypocone. A moderately strong cingulum borders the tooth between the hypostyle and the hypocone. In one premolar series, C.I.T. no. 1879, the cingulum actually traverses the base of the hypocone and is continuous with the cingulum of the protocone.

A narrow ridge joins the hypostyle with the metastyle. This tenuous connection is completed at a later stage of wear than is that between hypocone and ectoloph, but is usually earlier than the connection between protocone and ectoloph.

Crochets reaching forward from the metaconule appear on several third molars. The fossettes are rarely closed, and then only when the tooth has been greatly worn. In some specimens a few plications have been observed on the metaloph in the prefossette and postfossette areas.

Strong, massive external styles characterize the teeth. Cement is completely absent. The occlusal surface of the permanent upper cheek teeth varies in

shape. It may be square, or rectangular with the transverse width much greater than the anteroposterior.

The following measurements (in millimeters) give the maximum heights of the low, strongly curved crowns: C.I.T. no. 1879,  $P^2$ , 17.0 mm.;  $P^3$ , est. 18.5 mm.;  $P^4$ , 19.0 mm. C.I.T. no. 1239,  $M^1$ , 17.2 mm.;  $M^2$ , 17.7 mm. C.I.T. no. 1404,  $M^3$ , 16.5 mm.

*Upper deciduous dentition.* Only two teeth, both representing  $Dm^2$ , occur in the collection, C.I.T. nos. 2845 and 2846 (pl. 6, figs. 2, 3). In these the proto-loph is not connected with the ectoloph, and in C.I.T. no. 2845 the protocone is separated from the protoconule. The cingulum, though well developed along the anterior side of the teeth, is absent on the inner base of both protocone and hypocone.

The separation of metaloph from ectoloph forms an important diagnostic character. A small transverse ridge points inward from the ectoloph at the posterior end of the paracone crescent. The outer end of the metaloph ridge terminates just anterior to the transverse ridge of the ectoloph. The two ridges overlap and come very close to each other, but they are not joined together except perhaps at the very base.

The hypostyle is much more suppressed than in permanent teeth. The shape of the occlusal surface of  $Dm^2$  is like that of  $P^2$ : anteroposterior diameter along outer border, 29 mm.; greatest transverse diameter, 26.5 mm. The crown height in  $Dm^2$  is 14 to 15 mm.

*Lower permanent dentition.* The incisors, C.I.T. no. 680, are long-rooted, short-crowned, and not so procumbent as are the merychippine lower incisors. A strong dividing line distinguishes the upraised, thickly enameled crown from the root. Very shallow uncemented cups occur near the posterior border of the occlusal surface.

$P_1$ , C.I.T. no. 2847 (pl. 6, fig. 4), is a small, single-rooted tooth which from root to crown is concave anteriorly. The crown is laterally compressed, with a faint anterior tubercle and a large posterior tubercle.

The collections of the California Institute include only two well preserved series of lower molariform teeth, nos. 1880 and 1881 (pl. 5, figs. 3, 4). As with the upper cheek teeth,  $P_4$  is the largest and the remaining teeth are successively smaller in either direction from it.

In the molariform teeth the metaconid-metastylid column bears no pronounced gutter on its inner wall. There is sometimes a very slight groove near the summit of the column. With wear the column increases very rapidly in anteroposterior diameter.

The entostylid is distinct on unworn teeth. The posterior lobe of  $M_3$  is relatively small. The triangular entoconid becomes square with wear. The external walls of the protoconid and hypoconid display a strongly curved, finely fluted enamel surface. A very deep valley lies between the protoconid and hypoconid. No cement is present on the teeth.

A strong cingulum, which rises high on the anterior border of the tooth,

skirts the external basal border of the protoconid. A second cingulum originates in the protoconid-hypoconid valley, skirts the external basal border of the hypoconid, then rises sharply to the posterior border of the tooth.

The occlusal surfaces are relatively short and wide. Ratios of antero-posterior diameter to transverse diameter:  $P_3$ , 1.20-1.40;  $P_4$ , 1.15-1.36;  $M_1$ , 1.25-1.30;  $M_2$ , 1.23-1.39;  $M_3$ , 1.60-1.70.

The maximum crown height for all the lower molariform teeth is approximately 20 mm.

*Lower deciduous dentition.* The milk tooth,  $Dm_3$  or  $Dm_4$ , C.I.T. no. 2848 (pl. 6, fig. 6), resembles the permanent dentition in almost every respect. The height of the crown is less and the entostylid is stronger than in permanent teeth. Anteroposterior diameter, 28 mm.; transverse diameter, 18 mm.; crown height, 12 mm.

*Measurements (in millimeters) of dentition of Hypohippus near affinis*

AP, anteroposterior diameter

Upper dentition:	C.I.T. no. 1404	C.I.T. no. 1401
Length of series $P^1-M^3$ . . . . .	164	145
Length of series $P^1-P^4$ . . . . .	92	82
Length of series $M^1-M^3$ . . . . .	72	63
$P^1$ , anteroposterior diameter . . . . .	14.2	16.7
$P^1$ , greatest transverse diameter . . . . .	8.2	10.4
$P^2$ , AP along outer border . . . . .	30.0	26.5
$P^2$ , AP protoconule-hypostyle . . . . .	24.0	20.0
$P^2$ , greatest transverse diameter . . . . .	27.4	26.4
$P^3$ , AP along outer border . . . . .	29.2	25.0
$P^3$ , AP protoconule-hypostyle . . . . .	26.0	23.0
$P^3$ , greatest transverse diameter . . . . .	32.5	29.8
$P^4$ , AP along outer border . . . . .	30.5	25.5a
$P^4$ , AP protoconule-hypostyle . . . . .	27.2	23.2
$P^4$ , greatest transverse diameter . . . . .	33.8	32.5a
$M^1$ , AP along outer border . . . . .	28.5	24.9
$M^1$ , AP protoconule-hypostyle . . . . .	25.0	22.1
$M^1$ , greatest transverse diameter . . . . .	32.5	30.5
$M^2$ , AP along outer border . . . . .	28.8	23.0
$M^2$ , AP protoconule-hypostyle . . . . .	24.2	21.0
$M^2$ , greatest transverse diameter . . . . .	31.4	27.5
$M^3$ , AP along outer border . . . . .	23.2	20.4
$M^3$ , AP protoconule-hypostyle . . . . .	22.5	19.0
$M^3$ , greatest transverse diameter . . . . .	25.4	25.0
$I^1$ , greatest diameter . . . . .	14.4	....
$I^1$ , least diameter . . . . .	11.6	....
$I^2$ , greatest diameter . . . . .	12.8	11.6
$I^2$ , least diameter . . . . .	10.3	8.5
$I^3$ , greatest diameter . . . . .	9.7	9.2
$I^3$ , least diameter . . . . .	7.9	5.4
C, greatest diameter . . . . .	11.4	....
C, least diameter . . . . .	8.7	....
Diastema, $I^3-C$ . . . . .	18e	14
Diastema, $C-P^1$ . . . . .	23a	28a

a, approximate.

e, estimated.

Continued on next page

## Measurements - Continued

	No. 1880	No. 1881	No. 2847
Lower dentition:			
Length of series $P_2-M_3$ . . . . .	148	....	....
Length of series $P_2-P_4$ . . . . .	74.5	....	....
Length of series $M_1-M_3$ . . . . .	73.5	....	....
$P_1$ , anteroposterior diameter . . . . .	....	....	9.1
$P_1$ , transverse diameter . . . . .	....	....	5.0
$P_2$ , anteroposterior diameter . . . . .	24.0	....	23.6
$P_2$ , transverse diameter . . . . .	16.3	....	17.3
$P_3$ , anteroposterior diameter . . . . .	24.2	23.2	....
$P_3$ , transverse diameter . . . . .	17.5	19.2	....
$P_4$ , anteroposterior diameter . . . . .	24.8	24.0	....
$P_4$ , transverse diameter . . . . .	19.5	20.9	....
$M_1$ , anteroposterior diameter . . . . .	23.8	23.9	....
$M_1$ , transverse diameter . . . . .	18.4	19.0	....
$M_2$ , anteroposterior diameter . . . . .	24.0	22.5	....
$M_2$ , transverse diameter . . . . .	17.3	18.3	....
$M_3$ , anteroposterior diameter . . . . .	23.5	25.5	....
$M_3$ , transverse diameter . . . . .	14.7	15.0	....
No. 680			
$I_1$ , greatest diameter . . . . .			9.4
$I_1$ , least diameter . . . . .			9.0
$I_2$ , greatest diameter . . . . .			9.0
$I_2$ , least diameter . . . . .			8.3

*Relationships.* *Hypohippus nevadensis* Merriam (1913b) of the neighboring Esmeralda fauna presents several characters which find analogies in *H. near affinis* from Tonopah. The former species was first described from the Esmeralda (U.C. locality 1980) near Cedar Mountain, Nevada. Further material from Fish Lake Valley, Nevada, was assigned to this species by Stock (1926). A detailed comparison between the Tonopah species and *H. nevadensis* reveals a similarity in characters, but a discrepancy in size. Unfortunately for comparison, the material of the type *H. nevadensis* consists of deciduous upper cheek teeth and  $M^1$ .  $Dm^2$  from Tonopah is much smaller than Merriam's type, U.C. no. 21056, and somewhat smaller than the specimen from Fish Lake Valley, U.C. no. 27116. The largest  $M^1$  in the Tonopah collection is much smaller in all dimensions including height of crown than  $M^1$  of U.C. no. 27116. The deciduous teeth of *H. near affinis* resemble those of the Cedar Mountain species in separation of metaloph from ectoloph, in which respect also they differ from the Fish Lake Valley form. Whereas the metaloph and ectoloph are separate in  $M^1$  of U.C. no. 27116 from Fish Lake Valley, these crests are joined in all permanent cheek teeth from Tonopah except  $P^2$ , C.I.T. no. 1239. A crochet is present in  $Dm^2$  and  $Dm^3$  of U.C. no. 27116, but is weak in  $Dm^4$  and absent in  $M^1$ . In the Tonopah collection only one tooth, an  $M^3$ , bears a crochet. A cingulum traversing the entire inner border of the upper cheek teeth may be present or absent in the material from the three Nevadan localities.

Lower teeth of *H. near affinis* resemble those from Fish Lake Valley in

every respect except size. The latter lower teeth are larger by about the same amount as are the upper teeth.

Limb elements of the Tonopah species closely approximate in size those of U.C. no. 21056 from Cedar Mountain. It must be remembered, however, that the limb elements of *H. near affinis* are those of a large adult, whereas U.C. no. 21056 represents a very young individual.

In summary, the major difference between the Tonopah form and *Hypohippus nevadensis* from Cedar Mountain and Fish Lake Valley is one of size. The latter averages one-sixth to one-eighth larger lineally than the former. In *H. nevadensis* the importance of separation of metaloph from ectoloph and the development of a crochet may be overestimated. Merriam (1913b) based the new subgenus *Drymohippus* on this separation of lophs. After reviewing the Fish Lake Valley material, Stock (1926, p. 64) commented: "If the form from the Fish Lake Valley region has been correctly assigned to Merriam's species, this character appears to be subject to individual variation and cannot, therefore, be considered as distinguishing *Drymohippus*. Likewise, the development of a crochet in the milk teeth would not then offer a constant character distinguishing *Drymohippus* from other members of the *Hypohippus* group." (See also McGrew, 1938, p. 314.) In the figure of *Hypohippus equinus* Scott (1895), on P<sup>2</sup> the metaloph is apparently separate from the ectoloph. The Tonopah material, with metaloph and ectoloph joined in all except two milk teeth and in P<sup>2</sup>, bears out the contention that such variations may be common to many hypohippines.

*Hypohippus osborni* Gidley (1907, p. 930) is considerably smaller than the largest *H. near affinis*, although only slightly smaller than the smallest individuals referable to this species.

*Hypohippus near affinis* from Tonopah falls short of the type *H. affinis* (Leidy) in size. Material from Big Spring Canyon, A.M.N.H. no. 10834, which was assigned to the type *H. affinis* by Gidley (1906, p. 135), shows that the lower teeth of *H. affinis* are somewhat larger than those of the Tonopah form.

A molar series, P<sup>3</sup>-M<sup>3</sup>, U.C. no. 32019, from the Niobrara River U.C. locality Little Beaver A V336 is smaller than the corresponding teeth from Tonopah. In this specimen there is a firmer connection between metaloph and ectoloph, and a small conical cuspule is present at the lingual end of the protocone-hypocone valley of each tooth. A small crochet is developed in P<sup>4</sup>. The protocone and the protoconule show a tendency to remain separate in the premolars. In this latter character and in size, the Niobrara River specimen appears a little more primitive than *H. near affinis*, whereas on the basis of metaloph-ectoloph connection the Tonopah form may be slightly more primitive. *Hypohippus near affinis* is interpreted to be more advanced but situated on a closely allied side branch which retained the primitive separation of metaloph and ectoloph.

Well preserved series of upper and lower permanent teeth and upper milk

teeth of *Hypohippus affinis* in the Burge fauna have been illustrated by McGrew (1938). These teeth agree closely in size with those of *H. near affinis*. A partially erupted  $M^1$  in U.C. no. 28842 indicates that the Burge form is much higher-crowned. The tooth pattern of U.C. no. 28840 differs in the presence of a crochet on the metaloph, in better connection of metaloph and ectoloph, and in the development in the last two molars of a small conical cusplule at the lingual end of the protocone-hypocone valley. The lower molars U.C. no. 28840 are similar in pattern to those of *H. near affinis*, but are somewhat higher-crowned, and have a larger posterior lobe in  $M_3$ .

Known material of *Hypohippus* from Barstow is too fragmentary to afford any comparisons of value. On the basis of broken lower teeth U.C. nos. 21215 and 35421, the Barstow form appears larger than *H. near affinis*, yet in all probability it, too, lies near that species.

*Hypohippus near affinis* from Tonopah may have been ancestral to *Hypohippus nevadensis*. The former type represents a stage of development which is slightly more primitive than that shown in *H. affinis* from the Burge of Gordon Creek, and is more advanced than that of *H. cf. osborni* from the Niobrara River of U.C. locality Little Beaver A V336.

### *Merychippus calamarius* (Cope)

(Plate 7; plate 8, figures 2, 2a; plate 9, figures 2, 2a; text figures 4, 5)

*Skull*. Only a few minor characters are determinable from the sparse and fragmentary skull material. In C.I.T. no. 2839 the infraorbital foramen lies directly above the posterior part of  $P^3$  and the anterior border of  $P^4$ . The anterior border of the orbit reaches as far forward as the plane of contact between  $M^3$  and  $M^2$ . The diastema between  $I^3$  and C ranges from 19 to 24 mm. in length, and the diastema between C and  $P^1$  varies inversely in length from 32 to 26 mm.

*Mandible*. Although symphyseal sections and horizontal parts of rami were preserved in considerable abundance, no material is available to illustrate the region of the angle and the ascending ramus. In C.I.T. no. 2836 (pl. 7, fig. 5), the canine is immediately posterior to  $I_3$ . The diastema between C and  $P_2$  is from 43 to 49 mm. long. The mental foramen is located halfway between C and  $P_2$ . In young animals the tooth size and the diastemal length is the same as in adults. Growth in the mandible takes place by deepening of the jaw from 40 mm., just posterior to  $Dm_4$  in a young foal, C.I.T. no. 2833, to 50 mm., between  $P_4$  and  $M_1$  in a young adult, C.I.T. no. 2834. The mandible is also thickened by growth. The greatest increase in size and in length, however, takes place in the molar region, as the ascending ramus is pushed back to make room for the molar teeth.

Most of these characters are well illustrated in mandibles C.I.T. nos. 656, 678, and 2834 (pl. 7, figs. 2, 2a, 7, 8).

*Measurements (in millimeters) of mandible of Merychippus calamarius*

	C.I.T. no. 2834 (young adult)	C.I.T. no. 678 (youth)	C.I.T. no. 656 (foal)
Anteroposterior diameter of symphysis measured on inferior border from			
crotch to root of I <sub>1</sub> . . . . .	50a	49	40
Least width of symphyseal region . . . . .	28.4	23.0	19.0
Least depth of symphyseal region . . . . .	22.0	20.4	16.5
Depth normal to alveolar border			
anterior to P <sub>2</sub> . . . . .	32.9	31.0	21a
Depth normal to alveolar border			
anterior to M <sub>1</sub> . . . . .	51.4	43e	22e

a, approximate.

e, estimated.

*Tooth wear.* Advanced stages of wear efface details of the enamel pattern and destroy the original proportions of the occlusal surface. Hence, well worn teeth tend to lose many of the characters on which specific determinations are made. For this reason, in the following discussion, all remarks apply to teeth which are approximately one-third worn except as otherwise indicated. Teeth which are unworn to one-third worn are designated as *unworn*, teeth which are more than one-third worn are termed *worn*. The state of wear of any given tooth was determined by comparing the height of the crown with the maximum crown height for that tooth.

*Upper permanent dentition.* The limited extremes of variation in the abundantly represented merychippine form are illustrated by C.I.T. nos. 2840, 2841, 1311, 669, and 2839 (fig. 4, a-e, respectively). The incisors are strongly curved and relatively long-crowned with no sharp break between crown and root. The enamel gradually becomes thinner and disappears toward the root. In each incisor the grinding surface is deeply cupped and the enamel infold is filled with cement.

The upper canine is a strongly curved, peglike tooth. Occasionally the piercing end of the tooth, instead of being circular in cross section, is somewhat flattened on the lingual side of the anterior and posterior edges, so that the tooth appears as a small curved blade supported by a column on the lingual side.

P<sup>1</sup> is a small, short-crowned, double-rooted tooth located immediately anterior to P<sup>2</sup>. It is generally well worn at an early stage and is often lost soon after maturity. Because the angle of the surface of wear on this tooth may vary greatly, its enamel pattern appears in a number of diverse forms. Basically it consists of a prominent outer border, a strong metaconule, and a partially enclosed prefossette opening toward the front.

Separation of the protocone from the protoconule occurs in almost 90 per cent of the unworn molariform teeth. In only 14 per cent of the unworn teeth is the protocone rounded or oval. In the rest it has a spur projecting toward the protoconule. The protocone is generally inflated, although

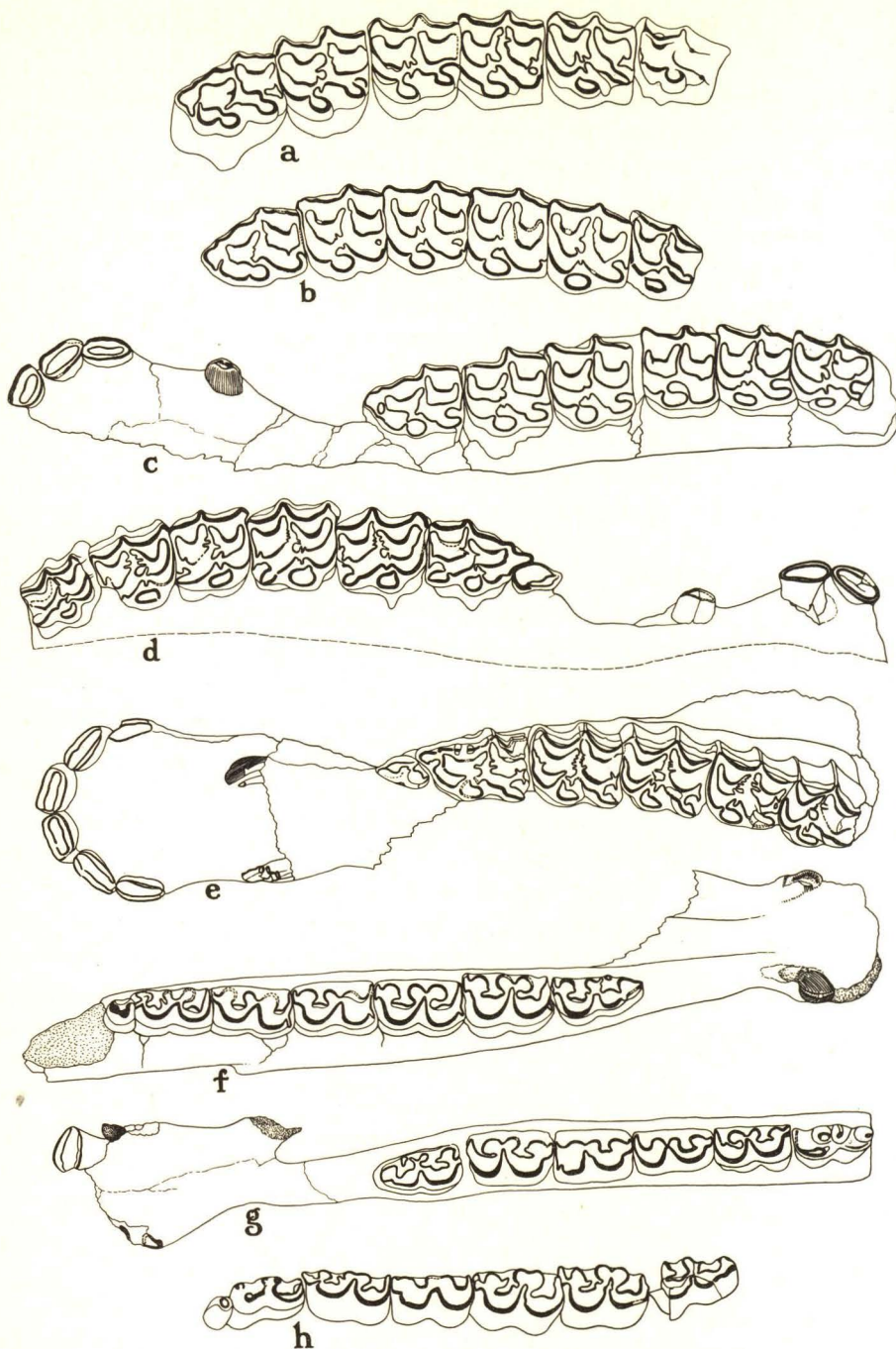


Fig. 4. *Merychippus calamarius* (Cope). Referred specimens, showing variation in enamel pattern. a, no. 2840, moderately worn; b, no. 2841, moderately worn; c, no. 1311, moderately worn; d, no. 669, slightly worn; e, no. 2839, unworn; f, no. 2834, moderately worn; g, no. 678, slightly worn; h, no. 2842, slightly worn. All figures  $\times 0.5$ .

Calif. Inst. Tech. Vert. Pale. Coll.

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it may be flattened on the lingual side. Indented protocones rarely occur. The long axis is oriented for the most part anteroposteriorly. The protocone usually lies lingual to the posterior half of the prefossette. In some cases, however, and always in  $M^3$ , it is more posterior, extending back to a position lingual to the metaconule. The protocone is always larger, more inflated, and more lingual in position than the hypocone.

The hypocone is practically always united with the metaconule. It is generally flattened, although it may be rounded in some specimens. The long axis of the hypocone is almost never oriented anteroposteriorly.

The pli caballin is generally single and acutely pointed, sometimes single and rounded, and rarely bifid or double. The hypostyle sometimes has no plications, but commonly has a single acute plication and rarely a double one.

The fossettes are usually closed in all teeth except  $P^2$ . The various plications range in number from none to quadruple folds. On the whole, the fossette borders would be called moderately to highly complex for a merychippine form. There appears to be a direct correlation between protocone separation and degree of complexity of the enamel pattern. The more complete the separation, the more complex the pattern.

The external styles are strong. Moderately heavy to heavy cement covers most of the teeth.

In  $M^1$  and  $M^2$  the ratios between anteroposterior and transverse diameters vary from 1.18-1.10 in absolutely unworn teeth to 0.90-0.76 in very worn teeth. Because of the cement covering on most of the teeth, inaccuracies enter into the measurements of the transverse diameters (Bode, 1931, p. 122).

The crowns of the molariform teeth are strongly curved (C.I.T. no. 2861, pl. 7, fig. 4a). In unworn teeth the radius of curvature of the external styles generally falls between 40 and 50 mm. The radius of curvature of the lingual side of the protocone ranges between 12 and 18 mm. In unworn upper teeth the maximum crown height is greater than in any merychippine species previously recorded (C.I.T. no. 2861, pl. 7, fig. 4).

*Measurements (in millimeters) of crown heights of upper teeth*

	A	B
$P^1$ . . . . .	9	...
$P^2$ . . . . .	35	37
$P^3$ . . . . .	39	41
$P^4$ . . . . .	42	45
$M^1$ . . . . .	40a	43a
$M^2$ . . . . .	44	47
$M^3$ . . . . .	36	41

a, approximate.

These measurements were taken of separate unworn teeth and of unerupted teeth in maxillary batteries. In column A, crown height is considered to be the shortest distance from root to grinding surface taken just anterior to the mesostyle, with the notch between the external roots furnishing one

measuring point and the indentation on the external wall of the tooth between paracone and metacone furnishing the other measuring point. The measurements in column B were taken by the method used by Bode in compiling data for a table comparing the crown heights of merychippine forms from Mascall, Coalinga, Barstow, and Tonopah (Bode, 1934, p. 56). The measuring points in this case were the base of the anteroexternal root and the tip of the paracone cusp.

*Upper deciduous dentition.* The incisors are large, deeply cupped teeth without cement.  $Dm^1$ , as it appears in C.I.T. no. 2835, is slightly longer than  $P^1$ . The metaconule is poorly developed, hence the tooth is bladelike in appearance and shows no tendency toward developing fossettes.

Character for character, the molariform deciduous teeth C.I.T. no. 2843 (pl. 7, figs. 6, 6a) resemble closely the permanent premolars, except for the expected differences between deciduous and permanent teeth. In the molariform deciduous teeth the protocone remains free until the crowns are more than half worn. The fossette borders are a little more complexly plicated than they are in the permanent series. Also in the deciduous teeth the cement varies from a thin film on the outer walls and none in the fossettes to a moderately thick external coating and a thin film in the fossettes. The following maximum crown heights were measured from the roots to the notch between the paracone and metacone cusps:  $Dm^3$ , approx. 16 mm.;  $Dm^4$ , approx. 17 mm.

*Lower permanent dentition.* A symphyseal section of the jaw with incisors and canines complete, C.I.T. no. 2836 (pl. 7, fig. 5), shows that the lower incisor teeth, like the uppers, are relatively long-crowned and have no sharp break between crown and root. As in the uppers, the grinding surface is characterized by deep cement-filled cups. The lower incisors differ from the upper in their more procumbent position, and their crowns are therefore not so sharply curved.

The lower canine is less curved than the upper. The root is circular in cross section. The piercing end of the tooth is flattened on the buccal as well as on the lingual side along the anterior and posterior edges. This gives the tooth the appearance of a central cone with anterior and posterior flanges.

$P_1$ , based on a single separate tooth, C.I.T. no. 2837 (pl. 7, fig. 1), is very small, with two rounded roots closely appressed. In an anteroposterior direction the tooth is pinched in where the crown and roots join. The crown is strongly compressed laterally, with sharp anterior and posterior edges.

Variation in the lower molariform teeth is illustrated by C.I.T. nos. 2834, 678, and 2842 (fig. 4, *f-h*, respectively). The stout premolars tend to be a little shorter anteroposteriorly and much wider transversely than the molars. In the molariform teeth the anteroposterior length of the metaconid-metastylid column is relatively great. The values for the ratio metaconid-metastylid length to anteroposterior length for  $P_3$  through  $M_2$  range from 0.35 to 0.53, and the mean value for each of these teeth falls between 0.41 and 0.45.

*Measurements (in millimeters) and ratios of measurements*

AP, anteroposterior length of tooth.

MCS, anteroposterior length of metaconid-metastylid column.

M/A, ratio of MCS to AP.

	Max. AP	Min. AP	Mean AP	Max. MCS	Min. MCS	Mean MCS	Max. M/A	Min. M/A	Mean M/A
P <sub>2</sub> (separate) . . . . .	25.5	21.8	24.0	6.7	5.0	5.9	0.28	0.20	0.243
P <sub>3</sub> (in place) . . . . .	24.2	21.4	23.2	11.2	8.5	9.9	0.48	0.35	0.429
P <sub>3</sub> and P <sub>4</sub> (separate) . . . . .	25.0	20.5	22.8	11.8	8.4	10.2	0.53	0.38	0.448
P <sub>4</sub> (in place) . . . . .	25.2	20.3	23.1	11.5	8.8	10.3	0.50	0.37	0.444
M <sub>1</sub> (separate) . . . . .	25.0	19.3	22.6	10.5	8.0	9.3	0.49	0.36	0.413
M <sub>2</sub> (separate) . . . . .	26.4	19.5	22.9	11.0	7.7	9.5	0.46	0.36	0.417
M <sub>3</sub> (separate) . . . . .	27.5	24.0	26.1	8.7	6.5	7.7	0.33	0.26	0.294

In P<sub>2</sub> the metaconid occasionally stands as a small separate column half-way between the metastylid and parastylid. In such cases the anteroposterior diameter across the metaconid and metastylid column is much greater than it is when the two are joined into one column, and the mean ratio of metaconid-metastylid length to anteroposterior length becomes 0.36.

The gutter on the inner wall of the metaconid-metastylid column is sharply incised to rounded. Though the gutter disappears with wear, it is always of pronounced depth in unworn teeth. P<sub>2</sub> characteristically has a small gutter and a metastylid which is often more highly developed than the metaconid. In all other teeth the metaconid surpasses the metastylid in size. The posterior lobe of M<sub>3</sub> is greatly extended.

The parastylid swings inward lingual to a plane tangent to the lingual side of the metaconid-metastylid column.

The entoconid may be in any form from triangular (often indented) to rounded to almost rectangular, but is generally rounded and strongly inflated.

The posterior extension of the entostylid, though commonly strong in unworn teeth and especially strong in the molars, varies considerably from one tooth to another. With increased wear the entostylid decreases in size.

The external walls of the protoconid and hypoconid are strongly curved in unworn teeth. One or two unworn teeth and a few worn teeth in the collection show a slight tendency toward flattening of the outer walls of these cusps. The sharp, deep V of the valley between the cusps generally points anteriorly. With wear the valley becomes more shallow and open.

As in the upper dentition, the lower teeth sometimes have little or no cement on the external walls, but most of the teeth would be characterized as moderately to heavily cemented.

The anteroexternal fold is present on more than 75 per cent of the lower teeth. It rarely appears in teeth less than one-fourth or more than three-fourths worn.

As in the upper cheek teeth, the shape of the occlusal surface varies primarily with the stage of wear of the tooth. Measurements on loose unworn teeth and on worn teeth in the jaw yielded the following results:

*Ratios of anteroposterior diameter to transverse diameter in lower teeth*

	Unworn teeth			Worn teeth
	Minimum	Maximum	Average	Average
P <sub>2</sub> . . . . .	1.81	2.26	2.01	....
P <sub>3</sub> and P <sub>4</sub> . .	1.60	1.98	1.76	1.57
M <sub>1</sub> . . . . .	1.93	2.50	2.23	1.47
M <sub>2</sub> . . . . .	2.04	2.60	2.36	1.81
M <sub>3</sub> . . . . .	2.46	3.27	2.90	....

The extent of plication of the enamel walls of the lower cheek teeth is very slight, hence the pattern would be termed simple.

On unworn teeth the maximum crown height is greater than in any merychippine previously recorded. In C.I.T. no. 2862 (pl. 7, fig. 3), the crown height of P<sub>1</sub> is 8.5 mm.; P<sub>2</sub>, 32 mm.; P<sub>3</sub>, 47 mm.; P<sub>4</sub>, 47 mm.; M<sub>1</sub>, 41 mm.; M<sub>2</sub>, 38 mm.; M<sub>3</sub>, 38 mm. These measurements were made on loose unworn teeth and on unerupted teeth in the mandible. The measuring points were taken as the notch between the roots on the external side and the notch between the metaconid and metastylid cusps.

*Lower deciduous dentition.* The incisors are large, deeply cupped, and uncemented. A symphyseal section of a newborn foal, C.I.T. no. 2838, bearing only the first incisors and canines, reveals that D<sub>c</sub> is flattened on the inner side. Dm<sub>1</sub>, C.I.T. no. 660, left ramus, appears as a small peglike tooth.

In the molariform deciduous teeth C.I.T. no. 656 (pl. 7, figs. 2, 2a), the ratio metaconid-metastylid length to anteroposterior diameter of the tooth is very constant. This constancy probably arises from the shortness of crown, which does not permit much variation with crown height. The ratio metaconid-metastylid length to anteroposterior diameter for Dm<sub>2</sub> ranges from 0.36 to 0.39 mm.; for Dm<sub>3</sub>, 0.45 to 0.50 mm.; for Dm<sub>4</sub>, 0.42 to 0.45 mm. These ratios for Dm<sub>3</sub> and Dm<sub>4</sub> correspond closely to similar ratios determined for the permanent premolars P<sub>3</sub> and P<sub>4</sub>. The ratio for Dm<sub>2</sub> is higher than all ratios for normal P<sub>2</sub>, although it is identical with the ratio determined for the second premolars in which the metaconid stands as a separate column from the metastylid.

In Dm<sub>3</sub> and Dm<sub>4</sub> the metaconid-metastylid column has about the same strength as it has in P<sub>3</sub> and P<sub>4</sub>. It is normally stronger, however, in Dm<sub>2</sub> than in P<sub>2</sub>.

The gutter on the inner wall is sharply incised and of about equal depth for all three deciduous molars, hence the gutter in Dm<sub>2</sub> is relatively much deeper than that in P<sub>2</sub>.

As in permanent premolars, the metastylid in Dm<sub>2</sub> is more highly developed than the metaconid, but the reverse is true of Dm<sub>3</sub> and Dm<sub>4</sub>. In contrast with the entoconid in permanent teeth, that in milk teeth is triangular to strongly indented. Only after considerable wear does it appear rounded. In Dm<sub>2</sub> and Dm<sub>3</sub> the entostylid is strong and is sharply curved lingually. In Dm<sub>4</sub> the very strong entostylid projects posteriorly with only a slight inward curvature. The strongly curved external walls show no flattening. The enamel shows a

distinctively finely fluted surface. The very deep valley between protoconid and hypoconid points anteriorly. Though a few of the teeth lack cement almost completely, most of them are thinly coated with it, and some might be termed moderately cemented. The anteroexternal fold is very well developed toward the base of the crown in  $Dm_3$  and  $Dm_4$ . It is slightly to moderately developed in  $Dm_2$ . In approximately two-thirds of the milk teeth in the collection, the external tubercle between protoconid and hypoconid is moderately developed to well developed. Lacking cement to round it off, the occlusal surface is very rough, even sharp-pointed in an unworn stage. Variations in shape of crown may be expressed by ratios between the anteroposterior diameter and the transverse diameter. These ratios vary in  $Dm_2$  from 1.98 to 2.31; in  $Dm_3$ , from 1.69 to 1.90; in  $Dm_4$ , from 1.74 to 2.05.

The enamel pattern of the lower milk molars is simple. The maximum crown height is as follows:  $Dm_1$ , 5 mm.;  $Dm_2$ , 16 mm.;  $Dm_3$ , 18 mm.;  $Dm_4$ , 22 mm. The measurements were made on unworn milk teeth. The measuring points were taken on the posteroexternal face of the tooth from the base of the hypoconid to the crest of the hypoconid cusp.

*Comparative measurements (in millimeters) of dentition of Merychippus calamarius*

	C.I.T. no. 2839	C.I.T. no. 669	C.I.T. no. 1311	C.I.T. no. 2840	C.I.T. no. 2841	Type specimen Santa Fe
Upper dentition:						
Length of series $P^2-M^3$ . . .	....	135	133	142	134	129.0
Length of series $P^2-P^4$ . . .	76.6	73.5	71.3	74.7	71.7	67.8
Length of series $M^1-M^3$ . . .	....	61.4	61.9	67.2	61.9	61.0
$P^1$ , anteroposterior diameter	14.9	13.5	....	....	....	....
$P^1$ , transverse diameter . .	8.4	7.2	....	....	....	....
$P^2$ , anteroposterior diameter	29.3	27.5	27.0	27.0	27.4	25.0
$P^2$ , transverse diameter . .	16.9	17.5	17.4	18.2	17.9	17.8
$P^3$ , anteroposterior diameter	24.0	23.0	22.0	24.1	22.3	21.5
$P^3$ , transverse diameter . .	20.0	20.5	20.0	20.5	22.1	21.0
$P^4$ , anteroposterior diameter	23.3	23.0	22.3	23.6	22.0	21.0
$P^4$ , transverse diameter . .	21.0	21.9	21.1	21.5	22.8	20.5
$M^1$ , anteroposterior diameter	21.0	19.7	19.8	21.2	20.7	19.4
$M^1$ , transverse diameter . .	19.6	21.4	20.8	21.8	24.2	19.6
$M^2$ , anteroposterior diameter	22.5	21.2	19.8	23.0	21.2	21.2
$M^2$ , transverse diameter . .	20.5	21.6	21.3	21.8	24.2	18.9
$M^3$ , anteroposterior diameter	....	20.5	22.3	23.0	20.0	19.1
$M^3$ , transverse diameter . .	....	17.9	20.1	19.0	21.4	17a
$I^1$ , greatest diameter . . .	13.4	13.5	11.5			
$I^1$ , least diameter . . . . .	8.1	8.0	8.0			
$I^2$ , greatest diameter . . .	13.8	14.5	13.6			
$I^2$ , least diameter . . . . .	7.0	7.3	7.8			
$I^3$ , greatest diameter . . .	11.7	13.6	11.4			
$I^3$ , least diameter . . . . .	5.8	6.3	6.4			
C, greatest diameter . . . .	10a	10.7	10.1			
C, least diameter . . . . .	....	7.0	7.3			
Diastema, $I^3-C$ . . . . .	23.0	19.0	21.9			
Diastema, $C-P^1$ . . . . .	27.5	31.3	....			

a, approximate.

*Continued on next page*

*Comparative measurements - Continued*

	No. 2834	No. 2842	No. 678	No. 2837	Type
Lower dentition:					
Length of series $P_2-M_3$ . . . . .	144	140	132*	....	....
Length of series $P_2-P_4$ . . . . .	73.4	70.2	67	....	....
Length of series $M_1-M_3$ . . . . .	70.6	69.4	65*	....	....
$P_1$ , anteroposterior diameter . . . . .	....	....	....	8.7	....
$P_1$ , transverse diameter . . . . .	....	....	....	5.0	....
$P_2$ , anteroposterior diameter . . . . .	24.6	24.4	22.9	....	....
$P_2$ , transverse diameter . . . . .	11.6	11.5	11.8	....	....
$P_3$ , anteroposterior diameter . . . . .	23.2	22.9	22.8	....	20.0
$P_3$ , transverse diameter . . . . .	13.6	12.8	14.5	....	13.2
$P_4$ , anteroposterior diameter . . . . .	24.3	23.1	20.3	....	21.4
$P_4$ , transverse diameter . . . . .	14.7	13.7	14.7	....	12.7
$M_1$ , anteroposterior diameter . . . . .	21.4	22.0	21.0	....	19.5
$M_1$ , transverse diameter . . . . .	12.8	11.5	12.0	....	10.5
$M_2$ , anteroposterior diameter . . . . .	21.3	23.3	20.0	....	18.6
$M_2$ , transverse diameter . . . . .	12.3	10.0	11.0	....	....
$M_3$ , anteroposterior diameter . . . . .	27.7	26.0	20.8*	....	24.8
$M_3$ , transverse diameter . . . . .	10.9	9.7	9.7	....	8.9
No. 2836					
$I_1$ , greatest diameter . . . . .	....	....	....	11.3	
$I_1$ , least diameter . . . . .	....	....	....	8.0	
$I_2$ , greatest diameter . . . . .	....	....	12.4	12.8	
$I_2$ , least diameter . . . . .	....	....	7.8	7.5	
$I_3$ , greatest diameter . . . . .	....	....	....	12.3	
$I_3$ , least diameter . . . . .	....	....	....	6.7	
$C$ , greatest diameter . . . . .	8.8	....	....	8.8	
$C$ , least diameter . . . . .	7.0	....	....	6.8	
Diastema, $C-P_2$ . . . . .	42	....	49	....	

\*Measurement does not include posterior lobe of  $M_3$ .

	No. 2843	No. 2844
Upper milk dentition:		
Length of series $Dm_2-Dm_4$ . . . . .	82.5	80.3
$Dm^1$ , anteroposterior diameter . . . . .	....	12.0
$Dm^1$ , transverse diameter . . . . .	....	7.0
$Dm^2$ , anteroposterior diameter . . . . .	34.0	30.5
$Dm^2$ , transverse diameter . . . . .	19.0	18.2
$Dm^3$ , anteroposterior diameter . . . . .	23.7	22.9
$Dm^3$ , transverse diameter . . . . .	21.7	21.4
$Dm^4$ , anteroposterior diameter . . . . .	25.0	24.5
$Dm^4$ , transverse diameter . . . . .	21.4	21.7
$Di^1$ , greatest diameter . . . . .	....	12.7
$Di^1$ , least diameter . . . . .	....	5.2
$Di^2$ , greatest diameter . . . . .	....	11.5
$Di^2$ , least diameter . . . . .	....	5.1
$Di^3$ , greatest diameter . . . . .	....	9.7
$Di^3$ , least diameter . . . . .	....	4.7
No. 656      No. 660		
Lower milk dentition:		
Length of series $Dm_2-Dm_4$ . . . . .	82.4	77.3
$Dm_1$ , anteroposterior diameter . . . . .	....	3a
$Dm_1$ , transverse diameter . . . . .	....	4a
$Dm_2$ , anteroposterior diameter . . . . .	29.9	26.6
$Dm_2$ , transverse diameter . . . . .	13.8	12.4

a, approximate.

## Comparative measurements - Continued

Lower milk dentition - continued:	No. 656	No. 660
Dm <sub>3</sub> , anteroposterior diameter . . . . .	24.6	24.0
Dm <sub>3</sub> , transverse diameter . . . . .	14.0	14.2
Dm <sub>4</sub> , anteroposterior diameter . . . . .	26.6	25.9
Dm <sub>4</sub> , transverse diameter . . . . .	13.3	13.5
D <sub>11</sub> , greatest diameter . . . . .	12.3	
D <sub>11</sub> , least diameter . . . . .	5.5	
D <sub>12</sub> , greatest diameter . . . . .	12.3	
D <sub>12</sub> , least diameter . . . . .	5.2	
D <sub>13</sub> , greatest diameter . . . . .	9.0	
D <sub>13</sub> , least diameter . . . . .	5.5	

*Relationships.* Unfortunately the neighboring Esmeralda localities (Stirton, 1936, p. 183) contain very scant protohippine remains. Of these only an M<sub>3</sub>, U.C. no. 19825 (Merriam, 1916a, pp. 187-188, fig. 21), offers diagnostic characters which approach those of *Merychippus calamarius*. The occlusal surface of this tooth is short. The anteroposterior diameter of the metaconid-metastylid column and of the posterior lobe are relatively much shorter than the corresponding features in third molars from Tonopah. The relative transverse width of the posterior lobe of M<sub>3</sub> surpasses that in *M. calamarius*. The inflation of the entoconid and absence of an anteroexternal fold in this instance seem to signify little as to the evolutionary stage of the tooth. The crown height of 36 mm. may be considered extremely great for a merychippine tooth as worn as this one is. In summary, the strong development of the third lobe and the relatively great height of crown may be taken as evidence that this specimen, U.C. no. 19825, probably belongs to a primitive form of the genus *Protohippus* or *Pliohippus*. Merriam (1916a, p. 188) stated that the tooth "represents a protohippine horse of approximately the stage of evolution seen in the form of *Merychippus* near *calamarius* of the Barstow fauna." To the author the tooth appears to be more advanced than *M. calamarius*, though its geologic age relative to the Tonopah merychippine horses cannot be stated with any surety.

*Merychippus intermontanus* Merriam (1915, 1919) from the Barstow fauna falls within the size limits of the largest individuals from Tonopah. A simple enamel pattern and early attachment of the protocone distinguish the upper cheek teeth and milk dentition from those of *M. calamarius*. None of the lower teeth of *M. intermontanus* carries the anteroexternal fold which develops so commonly in lower cheek teeth of *M. calamarius*.

Though the upper cheek teeth of *Merychippus sumani* Merriam (1911a, 1915, 1919) from the Barstow show a complexity of enamel pattern equal to that of *M. calamarius*, they are considerably smaller.

*Merychippus calamarius stylodontus* Merriam (1915, 1919) from the Barstow fauna closely approximates the Tonopah form in size, although the latter is larger. Furthermore, the enamel pattern of the Tonopah form is slightly more complex than that of the Barstow form. Merriam states (1919, p. 484) that *M. calamarius stylodontus* differs from the typical *M. calamarius* "in

relative simplicity of enamel folds of the walls bordering the fossettes. . . . It is considerably smaller than the typical form and the crowns seem narrower. The apparent difference in width may be due in part to differences in stages of wear of specimens compared, or to method of measurement." The author wishes to point out that the measurements previously recorded (Cope, 1877, p. 322; Merriam, 1919, p. 489) for *M. calamarius* obviously do not correspond to measurements made on the original plate (Cope, 1877, pl. 75, fig. 1). Thus discounting the question of width, it becomes apparent that *M. calamarius stylodontus* differs from the type *M. calamarius* in precisely the same manner as it does from the Tonopah merychippine species.

The teeth of the type *Merychippus calamarius* (Cope, 1875) from the Santa Fe do not differ from those of its equivalent from Tonopah in any important character. The upper teeth of the Santa Fe type may be described as slightly smaller and slightly more complex than typical Tonopah specimens. The lower teeth from Santa Fe show a relatively smaller posterior lobe in  $M_3$  and they do not carry any anteroexternal fold.

Plication	Tonopah	Santa Fe
P11 caballin . . . . .	Generally single	Single or double
P11 protoloph . . . . .	Single, rare	Single, rare
P11 protoconule on P <sup>2</sup> . . . . .	Absent	Present
on other teeth . . . . .	Single	Single
P11 prefossette on P <sup>2</sup> . . . . .	Single	Single
on other teeth . . . . .	Generally single	Double to quadruple
P11 postfossette . . . . .	Double or triple	Double or triple
P11 hypostyle . . . . .	Absent or single	Single or double

The material from Quatal Canyon (Gazin, 1930) which was designated *Merychippus sumani* Merriam suggests but does not approach *M. calamarius*. The upper teeth from Quatal Canyon are smaller, less cemented, and lower-crowned than those of *M. calamarius*. The lower teeth in the Quatal Canyon collection differ from *M. calamarius* in having a more shallow inner gutter, a deeper, more rounded external valley, and a smaller posterior lobe on  $M_3$ .

No teeth from the Mint Canyon fauna (Maxson, 1930; Stirton, 1933) approach those of *M. calamarius* in appearance.

The Ricardo species *Plihippus tantalus* Merriam, U.C. no. 19434 (1913c, fig. 4; 1919, fig. 189), and *Plihippus fairbanksi* Merriam, U.C. no. 19789 (1915, fig. 8; 1919, fig. 185), have both larger and higher-crowned teeth than does *Merychippus calamarius*. *Plihippus* near *mirabilis* (Leidy), U.C. no. 21323 (Merriam, 1919, fig. 188), is of about the same size as *M. calamarius*, but its enamel pattern is simpler and the tooth crown appears to be higher.

None of the protohippine horses of the Great Plains region approaches very closely *M. calamarius* from Tonopah. The bulk of the Equidae from the Snake Creek was at first tentatively referred to *Merychippus* cf. *insignis* Leidy (Matthew and Cook, 1909). Later, when the formation was divided into zones,

90 to 95 per cent of the Equidae from the Lower Snake Creek were referred to *Merychippus paniensis* Cope (Matthew, 1924). The type for *M. insignis* consists of  $Dm^2$  and  $Dm^3$ . These teeth differ from *M. calamarius* in being noticeably smaller and in lacking cement. The type *M. paniensis* is smaller and relatively low-crowned, though Matthew does state that some of the specimens in the fauna are as large and progressive as *M. calamarius*.

Among the Niobrara River (*sensu* McGrew and Meade, 1938) protohippines in the undescribed collections of the University of California, *Merychippus insignis* appears much smaller and perhaps more primitive than *M. calamarius*. A second species represented by U.C. no. 33068 (perhaps *M. republicanus*) differs in its constant protoconal separation, smaller size, and slightly more complex enamel pattern. A third species, which may represent *M. perditus*, appears longer-crowned and shows definite connection between protocone and protoconule at a very early stage of wear.

*Pliohippus supremus*, U.C. no. 32285, from the Burge (McGrew, 1938) is somewhat similar to *M. calamarius* in size and in enamel pattern, but it is longer-crowned and the protocone becomes attached at a much earlier stage of wear. Teeth of *Pliohippus pernix*, U.C. no. 32501, are larger and simpler than those of *M. calamarius*, and display an attachment of the protocone at an earlier stage of wear.

#### Comparative Osteology of Hypohippus and Merychippus

*Skeletal parts.* For the sake of convenience in discussion, the skeletal elements of *Merychippus calamarius* and *Hypohippus near affinis* are described together. Very few of the larger bones have been preserved completely. The hypohippine material occurs in a poorer state of preservation and specimens are much less abundant than those of the merychippine type. The ratio of frequency of occurrence is 2 to 10 merychippine elements to every one of *Hypohippus*.

For the most part, the skeletal material resembles that of *Equus* very closely in all features except size. Only those differences from *Equus* which appear in form and in the proportions of elements are described below at some length.

*Scapula.* In this element of the shoulder girdle the spine differs from that of *Equus* in its downward slope toward the neck without suggestion of an acromion.

#### Measurements (in millimeters) of scapula

	<i>Merychippus</i> C.I.T. no. 759	<i>Hypohippus</i> C.I.T. no. 2888
Anteroposterior diameter from tuber to posterior border of glenoid cavity . . . .	68	77.5
Transverse diameter across glenoid cavity .	40	49
Anteroposterior diameter across glenoid cavity . . . . .	44	56

*Humerus.* The head of the humerus is similar to that in *Equus*. In every other feature the humerus of *Merychippus* (fig. 5) differs from that of the modern horse. The bicipital groove is single, not double as in *Equus*. The anterior part of the lateral tuberosity is strongly produced so as to curve medially, and overhangs the bicipital groove. A large inner tuberosity extends posteriorly toward the articular surface of the head. The comparatively slender shaft is twisted. As compared with the corresponding feature in *Equus*, the deltoid ridge is inconspicuous and localized, having no crests extending out from it. The lateral condyloid crest is moderately developed. The coronoid fossa is not so deep as in *Equus*. The medial condyle is large and tapers from the medial border toward the synovial fossa. The lateral condyle is much smaller than the medial one, and medially is characterized by a low, rounded ridge. The lateral part of the lateral condyle is cylindrical rather than conical on its bearing surface. The forms of the medial and lateral condyles give the distal extremity a much more pronounced appearance of obliquity than is characteristic of *Equus*.

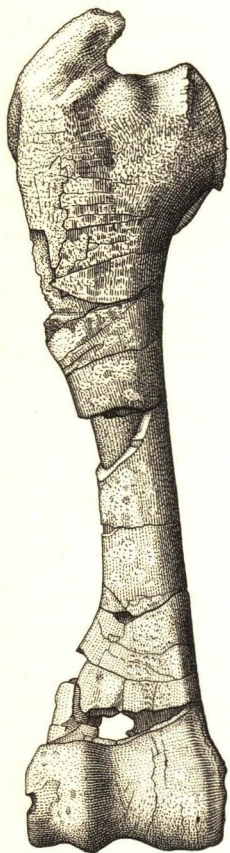


Fig. 5. *Merychippus calamarius* (Cope).  
Right humerus, no. 2863,  
anterior view.  $\times 0.5$ .

Calif. Inst. Tech.  
Vert. Pale. Coll.  
Upper Miocene, Tonopah,  
Nevada

In all these characters in which the humerus of *Merychippus* differs from that of *Equus*, it shows a strong similarity to that of a Recent artiodactyl such as the ox.

In the later evolution of the horses from the merychippine stock there has developed in the humerus a double bicipital groove with a median convexity (Osborn, 1930, p. 754; Scott, 1895, p. 101). The curved and overhanging prominence of the anterior part of the lateral tuberosity has been subdued and finally lost. The deltoid ridge and its accompanying proximal and distal crests have become strongly developed.

Only the distal ends of several humeri of *Hypohippus* are available in the Tonopah collections. These differ from the merychippine type and approximate closely in form the humerus of *Equus*. The lateral condyloid crest is fairly well developed. The medial condyle does not taper so strongly as it does in *Merychippus*, yet it is not quite so gently tapering as in *Equus*. The lateral condyle is marked by a pronounced shallow groove and is conical, increasing in diameter toward the lateral border as in *Equus*. The distal extremity of the humerus differs from that of *Equus* in having a rounded border at the median side of the medial condyle, whereas in *Equus* the bearing surface of this condyle is separated from the median border by a very sharp angular break.

*Measurements (in millimeters) of humerus*

	<i>Merychippus</i> C.I.T. no. 2863	<i>Hypohippus</i> C.I.T. no. 2889
Total length . . . . .	223	...
Smallest diameter of shaft:		
Anteroposterior . . . . .	27	...
Transverse . . . . .	22	...
Transverse diameter, proximal end . . . . .	62	...
Transverse diameter, distal end . . . . .	52	61

*Radius.* The humeral articular surface as well as the distal end of the radius of *Merychippus* differs from that of *Equus* in being proportionally narrower transversely. The sagittal ridge of the proximal end is a little more pronounced than it is in *Equus*. The dorsal surface of the shaft is strongly curved but the volar surface is flat.

*Measurements (in millimeters) of radius*

	<i>Merychippus</i> C.I.T. nos. 2864, 2865	<i>Hypohippus</i> C.I.T. no. 1308
Total length . . . . .	227	265a
Proximal end, anteroposterior diameter . . . . .	27.0	33.5
Proximal end, transverse diameter . . . . .	50.0	59.0
Distal end, anteroposterior diameter . . . . .	27.0	32.0
Distal end, transverse diameter . . . . .	44.5	49.5

a, approximate.

*Ulna.* Only fragments of the proximal end of the ulna are preserved. The structural characters of the proximal end are similar to those in the corresponding parts of the ulna in *Equus*.

*Carpus.* The scaphoid does not differ markedly from that of *Equus*. In the merychippine form this element has rounder articular surfaces and more concave borders. The lunar resembles that of *Equus* very closely. The proximal articular surfaces of the cuneiform are relatively farther apart than in *Equus*. These surfaces are always distinct from each other, with a nonarticular area between them. The anterior proximal articular surface and the distal articular surface are relatively narrower than those of *Equus*. The pisiform is longer anteroposteriorly than in *Equus*. It has two distinct surfaces for articulation with the cuneiform and one surface which articulates with the ulnar part of the fore-leg bone. The trapezium was not preserved. The trapezoid is a wedge-shaped bone with less articulating surface than in *Equus*. It never has a posterior facet for articulation with the magnum. It may or may not bear a posterior facet for articulation with the trapezium. The magnum is much narrower transversely than the corresponding bone in *Equus*. The unciform resembles that of *Equus*. The posterior surface for articulation with the magnum, however, is smaller than in the modern horse. A small posterior articular surface for metacarpal V is usually present.

In summary, the carpal bones of *Merychippus* and *Hypohippus* differ but little from each other in shape and proportions. In the course of evolution

from *Merychippus* to *Equus* the carpals were shortened anteroposteriorly, widened transversely, and flattened proximodistally.

*Measurements (in millimeters) of carpals*

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. nos. 2866-2872			C.I.T. nos. 2890-2896		
	AP	Tr	PD	AP	Tr	PD
Scaphoid . . . . .	26.0	17.5	19.7	29.3	20.0	23.6
Lunar . . . . .	24.1	19.4	19.0	27.0	19.7	23.0
Cuneiform . . . . .	24.0	11.2	15.0	32.5	15.3	20.0
Pisiform . . . . .	31.4	7.6	20.9	35e	8.0	22
Trapezoid . . . . .	12.9	12.5	12.4	15.6	14.0	16.0
Magnum . . . . .	23.9	25.2	16.5	30.3	30.0	19.7
Unciform . . . . .	18.5	11.7	16.2	22.4	12.2	20.4

e, estimated.

*Metacarpus*. The proximal end of metacarpal III in both *Merychippus* and *Hypohippus* is not so broad as in *Equus*. For both Miocene types the angle between the magnum and unciform articular facets varies from  $107^{\circ}$  to  $120^{\circ}$  and averages  $116^{\circ}$  (cf.  $160^{\circ}$  in *Equus*). *Merychippine* metacarpal III is broadly grooved on its volar surface between the rough areas for attachment of the lateral metacarpals. The volar groove appears deeper in *Hypohippus*. In both *Merychippus* and *Hypohippus* the keel on the distal articular surface of metacarpal III is strong posteriorly, but weak to totally absent on the anterior surface. In *Equus* this keel is strong all the way around.

Lateral metacarpals II and IV are well developed in both *Merychippus* and *Hypohippus* (pl. 8). The hypohippine side metacarpals are readily distinguished from the more slender merychippine forms by their massiveness. In both genera metacarpal II bears a facet for articulation of the trapezium. On the posterior side of its proximal end, metacarpal IV carries a small facet for the articulation of metacarpal V. Below this small facet and parallel to the main axis of the metacarpus is a broad, flat, slightly roughened area against which lay metacarpal V.

*Measurements (in millimeters) of metacarpus*

AP, anteroposterior diameter.

Tr, transverse diameter.

These measurements were made on mounted specimens. The approximations are controlled by measurements of unmounted specimens of the same general size.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. no. 2854 (1)			C.I.T. no. 2856 (2)		
	II	III	IV	II	III	IV
Metacarpal . . . . .	II	III	IV	II	III	IV
Length . . . . .	153	163	147	177a	192	173a
Proximal end, AP . . . . .	12	19	14	13	22	15
Proximal end, Tr . . . . .	9	26	10	12	28	13

a, approximate.

## Measurements of metacarpus - Continued

	<i>Merychippus</i> C.I.T. no. 2854 (1)			<i>Hypohippus</i> C.I.T. no. 2856 (2)		
Distal end, AP . . . . .	15	20	15	18	22	19
Distal end, Tr . . . . .	8	25.5	7	11	27.5	11
Least dimensions of shaft:						
AP . . . . .	7	14	8	12	15	12.5
Tr . . . . .	6	18	4	6	22	6

(1) *Merychippine* metacarpal III varies in length between 160 and 186 mm., and averages about 180 mm. long. Hence, this mounted specimen (C.I.T. no. 2854) is much smaller than the average for the Tonopah collection.

(2) *Hypohippine* metacarpal III varies in length from 183 to 192 mm., and averages 186 mm. The mounted specimen (C.I.T. no. 2856) is therefore larger than the average.

*Pelvis.* The acetabulum is the only part of the pelvic girdle which has been preserved. The *merychippine* acetabulum appears to resemble closely that of *Equus*. A single *hypohippine* acetabulum appears to be deeper and more nearly hemispherical than the others.

## Measurements (in millimeters) of acetabulum

	<i>Merychippus</i> C.I.T. no. 2874	<i>Hypohippus</i> C.I.T. no. 2898
Anteroposterior diameter . . . . .	42.0	46.5
Transverse diameter . . . . .	33.0	46.8

*Femur.* No complete femora are preserved in the collection. The proximal and distal ends of the femur of *Merychippus* closely resemble those of *Equus*. The shaft of the femur is proportionately more slender than in *Equus*, but the lesser trochanter and the third trochanter are well developed.

A distal end of a *Hypohippus* femur shows a trochlea proportionately much narrower than in *Equus*. The lateral condyle of the femur in *Hypohippus* is much larger than the medial condyle, whereas in *Equus* the lateral condyle is only slightly larger.

## Measurements (in millimeters) of femur

	<i>Merychippus</i> C.I.T. no. 2875	<i>Hypohippus</i> C.I.T. no. 2899
Length, estimated . . . . .	275	....
Distal end, transverse diameter . . . . .	61.5	76.5

*Tibia.* The tibia of *Merychippus* closely resembles that of *Equus* throughout. The shaft is slightly larger than that of *Equus* in proportion to the size of the extremities. The articular grooves of the distal end are slightly deeper and sharper in the tibia of *Merychippus*.

The distal end of a *hypohippine* tibia resembles that of *Equus* in every feature except a proportionately broader intermediate ridge on the articular surface.

*Measurements (in millimeters) of tibia*

	<i>Merychippus</i> C.I.T. no. 754	<i>Hypohippus</i> C.I.T. no. 2900
Length . . . . .	283	....
Distal end, transverse diameter . . . . .	45	57

*Patella.* Patellae of *Merychippus* and *Hypohippus* resemble that of *Equus*, except that the base is slightly more produced and the medial angle is less produced. These proportions give the bone the appearance of an elongate rhomb, when viewed from the front, rather than that of a square as in *Equus*.

*Measurements (in millimeters) of patella*

	<i>Merychippus</i> C.I.T. no. 2876	<i>Hypohippus</i> C.I.T. no. 2901
Anteroposterior diameter . . . . .	25	28a
Transverse diameter . . . . .	41	45a
Proximal-distal diameter . . . . .	46	55a

a, approximate.

*Tarsus.* A deep, narrow groove bordered by narrow, high ridges characterizes the trochlea of a merychippine astragalus, in which respect the principal element of the tarsus resembles that in *Equus*. The hypohippine astragalus, in contrast, has a trochlea with broad, shallow groove bounded by low, wide ridges. The merychippine astragalus further resembles that of *Equus* in having on the navicular facet a well defined nonarticular depression, which is either poorly represented or entirely absent in the hypohippine astragalus.

In the merychippine calcaneum, and to a lesser extent in the hypohippine, there is a deeper groove between the tuber calcis (proximal part of the body) and the sustentaculum tali (medial process) than in *Equus*. The articular facet for the cuboid is slightly more steeply inclined upward and backward than the corresponding facet in *Equus*.

The astragalar facet of the navicular has a shallow nonarticular depression in the merychippine form and no depression in the hypohippine. Only 1 specimen in more than 60 naviculars of *Merychippus* has a surface for articulation with the calcaneum. This articulation occurs commonly in *Equus*. On the distal surface there is no nonarticular groove separating the two surfaces of articulation for the ectocuneiform. Likewise on the distal surface there is no nonarticular groove between the ecto- and mesocuneiform surfaces. Both of these grooves are commonly found in naviculars of *Equus*. Finally, in *Merychippus* the ento-mesocuneiform surface is continuous and rounded, not broken by an angle as in *Equus*. The fused ento-mesocuneiform bone in *Merychippus* and *Hypohippus* differs little from that in *Equus*.

In only 3 out of 42 merychippine ectocuneiform bones does the nonarticular groove completely cross the proximal surface. The distal nonarticular groove may vary in shape, but is never large as in *Equus*. Both these nonarticular grooves are far less developed in *Hypohippus* than in *Merychippus*. The proximal

posterior articulation for the cuboid appears to make a fairly constant angle with the proximal posterior articulation for the navicular in any given type of horse. Large series of measurements yield the following values: *Merychippus*  $100^{\circ}$ , *Hypohippus*  $105^{\circ}$ , and *Equus*  $110^{\circ}$ .

The cuboid of *Merychippus* differs from that of *Equus* in having the anterior surface for articulation with metatarsal IV relatively larger than the facet for metatarsal III. The posterior lateral surfaces for articulation with the navicular and ectocuneiform make a prominence which projects inward from the middle of the medial surface. In *Equus* this prominence lies near the posterior end of the medial surface. The cuboid of *Hypohippus* is shorter anteroposteriorly and more cuboid in shape than that of either *Merychippus* or *Equus*. Furthermore, all the articular surfaces on the hypohippine cuboid appear larger, especially the facet for metatarsal IV. In the cuboid bone of both *Merychippus* and *Hypohippus* the tuberosity for attachment of the plantar ligament is much larger than in *Equus*.

Measurements (in millimeters) of tarsals

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. nos. 2877-2882			C.I.T. nos. 2902-2907		
	AP	Tr	PD	AP	Tr	PD
Astragalus . . . . .	28	36	42	32	42	44
Calcaneum . . . . .	35	33	84	42	37	93
Navicular . . . . .	26	30	10	31	31	12
Ento-mesocuneiform . . . . .	11	25	14	15	29	18
Ectocuneiform . . . . .	24	27	10	29	31	11
Cuboid . . . . .	28	17	21	30	19	26

*Metatarsus.* In both *Merychippus* and *Hypohippus* the proximal end of metatarsal III presents a nearly circular anterior outline, in contrast with the oval outline in *Equus*. Whereas a facet for the articulation of the mesocuneiform is always present in metatarsal III of *Equus*, in *Merychippus* the facet appears in only 2 out of more than 70 specimens. On the other hand, this mesocuneiform facet seems to be present on all 7 well preserved hypohippine third metatarsals. In both *Merychippus* and *Hypohippus* the distal keel, though prominent on the posterior surface, dies away on the anterior surface. The transverse diameter of the distal end of metatarsal III is relatively much greater in *Hypohippus* than in *Merychippus*.

Lateral metatarsals II and IV are well developed in both *Merychippus* and *Hypohippus* (pl. 9). The merychippine side toes are much more slender than the hypohippine, especially near the distal end. The proximal end of metatarsal IV is very massive in both forms, and is characterized on the posterior side by a large sloping surface for the attachment of ligaments.

*Measurements (in millimeters) of metatarsus*

Ap, anteroposterior diameter.

Tr, transverse diameter.

These measurements were made on mounted specimens.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. no. 2855 (1)			C.I.T. no. 2857 (2)		
Metatarsal . . . . .	II	III	IV	II	III	IV
Length . . . . .	170	183	171	202	217	203
Proximal end, AP . . . . .	15	24	20	18	27	26
Proximal end, Tr . . . . .	8	26	12	11	32	12
Distal end, AP . . . . .	14	19	14	22	24	23
Distal end, Tr . . . . .	8	25	7	12	33	14
Least dimensions of shaft:						
AP . . . . .	6	16	5	13	18	15
Tr . . . . .	2.5	18	3	5	24	5

(1) *Merychippine* metatarsal III varies in length between 182 and 216 mm., and averages 202 mm. Hence, this mounted specimen (C.I.T. no. 2855), almost the smallest in the collection, is much smaller than the average.

(2) *Hypohippine* metatarsal III varies in length between 212 and 221 mm., and averages 216 mm. This mounted specimen (C.I.T. no. 2857) is a little larger than average.

*Phalanges*. Owing to the variation in growth stages represented by the equids in the collection, the phalanges show considerable variability in size and proportions. Since no phalangeal series were found in undoubted association with upper limb bones, it is deemed undesirable to make distinction between the phalanges of the fore limb and those of the hind limb.

Digit III: The first phalanx of *Merychippus* is proportionally more slender than that of *Equus*, especially at the distal end. *Hypohippine* phalanx I, notably in the shaft, is much more robust than that of *Equus*. In the case of both Tonopah equids the median groove of the proximal articulation becomes shallower and disappears anteriorly. In *Equus* the groove is strong anteriorly as well as posteriorly. A single abnormal *merychippine* first phalanx in the collection, C.I.T. no. 2884, bears large lateral tuberosities or spurs which apparently functioned as aggrandized eminences for attachment of the collateral ligament. The form is in all likelihood a sport.

The *merychippine* second phalanx is longer and more slender than that of *Equus*. Proportionally, the second phalanx of the *Hypohippus* approximates that of *Equus* in length and breadth, but falls short in thickness of the distal end.

The third or ungual phalanx of *Merychippus* tends to be more slender and pointed than that of *Hypohippus*. Both are longer and narrower than the third phalanx of *Equus*. In the Tonopah forms the articular surface continues out toward the wings to make a bell-shaped pattern, as compared with the semicircular shape of the corresponding element in *Equus*. In the Miocene equids the wings, or angles, were either not developed or not ossified to the extent that they are in *Equus*. A well marked terminal cleft characterizes the ungual phalanges

of both *Merychippus* and *Hypohippus*. The angle of inclination between the ground plane and the anterior slope of the phalanx ranges from  $33^{\circ}$  to  $35^{\circ}$  in the Miocene forms, in contrast with approximately  $50^{\circ}$  in *Equus*.

The proximal sesamoids differ little except in size from those of *Equus*. No distal sesamoids were found in the entire collection.

*Measurements (in millimeters) of digit III*

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

These measurements were made on individual specimens in the collection and represent average-sized adults.

	<i>Merychippus</i> C.I.T. nos. 2885-2887			<i>Hypohippus</i> C.I.T. nos. 2908-2910		
	AP	Tr	PD	AP	Tr	PD
Phalanx I . . . . .	...	...	42	...	...	43
Proximal end . . . . .	22.5	30	...	25	36	...
Distal end . . . . .	14	24	...	16	30	...
Least diameter of shaft . . . .	11.5	20	...	12.5	27.5	...
Phalanx II . . . . .	...	...	30	...	...	34
Proximal end . . . . .	19	30	...	21	35	...
Distal end . . . . .	15	26	...	17.5	33	...
Least diameter of shaft . . . .	12.5	22.5	...	14	29	...
Phalanx III . . . . .	37	37	24	41	40	25.5

Digits II and IV: The lateral phalanges are small and more variable in size than those of digit III. The hypohippine first phalanx is deeper proximally, much broader throughout, and slightly longer than that of *Merychippus*. The second phalanx of *Hypohippus* is longer and slightly larger than that of *Merychippus*. No lateral ungual phalanges are included in the collection.

*Measurements (in millimeters) of digits II and IV*

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

These measurements were made on individual specimens in the collection and represent average-sized adults.

	<i>Merychippus</i> C.I.T. nos. 2912-2913			<i>Hypohippus</i> C.I.T. no. 2911		
	AP	Tr	PD	AP	Tr	PD
Phalanx I . . . . .	....	....	24.5	....	....	25.5
Proximal end . . . . .	14.5	10.0	....	18.4	12.6	....
Distal end . . . . .	11.0	9.3	....	11.5	11.5	....
Phalanx II . . . . .	13.5	11.5	12.5			

RHINOCEROTIDAE

This family of the Perissodactyla is represented in the Tonopah fauna by relatively few specimens. The only well preserved material consists of first premolars followed by milk teeth in both upper and lower dentitions, along

with a few skeletal elements. Based upon the teeth, a population count of the rhinocerotids in the collection totals three individuals, one adult and two young. In the highly cristate pattern of its deciduous upper molars and in its retention of a large crested  $P^1$  and a large simple  $P_1$ , the Tonopah rhinocerotid appears distinct from any species previously described, and is designated as follows:

*Aphelops? cristalatus*, n. sp.

(Plate 10; text figure 6)

*Type specimen.* A part of the left maxillary, C.I.T. no. 2806 (pl. 10, fig. 1), and a part of the left mandible, C.I.T. no. 2807. Specimen 2806 includes an unworn  $P^1$  and slightly worn  $Dm^2$ - $Dm^4$ . All the teeth are in good condition except for the middle part of the anterior end of  $Dm^2$ , which has been lost. Specimen 2807 has the lower dentition which corresponds to that of the type maxillary, i.e., an unworn  $P_1$  and slightly worn  $Dm_2$ - $Dm_4$ . All are in good condition except  $Dm_2$ . No. 2807 was found in the same horizon and only 2 feet from the maxillary. Undoubtedly it represents the lower jaw of the same individual.

*Referred material.*  $Dm^2$  and  $Dm^3$ , C.I.T. no. 762 (pl. 10, fig. 2); part of a ramus, C.I.T. no. 2808, bearing  $Dm_2$  and  $Dm_3$ ; a ramus, C.I.T. no. 2809, with  $Dm_2$ - $Dm_4$  (pl. 10, fig. 3); tibia, fibula, calcaneum, two astragali, cuboid, three lateral metapodials, and a phalanx.

*Specific characters.*  $P^1$  large, only slightly reduced, bearing an internal crest and three transverse cristae. Upper deciduous molars with several cristae always present, very strong crochet and moderate to strong antecrochet, union of crochet and crista occurring almost always.  $P_1$  large, almond-shaped.  $Dm_2$  long, very narrow, no protoconid-hypoconid valley. Limbs and feet normally proportioned as in modern rhinoceroses, not shortened as in *Teleoceras*.

*Mandible.* The young mandible, nos. 2807 and 2809, is quite slender and has very little depth. Much of this lack of depth may be ascribed to the youth of the individual, but the character reflects in part a customary shallowness of jaw in *Aphelops*. In mandible no. 2809, the depth of the inner side normal to the alveolar border, posterior to  $Dm_4$ , is 53 mm.; height from lower border of angle to condyle, 146 mm.

*Upper dentition.*  $P_1^*$  is a small tooth with very simple crown consisting of an outer crest along the length of the tooth and a parallel inner crest which is restricted to the posterior part of the tooth. Three cristae run transverse to these crests. A large anterior crista and a small intermediate crista arise from the external crest, and the small posterior crista originates on the internal crest.

\*Since the crown is not yet fully erupted and the following milk molars show considerable wear, the tooth is considered a  $P^1$ . See Matthew, 1932, note on p. 423.

Dm<sup>2</sup>, a molariform tooth, is more elongate than the posterior deciduous teeth. The anterior border is diagonal and curved, giving the tooth an almost triangular outline. The outer wall is convex externally, and smooth except for a low style (parastyle fold) external to the paracone. The proto-loph remains separate from the ectoloph until a very advanced stage of wear is reached. At this advanced stage a connection tends to be made by means of the median crest as well as by the anterior crest which projects inward from the ectoloph. There is no antecrochet arising from the proto-loph; the prefossette is open. The relatively large metaloph is connected with the ectoloph. The metaloph bears a very strong crochet which joins the posterior crista from the ectoloph and closes off a median fossette. At least two small cristae from the ectoloph and one small crista from the crochet project into this median fossette. The postfossette is open. A low cingulum traverses the entire anterior, internal, and posterior border of the tooth. An internal tubercle, small to large in size, lies on the internal border of the tooth in the protocone-hypocone valley.

Dm<sup>3</sup> is wider transversely than Dm<sup>2</sup> and is larger and more nearly square in outline. The parastyle fold is much larger than in Dm<sup>2</sup> and relatively much farther forward because the parastyle is not so greatly produced anteriorly. The proto-loph is firmly joined to the ectoloph and bears a bulky, rounded, but short antecrochet. The metaloph, slightly smaller than the proto-loph, is firmly joined to the ectoloph by the posterior crista. A long relatively strong crochet folds forward from the metaloph. Union between the crochet and one of the two median cristae from the ectoloph is not consummated in one specimen, C.I.T. no. 2806, and only tenuously effected in another, C.I.T. no. 762. A few small cristae project into the region of the median fossette. None of the fossettes is really closed. A low cingulum and internal tubercle tend to develop as in Dm<sup>2</sup>. In no. 2806 a very small median ridge runs along the bottom of the protocone-hypocone valley.

Dm<sup>4</sup> in no. 2806 is almost identical in pattern and structure with Dm<sup>3</sup> of no. 762. In size, especially in crown height, Dm<sup>4</sup> bulks somewhat larger than Dm<sup>3</sup>.

*Lower dentition.* In ramus no. 2807, P<sub>1</sub> is just emerging. This tooth is almond-shaped. Instead of coming to a point, however, the occlusal surface is marked by an elongate fossette which opens into a groove on the internal side of the tooth. Two very small folds lie on the external wall of the tooth.

Dm<sub>2</sub> in no. 2808 is a long, very narrow, triangular tooth with lophoid pattern. It differs from permanent P<sub>2</sub> of other aphelopines in its length. The absence of any marked valley on the external wall differentiates the tooth from the second lower deciduous teeth in other aphelopines.

Dm<sub>3</sub> and Dm<sub>4</sub>, both relatively long-crowned, consist of two lophs arranged as in typical rhinocerotids. The only anomaly is a small internal cusp which lies in the posterior valley of Dm<sub>4</sub>.

*Measurements (in millimeters) of dentition of Aphelops? cristatus*

All measurements are minimum over-all diameters.

Upper dentition:	C.I.T. no. 2806	C.I.T. no. 762
Length of series P <sup>1</sup> -Dm <sup>4</sup> . . . . .	154	....
Length of series Dm <sup>2</sup> -Dm <sup>4</sup> . . . . .	138	....
P <sup>1</sup> , anteroposterior diameter . . . . .	27.0	....
P <sup>1</sup> , transverse diameter . . . . .	21.5	....
P <sup>1</sup> , crown height . . . . .	28a	....
Dm <sup>2</sup> , anteroposterior diameter . . . . .	46.0	50.0
Dm <sup>2</sup> , transverse diameter . . . . .	43.0	48.4
Dm <sup>2</sup> , crown height . . . . .	24.5	30.0
Dm <sup>3</sup> , anteroposterior diameter . . . . .	48.0	53.6
Dm <sup>3</sup> , transverse diameter . . . . .	47.0	52.0
Dm <sup>3</sup> , crown height . . . . .	28.0	34.0
Dm <sup>4</sup> , anteroposterior diameter . . . . .	54.0	....
Dm <sup>4</sup> , transverse diameter . . . . .	52.5	....
Dm <sup>4</sup> , crown height . . . . .	38.0	....
	No. 2807	No. 2809
Lower dentition:		
Length of series P <sub>1</sub> -Dm <sub>4</sub> . . . . .	155	....
Length of series Dm <sub>2</sub> -Dm <sub>4</sub> . . . . .	133	135
P <sub>1</sub> , anteroposterior diameter . . . . .	16e	....
P <sub>1</sub> , transverse diameter . . . . .	8e	....
P <sub>1</sub> , crown height . . . . .	22a	....
Dm <sub>2</sub> , anteroposterior diameter . . . . .	35a	38
Dm <sub>2</sub> , transverse diameter . . . . .	17.8	18.5
Dm <sub>2</sub> , crown height . . . . .	23.0	27.0
Dm <sub>3</sub> , anteroposterior diameter . . . . .	47.0	45.5
Dm <sub>3</sub> , transverse diameter . . . . .	22.0	22.0
Dm <sub>3</sub> , crown height . . . . .	29.0	32.0
Dm <sub>4</sub> , anteroposterior diameter . . . . .	46.0	49.0
Dm <sub>4</sub> , transverse diameter . . . . .	25.2	24.0
Dm <sub>4</sub> , crown height . . . . .	34.0	37.0e
a, approximate.		
e, estimated.		

*Scapula.* The massive scapula, C.I.T. no. 2811, bears no acromion. The tuber is large and rugose with a short, heavy coracoid process. Anteroposterior diameter from tuber to posterior border of glenoid cavity, 123 mm.; transverse diameter across glenoid cavity, 69 mm.; anteroposterior diameter across glenoid cavity, 88 mm.

*Tibia and fibula.* The thick-set tibia, C.I.T. no. 1310, differs little from the characteristic rhinocerotid form. Only the extremities of the fibula are preserved. The tibial facet of the distal extremity of the fibula makes a very obtuse angle (approximately 145°) with the astragalar facet, in contrast with a presumably more acute angle on the teleocerine form. Length, 400 mm.; transverse diameter of distal end, 101 mm.

*Astragalus.* The trochlear surface, which is long anteroposteriorly, has a characteristic deep and broad groove. The fibular facet is almost vertical. The external calcaneal facet presents a strongly concave and convex surface and is separated from the internal calcaneal facet by a deep nonarticular groove. The internal calcaneal facet is rounded in outline. The navicular

facet is relatively short anteroposteriorly. The cuboid facet makes a low angle with the navicular facet and is long, narrow, and diagonal in position. The posterior region of the line of junction between cuboid and navicular facets bears a distally projecting prominence.

*Calcaneum*. A short tuber calcis and a large astragalar facet which curves up onto the anterior side of the cochlear process characterize the calcaneum. The outline of the astragalar facet on the sustentaculum tali is rounded. The surface for articulation with the cuboid is strongly concave.

*Measurements (in millimeters) of astragalus and calcaneum, C.I.T. no. 761*

	AP, anteroposterior diameter.		
	Tr, transverse diameter.		
	PD, proximal-distal diameter.		
	AP	Tr	PD
Astragalus . . . .	54	90	78
Calcaneum . . . .	72	86	131

*Cuboid*. The most striking feature of the cuboid is the extremely large size of the tuberosity for the plantar ligament.

*Metapodials*. Three metapodials in the collection appear to represent metatarsal II (two specimens) and metatarsal IV (one specimen). These metatarsals are relatively long, slender, smooth, and strongly keeled distally (figs. 6a, 6b).

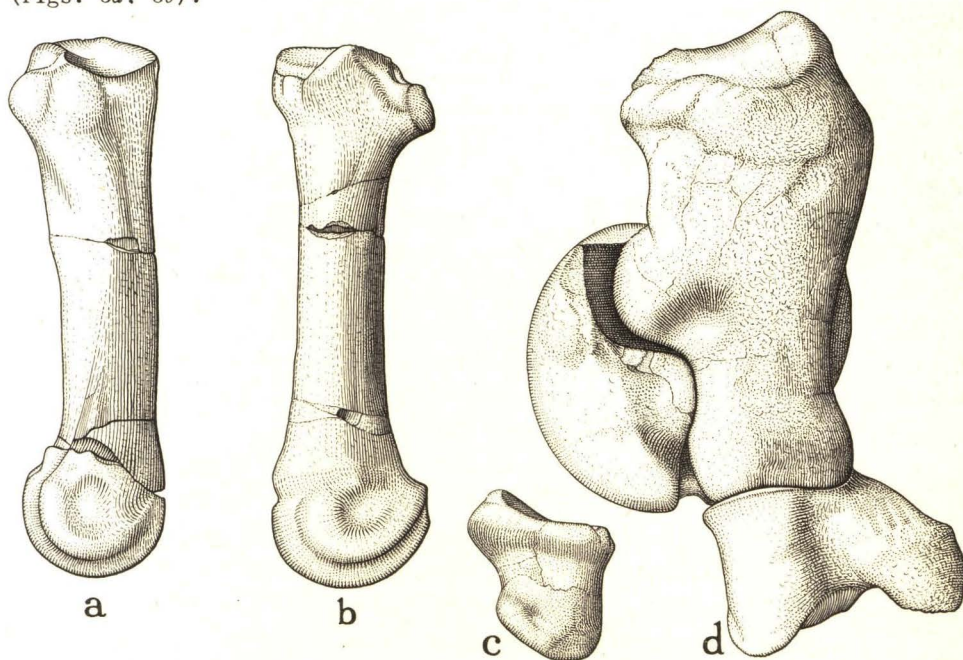


Fig. 6. *Aphelops? cristatus*, n.sp. Skeletal elements. a and b, metapodials, no. 2810; c, phalanx, no. 2812; d, calcaneum, astragalus, and cuboid, no. 761. Lateral views,  $\times 0.5$ .

*Phalanx.* A single side-toe phalanx I, though short, appears to be relatively narrow and high.

*Measurements (in millimeters) of metatarsals and phalanx*

AP, anteroposterior diameter.

Tr, transverse diameter.

	C.I.T. no. 2810		C.I.T. no. 2812
	Metatarsals		Digit II or IV,
	II	IV	phalanx I
Length . . . . .	142-162	141	37
Proximal end, AP . . . . .	38	40	37
Proximal end, Tr . . . . .	30	43	37
Distal end, AP . . . . .	40	41	26
Distal end, Tr . . . . .	31	31	29
Least dimension of shaft:			
AP . . . . .	21	22	
Tr . . . . .	23	26	

*Relationships.* The affinities of *Aphelops? cristalatus* clearly lie with *Aphelops* and *Peraceras* rather than with *Teleoceras*. In the absence of adequate skull material, however, the generic status of the Tonopah rhinoceros must remain tentative.

*Aphelops malacorhinus* Cope (Cope and Matthew, 1915, pl. 141) agrees closely with *A.? cristalatus* in respect to the broader points of size, tooth pattern, strong crochet, and weak antecrochet. It differs in having no cristae, and hence no union of crochet and crista to form a medifossette.

*Aphelops mutilus* Matthew (1924, 1932) is considered a progressive mutation of *A. malacorhinus*. It averages somewhat larger than *A.? cristalatus* in length of premolar tooth row and in transverse diameter of the teeth. The latter difference may be due in large part to the fact that the comparison is made between permanent teeth of one species and deciduous of the other. The teeth of *A.? cristalatus* are far more cristate than those of *A. mutilus*. This again may be a normal difference between milk and permanent teeth.  $P^1$  of *A.? cristalatus*, however, is distinguished by a long external crest, a moderately long inner crest, and three transverse cristae.  $P^1$  of *A. mutilus* and all other comparable rhinocerotids bear two internal cusps, of which the larger is posterior, rather than a single long crest. Transverse cristae are single or absent.

In view of these similarities and differences, *Aphelops? cristalatus*, progressive in tooth pattern but primitive in retaining well developed  $P^1_1$ , is regarded as an offshoot of the line which gave rise to *A. malacorhinus* from the Republican River bed (exact fauna not known; Stirton, 1936, p. 188) and to *A. mutilus* from the Coffee Ranch Quarry and from Higgins Quarry A of Texas.

*Aphelops ceratorhinus* Douglass (1903) differs from *A.? cristalatus* in smaller size and in absence of antecrochets and cristae.

*Aphelops megalodus* (Cope, 1873; Cope and Matthew, 1915) from Pawnee Creek is much smaller and distinctly more primitive in all its tooth characters.

*Aphelops meridianus* (Leidy) and material from New Mexico assigned to the species by Cope (1877, pp. 317-319, pls. 73, 74) is likewise a small and primitive form.

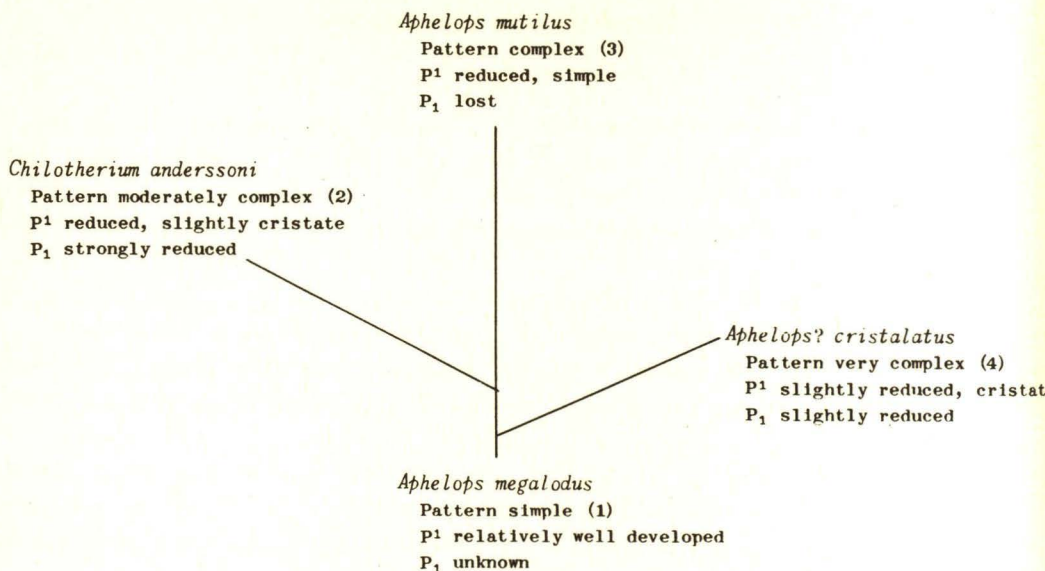
Until *Aphelops jemezianus* Cope (1877, pl. 73) is represented by better and more abundant material it will be impossible to determine any but its broadest relationships. No satisfactory comparison can be made between *A. jemezianus* and *A.? cristalatus*.

An upper milk molar from the valley of the Niobrara River was described and illustrated by Leidy (1858, p. 28; 1869, pl. 23, figs. 4, 5). The tooth resembles  $Dm^3$  (C.I.T. no. 2806) of *A.? cristalatus* very closely in pattern. The Niobrara River tooth is of indeterminate genus and species (Matthew, 1918, p. 207, without any specific reasons refers the tooth to *Teleoceras fossiger*).

*Aphelops* sp. Matthew (1918, fig. 13, A.M.N.H. 17222), consisting of  $P^1$ - $Dm^4$ , represents a form which is much smaller, with simpler tooth pattern, than that from Tonopah. The inner crest of so-called  $Dm^1$  (probably  $P^1$ ) consists of two rudimentary cusps rather than an elongate crest. No cristae are present, hence in no tooth of the series does the crochet unite with a crista to form a medifossette. A not far distant ancestor of *Aphelops? cristalatus* may have resembled this (Lower?) Snake Creek *Aphelops* sp. very closely.

As Matthew has conclusively demonstrated (Matthew, 1932, pp. 433-435), "Among the Old World Rhinocerotidae the group of species assembled by Ringström under *Chilotherium* make the nearest approach to the American *Aphelops*." An illustration of the milk dentition of *Chilotherium anderssoni* Ringström (1924, pl. 3) emphasizes the similarity between this Asiatic rhinocerotid of the *Hipparion* fauna and the American *Aphelops? cristalatus*. The milk teeth of *Chilotherium anderssoni* are of same length as those of the Tonopah form, but they are narrower transversely and are progressively higher-crowned from  $P^1$  through  $Dm^2$  to  $Dm^4$ . The outer crest and three transverse cristae of  $P^1$  resemble *A.? cristalatus* in form, but the metaloph is a conical cusp as in all species of *Aphelops* except *A.? cristalatus*. In each of the milk molars,  $Dm^2$  to  $Dm^4$ , the main medial crista is well developed, but there are no minor cristae such as appear in *A.? cristalatus*. The antecrochet and the posterior part of the cingulum are more strongly developed in *Chilotherium* than in *Aphelops*. In the lower jaw,  $P_1$  is a peglike tooth which is absent in most cases, in contrast with the relatively well developed  $P_1$  of *A.? cristalatus*.  $Dm_2$  to  $Dm_4$  are almost identical with the corresponding teeth of the Tonopah species, except that there is a strong protoconid-hypoconid valley in  $Dm_2$ , a feature which is characteristically absent in *A.? cristalatus*.

On the basis of dentition alone the following relationships seem indicated:



- (1) Simple: No crista; no crochet; weak antecrochet.
- (2) Moderately complex: Crista present or absent; strong crochet; moderate to strong antecrochet; occasional union of crochet and crista on premolars.
- (3) Complex: Crista always present; strong crochet; moderate to strong antecrochet; union of crochet and crista on premolars almost always.
- (4) Very complex: Several cristae always present; very strong crochet; moderate to strong antecrochet; union of crochet and crista on premolars almost always.

An astragalus, U.C. no. 19824, from the Esmeralda can be assigned questionably to *Aphelops*.

Some fragmentary teeth from High Rock Canyon, U.C. no. 11619, suggest that their crown pattern was cristate when unworn. This material, though slightly larger, is comparable in size with C.I.T. no. 2807. Since the High Rock Canyon material represents adults, however, a direct comparison with the youthful *A.? cristatus* is almost meaningless.

#### CAMELIDAE

The family is sparingly represented in the Tonopah fauna. A fairly well preserved palate and a single partial ramus with P<sub>2</sub>-M<sub>3</sub> provide the only moderately complete dentitions in the collection. The remainder of the collection consists of maxillary and mandibular fragments, isolated teeth, an axis, a few complete limb bones, many carpals, tarsals, and phalanges, a few metatarsals but no complete metacarpals, and an abundance of more fragmentary skeletal material.

An estimate based on the occurrence of astragali and teeth indicates that the fauna contained as a minimum population at least eight camelids, two young and six adults.

*Alticamelus? stocki*, n. sp.

(Plate 11; text figure 7)

*Type specimen.* A palate with  $P^1$ - $M^3$  of both sides complete (except both  $P^2$ 's broken off), left C, right  $I^3$ , both  $I^2$ 's, and the alveoli for both  $I^1$ 's, C.I.T. no. 1434 (pl. 11, figs. 1, 1a).

*Paratype specimen.* A ramus with  $P_2$ - $M_3$  complete, C.I.T. no. 2819 (pl. 11, figs. 2, 2a).

*Referred material.* A palate, C.I.T. no. 764; symphyseal section of jaw, no. 2820; milk teeth  $Dm^3$  and  $Dm^4$ , no. 2821;  $Dm_3$  and  $Dm_4$ , no. 2822; axis, no. 2828; ulnoradii, nos. 2823 and 2824; tibia, no. 2825; metatarsi, nos. 2826 and 2827; and all (except perhaps the very largest) camelid carpals, tarsals, and phalanges in the Tonopah collection.

*Specific characters.*  $I^1$  and  $I^2$  retained in fully adult individual. Premolars slightly more reduced than in other species of *Alticamelus*. Limb bones large and long, but proportionally not quite so long as in other alticamelids. I take pleasure in naming this species for Dr. Chester Stock.

*Skull.* In the best-preserved palate, C.I.T. no. 1434, the posterior palatine foramen lies just medial to the middle of  $P^3$ . This part is more anterior than the foramen in the second palate, no. 764. The relative shortness of all the diastemata constitutes an important diagnostic character.

## Measurements (in millimeters) of diastemata

	C.I.T. no. 1434	C.I.T. no. 764
$I^3$ -C . . . . .	11.5	16.0
C- $P^1$ . . . . .	....	15.0
$P^1$ - $P^2$ . . . . .	12.0	19.0

*Mandible.* The mandibular material is too fragmentary to display any important characters. A large mental foramen lies below  $P_1$ , and a second and smaller foramen is situated between  $P_4$  and  $M_1$ . Depth of mandible no. 2819 below  $M_1$ , 41 mm.; width of mandible below  $M_1$ , 23 mm.; diastema  $I^3$ -C, 15 mm.; diastema C- $P_1$ , 19 mm.; diastema  $P_1$ - $P_2$ , est. 18 mm.

*Upper dentition.* There is a deep conical alveolus for a moderately large  $I^1$  which projects anterolaterally.  $I^2$  is somewhat smaller than the first incisor and the crown is perhaps nonfunctional. The tooth curves inward.  $I^3$  is large, strong, and caniniform. The recurved canine bulks approximately as large as  $I^3$ . Caniniform  $P^1$  is a little more recurved than the canine and has a shorter crown, but its single root is just as massive as that of the canine.

The long, narrow, and double-rooted  $P^2$  is relatively large and bears cingulum-like ridges on the internal wall at either end of the tooth.  $P^3$  is similar to  $P^2$ , but the internal ridge is developed along the whole internal wall of the tooth so that it closes off a long, narrow fossette. In  $P^4$  the

internal wall reaches full development, being thick and strongly convex lingually. The premolars do not appear to be greatly reduced.

The molar teeth are large, simple, and typically camelid with their moderately high crowns (26 mm. on external side of an unworn tooth, C.I.T. no. 2831, measured from root to highest point in intercusp valley), very strong styles, and strong fold on the external enamel wall.

*Lower dentition.* The three strongly procumbent lower incisors are spatulate when unworn. The large canine and single-rooted  $P_1$ , both caniniform, approximate each other in size.

$P_2$  is slender, simple, moderately large, and double-rooted.  $P_3$  and  $P_4$  are relatively little reduced. The molars are large, simple, and moderately high-crowned.

*Milk dentition.*  $Dm^3$  is submolariform, with a strong anterior style, a narrow anterior crescent, and a posterior crescent.  $Dm^4$  is slightly higher-crowned than  $Dm^3$ . It is completely molariform, although smaller and lower-crowned than the true molars.

$Dm_3$  is a long and very slender tooth characterized by two deep infolds in its internal wall, one in its external wall, and a small enclosed posterior fossette.  $Dm_4$  with its three crescents is long, slender, and only moderately high-crowned.

*Measurements (in millimeters) of dentition of Alticamelus? stocki*

All measurements are made approximately at the wearing surface of the teeth. In measuring anteroposterior diameters of molars and milk molars, the parastyle was not included. No. 1434 (upper dentition) represents a fully adult camelid, in which the anterior crescentic infold of  $M^1$  has already partially disappeared with wear. No. 2819 (lower dentition) is so worn that the anterior crescent infold has disappeared in  $M_1$  and is almost completely worn away in  $M_2$ . The milk dentitions, both upper and lower, are little worn.

Upper dentition:	C.I.T. no. 1434
Length of series $P^2-M^3$ . . . . .	149
Length of series $P^2-P^4$ . . . . .	53
Length of series $M^1-M^3$ . . . . .	96
$I^3$ , anteroposterior diameter . . . . .	11a
$C$ , anteroposterior diameter . . . . .	11.5
$C$ , transverse diameter . . . . .	9.5
$P^1$ , anteroposterior diameter . . . . .	12.4
$P^1$ , transverse diameter . . . . .	8.2
$P^2$ , anteroposterior diameter . . . . .	14a
$P^2$ , transverse diameter . . . . .	7.5a
$P^3$ , anteroposterior diameter . . . . .	19.0
$P^3$ , transverse diameter . . . . .	11.4
$P^4$ , anteroposterior diameter . . . . .	18.0
$P^4$ , transverse diameter . . . . .	17.5
$M^1$ , anteroposterior diameter . . . . .	27.0
$M^1$ , transverse diameter . . . . .	22.0
$M^2$ , anteroposterior diameter . . . . .	35.5
$M^2$ , transverse diameter . . . . .	24.0
$M^3$ , anteroposterior diameter . . . . .	36.8
$M^3$ , transverse diameter . . . . .	21.0

a, approximate.

*Measurements - Continued*

Lower dentition:		No. 2819
Length of series P <sub>2</sub> -M <sub>3</sub> . . . . .		144
Length of series P <sub>2</sub> -P <sub>4</sub> . . . . .		44
Length of series M <sub>1</sub> -M <sub>3</sub> . . . . .		100
P <sub>2</sub> , anteroposterior diameter . . . . .		11.4
P <sub>2</sub> , transverse diameter . . . . .		5.3
P <sub>3</sub> , anteroposterior diameter . . . . .		15.6
P <sub>3</sub> , transverse diameter . . . . .		6.4
P <sub>4</sub> , anteroposterior diameter . . . . .		17.7
P <sub>4</sub> , transverse diameter . . . . .		9.2
M <sub>1</sub> , anteroposterior diameter . . . . .		24.5
M <sub>1</sub> , transverse diameter . . . . .		15.5
M <sub>2</sub> , anteroposterior diameter . . . . .		32.3
M <sub>2</sub> , transverse diameter . . . . .		19.1
M <sub>3</sub> , anteroposterior diameter . . . . .		42.5
M <sub>3</sub> , transverse diameter . . . . .		16.1
Upper milk dentition:		No. 2821
Dm <sup>3</sup> , anteroposterior diameter . . . . .		25.0
Dm <sup>3</sup> , transverse diameter . . . . .		13.0
Dm <sup>4</sup> , anteroposterior diameter . . . . .		24.0
Dm <sup>4</sup> , transverse diameter . . . . .		14.0
Lower milk dentition:		No. 2822
Dm <sub>3</sub> , anteroposterior diameter . . . . .		17.0
Dm <sub>3</sub> , transverse diameter . . . . .		7.3
Dm <sub>4</sub> , anteroposterior diameter . . . . .		33.0
Dm <sub>4</sub> , transverse diameter . . . . .		10.5

*Skeletal parts.* In relation to the size of the dentition, the skeletal parts in the camelid collection appear inordinately large. Yet since but one type of camelid is found in the fauna, these dentitions and skeletal parts are presumed to be of the same species.

*Axis.* The second cervical vertebra (no. 2828, fig. 7e), though large, is not particularly elongated for a camel of this size. The odontoid process is spoutlike. Length of centrum, 200 mm.; transverse diameter at anterior end, 79 mm.

*Ulnoradius.* The radius and ulna are as firmly fused together as in Recent *Lama*. Two examples of this bone are preserved in the collection, one moderately large, presumably of a young animal, the other of a very large adult (figs. 7a, 7b).

*Measurements (in millimeters) of radius*

	C.I.T. no. 2823	C.I.T. no. 2824
Total length . . . . .	448	575
Proximal end, transverse diameter . . . . .	67	74
Distal end, anteroposterior diameter . . . . .	47	55
Distal end, transverse diameter . . . . .	65	77



Fig. 7. *Alticamelus? stocki*, n. sp. a, ulnoradius, no. 2724, anterior view; b, ulnoradius, no. 2823, anterior view; c, tibia, no. 2825, anterior view; d, metatarsus, no. 2826, anterior view; e, axis, no. 2828, lateral view; f, phalanx, no. 2858, anterior view; g, phalanx, no. 2859, anterior view. All figures  $\times 0.33$ .

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada

*Carpus*. The carpal elements differ little from those of Recent *Lama*, except in their somewhat larger size. Although the size of the carpals varies somewhat, there do not appear to be any distinctive characters by which the elements can be segregated.

*Measurements (in millimeters) of carpals, C.I.T. nos. 2914-2920*

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters. The series which was measured is of average size.

	AP	Tr	PD
Scaphoid . . . .	39	22	30
Lunar . . . . .	38	24	34
Cuneiform . . . .	40	24	33
Pisiform . . . . .	49	24	38
Trapezoid . . . .	22	16	21
Magnum . . . . .	33	24	19
Unciform . . . . .	46	26	28

*Metacarpus*. No complete metacarpal elements occur in the collection. The proximal end of a large cannon bone corresponds in size to the large carpals and the large ulnoradius. This large metacarpus is strongly fused as in an adult. A pair of smaller metacarpals, agreeing in size with the smaller radius and carpals, is not completely fused into one bone and hence may represent a young individual. The step down from the proximal articular surface of metacarpal III to the articular surface of metacarpal IV is pronounced. Proximal end of metacarpus no. 2829, anteroposterior diameter, 45 mm.; transverse diameter, 59 mm.

*Tibia*. The long, fairly slender tibia of a young individual shows no noteworthy features (no. 2825, fig. 7c). The lateral malleolus is similar to that of *Lama*. Total length, 495 mm.; distal end, transverse diameter, 66 mm.

*Patella*. The patella, no. 2921, resembles that of *Lama*. Anteroposterior diameter, 30 mm.; transverse diameter, 38 mm.; proximal-distal diameter, 80 mm.

*Tarsus*. The tarsal bones of a young individual appear to correspond very closely to those of *Lama*. The astragalus is relatively narrow.

*Measurements (in millimeters) of tarsals C.I.T. nos. 2922-2926*

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

	AP	Tr	PD
Astragalus . . . .	37	40	64
Calcaneum . . . .	48	42	130
Navicular . . . . .	39	25	23
Cuboid . . . . .	50	31	27
Ectocuneiform . .	28	26	18

*Metatarsus.* The metatarsal bones of a young individual demonstrate that at first fusion is incomplete near the distal end of the shafts. Fusion is completed in an older, slightly larger individual. A few very large distal extremities of metapodials constitute some of the material which may represent a larger and different species of camelid. In Recent *Lama* the distal ends of the metacarpals are larger than the distal extremities of the metatarsals. Hence these large fragments need not necessarily represent another species, but may belong to the fore feet of an especially large individual. In C.I.T. no. 2827, the total length of the metatarsus is 407 mm.; transverse diameter of proximal end, 51 mm. The transverse diameter of the distal end of this specimen, a normal metatarsal, is 28 mm.; the corresponding measurement in no. 2830, a very large metapodial, is 36 mm.

*Phalanges.* In Recent *Lama* the phalanges of the manus may measure as much as one-ninth (11 per cent) larger in every dimension than do the phalanges of the pes. It is to be noted, however, that they maintain similar proportions in both manus and pes. Hence, in a collection of fossil camelid phalanges of a given species there should be little variation in proportions even though the size range seems considerable. On this account a few disproportionately massive phalanges may be associated with the metapodial material to represent a larger camelid.

*Measurements (in millimeters) of phalanges*

AP, anteroposterior diameter.  
Tr, transverse diameter.  
PD, proximal-distal diameter.

	AP	Tr	PD
Phalanx I, no. 2858 (normal specimen) . . . . .	..	..	96
Proximal end . . . . .	28	29	..
Phalanx I, no. 2859 (large specimen) . . . . .	..	..	99
Proximal end . . . . .	34	39	..

*Relationships.* At present the distinctions between the various Upper Miocene--Lower Pliocene camelids appear to be very poorly defined. Matthew (1901) reviewed the bases upon which these distinctions are made. When the structural features of the Tonopah camelid are compared with Matthew's revised list of generic characters (1918), the Nevadan type is found to differ from *Pliauchenia* and *Megatylopus* in having a complete dentition. The latter two genera have each but one incisor, and the premolar formulas are  $\frac{3}{2}$  and  $\frac{2}{2}$  respectively. *Miolabis* is much smaller and more primitive.

The Tonopah form differs from *Procamelus* in its complete dentition with not quite so much reduction of the premolars. The limb bones of the Tonopah camelid are relatively longer and larger.

*Protolabis* resembles *Alticamelus? stocki* only in the retention of its upper

incisors. It differs decidedly in its small, short limb bones and in the separate to imperfectly united metacarpals.

According to Stirton (1929, p. 293) there are a number of characters by which *Alticamelus* may be distinguished from *Procamelus*. The Tonopah material shows the following features diagnostic of *Alticamelus*: (1) The premolars are slightly less reduced than in *Procamelus*. (2) The parastyle, mesostyle, and anterior external rib are more prominent. (3) The diastemata between  $P^1$  and  $P^2$  and between C and  $P^1$  are relatively short. (4) The  $P_1$ - $P_2$  diastema (estimated) is much less. (5) The caniniform teeth are heavier than in *Procamelus*. (The upper canines in C.I.T. no. 1434 are of about the size seen in *Procamelus*, but  $I^3$  and  $P^1$  are larger. All the caniniform teeth are very large in no. 764.) (6) The first premolars, upper and lower, show no tendency to develop double roots. (7) The inner side of the lobes of the lower molars is slightly convex anteroposteriorly, but not much more so than in *Procamelus*.

All the characters listed above appear to be valid. Since the Tonopah camelid lies in or near the alticamelid group with respect to each of these characters, it apparently should be referred to the genus *Alticamelus*. If, however, the absence of the first and second upper incisors be considered a definite character of *Alticamelus*, then C.I.T. no. 1434, as a fully adult specimen with complete dentition, cannot be of that genus. In his description of *Alticamelus giraffinus*, Matthew (1901, p. 430, *A. altus*; Matthew and Cook, 1909, p. 402, renamed *A. giraffinus*) states that "the first and second upper incisors are represented by small crownless stumps, perhaps the remains of the milk dentition." The first two incisors in no. 1434 are much reduced in size and may have had little function, but their reduction is not so great as that described by Matthew and they are probably not milk teeth. Matthew (1924, fig. 54) has referred a figured specimen, A.M.N.H. nos. 18350 and 18869, to *Alticamelus* cf. *leptocolon*. The specimen is undescribed. The figure shows alveoli for all three incisors, but the specimen might be of the genus *Protolabis*.

Ratios of premolar reduction have been calculated by dividing the length of series  $M^1$ - $M^3$  by that of  $P^2$ - $P^4$ , and also by dividing the length of series  $M_1$ - $M_3$  by that of  $P_2$ - $P_4$ . These reveal that in all but one species of *Alticamelus* the premolar teeth are relatively less reduced than in nos. 1434 and 2819 from Tonopah. The one exception is an *Alticamelus* referred to *leptocolon*, A.M.N.H. nos. 18350 and 18869, by Matthew (1918). This ratio does not distinguish *Alticamelus*? *stocki* from *Protolabis* and *Procamelus*.

A second ratio was calculated to determine the limb proportions of the various Upper Miocene camelids. This ratio was derived by dividing the length of the series  $M_1$ - $M_3$  into the length of the metacarpal. Where these measurements were not available, length  $M^1$ - $M^3$  and length of metatarsal were used. It must be remembered that although the use of both of these "substitute" measurements gives approximately the same ratio, the use of only one

"substitute" may affect the ratio as much as several tenths of a point. Shortening of the tooth row with wear is another important source of error. This ratio actually does set apart the alticamelid group from the genera *Protolabis* and *Procamelus*. *Protolabis* has a much lower ratio. That of *Procamelus* is still lower. *Procamelus* with its moderately long limbs should have a higher ratio than available measurements indicate. Although additional material will probably yield higher ratios for *Procamelus*, these new ratios will undoubtedly remain distinctly lower than those for *Alticamelus*. In limb proportions *Alticamelus? stocki* falls nearest to the *Alticamelus* group, although it cannot be definitely included within that group.

*Comparative measurements (in millimeters) and ratios of limb elements and tooth rows of Alticamelus*

1. *A.? stocki*, Tonopah, C.I.T. For specimen numbers, see p. 153.
2. *A. alexandrae*, Barstow, U.C. no. 26015.
3. *A. procerus*, Lower? Snake Creek, A.M.N.H. no. 14070.
4. *A. sp. 1*, Snake Creek, undescribed (Davidson, 1923).
5. *A. giraffinus*, Pawnee Creek, A.M.N.H. no. 9109.
6. *A. leptocolon*, Pawnee Creek, A.M.N.H. no. 18350.

Lengths:	1	2	3	4	5	6
P <sup>2</sup> -M <sup>3</sup> . . . . .	149	117.5	157	.....	.....	111
P <sup>2</sup> -P <sup>4</sup> . . . . .	53	46.5	63	.....	.....	34
M <sup>1</sup> -M <sup>3</sup> . . . . .	96	74.5	98	.....	87	74
P <sub>2</sub> -M <sub>3</sub> . . . . .	144	130	164	143	154	.....
P <sub>2</sub> -P <sub>4</sub> . . . . .	44	45.5	56	48	49	.....
M <sub>1</sub> -M <sub>3</sub> . . . . .	100	84.5	108	95	105	.....
Axis . . . . .	200	172	.....	.....	250	.....
Radius . . . . .	448-575	480	.....	494	.....	417-464
Metacarpus . . . . .	.....	390	.....	399*	.....	362-389
Metatarsus . . . . .	403	.....	552	.....	624.4	355
Ratios:						
Upper, m/pm** . . . . .	1.81	1.60	1.55	.....	.....	2.18
Lower, m/pm . . . . .	2.18	1.85	1.93	1.98	2.14	.....
Metapodial . . . . .	4.2	4.6	5.6	4.2	7.1	4.8
Molar tooth row						

\*A metacarpus recorded for *Alticamelus sp. 1* (Davidson, 1923, p. 406) with length of 484 mm. is evidently not to be associated with a radius with length of 494 mm. Hence the metacarpus described as of *A. sp. 2* by Davidson and having a length of 399 mm. is used instead.

\*\*Ratio between lengths of molar and premolar tooth rows.

*Alticamelus alexandrae* Davidson (1923) from the Barstow Miocene has no I<sup>1</sup> and I<sup>2</sup>. The tooth row is shorter, the premolars are less reduced, and the limb bones are more elongate than in *A.? stocki*. The length of the axis is proportionally the same in both forms.

*Alticamelus procerus* Matthew and Cook (1909) from the Lower? Snake Creek differs from *A.? stocki* in absence of I<sup>1</sup> and I<sup>2</sup>, in longer tooth row, in less reduced premolars, and in more elongate limbs.

*Alticamelus giraffinus* Matthew (1901, *A. altus*) from Pawnee Creek, an old individual with a longer tooth row and less reduced premolars, differs striking-

ly from the Tonopah species in the extreme elongation of its limb elements and of its neck. This species, the type of the genus, has the stumps of  $I^1$  and  $I^2$ .

The skull, mentioned above, which was referred by Matthew (1924, fig. 54) to *A. cf. leptocolon* has a much shorter tooth row than no. 1434, but  $I^1$  and  $I^2$  are present. Because of lack of further illustrations and detailed description of this camelid, the two forms cannot be closely compared. Limb bones which have been designated *A. leptocolon* Matthew (1901, fig. 30; 1909, p. 115) are of the same proportions as the specimens from Tonopah, but somewhat smaller.

Some undescribed alticamelid species from Snake Creek (Davidson, 1923, pp. 402, 406) approximate in measurements the Tonopah material. The premolars of the Snake Creek form are somewhat less reduced. *Alticamelus priscus* Matthew (1924, p. 187) lacks sufficient description for any detailed comparison.

#### ANTILOCAPRIDAE

A large number of merycodont remains, including skull parts and horn cores, have been described from the Tonopah locality (Furlong, 1934). On the basis of this material, two new species were established: (1) *Merycodus loxocerus* Furlong, represented by no less than sixty individuals of all ages, and (2) *Merycodus hookwayi* Furlong, known by the remains of possibly more than three individuals.

Considerable variation in size and pattern of merycodont horn cores can be noted in a collection of this kind of material from a given locality. Sometimes several distinct types are represented. More commonly the types grade by small variations from one to another. With such variations possible, it would seem logical to use minor structural differences in horn-core development to distinguish species or varieties. It is deemed advisable to reserve for generic distinction the differences in dental characters and the major differences in the horn cores.

Furlong has already pointed out the characters of horn core and dentition which serve to distinguish the two Tonopah species from all others. No attempt was made, however, to determine the phylogenetic position of these species.

The best criteria for establishing the relationships of merycodonts are not found in the form and size of the horn cores, but in the length of the postsymphyseal diastema, the reduction of the premolars, the crown pattern of  $P_4$ , and the lengthening of the molar tooth crowns.

Frick has indicated the relative length of the postsymphyseal diastema by recording the ratio of the anteroposterior diameter of  $M_3$  to the diastema length. The selection of the length of  $M_3$  as dividend in the ratio, though moderately satisfactory for determining specific differences, is peculiarly unfortunate from the point of view of demonstrating the relative diastema length in species. The evolutionary trend in merycodonts is shown by an increase in size of  $M_3$  as well as by an increase in length of diastema. Hence, with both

values increasing in the normal evolution of the family, the ratio between  $M_3$  and diastema length may remain constant, even though both are greatly elongated relatively to the rest of the tooth row. Therefore, to emphasize more correctly the relative increase in diastema length, the anteroposterior diameter of  $M_1$  is suggested rather than the corresponding measurement of  $M_3$ .

The ratio of length of premolar tooth row to length of molar tooth row has been used to indicate the amount of shortening in the premolar series.

The phylogenetic significance of the crown pattern of  $P_4$  was discussed in a previous paper (Henshaw, 1938, pp. 65-67).

The length of the molar tooth crowns is probably the most important character in determining phylogenetic relationships. Though well shown in Frick's illustrations (Frick, 1937, figs. 41-47), this character unfortunately has not been considered in any large measure by other students of the merycodont antelope group.

#### *Merycodus loxocerus* Furlong

*Relationships.* Measurements taken on C.I.T. nos. 713 and 1298 indicate that the postsymphyseal diastema is relatively extremely short, only those of *Ramoceros coronatus* (Merriam) (Frick, 1937, p. 437) and *Merycodus sabulonis* (Matthew and Cook, 1909, p. 411) being shorter. The premolar-molar tooth-row ratio in *M. loxocerus* indicates less reduction of the premolar tooth row than in any other merycodont except the primitive *Merycodus agilis* Douglass from Madison Valley. The crown pattern of  $P_4$  often retains the primitive five-lobed form. The molar crown height on unworn teeth is very low in relation to anteroposterior length of tooth, e.g. in  $M_3$  approximately 12 mm. crown height to 12 mm. anteroposterior length.

All these characters emphasize the primitive nature of *Merycodus loxocerus*. The type of horn core found in this species agrees closely with some of those from the Barstow, e.g. *Merycodus alticornis* (Frick, 1937, p. 347 and fig. 38A), described as "shaft unusually slender and elongate." The lower teeth of the Tonopah form, however, appear more primitive than those of the Barstow (Frick, 1937, figs. 46, 47).

#### *Merycodus hookwayi* Furlong

*Relationships.* Measurements taken on the paratype, C.I.T. no. 712, show that the postsymphyseal diastema of *Merycodus hookwayi* is relatively shorter than in all species except *Ramoceros coronatus*, *Merycodus sabulonis*, *M. loxocerus*, and *M. agilis*. The slight premolar shortening exceeds only that in the primitive forms *M. agilis* and *M. loxocerus*, and equals that in *Ramoceros coronatus* and *Merycodus sabulonis*. The crown pattern of  $P_4$ , as in *M. loxocerus*, is of the five-lobed type. The height of crown of  $M_3$  is 16 mm. on an unworn tooth 14.5 mm. long.

*Merycodus hookwayi* represents a primitive merycodont which is slightly more

advanced than *Merycodus loxocerus*. Frick placed *M. hookwayi* in the genus *Meryceros*, yet he characterized that genus as having muzzle and diastema elongate. Furthermore, the horn cores of typical *Meryceros* all appear to be short-shafted. *Merycodus hookwayi*, with its long though moderately heavy-shafted horn core, and above all its shortened diastema and heavy premolars, appears to be more closely related to Frick's subgenus *Paracosoryx*.

For reasons previously discussed (Henshaw, 1939, pp. 25-26), this Tonopah species is referred to the genus *Merycodus*. The subgenus *Paracosoryx* appears to be valid.

Among Frick's figured specimens the one which appears closest to *M. hookwayi* is F.A.M. no. 31159 (Frick, 1937, fig. 39A; also p. 347). Frick referred this Barstow specimen to *M. (Paracosoryx) alticornis*, but made special note of the fact that the specimen appeared "as heavy, but considerably shorter than type." Unfortunately there are no teeth associated with this specimen from the Barstow.

*Merycodus (Paracosoryx) furlongi* (Frick), U.C. no. 26795 (Furlong, 1927, pl. 26, fig. 1; Frick, 1937, p. 348), differs in having forward-tilting horn cores with longer tines, and in having a much more advanced type of ramus and lower dentition.

Neither *M. loxocerus* nor *M. hookwayi* appears to have any counterpart among recorded merycodonts. They may represent a primitive type which developed into localized aberrant forms.

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## PLATES



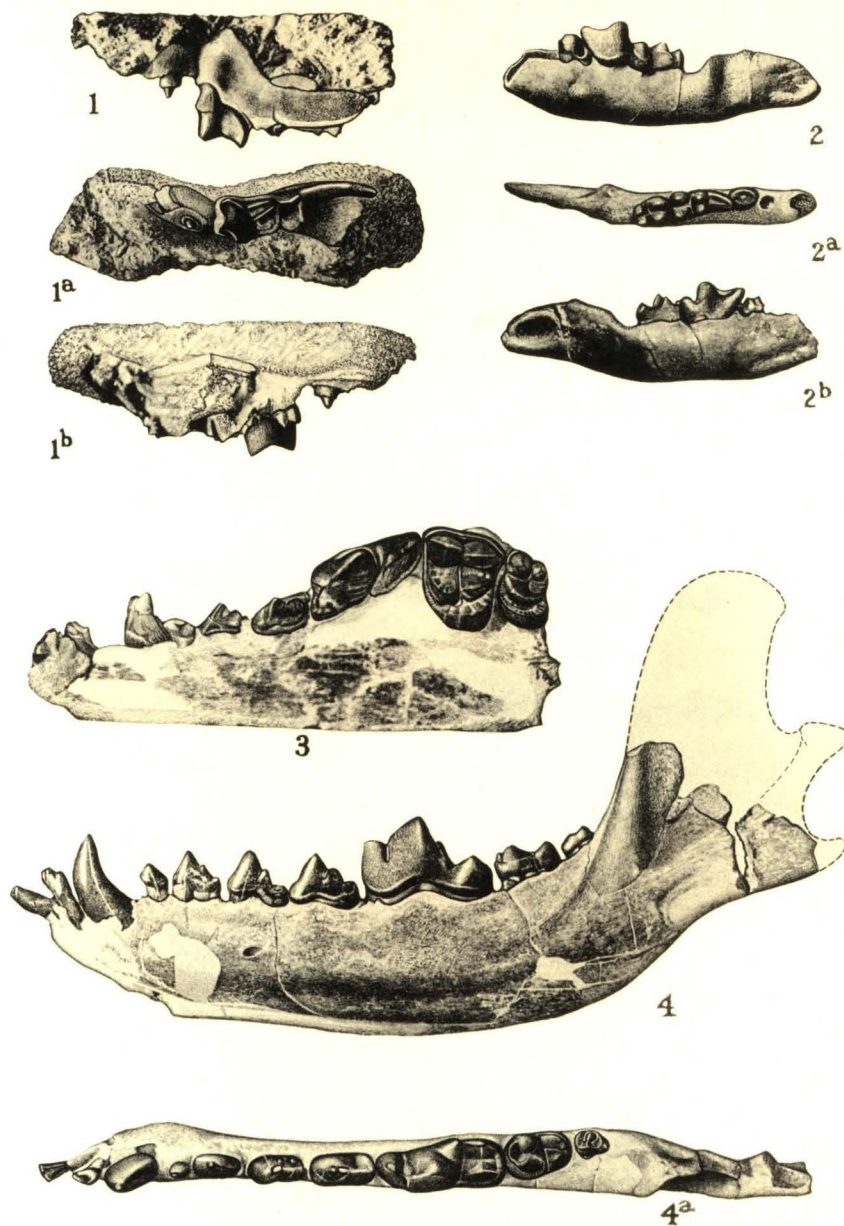
FIG. 1. View of Quarry A from the northwest. Quarry A is cut on side of hill in center of picture. Quarry C lies out of sight on back slope of same hill. Both quarries occur at approximately the same stratigraphic horizon. This horizon has been offset by minor faulting.



FIG. 2. Blasting to loosen overburden at Tonopah Quarry C. View from the east. Fossiliferous strata dip gently southward.



FIG. 3. Panorama of western slope of San Antonio Mountains, looking S.  $45^{\circ}$  W. to W. from a point 10 miles north of Tonopah, Nevada. Southern end of Big Smokey Valley lies in distance with Lone Mountain beyond. Location of Quarries A and C of Calif. Inst. Tech. Vert. Pale. Locality 172 is indicated on photograph.



FIGS. 1, 1a, 1b. *Metechinus fergusonii*, n. sp. Type specimen, no. 2817, left maxillary dentition. Fig. 1, lateral view; fig. 1a, occlusal view; fig. 1b, lingual view.  $\times 2.75$ .

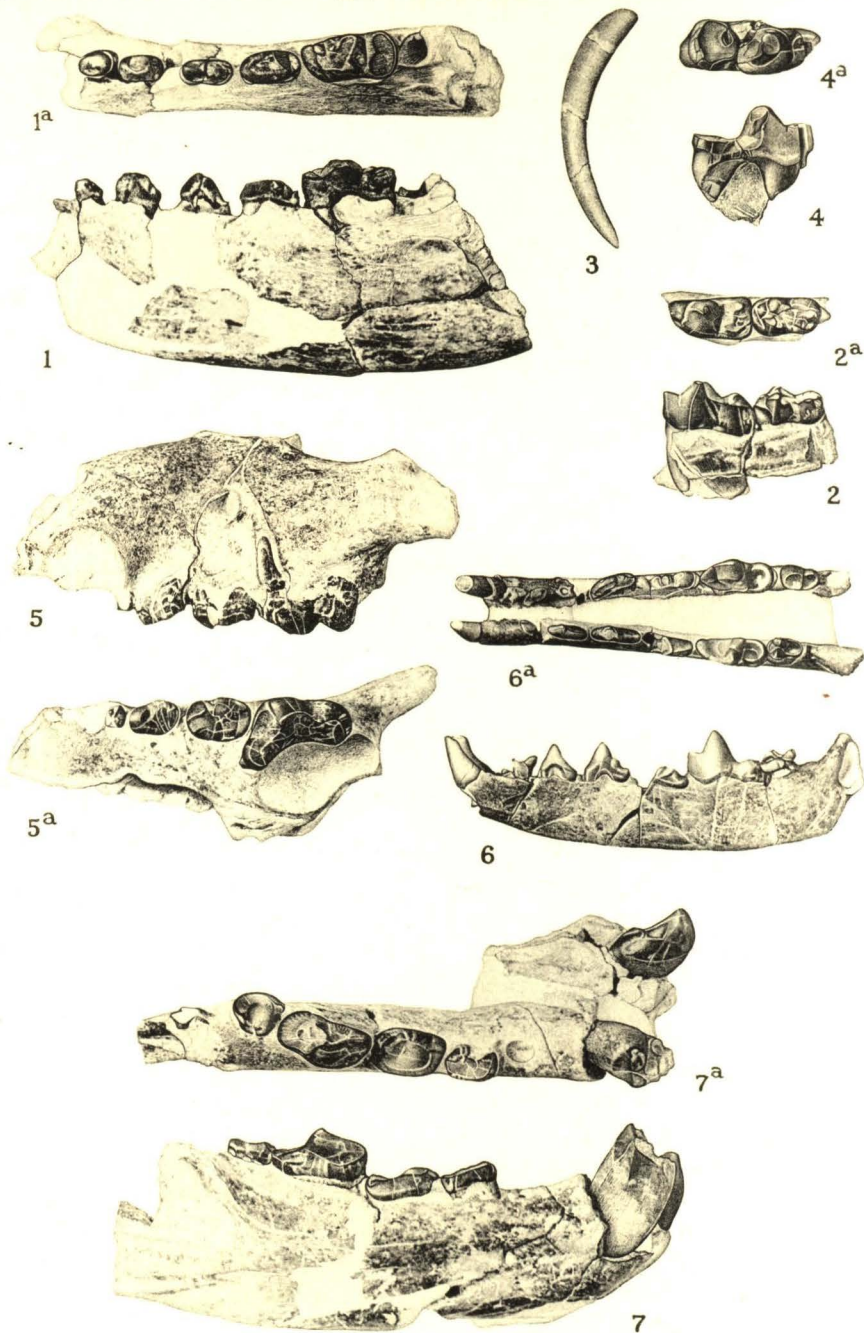
FIGS. 2, 2a, 2b. *Metechinus fergusonii*, n. sp. Type specimen, no. 2817, left ramus and dentition. Fig. 2, lateral view; fig. 2a, occlusal view; fig. 2b, lingual view.  $\times 2.75$ .

FIG. 3. *Tomarctus paulus*, n. sp. Type specimen, no. 1229, skull fragment with dentition, anterior teeth slightly crushed, occlusal view.  $\times 1.2$ .

FIGS. 4, 4a. *Tomarctus paulus*, n. sp. Type specimen, no. 1229, left ramus, ascending part restored from right side. Fig. 4, lateral view; fig. 4a, occlusal view.  $\times 1.2$ .

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



FIGS. 1, 1a. *Tomarctus? kelloggi* (Merriam). No. 1235, left ramus and dentition. Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a. *Tomarctus? kelloggi* (Merriam). No. 789, left  $M_1$ - $M_2$ . Fig. 2, lateral view; fig. 2a, occlusal view.

FIG. 3. *Tomarctus brevirostris* Cope. No. 2853, canine, lateral view.

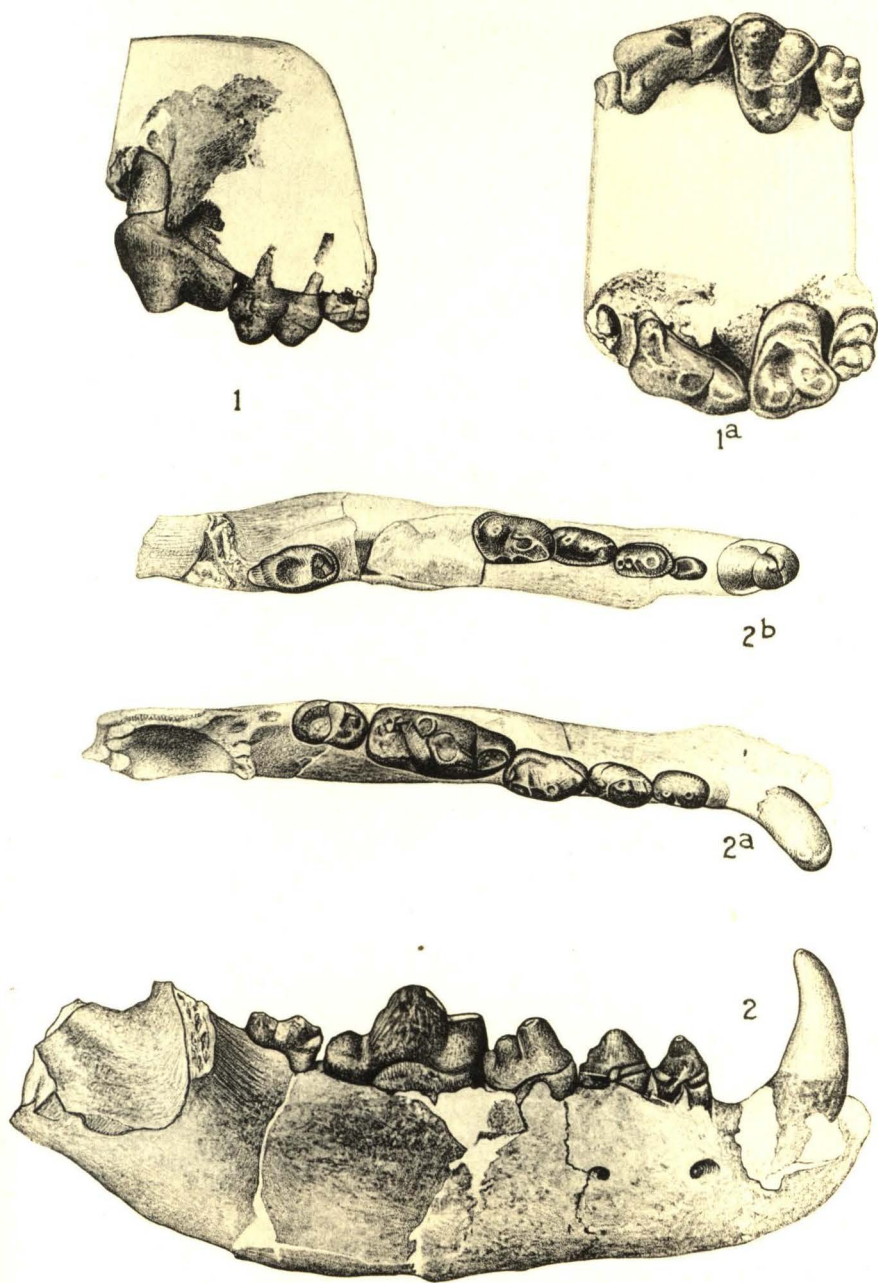
FIGS. 4, 4a. *Tomarctus brevirostris* Cope. No. 774,  $M_1$ . Fig. 4, lateral view; fig. 4a, occlusal view.

FIGS. 5, 5a. *Brachypsalis pachycephalus* Cope. No. 1231, left maxillary and dentition. Fig. 5, lateral view; fig. 5a, occlusal view.

FIGS. 6, 6a. *Leptocyon vafer* (Leidy). No. 780, mandible. Fig. 6, lateral view; fig. 6a, occlusal view.

FIGS. 7, 7a. *Brachypsalis pachycephalus* Cope. No. 1230, right ramus. Fig. 7, lateral view; fig. 7a, occlusal view.

All figures approximately natural size



*Aelurodon wheelerianus asthenostylus*, n. var.

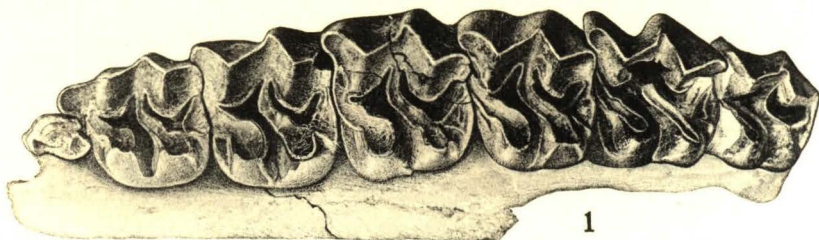
FIGS. 1, 1a. Type specimen, no. 781, maxillary with  $P^4$ - $M^2$ . Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a, 2b. Type specimen, no. 781, rami. Fig. 2, lateral view; figs. 2a, 2b, occlusal views.

All figures approximately  $\times 0.88$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



*Hypohippus near affinis* (Leidy)

FIG. 1. No. 1404, upper dentition.

FIG. 2. No. 1401, upper dentition.

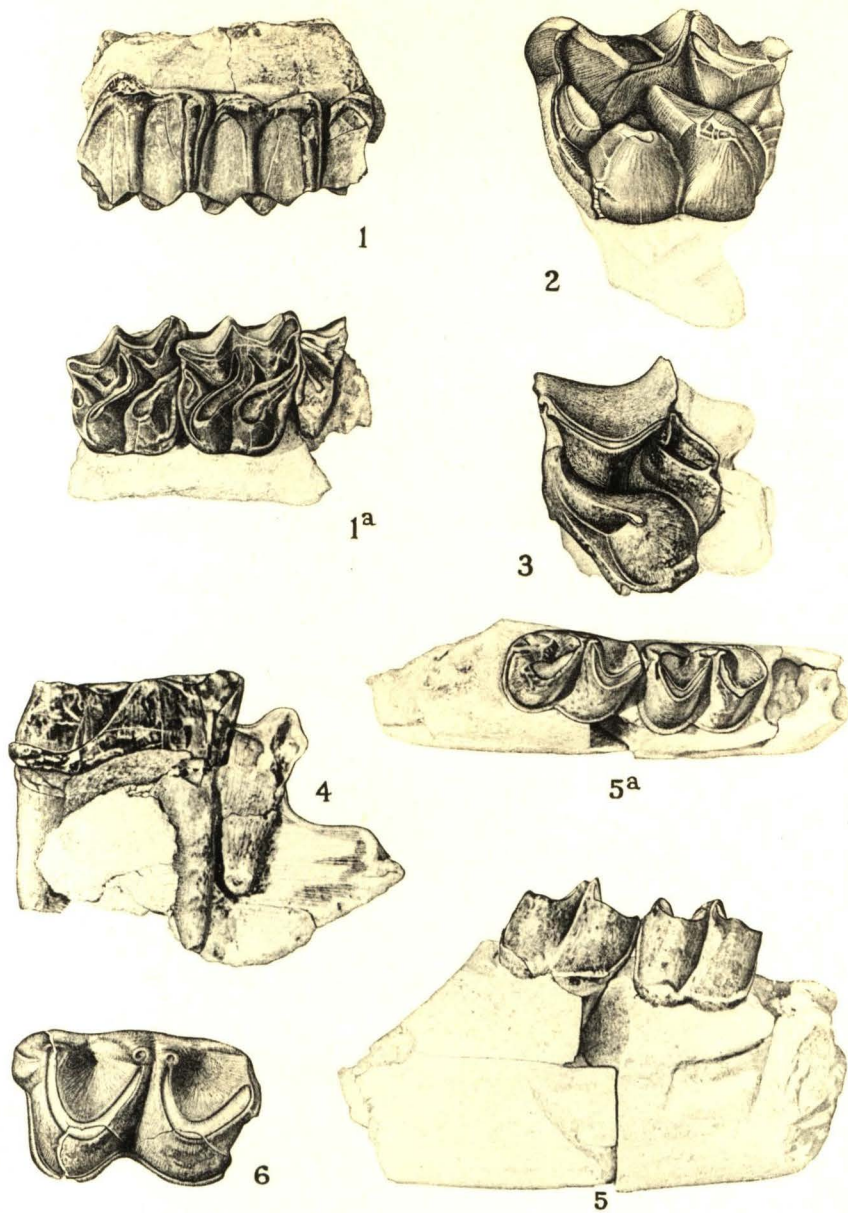
FIG. 3. No. 1880, lower dentition.

FIG. 4. No. 1881, lower dentition.

Occlusal views,  $\times 0.67$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



*Hypohippus near affinis* (Leidy)

FIGS. 1, 1a. No. 2860,  $M^1-M^2$ . Fig. 1, lateral view; fig. 1a, occlusal view.

FIG. 2. No. 2845,  $Dm^2$ , occlusal view.

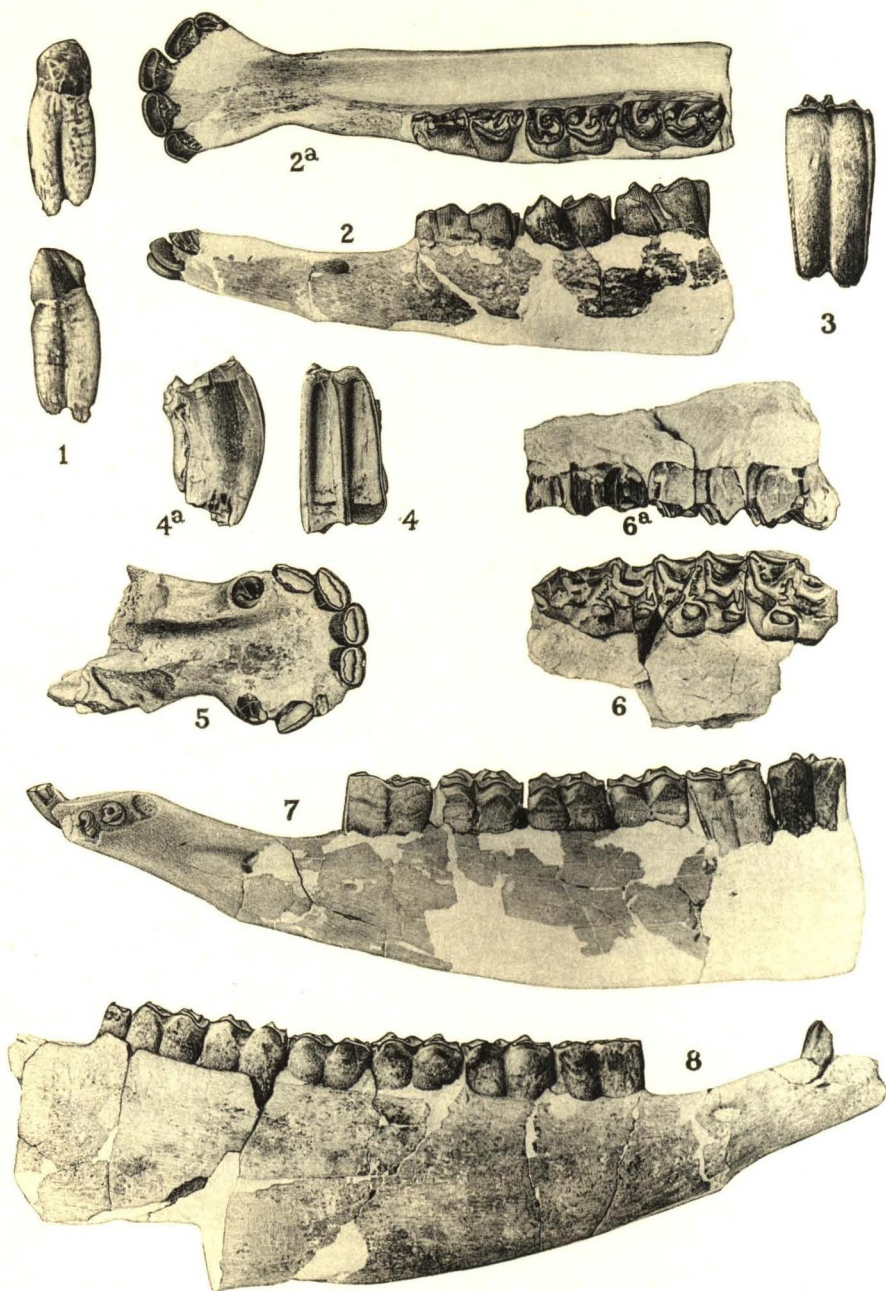
FIG. 3. No. 2846,  $Dm^2$ , occlusal view.

FIG. 4. No. 2847,  $P_1-P_2$ , lateral view.

FIGS. 5, 5a. No. 1878,  $P_3-P_4$ . Fig. 5, lateral view; fig. 5a, occlusal view.

FIG. 6. No. 2848, deciduous lower molar, occlusal view.

All figures  $\times 0.6$



*Merychippus calamarius* (Cope)

FIG. 1. No. 2837,  $P_1$ , lateral and lingual views. Natural size.

FIGS. 2, 2a. No. 656, lower milk dentition. Fig. 2, lateral view; fig. 2a, occlusal view.  $\times 0.5$ .

FIG. 3. No. 2862,  $P_4$ , lateral view.  $\times 0.5$ .

FIGS. 4, 4a. No. 2861,  $M^2$ . Fig. 4, lateral view; fig. 4a, occlusal view.  $\times 0.5$ .

FIG. 5. No. 2836, lower incisors and canines, occlusal view.  $\times 0.5$ .

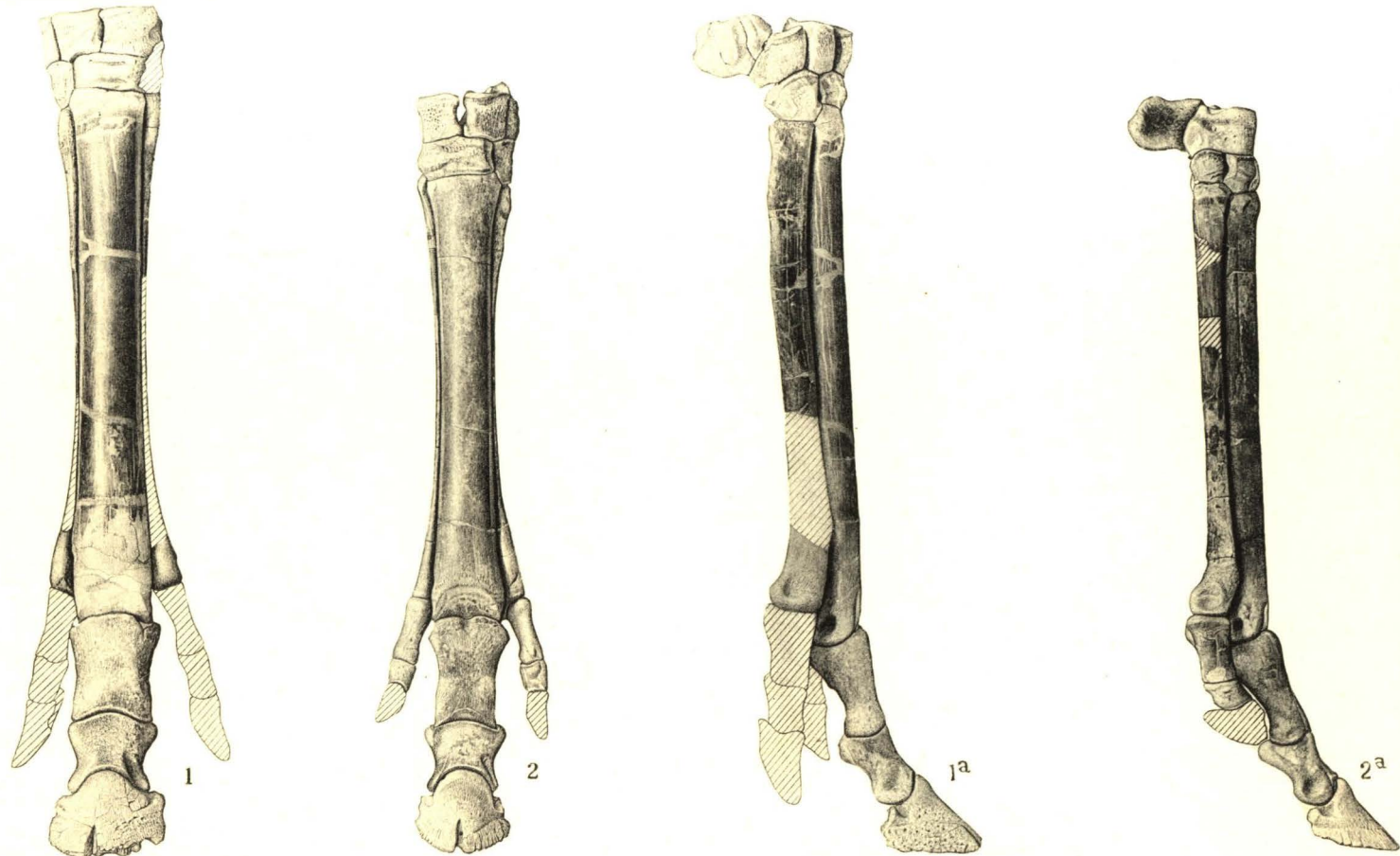
FIGS. 6, 6a. No. 2843, upper milk dentition. Fig. 6, lateral view; fig. 6a, occlusal view.  $\times 0.5$ .

FIG. 7. No. 678, ramus and dentition, lateral view.  $\times 0.5$ .

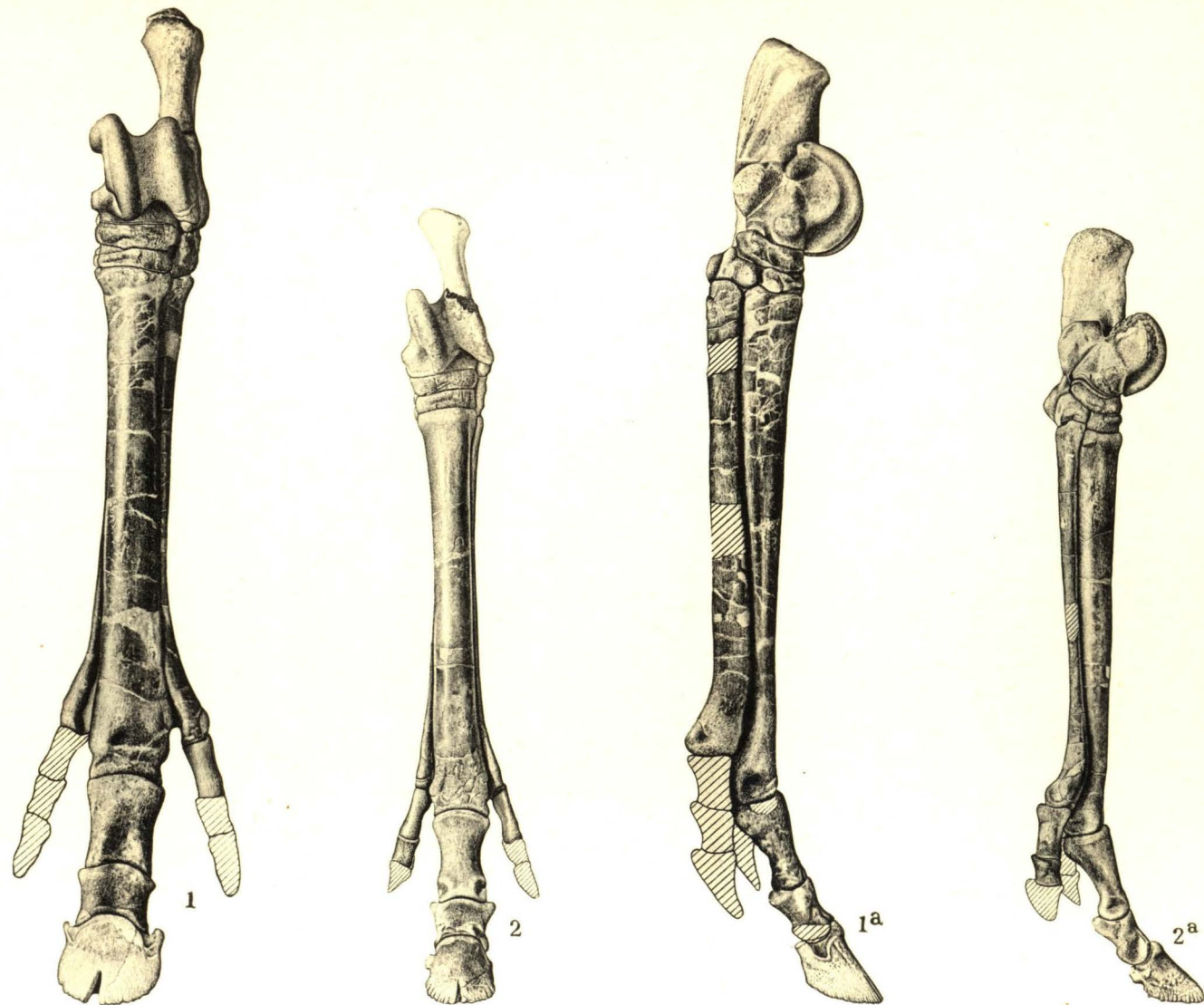
FIG. 8. No. 2834, ramus and dentition, lateral view.  $\times 0.5$ .

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



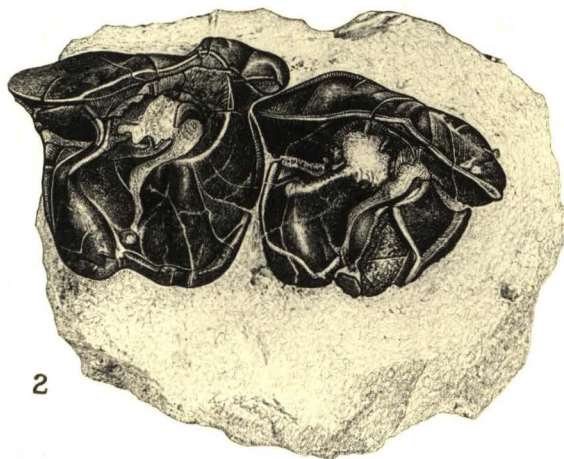
FIGS. 1, 1a. *Hypohippus* near *affinis* (Leidy). No. 2856, right manus. Fig. 1, anterior view; fig. 1a, lateral view.  
 FIGS. 2, 2a. *Merychippus calamarius* (Cope). No. 2854, left manus. Fig. 2, anterior view; fig. 2a, medial view.  
 All figures  $\times 0.4$



FIGS. 1, 1a. *Hypohippus* near *affinis* (Leidy). No. 2857, left pes. Fig. 1, front view; fig. 1a, medial view.  
 FIGS. 2, 2a. *Merychippus calamarius* (Cope). No. 2855, left pes. Fig. 2, front view; fig. 2a, medial view.  
 All figures  $\times 0.33$



1



2



3

*Aphelops? cristatus*, n. sp.

FIG. 1. No. 2806,  $P^1$ ,  $Dm^2$ – $Dm^4$ .

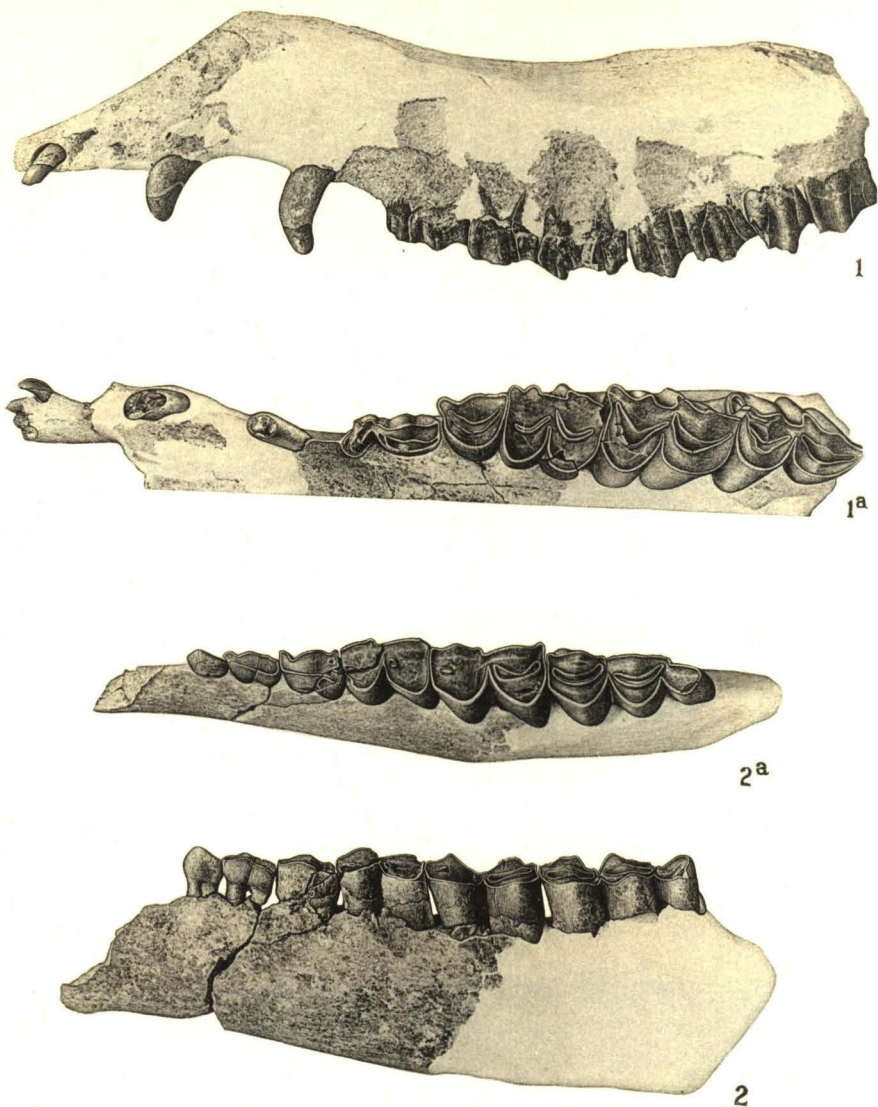
FIG. 2. No. 762,  $Dm^2$ – $Dm^3$ .

FIG. 3. No. 2809,  $Dm_2$ – $Dm_4$ .

Occlusal views,  $\times 0.67$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



*Alticamelus? stocki*, n. sp.

FIGS. 1, 1a. Type specimen, no. 1434, skull fragment with dentition. Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a. Paratype, no. 2819, ramus and dentition. Fig. 2, lateral view; fig. 2a, occlusal view.

All figures approximately  $\times 0.5$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada