

SYSTEMATICS, BIOGEOGRAPHY,  
AND EVOLUTION OF *CYNORCA*  
AND *DYSEOHYUS* (TAYASSUIDAE)

MICHAEL O. WOODBURNE

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 141 : ARTICLE 2      NEW YORK : 1969





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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 141, article 2, pages 271–356, text figures 1–14,  
plates 41–51, tables 1–17

*Issued May 16, 1969*

*Price: \$3.00 a copy*



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## INTRODUCTION

THE PRESENT PAPER is the first of a series of reports designed to review the Tertiary and Quaternary genera of fossil peccaries. A study of the taxonomic status and osteological and dental variation of the living peccaries has been recently completed. In that paper (Woodburne, 1968), it was concluded that the modern peccaries comprised two distinct genera, each having had a considerable, although largely unknown, independent historical development. Each genus is composed of a single modern species. The smaller and more widely distributed collared peccary is *Dicotyles tajacu* (Linnaeus), whereas the larger form, the white-lipped peccary, is referable to *Tayassu pecari* Link. Although each species possesses a relatively conservative morphology, observed individual variation within each taxon is moderately large. The amount of this variation has been assessed in the above-mentioned study so that the degree of dental and cranial variability encountered in the modern species populations can serve as a guide when fossil samples are considered.

During the study of fossil and recent tayassuids, initiated in collaboration with the late R. A. Stirton of the Museum of Paleontology, University of California, Berkeley, it became apparent that the Tertiary peccaries underwent two major evolutionary radiations. The first involved the appearance of the group in early Oligocene time, as manifested in such genera as *Perchoerus*, *Thinohyus*, *Chaenohyus*, *Desmathyus*, and *Hesperhyus*, and this radiation carried on into the Pliocene.

The second evolutionary radiation of the peccaries is first documented in the early Miocene with the genus *Cynorca* and its derivative *Dyseohyus* which are the subject of this report. Other genera, which are a part of the second, more modern manifestation of peccary evolution, include *Prosthennops*, *Mylohyus*, *Tayassu*, *Platygonus*, and *Dicotyles*.

Thus the genus *Cynorca* is important in that it stands in an annectant position between the primitive peccaries and the more modern types. As here constituted, *Cynorca* consists of four species: the genotypic species,

*C. proterva*, from the early late Miocene, mainly from eastern North America; a new taxon, *C. occidentale*, from the middle and late Miocene of western North America; *C. hesperia*, a monotypic form from the late Miocene of Oregon; and *C. sociale* from early to middle Miocene deposits in Texas and California. Other specimens of uncertain affinity are known from early to late Miocene deposits of Nebraska, California, Oregon, and Texas.

*Dyseohyus* is composed of two species: *D. fricki*, currently known only from the late Miocene of California; and *D. stirtoni*, new species, from approximately contemporaneous deposits in Colorado, Nebraska, and Texas. Sparse remains of a larger form of peccary probably related to *Dyseohyus* have been found in the late Miocene of Colorado and early Pliocene of Nevada.

## TAXONOMY

The genus *Cynorca* has never been adequately diagnosed, inasmuch as Cope considered it a squalodont and approached the specimens from that point of view. Now that it can be shown to pertain to a peccary that inhabited a large part of North America during Miocene time, the problem of distinguishing *Cynorca* from various other peccary genera again arises.

During a recently completed study of the cranial myology and osteology of *Dicotyles tajacu* (Woodburne, 1968), approximately 100 specimens of this species, as well as of the contemporaneous *Tayassu pecari*, were examined with regard to individual variation. In general, it was found that specimens of one genus differed from those of the other mainly in cranial characters and that, other than size, dental distinctions tended to be subtle. Part of this phenomenon seems to be due to the fact that, whereas the basic construction of peccary dentitions is conservative and not subject to such profound evolutionary changes as, for instance, are seen in certain members of the Equidae, the dental morphology of a given species population may show a rather considerable amount of detailed individual variation. This obviously

hinders the formulation of clear-cut and neatly exclusive statements when one population is compared with another, but it also indicates that caution should be exercised in naming new peccary taxa on the basis of a few dental irregularities. The problem is only compounded by the fact that fossil peccaries are rarely found in statistically valuable quarry samples, so that, even granting the probably wide dental variability of these paleopopulations, it is difficult to assess the direction, if any, in which the variation tends to be manifested.

From the above-mentioned study on Recent peccaries and from a study of a large portion of the available fossil tayassuid material, the following generalization seems to apply: that peccary genera tend to be distinguished by a combination of cranial and dental features, but that species are mainly separable only dentally. Because each species is apt to show a relatively wide range of dental variation, fossil peccary populations will tend to be broadly rather than narrowly characterized, with the corollary that these species often will be moderately long-ranging entities.

Partly because of the factors just discussed, there has been a great deal of complexity regarding the systematics of the living peccaries and some allegedly related small, late Cenozoic fossil species. Names such as *Dicotyles torquatus*, *D. fossilis*, *D. lenis*, and *D. hesperius*, to list those pertinent here, are commonly encountered in the early paleontological literature in reference to both fossil and Recent forms.

As far as the living peccaries are concerned, a recent study (Woodburne, 1968) produced rather strong evidence favoring the thesis that they constitute two separate genera. The larger, less well-known, and less-widespread white-lipped peccary is *Tayassu pecari* Link, 1795 (Hershkovitz, 1963). Under the name *Sus tajacu*, the smaller, better-known, and more-widespread collared peccary was originally included (Linnaeus, 1758) in the same genus as the modern European suid. Cuvier (1817) subsequently proposed the name *Dicotyles torquatus* for the collared peccary, but, because of Linnaeus' prior allocation, only the generic name still stands. The collared peccary should be known as

*Dicotyles tajacu* (Linnaeus, 1758).

Unfortunately, many of the classical North American vertebrate paleontologists considered *D. torquatus* a valid combination and referred both living and extinct peccaries to it. Most of the fossil forms were small and were purported to resemble the living collared peccary. As far as I can determine, *Dicotyles traunmulleri* of the Peruvian late Pliocene (Spillman, 1949) represents the only fossil form that may be awarded tentative recognition as a close relative of the collared peccary. A few specimens from latest Pleistocene or sub-Recent deposits of Argentina may be referable to the collared peccary, and others from deposits of the same general age in various places in South America may relate to the white-lipped peccary as well (Rusconi, 1931). In spite of these ancestral glimmerings in South America, there is no specimen from Pleistocene or earlier deposits in North America that can be said to pertain to either of the Recent genera.

For the above-mentioned reason referral of some of the middle and late Tertiary fossil peccaries to *Dicotyles torquatus*, *D. fossilis*, *D. lenis*, and *D. hesperius* is misleading and adds confusion to a group of animals for which the number of specimens is usually small, but, on the other hand, for which the number of taxa proposed and used has been relatively high. Some of the specimens in the original hypodigm of *Cynorca proterva* were allocated to *Dicotyles torquatus* by Cope (1867) and all the hypodigm materials were referred to *D. lenis* by Leidy (1869). With *D. fossilis* and its synonym, *D. lenis*, having been included in the Pleistocene genus *Mylohyus* by Lundelius (1960), some of the former complexity is cleared away. Specimens referred to *D. lenis* by Leidy are certainly not to be confused with those of *Mylohyus*, nor do they pertain to the living collared peccary, by whichever name it be known. My conclusion is that *Cynorca proterva* is a valid species, a peccary of approximately late Miocene age which inhabited coastal or interior areas with roughly comparable ecologies from Nebraska and Texas eastward to South Carolina and Maryland.

Because the present project is part of a revision of the Tayassuidae as a whole, the content of various generic names proposed



in the literature may be altered. Undocumented innovations are kept to a minimum, and I use the following conventions. The term "primitive peccaries," or "primitive genera," applies to *Perchoerus*, *Thinohyus*, and *Chaenohyus*. Either term could also apply to *Desmathyus* and *Hesperhys*, but these large forms obviously have nothing to do with the small genus *Cynorca* or its derivative, *Dyseohyus*. As will be developed subsequently, *Cynorca* stands at the base of the second major peccary radiation, i.e., that which resulted in the modern genera *Dicotyles* and *Tayassu* as well as the genera *Dyseohyus*, *Prosthennops*, *Mylohyus*, and *Platygonus*. *Cynorca* was apparently the direct ancestor only of *Dyseohyus*. As far as can be determined at the present time, *Platygonus*, *Mylohyus*, and *Prosthennops*, as classically constituted, are side branches, albeit successful ones, from the evolutionary pathway leading to the modern peccaries. Therefore, most comparisons are made with the primitive genera on the one hand and with *Dyseohyus* and *Dicotyles* or *Tayassu* on the other. Because of the serial nature of the projected reports on fossil peccaries, it is not possible to compare exhaustively each genus with every other genus until the last.

### DESCRIPTIVE TERMINOLOGY

In the subsequent cranial and mandibular descriptions, certain fossae, depressions, or other features are designated by the following names. Other structures not defined are those commonly used and should present no problems.

**BUCCINATOR FOSSA:** This fossa, to judge from evidence found in a dissection of *Dicotyles tajacu*, houses much of the upper origin of *M. buccinator*. In *Cynorca* and *Dyseohyus* the fossa lies lateral to the diasternal crest of the maxillary and forms a shallow, elongate fossa which diminishes anteriorly and posteriorly. Although fibers of *M. buccinator* may have extended backward along the supra-alveolar portion of the maxillary to the level of the infraorbital foramen, there is scant evidence of this on the bone itself.

**DIGASTRIC FOSSA:** This is an anteriorly elongate fossa on the internal surface of the mandible above its ventral edge which con-

tains the body of *M. digastricus*. Anteriorly the fossa narrows toward the rear of the symphysis; posteriorly, it is confluent with the pterygoid fossa.

**FACIAL CREST:** This is the usually sharp ventrolateral edge of the zygomatic arch, corresponding to the lateral border of the origin of *M. masseter*. The crest fades out posteriorly at the edge of the glenoid fossa and ends abruptly anteriorly at the anterolateral tip of the zygoma.

**FRONTAL DEPRESSION:** In *Cynorca* and *Dyseohyus* the frontal depressions are slightly depressed areas on the dorsal surface of the cranium medial to the dorsal rim of the orbits and posteromedial to the frontal eminences.

**FRONTAL EMINENCE:** On each side of the dorsal surface of the cranium anterolateral to the supraorbital foramina and anteromedial to the dorsal rim of the orbits, the frontal and adjacent portions of the nasal and maxillary bones are raised into an elongate eminence. The structures diminish distally in all directions and are bounded medially by the supraorbital-nasal grooves.

**GENIAL PITS:** These are depressions in the same general areas as the genial spine, commonly positioned more dorsally than the spine. There is usually one of these pits on each side of the midline.

**GENIAL SPINE:** This is a posteriorly projecting ridge or spine situated in the midline at the posteroventral edge of the symphysis.

**INFRATEMPORAL CRESTS:** A pair of crests are found at the rear of the infratemporal fossa. The more medial of the two crests passes upward along the lateral border of the anterior lacerate-rotundum foramen, and leads toward the base of the postorbital process of the frontal. Midway along its length this crest is developed into a broadly acuminate eminence, where a short, more dorsally directed branch curves anteriorly along the posterior surface of the orbital fossa. The second, more lateral, of the two infratemporal crests is separated from the first by a relatively broad, anteroventrally directed sulcus. The crest extends obliquely down the anterior surface of the squamosal toward the exposed anterior tip of the bulla.

**INFRATEMPORAL FOSSA:** An imperfectly delineated area anterior to the temporal fossa is bounded posteriorly by the anteriorly

facing portion of the squamosal lateral to the anterior lacerate-rotundum foramen, and anteromedially by the alisphenoid and posterior portion of the crest corresponding to the dorsal limit of the origin of *M. pterygoideus lateralis*. Dorsally, the infratemporal fossa is confluent with the orbital fossa, anteriorly with the pterygopalatine fossa, and its lateral border is defined by the coronoid process of the mandible, when in position.

**MID-SAGITTAL PLANE:** This is the vertical plane following the midline of the animal which divides it into bilaterally symmetrical halves. See sagittal plane.

**POSTDIGASTRIC SULCUS:** This is the concave portion of the profile of the ventral surface of the mandible just anterior to the angle.

**POSTTYMPANIC PROCESS:** That part of the squamosal that forms a more or less flat plate in the mastoid region of the cranium posterodorsal to the postglenoid process and lateral to the base of the paroccipital process is the posttympanic process. Laterally, it is fused to the tympanic process of the squamosal (see Pearson, 1927, fig. 1).

**PTERYGOID FOSSA:** This area on the internal surface of the mandible above the angle and below the articular condyle contains the insertion of the pterygoid muscles. The fossa narrows anteriorly and, in *Cynorca* and *Dyseohyus*, leads into the digastric fossa.

**PTERYGOPALATINE FOSSA:** An elongate fossa, bounded above by the ridge corresponding to the dorsal limit of the origin of *M. pterygoideus lateralis*, extends anteriorly toward the maxillary and sphenopalatine foramina. The ventral edge of the fossa is formed by the laterally recurved ventral flange of the palatine, alisphenoid, and associated pterygoid bones, whereas the lateral border of the fossa is delimited by the medial edge of the coronoid process of the mandible.

**SAGITTAL PLANE:** The sagittal plane is any plane parallel to the mid-sagittal plane, but not on the midline.

**TEMPORAL FOSSA:** This is the area bounded medially by the squamosal and parietal bones, laterally by the medial surface of the coronoid process of the mandible, and posteriorly by the postzygomatic and lambdoidal crests. Anteriorly the fossa is confluent with the infratemporal fossa.

**TYMPANIC PROCESS:** The posterior portion of the zygomatic part of the squamosal, which rises behind the lateral edge of the glenoid fossa to the tip of the external auditory meatus, is the tympanic process. It covers the anterior half of the meatus, and the posttympanic process covers the posterior half.

## MEASUREMENTS

Measurements on the available specimens were made as outlined below and, unless otherwise specified, all measurements are in millimeters.

**LENGTH, ANTERIOR TIP OF I<sup>1</sup> TO REAR OF CONDYLES:** This dimension (table 12) consists of two measurements: from the tip of I<sup>1</sup> to the rear of M<sup>3</sup>, and from M<sup>3</sup> to the point at which a plane perpendicular to that of the palatal surface intersects the rear of the condyles.

**LENGTH OF DIASTEMA FROM C<sup>1</sup> TO P<sup>2</sup>:** This is the distance from the rear edge of the alveolus of C<sup>1</sup> to the anterior edge of that of P<sup>2</sup>, as measured parallel to the palatal plane (table 12).

**WIDTH BETWEEN ALVEOLI OF P<sup>2</sup>:** This dimension (table 12) is taken between the lingual edges of the anterior root of P<sup>2</sup>.

**WIDTH BETWEEN ALVEOLI OF M<sup>3</sup>:** This is the transverse distance between the lingual edges of the alveoli of the anterolingual root of M<sup>3</sup> (table 12).

**LEAST WIDTH, ROSTRUM BEHIND CANINES:** This measurement, made from the ventral aspect of the cranium, is the least transverse dimension of the rostrum, which occurs just anterior to P<sup>2</sup> (table 12).

**HEIGHT, CONDYLES TO NUCHAL CREST:** This measurement is taken in the plane perpendicular to that of the palatal surface. Ventrally the calipers rest on the ventral edge of the condyles; dorsally they intersect the dorsal surface of the cranium near theinion (table 12).

**BREADTH ACROSS ZYGOMATIC ARCHES:** This dimension is also taken from the ventral aspect of the cranium. It represents the greatest transverse distance across the zygomatic arches. In the peccaries under discussion this occurs at the anterior edge of the glenoid fossa (table 12).

**BREADTH BETWEEN POSTORBITAL PRO-**



**CESSSES OF FRONTALS:** This parameter is measured from the dorsal aspect, with the calipers resting on the lateral surface of the postorbital processes (table 12).

**LENGTH AND WIDTH, UPPER INCISORS:** This measurement represents the greatest cross-sectional length of the tooth, parallel to the plane of the palatal surface, between its anterolingual and posterolingual edges. The width is taken perpendicular to the length (tables 1 and 14).

**LENGTH AND WIDTH, LOWER INCISORS:** For  $I_1$  and  $I_2$  the length was taken in an anteromedial direction across the ventrolabial base of the enamel. The width was taken posterodorsally, through the body of the tooth, in a plane perpendicular to that used for the length.  $I_3$  is oriented longitudinally so that its dimensions can be measured in the usual way (tables 2, 9, and 15).

**LENGTH AND WIDTH, CANINES:** The cross-sectional length of both upper and lower canines is measured along the long axis of the tooth at the base of the enamel. The width was measured perpendicular to this. In the living genera, and probably in these fossil forms as well, the width of the upper canine is essentially unaffected by tooth wear. The width of the lower canine is also unaffected by wear, although the length of both teeth is decreased as wear progresses (tables 1, 2, 4, 5, 9–11, 14, 15, and 17).

**LENGTH,  $I^1$  TO  $M^3$ :** This measurement was taken directly, from the anterior tip of  $I^1$  to the rear of  $M^3$ . Variability was probably introduced into the results (table 14) because of wear between adjacent members of the cheek-tooth series and occlusal wear on  $I^1$ .

**LENGTH AND WIDTH, UPPER CHEEK TEETH:** These results are obtained in the usual way. The length is the greatest longitudinal dimension of the tooth, taken somewhat above the base of the enamel. For the upper premolars, the direction of measurement is often aligned slightly anteromedially; for the molars it is roughly parallel to the long axis of the cranium. The width is measured perpendicular to the length, across the widest part of the tooth (tables 1, 4, 7, 8, 10, 14, 16, and 17).

**LENGTH,  $I_1$  TO CONDYLES:** This dimension (table 13) is the sum of two measurements: the length of  $I_3$  to  $M_3$ , and the length from

the rear of  $M_3$  to the rear of the condyles. The mechanical error introduced by this method is probably less than 5 per cent.

**LENGTH, DIASTEMA BETWEEN  $C_1$  AND  $P_2$ :** The results are given in table 13. The measurement was taken from the rear of the alveolus of  $C_1$  to the anterior alveolus for  $P_2$ .

**DEPTH, TIP OF CORONOID PROCESS TO ANGLE OF MANDIBLE:** The measurement may be taken directly with the jaws of the calipers oriented in a vertical plane parallel to that intersecting the ventral edges of the horizontal ramus and the angle. The results are presented in table 13.

**DEPTH BELOW  $P_2$ :** With the calipers oriented as in the previous measurement, the depth (table 13) is taken from the edge of the anterior alveolus of  $P_2$  to the ventral edge of the ramus directly below.

**DEPTH BELOW REAR OF  $M_1$ :** The orientation of the calipers is the same as above. A possible mechanical error of about 5 per cent may be introduced because of the necessity of estimating the point at which the ventral edge of the mandible would strike the lower jaw of the calipers. In this orientation the lower point of the calipers can project only slightly medial to the lateral surface of the mandible (table 13).

**WIDTH BETWEEN ALVEOLI OF  $P_2$ :** This is the transverse distance between the inner edges of the anterior alveoli of  $P_2$  (table 13).

**WIDTH BETWEEN ALVEOLI OF  $M_3$ :** The measurement (table 13) is determined in an analogous manner to that described above.

**WIDTH BETWEEN CONDYLES:** The points of the calipers are placed between the inner tips of the condyles (table 13).

**LENGTH,  $P_2$  TO  $M_3$ :** This is the greatest longitudinal dimension of the lower cheek-tooth series. The results are shown in tables 9 and 15.

**LENGTH AND WIDTH, LOWER CHEEK TEETH:** The length is the greatest anteroposterior diameter of the tooth; the width is the greatest transverse diameter (tables 2, 3, 5, 6, 9, 11, 15, and 17).

#### ABBREVIATIONS

Institutions in which collections were used in this work are abbreviated as follows:

A.M.C. Department of Geology, Texas A. and M. College, College Station

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

A.N.S.P., Academy of Natural Sciences of Philadelphia

F:A.M., Frick Laboratory, Department of Vertebrate Paleontology, the American Museum of Natural History

L.A.C.M., Los Angeles County Museum of Natural History

M.C.Z., Museum of Comparative Zoology, Harvard University

U.C.M.P., University of California Museum of Paleontology, Berkeley

U.C.R., Department of Geological Sciences, University of California, Riverside

U.S.G.S., United States Geological Survey

U.S.N.M., United States National Museum, Smithsonian Institution

U.T., University of Texas Vertebrate Paleontological Collections

Y.P.M., Peabody Museum, Yale University

The symbols used in all the tables and their significance are:

a, greatest width measured across anterior moiety  
e, width of anterior and posterior moieties equal  
p, greatest width measured across posterior moiety

+, measurement too small because of wear or abrasion

×, measurement approximate

### ACKNOWLEDGMENTS

Before the untimely death on June 14, 1966, of R. A. Stirton, he and I had been long engaged on a revision of the Oligocene and early Miocene peccaries, and, although any errors of fact and interpretation embodied in the succeeding pages of this report must necessarily be attributed to me, I gratefully acknowledge the ideas and observations so enthusiastically contributed by him. Regretful that these studies must be carried on without his help, I respectfully dedicate to R. A. Stirton this report, and the others that will follow.

During the tenure of this investigation, many individuals and institutions graciously made available type and other pertinent material from collections under their care. Appreciation for these and other hospitalities is extended to Dr. Horace G. Richards, Academy of Natural Sciences of Phila-

delphia; Dr. Theodore E. Downs, Los Angeles County Museum of Natural History; Dr. Malcolm C. McKenna, Mr. Morris F. Skinner, Mr. Ted Galusha, Mr. Beryl E. Taylor, and Mr. George Krochak, the American Museum of Natural History; Dr. C. L. Gazin, United States National Museum, Smithsonian Institution; Dr. John A. Wilson, University of Texas; Dr. Donald E. Savage, Museum of Paleontology, University of California, Berkeley; and Dr. Elwyn L. Simons, Peabody Museum of Natural History, Yale University. I have also benefited greatly from discussions with Dr. McKenna, Mr. Skinner, Mr. Galusha, Mr. Taylor, and Dr. Richard H. Tedford, the last-named also of the American Museum of Natural History.

The illustrations are the work of Messrs. Owen J. Poe and Karoly Fogassy, Miss Augusta F. Lucas, or myself.

Expenses that accrued during this study were partially defrayed by Intramural Grant No. 8044 from the Academic Senate, University of California, Riverside. Moreover, generous financial support was provided by the Frick Laboratory Fund of the American Museum of Natural History during the summer of 1966, so that I was able to spend my time examining specimens critical to this report as well as to my understanding of the phylogeny of the later Tertiary peccaries as a whole. In short, without Frick sponsorship this report would not have been possible.

This manuscript has been read by Dr. McKenna, Mr. Skinner, Mr. Galusha, Mr. Taylor, and Dr. Tedford, all of whom provided helpful suggestions. It should be understood, however, that the opinions expressed herein are not necessarily those of the above-named persons and that any errors of fact or interpretation are mine alone.

More than one-half of the specimens discussed in this report were obtained from quarries developed by members of the former Frick Laboratory. In order to avoid repetition of designations, such as Frick Laboratory Survey Quarry, the relevant quarry names are listed below. A shorter designation, e.g., Survey Quarry, is used in the text. A few of the Frick localities have not been given quarry names (indicated below by an asterisk) and are given the longer and more complete designation in the text.



## NEBRASKA

- Sioux County
  - Echo Quarry
  - Jenkins Quarry
  - Prosynthetoceras* Quarry
  - Ravine Quarry
- Dawes County
  - Observation Quarry
  - \*3 miles south and 9 miles west of Hay Springs

## COLORADO

- Weld County
  - \*2 miles northwest of Mastodon Quarry, near Grover
  - \*"Upper Horizon," near Grover

## WYOMING

- Goshen County
  - \*East side of road to Jay-Em, "16-mile district," near Lusk
  - \*"16-mile district, west end," near Lusk

## MONTANA

- Meagher County
  - \*Third wash northwest of White Sulphur Springs

## TEXAS

- San Jacinto County
  - Trinity Pit 1
- Tyler County
  - Woodville Locality 1 or 3

## NEVADA

- Esmerelda County
  - \*7 miles west of Blair Junction, near Tonopah

## CALIFORNIA

- San Bernardino County
  - Hemicyon Quarry
  - Steepside Quarry
  - Valley View Quarry

Standard cartographic locations of these localities are given, where possible, in the appropriate places in the text.

## STRATIGRAPHY AND CHRONOLOGY

THE SPECIMENS TREATED in the present study are of diverse provenance and were collected over a span of time ranging from the earliest days of vertebrate paleontology in America to the present. In the earlier period, material was often recovered by professional collectors, some of whom paid little attention to details of stratigraphy. In other cases, either original data have been lost, or information regarding locality data has been generalized to the extent that it is useful only in broad terms. Of course, during the interval between the early collections and the present, knowledge of the stratigraphy of local areas has increased and collecting procedures have become more refined. Moreover, the position of certain fossil aggregates with respect to the biochronological concepts Arikareean, Hemingfordian, and Barstovian (Wood and others, 1941) has fluctuated ever since these terms were introduced. It is not the purpose of this paper to revise these concepts, but, because of the diversity of opinions as to the content and scope of these and other Mammal Ages, the following comments are given in order to provide a frame of reference. In all subsequent paragraphs, such terms as Arikareean, Hemingfordian, Barstovian, or Clarendonian should be understood to refer to the equivalent North American Land-Mammal Ages proposed by Wood and his co-authors (1941).

Although it has been suggested that early Clarendonian faunas in North America best correspond to the faunas attributed to the late Miocene in Europe (Evernden, Curtis, Savage, and James, 1964, table 1), I retain the view of Wood and his co-authors (1941) and, for the purpose of this paper, attribute the Clarendonian to the early Pliocene. Likewise, in spite of attendant typological problems within Europe (see Savage, 1955), the following conventions are used here:

Arikareean = early Miocene  
Hemingfordian = middle Miocene  
Barstovian = late Miocene

Except for considerations involving early Clarendonian faunas, this arrangement is approximately correct and does little in-

justice to these concepts as they are currently used.

The paleontological literature contains many references to faunal assemblages that have an early or late position relative to the boundaries of a given Mammal Age. With one important exception (Savage, 1955), such usage has not been rigorously defined or defended and, although uncertainties remain as to what is meant by a Barstovian fauna, for instance, as compared with the type or typical Barstovian fauna, or by Hemingfordian faunas as compared with the type or typical Hemingfordian fauna, the approach taken here is that designations such as "early" and "late" are meaningful and have practical value. Recent attempts at indicating the presence of more than one fauna in, for instance, the Barstow Formation (Lewis, 1964, 1968) show that considerable detailed work must be done before the sequence of faunas encompassed within the various Mammal Ages can be adequately documented. The rigorous approach embodied in reports by McKenna (1965) and Savage (1955) points the way for the solution of such problems. In the meantime, however, it is still possible to evaluate the stage of evolution of a given faunal assemblage with that of another and to arrive at an interpretation as to whether the age of the first is earlier than, equal to, or later than, that of the second. In this report, the designation of a particular fauna as early or late represents a subjective evaluation by a particular author as to the position of the fauna with respect to others contained in a particular Mammal Age.

That the basis for such designation may be clearly understood, the following comments are provided for each of the localities mentioned in the text.

### ARIKAREEAN

OREGON: Inasmuch as the lower part of the John Day Formation of possibly late Oligocene age is sparsely fossiliferous, all specimens recorded as coming from the John Day River, John Day beds, or John Day Formation are regarded as being Arikareean

in age. Localities included in this category are L.A.C.M. (C.I.T.) 32 and the unnumbered localities that pertain to specimens of *Cynorca sociale* in the Peabody Museum of Natural History and the American Museum of Natural History. Material from U.C.M.P. V-6306, V-6416, and V-6417 is probably late Arikareean in age (J. M. Rensberger, personal communication, July 10, 1967).

TEXAS: Specimens of *Cynorca sociale* from the Garvin Gully fauna of the Oakville Formation in Texas are here considered to be either late Arikareean (Wilson, 1960) or early Hemingfordian (Wood and others, 1941) in age.

NEBRASKA: A single specimen of *Cynorca* cf. *C. sociale* from the "Loup Fork Tertiary" is probably Miocene in age. In view of its small size and probable relationship to *Cynorca sociale*, this temporal assignment can probably be refined to Arikareean.

#### HEMINGFORDIAN

WYOMING: According to the available field records certain specimens of *Cynorca occidentale*, new species, in the Frick collections were collected on the "east side of the road to Jay-Em," and high in the section "(above the brown sand)" of the "16-mile district" near Lusk, Wyoming. At least the latter are considered as having come from the Marsland Formation (*sensu* McKenna, 1965; = "Lower Marsland" = "upper Harrison" of other authors). Such remains are tentatively assigned an early Hemingfordian age.

CALIFORNIA: Specimens of *Cynorca sociale* from L.A.C.M. (C.I.T.) 503 are from the Phillips Ranch fauna of late Hemingfordian age. The age assignment is based primarily on the indigenous *Merychippus tehachapiensis*, the stage of evolution of which resembles that attained by *Merychippus primus* of faunas found in the Sheep Creek Formation in Nebraska. U.S.N.M. No. 23871 is an isolated right M<sup>3</sup> designated as *Dyseohyus* or *Cynorca*. The locality from which it was recovered is U.S.G.S. M-1016 in the Hemingfordian portion of the Caliente Formation in San Luis Obispo County, California. Whether the specimen is associated with early or late Hemingfordian faunal remains is yet to be documented.

NEBRASKA: Remains of *Cynorca occidentale*, new species, from Ravine Quarry are derived from rocks of the Sheep Creek Formation. Verbal communication from Morris F. Skinner indicates that the quarry lies 100 feet stratigraphically below the ash bed at the top of the formation. According to McKenna (1965) the fossils from the deposits of this formation, which lie below the ash dated by Evernden, Curtis, Savage, and James (1964) at 14.7 million years, are referable to the Hemingfordian North American Land Mammal Age. Furthermore, such fossils apparently correspond to the "limited or lower Sheep Creek fauna" specifically mentioned in the characterization of the Hemingfordian given by Wood and his co-authors (1941). Although there may be some debate as to the position of the upper boundary of the Hemingfordian biochron with respect to various parts of the Sheep Creek Formation (see McKenna, 1965, for a review), there is little doubt that the Sheep Creek (exclusive of the Lower Snake Creek beds) is the last formation to bear fossil aggregates to which a Hemingfordian age can be attributed. Accordingly, in this report specimens derived from rocks of the Sheep Creek Formation (*sensu* McKenna, 1965) are informally designated as late Hemingfordian in age. Fossils from deposits overlying or channeled into the Sheep Creek are considered as being post-Hemingfordian in age.

MONTANA: A single mandible of a peccary referred to as *Cynorca occidentale*, new species, was obtained from a Frick Laboratory locality in "lower beds," just above the base of the third wash northwest of White Sulphur Springs, Meagher County, Montana. The stage of evolution of this specimen is similar to that of specimens from Ravine Quarry. A tentative late Hemingfordian age is given to the Montana specimen.

OREGON: According to the specimen label, the type and sole specimen of *Cynorca hesperia* (Marsh) was collected from the upper John Day River, Oregon. Marsh (1871, p. 43) thought the specimen came from the same deposits as the type of *Platygonus condoni*, i.e., from "the Pliocene beds of Oregon" and it may be significant that in Marsh's 1871 paper no typical "John Day" fossils were included. It is possible that Condon's collection

was made south of Picture Gorge where mainly later (Mascall and Rattlesnake) deposits occur. Of course the Mascall and Rattlesnake formations were not recognized as different units in 1871, but, from the stage of evolution displayed by the specimen, it seems most likely that the holotype of *C. hesperia* was recovered from deposits of the Mascall Formation. The age of faunal elements of this formation has been considered to be either latest Hemingfordian or earliest Barstovian by Downs (1956, p. 328; 1961, p. 58), and early Barstovian on radiometric and faunal grounds by Evernden, Curtis, Savage, and James (1964).

#### BARSTOVIAN

NEBRASKA: A large number of the specimens of *Dyseohyus stirtoni*, new species, as well as sparse remains of *Cynorca proterva* considered in this report, are derived from Observation Quarry. According to the associated field records, the temporal position of the specimens from this quarry is considered as post Sheep Creek and pre Lower Snake Creek. Because faunas from the Sheep Creek Formation are considered here as late Hemingfordian, the age of the material from Observation Quarry is tentatively set at early Barstovian.

Specimens of *Dyseohyus stirtoni*, new species, from the following localities in western Nebraska are considered to be Barstovian in age: Survey Quarry in deposits which yield fossils equivalent in age to those derived from the Lower Snake Creek beds; Echo, *Prosynthetoceras*, and Jenkins quarries in Lower Snake Creek deposits.

CALIFORNIA: A somewhat meager but important collection of peccaries has been made from deposits of the Barstow Formation in the Barstow Syncline. Lewis (1964, 1968) recognized the presence of three faunal units in the Barstow Formation, as exposed in the Barstow Syncline and at Alvord Mountain, 25 miles to the east. The youngest faunal unit occurs in the upper third of the formation and has been characterized by the joint occurrence of *Merychippus intermontanus*, *M. sumani*, *Paracosoryx*, *Paramoceros*, and *Ustatochoerus* (Lewis, 1964, 1968). The rocks containing this faunal unit occur stratigraphically above the "lower marker tuff

bed" of Dibblee (1968), which is apparently the same tuff informally termed the "Skyline Tuff" by various vertebrate paleontologists in North America. Remains of *Dyseohyus fricki* from Hemicyon Quarry and L.A.C.M. (C.I.T.) 288 occur in the interval above the "lower marker tuff bed," and, for the purposes of this report, fossil mammals from this interval are considered to be of late Barstovian age.

The second faunal unit discussed by Lewis (1964, 1968) occurs in the middle third of the Barstow Formation, below the "lower marker tuff bed," and is apparently characterized by the occurrence of *Brachycrus buwaldi*, *Ramoceros* (*Merriamoceros*), and *Rakomeryx*. *Merychippus stylodontus* and *Merychys* (*Metoreodon*) may also be characteristic of this unit, but their presence here was not emphasized by Lewis (1968, p. 34). Specimens from Valley View Quarry (*Cynorca occidentale*, new species) and the upper level of Steepside Quarry (*Dyseohyus fricki*), and U.C.R. V-6401 (*D. fricki*) pertain to this faunal unit. In the present report, the second faunal unit of Lewis (1964, 1968) is considered to be of early Barstovian age.

None of the material covered in the present report is known to have been derived from the lowest part of the Barstow Formation which apparently yields *Merychippus teahapapiensis* of late Hemingfordian age. Other specimens in the Frick collection of *D. fricki* from the Barstow area have no exact stratigraphic data and are tentatively considered as being Barstovian in age.

*Cynorca occidentale*, new species, is represented in collections from L.A.C.M. (C.I.T.) 108 and 129 in the *Merychippus* zone (North Coalinga) in Fresno County, California. Downs (1956, 1961) has appraised the age of the fauna from this area and concluded that it was early Barstovian, an assignment followed in the present report.

Additional Barstovian material of *Cynorca occidentale*, new species, is derived from U.C.M.P. V-5666, Kent Quarry, in the Cuyama Badlands. U.C.M.P. V-5666, situated about 470 feet below the top of the middle part of the Caliente Formation, is one of the better localities in this rock unit and contains the most diverse Barstovian fauna of the region. Mammalian elements



with possible biostratigraphic significance from U.C.M.P. V-5666 include *Merychippus sumani*, *M. brevidontus*, and *Archaeohippus mourningi* (James, 1963).

According to Bode (1934, 1935), *A. mourningi* occurs together with *Merychippus californicus* and *M. brevidontus* in the early Barstovian *Merychippus* zone (North Colalinga), but at Barstow, *M. sumani* is associated with a late Barstovian assemblage, including *M. intermontanus* (Lewis, 1964, 1968).

*Archaeohippus mourningi* also occurs in the Barstow sequence (Merriam, 1913, 1919), but a firm statement as to its stratigraphic position has not been presented. *Archaeohippus mourningi* may range through much of Barstovian time; at present its chronostratigraphic significance is not determinable.

James (1963, p. 146) grouped the localities from the Barstovian part of the Caliente Formation into three faunas: the Dome Spring fauna, the Doe Spring fauna, and the Upper Dry Canyon fauna. U.C.M.P. V-5666 is among those contributing to the Dome Spring fauna, the uppermost of the faunal units. Rocks containing U.C.M.P. V-5666 are correlated with those bearing a biotite tuff at U.C.M.P. V-5672, which yielded a potassium-argon date of 15.2 million years (James, 1963, p. 138). This compares favorably with the 15.1 million years obtained by Evernden, Curtis, Savage, and James (1964) from a crystalline tuff about 50 feet stratigraphically above the "lower marker tuff bed" of Dibblee (1968). The Dome Spring fauna contains *Merychippus sumani*, *M. brevidontus*, and *Archaeohippus mourningi* in association with various other taxa (primarily those listed from U.C.M.P. V-5666; James, 1963, p. 137). It would seem to be temporally equivalent to the late Barstovian upper faunal unit of Lewis (1964, 1948) in the Barstow sequence. A possible discrepancy in regard to the composition of the Dome Spring fauna is found in conjunction with U.C.M.P. V-5670, discussed below.

The Doe Spring Canyon fauna of James (1963, p. 146) based on specimens of *Sciuropterus uphami*, *Merychippus sumani*, *Ramoceros* sp., and *Gomphotherium* sp., from U.C.M.P. V-5843, is tentatively correlated with the Dome Spring fauna (James, 1963,

p. 142), but note that *M. sumani* seems to be ubiquitous in the middle part of the Caliente Formation and that James (*loc. cit.*) did not indicate to which subgenus his *Ramoceros* pertains.

James' lower faunal unit, the Upper Dry Canyon fauna, occurs stratigraphically below the other two faunas and is comprised of *Merychippus sumani* in association with *Brachycrus buwaldi* and *Protolabis* sp. (1963, p. 146). The Upper Dry Canyon fauna may be interpreted as roughly equivalent to Lewis' (1964, 1968) second faunal unit in the Barstow Formation, of early Barstovian age. This interpretation is based on the fact that *B. buwaldi* is restricted to the lower part of the Barstovian sequence in the two areas and, if correct, indicates that the teilzone of *M. sumani* is of greater temporal duration in the Cuyama area than at Barstow. According to James (*ibid.*, p. 138) the highest occurrence of *B. buwaldi* is found at U.C.M.P. V-5670, 50–100 feet below U.C.M.P. V-5666. James included U.C.M.P. V-5670 among localities contributing to his Dome Spring fauna (*ibid.*, p. 146) although it is the lowest of the localities pertaining to that unit. Unless the teilzone of *B. buwaldi* ranges later in time in the Cuyama area than at Barstow, the boundary between early and late Barstovian faunas probably should be drawn between U.C.M.P. V-5666 and U.C.M.P. V-5670 in the Caliente Formation.

In view of the fact that the Cuyama specimens of *Cynorca occidentale*, new species, occur at U.C.M.P. V-5666, stratigraphically above the highest occurrence of *B. buwaldi*, they are considered to be of late Barstovian age.

Material representing *Dyseohyus* or *Cynorca* from L.A.C.M. (C.I.T.) 400, in rocks referred to the Punchbowl Formation, upper Cajon Valley, San Bernardino County, California, is associated with a large merychippine horse and with *Archaeohippus mourningi*. Until future work can yield a more refined determination, a Barstovian age is assigned to these specimens.

Specimens of *Cynorca occidentale*, new species, are known from U.S.G.S. M-1006 in the Caliente Formation, eastern Caliente Range, north of the Cuyama Badlands. At present it is impossible to assess the bio-

stratigraphic character of the fossil remains from this locality, although the bulk faunal list for this area of the Caliente Formation (Repenning and Vedder, 1961) indicates, in general, a Barstovian age.

COLORADO: The type of *Dyseohyus stirtoni*, new species, was collected from a locality 2 miles northwest of Mastodon Quarry near Grover, Colorado. According to Morris F. Skinner (personal communication, September, 1967): "Mastodon Quarry may eventually prove to be biostratigraphically approximately post Lower Snake Creek and pre Valentine." This comment suggests a late Barstovian age for fossil elements from this quarry. The late Barstovian age here given the type of *D. stirtoni*, new species, is consistent with its stage of evolution. Another specimen from the vicinity of Grover, Colorado, has no locality data. In this report it is designated as *?Dyseohyus* sp. and is given a tentative Barstovian age on the basis of its stage of evolution.

TEXAS: Material in the American Museum of Natural History identified as pertaining to *Cynorca proterva* and *Dyseohyus stirtoni*, new species, was obtained from Trinity Pit 1, in the Fleming Formation a short distance northeast of Coldspring, Texas. These remains may be approximately equivalent to the Cold Spring fauna to which Quinn (1955, pp. 74-75, table 22) gave a Hemingfordian age. Quinn (*ibid.*) also stated, however, that the elements of the Cold Spring fauna compare best with those from the Calvert Formation of Maryland, or from the Lower Snake Creek deposits of Nebraska. As reviewed by McKenna (1965) and as maintained in this report, the age of fossil remains from the Lower Snake Creek beds is best considered as post-Hemingfordian, and the same may be true for the fossil mammals of the Calvert Formation. Therefore, the age

of the Cold Spring fauna is taken as Barstovian. According to Morris F. Skinner (personal communication, January 4, 1968) the specimens associated with these peccary remains were derived from Trinity Pit 1 which is stratigraphically 200 feet below the levels that produced the Cold Spring fauna of Quinn. The specimens from Trinity Pit 1 are certainly of Barstovian rather than Hemingfordian age. Skinner (personal communication, February 13, 1968) regards the sample from Trinity Pit 1 as faunally equivalent to fossil assemblages from the Lower Snake Creek beds (*sensu* McKenna, 1965).

MARYLAND: Most East Coast specimens of *Cynorca proterva* are derived from the Calvert Formation in Maryland. The age of the Calvert has often been thought to be middle Miocene (Dall, 1904, pp. xciii, cl-cciii; Spangler and Peterson, 1950, p. 75; Thenius, 1959, pp. 206, 207) as based on various animal groups. Perhaps the age estimate most useful to vertebrate paleontologists in North America has been that of Gazin and Collins (1950, p. 3), e.g., latest Hemingfordian or early Barstovian, with greatest resemblance to faunal elements of the *Merychippus* zone (North Coalinga) of California. This latter fauna is considered as being post Mascall and pre Barstow by Downs (1956) and is probably early Barstovian in age. For the purposes of this report, the age of the fossils from the Calvert Formation is taken as early Barstovian.

#### CLARENDONIAN

NEVADA: *?Dyseohyus* sp. has also been recovered from a Frick locality 7 miles west of Blair Junction, near Tonopah, Nevada. According to records of the Frick collection in the American Museum of Natural History, other faunal elements associated with this specimen indicate an early Clarendonian age.

## SYSTEMATICS

### CYNORCA COPE, 1867

*Cynorca* COPE, 1867, p. 151.

TYPE: *Cynorca proterva* Cope, 1867.

DISTRIBUTION: Early to late Miocene of North America.

INCLUDED SPECIES: Type, and *Cynorca sociale* (Marsh, 1875), *Cynorca hesperia* (Marsh, 1871), and *Cynorca occidentale*, new species.

DIAGNOSIS: Cranium small, rostrum probably moderately elongate; postzygomatic crest probably continuous with lambdoidal crest; supraorbital canals converging anterior to supraorbital foramina; auditory bullae filled with cancellous tissue, bullae not smoothly globose as in *Thinohyus* or *Perchoerus*, but anteriorly acuminate, with even, lightly sulcate, external surface as in Recent genera; central axis of bulla directed anteroventrally rather than anteromedially, posttympanic process of squamosal sulcate as in primitive genera, not flat as in *Dyseohyus* and later genera; glenoid fossa with distinct lateral edge, not merging smoothly and gradually with lateral surface of tympanic process of squamosal as in primitive peccaries; glenoid fossa lower relative to ventral edge of bulla than in earliest of primitive genera; base of paroccipital process aligned nearly longitudinally; infraorbital foramen above  $P^4$ , cross section subovate to slitlike; amount of facial exposure of lacrimal small; anterior palatine foramina occurring between  $M^1$  and  $M^2$ ; upper diastemal crest forming medial border of elongate, but relatively narrow, ventrally facing, buccinator fossa; diastema between  $C^1$  and  $P^1$  relatively greater than in primitive genera; diastema between  $C^1$  and  $P^2$  about equal to combined length of  $P^2$ – $P^4$ ; dental formula  $I_3^3, C_1^1, P_3^{3-7}4, M_3^3$ ;  $I^1$  considerably larger than  $I^2$ ,  $I^1$  and  $I^2$  slanting anteroventrally,  $I^3$  directed nearly vertically;  $C^1$  with only faint lingual grooves and lateral ridges;  $P^1$  small, reduced when present;  $P^2$  and  $P^3$  with single, rounded main cusp and wide talon;  $P^4$  subtriangular, incipiently molari-form, protocone separated from metaconule by posterolingually directed postprotoconal

groove in some species; upper molars with moderate to strongly expanded lingual bases; in width  $M^1 < M^2 > M^3$ ;  $M^3$  variably reduced; lower incisors extending anteriorly,  $I_2$  lying posterolateral to  $I_1$ ;  $I_1$  and  $I_2$  subconical in cross section; lower canine with lateral ridges and lingual grooves developed only about halfway up from the alveolus; distance between canine and  $P_2$  about 20 per cent longer than combined length of  $P_2$ – $P_4$ ; talonid of  $P_2$  poorly developed;  $P_3$  with incipient anterior basal cuspid, undivided main cuspid, and poorly developed talonid;  $P_4$  with moderately broad anterior end, talonid narrow, small, and low; lower diastemal crests narrow but not sharp; in width  $M_1 < M_2 > M_3$ ; rami elongate, slender; postdigastric sulcus shallow; angle inflected; pterygoid and digastric fossae confluent; digastric fossa well developed.

DISCUSSION: As is true of a number of mammalian genera that were proposed during the classical period of American vertebrate paleontology, the genus *Cynorca* was based on material of limited taxonomic value. To promote an understanding of the problems involved in this case, the pertinent steps through which the genus came to be known are briefly reviewed. A more exhaustive documentation of these steps is presented by Gazin and Collins (1950, pp. 17–18).

The genus *Cynorca* was based on material included in a collection made by James T. Thomas near the Patuxent River in Charles County, Maryland, "...in the beds of the Yorktown epoch in places where they are exposed by the cutting of various streams. The localities are 20 miles to the eastward of the outcrops of the eocene beds and, as those of the pliocene are at a considerable distance eastward of the eastern shore of Chesapeake Bay, it is scarcely probable that there is any admixture of specimens from those formations. Two species in the collection of *Galera* and *Dicotyles* genera at present existing in South America, the latter within our own limits also, indicate the existence of a post-pliocene deposit in the neighborhood which has not been hitherto recognized..." (Cope, 1867, pp. 138–139).

The specimens include several species of sharks, a teleost, some turtles, crocodiles, cetaceans, and the peccary material. The last-named can be sorted into two lots on the basis of preservation: those of darkly stained and unleached appearance include a peccary canine and two squalodont teeth associated by Cope (*ibid.*, p. 151) under the name *C. proterva*; the other material, more lightly colored and of leached appearance, consists of jaw fragments and teeth designated as *Dicotyles torquatus*. The first lot was apparently considered by Cope as coming from Pliocene or earlier deposits, whereas the other, leached, material was said to be derived from later deposits because the specimens, identified as *D. torquatus* and *Galera macrodon*, pertain to terrestrial mammals: "...No beds regarded as postpliocene have yet been indicated from the shores of the Patuxent, though the below-mentioned species *D. torquatus* and *G. macrodon* have been most probably derived from such a deposit. These, with the other beds of other epochs, are buried under from 10 to 30 feet of rather fine gravel drift" (Cope, *ibid.*, p. 155). Other than these inferences, there is no explicit statement regarding an empirically determined difference in provenance of the two groups of specimens. On the other hand, it is possible that both lots could have come from the same deposit and that the apparent differences in preservation could be attributed to differential subaerial exposure. In this light, it may be significant that all the specimens under discussion here were catalogued under the same number (A.N.S.P. No. 11543) and were also given the same field number (234). Furthermore, comparison of these specimens with known Pliocene or Pleistocene peccaries indicates that the material in question is certainly not referable to any of the known genera of those epochs but is similar, on the other hand, to small fossil peccaries from Miocene deposits elsewhere in North America. The position taken here is that, although the alleged "post-pliocene" provenance of the specimens in question cannot be definitely disproved, the level of their structural development sheds considerable doubt on such an allegation.

Although Cope originally thought that the first and most fully described specimen, i.e.,

the nominal holotype of *Cynorca proterva*, belonged to a squalodont, as did the other two teeth included under that category in his 1867 notice, it shortly became clear that two kinds of animals were represented. Thus, in 1868, Cope indicated that the nominal holotype of *C. proterva* represented a "small *Dicotyles*" (1868, p. 185) and tried to restrict his name to the other, demonstrably squalodont material. It has subsequently been determined, however, that the nominal holotype must be the name bearer of the species and that *Cynorca proterva* must refer to a tayassuid (Kellogg, 1923; Gazin and Collins, 1950). Case (1904, pp. 7-8, pl. 10, figs. 4, 5) reproduced Cope's original description, but the figures are of squalodont teeth and do not correspond to the description. Therefore, as far as I am aware, no figures of the holotype canine have been published up to the present.

In 1950, Gazin and Collins referred additional peccary material from the Miocene of Calvert County, Maryland, to *Cynorca proterva*. Interestingly enough, the preservation of this material is identical to that of Cope's holotype and, whereas the geographical provenance of Cope's specimen differs from theirs, the newer remains do establish the presence of a small peccary in deposits of Miocene age in that part of Maryland. Even though the provenance of the alleged "post-pliocene" material referred to as *Dicotyles torquatus* may be in doubt, the fact that comparable specimens from the two areas (in this case, dP<sub>4</sub>'s) do not differ significantly is highly suggestive and favors the inference that all the peccary remains considered here are contemporaneous.

There are thus three lots of specimens involved in efforts to establish the validity of *Cynorca proterva*: (1) Cope's nominal holotype, a right upper canine; (2) the "post-pliocene" material collected by James Thomas, upper and lower canines, a deciduous fourth premolar, and two lower first molars; and (3) the specimens referred to as *C. proterva* by Gazin and Collins, including upper third molars, a lower deciduous fourth premolar, lower third and fourth premolars, two second lower molars, and a third lower molar.

When Cope's nominal holotype is con-



sidered by itself, there can be no doubt that it is a canine of a small adult peccary. Furthermore, the specimen is comparable to canines belonging to small tayassuids known from other Miocene deposits in North America, and the probability that it could pertain to any of the other currently known peccary genera is extremely low.

Although somewhat more abraded, the upper canine of lot 2 is not significantly different from Cope's, and the lower deciduous fourth premolar of lot 2 is not significantly different from that referred to as *C. proterva* by Gazin and Collins. By this comparison a link, although possibly a tenuous one, can be established among the three groups of specimens, allowing an assessment of the suite of characters attributable to this fossil sample. As far as can be determined on present evidence, the animals represented were probably contemporaneous, at least within the limits of a Mammal Age.

***Cynorca sociale* (Marsh, 1875)**

Plate 41, figures 1, 3-7; plate 42, figures 1, 3; text figures 1, 2; tables 1, 2

*Thinohyus socialis* MARSH, 1875, p. 249; 1894, p. 271, fig. 25 (holotype). STEHLIN, 1899, p. 113. SINCLAIR, 1905, p. 135.

*Thinohyus (Bothrolabis) socialis*: MERRIAM AND SINCLAIR, 1907, p. 186.

*Palaeochoerus socialis*: COPE, 1879, p. 50.

*Perchoerus socialis*: MATTHEW, 1909, p. 109.

TYPE: Y.P.M. No. 11785, associated right and left  $M^2-M^3$ ; protoloph of  $LM^2$  broken off as is posterolabial corner of heel on  $LM^3$ .

DISTRIBUTION: Early Miocene (Arikarean), John Day River, Oregon (Y.P.M. No. 11785). Early Miocene (Arikarean), John Day beds, L.A.C.M. (C.I.T.) 32, 1 mile east-northeast of the Cress Ranch, near Haystack Valley, Oregon (L.A.C.M. [C.I.T.] No. 497 and L.A.C.M. No. 18081). Late early Miocene (late Arikarean), upper part of John Day Formation from the following localities: U.C.M.P. V-6306, 6 feet below a massive gray bed on the southeast flank of the low, northeast-trending ridge opposite Haystack 21, Wheeler County, Oregon (U.C.M.P. No. 66862); U.C.M.P. V-6416, a greenish zeolitized claystone in the NE.  $\frac{1}{4}$ , NE.  $\frac{1}{4}$ , sect. 27, T. 8 S., R. 25 E., Kimberly Quadrangle, Wheeler County, Oregon (U.C.M.P. No.

66861); U.C.M.P. V-6417 in pale olive sandstones and claystones, SW.  $\frac{1}{4}$ , NE.  $\frac{1}{4}$ , sect. 23, T. 8 S., R. 25 E., Kimberly Quadrangle, Wheeler County, Oregon (U.C.M.P. No. 66863). Late early Miocene (late Arikarean) or possibly early middle Miocene (early Hemingfordian), Oakville Formation, Garvin Gully fauna from the following localities in Grimes County, Texas: Garvin Farm (U.T. No. 31084-111, A.M.C. No. 2894);  $2\frac{1}{4}$  miles north of Navasota and  $\frac{1}{4}$  mile east of the International-Great Northern Railroad tracks (U.T. No. 31084-61): Emory Estate, Navasota (U.T. No. 31084-20). Late middle Miocene (late Hemingfordian), Phillips Ranch fauna, Kinnick Formation, L.A.C.M. (C.I.T.) 503, NW.  $\frac{1}{4}$ , sect. 34, T. 31 S., R. 34 E., Kern County, California (L.A.C.M. No. 18080).

HYPODIGM: The type and L.A.C.M. (C.I.T.) No. 497, crushed palate with  $RI^1$ ,  $C^1$ ,  $P^1-M^2$ ,  $LI^{1-3}$ ,  $C^1$ ,  $P^2-4$ , and anterior portion of mandibles with  $RI_{1-3}$ ,  $C_1$ ,  $P_{2-3}$ ;  $RI_{1-3}$ ,  $C_1$ , and  $P_2$ ; L.A.C.M. No. 18080, right maxillary fragment with  $M^{1-2}$ ; L.A.C.M. No. 18081, fragment of left mandible with  $M_{2-3}$ ; U.C.M.P. No. 66861, frontal region of cranium, palatal fragments, and partial mandible with  $RP^2-M^3$ ,  $LM^{2-3}$ ,  $RP_3-M_3$ , and  $LP_3-M_2$ ; U.C.M.P. No. 66862, palate and otic and snout fragments with right and left  $P^2-M^3$ ; U.C.M.P. No. 66863, partial left mandible with  $P_4-M_3$  and fragmentary tarsal elements, including a nearly complete astragalus; U.T. No. 31084-61,  $LM^2$ ; A.M.C. No. 2894, partial right and left mandibles with  $RM_1$ ,  $LdP_4-M_1$ , isolated  $RM^2$ ,  $M^3$ ; U.T. Nos. 31084-111,  $LM^3$ , and 31084-50,  $RM^3$ .

DIAGNOSIS: Smallest species of genus; upper and lower molars not markedly expanded transversely and  $M^3$  not reduced as in *C. occidentale*, new species; no strong postmetaconid crest on lower molars and  $dP_4$  as in *C. proterva*; differing from all other species in that  $P_4$  lacks a bicusped heel and  $P^4$  lacks a deep, trenchant, postprotoconal groove. Bases of molar protocones and hypocones acuminate lingually.

DESCRIPTION: Fragments representing the following parts of the cranium are present: frontal area, part of the orbit, palate and maxillary base of the zygomatic arch, part

of the maxillary surrounding the canine, lateral surface of the snout bearing the infraorbital foramen, the auditory bullae, and adjacent parts of the otic region. The nasals are preserved in L.A.C.M. (C.I.T.) No. 497, but they are so crushed as to have no discernible important features. The frontals, also crushed in U.C.M.P. No. 66861, seem to have been relatively flat between the orbits, and the frontal depressions, situated just medial to the orbital rim on the dorsal surface of the cranium, are slightly developed. Posterior to this area, in the midline, the cranial surface is slightly arched. The area just lateral to the supraorbital foramina may have been slightly swollen, but the specimen is distorted in the critical places. It is doubtful that the cross section of the frontal region was so prominently domelike as in *Dyseohyus*, but it is also doubtful that the frontal depressions were so strongly developed as in more primitive peccaries. There is a slight suggestion that the area immediately anterior to the frontal eminences was concave, as in *D. fricki*. In U.C.M.P. No. 66861 the supraorbital foramina are 16.8 mm. apart, but this distance has been foreshortened about 15 per cent by crushing. Anterior to the foramina the supraorbital canals converge much as in most peccaries except *Tayassu*, before diverging toward the nasal region. The nasals are not sufficiently preserved in L.A.C.M. (C.I.T.) No. 497 to show whether or not they bear conspicuous extensions of the supraorbital canals as in *Dicotyles*. The general construction of the dorsal surface of the cranium in *C. sociale* is most like that of *Dyseohyus* or *Dicotyles* rather than like that in the more primitive peccaries.

Although the critical area is not particularly well preserved in the available material, the lateral surface of the snout seems to have been relatively smooth, generally as in *Dyseohyus*, and not strongly concave as in *Dicotyles*. In lateral view the profile of the infraorbital foramen in L.A.C.M. (C.I.T.) No. 497 leans backward in recumbent fashion. In dorsal view the foramen is readily visible and does not have the short, triangular appearance as seen in the more primitive peccaries. The configuration of the infraorbital foramen of *Cynorca* resembles that of *Dyseohyus*.

The sutures between the frontal, maxillary, nasal, jugal, and lacrimal bones are not distinctly preserved, but my interpretation of their possible configuration suggests that it is much like that of the living genus *Dicotyles*. The frontonasal suture extends anterolaterally from a point about 2 mm. anterior to the supraorbital foramen, then turns sharply anteriorly to join the maxillary. From this point the maxillofrontal suture traces posterolaterally to meet the jugal about 6 mm. anterior to the lacrimal tubercle. The dorsal edge of the jugal passes back toward the tubercle, but the lacrimal has only a minimal amount of exposure on the facial aspect of the cranium. This character represents a basic similarity to the living peccaries and *Dyseohyus* and a point of contrast with the more primitive types, but the evidence is tenuous at best and should be applied cautiously.

In U.C.M.P. No. 66861 a relatively shallow pocket about 8 mm. wide faces anteriorly from the anterior base of the zygomatic arch, dorsal to M<sup>1</sup>. This structure is only partially preserved, but probably extended dorsally onto the lateral surface of the face posterior to the infraorbital. If such a configuration can be interpreted from the available fragment, it would be similar to the condition seen in *Dyseohyus*. In the latter, the ventral surface of the root of the zygomatic arch is flat and faces ventrally. The anterior surface of the zygomatic root is rather sharply demarcated from the ventral surface and extends dorsally into the broad, elongate, slightly concave surface interpreted here as housing M. depressor labii superioris and M. depressor rostri (see Woodburne, 1968). This attachment area extends posterodorsally from the area of the infraorbital foramen toward the anterior edge of the orbit and further causes the dorsal surface of the zygomatic root to be excavated, producing a narrow prominent process at the anterior edge of the facial crest.

The surface of the palate (pl. 41, fig. 7) is relatively flat, being only slightly concave in cross section. The centers of the palatine foramina are 9.95 mm. apart in U.C.M.P. No. 66862 and lie internal to the anterior edge of M<sup>2</sup>. Shallow palatine grooves lead anteriorly from the foramina at least as far as P<sup>3</sup>, but

these structures are less distinctly developed than in the holotype of *C. occidentale*, new species. The evidence for the position of the palatine foramina with respect to the molar teeth in *C. occidentale*, new species, is somewhat equivocal, but in *C. sociale* the foramina are situated conspicuously farther posteriorly than in *Dyseohyus*.

Although it is poorly preserved, the evidence in L.A.C.M. (C.I.T.) No. 497 indicates that the diastemal crest posterior to P<sup>1</sup> is not strongly developed, but there is a suggestion that the crest formed the lateral boundary of a shallow, ventrally facing fossa in the diastemal area. The critical site is not preserved in U.C.M.P. No. 66862, so the presence of such a pit cannot be confirmed. If present, this feature in *C. sociale* would tend to point toward specimens of *Dyseohyus* in which the diastemal crests are relatively pronounced, and which form the medial border of an elongate groove, or depression, that may have a ventral, rather than lateral, primary orientation. This depression corresponds, at least in part, to the buccinator fossa described in *Tayassu* (Woodburne, 1968). To judge from L.A.C.M. (C.I.T.) No. 497, the distance from P<sup>1</sup> to P<sup>2</sup> was roughly 9.5 mm.; reconstruction of U.C.M.P. No. 66862 indicates that this diastema may have been as much as 15 mm. Both specimens are broken in this area so that only future discoveries can provide the answer as to which of these estimates is closer to the actual condition. Anterolateral to the diastema the canine buttress has a flat anterior surface but is otherwise not strongly developed (text fig. 2).

Material pertaining to the occiput and auditory region is present only in U.C.M.P. No. 66862, and in the following statements comparison is made primarily with the living *Dicotyles tajacu*. Because the fossil fragments are isolated from the cranium, it is not possible to determine their precise angular relationships with other parts of the skull, but for the purpose of description it is assumed that the nearly transverse plane passing through the postglenoid process is vertical with respect to the general orientation of the occlusal plane as in *Dicotyles*, *Dyseohyus*, and some of the more primitive peccaries.

With this orientation the planar configuration of many of the features displayed in these fragments is quite similar to that of *Dicotyles*. In particular the configuration of the glenoid fossa and the orientation of the surface to which the bulk of *M. obliquus capitis* anterior attaches in *Dicotyles* are similar to these features in *C. sociale*. The bulla (pl. 41, fig. 3) is narrower and more acuminate anteriorly in *C. sociale*, but in both the fossil and the members of the living genus it is filled with cancellous bone. The groove for the tympanohyal on the ventral surface of the bulla is narrower and shallower than in the modern genus. The position of the glenoid fossa relative to the ventral surface of the bulla is higher in *C. sociale* than in *Dyseohyus* and *Dicotyles*, but lower than in the earliest of the primitive peccaries. The degree of separation of the posterior lacerate and stylomastoid foramina is less than in the primitive peccaries and greater than in *Dicotyles*. In contrast to the more primitive peccaries and in agreement with the living genera, the bulla is not connected to the postglenoid process in *C. sociale*. Other conspicuous comparisons between *C. sociale* and *D. tajacu* indicate that the plane of orientation of the paroccipital process in the former is more obliquely oriented than in the latter, as seen in ventral view. Also, the surface of the squamosal along the lateral base of that process is definitely concave, forming a shallow, trough-like configuration which passes posterodorsally from the paroccipital process toward the external auditory meatus. The same area in *D. tajacu* is essentially flat. Laterally, the posttympanic process of the squamosal covering the mastoid region in *C. sociale* meets the tympanic process of the squamosal along a distinct groove. The line of junction of these two parts of the squamosal in *D. tajacu* is nearly smooth, and discernible only with difficulty in some specimens. Careful inspection of these otic fragments reveals no suggestion that the fusion of the squamosal with the mastoid is any less complete than in the living peccaries. *Cynorca* is apparently "amastoid" (Pearson, 1927) to the same degree as is *Dicotyles* or *Tayassu*.

Beyond its small size, relatively short diastemal region, well-developed genial pits,

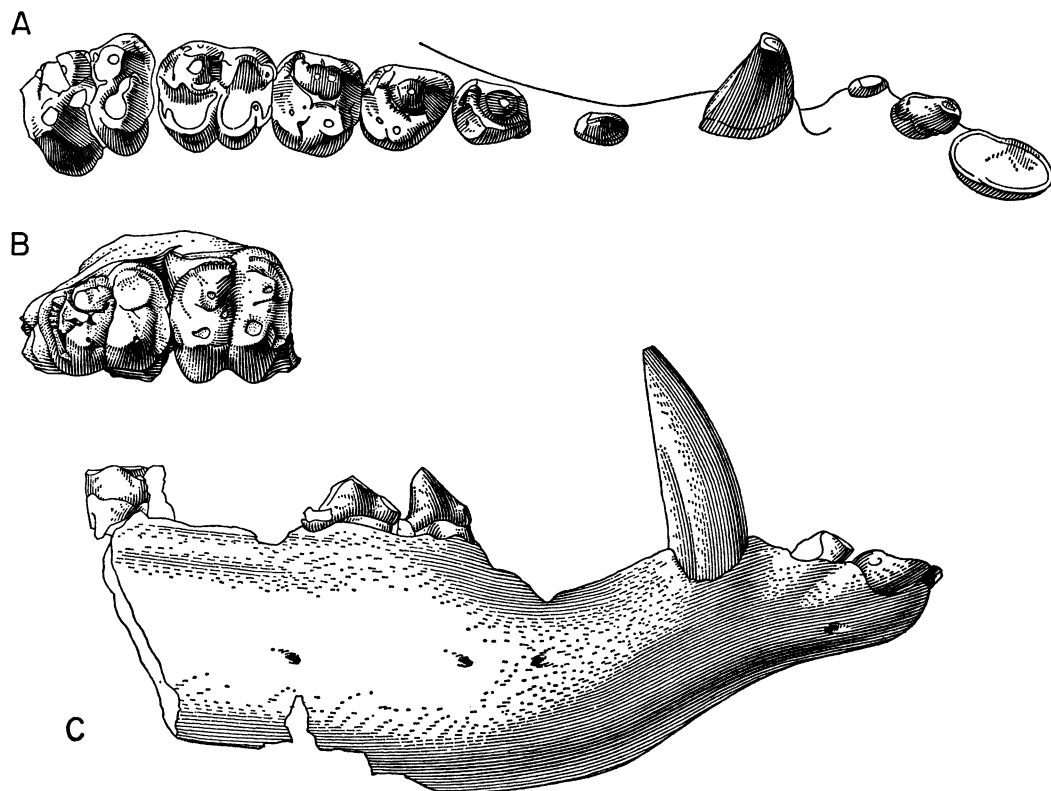


FIG. 1. *Cynorca sociale*. A. Occlusal view of right upper dentition, I<sup>1</sup>-M<sup>2</sup>, L.A.C.M. (C.I.T.) No. 497. B. Occlusal view of right M<sup>2</sup> and M<sup>3</sup> of holotype, Y.P.M. 11874. C. Labial view of right symphysis, with I<sup>1-3</sup>, C<sup>1</sup>, P<sup>2-3</sup>, and part of M<sup>1</sup>, L.A.C.M. (C.I.T.) No. 497. All  $\times 1.5$ .

and concave lateral profile in the symphyseal region ventral to the canines, the mandibles of *C. sociale* are not particularly remarkable (pl. 42, fig. 3; text fig. 1C). In lateral profile, the diastemal crests are shallowly concave, but are straight as seen from above. The dorsal surface of the symphysis forms an elongate groove and is not significantly expanded into a spoon-shaped depression anterior to the canines. The outer surface of the mandible is relatively flat and smooth, but, as is that in *C. occidentale*, new species, the digastric fossa is definitely discernible. The ventral border of the mandible is relatively straight, with only a slight post-digastric sulcus. The angle is not completely preserved in the available specimens, but, to judge from the condition in U.C.M.P. No. 66863, it was inflected to some extent.

**UPPER DENTITION:** The upper incisors (text fig. 1A) are arranged in a V shape. The canines apparently lie on a line labial to I<sup>3</sup>,

although such a position is not determinable from the available material. Except for P<sup>1</sup>, which lies near the canine, the cheek teeth form a continuous series which is bowed outward, particularly opposite M<sup>2</sup>. The first incisor is broadly worn in the available material but seems not to have been basically different from that of *C. occidentale*, new species. The second incisor is a shearing tooth with a single apex forward of the midpoint and connected by linear crests to the anterior and posterior edges of the crown. The anterior crest is shorter than the posterior, and together these crests separate the somewhat convex labial surface of the tooth from the slightly concave lingual surface. Posterior to I<sup>2</sup>, I<sup>3</sup> is a simple, transversely compressed, shearing tooth with nearly straight labial and lingual sides sloping gently toward the apex.

The canine bears the usual peccary configuration and is slightly smaller than that of the holotype of *C. proterva*. Available canines



of *C. sociale* are abraded but seem to resemble those of *C. proterva* in the degree to which the various ridges and grooves are developed.

The first premolar (text fig. 1A) is a small, simple, single-cusped tooth with two roots. It is situated about 5 to 8 mm. posterior to the lingual edge of the canine and is separated from  $P^2$  by a diastema of at least 9.5 mm. and possibly as much as 15 mm. The small size of  $P^1$ , the development of a pronounced diastema between it and  $P^2$ , and the fact that  $P_1$  has already been eliminated by evolution suggest that  $P^1$  was also being subjected to such a process. In *Dyseohyus*, the major

derivative of *Cynorca*, the elimination of  $P^1$  is complete. Whether the tooth was never present in *C. proterva*, *C. hesperia*, or *C. occidentale*, new species is not presently determinable. The second premolar (pl. 41, fig. 7; text figs. 1A, 2) is more complex than  $P^1$ , with a single, subconical main cusp and a transversely expanded heel. The morphology of  $P^2$  is variable in detail, particularly with respect to the degree by which the heel is separated from the main cusp. In U.C.M.P. No. 66862, the degree of separation of the two parts of the tooth is slight, the heel is broader in comparison with the width of the main cusp, and there

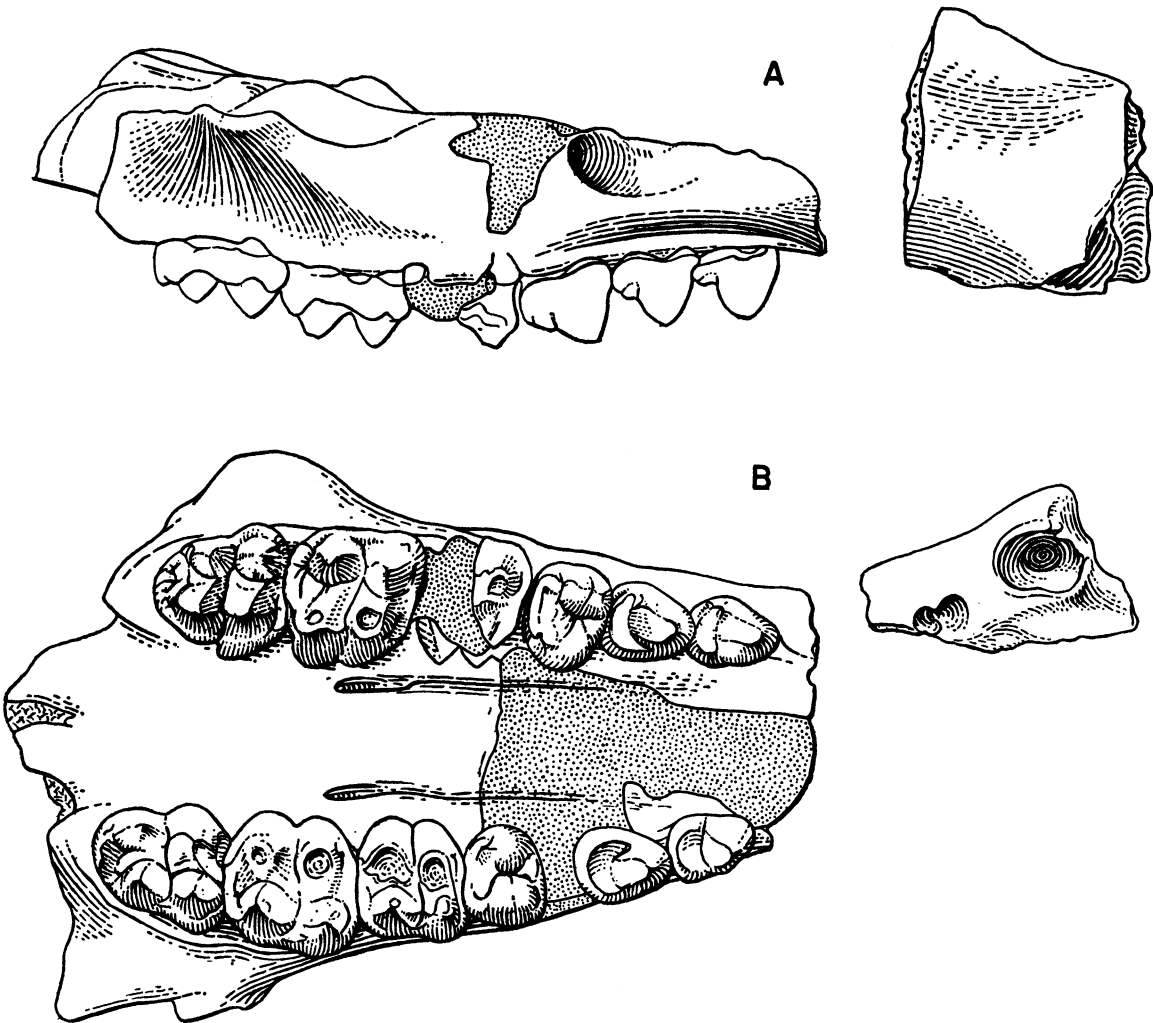


FIG. 2. *Cynorca sociale*, cheek teeth and snout fragment, U.C.M.P. No. 66862, with fragments oriented in approximately original position. A. Labial view. B. Palatal view. All  $\times 1.5$ .

is no lingual cingular extension of the heel. In U.C.M.P. No. 66861, the tooth is essentially like that just described except for a more prominent development of the groove between the heel and the main cusp. In L.A.C.M. (C.I.T.) No. 497, however, the two parts of the tooth are well separated, the heel is considerably wider than the main cusp, and it extends anteriorly along the lingual base of that cusp. The composition of the heel, i.e., two parallel, slightly curved, transverse ridges, is also best developed in L.A.C.M. (C.I.T.) No. 497. In each individual, the third premolar is

essentially a larger version of P<sup>2</sup>, except in having a slight lingual cingulum in the two University of California specimens. The fourth premolar (pl. 41, fig. 7; text figs. 1A, 2), however, is more molariform than the others, showing incipient separation of the paracone and metacone in the body of the main cusp, and the presence of the protocone lingual to it. The degree of separation of the parametacone is not so well developed as in *C. occidentale*, new species, or in *C. hesperia*. In *C. sociale* the protocone bears anterolabially and posterolabially directed arms which are partially subdivided by grooves

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF THE UPPER DENTITION OF *Cynorca sociale*

	L.A.C.M. No. 497	L.A.C.M. No. 18080	U.C.M.P. No. 66861	U.C.M.P. No. 66862	Y.P.M. No. 11785	A.M.C. No. 2894	U.T. No. 31084-61	U.T. No. 31084-111	U.T. No. 31084-20
I <sup>1</sup>									
Length	8.60	—	—	—	—	—	—	—	—
Width	5.30	—	—	—	—	—	—	—	—
I <sup>2</sup>									
Length	5.45	—	—	—	—	—	—	—	—
Width	3.65	—	—	—	—	—	—	—	—
I <sup>3</sup>									
Length	4.00	—	—	—	—	—	—	—	—
Width	2.80×	—	—	—	—	—	—	—	—
C <sup>1</sup>									
Length	8.35	—	—	—	—	—	—	—	—
Width	5.50	—	—	—	—	—	—	—	—
P <sup>1</sup>									
Length	4.80	—	—	—	—	—	—	—	—
Width	2.20	—	—	—	—	—	—	—	—
P <sup>2</sup>									
Length	7.05	—	7.45	7.60	—	—	—	—	—
Width	5.95p	—	5.15p	5.50p	—	—	—	—	—
P <sup>3</sup>									
Length	8.30	—	8.30	8.50	—	—	—	—	—
Width	7.75p	—	7.20p	6.60p	—	—	—	—	—
P <sub>4</sub>									
Length	8.25	—	7.60	8.10	—	—	—	—	—
Width	9.10a	—	9.05a	8.50a	—	—	—	—	—
M <sup>1</sup>									
Length	10.40	10.45	8.85	9.55	—	—	—	—	—
Width	10.00p	10.45e	10.50	10.85p	—	—	—	—	—
M <sup>2</sup>									
Length	12.45	10.85	10.60	11.30	11.00	10.95	11.00	—	—
Width	10.95p	10.95p	11.30p	11.55p	12.40a	10.00	11.10	—	—
M <sup>3</sup>									
Length	—	—	11.00	11.20	12.10	11.60	—	11.50	10.85
Width	—	—	11.10a	10.95	10.10a	9.45	—	9.95	9.30
Length, P <sup>2</sup> -M <sup>3</sup>	—	—	—	54.80	—	—	—	—	—

into structures corresponding to the protoconule and metaconule. The protoconule attaches to the low anterior cingulum. At least in U.C.M.P. No. 66862 the metaconule abuts against another, smaller, conule which is situated between the posterolingual base of the parametacone and the posterior cingulum. The latter extends along the posterior surface of the tooth and turns sharply anteriorly along the labial edge to come in contact with the posterior base of the parametacone. In L.A.C.M. (C.I.T.) No. 497 the structures in the region of the heel are more worn, so that coronal details are not readily determinable. There is nothing to suggest, however, that the basic construction of  $P^4$  in L.A.C.M. (C.I.T.) No. 497 is dissimilar from that in U.C.M.P. No. 66862. In U.C.M.P. No. 66861,  $P^4$  is even more worn. In none of these specimens is there any suggestion of the strong, deep, postprotoconal groove separating the protocone from the metacone as seen in *C. occidentale*, new species, or *C. hesperia*.

The molars of *C. sociale* (pl. 41, figs. 5-7; text figs. 1A, B, 2) are not fundamentally different from those in other species of the genus. The first molar is only slightly wider than  $P^4$ ;  $M^2$  is the widest tooth of the cheek-tooth series and  $M^3$  is not reduced, particularly relative to  $M^1$ . Anterior and posterior cingula are relatively broad in the John Day specimens (including the holotype, text fig. 1B); labial cingula are variably developed. The lingual bases of the molars are moderately to strongly expanded, particularly with respect to  $M^2$ . The proportions of some of the molars seem to be variable;  $M^1$  of L.A.C.M. No. 497 is relatively more elongate than in most other specimens. Specimens from various Texas localities are less expanded lingually than those from Oregon, and the molars of L.A.C.M. No. 18080 from the late Hemingfordian of California are about intermediate in degree of expansion. Whereas the Texas and California specimens differ in certain details from those from Oregon, the amount of variation is not out of line with that observed in populations of the living peccaries (Woodburne, 1968) and these specimens all resemble one another in general size and in the unreduced nature of  $M^3$ . The present evidence points most compellingly

to the inclusion of these specimens in *C. sociale*.

**LOWER DENTITION:** Although worn, the lower incisors are preserved in L.A.C.M. (C.I.T.) No. 497. No occlusal details can be made out on  $I_1$  and  $I_2$ , although  $I_2$  was probably larger than  $I_1$ . The third incisor is a simple, transversely compressed tooth.

The canines are similar to those of *C. proterva* or *C. occidentale*, new species, except for being smaller. The degree of development of grooves and ridges is the same in the three species.

Genetic elimination of  $P_1$  has taken place in *C. sociale* along with concomitant elongation of the postcanine diastema. This is the first time in the history of the Tayassuidae that either of these two phenomena has been recorded. As represented in L.A.C.M. (C.I.T.) No. 497 (text fig. 1C),  $P_2$  is a simple, single-cusped tooth with a small heel and a slightly developed anterior basal conulid. As preserved, the heel is featureless.  $P_3$  is a larger version of  $P_2$ , with a more prominent anterior basal conulid, which gives the tooth a more symmetrical lateral profile. The heel is not well preserved in the available specimens. In  $P_4$  the trigonid is composed of a pair of closely appressed cuspids, but the heel is only a single-cusped structure (pl. 42, fig. 1). The anterior conulid is small. The tooth is short and relatively broad, with the length of the heel being about one-half that of the anterior portion of the tooth. The single cuspid of the heel is situated on a broad base and connects to the main cuspid by a short longitudinal crest. Labial and lingual cingula are faintly developed. The deciduous fourth premolar, preserved in A.M.C. No. 2894 (pl. 41, fig. 4), has the standard basic peccary configuration and resembles that of *C. proterva* to a large degree. Although a postmetaconid crest is present, it is not developed so prominently as that in *C. proterva*, and in contrast to the latter, there is no postmetaconid crest on  $M_1$  of A.M.C. No. 2894.

In general, the lower molars of *C. sociale* have a smooth, somewhat bilobate occlusal outline with only occasional specimens having a short labial cingulum at the transverse valley. The second molar is the widest tooth, but  $M_3$  is not reduced to any appreciable

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER DENTITION OF *Cynorca sociale*

	L.A.C.M. No. 497	L.A.C.M. No. 18081	U.C.M.P. No. 66863	U.C.M.P. No. 66861	A.M.C. No. 2894	U.T. No. 31084-96
I <sub>1</sub>						
Length	3.10	—	—	—	—	—
Width	3.20	—	—	—	—	—
I <sub>2</sub>						
Length	3.65	—	—	—	—	—
Width	4.20	—	—	—	—	—
I <sub>3</sub>						
Length	4.00	—	—	—	—	—
Width	2.55	—	—	—	—	—
C <sub>1</sub>						
Length	6.80	—	—	—	—	—
Width	6.00	—	—	—	—	—
P <sub>2</sub>						
Length	6.50	—	—	—	—	—
Width	2.95	—	—	—	—	—
P <sub>3</sub>						
Length	—	—	—	7.90	—	—
Width	—	—	—	4.25p	—	—
dP <sub>4</sub>						
Length	—	—	—	—	13.05	—
Width	—	—	—	—	6.65p	—
P <sub>4</sub>						
Length	—	—	9.50	8.85	—	—
Width	—	—	6.15	5.65p	—	—
M <sub>1</sub>						
Length	—	—	9.90	9.35	10.95	10.75
Width	—	—	7.70p	7.20p	7.95p	7.50p
M <sub>2</sub>						
Length	—	10.75	11.20	10.70	—	—
Width	—	8.35a	9.05a	8.55a	—	—
M <sub>3</sub>						
Length	—	13.00	13.00	—	—	—
Width	—	8.05a	8.25a	7.60+	—	—

extent. Specimens from Texas (pl. 41, figs. 1, 4) are slightly larger than those from Oregon (pl. 42, fig. 1), and the Texas teeth are generally the more rugose. Size and rugosity, however, are variable in the Texas sample, and M<sub>2</sub> of U.C.M.P. No. 66891 approaches the Texas material in robustness. The possibility that the Texas material represents a distinct population from that of Oregon cannot be definitely disproved at this time, but the range of variation encountered is not too extreme to be encompassed in a single peccary species.

DISCUSSION: Inasmuch as *C. sociale* is suitably generalized to be potentially an-

cestral to both *C. proterva* and *C. occidentale*, new species, it is tempting to suppose that, as represented by the Texas material, the eastern population of *C. sociale* gave rise to *C. proterva*, whereas a western population gave rise to *C. occidentale*, new species. Because of the meager material available, however, the validity of this possibility cannot be tested, and additional complexities are introduced when consideration is extended to *C. hesperia*. The taxonomic status of this species is open to doubt. If it should eventually prove to belong to *C. proterva*, the integrity of the almost mutually exclusive distribution patterns proposed for *C. proterva*

and *C. occidentale*, new species, would be compromised. In that case, theoretical considerations of the centers of origin of species derived from *C. sociale* would need to be revised (see p. 341).

*Cynorca sociale* is definitely advanced over such primitive genera as *Perchoerus*, *Thinohyus*, and *Chaenohyus*. Characters in *C. sociale* that demonstrate this relationship include the nature of its bullae and associated features, the configuration of its glenoid fossa, the small facial exposure of the lacrimal, the presence of upper and lower diastemal crests, the incipient presence of buccinator fossae, the apparent presence of heel structures in  $I^1$  and  $I^2$ , the extremely small size of  $P^1$ , and the absence of  $P^1$ . In most of these same features, *C. sociale* is in an early stage of development relative to the more modern peccary genera.

#### *Cynorca* cf. *C. sociale*

Plate 41, figure 2; text figure 3; table 3

*Perchoerus socialis* COPE AND MATTHEW, 1915, pl. 111, fig. 3. PEARSON, 1923, p. 94, fig. 16e.

*Dicotyles* sp. SCOTT AND OSBORN, 1890, p. 76, fig. 6.

DISTRIBUTION: Early Miocene (Arikarean), John Day Formation, Camp Creek, Crooked River, Oregon (A.M.N.H. No. 7393). ?Early Miocene (?Arikarean), "Loup Fork Tertiary," Nebraska (M.C.Z. No. 17744).

HYPODIGM: A.M.N.H. No. 7393, fragment of right mandible with  $P_3$ – $M_3$ ; M.C.Z. No. 17744, fragment of left mandible with  $P_4$ – $M_2$ .

DESCRIPTION: These two specimens are among those for which there are few stratigraphic data. The dentition of A.M.N.H. No. 7393 is simple and does not differ fundamentally from that of *C. sociale*. The main reason for not including it in the hypodigm of that species is that this specimen is about

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF THE  
LOWER CHEEK TEETH OF *Cynorca* CF.  
*C. sociale*

		A.M.N.H. No. 7393	M.C.Z. No. 17744
$P_3$	Length	9.30	—
	Width	4.50	—
$P_4$	Length	10.95	8.80
	Width	6.85	5.65
$M_1$	Length	11.50	9.35
	Width	8.15p	6.50p
$M_2$	Length	12.35	10.80
	Width	9.10a	8.20a
$M_3$	Length	—	—
	Width	8.80a	—

25 per cent larger than *C. sociale*. In addition,  $P_4$  is conspicuously longer than that in *C. sociale*, has a much more distinctly developed heel, and the occlusal outline of the molars is sharply constricted between the anterior and posterior moieties, producing a more strongly bilobate appearance than is considered typical of *C. sociale*. Such a configuration is more commonly encountered in *Perchoerus*.

In contrast to A.M.N.H. No. 7393, the dentition of M.C.Z. No. 17744 is quite small. Except for  $M_1$ , which is smaller, the dimensions of this specimen resemble those of U.C.M.P. No. 66861. The small size of the specimen and simple heel of  $P_4$  would be the more compelling reasons for including it in *C. sociale*, but the conservative nature of tayassuid lower dentitions dictates caution. Should this specimen prove referable to *C. sociale*, its importance would lie in demon-

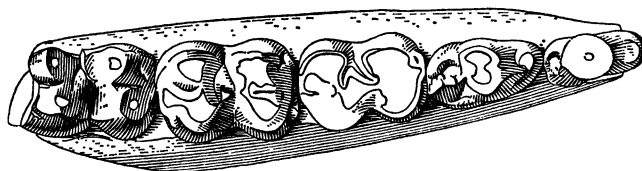


FIG. 3. *Cynorca* cf. *C. sociale*, occlusal view of right  $P_3$ – $M_3$ , A.M.N.H. No. 7393.  $\times 1.5$ .



strating an extension of the geographic range of the species into Nebraska.

*Cynorca proterva* Cope, 1867

Text figure 4; tables 4 and 5

*Cynorca proterva* COPE, 1867, p. 151; 1868, p. 185. KELLOGG, 1923, p. 28.

*Squalodon protervus* COPE, 1867, p. 151. CASE, 1904, p. 7.

*Dicotyles torquatus*: COPE, 1867, p. 155.

*Dicotyles lenis*: LEIDY, 1869, p. 384.

Cf. *Cynorca proterva*: GAZIN AND COLLINS, 1950, pp. 4, 17, fig. 7.

TYPE: A.N.S.P. No. 11543a, left upper canine. Nine specimens are identified as A.N.S.P. No. 11543, one of which is the type. For convenience I have arbitrarily added alphabetical designations (a-f) to seven of the specimens catalogued under this number; the other two are not definitely identifiable as peccaries.

DISTRIBUTION: Early late Miocene (early Barstovian), Calvert Formation, Patuxent River, Charles County, Maryland (A.N.S.P. Nos. 11543a-11543f). Early late Miocene (early Barstovian), Calvert Formation, from the following localities in Calvert County, Maryland; Plumb Point (U.S.N.M. Nos. 18493, 18494), Scientists Cliffs (U.S.N.M. No. 17080), 1 mile south of Chesapeake Beach (U.S.N.M. No. 19110), south Chesapeake Beach (U.S.N.M. No. 21835), and 0.7 mile south of Randle Cliff Beach (U.S.N.M. No. 18429). Late Miocene (Barstovian), Trinity Pit 1, Fleming Formation, south bank of Trinity River, 7 miles northeast of Coldspring, San Jacinto County, Texas (F:A.M. No. 73662). Early late Miocene (early Barstovian) from sediments occupying a stratigraphic position between the Sheep Creek and Lower Snake Creek deposits in Observation Quarry, NW.  $\frac{1}{4}$ , NW.  $\frac{1}{4}$ , SE.  $\frac{1}{4}$ , sect. 4, T. 31 N., R. 47 W., Dawes County, Nebraska (F:A.M. No. 73664).

HYPODIGM: Type, and A.N.S.P. No. 11543b, LC<sup>1</sup>; A.N.S.P. No. 11543c, RC<sub>1</sub>; A.N.S.P. No. 11543d, fragments of associated right and left mandibles, with RM<sub>1</sub> and LdP<sub>4</sub>-M<sub>1</sub>; A.N.S.P. No. 11543e, RC<sub>1</sub>; A.N.S.P. No. 11543f, LM<sub>1</sub> (see below for a discussion of the problems concerning A.N.S.P. No. 11543f); U.S.N.M. No. 18493, LM<sup>3</sup>; U.S.N.M. No. 18494, LM<sup>3</sup>; U.S.N.M.

No. 17080, RP<sub>4</sub>; U.S.N.M. No. 19110, LM<sub>2</sub>; U.S.N.M. No. 18429, fragment of right mandible with M<sub>2</sub>-M<sub>3</sub>; U.S.N.M. No. 21835, RP<sub>4</sub>, LdP<sub>4</sub>, and RM<sub>1</sub>; F:A.M. No. 73662, fragment of mandible with LdP<sub>4</sub>, M<sub>2</sub>-M<sub>3</sub>; F:A.M. No. 73664, RM<sup>3</sup>.

DIAGNOSIS: Among larger species of genus; molars not transversely expanded and M<sub>3</sub><sup>3</sup> not reduced as in *C. occidentale*, new species; differing from *C. sociale* in lacking acuminate lingual bases of protocone and hypocone, and in having a bicusped talonid on P<sub>4</sub>; unique in having a postmetaconid ridge on dP<sub>4</sub> and some lower molars.

DESCRIPTION: The hypodigm consists of a number of isolated teeth and fragments of mandible which, taken together, represent the upper and lower canines, dP<sub>4</sub>, P<sub>3</sub>-M<sub>3</sub>, and M<sup>3</sup>. Inasmuch as the type represents a peccary of the same size as the other specimens of the hypodigm, and comes from the same general biochron, the taxon *Cynorca proterva* is here considered to be sufficiently represented for adequate diagnosis, even though the type alone would not be specifically distinguishable from other species of this genus.

As indicated above, either individually or collectively, specimens gathered together under A.N.S.P. No. 11543 have been subjected to diverse taxonomic treatment in the past. A.N.S.P. No. 11543d, fragments of mandible with right M<sub>1</sub> and left dP<sub>4</sub>-M<sub>1</sub>, was referred to as *Dicotyles torquatus* by Cope (1867, p. 155), and all the specimens labeled as A.N.S.P. No. 11543 were referred to *Dicotyles lenis* by Leidy (1869, pp. 384-385). In particular, A.N.S.P. No. 11543f, left M<sub>1</sub>, is labeled as cotype of *D. lenis* and, as stated by Leidy (*ibid.*, p. 385), apparently came from the "shores of Ashley River, South Carolina." Since all specimens labeled A.N.S.P. No. 11543 are also identified by field number 234, the locality notation of A.N.S.P. No. 11543f is insufficient by itself to demonstrate a "post-Pliocene" provenance for the genus *Cynorca*, but may be taken as tentative evidence for an extension of the geographic range of the taxon. This tooth is certainly distinct in degree of morphological development from the type of *D. fossilis* which was included by Leidy (1869, p. 384) in *D. lenis*. As indicated by Lundelius (1960, p. 30),

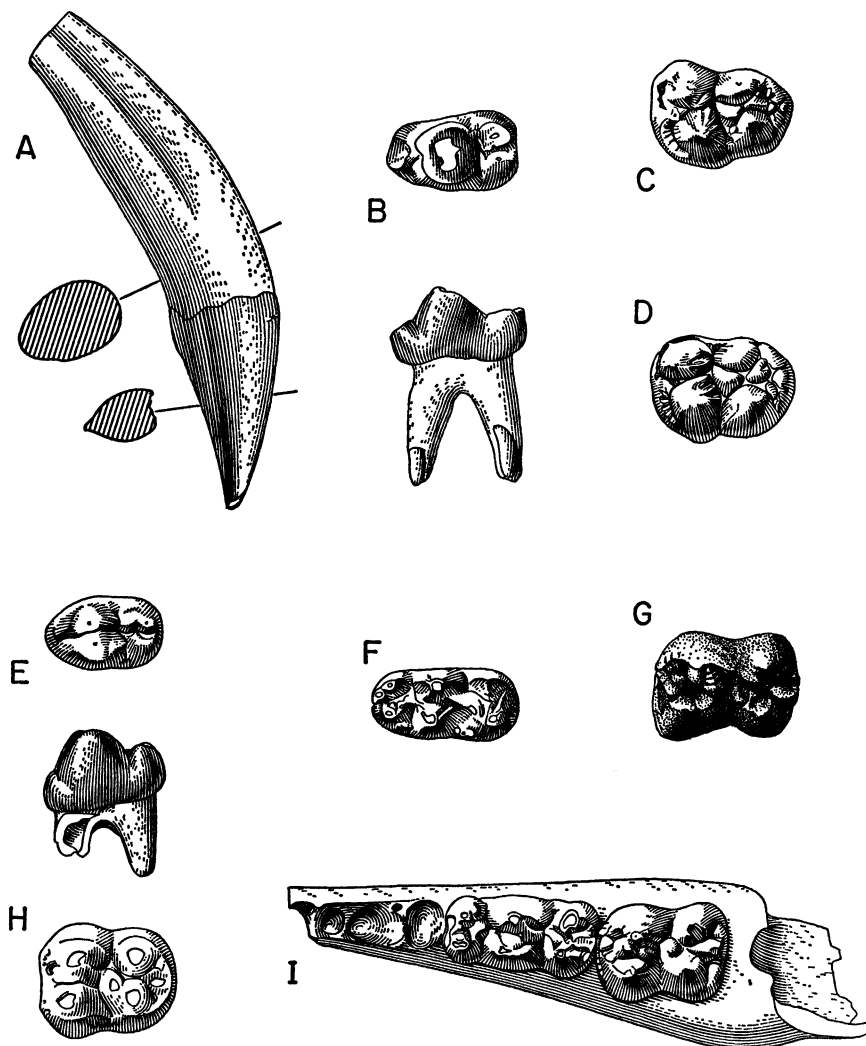


FIG. 4. *Cynorca proterva*. A. Right C<sup>1</sup>, holotype, A.N.S.P. 11543a, labial view. B. Right P<sub>4</sub>, U.S.N.M. No. 17080, occlusal and lingual views. C. Left M<sup>3</sup>, U.S.N.M. No. 18493, occlusal view. D. Left M<sup>3</sup>, U.S.N.M. No. 18494, occlusal view. E. Right P<sub>4</sub>, U.S.N.M. No. 21835, occlusal and lingual views. F. Left dP<sub>4</sub>, U.S.N.M. No. 21835, occlusal view. G. Left M<sub>1</sub>, A.N.S.P. No. 11543f, occlusal view. H. Left M<sub>2</sub>, U.S.N.M. No. 19110, occlusal view. I. Fragment of left mandible with dP<sub>4</sub>-M<sub>1</sub>, A.N.S.P. No. 11543d, occlusal view. All ×1.5.

Leidy gave no reason for wanting to substitute *D. lenis* for the prior name *D. fossilis*, and *D. fossilis* is currently considered as a species of the Pleistocene genus *Mylohyus*.

UPPER DENTITION: Two left upper canines are available for description: A.N.S.P. No. 11543a, the holotype (text fig. 4A), and A.N.S.P. No. 11543b. The former is some-

what larger than the latter (see table 4), possibly owing in part to postmortem abrasion. In both specimens the tip of the tooth is worn off, and the enamel has been breached along the leading edge, exposing a strip of dentine. In the modern *Dicotyles tajacu*, a distinct crest is present in the basal one-third of the canine at its anterolabial and

TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF THE UPPER DENTITION OF *Cynorca proterva*

	A.N.S.P. No. 11543a, Type	A.N.S.P. No. 11543b	U.S.N.M. No. 18493	U.S.N.M. No. 18494	F:A.M. No. 73664
C <sup>1</sup>					
Length	9.65	8.35+	—	—	—
Width	6.45	5.75	—	—	—
M <sup>3</sup>					
Length	—	—	12.50	12.50	12.35
Width	—	—	10.00a	9.60a	9.40a

anterolingual corners. Each crest then diminishes sharply in amplitude as it curves apically toward the tip of the tooth. Remnants of these structures are present in A.N.S.P. Nos. 11543a and 11543b, but in both teeth most of the enamel on which the basal portions of these crests would be situated has been worn away. The greatest transverse and longitudinal dimensions of each tooth occur at the root 6 to 7 mm. below the base of the enamel, after which the root tapers toward its proximal tip. The root of the holotype is much less abraded than that of A.N.S.P. No. 11543b and shows the shallow, but distinct lingual groove and the similarly developed labial ridge commonly encountered in peccaries. The groove is not expressed in the enamel of the crown, but on the labial side the ridge continues with diminishing amplitude toward the apex of the tooth. These specimens resemble canines of other peccaries in their recurved outline and the development of the wear facet on the anterior surface of their crowns. The delicate construction of the canines of *C. proterva* contrasts distinctly with the more rugose nature of these teeth in most larger peccaries except for *Dyseohyus* and *Dicotyles*.

No upper premolars are present in the hypodigm of *C. proterva*, and of the molars only M<sup>3</sup> is represented. The molars from Maryland are from the left side and are designated by U.S.N.M. Nos. 18493 and 18494, respectively (text fig. 4C, D). A right M<sup>3</sup> from Nebraska is represented by F:A.M. No. 73664. All are of typical peccary construction and do not seem to be particularly reduced. In both Maryland specimens the cusps are bunodont, with smooth rounded

apices and crenulate enamel sides. In F:A.M. No. 73664, the cusps are sharper. Labial and lingual cingula are faintly developed in the Maryland specimens and are absent from the Nebraska tooth. The teeth taper slightly posteriorly, with U.S.N.M. No. 18493 being the most strongly affected. All four principal cusps are present, as are the protoconule and metaconule and anterior and posterior cingula. The subsidiary conules take the form of small pyramidal cusps and are separated from adjacent tooth structures by narrow grooves. The heel consists primarily of a small cusp, bifurcated in the eastern specimens, which lies posterior to the metaconule between the metacone and hypocone, and leads posteriorly toward the terminal arcuate row of two to three small cusps. The proportions of these teeth are best considered as relatively elongate, rather than transversely expanded, in contrast to the homologous teeth of *C. occidentale*, new species, from the West coast.

LOWER DENTITION: The lower canines available are A.N.S.P. No. 11543c and A.N.S.P. No. 11543e. The latter is too abraded to contribute significantly to the description. A.N.S.P. No. 11543c is abraded on the lingual surface of the crown and on the labial surface of the root, but its tayassuid character is readily apparent. This is seen in the recurved profile, the essentially triangular cross section, and the presence of a labial ridge on the crown which diminishes slightly apically. Although this specimen is larger than specimens of earlier species of this genus, it is still smaller than the comparable canine in any other genus of peccary with the possible exception of the

[illegible]

the talonid. The talonid is most strongly developed posterolabially, consisting, in at least U.S.N.M. No. 21835, of two conulids which are arranged longitudinally. Although the posterolingual part of the talonid in this specimen consists of a single conulid, it is as high as its labial counterpart. In U.S.N.M. No. 17080, the talonid is worn, but remnant features suggest that its construction is essentially like that in U.S.N.M. No. 21835. In neither of these specimens is there any additional basal cingulum, and, in both, the talonid is separated from the trigonid by a transverse groove. The chief variation in  $P_4$  of *C. proterva* is in the development of the anterior basal conulid. This structure is prominent in U.S.N.M. No. 17080, but it is only a small nubbin in U.S.N.M. No. 21835. The former tooth is therefore much more elongate and more massive than in any other species of *Cynorca* yet known, but the morphology of the latter is quite like that found in *C. occidentale*, new species, from western North America.

The first lower molar is represented by A.N.S.P. No. 11543d (text fig. 4I), A.N.S.P. No. 11543f (text fig. 4G), and U.S.N.M. No. 21835. These are small, relatively elongate teeth with unswollen cuspids. The four major cuspids and subsidiary conulids are present. As in  $dP_4$ , there is a longitudinally oriented ridge on the posterior surface of the metaconid situated lingual to the posteriolabially directed arm that descends from the apex of the same cuspid. Although it would be expected that the presence and degree of development of this longitudinally oriented structure would be subject to intraspecific variation, they are remarkably constant. The structure is found not only in specimens from Charles County (A.N.S.P. No. 11543d) and Calvert County (U.S.N.M. No. 21835), Maryland, as well as in the isolated tooth (A.N.S.P. No. 11543f) from Ashley River, South Carolina, but also in all teeth of the mandible from San Jacinto County, Texas (F:A.M. No. 73662). Inasmuch as it is relatively improbable that four different collectors working in four different areas would find specimens relating to a minor variant of a fossil population, the approach taken here is that the presence of the longitudinally directed postmetaconid crest in  $M_1$

and  $dP_4$  (see above) can be considered a primary feature of *C. proterva*. Also inherent in this approach is the postulate that, as far as can be determined from the morphology of the available specimens, the collections sampled a fossil population that was contemporaneous, at least within the available limits of biochronological or geochronological resolution.

Second lower molars, represented by U.S.N.M. Nos. 19110 (text fig. 4H), U.S.N.M. No. 18429, and F:A.M. No. 73662, are larger than, but otherwise essentially similar to,  $M_1$ . The teeth are still relatively elongate as compared with those of *C. occidentale*, new species, and resemble  $M_1$  chiefly in possessing the longitudinal postmetaconid crest. This is particularly evident in F:A.M. No. 73662 in which the tooth is unworn. Both of the specimens in the United States National Museum are in a later stage of wear than the available first molars, so the degree to which the postmetaconid crest is developed cannot be determined. To judge from U.S.N.M. No. 19110, however, in which the posterior base of the metaconid is elongated to the extent that the transverse valley is obstructed, a longitudinal postmetaconid ridge was probably well developed.

As shown by U.S.N.M. No. 18429 (Gazin and Collins, 1950, fig. 7) and F:A.M. No. 73662,  $M_3$  of *C. proterva* is an elongate, narrower version of  $M_2$  in which the talonid is strengthened by an expansion of the central, terminal conulid. As in  $M_1$  and  $M_2$  there are no cingula other than a narrow anterior cingulum and a short structure at the labial mouth of the transverse valley. This tooth is considerably longer and relatively narrower than  $M_3$  of *C. occidentale*, new species, and in F:A.M. No. 73662 the presence of the postmetaconid crest is still demonstrable.

Only a small portion of the mandible is present in U.S.N.M. No. 18429 and F:A.M. No. 73662. The ascending ramus rises past the rear of  $M_3$  in U.S.N.M. No. 18429 and continues as a broad convexity below the anterior root of  $M_2$ , at which point the specimen is broken. In F:A.M. No. 73662  $M_3$  is not fully erupted, and  $dP_4$  is still in place, so that the adult configuration of the mandible is not determinable. Posteriorly the ventral

border of the coronoid fossa lies at about the level of the alveolar border. Below this, the attachment area for *M. masseter lateralis* is poorly defined but seems to extend forward to, or slightly beyond, a line passing ventrally from the hypoconid of *M*<sub>3</sub>. Medially the pterygoid and digastric fossae are continuous, but the concave configuration of the former and concomitant medial curve of the preserved portion of the angle suggest that the latter may have been inflected to some extent. This feature is in direct contrast to the condition in more primitive peccaries such as *Thinohyus* and *Perchoerus* and is a point of similarity relative to *Dyseohyus* and various later peccaries, including the living white-lipped peccary, *Tayassu pecari*.

**DISCUSSION:** The biochronologic range of *Cynorca proterva* may be restricted to the early Barstovian. The imprecise nature of this statement stems from uncertainties concerning the correlation of faunas with which it is associated with those for which temporal position is more firmly established. Part of the difficulty is due to the apparent restriction of *C. proterva* to coastal areas. The major exception is F:A.M. No. 73664 which comes from Observation Quarry in western Nebraska. The possibility that *C. proterva* occupied a coastal habitat, which may have extended as a gallery situation to the interior of North America, is explored below.

Although the current representation of *Cynorca proterva* is rather meager, the features displayed by the available material warrant specific separation from other species of the genus. Although the collateral species from western North America, *C. occidentale*, new species, is about the same size as *C. proterva*, the dentition of the former is more robust. As far as can be determined, neither of these two species is demonstrably more advanced than the other, and both could have arisen from the early to middle Miocene species *C. sociale*.

***Cynorca* cf. *C. proterva***

Plate 42, figure 2; table 6

**DISTRIBUTION:** Late middle Miocene (late Hemingfordian), from a Frick locality "3 miles south and 9 miles west of Hay Springs," NE.  $\frac{1}{4}$ , sect. 30, T. 31 N., R. 47 W., in

deposits equivalent to the Sheep Creek Formation, Dawes County, Nebraska.

**HYPODIGM:** F:A.M. No. 73663, associated fragments of juvenile mandible with right *dP*<sub>3</sub>-*M*<sub>2</sub> and left *dP*<sub>4</sub>-*M*<sub>1</sub>.

**DESCRIPTION:** In *dP*<sub>3</sub> the main cuspid is in a central position above the two roots, and between a low anterior conulid and the equally low heel. Occlusal wear has eliminated most surface features of these lower parts of the tooth, but each probably consisted of a single cuspid. The occlusal outline is broadly bilobate, because the anterior and posterior parts of the tooth are distinctly wider than the central portion.

The proportions of *dP*<sub>4</sub> are relatively elongate and, as in *dP*<sub>3</sub>, the minimum width of the tooth is measured across the central portion. This tooth bears the usual six cuspids and, except for its smaller size, lower crown height, and more regularly rectangular occlusal outline, differs little from specimens of *C. proterva*. As in *C. proterva* the base of the metaconid in F:A.M. No. 73663 is broadly expanded posteriorly, indicating the presence of a postmetaconid crest.

The molars are smaller than those of typical *C. proterva*, and seem to have somewhat more elongate proportions. The postmetaconid crest is not present in the molars of F:A.M. No. 73663.

**DISCUSSION:** As indicated by the larger dentition, this specimen is not a representa-

TABLE 6  
MEASUREMENTS (IN MILLIMETERS) OF THE  
LOWER CHEEK TEETH OF *Cynorca* CF.  
*C. proterva* (F:A.M. No. 73663)

		Right	Left
<i>dP</i> <sub>3</sub>	Length	9.05	—
	Width	4.55p	—
<i>dP</i> <sub>4</sub>	Length	12.50	12.55
	Width	5.80p	5.85p
<i>M</i> <sub>1</sub>	Length	10.90	10.90
	Width	7.35p	7.15p
<i>M</i> <sub>2</sub>	Length	12.20	—
	Width	8.55a	—



tive of *Cynorca sociale*; the elongate proportions of the teeth preclude affinity with this species as well as with *C. occidentale*, new species, and *Dyseohyus fricki*. The occlusal outlines of  $dP_3$  and  $dP_4$  of F:A.M. No. 73663 are markedly different from those in *D. fricki*, and *D. stirtoni*, new species. Unfortunately  $dP_3$  is unknown in typical *C. occidentale*, new species, but including F:A.M. No. 73663 in the lineage leading to, or near, that of *C. proterva* seems to express best the characters it displays.

***Cynorca hesperia* (Marsh, 1871)**

Text figure 5; table 7

*Dicotyles hesperius* MARSH, 1871, p. 42.

*Dicotyles hesperius*: COPE AND WORTMAN, 1884, p. 18. WILCKENS, 1885, p. 306. STEHLIN, 1899, pp. 115, 194.

*Chaenohyus? hesperius*: COPE, 1879, p. 373.

*Tayassu hesperius*: COLBERT, 1938, p. 216.

TYPE AND HYPODIGN: Y.P.M. No. 11899, fragment of right maxilla with  $P^4$ - $M^3$ .

DISTRIBUTION: Late middle Miocene (late Hemingfordian) or early late Miocene (early Barstovian), Mascall Formation, John Day region, Oregon. According to the specimen label, the maxillary fragment was collected by Thomas Condon from the upper John Day River, Oregon. Marsh (1871, p. 43) thought that the specimen came from the same deposits as the type of *Platygonus condoni*,

i.e., from "the Pliocene beds of Oregon," but this reference is interpreted here as probably to deposits now known as Mascall (see p. 283).

DIAGNOSIS: Definitely smaller than *C. occidentale*, new species, slightly smaller than *C. sociale* and possibly *C. proterva*; relatively elongate proportions of molars similar to those of *C. sociale* and presumably those of *C. proterva*, but differing from those of *C. sociale* in presence of deep trenchant groove that passes lingually between protocone and metacone of  $P^4$ ; similar, in construction of  $P^4$ , to *C. occidentale*, new species, but differing from that species in proportions and gracile nature of molars and unreduced condition of  $M^3$ .

DESCRIPTION: The specimen is of an adult peccary showing wear on the major cusps of all teeth, with the occlusal pattern of  $M^1$  developed to almost its maximum extent. In  $P^4$ , the protocone, paracone, and metacone are well developed, but the protoconule and metaconule consist of small conules. Posterior to the metaconule a broad heel is developed and continues as a narrow cingulum to the rear of the metacone and to the posterior base of the protocone. The metacone and metaconule are separated from the heel by an arcuate groove which joins a deep, posterolingually directed groove passing between the protocone on one hand and the metaconule and the heel on the other. This latter groove also leads anteriorly along the labial base of the protocone and bifurcates at the protoconule. A narrow anterior cingulum lies along the base of the paracone and partly along that of the protocone.

In its construction,  $P^4$  of *C. hesperia* resembles that of *C. occidentale*, new species, and, were it not for the fundamental difference between the molars of these two species, they would be considered synonymous.

All major cusps and conules are developed on the molars and present no striking differences in basic construction from those of other species of the genus. Except for the heel of  $M^3$ , the molars of *C. hesperia* are lightly cingulate, but it is in the proportions of these teeth that this species differs from the essentially contemporaneous and geographically proximal species, *C. occidentale*, new species. The molars of *C. hesperia* are

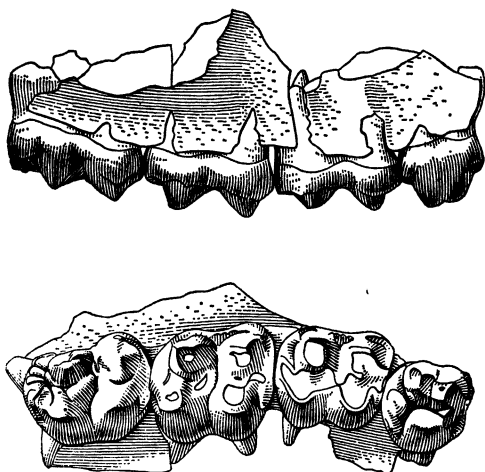


FIG. 5. *Cynorca hesperia*, holotype, maxillary fragment with right  $P^4$ - $M^3$ , Y.P.M. No. 11899, occlusal view.  $\times 1.5$ .

relatively slender, and  $M^3$  is not reduced, but those of *C. occidentale*, new species, are basally expanded and have swollen cusps and a reduced  $M^3$ .

DISCUSSION: The construction of  $P^4$  of *C. hesperia* differs from that in *C. sociale* chiefly in the deep, trenchant nature of the postprotoconal groove. This structure is not so well developed in the latter species, although the construction and proportions of its molars are not significantly different from those of *C. hesperia*. It is quite likely that *C. hesperia* is a direct descendant of *C. sociale*. In spite of the similarity in premolar morphology between *C. hesperia* and *C. occidentale*, new species, differences in the construction of their respective molar dentitions preclude close affinity. Probably both species arose from a structural level, such as is found in *C. sociale*, and paralleled each other in premolar evolution while achieving different molar specializations. Based on present knowledge, *C. hesperia* cannot be included with either *C. sociale* or *C. occidentale*, new species, and in these terms represents a separate species. Final judgment as to the taxonomic position of the Mascall peccary must await the discovery of comparative dental material of *C. proterva*. Except for  $M^3$ , the upper molar and premolar morphology of the eastern species of *Cynorca* is unknown, but in view of the probably elongate, non-swollen character of its upper molars (as based on the condition of  $M^3$  and the lower dentition), *C. proterva* may prove similar to *C. hesperia*. If so, *C. hesperia* would become a synonym of *C. proterva*.

*Cynorca occidentale*,<sup>1</sup> new species

Plate 42, figure 4; plates 43–46;  
text figure 6; tables 8, 9

TYPE: F.A.M. No. 73660, palate with right and left  $P^2$ – $M^3$ , symphysis and right mandible with right  $I_{1-3}$ ,  $C_1$ ,  $P_2$ – $M_3$ , and left  $I_1$  and  $C_1$ .

DISTRIBUTION: Late late Miocene (late Barstovian), U.C.M.P. V-5666, Dome Springs fauna, Kent Quarry, 470 feet below the top of the middle part of the Caliente Formation, Cuyama Badlands, Ventura

<sup>1</sup> From the Latin *occidens*, in reference to the distribution of the species in western North America.

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF THE  
UPPER CHEEK TEETH OF *Cynorca hesperia*  
(Y.P.M. No. 11899)

$P^4$	
Length	7.45
Width	8.25
$M^1$	
Length	10.20
Width	9.15p
$M^2$	
Length	11.05
Width	10.45a
$M^3$	
Length	11.55
Width	9.40a

County, California (U.C.M.P. No. 68027). Early late Miocene (early Barstovian), Valley View Quarry, 200 feet below the "lower marker tuff bed" of Dibblee (1968), second faunal unit of Lewis (1964, 1968), middle third of the Barstow Formation, SE.  $\frac{1}{4}$ , NW.  $\frac{1}{4}$ , sect. 24, T. 11 N., R. 2 W., Barstow Syncline, San Bernardino County, California (F.A.M. No. 73660). Early late Miocene (early Barstovian), L.A.C.M. (C.I.T.) 108 and 109, Temblor Formation, *Merychippus* zone, SW.  $\frac{1}{4}$ , sect. 28, T. 18 N., R. 15 E., Domengine Creek, North Coalinga district, Fresno County, California (L.A.C.M. Nos. 18082, 18083, and 18084). Late Miocene (Barstovian), U.S.G.S. M-1006, Caliente Formation, Caliente Range, San Luis Obispo County, California (U.S.-N.M. No. 22927). Late middle Miocene (late Hemingfordian), Ravine Quarry, Sheep Creek Formation, SW.  $\frac{1}{4}$ , sect. 34, T. 26 N., R. 55 W., Antelope Draw, Sioux County, Nebraska (F.A.M. No. 73668). ?Late middle Miocene (?late Hemingfordian), from a Frick locality in "lower beds," in the third wash northwest of White Sulphur Springs, Meagher County, Montana (F.A.M. No. 37667); age determination based on similarity of this specimen to F.A.M. No. 37668. Early middle Miocene (early Hemingfordian), Frick locality "16-mile district, west end," Marsland Formation (*sensu* McKenna, 1965), near Lusk, Goshen County, Wyoming (F.A.M. Nos. 73665, 73680). Early middle Miocene (early Hemingfordian), from a

Frick locality in "beds on east side of the road to Jay-Em," Marsland Formation (*sensu* McKenna, 1965), near Lusk, Goshen County, Wyoming (F:A.M. No. 73666).

**HYPODIGM:** Type, and U.C.M.P. No. 68027, associated right P<sup>2</sup>, P<sup>4</sup>-M<sup>3</sup>, and left I<sup>1</sup>, P<sup>2</sup>, P<sup>4</sup>; U.S.N.M. No. 22927, left partial mandible with P<sub>3</sub>-M<sub>3</sub>; F:A.M. No. 73668, right partial mandible with P<sub>4</sub>-M<sub>3</sub>; F:A.M. No. 73665, fragment of associated right juvenile mandible with dP<sub>4</sub>-M<sub>2</sub>, left talonid of M<sub>1</sub>, and isolated right M<sub>2</sub>; F:A.M. No. 73667, partial right mandible with P<sub>4</sub>-M<sub>3</sub>; F:A.M. No. 73666, juvenile palate with right dP<sup>3-4</sup>, M<sup>1-2</sup>, left dp<sup>3-4</sup>, M<sup>1</sup>, F:A.M. No. 73680, left juvenile jaw with P<sub>3</sub>, partial dP<sub>4</sub>, M<sub>2</sub>, partial M<sub>3</sub>; L.A.C.M. Nos. 18082, 18083, and 18084, all right M<sup>3</sup>'s.

**DIAGNOSIS:** Among larger species of *Cynorca*, slightly larger than *C. proterva*, definitely larger than *C. hesperia* or *C. sociale*; upper molars transversely expanded, individual cusps tending to be bulbous at base; lower molars relatively not so elongate as those of *C. proterva*, M<sub>2</sub> usually markedly wider than M<sub>1</sub>; P<sup>4</sup> with deep, trenchant, lingually opening, postprotoconal groove; P<sub>4</sub> with bicusped talonid; M<sub>3</sub> reduced.

**DESCRIPTION:** Except where noted, the description of the holotype suffices for comparable elements of other specimens. The palatal fragment is slightly crushed and is traversed by a few small, oblique cracks. Remnants of the infraorbital foramina suggest that they may have been somewhat slitlike in cross section. The foramen was probably above P<sup>4</sup>. The palatal surface is nearly smooth and flat between the cheek teeth, being interrupted only by the palatine foramina and grooves. The exact location of the foramina is difficult to determine. They seem to emerge medial to the base of P<sup>4</sup>, but possibly were opposite M<sup>2</sup> (pl. 43, fig. 3). In F:A.M. No. 73666 (pl. 42, fig. 4) the palatine foramina are opposite the rear half of M<sup>1</sup>, even though the specimen is of an immature animal, with dP<sup>3</sup> and dP<sup>4</sup> still functional. In the adult the foramina would be even farther back. In the holotype the palatine foramina are separated from each other by a distance of 13.3 mm. The corresponding distance is 10.0 mm. in F:A.M. No. 73666. Anteriorly, the palatine grooves converge somewhat so that

they are 9.0 mm. apart at the anterior end of P<sup>2</sup>. In conformity with this configuration, the tooth rows converge anteriorly; the transverse distance between the lingual bases of M<sup>3</sup> protocones is 25.0 mm. and that between the lingual base of the major cusp of P<sup>2</sup> is 22.8 mm. In the holotype the transverse distance between the protocone alveoli of M<sup>1</sup> is 22.35 mm.; in F:A.M. No. 73666 this distance is 16.85 mm. Although a line passing through the lingual edges of the cheek teeth is somewhat irregular because of the expanded lingual base of M<sup>2</sup>, a line passing along the labial bases of the cheek teeth would be smoothly convex. Thus the tooth rows not only diverge posteriorly but are also somewhat bowed outward at M<sup>1</sup> and M<sup>2</sup>. As preserved, the bone of the palate extends only 7.2 mm. anterior to the left P<sup>2</sup>, and there is no evidence for or against the presence of P<sup>1</sup>. If P<sup>1</sup> was present, it was separated from P<sup>2</sup> by a diastema greater than 7.2 mm.

**UPPER DENTITION:** The first incisor, represented in U.C.M.P. No. 68027, is a relatively brachyodont tooth with a recurved anterior edge which leads toward the apex. A wear facet on the posterior surface is tear-shaped in occlusal view (text fig. 6A) and widens toward the base of the crown. A longitudinal, lenticular exposure of dentine at the postero-lingual base of the wear facet suggests the presence of a small, ridgelike development in this position. A similar ridge seems to have been present along the labial border of the occlusal surface as well, so that in the unworn condition a shallow longitudinal concavity was probably present in the intervening space. In occlusal outline, the lingual edge is smoothly convex, but the labial surface of the tooth is slightly concave. Although I<sup>1</sup> is larger in *C. occidentale*, the basic construction of the tooth is similar to that in *C. sociale*. Both of these species differ from the Recent *Dicotyles* and *Tayassu* in the slight development of the lingual and labial crests.

As represented in F:A.M. No. 73666, dP<sup>3</sup> (pl. 42, fig. 4) has an anteriorly triangular occlusal outline and bears three principal cusps, all of which are partly worn. The anteriormost of these (?paracone) is centered over the anterior half of the tooth and bears a low, short, longitudinal crest which descends into the transverse valley to

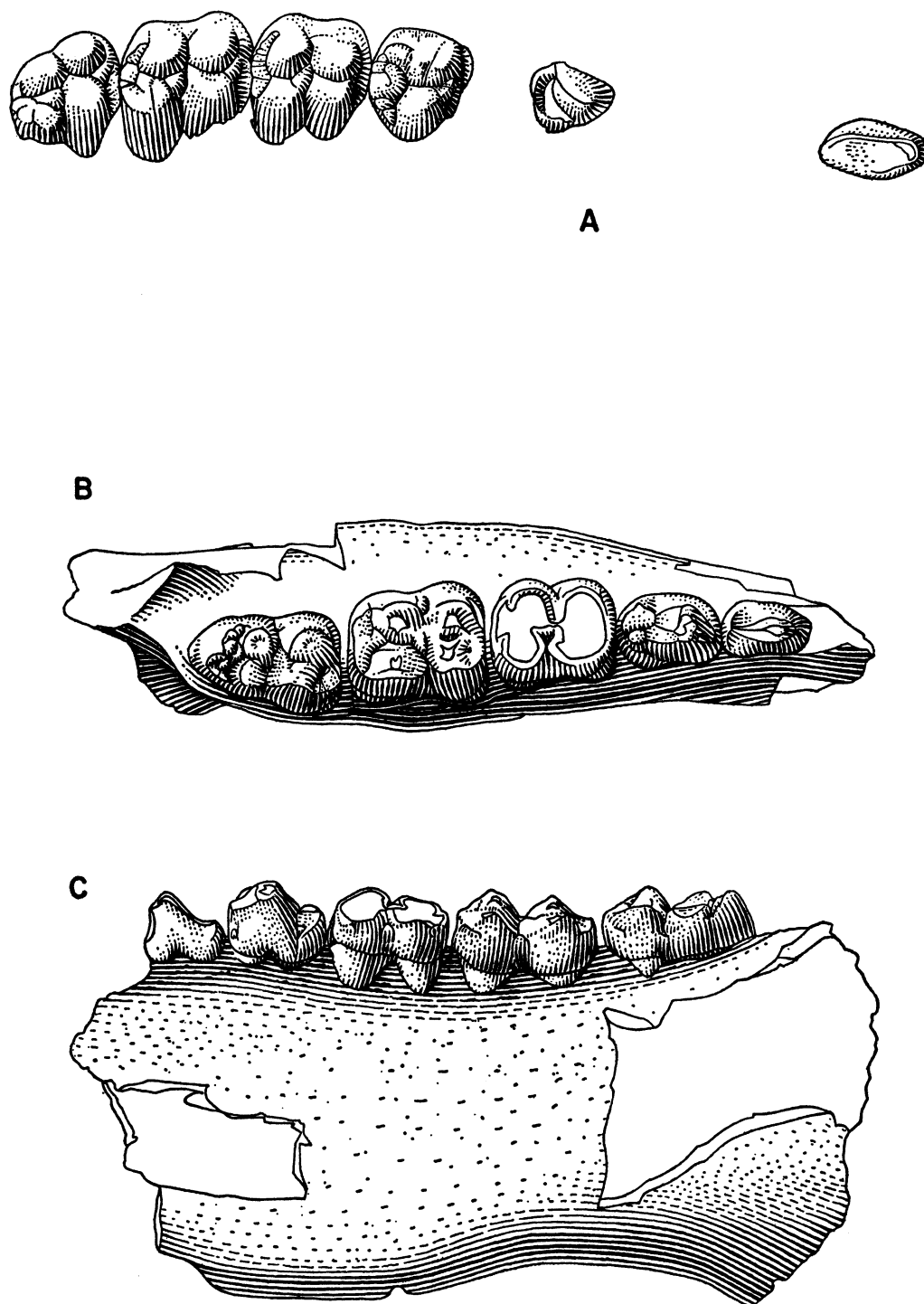


FIG. 6. *Cynorca occidentale*, new species. A. Left I<sup>1</sup>, right P<sup>2</sup>, P<sup>4</sup>-M<sup>3</sup>, U.C.M.P. No. 68027 (space between I<sup>1</sup> and P<sup>2</sup> not representative of actual distance), occlusal view. B, C. Mandible with left P<sub>3</sub>-M<sub>3</sub>, U.S.N.M. No. 22927. B. Occlusal view. C. Labial view.  $\times 1.5$ .

meet a similar crest from the ?metacone. Lingual to the ?metacone, the ?hypocone occupies the posterolingual corner of the tooth and is connected to the former cusp by a short, transverse crest. The ?hypocone also reaches the narrow posterior cingulum by means of a short, posterolabially directed crest. At the anterior base of the tooth is the remnant of a low cingulum. Except for having a more irregularly trapezoidal occlusal outline and for having less strongly developed features, dP<sup>4</sup> is essentially like M<sup>1</sup>. The primary differences in dP<sup>3</sup> between *C. occidentale* and *Tayassu* or *Dicotyles* is the presence of a ?protocone in the anterolingual quadrant of the teeth of the living forms. As for dP<sup>4</sup>, the tooth in the living genera is less broadly expanded and less irregular in outline. Comparison with the more worn deciduous premolars in the holotype of

*Dyseohyus fricki* reveals no differences other than size.

Although P<sup>1</sup> is still present in *C. sociale*, its presence cannot be established in any other species of *Cynorca*. In *C. occidentale*, P<sup>2</sup> (pl. 43, fig. 3; text fig. 6A) is subtriangular in occlusal outline. A large, conical, main cusp occupies most of the occlusal surface which bears a very weak longitudinal crest at its posterior base. Posterior and medial to this a crescentic talon extends anteriorly toward, but does not reach, the anterior end of the tooth. The talon is expanded posterolingually; its occlusal surface is developed into a relatively sharp crescentic ridge. A distinct commissure lies along the base of the main cusp, separating it from the talon. In U.C.M.P. No. 68027, P<sup>2</sup> is essentially like that in the holotype but, being less worn, shows a more cusped talon.

TABLE 8  
MEASUREMENTS (IN MILLIMETERS) OF THE UPPER DENTITION OF *Cynorca occidentale*,  
NEW SPECIES

	F:A.M. No. 73360, Holotype	F:A.M. No. 73666	U.C.M.P. No. 68027	F:A.M. No. 73665	L.A.C.M. No. 18082	L.A.C.M. No. 18083	L.A.C.M. No. 18084
P <sup>2</sup>							
Length	8.05	—	—	—	—	—	—
Width	6.35p	—	—	—	—	—	—
dP <sup>3</sup>							
Length	—	10.25	—	—	—	—	—
Width	—	6.90p	—	—	—	—	—
P <sup>3</sup>							
Length	8.95	—	7.80+	—	—	—	—
Width	7.10p	—	6.10+	—	—	—	—
dP <sup>4</sup>							
Length	—	9.10	—	—	—	—	—
Width	—	9.70p	—	—	—	—	—
P <sup>4</sup>							
Length	8.15	—	8.70	—	—	—	—
Width	9.10p	—	9.60	—	—	—	—
M <sup>1</sup>							
Length	10.95	10.90	11.80	—	—	—	—
Width	10.75p	11.05p	12.05p	—	—	—	—
M <sup>2</sup>							
Length	12.90	11.50	12.80	13.25	—	—	—
Width	13.00a	11.50e	—	11.65a	—	—	—
M <sup>3</sup>							
Length	11.05	—	10.20	—	11.45	11.40	11.20
Width	10.40a	—	10.45a	—	10.60	10.90a	10.35a
Length, P <sup>2</sup> -M <sup>3</sup>	62.10	—	—	—	—	—	—

The third premolar is similar to P<sup>2</sup> except that the greatest width is measured nearer the transverse midline rather than more posteriorly. Also, a broad heel area is developed into a number of cusps, lying largely lingual to the arcuate groove marking the base of the main cusp or paracone. Lingual to this an incipient ?protocone is probably represented by the slightly swollen anterior part of the cingulum. Posterolingual to the ?protocone a small conical ?metaconule lies between the paracone and the posterior cingulum. A short groove separates the ?protocone and ?metaconule.

The outline of P<sup>4</sup> is also subtriangular, but the apex is lingual rather than anterior. The main, labial cusp is twinned (the parametacone), and it is not so high or prominent relative to the other components of the tooth as in P<sup>2</sup> and P<sup>3</sup>. The transverse commissure which effects the twinning of the parametacone extends about halfway toward the base on the labial side of the tooth and reaches the longitudinal groove at the lingual base of the cusp. The apex of the protocone lies nearly on the transverse midline of the tooth but is anterior to the point of greatest width. Posteriorly, the protocone is separated from the metaconule by the posterolingually directed, deep, trenchant, postprotoconal groove, as foreshadowed in P<sup>3</sup>. The metaconule is composed of a number of small conules, separated into an anterior and a posterior set by a short transverse commissure. A narrow anterior cingulum is developed and nearly reaches the short protoconule in the anterior midline of the tooth. In general, the constituents of P<sup>4</sup> are like those of P<sup>3</sup>, but more elaborate, and situated somewhat more posterolabially.

The outline of M<sup>1</sup> (pl. 42, fig. 4; pl. 43, fig. 3; text fig. 6A) is broadly rectangular, with the lingual bases of the protocone and hypocone being distinctly expanded. The paracone and metacone are situated anteriorly relative to the lingual pair, and rather short but relatively broad anterior and posterior cingula are continuous with the labial cingulum. Because of the lingual expansion of the protocone and hypocone, the labial surface of the tooth slants internally toward the tips of the paracone and metacone at a steeper angle than the lingual

surfaces of the protocone and hypocone. A sinuous transverse commissure separates the anterior half from the posterior half of the tooth. The paracone and metacone are conical in the unworn state (with the exception that faint crests are developed at the posterolabial corner of the paracone and at the anterolabial and posterolabial corners of the metacone), but the protocone and hypocone are developed into bunoselenodont cusps by the addition of short, relatively broad crests to their anterolabial and midlabial surfaces. The anterolabial crest (protoconule) is the better developed of those associated with the protocone; it connects to the anterior cingulum and to a very short anterolingual crest which projects from the base of the paracone. The midlabial crest from the protocone is poorly expressed and is cut off by the main transverse groove and by the crescentic groove which delimits the lingual base of the paracone. In U.C.M.P. No. 68027 the midlabial crest from the protocone is poorly expressed and is similar in this respect to M<sup>1</sup> of F:A.M. No. 73666.

The anterolabial crest (metaconule) which extends from the hypocone terminates in the transverse valley just adjacent to the posterolingual base of the paracone, and a faint subsidiary crest lies along the lingual base of the metaconule. This latter structure is not present in U.C.M.P. No. 68027 or F:A.M. No. 73666. The midlabial crest of the hypocone is poorly developed in the holotype, but persists as a broad, flat structure in U.C.M.P. No. 68027, and as a short ridge in F:A.M. No. 73666. The posterior cingulum reaches nearly to the apex of the hypocone, increasing the bunoselenodont character of that cusp.

The second molar is constructed essentially like M<sup>1</sup>. It is larger, the crests from the protocone and hypocone are more distinctly developed, the protoconule and metaconule are delimited by commissures along the anterolabial crests from the protocone and hypocone, respectively, the labial cingulum is less strongly developed, and the lingual basal expansion of the tooth is more apparent. The same variations in detail noted for M<sup>1</sup> in other specimens of this species also apply to M<sup>2</sup>. In addition, M<sup>2</sup> of F:A.M. No. 73666 is shorter than in the other two indi-



viduals. The third molar is considerably reduced relative to  $M^2$  and is more irregularly trapezoidal because of the conspicuous reduction in width of its posterior moiety. The component parts of  $M^3$  are essentially those of  $M^2$ , but the individuality of the secondary conules has been emphasized to the detriment of the bunoselenodonty of the lingual cusps, particularly in U.C.M.P. No. 68027. The labial cingulum is absent.

LOWER DENTITION: The incisors are straight, elongate, nearly cylindrical teeth

which extend out of their alveoli at an angle of about 12 degrees relative to a horizontal line passing along the tips of the cheek teeth (pl. 46). The crown of  $I_3$  is not present.  $I_2$  is slightly larger than  $I_1$ , and both are less spatulate than in *Dyseohyus* or the living peccaries.

The lower canines have a triangular cross section, anterior apex, and somewhat concave posterior surface (pl. 46). On the labial surface a low ridge, delimited on each side by a narrow groove, extends about halfway

TABLE 9  
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER DENTITION OF *Cynorca occidentale*,  
NEW SPECIES

	F:A.M. No. 73660, Holotype	U.S.N.M. No. 22927	F:A.M. No. 73668	F:A.M. No. 73667	F:A.M. No. 73665	F:A.M. No. 73680
$I_1$						
Length	3.90	—	—	—	—	—
Width	4.10	—	—	—	—	—
$I_2$						
Length	4.50	—	—	—	—	—
Width	4.20	—	—	—	—	—
$C_1$						
Length	10.10+	—	—	—	—	—
Width	7.50+	—	—	—	—	—
$P_2$						
Length	7.75c	—	—	—	—	—
Width	3.80c	—	—	—	—	—
$dP_3$						
Length	—	—	—	—	—	—
Width	—	—	—	—	—	—
$P_3$						
Length	8.75	8.35	—	—	—	9.40
Width	4.85p	5.00p	—	—	—	6.05p
$dP_4$						
Length	—	—	—	—	12.65	—
Width	—	—	—	—	6.25p	8.25p
$P_4$						
Length	9.30	9.40	9.90	9.95	—	—
Width	6.25	6.80	7.05	6.50p	—	—
$M_1$						
Length	11.30	11.25	10.55	10.10	11.65	—
Width	8.65a	9.55p	8.35a	8.10p	8.45a	—
$M_2$						
Length	12.50	13.65	11.50	11.70	13.35	12.50
Width	10.90a	11.60a	9.90a	9.25a	—	9.85p
$M_3$						
Length	13.70	14.55	13.95	13.80	—	—
Width	9.35	10.10a	10.15a	—	—	8.35+
Length, $P_2-M_3$	65.40	—	—	—	—	—

from the alveolus toward the tip. The lingual surface is smooth. The incompletely erupted canines are slender and elongate and extend 35.8 mm. above their alveoli. These teeth are conspicuously larger than in *C. proterva* or *C. sociale*.

The length of the cheek tooth series is 65.40 mm. There is no  $P_1$ ;  $P_2$  (pl. 43, fig. 1; pl. 46) is a simple tooth with a large, pointed main cuspid, a very small talonid, and only a suggestion of an anterior basal conulid. Also,  $P_3$  is somewhat (0.30 mm.) wider above the posterior root than above the anterior; in  $P_2$  the anterior and posterior widths are essentially the same. The third premolar of U.S.N.M. No. 22927 (text fig. 6B) is smaller than, but otherwise similar to, that of the holotype (pl. 43, fig. 1; pl. 46). In  $P_4$ , the main conulid is divided by a slightly oblique groove into labial and lingual halves. A small conulid is slightly demarcated from the labial half, high up on its anterior surface. A weak crest continues down from this conulid toward the anterolingual corner of the tooth to join the equally weak anterior cingulum. A slightly stronger crest extends posterolabially down the rear surface of the lingual half of the main cuspid but is prevented from continuing onto the talonid by the transverse groove that separates that element from the trigonid. The talonid is composed of two conulids, the labial of which is the larger. The talonid accounts for only about one-fifth of the total length of the tooth, and its vertical height is only about one-half of that of the trigonid. Posterior, labial, and lingual cingula are absent. In U.S.N.M. No. 22927,  $P_4$  (text fig. 6B) is somewhat wider posteriorly and its features are slightly more massive than in the holotype. An increased posterior width is also found in  $P_4$  of F:A.M. No. 73667 (pl. 43, fig. 2) in which the talonid is composed of a single central main conulid and two smaller flanking structures. The crown of  $P_4$  in F:A.M. No. 73668 is rather complexly crenulate, possibly owing partly to its unworn nature. The width of the trigonid relative to the talonid is essentially the same as in the holotype, but in F:A.M. No. 73668, the talonid is more strongly developed.

The first molar of the holotype (pl. 43, fig. 1) is the only tooth of the lower series

showing any appreciable wear. The protoconid and hypoconid are situated slightly anterior to the metaconid and entoconid, all four cuspids being basically bunodont. A sinuous transverse valley separates the tooth into an anterior and a posterior moiety. In detail, the paralophid connects broadly to the base of the protoconid and arcs lingually to reach the base of the metaconid. Below the paralophid, the slender anterior cingulum extends across the tooth. Short, broad crests diverge anterolabially and posterolabially from the metaconid and are prevented from reaching the protoconid by the irregular but essentially longitudinal commissure at its base.

In the talonid the situation is reversed. The lingual element, the entoconid, is essentially unmarked (a faint groove is developed along its anterolabial surface), but the labial element, the hypoconid, sends off stout, low, anterolingual and posterolingual crests and has a somewhat bunoselenodont aspect. The posterolingual crest is developed into a low hypoconulid at the lingual base of a short, posterior cingulum. A labial cingulum occurs only at the transverse valley. The lingual cingulum is not developed.

The second molar is constructed essentially like  $M_1$ . The two crevices partially disrupting the paralophid are more apparent in  $M_2$  and the other surface details are more vividly represented than in  $M_1$ . The most conspicuous differences to be noted when  $M_1$  is compared with  $M_2$  are the greater relative and actual anterior width of  $M_2$ , its larger size, and the presence of additional, midlabial and posterolabial grooves on the surface of the entoconid. The presence of these grooves is best documented in the holotype.

The third molar is similar to  $M_2$  with the exception of its decreased width and the development of an enlarged hypoconulid. The hypoconulid consists of a roughly T-shaped array of four conulids in the holotype, and this pattern is essentially like that in U.S.N.M. No. 22927 (text fig. 6B). In F:A.M. No. 73668 (pl. 44, fig. 1) a pair of terminal conulids lie posterior to a central conulid, but in F:A.M. No. 73667 a rhomboid configuration of four conulids is positioned mainly posterior to the hypoconid (pl. 43, fig. 2).

The horizontal ramus is crushed dorso-ventrally in the holotype (pl. 46), but the ventral border seems to have been relatively straight. It is only slightly convex in F:A.M. Nos. 73667 and 73668 (pl. 45). Below the premolars the labial and lingual surfaces are relatively flat. Both sides develop elongate convexities below the molars, but the construction of this area of the mandible seems rather typical of peccaries in general. In F:A.M. No. 73667 and U.S.N.M. No. 22927, enough is preserved of the angle to show that it was slightly inflected. In the holotype this area of the mandible has been artificially flattened. Anterior to this the area of the postdigastric sulcus may be somewhat distorted in the holotype, but the shallow nature of the sulcus is demonstrated in other specimens. As seen from below, the ventral edge of the horizontal ramus of the holotype is nearly straight, possibly owing to post-mortem alteration, as this edge of the ramus is slightly bowed outward in other specimens. Posterior to the canines, the diastemal crest is narrow, but not sharp, and is concave in lateral view. The mental foramen is 12.55 mm. below the crest, 7.70 mm. anterior to  $P_2$ . The length of the canine-premolar diastema is 31.40 mm. Below the diastemal region the ventral surface of the symphysis is nearly straight in lateral view and extends anterodorsally nearly parallel with the trend of the incisors.

In stage of wear, the four specimens representing lower dentitions of *C. occidentale* may be placed in the following series, youngest to oldest: F:A.M. No. 73667,  $P_4$  not completely erupted; F:A.M. No. 73668,  $P_4$  erupted, with slight wear on  $M_1$ - $M_2$ ,  $M_3$  unworn; F:A.M. No. 73660,  $P_4$  erupted, with slight wear,  $M_1$ - $M_3$  with progressively decreasing wear; U.S.N.M. No. 22927,  $P_4$  in moderate wear,  $M_1$  nearly completely worn,  $M_2$ - $M_3$  strongly worn.

The depth of the mandible of the holotype below the alveolar border at the anterior edge of  $M_1$  is 32.40 mm. In U.S.N.M. No. 22927 this measurement is 33.75 mm.; the same measurement in F:A.M. No. 73667 is 22.90 mm. and 21.80 mm. in F:A.M. No. 73668.

DISCUSSION: As constituted here, the bio-chronologic range of *Cynorca occidentale* is

early Hemingfordian to late Barstovian. As shown by the palatal width between the alveoli of  $M^1$  and by some of its dental dimensions, one of the early Hemingfordian representatives of *C. occidentale* (F:A.M. No. 73666) is smaller than the holotype. On the other hand, the dentition of the apparently contemporaneous F:A.M. No. 73665 is indistinguishable from the holotype material.

Both late Hemingfordian members of this species, F:A.M. Nos. 73667 and 73668, have conspicuously smaller mandibles than are found in either the holotype or in U.S.N.M. No. 22927. In addition, the size of  $M_2$  in these late Hemingfordian specimens is distinctly smaller than in the Barstovian material. Furthermore, the massiveness of  $M_2$  in relation to  $M_1$  or  $M_3$  in the Barstovian members of the species is in decided contrast to the small relative development of this tooth in F:A.M. Nos. 73667 and 73668. Although  $M_2$  of the early Hemingfordian F:A.M. No. 73665 is partially hidden in its crypt, it seems to have been as massive as its counterpart in the holotype.

Whether the differences shown by some of the late Hemingfordian members of *C. occidentale* reflect individual variation emphasized by the temporal separation of the specimens in question, or are of phyletic importance, cannot be answered conclusively at present. For the time being the specimens are included in this species. Should the discovery of additional material warrant separating them at the specific level, such a species probably would be related to *C. occidentale*.

As seen by the dental and other features presented above, *C. occidentale* occupies a different adaptive zone than the roughly contemporaneous species, *C. proterva*. Inasmuch as both species are potentially derivable from *C. sociale*, the two adaptive zones would have had to separate sometime in the Arikareean or possibly earliest Hemingfordian. Both *C. proterva* and *C. occidentale* are specialized in their own ways, and neither can be shown to be structurally closer to *C. sociale*. The proposition that *C. occidentale* occupied a drier, intermontane habitat in contrast to the moister, lowland habitat of *C. proterva* is discussed below.

**DYSEOHYUS** Stock, 1937*Dyseohyus* Stock, 1937, p. 398, pl. 1.TYPE: *Dyseohyus fricki* Stock, 1937.

DISTRIBUTION: Apparently restricted to the late Miocene of California, Colorado, Nebraska, and Texas.

INCLUDED SPECIES: Type, and *D. stirtoni*, new species.

DIAGNOSIS: Skull relatively gracile, rostrum elongate, postzygomatic crest continuous from external auditory meatus to lambdoidal crest; supraorbital canals converging only slightly anterior to supraorbital foramina; auditory bullae filled with cancellous tissue, broader than in *Cynorca*, longer than in *Dicotyles*; post-tympanic process of squamosal essentially flat as in living genera, glenoid fossa with distinct lateral edge as in *Cynorca*, without strong anterior edge seen in living genera; glenoid fossa situated below level of bulla; palatal surface extending posteriorly far beyond rear of  $M^3$ ; paroccipital processes with nearly longitudinal basal alignment; surface of jugal and maxillary excavated just anterior to orbit for insertion of depressor snout muscles; facial crest not continuing anteriorly above infraorbital foramen; width of nasals apparently not markedly restricted between premaxillae; infraorbital foramen above  $P^3/P^4$  or  $P^4/M^1$ ; cross section subcircular; scar of attachment of masseteric muscles elongate, tapering posteriorly, and facing ventrally and slightly laterally; small amount of facial exposure of lacrimal; anterior palatine foramina occurring between  $P^4$  and  $M^1$ ; upper diastemal crest forming medial border of elongate, narrow, ventrally facing, buccinator fossa; diastema between  $C^1$  and  $P^2$  about equal to combined length of  $P^2-P^4$ ; dental formula  $\frac{3}{1}, \frac{1}{1}, \frac{3}{2}, \frac{3}{2}$ ;  $I^1$  considerably larger than  $I^2$ ;  $I^1$  and  $I^2$  slanting anteroventrally,  $I^3$  directed nearly vertically; upper canine without distinct lateral ridges and grooves;  $P^2$  with single, rounded main cusp, wide crescentic talon which extends forward to anterior end of tooth;  $P^3$  with single to twinned main cusp, protocone tending to be separated by incomplete commissure from metaconule;  $P^4$  subrectangular, protocone separated from metaconule by posterolingually directed, postprotoconal groove; upper molars rather elongate to relatively

broad, in width  $M^1 < M^2 > M^3$ ;  $M^8$  not reduced; lingual bases of molars variably expanded; lower incisors extending anteriorly,  $I_2$  lying posterolateral to  $I_1$ ,  $I_1$  and  $I_2$  spatulate; diastema between  $I_3$  and canine small (about 4.0 mm.); lower canine with lateral ridges and grooves developed to tip; diastema between canine and  $P_2$  equal to or greater than length of premolar series;  $P_2$  with well-developed talonid consisting of one or more cuspids, with the greatest basal dimension oriented transversely;  $P_3$  with distinct anterior basal cuspid; prominent, incipiently bifid main cuspid and distinct talonid composed of cluster of three cuspids arrayed in crescent;  $P_4$  with rather broad anterior end, labial and lingual portions of twinned main cuspid of essentially equal size, aligned nearly transversely with respect to each other, talonid broader and relatively more massive, in height and length, than in *Cynorca*; lower diastemal crests sharp; in width,  $M_1 < M_2 > M_3$ ; mandible relatively broad but shallow, elongate; postdigastric sulcus shallow; ventral tips of angle inflected; pterygoid and digastric fossae confluent; digastric fossa well developed.

DISCUSSION: The genus *Dyseohyus* was originally described (Stock, 1937) from upper Miocene rocks in the Barstow Syncline and, for the most part, its presence has been restricted largely to that locality. Repenning and Vedder (1961) listed *Dyseohyus* from the Branch Canyon-Caliente Formation in the Caliente Range, San Luis Obispo County, California, but some of these specimens have been referred to *Cynorca occidentale*, and the taxonomic allocation of others is uncertain. Based entirely on specimens in the Frick Collection in the American Museum of Natural History, the genus *Dyseohyus* is seen to have been rather widely distributed in western North America from California to Nebraska, Colorado, and Texas during late Miocene time. *Dyseohyus* apparently arose from an early or middle Miocene population of *Cynorca sociale* (but see p. 349).

***Dyseohyus fricki*** Stock, 1937Plate 47, figure 1; text figures 7-10;  
tables 10-13*Dyseohyus fricki* Stock, 1937, p. 398, pl. 1.

TYPE: L.A.C.M. (C.I.T.) No. 2039, nearly

complete skull and fragments of mandible from L.A.C.M. (C.I.T.) 288, roughly 200 feet above a stratigraphic position equivalent to the "lower marker tuff bed" of Dibblee (1968) in the SE.  $\frac{1}{4}$ , NW.  $\frac{1}{4}$ , sect. 24, T. 11 N., R. 2 W., San Bernardino County, California.

**DISTRIBUTION:** Late Miocene (Barstovian) of the upper two-thirds of the Barstow Formation, San Bernardino County, California, from the following localities: L.A.C.M. (C.I.T.) 288 (holotype, see above); upper level of Steepside Quarry, roughly 900 feet below the "lower marker tuff bed" in the S.E.  $\frac{1}{4}$ , NW.  $\frac{1}{4}$ , sect. 23, T. 11 N., R. 2 W. (F:A.M. No. 73670); U.C.R. V-6401, also about 900 feet below the "lower marker tuff bed" in the NW.  $\frac{1}{4}$ , NW.  $\frac{1}{4}$ , sect. 23, T. 11 N., R. 2 W. (U.C.R. No. 11295); Hemicyon Quarry, about 250 feet above the "lower marker tuff bed" in the N.  $\frac{1}{2}$ , SW.  $\frac{1}{2}$ , SE.  $\frac{1}{4}$ , sect. 14, T. 11 N., R. 2 W. (F:A.M. No. 73671). Other specimens (F:A.M. Nos. 73672 and 73673) have no precise stratigraphic data, but come from the Barstow Formation. The local teilzone of *D. fricki*, then, is generally equivalent to the intervals characterized by elements of the first and second faunal units of Lewis (1964, 1968).

**HYPODIGM:** Type, and F:A.M. No. 73670, somewhat distorted but largely complete cranium with  $RP^3$ - $M^2$ ,  $LC^1$ ,  $P^3$ - $M^3$ , and portion of the mandible anterior to angles, including symphysis,  $RC_1$ ,  $P_3$ - $M_3$  and  $LP_2$ - $M_2$ ; U.C.R. No. 11295,  $LP^4$ ; F:A.M. No. 73671, fragment of left mandible with  $dP_3$ ,  $dP_4$ ,  $M_2$ , and  $M_3$ ; F:A.M. No. 73673, fragment of right mandible with  $M_1$ - $M_3$ ; F:A.M. No. 73672, fragment of right mandible with  $M_1$  and crushed  $M_2$ .

**DIAGNOSIS:** Differs from *D. stirtoni*, new species, in the following features: dorsal surface of nasals flat; anterior palatine foramina opposite anterior tip of  $M^1$ ; palate extending posteriorly midway between  $M^3$  and glenoid fossa; weak separation of parametacone of  $P^4$ ; upper molars short, wide;  $dP_3$  and  $dP_4$  small,  $dP_4$  irregularly narrowed anteriorly;  $P_4$  small, relatively brachyodont; lower molars relatively short; genial spine present on symphysis; ventral surface of mandible smooth below canines.

**DESCRIPTION:** The holotype cranium of *Dyseohyus fricki* (text figs. 7-9) has been

restored in plaster in many places, but, except for the lambdoidal crests and pterygoid bones, essentially all features of the cranium are preserved. As far as can be determined the specimen is completely undistorted. The holotype apparently represents a young adult individual. Although the left deciduous premolar series is still in place, the teeth are almost completely worn down. On the right side, the adult set of premolars is exposed and has almost reached the position of occlusion. Although cranial sutures are still largely visible, owing to the youth of the specimen some of the processes, scars, and ridges may not be so robust as would be expected in a fully adult animal. The following description of the cranium has been supplemented by study of F:A.M. No. 73670, which is somewhat crushed. Significant differences between the two specimens are pointed out. Unless otherwise specified, the cranium is oriented with the occlusal plane of the cheek teeth falling as nearly as possible on a horizontal surface.

In the over-all view the cranium of *D. fricki* is moderately elongate and slender, with a domelike, dorsal, frontoparietal surface and a short postorbital portion. The degree of development of the sagittal crest is great in F:A.M. No. 73670. Anterolateral to the domelike portion of the dorsum, the frontal depressions are rather weakly developed. The upper rim of the orbit, just lateral to these, is thus not so sharply demarcated from the more medial portions of the dorsum as in *Perchoerus* or *Thinohyus*. The supraorbital foramina, situated at the anterior edge of the frontal depressions, lie on a vertical transverse plane passing somewhat posterior to the lacrimal tuberosities, a position similar to that in *Perchoerus* and *Thinohyus* but posterior to that seen in *Dicotyles* or *Tayassu*. In the living genera the supraorbital foramina are either directly above or anterior to the lacrimal tubercle. In the holotype, the foramina are 29.5 mm. apart. In F:A.M. No. 73670 the distance is 30.1 mm., but the dorsal surface has been flattened somewhat so the measurement may be too large. Anterior to the foramina, the supraorbital-nasal canals extend toward the tip of the snout, converging to a minimum distance of 21.0 mm., 28.0 mm. anterior to

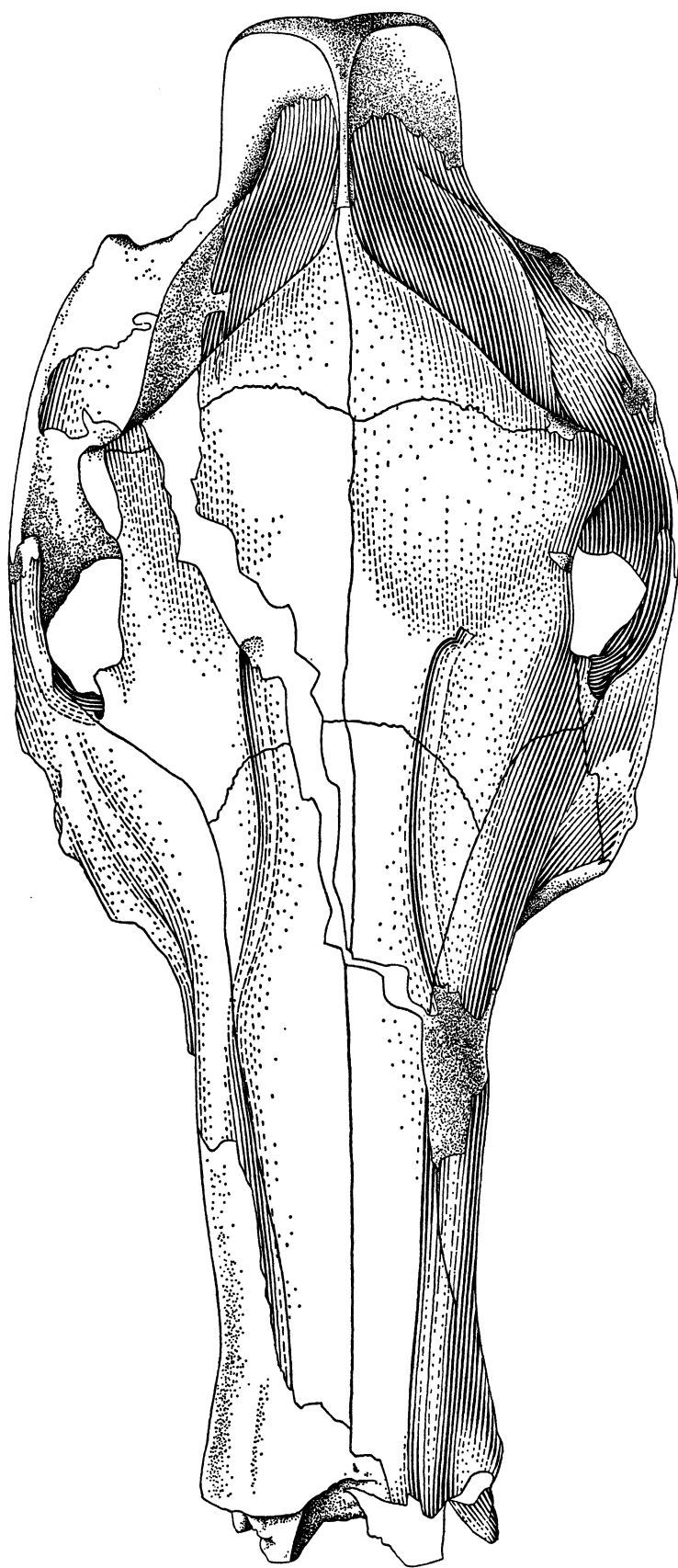


FIG. 7. *Dysochotys fricki*, cranium, holotype, L.A.C.M. (C.I.T.) No. 2039, dorsal view; restored areas stippled.  $\times 1$ .



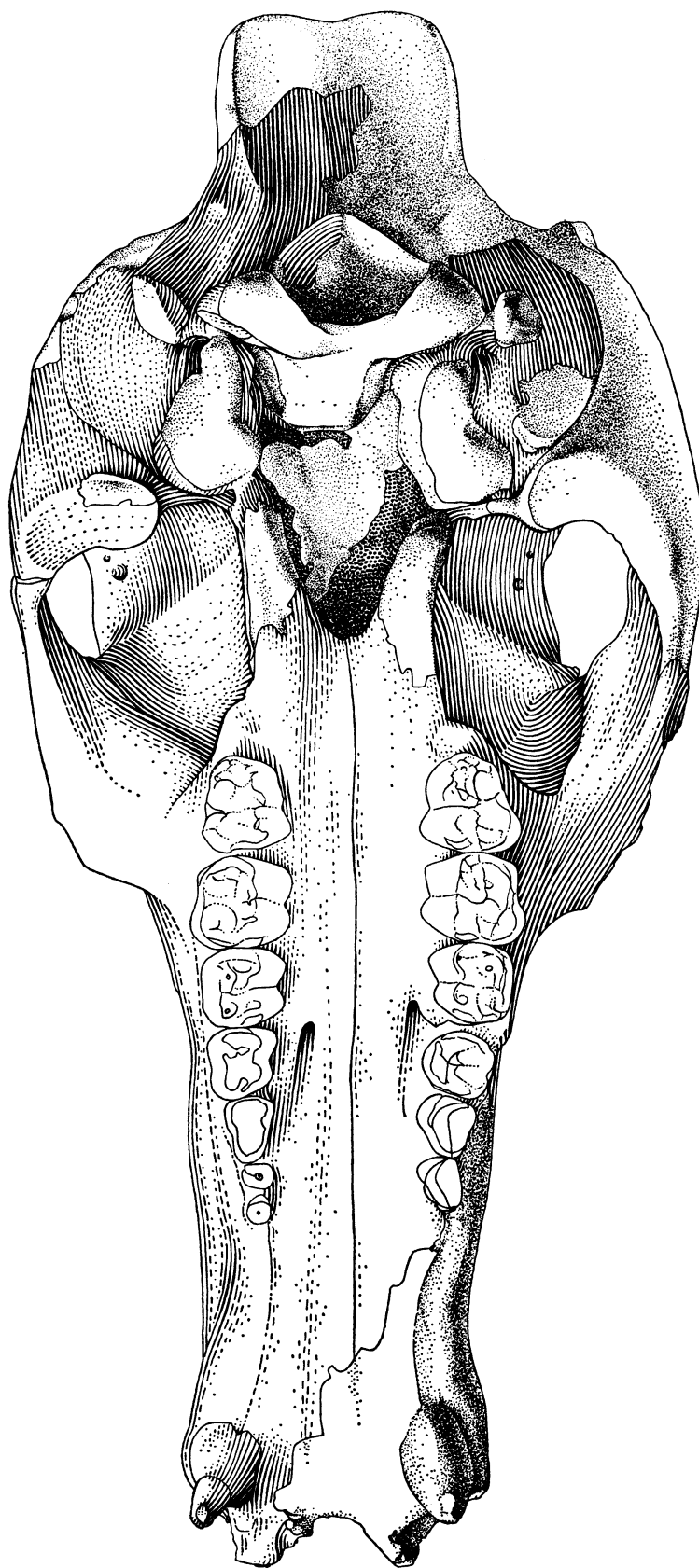


FIG. 8. *Dyseohyus fricki*, cranium, holotype, L.A.C.M. (C.I.T.) No. 2039, ventral view; restored areas stippled.  $\times 1$ .

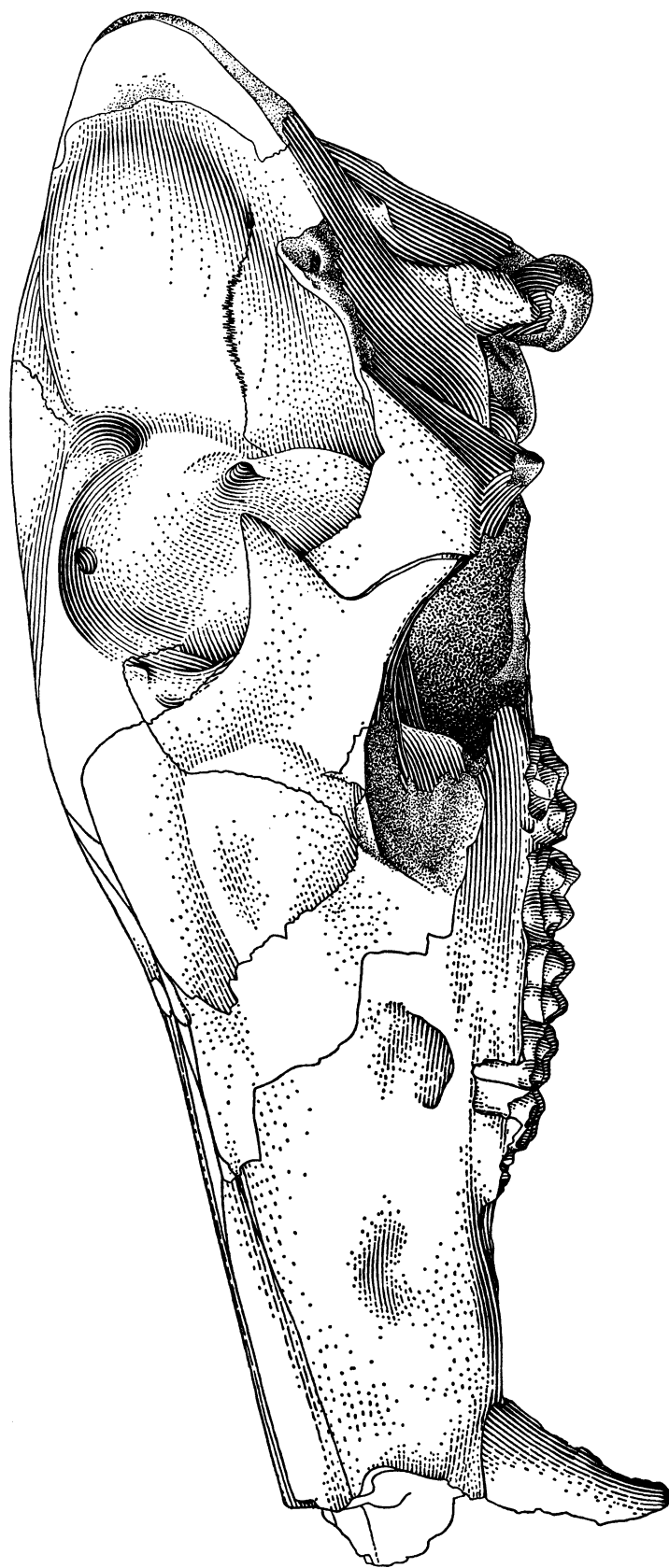


FIG. 9. *Dyseokyus fricki*, cranium, holotype, L.A.C.M. (C.I.T.) No. 2039, lateral view; restored areas stippled.  $\times 1$ .

the lacrimal tubercle. Approximately 29.5 mm. farther on, the canals have diverged to their maximum separation, 33.5 mm. in the holotype. From this point the canals converge somewhat as they continue anteriorly, and, although the critical area is not preserved in the available specimens, they probably emerge from the snout at the postero-dorsal corner of the narial notch. Antero-lateral to the supraorbital foramina the surface of the frontal and adjacent parts of the maxillary and nasal bones bulges upward somewhat, forming a slightly elongate frontal eminence. This fades out posteriorly into the frontal depression and anteriorly onto the dorsolateral surface of the snout. The raised frontal eminences, coupled with the elevated part of the frontal between the supraorbital foramina, adds to the broad, rounded, dome-like aspect of the dorsal surface of the cranium and contrasts strongly with the concave slope of the snout immediately anterior to it (text fig. 9). This concave surface of the snout, visible in terms of the profile of its lateral as well as dorsal surfaces, is best developed in the area of greatest divergence of the supraorbital canals. Anterior to this the dorsal and lateral surfaces of the snout are smooth and straight; but the concave pre-frontal region seems to be unique to *D. fricki*, and possibly *C. sociale*, as it is not found in either the living peccaries or in *Thinohyus* or *Perchoerus*. In the primitive peccaries the dorsal profile of the cranium descends essentially smoothly from the frontal region to the tip of the snout, and the cross section of the snout is narrow dorsally. In *Dicotyles* and *Tayassu* the lateral profile of the snout is essentially similar to that of the primitive peccaries, but its cross section is much broader and flatter, particularly in the region anterior to the canines, and resembles that of *D. fricki*.

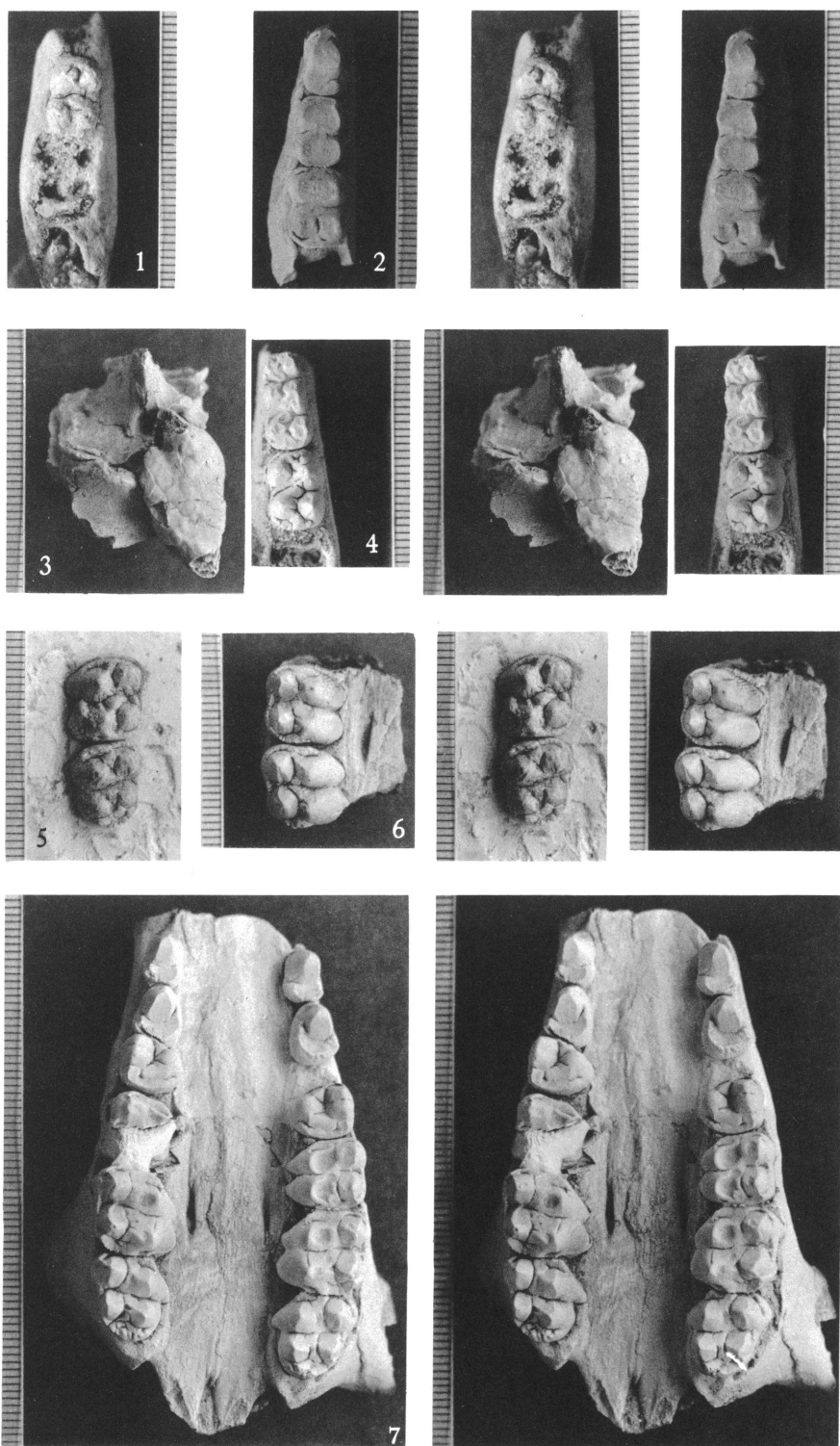
Because of the missing areas, only the posterior tips of the premaxillaries are preserved in the holotype. They extend backward as narrow strips between the nasal and maxillary bones to a point above the anterior end of P<sup>2</sup>, a position posterior to that reached in *Dicotyles* or *Tayassu*. The snout of the primitive genera is not so long, relatively, as in *D. fricki*. The posterior tip of the premaxillaries extends back to a point above the

TABLE 10  
MEASUREMENTS (IN MILLIMETERS) OF THE  
UPPER DENTITION OF *Dyseohyus fricki*

	L.A.C.M. No. 2039, Holotype	F:A.M. No. 73670	U.C.R. No. 11295
C <sup>1</sup>			
Length	12.20×	12.50+	—
Width	9.00	8.60+	—
P <sup>2</sup>			
Length	7.20+	—	—
Width	6.50+p	—	—
dP <sup>3</sup>			
Length	9.70	—	—
Width	7.60p	—	—
P <sup>3</sup>			
Length	9.25	8.75×	—
Width	8.40p	7.80p	—
dP <sup>4</sup>			
Length	9.95	—	—
Width	10.00p	—	—
P <sup>4</sup>			
Length	9.85	9.10	9.20
Width	10.35p	10.10p	10.80
M <sup>1</sup>			
Length	11.80	11.75	—
Width	11.80×	11.60p	—
M <sup>2</sup>			
Length	13.25	12.90	—
Width	14.00×	12.90a	—
M <sup>3</sup>			
Length	14.20	—	—
Width	13.60×	11.00a	—
Length, P <sup>2</sup> -M <sup>3</sup>	64.40	—	—

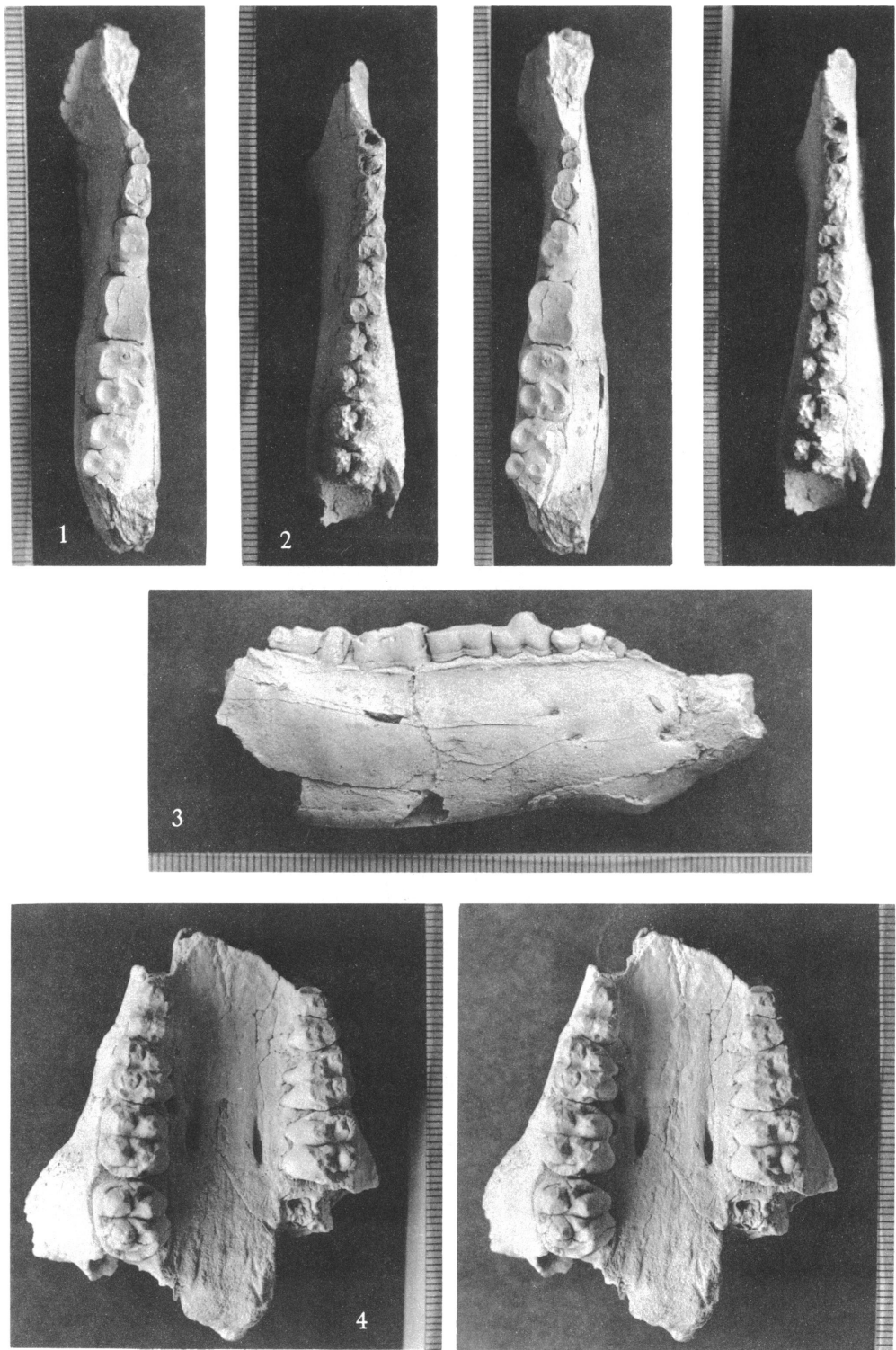
anterior edge of P<sup>3</sup> in *Thinohyus* and above P<sup>2</sup> in *Perchoerus*.

The nasals are nearly flat, forming a slightly convex upper surface of the snout. This surface continues back to a point above M<sup>1</sup> and then expands upward to meet the frontals, medial to the frontal eminences described previously. The straightness of the nasal suture as it passes the premaxillaries and continues posteriorly is prophetic of the condition in *Tayassu* as is the extensive flat upper surface of the snout. In *Dicotyles* the width of the nasals diminishes sharply between the premaxillaries, and the flat upper surface of the snout does not extend so far posteriorly. In the primitive peccaries, the configuration of the nasal suture is much like

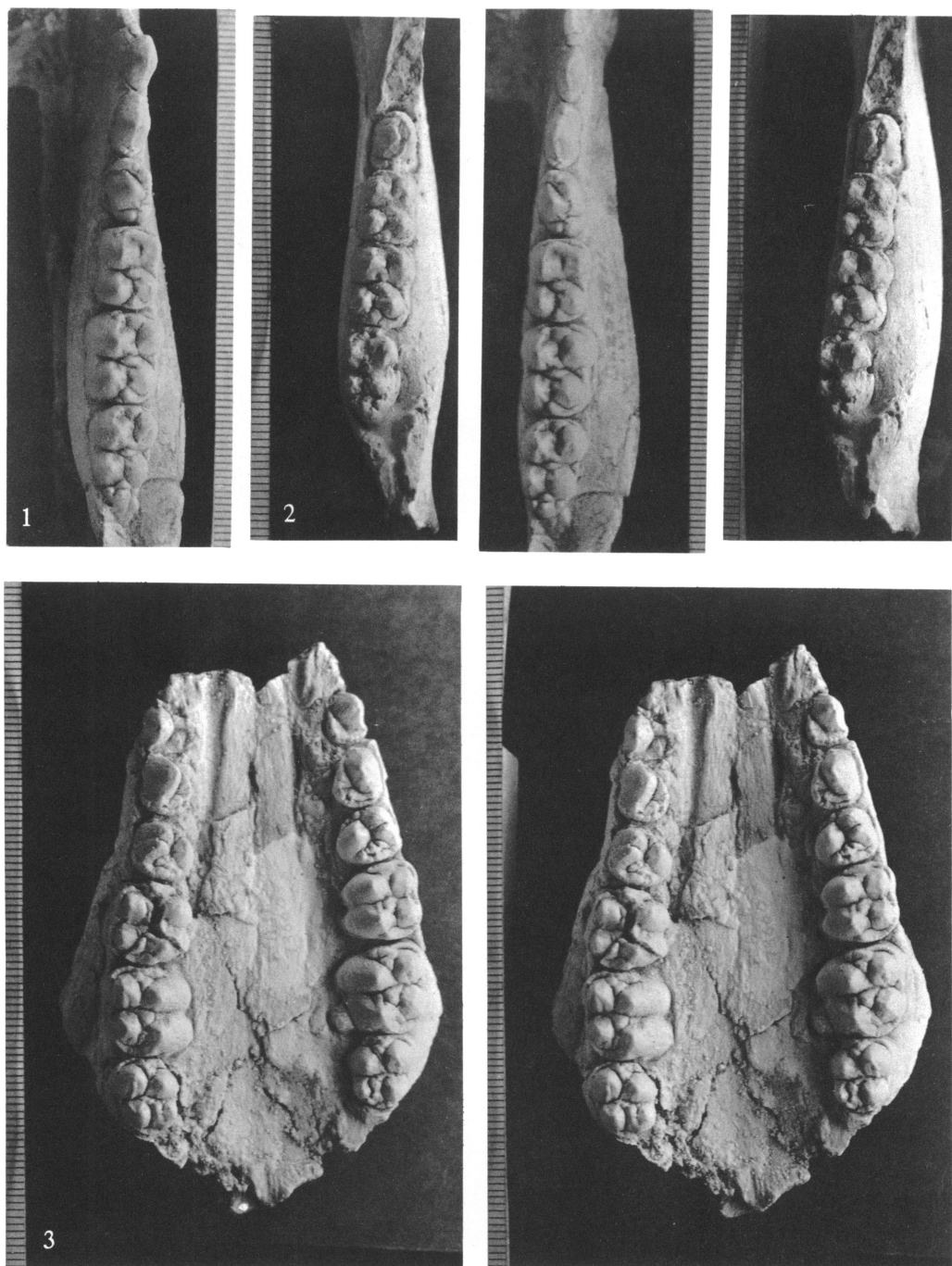


1. *Cynorca sociale*, right  $M_1$ , A.M.C. No. 2894, occlusal view
2. *Cynorca* cf. *sociale*, fragment of left mandible with  $P_4$ - $M_2$ , M.C.Z. No. 17744, occlusal view
- 3-7. *Cynorca sociale*. 3. Left bulla, U.C.M.P. No. 66862, ventral view. 4. Left  $dP_4$ - $M_1$ , A.M.C. No. 2894, occlusal view. 5. Left  $M^2$ , U.T. No. 31084-61, and left  $M^3$ , U.T. No. 31084-111, occlusal view. 6. Right  $M^2$ - $M^3$ , L.A.C.M. No. 31080, occlusal view. 7. Palate with right and left  $P^2$ - $M^3$ , U.C.M.P. No. 66862, occlusal view

All natural size

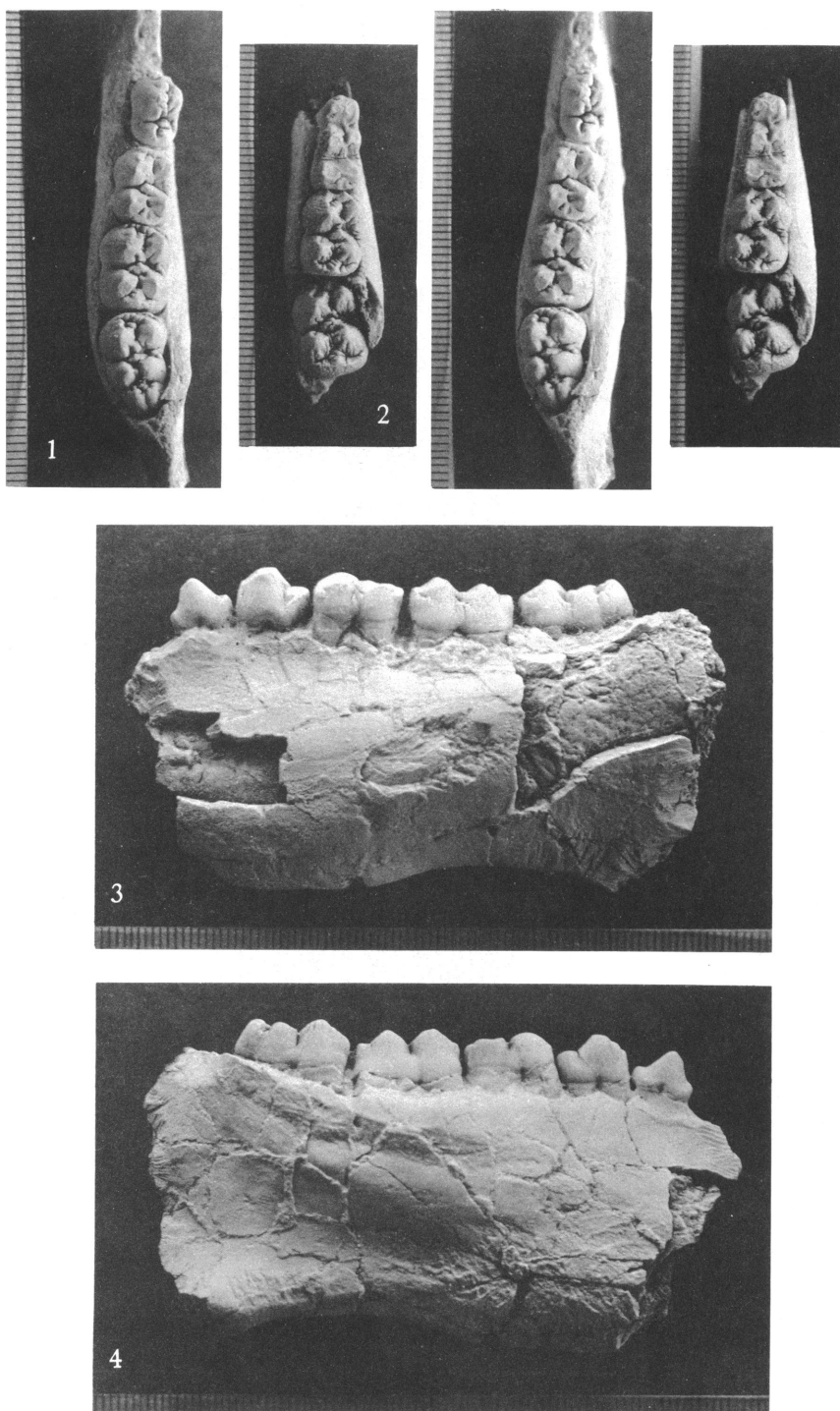


1. *Cynorca sociale*, right mandible with P<sub>3</sub>-M<sub>3</sub>, U.C.M.P. No. 66861, occlusal view
  2. *Cynorca* cf. *C. proterva*, right mandible with dP<sub>3</sub>, dP<sub>4</sub>, M<sub>1</sub>, and M<sub>2</sub>, F:A.M. No. 73663, occlusal view
  3. *Cynorca sociale*, right mandible with P<sub>3</sub>-M<sub>3</sub>, U.C.M.P. No. 66861, labial view
  4. *Cynorca occidentale*, new species, juvenile palate with right dP<sub>3</sub>, dP<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>, and left dP<sub>3</sub>, dP<sub>4</sub>, M<sub>1</sub>, F:A.M. No. 73666, occlusal view
- All natural size



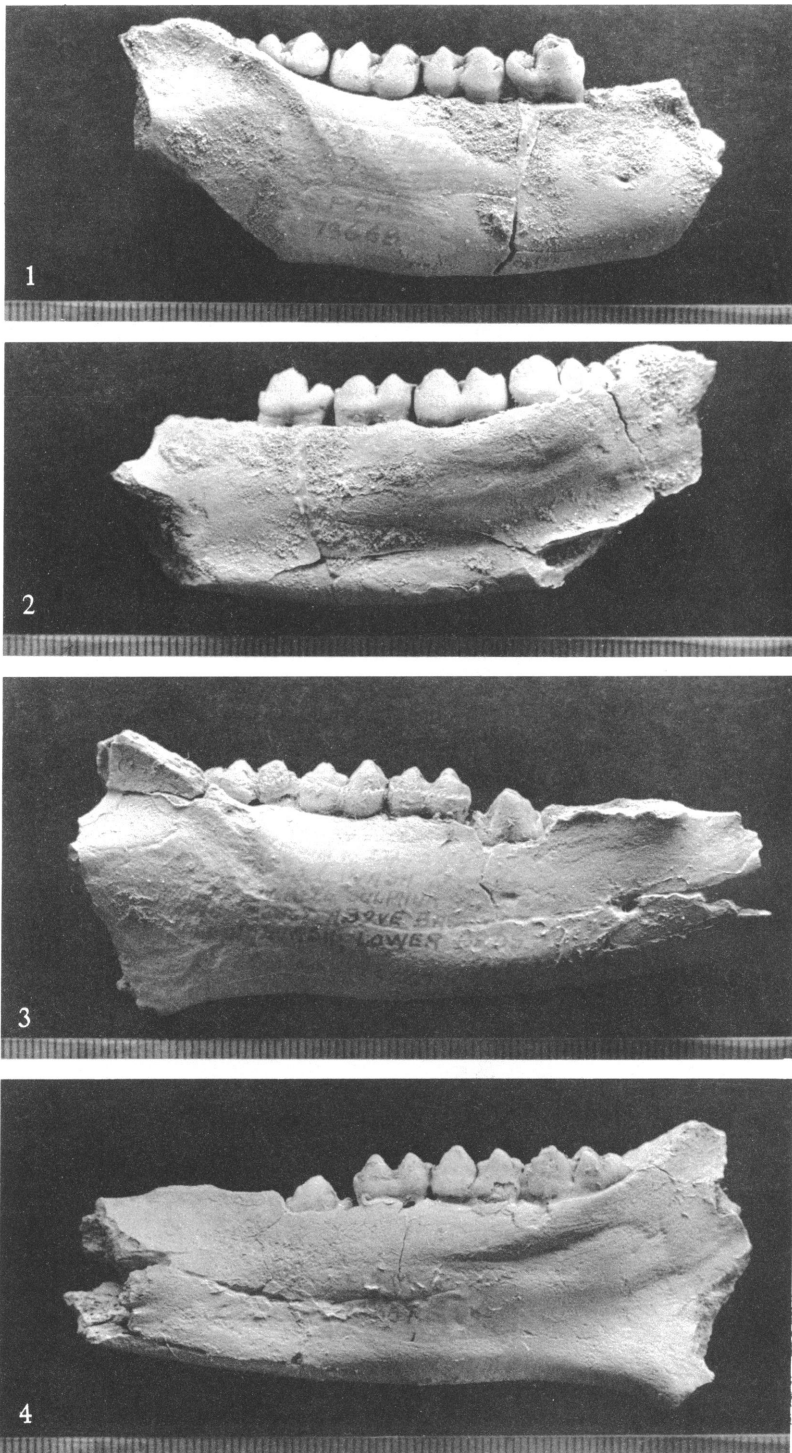
*Cynorca occidentale*, new species. 1. Holotype, right mandible with P<sub>2</sub>-M<sub>3</sub>, F:A.M. No. 73660, occlusal view. 2. Right mandible with P<sub>4</sub>-M<sub>3</sub>, F:A.M. No. 73667, occlusal view. 3. Holotype, palate with right and left P<sup>2</sup>-M<sup>3</sup>, F:A.M. No. 73660, occlusal view  
All natural size



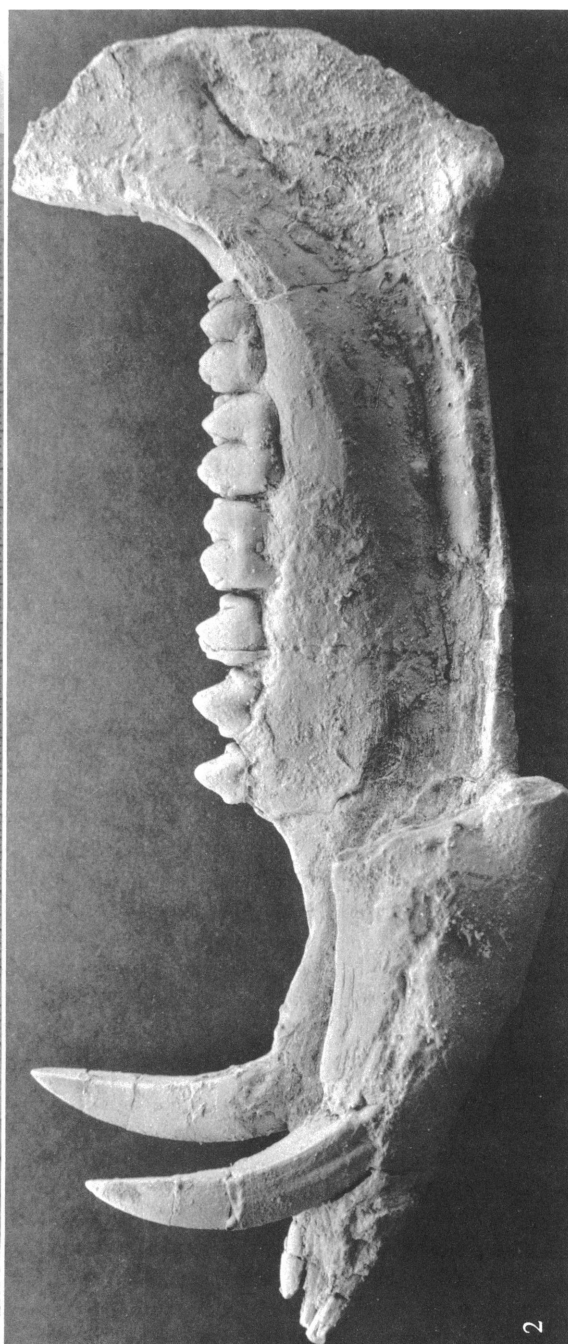
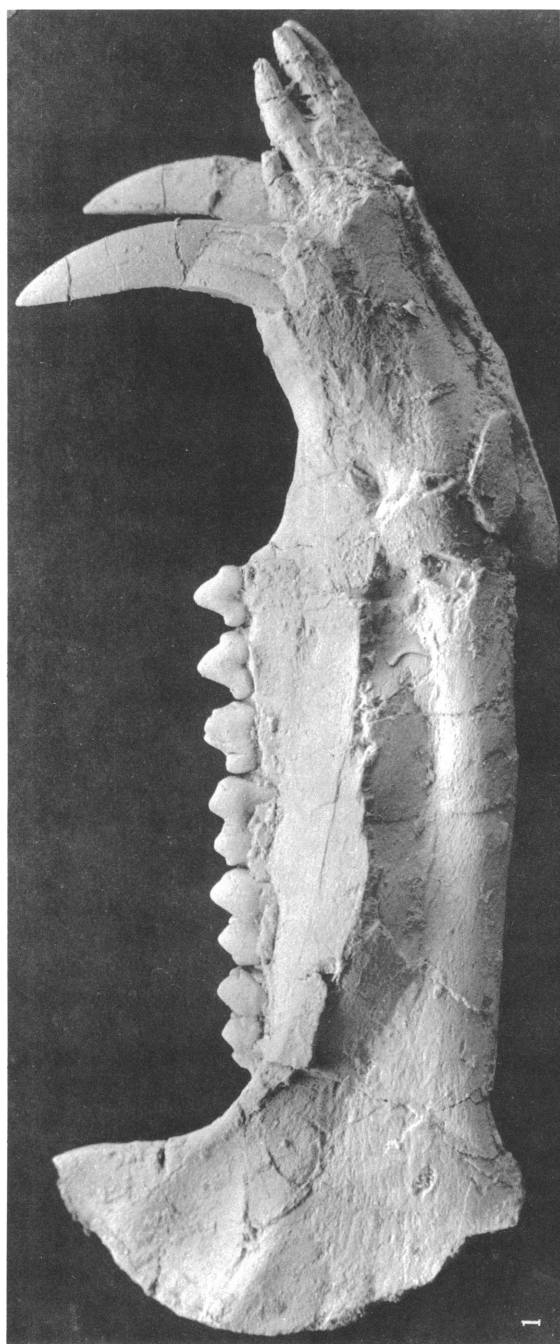


*Cynorca occidentale*, new species. 1. Right mandible with P<sub>4</sub>-M<sub>3</sub>, F:A.M. No. 73668, occlusal view. 2. Right mandible with dP<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>, F:A.M. No. 73665, occlusal view. 3, 4. Left mandible with P<sub>3</sub>-M<sub>3</sub>, U.S.N.M. No. 22927. 3. Labial view. 4. Lingual view.  
All natural size

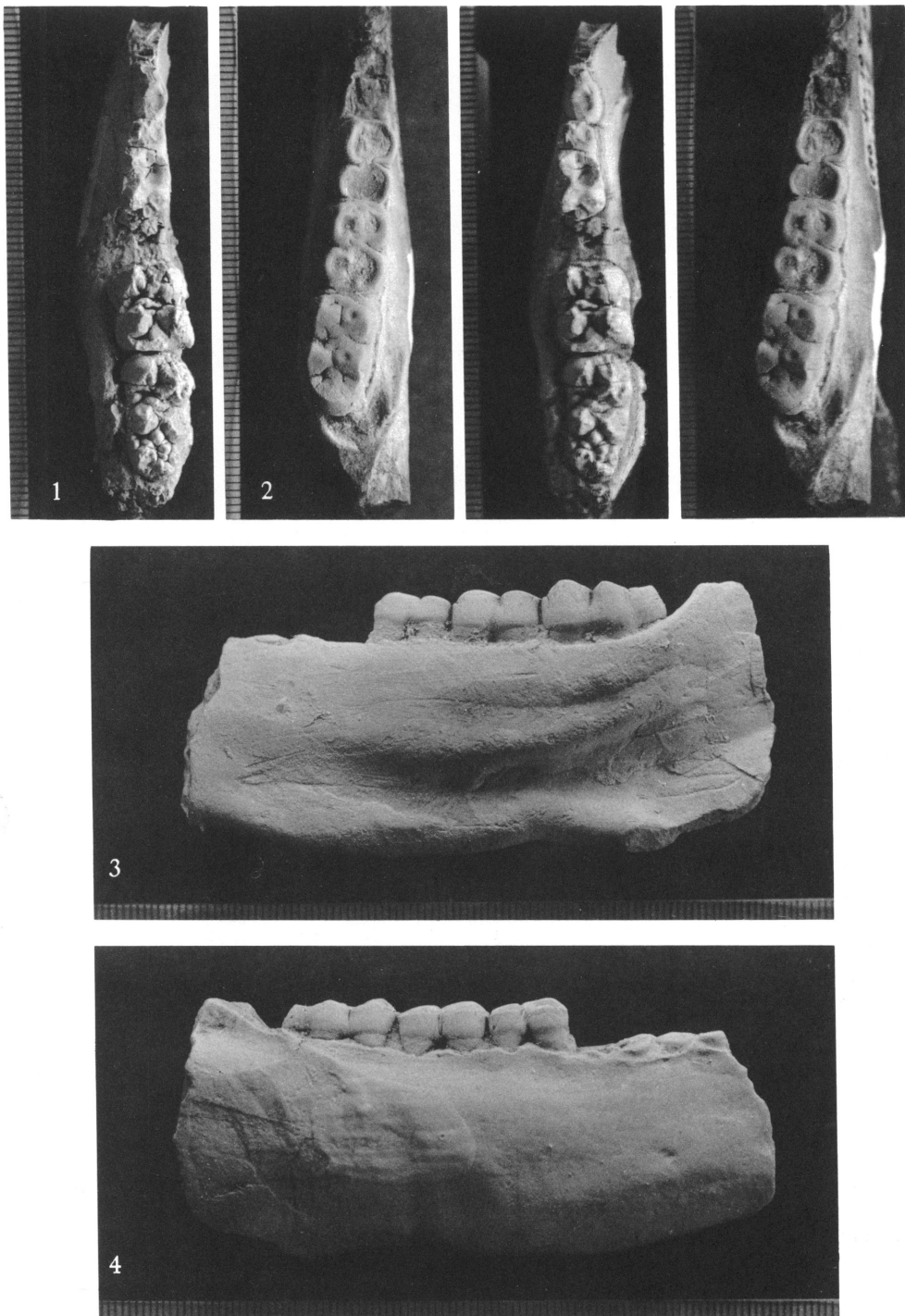




*Cynorca occidentale*, new species, right mandibles with  $P_4$ - $M_3$ . 1, 2. F:A.M. No. 73668. 1. Labial view. 2. Lingual view. 3, 4. F:A.M. No. 73667. 3. Labial view. 4. Lingual view. All natural size



*Cynorca occidentale*, new species, holotype, symphysis and right horizontal ramus with right  $I_{1-3}$ ,  $C_1$ ,  $P_2-M_3$ , and left  $I_1$  and  $C_1$ , F.A.M. No. 73660. 1. Labial view. 2. Lingual view. Both natural size



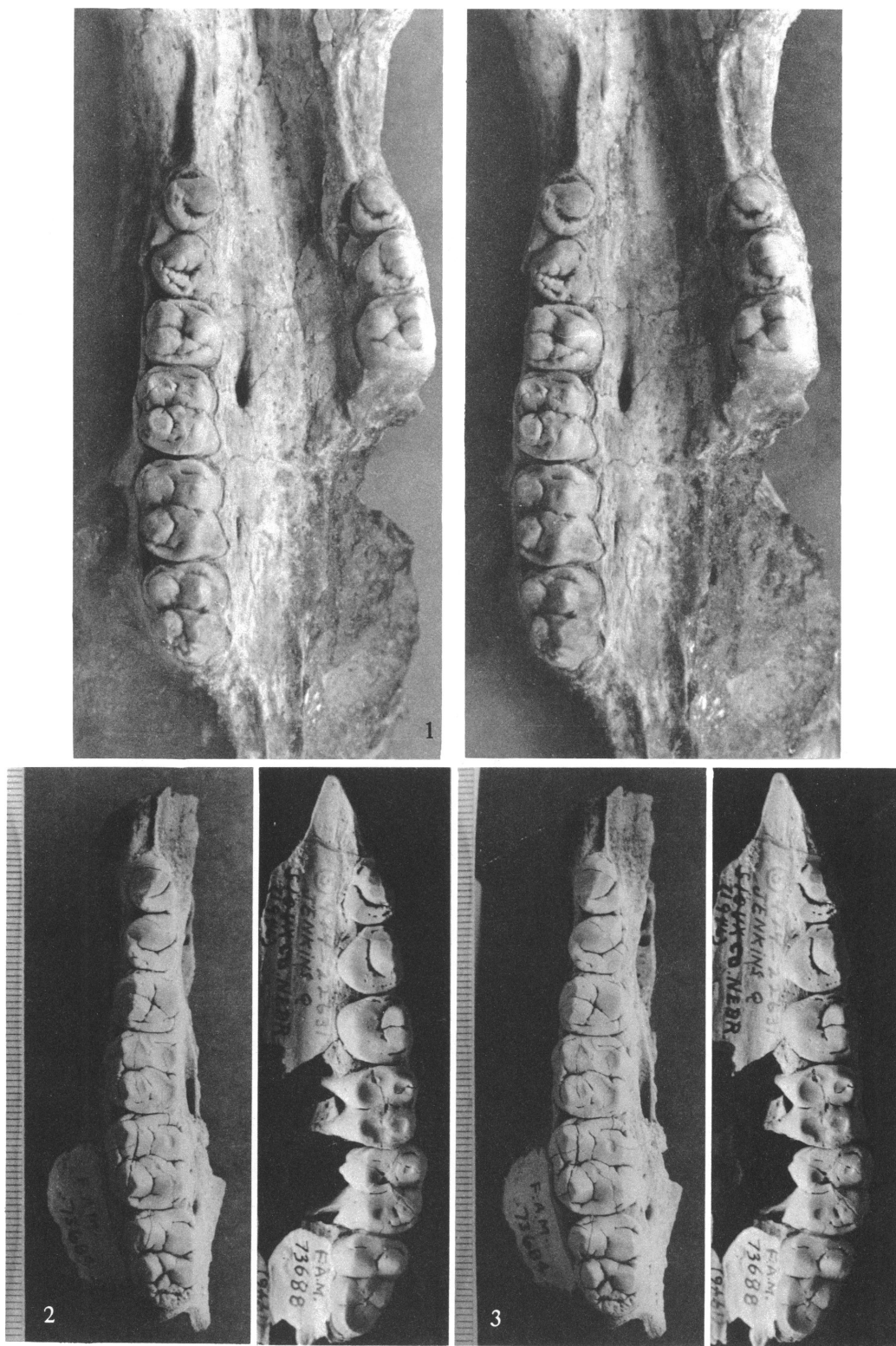
1. *Dyseohyus fricki*, fragment of left juvenile mandible with dP<sub>3</sub>, dP<sub>4</sub>, M<sub>2</sub>, M<sub>3</sub>, F:A.M. No. 73671, occlusal view

2-4. *Dyseohyus* or *Cynorca*, right mandible with M<sub>1</sub>-M<sub>3</sub>, F:A.M. No. 73661. 2. Occlusal view. 3. Lingual view. 4. Labial view

All natural size



*Dysochotys stirtoni*, new species, holotype, cranium, F.A.M. No. 73679. 1. Lateral view. 2. Dorsal view. Both  $\times \frac{3}{4}$

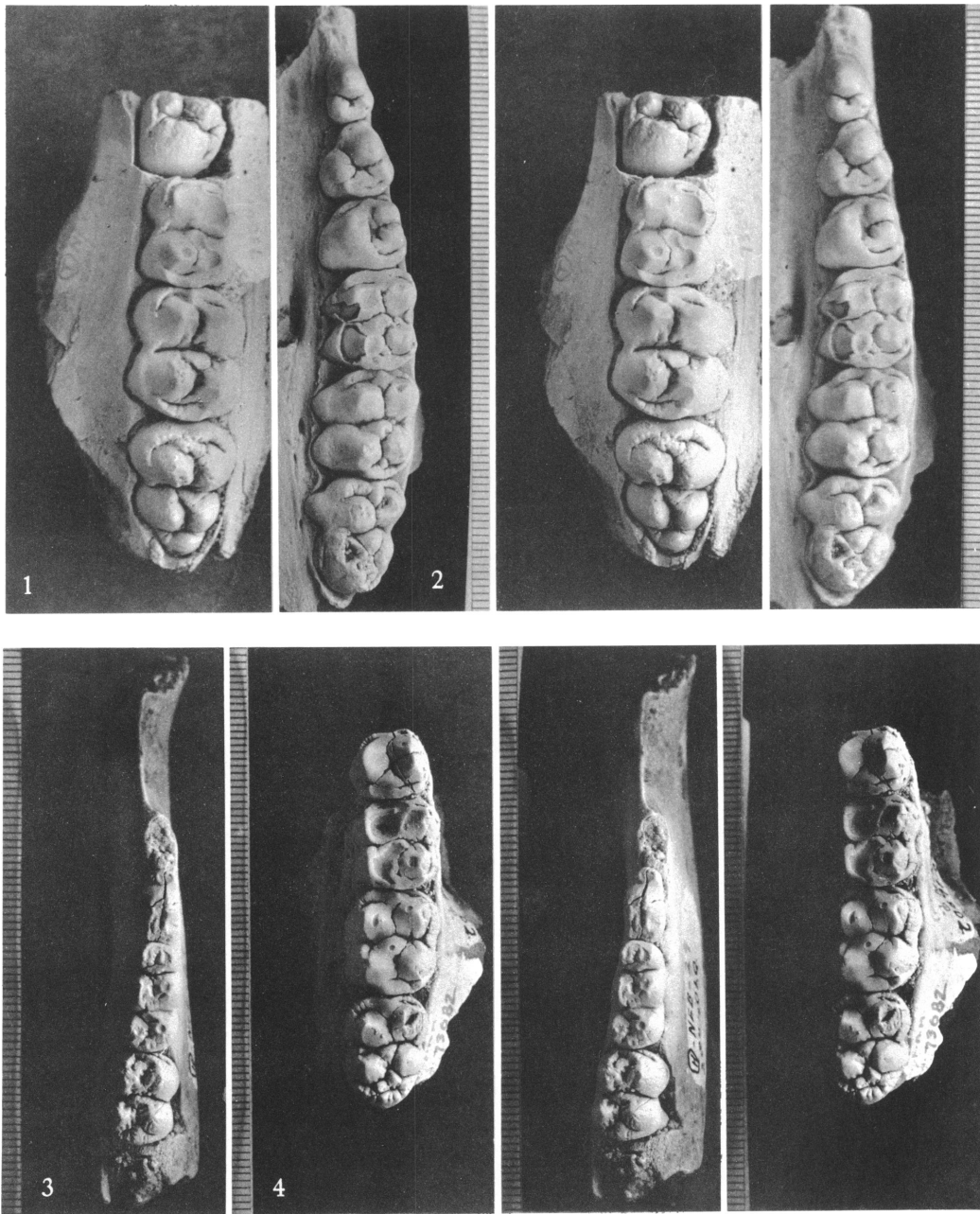


*Dyseohyus stirtoni*, new species. 1. Holotype, cranium with right P<sup>2</sup>-M<sup>3</sup>, left P<sup>2</sup>-P<sup>4</sup>, F:A.M. No. 73679, occlusal view. 2. Right P<sup>2</sup>-M<sup>3</sup>, F:A.M. No. 73684, occlusal view. 3. Left P<sup>2</sup>-M<sup>3</sup>, F:A.M. No. 73688, occlusal view. All natural size





*Dyseohyus shirtoni*, new species. 1. Holotype, right P<sub>2</sub>-M<sub>3</sub>, F.A.M. No. 73679, occlusal view. 2. Holotype, right mandible, F.A.M. No. 73679, lateral view. 3. Right P<sub>2</sub>-M<sub>3</sub>, F.A.M. No. 73679, lateral view. 4. Right P<sub>2</sub>-M<sub>3</sub>, F.A.M. No. 73686, occlusal view. 5. Right P<sub>2</sub>-M<sub>3</sub>, F.A.M. No. 73686, lateral view. All X  $\frac{3}{4}$ .



1, 2. *?Dyseohyus* sp. 1. Right P<sup>4</sup>-M<sup>3</sup>, F:A.M. No. 73681, occlusal view; P<sup>4</sup> rotated clockwise 90 degrees. 2. Left P<sup>2</sup>-M<sup>3</sup>, F:A.M. No. 73678, occlusal view  
 3, 4. *Dyseohyus stirtoni*, new species. 3. Fragment of right juvenile mandible with dP<sub>3</sub>, dP<sub>4</sub>, M<sub>1</sub>, F:A.M. No. 73689, occlusal view. 4. Left P<sup>4</sup>-M<sup>3</sup>, F:A.M. No. 73682, occlusal view  
 All natural size





that in *D. fricki*, although the dorsal surface of the snout is not flat, but sharply convex. Posteriorly, the nasals expand laterally somewhat before coming in contact with the frontals, and the frontonasal suture forms an anteriorly convex arc.

The surface of the maxillary, below its contact with the premaxillary and nasal elements, is predominantly flat and smooth, particularly in the area above and anterior to the infraorbital foramen. Posterior to the canine buttresses, which are more strongly developed in F:A.M. No. 73670 than in the holotype, the surface of the maxillary is slightly convex, as it is in the region anterior to the lacrimal tubercle and anterior to the frontal eminences. The convexity of the maxillary in this area is emphasized by the broad and moderately deep excavation found just below, on the anterior border of the jugal above the tip of the facial crest (text fig. 9). Such a concavity is not developed in any of the primitive peccaries, but is generally similar to that found in some later forms, as discussed further below. The maxillofrontal suture leaves its contact with the nasals 25 mm. anterior to the supraorbital foramen and follows an anteroventrally concave arc to meet the lacrimojugal junction 11 mm. anterior to the lacrimal tuberosity. Thence, the maxillojugal suture leads anteroventrally to the dorsal edge of the excavation for the origin of Mm. depressor rostri and dilator naris lateralis and bends sharply downward, obliquely traversing this concavity, and continues toward the anterior edge of the facial crest. The course of the maxillojugal suture, as it continues under the zygomatic arch and into the pterygopalatine fossa, is obscured.

In the absence of the tip of the snout, the palatal course of the premaxillomaxillary suture is not visible, and the maxillopalatine suture is not determinable. The diastemal crests are relatively sharp, and each bounds a sulcus, best developed in F:A.M. No. 73670, which lies between the canine and P<sup>2</sup>, tapering both anteriorly and posteriorly. The structure, which probably can be designated as the buccinator fossa, is visible from lateral and ventral aspect, although the way in which the fossa definitely lies medial to the lateral surface of the snout is suggestive of

the condition in *Tayassu*. The basic orientation of the fossa seems, then, to be ventral rather than lateral. To summarize, the snout of *D. fricki* is moderately long and lightly built. The site of origin of M. dilator naris lateralis and probably M. depressor rostri lies in an excavation above the facial crest and anterior to the orbits, the infraorbital foramen has a slitlike cross section, does not lie within a pronounced depression, and the basic orientation of the buccinator fossa is ventral. These are features in which *D. fricki* shows a basic resemblance to *Tayassu* and differs from *Dicotyles*. In contrast to both Recent genera, there is no continuation of the facial crest anterior to the zygomatic arch. Unlike *Tayassu*, there is no expanded maxillary sinus in *D. fricki*, and thus there is no corresponding expansion of the area lateral to the diastemal crest.

Posterior to the relatively slitlike infraorbital foramen, the anterior base of the zygomatic arch projects sharply outward so that the anterior tip of the facial crest lies well lateral to the flat, supra-alveolar surface of the maxillary (text figs. 7, 8). Posterior to this the nearly flat sides of the zygomatic arch diverge slightly from a sagittal plane, reminiscent of the primitive genera and similar to *Tayassu*, but not *Dicotyles*. Beneath this the flat ventral surface of the zygomatic arch, which corresponds to the site of origin of the masseteric muscles, is broadest anteriorly, tapers posteriorly, and faces ventrolaterally (text fig. 8). Even in F:A.M. No. 73670, where the dorsoventral flattening of the specimen would only accentuate the ventral orientation of this surface, the site of origin of the masseteric muscles still faces ventrolaterally, as in *Tayassu*. Although F:A.M. No. 73670 represents a more rugose individual than the holotype, the facial crest at the lateral edge of the ventral surface of the zygomatic arch is not strongly developed. There is no suggestion that the condition in *D. fricki* approached that in *Dicotyles*, in which the facial crest is strongly produced ventrally. As far as the cranium is concerned, the orientation of the masseteric muscles of *D. fricki* was probably more like the condition in *Tayassu* than that in *Dicotyles*.

At the anterodorsal edge of the zygomatic arch only a small, triangular segment of the

lacrimal is exposed. The lacrimal tuberosity lies just below the lacrimofrontal suture and just above the lacrimal foramen (text fig. 9). The lacrimojugal suture passes obliquely downward below this before disappearing into the orbit, where its continued pathway is not discernible. The frontolacrimal suture traverses the anteromedial edge of the orbit, extending ventrally to the region of the sphenopalatine and maxillary foramina. The relations of these foramina to each other and to the posterior palatine foramen are not exactly determinable in the available specimens, although there is no evidence that they were not arranged essentially as in the living genera.

The sutures of the alisphenoid, palatine, and pterygoid bones within the pterygopalatine and infratemporal fossae are not determinable; the pterygoids are totally missing. Such indications as may be seen, however, promote the suggestion that the sutural arrangements of the alisphenoid and palatine bones were essentially as in the modern species.

In palatal aspect (text fig. 8), the sutures between the three bones listed above are not visible but, except for the absence of the palatamaxillary suture, noted above, the remaining features of the palate are readily determinable. The palatal surface is smooth and bears only a slightly developed midsagittal ridge between the molar teeth in the holotype. In F:A.M. No. 73670 the ridge is not developed, and in both specimens the palatal surface is slightly convex transversely. The anterior palatine foramina are opposite the anterior edge of  $M^1$  in both specimens, and anterior to this the slightly developed palatine canals continue toward the tip of the snout, reaching at least to the canines. The surface of the palate extends posterior to the cheek teeth to a point midway between the rear of  $M^3$  and the anterior edge of the glenoid fossa. The opening of the choanal fossa is in relatively the same position as in the living genera, although its actual distance from  $M^3$  in *D. fricki* is greater than the distance in *Dicotyles*. In most primitive genera as well as in *C. sociale* and probably *C. occidentale*, the choanal fossa opens out almost immediately behind  $M^3$  in sharp contrast to the condition in *D. fricki*. The palatal

surface between and posterior to  $M^3$  is slightly concave, but not to the extent common in the living genera. The cheek teeth form a smooth, broad, outwardly convex arc, and their over-all size relative to that of the cranium is greater in the holotype than in F:A.M. No. 73670.

Posterior to the choanal fossa, the bullae are only partially preserved but seem to have been somewhat broader and more massive than those of *C. sociale*. In relative length and breadth, the bullae of *D. fricki* are intermediate between the bulla of *C. sociale* and that of *Dicotyles*. The positions of the various foramina around the bullae are about the same as in *C. sociale*. One of the more profound differences between the bullae of *D. fricki* and those of *C. sociale* is their position relative to the glenoid fossae. In *C. sociale* and in the more primitive genera the anterior tip of the bulla actually projects below the level of the glenoid fossa; in all but the earliest forms, the tip of the postglenoid process is at the same level as the ventral surface of the bulla. In *D. fricki* and in the Recent genera, the glenoid fossa has dropped in position so that it is below the level of the bulla, and the degree of vertical separation of these two structures is the same for *D. fricki* as for *Dicotyles* and *Tayassu*. The anterior edge of the glenoid fossa forms only a slightly projecting lip at the squamosojugal suture in *D. fricki*. The configuration here is more pronounced than in the primitive forms, whereas in the living genera this area is developed into a structure that is nearly as pronounced as the postglenoid process. As in all peccaries, the jugal does not enter into the glenoid fossa in *D. fricki*.

The area between the bullae is not well preserved in either of the two available crania, but in F:A.M. No. 73670 a pair of basilar eminences are developed into subconical structures at the basispheno-basisoccipital suture. Posterior to this, the condyles have no particularly distinctive features.

The occiput of *D. fricki* is nearly identical to that of *Dicotyles* and *Tayassu*. Points of difference in *D. fricki* include the more longitudinal rather than nearly transverse orientation of the paroccipital processes and the more oblique orientation of the posttym-

panic process of the squamosal as seen in ventral view. Another divergence from the condition in *Dicotyles* or *Tayassu* is the slightly less sharply developed postzygomatic-lambdoidal crest just dorsolateral to the small, semipyramidal eminence that lies on the exoccipital, dorsolateral to the foramen magnum. This eminence, variably present in the living peccaries, is associated with the insertion of *M. rectus capitis dorsalis minor*. The area of the occiput involved with the insertion of *M. rectus capitis dorsalis major* is as in *Dicotyles* and *Tayassu* except that, as restored in plaster, the lambdoidal crests of the holotype have been represented as being too small. From the size of the cranium the lambdoidal crests of *D. fricki* should have been about the same size as, or slightly larger than, those of *Dicotyles*. Such occipital sutures as can be made out in the holotype of *D. fricki* are similar to those of the living peccaries, with the squamoso-exoccipital suture passing by the lateral base of the paroccipital process and rising, slightly dorsomedially, past the eminence for *M. rectus capitis dorsalis minor*, to meet the parietal near the base of the lambdoidal crest.

As determined from the available material, the occiput of *C. sociale* differs from that of *D. fricki* in the concave nature of the post-tympanic process of the squamosal and the degree of separation of the lateral edge of that process from the adjacent tympanic area of the same bone. The plane of orientation of the paroccipital process is the same in both *C. sociale* and *D. fricki*, but the other features just mentioned indicate that the occiput of *C. sociale* is the more primitive.

The occiput of *D. fricki* is thus substantially of modern aspect in contrast to that of the primitive genera, with the occipital surface forming a nearly flat plane and the continuously developed postzygomatic-lambdoidal crest separating the temporal fossa from the occipital region.

The temporal and parietal regions (text figs. 7, 9) of the cranium of *D. fricki* are like those of peccaries in general, with a single, narrow, sagittal crest forming the postero-medial border of the temporal fossa. Anteriorly, the parietal crests diverge from the sagittal crest, extending to the postorbital

processes. Below and posterior to the parietal crests the outer surface of the cranium is conspicuously bowed outward so that it is considerably more expanded than in *Dicotyles* or *Tayassu*. In the living peccaries, the length of the sagittal crest is actually and relatively much less than in *D. fricki* and, although the parietal crests are still oriented at an angle of about 45 degrees relative to the midline, their position has shifted posteriorly in comparison with that found in the Miocene genus. Without changing the position of adjacent structures, such as the postzygomatic-lambdoidal crest, the backward shift of the parietal crests allows for the flatter subjacent cranial surface in the Recent genera.

As shown in F.A.M. No. 73670, the adult outline of the parietal crests is posteriorly concave, which, with the bulbous configuration of the subjacent cranial surface, is reminiscent of the primitive peccaries. Anterior to the parietal crests, the frontoparietal suture describes a pair of anteriorly concave arcs as it traverses the dorsal surface of the cranium from the midline to the post-orbital processes. In lateral view, the suture continues ventrally to join the squamosal in the shallow, anteroventrally oriented sulcus which lies between the infratemporal crests. From this point the parietosquamosal suture extends almost directly across the temporal fossa to the lambdoidal crest. Just above the suture in the posterior third of the fossa is the parietal foramen. Returning to the infratemporal fossa, the infratemporal crests lead anteroventrally into the fossa essentially as in the living peccaries, with the medial of the two crests bounding the large anterior lacerate-rotundum foramen which is largely obscured by matrix. The optic foramen lies medial and slightly dorsal to the latter. In further resemblance to the living peccaries, and in contrast to the more primitive genera, a lacrimal bulla (Pearson, 1923, p. 69) does not protrude from the anteromedial base of the zygomatic arch. The degree of development of the area referred to as the ethmoidal bulla by Pearson (1923, p. 70) and which forms the dorsal limit for the origin of *M. pterygoideus lateralis* in the pterygopalatine fossa is similar to that in *Dicotyles*. Such a structure is not present in the skulls of the

primitive peccaries. In summary, the cranium of *Dyseohyus fricki* is essentially of modern aspect, with only a few features reminiscent of an earlier level of organization. Cranially, *D. fricki* is more advanced than *C. sociale* and, except for a few details, is already at the level found in the living peccaries.

UPPER DENTITION: The incisors of *D. fricki* are not present in the available material, and the preservation of the canine reveals little more than its general tayassuid shape.

The deciduous premolars in the holotype (text fig. 8) are nearly worn out, and  $dP^2$  is represented only by broken roots. In occlusal outline,  $dP^3$  generally resembles that found in F.A.M. No. 73666, *C. occidentale*, although the tooth in *D. fricki* is relatively somewhat broader and shorter. The occlusal surface of  $dP^4$  is well worn but, except for being larger and somewhat less acuminate anteriorly, resembles that in F.A.M. No. 73666.

$P^1$  is completely absent from the permanent dentition (text fig. 10).  $P^2$  is not completely preserved, but it is composed of a strong main cusp which, in the unbroken state, would be backed by a strong heel. To judge from the configuration of  $P^3$ , the slightly developed anterior cingulum in  $P^2$  probably would have been connected to the talon by means of a lingual cingulum. In  $P^3$ , the strong central cusp is bounded posteriorly by the heel which diminishes in width anteriorly and forms a cingulum that is continuous to the anterior tip of the tooth. In detail, the talon consists of an outer ridge, the posterolingual basal expansion of which accounts for the bulk of the structure, and a short, transversely oriented ridge which lies posterior to the main cusp. The longitudinal crest on the posterior surface of this cusp trends posterolabially between the apex and the base of the tooth. The anterior longi-

tudinal crest essentially follows the midline to the anterior tip of the tooth. In contrast to the general simplicity of  $P^3$ ,  $P^4$  is incipiently molariform. The paracone and metacone are definitely separated, although the line of demarcation does not extend completely to the base on the labial surface. The protocone is prominent. It is traversed by an arcuate ridge that connects to the base of the paracone anteriorly and to the posterior cingulum posteriorly. Below the anterior protoconal crest an anterior cingulum traverses the base of the tooth, and a posterior cingulum is similarly developed behind the metacone and metaconule. The metaconule is well developed and is separated from the protocone by the well-defined postprotoconal groove. In contrast, the protoconule is not distinctly demarcated from the protocone.  $P^4$  has a subcircular, somewhat heart-shaped occlusal outline caused by the midlabial indentation of the base of the tooth and concomitant local absence of the already weak labial cingulum.

The molars present no peculiarities in cusp position or development. The most characteristic features of the molars of *D. fricki* are their relatively short, broad proportions and the expansion of their lingual bases. The latter character may be subject to individual variation, but, in addition to their expanded nature, the lingual bases of the protocone and hypocone narrow conspicuously to form moderately sharp apices, instead of being smoothly convex. The anterior cingula are relatively broad and terminate lingually at a point slightly lingual to a line passing between the tips of the protocone and hypocone. The expanded base of the protocone thus extends much farther lingually than the anterior cingulum, and its anterolingual surface has a strongly oblique orientation in occlusal view. In some specimens of *D.*



FIG. 10. *Dyseohyus fricki*, cheek teeth,  $P^2$ - $M^3$ , holotype, L.A.C.M. (C.I.T.) No. 2039, occlusal view.  $\times 1.5$ .

*stirtoni*, new species (F:A.M. No. 73687), expanded lingual bases of the protocone and hypocone approach the condition in *D. fricki*, but in the former the lingual apices of the cusps are more widely separated from each other and the tooth proportions are more elongate. Most molar features in *D. fricki* seem to represent larger versions of those seen in *Cynorca sociale*, and this similarity even extends to the strong oblique orientation of the anterolingual bases of the molars and the acuminate bases of the protocones and hypocones, as seen in occlusal view.

At first glance the upper molars of *D. fricki* seem to resemble those of *C. occidentale*. Closer scrutiny indicates, however, that the molars of *C. occidentale* are basically small teeth with disproportionately expanded lingual bases. The molars of *D. fricki* are larger and their component parts seem to be in proportion with one another. Furthermore, the details in which the molars of *D. fricki* resemble those of *C. sociale* are not present in *C. occidentale*.

**LOWER DENTITION:** The lower dentition of *D. fricki* is poorly represented. No incisors are available for description, and the state of  $C_1$  resembles that of its upper counterpart. As in species of *Cynorca*  $P_1$  is not present, and  $P_2$ , which is invariably present, is poorly preserved. In F:A.M. No. 73670 the tooth apparently consisted of a small version of  $P_3$  which, to extrapolate from other species of the genus, had a small or incipiently developed anterior basal conulid. In  $P_3$  this conulid is also incipiently developed and, to judge from F:A.M. No. 73670, the main cuspid was probably incipiently bifid. The heel bears two weakly developed longitudinal crests and a transverse posterior ridge. The permanent fourth premolar has only a slightly developed anterior basal conulid, but the longitudinal groove dividing the main cuspid into two halves is relatively trenchant, as seen in the holotype. The talonid is poorly developed, bearing a weak, labial, longitudinal ridge but no lingual longitudinal ridge, and a posterior proliferation of small conulids probably representing a single larger structure. The essentials of this description can be seen in F:A.M. No. 73670 as well, although  $P_4$  and the molar teeth are nearly completely worn in this specimen.

As shown in F:A.M. No. 73671,  $dP_3$  is a simple, elongate tooth with the main cuspid having a nearly central position relative to the anterior and posterior roots (pl. 47, fig. 1). Although wear has obliterated many of the surface features, remnants of a low, anterior, basal conulid can still be seen. Behind the main cuspid the heel is apparently composed of a single broadly based cuspid. The deciduous fourth premolar of *D. fricki* is the usual six-cusped structure. Although its surface is relatively well worn, the closely appressed nature of the anterior pair of cuspids is still visible. Also visible is the markedly asymmetrical occlusal outline of the anterior third of the tooth.

$DP_3$  and  $dP_4$  of *D. stirtoni*, new species, are much more massive (pl. 51, fig. 3) than comparable teeth in *D. fricki*. Moreover,  $dP_3$  in *D. stirtoni*, new species, has an apparently bifid main cuspid and heel composed of two conulids. The occlusal outline of  $dP_4$  in *D. stirtoni*, new species, is more rectangular than in *D. fricki*, and the anterior pair of conulids are not so closely appressed.

The first molar is best represented by F:A.M. No. 73672 but has no particular distinguishing features. A labial cingulum is present opposite the transverse valley. Only a weakly developed postmetaconid crest is present, and the individual cusps are not noticeably swollen or expanded. The basal outline of the tooth is not bilobate because of the labial cingulum and because there is no indentation between the bases of the metaconid and entoconid. As represented by F:A.M. Nos. 73670, 73671 (pl. 47, fig. 1), 73673, and the holotype,  $M_2$  is a larger version of  $M_1$ , being possibly somewhat more heavily cingulate labially. As represented by the holotype, the cusps of  $M_3$  are rather lightly built and sharply crested, probably owing to their early stage of wear and individual bias. In F:A.M. No. 73671 (pl. 47, fig. 1) the cuspids are heavier and the secondary conulids are bulkier. In the holotype,  $M_3$  has no labial cingulum, tapers posteriorly, and bears a hypoconulid consisting essentially of an anteriorly concave arcuate ridge which is raised into a small labial and lingual cuspid.

The lower cheek teeth contrast with those of *C. sociale*, *C. occidentale*, and *C. proterva* in their larger size, the more strongly bifid

main cuspid of  $P_4$ , and the possibly incipiently bifid main cuspid of  $P_3$ . In contrast to that of *C. occidentale*,  $M_2$  of *D. fricki* is not reduced, and there is no tendency toward swelling of the cuspids on the individual teeth. Also, the sharp discrepancy in the widths of the anterior and posterior halves of  $M_1$  and  $M_2$  in some specimens of *C. occidentale* has not been observed in *D. fricki*. Contrasts with *C. proterva* tend to be mainly in terms of size, but the occlusal outlines of the lower molars of the latter are more sharply bilobate owing partly to the absence of a labial cingulum. *Dyseohyus fricki* is more advanced than *C. sociale* in its larger size, in having lost  $P^1$ , and in the more complex nature of the premolar dentition. The proportions of the lower molars in *D. fricki* are similar to those of *C. sociale*.

The mandible of *D. fricki* is best represented in F.A.M. No. 73670, a specimen containing only the symphysis, teeth, and parts of the horizontal rami. The rami are flat internally and moderately convex laterally below the alveolar border of the molars. In dorsal view the rami converge toward the symphysis which is bowed outward around the base of the canine, then probably narrow anteriorly, although the critical area is not completely preserved. The prominent diastemal crests form laterally concave arcs between  $P_2$  and  $C_1$ , and between the crests the broadly sulcate dorsal surface of the symphysis rises gradually and evenly anteriorly. Anterior to the canines this surface broadens in a somewhat spatulate fashion. On the posterior surface of the symphysis the genial spine forms a prominent, but thick

TABLE 11  
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER DENTITION OF *Dyseohyus fricki*

	L.A.C.M. No. 2039, Holotype	F.A.M. No. 73670	F.A.M. No. 73671	F.A.M. No. 73673	F.A.M. No. 73672
$C_1$					
Length	—	12.25	—	—	—
Width	—	10.95	—	—	—
$P_2$					
Length	—	8.40	—	—	—
Width	—	4.00p	—	—	—
$dP_3$					
Length	—	—	8.25	—	—
Width	—	—	4.25p	—	—
$P_3$					
Length	9.40	9.46	—	—	—
Width	5.95p	5.10p	—	—	—
$dP_4$					
Length	—	—	13.15	—	—
Width	—	—	7.00p	—	—
$P_4$					
Length	10.40	9.70	—	—	—
Width	7.60p	6.55p	—	—	—
$M_1$					
Length	—	12.35	—	11.60	12.25
Width	—	9.50p	—	9.35p	9.40p
$M_2$					
Length	13.30	12.90	12.60	13.20	—
Width	11.00a	11.65a	10.90a	10.85a	—
$M_3$					
Length	18.60	—	17.35	—	—
Width	11.45a	10.05a	10.15a	9.75a	—



TABLE 12  
CRANIAL MEASUREMENTS (IN MILLIMETERS) OF *Dyseohyus*

	<i>D. fricki</i>		<i>D. stirtoni</i> , New Species
	L.A.C.M. No. 2039	F:A.M. No. 73670	F:A.M. No. 73679
Length from tip of I <sup>1</sup> to rear of condyles	—	—	226.25×
Length, diastema from C <sup>1</sup> to P <sup>2</sup>	29.50	28.25	28.85
Width between alveoli of P <sup>2</sup>	18.90	23.50	19.70+
Width between alveoli of M <sup>3</sup>	18.50	21.10	19.30
Least width of rostrum	36.00	33.45	38.40
Height from condyles to nuchal crest	73.80×	—	72.70×
Breadth across zygomatic arches	96.40	—	—
Breadth between postorbital processes of frontals	77.90	83.30×	77.50+

rather than narrowly acuminate, process. The presence or absence of genial pits in this area cannot be definitely established. In lateral view the ventral surface of the symphysis is smoothly convex rather than having a shallow, but conspicuous, concavity below the incisor roots as in *C. sociale*. Because of the manner of preservation, the nature of the angle, coronoid process, and the pterygoid and digastric fossae cannot be evaluated in F:A.M. No. 73670. In F:A.M. No. 73673 the configuration of the digastric fossa below M<sub>2</sub> and M<sub>3</sub> seems to have been like the condition in *C. sociale*, *C. occidentale*, and *C. proterva*.

The mandible of *D. fricki* is more robust than that of *C. sociale*, *C. proterva*, or of *C. occidentale*, and the diastemal crests (not known in *C. proterva*) are thicker and heavier. As far as is currently known, a genial spine is developed only in *D. fricki*. The difference in the profile of the ventral symphyseal surface between this species and *C. sociale* is pointed out above. To judge from the crushed and somewhat distorted holotype mandible of *C. occidentale*, the configuration of this surface may have resembled that of *D. fricki*.

DISCUSSION: The biochronological range of *Dyseohyus fricki* is early to late Barstovian. Geographically, this species seems restricted to western North America. As indicated above, the cranium of *D. fricki* is larger than that of *C. sociale* and presumably the crania of *C. proterva* and *C. occidentale*. Other cranial comparisons can be made chiefly with *C. sociale* and *D. stirtoni*, new

species. The cranium of *D. fricki* is advanced over that of species of *Cynorca* in the more posterior position of the anterior palatine foramina, the posterior prolongation of the palatal surface, the lower position of the glenoid fossa, the flatter posttympanic process of the squamosal, and the well-fused contact of the lateral edge of that process with the adjacent tympanic process of the same bone. The dentition of *D. fricki* differs from that of species of *Cynorca* in its larger size, the acuminate lingual bases of the molar protocones and hypocones (except *C. sociale*), and the more strongly bifid main cuspid of P<sub>4</sub>. The mandible of *D. fricki* differs from that of contemporary species of *Cynorca* in size and robustness and from that of *C. sociale* in the smooth profile of the ventral symphyseal surface.

As discussed below, *D. fricki* is more primitive than *D. stirtoni*, new species. The molar proportions of *D. fricki* are essentially those of *Cynorca sociale*, so that, although certain dental and cranial features indicate that *D. fricki* is more advanced, its ultimate ancestry seems to lie with *C. sociale*.

***Dyseohyus stirtoni*,<sup>1</sup> new species**

Plates 48–50; plate 51, figures 3, 4;  
tables 12–15

TYPE: F:A.M. No. 73679, nearly complete skull and mandible and partial skeleton.

DISTRIBUTION: Early late Miocene (early Barstovian), Observation Quarry, NW.  $\frac{1}{4}$ ,

<sup>1</sup> Named in honor of the late R. A. Stirton in recognition of his contributions to the study of fossil peccaries.

TABLE 13  
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER JAW OF *Dyseohyus*

	<i>D. fricki</i> F:A.M. No. 73670	<i>D. stirtoni</i> , New Species F:A.M. No. 73679	F:A.M. No. 73686	F:A.M. No. 73683
Length from I <sub>1</sub> to condyles	—	183.50	—	—
Length of diastema between C <sub>1</sub> and P <sub>2</sub>	35.35	31.95	—	—
Depth from tip coronoid process to angle of mandible	—	74.90	—	—
Depth below P <sub>2</sub>	32.50	28.40	32.40	26.40
Depth below rear of M <sub>1</sub>	—	32.60	34.15	30.90
Width between alveoli of P <sub>2</sub>	23.95	22.45	—	—
Width between alveoli of M <sub>3</sub>	31.80	28.65	—	—
Width between condyles	—	55.95	—	—

NW.  $\frac{1}{4}$ , SE.  $\frac{1}{4}$ , sect. 4, T. 31 N., R. 47 W., Dawes County Nebraska (F:A.M. Nos. 73695, 73689, 73690, 73691–73693); late Miocene (Barstovian), Survey Quarry, NW.  $\frac{1}{4}$ , NE.  $\frac{1}{4}$ , sect. 24, T. 31 N., R. 47 W., Dawes County, Nebraska (F:A.M. No. 73694); late Miocene (Barstovian), Jenkins Quarry, Lower Snake Creek channels, Sinclair Draw, SW.  $\frac{1}{4}$ , sect. 3, T. 25 N., R. 55 W., Sioux County, Nebraska (F:A.M. Nos. 73682–73685, 73688); late Miocene (Barstovian), Echo Quarry, Lower Snake Creek channels, Antelope Draw, SE.  $\frac{1}{4}$ , sect. 33, and SW.  $\frac{1}{4}$ , sect. 34, T. 25 N., R. 55 W., Sioux County, Nebraska (F:A.M. No. 73686); late Miocene (Barstovian), *Prosynthetoceras* Quarry, Lower Snake Creek channels, Ranch House Draw, NW.  $\frac{1}{4}$ , sect. 3, T. 25 N., R. 55 W., Sioux County, Nebraska (F:A.M. No. 73687). Late Miocene (Barstovian), 2 miles northwest of Mastodon Quarry, SE.  $\frac{1}{4}$ , SW.  $\frac{1}{4}$ , sect. 23, T. 10 N., R. 60 W., 8 miles east and 4 miles south of Grover, Weld County, Colorado (F:A.M. No. 73679). Late Miocene (Barstovian), Trinity Pit 1, Fleming Formation, 7 miles northeast of Coldspring, San Jacinto County, Texas (F:A.M. Nos. 73674, 73675, 73677).

**HYPODIGM:** Type, and F:A.M. No. 73690, rostrum, including right canine; F:A.M. No. 73682, LP<sup>4</sup>–M<sup>3</sup>; F:A.M. No. 73684, RP<sup>2</sup>–M<sup>3</sup>; F:A.M. No. 73688, palate with RP<sup>4</sup>–M<sup>3</sup>, LP<sup>2</sup>–M<sup>3</sup>; F:A.M. No. 73693, LP<sup>4</sup>; F:A.M. No. 73691, LM<sup>1</sup> and LP<sup>4</sup>; F:A.M. No. 73687, RM<sup>2</sup>; F:A.M. No. 73686, right mandible,

lacking symphysis, with P<sub>2</sub>–M<sub>3</sub>; F:A.M. No. 73683, left horizontal ramus with P<sub>2</sub>–M<sub>3</sub>; F:A.M. No. 73685, symphysis and left ramus with right and left I<sub>1</sub>, C<sub>1</sub>, and LdP<sub>2</sub>, P<sub>2</sub>–M<sub>2</sub>; F:A.M. No. 73689, fragment of right mandible with dP<sub>3</sub>, dP<sub>4</sub>, M<sub>1</sub>; F:A.M. No. 73695, fragment of left mandible with P<sub>2</sub>–M<sub>3</sub>; F:A.M. No. 73694, fragment of right mandible with P<sub>2</sub>–P<sub>3</sub>; F:A.M. No. 73677, fragment of right mandible with M<sub>2</sub>–M<sub>3</sub>; F:A.M. No. 73674, symphysis with right and left I<sub>1–2</sub>, LC<sub>1</sub>; F:A.M. No. 73675, RP<sub>4</sub>; F:A.M. No. 73692, LM<sub>1</sub>.

**DIAGNOSIS:** Differing from *D. fricki* in the following ways: dorsal surface of nasals transversely convex; posterior palatine foramina opposite anterior half or posterior half of M<sup>1</sup>; palate extending posteriorly nearly to level of glenoid fossa, parametacone of P<sup>4</sup> relatively well separated; molars relatively elongate and narrow, M<sup>3</sup> elongate; dP<sub>3</sub> and dP<sub>4</sub> larger than in *D. fricki*; dP<sub>4</sub> regularly rectangular; P<sub>4</sub> large, relatively robust; lower molars relatively elongate; no genial spine on posterior surface of symphysis; ventral surface of symphysis concave below canines.

**DESCRIPTION:** The holotype cranium has a slightly skewed cross section owing to post-mortem crushing, so most areas are somewhat distorted (pl. 48). Missing portions of the cranium include the left zygomatic and temporal regions, both otic areas, except for the right external auditory structure, and the left half of the palate behind P<sup>4</sup>. The

lambdoidal crests and most of the occipital surface have also been lost. Except for a few cracks, the mandibles are in perfect condition. The following description is based largely on the holotype, with statements as to variation being drawn from other specimens as noted. The specimens are oriented as outlined for *D. fricki*.

The holotype of *D. stirtoni* has an adult dentition with all teeth showing at least some wear. In addition, cranial sutures are largely obliterated. The general proportions and features of the cranium of *D. stirtoni* seem to be essentially like those described for *D. fricki*. The narial aperture, not preserved in the Barstow species, has a high, subovate cross section in *D. stirtoni* and is narrower dorsally than ventrally. In lateral view (pl. 48, fig. 1), the profile of the aperture is recumbent in F:A.M. No. 73679 and sweeps upward to the small narial notch. In the midline, the nasals project 5.25 mm. anterior to the notch.

Posterior to the tip of the snout the flange-like canine buttresses are strongly developed in the holotype, but are less prominent in F:A.M. No. 73690. Although these structures are weak in the holotype of *D. fricki*, the referred skull of that species, F:A.M. No. 73670, approaches the condition seen in *D. stirtoni*.

Above the canine buttresses the dorsal surface of the nasals is high and relatively narrow (pl. 48). The condition seen in the partial rostrum, F:A.M. No. 73690, is less distorted than in the holotype of *D. stirtoni*. If this specimen is representative of the species, then *D. stirtoni* differs from *D. fricki* in having a high and relatively narrow nasal surface.

The morphology of the upper surface of the cranium of *D. stirtoni* differs little from that of *D. fricki*, although the concave profile seen anterior to the frontonasal suture in *D. fricki* may prove to be absent from *D. stirtoni* when less distorted material becomes available. The supraorbital foramina and canals of *D. stirtoni* have the same configuration as in *D. fricki*, and it is probable that the degree of convexity of the dorsal surface of the cranium in *D. stirtoni* was originally similar to that in *D. fricki*. Frontal eminences and depressions are similar in the two species.

Cranial sutures visible on the dorsum of the cranium of *D. stirtoni* are those between the frontal and nasal bones, the adjacent frontomaxillary suture, and the premaxillonasal, maxillonasal, and premaxillomaxillary sutures. All these have the same basic configuration as in *D. fricki*. The frontolacrimal suture in *D. stirtoni* is not visible, and the frontoparietal suture is fused.

In lateral view the cranium of *D. stirtoni* is like that of *D. fricki*. This similarity extends to such features as the position of the anterior base of the zygomatic arch relative to  $M^2$ , the relative depth of the maxillary portion of the arch below the orbit, the flat, unexcavated nature of the lateral surface of this structure, the orientation and shape of the ventral surface of the zygomatic arch, the position of the fossa for the origin of *Mm. dilator naris lateralis* and depressor rostri, and the profile of the diastemal crest. In the holotype (pl. 48, fig. 1) the infraorbital foramen lies above the anterior end of  $P^4$  and the adjacent part of  $P^3$ , but in other specimens (F:A.M. Nos. 73682 and 73684) it lies wholly above  $P^4$ . Essentially this position is that found in *D. fricki*.

Features of the orbit, temporal, and infratemporal fossae in *D. stirtoni* are obscured by matrix and crushing, so that comparisons with *D. fricki* cannot be made.

In ventral view, the tip of the snout of *D. stirtoni* is narrow and elongate anterior to the canines. All three incisors are present, the alignment of the two rows forming a rather tight chevron. Between them, the two narrow and elongate incisive foramina, which measure 7.85 mm. by 2.90 mm. in F:A.M. No. 73690, lie internal to  $I^2$  and are separated from each other by a distance of 1.85 mm. Posterior to this the palatal surface is smooth and flat, with the anterior palatine grooves fading out medial to the notches for the reception of the lower canines. The anterior palatine foramina lie opposite the anterior half of  $M^1$  in the holotype (pl. 49, fig. 1). Although the fragmentary nature of the specimen hinders a definite statement, these foramina appear to lie opposite the rear half of  $M^1$  in F:A.M. No. 73688. The position of the anterior palatine foramina in *D. stirtoni* is therefore somewhat posterior to that found in *D. fricki*. In *D. stirtoni*, the diastemal

crests are nearly straight and sharp, and lie medial to well-defined buccinator fossae. Although the nature of the corresponding material in *D. fricki* does not permit a definite conclusion, it is possible that these structures are better developed in *D. stirtoni*.

Even though the preservation of the palate posterior to the molars in *D. stirtoni* is not so complete as one could wish, it is clear that the opening of the choanal fossa lies essentially opposite the glenoid fossa. Such a position is definitely more posterior than that found in *D. fricki*. Unfortunately, the crushed nature of the specimen prevents a judgment as to whether the glenoid fossa in *D. stirtoni* was as low relative to the tooth row and auditory bullae as in *D. fricki*. The bullae and associated areas of the cranium are not preserved in *D. stirtoni*. The glenoid fossa and occipital condyles apparently have the same configuration as in *D. fricki*. As seen in ventral and posterior views, the degree of fusion of the posttympanic process of the squamosal with the tympanic process of the same bone in *D. stirtoni* is similar to that in *D. fricki*, and it probably would be safe to suggest that the straight, linear tympanic process which ascends to the external auditory meatus in *D. stirtoni* will prove to be similar to that in *D. fricki* when pertinent material becomes available.

In summary, the cranium of *D. stirtoni* is the same size as that of *D. fricki* and resembles it in most features. The most notable differences in *D. stirtoni* seem to be the probable absence of a concavity of the dorsal surface anterior to the frontals, the narrower, more transversely arcuate dorsal surface of the nasals, the possibly greater development of the buccinator fossae and adjacent diastemal crests, the more posterior position of the anterior palatine foramina, and the greater posterior extension of the palate and associated aperture of the choanal fossa.

**UPPER DENTITION:** As mentioned above, all three upper incisors are present in *D. stirtoni*. These diminish in size from  $I^1$  to  $I^3$ ,  $I^1$  being more than twice the size of  $I^2$ . Both  $I^1$  and  $I^2$  have elongate, irregular, occlusal outlines, but  $I^3$  is caniniform.  $I^1$  and  $I^2$  project anteroventrally, but  $I^3$  extends vertically and is slightly recurved (pl. 48, fig. 1). In occlusal pattern,  $I^1$  was probably of the general tayassuid configuration, but the

tooth in the holotype, the only available specimen, is well worn. The second incisor apparently consists of an anteriorly situated cusp with a broad, low, posterior base. Whether or not a crest was present behind the main cusp is not determinable.  $I^2$  and  $I^3$  are less bladelike than in *C. sociale* and have a more prominent heel structure than in the primitive genera. All incisors in *D. stirtoni* are lower-crowned than in individuals of *Perchoerus* and *Thinohyus*.

The canine of *D. stirtoni* is laterally compressed and, in contrast to the primitive genera, bears no distinct markings of any sort on its labial and lingual surfaces. This situation is similar to that in *D. fricki*.

As regards the premolars,  $P^1$  is absent,  $P^2$  and  $P^3$  are non-molariform, and  $P^4$  is almost molariform (pl. 49; pl. 51, fig. 4). The second premolar is smaller than the third and consists of a prominent, anteriorly situated main cusp and a variably developed heel. As shown in the holotype, the latter consists of a thick posterior cingulum which thins as it extends around to the anterolingual base of the tooth. In the holotype the cingulum of the right  $P^2$  projects strongly posterolingually, giving the tooth a triangular occlusal outline, but in the left  $P^2$  this outline is nearly circular. The premolars of *D. stirtoni* also show a rather wide range of individual variation of the fundamental plan just described. In specimens such as F:A.M. No. 73684 (pl. 49, fig. 2) the basal outline of the main cusp is more elongate and the heel is a simple, thick, slightly arcuate structure occupying the posterior and posterolingual parts of the tooth. In this specimen, unlike the holotype, the narrow anterior cingulum does not extend across the lingual base of the main cusp. In F:A.M. No. 73688,  $P^2$  is essentially like that of F:A.M. No. 73684 except that the anterior cingulum is heavier and the heel, which is also heavier, is composed of a pair of transverse crests in its labial half (pl. 49, fig. 3).

The third premolar is essentially like  $P^2$ , but differs in being larger and broader. The kind of variation seen when one  $P^3$  is compared with another is like that described for  $P^2$ . In the holotype,  $P^3$  presents its most radical departure from the general plan; the main cusp is incipiently bifid, and definite protoconal and hypoconal areas have been

TABLE 14

MEASUREMENTS (IN MILLIMETERS) OF THE UPPER DENTITION OF *Dyseohyus stirtoni*, New Species

	F:A.M. No. 73679	F:A.M. No. 73690	F:A.M. No. 73682	F:A.M. No. 73684	F:A.M. No. 73688	F:A.M. No. 73693	F:A.M. No. 73691	F:A.M. No. 73687
I <sup>1</sup>								
Length	11.05	—	—	—	—	—	—	—
Width	6.00	—	—	—	—	—	—	—
I <sup>2</sup>								
Length	5.80	—	—	—	—	—	—	—
Width	3.65	—	—	—	—	—	—	—
I <sup>3</sup>								
Length	3.95	—	—	—	—	—	—	—
Width	3.20	—	—	—	—	—	—	—
C <sup>1</sup>								
Length	13.15	10.70	—	—	—	—	—	—
Width	7.75	7.30	—	—	—	—	—	—
P <sup>2</sup>								
Length	8.70+	—	—	9.60	10.00	—	—	—
Width	8.05p	—	—	7.55p	8.00p	—	—	—
P <sup>3</sup>								
Length	10.05	—	—	10.35	10.50	—	—	—
Width	10.30	—	—	8.85p	9.90p	—	—	—
P <sup>4</sup>								
Length	10.40	—	9.45	9.80	10.70	10.00	—	—
Width	11.55a	—	11.05e	11.15e	11.20a	10.60a	—	—
M <sup>1</sup>								
Length	12.90	—	12.45	12.75	12.65	—	12.65	—
Width	11.60p	—	12.30a	12.40a	11.65p	—	11.20a	—
M <sup>2</sup>								
Length	15.25	—	14.20	14.80	14.00	—	—	12.90
Width	12.45a	—	13.55a	13.60a	12.65a	—	—	12.45
M <sup>3</sup>								
Length	14.60	—	15.05	15.40	16.50	—	—	—
Width	12.20a	—	11.70a	12.05a	11.50a	—	—	—
Length, P <sup>2</sup> -M <sup>3</sup>	70.75	—	—	69.70	72.05	—	—	—
Length, I <sup>1</sup> -M <sup>3</sup>	147.40	—	—	—	—	—	—	—

differentiated in the heel structure. In addition, the occlusal outline of this tooth is almost circular as compared with the more definitely triangular appearance of the other specimens.

In P<sup>4</sup> the degree of molarization has increased to the extent that the paracone and metacone are distinct cusps, closely appressed in most specimens, but more strongly separated in the holotype. A discrete protocone is present, and posterolabial to this is a recognizable metaconule. Except for F:A.M. No. 73693, the postprotoconal groove in *D. stirtoni* is not so trenchant as in the holotype

of *D. fricki*, or in *Cynorca occidentale* and *C. hesperia*. A protoconule is not developed to the same extent as the metaconule, but a short arm extends from the protocone to the anterior cingulum and adjacent antero-lingual base of the paracone. Anterior and posterior cingula are present. These end abruptly along the sides of the protocone, and do not extend as far as the level of its lingual tip. Labial and lingual cingula are absent.

The molars of *D. stirtoni* (pl. 49) are much like those in *D. fricki*, but with the following differences: the proportions of the teeth are

TABLE 15  
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER DENTITION OF *Dryoschys stirtoni*, New Species

	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.	F.A.M. No.
	73679	73674	73685	73689	73683	73686	73694	73695	73677	73675	73691	73692
I <sub>1</sub>	Length	5.50	4.70	5.20	—	—	—	—	—	—	—	—
	Width	4.30	3.95	5.05	—	—	—	—	—	—	—	—
I <sub>2</sub>	Length	5.20	4.65	—	—	—	—	—	—	—	—	—
	Width	5.00	3.85	—	—	—	—	—	—	—	—	—
I <sub>3</sub>	Length	4.55	—	—	—	—	—	—	—	—	—	—
	Width	2.65	—	—	—	—	—	—	—	—	—	—
C <sub>1</sub>	Length	10.65	9.30	—	—	—	—	—	—	—	—	—
	Width	8.85	8.60	—	—	—	—	—	—	—	—	—
dP <sub>2</sub>	Length	—	—	6.55	—	—	—	—	—	—	—	—
	Width	—	—	3.20a	—	—	—	—	—	—	—	—
dP <sub>3</sub>	Length	—	—	—	9.90	—	—	—	—	—	—	—
	Width	—	—	—	5.55e	—	—	—	—	—	—	—
dP <sub>4</sub>	Length	—	—	—	14.30	—	—	—	—	—	—	—
	Width	—	—	—	7.60p	—	—	—	—	—	—	—
P <sub>2</sub>	Length	9.65	—	7.80	—	8.10	9.55	8.90	—	—	—	—
	Width	4.90p	—	3.90a	—	—	5.80p	4.70p	—	—	—	—
P <sub>3</sub>	Length	10.80	—	9.30	—	10.65	11.00	8.95	—	—	—	—
	Width	6.10p	—	5.40p	—	6.05p	7.25p	5.80	—	—	—	—
P <sub>4</sub>	Length	11.30	—	11.15	—	12.40	11.95	—	—	11.10	11.00	—
	Width	7.75a	—	7.80a	—	8.30p	8.75p	—	—	—	7.30a	—
M <sub>1</sub>	Length	12.90	—	12.55	12.45	12.75	13.30	—	—	—	—	12.05
	Width	10.65p	—	9.30a	10.25a	10.70a	10.60a	—	—	—	—	8.90p
M <sub>2</sub>	Length	14.65	—	14.00	—	14.60	15.15	—	—	—	—	—
	Width	11.85p	—	—	—	12.80a	13.00a	—	14.05	15.00	—	—
M <sub>3</sub>	Length	19.10	—	—	—	19.20	20.40	—	12.30a	11.95	—	—
	Width	10.90a	—	—	—	12.00a	12.55a	—	19.05	17.95	—	—
Length, P <sub>2</sub> -M <sub>3</sub>	—	—	—	—	77.70	80.95	—	—	10.95a	11.45a	—	—

more elongate in *D. stirtoni*, the bases of the protocone and hypocone are not expanded lingually, and  $M^3$  is not reduced in length. In F:A.M. No. 73688,  $M^3$  of *D. stirtoni* is considerably elongated. In other specimens, as in the holotype,  $M^3$  is narrower than, but about the same length as,  $M^2$ . In *D. stirtoni* the anterior cingula of the molars reach farther lingually than in *D. fricki*.

*Dyseohyus stirtoni* differs from *D. fricki* in having more robust premolars, a larger metacone and differently arranged cingula on  $P^4$ , more elongate upper molars, and upper molars without expanded lingual bases and with anterior cingula which extend farther lingually. The rather wide range of variation seen in the premolar dentition of *D. stirtoni* is interpreted as being characteristic of a progressive species. *Dyseohyus stirtoni* appears to be the most progressive member of its genus and it is either the direct ancestor of, or is associated with, the lineage that produced *Prosthennops niobrarensis*.

**LOWER DENTITION:** All three lower incisors are present in some specimens of *D. stirtoni*, but  $I_2$  is actually preserved only in the holotype. Whether  $I_2$  was in the process of being eliminated from this species or not is not determinable, but this tooth was apparently never present in F:A.M. No. 73685, a young individual in which all deciduous teeth except  $dP_2$  are preserved.

All three incisors are somewhat spatulate, and all are directed anteriorly (pl. 50, fig. 2). The second incisor is the largest, and  $I_3$  is the smallest. The second incisor is also less conical than that in *Cynorca occidentale*; incisors of *C. sociale* are too heavily worn for adequate comparison.

The canine is essentially like that of *Cynorca* but larger. A well-defined midlabial ridge rises from the alveolus toward the tip of the tooth, but the lingual surface is smooth (pl. 50, fig. 2).

The first premolar has been eliminated in all specimens of *D. stirtoni* examined. As shown in F:A.M. No. 73685,  $dP_2$  is a simple, narrow, two-rooted tooth with a main cuspid situated over the anterior root. The main cuspid slopes down to a small, only slightly expanded heel posteriorly. The remaining elements of the deciduous dentition are represented in F:A.M. No. 73689 (pl. 51,

fig. 3). The main cuspid of  $dP_3$ , situated over the center of the tooth, is bifid, and each part bears a low ridge which extends to the heel. The latter is composed of a pair of low conulids which are only slightly separated from each other at the midline. An anterior conulid lies slightly labial to the midline and, in this specimen, shows a moderate degree of wear. The occlusal outline of  $dP_3$  is slightly asymmetrical, owing primarily to the labial position of the anterior conulid. The only specimen of *D. fricki* available for comparison is F:A.M. No. 73671, in which  $dP_3$  is considerably smaller than that of *D. stirtoni* and more lightly constructed (pl. 47, fig. 1). Although a definitive statement cannot be made because of the stage of wear in F:A.M. No. 73671, it apparently did not have a bifid main cuspid.

In *D. stirtoni*,  $dP_4$  is the usual elongate six-cuspid tooth. The tooth is definitely larger than that of *D. fricki*, more regularly rectangular, and the cuspids seem to be somewhat more massive (pl. 51, fig. 3).

$P_2$  (pl. 50) is well represented in the collection and consists of a high, somewhat anteriorly placed, main cuspid bearing faint median crests which connect to a minute anterior conulid and to the larger heel. The main cuspid is single and elongate, but the talonid has a transverse orientation and in some specimens consists of a pair of small conulids which are poorly separated from each other. In most features,  $P_3$  is only a larger replica of  $P_2$ , with the exception that in a few specimens, such as the holotype, the incipiently bifid nature of the main cuspid may be noted. In addition, the talonid of  $P_3$  tends to be higher relative to the main cuspid and of more complex construction than in  $P_2$ . In  $P_4$  (pl. 50), however, molarization has proceeded to the extent that the main cuspid is strongly bifid. As in  $P_3$  the anterior basal conulid is small, but the heel in  $P_4$  is well developed and is definitely higher relative to the main conulid than that in either  $P_3$  or  $P_2$ . In the holotype, the talonid consists of a single conulid with a short arcuate crevice crossing its apex and continuing down its anterolingual surface. A similar crevice occurs on the labial side of the tooth, except that it does not curve onto the apex of the talonid. In other specimens,

the talonid consists of a more complex rhomboid array of smaller conulids. Comparison with  $P_4$  of *D. fricki* indicates that in *D. stirtoni* the tooth is larger and more robust.

Molars of *D. stirtoni* (pl. 50; pl. 51, fig. 3) are essentially like those in *D. fricki*. The range of variation expressed in the hypodigm of *D. stirtoni* is such as to encompass the dental characters of the molars of *D. fricki*, including size. In most specimens of *D. stirtoni*,  $M_1$  and  $M_2$  are relatively narrower and more elongate than those in *D. fricki*, but specimens of the former species, such as F:A.M. No. 73686, show overlap in this regard.

The mandible of *D. stirtoni* is perfectly preserved in the holotype. In dorsal view, the symphysis of this specimen is slightly spoon-shaped posterior to the incisors, but narrows between the canines and descends slightly toward the genial pits. The small genial spine seen in specimens of *D. fricki* is not present in *D. stirtoni*. Three mental foramina are visible on the left side in the holotype, one below the center of  $P_2$  and the other two below the diastemal crests. In the mandible fragment F:A.M. No. 73683, the only foramen preserved lies below the center of  $P_3$ . Posterior to the symphysis the diastemal crests are slightly arcuate and cheek-tooth rows are nearly straight and parallel.

In lateral view (pl. 50, fig. 2), there is a concavity in the profile of the ventral surface of the symphysis below the canines. This feature is not present in *D. fricki*. Posterodorsal to this the diastemal crests are almost straight, possibly less concave than in *D. fricki*.

Except for a broad bulge below  $M_2$ , which diminishes anteriorly, the lateral side of the horizontal ramus is relatively flat and smooth (pl. 50, figs. 2, 4). The alveolar border of the cheek teeth falls nearly on a straight line, whereas below  $P_4$ ,  $M_1$ , and  $M_2$  the ventral edge of the horizontal ramus is slightly bowed downward. The resulting postdiastemic sulcus, posteriorly, accentuates the ventrally projecting angle. The ventral edge of this structure has a strongly arcuate profile, but its posterior edge climbs steeply in a slight anterodorsal direction to the base of the articular condyle. The lateral surface of the angle is nearly flat in contrast to the

well-defined coronoid fossa above. The leading edge of the ascending ramus is nearly straight except where it leaves the body of the horizontal ramus opposite the posterior half of  $M_3$ .

The medial surface of the mandible (pl. 50, fig. 5) is marked by the elongate, shallow, and narrow digastric fossa, which is confluent with the pterygoid fossa that occupies the medial surface of the angle. The ventral edge of the angle is conspicuously inflected, and posteriorly a small number of irregular pits and ridges reflect the attachment of the pterygoideus musculature. Anteroventral to the condyle the ovate mandibular canal opens posteriorly and ranges in position from just above to just below the level of the occlusal plane of the cheek teeth. Anterior to the foramen and immediately posterior to  $M_3$  the nearly flat, anteromedially directed site of origin for *M. depressor labii inferioris* is well exposed on the anterior surface of the ascending ramus. The medial surface of the tip of the coronoid process is marked by a semi-strap-shaped insertion area for *M. temporalis*. This surface faces somewhat posterodorsally, and in apparent association the tip of the coronoid process is reflected outward. Because of the rather poor representation of the mandible in *D. fricki*, the only apparent differences between it and that of *D. stirtoni* are the concavity of the ventral surface of the symphysis below the canines and the somewhat straighter profile of the diastemal crests in the latter species.

**DISCUSSION:** The biostratigraphic range of *Dyseohyus stirtoni* is restricted to the Barstovian. As shown by the possibly greater development of the buccinator fossa, and by the greater posterior extension of the palate, *D. stirtoni* is more advanced than *D. fricki*. Similarly, the tendency for certain members of *D. stirtoni* to have more complex, higher-crowned, and more molariform premolars than *D. fricki* illustrates the more progressive nature of the former. Additional evidence in this vein is seen in the fact that, whereas the molar proportions of *D. fricki* are substantially those of *Cynorca sociale*, the more elongate molar proportions of *D. stirtoni* resemble those of such later species as *Prosthennops niobrarensis*. Whether *D. stirtoni* was ancestral to *P. niobrarensis* or not



remains to be documented, but study of material in the Frick collections seemingly referable to that species indicates that such is a definite possibility.

The ancestry of *D. stirtoni* is not currently resolvable because of the absence of adequate cranial material for the species of *Cynorca*. Certain specimens, treated below, indicate that the lineage leading toward *D. stirtoni* may extend back to Arikareean time. If so, the ultimate ancestor of *D. stirtoni* is probably best considered as *Cynorca sociale*, although the point at which this lineage became separated from that leading to *D. fricki* is uncertain (see text fig. 14).

**?Dyseohyus sp.**

Plate 51, figures 1-2; table 16

**DISTRIBUTION:** ?Late Miocene (?Barstovian), from a Frick locality in the "upper horizon" near Grover, Colorado (F:A.M. No. 73678). Early Pliocene (early Clarendonian), from a Frick locality 7 miles west of Blair Junction, Esmerelda County, Nevada (F:A.M. No. 73681).

**HYPODIGM:** F:A.M. No. 73678, palate with right P<sup>3</sup>-M<sup>3</sup> and left P<sup>2</sup>-M<sup>3</sup>; F:A.M. No. 73681, right palatal fragment with P<sup>4</sup>-M<sup>3</sup>. P<sub>4</sub> is rotated 90 degrees and is only partly erupted. M<sup>3</sup> is also only partly erupted.

**DESCRIPTION:** Only the base of the zygomatic arch is preserved in F:A.M. No. 73678. Anterior to this, the large infraorbital foramen has a nearly ovate cross section and opens above the rear half of P<sup>3</sup> and the anterior half of P<sup>4</sup>. The palatal surface is smooth and flat. This surface is broken posterior to M<sup>3</sup>, so whether or not it extended as far posteriorly as in *D. fricki* or in *D. stirtoni* is not determinable. The anterior palatine foramina are situated medial to P<sup>4</sup> on the right side and medial to M<sup>1</sup> on the left. Anterior to these, the palatine grooves are only faintly developed.

The cheek-tooth dentition of F:A.M. No. 73678 is only slightly arcuate; P<sup>2</sup> has a single main cusp and a broad posterior heel. The occlusal outline of the tooth is thus triangular. The extreme anterior tip of this tooth is broken off, but there appears to have been no distinct basal conule in this position. The heel is massive and consists of a single, anteriorly concave, transverse struc-

ture. In F:A.M. No. 73678 the main cusp is less massive and lower-crowned than in *D. stirtoni* and may have resembled the imperfectly preserved P<sup>2</sup> of *D. fricki*.

In contrast to all specimens of *Dyseohyus* except the holotype of *D. stirtoni*, P<sup>3</sup> of F:A.M. No. 73678 has a paracone, a small, but distinctly developed metacone, and a protocone. In fact the protocone and paracone of this specimen are more definitely developed than those of *D. stirtoni*. A narrow postprotoconal groove further separates the protocone from the metaconule and posterior cingulum in F:A.M. No. 73678. In further contrast to the holotype of *D. stirtoni*, the occlusal outline of this P<sup>3</sup> is anteriorly elongate. As there is only a small anterior cingulum, most of this elongation is developed in the base of the paracone. A somewhat similar but less extreme configuration is seen in P<sup>3</sup> of the holotype of *D. fricki* and in F:A.M. No. 73688, a representative of *D. stirtoni*. In the degree of development of its metacone and metaconule, P<sup>3</sup> of F:A.M. No. 73678 is more molariform than that in *D. stirtoni* and in *D. fricki*.

TABLE 16  
MEASUREMENTS (IN MILLIMETERS) OF THE  
UPPER CHEEK TEETH OF ?*Dyseohyus* SP.

		F:A.M. No. 73678		F:A.M. No. 73681
		Right	Left	
P <sup>2</sup>				
	Length	—	9.75	—
	Width	—	6.80	—
P <sup>3</sup>				
	Length	11.20	11.40	—
	Width	10.55	10.50	—
P <sup>4</sup>				
	Length	11.00	10.55	11.90
	Width	12.35	12.55	12.55
M <sup>1</sup>				
	Length	14.25	14.50	14.65
	Width	12.80p	12.60p	12.70p
M <sup>2</sup>				
	Length	15.35	15.45	17.70
	Width	14.65a	14.70a	15.60a
M <sup>3</sup>				
	Length	17.05	16.25	19.80
	Width	14.15a	13.75a	15.40a
Length, P <sup>2</sup> -M <sup>3</sup>		—	75.35	—

In F:A.M. No. 73681,  $P^4$  is rotated 90 degrees out of its normal alignment, causing the protocone to lie adjacent to  $M^1$ . The fourth premolar of both F:A.M. Nos. 73678 and 73681 is composed of a paracone, metacone, and protocone. The cusps are relatively massive, and the paracone and metacone are of nearly equal size in F:A.M. No. 73678. In F:A.M. No. 73681, the three cusps are well separated, but the metacone is considerably smaller than the paracone. In both specimens the protocone merges freely with an anterolabially directed crest as well as with the posterior cingulum. There is only a faint suggestion of the development of either a protoconule or metaconule, the latter being completely absent from F:A.M. No. 73681. In both specimens, a postprotoconal groove is not developed. These premolars are thus not so molariform as those found in *Dyseohyus* or even some species of *Cynorca*, and this condition is all the more notable when compared with the relatively advanced structure of  $P^3$ .

The occlusal proportions of the molars would be relatively elongate were it not for the markedly expanded lingual bases of their protocones and hypocones. This condition is most strongly developed in  $M^2$ ; in  $M^3$  the base of the hypocone is not expanded. Therefore,  $M^2$  is conspicuously wider than  $M^1$  and at least slightly wider than  $M^3$ . Although  $M^3$  tapers posteriorly it is not reduced. It is larger than  $M^1$ . The individual cusps are not so large as might be expected from the massive basal dimensions of the teeth. Except for being constricted by the metaconule, the transverse valleys between the anterior and posterior moieties are unobstructed. The bases of the cusps are not swollen anteroposteriorly. In fact, the anteriorly flattened metaconule and nearly straight transverse valley combine to give the molars of F:A.M. No. 73681 a nearly bilophodont aspect.

**DISCUSSION:** Except for the construction of  $P^4$ , which is somewhat enigmatic, the relatively elongate molar proportions of F:A.M. Nos. 73678 and 73681 constitute a point of similarity to *D. stirtoni*. The expanded lingual bases of the molars and the construction of  $P^2$  are, however, like those in *D. fricki*. The morphology of  $P^3$  is more advanced than that of all specimens of *D.*

*fricki* and of *D. stirtoni*, with the possible exception of the holotype. In contrast to the advanced nature of  $P^3$ , the apparently primitive construction of  $P^4$  seems out of place. The importance of the advanced characters of the molars and third premolar may be diminished by the primitive structural level of  $P^4$ , but the significance of this phenomenon cannot be evaluated at the present time. In view of the general size of their dentitions and because of the relatively advanced character of  $P^3$ , F:A.M. Nos. 73678 and 73681 are tentatively recognized as *?Dyseohyus* sp. Should this taxonomic unit become represented by more complete material, it would probably warrant at least a new species name.

#### DYSEOHYUS OR CYNORCA

Plate 47, figures 2-4; table 17

**DISTRIBUTION:** Late early Miocene (late Arikareean) or early middle Miocene (early Hemingfordian), Garvin Farm, Grimes County, Texas (A.M.C. No. 2894, see below, and U.T. No. 31084-68). Late middle Miocene (late Hemingfordian), U.S.G.S. M-1016, Caliente Formation, NW.  $\frac{1}{4}$ , sect. 26, T. 11 N., R. 26 W., San Luis Obispo County, California (U.S.N.M. No. 23871). *?Late* Miocene (*?Barstovian*), Woodville 1 or 3, Rush Creek, Tyler County, Texas (F:A.M. No. 73661). Late Miocene (*Barstovian*), Trinity Pit 1, Trinity River, Fleming Formation, 7 miles northeast of Cold Spring, San Jacinto County, Texas (F:A.M. No. 73676). Late Miocene (*Barstovian*), L.A.C.M. (C.I.T.) 400, "Punchbowl" Formation, upper Cajon Valley, E.  $\frac{1}{4}$ , sect. 2, T. 3 N., R. 7 W., San Bernardino County, California (L.A.C.M. [C.I.T.] No. 5309).

**MATERIAL:** In general the specimens discussed here are smaller than specimens of *Dyseohyus* and larger than those of *Cynorca*. These specimens are not treated as a hypodigm because there is no assurance that they pertain to a single taxonomic unit: A.M.C. No. 2894, isolated left  $M_2$  (other specimens catalogued under this number are described as *Cynorca sociale*); U.T. No. 31084-68, fragment of mandible with right  $M_1$ - $M_2$ ; U.S.N.M. No. 23871, right  $M^3$ ; F:A.M. No. 73661, partial right mandible with  $M_1$ - $M_2$ ; F:A.M. No. 73676, seven isolated teeth, including a well-worn right  $?M^1$ , an unworn

TABLE 17  
MEASUREMENTS (IN MILLIMETERS) OF THE DENTITION OF SPECIMENS DESIGNATED AS  
*Dyseohyus* OR *Cynorca*

	U.S.N.M. No. 23871	F:A.M. No. 73676	F:A.M. No. 73661	A.M.C. No. 2894	U.T. No. 31084-68	L.A.C.M. No. 5309
RM <sup>1</sup>						
Length	—	10.65	—	—	—	—
Width	—	10.30a	—	—	—	—
LM <sup>1</sup>						
Length	—	12.00	—	—	—	—
Width	—	11.00a	—	—	—	—
M <sup>2</sup>						
Length	—	13.35	—	—	—	—
Width	—	11.50a	—	—	—	—
M <sup>3</sup>						
Length	13.00	13.75	—	—	—	—
Width	11.45a	11.30a	—	—	—	—
C <sub>1</sub>						
Length	—	6.95	—	—	—	—
Width	—	7.50	—	—	—	—
P <sub>3</sub>						
Length	—	—	—	—	—	9.40
Width	—	—	—	—	—	5.60p
P <sub>4</sub>						
Length	—	—	—	—	—	9.85
Width	—	—	—	—	—	7.15p
M <sub>1</sub>						
Length	—	—	11.20	—	11.75	10.45
Width	—	—	8.60a	—	8.40p	8.25p
M <sub>2</sub>						
Length	—	13.75	12.55	12.55	13.20	—
Width	—	10.40p	10.25a	10.10a	—	—
M <sub>3</sub>						
Length	—	—	16.70	—	—	15.65
Width	—	—	10.65a	—	—	9.50a×

left ?M<sup>1</sup>, an unworn right M<sup>2</sup>, a moderately worn right M<sup>3</sup>, left C<sub>1</sub>, the root of another left C<sub>1</sub>, and a moderately worn right ?M<sub>2</sub>; also included in F:A.M. No. 73676 is a massive left C<sub>1</sub> which is not that of a peccary. L.A.C.M. (C.I.T.) No. 5309 is a fragment of left mandible with P<sub>3</sub>—M<sub>1</sub>, M<sub>3</sub>.

DESCRIPTION: The worn ?M<sup>1</sup> (F:A.M. No. 73676) has almost no pattern left, but its moderately bilobate occlusal outline and relatively elongate proportions are still visible. Molars of this general character are found in *D. stirtoni*, but the tooth in question is smaller than M<sup>1</sup> of that species. To judge from the size of M<sup>3</sup> in *C. proterva* this ?M<sup>1</sup> is larger than would be probable for that species.

The bilobate character of the unworn M<sup>1</sup> in F:A.M. No. 73676 is even more conspicuous and resembles comparable teeth in the referred cranium of *D. fricki* (F:A.M. No. 73670). On the other hand, the occlusal outline in the specimen in question is more regular than that in *D. fricki* and lacks the prominently oblique orientation of the anterolingual base of the protocone seen in that species.

Although smaller than most specimens of *D. stirtoni*, the unworn M<sup>2</sup> of F:A.M. No. 73676 has moderately elongate proportions. In addition, the bases of the protocone and hypocone are expanded lingually in this specimen, but not to the extent seen in *C. occidentale* and in *D. fricki*. As well as not

being bilobate, the occlusal outline of this  $M^2$  differs from that of *D. fricki* in the same manner as just described for  $?M^1$ .

The third molar of F:A.M. No. 73676 is elongate and not reduced in comparison with  $?M^1$  and  $M^2$ . The proportions and occlusal outline of this tooth are like those of *D. stirtoni*, *C. proterva*, and *C. sociale*, but the specimen is smaller than the first species and larger than the latter two.

The left  $C_1$  in F:A.M. No. 73676 is worn, with enamel present only on the upper third of the tooth. A strongly developed wear facet is present on the posterior surface, augmenting the triangular cross section of the crown. As preserved, there are essentially no labial or lingual grooves. The specimen is about the same size as those in the hypodigm of *C. proterva*.

The right  $M_2$  in F:A.M. No. 73676 is slightly smaller than specimens of *D. stirtoni*, but its elongate proportions constitute a point of similarity to that species.

In summary, if the specimens catalogued as F:A.M. No. 73676 all pertain to the same taxon, such a taxon would be characterized as being slightly smaller than *D. stirtoni* but otherwise resembling it in having elongate molar proportions and an unreduced  $M^3$ . Unfortunately, the premolar dentition is not represented in this material.

Apparently contemporaneous material from Texas, F:A.M. No. 73661, allows assessment of some of the features of the lower dentition. In this specimen, all three lower molars are associated in one mandible. The proportions of these molars are relatively elongate,  $M_2$  is not markedly wider than  $M_1$ , and  $M_3$  is not reduced. In these terms, the specimen, although smaller, resembles *D. stirtoni*. The mandible of F:A.M. No. 73661 is larger than that of *C. sociale* and *C. proterva*, but smaller than that of *C. occidentale* and the species of *Dyseohyus*. In F:A.M. No. 73661 the depth of the mandible below the alveolar border just anterior to  $M_1$  is 29.00 mm., as compared with 23.20 mm. for *C. sociale* and at least 32.40 mm. in *C. occidentale*. A similar measurement cannot be made for *C. proterva*, but it would be approximately the same as for *C. sociale*. The comparable dimension in *D. fricki* is probably more than 30 mm., and in *D. stirtoni* it

ranges from 30.75 mm. to 32.90 mm. As for the rest of the mandible, the remnant base of the ascending ramus in F:A.M. No. 73661 indicates that this structure rose past the posterior tip of  $M_3$ . Below this the labial surface of the mandible is slightly convex, but lingually the digastric fossa and the preserved portion of the pterygoid fossa are as in specimens of both *Cynorca* and *Dyseohyus*. Most of the angle is broken off in this specimen, but enough remains to show that it was inflected.

Texas specimens of possible late Arikareean (Wilson, 1960) age may be related to those just described. Lower molars catalogued as U.T. No. 31084-68 and A.M.C. No. 2894 have relatively elongate proportions. They approach *C. occidentale* in size, but  $M_2$  is not remarkably wider than  $M_1$ . If smaller, these teeth might be referable to *C. sociale*. Their coronal construction is more open than in *C. proterva* and they are smaller than representatives of *Dyseohyus*. The molars of U.T. No. 31084-68 are essentially the same size and shape as F:A.M. No. 73661, and  $M_2$  in both of these specimens is only slightly smaller than that of F:A.M. No. 73676.

All the specimens described above do not fit well with any of the material currently assigned to any of the species of *Cynorca* or *Dyseohyus*. As indicated primarily by the proportions of their molars, they may represent a lineage related to that of *D. stirtoni*. The lineage perhaps extends back into late Arikareean time. *Cynorca sociale* is of sufficiently generalized construction and is suitably placed in time to have been either ancestral to, or near the ancestry of, this lineage. Whether the specimens under discussion ultimately belong in *Cynorca* or *Dyseohyus* must be decided on the basis of better material than is currently available. Furthermore, it is by no means proved that the specimens described here all pertain to a single species or lineage; the available morphologic features merely suggest it.

A California population possibly allied to that just described from Texas is represented by U.S.N.M. No. 23871 and L.A.C.M. (C.I.T.) No. 5309. U.S.N.M. No. 23871, a right  $M^3$ , is smaller than  $M^3$ 's referred to *Dyseohyus*, and larger than those referred to *Cynorca*. Of the available material, this speci-

men most closely resembles the fragmentary teeth in the referred cranium of *D. fricki* F:A.M. No. 73670. U.S.N.M. No. 23871 ( $M^3$ ) is similar in general size to, but is shorter than,  $M^3$  of F:A.M. No. 73676 from Texas. The California specimen is thus in an analagous position relative to *Dyseohyus* as is the Texas material, except that the closest resemblance is shown to the western species, *D. fricki*, rather than to *D. stirtoni*.

A similar statement can be made relative to L.A.C.M. (C.I.T.) No. 5309. In this specimen,  $P_3$  and  $P_4$  are about the same size as those in *D. fricki*, are smaller than those in *D. stirtoni*, and larger than those in *Cynorca*. In contrast,  $M_1$  and  $M_3$  are almost the same size as these teeth in F:A.M. No. 73661, the Texas mandible of *Dyseohyus* or *Cynorca*, and are smaller than those of either *D. fricki* and *D. stirtoni*. Thus a simple allometric increase in size of the lower dentition would not result in a specimen similar to *D. fricki*. The fact that in almost all respects,  $M_1$  and  $M_3$  of L.A.C.M. (C.I.T.) No. 5309 are essentially identical to F:A.M. No. 73661 suggests that the California material should be referred to the category *Dyseohyus* or *Cynorca*, at least until additional evidence is forthcoming.

DISCUSSION: Two lots of specimens seem to have reached a stage of evolution intermediate between that of *Cynorca sociale* and that of *Dyseohyus*. In regard to the Texas sample, there may be no intrinsic reason to consider the material catalogued as F:A.M. No. 73676 as pertaining to one species. On the other hand it may be noteworthy that if  $M^1$ ,  $M^2$ , and  $M^3$  are so considered, the general observations drawn concerning rela-

tive tooth proportions are the same as for the teeth in F:A.M. No. 73661, in which  $M_1$ – $M_3$  are definitely associated. If the upper dentition of F:A.M. No. 73676 is considered as pertaining to the same species as F:A.M. No. 73661, such a species could be characterized as being slightly smaller than *C. occidentale* and definitely smaller than *Dyseohyus*. In addition, this presumed species would not have the markedly wider  $M^2$  of *C. occidentale*. Even with the ?late Arikareean (Wilson, 1960) material from Texas included, the molar occlusal outlines, general molar proportions, and unreduced nature of  $M^3$  displayed by the presumed species would point to affinity with *D. stirtoni*. Because of the uncertainties described above, a species based on the characters just outlined is not proposed at this time.

In some respects, the western sample of this taxonomic category seems to be ancestral to *D. fricki*. In other features, closest resemblance is shown to members of the Texas sample of *Dyseohyus* or *Cynorca*. It is possible that the two samples reflect approximately parallel evolution from local populations of *C. sociale*, each lineage leading toward a different species of *Dyseohyus*. It is also possible that the specimens designated as *Dyseohyus* or *Cynorca* are members of a largely unrecorded panmictic population which was widely distributed in North America and that a single ancestor, from which both species of *Dyseohyus* were derived, was drawn from this population. Decision between alternatives such as these, and elucidation of the exact ancestry of each of the species of *Dyseohyus*, must be deferred until better material becomes available.

## GENERAL DISCUSSION

### BIOGEOGRAPHY

IT IS ALMOST axiomatic that studies on the paleogeography and paleogeomorphology of an area can produce only tentative and generalized results. Such is certainly the case for continental North America during Miocene time. Nevertheless, it is my opinion that such studies, when coupled with the admittedly imperfect information on faunal occurrences and composition, can yield tentative but useful biogeographic reconstructions. Moreover, as exemplified by Dice (1943), ecologists have been able to formulate subdivisions of the modern biota. These subdivisions do not arise *de novo* but have had an undocumented developmental history. Therefore, just as it is imprecise to speak of North America as constituting a single modern faunal province, it is equally imprecise to consider this continent to have been such an entity in the past.

In the following paragraphs, the distribution of the species of *Cynorca* and *Dyseohyus* are examined in light of their possible ecological preferences and in terms of the possible distribution of contemporaneous, broadly defined, ecological and physiographic systems. Because of the small number of peccary specimens involved, such reconstructions as can be made (text figs. 11–13) may be subject to revision as additional evidence accumulates. The reason for the following attempt to fit the species of *Cynorca* and *Dyseohyus* into an interpretive reconstruction of the Miocene physiographic and climatic setting of North America is to emphasize the fact that each fossil species represents a former biological system, the evolution and dispersal of which developed in response to the surrounding ecological and climatic conditions. The evolution and dispersal of these species should thus be considered from various points of view, including but not limited to their skeletal morphology. Almost as a by-product of this discussion, the thesis may be advanced that, by late Miocene time, the species of *Cynorca* and *Dyseohyus* had differentiated not only ecologically but also geographically into differ-

ent areas of the North American continent. It is possible that the geographic differentiation of these peccaries may have coincided with that displayed by other mammalian species (see Shotwell, 1961; and Black, 1963, for examples). The evidence accumulated by these and other workers suggests that certain faunal provinces were present in North America during the Miocene, but the documentation of these provinces is not the purpose of this report.

A broad framework for discussing the features of the North American continent was provided by Eardley (1962, pls. 14, 15). The coastline was considerably farther inland than it is at the present time along the Atlantic and Gulf coasts, but along the Pacific there were numerous marine embayments. In the interior, relatively low mountains of the Cordilleran chain of the west and the Rockies to the east were undergoing uplift. Streams flowing eastward from the Rockies (Lugn and Lugn, 1956) apparently followed paths approximately corresponding to those now followed by the present major river systems, and emptied into the proto-Mississippi system. To the east the Appalachian region remained a positive area, accompanied by broad arching.

**EASTERN AND GULF COASTS:** During the Miocene these coastal areas were apparently moist lowland situations which existed under a warm-temperate climate and supported vegetation similar to that now found in coastal South Carolina and adjacent areas (Berry, 1916; Stenzel, Turner, and Hesse, 1944). Coastal South Carolina is now in the Austroriparian Biotic Province of Dice (1943), characterized as containing swamps and marshes with enough rainfall (about 50 inches per year) to support hardwood forests. The presence of essentially modern forests in this area during the Miocene is supported by an analysis by Graham (1965). As shown by the distribution of fossil crocodilians (see below) a habitat similar to that found in these coastal areas probably extended up the drainage system of the proto-Mississippi River and its tributaries, to reach into the western parts of the Plains states.

**THE PLAINS STATES:** As indicated by Van Houten (1961, figs. 4, 5) areas in eastern Colorado, Wyoming, Montana, and adjacent parts of the Dakotas, Nebraska, and Kansas, received large quantities of detrital material derived from erosion of the rising elements of the Rocky Mountain system. From the studies of Luginbuhl and Luginbuhl (1956), from personal observation, and from discussions with members of the former Frick Laboratory, it seems that many of the major Miocene river systems in, for instance, western Nebraska, followed paths now taken by the modern streams of the area. Flint (1957, fig. 10-2) showed that the pre-glacial continental divide may have trended east-northeast through central South Dakota. South of this the major east-flowing streams seem to have met the proto-Mississippi-Missouri system in the southern Ohio Valley.

With the use of the study of MacGinitie (1962) as a basis for extrapolation, the topography of the area in western Nebraska, at least, was probably of lower relief than that found there at present, i.e., "extensive, nearly flat plains, traversed by wide river valleys of small gradient" (*ibid.*, p. 76).

MacGinitie (*ibid.*, p. 81) has shown that, in western Nebraska during the late Miocene, the plants found along the borders of the major streams are those commonly found today in the swamp cypress association of the central and coastal states. The presence of luxuriant vegetation along the streams is consistent with the presence of fossil crocodilians in deposits of the middle Miocene Sheep Creek Formation and later rock units in western Nebraska (Matthew, 1924; Woodburne, 1959) and supports the inference that winter temperatures seldom, if ever, reached the freezing point in this area during Miocene time. (See also Estes and Tihen, 1964, and references cited therein for similar conclusions based on lower vertebrate faunas from the lower part of the Valentine Formation.) Moreover, the western Plains states are one of the last areas where fossil crocodilians are recorded during Miocene and Pliocene time in the interior of North America. The gradual restriction of crocodilians to coastal areas of North America during the later Tertiary seems to reflect a similar restriction of the moist, warm-temperate to subtropical cli-

mate under which they lived. The evidence from the stream-border segment of the Kilgore flora and the distribution of fossil crocodilians suggest that an ecological situation similar to that found along the eastern and Gulf coasts during the Miocene extended into the interior of North America along the courses of the major river systems.

The upland plains element of the Kilgore flora is apparently most like that found on the eastern side of the Sierra Madre in Mexico and, with a rainfall of approximately 30 inches per year, existed under relatively dry conditions (MacGinitie, 1962, p. 97), but whether extensive grasslands had developed in the Great Plains in middle to late Miocene time or not is open to question (MacGinitie, 1962, p. 99).

**COLORADO PLATEAU:** According to Van Houten (1961, fig. 4), the Colorado Plateau was largely a positive area from the Oligocene to middle Miocene; mainly volcanic debris accumulated around the margins. During the late Miocene and Pliocene (*ibid.*, fig. 5), sediments encroached on the highlands which became largely restricted toward southeastern Utah. Throughout all of the Miocene, however, elements of the Rocky Mountains continued to exist as disjunct, linear positive elements that experienced local uplift.

In the words of Hunt (1956): "During early Miocene time, as block faulting progressed in the Basin and Range province, the Colorado Plateau probably became well defined...and reached an altitude distinctly higher than the basins, although perhaps not so high as the ranges... At this point... degradation began" (p. 77). As uplift continued, the tributaries of the proto-Colorado River system began to be entrenched, and the once relatively broad valleys became constricted as escarpments developed and local mountains were elevated. "During the late Miocene to middle Pliocene time...the Colorado Plateau rose higher above the basins of the Basin and Range province. As a result of this general uplift, the Plateau was tilted northeastward" (*ibid.*, p. 85).

Paleobotanical evidence summarized by Axelrod (1958) indicates that the Madro-Tertiary Geoflora, which was adapted to relatively dry conditions, arose in the southern Rocky Mountains and adjacent Mexico



by at least the late Oligocene. As drier conditions spread in the Miocene, elements of this flora are found in progressively more peripheral positions with respect to this presumed center of origin. Although the concept of geofloras as dynamic, biologically cohesive entities has come under scrutiny (MacGinitie, 1962, pp. 86, 87), designating a floral assemblage as Madro-Tertiary still carries with it the inference that the assemblage is composed of plants that lived under a generally warm climate, with an annual rainfall of less than 30 inches.

During the Miocene uplift of the Colorado Plateau, it is probable that much of the Colorado Plateau existed under conditions that would support elements of the Madro-Tertiary Geoflora (see Shotwell, 1961, fig. 7), but the mountains and higher hills may have been clothed by members of the Arcto-Tertiary Geoflora that were adapted to moister, but somewhat cooler conditions.

**CORDILLERAN REGION:** This area covers California, Nevada, Oregon, and neighboring parts of adjacent states. Van Houten (1961) has indicated that in the interval from Oligocene to middle Miocene time, "Vigorous volcanic activity along the Sierra Nevada-Cascade belt produced great masses of andesitic lava flows, mudflows, and pyroclastic deposits that built up a low topographic barrier a thousand feet high" (p. 617). Some of this material spilled over into the Great Basin which was about 2000 feet above sea level. "The deformation and volcanic accumulation apparently did not interfere with external drainage to the west or alter the climate significantly, however" (p. 617).

By way of contrast aggradation apparently did not occur in the northern part of the old Nevadan miogeosynclinal belt. Farther to the south, however, in southern Nevada and adjacent west central Utah, a series of "ignimbrites . . . and associated lavas and pyroclastic debris . . . mantled a broad terrane of low relief" (p. 617). To the west the rest of California was largely a positive area undergoing degradation, except for areas peripheral to the San Joaquin, Ventura, and Los Angeles embayments.

In late Miocene to early Pliocene time the northern part of the old Nevadan miogeosyncline was the site of accumulation of vol-

canic debris which built some areas up to "3,000-4,000 feet above sea level" (*ibid.*, p. 620). To the south numerous local basins developed and received considerable quantities of debris. The only highlands where deposition was not occurring were found locally in extreme southern California and adjacent Arizona and northwestern California and adjacent Oregon.

At least in late Miocene time most of Nevada, parts of adjacent Utah, southwestern California, and western Arizona were relatively dry and warm, and accommodated floras of Madro-Tertiary character. To the north and along the tops of the ranges in Nevada and Utah, conditions were moister, somewhat cooler, and less extreme. The associated flora is of Arcto-Tertiary type (Axelrod, 1956, fig. 16).

To fill in some of the remaining gaps in this climatological reconstruction, the following brief discussion of five more floral associations is presented. These are relevant to discussions on the distribution of *Cynorca* and *Dyseohyus*.

The Valley Springs flora is on the western slopes of the Sierras in north central California (text fig. 11). This flora (Axelrod, 1944a, pp. 217-220) is composed of a mixture of Madro-Tertiary and Arcto-Tertiary elements. Axelrod suggested a late Miocene age for this flora, but it may be as old as late early Miocene (Evernden and James, 1964).

A late middle Miocene age was assigned to the Upper Cedarville flora by Chaney (1959, pp. 116-118). This flora, situated in far northeastern California, was given a late early Miocene age by Evernden and James (1964).

South of the other two localities, in the Kinnick Formation, elements of the Tehachapi flora have been recovered. The flora (Axelrod, 1939) is of Madro-Tertiary aspect. In the present report the mammals from the Kinnick Formation have been assigned a late middle Miocene age.

In Oregon, the Alvord Creek flora (Axelrod, 1944b) seems to be of Arcto-Tertiary aspect. Axelrod suggested an early Pliocene age for this flora, but it may be as old as late early Miocene (Evernden and James, 1964).

The Mascall flora, recovered from the same formation as the Mascall fauna, is of

latest middle Miocene or earliest late Miocene age. The flora is of Arcto-Tertiary affinities and has essentially the same swamp-cypress association found in the stream-border assemblage of the Kilgore flora (MacGinitie, 1962, p. 81). The broad climatic picture for the Mascall is probably slightly cooler than that of the Kilgore.

**DISTRIBUTION OF *Cynorca*:** Although the

age of some of the John Day specimens of *Cynorca sociale* is uncertain, the earliest record of this species may be no older than late Arikareean. Since the Bridge Creek flora (Chaney, 1952) of approximately middle Oligocene age (Evernden and James, 1964), the early Miocene Alvord Creek flora, and the ?late early Miocene Upper Cedarville flora are of Arcto-Tertiary aspect, it would

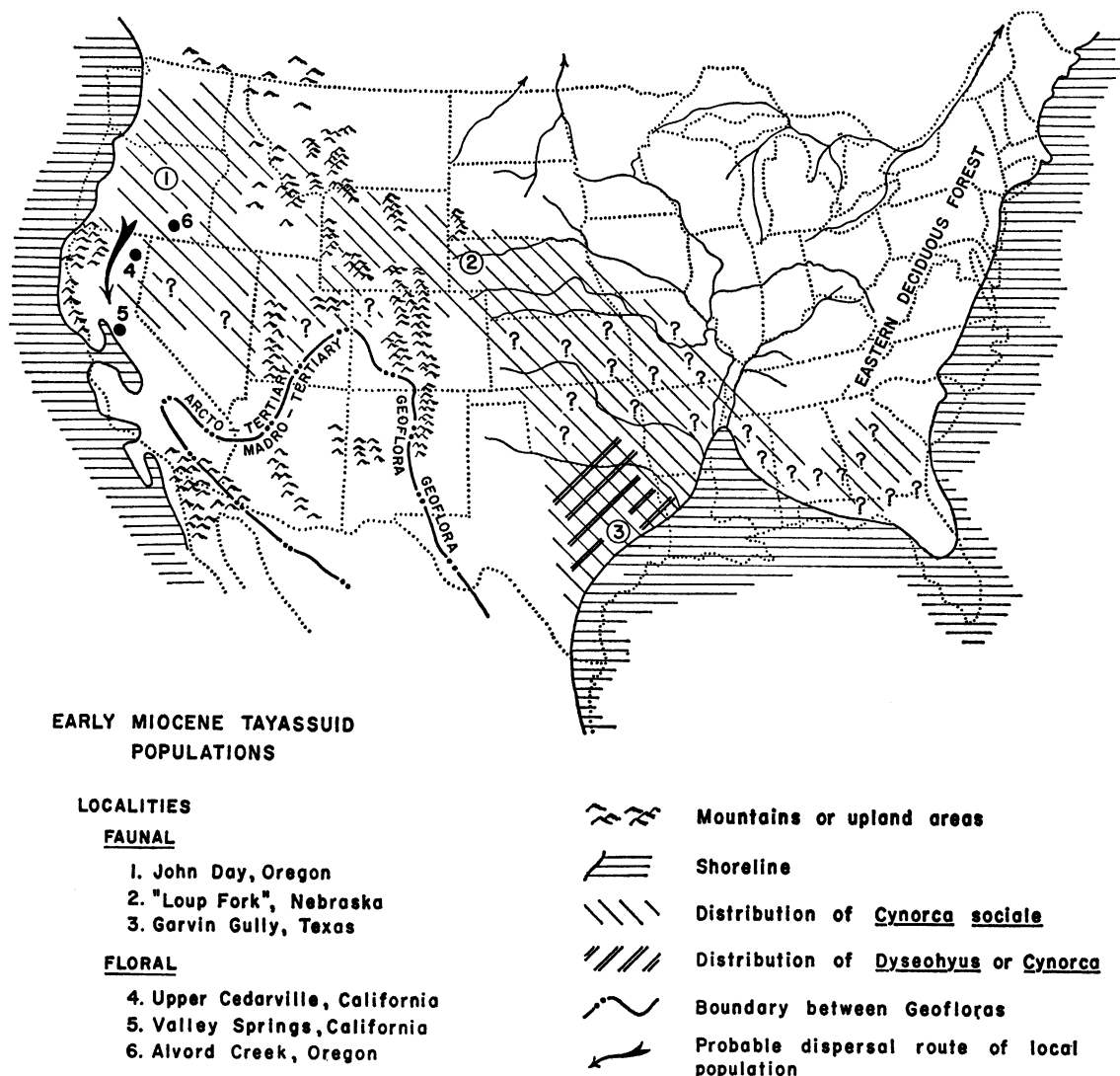


FIG. 11. Distribution of the early Miocene species of *Cynorca* in relation to the broad physiographic and climatic elements of North America. Reconstructions of the coastlines are adapted from Eardley (1962); river systems, from Flint (1957); distribution of tectonic elements, from Hunt (1956) and Van Houten (1961). Paleobotanical and climatic reconstructions are from sources cited in the text. Boundaries between geofloras are approximate.

seem that the contemporaneous biota of the John Day region lived under a moist-temperate climate.

Although no floral elements are associated with it, the Texas population of *C. sociale* probably lived under moist, lowland conditions. Temperatures may have been somewhat milder than those in Oregon.

No Arikareean peccaries are known from the southern Cordilleran region and adjacent Colorado Plateau. To the north, however, there seems to have been some faunal interchange between Oregon and the Plains states. Members of the tayassuid genus *Chaenohyus* from faunas of the Sharps Formation in South Dakota are sufficiently like those from the John Day Formation of Oregon to warrant their tentative inclusion in a single species. Some other genera from the Sharps Formation, including the primate *Ekgmowechashala*, and certain beavers, are closely related to forms that occur in the faunas of the John Day Formation (J. M. Rensberger, personal communication, December 27, 1967). In addition, the likelihood that there was an avenue for tayassuid dispersal between these two areas in Miocene time may be strengthened by the single representative of *Cynorca* cf. *C. sociale* from deposits of probable Arikareean age in Nebraska. The early Miocene climate of Nebraska was probably such as to support animals and plants with the same general ecological requirements as lived in the John Day region, but such support has not yet been firmly established. The late Miocene Kilgore flora of north-central Nebraska has many elements in common with those of the somewhat earlier Mascall flora of Oregon (MacGinitie, 1962, p. 81), and it is possible that a corresponding degree of ecological similarity between the two areas was also present in the early Miocene.

If the situation is viewed broadly, the main late Arikareean and early Hemingfordian population of *Cynorca sociale* may have extended from Oregon eastward to the Plains states, and southward along tributaries of the old Mississippi-Missouri drainage system to the Gulf coast (text fig. 11). Ecologically, it would seem entirely plausible that members of this species lived along the Atlantic coast as well.

That *C. sociale* appears to be absent from the southwestern regions of North America may be only because our knowledge of Arikareean faunas in that area is meager. On the other hand, MacGinitie (1962, p. 83) wrote: "As more research is accomplished on the Rocky Mountain and adjacent fossil floras, it is becoming increasingly clear that, in the interval from late middle Eocene to upper Miocene, truly mesic plant formations existed only on the higher elevations and on the borders of streams and lakes. The interfluvial and foothill areas supported a subhumid, open, shrubby forest and subtropical scrub to evergreen oak-pine woodland." This reference is to the "evergreen oak woodland of the southwestern United States and northern Mexico, which was well represented in the California-Nevada-Colorado-Texas-Oklahoma region by the Sierra Madrean Woodland Element into Pliocene time" (Axelrod, 1950, p. 251). The valleys and lowlands of the Colorado Plateau and associated areas to the south and west may have lacked the ecological requirements to support populations of *C. sociale* in the early Miocene.

The foremost exception to the hypothesis that *Cynorca sociale* preferred to live in areas having a relatively moist climate is found in the single specimen representing a late Hemingfordian population of this species in the Phillips Ranch fauna. The deposits that yield this fauna (text fig. 12) in southern California also produce the Tehachapi flora of Madro-Tertiary aspect. Adaptation to such conditions is out of line with the data applicable to the other members of this species and, as such, is somewhat unexpected. This representative of *C. sociale* is the latest known, and it may be that, in order to survive, this species was forced to explore ecological situations that were peripheral to its former niche.

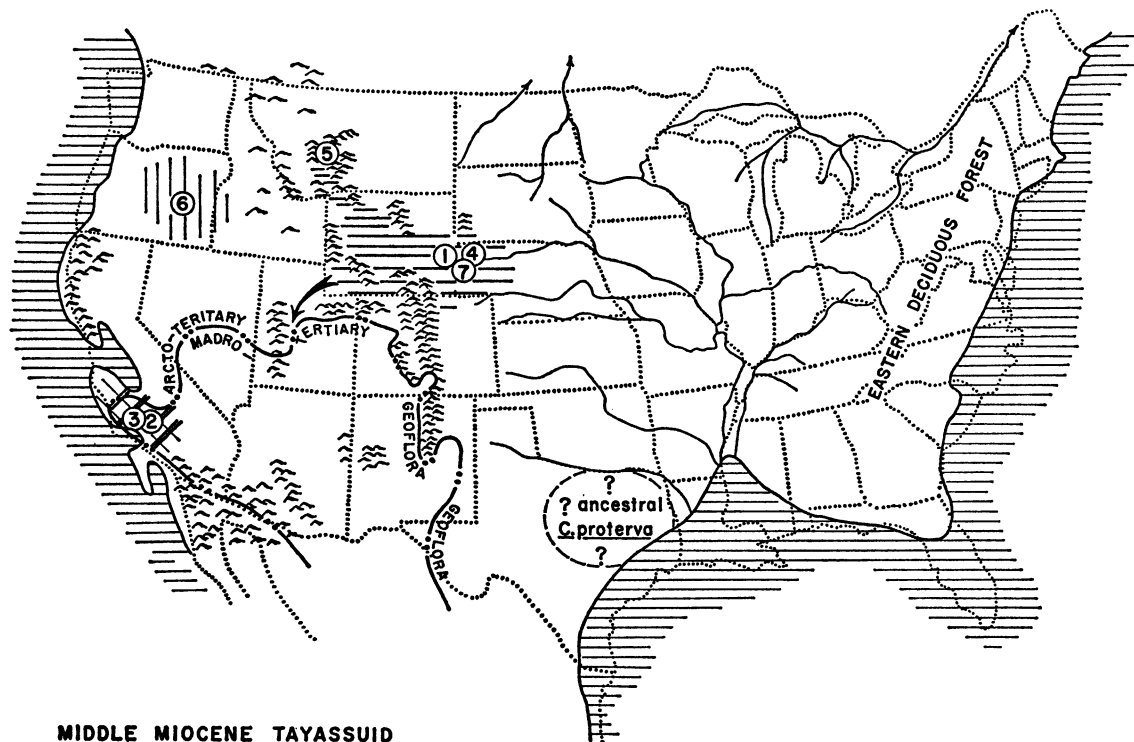
*Cynorca proterva* apparently had a geographical distribution similar to the eastern portion of that proposed for *C. sociale*. Based on information afforded by the stream-border association of the Kilgore flora and the distribution of Miocene and Pliocene crocodilians, *C. proterva* apparently preferred to live in moist, warm-temperate situations. A microclimate of this character may have extended westward from the coastal areas,

along the borders of the major streams as far as Nebraska (text fig. 13). Such a climate was undoubtedly well developed along the Gulf and Atlantic coasts where *C. proterva* is best known.

*Cynorca hesperia* is a monotypic form with a restricted occurrence in Oregon (text fig. 12). If it can be said to have been derived

from deposits of the Mascall Formation, it may have lived under moist, cool-temperate conditions. The Mascall flora from the same formation is of Arcto-Tertiary aspect.

For the most part, *Cynorca occidentale* is distributed in areas thought to be under the influence of a relatively dry, warm climate (text fig. 13). The localities of the specimens



# MIDDLE MIOCENE TAYASSUID POPULATIONS

## LOCALITIES

### FAUNAL

1. Near Lusk, Wyo.
2. Phillips Ranch, Calif.
3. Caliente Range, Calif.
4. Ravine Quarry, Neb.
5. Near White Sulphur Springs, Mont.
6. Mascall, Ore.
7. Near Hay Springs, Neb.

### FLORAS

2. Tehachapi, Calif.
6. Mascall, Ore.

- Mountains or upland areas
- Shoreline
- Distribution of *Cynorca sociale*
- Distribution of *Dyseoehyus* or *Cynorca*
- Distribution of *Cynorca hesperia*
- Distribution of *Cynorca occidentale*
- Boundary between Geofloras
- Probable dispersal route of local population

FIG. 12. Distribution of the middle Miocene species of *Cynorca* in relation to the broad physiographic and climatic elements of North America. Reconstructions of the coastlines are adapted from Eardley (1962); river systems, from Flint (1957); distribution of tectonic elements, from Hunt (1956) and Van Houten (1961). Paleobotanical and climatic reconstructions are from sources cited in the text. Boundaries between geofloras are approximate.

from the California late Miocene correspond to areas associated with elements of the Madro-Tertiary Geoflora (Axelrod, 1956, fig. 16). Interestingly enough, early and late Hemingfordian members of the species existed in areas thought to be associated with Arcto-Tertiary floral elements (text fig. 12). Whether *C. occidentale* actually lived in association with elements of this floral type or inhabited the drier parts of the valleys and basins in middle Miocene time remains to be seen. It is possible that a shift in the geographic range of *C. occidentale* from a northeasterly position to a more southwesterly position during the middle to late Miocene interval reflects a gradual change in environmental adaptation.

The reconstruction of highlands and adjacent lower areas in western North America during the pertinent time interval (Van Houten, 1961, figs. 4, 5) suggests that the most likely avenue of dispersal between the northwestern Plains states and southern California was across western Wyoming, northeast Utah, and central or southern Nevada.

**DISTRIBUTION OF *Dyseohyus*:** *Dyseohyus fricki* is known only from a limited area in southern California (text fig. 13) and apparently lived under the somewhat drier and warmer climate indicated by the presence of elements of the Madro-Tertiary Geoflora. The late Hemingfordian and Barstovian specimens of *Dyseohyus* or *Cynorca* from the Caliente Range and upper Cajon Valley in California (text figs. 12, 13) are in some ways similar to *D. fricki* and, in view of the relative geological and geographical proximity of Madro-Tertiary floral elements, may have lived under similar conditions. The presence of the mixed Arcto-Tertiary, Madro-Tertiary aspect of the broadly contemporaneous Valley Springs flora as far north as central California (text fig. 11) suggests that climatic conditions were becoming more xeric along the western flank of the Sierras from middle Miocene time on. *Dyseohyus fricki* may have evolved from a late Hemingfordian or early Barstovian population of *Dyseohyus* or *Cynorca* that had invaded the expanding drier areas of the West coast after having branched off from a local population of *Cynorca sociale*.

In contrast to *D. fricki*, *D. stirtoni* is known from upper Miocene deposits of Nebraska, Colorado, and Texas. Such a distribution pattern (text fig. 13) suggests that it may have been adapted to somewhat moister conditions than was *D. fricki*. On the other hand, it is much better represented in the collections from the Plains states than is *Cynorca proterva*. If this better representation can be tentatively taken as evidence that *D. stirtoni* was more successfully adapted to the local conditions than was *C. proterva*, it may have lived widely over the area, including the interfluvies and plains in which the vegetation reflects sub-humid conditions. Specimens of *Dyseohyus* or *Cynorca* from Texas more closely resemble *D. stirtoni* than *D. fricki*. The pertinent material ranges in age from late Arikareean or early Hemingfordian to approximately Barstovian. If this material can be considered as representing one species, such a population may have been largely restricted to this area in southeastern Texas. As such it probably arose, and continued to live under, warm moist conditions (text figs. 11, 13). If this population gave rise to *D. stirtoni*, the latter may have explored a somewhat drier habitat, in the same sense as did *D. fricki*.

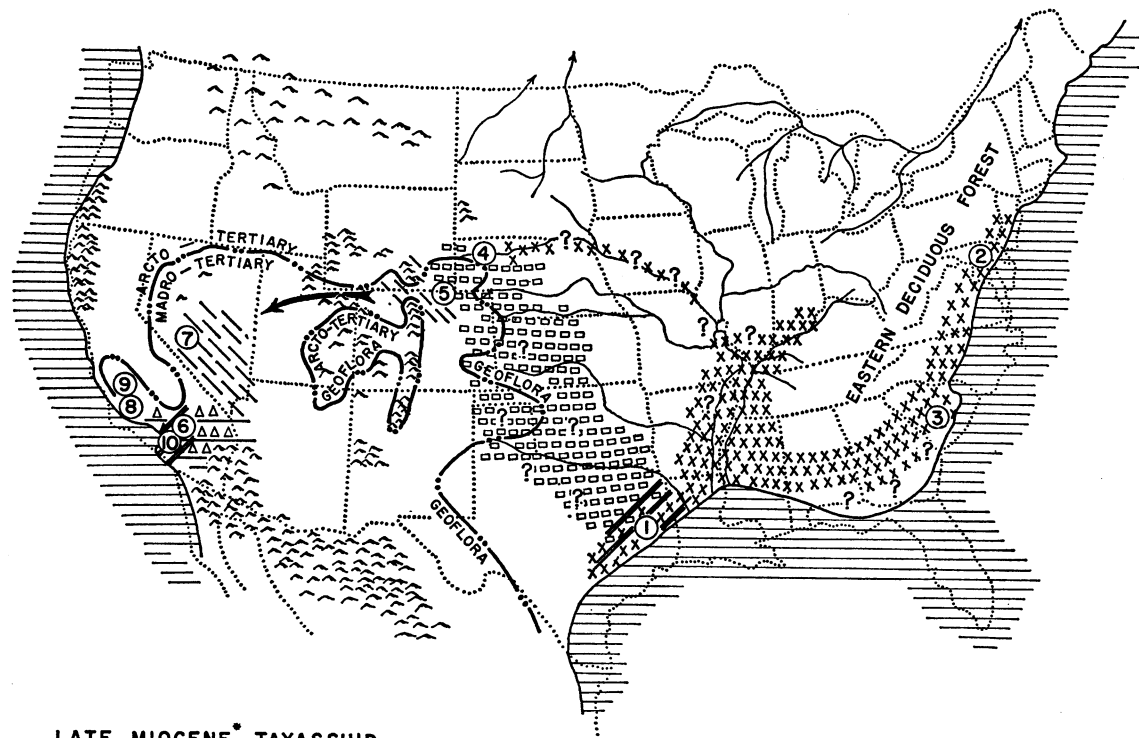
The large peccary designated as ?*Dyseohyus* sp. is poorly represented. Its presence in upper Miocene deposits in eastern Colorado and lower Pliocene deposits in southwestern Nevada suggests, however, that it was adapted to the relatively xeric conditions indicated by the probable presence of elements of the Madro-Tertiary Geoflora. In spite of its meager representation, the members of this taxon represent the only peccary population yet discussed which, at least potentially, inhabited the northeast-southwest area connecting the Plains states to southern California (text fig. 13).

**SUMMARY:** As far as can be determined from imperfect evidence, dry highlands that were apparently developing during the Miocene in the southern Rockies and adjacent Mexico constituted a major barrier to peccary distribution. In early Miocene time a broad ecologic province may have extended from the Atlantic and Gulf coasts, through the Plains states, and westward

across Wyoming and Idaho to Oregon (text fig. 11). This province was associated with a moist, warm-temperate climate, and was occupied by *Cynorca sociale*.

In middle Miocene time derivatives of this species began to evolve. The lineage leading

to *Dyseohyus fricki* may have extended from Oregon into southern California and, as it did so, adapted to warmer and drier conditions. The late Hemingfordian representative of *C. sociale* could be a reflection of this morphologically and adaptively evolutionary



# LATE MIOCENE\* TAYASSUID POPULATIONS

## LOCALITIES

1. Cold Springs, Tex.
2. Calvert Fm., Md.
3. Ashley R., S. Ca.
4. Various locs., Neb.
5. Near Grover, Colo.
6. Barstow Syncline, Calif.
7. Blair Jct., Nev.\* (CLARENDONIAN)
8. Cuyama Badlands, Calif.
9. Merychippus zone, Calif.
10. Cajon Valley, Calif.

- Mountains or highlands
- Shoreline
- Distribution of *Dyseohyus* or *Cynorca*
- Distribution of *Cynorca occidentale*
- Distribution of *Cynorca proterva*
- Distribution of *Dyseohyus fricki*
- Distribution of *Dyseohyus stirtoni*
- Distribution of ? *Dyseohyus* sp.
- Boundary between Geofloras

FIG. 13. Distribution of the late Miocene species of *Cynorca* and *Dyseohyus* relative to the broad physiographic and climatic elements of North America. Reconstructions of the coastlines are adapted from Eardley (1962); river systems, from Flint (1957); distribution of tectonic elements, from Hunt (1956) and Van Houten (1961). Paleobotanical and climatic reconstructions are from sources cited in the text. Boundaries between geofloras are approximate. Note that the Nevada sample of ?*Dyseohyus* sp. is of Clarendonian age. This population may have moved from Colorado to Nevada during this time or may have already occupied much of the area in the late Miocene.

process. Possibly beginning in Colorado, Montana, or Nebraska, a local population of *C. sociale* may have given rise to *C. occidentale* which also went through an adaptation to drier conditions during the middle Miocene. The population from which the large ?*Dyseohyus* sp. arose is unknown. It apparently occupied an area of relatively xeric conditions extending southwestward from Colorado to Nevada.

Other species apparently retained the original general ecologic adaptation of *C. sociale*. If *C. hesperia* is a valid entity, it probably represents evolution in place from a local population of the former species. It is likewise possible that *C. proterva* arose from a population of *C. sociale* centered near the Gulf coast. In the same area, a population with a morphology approximately intermediate between that of *C. sociale* and that of *Dyseohyus stirtoni* apparently occupied another segment of the general moist, warm-temperate habitat. *Dyseohyus stirtoni* may have arisen from this intermediate population, subsequently developing into the dominant peccary of the *Dyseohyus-Cynorca* complex in an area extending from the Plains states as far south as Texas.

In terms of the fossil peccaries treated in this report, a single biotic province could have extended from Oregon to Nebraska, and south to Texas and possibly the Atlantic coast in the early Miocene. In middle Miocene this province was undergoing disintegration. Local centers of biological diversity are found in Texas, the Montana-Wyoming-Nebraska area, and in southern California.

By the late Miocene *Dyseohyus fricki* and *Cynorca occidentale* were apparently confined to a relatively dry, southern province of the West coast. *Dyseohyus* sp. may indicate the presence of a province in the southern Great Basin, Colorado Plateau, and adjacent areas in which the climatic conditions were also relatively dry. *Dyseohyus stirtoni* occupied a third province east of the Rockies from Nebraska to Texas. This province apparently overlapped the peripheral digitations of a primarily coastal province characterized by the presence of *Cynorca proterva*. The validity of an additional province in the northwestern states (characterized by *Cynorca hesperia*) remains to be tested. Whether

the biotic provinces inferred from tayassuid evidence will prove to resemble those constructed from other biotic data or not remains to be seen. These provincial reconstructions represent imperfect interpretations based on oddments of preservation. If they do no more than promote critical thought on the subject, the purpose of this exercise will have been accomplished.

#### EVOLUTION OF *CYNORCA* AND *DYSEOHYUS*

Although data on the morphology of its cranium are rather meager, *Cynorca* can be shown to be the first member of the second major evolutionary radiation of the Tayassuidae. This radiation produced the living peccaries *Dicotyles* and *Tayassu* and, seemingly, the common Pliocene and Pleistocene genera of North and South America.

As represented by *Perchoerus* and *Thinohyus*, the following summary of the salient features of the primitive peccaries will provide a frame of reference for evaluating the phyletic position of *Cynorca*. In these primitive peccaries, the snout is devoid of well-defined depressions that can be associated with muscle origins. The buccinator fossa, for instance, is not present, and because of the presence of a complete premolar dentition there are no diastemal crests. In addition, the lateral surfaces of the snout diverge evenly posteriorly and merge with the anterior end of the zygomatic arch. In these primitive forms the facial crest does not have a distinctly developed anterior tip. The lacrimal is broadly exposed anterior to the orbit.

In ventral view the palate extends posterior to M<sup>3</sup> in varying degrees. In other features, P<sup>4</sup> is non-molariform and there are no long diastemata posterior to P<sup>1</sup>.

Farther posteriorly the ventral surface of the bulla lies below the level of the glenoid fossa in the primitive genera, and the bulla is not filled with cancellous tissue. There is a direct bony connection between the medial base of the glenoid and the adjacent bulla as well as a broad connection between the latter and the paroccipital process. Above the bullae, the posttympanic process of the squamosal is sulcate, and the base of the paroccipital process forms a heavy triangular

boss which projects laterally. Dorsomedial to the paroccipital process the lambdoidal crest descends nearly vertically to merge with the occiput above the lateral edge of the foramen magnum. Anterior to the basal half of the lambdoidal crest the occipital and temporal regions are freely confluent because the postzygomatic crest blends into that portion of the squamosal which forms the medial surface of the temporal fossa. The postzygomatic crest thus lies anterior to, and does not come in contact with, the lambdoidal crest.

Except for the less well-developed digastric fossa and the shorter postcanine diastema, the mandible of the primitive peccaries is not remarkably different from that of *Cynorca*.

Although not all the above features can be compared with those of *Cynorca*, the more advanced nature of this genus with respect to *Perchoerus* or *Thinohyus* can still be shown by the available material. The incipiently developed buccinator fossa in *C. sociale* not only heralds the larger structure in *Dyseohyus* and the Recent genera but is also associated with a definite diastema between  $P^1$  and  $P^2$ . Furthermore, the extremely small size of  $P^1$ , its isolation from the rest of the premolar dentition, and the absence of  $P_1$  indicate that the first upper premolar is in the process of phyletic reduction. Although it is not now possible to determine whether or not  $P^1$  was similarly lost in later species of *Cynorca*, it is certainly absent from *Dyseohyus* and the later peccaries. *Cynorca* has little definite evidence to offer regarding the presence of depressions on the lateral surface of the snout for the origin of such muscles as Mm. dilator naris lateralis and depressor rostri. On the other hand, available fragments of the base of the zygomatic arch in *C. sociale* are similar to comparable areas in *Dyseohyus*, which permits the tentative suggestion that depressions for such muscles listed above might have been present in the small Miocene genus (see p. 290).

The palate ends closely behind  $M^3$  in *Cynorca*, a position similar to that found in some specimens of *Perchoerus* and *Thinohyus*. *Cynorca sociale* is advanced over the primitive peccaries in the presence of diastemata, the reduced nature of  $P^1$ , and the absence of  $P_1$ . The last premolar is still non-molariform

in this species, but in later members of the genus, as well as in its derivative, *Dyseohyus*,  $P^4$  is increasingly molariform.

The glenoid fossa in *C. sociale* lies at a lower level relative to the ventral edge of the bulla than in the earliest of the primitive peccaries. The bullae of *C. sociale* are advanced in having a cancellous internal filling and lacking bony connections with the glenoid and with the paroccipital process. *Cynorca* is primitive in its sulcate posttympanic process, but advanced in its lightly constructed paroccipital process. Unfortunately the status of the degree of confluence between the temporal and occipital regions is not determinable from the specimens at hand. The system of a continuous lambdoidal-postzygomatic crest in *Dyseohyus* is prophetic of the sharp separation between these two regions in the later peccaries, and it is possible that *Cynorca* was intermediate between the primitive genera and *Dyseohyus*.

Unfortunately the configuration of the lacrimal is not definitely determinable in *Cynorca*, but, as indicated on page 290, it was probably like that of *Dyseohyus* and not that of the primitive peccaries.

In addition, the mandibles of *Cynorca* and *Dyseohyus* are notable for their well-developed digastric fossa and relatively long postcanine diastema.

As shown by the available material, *Cynorca* is apparently the ancestor of *Dyseohyus* and certainly is more similar to that genus than it is to *Thinohyus* or *Perchoerus*. Similarities between *Cynorca* and *Dyseohyus* include the presence of the buccinator fossa, the adjacent diastemal crest, the prominent postcanine diastema, the probable configuration of the lateral surface of the snout, the presence of cancellous tissue in the bullae, the absence of a strong connection between the bulla and both the postglenoid and paroccipital processes, the slender nature of the paroccipital process, the absence of  $P_1$ , the presence of a long, lower, postcanine diastema, and the presence of a well-developed digastric fossa in the mandible.

Furthermore, the more advanced position of *Dyseohyus* relative to its probable ancestor, *C. sociale*, is shown by the loss of  $P^1$ , the more molariform upper premolars, the



anterior position of the anterior palatine foramina, the posterior extension of the palate, the lower position of the glenoid fossa relative to the bulla, and the flat posttympanic process of the squamosal.

The structural position of *Dyseohyus* relative to the later peccary genera is yet to be documented in detail. In general, however, such features as the phyletic loss of  $P_1^1$ , the presence of definite postcanine diastemata, the presence of fossae or depressions which may be associated with the origins of Mm. buccinator, dilator naris lateralis, and depressor rostri, the limited facial exposure of the lacrimal, the posterior elongation of the

palate, the low position of the glenoid fossa relative to the bullae, and the definite separation of the temporal and occipital regions show that *Dyseohyus* is certainly at the proper stage of development to be the potential ancestor of most later peccaries, including the living *Tayassu*. As pointed out elsewhere (Woodburne, 1968), the ancestry of *Dicotyles* is not readily resolvable at present, although it seems to have been associated to some extent with the lineage that produced *Platygonus*. Whether or not the ultimate ancestry of the broad *Platygonus-Dicotyles* lineage is to be found in *Dyseohyus* remains to be seen.

### A PHYLOGENY OF CYNORCA AND DYSEOHYUS

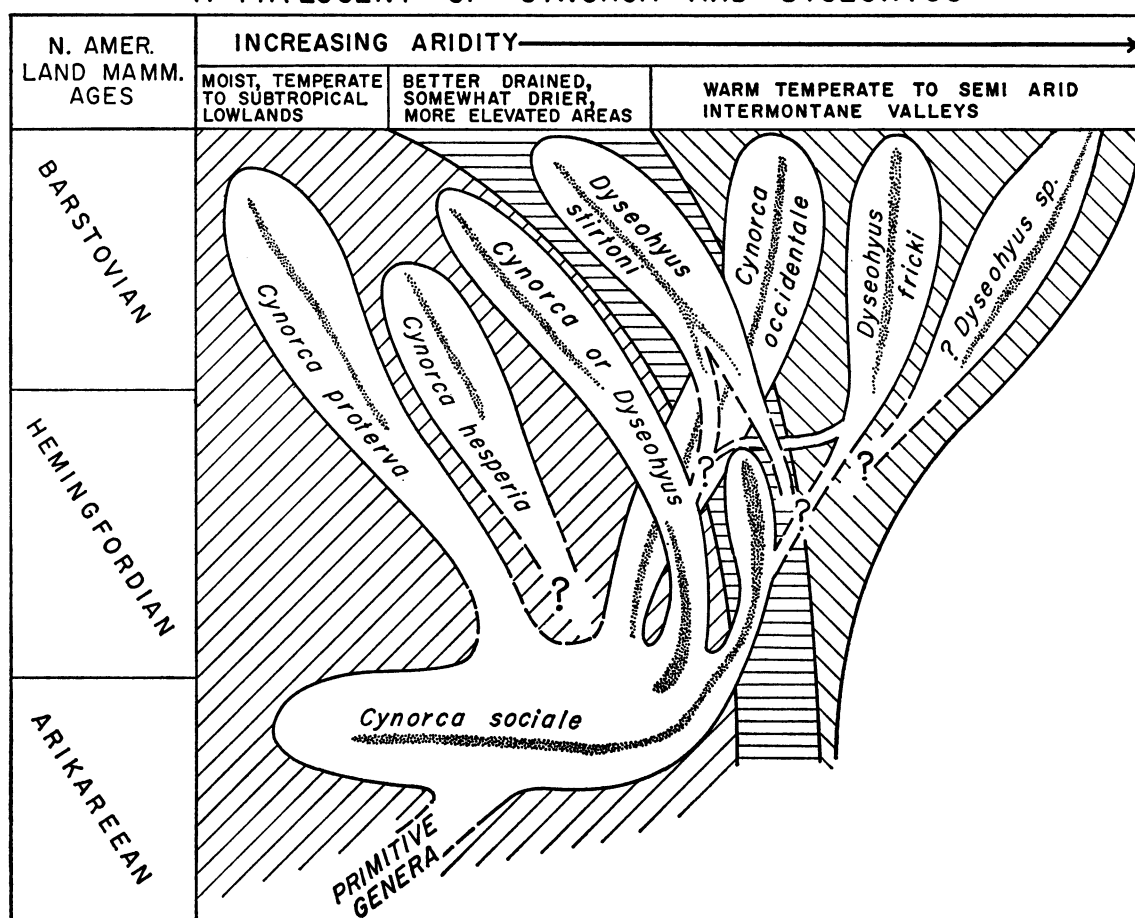


FIG. 14. Phylogeny of *Cynorca* and *Dyseohyus* in conjunction with the major climatic adaptive zones entered by the various species. The lobes indicate the probable extent of the lineages. The stippling within the lobes indicates the actual biochronological extent of the relevant specimens. *Dyseohyus* sp. continues into the Clarendonian.

For reasons presented above, *Cynorca sociale* is probably the ancestor of the later species of that genus as well as of *Dyseohyus*. The basal species of *Cynorca*, *C. sociale*, may have been relatively widely distributed, particularly if the Nebraska material treated as *Cynorca* cf. *C. sociale* is included, and ranges from Arikareean to Hemingfordian. *Cynorca sociale* may have given rise to three other species of the genus, but the taxonomic status of the late Hemingfordian to early Barstovian *C. hesperia* is uncertain. *Cynorca occidentale* apparently ranges from early Hemingfordian to late Barstovian. In Barstovian members of *C. occidentale* and in *C. hesperia*, P<sup>4</sup> is more molariform than that in *C. sociale*, but, because of the absence of comparable material in *C. proterva*, it is not possible to determine whether or not incipient premolar molarization was a general evolutionary feature of *Cynorca*. Since *C. proterva* is known from early Barstovian faunas, in order to be general, such an advance would have had to have occurred by at least late Hemingfordian time. Because the molar specializations achieved by the later species of *Cynorca* differ in individual ways, from species to species, from the basic plan seen in *C. sociale*, neither *C. proterva*, nor *C. hesperia*, nor *C. occidentale* is demonstrably intrinsically more primitive or more advanced than any other. Each of the three species probably lived during the same period of time, notwithstanding the earlier demonstrable geochronologic range of *C. occidentale*. In addition, none of the three species apparently gave rise to any other taxon.

Of the two species of *Dyseohyus*, *D. fricki* is the more primitive. At least the proportions of its molars and the relative degree of specialization of its premolars more closely approximate the stage of evolution occupied by *C. sociale* than do the comparable elements of *D. stirtoni*. Both *D. fricki* and *D. stirtoni* lived during about the same interval of time, and their respective lineages were well established by the Barstovian.

Information concerning the derivation of *Dyseohyus* from *Cynorca* is not abundant. If specimens designated as *Dyseohyus* or *Cynorca* (p. 334) are associated with the lineage leading between these two genera, the follow-

ing reconstruction may indicate the mode of this evolution.

The western specimens of *Dyseohyus* or *Cynorca* from California are in some ways intermediate between *Cynorca sociale* (as represented by the Oregon material) and *Dyseohyus fricki*. On this basis, the evolutionary pathway by which *D. fricki* was evolved may have followed this route and may have occurred in western North America.

Similarly, there is some reason to consider the Texas material of *Dyseohyus* or *Cynorca* to be intermediate between the Texas population of *C. sociale* and the large Barstovian peccary from this area designated as *Dyseohyus stirtoni*.

If so and if the Oregon and Texas samples of *C. sociale* are considered as geographic demes of the same species population, the genus *Dyseohyus* may be polyphyletic at the taxonomic level of a deme or subspecies. If so, the genus *Dyseohyus* would be a horizontal grade rather than a vertical clade, and philosophical considerations concerning the desirability of monophyletic derivation of taxonomic units would dictate that *D. fricki* and *D. stirtoni* be placed in separate genera.

The reason that such a procedure is not advocated at this time is based on the following lines of thought. First, the number of specimens available for all populations of *C. sociale* is extremely small; consequently the degree of variation originally manifested on either a local or a pan-populational scale is not determinable. Second, the localities at which *C. sociale* has been recorded are few, and, although a possible distribution pattern for the species has been reconstructed (text fig. 11), it is highly interpretive. Therefore, boundaries between populations representing fossil demes or subspecies cannot be constructed, and adequate characterization of these populations cannot be supplied. It is not possible to make a firm choice as to whether *C. sociale* consisted of a number of morphologically disjunct groups or of a single, large, almost completely panmictic population.

In similar fashion, the vertical component of the population or populations leading toward *Dyseohyus* is at best imperfectly sampled; the spatial as well as morpho-

logical characteristics of such populations are almost unknown. In summary, although the meager evidence may be somewhat suggestive, documentation of the polyphyletic derivation of *Dyseohyus* from two local centers of *C. sociale* is manifestly impossible at the present time.

Although such derivation of the species of *Dyseohyus* may have occurred, the genus *Dyseohyus* still arose from a single species of *Cynorca*. Such a derivation tends to diminish the necessity for separating *D. fricki* and *D. stirtoni* generically and shows that, broadly speaking, *Dyseohyus* is still a clade. Combining the two species under one genus, at least for the time being, also makes sense from the viewpoint of their osteological characters. If separated, the degree of morphological distinction that would be present between the two monotypic genera would be less than that commonly found between most other peccary genera. In conclusion, be it ultimately shown to be a grade instead of a clade, the genus *Dyseohyus* as currently constituted occupies a clearly demonstrable intermediate position between *Cynorca* and the later peccaries. Moreover, *D. fricki* and *D. stirtoni* are more like each other than either is to any other genus or

species of peccary. To separate these two species into different genera without better evidence than is now available would be premature and would introduce unnecessary confusion and complexity into the situation.

The phyletic position of the two specimens referred to ?*Dyseohyus* sp. cannot be evaluated at this time. Although these specimens are larger than those of either *D. fricki* or *D. stirtoni*, they display features found in both of these better-known species.

The advanced nature of *D. stirtoni* is noted above (p. 332), and, of the species of *Cynorca* or *Dyseohyus*, this is the only taxon that is in a potentially demonstrable annectant position with respect to a later peccary species, *Prosthennops niobrarensis*. Thus, although the details of the origin of *Cynorca* from the primitive peccaries remains to be documented, a genetic thread can be traced from *Cynorca* to *Dyseohyus* and from *Dyseohyus* to the later peccaries. In this light, *Cynorca* occupies the basal position of the second major peccary radiation. This radiation produced such genera as *Prosthennops*, *Mylohyus*, *Tayassu*, *Platygonus*, and *Dicotyles*. A phylogeny of *Cynorca* and *Dyseohyus* is presented in text figure 14.

## SUMMARY

THE GENUS *Cynorca* COPE, 1867, is a small peccary of Miocene age which stands at the base of the second evolutionary radiation of the Tayassuidae. Although its ancestry has not been brought to light, the genus probably arose from *Thinohyus* or *Perchoerus*, primitive genera that range in age from early Oligocene to early Miocene. The oldest known species of *Cynorca* is *C. sociale* (Marsh, 1875), recorded from deposits of early Miocene age in Oregon, Texas, and possibly Nebraska. *Cynorca sociale* was probably adapted to a relatively moist, temperate climate.

Three species of *Cynorca* are recognized as having been derived from *C. sociale*. *Cynorca proterva* Cope (1867), the genotypic species, is known from deposits of probably early late Miocene age in Maryland, South Carolina, Texas, and Nebraska. Although the evidence is imperfect, it is likely that *C. proterva* arose from a local, coastal population of *C. sociale* sometime in the early or middle Miocene. Inasmuch as *C. proterva* has been recorded from primarily Eastern and Gulf coastal localities, it almost certainly preferred moist, lowland habitats. This species apparently also ranged into areas such as western Nebraska along the courses of the major east-flowing tributaries of the proto-Mississippi River system. *Cynorca occidentale*, new species, is first found in middle Miocene deposits of the Montana-Wyoming-Nebraska area after having differentiated from a local population of *C. sociale*. Thereafter, in the late Miocene, *C. occidentale* was apparently restricted to areas of more xeric conditions in southern California. A third species, *C. hesperia* (Marsh, 1871), is of uncertain status. If a valid species, it lived in Oregon in late middle Miocene or early late Miocene time and was probably derived

from a northwestern population of *C. sociale*.

*Dyseohyus* Stock, 1937, is a larger and more advanced derivative of *Cynorca*. The more primitive of the two species, *D. fricki* Stock, 1937, is restricted to the late Miocene of California. *Dyseohyus fricki* is found in some of the same deposits as *C. occidentale* and probably was also adapted to relatively xeric conditions. *Dyseohyus fricki* may have been derived from a segment of the Oregon population of *C. sociale* that was invading drier habitats.

The more advanced species of *Dyseohyus*, *D. stirtoni*, new species, is found in deposits of late Miocene age in Colorado, Nebraska, and Texas. *Dyseohyus stirtoni* was apparently adapted to somewhat drier conditions than the geologically and geographically proximal species, *C. proterva*. Specimens known as *Dyseohyus* or *Cynorca* from Texas range in age from early to late Miocene. If this group of specimens represents a single species, it may have given rise to *D. stirtoni* and was, in turn, derived from *C. sociale*. Inasmuch as both *D. fricki* and *D. stirtoni* were probably derived from the same species of *Cynorca* (*C. sociale*), they can be considered as pertaining to one genus. *Dyseohyus*, as currently constituted, might be polyphyletic at the subspecies level, but the evidence is not adequate for a definitive decision. Aside from *C. sociale*, which was ancestral to *Dyseohyus*, and *D. stirtoni*, which probably gave rise to some of the later peccary species such as *Prosthennops niobrarensis*, all other species of the two genera reviewed in this report are terminal lineages. A large form, ?*Dyseohyus* sp., from the late Miocene of Colorado and early Pliocene of Nevada, is aberrant and of uncertain ancestry. As far as can be determined, it, too, represents a terminal lineage.

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