THE SPECIES OF *NIMRAVUS* (CARNIVORA, FELIDAE)

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CONTENTS

INTRODUCTION

THE PRESENT PUBLICATION is intended as an essentially complete survey of *Nimravus* and a discussion of certain stratigraphical problems in South Dakota and Nebraska. In many respects it might be termed a progress report, that is, it represents the current status of my knowledge regarding the evolution of *Nimravus*, together with the many problems of phylogeny, correlation, taxonomy, and paleogeography. Our present understanding of felid relationships is subject to modification as additional raw materials become available; therefore, other interim or progress reports are to be expected subsequently from other students. The end to our search for a complete understanding of this multi-dimensional science is nowhere in sight.

Knowledge of the variability in modern felids has been an asset throughout the entire study. Many of the morphological differences observed and cited by earlier authors as criteria for distinguishing between certain fossil species and genera can be more logically interpreted as individual variations or sexual dimorphism in a single species. Many of the living felids are noted for their wide geographic distribution. For example, the jaguar is found today in an area covering some five million square miles.

Many authors have attached taxonomic significance to the size of the carnassial notch, but the rami representing submature to old individuals of *Dinictis felina* and *Nimravus brachyops* demonstrate beyond doubt that the width of the notch gradually increases as the individual ages. Presence or absence of the serrations on the posterior border and lingual keel of the canine has also been cited as a feature of taxonomic value, but the denticulate border may be obscured by advanced age or the enamel on the canine can be removed by being chipped.

In some groups of fossil vertebrates there is an abundance of names and objects. However, in the fossil felids the former predominates in most instances. The exceptions to this are the large number of examples representing species of *Smilodon, Panthera, Dinictis,* and *Hoplophoneus. Nimravus brachyops* is represented by a greater number of ex-

amples than one might think. The present work represents the first time that all North American specimens were brought together for study.

Since the beginning of the present century no examples of *Nimravus brachyops* from the John Day have become part of any museum collection. Yet Sternberg, Wortman, Snook, Davis, Osmont, Day, and Condon met with singular success in this part of the Oregon Tertiary from 1874 to 1900. Why the earlier workers were more successful in obtaining representatives of this species is unknown to me. Cope described all but one of the species from the John Day.

Darton found and Lucas described the first example of *N. brachyops* in the Great Plains. Since 1898 the number of specimens has increased through the efforts of the University of Nebraska, South Dakota School of Mines, and Frick Laboratory field parties.

The lone example from California was described by Stock.

In only two instances, to my knowledge, do we have the desired association of the skull and the postcranial elements. Because of this and the fragmentary condition of these partial skeletons little can be written about the comparative morphology of *Nimravus*. This lack of preservation or association should not appear abnormal, because similar conditions exist in most other felid genera.

During the late Oligocene in the Great Plains, *Nimravus* and *Pogonodon* appear to have been the dominant genera of felids. *Dinictis* and *Hoplophoneus* were in the minority as far as our knowledge goes to date. Our present information on *Eusmilus*, as the name has been previously used, does not permit a definite statement.

That part of the Sespe formation in California which is late Oligocene in age has yielded only two genera of felids—*Nimravus* and "*Hoplophoneus.*"[1]

To date we know nothing of *Dinictis* and

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[1] Stock described *Nimravus meridianus* and *Hoplophoneus belli* from Kew Quarry. Regarding the latter, I do not believe the species is correctly allocated, and it should be compared with *Eusmilus bidentatus* from Quercy.

Hoplophoneus in the early Miocene deposits of the Great Plains. The occurrence of *Pogonodon* is questionable. *Nimravus*, based on the number of specimens, was the dominant genus.

From the John Day of Oregon we seem to have four valid genera. *Nimravus* is the most common form, followed by *Pogonodon, Dinaelurus,* and *Eusmilus.*[1]

Appreciation is expressed to Dr. Glenn L. Jepsen for his patience and timely guidance throughout the course of this work. As part of an extensive review of the Felidae, Dr. Childs Frick has very kindly made available his collection of Oligocene and early Miocene felids for consideration at this time. The specimens have proved most valuable, and his financial assistance has made it possible to continue the investigation. Drs. Erling Dorf, B. F. Howell, and F. V. Van Houten advised and constructively criticized the manuscript. Various problems relating to the Oligocene stratigraphy and nomenclature have been profitably discussed with Messrs. Morris F. Skinner and Charles H. Falkenbach. They have also provided many data for the specimens collected by them and their associates. Dr. H. M. Martin, the School of Veterinary Medicine, University of Pennsylvania, examined the thin sections of the mandibular torus.

Assistance provided by the William Berryman Scott Fund has made it possible to examine the types and referred examples presently under consideration.

The photographic work has been accomplished by Mr. W. S. Starks. The library facilities in the American Museum of Natural History and at Princeton University were used to the greatest extent. To the respective staffs, my thanks are given for all assistance. The discussions with the late Dr. John T. Zimmer on taxonomic problems were most helpful. Mr. Floyd Blair of the Frick Laboratory and Mrs. R. H. Nichols of the Ameri-

can Museum of Natural History were most helpful in locating specimens. Thanks are due to the numerous collectors whose field investigations have resulted in vastly increasing the data for the described species.

It has been necessary to examine the felid collections in many institutions throughout the United States. For the cooperation extended, my thanks go to the following people for the loan of various specimens: Drs. George Gaylord Simpson and Harold E. Anthony, the American Museum of Natural History; Dr. Childs Frick, Frick Laboratory, the American Museum of Natural History; Dr. C. Bertrand Schultz, University of Nebraska State Museum; Dr. Glenn L. Jepsen, Princeton University; Dr. James D. Bump, South Dakota School of Mines and Technology; Dr. L. S. Cressman, Museum of Natural History, University of Oregon; Dr. C. Lewis Gazin, United States National Museum; Dr. Joseph T. Gregory, Peabody Museum of Natural History, Yale University; Dr. H. G. Richards, Academy of Natural Sciences of Philadelphia; Dr. Robert P. Sharp, California Institute of Technology; Drs. R. A. Stirton and D. E. Savage, Museum of Paleontology, University of California; and Dr. Robert W. Wilson, Museum of Natural History, University of Kansas.

The observations recorded on the following pages are essentially correct. However, some of the interpretations can be verified or refuted only by additional raw material or the reëxamination or interpretation of the data available to me. The responsibility for all errors is mine.

Essential information regarding each species is given in a standardized sequence which is self-explanatory: Accepted name and synonyms, with citations, type, syntypes, and lectotype (chosen wherever syntypes were originally used) or neotype, hypodigm, age and locality, and diagnosis. The necessary association of catalogue number, object, locality, rock unit, or time rock is presented under the heading hypodigm. The word "hypodigm," as herein used, means all the specimens referred to a species. Those items considered as essential for genera are also given. Additional information, such as changes in the allocation of the specific name, morphological description, reasons for syn-

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[1] *Eusmilus* is used here as the correct name for *Hoplophoneus cerebralis* Cope. Stock's "*H.*" *belli* and the species described by Cope seem to be congeneric. The type is the only known example in each instance. I have compared Cope's type with the figures and description of *Eusmilus bidentatus* (Piveteau, 1932), and the suggested allocation of the North American species seems reasonable.

onymy, and views on affinities are considered in the discussions.

As a result of continued research in the different divisions of the biological sciences, type terminology or nomenclature has become so complex that it tends to exemplify overspecialization. For example, Frizzell (1933) and Fernald (1939) list, define, and give the author for more than one hundred type terms. In this instance, at least, it seems that confusion and misunderstanding increase in direct proportion to the magnitude and complexity of the terminology. Simpson's (1940; 1945, pp. 26–33) discussion of type concepts merits the serious study of every student of taxonomy. Another very useful and recent discussion is that of Mayr, Linsley, and Usinger (1953).

The following are recognized as useful and necessary:

TYPE: As herein used, the term refers to either the type species of a genus or the type specimen of a species. It is evident that the word may have the same connotation as "generotype" or "holotype." Regarding "genotype," the International Commission for Zoological Nomenclature recommends that the term not be used because of possible confusion with the same word as used in genetics.

SYNTYPE: One of several coordinate specimens or species given equal value as types in the original proposal of a specific or generic name.

LECTOTYPE: A syntype (specimen or species) selected by the first reviser to serve as the type specimen for a species or as the type species for a genus.

NEOTYPE: This term is used for a substitute specimen, proposed under prescribed conditions for a type that is lost.

A considerable number of synonymous terms have been proposed for the various parts of felid teeth. For example, in the upper carnassial the paracone has been identified as the "parametacone," "protocone," and "amphicone"; the parastyle has been known as the "prostyle"; "tritocone" and "metastyle" have been used in place of the name "metacone"; and "protocone" and "deuterocone" have been used for the same structure. The terminology of the lower carnassial is fairly well standardized, although there has been

some confusion between the talonid and metaconid. Except in one instance, no disagreement has occurred in the usage of the terms "paraconid" and "protoconid" on the M_1.

In the description of P^3 and P_{3-4} the most prominent cusp has been termed "paracone" ("parametacone," Wood) and "protoconid," respectively. For the greatest part, the names "anterior" and "posterior" accessory cusp have been used for any additional structure adjacent to the paracone and protoconid. This noncommittal nomenclature can serve a distinct purpose, but in some felid genera it adds to the existing confusion.

The dental nomenclature used herein follows Wood (1927) and Butler (1946). "Talonid" is a term for the most posterior part of M_1, and it may represent the entoconid, the hypoconid, or the hypoconulid of an early tribosphenic molar.

Normal wear on the carnassials varies with the age of each individual and is indicated by W (unworn or very slightly worn) to W4 (extremely worn). These symbols are most applicable to M_1, but difficulty will be experienced in any attempt to apply them too rigidly because the process of wear is continuous. In a large sample of one population, there will be little difference between individuals classified as W and those representing W1. The same is true for W1 to W4. The degree of ossification at the sutures of a skull has been considered as a possible means of determining relative age, but several postmortem processes which cause separation of the various bones discourage its use.

Examples of W and W4 are represented in figure 2.

The terms "jaw" and "ramus," as herein used, are synonymous. "Mandible" refers to the left and right ramus when articulated or associated.

All measurements are recorded in millimeters.

Abbreviations used in the text and tables are:

L, length
W, width
ca., approximate
N, number of specimens measured
OR, observed range
M, arithmetic mean

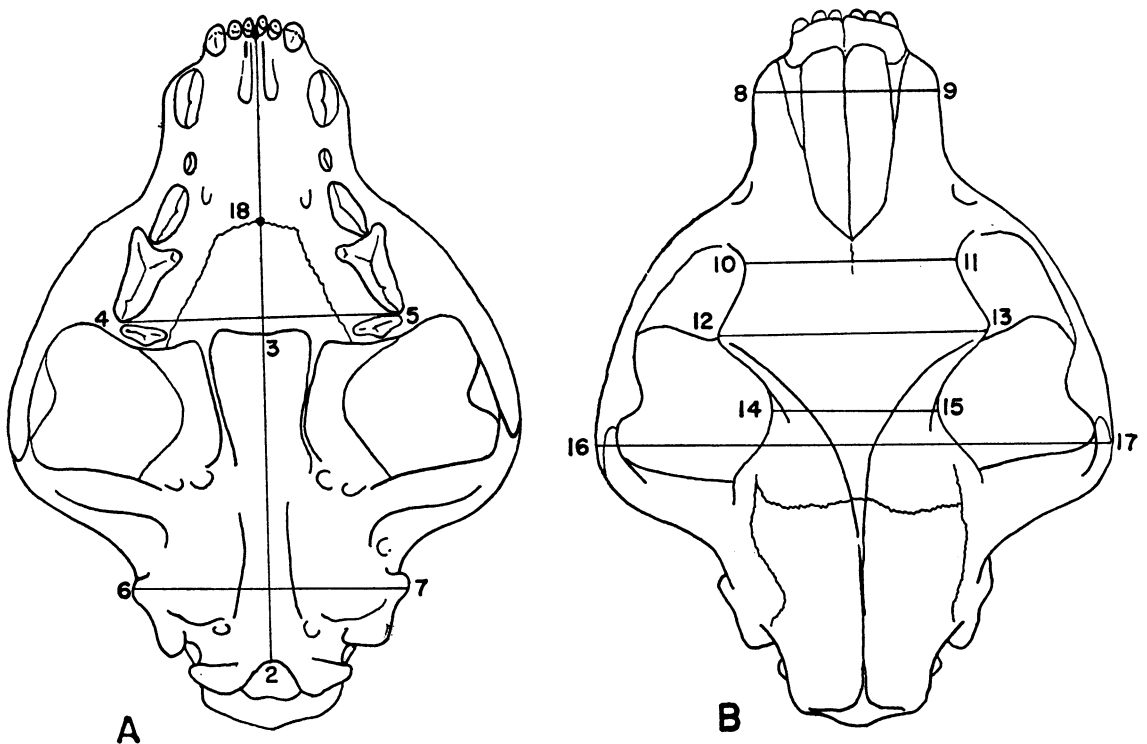As illustrated in figure 1, some of the points

FIG. 1. Idealized diagram of a felid skull, showing the location of measurements. A. Dorsal view. B. Ventral view. *Key:* 1–2, prosthion–basion; 1–3, prosthion–staphylion; 4–5, width at posterior part of P^4; 6–7, width at mastoid processes; 8–9, rostral width; 10–11, interorbital breadth; 12–13, breadth at postorbital processes; 14–15, breadth at postorbital constriction; 16–17, breadth across zygomata; 2–18, basion to maxillary-palatine suture; 1–18, prosthion to maxillary-palatine suture.

of measurement are set forth on an idealized diagram of a felid skull. The following measurements are also used:

C/–P^4
P^{3-4}
LP^4
WP^4
LP^3
LC/
WC/

The locations of specimens are abbreviated as follows:

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

A.M.N.H.: M., the American Museum of Natural History, Department of Mammals

C.I.T., California Institute of Technology

M.C.Z., Museum of Comparative Zoölogy at Harvard College

P.U., Princeton University Geological Museum

S.D.S.M., South Dakota School of Mines and Technology

U.C.M.P., University of California, Department of Paleontology

U.N.S.M., University of Nebraska State Museum

U.O., University of Oregon, Museum of Natural History, Condon Collection

U.S.N.M., United States National Museum, Division of Vertebrate Paleontology

Y.P.M., Yale University, Peabody Museum of Natural History

Doubtful assignments are indicated by a question mark after the part of the name to which doubt relates. A question mark in front of the generic name indicates that both the generic and specific names are in doubt (Schenk and McMasters, 1948).

The photographs of certain specimens have been reversed for the purpose of uniformity. Wherever this occurs, it is indicated in the explanation to the plate or figure.

STRATIGRAPHY AND STRATIGRAPHICAL NOMENCLATURE

ACCORDING TO PARRISH (1915, p. 60), the White River Badlands of South Dakota were first discovered in 1746 by the de la Verendrye brothers, French-Canadian explorers who made their way westward as far as the Big Horn Mountains in what is now Wyoming. Before the arrival of these explorers, the area was known to various Indian tribes.

In 1846 Hiram A. Prout, of St. Louis, sent to Dana and Silliman of Yale College a cast of a remarkable fossil that he had received from an acquaintance residing at one of the trading posts of the St. Louis Fur Company on the Missouri River. Prout's brief notes and a sketch were published in the American Journal of Science (1846, pp. 288–289). The following year Prout stated that this fossil was found in the "Mauvais Terre, on the White River, one of the western confluents of the Missouri" (Prout, 1847). This was the famous specimen described by Prout as a "gigantic *Palaeotherium*" (lower jaw of a brontothere) and was the first scientific account of a specimen from the area later to be known as the Big Badlands. In 1847 Leidy described certain fossils that had been collected and sent in by employees of the American Fur Company. Shortly thereafter Hayden, Meek, Owen, Evans, and Culbertson conducted explorations in South Dakota. Marsh and Cope began their studies of the Nebraska, Colorado, Wyoming, South Dakota, and North Dakota White River faunas and deposits about 1873. Since that time many institutions have obtained large collections, and the stratigraphic and paleontological results have been presented in numerous publications, varying from brief notes to monographs. The detailed history of the explorations has been discussed by O'Hara (1920), Osborn (various dates, especially 1929), Scott and Jepsen (1936), MacDonald (1951), and others.

Meek and Hayden recognized and named the White River sediments as a distinct sequence of rocks in the Big Badlands of South Dakota. In 1862 they used the name for about 1000 feet of white and light-drab claystone, with minor amounts of sandstone and fresh-water limestone. The fossils listed by these writers, which were described by Leidy and others, are for the most part characteristic of the Oligocene as it is presently delimited. In Leidy's time, and for some time after that, it was customary to refer the White River sediments to the Miocene epoch. Stratigraphers and paleontologists have generally restricted the usage of White River to the Oligocene as either a formation, a group, or a series. The White River as used by Meek and Hayden probably included deposits now considered Miocene or Pliocene in age.

Prior to 1938 the following subdivisions of the White River group had been recognized in Nebraska and South Dakota:

Brule formation
  Protoceras-Leptauchenia beds
  Oreodon beds
Chadron formation
  Titanotherium beds

The lowest Tertiary rocks in northwestern Shannon (formerly Washington) County, South Dakota, were named after the most abundant and characteristic fossil, *Titanotherium* Leidy, 1852. Meek and Hayden designated these deposits the *Titanotherium* beds about 1857. Hatcher's (1893) threefold division of the *Titanotherium* beds was based primarily on faunal evidence, and Osborn (1929) did not question the data provided by Hatcher. Clark (1937) demonstrated the discrepancies in Hatcher's concept of the faunal zones and Osborn's interpretation of the titanothere lineages.

It is difficult to trace the exact history of the use of the term "*Oreodon* beds," but it is a modification of Meek and Hayden's Turtle bed or Turtle-*Oreodon* bed.

Wortman proposed a threefold division of the White River in 1893: *Titanotherium* beds, *Oreodon* beds, and *Protoceras* beds. The last-named were to include the upper part of the sediments previously allocated to the *Oreodon* beds. Osborn's (1909) division of the White River approximates the following:

Leptauchenia zone
  Leptauchenia clays, 100 feet
  Protoceras sandstone, 50–75 feet
Oreodon zone
  Upper, 100 feet

Middle, 75–100 feet
Lower nodular layer, 10–20 feet
Lower, 70 feet–*Metamynodon* sandstone, 70 feet
Titanotherium zone
Upper, 30 feet
Middle, 100 feet
Lower, 50 feet

The *Oreodon* beds in the Big Badlands have a thickness of about 200 feet. They are composed of arenaceous claystones, lenticular sandstones, conglomerates, and layers of nodules or concretions. The general color is a yellowish gray buff, but horizontal banding is present in shades of red, brown, or green. The amount of calcium carbonate cement ranges from 10 to 15 per cent in the clays to 30 per cent in the nodules (Bump, 1951). The lithology and stratigraphy of the lower, middle, and upper *Oreodon* beds of the Big Badlands have been described by Sinclair (1921), Wanless (1922, 1923), Bump (1951), and others.

Overlying the upper *Oreodon* beds are the *Leptauchenia* beds (including most of the *Protoceras* sandstones and conglomerates) varying from 60 to 200 feet in thickness. The contact of the *Leptauchenia* beds with the underlying sediments has been described by Wanless (1923, pp. 226–227, pl. 1, fig. 1). Wherever this "marker" bed is absent, the determination can be established best by the fauna, and *Leptauchenia* is the most distinctive fossil. The *Protoceras* channel sandstone and conglomerate generally occur in the lower and middle part of the *Leptauchenia* beds, and their lithology is subject to considerable variation (see Wanless, 1923, p. 229). At the head of Quinn Draw, northeast of Indian Stronghold, the *Protoceras* channels have cut into the upper *Oreodon* beds. Adjacent to and above the *Protoceras* channels are bedded siltstone, fine-grained sandstone, and nodular buff siltstone. The uppermost part of the *Leptauchenia* beds (see Wanless, 1923, pl. 7, fig. 1; and Bump, 1951, fig. 7) is noted for the occurrence of a grayish white ash which can be recognized at many localities in the Big Badlands and averages about 35 feet in thickness. The authors who use the terms "zone" or "beds" recognize this ash as the top of the *Leptauchenia* zone or beds, but, as many collectors have observed, *Leptauchenia* is quite abundant throughout the sediments 200 or more feet in thickness above the ash. The writer's collecting in the *Leptauchenia* zone has been at Cedar Pass, The Pinnacles, Wolf Table, Cedar Butte, Sheep Mountain, Quiver Hill, and other localities. The exact number of specimens of *Leptauchenia* that have been collected is not known, but their remains are equally numerous above and below the ash. The term "beds," when preceded by the name of an organism, obviously means beds (rocks or sediments) in which that particular plant or animal is found. Therefore, "*Leptauchenia* zone" is synonymous with "*Leptauchenia* beds," and these names should logically refer to all rocks in which *Leptauchenia* occurs—a much greater thickness of sediments than that allocated by most authors when they use these terms. The fact must be realized that the true limits of *Leptauchenia* are not known and probably never will be known.

Such terms as "*Titanotherium* zone," "*Oreodon* zone," and "*Leptauchenia* zone" (including *Protoceras* channel sandstone and conglomerate) have a certain amount of utility. The term "beds" is not part of the formal stratigraphic nomenclature but may be, when certain requirements are met (Ashley *et al.*, 1933, art. 16).[1]

The concepts associated with faunal zones are useful, but the actual ranges of genera are unknown. Redefinitions based on subsequent discoveries or more thorough investigations expand or contract the generic and specific ranges, and names may be changed through synonymy. *Oreodon* Leidy, 1851, has been reduced to synonymy with *Merycoidodon* Leidy, 1848, and *Titanotherium* Leidy, 1852, according to Simpson (1945), equals *Menodus* Pomel, 1849, but the synonymy of *Titanotherium* is considerably more complex than that of *Oreodon* and *Merycoidodon*. One of the best examples demonstrating the unwieldiness of generic names, when used to identify a particular zone, has been presented by

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[1] From the simple and straighforward publication by Ashley and his co-authors, there has occurred a pronounced change of thought concerning stratigraphic classification and nomenclature. Persons interested in the changes during the past 25 years are referred to the bibliography in Frye (1958). The American Commission on Stratigraphic Nomenclature is preparing a recommended code of classification and nomenclature.

Jepsen (1940, p. 235): "Willmarth (1938, p. 861) follows Osborn (1929, pp. 57–59, 68 seq.) in calling the Gray Bull beds the '*Systemodon-Coryphodon-Eohippus* zone.' *Systemodon* Cope, 1881, has been reduced to synonymy with *Hyracotherium* Owen, 1840, and Hay in 1899 proposed *Homogalax* for the species other than the genotype, which had been placed in *Systemodon*. *Eohippus* Marsh, 1876, is a synonym of *Hyracotherium*. Thus, the Gray Bull beds might be called the *Homogalax, Coryphodon, Hyracotherium* zone, but only the first of these genera is diagnostic of the zone; *Coryphodon* occurs lower and higher and *Hyracotherium* is also found in higher levels."

The names "*Titanotherium*," "*Oreodon*," and "*Leptauchenia*" beds or zone have been applied to the White River deposits in Nebraska before and after Darton proposed the Chadron formation and Brule clays. Darton (1899, p. 736) wrote: "The White River beds in their extension from South Dakota into Nebraska, present some difference in stratigraphic range and relations. They expand considerably and include, at their top, beds which appear not to be represented in the typical regions. Accordingly, to afford distinct definitions for the members in Nebraska, I have introduced the designation *Brule clay* and separated the underlying *Titanotherium* beds as the *Chadron formation*." The section from Round Top to Adelia (Darton, 1899, p. 757, fig. 226), Sioux County, Nebraska, is now considered the type of the Brule formation. Darton mentioned a marked unconformity at the top of the Brule, but the present writer has made a detailed examination of the area, and no evidence could be found to substantiate this observation.

Since the time Darton described the Brule clay, it has become known as the Brule formation, and the White River has usually been changed to a higher category (group or series). For many years the lower part of the Brule was described as the *Oreodon* beds or zone and the upper part as the *Leptauchenia* beds or zone. Schultz and Stout (1938) replaced *Oreodon* and *Leptauchenia* zone ("as they occur in northwestern Nebraska" quoted below) for a more desirable and practical nomenclature. They wrote: "A

lithologic break, and in places a significant and pronounced disconformity, divide the Brule formation into two widespread lithologic units, which, it is suggested, should now be considered as stratigraphic members. For the lower or *Oreodon* zone portion of the Brule formation as it occurs in northwestern Nebraska the name Orella member is proposed. Typical exposures of this member, attaining a thickness of about 150 feet, are to be found about 2½ miles southwest of Orella station in the vicinity of Toadstool Park, in sec. 8, T. 33 N., R. 53 W., Sioux County, Nebraska. Here the Orella member is disconformably overlain by the massive clays [siltstone and tuffaceous siltstone] of the upper or *Leptauchenia* zone portion of the Brule formation for which the name Whitney member is proposed. This member occurs typically and attains a thickness of about 290 feet to the east [southeast] of Toadstool Park along the escarpment near Round Top, in sec. 16 and 21, T. 33 N., R. 53 W."

The original description of the Orella and Whitney should have been more complete. Until agreement is reached on the upper limits of the Whitney and the nature of the division between the Orella and Whitney, it is difficult to use the names, even in the type area, with any degree of precision.

Oligocene and Miocene sediments are well exposed in the valley of the North Platte River in western Nebraska and eastern Wyoming. The deposits which have yielded remains of titanotheres are very similar lithologically to the Chadron formation as it is exposed along the White River. At Scotts Bluff Monument the lower part of the section appears similar to the type Orella member, and above this there are beds resembling the Whitney. These have been referred to the Brule formation. An erosional unconformity separates the Brule in this area from the overlying Gering formation (Darton, 1899). As yet a reappraisal is not available of Darton's (1899, 1903, 1905) investigations. Lugn (1939) has mentioned the amount of relief on the Brule surface as being more than 250 feet. Some individuals have considered Scotts Bluff Monument as the type Gering but Schlaikjer (1935) wrote: "I have inspected the Gering formation at the type locality south of Gering, Nebraska, and have made a

preliminary study of it from that locality westward to Wyoming. It appears to be nothing more than an exaggerated eastward extension of the same conditions that prevail at the base of the lower Harrison in the Goshen Hole area. In other words, the Gering represents only a local phase of the lower Harrison and ought not to be regarded as a separate formation any more than the *Metamynodon* or *Protoceras* channel phases of the Brule should be regarded as distinct formations of the Oligocene." Schlaikjer's opinion of the Gering does not seem to be justified, for nowhere does he mention an examination of the type Harrison.

Galbreath's (1953) study has added much to our knowledge of the Oligocene stratigraphy and paleontology in northeastern Colorado. The historical aspect of the North Dakota Oligocene sediments and the results of stratigraphical studies have been presented by Skinner (1951).

It is highly desirable, in view of the presently accepted standards of stratigraphic nomenclature, to improve the terminology used for the White River deposits in South Dakota. It is not feasible for the writer to make the changes at this time, but the application of geographic names of formational or member status to the South Dakota deposits would clarify some of the existing problems. The present status of our knowledge does not warrant the usage of "Orella member" and "Whitney member" in the Sheep Mountain-Cuny Table area. New names, of member rank, to replace "*Oreodon* beds" and "*Leptauchenia* beds" seem most desirable. Wood (1949, p. 86) is of the opinion that Orella and Whitney can be used satisfactorily in South Dakota as witnessed by his statement: "The Oligocene of the Big Badlands of South Dakota and of northwestern Nebraska forms one essentially continuous unit, in which formations, members, facies, and faunal zones generally extend across the State line as though it had not formed a barrier during Oligocene time. The fact that type localities are scattered on both sides of the line is of no possible interest to anyone, unless, conceivably, to a state geologist." No one has published the information that demonstrates the relationships of the rocks between northern Sioux and Dawes counties, Nebraska, and

Pennington and Shannon counties, South Dakota. Until this has been accomplished, it does not seem practical to use the names "Orella" and "Whitney" in the Big Badlands. Lithologically, the *Oreodon* beds in the Sheep Mountain and Cedar Pass areas are not similar to the Orella member in Nebraska, except in a very general way. Moreover, there is less similarity between the Whitney in Nebraska and the typical *Leptauchenia* beds in central and northern Shannon County.

Most of the correlations between the two states have been based on faunal similarities. According to most authors, the faunas from the Orella and *Oreodon* zone are so similar that they seem to represent equal amounts of time. The Whitney, on faunal evidence, has been considered equivalent in time to the *Leptauchenia* beds (as used by Wanless, 1923, and presumably Wood, *et al.*, 1941, followed Wanless' usage). In 1941 the provincial age names "Chadronian," "Orellan," and "Whitneyan" were proposed by Wood and his coauthors (1941, pp. 17, 27, 36), and they correctly interpreted the original description of the Orella and Whitney to indicate an equivalence with the *Oreodon* and *Leptauchenia* beds. As the committee stated on page 27: "Oreodon beds = middle White River = lower Brule = Orella member, Orellan"; and on page 29: "*Protoceras-Leptauchenia* beds = upper White River = upper Brule = Whitney member, Whitneyan." It is evident from the preceding that the provincial terms have been limited by events (rocks), and from the original description of the Orella and Whitney members there seems to be only one possible interpretation: Orella member is equivalent to the *Oreodon* zone or beds, and Whitney equals the *Leptauchenia* zone or beds.

In 1944 Morris F. Skinner obtained a well-documented collection of fossils from the type Orella and Whitney for the purpose of comparison with a similar collection from South Dakota. The oreodonts indicate the equivalence in time of the upper *Oreodon* beds with the lower part of the Whitney. This correlation is expressed in a preliminary chart by Falkenbach and Schultz (1951, p. 49), and the evidence substantiating the correlation is to be presented later by these writers. The accuracy of the correlation is not questioned,

but (on pp. 49–50) these writers quote Schultz and Stout (1938): "For the lower or *Oreodon* zone portion of the Brule formation as it occurs in northwestern Nebraska the name Orella is proposed . . . Here the Orella member is disconformably overlain by massive clays of the upper or *Leptauchenia* zone of the Brule formation for which the name Whitney member is proposed." Then they add the following comment: "No mention was made by these writers [Schultz and Stout] of how the Nebraska Brule deposits correlated with those of South Dakota . . . Undoubtedly the names 'Oreodon zone' and 'Leptauchenia zone' should not have been applied to the Nebraska area because there is a certain implication of correlation."

If it is assumed that agreement will be attained on the correlation of the upper *Oreodon* beds with the lower part of the Whitney, a problem in age terminology becomes apparent. Are the upper *Oreodon* beds and its fauna Orellan or Whitneyan? As mentioned above (Wood *et al.*, 1941), the Orella member and *Oreodon* beds are included in the Orellan; the Whitneyan included the Whitney member and *Leptauchenia* beds. As here used, the upper *Oreodon* zone is early Whitneyan in age. Bump (1951) has used the names "Orella member" for the *Oreodon* beds and "Whitney" for the *Leptauchenia* beds. Lower, middle, and upper Orella were synonymous with the threefold division of the *Oreodon* beds, and the discussion was limited to a general review of the South Dakota deposits. With the use of the correlation suggested by Falkenbach and Schultz, the upper Orella as used by Bump is equivalent faunally to the lower part of the Whitney in Nebraska but is not equivalent in time to the Whitney as he used it in South Dakota.[1]

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[1] Bump (1956) has proposed two new names for the rock units in the Big Badlands of South Dakota. The lower member of the Brule formation, which includes a major portion of the classic *Oreodon* beds, was designated the "Senic member." The upper member, which includes the *Protoceras* channels and part of the *Leptauchenia* beds (up to the base of the lower or white ash as exposed at Sheep Mountain) was designated the "Poleslide member." In the listing of specimens I have used the name "Poleslide."

Schultz and Stout (1955) have recently reviewed the classification of the White River sediments in western Nebraska.

As mentioned above, most authors have considered the white ash layer at Sheep Mountain as the top of the *Leptauchenia* beds. The stratigraphically higher sediments which are well developed at Cedar Pass, Cedar Butte, and 6 miles northeast of Imlay have been referred to the Rosebud beds and considered Miocene in age (Wanless, 1923). Matthew and Gidley (1904, pp. 245–246), in their original description of the Rosebud, wrote: "The lower formation above mentioned, for which we propose the local term *Rosebud beds*, is best exposed along the Little White River and in the vicinity of the Rosebud Agency. These beds closely resemble portions of the upper Oligocene beds, both in character and general appearance, except that they contain a little more sand." An understanding of the Rosebud as a lithic unit and its contained fauna must begin along the Little White River and in the vicinity of Rosebud, Todd County, South Dakota. In 1907 Matthew (p. 107) extended the name "Rosebud" to include certain deposits along Porcupine Creek in the southern part of Shannon County, South Dakota. This is not the type Rosebud as believed by some authors (for example, Wanless, 1923, p. 232). Until the type Rosebud is considered in its proper perspective, it is inadvisable at this time to include the rocks mentioned by Matthew in 1907, and by Wanless in 1923, as representative of the Rosebud.

The John Day felids here considered do not aid in refining the latest interpretation of the relationships between the Oregon deposits and various lithic units in the Great Plains. Two of the reasons for this are: (1) the scanty stratigraphic information available because most of the specimens were collected prior to 1910, and (2) no felids are known from deposits in the Great Plains that can be definitely identified as middle Arikareean, and only one specimen is known that is probably late Arikareean in age. Schultz and Falkenbach (1949, pp. 89–93) have reviewed the more important literature concerning the previous interpretations and conclude: "The examples [of Promerycochoerinae] from the John Day indicate a geologic age approximating that of the Harrison [late Arikareean] of Nebraska and Wyoming. The forms considered as coming from middle John Day are

comparable in size with those from the Harrison, while specimens from the upper John Day are somewhat larger. This may indicate that the upper John Day represents a portion of that interval of time which must be accounted for between the final deposition of the Harrison formation and the beginning of the Marsland sedimentation in the Great Plains. The upper John Day oreodonts, however, show closer affinities to the Harrison forms than to those of the Marsland [early Hemingfordian]." These writers also point out the absence of *Leptauchenia* and *Cyclopidius* in the John Day and the Harrison formations. It is very possible that the scanty fauna and flora from the lower part of the John Day are late Oligocene in age, and that part of the middle John Day is earlier in age than late Arikareean.

A restudy of the entire fauna from the John Day and the early Miocene deposits in the Great Plains may prove necessary, if we are to refine the present estimates of relative age.

SYSTEMATICS

ORDER **CARNIVORA** BOWDICH, 1821

FAMILY **FELIDAE** GRAY, 1821

SUBFAMILY **NIMRAVINAE** TROUESSART, 1885

NIMRAVUS COPE, 1879

Nimravus COPE, 1879, Proc. Acad. Nat. Sci. Philadelphia, vol. 31, p. 168.

Archaelurus COPE, 1879, Amer. Nat., vol. 13, p. 798a.

Ailurictis TROUESSART, 1886, La grande encyclopédie, Paris, vol. 1, p. 954 (= *Aelurogale* Filhol, 1872, Ann. Sci. Geol. Paris, vol. 3, art. 7, p. 10; 1872, Compt. Rendu Acad. Sci. Paris, vol. 75, pt. 2, p. 94; nec *Ailurogale* Fitzinger, 1869).

TYPE: *Machairodus brachyops* Cope.

TYPES OF SYNONYMS: Of *Archaelurus*, *A. debilis*. Of *Ailurictis*, *A. intermedius*. Of *Aelurogale*, *A. intermedia*.

INCLUDED SPECIES: *Nimravus brachyops*, *N. intermedius*, *N.? jourdani*, and *Nimravus* sp.

DISTRIBUTION: Late Oligocene and early Miocene of North America, middle or late Oligocene of Europe, and Oligocene of Asia.

DIAGNOSIS: The postparietal pit is small, and a preorbital fossette is present. The superior surface of the malar anterior to the orbit forms a flattened surface which dips anteriorly and somewhat laterally. Length of the alisphenoid canal is reduced. Posterior part of the palatine is anterior to M^1. The P^3 is high crowned, with no parastyle. The upper carnassial has a very slight development of what might be termed a parastyle, anterior border emarginate, with the degree of emargination increased by continued wear, and the protocone is anteriorly directed. The upper molar appears transversely reduced, primarily because the inclination of the crown (with the palate considered as a horizontal plane) is 80 to 90 degrees. The flange is not developed on the jaw, and the inferior border of the ramus is convex below the diastema and M_2. A digastric crest is present. A unique bilateral structure occurs on the external alveolar border below the posterior part of P_4 and M_3 and is herein designated the alveolar torus. P_{3-4} are high-crowned teeth, and the paraconid on P_3 is variable in occurrence and degree of development. M_1 lacks a metaconid but retains a well-developed talonid.

The dental formula varies from $\frac{3131}{3121}$ to $\frac{3141}{3133}$.

DISCUSSION: *Nimravus* is a well-established generic name in paleontological literature. As a result of two proposals approved and adopted by the Fourteenth International Congress of Zoology, the name may be supplanted by an earlier one which has been considered, in most instances, as preoccupied. The first proposal (Hemming, 1953, p. 78) is as follows: "A generic name is not to be treated as a homonym of another such name if it differs from it in spelling by even one letter." The second (pp. 80–81) is that names based on words transliterated into the Latin alphabet from other alphabets and differing in spelling only by reason of difference of transliteration are not to be treated as homonyms of one another.

In 1869 the name *Ailurogale* was proposed by Fitzinger (type: *Felis planiceps* Vigors and Horsfield, 1828; one of the recent felids of Borneo and Sumatra).[1]

In 1872 the name *Aelurogale* was proposed by Filhol (type: *Aelurogale intermedia* Filhol) for a jaw from the Phosphorites du Quercy. Subsequently Trouessart (1886) recognized the similarity between these two generic names, said that Filhol's was preoccupied, and proposed the name *Ailurictis* (type: *Aelurogale intermedia* Filhol). Most students of felid evolution and taxonomy have followed Trouessart.

The adoption of the two above-mentioned proposals now permits recognition of the name *Aelurogale*. However, in the interests of preserving a well-established name and for universality and stability of nomenclature, I prefer to retain the name *Nimravus*. Prior to the publication of the Copenhagen Decisions, the articles and opinions of zoological nomenclature would require that the name *Nimravus* be used for a taxon previously known as *Pogonodon* and the name *Archaelurus* for that previously known as *Nimravus*. Such a change in concept of names is most

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[1] *Felis planiceps* has been used, according to Palmer, Kretzoi, and others, as the type of the following genera: *Aelurin* or *Ailurin* Gervais, 1855; *Ictailurus* Severtzow, 1858; *Ailurogale* Gill, 1871; and *Plethaelurus* Cope, 1872. Severtzow's name is that currently recognized as valid.

undesirable and would lead to a greater confusion in felid nomenclature than that which already exists.

A complete review of the use of *Nimravus*, *Archaelurus*, and *Ailurictis* (= *Aelurogale*) as valid or synonymous names is unnecessary, but what follows serves to illustrate the diverse uses of names and differing opinions. Adams (1897), for example, considered *Archaelurus*, *Ailurictis*, and *Nimravus* as synonymous, hence names for the same sort of animal. Presumably Matthew (1910) recognized *Archaelurus*, *Ailurictis*, and *Pogonodon* as subgenera of *Nimravus*, but his taxonomic treatment of these names is difficult to understand. Kretzoi (1929) and Simpson (1945) thought that *Ailurictis*, *Nimravus*, and *Archaelurus* were distinct genera, but Piveteau (1932) was of the opinion that these three generic names represented the same sort of animal. Scott and Jepsen (1936) believed that the names *Archaelurus* and *Nimravus* represented distinct genera.

Archaelurus was differentiated from *Nimravus* principally on the following structures. The first upper and second lower premolars are present, and the posterior part of the upper canines lack serrations in *Archaelurus*. In this instance the presence or absence of P^1 and P_2 does not, in my opinion, constitute a valid generic separation, because the teeth are variable in occurrence and may be either single or double rooted. The canine in the type is imperfectly preserved, but, from what remains, minute serrations can be seen at the base of the posterior border. Its reduced development is attributed to sexual dimorphism and imperfect preservation.

Adams (1897) and Piveteau (1932) have discussed the similarity of *Ailurictis* and *Nimravus*. There is nothing in the various descriptions and figures which leads me to believe that these two names represent different sorts of animals. The specimens and casts also substantiate this conclusion.

The general morphology of the skull, jaw, and postcranial elements has been described by Cope, Merriam, Eaton, Filhol, Piveteau, and others. Hence it is not repeated here, and the following remarks pertain to those structures not considered in sufficient detail by previous authors.

The groove anterior to the masseteric fossa (paralleling the ascending ramus) and the lingual pit on the zygomata show a greater degree of development in *Nimravus* than in other groups of Oligocene and early Miocene felids. Wherever that area of the jaw posterior to M_2 is present, this groove has been observed, although its extent dorsoventrally, its depth and general degree of development, is somewhat variable. The lingual zygomatic pit may have served as an added area for the origin of the masseteric muscle. If this interpretation is correct, it would seem that additional leverage could be provided for the scissor-like action of the carnassials.

A flange, typical of many North American Oligocene felids, is absent. The rounded ridge outlining the anterior end of the lateral surface of the ramus extends downward and backward, swinging around the antero-inferior angle to form a crest on the inferior surface. This crest extends backward to a point below the posterior end of P_2 or P_3, and posterior delimitation of the crest is difficult if not impossible as it becomes part of the inferior ramal border. Adjacent to the crest and towards the symphysis, a depression is present, which is assumed to be the anterior insertion area of the digastric muscle. The term "digastric crest" is suggested for the feature. When the mandible is viewed inferiorly, the crests continue lingually towards one another. Subsequent students must decide if this structure could represent an early stage in the development of a flange or the late stage in the reduction of a flange.

The unique bilateral structure on the external alveolar border (posterior P_4–M_3) of *Nimravus* has received at least four different names and is herein called, to avoid any pathological implication, the "alveolar torus."

Cope (1879d, p. 372) said of the alveolar torus: "The osseous callus below the true molars is a remarkable character, unique in the order of the Carnivora. It is evidently a provision against the weakness of the mandibular rami, at the point of greatest strain." In a subsequent description of *Archaelurus debilis*, Cope (1880, p. 842) again mentioned that the structure strengthened the mandible, and in a detailed description of *A. debilis* (A.M.N.H. No. 6930) in 1884 (p. 955), he stated: "The osseous tuberosity beneath the

inferior true molar teeth is a most peculiar feature. It looks as though the external alveolar border has been greatly extended, and then folded down and attached to the side of the ramus. Its free borders are a vertical and a horizontal, which are connected by a rounded angle. The ascending border passes into the base of the coronoid by a roughened ridge. The inferior border and external face are also slightly roughened." In his discussion of *Nimravus gomphodus*, Cope (1884) observed that the " . . . exostosis below the last two molars is wanting. It is represented by a thickening of the external alveolar border, which is larger in some specimens than in others." How the exostosis could be absent (the usual meaning of "wanting") and still be variable in size is difficult to understand. Cope's remarks were about the type of *Nimravus gomphodus*, A.M.N.H. No. 6933, in which the torus is reduced but not absent.

Merriam (1906) limited his remarks on the exostosis to a few comments on the variable size of the structure.

In 1910, Matthew's examination of *Nimravus* prompted the following comments: "Several of the species from the John Day beds show a peculiar bony outgrowth beneath the lower carnassial, correlated with a precocious reduction of the upper and enlargement of the lower canines, and designed apparently to shift the support of the lower carnassial outwards in such a way as to afford space for a more powerful masseter attachment than the construction of the skull and jaws would otherwise admit. This constitutes a precocious adaptation functionally analogous to the widening of the palate and jaws of the modern Felidae."

Eaton (1922) described four the the John Day felids in the Marsh Collection and mentioned the exostosis as strongly developed in three specimens of *Nimravus debilis* and slightly developed in a fourth individual of *Nimravus*.

Filhol, in 1872 and subsequent publications, described the remains of *Aelurogale intermedius* from the French Oligocene (Phosphorites du Quercy). Piveteau (1932) has figured and discussed additional specimens with the following comments (p. 116) on the alveolar torus: "*Un curieux caractère des mandibules de* Nimravus, *caractère signalé*

depuis longtemps par Cope dans les espèces américaines, c'est la présence, sous la tuberculeuse et le talon de la carnassière, d'une exostose dont la nature et la signification sont difficiles à préciser (Voir pl. II, fig. 8). Peut-être faudrait-il y voir une disposition en relation avec l'insertion du masséter. En tout cas, sa présence sur toutes les mandibules des Phosphorites, comme sur toutes celles de l'Amérique du Nord, ne permet pas de lui attribuer caractère pathologique."

Stock (1933) in describing the only known species of *Nimravus* from the Sespe formation (Kew Quarry) stated: "No extensive exostosis is evident along the alveolar border of M_1 in the Sespe specimen. A prominent lateral border below and in front of the alveolus for the second molar may represent 'the beginning of an exostosis. In view of the frequent development of a swelling along the lateral border of M_1 and M_2 in the John Day representatives of the *Nimravus* group, the absence of a clear example of exostosis in the Sespe specimen appears rather unique. As indicated, there is a suggestion of an increase in size of surface in the enlarged ridge, but the latter is of short extent and in front of this the lateral wall is flattened. Merriam has shown that the exostosis is of variable size in specimens from the John Day beds. Although moderately developed in *N. confertus*, the exostosis is much better defined in this form than in *N. meridianus*." Although the torus is not extensively developed on the holotype of *meridianus*, it is definitely present.

MacDonald (1950) has mentioned the variable development of the exostosis.

Development of the torus is usually confined to the area along the alveolus from the midpoint of M_1 posteriorly to M_{2-3}, but a slight swelling is present between the posterior part of P_4 and the central part of M_1 in A.M.N.H. No. 6934. The smallest size of the torus is seen in S.D.S.M. No. 348 (type of *Nimravus bumpensis*, Whitneyan) in which it appears as a low, slightly swollen ridge extending somewhat posteriorly to M_2 and anteriorly to the central part of M_1. The extreme condition is present in A.M.N.H. No. 6930 (type of *A. debilis*, Arikareean). In this specimen the inferior border of the torus extends ventrally about one-third of the distance to the inferior border of the ramus, and
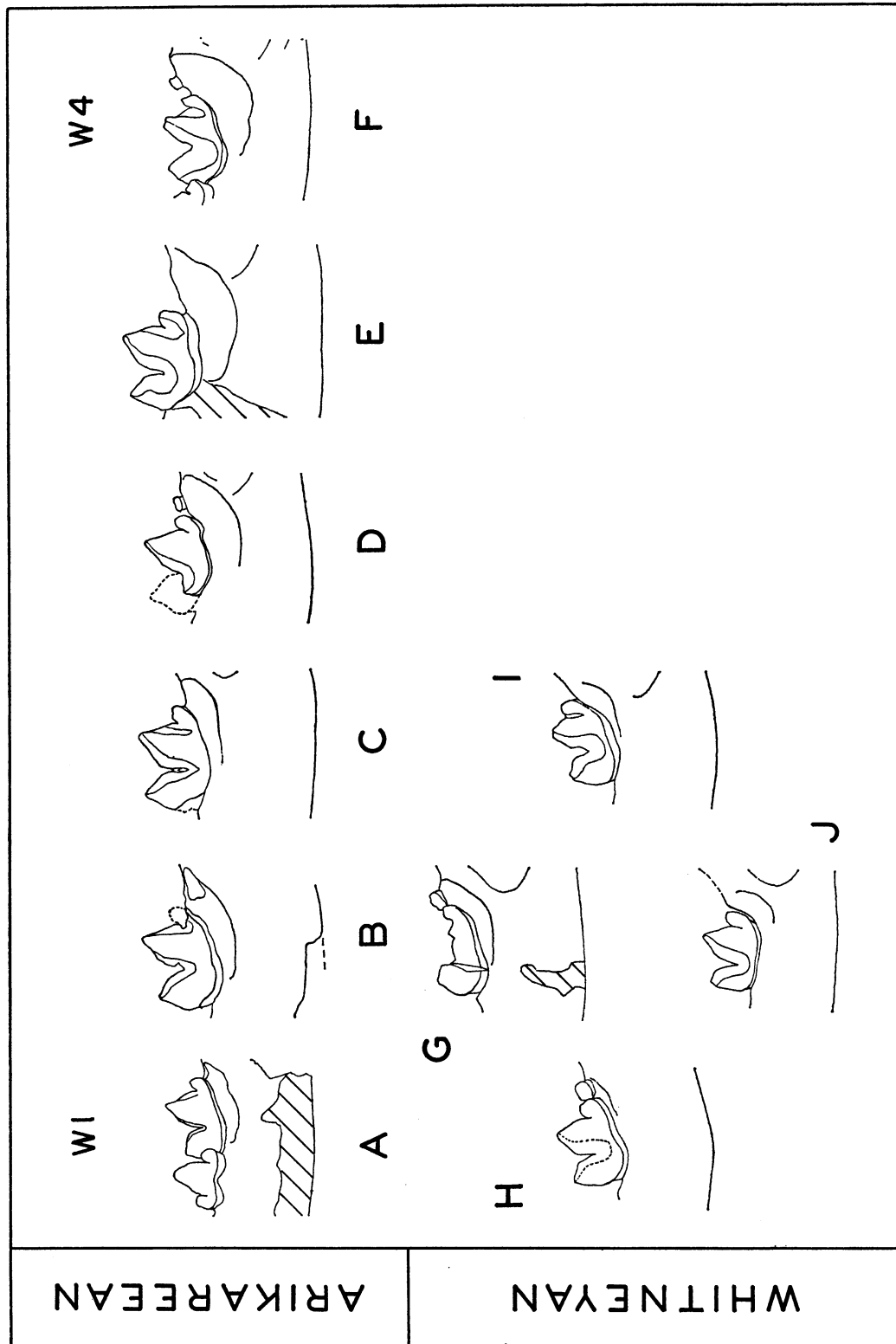
FIG. 2. Rami of *Nimravus brachyops*, showing increase in size of alveolar torus with increase in wear on the lower carnassial. Late Oligocene of Nebraska, South Dakota, and California; early Miocene of Oregon. A. A.M.N.H. No. 6936, left jaw. B. U.C.M.P. No. 1680, left jaw. C. A.M.N.H. No. 6935, right jaw, reversed. D. A.M.N.H. No. 6934, left jaw. E. U.C.M.P. No. 1679, left jaw. F. A.M.N.H. No. 6930, left jaw. G. S.D.S.M. No. 4053, right jaw, reversed. H. S.D.S.M. No. 348, left jaw. I. C.I.T. No. 462, right jaw, reversed. J. U.N.S.M. No. 25491, left jaw. ×0.6.

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the posterior border covers the anterior part of the masseteric fossa. On the surface of the torus numerous minute holes are present. The cross section of the structure shows that these are foramina filled with matrix which penetrate to the inner cancellous bone. In some examples the surface is striated, and the combination of foramina and striae gives the surface a rugose appearance.

The development of the torus controls the elevated position of M_{2-3} with respect to M_1 in two ways: (1) the crown height of the M_2 is increased above the talonid of M_1, and (2) the M_2 becomes tilted forward to a greater degree as the torus increases in size.

Development of the alveolar torus occurs in all but one of the North American examples of *Nimravus brachyops*.

Although the size of the torus varies among individuals, the pattern of its development in North America seems to be correlated with individual and geological age. It is smaller in the less mature and geologically older individuals and, conversely, larger in the more adult and geologically younger individuals.

All the most recent faunal studies indicate an early Miocene age for the middle and upper John Day, hence later in age than the sediments herein allocated to the Poleslide member (Whitneyan). Wherever it is possible to compare similar wear on the M_1 of specimens from the John Day with those from the upper part of the Brule formation in the Great Plains, the torus is seen to be larger in the Oregon specimens. As far as can be determined, this correlation of individual age and geological time has not been previously noted. The present study represents the first time all the groups of individuals recognized as species of *Nimravus* have been brought together for examination. The size of the torus and wear on the M_1 is presented in plate 10 and text figure 2.

Although the torus has been the subject of much consideration, no function can as yet be ascribed to it. Some hypotheses, however, may be discarded as improbable.

One possibility is that the torus might have served as an insertion area for a muscle or muscles. The origin of the buccinator muscle in living felids is on the outer surface of the maxillary bone in the depression between the infraorbital foramen and P^2. The fibers pass ventrally, diverging and mingling with those of the deep part of the orbicularis oris. Jayne (1898) indicates a posterior extension of the buccinator, a muscle that aids in raising the upper lip, to the area below M_1.

The possibility exists that either the temporal or the masseteric muscle was inserted at the area occupied by the torus, but this is not the case in modern felids. If the assumption is made that the torus served as a surface for a muscle insertion, it is difficult to explain the increase in the size of the structure. Any part of the masseteric muscle inserted below M_1 would seriously impede the process of chewing, because in this area there occurs the scissors-like action of the carnassials. All the chewing depends on the proper occlusion between the premolars and molars, with P^4 and M_1 being most effective in shearing the food. All the living felids can perform the process of chewing without the added insertion of the masseteric below the M_1, and there seems little reason to believe that such an insertion would be necessary for *Nimravus*.

A lingual mandibular torus occurs in *Sinanthropus pekinensis* and several races of historic and modern man. According to Weidenreich (1936, p. 55), " . . . the percentage of its occurrence is slightly higher in prehistoric or historic man than in present man." Of the tubercular type, Weidenreich (*loc. cit.*) stated: "A cross section was made in which was found that the whole protuberance was of very hard and ivory-like consistency. It is strictly confined to the compact layer of the inner side of the jaw . . . and not mingled with any spongy substance at all. Microscopic examination reveals that it consists throughout of a highly dense lamellar bone provided with very scanty and narrow Haversian canals . . . the tori mandibulares in *Sinanthropus* and recent man are completely identical in their position, appearance and internal structure."

Fürst (1908) believed that the mandibular torus in man is the result of mechanical causes. Hrdlička (1910) considered the structure to be the result of extraordinary pressure along the teeth most concerned in chewing. Hooton (1918) objected to these interpretations and thought that it would be natural to expect the concentration of the bony reënforcement opposite the molars

rather than opposite the premolars. Weidenreich (*ibid.*, p. 58) did not accept any of the previous interpretations and (p. 60) stated, "As to the tubercule type . . . I am inclined to accept the suggestion that the protuberances and pillars left during the reduction which the formerly much bulkier alveolar process has undergone in the course of human evolution."

Matthew (1910) suggested that the alveolar torus in *Nimravus* served to strengthen the jaw. If this were true, it would seem that the structure would be approximately the same size in all specimens regardless of individual age. Furthermore, strengthening could be more satisfactorily accomplished by a deepening and thickening of the ramus.

The possibility has been considered that the torus might represent a diseased condition. It is difficult to determine which authors have entertained this idea because of the failure in most instances to state what was meant by the use of the term "exostosis." According to some texts the word "exostosis" can be used for any bony swelling or protuberance. Others use the term for a bony tumor. Two thin sections of the torus have been prepared from A.M.N.H. No. 6934. The slides have been examined by Dr. H. M. Martin, the School of Veterinary Medicine, Dr. Boyle, the Dental School, and others, all at the University of Pennsylvania. Dr. Martin[1] has mentioned that all who have examined the section of the torus agreed that it appeared to be normal bone. With this statement in mind, it appears useless to speculate about the number of interesting possibilities that could be developed if the internal structure of the torus suggested a pathological condition.

As yet I can offer no satisfactory explanation as to the function of the alveolor torus. Whether or not there is a genetic relationship between this structure and the apparently abnormal development of the bony growth in the external auditory meatus remains to be determined.

Nimravus has been commonly cited as representing the ancestral group that gave rise to *Pseudaelurus*. For example, Matthew (1910) stated that "The series *Dinictis-Nimravus* [including *Archaelurus* and *Pogonodon*

as synonyms]-*Pseudaelurus-Felis* are in direct succession, structurally and geologically." This lineage has been widely accepted although it is not without opponents. At no time did Scott (1913; 1936, *in* Scott and Jepsen; 1937) include *Nimravus* in the lineage leading to *Pseudaelurus* and *Felis* but suggested that *Nimravus* survived in the late Miocene and Pliocene, then became extinct, or continued to the Recent to provide an ancestor for *Acinonyx*. *Nimravus* is unknown in the late Miocene or Pliocene of North America, and its relationship to *Acinonyx* is very questionable. Two of the possible interpretations about *Nimravus* subsequent to the John Day (Arikareean) are that it became extinct and that the group continued during the balance of the Miocene but has yet to be discovered. When this occurs the range would be extended, but until then it seems reasonable to conclude that *Nimravus* became extinct in North America during the late Arikareean or early Hemingfordian.

Hibbard (1934) suggested that *Nimravus* was the ancestral group that gave rise to *Pratifelis* (Hemphillian). However, first, *Pratifelis* is inadequately known; second, the hiatus in our knowledge of known ranges is great; and, finally, the significant structural similarity between the two genera, if any, is indeed obscure.

Nimravus was a relatively conservative genus, that is, the structural changes that occurred during the late Oligocene and early Miocene were very slight. In order to conform with Matthew's idea of a direct relationship to *Pseudaelurus*, the necessary structural changes would have had to occur during a relatively short span of time. Perhaps there was a pre-Arikareean dichotomy, but again there seems to be no evidence to substantiate such an interpretation. The same is equally true for *Dinictis* and *Nimravus*, as a late Eocene or early Oligocene dichotomy is a possibility, but we lack the supporting evidence. At present I cannot suggest much that would clarify the ancestral-descendant relationships of *Nimravus*. *Dinictis* is a possible ancestor, but *Pseudaelurus* is an improbable descendant. In my opinion the taxon *Nimravus* approaches a real and definite evolutionary entity, not an artificial category or an arbitrary bundling together of diversified species.

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[1] Personal communication.

Because the continent on which *Nimravus* originated is unknown and the temporal relationships between the two hemispheres are questionable, it is not possible at the present time to determine whether the migration took place from Europe to Asia and thence to North America or if it occurred in the reverse direction. However, a land bridge or connection between North America and Asia must have existed during the Oligocene to permit the spread of the genus from one continent to another.

Nimravus brachyops Cope, 1878

Machairodus brachyops COPE [in part], 1878, Proc. Amer. Phil. Soc., vol. 18, p. 72.

Hoplophoneus brachyops COPE [in part], 1879, Amer. Nat., vol. 13, p. 197.

Nimravus brachyops COPE [in part], 1879, Proc. Acad. Nat. Sci. Philadelphia, vol. 31, p. 170.

Archaelurus debilis COPE, 1879, Amer. Nat., vol. 13, p. 798a; 1880, Amer. Nat., vol. 14, p. 842, figs. 3-4; 1884, Rept. U. S. Geol. Surv. Terr. (Hayden), vol. 3, p. 953, fig. 37, pl. 72.

Nimravus gomphodus COPE, 1880, Amer. Nat., vol. 14, p. 884, fig. 7; 1884, Rept. U. S. Geol. Surv. Terr. (Hayden), vol. 3, p. 964, pl. 72a, figs. 1-3, pl. 73.

Nimravus confertus COPE, 1880, Amer. Nat., vol. 14, p. 884, fig. 10; 1884, Rept. U. S. Geol. Surv. Terr. (Hayden), vol. 3, p. 972, pl. 71a, fig. 17.

Nimravus brachyops Cope, MIVART, 1881, The cat, p. 434, fig. 186.

Dinictis major LUCAS, 1898, Amer. Jour. Sci., ser. 4, vol. 6, p. 399.

Archaelurus debilis major MERRIAM, 1906, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 5, p. 39, fig. 15, pl. 4.

Archaelurus debilis merriami HAY, 1930, Publ. Carnegie Inst. Washington, no. 390, vol. 2, p. 543.

Nimravus meridianus STOCK, 1933, Publ. Carnegie Inst. Washington, no. 440, p. 39, pl. 3, fig. 1.

Nimravus bumpensis SCOTT AND JEPSEN, 1936, Trans. Amer. Phil. Soc., vol. 28, pt. 1, p. 147 pl. 21.

Nimravus altidens MACDONALD, 1950, Jour. Paleont., vol. 24, p. 601, fig. 1.

Dinictis cyclops Cope, HOUGH, 1953, Prof. Paper U. S. Geol. Surv., no. 243-G, p. 105, fig. 9.

LECTOTYPE: A.M.N.H. No. 6935. Partial right ramus, W1-2, John Day formation, probably collected by Sternberg. Although Cope (1878, p. 72) mentioned a "left mandibular ramus with parts of the skeleton," a right ramus, A.M.N.H. No. 6935, is the only specimen from the Cope Collection to agree with the description and dimensions. I interpret the word "left" as a *lapsus calami* on the part of Cope. As additional evidence to support the opinion that this specimen is one of the syntypes, the American Museum records, presumably based on information from W. D. Matthew, cite the first mention of this specimen as "Cope, 1878, Proc. Amer. Phil. Soc., vol. 18, pp. 72-73." The "parts of skeleton" mentioned by Cope have not been definitely located except for a left femur. The degree of association between the jaw and femur is, of course, unknown to me. In the explanation to plate 74, Cope (1884) mentioned that the two objects were from one individual, and presumably this portion of the rear limb can be considered as part of the lectotype. In view of any future taxonomic difficulties and also those that are discussed on the following pages, I designate the jaw, A.M.N.H. No. 6935, as the lectotype of *Nimravus brachyops* (Cope, 1884, pl. 74, fig. 1; Matthew, 1910, fig. 7B), because it is the only one of the syntypes that agrees with Cope's (1879b) diagnosis.

SYNTYPES: In addition to the lectotype, Cope had the following at hand: A.M.N.H. No. 6931, skull W2 and A.M.N.H. No. 6940, left maxilla and skeletal fragments. All specimens are presumably from the middle or upper part of the John Day formation and were collected by C. H. Sternberg, 1878. Several isolated teeth were mentioned by Cope as belonging to the species (*Machairodus brachyops*, 1878), but these have not been located. A.M.N.H. No. 6939, a partial skull, is another one of the syntypes and is herein allocated to one of the species of *Pogonodon*.

TYPES OF SYNONYMS: Of *Archaelurus debilis*: A.M.N.H. No. 6930, skull, mandible, and cervical vertebra, W4, middle or upper part of the John Day formation, Turtle Cove, Grant County, Oregon; collected by J. L. Wortman, 1879; female. Of *Nimravus gomphodus*: A.M.N.H. No. 6933, skull, left ramus, cervicals, and two dorsals, W1-2, middle? part of the John Day formation; collected by J. L. Wortman, 1879; male. Of *Nimravus confertus*: A.M.N.H. No. 6936, partial left ramus, W1, middle part of the John Day formation, Turtle Cove, Grant County, Oregon; collected by J. L. Wortman, 1879; female?

Of *Dinictis major*: U.S.N.M. No. 3957, partial skull and skeleton, W2–3, Gering formation, Birdcage Gap, southwest of Bridgeport, Morrill County, Nebraska; collected by N. H. Darton. According to the original description by Lucas a ramus was also found. The jaw in question has yet to be relocated; female. Of *Archaelurus debilis major*: U.C.M.P. No. 1681, skull, W1–2, middle part of the John Day formation, U.C.M.P. locality V898, Logan Butte, Crook County, Oregon; collected by Davis and Osmont, 1900; male.

Of *Archaelurus debilis merriami*: The type of this name is the same as that of *A. debilis major*, U.C.M.P. No. 1681. Of *Nimravus meridianus*: C.I.T. No. 462, partial right ramus, W2–3, Kew Quarry, upper part of the Sespe formation, Los Posas Hills, Ventura County, California. Of *Nimravus bumpensis*: S.D.S.M. No. 348, skull and mandible, W1–2, Poleslide member, Brule formation, east side of Cuny Table, Shannon County, South Dakota; female. Of *Nimravus altidens*: S.D.S.M. No. 4053, partial right ramus, W2, Poleslide
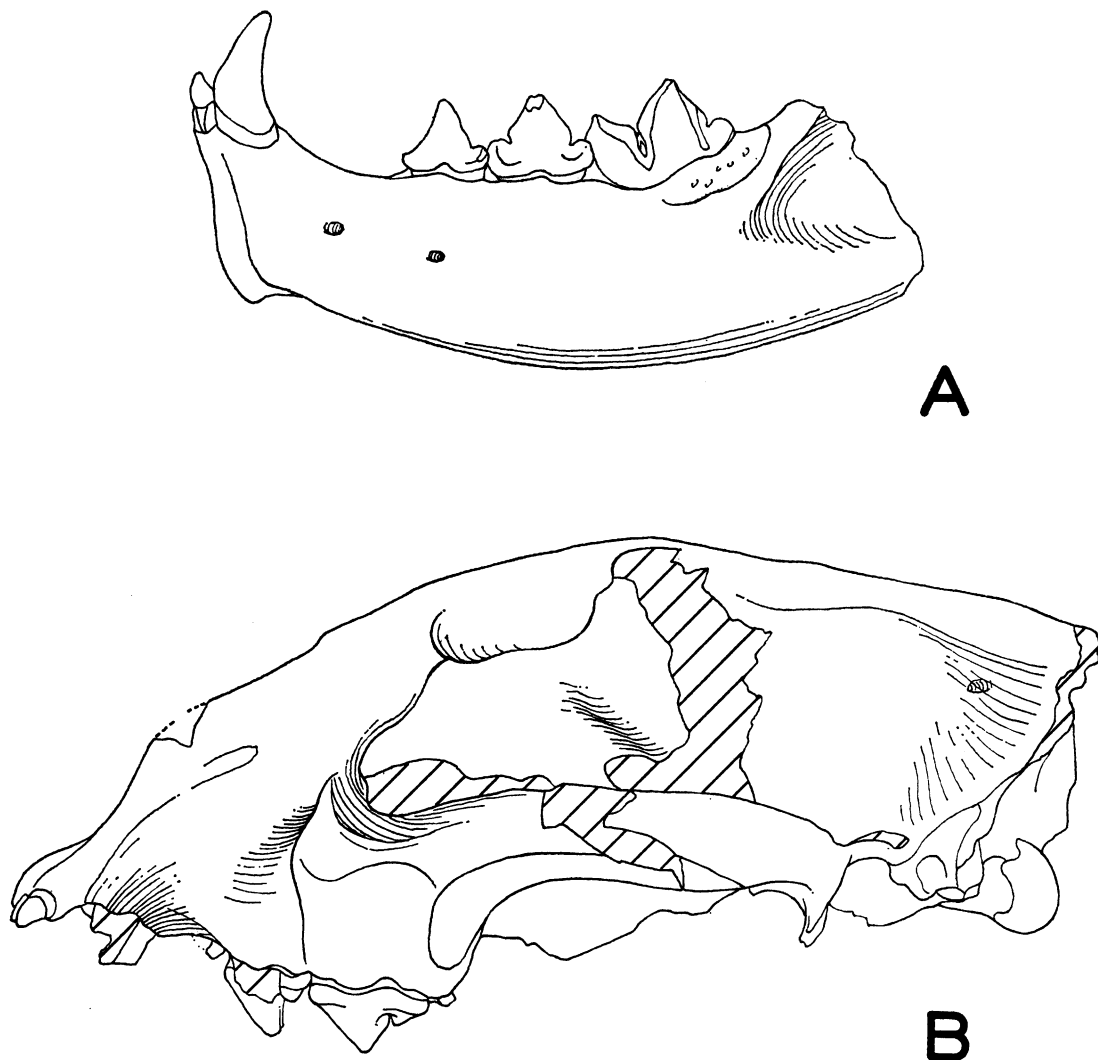

FIG. 3. *Nimravus brachyops* Cope. A. Lectotype, A.M.N.H. No. 6935, right jaw, reversed. B. Syntype, A.M.N.H. No. 6931, skull. Lateral views. Both from the John Day formation, Oregon. ×¾.

Fig. 4. *Nimravus brachyops* Cope. Syntype, A.M.N.H. No. 6940, left maxilla, lateral view; John Day formation, Oregon. ×¾.

member, Brule formation, *Protoceras* channel, 7 miles east of Rockyford, Shannon County, South Dakota.

HYPODIGM: In addition to the above types the following are herein allocated:

MIDDLE AND UPPER PART OF THE JOHN DAY FORMATION, OREGON

FEMALES: Y.P.M. No. 10046, skull and mandible; Y.P.M. No. 10519, partial skull and mandible; A.M.N.H. No. 6931, skull, W2.

MALES: Y.P.M. No. 10517, skull, mandible, and cervicles, W3; Y.P.M. No. 10044, skull, mandible, and atlas, W3; Y.P.M. No. 10045, skull and mandible; Y.P.M. No. 14388, partial skull, mandible, metatarsals, W2; Y.P.M. No. 14385, partial skull, M_1, phalanges; U.C.M.P. No. 1679, partial left ramus, W2–3.

SEX UNKNOWN: U.O. No. 607, skull and mandible, W2; U.S.N.M. No. 16558, skull, W1–2; Y.P.M. No. 14384, partial skull; U.O. No. F-683, partial skull; A.M.N.H. No. 6932, partial skull and postcranial elements; Y.P.M. No. 14394, partial skull, W1–2; U.C.M.P. No. 1685, right maxilla, W1–2; A.M.N.H. No. 6940, left maxilla and postcranial elements; Y.P.M. No. 14932, left maxilla and teeth, W1–2; Y.P.M. No. 14391, partial left and right rami, W2–3; U.C.M.P. No. 1680, partial left ramus and vertebra, W1; A.M.N.H. No. 6934, partial left ramus, W2; Y.P.M. No. 14393, partial left ramus, W3; Y.P.M. No. 14390, partial right ramus, W2–3; U.C.M.P. No. 2256, left pes; U.C.M.P. No. 110, tibia, caudals, metatarsals; Y.P.M. No. 14389, M_1, W1–2.

GERING FORMATION, NEBRASKA

U.N.S.M. No. 1091, skull, ulna, and partial humerus (the latter may represent another individual), probably male, W2–3, Morrill County

Locality 109, Black Hank Canyon, 3 miles west of Redington Gap, Morrill County.

BRULE FORMATION, WHITNEY MEMBER, NEBRASKA

U.N.S.M. No. 25491, partial skull and mandible, W2, from the type Whitney, about 2 feet above the top of the upper ash (see Falkenbach and Schultz, 1951, p. 49, fig. 2), Sioux County; U.N.S.M. No. 25744, partial skull, W2, about 50 feet below the lowest ash layer, north-northwest of Morrill County Locality 111, southeast of Bridgeport, Morrill County.

The John Day specimens were collected by Condon, Wortman, Sternberg, Snook, Davis, Osmont, and Day. The South Dakota School of Mines specimens were collected by James Bump.

AGE AND LOCALITIES: Whitneyan age: Poleslide and Whitney members of the Brule formation, upper part of the Sespe formation (Kew Quarry, Las Posas Hills); Nebraska, South Dakota, California. Arikareean age: Gering and John Day formations; Nebraska, Wyoming, and Oregon.

DIAGNOSIS: The only criteria available now for distinguishing between the three herein recognized species of *Nimravus* are their geographic distribution and difference in relative age. I cannot, with the available materials and excellent figures in Piveteau's study, distinguish any consistent morphological differences between *N. brachyops* and *intermedius*.

DISCUSSION: A critical reading of Cope's publications on various John Day felids demonstrates, in terms of modern taxonomy, that *Nimravus gomphodus* is not the type species of *Nimravus*, although it is commonly cited as such. The type is *Nimravus brachyops*.

The first felid from the John Day was described by Cope (1878, pp. 72–73) as *Machairodus brachyops;* no type was designated in this or subsequent publications; and four of the syntypes have been identified as follows: "This species . . . is represented in my collection by parts of two crania; by an entire cranium; by a left mandibular ramus with parts of the skeleton and by several isolated teeth." His remarks regarding one of the "crania" are as follows: "In the first cranium the sagittal crest is well developed. The canine tooth has an oval section at the base of the crown whose long diameter somewhat exceeds the distance between it and the ante-

TABLE 1

DIMENSIONS OF COPE'S "FIRST CRANIUM" OR "PARTIAL CRANIUM" (A.M.N.H. No. 6939)

	Cope (1878, pp. 72–73)	Present Author
Length of muzzle in front of canine	17.0	—
Diameter of canine at base		
Anteroposterior	18.0	19.0
Transverse	11.0	10.5
Distance from canine to "p.M.2" (P^3)	17.0	17.0

TABLE 2

DIMENSIONS OF COPE'S "SECOND SPECIMEN" OR "PARTIAL CRANIUM" (A.M.N.H. No. 6940)

	Cope (1878, pp. 72–73)	Present Author
Length of base of series to canine	62.0	ca. 60.0
Length of base of second premolar (P^3)	18.0	18.8
Length of base of sectorial (P^4)	25.0	ca. 25.0
Elevation to summit of infraorbital foramen	33.0	—

TABLE 3

DIMENSIONS OF COPE'S "SECOND" OR "ENTIRE CRANIUM" (A.M.N.H. No. 6931)

	Cope (1878, pp. 72–73)	Present Author
Total length of cranium	192.0	ca. 193.0
Greatest width of cranium	123.0	ca. 127.0
Length of dental series with C/	77.0	77.0
Diameter of C/ at base		
Anteroposterior	12.0	13.0
Transverse	8.0	ca. 8.0
Distance between C/ and second premolar (P^3)	19.0	17.0
Length of base of second premolar (P^3)	19.0	19.0
Length of base of sectorial	23.0	23.0

TABLE 4

DIMENSIONS OF COPE'S "MANDIBULAR RAMUS" (A.M.N.H. No. 6935)

	Cope (1878, pp. 72–73)	Present Author
Length of inferior dental series with /C	94.0	92.0
Length of diastema	25.0	ca. 24.0
Length of base of first premolar (P$_3$)	15.0	15.0
Length of base of sectorial	27.0	27.6
Depth of ramus below second premolar	32.0	31.0
Depth of ramus below superior canine	27.0	—

rior base of the second premolar [P³]. The infraorbital foramen is large." The dimensions listed by Cope for the "first cranium" or one of the "partial crania" are presented here in table 1. All the John Day felids in the American Museum of Natural History have been examined, and A.M.N.H. No. 6939, a rather fragmentary skull, is the only specimen that agrees with these dimensions, but it is difficult to determine precisely where Cope measured the length of the muzzle.

"The second specimen [Cope, 1878, p. 72], the left maxillary and part of malar bones with teeth, shows that the length of the base of the sectorial tooth equals the space between it and the middle of the first premolar. The superior aspect of the proximal portion of the malar bone is horizontal." The dimensions listed by Cope for the "second specimen" or one of the "partial crania" are presented here in table 2. A left maxilla now catalogued as A.M.N.H. No. 6940 is the only specimen that approximates the dimensions listed by Cope and agrees with his description.

Regarding the second cranium, Cope (1878, pp. 72–73) wrote: "The characters displayed by the second cranium ["entire cranium" above] lead me to suspect that it is that of a female. A striking feature of the superior dental series is the small size of the canine, which is also not much compressed at the base. As regards the cranium, the sagittal crest is only distinct over the posterior part of the brain case; the zygomata are not very widely expanded, and the muzzle is narrowed. The external infraorbital foramen is large." The dimensions given by Cope for this specimen are presented here in table 3. A.M.N.H. No. 6931 is the only skull that corresponds to the measurements and description.

Cope's comments (1878, pp. 72–73) regarding the jaw are as follows: "The mental border of the mandibular ramus is not flared downwards but is continuous, but the external is separated from the anterior and inferior faces by strong angles. The diastema is long. Three molars, all large; the first [P₃] without anterior basal tubercle, the second [P₄] with a large one. Sectorial tooth the longest, with well developed simple cutting heel." The dimensions given by Cope are presented here in table 4. A partial right ramus

now catalogued as A.M.N.H. No. 6935 is the only specimen that approximates Cope's dimensions and description. Although Cope mentioned "a left mandibular ramus with parts of the skeleton," this right jaw is the only one in the Cope Collection of the American Museum of Natural History to agree with his statement. I interpret the word "left" as a *lapsus calami* on the part of Cope. As additional evidence to support the opinion that this specimen is one of the syntypes, the American Museum records, presumably based on information from Matthew, cite the first mention of this jaw as "Cope, 1878, Proc. Amer. Phil. Soc., vol. 18, pp. 72–73." The records of this institution also cite the first mention of the other syntypes as the just-mentioned periodical.

It is my opinion that these four specimens, now numbered A.M.N.H. Nos. 6935, 6939, 6940, and 6931, constitute, in part, the basis for Cope's description of *Machairodus brachyops*. It is difficult to determine which postcranial elements were associated with the ramus, and to date only a left femur has been located. (Regarding this limb, see the remarks under the discussion of the lectotype.) The several isolated teeth mentioned by Cope have not been located.

The first taxonomic change occurred in February of 1879 (1879a), when Cope considered *brachyops* to have closer affinities with the various species of *Hoplophoneus* as indicated by the following note: "Fine specimens of the *Machairodus brachyops* Cope show that it possessed an inferior tubercular tooth. It therefore belongs to the genus *Hoplophoneus* Cope." No specimens were mentioned. If the "tubercular tooth" can be interpreted as M_2, Cope had at hand additional material from the John Day, as A.M.N.H. No. 6935 does not have an M_2 nor is there any indication of an alveolus. It should be noted that the presence of this tooth is not normal for *Hoplophoneus*. In 1884 Cope mentioned that this ramus was referred to *Hoplophoneus* because " . . . it is exceptionally without tubercular tooth." The lack of specific information permits only one reasonable interpretation—all the syntypes were considered by Cope under the name *H. brachyops*.

The next taxonomic change occurred in August of 1879 (1879b, pp. 168–169) when

the generic name *Nimravus* (p. 168) occurred for the first time in the literature. On the following page (p. 170) Cope cited [*Nimravus*] *brachyops* in a list of extinct and living felids. At this time (August, 1879) *Nimravus* was a monotypical genus, with the species *Nimravus brachyops* as its type. As long as *Nimravus* is recognized as a valid genus, or if it is considered a synonym, *N. brachyops* must be the type species, although most authors, for reasons unknown to me, have regarded *Nimravus gomphodus* (1880) as the type species.

Although Cope did not mention any specimens with this listing of the name *N. brachyops*, there is no indication that any of the syntypes were removed from the species.

Because the diagnosis of a genus and that of a species are the same for monotypical genera, Cope's diagnosis (no flange, premolars $\frac{2}{2}$) applies to both categories. Therefore, one or all of the objects should have the structures set forth as being diagnostic. In this instance the jaw is the only one of the syntypes that has no flange and two lower premolars. Cope's indication of two premolars in the superior dentition may be a *lapsus calami*, because three are present in the maxilla and the skull, P^2 and part of P^3 are present, and P^4 is missing in the partial skull. One of my reasons for selecting the partial jaw as the lectotype is that it is the only object that agrees with the diagnosis.

The next contribution by Cope to the felids of North America was in 1880. A.M.N.H. No. 6931 (Cope's "complete cranium" or "female" of 1878) was referred to *Archaelurus debilis*, as indicated in the following (1880, p. 843): "The first description of this species [*A. debilis*] was given by myself under the head of *Nimravus brachyops* (*Machaerodus brachyops*. Paleont. Bull. 30, p. 10, Dec. 1878), from a skull found by Mr. Sternberg, under the impression that it might belong to a female of that species. Subsequently, a nearly perfect cranium [A.M.N.H. No. 6930, the type of *A. debilis*] obtained by Mr. Wortman, demonstrated the distinctness of the animal both as to species and genus." A.M.N.H. No. 6935 was not mentioned in the 1880 publication, but it was removed from *brachyops* because Cope's statement in his discussion of the species, "Although I do not possess a mandible [of *brachyops*]," leaves

no doubt that the jaw had been removed and considered elsewhere, probably with *Nimravus gomphodus*, as the femur presumably associated with this jaw is figured (p. 844, fig. 6) as *N. gomphodus* (referred). A.M.N.H. No. 6940, the "left maxillary and malar bone with teeth," and A.M.N.H. No. 6939, the "partial cranium with the well developed sagittal crest" are mentioned under *Pogonodon brachyops*. Five vertebrae are figured as *P. brachyops*; these are at the present time numbered A.M.N.H. No. 6940. The association of the vertebrae and maxilla is explained by Cope in 1884. The description is complete enough to determine the presence of A.M.N.H. No. 6939 with *P. brachyops* by the following: "This species was the first of the Oregon felines of which bones were obtained. It was first sent here by Mr. C. H. Sternberg from the Truckee Miocene bad-lands of the John Day valley, Oregon . . . It [*brachyops*] differs from the species of that genus [*Nimravus*] and *Archaelurus* in the following points: (1) the truncate triangular post-tympanic process; (2) the transverse frontomaxillary suture; (3) the preorbital impressed depression; (4) the superior position of the postparietal foramen."

In 1884 Cope mentions all the syntypes. A.M.N.H. No. 6935 was definitely referred to *Nimravus gomphodus*, and, for the first time, the ramus was figured, and the associated femur illustrated again. Cope mentioned (1884, p. 964): " . . . an entire [much of the bone posterior to the alveolar torus is missing] mandibular ramus with all the teeth, and a femur both having been found lying close together in the rock." It cannot be proved that the femur and the jaw are parts of the same individual, and in such cases it is futile to speculate about the degree of association. It is difficult to interpret certain comments Cope made about *N. gomphodus*, but in the following excerpt from page 972, it is quite evident that A.M.N.H. No. 6935 was originally considered as an example of *brachyops*: "The first notice of this species [*gomphodus?*] was based on a mandible. As it is exceptionally without tubercular tooth [M_2], I referred it to the genus *Hoplophoneus*; and since its proportions are very similar to those of the *Pogonodon brachyops* [alias *M. brachyops*, *H. brachyops*, and *N. brachyops*], of which no

mandible had been found up to that time, I identified it with that species [*brachyops*]." Cope did not change the allocation of the other syntypes between 1880 and 1884, as A.M.N.H. No. 6931 is referred to *Archaelurus debilis*, and A.M.N.H. Nos. 6939 and 6940 are mentioned under *Pogonodon brachyops*.

Two of the syntypes (A.M.N.H. Nos. 6935 and 6931) have been removed from *brachyops*, and they are not the types of any later species, at least to and including the present report. The other syntypes, A.M.N.H. Nos. 6939 and 6940, remained with *brachyops*, and the species was allocated by Cope to *Pogonodon*. These syntypes are not the types of a subsequently described species, nor is *brachyops* the type species of *Pogonodon*. Cope's manipulation of specimens and species from 1878 to 1884 left *Nimravus* without a type species.

Although various nomenclatural codes were proposed following Linné's "Philosophia Botanica" (1751), no single code had attained international acceptance until, in 1889, the First International Zoological Congress adopted the one proposed by Raphael Blanchard. In 1901, at the Fifth Congress in Berlin, a 15-member committee submitted a revised code that is essentially the International Code of today. In 1884, at least two procedures were available for recognizing a type species which is evident from a discussion of nomenclature by Packard and Cope (1884, p. 907): "The type of a genus shall be the species which stands first on the list made by the original describer. This method has been generally discarded, and the law of exclusion been adopted in its stead. That is, the species remaining after others have been subtracted as representing new genera, bears the earliest generic name." Cope followed the "law of exclusion."

As mentioned above, the type species was automatically determined by the first association of the names *brachyops* and *Nimravus*. Although Cope did not, in this instance, select an object to serve as the name bearer, it was not a custom even among many of his contemporaries to designate types; therefore, to criticize adversely procedures of 1880 is not justified by using present methods as a standard of comparison.

The lectotype, as herein designated, is the partial jaw (A.M.N.H. No. 6935). However, in an explanation of plates, Adams (1896, p. 444, pl. 12) lists "Figure 5. *Dinictis brachyops* (Cope's type, Amer. Mus., posterior portion reversed)," and A.M.N.H. No. 6939, the partial skull, is figured. To some investigators, this selection by Adams might be considered as ambiguous. However, the opinions and articles available to and including the 1948 meeting of the International Congress would permit this figure caption by Adams to be valid for the selection of a type. Adams' statement does not meet the requirements for type selection according to the policies established by the 1953 Copenhagen Decisions.

That which follows illustrates the resulting confusion, if A.M.N.H. No. 6939 were designated as the type of *N. brachyops*. Two of the diagnostic structures present on this specimen are (1) the remnants of a relatively high thin sagittal crest and (2) a large postparietal pit. These same structures occur on the types and only known examples of *Pogonodon platycopis* (1880), *P. davisi* (1906), and *P. serrulidens* (1922) and are not found in any of the specimens allocated to the different species of *Nimravus* as the name is commonly used. Because the names *Nimravus* and *N. brachyops* have priority over *Pogonodon* (1880) and the specimens representing these species have similar structures, *Pogonodon* would become a synonym of *Nimravus*. A generic name would then be needed for *gomphodus*, *debilis*, *confertus*, *major*, *bumpensis*, and others. *Archaelurus* would be available for those that had been considered as species of *Nimravus*, and the name *Nimravus* would then be used for the concept previously associated with the name *Pogonodon*.

Subsequent to the description of *Nimravus brachyops*, seven very similar species and one subspecies, from the late Oligocene and the early Miocene deposits of North America, have been allocated to *Dinictis*, *Nimravus*, and *Archaelurus*. In all but two instances, each species was described on the basis of one specimen. There appears to be no known evidence that would support the recognition of more than one species of *Nimravus* in North America, and no clearly defined morphological differences have been observed that differentiate between the geographically and

temporally separated groups of individuals. Although minor modifications did occur with the passage of time, the differences noted by previous authors as having specific or sub-specific value might be more logically inter-preted as individual variations or sexual dimorphism in a single species.

Archaelurus debilis, when first described, consisted of the excellent type skull, mandi-ble, and atlas. Later (1884) Cope referred to the species another skull (one of the syntypes of *N. brachyops*) and the anterior part of a skull with associated postcranial elements. Because *Archaelurus* was and has been mono-typic, the diagnosis discussed in the generic synonymy is applicable here and need not be repeated. Subsequent remarks made in refer-ence to *A. debilis* are considered in connection with the other synonymous species and that which follows. At first glance it (especially the type and second referred skull) appears quite distinct from the type of *N. gomphodus*, but on analysis the differences are due merely to differences in age and sex. The true dis-tinctions are slight and involve principally minor differences of size and proportions, which all suggest, on analysis, to be within the known range of *N. brachyops*. This study represents the first time all available speci-mens were brought together for examination. Therefore, one result is a better understand-ing of the known range and degree of varia-tion. Additional data regarding the proveni-ence of the individual specimens within the John Day formation would be desirable, but all were collected between 1874 and 1900. The type enters well into this taxonomically homogeneous sample and is included in the statistical data below. Sex determination is also discussed below.

Nimravus gomphodus was based primarily on the major part of a skull, left ramus, cervi-cal, and two dorsal vertebrae. Later (1884) Cope referred to the species a partial right ramus (the lectotype of *N. brachyops*) and femur, and a partial left ramus. The type of *gomphodus* retains the M_2, while it is absent in that of *brachyops*, and there is a difference in the size of the alveolar torus. The variabil-ity of the latter structure is discussed above, and the presence or absence of the second lower molar is not taxonomically significant. Reference has been made by some authors to

the straightness of the upper canine in the type. Post-mortem breaking and subsequent filling of the cracks with a tuffaceous siltstone have changed the lateral outline of the tooth.

Nimravus confertus was defined principally on two characteristics: (1) the small size of the type, and (2) the fact that the crown of the inferior canine was directed backward. When correctly restored, the position of the crown would be more anterior. The mor-phology of the type also is well within the range of variation of *N. brachyops*.

The specimen Mivart figured under the name *Nimravus brachyops* is A.M.N.H. No. 6933, the type of *N. gomphodus*. No explana-tion was given for his association of the name and object.

Dinictis major was based on the anterior part of a skull, a jaw, and several postcranial elements. The original comparison was with *F. concolor* and the jaguar. According to Lucas, the distinctive characters were the large size of the animal, the feeble develop-ment of the flange, the robust character of the feet, and the presence of an ungual shield. The convex inferior border of the jaw was also mentioned. No change in the generic alloca-tion of *major* occurred until 1930, when Hay transferred the species to *Nimravus*. Scott and Jepsen (1936) preferred to follow the original designation of Lucas. The skull of the type is crushed transversely, and only the anterior half is preserved. However, there re-mains enough of the specimen to permit a satisfactory diagnosis. The planar surface on that part of the malar anterior to the orbit is well defined. The teeth in the holotype are worn, however; P^3 is relatively high crowned, the protoconid of P^4 has not lost its character-istic shape and position, and the relationship of the crown of M^1 to the palate is similar to that in other species of *Nimravus*. Lucas did not mention the presence of an alveolar torus on the holotype, and in his description of the ramus he stated: "The anterior cusp is obso-lete on the second [P_3] lower premolar, large on the third [P_4] lower premolar. The mandi-ble is rather deep, convex on the lower edge, and with the flange for the upper canine al-most obsolete." Unfortunately the jaw is missing at the present time. Lucas recorded the length of the lower molar series as 65 mm., and this dimension is the same in the

type of *N. bumpensis*. I can find no structural differences in the skull of *major* that would be considered diagnostic in the separating of it from other North American species of *Nimravus*. The postcranial elements are insufficiently known for a satisfactory comparison.

Archaelurus debilis major was based on an essentially complete skull, a fragmentary skull, three partial rami, and associated and isolated postcranial elements. Merriam's diagnosis, as best as I can determine, is given below:

1. Large forms.
2. Reduced exostosis.
3. Wide masseteric fossa.
4. P$_3$ with paraconid.

The size difference I do not consider as diagnostic and prefer to consider the skull as a male of *Nimravus brachyops*. Reduction of the alveolar torus or exostosis and its significance are discussed above. Merriam (1906) stated: "Practically the only character which seems distinctive is found in the form and size of the masseteric fossa. In *N. gomphodus* its inferior margin is separated from the lower border of the horizontal ramus by a wide bar. In *A. debilis* the fossa extends farther forward and reaches down to the inferior margin of the jaw, which it may follow for some distance." These observations of Merriam are correct, if only the types of *Nimravus debilis* and *N. gomphodus* are compared. If all known rami of the John Day *Nimravus* are compared, the development of the inferior part of the masseteric fossa is found to be extremely variable. To test the variability of this feature, more than 30 sexed specimens of *Panthera onca* in the American Museum collection have been examined, and in this form the variation of shape and size of the structure can be attributed to sexual dimorphism and individual variation within a species. For example, the inferior border of the masseteric fossa in a female jaguar (A.M.N.H.: M. No. 36949) is similar to that in the larger specimens here considered as males of *Nimravus brachyops*, and this structure in a male jaguar (A.M.N.H.:M. No. 36950) is like that in the smaller specimens believed to be females of *N. brachyops*. The P$_3$ paraconid is one of those structures that grades from present to absent and is of little taxonomic value.

Hay (1930) proposed *Archaelurus debilis merriami* to replace Merriam's subspecies, *major*. No reasons were given by Hay for this change.

Nimravus meridianus was based on a partial right ramus and was distinguished from *N. confertus* as follows:

1. Longer diastema.
2. Slightly smaller size.
3. No marked angulation of the antero-inferior border.
4. Further extension of the symphysis posteriorly.

None of these in my opinion involves a valid separation, and there is no basis for thinking that *meridianus* was specifically distinct from the other species of *Nimravus* in North Amer-

TABLE 5

MEASUREMENTS OF THE TYPE OF *Nimravus major* AND THAT OF *Nimravus bumpensis*

	N. major U.S.N.M. No. 3957	N. bumpensis S.D.S.M. No. 348
LC/	15.5	14.5
LP^3	18.4	18.5
LP^4	23.5	23.2
WP^4	12.0	13.0
P$^{3-4}$	40.9	40.0
C/–P^4	70.3	ca. 70.0

ica, although in their known distribution they were separated in space and time. The geographic difference is less than the range found in *Felis concolor*, *F. rufus*, or *Panthera onca*.

Nimravus bumpensis was based on a fine skull and mandible. Scott and Jepsen (1936) described and figured[1] the first species from the late Oligocene of South Dakota. In the original description of *bumpensis*, the zygomatic arches were said to curve out much less boldly from the sides of the skull than those in the type of *N. gomphodus*, thus narrowing the temporal openings conspicuously. However, the narrowing was produced, at least in part, by transverse crushing. Although Scott and Jepsen considered Hay's allocation of *major* as untenable, a detailed examination

[1] The type is reproduced as $\times\frac{2}{3}$ on plate 21 in Scott and Jepsen (1936), not $\times\frac{1}{1}$ as stated on page 153.

TABLE 6

DIMENSIONS OF TYPES

Jaw Dimensions	Nimravus brachyops	Nimravus confertus	Nimravus meridianus	Nimravus altidens
/C–condyle	—	—	—	—
/C–M_1	92.0	—	—	ca. 78.0
P_3–M_1	58.0	48.5	46.2	49.0
P_{3-4}	33.0	30.0	—	30.0
LM_1	27.5	22.5	21.8	22.0
LP_4	19.0	16.0	15.2	16.4
LP_3	15.0	13.5	12.6	14.0

of Lucas' type has demonstrated that Hay was correct. In fact the similarity of the two types, *bumpensis* and *major*, is so great that they should be regarded as members of the same species. There is the possibility that the two types are females because of similarity in size and morphology (see table 5). The development of the sagittal crest in the South Dakota specimen also agrees well with that of specimens from the John Day which I be-

TABLE 7

DIMENSIONS OF TYPES

Skull and Jaw Dimensions	Nimravus gomphodus	Archaelurus debilis	Archaelurus debilis major	Dinictis major	Nimravus bumpensis
Prosthion–basion	—	173.0	ca. 208.0	—	164.0
Prosthion–staphylion	—	74.5	ca. 86.0	70.0	ca. 75.0
Width at posterior P^4	—	ca. 80.0	ca. 82.0	ca. 65.0	ca. 65.0
Width at mastoid process	—	67.0	80.0	—	58.0
Rostral width	—	52.0	ca. 63.0	ca. 50.0	ca. 40.0
Interorbital breadth	—	47.0	51.0	—	ca. 40.0
Breadth at postorbital processes	—	64.0	71.0	—	ca. 60.0
Breadth at postorbital constriction	39.0	37.0	ca. 40.0	—	35.0
Breadth across zygomata	ca. 142.0	ca. 134.0	ca. 150.0	—	—
Basion to maxillary-palatine suture	—	119.0	141.0	—	ca. 110.0
Prosthion to maxillary-palatine suture	—	53.5	ca. 67.0	ca. 51.0	ca. 55.0
C/–P^4	73.0	72.0	78.0	70.0	70.0
P^{3-4}	42.5	43.5	45.0	41.0	40.0
LP^4	25.0	24.5	25.5	23.5	23.2
LP^3	18.5	19.5	20.0	18.4	18.5
LC/	16.0	ca. 13.5	16.0	15.5	ca. 15.0
/C–condyle	152.0	136.0	—	—	130.0
/C–M_1	89.0	81.0	—	—	84.0
P_3–M_1	57.5	54.0	—	—	50.5
P_{3-4}	35.0	33.0	—	—	30.5
LM_1	ca. 25.0	24.3	—	—	22.8
LP_4	ca. 19.5	17.5	—	—	16.4
LP_3	16.0	15.0	—	—	14.0

TABLE 8

METRICAL DATA ON *Nimravus brachyops* FROM THE JOHN DAY FORMATION

Skull and Jaw Dimensions	N	OR	M
Prosthion–basion	7	*ca.* 170.0–*ca.* 208.0	187.7
Prosthion–staphylion	9	*ca.* 65.0–*ca.* 86.0	74.1
Width at posterior P^4	8	74.0–*ca.* 85.0	78.7
Width at mastoid process	8	*ca.* 66.0–80.0	72.4
Rostral width	11	*ca.* 48.0–67.0	55.1
Interorbital breadth	12	*ca.* 45.0–54.0	49.0
Breadth at postorbital processes	10	62.0–*ca.* 80.0	69.0
Breadth at postorbital constriction	13	37.0–*ca.* 43.0	40.1
Breadth across the zygomata	10	*ca.* 128.0–*ca.* 150.0	137.1
Basion to maxillary-palatine suture	6	119.0–141.0	132.3
Prosthion to maxillary-palatine suture	8	49.0–*ca.* 67.0	58.2
$C/-P^4$	13	67.0–*ca.* 80.0	72.4
P^{3-4}	13	40.5–45.0	43.1
LP^4	16	23.0–25.5	24.3
LP^3	14	17.0–20.0	18.9
$LC/$	11	*ca.* 13.0–17.0	16.8
$/C$–condyle	6	129.0–158.0	145.1
$/C-M_1$	8	*ca.* 75.0–*ca.* 98.0	87.9
P_3-M_1	9	48.5–58.0	55.2
P_{3-4}	11	30.0–35.8	33.5
LM_1	9	22.5–27.5	25.4
LP_4	11	16.0–*ca.* 19.5	18.3
LP_3	9	13.5–*ca.* 16.5	15.0

TABLE 9

METRICAL DATA ON *Nimravus brachyops* FROM THE GERING FORMATION

Skull and Jaw Dimensions	N	OR	M
Prosthion–basion	2	*ca.* 175.0–*ca.* 185.0	180.0
Prosthion–staphylion	2	70.0–*ca.* 74.0	72.0
Width at posterior P^4	3	*ca.* 65.0–81.0	75.7
Width at mastoid process	1	80.0– —	—
Rostral width	3	*ca.* 50.0–63.0	57.7
Interorbital breadth	2	*ca.* 45.0–48.0	46.5
Breadth at postorbital processes	1	73.0– —	—
Breadth at postorbital constriction	2	*ca.* 40.0–42.0	41.0
Basion to maxillary-palatine suture	2	123.0–*ca.* 135.0	129.0
Prosthion to maxillary-palatine suture	3	*ca.* 51.0–*ca.* 55.0	53.3
$C/-P^4$	3	70.0–*ca.* 73.0	71.7
P^{3-4}	3	41.0–43.0	42.0
LP^4	3	*ca.* 23.0–24.0	23.5
LP^3	3	18.0–18.5	18.3
$LC/$	3	15.5–18.0	16.5
$/C-M_1$	1	86.0 —	—
P_3-M_1	1	52.0 —	—
P_{3-4}	1	31.5 —	—
LM_1	1	23.0 —	—
LP_4	1	17.0 —	—
LP_3	1	14.0 —	—

lieve represent females. Scott and Jepsen defined *bumpensis* principally on these characters:

1. Smaller than *N. gomphodus* and about equal to *N. confertus*.
2. Incisors smaller and more reduced than in *N. gomphodus*.
3. Canines proportionately shorter and thicker than in *N. gomphodus*.
4. Wider carnassial notch than in *gomphodus* and almost as wide as that in the type of *A. debilis*.
5. Suborbital portion of the maxillary much narrower and bringing the infraorbital foramen down to a very inferior position.
6. Occiput a different shape and paroccipital processes shorter and pointing more directly backward.

Of these, characters 1, 2, 5, and 6 are not distinctive from the known sample of *N. brachyops* from the John Day; 4 is the result of wear; and 3 is within the range seen in many of the modern felids.

Subsequent to the description of *bumpensis*, another species of *Nimravus* was de-scribed from the late Oligocene of South Dakota. MacDonald (1950) proposed the name *altidens* for a new species of *Nimravus*. The stratigraphic provenience of the type jaw was given as: " . . . the oldest known species in the genus. It is older than *Nimravus bumpensis* (1936) as indicated by its occurrence in the *Protoceras* sandstones below the level of the particular zone of the *Leptauchenia* beds where Scott and Jepsen's specimen was found." The specific name *altidens* refers to the elevated position of M_2. This elevation of M_2, with respect to M_1, is controlled by the development of the torus and is of dubious value in taxonomy. Three of the differences in the types of *bumpensis* and *altidens* mentioned by MacDonald (location of mental foramina, size of the M_2, and size of the talonid on M_1) are interpreted as individual variation. The crenulated enamel on P_3–M_1, said to be present in the holotype of *bumpensis* and absent in that of *altidens*, is visible both microscopically and macroscopically. A paraconid is present on the P_3 in the type of *altidens*. This feature is absent in
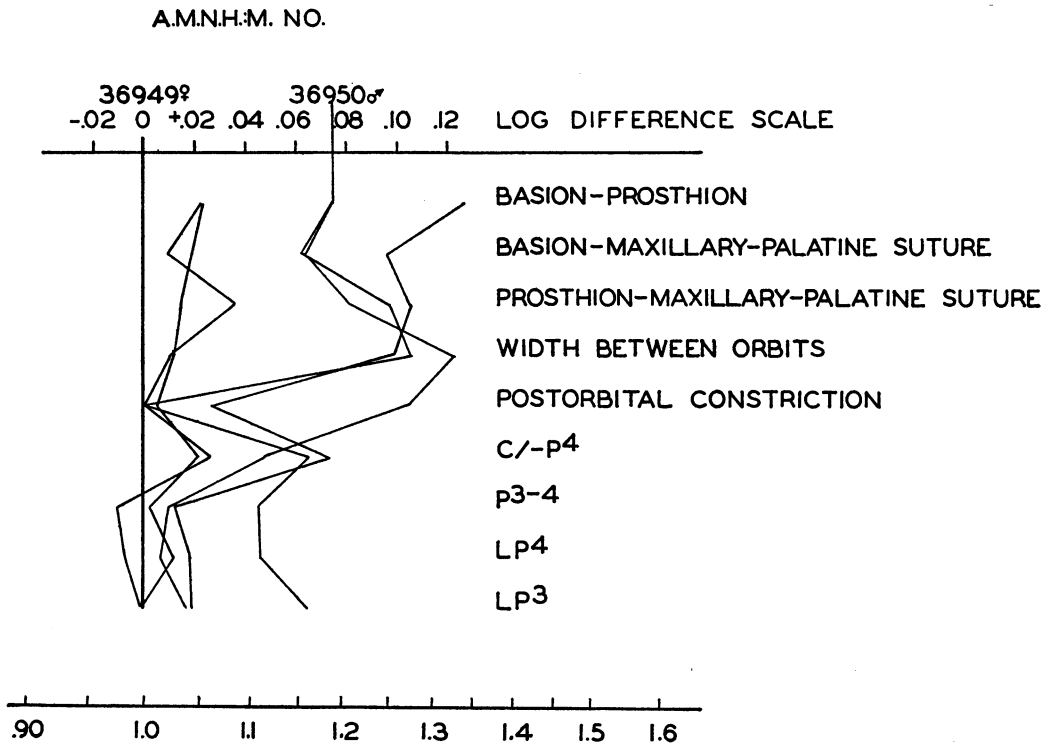

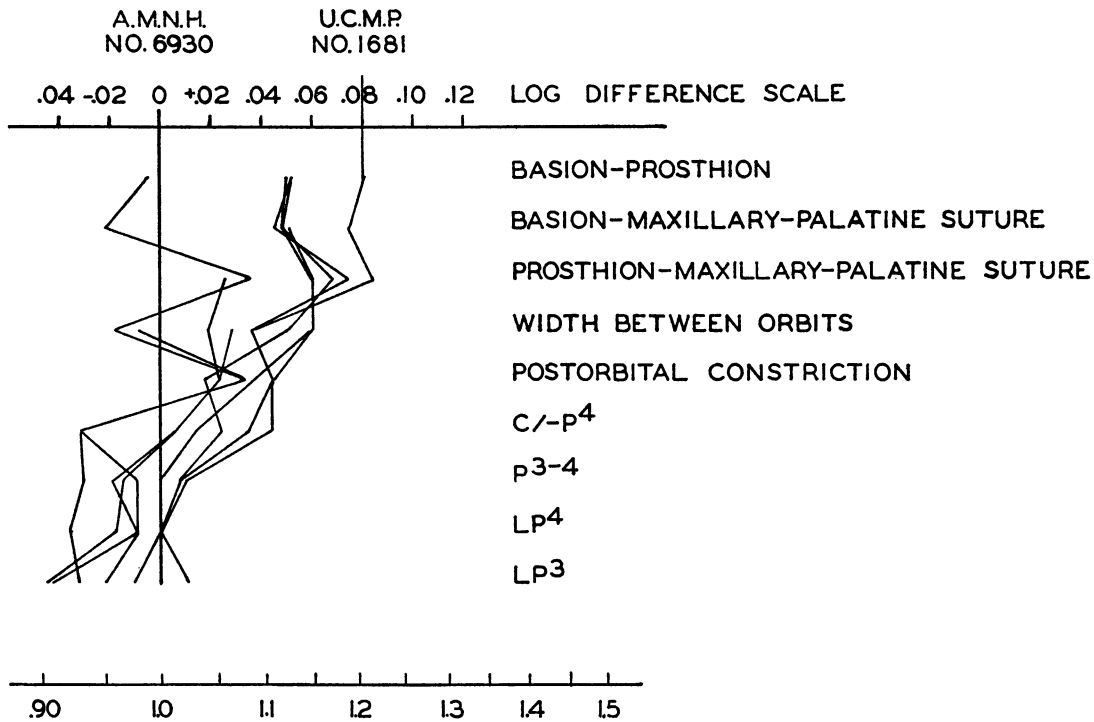FIG. 5. Ratio diagram of the recent jaguar, *Panthera onca milleri*.

A.M.N.H.   U.C.M.P.
NO. 6930   NO. 1681

.04 -.02   0 +.02 .04 .06 .08 .10 .12   LOG DIFFERENCE SCALE

BASION–PROSTHION

BASION–MAXILLARY–PALATINE SUTURE

PROSTHION–MAXILLARY–PALATINE SUTURE

WIDTH BETWEEN ORBITS

POSTORBITAL CONSTRICTION

$C/-P^4$

P^{3-4}

LP^4

LP^3

.90   1.0   1.1   1.2   1.3   1.4   1.5

FIG. 6. Ratio diagram of *Nimravus brachyops* from the John Day formation, Oregon.

bumpensis, and the anterior border of the protoconid is concave. The large sample of *N. brachyops* from the John Day indicates the variability in the development of the paraconid on P_3, and a larger series from the late Oligocene will undoubtedly reveal the same degree of variation. If *N. bumpensis* can ever be recognized as a valid species or subspecies, it is my opinion that *altidens* should be considered as a synonym.

Hough (1953, fig. 9) apparently did not question the identification on the label of U.S.N.M. No. 16558 as *Dinictis cyclops*, but none of the structures, features, or characters of this specimen permits its allocation to any species of *Dinictis*. The high crown of P^3, the shape and position of the protocone on P^4, the reduced M^1, and the flattened surface on that part of the malar anterior to the orbit are features not associated with *Dinictis*. The specimen is a typical example of *N. brachyops*.

The ratio diagrams developed by Simpson (1941) have been used to demonstrate the variable proportions that occur in both sexes of *Panthera onca milleri*. The standard of comparison in figure 5 is definitely a female,

and from the sample available it is evident in the ratio diagram that the males tend to form one group and the females another. If a much larger sample were available, there probably would be a gradation between the two groups. As mentioned above, the development of the sagittal crest and size of the individual have been used with moderate success in determining the sex of recent cats. In male jaguars the sagittal crest is higher, and the individuals are usually larger than the females. The ratio diagrams therefore serve another function—an aid to the approximation of the sex of specimens.

Sexual dimorphism in *Nimravus brachyops* from the John Day is suggested by the smaller size of some of the skulls and jaws and lesser development of the sagittal crest. These three specimens I consider as females: the type of *Archaelurus debilis* (A.M.N.H. No. 6930), A.M.N.H. No. 6931, and Y.P.M. No. 10046 (figured by Eaton, 1922). Others with a heavier and higher sagittal crest and larger over-all dimensions I consider as males; the types of *Nimravus gomphodus* Cope, *Archaelurus debilis major* Merriam, and Y.P.M.

Nos. 10517 and 10045 (figured by Eaton, 1922). In figure 6 several of the most complete specimens from the John Day have been compared with A.M.N.H. No. 6930 (the type of *Archaelurus debilis*). U.C.M.P. No. 1681 is the type of *Archaelurus debilis major*, and one of the lines at +0.05 represents the type of *Nimravus gomphodus*. Two groups tend to form in the ratio diagram for the John Day felids which is similar to that for the jaguar. It seems more logical to interpret the specimens as representing the dimorphic sexes rather than different species of one or more genera.

Presence of the M_3 is indicated in Y.P.M. No. 10517 by a right root, in Y.P.M. No. 14393 and in U.C.M.P. No. 1680 by a left alveolus. The occurrence of M_3 in cats is exceptional, and I have seen only one other specimen (U.N.S.M. No. 25525, referred example of *Dinictis felina*) in which the M_3 is present. This tooth, unopposed by an upper, is not functional in *N. brachyops*. It is possible that the presence of an M_3 in *Nimravus* is, in some way, associated with the development of the alveolar torus. To date the occurrence of this tooth has been noted in only those specimens from the John Day.

One peculiar structure limited to *Nimravus brachyops* is an ossicle in the external auditory meatus (not to be confused with the auditory ossicles—malleus, stapes, and incus). The function, if any, is unknown. Four specimens retain its development on either the left or right side, as follows:

A.M.N.H. No. 6933, left; John Day
A.M.N.H. No. 6931, right; John Day
A.M.N.H. No. 6930, right; John Day
U.S.N.M. No. 1091, left; Gering

Those specimens in which the tympanic bulla is present on one or both sides and in which the ossicle does not occur are:

Y.P.M. No. 10045; John Day
U.O. No. 607; John Day
S.D.S.M. No. 348; Poleslide member

As yet I am not positive that the structure is bilateral in its development. Additional preparation on U.N.S.M. No. 1091 has demonstrated the hollow nature of the ossicle. In this specimen the ossicle is conical in shape, with the superior surface flattened and the long axis paralleling the lateral and superior surface of the tympanic bulla. The small bone approximates 10–12 mm. in length and 3–5 mm. in width. The restriction of the external auditory meatus is about 2 mm. in U.N.S.M. No. 1091.

Of the John Day specimens, A.M.N.H. No. 6930 is the best preserved, and there is a suggestion that the bone is hollow. Cope (1884) observed the presence of the bone as " . . .

TABLE 10

METRICAL DATA ON *Nimravus brachyops* FROM THE WHITNEY AND POLESLIDE MEMBERS

Skull and Jaw Dimensions	N	OR	M
Prosthion–basion	2	164.0–*ca*. 190.0	177.0
Prosthion–staphylion	2	*ca*. 75.0–*ca*. 75.0	75.0
Width at mastoid process	3	58.0–72.0	66.6
Rostral width	2	*ca*. 40.0–60.0	50.0
Breadth at postorbital constriction	3	35.0–*ca*. 42.0	39.0
Basion to maxillary-palatine suture	2	*ca*. 110.0–*ca*. 127.0	118.5
Prosthion to maxillary-palatine suture	2	*ca*. 55.0–*ca*. 60.0	57.5
P^{3-4}	2	40.0–*ca*. 40.0	40.0
LP^4	3	20.0–23.2	22.3
$LC/$	3	*ca*. 11.0–*ca*. 17.0	14
$/C-M_1$	3	*ca*. 68.0–84.0	77.0
P_3-M_1	3	47.0–50.5	48.8
P_{3-4}	2	30.0–30.5	30.2
LM_1	3	21.0–22.8	21.9
LP_4	3	15.5–16.4	16.1
LP_3	3	13.5–14.0	13.8

		West Coast	Great Plains	North America	
Early Miocene	Arikareean	*Nimravus brachyops*	*Nimravus major*	*N. brachyops brachyops* *N. b. major*	*Nimravus brachyops*
Late Oligocene	Whitneyan	*Nimravus meridianus*	*Nimravus bumpensis*	*N. b. meridianus* *N. b. bumpensis*	

FIG. 7. Three possible combinations of names for the North American species of *Nimravus*.

probably a tympanic bone, which is thickened so as to resemble somewhat a sesamoid." The bone is firmly ossified to the remnants of the tympanic bulla, and it partially obscures the opening to the postglenoid foramen in the United States National Museum example.

It is doubtful if the presence of the ossicle was advantageous, and it seems reasonable to conclude that the constriction of the external auditory meatus reduced the individual's ability to hear.

One of the unique specimens from the Gering formation is U.N.S.M. No. 1091. In this individual the right canine has penetrated through the right humerus of another (?) felid. The piercing may be due to the weight of the overlying sediments, as the skull has been crushed dorsoventrally, or the penetration of the canine might have occurred during a battle between two males. The posterior surface of the humerus is broken near the upper extremities of the anconeus, and the anterior surface is preserved, proximally to the upper part of the deltoid ridge. The acromial head of the deltoid muscle originates at the point where the tip of the canine

emerges through the bone. The tip of this tooth is fractured and displaced somewhat posteriorly to its normal position. Around the area where the canine emerges, the bone is splintered and elevated towards the protruding tip of the tooth. This same specimen is one of the few in which the ventral flaring of the basi-occiput is well shown. The thin tympanic bulla is present around the posterior and the anteromedial margin of the petrosal and continues ventrally to join or abut against the lateral margin of the basi-occiput. A structure that might be referred to the entotympanic process is also present.

The nomenclature herein used for *Nimravus* in North America seems the least artificial. This chorocline and chronocline (*N. brachyops*) might be given any taxonomic rank in the Linnean system, depending on how great is the morphological difference between known early and late members. In this instance, my judgment is that the cline is of specific scope. The interpretation of the available data is that at any one time there was only one species and the genetically continuous, ancestral-descendant series of populations changed little in morphology.

When additional materials are available, subspecific names might be used for these spatiotemporally separated samples. At such time *Nimravus brachyops* could consist of the following subspecies: *N. b. brachyops*, *N. b. major*, *N. b. meridianus*, and *N. b. bumpensis*.

Nimravus intermedius (Filhol, 1872)

Aelurogale intermedia FILHOL, 1872, Ann. Sci. Geol. Paris, vol. 3, p. 10, pl. 16, figs. 23–25; 1872, Compt. Rendu Acad. Sci. Paris, vol. 75, pt. 2, pp. 93–94; 1877, Ann. Sci. Geol. Paris, vol. 8, p. 30, pl. 3, figs. 209–212.

Ailurictis intermedius (Filhol), TROUESSART, 1886, La grande encyclopédie, Paris, vol. 1, p. 954.

Nimravus intermedius (Filhol), PIVETEAU, 1932, Ann. Paleont., vol. 20, pp. 107–163.

TYPE: When the name *Aelurogale intermedia* was proposed (Filhol, 1872a, 1872b), a right jaw was figured (1872a), and as far as I can determine it was never refigured by Filhol or Piveteau. Presumably this specimen should be designated the type, providing its whereabouts can be determined.

According to Piveteau (1932, pl. 1, fig. 2; pl. 3, fig. 3) the type consists of a left maxilla and jaw in the collections of the Muséum National d'Histoire Naturelle, Paris. If these represent the same individual, they could serve as the neotype, on the assumption, of course, that the one described by Filhol cannot be found.

HYPODIGM: The following specimens, including the two Piveteau considered as representing the type, in the Muséum National d'Histoire Naturelle, Paris: two left maxillae, a partial skull, two upper canines, six left and two right jaws, and a dP4. All were figured by Piveteau (1932, pl. 1, figs. 1–6, pl. 2, figs. 5, 6, 8, 9, pl. 3, figs. 2, 3, 6, and pl. 4, figs. 2–3).[1]

Lydekker (1887) has referred the following specimens from Caylux (Tarn-et-Ga-

ronne) to *N. intermedius;* all are at the British Museum (Natural History): No. 2369a, left maxilla; No. 2369, left immature maxilla; No. 2370, left ramus; No. 2371, left ramus; No 2372, left ramus; and No 2373, right ramus.[2]

Three of the North American institutions having specimens or casts are as follows: M.C.Z. No. 8938, left ramus; A.M.N.H. No. 11067, left ramus; P.U. No. 11569, left ramus; P.U. No. 11827, cast of left ramus and left maxilla (figured by Piveteau, 1932, pl. 4, fig. 2).

The two deciduous teeth and postcranial elements figured by Schlosser (1890, pl. 9, figs. 23–25, 55, pl. 6, figs. 3, 14–15, 19–20, 23–24) are tentatively allocated.

AGE AND LOCALITIES: Phosphorites du Quercy, Tarn-et-Garonne, Stampien, middle Oligocene.

DISCUSSION: Piveteau (1932) has adequately reviewed and described this European species.

Those rami figured by Piveteau as *N. intermedius* race *major* may represent males of the *intermedius* population. The allocation of *edwardsi*, *mutata* (=*acutata?*), and race *minor* to *Nimravus* may be correct, but I suspect that they represent another taxon.

Nimravus? jourdani (Kretzoi, 1929)

Aelurogale intermedia? FILHOL, 1883, Arch. Mus. Hist. Nat. Lyon, vol. 3, p. 59, pl. 4, fig. 2.

?Aelurogale intermedia Filhol, DEPÉRET, 1887, Arch. Mus. Hist. Nat. Lyon, vol. 4, p. 130.

Aelurogale intermedia Filhol, DEPÉRET, 1892,

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[1] A left maxilla figured as *N. intermedius* race *major* by Piveteau in my opinion represents the same sort of animal as *Dinailurictis bonali* Helbing. The P4 length of the Quercy specimen is either 33 or 36.5 mm. depending upon which view, occlusal or lateral, is used for measuring. Either dimension is well beyond the known range of *N. brachyops* and *intermedius*. The upper carnassial also lacks the emargination on the anterior border, a structure that is characteristic of the known species of *Nimravus*.

[2] Lydekker also allocated a left P4 to *intermedius* and recorded the length as 32 mm. This specimen may prove referable to *Dinailurictis bonali*. Kretzoi has made one of the syntypes (P3–4) of *bonali* the type of *Ailurictis helbingi*, but the species belongs in another taxon because the P3 is relatively low-crowned, P4 does not have the deeply emarginate anterior border, and the lingual surface of the upper carnassial is unlike that of *N. brachyops* and *intermedius*. If the maxilla figured by Piveteau is allocated to *bonali* or *helbingi*, then M1 is transversely elongate as in *Dinictis* and *Pogonodon* and not reduced as in *Nimravus*. One of the problems with *Dinailurictis bonali* is the lack of association between the upper canines and the partial maxilla; hence we do not know if they represent similar or dissimilar sorts of animals. Until additional and more complete specimens are discovered at Quercy, La Tuque, or some other place, we will not know the relationship between the teeth in question.

Arch. Mus. Hist. Nat. Lyon, vol. 5, p. 19, pl. 1, figs. 2–3.

Ailurictis jourdani KRETZOI, 1929, 10th Congr. Internatl. Zool. Budapest, p. 1295.

Ailurictis jourdani Kretzoi, ZAPFE, 1950, Sitzber. Math. Naturwiss. Kl. Wien, div. 1, vol. 159, pp. 136–137, fig. 17.

TYPE: Superior canine in the Muséum d'Histoire Naturelle de Lyon. Figured by Filhol (1883, pl. 4, fig. 2). La Grive-Saint-Alban (Isère), Tortonian.

AGE AND LOCALITIES: La Grive-Saint-Alban (Isère), Tortonian and Spaltenfullung von Neudorf an der March (Czechoslovakia), Helvetian.

DISCUSSION: The two canines and a lower carnassial described by Filhol (1883) and Depéret (1892) from Grive-St.-Alban and those specimens from the fissure fillings of Neudorf described by Zapfe (1950) have generally been considered as representing this species. The canines in the North American species of *Nimravus* do not seem particularly diagnostic, and the possibility exists that these from the European Miocene represent a pseudaelurine. A marked similarity exists between the M_1 figured by Depéret and that of *Nimravus intermedius* from the Phosphorites du Quercy.

A diagnosis for *N.? jourdani* is delayed until more specimens become available, and it seems that the European students are in a better position for determining the status of this species. In view of the limited number of specimens and the difficulty experienced in working with isolated teeth, *jourdani* may not represent, as suggested by Kretzoi, the terminal species of the *Nimravus* lineage in Europe.

According to Filhol (1883) the type of *N. jourdani* was apparently the object that Jourdan (1862, p. 132) used to establish the name *Prionedes*. I have not seen the article by Jourdan, but subsequent publications by other authors lead me to believe that no species was mentioned. Only additional confusion in the already complex felid nomenclature would result should *Prionedes* ever become an established name. I prefer to consider it as having no status.

Nimravus sp.

EXAMPLE: A.M.N.H. No. 21638, partial left ramus, W1–2, Hsanda Gol formation, Oligocene, "Grand Canyon" north of Tsagan Nor, Outer Mongolia.

DISCUSSION: Previous to this report *Nimravus* was known only in North America and Europe, but now the distribution can be extended to Asia. From the Hsanda Gol formation in Outer Mongolia the American Museum Asiatic Expedition of 1925 secured a collection rich in rodents, carnivores, and insectivores. Among these complete and remarkably well-preserved specimens is a fragmentary jaw with the M_1 (length 20.5 mm.), alveolus of M_2, and the diagnostic alveolar torus.

Additional materials are necessary for a determination of whether or not the jaw fragment represents a new species of *Nimravus*. Presumably the specimen could be described as representing a new species because of its location in relation to specimens from western Europe and North America.

At least three different opinions have been published about the age of the Hsanda Gol. Originally this formation was judged to be of Miocene age. Subsequent studies of the fauna by Matthew and Granger changed the allocation of the Berkey and Morris dating to Oligocene. Chardin and LeRoy place the Hsanda Gol in the Aquitanian and use this stage name as a unit apart from the Oligocene and Miocene. They placed a special emphasis on the Aquitanian, Pontian, and Villafranchian, because these three ages, which are usually thought of as transitional intervals, have a dominant individuality of their own in the continental Tertiary of eastern Asia.

A review of the fauna from the Hsanda Gol is definitely beyond the scope of the present investigation, but such a restudy may prove necessary if we are to refine the present estimates of its relative age.

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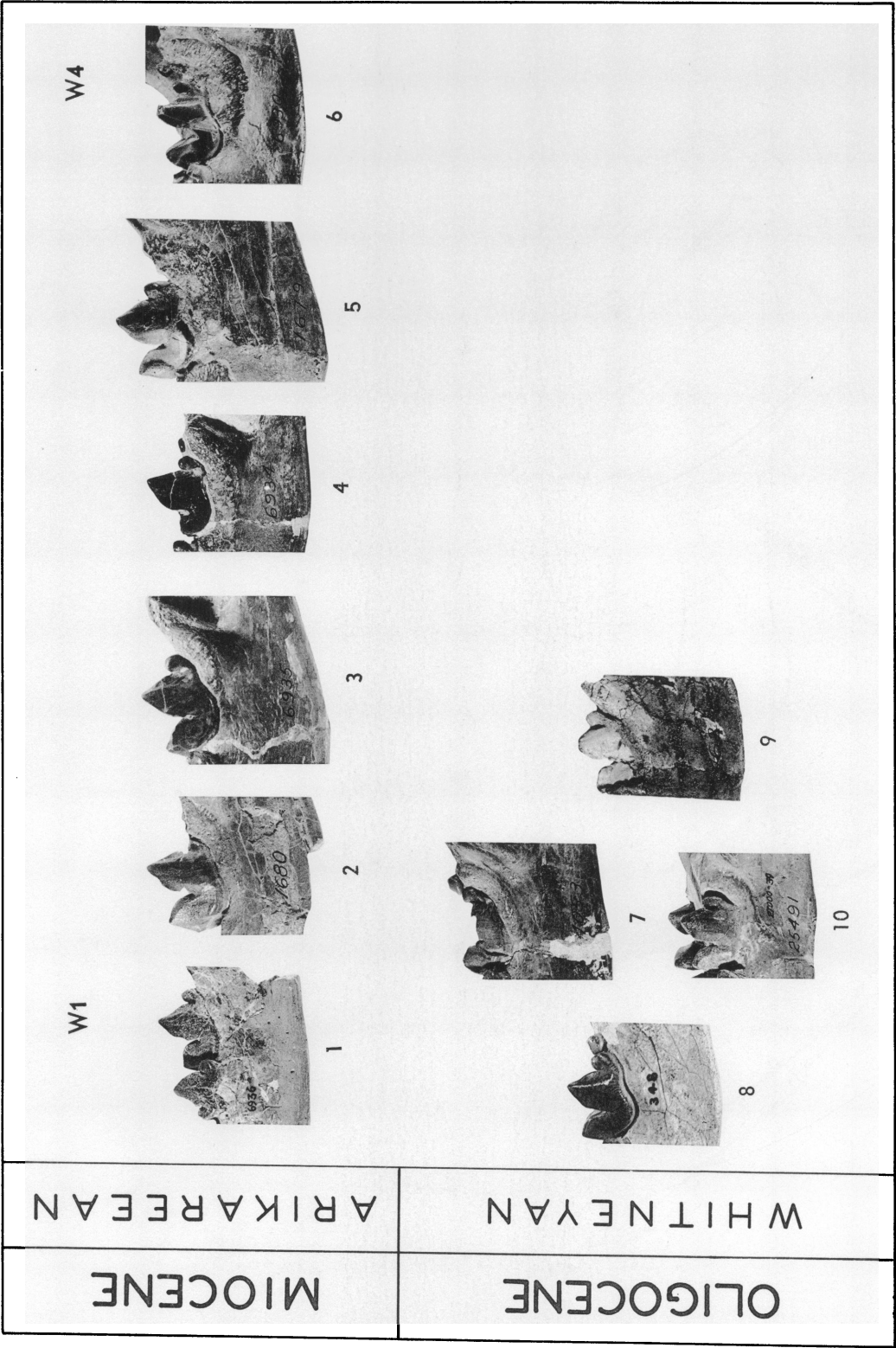
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PLATES 9–22
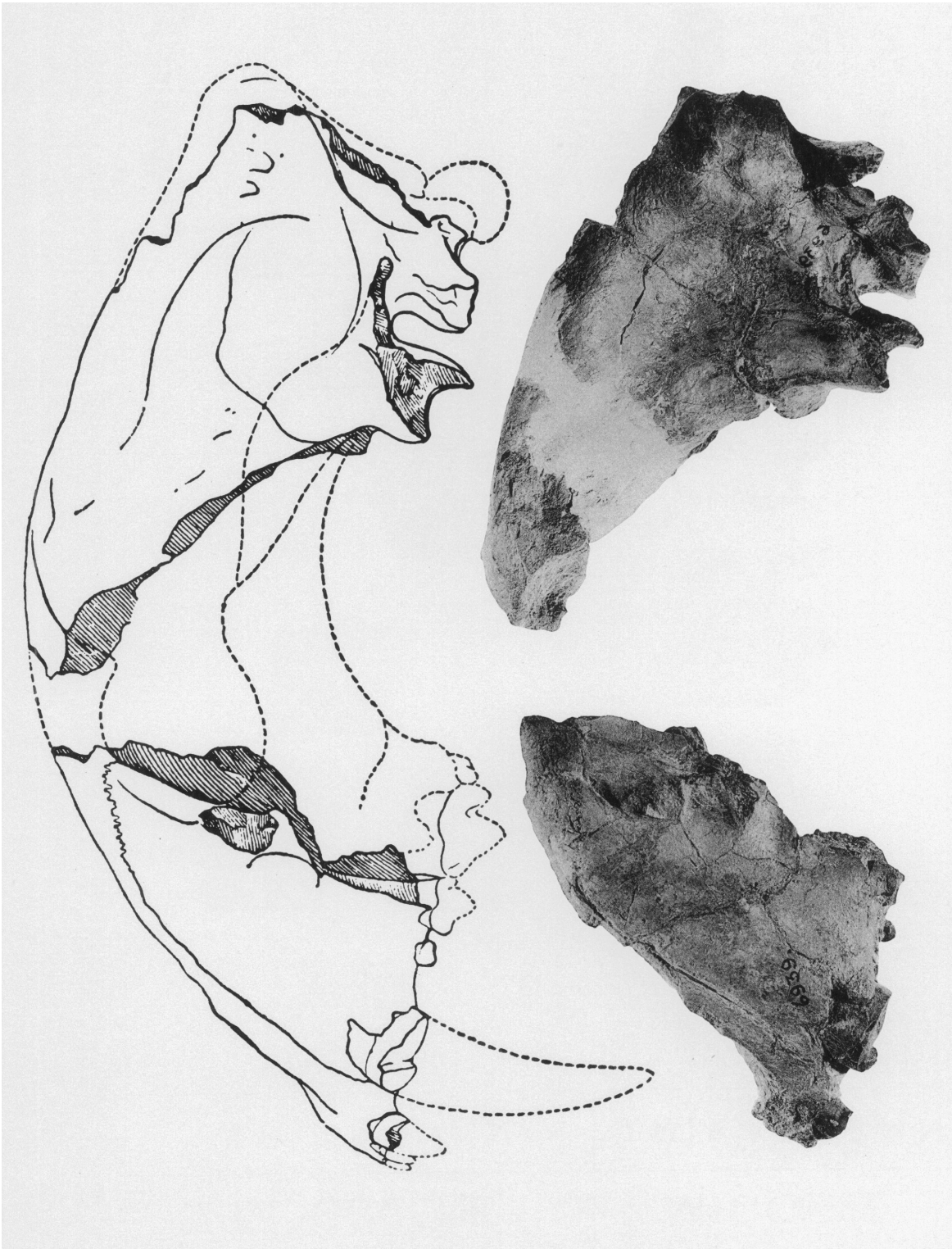
"*Nimravus brachyops*" Cope, syntype, A.M.N.H. No. 6939, partial skull, lateral view; John Day formation, Oregon. Posterior part of skull reversed. Line drawing after Adams, 1896. Both approximately × ¾.

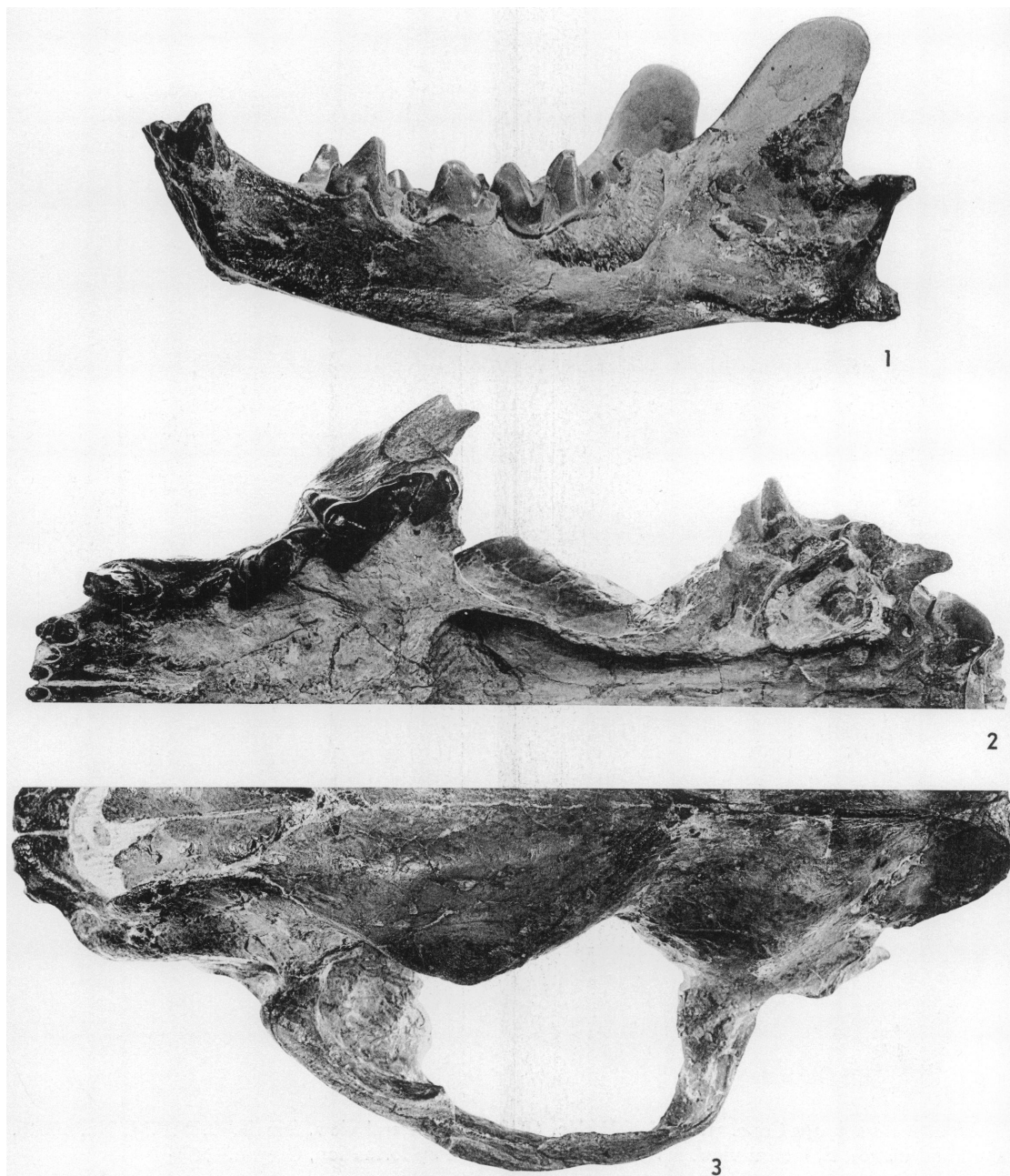*Nimravus brachyops* Cope, Y.P.M. No. 10517, skull, male, lateral view; John Day formation, Oregon. × 1

Nimravus brachyops Cope, Y.P.M. No. 10517, skull, male. 1. Ventral view. 2. Dorsal view. John Day formation, Oregon. × ¾
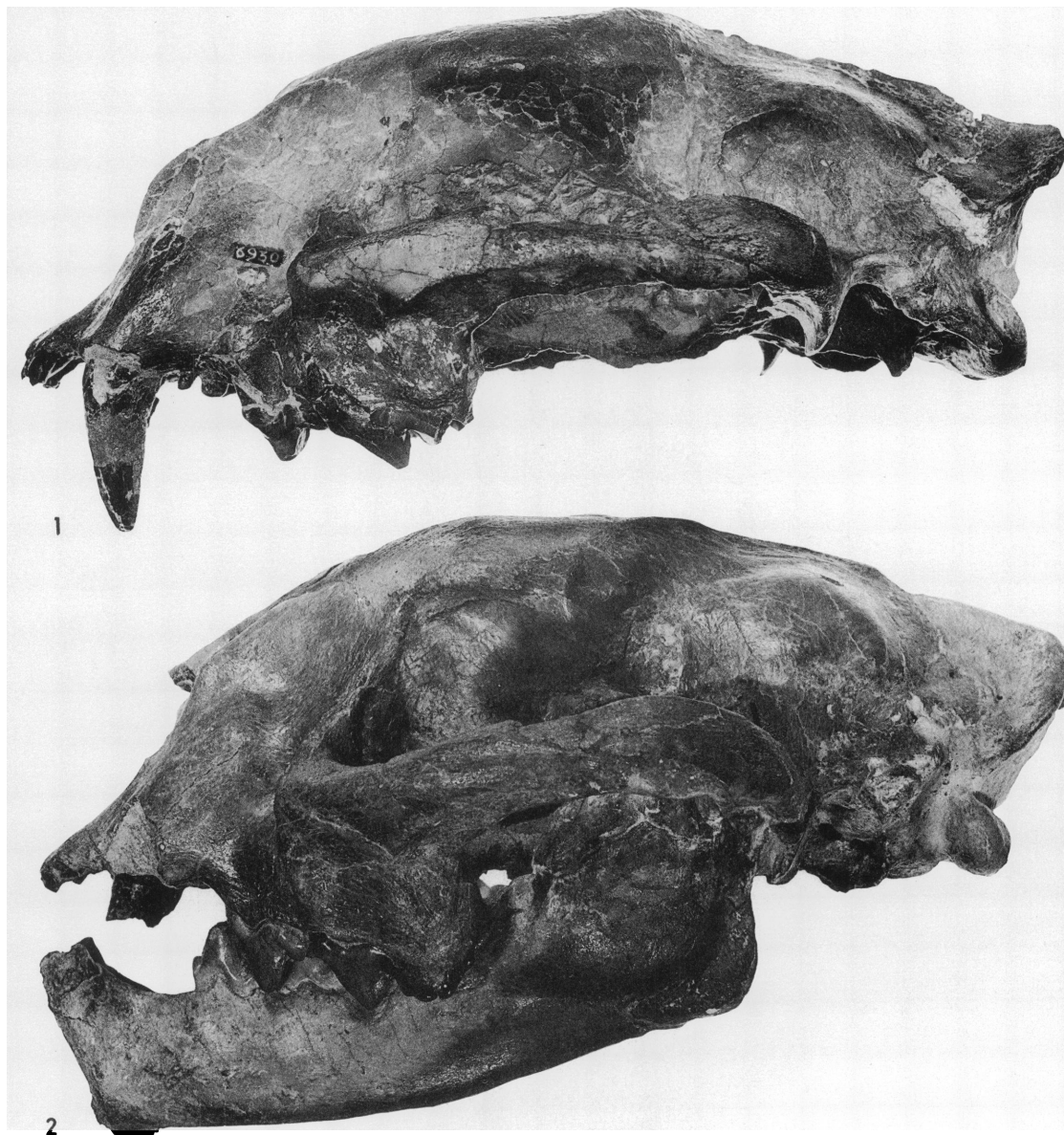
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Nimravus brachyops Cope, U.C.M.P. No. 1681, skull, male. 1. Ventral view. 2. Dorsal view. John Day formation, Oregon. × ¾

Nimravus brachyops Cope, A.M.N.H. No. 6930. 1. Mandible, lateral view. 2. Skull, ventral view, reversed. 3. Skull, dorsal view, female. John Day formation, Oregon. × ¾

Nimravus brachyops Cope. 1. A.M.N.H. No. 6930, skull, lateral view, female. 2. Y.P.M. No. 10046, skull and mandible, lateral view, reversed, female. John Day formation, Oregon. × ¾
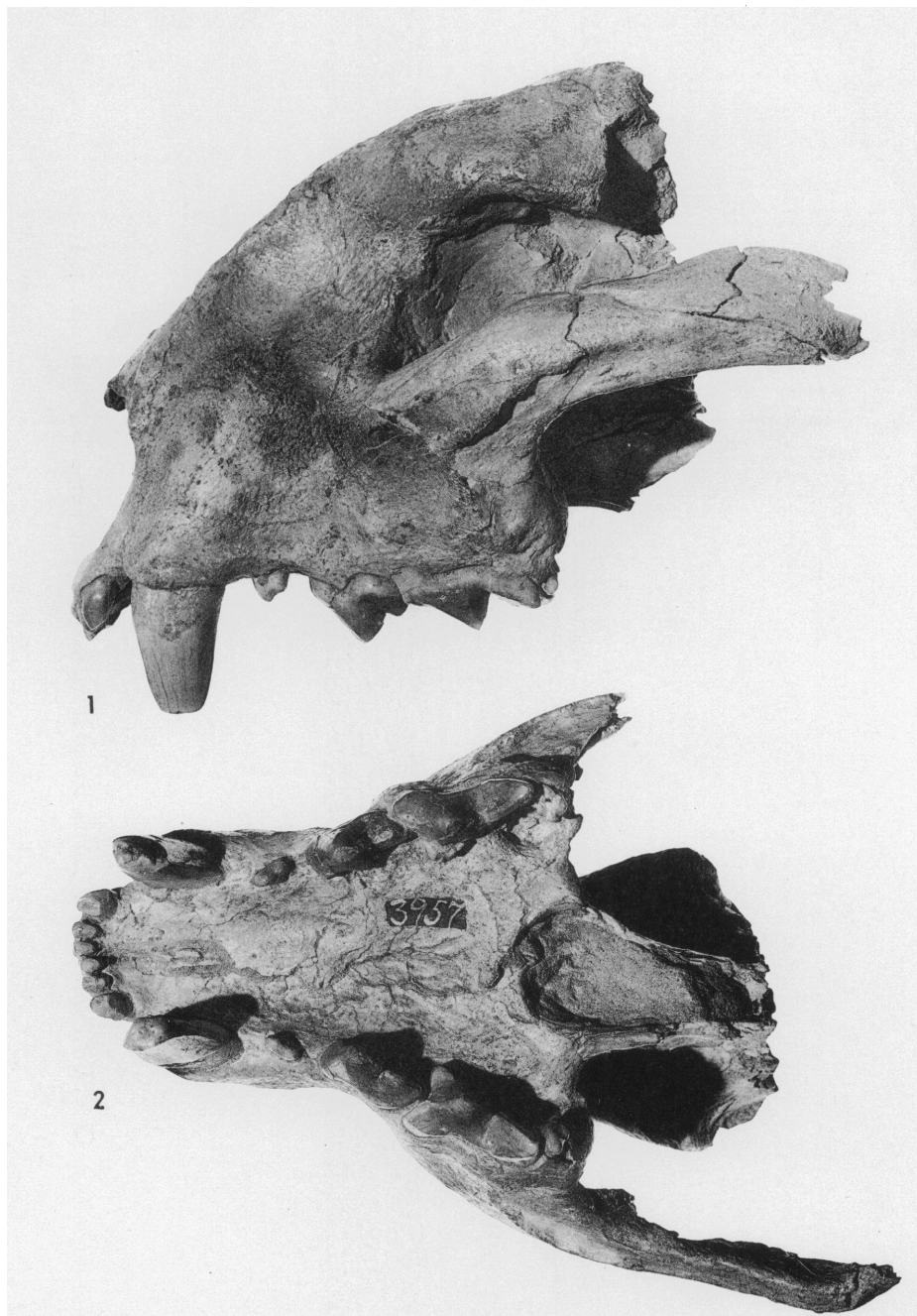
*Nimravus brachyops* Cope, Y.P.M. No. 10046, skull, dorsal view, female; John Day formation, Oregon. × 1

Nimravus brachyops Cope, U.N.S.M. No. 1091, skull, ventral view, male; Gering formation, Nebraska. ×1
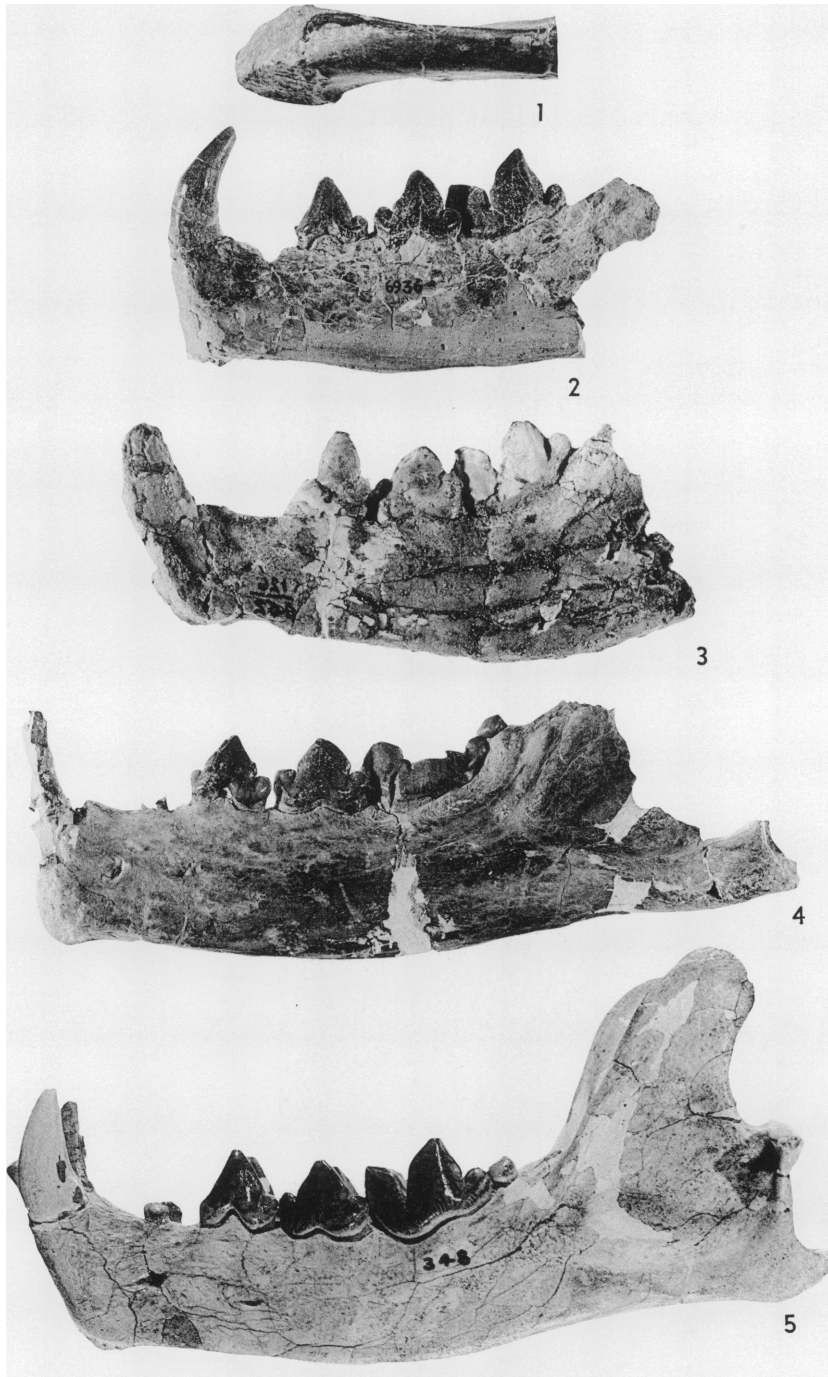
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Nimravus brachyops Cope, U.S.N.M. No. 3957, partial skull, female. 1.
Lateral view, reversed. 2. Ventral view. Gering formation, Nebraska. × ¾
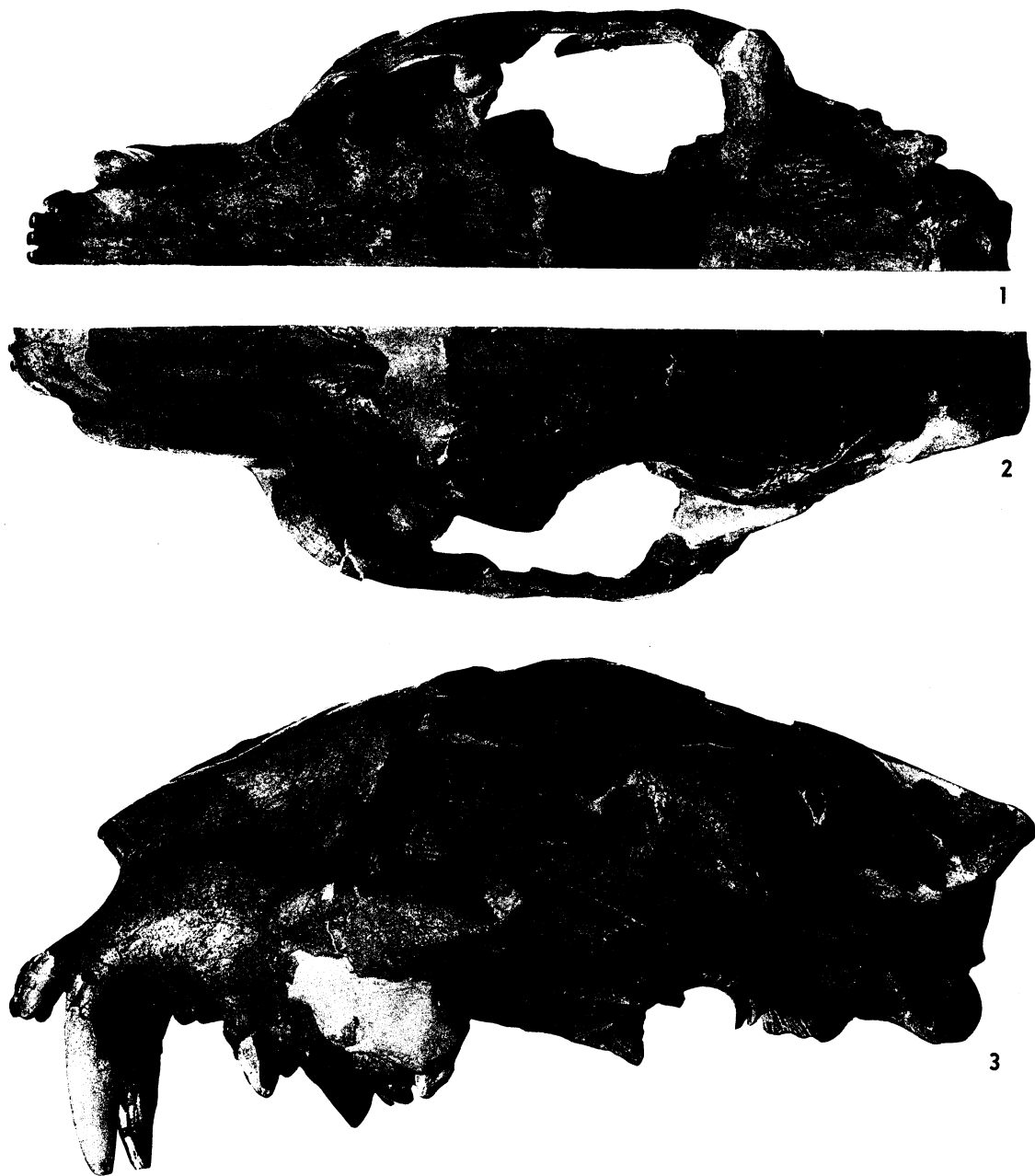
Nimravus brachyops Cope, S.D.S.M. No. 348, skull, female. 1. Ventral view. 2. Dorsal view. 3. Lateral view. Poleslide member, Brule formation, South Dakota. × ¾

Nimravus brachyops Cope. 1. A.M.N.H. No. 6935, jaw, ventral view, reversed; John Day formation, Oregon. 2. A.M.N.H. No. 6936, jaw, lateral view; John Day formation, Oregon. 3. C.I.T. No. 462, jaw, lateral view, reversed; Sespe formation, California. 4. S.D.S.M. No. 4053, jaw, lateral view, reversed; Poleslide member, Brule formation, South Dakota. 5. S.D.S.M. No. 348, mandible, lateral view; Poleslide member, Brule formation, South Dakota. × ¾