

PROMERYCOCHOERINAE, A NEW SUBFAMILY OF OREODONTS

C. BERTRAND SCHULTZ AND
CHARLES H. FALKENBACH

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INTRODUCTION

THE PRESENT REPORT, the fourth in the series concerning a revision of the oreodonts (Merycoidodontidae), deals with six closely related genera and subgenera, *Promerycochoerus* Douglass, *P. (Parapromerycochoerus)*, new subgenus, *P. (Pseudopromerycochoerus)*, new subgenus, *Mesoreodon* Scott, *Promesoreodon*, new genus, and *Merycoides* Douglass, which are here listed under the new subfamily Promerycochoerinae. The subfamily includes forms with moderately small to very large-sized skulls, second in size only to some of the forms referred to the Desmatochoerinae, to be discussed in a later paper. The Promerycochoerinae are widely distributed and have been reported from the Whitney through the Harrison or their approximate equivalents in age. The geological distribution of the Promerycochoerinae, compared with that of the Merycochoerinae, Ticholeptinae, and Merychyinae (the three subfamilies previously reported on by the writers), is presented in chart 1 (p. 80). The geographic distribution of these same subfamilies is compared in chart 2 (p. 82).

The occurrence of similar forms of the Promerycochoerinae in the John Day and in the central Great Plains suggests the approximate equivalence in age of the two areas. The interpretation of the comparable stratigraphic relationships of the Oregon deposits with those of the central Great Plains is illustrated in chart 3 (p. 83). (See discussion, p. 89.)

When the writers first undertook the study of the oreodonts and their distribution it soon became apparent that many of the species currently referred to *Promerycochoerus* were unrelated and that many of the oreodont genera had to be considered before a revision of this genus could be undertaken. The method of approach in the present revision has been discussed in a recent report.¹

In the following pages, 331 numbered skulls, mandibular rami, and skeletal elements are listed or described under the four named genera (of which one is new) and two

subgenera (both of which are new). Sixty of these specimens, representing 16 species and eight subspecies (of which four species and four subspecies are new), are illustrated in detail (including 10 refigured types) in 26 text figures. The drawings are reproduced at one-third and one-half actual size. Figure 1, an outline drawing, is reproduced at one-half natural size for comparison with figures of the same scale in this and previous reports.

The figures illustrate the range in size, shape, and proportions of the skulls, rami, and skeletal elements; individual variation is shown by drawings of specimens found associated in the field.

The writers reiterate their appreciation of the aid and encouragement of the scientists and associates to whom acknowledgment has previously been made²; and to Chancellor R. G. Gustavson of the University of Nebraska for encouragement in the continuation of the research; Dr. Frederic B. Loomis of Amherst College, Mr. Eustace L. Furlong and Dr. Chester Stock of the California Institute of Technology, Dr. Elmer S. Riggs of the Chicago Natural History Museum, Dr. Glenn L. Jepsen of Princeton University, Dr. Charles L. Camp of the University of California, and Dr. Malcolm R. Thorpe of the Yale Peabody Museum for the loan of, or the privilege of examining, the various specimens listed in this paper. To all these and many others the writers are grateful for making the present report possible.

The new material and the stratigraphic data used in this study have been gathered by party leaders and their associates to whom acknowledgments have previously been made² and by Messrs. E. L. Blue, Frank Crabill, Robert Long, and Eugene Vanderpool of the University of Nebraska State Museum. The Frick Laboratory and the University of Nebraska State Museum collections served as the basis for the present revision, except for the John Day forms.

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1947, Bull. Amer. Mus. Nat. Hist., vol. 88, art. 4, pp. 166-167.

² Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, Bull. Amer. Mus. Nat. Hist., vol. 77, art. 5, p. 216; 1941, *ibid.*, vol. 79, art. 1, p. 4; 1947, *ibid.*, vol. 88, art. 4, p. 165.

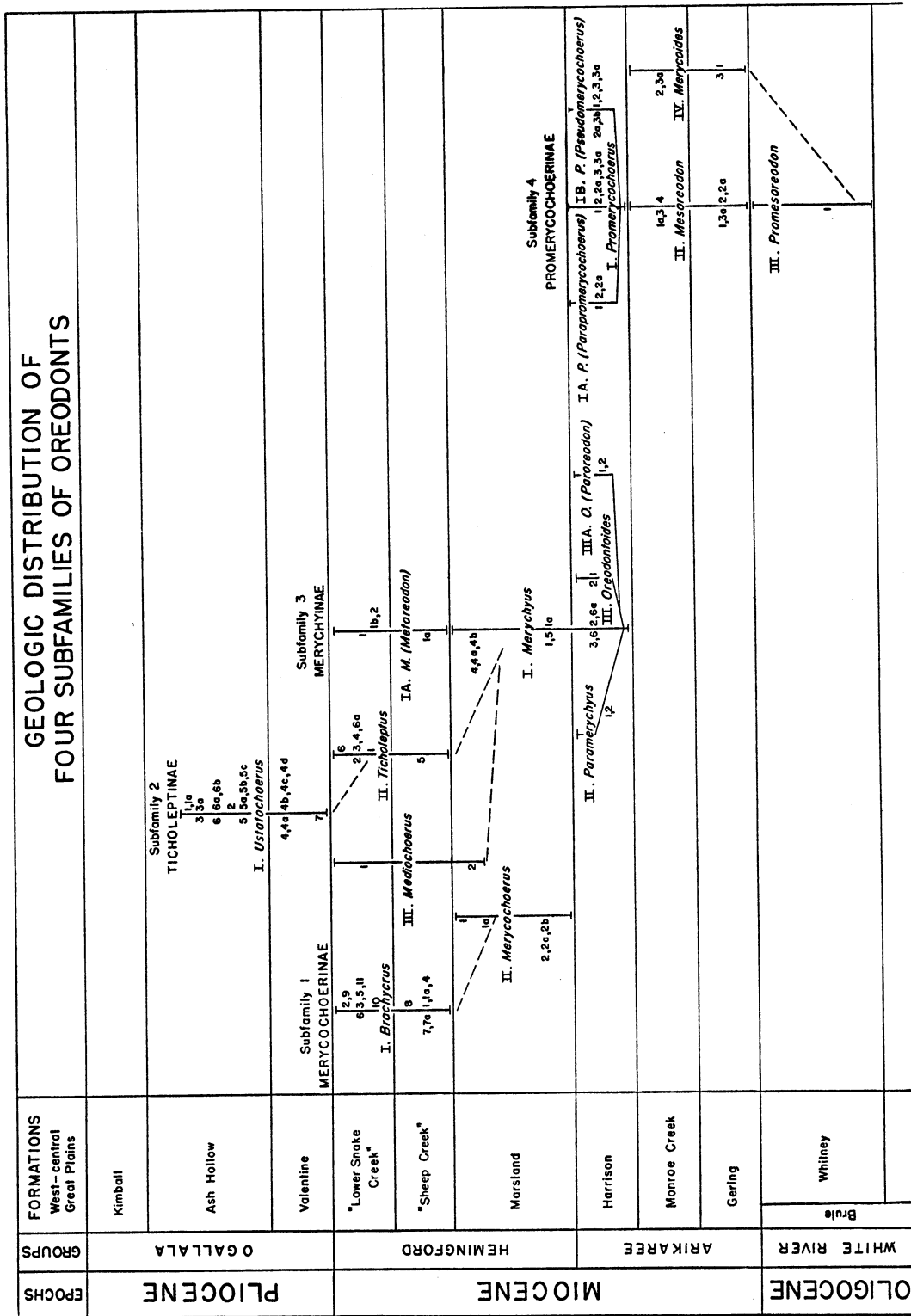


CHART 1. Stratigraphic distribution of the four subfamilies: Merycochoerinae (subfamily 1, Schultz, C. Bertrand, and Charles H. Fal-
kenbach, 1940, *ibid.*, vol. 77, art. 5, pp. 213-306), Ticholeptinae (subfamily 2, 1941, *ibid.*, vol. 79, art. 1, pp. 1-105), Merychyinae (sub-
family 3, 1947, *ibid.*, vol. 88, art. 4, pp. 161-285), and Promerycochoerinae (subfamily 4, present report).

EXPLANATION OF CHART 1. The known geological limitations of each genus and subgenus are indicated by a solid vertical line with a horizontal bar at either end. Where the relationship between two genera is not definite a broken line is used. The middle and upper Tertiary section of the west-central Great Plains (northeastern Colorado, Nebraska, South Dakota, and eastern Wyoming) is used as the basis for the geological scale. The limited meanings of the "Lower Snake Creek" and "Sheep Creek" are here used (footnote 2, p. 83).

The numbers in the tables of contents of the four oreodont papers mentioned above are used as the key for the identification of the species and subspecies. The numbers to the left of the vertical line indicate species or subspecies from the west-central Great Plains; those to the right, from localities outside this area.

- Subfamily 1. Merycochoerinae
I. *Brachycerus* Matthew
1a. *B. buwaldi* (Merriam)
1a. *B. buwaldi barstowensis* Schultz and Falkenbach
2. *B. alitramus* (Douglass)
3. *B. elrodi* (Douglass)
4. *B. madisonius* (Douglass)
5. *B. laticeps* (Douglass)
6. *B. stowneae* (Sinclair)
7. *B. wilsoni* Schultz and Falkenbach
7a. *B. wilsoni longensis* Schultz and Falkenbach
8. *B. rusticus* (Leidy)
9. *B. sweetwaterensis* Schultz and Falkenbach
10. *B. naughtani* Schultz and Falkenbach
11. *B.* species undetermined
II. *Merycochoerus* Leidy
1. *M. proprius* Leidy
1a. *M. proprius magnus* (Loomis)
2. *M. mathewi* Loomis; 2a, 2b, geographic varieties
3. *M.* species undetermined
Subfamily 2. Ticholeptinae
I. *Ustatocochus* Schultz and Falkenbach
1. *U. californicus* (Merriam)
1a. *U. californicus rabi* Schultz and Falkenbach
2. *U. compressidens* (Douglass)
3. *U. major* (Leidy)
3a. *U. major texanus* Schultz and Falkenbach
4. *U. medius* (Leidy); 4a, 4b, geographic varieties
4c. *U. medius mohavensis* Schultz and Falkenbach
4d. *U. medius novomexicanus* (Frick)
5. *U. profectus* (Matthew and Cook); 5a, geographic variety
5b. *U. profectus espanolensis* Schultz and Falkenbach
5c. *U. profectus studei* Schultz and Falkenbach
6. *U. curtus* (Loomis)
III A. *Oreodontoides* (*Paroreodon*) (Thorpe)
1. *O. (P.) marshi* (Thorpe)
2. *O. (P.) stocki* Schultz and Falkenbach
Subfamily 4. Promerycochoerinae
I. *Promerycochoerus* Douglass
1. *P. carrikieri* Peterson
2. *P. latidens* Thorpe; 2a, geographic variety
3. *P. superbus* (Leidy)
3a. *P. superbus chelydra* (Cope)
1A. *Promerycochoerus* (*Parapromerycochoerus*) Schultz and Falkenbach
1. *P. (P.) barbouri* Schultz and Falkenbach
2. *P. (P.) macrostegus* (Cope)
2a. *P. (P.) macrostegus furlongi* Schultz and Falkenbach
II. *Promerycochoerus* (*Pseudopromerycochoerus*) Schultz and Falkenbach
1. *P. (P.) inflatus* (Thorpe)
2. *P. (P.) minor* (Douglass)
2a. *P. (P.) minor pygmyus* (Loomis)
3. *P. (P.) montanus* (Cope); 3a, geographic variety
3b. *P. (P.) montanus pinensis* Schultz and Falkenbach
II. *Mesoreodon* Scott
1. *M. cheeki* (Schlaikjer)
1a. *M. cheeki scotti* (Schlaikjer)
2a. *M. chelonyx* Scott
2a. *M. chelonyx wheeleri* (Koerner)
3. *M. megalodon* Peterson
3a. *M. megalodon sweeti* Schultz and Falkenbach
4. *?* *M. hesperus* (Stock)
III. *Promesoreodon* Schultz and Falkenbach
1. *P. scartoni* Schultz and Falkenbach
IV. *Merycoides* Douglass
1. *M. cursor* Douglass
2. *M. giganteus* Schultz and Falkenbach
3. *M. nebraskensis* Schultz and Falkenbach
3a. *M. nebraskensis blairi* Schultz and Falkenbach

CHART 2

GEOGRAPHIC DISTRIBUTION OF FOUR SUBFAMILIES OF OREODONTS

| | Calif. | Colo. | Ida. | Kan. | Mont. | Nebr. | Nev. | N. Mex. | Oreg. | S. Dak. | Tex. | Wyo. |
|--|--------|-------|------|------|-------|-------|------|---------|-------|---------|------|------|
| Merycochoerinae, subfamily 1 | | | | | | | | | | | | |
| <i>Merycochoerus</i> | | X | | | | X | | | | X | | X |
| <i>Brachycrus</i> | X | | | | X | X | | X | | | | X |
| Ticholeptinae, subfamily 2 | | | | | | | | | | | | |
| <i>Ustatochoerus</i> | X | X | | X | X | X | | X | | X | X | |
| <i>Ticholeptus</i> | X | | | | X | X | X | | X | | X | |
| <i>Mediochoerus</i> | | | | | | X | | | | | | |
| Merychyinae, subfamily 3 | | | | | | | | | | | | |
| <i>Merychys</i> | X | X | X | | X | X | | | | X | | X |
| <i>M. (Metoreodon)</i> | X | | | | | X | | X | | | | |
| <i>Paramerychys</i> | | | | | | | | | | X | | X |
| <i>Oreodontoides</i> | | | | | | | | | X | X | | |
| <i>O. (Paroreodon)</i> | | | | | | | | | X | | | |
| Promerycochoerinae, subfamily 4 | | | | | | | | | | | | |
| <i>Promerycochoerus</i> | | | | | X | X | | | X | X | | X |
| <i>P. (Parapromerycochoerus)</i> | | | | | | | | | X | X | | X |
| <i>P. (Pseudopromerycochoerus)</i> | | | | | X | | | | X | X | | X |
| <i>Mesoreodon</i> | X | | | | X | X | | | | | | X |
| <i>Promesoreodon</i> | | | | | | | | | | X | | |
| <i>Merycoides</i> | | | | | X | X | | | | | | X |

A list of abbreviations of institutions cited is as follows:

A.C., Amherst College
A.M., the American Museum of Natural History
C.I.T., California Institute of Technology
C.M., Carnegie Museum of Pittsburgh
C.N.H.M., Chicago Natural History Museum
F:A.M., Frick Collection American Mammals
(the American Museum of Natural History)

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

P.U., Princeton University

U.C., University of California

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

U.O., University of Oregon

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

W.M., Walker Museum

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

CHART 3

AN INTERPRETATION OF THE STRATIGRAPHIC RELATIONSHIPS OF CERTAIN DEPOSITS
IN THE GREAT PLAINS AND OREGON

| Epoch | Group | West-Central Great Plains | | Oregon | Index Oreodont Genera ¹ |
|-----------|-------------|----------------------------------|---|-----------------------------------|------------------------------------|
| | | Nebraska-Wyoming Section | South Dakota | | |
| PLIOCENE | Ogallala | Ash Hollow | | | <i>Ustatochoerus</i> |
| | | Valentine | | | |
| MIOCENE | Hemingford | "Lower Snake Creek" ² | | Mascall | <i>Brachycrus</i> |
| | | "Sheep Creek" | | | |
| | | Marsland (="Upper Harrison") | "Upper Rosebud" (in part) ³ | | <i>Merycochoerus</i> |
| | Arikaree | Harrison | | Upper John Day Middle John Day | <i>Promerycochoerus</i> |
| | | Monroe Creek | "Lower Rosebud" | | <i>Mesoreodon</i> |
| | | Gering | | | |
| OLIGOCENE | White River | Upper Brule | Whitney (="Leptauchenia zone") | | <i>Promesoreodon</i> |

¹ The genera listed are restricted to the formations indicated on this chart.² The limited meanings of the "Lower Snake Creek" and the "Sheep Creek" are here used. See Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, *ibid.*, vol. 77, art. 5, p. 242; 1941, *ibid.*, vol. 79, art. 1, p. 76.³ A portion of the deposits in South Dakota assigned to the "Upper Rosebud" are Pliocene in age.

DESCRIPTION OF PROMERYCOCHOERINAE, NEW SUBFAMILY 4¹

THE NEW SUBFAMILY, Promerycochoerinae, includes *Promerycochoerus* Douglass, *P. (Parapromerycochoerus)*, new subgenus, *P. (Pseudopromerycochoerus)*, new subgenus, *Mesoreodon* Scott, *Promesoreodon*, new genus, and *Merycoides* Douglass. The subfamily is characterized by small- to large-sized forms exhibiting a tendency towards brachycephalic skulls; a narrow supraoccipital region which is not fan shaped as in *Merycochoerinae*, *Ticholeptinae*, and *Merychyinae*; a small and shallow lacrimal fossa; an inflated muzzle with facial constriction; inflated bullae; brachyodont teeth; large C/ and P₁; and a posterior intermediate crest on P₃.

Remains of *Promerycochoerus*, *P. (Parapromerycochoerus)*, and *P. (Pseudopromerycochoerus)* have been discovered only in deposits which are approximately equal in age to the Harrison. *Mesoreodon* and *Merycoides* have been recorded from the earlier Gering and Monroe Creek formations or from geologic horizons which are considered to be equivalent in age. *Promesoreodon* is restricted to the still earlier Whitney member of the Brule formation.

I. PROMERYCOCHOERUS DOUGLASS

Promerycochoerus DOUGLASS, 1901, Amer. Jour. Sci., vol. 11, p. 82. MATTHEW, 1901, Mem. Amer. Mus. Nat. Hist., vol. 1, pt. 7, p. 396. LOOMIS, 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 17. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 104.

Paracotylops MATTHEW (in Merriam), 1901, Bull. Dept. Geol. Univ. California, vol. 2, no. 9, p. 296. THORPE, 1937, loc. cit.

GENOTYPE: *Promerycochoerus superbus* (Leidy).

CHARACTERS

SKULL: Large (slightly larger than examples of *Merycochoerus*); basal length rang-

ing from 266 to 350 mm.; width, from 190 to 322 mm.; brachycephalic; supraoccipital region narrow, produced posteriorly beyond occipital condyles with lateral wings moderately spread (in contrast to the fan-shaped occipital region of *Merycochoerus*); brain case inflated, comparatively small for size of skull; frontals wide, but with considerable individual variation; nasals long, with superior surface rounded and tendency towards slight anterior retraction; orbit rounded; malar deep below the orbit; zygomatic arch robust (lighter in supposed female examples); inferior border of arch curving downward from malar, then upward almost to the level of the sagittal crest, with tendency to extend posteriorly beyond the area above the postglenoid process; lacrimal fossa moderately small and shallow; infraorbital foramen above region of P₃-P₄; facial area depressed above the premolars; muzzle laterally expanded; premaxillae fused for short distance; occipital condyles moderately heavy; paroccipital process wide at base with lateral twist forward and with axis at angle to skull; bulla large, inflated, and round to oval in outline; postglenoid process blocky, and extended laterally; posterior palate projecting for slight distance beyond M₃.

MANDIBLE: Moderately robust but not to degree noted in *Merycochoerus*; postsymphysis below region of P₃-P₄; ramus shallow; ascending ramus long anteroposteriorly and comparatively shallow; condyle moderately large, placed at slight inward angle; inferior border of ramus usually parallel to alveolar border to a point below the posterior lobe of M₃, from which it curves downward sharply; posterior border of ascending ramus with a prominent inward curve at base.

DENTITION: Brachyodont; heavy; large, massive C/ and P₁; premolars slightly crowded but with tendency for a small diastema between P₁ and P₂; prominent anterior intermediate crest on P₂ and P₃ (often obscured by wear); weak posterior intermediate crest on P₃; anterior and posterior portions of P₄ separated by a high point or cusp.

LIMBS: Moderately robust; more massive and somewhat longer than examples of

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, Bull. Amer. Mus. Nat. Hist., vol. 77, art. 5, p. 215 (subfamily 1, *Merycochoerinae*); 1941, *ibid.*, vol. 79, art. 1, p. 6 (subfamily 2, *Ticholeptinae*); 1947, *ibid.*, vol. 88, art. 4, p. 168 (subfamily 3, *Merychyinae*). George G. Simpson (1945, Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 149, 263) tentatively placed *Promerycochoerus* under the subfamily *Merycochoerinae* (see discussion in present paper, p. 88).

DISTINCTIVE CHARACTERS OF THE PROMERYCOCHOERINAE¹

| DIAGNOSTIC CHARACTERS | <i>Promerycochoerus</i> (P. 84, figs. 1-5, 11-14, 25, 26) | <i>P. (Parapromerycochoerus)</i> (P. 114, figs. 5-7, 11, 12) | <i>P. (Pseudopromerycochoerus)</i> (P. 121, figs. 6, 8-12, 25, 26) | <i>Mesoreodon</i> (P. 131, figs. 7, 15-20, 25, 26) | <i>Promesoreodon</i> (P. 152, figs. 21-25, 25) | <i>Merycoides</i> (P. 153, figs. 7, 21-24) |
|--|--|---|---|---|---|--|
| Anterior nasal-maxilla contact above | P ¹ | P ¹ | P ¹ -P ² | P ¹ | P ¹ | P ² |
| Infraorbital foramen above | P ² -P ⁴ | P ⁴ -M ¹ | P ⁴ | P ² -P ⁴ | P ³ | P ² -P ⁴ |
| Bulla | Tendency to be moderately high and suboval in outline | Moderately high and narrow | High and narrow | Moderately high to high, suboval | Moderately high, suboval | Low to moderately high, suboval |
| Zygomatic arch | Robust | Robust, rising higher than in <i>Promerycochoerus</i> | Light | Light to moderately robust | Light | Light |
| Inferior border of ramus | Abrupt downward curve below 3d lobe of M ₃ | As in <i>Promerycochoerus</i> | As in <i>Promerycochoerus</i> | Gradual downward curve | (Unknown) | Gradual downward curve |
| Dentition | Brachyodont (less so than in <i>Mesoreodon</i>) | Brachyodont (lighter than in <i>Promerycochoerus</i>) | Brachyodont | Brachyodont | Brachyodont (more so than <i>Mesoreodon</i>) | Brachyodont (similar to <i>Promesoreodon</i>) |
| Anterior intermediate crest on premolars | P ² -P ³ | P ² -P ³ | P ² -P ³ | P ¹ -P ³ | P ¹ -P ³ | P ¹ -P ³ |
| Limbs | Moderately heavy | Moderately heavy | Lighter than in <i>Promerycochoerus</i> | Moderately short and heavy | Short and light | Lighter than in <i>Mesoreodon</i> |

¹ Compare with Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, 1941, and 1947, *ibid.*, pp. 216, 6, and 168, respectively.

CHART 4

GEOGRAPHIC DISTRIBUTION OF

Promerycochoerus, *Promerycochoerus* (*Parapromerycochoerus*), *Promerycochoerus* (*Pseudopromerycochoerus*),
Mesoreodon, *Promesoreodon*, and *Merycoides*

[illegible]

CHART 4—(Continued)

| | | Lower Miocene Localities | | | | | | | | | | | | Oligocene Localities | | | | | |
|------------|---|--------------------------|-------------|---------------|-------------|--------------|-----------|----------------|----------------|---------------|-------------|------------------|--------------|----------------------|--------------|------------|--------------|----------------|----------------|
| | | Calif. | Montana | | | South Dakota | | | | Oreg. | Nebraska | | | Wyoming | | | South Dakota | | |
| | | Ventura Co. | Granite Co. | Jefferson Co. | Meagher Co. | Shannon Co. | Tripp Co. | Washabaugh Co. | Washington Co. | John Day Area | Morrill Co. | Scotts Bluff Co. | Sheridan Co. | Sioux Co. | Converse Co. | Goshen Co. | Niobrara Co. | Washabaugh Co. | Washington Co. |
| Mesoreodon | <i>M. cheeki</i> (1) (Gering) | | | | | | | | | | X | | | | | T | X | | |
| | <i>M. cheeki scottii</i> (1a) (Monroe Creek) | | | | | | | | | | X | | | X | X | | T | | |
| | <i>M. chelonyx</i> (2) (Gering equiv.) | | | X | T | | | | | | | | | | | | | | |
| | <i>M. chelonyx wheeleri</i> (2a) (Gering equiv.) | | | | T | | | | | | | | | | | | | | |
| | <i>M. megalodon</i> (3) (Monroe Creek) | | | | | | | | | | X | | | T | | | X | | |
| Promesodon | <i>M. megalodon sweeti</i> (3a) (Gering) | | | | | | | | | | T | | | | | X | X | | |
| | ? <i>M. hesperus</i> (4) (Monroe Creek equiv.) | T | | | | | | | | | | | | | | | | | |
| Merycoides | <i>P. scanloni</i> (1) (U. Brule = Whitney) | | | | | | | | | | | | | | | | | T | X |
| | <i>M. cursor</i> (1) (Gering equiv.) | | | T | | | | | | | | | | | | | | | |
| | <i>M. giganteus</i> (2) (Monroe Creek) | | | | | | | | | | | | | | | | T | | |
| | <i>M. nebraskensis</i> (3) (Gering) | | | | | | | | | | | | T | | | | | | |
| | <i>M. nebraskensis blairi</i> (3a) (Monroe Creek) | | | | | | | | | | | | | | | | | | |

¹ T, Locality of holotype (and referred specimens when known).² In all instances an approximate equivalent is inferred.

Merycochoerus matthewi from the lower Marsland formation.

MEASUREMENTS: Tables 1, 2, and 3.

ILLUSTRATIONS: Figures 1-5, 11-14 (skulls, mandibles, and dentitions); 25, 26 (limbs).

DISCUSSION

It seems desirable to discuss in some detail the establishment of the genus *Promerycochoerus*. The generic name was first used by Earl Douglass¹ only provisionally, because Douglass was acquainted with the fact that W. D. Matthew had prepared a manuscript for publication describing the same genus. John D. Merriam also was interested in the oreodonts from the John Day beds and had the use of Matthew's manuscript. Merriam² published the following statement, using Matthew's "manuscript" name, *Paracotylops*: "As *Merycochoerus* does not occur in the John Day, the upper division will be called the *Paracotylops* beds. This name is based on the new generic name proposed by W. D. Matthew for the Upper John Day oreodonts, originally supposed to be *Merycochoerus*." Since this was in the same year (1901) that Douglass published his report, perhaps Matthew had not received Douglass' paper prior to forwarding the manuscript to Merriam, or had failed to replace the name *Paracotylops* with *Promerycochoerus*.

Matthew,³ upon receiving Douglass' paper, however, changed his own manuscript and published the following statement: "Mr. Douglass used this name [*Promerycochoerus*] only 'provisionally' (Am. Jour. Sci., 1901, vol. 11, p. 82) in order to avoid anticipating my previously written but until now unpublished work on the subject. While appreciating his courtesy in the matter, I think it will avoid possible confusion to use his name, as it was published with a valid definition."

William J. Sinclair,⁴ also reporting on the same subject, stated: "It now appears that *Promerycochoerus* should be retained as a generic name, and consequently, at Professor Merriam's suggestion, the name of beds of the

upper division has been changed from *Paracotylops* to *Promerycochoerus* beds."

Unfortunately the type material of *Promerycochoerus superbis* (Leidy), the genotypic species, includes only fragmentary specimens. The holotype designated by Douglass apparently has been lost. Since 1888, the skull A.M. 7431 in the Cope collection from the John Day, the first well-preserved specimen of *P. superbis* to be illustrated,⁵ has been figured⁶ and widely cited as a typical example of this species. The specimen (this paper, fig. 11) is an excellent example upon which to base generic and specific characters. As far as it is possible to compare, Leidy's original illustration of the holotype agrees readily with the specimen from the Cope collection. The balance of the Leidy material is so incomplete that it is of no value in establishing definite generic or specific characters (see p. 107 for additional discussion concerning *P. superbis*).

In the past—primarily, perhaps, because geologic data have been lacking and the significant morphological characters have not been appreciated—a number of species referable to other genera have been erroneously assigned to *Promerycochoerus*.

As the name implies, it has been assumed that *Promerycochoerus* gave rise to *Merycochoerus*. Peterson⁷ discussed to some extent the geologic history and the morphologic relationship of *Promerycochoerus* and *Merycochoerus*. The present writers plan to discuss the stratigraphic occurrence of these two genera and to review the ancestral possibilities of *Merycochoerus* in a forthcoming report on another subfamily. Concerning the phylogenetic relationship of the two genera, however, Peterson is here quoted: "Even granting that a long time elapsed between the formation of the deposits in which *Promerycochoerus* occurs and the deposits in which *Merycochoerus* is found [Harrison and Marsland, respectively] we are nevertheless confronted

⁵ Cope, E. D., 1888, Amer. Nat., vol. 22, pl. 26, fig. 2 (in part).

⁶ Scott, W. B., 1890, Morph. Jahrb., vol. 16, pl. 14, fig. 10; Zittel, K. A. von, 1911, Grundzuge der Paläontologie (Paläozoologie), div. 2, Vertebrata, fig. 675b; 1923, op. cit., fig. 716b.

⁷ Peterson, O. A., 1914, Ann. Carnegie Mus., vol. 9, nos. 1-2, p. 215.

¹ Douglass, Earl, 1901, loc. cit.

² Merriam, John C., 1901, loc. cit.

³ Matthew, W. D., 1901, *ibid.*, p. 398.

⁴ Sinclair, William J., 1901, Jour. Geol., vol. 9, no. 8, p. 703.

in the anatomy of *Promerycochoerus* with features which are obstacles to our regarding this genus as the direct ancestor of *Merycochoerus* . . . "

Peterson, using "*P. vantasselensis*" (= *P. carrikeri*) as an example, further pointed out that there is "no tendency of the superior incisors to become larger, no sudden retraction of the muzzle in front of the jugal, no shifting backward of the infra-orbital foramina. . . ." To this the present writers, who are in agreement with Peterson concerning the constancy of these characters in *Promerycochoerus*, might add that there is no tendency for the premaxillae to become joined for a longer distance, or for the brain case to become shortened. The large inflated bullae of *Promerycochoerus* are definitely different from the bullae of *Merycochoerus*, which are high and narrow. In the subgenus *P. (Parapromerycochoerus)*, however, the bullae are smaller and there is a tendency towards a slight anterior retraction of the nasals (see p. 114).

The amount of time unaccounted for between the closing of the Harrison formation—the age of the occurrence of *Promerycochoerus* and *P. (Parapromerycochoerus)*—and the beginning of the lower Marsland—the age of the earliest occurrence of *Merycochoerus*—or their approximate equivalents is thus far indeterminate. The few known lines of oreodonts that survived this hiatus did not change nearly so much as would be necessary for either *Promerycochoerus* or *P. (Parapromerycochoerus)* to give rise to *Merycochoerus*.

The writers further agree with Peterson that forms changed slowly. In the development of the oreodonts, the changes in some instances were more rapid than in others. It must be stressed that the rate of change in the various contemporaneous lines was not a constant factor. The seemingly sudden change from one genus to another must be due to the fact that the history of the line is not complete. A cause of the incomplete picture may be that the forms from the Harrison formation of the west-central Great Plains have been collected chiefly from the upper portion of the beds, because the lower section is usually represented by vertical bluffs which make collecting difficult. In other cases cer-

tain parts of a bed definitely are not productive of fossil remains.

In view of such definite evidence that *Promerycochoerus* did not give rise to *Merycochoerus*, the present writers prefer to place *Merycochoerus* under the Merycochoerinae and *Promerycochoerus* under the Promerycochoerinae. Simpson¹ provisionally considered both under one subfamily.

The genera *Desmatochoerus* Thorpe and *Hypselochoerus* Loomis are intentionally not shown in the synonymy with *Promerycochoerus* and will be discussed in a later paper on the subfamily Desmatochoerinae. Thorpe² considered both these genera to be synonymous with *Promerycochoerus*.

The occurrence of *Promerycochoerus* in the John Day deposits has been of interest for almost a half century. The genotypic species *P. superbus* was based on material from the John Day. Examinations of the various subsequent oreodont collections from this area have demonstrated that very little field or geological data for the various specimens are available. The collection in the California Institute of Technology is perhaps the best documented from this standpoint. The American Museum collection (Cope), which recently has been prepared by Carl C. Sorensen, includes the most complete material.

A brief review of the more important literature concerning the John Day beds may serve to clarify the opinions of various workers concerning the occurrence of *Promerycochoerus*. Chart 3 is an interpretation of the stratigraphic relationships of the John Day beds of Oregon to the Miocene deposits of the Great Plains.

Merriam,³ in a discussion of correspondence with J. L. Wortman, stated: "The collections made by the University of California parties have all been labeled as accurately as possible in the field with reference to horizons. . . . Judging from field observations alone, Dr. Wortman would be justified in his classification. The large *Paracotylops* [*Promerycochoerus*] forms were found to be principally, if not entirely, confined to the upper beds. . . ."

¹ Simpson, George Gaylord, 1945, Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 149, 263.

² Thorpe, Malcolm R., 1937, *loc. cit.*

³ Merriam, John C., 1901, Bull. Dept. Geol. Univ. California, vol. 2, no. 9, p. 297.

This statement seems to be the first appearance of the supposition that *Promerycochoerus* occurs primarily in the upper John Day.

In a suggested correlation of the John Day and the Mascall, Merriam and Sinclair¹ reported: "The Upper John Day has its closest affinities with the Middle John Day, and is probably in greater part Upper Oligocene, although it may overlap on the Lower Miocene. The Middle John Day is to be correlated with the *Protoceus* [*Protoceras*] horizon of the White River Oligocene. The lower limit of the Upper John Day is determined by the downward range of *Promerycochoerus* in the beds.

"This genus, which also occurs in the Mascall, and *Mylagaulodon angulatus*, gen. and sp. nv., and later types unite in a measure the gap between Upper John Day and the Mascall faunas."

It is evident from the above statement that the lower limit of the upper John Day is indefinite and the division of the upper from the middle John Day remains open to question. In reference to the occurrence of *Promerycochoerus* from the Mascall, it should be stated that "*Promerycochoerus*" *obliquidens* (Cope), listed by Merriam and Sinclair in the faunal list for the Mascall, does not belong to this genus but rather to *Ticholeptus*.²

Matthew,³ in making a comparison of the Rosebud fauna with that of the John Day, stated: "The Rosebud fauna is very clearly related to the John Day. The great majority of the species in the lower Rosebud and many of those of the upper beds can be referred to John Day genera but show, whenever adequate comparisons can be made, a very considerable advance upon species of the John Day."

Later Peterson⁴ added: "It has been pointed out by Matthew and the writer⁵ that in the Lower Arikaree deposits of the plains we not only have many new genera, but those which are related to forms found

in the John Day beds are always farther along in the trend of their evolutionary development, showing that they belong to a later period than the John Day."

These conclusions are not substantiated by the oreodont material now available. In the genus *Promerycochoerus*, *P. superbus* (presumably from the middle John Day) is the approximate size of examples of *P. carrikeri* from the Harrison formation. It can hardly be said that one is more primitive than the other. It is true, however, that in *P. carrikeri* the posterior border of the zygomatic arch is always hooked, while its ancestral form, *Mesoreodon megalodon*, has a straight posterior border on the zygomatic arch which is similar to that found on examples of *P. superbus*. Yet in *P. latidens* (presumably from the upper John Day), the examples of the skulls tend to be larger than either *P. superbus* or *P. carrikeri* and do have a straight posterior border of the zygomatic arch. Furthermore, in examples of *P. superbus chelydra* (presumably from the middle John Day), the skull is of a size approximately equal to examples of *P. carrikeri* and has a hooked posterior border to the zygomatic arch. Hence, in this instance, one could not say that either form is more primitive.

In general the examples of the *Promerycochoerinae*, which presumably come from the middle John Day, are equal in size and characters to those forms from the Harrison of the west-central Great Plains. The specimens reported from the upper John Day are larger than those from the Harrison but are still typical of the Plains forms and are not so specialized as *Merycochoerus* from the Marsland formation of the Plains.

Matthew's conclusions, as previously quoted, were drawn mostly from the carnivore and rodent material. Until a stratigraphic study of the occurrence of these remains is made, it does not seem possible to determine definitely that the fossils of one area show more primitive characters than those from the other area. Peterson's conclusions were based in part on a misconception of the Miocene stratigraphy in the west-central Great Plains. For example, he considered *P. carrikeri* as coming from the "Monroe Creek Beds." Yet *Promerycochoerus*

¹ Merriam, John C., and William J. Sinclair, 1903, Jour. Geol., vol. 11, no. 1, p. 96.

² Schultz, C. Bertrand, and Charles H. Falkenbach, 1941, Bull. Amer. Mus. Nat. Hist., vol. 76, art. 1, p. 82.

³ Matthew, W. D., 1907, Bull. Amer. Mus. Nat. Hist., vol. 23, art. 9, p. 173.

⁴ Peterson, O. A., 1914, Ann. Carnegie Mus., vol. 9, nos. 1-2, p. 218.

⁵ Peterson, O. A., 1906, *op. cit.*, vol. 4, no. 1.

forms are known only from the Harrison formation or its approximate equivalents.

It should also be stated that there are other forms of oreodonts from the John Day which are generically different from those of the Great Plains, but which are reported to be associated with *Promerycochoerus*. Perhaps the smaller of these John Day forms occur in a lower horizon than the *Promerycochoerus* specimens, but these smaller examples also are different from the forms from the Gering and Monroe Creek formations of the Great Plains.

In the *Promerycochoerinae* it is evident that vertical lines of development in some instances evolved locally after a first migration had taken place. That is, the lines in the John Day region evolved locally as did the lines in the Great Plains. This difference in the vertical line of development in separate localities is also quite apparent in the genus *Brachycrus*,¹ which shows four independent lines of progress in California, Nebraska, Montana, and Wyoming.

There are two possible explanations for the fact that the species of *Promerycochoerinae* from the upper John Day are larger than those from the west-central Great Plains:

1. Most of the examples of *Promerycochoerus carrikeri* from Nebraska and Wyoming have been collected from horizons close to the top of the Harrison formation as known in those areas. It is possible that the species representing this subfamily from the middle John Day are of the same geological age as those from the lower part of the Harrison formation. If so, the John Day lines may have evolved contemporaneously at a faster rate than those from the Great Plains, thus resulting in larger forms. An example supporting this possibility is found in *P. (Parapromerycochoerus)* where *P. (P.) macrostegus furlongi*, new subspecies, from presumably middle John Day deposits, is definitely larger than the closely related new species *P. (P.) barbouri* from the Harrison of the Great Plains.

2. The upper John Day may represent the period of time between the close of the Harrison and the beginning of Marsland

times in the Plains, but it is distinctly a part of Harrison, not Marsland, times. The genus *Merycochoerus* is known only from the Marsland formation or its equal, and no examples of this genus have been reported from the John Day beds. In some lines of oreodonts from the John Day beds, the increase in size between the middle and upper beds appears to be greater than that found later in the few generic lines that survived the hiatus between the Harrison and Marsland formations of the plains.

Matthew,² in a discussion of "The Pacific coast mammal faunas," stated: "The oldest of these is the John Day, which I regard as essentially a unit, although the occurrence of *Promerycochoerus* only in the upper part seems to divide it. There is very little else to separate the upper John Day, so far as has been shown, and both the upper and lower³ fauna are very largely identical with that of the Lower Rosebud, with the important exceptions that *Parahippus* is not found and that *Promerycochoerus* occurs only in the upper levels. For these reasons one may consider the John Day slightly older than the Rosebud, but decidedly later than the Upper White River [*Protoceras* beds]. I do not think there is any adequate reason to place it in a separate intermediate division but would rather class it with the Lower Rosebud."

The present writers consider that at least the upper portion of the "Lower Rosebud" is equal to the Harrison. It is not clear what Matthew used as a basis for his statement that "*Promerycochoerus* is found only in the upper John Day," but presumably it was Merriam's discussion (p. 89). On the basis of the various quotations and statements thus far given it may be seen that Matthew's conclusions as to the age of the John Day beds agree with the oreodont evidence, except for his statement that *Promerycochoerus* is limited to the upper John Day only.

Chester Stock⁴ gives additional evidence concerning the relationships of the faunas of

² Matthew, W. D., 1924, Bull. Geol. Soc. Amer., vol. 35, pt. 4, p. 751.

³ "Lower" apparently refers to the fauna from the middle John Day since oreodonts are unknown from the lower John Day.

⁴ Stock, Chester, 1930, Carnegie Inst. Washington Publ., no. 404, p. 31.

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, Bull. Amer. Mus. Nat. Hist., vol. 77, art. 5, p. 218.

the John Day: "In the Tertiary sequence of the John Day region of north-central Oregon the genus *Promerycochoerus* makes a sudden appearance in the upper John Day. The absence of this oreodont in the middle division of the John Day and the prevalence of the type in the upper deposits, early led Wortman to designate the latter as the *Merycochoerus* [*Promerycochoerus*] beds. Further palaeontological explorations in this region have tended to emphasize this distinction. Curiously enough, while much intensive collecting has been conducted in the John Day, members of the *Leptauchenia-Cyclopidius* group have been conspicuously absent from the entire assemblage."

This statement relating to the absence of *Leptauchenia* and *Cyclopidius* in the John Day is significant, since these two genera are not represented in the faunas of the Harrison or later formations of the Great Plains.¹ The geologic distribution of these two forms will be considered in a forthcoming paper on the Leptaucheninae by the writers. It should be mentioned here, however, that species representing subfamily Leptaucheninae are known from the lower Miocene deposits of California² and Montana. These forms seem to be closely allied to the forms from the Gering and Monroe Creek of the west-central Great Plains. If a fauna is ever found in the lower John Day perhaps it will include *Leptauchenia* and *Cyclopidius*.

It is apparent that Matthew's and Stock's conclusions were based on previous statements made by other writers and on fossil collections at hand at the time of writing. In the California Institute of Technology collections from the John Day area, however, there is a skull of *P. (Parapromerycochoerus) chelydra* with field data reading "middle John Day," thus supporting the contention that *Promerycochoerus* is not limited to the upper John Day.

The present writers, on a recent trip (March, 1945) to the Pacific coast to examine the collections of John Day oreodonts at the California Institute of Technology, the University of California, and the University of

Oregon, had many discussions concerning the John Day geology with J. P. Buwalda, Ralph W. Chaney, Chester Stock, and Eustace L. Furlong. It seemed to be generally agreed that there are no definite field markers within the John Day beds, and especially no mark of separation between the middle and upper John Day. From these discussions it was also gathered that *Promerycochoerus* occurred in both the middle and upper John Day. The data occurring with many specimens from the John Day in the various collections indicate "upper or middle John Day," but it is apparent that the upper zone of one collector may not be the same as the upper zone of another worker.

Thorpe³ in 1937 tried to separate the material into upper and middle John Day on the basis of the matrix ("green matrix = middle John Day," etc.) in which the specimen was embedded. This method is not practical, as was demonstrated when Carl C. Sorensen prepared the Cope collection at the American Museum. At that time it was common to find a specimen with both green and gray matrix adhering to the bone. C. Lewis Gazin of the United States National Museum has informed the writers that he has had the same experience with the colors of the John Day sediments, and that they are not to be depended upon for identification of definite geologic horizons.

The present writers wish to make it clear, therefore, that the horizons mentioned in this paper in connection with John Day oreodont material are somewhat questionable. Owing to the absence of these geologic data the classification of the John Day forms is based primarily on morphological characters. The development of the *Promerycochoerinae* in the west-central Great Plains, where adequate stratigraphic information is available, also has been considered in the John Day problem. The examples from the John Day indicate a geologic age approximating that of the Harrison of Nebraska and Wyoming. The forms considered as coming from middle John Day are comparable in size with those from the Harrison, while specimens from the upper John Day are somewhat larger. This may indicate that the

¹ Based on geologic evidence obtained by the present writers.

² Stock, Chester, 1930, *loc. cit.*

³ Thorpe, Malcolm R., 1937, *loc. cit.*

upper John Day represents a portion of that interval of time which must be accounted for between the final deposition of the Harrison formation and the beginning of Marsland sedimentation in the Great Plains. The upper John Day oreodonts, however, show closer affinities to the Harrison forms than to those of the Marsland.

DISTRIBUTION

Promerycochoerus remains are known from three species and two subspecies, from the lower Miocene of Montana, Nebraska, Oregon, South Dakota, and Wyoming (see distribution chart, p. 86).

SUMMARY OF SPECIES AND TYPES

Three species and one subspecies of *Promerycochoerus* from five lower Miocene localities are here recorded:

1. *Promerycochoerus carrikeri* Peterson, from Sioux County, Nebraska, referred remains from Sheridan County, Nebraska,

Niobrara and Goshen counties, Wyoming, and Shannon, Washabaugh, and Washington counties, South Dakota. (Harrison formation.)

HOLOTYPE: Skull, mandible, and most of skeleton, C.M. 1080.

2. *Promerycochoerus latidens* Thorpe, from the John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Skull, Y.P.M. 10961.

2a. *Promerycochoerus latidens*, geographic variety, from Meagher County, Montana. (Approximate Harrison equivalent.)

EXAMPLE: Partial skull, F:A.M. 45421.

3. *Promerycochoerus superbis* (Leidy), from the John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull (lost).

EXAMPLE: Skull and partial mandible, A.M. 7431. Figures 2-5, 11, 12.

3a. *Promerycochoerus superbis chelydra* (Cope), from the John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Skull, A.M. 7430. Figures 2-5.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PROMERYCOCHOERUS

TOTAL AVAILABLE SPECIMENS: 154

1. *Promerycochoerus carrikeri* Peterson

From the Harrison formation, Sioux County, Nebraska; referred specimens from Sioux and Sheridan counties, Nebraska, Niobrara and Goshen counties, Wyoming, and Shannon, Washabaugh, and Washington counties, South Dakota

Promerycochoerus carrikeri PETERSON, 1906, Ann. Carnegie Mus., vol. 4, no. 1, p. 26, pl. 9; 1914, *ibid.*, vol. 9, nos. 1, 2, p. 149, figs. 1-32, pls. 33-39. ORTMANN, 1909, Aus der Natur, Leipzig, Jahrg. 5, p. 22, fig. 1. PIRSSON AND SCHUCHERT, 1915, Textbook . . . geology, fig. 506. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 106, figs. 68-70, pl. 10, fig. 1, pl. 45, fig. 1.

Promerycochoerus vantassensis PETERSON, 1906, *ibid.*, vol. 4, no. 1, p. 36, pl. 11; 1914, *ibid.*, vol. 9, nos. 1, 2, p. 198, figs. 33-40, pl. 40. O'HARA, 1920, South Dakota School Mines, Dept. Geol., bull. no. 13, p. 126, fig. 63. LOOMIS, 1923, Amer. Jour. Sci., ser. 5, vol. 6, p. 223, fig. 11. THORPE, 1937, *ibid.*, vol. 3, pt. 4, p. 147, figs. 108-110, pl. 45, fig. 2.

Promerycochoerus thomsoni LOOMIS, 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 22, figs.

9 (in part), 10. THORPE, 1937, *ibid.*, vol. 3, pt. 4, p. 145, fig. 106, pl. 19, figs. 1-2.

CHARACTERS

SKULL: Large; sagittal crest very high and prominent; brain case small for size of skull but with prominent ridges; frontals moderately broad to broad (somewhat narrower in supposed female examples); nasals long and heavy, with slight anterior retraction; anterior nasal-maxilla contact in region above P¹; orbit of moderate size, somewhat rounded in outline with longer axis almost vertical to skull; zygomatic arch from moderately robust to robust (less robust in supposed female examples and very robust in old individuals); posterior superior border of zygomatic arch with an inward curved hook (present even in immature individuals); infraorbital foramen in area above P²-P⁴; lacrimal fossa shallow; paroccipital process wide at base, tapering to somewhat rounded point, with small space between it and the bulla; postglenoid process large and robust, wide transversely.

MANDIBLE: Moderately robust; post-

symphysis below P_3 ; condyle heavy, wide transversely and situated almost perpendicular to the longitudinal axis of the tooth row.

DENTITION: Brachyodont; C/ large; /C two to three times the size of I_3 ; usually a small diastema between C/ and P^1 and between P^1 and P^2 ; no diastemata between teeth in inferior dentition; superior premolars not crowded, longitudinal axis of individual premolars almost parallel with external alveoli border; inferior premolars crowded and overlapping; M_1^1 – M_3^2 graduating from small to large; M_3^2 with prominent heel; external styles of superior molars very prominent.

LIMBS: Medium length; approximate length of examples of *Merycochoerus matthewi*, but more robust.

MEASUREMENTS: Tables 1, 2, and 3.

ILLUSTRATIONS: Figures 1–5, 11–14, 25, 26.

DISCUSSION

The material referred to this species from the area 16 miles north and east of Lusk is from approximately one geological level in the Harrison. This eliminates the possibility of geological variation within this particular collection of specimens. The variation in size of the skulls and dental series, as well as the differences in the ratios of the length to the width of the skulls and of the length of the molar series to the premolar series, is demonstrated in table 3. A great amount of individual variation is noted, and the indices are of no apparent value. Thorpe¹ used the indices to show relative differences within the holotypes, but when a group of specimens of one species is compared the variation of indices is so great that they do not appear to be diagnostic.

The variation in the size of the limb elements is considerable but on an average no greater than that found in *Merycochoerinae* and *Ticholeptinae*. The metapodials of the associated specimens F.A.M. 33352 and 33353 indicate considerable variation; the shaft of one is very slender and the other broad. The facets of the astragali and calcanea also vary considerably.

The amount of sex variation is not definite in this species, but the writers have consid-

ered the narrower skulls with the lighter zygomatic arches as probably female. The depth of the malar below the orbit seems to be of little value in sex determination.

Characters that appear to be constant in the skull are the hooked posterior border of the zygomatic arch, the comparatively long point of contact of the fused maxillae, and the anterior nasal-maxilla contact above P^1 .

The variable characters in this species include the following: the width of the sagittal crest²; the degree of massiveness of zygomatic arches; the amount of protrusion of the arches below the tooth row; the depth of the malar below the orbit; the anterior retraction of the nasal; the width of the frontals; the proportions of length to width of the skull; the ratios of the length of the premolar to the molar series; and the size of bullae.

Peterson,³ in the original description of this species, considered the type specimen as coming from the Monroe Creek beds. The present writers consider that this was a misidentification of the beds and that the material actually was found in the Harrison. In the area where the holotype was found the Monroe Creek beds are represented by almost vertical bluffs which are inaccessible for prospecting. Furthermore most of the material from this area has been collected from the upper portion of the deposits, which are of Harrison age. All examples of this species in the Frick Laboratory and the University of Nebraska State Museum collections have been taken from the upper portion of the Harrison beds. No evidence of *Promerycochoerus* has thus far been found in the Monroe Creek formation by collecting parties from either of the above-mentioned institutions.

Peterson⁴ presented a thorough description of the osteology of *Promerycochoerus carrikeri*. The above-mentioned individual and sex variation was not included.

The group of three individuals displayed in the Carnegie Museum represents the finest examples known of this species (see p. 95 for listings of these specimens). Considerable variation is apparent in the length

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

² See Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, *Bull. Amer. Mus. Nat. Hist.*, vol. 77, art. 5, fig. 16 (*Merycochoerinae*).

³ Peterson, O. A., 1906, *loc. cit.*

⁴ Peterson, O. A., 1914, *loc. cit.*

and width of the skulls and in the dental series, but the lengths of the limb elements of these examples do not vary so much as in the total amount of material here considered. Although in the Frick Laboratory collections there is a group of seven associated individuals (see fig. 7), they are not so well articulated as those in the Carnegie group. However, this group includes immature individuals. Although considerable variation is noted in this associated family group, the variation is not nearly so much as may be found if the whole population of the region is considered.

The average basal lengths of skulls of this species do not differ noticeably from those of *P. superbus* and *P. superbus chelydra*, but are considerably smaller than those of *P. latidens*. The P_1^1 - M_3^3 measurements are within

the range of all three of the forms just mentioned.

The present writers consider both *P. vanttasselensis* and *P. thomsoni* to be synonymous with *P. carrikeri* and the difference heretofore noted to be nothing more than sex or individual variation. In the type description of "*P. thomsoni*," Loomis¹ compared various species of *Promerycochoerus*, but failed to take into consideration *P. carrikeri*, a species from the same geologic horizon (Harrison). The large, heavy, hooked posterior borders of the zygomatic arches of three supposed male specimens and the light, non-hooked posterior border of the "female" example evidently were not considered to be diagnostic characters by Loomis.

Eighty-three specimens are here recorded:

HOLOTYPE

Skull with I^1 - M^3 , mandible with I_1 - M_3 ,
and most of skeleton. (w)²
?Male example

C.M. 1080

From the Harrison formation, head of Warbonnet Creek, Sioux County-Nebraska; collected by O. A. Peter, son, 1901

Figured by Peterson, 1906, pl. 9 (in part); 1914, pls. 33 (in part) and 34 (in part); Ortmann, 1909, fig. 1; Pirsson and Schuchert, 1915, fig. 506; Thorpe, 1937, fig. 68

REFERRED SPECIMENS ASSOCIATED WITH HOLOTYPE

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Skull with I^1 - M^3 , mandible with I_1 - M_3 ,
and most of skeleton. (w)
?Male example

C.M. 1079

Figured by Peterson, 1906, pl. 9 (in part); 1914, fig. 3, nos. 2-3; pls. 33 (in part) and 34 (in part); Ortmann, 1909, fig. 1; Pirsson and Schuchert, 1915, fig. 506

Skull with I^1 - M^3 , mandible with I_1 - M_3 ,
and most of skeleton. (w+)
?Male example

1078

Figured by Peterson, 1906, pl. 9 (in part); 1914, pls. 33 (in part) and 34 (in part); Ortmann, 1909, fig. 1; Pirsson and Schuchert, 1915, fig. 506

The three above skeletons, which are displayed at the Carnegie Museum in Pittsburgh, were left articulated as found in the original matrix. They represent one of the finest examples of associated material so far reported in the oreodonts. The individual variation demonstrated by these specimens is shown in table 1, page 112.

¹ Loomis, Frederic B., 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, pp. 22-23.

² Abbreviations used in descriptions: alv., alveolus or alveoli; br., broken; erupt., erupting; rt., root or roots. Stage of wear of teeth: (i), immature; (m), mature; (w), worn.

REFERRED FROM (A) SIOUX AND (B) SHERIDAN COUNTIES, NEBRASKA, (C) NIOBRARA AND (D) GOSHEN COUNTIES, WYOMING, (E) SHANNON, (F) WASHABAUGH, AND (G) WASHINGTON COUNTIES, SOUTH DAKOTA

A. FROM SIOUX COUNTY, NEBRASKA

(C.M. specimens collected by O. A. Peterson)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|--|-----------|--|
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , partial scapula, humerus, pelvis, ver- tebrae, ribs, and skeletal fragments. (w+) ?Male example | C.M. 1047 | From head of Warbonnet Creek Figured by Peterson, 1914, figs. 4-13, 14 (in part), 26-27; O'Hara, 1920, fig. 63 (in part); Thorpe, 1937, pl. 35 (in part) |
|--|-----------|--|

The above skull and mandible are mounted on the composite skeleton, C.M. 1081, which also includes parts of specimens C.M. 109 and 1228. Peterson, 1914, page 195, stated that the number of the skull and mandible of the composite skeleton is C.M. 109, but this appears to be in error. At the present time the skull and mandible, C.M. 1047, are mounted with the composite skeleton, C.M. 1081. The skull and mandible, C.M. 109, are in a storage case at the Carnegie Museum.

SKULL, 2 MANDIBLES, AND SKELETAL ELEMENTS

| | | |
|---|-----|---|
| Skull with I ¹ (br.)-M ³ , mandible with I ₁ -M ₃ (I ₂ alv. and I ₃ br.), partial scapula, partial humerus, radius, 2 partial femora, manus and pes ele- ments. (w ₊ ⁺) ?Male example | 109 | From near the head of Monroe Creek Figured by Peterson, 1914, figs. 1-2, pl. 38 (in part); Thorpe, 1937, figs. 69-70; pl. 10, fig. 1 |
| Partial mandible with /C-P ₂ (P ₁ erupt., P ₂ -M ₂ alv.). (I) | | |

The partial immature mandible is listed under the same number (C.M. 109) as the mature skull and mandible. The limbs associated with the two specimens belong to a mature individual and therefore are here considered as part of the mature example. Peterson, 1914, stated that the skull and mandible, C.M. 109, were mounted on the composite skeleton, C.M. 1081, which appears to be in error (see specimen C.M. 1047 listed above).

SKELETAL ELEMENTS

| | | |
|---|------|---|
| Partial skeleton posterior to the fifth dorsal, lacking skull and mandible | 1081 | From the same level as the holotype, 9 feet from the group of three indi- viduals Figured by Peterson, 1914, figs. 14 (in part), 15-25, 28-32, pls. 34 (in part) and 35 (in part); O'Hara, 1920, fig. 63 (in part); Thorpe, 1937, pl. 45 (in part) |
|---|------|---|

The partial skeleton is part of the composite mount mentioned above in connection with C.M. 1047. Thorpe¹ stated that the mounted skeleton, "C.M. 1080," was the holotype of this species, but Peterson² definitely stated that the mounted skeleton (actually C.M. 1081) is made up of three individuals and is not the holotype. The holotype, C.M. 1080, is not a free mount and is displayed in the original matrix in a slab with associated specimens, C.M. 1078 and 1079.

¹ Thorpe, Malcolm R., *ibid.*, vol. 3, pt. 4, caption of pl. 45.

² Peterson, O. A., 1914, *ibid.*, vol. 9, nos. 1, 2, p. 195, pl. 35.

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

- Anterior portion of skull with I¹-M³(br.), C.M. 1228 Figured by Peterson, 1914, pl. 24 (in part); O'Hara, 1920, fig. 63 (in part); Thorpe, 1937, pl. 45 (in part)
partial mandible with I₁-M₃, and partial skeleton. (w)
Part of the skeleton is included in the composite mount with C.M. 1081 and 1047.

2 SKULLS AND ASSOCIATED MANDIBLES

- Skull with I¹-I² alv. and I²-M³ and mandible (attached) with I₁-M₃. (M) U.N.S.M. 28014¹ From 2 mi. N. of Harrison-Van Tassel road, $\frac{1}{2}$ mi. E. of Wyoming state line
Skull with I¹-M³ and mandible with I₁-M₃. (w+) 28007 From 2 mi. N. of Harrison-Van Tassel road, $\frac{1}{4}$ mi. E. of Wyoming state line

SKULL, MANDIBLE, AND SKELETON

- Skull with I¹-M³, mandible with I₁-M₃, and mounted skeleton. (w+) C.N.H.M. P12036 From Niobrara River, near Agate; collected by Olcott, 1906

SKULL AND ASSOCIATED MANDIBULAR RAMUS

- Skull with I¹(alv.)-M³ (P³ and M¹ alv.) and right ramus with I₁-C alv. and P₁-M₃ (M₁ br.). (w) C.N.H.M. P12034 From Niobrara River, near Agate; collected by Olcott, 1906

FROM S. OF HARRISON:

3 ASSOCIATED INDIVIDUALS

- Skull with I¹-M³, mandible with I₁-M₃, scapula, femur, tibia, astragalus, calcaneum, pelvis, vertebrae, and ribs (w) F:A.M. 45420A
?Male example
Fragments of skull with P¹(erupt.)-dP²-M¹(germ), partial mandible with dP₂-M₁(germ) (P₄ absent), and partial scapula (i) 45420B
Partial left ramus with dP₁-M₁(erupt.) (P₂-P₄ alv.) (i) 45420C

SKULL AND SKELETAL ELEMENTS

- Skull with I¹-M³ (C/ rt. and P¹ br.), 2 humeri (1 partial), partial radius, 2 partial ulnae, partial manus, femur, tibia, astragalus, calcaneum, and atlas vertebra (w+) 42312
?Female example

The bulla of this specimen is somewhat smaller than that found in other examples of this species.

SKULL

- Skull with I¹(alv.)-M³ (I²-I³ rt. and P²-P³ alv.) (M+) 37601
?Female example

MANDIBLE

- Mandible with I₁-C alv. and P₁-M₃ (w) 45401

MANDIBLE

- Mandible with I₁-M₃. (w+) A.M. 13777 From N. of Niobrara River; collected by Olcott, 1907

B. FROM PINE RIDGE, N. OF RUSHVILLE, SHERIDAN COUNTY, NEBRASKA

PARTIAL SKULL

- Anterior portion of skull with I¹-M³ (w+) U.N.S.M. 28011

¹ It will be noted that new permanent file numbers for University of Nebraska State Museum specimens are used in this paper. Heretofore, a number prefixed to a date was used in the oreodont publications. This latter number, however, was assigned in the field and is now considered to be a field number. Henceforth, only the permanent file numbers will be used in the oreodont studies.

C. FROM NIOBRARA COUNTY, WYOMING

(C.M. specimens are recorded from Converse County, Wyoming, but Converse County has been divided since the time the material was collected and this area is now known as Niobrara County)

FROM VAN TASSELL CREEK AREA:

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Skull with I¹-M³ (M¹ alv.), mandible with I₁-M₃, partial scapula, partial humerus, tibia, manus and pes elements, pelvis, and vertebrae. (w+) C.M. 1230 Figured by Peterson, 1906, pl. 11; 1914 figs. 33-40, pl. 40; Thorpe, 1937, figs. 108-110
?Male example

Holotype of *P. vantassensis* Peterson

Partial right ramus with I₂-M₃ (I₂-I₃ rt. and P₂ br.) (w+) C.M. 1230
The above two specimens have the same number.

Crushed skull with C/-M³ (M¹ alv.), mandible with I₁-I₃ rt. and /C-M₃ (P₁ br.), partial humerus, 2 radii (1 partial), partial tibia, astragalus, and fragments (w) 1232
?Female example

Fragments of the second individual were associated with C.M. 1232.

Skull with I¹-I³ alv. and C/-M³, 2 partial ulnae, partial tibia, partial pes, and skeletal fragments (w) 1232A
?Male example

The above two specimens were found associated in one field block.

FROM N. OF KEELINE:

ASSOCIATED SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P³(br.)-M³, mandible with I₁-C rt. and P₁(br.)-M₃, partial scapula, 2 partial humeri, femur, partial tibia, and skeletal fragments (M+) F:A.M. 33324
?Male example

SKULL

Skull with C/-M³ (P²-P³ alv.) (M) 33327
?Female example

MAXILLA, IMMATURE

Partial left maxilla with I¹-I³ alv. and C/(erupt.)-dP²-M²(erupt.) (I) 45387

2 MANDIBLES AND HUMERUS

Mandible with I₁-I₃ alv. and /C-M₃(erupt.) (P₂ and P₄ alv.) and partial humerus (-M) 45388
Mandible with I₂-M₃ (P₁ br.) (w+) 45390

3 MANDIBULAR RAMI

Right ramus with I₁-C alv. and P₁(br.)-M₃ (P₄ alv.) (w) 45389

Two left rami with

I₁(alv.)-M₃ (I₂-I₃ rt., P₄ br., and M₁ alv.) (w+) 45391
P₄-M₃ (w+) 45392

SKELETAL ELEMENTS

Two humeri, 2 radii, 2 partial pedes, vertebrae, and skeletal fragments 45404
Partial femur, 2 tibia (1 partial), 2 partial pedes 45405

The above elements are considerably lighter than other examples of this species.

Femur, tibia, astragalus, and calcaneum 45406

FROM QUARRY "Z," N. OF KEELINE:

| SKULL | | F:A.M. |
|--|------|--------|
| Skull with I ¹ -M ³ alv. and C/-M ³ | (w+) | 33326 |
| ?Male example | | |

| MANDIBLE | | |
|--|------|-------|
| Mandible with I ₁ -M ₃ | (M+) | 45393 |

2 MANDIBULAR RAMI AND PELVIS

| | | |
|---|--------------------------------|-------|
| Right ramus with I ₁ -C alv. and P ₁ -M ₃ (P ₂ and P ₄ alv.) | (w ₁ ⁺) | 45394 |
| Partial right ramus with P ₁ (erupt.)-M ₃ (alv.) (P ₂ and P ₄ -M ₁ alv.), and partial pelvis | (I) | 45395 |

SKELETAL ELEMENTS

| | |
|----------------------------------|----------|
| Two humeri (1 partial) | 45416A-B |
| Radius | 45407 |
| Two ulnae (1 partial) | 45408A-B |
| Femur | 45409 |
| Three tibiae | 45410A-C |

FROM N. OF MANVILLE (NORTH RIDGE, 77 HILL):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|--|--------------------------------|-------|
| Skull with I ¹ -M ³ , mandible with I ₂ -M ₃ , scapula, humerus, radius, 2 ulnae (1 partial), partial manus, 2 femora, 2 tibiae, astragalus, calcaneum, partial pelvis, and ribs | (w ₁ ⁺) | 33323 |
| ?Male example | | |

Found eight feet below F:A.M. "Rhino Quarry" on 77 Hill associated with *Merychys siouxensis* F:A.M. 33365 (Schultz and Falkenbach, 1947, p. 226).

2 MANDIBLES

| | | |
|--|--------------------------------|-------|
| Partial mandible with I ₁ -M ₂ (br.) | (w ₁ ⁺) | 45396 |
| Mandible with I ₁ -M ₃ (C br.) | (w+) | 45397 |

FROM N. OF NODE (NORTH RIDGE):

PARTIAL SKULL AND RAMAL FRAGMENTS

| | | |
|--|------|-------|
| Anterior portion of skull with I ¹ -M ³ alv. and C/-M ³ and ramal fragments . . . | (w+) | 33325 |
|--|------|-------|

FROM 14 MI. N. AND E. OF LUSK (NORTH RIDGE):

7 ASSOCIATED SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

| | | |
|--|--------------------------------|-------|
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and skeletal elements. Figs. 1-5, 11, 12, 14 | (w ₁ ⁺) | 33352 |
| ?Female example | | |
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and skeletal elements of definite association. Figs. 4, 12-14, 25, 26 | (w ₁ ⁺) | 33353 |
| ?Female example | | |
| Skull with I ¹ -dP ² -M ³ , mandible with I ₁ -dP ₂ -M ₃ , and skeletal elements. Figs. 13, 14 | (I) | 33354 |
| Skull with I ¹ -dP ² -M ² (erupt.) (C/ erupt.), mandible with I ₁ -dP ₂ -M ₃ (erupt.), and skeletal elements. Figs. 5, 13, 14 | (I) | 33355 |
| Partial skull with I ¹ -dP ¹ -M ¹ (erupt.) (C/ erupt.), mandible with I ₁ -dP ₂ -M ₂ (erupt.), and skeletal elements. Fig. 14 | (I) | 33356 |
| Partial skull with M ¹ -M ³ (erupt.), mandible with I ₁ -P ₁ rt. and P ₂ (br.)-dP ₂ -M ₃ (erupt.), and skeletal elements. Fig. 14 | (I) | 33357 |

F:A.M.
33357A

Posterior portion of skull, lacking dentition and skeletal elements. Fig. 14 . . .

These seven individuals were found associated. The skulls, mandibles, and limb elements have been removed from the matrix for study. The skull and mandible, F:A.M. 33353, have definite association with skeletal elements. The exact association of the other skulls and mandibles with definite limbs is uncertain because the bones of the skeletons were intermingled and not too well articulated (see fig. 14). For convenience in listing, "skeletal elements" are included with each skull.

FROM 16 MI. N. AND E. OF LUSK (NORTH RIDGE):

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

- Skull with I¹-I² alv. and I³-M³ (P⁴-M¹ alv.), mandible with I₁-M₃ (I₂-I₃ and P₁ alv.), 2 partial scapulae, partial femur, vertebrae, ribs, and pelvis . . . (w††) 33310
 ?Male example
 Skull with C/(br.)-M³ (P¹ br.), mandible with I₂-M₃, and most of skeleton . . . (w) 33321
 ?Male example

SKULL, MANDIBULAR RAMUS, AND SKELETAL ELEMENTS

- Skull with I¹-M³ (w†) 42302A
 ?Male example
 Right ramus with I₁(alv.)-M₃ (P₂ rt.) (w††) 42302B
 Radius, partial tibia, 2 atlas vertebrae, and other vertebrae 42302A-B

The above specimens (Nos. 42302A-B) were found associated in one field block. The skull and ramus belong to two different individuals, so it is impossible to determine with which specimen the skeletal elements were actually associated.

SKULL

- Skull with I¹-I² alv. and I³(rt.)-M³ (w) 33322
 ?Male example

2 SKULLS AND 1 MANDIBULAR RAMUS, IMMATURE

- Skull with I¹-C/(erupt.)-dP²-M²(erupt.) and left ramus with I₁-P₁(erupt.)-dP₂-M₂(erupt.) (i) 42316
 Partial skull with I¹-I³ alv. and dC/-dP²-M²(erupt.) (P¹ alv. and C/erupt.) . . . (i) 42315

SKELETAL ELEMENTS

- Two partial scapulae, humerus, 2 radii (1 partial), 2 ulnae (1 partial), 2 manus, 2 femora, 2 tibiae, 2 pedes, pelvis, vertebrae, and ribs (-m) 45402
 Two femora, 2 tibiae, fibula, 2 pedes, pelvis, and vertebrae 45403

FROM N. OF LUSK IN THE VICINITY OF U.S. HIGHWAY NO. 85 (NORTH RIDGE):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

- Skull with C/-M³, mandible with I₁-I₃ alv. and /C-M₃, humerus, radius, and ulna (w†) 42301
 ?Male example

Both superior third molars have a definite style.

SKULL AND MANDIBULAR RAMUS

- Skull with I¹-M³ and left ramus with /C-M₃ (w†) 45385
 ?Male example

MAXILLA AND MANDIBULAR RAMUS

- Left maxilla with P²-M³ (M¹ alv.) and partial left ramus with P₁(br.)-M₃(br.) (P₂ and M₁-M₂ br.) (w) 45415

SKULL AND HUMERUS

- Skull with I¹-M³ and humerus (w††) 37600
 ?Male example

2 SKULLS

F:A.M.

| | | |
|---|--------------------|-------|
| Partial skull with I ¹ -M ³ (I ³ rt., C/ br., and M ¹ alv.) | (w $\frac{1}{2}$) | 42303 |
| Skull with I ¹ (rt.)-M ³ | (w) | 42304 |

?Female example

MANDIBLE AND SKELETAL ELEMENTS

| | | |
|---|----------------------|-------|
| Partial mandible with I ₁ -P ₁ alv. and P ₂ -M ₃ (P ₃ alv.), humerus, ulna, 2 femora, tibia, vertebrae, and skeletal fragments | (w $\frac{1}{2}$ ++) | 45386 |
|---|----------------------|-------|

2 MANDIBLES, ONE IMMATURE

| | | |
|---|------|-------|
| Two mandibles with I ₁ -dP ₄ -M ₃ (erupt.) | (i) | 45398 |
| I ₁ -I ₃ alv. and /C-M ₃ | (w+) | 45399 |

MANDIBULAR RAMUS

| | | |
|---|--------------------|-------|
| Partial left ramus with I ₁ (rt.)-M ₃ (br.) | (w $\frac{1}{2}$) | 45400 |
|---|--------------------|-------|

FROM S. OF VAN TASSELL:

SKULL

A.M.

| | | |
|---|------|-------|
| Skull with I ¹ -M ³ , atlas, and skeletal fragments | (w+) | 13775 |
|---|------|-------|

?Female example

The bullae of this specimen are smaller than in average examples of this species and in this respect are similar to those of *P. (Parapromerycochoerus) chelydra* from the John Day.

FROM NEAR VAN TASSELL (W.M. specimens collected by Paul Miller and A.C. specimens collected by Frederic B. Loomis, 1920):

2 SKULLS, MANDIBLE, AND SKELETON

W.M.

| | | |
|--|----------------------|------|
| Crushed skull, mandible, and skeleton | (w $\frac{1}{2}$ ++) | 1478 |
| Skull with I ¹ -M ³ and mandible with I ₁ -M ₃ | (w) | 1478 |

This specimen was found associated with an example of "*Ticholeptos*" *petersoni*.

SKULL, MANDIBLE, AND SKELETON, IMMATURE

| | | |
|--|-----|----------------|
| Partial skull with I ¹ -P ³ (germ)-dP ⁴ -M ³ (germ), mandible (attached), and skeleton (mounted) | (i) | A.C. 20-140 |
|--|-----|----------------|

Figured by Loomis, 1923, fig. 1; Thorpe, 1937, pl. 45, fig. 2.

Although this skull and mandible represent an immature individual, the skeletal elements seem to belong to a mature one.

D. FROM E. OF RAWHIDE BUTTES, GOSHEN COUNTY, WYOMING
(Collected by Paul Miller, 1927)

SKULL AND MANDIBLE

F:A.M.

| | | |
|--|----------------------|-------|
| Partial skull with I ¹ -M ³ and mandible with I ₁ -M ₃ | (w $\frac{1}{2}$ ++) | 45411 |
|--|----------------------|-------|

?Female example

The exact location of this specimen is unknown to the writers.

E. FROM SHANNON COUNTY, SOUTH DAKOTA
(Collected by Albert Thomson, 1906, 1907, and 1921)

SKULL

| | | |
|--|------------|---|
| Partial skull with I ¹ -I ³ alv. and C/-M ³ (P ¹ -P ² and M ¹ alv.) (w+) | A.M. 12951 | From Porcupine Creek, 4 mi. N.N.W. of Porcupine Post Office |
|--|------------|---|

?Male example

MANDIBLE

- Partial mandible with /C(alv.)-M₃. (w) A.M. 12966 From the divide E. of Porcupine Creek, 7 mi. N. of the post office, 1921

F. FROM WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

- Skull with I²-M³ and mandible (attached) with I₁-M₃. (w⁺⁺) A.M. 13818 From 10 mi. S.W. of Eagles Nest Butte
?Male example

SKULL

- Skull with I¹-M³ (I²-I³ alv.). (w+) 13819 From 10 mi. S.W. of Eagles Nest Butte
?Male example
Holotype of *Promerycochoerus thomsoni* Loomis
Figured by Loomis, 1924, fig. 10; Thorpe, 1937, figs. 106-107, pl. 19, figs. 1-2

In 1924 Loomis¹ proposed the new species *P. thomsoni*, selecting specimen A.M. 13819 as the holotype, and considered specimens A.M. 13818, 12951, and the holotype as examples of the male. The specimen A.M. 12948 was referred to the species as an example of the female. The present writers consider the latter as belonging to the subgenus *P. (Pseudopromerycochoerus)* (see p. 129).

G. FROM WASHINGTON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

- Skull and mandible A.M. 12944 From Wounded Knee Creek, 4 mi. south of Madison

This specimen has been sent to the Chinese Geological Survey, Peiping, China, on exchange.

2. *Promerycochoerus latidens* Thorpe

From questionably upper John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon; and (2a) a geographic variety from Meagher County, Montana

Promerycochoerus latidens THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 1, p. 232, figs. 2a-c.

Promerycochoerus chelydra latidens (Thorpe) THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 115, figs. 74-76.

CHARACTERS

SKULL: Large and massive (lighter in supposed female examples); supraoccipital region produced posteriorly beyond the occipital condyles with lateral wings not widely spread; sagittal crest high; brain case inflated; frontals wide (narrower in supposed females); anterior nasal-maxilla contact in region above the anterior portion of P₁; malar deep below the orbit; zygomatic arch robust (lighter in supposed female examples), with straight posterior border, i.e., not hooked

as in *P. carrikeri*; occipital condyles of moderate size; paroccipital process with more lateral twist than in examples of *P. superbus* or *P. carrikeri*; bulla more suboval in outline than in examples of *P. superbus*; postglenoid process robust, larger than in examples of *P. superbus*; posterior palate projecting posteriorly beyond M³, but not to the extent found in examples of *P. (Pseudopromerycochoerus)*.

MANDIBLE: Massive; postsymphysis below anterior portion of P₃.

DENTITION: Average dental series longer than in examples of *P. superbus*, but approximately equal to that of *P. carrikeri*.

LIMBS: Robust; somewhat larger than in average examples of *P. carrikeri*; heavier and longer than in examples of *P. (Pseudopromerycochoerus) montanus*.

MEASUREMENTS: Tables 1 and 2.

ILLUSTRATIONS: Figures 2-4, 11, 12, 25, 26.

DISCUSSION

The holotype (skull) is incomplete and is

¹ Loomis, Frederic B., 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 22.

slightly smaller than the referred, illustrated skull, A.M. 7442. The holotype and the referred specimens, however, are larger on the average than examples of *P. superb* and *P. carrikeri*, although in some instances they approach the basal length of the latter. The specific characters of the limbs are based on the geographic variety, since no specimens are known from the John Day collection.

The geographic variety from Montana is not separable from the John Day species. Perhaps when additional material is available a difference in size range will be apparent (see discussion, p. 105).

Thorpe¹ considered *P. latidens* as a subspecies of *P. chelydra* and also suggested that the former species might represent the male of *P. chelydra*. Specimens of the latter form that are available to the writers demonstrate, however, that neither consideration is valid. *P. latidens* is considered as coming from the upper John Day but the geologic data are questionable, as they are for most oreodonts from the Oregon locality. *P. superb* is considered as a middle John Day form and as the ancestor of *P. latidens*. (See discussion of John Day beds, p. 89.)

Thirty-six specimens are here recorded:

• HOLOTYPE

| | | |
|--|--------------|--|
| Partial skull with P ¹ -M ³ (P ¹ -P ² br.). (w ⁺⁺) ?Male example | Y.P.M. 10961 | From North Fork of the John Day River, John Day Valley, Oregon; collected by L. S. Davis, 1875 Figured by Thorpe, 1921, figs. 2a-c; 1937, figs. 74-76 |
|--|--------------|--|

REFERRED FROM THE JOHN DAY VALLEY, OREGON

3 SKULLS AND MANDIBLES

| | | |
|---|-------------|--|
| Skull with I ¹ (alv.)-M ³ and mandible (attached) with I ₁ -M ₃ (P ₄ -M ₁ br.). (w) ?Female example | A.M. 7458 | From the John Day Valley; Cope collection |
| Partial skull with I ¹ -M ³ (I ¹ -I ³ alv.) and mandible (attached) with I ₁ -M ₃ . (w) | 7459 | From the John Day Valley; Cope collection |
| Skull with I ¹ -C/ br. and P ¹ -M ³ , mandible (attached) with P ₄ -M ₃ , and atlas (attached). (w) ?Male example | C.I.T. 1768 | From C.I.T. coll. loc. no. 229, Sutton Mountain, in canyon north of bridge across Bridge Creek; upper John Day |

SKULL

| | | |
|---|-----------|--|
| Skull with I ¹ -I ³ rt. and C/-M ³ (P ¹ -P ² rt., P ³ and M ¹ alv.). (w+) ?Male example | A.M. 7442 | From Camp Creek, Crooked River, John Day Valley, Oregon; collected by J. L. Wortman, 1879 Figs. 2-4 |
|---|-----------|--|

7 PARTIAL SKULLS

| | | |
|---|-------|---|
| Partial skull with C/(rt.)-M ³ (br.) (all teeth damaged). (w) ?Female example | 7441 | From the John Day Valley; Cope collection |
| Inferior anterior portion of skull with P ¹ -M ³ . (w) | 7441A | From the John Day Valley; Cope collection |

The above two specimens seem to have been found associated in the field. The second specimen is not complete enough for identification, but the teeth agree with the first specimen.

| | | |
|---|------|---|
| Partial skull with I ¹ -P ² rt. and P ³ (br.)-M ³ (all teeth damaged). (w+) | 7453 | From Camp Creek, Crooked River, John Day Valley; collected by J. L. Wortman, 1879 |
|---|------|---|

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

| | | |
|--|----------|---|
| Partial skull with C/(br.)-M ³ | U.C. 588 | No definite data, ?John Day Valley, 1899 |
| Partial skull with C/-P ⁴ rt. and M ¹ (br.)-M ³ . (w+) ?Male example | 643 | No definite data, ?John Day Valley, 1899-1900 |

The bulla of the above skull is large but is more oblong in outline than are the bullae found in the usual examples of this species.

| | | |
|--|------|--|
| Partial skull with C/-M ² rt. and M ³ (br.) ?Male example | 1637 | No definite data, ?John Day Valley, 1899 |
|--|------|--|

The size and outline of the bulla of the above skull are intermediate between those of examples of this species and those of *P. (Parapromerycochoerus) macrostegus*.

TENTATIVELY REFERRED¹

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|--|-----------|--------------------------|
| Fragments of skull with M ¹ -M ³ , fragments of mandible with M ₂ and M ₃ (br.), and partial pes. (w ₁ ⁺) | A.M. 7449 | From the John Day Valley |
|--|-----------|--------------------------|

Tentatively referred on the basis of the anterior twist of the paroccipital process.

FRAGMENTS OF SKULL AND MANDIBULAR RAMUS

| | | |
|--|------|--------------------------|
| Partial muzzle with C/, partial right maxilla with P ² -P ⁴ (br.), partial right ramus with P ₁ -M ₃ , and fragments. (w+) | 7451 | From the John Day Valley |
|--|------|--------------------------|

Tentatively referred on size only.

SKULL AND MANDIBULAR RAMUS

| | | |
|--|------|--|
| Partial left side of skull with C/-M ³ rt., partial left ramus with /C-P ₄ rt. and M ₁ br., and fragments. (w ₁ ⁺) | 7434 | From Bridge Creek, the John Day Valley, Wasco County; collected by Charles Sternberg, 1878 |
|--|------|--|

The above specimen was tentatively referred on size. The heavy arch suggests a male example.

2 PARTIAL SKULLS

| | | |
|--|-------------|---|
| Anterior portion of skull with C/(br.)-M ³ (br.) (P ¹ -P ² br. and P ³ absent). (w+) | C.I.T. 1732 | From C.I.T. coll. loc. no. 229, Sutton Mountain, in canyon north of bridge across Bridge Creek, John Day Valley |
|--|-------------|---|

Tentatively referred on size only.

| | | |
|--|-----------|--|
| Anterior portion of skull with I ¹ -I ³ rt. and C/(br.)-M ³ (P ¹ br.). (w) Approaches <i>P. superbus</i> in size. | U.C. 1177 | From U.C. coll. loc. no. 858, large exposures near camp in Koehley basin, the John Day Valley; collected by W. S. Sinclair |
|--|-----------|--|

6 MANDIBULAR RAMI

| | | |
|--|-----------|---|
| Symphysis of mandible with I ₁ -P ₁ (/C br. and embedded in matrix with lower dentition) | A.M. 7446 | From North Fork of John Day River; collected by Charles Sternberg, 1879 |
|--|-----------|---|

The above specimen was tentatively referred on size only. The American Museum card catalogue also lists "upper jaws" but these were not located by the writers.

| | | |
|---|------|---|
| Partial left ramus with P ₂ (rt.)-M ₂ (br.) (P ₄ -M ₁ br.) and partial left ramus with M ₁ -M ₂ br. (w) | 7470 | From Camp Creek, Crooked River, the John Day Valley; collected by J. L. Wortman, 1879 |
|---|------|---|

¹ Specimens too incomplete for definite determination.

Two individuals are represented under the above number. The two specimens may belong to the genus *Promerycochoerus* or to either of the two subgenera represented in the John Day beds.

| | | |
|---|-----------|--|
| Fragments of right ramus with M_2 - M_3 (br.). (w+) | A.M. 7493 | From Bridge Creek, Wasco County, the John Day Valley; collected by J. L. Wortman, 1878 |
| Partial left ramus with M_2 (br.)- M_3 . (w) | 7494 | From Bridge Creek, the John Day Valley, Wasco County; collected by J. L. Wortman, 1878 |

The two above specimens were tentatively referred on size only and may belong to *P. (Parapromerycochoerus) macrostegus*.

| | | |
|--|------|--------------------------|
| Partial mandible with I_1 (rt.)- M_3 (br.) (/C br. and P_5 - M_2 br.). (w) | 7732 | From the John Day Valley |
|--|------|--------------------------|

Tentatively referred because of the downward curve of the posterior portion of the inferior border of the ramus. Possibly referable to *P. superbus*.

2A. GEOGRAPHIC VARIETY FROM WHITE SULPHUR SPRINGS LOCALITY, MEAGHER COUNTY, MONTANA

DISCUSSION

The available material representing this geographic variety is not well preserved. The bullae of the skulls are damaged, and the skeletal elements are not numerous. Probably as much individual variation may be expected in this form as in other examples of the *Promerycochoerinae*.

Koerner¹ referred the Yale specimens here listed to "*Promerycochoerus*" *montanus*. The writers have available a good skull, A.M. 21338, of the latter species collected by Charles C. Mook from the same general area as the holotypes of both this species and *P. (Pseudopromerycochoerus) montanus*, and have noted definite differences between the two forms (see discussion of *P. (P.) montanus*, p. 126). As stated by Koerner, some of the Yale specimens here referred to this variety were collected by Charles H. Falkenbach and presented to the Yale Peabody Museum by the Frick Laboratory. The American Museum specimens are from the Cope collection.

In the description and discussion of his collection from the White Sulphur Springs area of Montana, Koerner makes a preliminary division of the beds into the Fort Logan and Deep River formations. The present writers believe that there are at least three distinct horizons in this area. The lower beds appear to be of an age approximately equal

to the Gering of the west-central Great Plains, the middle horizon approximately equal to the Harrison, and the upper level approximately equal to the Sheep Creek (including "Lower Snake Creek") deposits of Sioux County, Nebraska. The equivalence of the Gering to the lower deposits at Sulphur Springs is demonstrated on page 141, in the discussion of *Mesoreodon chelonys* Scott; the equivalence of the Harrison to the middle beds is indicated in the present discussion of this geographic variety; and the Sheep Creek affinities of the upper horizon are shown in a discussion of *Ticholeptus zygomatus* Cope by Schultz and Falkenbach.² In the latter instance the writers pointed out the close relationship of *Ticholeptus zygomatus* Cope and *T. hypsodus* Loomis, the former from the Smith River Valley of Meagher County, Montana, and the latter from the "Lower Snake Creek" horizon of Sioux County, Nebraska. *Ticholeptus* is known only from the upper part of the Hemingford group or its equivalent. *Ticholeptus* and *Brachycrus*³ remains are found associated in the same deposits. In 1940 the association of the two genera was recorded on the basis of material available only from Nebraska deposits. Since then, a fragmentary skull and ramus of *Brachycrus* have been located in the American

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1941, Bull. Amer. Mus. Nat. Hist., vol. 79, art. 1, pp. 76, 85.

² Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, *ibid.*, vol. 77, art. 5, p. 218.

³ Koerner, Harold E., 1940, Amer. Jour. Sci., vol. 238, p. 852.

Museum collection, which prove that the two genera were also associated in the White Sulphur Springs area of Montana. These two specimens from Montana, A.M. 21321 and 21322, a partial skull and a lower jaw, which may be of the same individual as the skull, were prepared recently by Frank Miller. The skull definitely belongs to the genus *Brachycrus* and will be figured and discussed in a later paper on the oreodonts by the writers.

Both Cope¹ and Scott² thought that the fragmentary limb elements found in the Montana deposits were of the same species as the holotype, *P. (Pseudopromerycochoerus) montanus*. On the basis of additional limb material of both *P. latidens* and *P. (P.) mon-*

tanus, the present writers believe that since the latter species has somewhat lighter and shorter limbs than the former, the limb elements referred to by Cope and Scott belong to this geographic variety and not to *P. (P.) montanus*.

Later Scott³ further discussed the skeletal elements of "*P.*" *montanus* on the basis of new additional material in the Princeton collection. He described a large amount of variation within the skulls. Three of these specimens, P.U. 10437, 10441, and 10484, are here referred to this geographic variant because they possess the characters of *P. latidens* and are more massive and larger than *P. (P.) montanus* (see p. 126).

REFERRED FROM WHITE SULPHUR SPRINGS, MEAGHER COUNTY, MONTANA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|--|------|-----------------|
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , partial humerus, partial femur, tibia, astragalus, calcaneum, and 2 partial pedes | (w+) | Y.P.M. 14011 |
|--|------|-----------------|

5 SKULLS AND MANDIBULAR RAMI

| | | |
|---|------|-------|
| Partial skull with I ¹ -M ³ and mandible with I ₁ -M ₃ | (w+) | 13962 |
| Posterior portion of skull with P ³ (br.)-M ³ , left ramus with P ₁ (br.)-M ₃ , and atlas | (m+) | 13963 |
| Skull with I ¹ (alv.)-M ³ and partial mandible with I ₁ -M ₃ (/C absent) | (w+) | 14012 |

?Female example

The bullae of the skull are small and high, approaching those found in examples of *Promerycochoerus (Parapromerycochoerus)*. Collected by Charles H. Falkenbach and presented to the Yale Peabody Museum.

| | | |
|--|------|-------|
| Left side of skull with C/(br.)-M ³ (P ¹ br.) and left ramus with /C-M ₃ (P ₁ -P ₄ br.) | (w†) | 14013 |
| Anterior portion of skull with I ¹ -M ³ and mandible with I ₁ -M ₃ | (m+) | 14014 |

4 MANDIBULAR RAMI, ETC.

| | | |
|---|------|-------|
| Partial mandible with I ₁ -/C alv. and P ₁ -M ₃ | (w+) | 13964 |
| Partial right ramus with I ₁ (alv.)-M ₃ (br.) (I ₂ and /C alv. and P ₂ br.) | (w+) | 13961 |

| | | |
|---|------|--------------|
| Partial left ramus with I ₁ -/C alv. and P ₁ -M ₃ . Figs. 11, 12 | (w+) | A.M. 8108 |
|---|------|--------------|

| | | |
|---|------|------|
| Anterior portion of mandible with I ₁ -P ₃ , 2 partial humeri, partial radius, partial ulna, partial tibia, partial fibula, astragalus, calcaneum, manus and pes elements, and ribs | (w+) | 8109 |
|---|------|------|

Figured by Cope, E. D., 1889, Amer. Nat., vol. 23, figs. 5-6 (in part), 9A; this paper, fig. 26.

| | | |
|---|-----|------|
| Partial right ramus with I ₁ -M ₃ | (w) | 8110 |
|---|-----|------|

SKULL

| | | |
|--|--------------|---|
| Partial skull with C/(br.)-M ³ (br.) (P ¹ and P ⁴ br.). (w†) ?Male example | F:A.M. 45421 | From S. of road between 1st and 2d wash W. of White Sulphur Springs, Meagher County, Montana; collected by Nelson J. Vaughan, N. Z. Ward, and Charles H. Falkenbach, 1942 |
|--|--------------|---|

¹ Cope, E. D., 1884, *Merycochoerus montanus* Cope (in part), Proc. Amer. Phil. Soc., Philadelphia, vol. 21, p. 531; (in part) 1884, Paleont. Bull., no. 39, p. 23; Proc. Amer. Phil. Soc., Philadelphia, vol. 22, p. 23; (in part) 1889, Amer. Nat., vol. 23, fig. 9a.

² Scott, W. B., 1890, Morph. Jahrb., vol. 16, p. 342, figs. 5-6.

³ Scott, W. B., 1893, Trans. Amer. Phil. Soc., Philadelphia, new ser., vol. 18, p. 151.

SKELETAL ELEMENTS

| | |
|---|-----------------|
| Partial humerus, radius, partial ulna, calcaneum, manus, and pes elements. Figs. 25, 26 (in part) | F:A.M. 45422 |
|---|-----------------|

FRAGMENTS OF SKULL

| | |
|--|---------------|
| Fragments of skull including part of the zygomatic arch | P.U. 10441 |
| Indicates a larger and more massive skull than <i>P. (P.) montanus</i> . | |

LIMB ELEMENTS

| | |
|---|-------|
| Humerus and skeletal fragments. Fig. 25 (in part) | 10484 |
| Femur. Fig. 26 | 10437 |

Both above specimens are larger and more massive than examples of *P. (P.) montanus*.

3. *Promerycochoerus superbis* (Leidy)

From questionably middle John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Oreodon superbis LEIDY, 1870, Proc. Acad. Nat. Sci. Philadelphia, vol. 22, p. 111. LEIDY, 1873 (in F. V. Hayden), Rept. U. S. Geol. Surv. Terr., pl. 1, fig. 1, pl. 2, fig. 16, pl. 7, figs. 7, 8, 9 (in part).

Eporeodon superbis (Leidy) MARSH, 1875, Amer. Jour. Sci., ser. 3, vol. 9, p. 249.

Eucrotaphus superbis (Leidy) COPE, 1879 (1880), Bull. U. S. Geol. and Geogr. Surv. Terr., vol. 5, p. 59.

Merycochoerus superbis (Leidy) COPE, 1884, Proc. Amer. Phil. Soc., Philadelphia, vol. 21, p. 522; 1888, Amer. Nat., vol. 23, p. 1094, pl. 26, fig. 2. SCOTT, 1890, Morph. Jahrb., vol. 16, pl. 14, fig. 10.

Promerycochoerus superbis (Leidy) DOUGLASS, 1901, Amer. Jour. Sci., ser. 4, vol. 11, p. 82; 1907, Ann. Carnegie Mus., vol. 4, no. 2, p. 87. ZITTEL, 1911, Grundzuge der Paläontologie (Paläozoologie), div. 2, Vertebrata, p. 483, fig. 675b; 1923, op. cit., fig. 716b. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 141, figs. 97-105, pl. 50, figs. 3-4.

Paracotylops superbis (Leidy) MATTHEW, 1901 (in J. C. Merriam), Bull. Dept. Geol. Uni. California, vol. 2, no. 9, p. 296.

Merycochoerus temporalis BETTANY, 1876, Quart. Jour. Geol. Sci., London, vol. 32, p. 269, pl. 17.

CHARACTERS

SKULL: Approximate size of *P. carrikeri*; smaller than examples of *P. macrostegus*; supraoccipital wings moderately spread, greatly produced posterior to the occipital condyles; sagittal crest moderately long, high, and sloping down posteriorly; frontals moderately wide; nasal long and rounded laterally, but not noticeably retracted; an-

terior nasal-maxilla contact usually above P^1 ; zygomatic arch with straight internal posterior border (not hooked as in *P. carrikeri*), and extending posteriorly beyond the region above the postglenoid process, not to the degree found in examples of *P. carrikeri*, but more so than in examples of *P. (Pseudopromerycochoerus)*; infraorbital foramen above region of posterior portion of P^4 ; lacrimal fossa larger and deeper than in *P. carrikeri*; slight facial depression above premolar region; muzzle joined for short distance; occipital condyles of moderate size; paroccipital process wide at base with slight forward twist; bulla well inflated, high and suboval in outline, extending downward beyond the inferior border of the postglenoid process; postglenoid process robust and high; posterior palate projecting posteriorly beyond M^3 (not to the extent found in examples of *P. superbis chelydra*).

MANDIBLE: Moderately robust; ramus of same depth until reaching a point below M_3 ; inferior border straight to a point below the posterior of M_3 , then curving gradually downward.

DENTITION: Equal to smaller examples of *P. carrikeri*; average smaller than average examples of *P. carrikeri* or *P. latidens*.

MEASUREMENTS: Tables 1 and 2.

ILLUSTRATIONS: Figures 2-5, 11, 12, 25, 26.

DISCUSSION

Leidy's original description was based on many individuals, represented by a partial skull, maxillae, and partial rami. Most of these specimens are now in the Yale Peabody Museum collection. The exceptions are a partial skull which apparently has been lost

and a specimen bearing Condon collection number 516. Most of the Condon collection is now in the University of Oregon at Eugene. The Condon specimen, No. 516, was not found by Falkenbach, however, during a recent visit to that institution.

Cope¹ referred this species to *Merycochoerus*, and later he figured a skull, A.M. 7431, with the legend "*Merycochoerus superbus*." This figured skull is an excellently preserved specimen and is the basis for the specific characters given in this paper. A mandible in the Cope collection at the American Museum has been found to belong to the same individual as the skull. In 1888 Cope further stated: "Of this fine species [*P. superbus*] I have nine crania extracted from the matrix and a good many not cleaned." It is not known to which nine crania he referred, for no numbers were given for the material.

Cope² and later Thorpe³ considered "*Merycochoerus temporalis*" Bettany to be in synonymy with "*M. superbus*." The present writers also agree with this conclusion. Bettany's illustration⁴ demonstrates that the skull of "*M. temporalis*" possesses a large bulla. It is not known if Leidy noted a bulla on the holotype of *P. superbus*.

Douglass⁵ in discussing *P. superbus* quotes the following from the original description⁶ of "*Oreodon superbus*": "The species, which I propose to distinguish under the name *Oreodon superbus*, is indicated by a mutilated skull, together with mutilated crania and portions of jaws with and without teeth, of half a dozen or more individuals." Douglass then suggested: "What we should undoubtedly consider as the type of this species is the skull represented in Fig. I, Pl. I, of Leidy's Extinct Vertebrate Fauna."⁷

Thorpe,⁸ however, did not include the figured skull as part of the cotypes but did list some of the specimens figured by Leidy and others that were not figured. He also did not take into account Douglass' statement about this same skull.

The fact that Cope⁹ illustrated the well-preserved skull, A.M. 17431, and referred it to *P. superbus* has not been properly considered in the past by those working with the oreodonts. In the absence of the Leidy skull, the present writers consider this skull as referable to this species and thus use it as the basis for the specific description and discussion. The balance of Leidy's original material is so fragmentary that comparisons are nearly impossible. Considering the portions which are preserved, no specific differences are noted between Leidy's original material and Cope's referred specimen.

Promerycochoerus superbus and *P. superbus chelydra* are here considered as coming from the middle John Day (see discussion of the John Day beds, p. 89). The two forms are about the same size and are not easily distinguishable, except for the hooked posterior border of the zygomatic arch in the latter.

Promerycochoerus superbus is readily separated from *P. latidens* by its smaller size, lighter construction, and flattened skull. It is also recognized as being different from examples of *P. carrikeri* in having a straight posterior border of the zygomatic arch, smaller average size, and being somewhat lighter. *P. superbus* is separated from examples of *P. (Pseudopromerycochoerus)* by the posterior protrusion of the zygomatic arch and the less protracted posterior palate. *P. superbus* was probably ancestral to *P. latidens*.

Thirty specimens are here recorded:

HOLOTYPE¹⁰

A mutilated skull which could not be located by the writers

From Bridge Creek, John Day Valley
Oregon; collected by John Condon
Figured by Leidy, 1873, pl. 1, fig. 1

¹ Cope, E. D., 1884, *loc. cit.*; 1888, *loc. cit.*

² Cope, E. D., 1884, *ibid.*, p. 522.

³ Thorpe, Malcolm R., 1937, *ibid.*, p. 141.

⁴ Bettany, G. T., 1876, *ibid.*, pl. 17.

⁵ Douglass, Earl, 1907, *ibid.*, p. 87.

⁶ Leidy, Joseph, 1870, *ibid.*, p. 111.

⁷ Leidy, Joseph, 1873 (*in* F. V. Hayden), Rept. U. S. Geol. Surv. Terr.

⁸ Thorpe, Malcolm R., 1937, *loc. cit.*

⁹ Cope, E. D., 1888, *op. cit.*, pl. 26, fig. 2.

¹⁰ By designation of Douglass, 1907, *loc. cit.*

EXAMPLE

| | | |
|--|-----------|---|
| Skull with I ¹ -M ³ and partial mandible with I ₁ (rt.)-M ₃ (I ₂ rt.). (w) | A.M. 7431 | From the Cope collection Figured by Cope, 1888, pl. 26, fig. 2 (in part); Scott, 1890, pl. 14, fig. 10; Zittel, 1911, fig. 675b; 1923, fig. 716b. This paper, figs. 2-5, 11, 12 |
|--|-----------|---|

The mandible was not recognized as belonging to the same individual as the skull until after 1888.

REFERRED FROM THE JOHN DAY VALLEY, OREGON

FROM BRIDGE CREEK (collected by Thomas Condon):

MATERIAL INCLUDED IN ORIGINAL DESCRIPTION

| | | |
|--|--------------|---|
| Partial right ramus with P ₂ (rt.)-M ₁ . (w ⁺) | Y.P.M. 10153 | Figured by Leidy, 1873, pl. 2, fig. 16, pl. 7, fig. 9 (in part); Thorpe, 1937, fig. 102 |
| When originally drawn this specimen had P ₂ -M ₂ (br.) present. Thorpe's illustration must have been taken from Leidy's, as both illustrations are identical. The M ₂ of the specimen is now absent. | | |
| Partial right ramus with P ₄ (rt.)-M ₃ (M ₂ br.). (w ⁺) | 10153A | Figured by Leidy, 1873, pl. 7, figs. 7-8; Thorpe, 1937, figs. 100-101 |

MATERIAL POSSIBLY INCLUDED IN ORIGINAL DESCRIPTION

MAXILLA AND MANDIBULAR RAMUS

| | |
|---|-----------------|
| Partial left maxilla with C/(br.)-P ⁴ and partial left ramus with I ₅ -C br. and P ₁ -M ₁ (br.) (P ₄ br.) (w) | Y.P.M. 10152 |
| Figured by Thorpe, 1937, fig. 9 (in part). | |

2 MAXILLAE

| | |
|---|--------|
| Partial left maxilla with M ¹ (alv.)-M ³ (w+) | 10151 |
| Figured by Thorpe, 1937, figs. 97-98. | |
| Partial left maxilla with P ³ -M ² (w+) | 10151C |

9 MANDIBULAR RAMI

| | | |
|---|--------|--|
| Five partial right rami with | | |
| P ₂ (rt.)-P ₄ (rt.) (w+) | 10151A | |
| I ₅ -P ₁ alv. and P ₂ -P ₃ rt. | 10151B | |
| M ₁ -M ₃ rt. | 10967C | |
| /C-P ₄ rt. | 10968 | |
| M ₁ br. (w ⁺) | 10968C | |
| Four partial left rami with | | |
| M ₂ -M ₃ (br.) (w+) | 10967A | |
| M ₃ br. (w ⁺) | 10967B | |
| P ₁ -P ₃ rt. and P ₄ -M ₁ (br.) (w ⁺) | 10968A | |
| P ₁ -P ₃ rt. | 10968B | |

Of the foregoing specimens, Thorpe¹ considered the Yale examples, Y.P.M. 10151, 10152, 10153, 10153A, 10967, and 10968 as cotypes of this species.

FROM THE JOHN DAY VALLEY (collected by various expeditions):

SKULL, MANDIBLE, AND HUMERUS

| | | |
|--|-----------|---|
| Partial crushed skull with I ¹ -M ³ (P ¹ br., P ² -P ³ absent, and P ⁴ -M ³ br.), partial mandible with M ₂ -M ₃ (br.), humerus, and fragments. (w ⁺) ?Female example | A.M. 7733 | From the Cope collection Fig. 25 (in part) |
|--|-----------|---|

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

SKULL AND MANDIBULAR RAMUS

- Anterior portion of skull with I¹-I³ alv. and C/-M³ (P¹ br. and P²-P³ rt.) and partial left ramus with P₁-P₃ rt. and P₄(br.)-M₂. (w+)

Y.P.M. 10983

Collected by Yale Expedition, 1879

Accessory styles on M³.

4 SKULLS

- Posterior portion of skull with P²(br.)-M³. (M)
- Partial skull with I¹-M³. (w+)
- Partial skull with I¹(alv.)-M³ (C/ br.). (w)

Y.P.M. 10154

From Bridge Creek; collected by S. Snook

10981

From Bridge Creek; collected by Daws and Day, 1876

A.M. 7445

From the Cope collection

The postglenoid process is heavier than that in average specimens referred to this species and resembles examples of *P. latidens* in this respect.

- Partial skull with C/(br.)-M³ (P¹-P³ rt.). (w)

C.I.T. 1734

From C.I.T. coll. loc. no. 229, Sutton Mountain, in canyon north of bridge across Bridge Creek, 1927

The C.I.T. catalogue states "Upper John Day," same locality as the referred specimen, *P. latidens*, C.I.T. 1768.

MANDIBULAR RAMUS AND PELVIS

- Partial left ramus with P₃(rt.)-M₂(br.) and partial pelvis. (w^{††})

Y.P.M. 10989

Thorpe, 1937, considered specimens Y.P.M. 10154, 10978, 10983, 10989, and 10991 as plesiotypes of *P. superbis*. The present writers were not able to locate specimen 10978 and found only a pelvis bearing 10991. Thorpe also listed as part of the cotypes specimen 516 of the Condon collection. In 1945, however, Falkenbach could not locate the specimen in the Condon collection at the University of Oregon at Eugene.

TENTATIVELY REFERRED FROM THE JOHN DAY VALLEY, OREGON

FRAGMENTS OF SKULLS, 2 INDIVIDUALS

- Posterior portions of 2 skulls with C/-M¹ br. and with C/-P⁴ (P¹ br., P² absent, and P³ br.). (w)

A.M. 7462

From Bridge Creek, Wasco County; collected by Charles Sternberg, 1878

Two individuals are included under this number. A partial occipital region of a skull bears the same number but it is without contact with either muzzle. It does possess incomplete bullae which suggest this species. There is, however, no evidence that another skull fragment (the postoccipital region) with the same number belongs to either muzzle.

SKULL AND LIMB ELEMENTS

- Anterior portion of skull with P¹-P² rt., P³-P⁴ absent, and M¹-M² br., partial humerus, radius, femur, and pes. (w[†])

7473

From the Cove, John Day Valley; collected by Wortman, ?1878
Fig. 26 (in part)

The above skull approximates the size of that of this species, and the limb elements are similar to those of *P. carrikeri*.

2 SKULLS

- Partial skull with C/-P³ rt. and P⁴(br.)-M³ (M¹ br.). (M)

7447

From the Cope collection

The size of the above skull and the position of the nasal-premaxilla contact suggest this species.

- Partial skull with P³(br.)-M³. (w)

7478

From the Cope collection

The size of the above skull is equal to that of examples of this species, but the bulla and the postglenoid process are more like those of *P. latidens*.

MANDIBLE

Partial mandible with I₁-C alv. and P₁(br.)-M₃ (P₂-P₄ alv. and M₁ br.).
(M+)

A.M. 7734 From the Cope collection

The dental series is shorter and the ramus is much shallower than in other examples of this species.

SKELETAL ELEMENTS

Three radii (2 partial), 2 partial ulnae, 7477 From the Cope collection
partial manus, partial femur, 3 partial
tibiae, partial fibula, partial cal-
caneum, and partial pes Figs. 25, 26 (in part)

There are two individuals represented under the above number. In comparison with the humerus, A.M. 7737, referred to this species, and with examples of *P. carrikeri*, the limb elements suggest *P. superbus*. Limb elements of the John Day Promerycochoerinae are not well known and therefore these specimens may belong to another species from the John Day.

Fragment of ulna, 2 astragali (1 partial), 7907 From the Cope collection
calcaneum, partial manus, partial pes,
and fragments Fig. 26 (in part)
Similar to A.M. 7477.

3a. *Promerycochoerus superbus chelydra* (Cope)

From questionably middle John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Merycochoerus chelydra COPE, 1884, Proc. Amer. Phil. Soc., Philadelphia, vol. 21, p. 523.

Promerycochoerus chelydra (Cope) DOUGLASS, 1901, Amer. Jour. Sci., vol. 11, p. 82. PETERSON, 1914, Ann. Carnegie Mus., vol. 9, nos. 1, 2, p. 219, pl. 41. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 112, figs. 71-73.

CHARACTERS

SKULL: Large, average slightly smaller but within the range of *P. superbus*; sagittal crest high, rising considerably above the frontal plane; frontals moderately wide; anterior nasal-maxilla contact in region above C/ and P¹; zygomatic arch with a hooked superior, posterior border (as in *P. carrikeri*); lacrimal fossa moderately large, but not deep; bulla high, narrow, somewhat smaller than in examples of *P. superbus*; posterior palate projecting for considerable distance beyond M³, but not so far as in *P. (P.) macrostegus*.

MANDIBLE: Moderately robust; similar to that of *P. superbus*.

DENTITION: Similar to that of *P. superbus*.

LIMBS: Unknown; ball of femur of A.M.

7901 similar to examples of *P. carrikeri*.

MEASUREMENTS: Table 1.

ILLUSTRATIONS: Figures 2-5, 11, 12.

DISCUSSION

This subspecies also has many characters in common with examples of *Promerycochoerus superbus*, but differs noticeably in having a comparatively small bulla. The hooked posterior border of the zygomatic arch, similar to that of *P. carrikeri*, suggests a close relationship with that species, possibly as a geographic variant. It is reasonable to expect that both this subspecies and *P. carrikeri* had a common ancestor in Gering or Monroe Creek times on the west-central Great Plains. At the time of the branching of the two lines of development, the hooked posterior border of the zygomatic arch was evident in both forms, but predominated in *P. carrikeri*, gradually disappeared in *P. superbus*, but remained in this subspecies.

There is individual variation in the bullae of the listed specimens of this subspecies, but it lies within the range of individual variation to be expected. The fragmentary limb elements suggest limbs similar to those of *P. carrikeri*.

Five specimens are here recorded:

TABLE 1

Promerycochoerus DOUGLASS. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND RAMI

| SKULL | <i>P. carrikeri</i> Peterson | | | | |
|---|---------------------------------------|---------------------------|---------------------------|------------------------------|------------------------------|
| | Holotype C.M. 1080 ² | Referred | | | |
| | | C.M. 1079 ² | C.M. 1078 ² | F:A.M. 33352 ³ | F:A.M. 33353 ³ |
| Stage of wear of teeth | (w) | (w) | (w+) | (w‡) | (w‡) |
| Length (max., including supraoccipital crest and incisors) | 332.5 | 330 | 377 | 352 | 336 |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | ((298)) | ((295)) | ((325)) | 298 | 305 |
| Condylbasal length | 309 | 308 | 336 | 311 | 298 |
| Width (max.) | 296 | 320 | 322 | 254 | 232 |
| Width of brain case (max.) | 92 | 90 | 96.5 | 74 | 81 |
| Width, interorbital (min.) | 94.5 | 87 | 97 | 72 | 78 |
| Distance from anterior rim of orbit to anterior base of canine | 146.5 | 146.5 | 166 | 146.5 | 140 |
| Distance from anterior rim of orbit to supraoccipital crest | 188 | 194 | 217 | 206 | 195 |
| Distance from ventral portion of occipital condyles to top of supraoccipital | 130 | — | 155 | 123 | 118 |
| Width of muzzle at infraorbital foramina | 84.5 | 83.5 | 90 | (73) | 85 |
| Width across canines (max.) | 125 | 118.5 | 121 | 82.5 | 99 |
| Width of palate between fourth premolars | — | — | — | 34 | 42 |
| Width of palate between canines | — | 71 | 71 | 46.5 | 65 |
| Length, C/M ³ incl. | 179.5 | 178 | 195.5 | 171 | 166 |
| Length, P ¹ -M ³ incl. | 144.5 | 137 | 156 | 145 | 144 |
| Length, P ¹ -P ⁴ incl. | 71.5 | 68 | 74 | 68 | 68 |
| Length, M ¹ -M ³ incl. | 76.5 | 71 | 86 | 78 | 79 |
| Width of M ³ (max.) | — | — | — | 27 | 30 |
| Width across condyles | — | — | — | 56 | 55 |
| Depth of malar below orbit | — | — | — | 32.5 | 38 |
| RAMUS | | | | | |
| Stage of wear of teeth | | | | | |
| Length (max., including incisors) | 278.5 | 275.5 | 292 | 273.5 | 264 |
| Length, /C to condyle incl. | 252.5 | 256 | 277 | 254 | 248 |
| Depth of jaw under coronoid | 115 | 108 | — | 119 | 106 |
| Depth of jaw below anterior edge of M ₃ | 52 | 50 | 60 | 47.5 | 49 |
| Length, /C-M ₃ incl. | 185 | 185.5 | 198 | 176 | 175 |
| Length, P ₁ -M ₃ incl. | 171 | 173 | 182 | 162.5 | 160.5 |
| Length, P ₁ -P ₄ incl. | 86 | 89 | — | 76 | 75.5 |
| Length, M ₁ -M ₃ incl. | 86 | 85 | — | 88 | 85 |

¹ Measurements in millimeters; (), approximate; (()), estimated.² Three associated specimens.³ Two of seven associated individuals.

TABLE 1—Continued

| | <i>P. latidens</i> Thorpe | | | <i>P. superbus</i> (Leidy) | <i>P. superbus chelydra</i> (Cope) |
|---|-----------------------------|--------------------------|-----------------------------|----------------------------|------------------------------------|
| | Holotype Y.P.M. 10961 | Referred A.M. 7442 | Referred F:A.M. 45421 | Referred A.M. 7431 | Holotype A.M. 7430 |
| SKULL | | | | | |
| Stage of wear of teeth | (w $\frac{1}{2}$ ++) | (w+) | (w $\frac{1}{2}$) | (w) | (w+) |
| Length (max., including supraoccipital crest and incisors) | ((390)) | (380) | (397) | 355 | (341) |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | ((350)) | 332 | 338.5 | 290 | 287 |
| Condylbasal length | — | 345 | 355 | 301 | 298 |
| Width (max.) | 275 | 286 | (283) | 236 | 250 |
| Width of brain case (max.) | 110.5 | 94 | 104 | 87 | 85 |
| Width, interorbital (min.) | 112 | 95 | (118) | 94 | 88 |
| Distance from anterior rim of orbit to anterior base of canine | — | 162.5 | 171.5 | 150 | 138 |
| Distance from anterior rim of orbit to supraoccipital crest | 235 | 208 | 233 | 206 | (206) |
| Distance from ventral portion of occipital condyles to top of supraoccipital | 118 | — | — | 109 | 113 |
| Width of muzzle at infraorbital foramina | 102 | 82.5 | (110) | 84 | 74 |
| Width across canines (max.) | — | 101 | — | 85 | (84) |
| Width of palate between fourth premolars | 54 | — | — | 46 | (43) |
| Width of palate between canines | — | 56.5 | — | 47 | 44 |
| Length, C/—M ³ incl. | — | 179.5 | (187) | 164 | 157 |
| Length, P ¹ —M ³ incl. | 147.5 | — | (154.5) | 139 | 131 |
| Length, P ¹ —P ⁴ incl. | 70 | — | 76 | 64 | 62 |
| Length, M ¹ —M ³ incl. | 78.5 | 85 | 81.5 | 77 | 69 |
| Width of M ³ (max.) | 32 | — | 29.5 | 27.5 | 26.5 |
| Width across condyles | 64 | 63 | 68 | 61 | 62 |
| Depth of malar below orbit | 53 | (46.5) | (54) | 41 | 36.5 |
| RAMUS | | | | | |
| | | | A.M. 8108 | | Referred A.M. 7901 |
| Stage of wear of teeth | — | — | (w+) | — | (w $\frac{1}{2}$) |
| Length (max., including incisors) | — | — | — | — | — |
| Length, /C to condyle incl. | — | — | — | — | — |
| Depth of jaw under coronoid | — | — | — | — | — |
| Depth of jaw below anterior edge of M ₃ | — | — | 60 | 52 | 49 |
| Length, /C—M ₃ incl. | — | — | — | 163 | 173 |
| Length, P ₁ —M ₃ incl. | — | — | 174.5 | 151 | 158.5 |
| Length, P ₁ —P ₄ incl. | — | — | 88.5 | 73 | 80.5 |
| Length, M ₁ —M ₃ incl. | — | — | 85 | 79 | 83.5 |

HOLOTYPE

| | | |
|---|-----------|--|
| Skull with I ¹ -I ³ rt. and C/(br.)-M ³ (P ⁴ rt.). (w+) | A.M. 7430 | From the John Day Valley, Oregon Figured by Peterson, 1914, pl. 41; Thorpe, 1937, figs. 71-73 This paper, figs. 2-5 |
|---|-----------|--|

The molar dentition of the holotype was not exposed from the matrix until 1944. This explains the vague molar details in the illustrations by Peterson and Thorpe.

REFERRED FROM THE JOHN DAY AREA, OREGON

2 SKULLS AND MANDIBLES

| | | |
|--|-----------|--|
| Partial skull with P ¹ -P ³ br. and P ⁴ -M ³ and fragments of mandible with M ₃ . (w ₊ ⁺) ?Male example | A.M. 7448 | From Camp Creek, Crooked River; collected by J. L. Wortman, 1879 |
| Posterior portion of skull without dentition and mandible with I ₁ -M ₃ , ball of femur, and pelvic fragments. (w ₊ ⁺) | 7901 | Figs. 11, 12 (in part) |

Fragments associated with the skull demonstrate that the zygomatic arch had a hooked posterior border.

2 SKULLS

| | | |
|---|--------------|--|
| Partial skull with C/-P ⁴ rt. and M ¹ (br.)-M ³ . (w ₊ ⁺) | Y.P.M. 10979 | |
| Partial skull with P ¹ -M ³ . (w+) | 10879 | From Haystack Valley; collected by L. S. Davis, 1875 |

IA. *PROMERYCOCHOERUS* (*PARAPROMERYCOCHOERUS*), NEW SUBGENUS

GENOTYPE: *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species.

DESCRIPTION

SKULL: Moderately large to large; ranging in basal length from 221 to 325 mm.; in width from 183 to 265 mm.; dolichocephalic; supra-occipital wings moderately spread, protruding posteriorly beyond the occipital condyles; sagittal crest moderately long and light; brain case expanded laterally; frontals usually wide; nasals with tendency to be somewhat retracted anteriorly; anterior nasal-maxilla contact above P¹; malar deep below orbit; zygomatic arch robust and extending upward to approximate level of the superior border of the sagittal crest; posterior border of the orbit and the posterior border of the zygomatic arch forming a wide U-shaped opening (when viewed from side); superior, posterior border of the zygomatic arch straight and not hooked as in *P. carrikeri* but extending posteriorly beyond the postglenoid process; infraorbital foramen above region of P⁴-M¹; lacrimal fossa small, but usually deep; de-

pression above premolar region; premaxillae joined for short distance (similar to examples of *Promerycochoerus*); muzzle inflated laterally and extended anteriorly; occipital condyles moderately robust; paroccipital process wide at base, tapering to lower border, and with axis more or less perpendicular to the length of the skull; bulla small but high, laterally compressed, approaching the type of bullae found in examples of *Merycochoerus* [bullae large and suboval in outline in *Promerycochoerus*, and extending below the level of the inferior border of the postglenoid process, while in *P. (Parapromerycochoerus)* bullae usually extending downward to about the level of the inferior border of the postglenoid process]; postglenoid process heavy to robust, suboval in outline; posterior palate projecting farther posteriorly than in examples of *Promerycochoerus*.

MANDIBLE: Light to moderately robust; postsymphysis below area of P₃; inferior border gradually increasing in depth posteriorly to a point below the posterior lobe of M₃, then forming a downward curve; ascending ramus somewhat higher than in examples of *Promerycochoerus* and lacking the inferior inward

TABLE 2

Promerycochoerus DOUGLASS. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

| | <i>P. carrikeri</i> Peterson | | | | |
|---|---------------------------------------|---------------------------|---------------------------|------------------------------|------------------------------|
| | Holotype C.M. 1080 ² | Referred | | | |
| | | C.M. 1078 ² | C.M. 1079 ² | F:A.M. 33352 ³ | F:A.M. 33353 ³ |
| Length of scapula (max.) | 235 | 230 | — | — | 196 |
| Length of humerus (articular) | 222.5 | 227 | — | — | 200 |
| Length of radius (articular) | 167.5 | 174 | 172 | — | 158.5 |
| Length of ulna (max.) | 239 | 253 | 247 | — | 227 |
| Length of metacarpal III (max.) | — | — | — | — | 77 |
| Length of femur (articular) | 258 | 268 | 252 | 239 | 238 |
| Length of tibia (articular) | 195 | 214 | 207 | 195 | 191.5 |
| Length of metatarsal III (max.) | 80 | — | 75 | — | 71 |
| Length of calcaneum (max.) | 88 | 81 | 82 | — | 83 |

TABLE 2—Continued

| | <i>P. latidens</i> Thorpe | | <i>P. superbis</i> (Leidy) | |
|---|---------------------------|-----------------|----------------------------|------|
| | Referred | | Referred | |
| | P.U. | F:A.M. 45422 | A.M. | |
| Length of scapula (max.) | — | — | — | — |
| Length of humerus (articular) | 223 | 10484 | — | — |
| Length of radius (articular) | — | (178) | 161.5 | 7477 |
| Length of ulna (max.) | — | — | — | — |
| Length of metacarpal III (max.) | — | 81 | 81 | 7907 |
| Length of femur (articular) | 268 | 10437 | — | — |
| Length of tibia (articular) | — | — | (185) | 7477 |
| Length of metatarsal III (max.) | — | 86 | — | — |
| Length of calcaneum (max.) | — | — | 88 | 7907 |

¹ Measurements in millimeters; (), approximate.² Three associated individuals.³ Two of seven associated individuals.

curve of that genus; condyle large, similar to examples of *Promerycochoerus*.

DENTITION: Equal to examples of *Promerycochoerus* but with a tendency towards being lighter; C/ and P₁ large; P₁–P₃ with prominent anterior intermediate crest, in examples where wear allows observation.

LIMBS: Similar to examples of *Promerycochoerus carrikeri*.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 5–7, 11, 12 (skulls, mandibles, and dentitions).

DISCUSSION

The proposed new subgenus has many characters in common with *Promerycochoerus* and differs chiefly from that genus in having smaller bullae and also a slight tendency towards more anterior retraction of the nasals. These two characters are not always preserved, and therefore the writers realize that in the incomplete specimens it is impossible to make definite identification. The questionable specimens are here listed under "tentatively referred" with notations for the

TABLE 3

Promerycochoerus carrikeri PETERSON. INDICES OF VARIOUS MEASUREMENTS

| Specimen | Width of Skull | Length of Superior Premolars | Wear |
|----------------|-----------------|------------------------------|------|
| | Length of Skull | Length of Superior Molars | |
| U.N.S.M. 28014 | — | .72 | M |
| F:A.M. 33327 | .68 | .80 | M+ |
| F:A.M. 42304 | .69 | .85 | M+ |
| F:A.M. 37601 | .65 | .82 | M+ |
| F:A.M. 33321 | .75 | .80 | W |
| F:A.M. 33322 | .75 | .84 | W |
| C.M. 1080 | .89 | .91 | W |
| C.M. 1079 | .93 | .95 | W |
| C.M. 1047 | — | .90 | W+ |
| W.M. 12034 | .71 | .69 | W |
| A.M. 12951 | — | .94 | W |
| F:A.M. 33326 | .77 | .80 | W+ |
| A.M. 13775 | .80 | .73 | W+ |
| F:A.M. 42312 | .63 | .76 | W+ |
| C.M. 1078 | .85 | .86 | W+ |
| C.M. 1047 | — | .90 | W+ |
| C.M. 1230 | .72 | .70 | W+ |
| W.M. 12036 | — | .71 | W+ |
| U.N.S.M. 28007 | — | .72 | W+ |
| U.N.S.M. 28011 | — | .91 | W+ |
| A.M. 13819 | .75 | .78 | W+ |
| F:A.M. 33323 | .79 | .82 | W+ |
| F:A.M. 33352 | .72 | .87 | W+ |
| F:A.M. 33353 | .69 | .86 | W+ |
| F:A.M. 42301 | .73 | .80 | W+ |
| F:A.M. 42302A | .73 | .90 | W+ |
| F:A.M. 42303 | .73 | .90 | W+ |
| F:A.M. 45385 | .76 | .88 | W+ |
| F:A.M. 37600 | .74 | .86 | W++ |
| F:A.M. 45411 | .61 | .89 | W++ |
| C.M. 109 | .83 | .90 | W++ |
| A.M. 13818 | .80 | .91 | W++ |
| F:A.M. 33310 | .80 | .94 | W++ |

individual specimens as to why they are considered as referable to the species.

It is evident that *P. (Parapromerycochoerus) barbouri* or a form quite similar to that species gave rise to *P. (P.) macrostegus furlongi* of the John Day. It is also apparent that *P. (P.) macrostegus furlongi* from questionably middle John Day deposits gave rise to *P. (P.) macrostegus* from questionably upper John Day. (See discussion of the possible sequence of forms from the John Day, p. 90.)

DISTRIBUTION

Remains of *P. (Parapromerycochoerus)* are known from the Harrison formation or its

approximate equivalent in Oregon, South Dakota, and Wyoming. (See distribution chart, p. 86.)

SUMMARY OF SPECIES AND TYPES

Two species and one subspecies of *Promerycochoerus (Parapromerycochoerus)* from three lower Miocene localities are here recorded:

1. *Promerycochoerus (Parapromerycochoerus) barbouri*, new species, from Niobrara County, Wyoming; referred specimens from Shannon and Washington counties, South Dakota. (Harrison.)

HOLOTYPE: Skull, F:A.M. 33315. Figures 5-7.

2. *Promerycochoerus (Parapromerycochoe-*

rus) *macrostegus* (Cope), from the John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Skull and mandible, A.M. 7444. Figures 5-7, 11, 12.

2a. *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus furlongi*, new subspecies, from the John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Skull, C.I.T. 1727. Figures 5-7.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PROMERYCOCHOERUS (PARAPROMERYCOCHOERUS)

TOTAL AVAILABLE SPECIMENS: 21

1. *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*,¹ new species

From the Harrison formation, Niobrara County, Wyoming; referred remains from Shannon and Washington counties, South Dakota

DESCRIPTION

SKULL: Smaller than in average examples of *P. carrikeri* from the same formation; sagittal crest slightly less in length and height than in *P. (Parapromerycochoerus) macrostegus*; moderately wide frontals; nasal with more anterior retraction than in *P. carrikeri*; anterior nasal-maxilla contact above posterior portion of P₁; zygomatic arch with straight posterior border, not hooked as in examples of *P. carrikeri*; postglenoid process not so robust as that found in examples of *P. (P.) macrostegus*.

MANDIBLE: Comparatively light; inferior border increasing in depth posteriorly, with slight downward curve posterior of M₃, curve

¹ Named in honor of the late Dr. Erwin Hinckley Barbour, Director (1891-1941) of the University of Nebraska State Museum, who encouraged the writers in their research on the oreodonts.

decidedly more abrupt in *P. (P.) macrostegus*.

DENTITION: Average length of dental series less than in examples of *P. carrikeri*, *P. (Parapromerycochoerus) macrostegus*, and *P. (P.) macrostegus furlongi*.

LIMBS: Unknown.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 5-7, 11, 12.

DISCUSSION

The proposed new species, although found in the same beds as examples of *P. carrikeri*, is distinguishable from that species by the smaller size, smaller bulla, absence of the hooked posterior border of the zygomatic arch, and the more extended posterior palate. The referred ramal specimens compare readily with the associated skull and ramus, A.M. 12965. Sex variation is based on the light and heavy zygomatic arches.

The new species is not well represented by examples in museum collections. To date material is known only from South Dakota and Wyoming. The F:A.M. specimens were collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1932-1938, and the A.M. material by W. D. Matthew and Albert Thomson, 1906-1907.

Six specimens are here recorded:

HOLOTYPE

Skull with I¹(alv.)-M³. (w+)
?Male example

F:A.M. 33315

From N. of Keeline, Niobrara County,
Wyoming, 1932
Figs. 5-7

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING, (B) SHANNON AND (C) WASHINGTON COUNTIES, SOUTH DAKOTA

A. FROM NIOBRARA COUNTY, WYOMING

MANDIBLE

Partial mandible with I₁-I₂ rt. and I₃-M₃
(/C br.). (M)

F:A.M. 45417

From N. Ridge, $\frac{1}{2}$ mi. W. of U. S. Highway No. 85, 1938
Figs. 11, 12

MANDIBULAR RAMUS

Partial left ramus with I₁-P₁ alv. and F:A.M. 45418 From 77 Hill, N. of Manville, 1932
P₂-M₃. (w+)

B. FROM SHANNON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBULAR RAMUS

Partial skull with I²-M³ (I³ rt.) and partial right ramus with P₁ and P₄-M₃ (M₁ br.). (w†)
?Female example A.M. 12965 From the divide E. of Porcupine Creek, 7 mi. N.N.W. of Porcupine Post Office, 1906

SKULL

Partial skull with I¹-M³. (m) 12950 From Porcupine Creek, 4 mi. N.N.W. of Porcupine Post Office, 1906
?Female example

C. FROM WASHINGTON COUNTY, SOUTH DAKOTA

SKULL

Skull with I¹-M³. (w+) A.M. 13816 From 5 mi. S. of Kyle Post Office, 1907
?Male example

The bullae are slightly larger than those of the holotype and the nasals show less retraction. Both of these variant characters, however, are within the individual variation that may be expected.

Loomis¹ considered this specimen as a male example of "*Promerycochoerus*" *gregoryi* Loomis, which species will be considered under another genus in a forthcoming paper by the writers.

2. *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope)

From questionably upper John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Merycochoerus macrostegus COPE, 1884, Proc. Amer. Phil. Soc., Philadelphia, vol. 21, p. 526; 1888, Amer. Nat., vol. 22, pl. 26, fig. 1. SCOTT, 1890, Morph. Jahrb., vol. 16, pl. 14, figs. 8-9.

Promerycochoerus macrostegus (Cope) DOUGLASS, 1901, Amer. Jour. Sci., ser. 4, vol. 11, p. 82. MATTHEW, 1901, Mem. Amer. Mus. Nat. Hist., vol. 1, pt. 7, p. 398, fig. 19. OSBORN, 1910, Age of mammals, fig. 115. ZITTEL, 1911, Grundzuge der Paläontologie (paläozoologie), div. 2, Vertebrata, p. 483, fig. 675a; 1923, *op. cit.*, p. 572, fig. 716a. ABEL, 1919, Die Stamme der Wirbeltiere, fig. 607. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 132, figs. 89-90, pl. 13, fig. 3.

Promerycochoerus marshi THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 1, art. 15, p. 236, figs. 4a-b; 1925, Jour. Mammal., vol. 6, fig. 1. WEBER AND ABEL, 1928, Die Säugetiere, fig. 405. THORPE, 1937, *ibid.*, p. 135, figs. 92-93.

CHARACTERS

SKULL: Largest known form of the subgenus but with somewhat less height than examples of *P. (P.) macrostegus furlongi*;

¹ Loomis, Frederic B., 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 23 (misprinted as A.M. 12816).

nasals retracted for short distance; nasal-maxilla contact in region above posterior portion of P₁; zygomatic arch with straight posterior border and not hooked as in examples of *P. carrikeri*; infraorbital foramen above region of anterior portion of M₁; lacrimal fossa moderately small but deeper than in *Promerycochoerus*; bulla greatly compressed laterally; postglenoid process slightly longer than in examples of previously mentioned species; posterior palate projection extremely produced beyond M³ similar to *P. (Pseudopromerycochoerus)*.

MANDIBLE: Inferior border of ramus with abrupt downward curve below the last lobe of M₃.

DENTITION: Longest series of subgenus; within the size range of *P. carrikeri*; inferior and superior premolars not crowded.

LIMBS: Similar to those of *P. carrikeri*.
MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 5-7, 11, 12.

DISCUSSION

Thorpe² stated that the posterior portion of the zygomatic arch "rises to the plane of the summit of the sagittal crest," and that "the nasal bones are long but proportionally

² Thorpe, Malcolm R., *loc. cit.*

reduced." A close examination of the holotypic skull shows that the sagittal crest has been restored and might well have been higher. In other examples of this species there is an apparent anterior rise and a posterior descent of the crest. The only point of surface of the sagittal crest of the holotype is the anterior edge of the lateral wings of the occiput, which is the point from which the crest descends in most examples. The anterior nasal-maxilla contact in this form is situated considerably more to the rear than in examples of *P. (P.) macrostegus furlongi*, which appears to have been ancestral to this species. The anterior tip of the nasals of the holotype have been restored, but should extend farther anteriorly.

Both illustrations of the holotype by Matthew¹ and Thorpe² show the retracted nasal as being complete except for a small notch on the right side at about the nasal-maxilla contact. The referred skull A.M. 7450 demonstrates a rise to the sagittal crest and a longer nasal. The present writers consider the holotype as an example of the female of this species. The holotypic skull is narrower than in other examples referred to the species, a character which is usually diagnostic in determining sex variation.

"*P. marshi*" Thorpe is here considered synonymous with *P. (P.) macrostegus*. Thorpe³ considered the holotypic skull of the former to be about the same length and breadth as in the holotype of *P. (P.) macrostegus*. The present writers would estimate the skull in question as being considerably wider than in the holotype of *P. (P.) macrostegus* and also would consider it to represent a male of that species. Thorpe further stated that the

holotype of "*P. marshi*" was more robust than the holotype of this species. Again this character probably represents sex variation. Other characters of difference between the two holotypes pointed out by Thorpe are here considered to be individual variation.

The holotypic skull and mandible of "*P. marshi*" are still joined by matrix, and until the present study was made the bullae were not exposed. The bullae proved to be small and typical of examples of *P. (P.) macrostegus*. In all the specimens discussed, the nasal-maxilla contact is above the posterior portion of P¹.

Thorpe listed the forms here discussed as coming from the upper John Day. The present writers agree with Thorpe in this, but no definite data of their occurrence are available (see discussion of John Day beds, p. 89).

The present writers consider the synonymy of the two species discussed above to be an example of what may occur when individual and sex variation is not considered. Since no two skulls are identical the term *duplicate* is not an appropriate one when dealing with fossils. The two types of variation and the geological occurrence of forms must always be considered; otherwise each specimen may appear to be a new species. There is no logical reason to recognize two distinct species if the holotypes come from supposedly the same locality and geologic level and have the same characters and size, differing only in very minor details. On the basis of occurrence of oreodonts in the west-central Great Plains, it is necessary to consider these forms in synonymy.

Fourteen specimens are here recorded:

HOLOTYPE

Skull with I¹-I³ rt. and I²-M³ and mandible with I₁-I₃ alv. and /C(br.)-M₃. (w⁺*)
?Female example

A.M. 7444

From the John Day Valley,⁴ Oregon; collected by Charles Sternberg
Figured by Cope, 1888, pl. 26, fig. 1;
Scott, 1890, pl. 14, figs. 8-9; Matthew, 1901, fig. 19; Osborn, 1910, fig. 115; Zittel, 1911, fig. 675a; 1923, fig. 716a; Abel, 1919, fig. 607; Thorpe, 1937, figs. 89-90, pl. 13, fig. 3
This paper, figs. 5-7, 11, 12

¹ Matthew, W. D., 1901, *loc. cit.*

² Thorpe, Malcolm R., 1937, *loc. cit.*

³ Thorpe, Malcolm R., 1921, *loc. cit.*; 1937, *loc. cit.*

⁴ Thorpe, 1937, *loc. cit.*, gives the locality as "Bridge Creek." The American Museum catalogue records the data as John Day Valley only.

REFERRED FROM THE JOHN DAY VALLEY, OREGON

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

| | | |
|--|--------------|--|
| Skull with I ¹ -M ³ , mandible with I ₁ -P ₃ rt. and P ₄ -M ₃ , partial humerus, partial tibia, calcaneum, astragalus, partial pes, and vertebrae. (w+) ?Female example | Y.P.M. 10955 | From indefinite locality; collected by L. S. Davis, 1876 |
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and vertebrae. (w+) ?Female example | 10957 | From indefinite locality; collected by L. S. Davis, 1876 |
| Partial skull with I ¹ -M ³ , mandible with I ₁ -C rt. and P ₁ (br.)-M ₃ , and partial tibia. (w+) | 10975 | From Turtle Cove; collected by L. S. Davis, 1876 |

2 SKULLS AND ASSOCIATED MANDIBLES

| | | |
|--|-------------|--|
| Skull with I ¹ -M ³ and mandible (attached) with I ₁ -M ₃ . (w ⁺) ?Male example Holotype of " <i>P. marshi</i> " Thorpe. (Y.P.M. 10999) | 10999 | From Haystack Valley; collected by L. S. Davis, 1876 Figured by Thorpe, 1921, figs. 4a-b; 1925, fig. 1; 1937, figs. 92-93; Weber and Abel, 1928, fig. 405 |
| Skull with I ¹ -I ² rt. and I ³ -M ³ , mandible (attached) with I ₁ -I ₂ rt. and I ₃ (br.)-M ₃ , and atlas. (w ⁺) ?Female example | C.I.T. 2696 | From the upper John Day, C.I.T. coll. loc. no. 30, between Gates and Simpson ranches, Kahler Basin; collected by John H. Maxson |

4 SKULLS

| | | |
|---|-------------|--|
| Skull with I ¹ (rt.)-M ³ . (w) ?Female example | A.M. 7450 | From indefinite locality |
| Partial skull with M ² -M ³ . (m+) | C.I.T. 1735 | From C.I.T. coll. loc. no. 23, in draw S. of Sheep Mountain, on E. side of John Day River; "middle John Day" |

The catalogue at the California Institute of Technology indicates "middle John Day," but the writers question this assignment and consider the above specimen as having come from the upper John Day.

| | | |
|--|----------|--|
| Partial skull without dentition | U.C. 585 | From indefinite locality |
| Skull with I ¹ -C/ rt. and P ¹ (br.)-M ³ . (w+) | U.O. 685 | From North Fork of the John Day River; Condon collection |

The bullae of this skull are larger than in average specimens referred to this species but not so large as in examples of typical *Promerycochoerus*. The nasal-maxilla contact is slightly more forward than in average examples of this species, perhaps owing to individual variation or to a difference in stratigraphic position.

TENTATIVELY REFERRED FROM THE JOHN DAY VALLEY, OREGON

2 ASSOCIATED INDIVIDUALS

| | | |
|--|-----------|---|
| Muzzle of skull with I ¹ -C/rt., symphysis of mandible with I ₁ -C, partial right ramus with P ₁ -P ₃ , and partial right ramus with P ₄ (br.)-M ₃ (br.) (M ₁ rt.). (w) | A.M. 7437 | From the North Fork of the John Day River; collected by L. S. Davis, 1879 |
|--|-----------|---|

Tentatively referred because of the deep downward curve of the inferior border of the ramus.

SKULL AND MANDIBLE

Anterior portion of skull with I¹-M³ and partial mandible (attached) with I₁-M₃. (w+) A.M.7467 From indefinite locality

Tentatively referred owing to the position of the nasal-maxilla contact above the posterior portion of P¹.

2 MANDIBLES, ETC.

Partial mandible with I₁-M₃ (P₁ br. and P₂ absent). (w) 7440 From indefinite locality

Tentatively referred because of the deep downward curve of the posterior portion of the inferior border of the ramus.

Partial mandible with P₂(br.)-M₃(br.) (M₁-M₂ br.), and partial humerus. (w⁺⁺) 7463 From indefinite locality

Tentatively referred because of the deep downward curve of the posterior portion of the inferior border of the ramus. The partial humerus approximates examples of *P. carrikeri* and the tentatively referred examples of *P. superbus*.

2a. *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus furlongi*,¹ new subspecies

From questionably middle John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

(more anterior than in *P. (P.) macrostegus*); posterior palatal projection extended posteriorly but not to the degree found in *P. (P.) macrostegus*.

MANDIBLE: Unknown.

DENTITION: Approximates size of *P. superbus*; smaller than examples of *P. (P.) macrostegus*.

LIMBS: Unknown.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 5-7.

One specimen is here recorded:

CHARACTERS

SKULL: Approximate size of *P. superbus* and *P. superbus chelydra*; smaller than in examples of *P. (Parapromerycochoerus) macrostegus*; infraorbital foramen above P⁴; anterior nasal-maxilla contact above P¹

HOLOTYPE

Skull with I¹-I³ rt. and C/(br.)-M³ (P¹ rt.) (w⁺)
?Female example

C.I.T. 1727

From C.I.T. coll. loc. no. 2, N. 08°; E. of Sheep Mt., S. 66°; E. of Cant Ranch, on E. side of principal gully in N. face of Sheep Mt., John Day Valley, Oregon; collected by E. L. Furlong
Figs. 5-7

IB. *PROMERYCOCHOERUS* (*PSEUDOPROMERYCOCHOERUS*), NEW SUBGENUS

SUBGENOTYPE: *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope).

DESCRIPTION

SKULL: Large, basal length ranging from 221 to 350 mm. and width from 149 to 276 mm.; supraoccipital region protruding posteriorly beyond the occipital condyles, with

¹ Named in honor of E. L. Furlong, who has made so many contributions to the paleontology of the Pacific coast region.

lateral wings small and moderately flared outward; sagittal crest narrow and high, but not so long as in examples of *Promerycochoerus*; brain case inflated, rounded, and slightly elongated; frontals wide; nasals large, moderately robust, with slightly rounded anterior superior surface, but not to the degree found in average examples of *Promerycochoerus*, and with slight anterior retraction; nasal-maxilla contact above anterior portion of P¹ to anterior portion of P²; malar deep below orbit; zygomatic arch, especially posterior portion, light in comparison with ex-

amples of *Promerycochoerus*; zygomatic arch with gradual rise posteriorly from below orbit and not extending downward or posteriorly so far as in examples of *Promerycochoerus*; posterior tip of arch approximately above the postglenoid process (in *Promerycochoerus* the zygomatic arch usually extending for some distance posterior to the postglenoid process, thus forming a definite narrow U-shape from side view); lacrimal fossa approximately equal to that in *Promerycochoerus*; infraorbital foramen above region of P⁴; facial depression above the premolar region; premaxillae joined for short distance; muzzle with outward flare (resulting from constriction in facial region); posterior palate projecting for considerable distance beyond M³, somewhat more than in examples of *Promerycochoerus*; occipital condyles moderately robust; paroccipital process moderately wide at base and set at slight angle to longitudinal axis of skull; bulla well inflated and usually oblong in outline; postglenoid process robust, similar to that in average examples of *Promerycochoerus*.

MANDIBLE: Approximately equal to examples of *Promerycochoerus*; postsymphysis in the area below P₂; ramus shallow; inferior border of ramus with rather sharp downward curve below second lobe of M₃; ascending ramus similar to examples of *Promerycochoerus*, with posterior border almost straight, lacking inward curve of examples of *Promerycochoerus*; condyle moderately heavy, similar to examples of *Promerycochoerus*.

DENTITION: Brachyodont; premolars not crowded as in examples of *Promerycochoerus*, otherwise quite similar to examples of that genus.

LIMBS: Approximately equal in size or larger than those of examples of *Promerycochoerus*, but with a tendency towards being somewhat lighter.

MEASUREMENTS: Tables 4, 5.

ILLUSTRATIONS: Figures 6, 8–12 (skulls, mandibles, and dentitions); 25, 26 (limbs).

DISCUSSION

The proposed new subgenus embraces forms with skulls which differ from those of *Promerycochoerus* in having shorter and lighter sagittal crests, shorter and lighter zygomatic arches, and greatly projected posterior pal-

ates. The ascending ramus differs from that genus in being almost straight (vertically) and in displaying a less crowded condition in the premolar series.

It is of interest to note that the large forms of the subgenus are known only from South Dakota, Montana, and Oregon. The small ones are represented in South Dakota and Wyoming. The large forms—*P. (Pseudopromerycochoerus) inflatus*, *P. (P.) montanus*, and *P. (P.) montanus pinensis*—here recorded differ slightly except in size, and no definite specific characters are apparent. Perhaps when more material of the subgenus is known from Montana and Oregon, a range of size difference may be recorded or other character differences be demonstrated. The writers consider the large subspecies as a geographic subspecies. The two small forms—*P. (P.) minor* and *P. (P.) minor pygmyus*—seem to represent a dwarf line. Possibly additional material may show that this species and subspecies should be referred to a new genus.

DISTRIBUTION

Promerycochoerus (Pseudopromerycochoerus) remains have been found in widely distributed areas. Three species and two subspecies are known from lower Miocene deposits (Harrison formation or its approximate equivalent) of Montana, Oregon, South Dakota, and Wyoming (see distribution chart, p. 86).

SUMMARY OF SPECIES AND TYPES

Three species and two subspecies of *Promerycochoerus (Pseudopromerycochoerus)* from five lower Miocene localities are here recorded:

1. *Promerycochoerus (Pseudopromerycochoerus) inflatus* (Thorpe), from John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull, Y.P.M. 10233. Figures 8–10.

2. *Promerycochoerus (Pseudopromerycochoerus) minor* (Douglass), from Granite County, Montana. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull and partial mandible, C.M. 769. Figures 10, 12.

2a. *Promerycochoerus (Pseudopromerycochoerus) minor pygmyus* (Loomis), from

Shannon County, South Dakota; referred remains from Goshen County, Wyoming. (Harrison.)

HOLOTYPE: Partial skull, A.M. 12967. Figures 8-10.

3. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), from Meagher County, Montana; and (3a) geographic variety from John Day Valley, Oregon. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull and partial mandible, A.M. 8107. Figures 10, 12.

3b. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, from Shannon County, South Dakota; referred remains from Washington and Tripp counties, South Dakota. (Harrison.)

HOLOTYPE: Skull and ramus, A.M. 12948. Figures 6, 8-12.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PROMERYCOCHOERUS (PSEUDOPROMERYCOCHOERUS)

TOTAL AVAILABLE SPECIMENS: 35

1. *Promerycochoerus* (*Pseudopromerycochoerus*) *inflatus* (Thorpe)

From questionably upper John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Promerycochoerus inflatus THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 1, p. 235, fig. 3.

Promerycochoerus macrostegus inflatus (Thorpe) THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 134, fig. 91.

CHARACTERS

SKULL: Decidedly larger and more massive than in *P. (Pseudopromerycochoerus) montanus*; anterior nasal-maxilla contact above P¹.

MANDIBLE: Unknown.

DENTITION: Series longer than in *P. (P.) montanus*.

LIMBS: Unknown.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 8-10.

DISCUSSION

Thorpe¹ described *P. inflatus* in 1921 but later considered it to be a subspecies of *P. (P.) macrostegus*. The holotypic skull of *P. (P.) inflatus* is somewhat longer and wider than that of *P. (P.) montanus*. The holotypic skull of *P. (P.) inflatus* is badly crushed and expanded and, as stated by Thorpe, "It is very robust and massive and is peculiar in that the bone of all parts of the skull is slightly spread apart and the interstices are filled with matrix. . . ." The dental series alone may be reduced 20 mm. if the crushing and spreading of the skull are considered.

The bullae of *P. (Pseudopromerycochoerus) inflatus* differ from those of *P. (Parapromerycochoerus) macrostegus* in being rather wide with a concave surface. On examination of this region on the skull, Y.P.M. 10233, it was found that the bulla has been placed on the skull with plaster, and it appears that the portion of the bulla with the concave surface should be turned so that it would face the postglenoid process or the paroccipital process. This would give the bulla an outline similar to that in *P. (Pseudopromerycochoerus) montanus*.

One specimen is here recorded:

HOLOTYPE

Partial skull with C/-M³ (P² rt.). (w+) ?Male example

Y.P.M. 10233

From Bridge Creek, the John Day Valley, Oregon; collected by Thomas Condon

Figured by Thorpe, 1921, fig. 3; 1937, fig. 91

This paper, figs. 8-10

¹ Thorpe, Malcolm R., 1921, *loc. cit.*; 1937, *loc. cit.*

2. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass)

From lower Miocene deposits (approximately equal in age to the Harrison of the Great Plains), Granite County, Montana

Promerycochoerus minor DOUGLASS, 1903, Ann. Carnegie Mus., vol. 2, no. 2, p. 168, fig. 12.

Promerycochoerus hollandi minor (Douglass) THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 127, fig. 83, pl. 16.

CHARACTERS

SKULL: Small, smallest known species of the subgenus; nasals slightly retracted; anterior nasal-maxilla contact above the region of P¹; zygomatic arch light, extending posteriorly slightly beyond the postglenoid process; infraorbital foramen above posterior portion of P²; lacrimal fossa small and shallow; paroccipital process tapering rapidly downward; bulla of medium size, inflated, and suboval in outline; postglenoid process almost as wide laterally as anteroposteriorly and with a sloping external border.

MANDIBLE: Small; similar to that of examples of other species of the subgenus.

DENTITION: Series small, equal to that of *P. (P.) minor pygmyus*; smaller than in other species of the subgenus.

LIMBS: Unknown.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 10, 12.

DISCUSSION

The holotype, the only known specimen representing this species, lacks the entire occipital region, thus making comparisons dif-

ficult. The bulla and paroccipital process associated with the holotype, although separated from the skull, undoubtedly are a part of it. The portions of the skull that are preserved, as well as the mandible, are similar to the holotype and referred examples of the subspecies, *P. (P.) minor pygmyus*.

Douglass¹ in the original description stated: "I refer it provisionally to this genus [*Promerycochoerus*] principally on account of the form and size of the zygomatic arches. It seems to be intermediate between *Eporeodon* and *Promerycochoerus*. It is a small species of *Promerycochoerus*, but larger than *Eucrotaphus*."

This species has characters which are similar to *Promerycochoerus*, but it also has the important characters of the subgenus *P. (Pseudopromerycochoerus)*. For example, the zygomatic arch does not extend noticeably beyond the postglenoid process as it does in the examples of *Promerycochoerus*.

Thorpe² treated this species as a subspecies of "*Promerycochoerus*" *hollandi* on the basis of "their many similar characters." The present writers consider that the species *hollandi* belongs to another subfamily of oreodonts and fail to see any important similar characters in *hollandi* and *P. (P.) minor*. Detailed comparisons will be made in a forthcoming paper. Thorpe did not make any comparisons of *P. (P.) minor* with *P. (P.) minor pygmyus* and considered the latter as a subspecies of "*Promerycochoerus vanttasselensis*," which is here placed in synonymy with *P. carrikeri* (see discussion, p. 95).

One specimen is here recorded:

HOLOTYPE

Anterior portion of skull with I²-M³, partial mandible with I₁-M₃, and fragments. (M+)

C.M. 769

From E. of Drummond, on the Hellgate River, Granite County, Montana; collected by Earl Douglass

Figured by Douglass, 1903, fig. 12; Thorpe, 1937, fig. 83; pl. 16

This paper, figs. 10, 12

2a. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis)

From the Harrison formation, Shannon County, South Dakota; referred remains from Goshen County, Wyoming

Promerycochoerus pygmyus LOOMIS, 1924, Bull.

Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 27, fig. 13.

Promerycochoerus vanttasselensis pygmyus (Loomis) THORPE, 1937, Mem. Peabody Mus. vol. 3, pt. 4, p. 150, fig. 111 (in part), pl. 20, figs. 2, 3.

¹ Douglass, Earl, 1903, *loc. cit.*

² Thorpe, Malcolm R., 1937, *loc. cit.*

CHARACTERS

SKULL: Approximate size of that of *P. (P.) minor*; supraoccipital region extending for short distance beyond the occipital condyles; supraoccipital wings moderately spread; sagittal crest prominent, but not very high; brain case inflated and rounded; frontals moderately wide; nasals moderately heavy with slight anterior retraction; anterior nasal-maxilla contact in area above the midportion of P^1 ; malar moderately deep below the orbit; zygomatic arch light, not extending posteriorly to the area above the postglenoid process; infraorbital foramen in area above the anterior portion of P^4 ; lacrimal fossa moderately small and moderately deep for size of skull; premaxillae joined for short distance; muzzle slightly expanded; occipital condyle light; paroccipital process small, tapering into a triangular shape; bulla inflated, rounded, and small, but proportionately equal in size to the bullae of larger species of this subgenus; postglenoid process moderately large and moderately robust; posterior palate projecting posteriorly well beyond M^3 , with a deep V-shaped posterior border (rounded in other species of this subgenus).

MANDIBLE: Moderately robust; postsymphysis usually below the anterior portion of P_3 ; ramus shallow; inferior border straight to a point below anterior lobe of M_3 , from which it curves downward rather abruptly; ascending ramus slightly higher proportionately than in other species of this subgenus; condyle moderately light, set at slight angle to the tooth row.

DENTITION: Series of about equal length to the holotype of *P. (P.) minor*, but decid-

edly smaller than examples of other species of this subgenus; premolars not crowded; P_2 and P_3 set at slight angle to alveolar border.

LIMBS: Considerably smaller than, but same proportions as, examples of *P. carrikeri* and *P. (Pseudopromerycochoerus) montanus*.

MEASUREMENTS: Tables 4 and 5.

ILLUSTRATIONS: Figures 8-12, 25, 26.

DISCUSSION

The subspecies is best represented from South Dakota, with only one referred specimen from Wyoming. As discussed on page 124, this subspecies is very similar to *P. (P.) minor*, that is, as far as is possible to make comparisons with the incomplete holotype of that species.

Loomis, when designating the holotype, referred specimen A.M. 12968 to this form and figured an associated partial manus. Also with the manus are other skeletal elements including a complete humerus, ulna, and radius, which are here figured for the first time (fig. 25).

Thorpe¹ considered this form as a subspecies of "*Promerycochoerus vantassensis*" Peterson, but this latter species is here considered as synonymous with *P. carrikeri*. It is not clear why Thorpe separated the two forms, *P. (P.) minor* and *P. (P.) m. pygmyus*, referring the former to a subspecies of "*P.*" *hollandi* and the latter to "*P. vantassensis*." The only point in common between "*P.*" *hollandi* and *P. (P.) minor* is that they came from Montana. Loomis evidently did not compare the examples of *P. pygmyus* with the holotype of *P. minor*.

Four specimens are here recorded:

HOLOTYPE

Skull (lacking postoccipital wings, frontals, and right zygomatic arch) with I^1 - M^3 . (w)

A.M. 12967

From the "lower Rosebud" (= Harrison in part) formation, Porcupine Creek, 2 mi. N.W. of Porcupine Post Office, Shannon County, South Dakota; collected by W. K. Gregory and Albert Thomson, 1906

Figured by Loomis, 1924, fig. 13; Thorpe, 1937, fig. 111 (in part); pl. 20, figs. 2-3

This paper, figs. 8-10

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

REFERRED FROM (A) SHANNON COUNTY, SOUTH DAKOTA, AND
(B) GOSHEN COUNTY, WYOMING

A. FROM SHANNON COUNTY, SOUTH DAKOTA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

- | | | |
|---|------------|--|
| Skull (crushed) with I ¹ (rt.)-M ³ , mandible with I ₁ -M ₃ , 2 humeri (1 partial), radius, ulna, partial manus, femur, partial tibia, pelvis, vertebrae, and ribs. (w) | A.M. 12968 | From Porcupine Creek, 3 mi. N.W. of Porcupine Post Office; collected by Albert Thomson, 1906 Figured by Loomis, 1924, fig. 13 (in part); Thorpe, 1937, fig. 111 (in part) This paper, figs. 11, 12, 25, 26 |
|---|------------|--|

SKULL AND MANDIBLE

- | | | |
|---|-------|---|
| Partial skull with I ² -M ³ and mandible (attached) with I ₁ (rt.)-M ₃ . (w ⁺⁺) | 12971 | From Porcupine Creek, 6 mi. E. of Porcupine Post Office; collected by W. K. Gregory, 1906 |
|---|-------|---|

B. FROM 6 MI. N.W. OF LINGLE, GOSHEN COUNTY, WYOMING
(Collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1931)

SKULL AND MANDIBLE

F:A.M.

- | | | |
|--|------|-------|
| Partial skull with I ¹ -M ³ and partial mandible with I ₁ -M ₃ | (w+) | 33335 |
|--|------|-------|

3. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope)

From the Deep River deposits (approximately equal in age to the Harrison of the Great Plains), Meagher County, Montana

Merycochoerus montanus COPE, 1884, Proc. Amer. Phil. Soc., Philadelphia, vol. 21, p. 531; 1884, *ibid.*, vol. 22, p. 23; 1884, Paleont. Bull., no. 39, p. 23; 1889, Amer. Nat., vol. 23, p. 113. SCOTT, 1890, Morph. Jahrb., vol. 16, p. 342, figs. 5, 6; 1895, Trans. Amer. Phil. Soc., Philadelphia, new ser., vol. 18, p. 151.

Promerycochoerus montanus (Cope) DOUGLASS, 1901, Amer. Jour. Sci., ser. 4, vol. 11, p. 82. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 138, pl. 17. KOERNER, 1940, Amer. Jour. Sci., vol. 238, no. 12, p. 852.

CHARACTERS

SKULL: Supraoccipital wings slightly larger than in examples of *P. (P.) montanus pinensis*; posterior portion of sagittal crest more robust than in the subspecies; exoccipital pits deep; nasals with slight anterior retraction; anterior nasal-maxilla contact above region just anterior of P¹; infraorbital foramen above the posterior portion of P⁴ to the anterior portion of M¹; bulla oblong in outline.

MANDIBLE: Typical of subgeneric description.

DENTITION: Typical of subgeneric description.

LIMBS: Short and heavy; shorter and lighter than in examples of *P. latidens*.

MEASUREMENTS: Tables 4 and 5.

ILLUSTRATIONS: Figures 8-12, 25, 26.

DISCUSSION

In the discussion under *Promerycochoerus latidens*, geographic variety (p. 105), it was pointed out that the holotype of *P. (Pseudopromerycochoerus) montanus* is incomplete and lacks any skeletal elements. In the Cope collection in the American Museum, however, there are several rami and a symphysis of a mandible associated with fragmentary limb elements. A partial skull, mandible, and skeletal elements, F:A.M. 45422A-B, are also referred to this species. These limb elements, in comparison with Cope's specimens, are somewhat lighter and shorter. The writers consider most of Cope's material as referable to *P. latidens*, geographic variety, rather than to *P. (P.) montanus*.

Scott¹ discussed the characters of the skull, rami, and skeletal elements of *P. (P.) montanus*, basing his conclusions on material in

¹ Scott, W. B., 1895, *loc. cit.*

the Princeton collection. The most important specimen is P.U. 10432, partial skull and mandible (attached). The more massive construction of the skull suggests that it is an example of a male. Scott's specimen is considerably more massive than the holotype, A.M. 8107, or the nearly complete referred skull, A.M. 21338, all three of which came from the same general area. Also among Scott's material there are three specimens which are here referred to *P. latidens*, geographic variety, from the same area as the example of *P. (P.) montanus*. Among the skull fragments, there is a partial zygomatic arch, P.U. 10441, which is larger and more massive than that of *P. (P.) montanus*. Also there is a humerus and associated fragments, P.U. 10484, and a femur, P.U. 10437, which compare readily with examples of *P. latidens*, but they are too large and massive to be referred to *P. (P.) montanus* (see p. 107).

It is of interest that Scott indicated that the Princeton material which is considered as

referable to *P. (P.) montanus* came from the upper horizon of the Smith River Valley of Montana. This is also true of the *P. latidens* material from the same area. However, the statement should be modified to read "the upper part of the lower Miocene of the area," which represents an approximate Harrison equivalent, since a later Miocene horizon is also present. Evidence of a "Sheep Creek" or "Lower Snake Creek" equivalent is strengthened by the fact that *Brachycrus* is also found in the same locality (see discussion, p. 105). *Mesoreodon chelonys* is also recorded from the same area but it is restricted to the lower part of the Miocene beds (see p. 140).

Cope¹ in the original description of *P. (P.) montanus* mentions a second individual, presumably referring to either the left ramus, A.M. 8108, or right ramus, A.M. 8110, here referred to *P. latidens*, geographic variety (see p. 106).

Fourteen specimens are here recorded:

HOLOTYPE

| | | |
|--|-----------|---|
| Posterior portion of skull with M ¹ -M ³ and partial mandible with P ₄ -M ₃ . (w) ?Female example | A.M. 8107 | From Smith Creek, Deep River, ?Meagher County, Montana; col- lected by J. C. Isaac, 1880 Figured by Thorpe, 1937, pl. 17 This paper, figs. 10, 12 |
|--|-----------|---|

REFERRED FROM WHITE SULPHUR SPRINGS AREA, MEAGHER COUNTY, MONTANA

ASSOCIATED SKULL, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

| | | |
|---|-----|------------------|
| Anterior portion of skull with C/(br.)-M ³ (br.), (P ² br., P ³ -P ⁴ absent) and partial mandible with I ₁ -M ₃ (P ₁ br.). Figs. 11-12 (in part) | (w) | F:A.M. 45422A |
| Partial left ramus with P ₅ -M ₃ | (w) | 45422B |

The heel of M₃ is slightly larger than that of example F:A.M. 45422A.

| | | |
|--|--|----------|
| Partial humerus, 2 radii (1 partial), 2 ulnae (1 partial), 2 partial manus, calcaneum, and partial pes. Figs. 25, 26 (in part) | | 45422A-B |
|--|--|----------|

The three specimens listed above were found associated in the field and therefore the limbs may belong to either F:A.M. 45422A or F:A.M. 45422B. The material was collected by N. J. Vaughan, N. Z. Ward, and Charles H. Falkenbach, 1942.

SKULL

| | | |
|---|-----|---------------|
| Almost complete skull with I ¹ -I ³ alv. and C/-M ³ . Figs. 8-10 | (w) | A.M. 21338 |
|---|-----|---------------|

The above specimen was collected by Charles C. Mook and C. Williams, 1925.

MANDIBULAR RAMUS

| | | |
|--|-----|------|
| Partial right ramus with P ₅ -dP ₄ -M ₁ (br.) | (i) | 8111 |
|--|-----|------|

The above specimen was collected by J. C. Isaac, 1877.

¹ Cope, E. D., 1884, *loc. cit.*

| SKULL AND MANDIBLE | | P.U. |
|--|--|---------------------|
| Partial skull with I ¹ -M ³ , mandible (attached) with I ₁ -M ₃ , and fragments . . . (w+) | | 10432 |
| ?Male example | | |
| SKULL | | |
| Anterior portion of skull with P ¹ -M ³ rt. | | 10433 |
| MANDIBLE | | |
| Partial mandible with /C-P ₁ rt. and P ₂ (br.)-M ₃ (w+) | | 10403A ¹ |
| LIMB ELEMENTS | | |
| Partial manus | | 10423 |
| Femur, partial radius, and partial ulna | | 10424 |

3A. GEOGRAPHIC VARIETY FROM QUESTIONABLY MIDDLE JOHN DAY DEPOSITS (APPROXIMATE HARRISON EQUIVALENT), THE JOHN DAY VALLEY, OREGON

NOTE: The referred material listed below differs slightly from examples of *P. (P.) montanus* in that there is a tendency for the supraoccipital wings to be less expanded and the frontals narrower. These differences, however, are within the individual variation found in any one species of other oreodonts.

PARTIAL SKULL AND MANDIBLE

| | | |
|---|---------------|---|
| Partial skull with I ¹ -I ³ alv. and C/-M ³ , and partial mandible with /C(br.)-M ₃ (P ₁ -P ₄ br.). (w) | U.S.N.M. 7841 | From Bridge Creek; collected by William Day, 1883 |
|---|---------------|---|

2 SKULLS

| | | |
|--|---------------|--|
| Skull with I ¹ -M ³ . (m+) | U.S.N.M. 7831 | From Deer Mountain, Camp Creek; collected by L. S. Davis, 1882 |
| Skull with I ¹ -M ³ . (w) | A.M. 7452 | From North Fork of the John Day River; Cope collection Figs. 8-10 |

3b. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies

From the Harrison formation, Shannon County, South Dakota; referred remains from Washington and Tripp counties, South Dakota

Promerycochoerus species GREGORY, 1920, Bull. Amer. Mus. Nat. Hist., vol. 42, art. 2, p. 189, fig. 159.

Promerycochoerus thomsoni ("female" example only) LOOMIS, 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 22, figs. 9, 11. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 145, fig. 107, pl. 19, fig. 2, pl. 20, fig. 1.

Hypselochoerus gregoryi (referred) LOOMIS, 1933, Bull. Geol. Soc. Amer., vol. 44, p. 729, fig. 9.

DESCRIPTION

SKULL: Supraoccipital region smaller and wings less expanded than in *P. (P.) montanus*; infraorbital foramen in region above posterior border of P⁴ and anterior portion of M¹;

¹ Koerner, H. E., 1940, *loc. cit.*, cited number as 10403.

exoccipital pits not so deep as found in examples of *P. (P.) montanus*; paroccipital process not so wide at base as may be expected for the large-sized skull; bulla well inflated and usually oblong in outline; postglenoid process moderately robust and high with external border more or less straight.

MANDIBLE: See subgeneric description.

DENTITION: See subgeneric description.

LIMBS: Moderately short and light, longer than in examples of *Promerycochoerus carikeri*.

MEASUREMENTS: Table 4.

ILLUSTRATIONS: Figures 6, 8-12.

DISCUSSION

The holotypic skull and ramus, A.M. 12948, of the proposed subspecies has been referred to and illustrated by Gregory,² Loomis,³ and Thorpe.⁴ Gregory mentioned the

² Gregory, W. K., 1920, *loc. cit.*

³ Loomis, Frederic B., 1924, *loc. cit.*

⁴ Thorpe, Malcolm R., 1937, *loc. cit.*

illustration of the specimen in connection with a comparative osteological discussion, and he identified it as "*Promerycochoerus* species."

Loomis later considered the same specimen to be a female example of "*Promerycochoerus thomsoni*." A comparison of the characters of the genus *Promerycochoerus* with those of the new subgenus *P. (Pseudopromerycochoerus)* definitely demonstrates that this holotype, A.M. 12948, does possess the characters of the proposed new subgenus, thus separating it from the genus *Promerycochoerus*.

Thorpe accepted the sex determination suggested by Loomis in the following statement: "From the standpoint of relationship, I should refer the male skull [A.M. 13819] to *P. vantasselensis* and that of the female [A.M. 12948] to *P. carrikeri*. . . ." The present writers, however, consider "*P. thomsoni*" and "*P. vantasselensis*" to be synonymous with *P. carrikeri* Peterson (see p. 93).

In 1933, Loomis¹ considered another specimen, A.C. 1931-109, as referable to "*Hypselochoerus*" *gregoryi*. An examination of the skull of this specimen, however, reveals that most of the occipital region has been restored incorrectly. The supraoccipital wings actually do not project beyond the condyles; thus the length of the skull would be considerably shortened. The skull of Loomis' specimen has an estimated length of 375 mm. and a width of at least 256 mm., whereas in the

holotype of "*H. gregoryi*" the respective measurements are 309 mm. and 150 mm. In the original description of "*Hypselochoerus gregoryi*" by Loomis, he states that it has an "excessively long skull, with moderately wide zygomatic arches." This description hardly applies to the skull A.C. 1931-109.

Thorpe² considered the species *gregoryi* under the genus *Promerycochoerus*, and referred to Loomis' skeletal description, pointing out that the discovery of this skeleton was the basis for the genus "*Hypselochoerus*" Loomis. Thorpe further stated that the holotypes of "*P. gregoryi*" and "*P. curvidens*" are exceedingly close to each other in general characters and that if Loomis' species, "*P. gregoryi*," warrants a subgeneric rank, it should be placed in *Desmatochoerus* Thorpe. Thorpe considered *Hypselochoerus* and *Desmatochoerus* in synonymy with *Promerycochoerus*. The writers, however, do not agree with the synonymy and will discuss this matter in a later paper.

Further complicating the study of specimens previously referred to the genus *Hypselochoerus* is the example A.M. 13816 (misprinted in Loomis, 1924, as 12816), which Loomis³ designated as a male example of "*H. gregoryi*." The present writers, however, have referred this specimen to *P. (Parapromerycochoerus) barbouri* (see p. 118).

Fifteen specimens are here recorded:

HOLOTYPE

Skull with I¹-M³ and left ramus with I₁(alv.)-M₃. (w+)

A.M. 12948

From the "lower Rosebud" (equal to Harrison formation), Porcupine Creek, 4 mi. N.N.W. of Porcupine Post Office, Shannon County, South Dakota; collected by W. D. Matthew, 1906

Figured by Gregory, 1920, fig. 159; Loomis, 1924, figs. 9 and 11; Thorpe, 1937, fig. 107, pl. 119, fig. 3, pl. 20, fig. 1

This paper, figs. 6, 8-12

Loomis⁴ considered this specimen as a female example of "*Promerycochoerus thomsoni*" Loomis.

¹ Loomis, Frederic B., 1933, *loc. cit.*

² Thorpe, Malcolm R., 1937, *ibid.*, p. 121.

³ Loomis, Frederic B., 1924, *loc. cit.*

⁴ Loomis, Frederic B., 1924, *ibid.*, p. 22.

REFERRED FROM (A) SHANNON, (B) WASHINGTON, AND
(C) TRIPP COUNTIES, SOUTH DAKOTA

A. FROM SHANNON COUNTY, SOUTH DAKOTA

SKULL, MANDIBLE, AND SKELETON

- Partial skull with I¹-M³, mandible with I₁-M₃, and skeleton (mounted in plaque) A.C. 1931-109 From Porcupine Creek, 5 mi. N.N.W. of Porcupine Post Office; collected by Frederic B. Loomis and party, 1931
Figured by Loomis, 1933, fig. 9; Thorpe, 1937, pl. 44, fig. 1

According to Thorpe, 1937, *loc. cit.*, the catalogue number of this specimen is A.C. 31-104.

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

- Skull (crushed laterally) with I²-M³, mandible (attached) with I₁-M₃, partial scapula, vertebrae, and pelvis. A.M. 12955 From Porcupine Creek, 4 mi. N.N.W. of Porcupine Post Office; collected by Albert Thomson, 1906
(w+)
?Female example

3 SKULLS AND MANDIBULAR RAMI

- Inferior portion of skull with P¹(br.)-M³ (P²-P³ br.), partial right ramus with P₃-M₃(br.) (M₁ br.), and fragments. 12956 From Porcupine Creek, 3 mi. N.N.W. of Porcupine Post Office; collected by W. D. Matthew, 1906
(w⁺)
?Male example
- Skull (crushed laterally) with I¹-M³ and mandible (attached) with I₁(rt.)-M₃. 12959 From the divide E. of Porcupine Creek, 7 mi. N.N.W. of Porcupine Post Office; collected by Albert Thomson, 1906
(w⁺⁺)
?Male example
- Anterior portion of skull with C/-M³ and partial mandible (attached) with I₅-M₃. (w) 12963 From the divide E. of Porcupine Creek, 7 mi. N.N.W. of Porcupine Post Office; collected by Albert Thomson, 1906

3 MANDIBULAR RAMI

- Partial mandible with P₁(rt.)-M₃ (P₂ absent). (w+) 12958 From the divide E. of Porcupine Creek, 7 mi. N.N.W. of Porcupine Post Office; collected by Albert Thomson, 1906
- Partial mandible with I₁-M₃(br.). (w) F:A.M. 37228 From 2 mi. N.N.W. of Porcupine Post Office, W. side of Porcupine Creek; collected by Ralph Mefferd and Morris Skinner, 1937
- Right ramus with I₁-P₁ alv. and P₂-M₃. A.M. 12954 From Porcupine Creek, 4 mi. N.N.W. of Porcupine Post Office; collected by W. D. Matthew, 1906
(w⁺)

B. FROM WASHINGTON COUNTY, SOUTH DAKOTA

3 SKULLS

- Skull (crushed) with I²-M³. (w+) A.M. 12940 From Wounded Knee Creek, 5 mi. S.E. of Manderson; collected by Albert Thomson, 1906
?Male example
- Anterior portion of skull with C/-M³(br.). (w) 12943 From Wounded Knee Creek, 4 mi. S.E. of Manderson; collected by W. D. Matthew, 1906
?Male example
- Skull with I³-dP³-M³(erupt.). (i) 12945 From "base of Rosebud," Wounded Knee Creek, 3 mi. S.E. of Manderson; collected by W. D. Matthew, 1906

TWO PARTIAL SKULLS AND SKELETAL ELEMENTS ASSOCIATED

- Five portions of skull with I¹(alv.)-M³ (C/ rt. and P²-P³ absent), mandible with I₁-M₃, pelvis, and fragments. (w+)
 ?Female example
 Partial skull with dP²-M²(br.). (i) A.M. 13815A From 5 mi. S. of Kyle Post Office; collected by Albert Thomson, 1907
 13815B Associated with above specimen

TENTATIVELY REFERRED

C. FROM EAST END OF TURTLE BUTTE, 3½ MI. N.W. OF WEWELA, TRIPP COUNTY, SOUTH DAKOTA

(Collected by Morris Skinner and associates, 1937)

PARTIAL SKULL, MANDIBLE, AND FRAGMENTS

F:A.M.

- Partial crushed skull with P¹(br.)-M³, mandible with I₁-M₃, astragalus, and fragments (w) 37582

II. MESOREODON SCOTT

Mesoreodon SCOTT, 1893, Amer. Nat., vol. 27, p. 659. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 97. KOERNER, 1940, Amer. Jour. Sci., vol. 238, p. 847.

GENOTYPE: *Mesoreodon chelonys* Scott.

CHARACTERS

SKULL: Medium size; ranging in basal length from 211 to 259 mm. and in width from 131 to 191 mm.; smaller and shallower than in examples of *Promerycochoerus*, larger and higher than in examples of *Promesoreodon*; supraoccipital region similar to that of *Promerycochoerus* (protruding posteriorly beyond the occipital condyles with lateral wings not greatly expanded but extending considerably beyond the condyles); exoccipital with deep pits (or possibly foramina); sagittal crest long and high but less so than in *Promerycochoerus* and more so than in *Promesoreodon*; brain case wide and inflated; nasals long, moderately robust to robust and anterior border from no retraction to slight retraction; anterior nasal-maxilla contact above P¹; malar moderately deep below the orbit; zygomatic arch from moderately light to medium heavy with highest point not extending upward to the plane of the sagittal crest, thus forming more of a half-circle than a U-shape (when viewed laterally); infraorbital foramen above P²-P⁴; lacrimal fossa large, not so deep proportionately as in examples of *Promesoreodon*; slight depression on the side of the face above the premolar region; muzzle somewhat in-

flated; premaxillae joined for very short distance; occipital condyles moderately heavy; paroccipital process tapering gradually downward, adhering to the bulla, with axis at pronounced angle to the bulla; bulla inflated, from medium size to moderately large, laterally compressed (suboval in outline), extending downward beyond the inferior border of the postglenoid process (see following discussion); postglenoid process moderately robust, with shape varying from squarish to anteroposteriorly compressed; posterior palate projecting for short distance posterior of M³.

MANDIBLE: Moderately robust; postsymphysis in area below P₃; symphysis strong, with a tubercle usually present at base of postsymphysis; ramus increasing in depth posteriorly; inferior ramal border slightly concave (not to the degree found in the genus *Brachycrus*), with gradual downward curve below the posterior portion of M₃; ascending ramus high, with slight inward curve of posterior border (similar to *Promerycochoerus*); condyle moderately large.

DENTITION: Brachydont (similar to *Promerycochoerus*, but less than in *Promesoreodon*); C/ large; /C small; P₁ large, somewhat spatulate shaped in outline; tendency towards slight diastema between P¹ and P² (more pronounced in some species than in others); premolars varying in size, resulting in crowding of the premolar region in some individuals; average examples of the premolar series set more or less straight with

TABLE 4

Promerycochoerus (*Parapromerycochoerus*), NEW SUBGENUS, AND *Promerycochoerus*
(Pseudopromerycochoerus), NEW SUBGENUS. COMPARATIVE MEASUREMENTS¹
 OF SKULLS AND RAMI

| | <i>P. (Parapromerycochoerus)</i> | | | <i>P. (Pseudopromerycochoerus)</i> | | |
|--|-------------------------------------|------------------------------------|--|------------------------------------|---------------------------------|--------------------------------------|
| | <i>barbouri</i> , new species | <i>macro- stegus</i> (Cope) | <i>macro- stegus furlongi</i> , new sub- species | <i>inflatus</i> (Thorpe) | <i>minor</i> (Doug- lass) | <i>minor pygmyus</i> (Loomis) |
| SKULL | Holotype F:A.M. 33315 | Holotype A.M. 7444 | Holotype C.I.T. 1727 | Holotype Y.P.M. 10233 | Holotype C.M. 769 | Holotype A.M. 12967 |
| Stage of wear of teeth | (w+) | (w $\frac{+}{+}$) | (w $\frac{+}{+}$) | (w+) | (M+) | (w) |
| Length (max., including supraoccipital crest and incisors) | 320 | (383) | 347 | ((392)) | — | ((255)) |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | 276.5 | (320) | 287.5 | ((355)) | — | 221 |
| Condylbasal length | 288 | (325) | 301 | ((336)) | — | 229 |
| Width (max.) | 222 | 248 | 231 | ((276)) | 149 | ((163)) |
| Width of brain case (max.) | 86 | 90 | 82 | — | — | — |
| Width, interorbital (min.) | 93 | 90 | (86.5) | 128 | 72 | — |
| Distance from anterior rim of orbit to an- terior base of canine | 136 | 164 | 145 | 168 | 78 | 103.5 |
| Distance from anterior rim of orbit to supra- occipital crest | — | (214) | 202 | ((224)) | — | — |
| Distance from ventral portion of occipital condyles to top of supraoccipital | — | ((212)) | — | — | — | — |
| Width of muzzle at infraorbital foramina | 84 | 91 | 76 | 132.5 | — | 64 |
| Width across canines (max.) | — | 85 | 79 | 107 | — | 63.5 |
| Width of palate between fourth premolars | 47 | 47 | 42 | 78 | — | 39 |
| Width of palate between canines | 40 | 47 | 43 | 50 | — | 37.5 |
| Length, C/-M ³ incl. | 153.5 | 180 | 160.5 | 207 | 123 | 122.5 |
| Length, P ¹ -M ³ incl. | 133.5 | 152 | (134) | 173.5 | 104.5 | 104.5 |
| Length, P ¹ -P ⁴ incl. | 58.5 | 73 | (62) | 79.5 | 50 | 47 |
| Length, M ¹ -M ³ incl. | 78 | 81 | 73 | 97.5 | 58 | 59.5 |
| Width of M ³ (max.) | 28 | 27 | 27.5 | 30 | 21 | 22 |
| Width across condyles | 54 | — | 57 | — | — | 45 |
| Depth of malar below orbit | 34 | 38 | 33 | 51.5 | — | 27 |
| RAMUS | Referred F:A.M. 45417 | | | | | Referred A.M. 12968 |
| Stage of wear of teeth | (M) | | | | | (w) |
| Length (max., including incisors) | 220.5 | 278 | — | — | — | 211 |
| Length, /C to condyle incl. | — | 267 | — | — | — | 186 |
| Depth of jaw under coronoid | — | 123 | — | — | — | 117 |
| Depth of jaw below anterior edge of M ₃ | 37 | 52 | — | — | — | 63.5 |
| Length, /C-M ₃ incl. | 139.5 | 178 | — | — | 127.5 | 132 |
| Length, P ₁ -M ₃ incl. | 132 | 167 | — | — | 117.5 | 123 |
| Length, P ₁ -P ₄ incl. | 62 | 81 | — | — | 54 | 55 |
| Length, M ₁ -M ₃ incl. | 71 | 86 | — | — | 65 | 69 |

TABLE 4—Continued

| | <i>P. (Pseudopromerycochoerus)</i> | | | |
|---|------------------------------------|---------------------------|--------------------------|---|
| | <i>montanus</i> (Cope) | | | <i>montanus pinensis</i> , new sub-species |
| SKULL | Holotype A.M. 8107 | Referred A.M. 21338 | Referred A.M. 7452 | Holotype A.M. 12948 |
| Stage of wear of teeth | (w) | (w) | (w) | (w+) |
| Length (max., including supraoccipital crest and incisors) | — | 353 | 340 | 357 |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | — | 294.5 | (298) | 304 |
| Condylbasal length | — | 308 | 304 | 317.5 |
| Width (max.) | 184 | 210 | (212) | 220 |
| Width of brain case (max.) | 75 | 84 | 88 | 90 |
| Width, interorbital (min.) | 100 | 94 | 88 | 96 |
| Distance from anterior rim of orbit to anterior base of canine | — | 145 | 145 | 161 |
| Distance from anterior rim of orbit to supraoccipital crest | 216 | 204 | (192) | 193 |
| Distance from ventral portion of occipital condyles to top of supraoccipital | 117 | 111.5 | — | 111 |
| Width of muzzle at infraorbital foramina | 92 | 95 | — | 110 |
| Width across canines (max.) | — | 82 | 80 | 89 |
| Width of palate between fourth premolars | — | 55 | 46 | 57 |
| Width of palate between canines | — | 43 | 40 | 47 |
| Length, C/-M ³ incl. | — | 172.5 | 167.5 | 175 |
| Length, P ¹ -M ³ incl. | — | 148 | 142.5 | 149.5 |
| Length, P ¹ -P ⁴ incl. | — | 68 | 65.5 | 73 |
| Length, M ¹ -M ³ incl. | 82 | 81.5 | 79.5 | 79 |
| Width of M ³ (max.) | 26 | 28 | 27.5 | 30 |
| Width across condyles | — | 57 | — | 53.5 |
| Depth of malar below orbit | — | 42 | 35 | 43 |
| RAMUS | | F:A.M. 45422A | U.S.N.M. 7841 | |
| Stage of wear of teeth | — | (w) | (w) | |
| Length (max., including incisors) | — | — | — | 285 |
| Length, /C to condyle incl. | — | — | — | 162 |
| Depth of jaw under coronoid | — | — | — | 128 |
| Depth of jaw below anterior edge of M ₃ | — | 50 | 51 | 63 |
| Length, /C-M ₃ incl. | — | 167 | (171) | 181 |
| Length, P ₁ -M ₃ incl. | — | (155) | 164.5 | 167 |
| Length, P ₁ -P ₄ incl. | — | 72 | 78.5 | 82 |
| Length, M ₁ -M ₃ incl. | 87.5 | 82.5 | 87 | 86 |

¹ Measurements in millimeters; (), approximate; (()), estimated.

TABLE 5

Promerycochoerus (*Pseudopromerycochoerus*), NEW SUBGENUS. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

| | <i>P. (P.) montanus</i> (Cope) | <i>P. (P.) minor pygmyus</i> (Loomis) |
|---|-----------------------------------|--|
| | Referred F:A.M. 45422A-B | Referred A.M. 12968 |
| Length of humerus (articular) | — | 155.5 |
| Length of radius (articular) | 184 | 128.5 |
| Length of ulna (max.) | 232 | 178.5 |
| Length of metacarpal III (max.) | 79 | 62 |
| Length of femur (articular) | — | 198 |
| Length of calcaneum (max.) | 72.5 | — |

¹ Measurements in millimeters.

the alveolar border; heel developed to varying degree on M³; external styles of superior molars prominent; anterior intermediate crest developed on P¹, P², and P³ in unworn or slightly worn premolar series (in *Promerycochoerus* this development on P² and P³ only); posterior intermediate crest present on P₃ (in *Promerycochoerus* this development weak); anterior basin or pit sometimes present on P⁴.

LIMBS: Moderately short and moderately heavy; decidedly lighter and shorter than in examples of *Promerycochoerus*.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 7, 15–20 (skulls, mandibles, and dentitions); 25, 26 (limbs).

DISCUSSION

The genus *Mesoreodon* is here considered as ancestral to *Promerycochoerus* and its subgenera. The bullae in examples of *Mesoreodon* show tendencies towards the large bullae of *Promerycochoerus* and also the small high bullae of *P. (Parapromerycochoerus)*. Since the bullae of specimens of *Mesoreodon* show gradation in either direction, it seems impossible at this time to separate or group the material on this basis. It is apparent that the known species of *Mesoreodon* are close to the dividing line of the genus *Promerycochoerus*, *P. (Parapromerycochoerus)*, and *P. (Pseudopromerycochoerus)*.

In the genus *Mesoreodon*, the posterior border of the zygomatic arch does not extend beyond the area above the postglenoid proc-

ess, which is also true in *P. (Pseudopromerycochoerus)*. In the side view of the latter, the zygomatic arch forms a U-shaped outline, while in *Mesoreodon* the outline is more circular, similar to that of *Promerycochoerus*.

A study of *Mesoreodon* demonstrates what may be expected in any phylogenetic line, i.e., the ancestral form has many characters in common with the related genera and subgenera which developed at a later time. These characters are diagnostic in interpreting the relationships of the various closely allied genera and subgenera.

Scott,² Douglass,³ Thorpe,⁴ and Koerner⁵ compared *Mesoreodon* with the genus *Eporeodon*. The present writers doubt that the genotypic species, *E. occidentalis*, from the John Day beds, was considered when these comparisons were made. The holotypic specimen of *E. occidentalis* differs from examples of *Mesoreodon* in having a much less overhanging supraoccipital region, a less prominent sagittal crest, an exceptionally higher but comparatively narrower bulla, and a more brachyodont dentition. It is apparent that *Mesoreodon* is more closely related to *Promerycochoerus* than to *Eporeodon*.

DISTRIBUTION

The genus *Mesoreodon* is from the Gering

² Scott, W. B., 1893, *loc. cit.*

³ Douglass, Earl, 1906, *Nat. Sci.*, vol. 24, no. 618, p. 565.

⁴ Thorpe, Malcolm R., 1937, *loc. cit.*

⁵ Koerner, H. E., 1940, *loc. cit.*

and Monroe Creek formations or their approximate equivalent in Montana, Nebraska, and Wyoming (see distribution chart, p. 87).

SUMMARY OF SPECIES AND TYPES

Three species, three subspecies, and one questionably referred species of *Mesoreodon* from eight lower Miocene localities are here recorded:

1. *Mesoreodon cheeki* (Schlaikjer), from Goshen County, Wyoming; referred specimens from Niobrara County, Wyoming, and Morrill County, Nebraska. (Gering.)

HOLOTYPE: Skull, mandible, and most of skeleton, M.C.Z. 17765.

1a. *Mesoreodon cheeki scotti* (Schlaikjer), from Niobrara County, Wyoming; referred specimens from Converse County, Wyoming, and Morrill and Sioux counties, Nebraska. (Monroe Creek.)

HOLOTYPE: Skull, mandible, and partial skeleton, M.C.Z. 17480.

2. *Mesoreodon chelonys* Scott, from Meagher County, Montana; referred specimen

from Jefferson County, Montana. (Approximate Gering equivalent.)

HOLOTYPE: Skull, mandible, and scapula, P.U. 10425. Figures 15, 16, 18, 19.

2a. *Mesoreodon chelonys wheeleri* (Koerner), from Meagher County, Montana. (Approximate Gering equivalent.)

HOLOTYPE: Skull, Y.P.M. 13950.

3. *Mesoreodon megalodon* Peterson, from Sioux County, Nebraska; referred specimens from Morrill County, Nebraska, and Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Partial skull and partial mandible, C.M. 1325. Figures 19, 20.

3a. *Mesoreodon megalodon sweeti*, new subspecies, from Morrill County, Nebraska; referred specimens from Goshen and Niobrara counties, Wyoming. (Gering.)

HOLOTYPE: Skull, mandible, and partial skeleton, U.N.S.M. 28012. Figures 16–18, 20.

4. ?*Mesoreodon hesperus* (Stock), 1930, from Ventura County, California. (Approximate Monroe Creek equivalent.)

HOLOTYPE: Partial mandible, U.C. 27003. Figure 20.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MESOREODON

TOTAL AVAILABLE SPECIMENS: 110

1. *Mesoreodon cheeki* (Schlaikjer)

From the Gering formation, Goshen County, Wyoming; referred specimens from Niobrara County, Wyoming, and Morrill County, Nebraska

Eporeodon cheeki SCHLAIKJER, 1934, Proc. Boston Soc. Nat. Hist., vol. 40, no. 3, p. 220; 1935, Bull. Mus. Comp. Zool., vol. 76, no. 4, p. 170, pls. 27–29.

Eporeodon major cheeki (Schlaikjer) THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 76, pl. 7, pl. 39, fig. 2.

CHARACTERS

SKULL: Medium size, approximately equal to the average examples of *M. chelonys*; lighter construction than that of *M. megalodon sweeti*; sagittal crest not so high as that of *M. megalodon sweeti*, but approximately equal to that of *M. chelonys*; zygomatic arch light, approximately equal to that of *M. chelonys*, but with posterior border not ex-

tending so far posteriorly as in *M. megalodon sweeti*; lacrimal fossa smaller and shallower than that in *M. chelonys*; postglenoid process not so robust as in *M. megalodon sweeti*.

MANDIBLE: Similar to that of *M. chelonys*; lighter than that of *M. megalodon sweeti*.

DENTITION: Length of dental series same as in *M. chelonys*.

LIMBS: Equal in size to those of *M. chelonys*, smaller than average examples of *M. megalodon*.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 7, 15, 17–19, 25.

DISCUSSION

In the original description of this species, Schlaikjer¹ stated that the geological occurrence of the holotype was "Lower Miocene (Lower Harrison)." Schlaikjer considered all of the lower Miocene (Gering, Monroe Creek, Harrison) in this area of Wyoming as "Lower Harrison." The holotype, however, actually

¹ Schlaikjer, Erich M., 1934, *loc. cit.*

came from a horizon here considered as Gering. The Frick Laboratory also has made a collection from this same locality. Both of the present writers have collected fossils from this and adjacent areas, and have studied the lithology of the various deposits. In the Gering, Monroe Creek, and the Harrison formations, definite lithologic differences have been noted. The oreodonts from the three formations also are distinguishable from each other specifically or subspecifically, and several phylogenetic lines thus can be established.

Schlaikjer considered *Mesoreodon cheeki* as

belonging to the genus *Eporeodon*, probably basing his conclusions on species referred to that genus and not on the genotypic species, *E. occidentalis*, from the John Day beds (see discussion, p. 138). *Mesoreodon cheeki* shows close affinities to *M. chelonys*, and additional material may demonstrate that the Wyoming form is a subspecies of *M. chelonys* or only a geographic variety.

The F:A.M. specimens were collected by Nelson J. Vaughan, Everett De Groot, John Lynch, Gene Roll, and Charles H. Falkenbach, 1935-1939.

Ten specimens are here recorded:

HOLOTYPE

Skull with I¹-M³, mandible with I₁-M₃,
and most of skeleton. (w)

M.C.Z. 17765

From S.E. $\frac{1}{4}$, sec. 21, T. 20 N., R. 60 W.,
Goshen County, Wyoming; collected
by Erich Schlaikjer, 1933

Figured by Schlaikjer, 1935, pls. 27-29;
Thorpe, 1937, pls. 7, 39, fig. 2

REFERRED FROM (A) GOSHEN AND (B) NIOBRARA COUNTIES, WYOMING, AND (C) MORRILL COUNTY, NEBRASKA

A. FROM HORSE CREEK AREA, GOSHEN COUNTY, WYOMING (SAME GENERAL AREA AS TYPE)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|---|------|-----------------|
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , partial scapula, humerus, radius, ulna, vertebrae, and ribs. Figs. 7, 15, 17-19, 25 | (w†) | F:A.M. 45430 |
|---|------|-----------------|

SKULL

| | | |
|--|------|-------|
| Right side of skull with C/-M ³ | (w†) | 37567 |
|--|------|-------|

B. FROM NIOBRARA COUNTY, WYOMING

FROM LITTLE MUDDY CREEK:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|--|-----|-------|
| Posterior portion of skull with P ⁴ -M ³ , partial mandible with M ₁ -M ₃ , scapula, partial humerus, radius, ulna, 2 femora, 2 tibiae, pes, pelvis, vertebrae, and ribs | (w) | 33359 |
| ?Female example | | |

2 ASSOCIATED INDIVIDUALS

| | | |
|--|-----|--------|
| Partial skull with C/-dP ² -M ³ (germ), mandible with P ₁ -dP ₄ (br.)-M ₃ (germ) (dP ₁ -dP ₃ rt.), and fragments | (I) | 37577A |
| Partial left maxilla with dP ⁴ (br.)-M ³ (germ) and partial right ramus with M ₁ (br.)-M ₃ (germ br.) | (I) | 37577B |

SKULL AND RAMUS, IMMATURE

| | | |
|---|-----|-------|
| Partial skull with I ¹ (alv.)-dP ² -M ³ (erupt.) and partial right ramus with dP ₄ -M ₃ br. | (I) | 44933 |
|---|-----|-------|

SKULL

| | | |
|--|------|-------|
| Partial skull with C/-M ³ | (w+) | 42309 |
| ?Male example | | |

FROM WILLOW CREEK:

SKULL AND MANDIBLE, IMMATURE

F:A.M.

Partial skull with C/(br.)-dP²-M² and partial mandible with I₁(rt.)-dP₁-M₂ . (I)

44925

C. FROM WILD CAT RANGE, MORRILL COUNTY, NEBRASKA

SKULL AND MANDIBLE

Partial skull with C/-P² rt. and P²-M²
and partial mandible with P₂(br.)-M₂.
(w†)

U.N.S.M. 28015

From Gering Formation, Wild Cat
Range, Round House Rock, Pumpkin
Creek, Morrill County, Nebraska; col-
lected by South Field Party, 1937

1a. *Mesoreodon cheeki scotti* (Schlaikjer)

From Monroe Creek formation, Niobrara County,
Wyoming; referred remains from Converse
County, Wyoming, and Sioux
County, Nebraska

Mesoreodon scotti SCHLAIKJER, 1934, Proc. Bos-
ton Soc. Nat. Hist., vol. 40, no. 3, p. 223; 1935,
Bull. Mus. Comp. Zool., vol. 76, no. 4, p. 171, pl.
32. THORPE, 1937, Mem. Peabody Mus., vol. 3,
pt. 4, p. 103, pl. 44, fig. 2.

CHARACTERS

SKULL: Approximate length of examples of
M. cheeki, with a tendency to be wider than
examples of that species; other characters
equal to those of *M. cheeki*.

MANDIBLE: Approximate size of examples
of *M. cheeki*.

DENTITION: Length of series well within
the individual variation of examples of *M.*
cheeki but with a tendency for series to be
heavier.

LIMBS: Approximately equal to those of
M. cheeki, with tendency to be shorter than
those in that species.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 15, 16, 18, 19, 25,
26.

DISCUSSION

In describing this form, Schlaikjer pointed
out the following characters: "Skull inter-
mediate in size between *M. chelonys* Scott and
M. megalodon Peterson. Much broader across
zygomatic arches. Face rather low and broad.
P₂ with the posterior, intermediate crest just
meeting the posterior crest. Radius and tibia
proportionately short . . . Remainder of skel-
eton intermediate in size between *M. chelonys*
and *M. megalodon*."

The holotype is a skeleton mounted in a
plaque with the skull embedded, and con-
siderable restoration is apparent. These cir-
cumstances make the measuring of the spec-
imen difficult. Some of the measurements
taken by the present writers vary from those
given by Schlaikjer.

The holotype of *M. megalodon* is far from
complete, but the available measurements
are here cited for comparison with those of a
referred specimen of the same species and
those of the holotypes of *M. chelonys*, *M.*
cheeki, and *M. cheeki scotti*.

| | <i>M. megalodon</i> | | <i>M. chelonys</i> | <i>M. cheeki</i> | <i>M. cheeki scotti</i> |
|--|---------------------|----------------------|--------------------|------------------|-------------------------|
| | Holotype | Referred | Holotype | Holotype | Holotype |
| | C.M. | F:A.M. | P.U. | M.C.Z. | M.C.Z. |
| | 1235 | 33318 | 10425 | 11785 | 17480 |
| Total length of skull | — | ((300)) ¹ | ((250)) | 258 | 259 |
| Width of skull | — | 199 | ((131)) | 149 | (180) |
| Distance from anterior base of orbit to anterior base of C/ | 113 | ((120)) | 97 | 93 | 95 |
| Breadth across canines | 66 | — | 45 | 54 | 58 |
| Length of superior premolar series | 60 | 59 | — | 54 | 51 |
| Length of superior molar series | — | 70 | 56.5 | 60 | 61.5 |

¹ Measurements in millimeters; (), approximate; (()), estimated.

The foregoing measurements indicate that the holotypes of *M. cheeki* and *M. cheeki scotti* are similar except for the width of the skulls. *M. chelonys* has a shorter skull than either, a distinction pointed out by Schlaikjer. The comparable measurements of the holotype of *M. megalodon* indicate a skull somewhat larger than that found in the other species. *M. megalodon* and *M. cheeki scotti* both come from the same geological formation (Monroe Creek), but the latter form is more closely related to *M. cheeki* and *M. chelonys* from the Gering formation or its approximate equivalent. The above comparison, however, does not take into account the range of size acceptable within a single species.

Thorpe¹ apparently accepted and agreed with Schlaikjer's statements. The conclusions drawn by both Schlaikjer and Thorpe are based on a skeleton referred to *M. megalodon* by Loomis,² but the present writers do not consider it referable to the genus *Mesoreodon*. The identification of this skeleton will be discussed in a forthcoming paper.

Schlaikjer,³ in drawing his conclusion, stated:

"It is a significant fact that *Mesoreodon chelonys*, *M. scotti*, *M. megalodon*, *Eporeodon cheeki*, *Promerycochoerus hatcheri*, and *P. loomisi* were all found at exactly the same geological level. This is a striking example of primitive forms, representative of ancestral stages, existing along with more specialized descendants. *Eporeodon cheeki*, for example, represents one of the last members, surviving over into early Miocene times as a living fossil, of a dominantly later Oligocene genus which was ancestral to at least a half dozen early Miocene genera. A study, therefore, of any group of oreodonts from a given geological level, especially of the later Oligocene or early Miocene, reveals four outstanding factors in the evolution of the oreodonts.

"1. In dental characters and in the majority of the skull and skeletal structures, change is gradual and such changes are primarily changes of proportions.

"2. The occurrence of primitive forms, or living fossils, existing along with, and fre-

quently not far removed structurally from more advanced types.

"3. The presence of representatives of various phylogenetic lines which are less progressive in their evolutionary development and more restricted in their adaptive radiation than other lines.

"4. Extreme variability which may be accounted for chiefly by sexual dimorphism, individual variation, and hybridization."

Many difficulties in the past have been caused by workers who do not consider the genotypic species of a genus when making comparisons of new material. For an example, in Schlaikjer's⁴ description of "*Eporeodon*" *cheeki*, it is questionable which specimen he used as typical of the genus *Eporeodon*. It is apparent that he did not use the holotype of the genotypic species, *Eporeodon occidentalis*, from the John Day as a basis for comparison, but rather he employed material belonging to some other species that had been referred to *Eporeodon*. The writers consider *E. occidentalis* from the John Day as coming from a horizon approximately equal to that of the Harrison of the west-central Great Plains. Furthermore, the present writers do not consider that the genus *Eporeodon*, as such, existed during Oligocene times. It is true that many species of oreodonts from the Oligocene have been referred to that genus, but these references do not seem to be valid.

The following conclusions have been reached in regard to the relationship of *M. cheeki* to other oreodonts:

1. The species *cheeki* is considered here as not referable to the genus *Eporeodon* but to *Mesoreodon* and therefore is not a "living fossil" which has lingered on from some Oligocene *Eporeodon*.

2. *Mesoreodon cheeki scotti* is closely related to *M. cheeki* and not intermediate structurally between *M. chelonys* and *M. megalodon*. Although from the same formation (Monroe Creek) as the latter form, *M. cheeki scotti* appears to be specifically separate. If the term "living fossil" could be used in this case, it would apply to *M. cheeki scotti*, which was only slightly different in Monroe Creek times from the Gering species *M. cheeki*.

The statement concerning the various

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

² Loomis, Frederic B., 1933, *Bull. Geol. Soc. Amer.*, vol. 44, p. 727, figs. 4-6.

³ Schlaikjer, Erich M., 1934, *ibid.*, p. 229.

⁴ Schlaikjer, Erich M., 1934, *ibid.*, p. 220.

forms living at the same time is partly without foundation. Schlaikjer considered all of the lower Miocene beds in the area in which he worked as "Lower Harrison." As a matter of fact, the area embraces deposits of Gering, Monroe Creek, and Harrison age (see p. 135). *Mesoreodon chelonys*, *M. cheeki*, and "*Promerycochoerus*" *loomisi* all occur in the Gering or its equivalent, but *Mesoreodon megalodon* and *M. cheeki scotti* come from the Monroe Creek formation. None of these forms has been reported from typical Harrison.

4. The writers agree with Schlaikjer that changes in dental characters, skulls, and skeletal parts are gradual, but do not agree that such changes are always primarily changes in proportions. It appears that another change, which must be considered, is size. Proportions and shapes vary greatly in individual specimens of one species (see Schultz and Falkenbach, "Merychyinae, a subfamily of oreodonts"¹).

5. The existence of primitive forms or "living fossils" along with more advanced

forms needs some clarification. It may be said in a general way that primitive and advanced forms representing different genera do occur together, but it is a rarity to find species within the same genus which do not show marked differences when geologic evidence is considered. In the case of *M. cheeki scotti* from the Monroe Creek an insignificant size difference alone seems to separate it from the Gering form, *M. cheeki*. The Monroe Creek subspecies, however, is slightly more robust than *M. cheeki*.

Mesoreodon cheeki scotti is here considered to be a geological subspecies from the Monroe Creek formation, evolving from *M. cheeki* of the Gering. The holotype of this subspecies and the two referred specimens come from the same location, Muddy Creek, Niobrara County, Wyoming. The wider skulls are here considered to be males. The F:A.M. material was collected by John Lynch, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1931 and 1937.

Eleven specimens are here recorded:

HOLOTYPE

| | | |
|---|--------------|---|
| Skull, mandible, and partial skeleton. (w+) ?Male example | M.C.Z. 17480 | From Muddy Creek, Niobrara County, Wyoming; collected by F. B. Loomis, 1924 Figured by Schlaikjer, 1935, pl. 32; Thorpe, 1937, pl. 44, fig. 2 |
|---|--------------|---|

REFERRED FROM (A) NIOBRARA AND (B) CONVERSE COUNTIES, WYOMING, AND (C) SIOUX COUNTY, NEBRASKA

A. FROM TYPE AREA, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

| | | |
|---|--------------------|-----------------|
| Anterior portion of skull with I ¹ -I ² alv. and I ³ -M ³ , mandible with I ₁ -M ₃ , partial scapula, humerus, partial radius, partial ulna, femur, and fragments. Figs. 25, 26 | (w $\frac{+}{-}$) | F:A.M. 33532 |
|---|--------------------|-----------------|

2 ASSOCIATED INDIVIDUALS

| | | |
|---|-----|--------|
| Partial skull with I ³ -dP ² -M ³ (erupt.) (C/ br.) and partial left ramus with P ₁ -dP ₂ -dP ₃ | (I) | 45427A |
| Partial mandible with I ₁ -M ₃ (br.) (P ₁ br.) | (M) | 45427B |

The above two specimens were found associated in one field block.

SKULL AND MANDIBLE

| | | |
|---|-----|-------|
| Partial skull with C/(br.)-M ³ and mandible with I ₁ -M ₃ (/C br.). Figs. 15, 16, 18, 19 | (M) | 44921 |
| ?Female example | | |

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1947, Bull. Amer. Mus. Nat. Hist., vol. 88, art. 4, p. 262, charts 3, 4.

2 SKULLS

F:A.M.

| | | |
|---|-------------------|-------|
| Partial skull with I ¹ -M ² (br.) (I ² rt. and M ¹ br.) | (w ⁺) | 44924 |
| Partial skull with P ¹ (br.)-dP ² -M ² | (i) | 45428 |

B. FROM 3 MI. S.E. OF DOUGLAS, CONVERSE COUNTY, WYOMING

(Collected by Gene Roll and Charles H. Falkenbach, 1941)

SKULL AND SKELETAL ELEMENTS

| | | |
|--|-------------------|-------|
| Posterior portion of skull with P ⁴ (br.)-M ³ , 2 partial scapulae, radius, ulna, partial pes, vertebrae, and fragments. Figs. 25, 26 | (w ⁺) | 44937 |
|--|-------------------|-------|

C. FROM JOE SANFORD RANCH, NORTH OF MITCHELL, SIOUX COUNTY, NEBRASKA

(Collected by Morris F. Skinner and Associates, 1942)

SKULL AND MANDIBLE

F:A.M.

| | | |
|---|--------------------|-------|
| Partial skull with P ² -M ³ and partial mandible with I ₁ -P ₂ rt. and P ₂ -M ₃ | (w ⁺⁺) | 44938 |
|---|--------------------|-------|

?Female example

TENTATIVELY REFERRED

D. FROM MUDDY CREEK, NIOBRARA COUNTY, WYOMING, 1933

SKULL

F:A.M.

| | | |
|--|-------------------|-------|
| Anterior portion of skull with C/-M ² (br.) | (w ⁺) | 44916 |
|--|-------------------|-------|

E. FROM LEDINGHAM RANCH, SOUTHERN SIOUX COUNTY, NEBRASKA

(Collected by Morris F. Skinner and Associates, 1942)

SKULL AND MANDIBLE

F:A.M.

| | | |
|--|-------------------|-------|
| Partial skull with C/(rt.)-M ³ and mandible with I ₁ -M ₃ | (w ⁺) | 44939 |
|--|-------------------|-------|

?Female example

The above two specimens approach the size of small examples of *M. megalodon* Peterson.

2. *Mesoreodon chelonys* Scott

From Miocene deposits (approximately equal in age to the Gering of the Great Plains), Smith River Valley, Meagher County, Montana; referred specimens from Jefferson County, Montana

Mesoreodon chelonys SCOTT, 1893, Amer. Nat., vol. 27, p. 659; 1895, Trans. Amer. Phil. Soc., Philadelphia, new ser., vol. 18, p. 125, pl. 3, fig. 29, pl. 4, figs. 32-34, pl. 5, figs. 35-42, pl. 6, figs. 46, 47. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 98, fig. 65, pl. 9, fig. 4, pl. 11, figs. 1-2.

Mesoreodon intermedius SCOTT, 1893, *loc. cit.*; 1895, *ibid.*, new ser., vol. 18, p. 145, pl. 5, figs. 44, 45. THORPE, 1937, *ibid.*, vol. 3, pt. 4, p. 102, pl. 11, fig. 3.

Mesoreodon (?) *latidens* DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, no. 2, p. 102, pl. 25.

Merycoides laticeps (misprint for *latidens*) (Douglass), LOOMIS, 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 9.

Merycoides latidens (Douglass), THORPE, 1937 *ibid.*, vol. 3, pt. 4, p. 173, fig. 125, pl. 26.

Mesoreodon danai KOERNER, 1940, Amer. Jour. Sci., vol. 238, p. 847, pl. 4, figs. 1-2.

CHARACTERS

SKULL: Medium size, with average examples equal to those of *M. cheeki*; sagittal crest prominent, moderately high; nasals without noticeable anterior retraction; posterior border of zygomatic arch similar to that of *M. cheeki* but not extending posteriorly so far as in *M. megalodon* or *M. megalodon sweeti*; infraorbital foramen above P⁴; lacrimal fossa larger and deeper than in examples of *M. cheeki*; occipital condyles moderately large (considerable individual variation); paroccipital process not so wide at base as that in examples of *M. cheeki*, but with same angular position to the bulla as in

that species; bulla inflated, somewhat oblong anteroposteriorly; postglenoid process heavy and wider laterally than anteroposteriorly.

MANDIBLE: Similar in size and shape to examples of *M. cheeki*.

DENTITION: Similar to that of *M. cheeki*; tendency for slight diastema between P¹ and P² (not a constant character).

LIMBS: Moderately short; shorter and lighter than those in *Promerycochoerus*; equal to examples of *M. cheeki* in size and construction.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 15, 16, 18, 19, 26.

DISCUSSION

The original material of *M. chelonys* studied by Scott consisted of many individuals and included partial skulls, rami, and skeletal elements. In 1895, Scott¹ illustrated various specimens of *M. chelonys* without identifying numbers. The writers have attempted to match the illustrations with the material in Scott's collection and have succeeded except for the following: plate 4, figure 32; plate 5, figure 35 (skull only), figures 39, 40, and 42. (See listings of specimens for other figures.)

Thorpe² reproduced some of Scott's figures with Princeton numbers: figure 65 as "P.U. 10425" (this specimen actually is P.U. 11769); plate 9, figure 4 as "P.U. 10425," and the ramus as "P.U. 10418." The skull in plate 9, figure 4, of Thorpe's monograph has not been identified with any of Scott's skull material and is believed to be a reconstruction, perhaps based on several skulls. It is possible that Thorpe was misled by Scott's legend on plate 5, figure 34, which reads, "*Mesoreodon chelonys*: Block containing cervical and thoracic vertebrae, scapula, etc., referred to same individual as male skull (Pl. V, Fig. 35) . . ." This particular block includes the specimen P.U. 10425, which in turn includes a skull and mandible, but not the skull and ramus illustrated in Scott's plate 5, figure 35, or Thorpe's plate 9, figure 4. The holotype of *Mesoreodon chelonys*, P.U. 10425, is here illustrated for the first time, figures 15, 16, 18, 19.

Scott³ also described "*Mesoreodon inter-*

medius," basing the new species on a metacarpal III and partial metacarpal IV, holotype, P.U. 10416, and a second individual, P.U. 10419, consisting of two phalanges, and indicated: "Metapodials slender and elongated, and ungual phalanges like those of *Merychys*. Lower beds."

Later Scott⁴ further discussed the species and stated: "This species is represented by foot-bones belonging to two different individuals, which are so different in their proportions from those of the foregoing species [*M. chelonys*] that they must be referred to another animal. The only skull which can with any probability be regarded as belonging to "*M. intermedius*" is a small one belonging to a very immature individual [?partial skull and partial mandible, P.U. 10406] and therefore of little value for systematic purposes. The milk teeth are still in place, the permanent canines just beginning to appear, and the first permanent upper molar already protruded. This latter tooth is somewhat like that of *Merychys* . . ."

At the time, Scott considered *Ticholeptus* to be synonymous with *Merychys* and possibly was comparing *T. zygomaticus* with "*M. intermedius*," since both forms came from the same area, although not from the same horizon. According to Scott the holotypes of both *M. chelonys* and *M. intermedius* came from the lower beds in this area. The lower beds are here considered to be approximately equal to the Gering of the Great Plains. *Ticholeptus* comes from the highest reported fossil-bearing horizon, which is considered as an approximate equivalent of either the "Sheep Creek" or "lower Snake Creek" of Sioux County, Nebraska. *Merychys* may be present in the intermediate deposits of the Montana area, but to date it has not been reported. These latter beds contain the remains of *Promerycochoerus* and are considered as approximately equal to the Harrison of the Great Plains. *Merychys* also is reported from this geologic horizon in the Great Plains.

The writers have studied Scott's Smith River Valley collection and see no reason to consider the immature specimen referred to "*M. intermedius*" by Scott as specifically dif-

¹ Scott, W. B., 1895, *loc. cit.*

² Thorpe, Malcolm R., 1937, *loc. cit.*

³ Scott, W. B., 1893, *ibid.*, p. 661.

⁴ Scott, W. B., 1895, *loc. cit.*

ferent from immature maxillae in the same collection identified as *M. chelonys* by Scott. The holotypic metapodials of "*M. intermedius*" are within the range of individual variation found within any species and well within the range that might be expected in *M. chelonys*. In view of these considerations along with the reported geological evidence, "*M. intermedius*" is here placed in synonymy with *M. chelonys*.

It is not certain that Thorpe¹ considered all three specimens as part of the holotype. The specimen number of the holotype, P.U. 10416, was the only one cited and it was reported by Thorpe as follows:

"Holotype, Cat. No. 10416 P.U.M., right Mc. III, proximal three-fourths of Mc. IV, proximal and distal phalanges of Mt. III, and skull of a very immature individual, with milk dentition.

"SPECIFIC CHARACTERS: The skull has almost no systematic value, although it indicates affinities with *Mesoreodon*.

"As compared with *M. chelonys*, the metapodials are markedly longer and slenderer, and the keels of the distal trochleae are more anteriorly extended . . . In general, these metacarpals bear a striking resemblance to those of *Merychyus*, except that the trapezoid facet on Mc. III is smaller and there are differences sufficient to exclude this species from that genus. It may be a female, but at present we have no way of determining its exact position."

The holotypic metapodials represent a mature individual and could not be from the same individual as the immature skull. The Princeton University records also show the three specimens in question to be from three different individuals.

Mesoreodon chelonys wheeleri (Koerner)² has a skull with a considerably longer basal length. The metapodials of this form, however, are unknown, but one would expect a longer foot than in *M. chelonys*.

The outstanding character that separates *M. cheeki*³ from *M. chelonys* is the larger and deeper lacrimal fossa of the latter. In basal lengths the means of both forms are equal. The latter species is better represented in

collections and has a larger range in basal measurements.

Douglass⁴ in the original description of "*M. (?) latidens*" questioned the genus and stated: "This species is placed provisionally in this genus. It is quite different from the type specimen of *Mesoreodon chelonys*, which is very close to some of the Upper Oligocene forms such as *Eucrotaphus* or *Eporeodon*, but other skulls from the Princeton collection (Nos. 10410 and 10418) seem to the writer to be somewhat different from the type and more nearly related to the present species which is undoubtedly somewhat later in age."

The present writers believe that the above quotation amplifies the fact that Scott in describing the species *chelonys* considered possible individual variation and Douglass did not. Later, in a review of the two species in question, Loomis⁵ stated: "*Mesoreodon* was founded on *M. chelonys*, which is related to *M. megalodon*. Both of these have skulls tending to the same form as that characteristic of *Promerycochoerus*, but at the [same] time they have a skeleton which is about like that of *Eporeodon* or *Merycoidodon* . . . The other species which have been referred to *Mesoreodon*, such as *M. longiceps* and *M. laticeps* [misprint for *latidens*] are far from the type species and close to the form which Douglass called *Merycoides* . . . In the true *Mesoreodon*, the front half of the upper third premolar is shortened, and the anterior intermediate crest, though small, is well developed. The posterior crescent incloses a basin on the rear of the tooth."

As discussed by the present writers at various times, the age of the individual is an important factor when variation in the characters of the premolars is considered. The lengthening or shortening of either the anterior or the posterior portion of the tooth is controlled by the wear of that tooth. In a discussion of "*M. latidens*" this particular consideration does not affect the conclusions, since the holotype of that species has all the tooth characters for *Mesoreodon* as pointed out by Loomis. However, Loomis' decision to

⁴ Douglass, Earl, 1907, *loc. cit.*

⁵ Loomis, Frederic B., 1924, *Bull. Amer. Mus. Nat. Hist.*, vol. 51, art. 1, p. 9. The present writers have inserted the word *same* in the quotation from Loomis, since the word *time* appears twice as the result of a misprint.

¹ Thorpe, Malcolm R., 1937, *ibid.*, p. 102.

² See p. 145.

³ See p. 135.

place the species "*latidens*" in the genus *Merycoides* was not justified.

Thorpe¹ accepted Loomis' conclusions and considered the species "*latidens*" to belong to the genus *Merycoides*. Thorpe's comparisons were with *Merycoides cursor* and the only mention of *Mesoreodon chelonys* was in the following: "A few foot bones, found with the holotype [*M. latidens*]", closely resemble those figured by Scott as *Mesoreodon chelonys*."

The characters and measurements of the holotype of "*M. latidens*" compare readily with the holotype and referred material of *M. chelonys*, and "*M. latidens*" is here considered to be synonymous with the latter.

The holotypic skull of "*M. danai*," described by Koerner,² is a very poorly preserved specimen in two pieces with no apparent contact between the posterior and anterior portions. Koerner stated that in the genus

Mesoreodon, P⁴ has one or no pit. In his description of "*M. danai*" it is stated that the holotype has no pit on P⁴. The dentition of the holotype is well worn. The present writers do not consider the presence or absence of a pit on P⁴ to be of diagnostic value, and wish to point out that the age of the individual may control the appearance of the pit.

Koerner further stated that in the genus *Eporeodon* P⁴ has either one or two pits. If these pits were to be used as generic characters, one would not know if the specimen were *Mesoreodon* with one pit or *Eporeodon* with a single pit.

The close resemblance between "*M. danai*" and *M. chelonys* and the fact that the forms apparently came from the same beds and same formation leave very little doubt that these forms are synonymous.

Twenty-five specimens are here recorded:

HOLOTYPE

| | | |
|---|------------|--|
| Partial skull with C/-P ¹ rt. and P ² -M ³ (P ² -P ³ and M ¹ br.), partial mandible with P ₁ (br.)-M ₃ , partial scapula, partial humerus, vertebrae, and thyroid apparatus. (w+) | P.U. 10425 | From Smith River Valley, Meagher County, Montana; collected by Princeton University field party, 1891 Figured by Scott, 1895, pl. 3, fig. 29; pl. 4, fig. 34; Thorpe, 1937, pl. 11, figs. 1-2 ³ |
| | | This paper, figs. 15, 16, 18, 19 |

REFERRED FROM TYPE AREA, (A) MEAGHER AND (B) JEFFERSON COUNTIES, MONTANA

(P.U. material collected by Princeton University field party, 1891, Y.P.M. specimen by H. E. Koerner, and F.A.M. specimen by N. Z. Ward, N. J. Vaughan, and Charles H. Falkenbach)

A. FROM MEAGHER COUNTY, MONTANA

| 2 PARTIAL SKULLS AND MANDIBLES | | P.U. |
|--|--|-------|
| Partial skull with I ¹ -M ³ (I ² -M ³ rt.) and partial mandible with I ₁ -M ₃ (w ₊ ⁺⁺) | | 10418 |
| Figured by Scott, 1895, pl. 5, fig. 35 (ramus only); Thorpe 1937, pl. 9, fig. 4 (ramus only). | | |
| Partial skull with C/-dP ³ -dP ⁴ rt. and M ¹ -M ² and partial mandible with /C-dP ₃ -dP ₄ rt. and M ₁ -M ₂ (I) | | 10406 |

2 PARTIAL SKULLS

| | |
|---|-------|
| Partial skull with I ³ -M ³ (br.) (C/ rt. and M ² br.) (w ₊ ⁺⁺) | 10410 |
| Partial skull with C/-M ³ (w ₊) | 11769 |

Figured by Scott, 1895, pl. 5, fig. 36; Thorpe, 1937, fig. 65 (of which the legend reads P.U. 10425).

The dentition on the right side is worn more than on the left side.

¹ Thorpe, Malcolm R., 1937, *loc. cit.*

² Koerner, H. E., 1940, *loc. cit.*

³ Thorpe, Malcolm R., 1937, *ibid.*, vol. 3, pt. 4, pl. 9, fig. 4, states that the skull and ramus are P.U. 10425. The mandible, however, is P.U. 10418, but the skull as drawn cannot be assigned to any of Scott's material. Perhaps the figured skull is a restoration based on the several skulls in the Princeton collection. Thorpe's figure 65 also shows P.U. 10425 but the illustration is of skull P.I. 11769.

| 2 MAXILLAE | | | P.U. |
|---|--------------------------------|---|--------|
| Left maxilla with C/(rt.)-M ³ and atlas | (M+) | | 10443 |
| Right maxilla with C/(rt.)-dP ³ -M ³ (erupt. and br.) | (I) | | 10436 |
| 2 PARTIAL MANDIBLES, ETC. | | | |
| Brain cast, partial mandible with P ₄ -M ₃ , and partial humerus | (w ₊ ⁺) | | 10409 |
| Symphysis of mandible with I ₁ -C rt. and P ₁ -P ₃ | (w+) | | 10448 |
| 2 PARTIAL LEFT MANDIBULAR RAMI | | | |
| Two partial left rami with | | | |
| P ₁ (rt.)-M ₃ (P ₂ -P ₃ rt.) | (w) | | 10433A |
| P ₁ (erupt.)-dP ₂ -M ₂ (br.) (dP ₄ -M ₁ br.) | (I) | | 10449 |
| LIMB ELEMENTS | | | |
| Partial radius, partial ulna, and partial manus | | | 10413 |
| Manus | | | 10414 |
| Metacarpal III and partial metacarpal IV | | | 10416 |
| Holotype of " <i>M. intermedius</i> " Scott | | | |
| Figured by Scott, 1895, pl. 5, fig. 43; Thorpe, 1937, pl. 11, fig. 3. | | | |
| Tibia, astragalus, calcaneum, and partial pes | | | 10421 |
| Partial tibia, astragalus, calcaneum, and partial pes | | | 10444 |
| Figured by Scott, 1895, pl. 5, fig. 41. | | | |
| Partial femur, tibia, and cervical vertebrae | | | 10445 |
| Partial tibia, astragalus, and calcaneum | | | 10455 |
| Partial humerus, 2 partial radii, 2 partial ulnae, 2 partial manus, partial femur, | | | |
| partial tibia, astragalus, and calcaneum | | | 10470 |
| Partial scapula, humerus, radius, partial ulna, and partial pelvis | | | 11373 |
| Figured by Scott, 1895, pl. 4, fig. 33; pl. 5, figs. 37-38; and pl. 6, figs. 46-47. | | | |
| Femur and tibia | | | 11374 |
| SKULL AND MANDIBULAR RAMUS | | | |
| Partial skull with C/-M ³ and partial left ramus with P ₃ (br.)-M ₃ . (w+) | Y.P.M. 13949 | From sec. 15, T. 10 N., R. 5 E. Figured by Koerner, 1940, pl. 4, fig. 122 | |
| Holotype of " <i>Mesoreodon danai</i> " Koerner | | | |
| SKULL | | | |
| Partial skull with C/(rt.)-M ³ . (M+) | F:A.M. 44955 | This paper, fig. 18 | |
| Premolars unusually large. | | | |
| B. FROM JEFFERSON COUNTY, MONTANA | | | |
| (Collected by Earl Douglass, 1901) | | | |
| SKULL, MANDIBLE, AND SKELETAL ELEMENTS | | | |
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and foot bones. (w ₊ ⁺) | C.M. 908 | From Canyon Ferry, 20 mi. E. of Helena Figured by Douglass, 1907, pl. 25; Thorpe, 1937, fig. 125; pl. 26 This paper, fig. 18 | |
| Holotype of " <i>M. latidens</i> " Douglass | | | |
| SKULL | | | |
| Skull with C/-M ³ , partial tibia, partial fibula, calcaneum, partial pes, and fragments. (w ₊ ⁺) | 1234 | From Canyon Ferry Fig. 26 (in part) | |
| In basal length this specimen approaches the examples of <i>M. chelonys wheeleri</i> (Koerner). | | | |

2a. *Mesoreodon chelonys wheeleri* (Koerner)

From lower Miocene deposits (approximately equal in age to the Gering of the Great Plains), Meagher County, Montana

Mesoreodon wheeleri KOERNER, 1940, Amer. Jour. Sci., vol. 238, p. 848, pl. 5.

CHARACTERS

SKULL: Larger than in examples of *M. chelonys*, but appropriate size of small examples of *M. megalodon*; infraorbital foramen above P^3 - P^4 ; bulla slightly larger than in examples of *M. chelonys*.

MANDIBLE: Typical of examples of *M. chelonys* except for larger size.

DENTITION: Average series longer than in examples of *M. chelonys*; approximate size of average examples of *M. megalodon sweetii*.

LIMBS: Unknown.

MEASUREMENTS: Table 6.

ILLUSTRATIONS: Figures 15, 17, 18, 20.

DISCUSSION

This form, originally described with full

specific status, is considered here as a subspecies of *M. chelonys*. Both the species and the subspecies came from the same area and deposits, and the only outstanding difference is the larger size of the subspecies. The average skulls of *M. chelonys* are slightly larger than the average examples of *M. cheeki*, while those of the subspecies are equal to the smaller examples of *M. megalodon*. With additional material from the Montana area, it may be demonstrated that *M. chelonys* represents the minimum and *M. chelonys wheeleri* the maximum size of one species, or that the subspecies may be from slightly higher deposits in the Miocene section of the area.

There is a possibility that this subspecies represents the same form as "*M. intermedius*" Scott.¹ Unfortunately there is not sufficient material available to show the relationship of these two oreodonts. "*Mesoreodon intermedius*," however, is not considered as a valid species in this paper (see p. 140).

Two specimens are here recorded:

HOLOTYPE

Skull with I^1 - I^3 alv. and C/- M^3 (P^1 - P^2 rt.). (w_1^+)

Y.P.M. 13950

From sec. 15, T. 10 N., R. 5 E., Meagher County, Montana; collected by H. E. Koerner, 1935-37

Figured by Koerner, 1940, pl. 5

REFERRED FROM WHITE SULPHUR SPRINGS, TYPE AREA

(Collected by Nelson J. Vaughan, Joseph Rooney, and Charles H. Falkenbach, 1942)

SKULL AND MANDIBLE

Skull with I^1 (br.)- M^3 and mandible with I_1 - P_1 br. and P_2 - M_2 . (w_1^+)

F:A.M. 45423

Figs. 15, 17, 18, 20

3. *Mesoreodon megalodon* Peterson

From Monroe Creek formation, Sioux County, Nebraska; referred remains from Morrill County, Nebraska, and Niobrara County, Wyoming

Mesoreodon megalodon PETERSON, 1906, Ann. Carnegie Mus., vol. 4, no. 1, pp. 24-26, figs. 2, 3, and *Mesoreodon melagodon* (undoubtedly a misprint), *ibid.*, p. 24. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 102, figs. 4, 66, 67, pl. 10, figs. 3-5.

CHARACTERS

SKULL: Larger, more massive, and broader than examples of *M. cheeki*; approximately

equal in length to that of *M. chelonys wheeleri* but broader; sagittal crest higher than in *M. cheeki*; frontals wide; malar deep below the orbit; zygomatic arch more massive and extending upward and posteriorly farther than in examples of *M. cheeki*; lacrimal fossa larger than in examples of *M. cheeki*; infraorbital foramen located above the posterior portion of P^3 and extending to the anterior portion of P^4 ; paroccipital process wide at base, and wider and tapering more rapidly than in examples of *M. cheeki*; bulla well

¹ Scott, W. B., 1893, Amer. Nat., vol. 27, pp. 659, 661.

inflated, comparatively large and suboval in outline, larger than in examples of *M. cheeki*; postglenoid process more robust and wider transversely than in examples of *M. cheeki*.

MANDIBLE: More massive than examples of *M. cheeki*.

DENTITION: Dental series longer and heavier than in examples of *M. cheeki*.

LIMBS: Longer and heavier than in *M. cheeki*.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 7, 16, 17, 19, 20, 25, 26.

DISCUSSION

Mesoreodon megalodon is restricted to the Monroe Creek formation and is in the same phylogenetic line as *M. megalodon sweeti* from the Gering formation. It appears that *M. megalodon* represents a stage in the line of development almost intermediate between *M. megalodon sweeti* and *Promerycochoerus carrikeri* (from the Harrison formation).

Examples of *M. megalodon*, where the stage of the wear permits the observance, demon-

strate the presence of *Mesoreodon* characters on the anterior intermediate crest on P¹-P³. In the lower dentition, the posterior intermediate crest is present on P₃. In the genus *Promerycochoerus*, the anterior intermediate crest is present on P²-P³ only.

Loomis¹ referred a skeleton to *M. megalodon*, an identification which was accepted by Thorpe.² In referring to the specimen, Loomis stated that the limb elements "stand in marked contrast" to those figured by Scott³ as *Mesoreodon chelonys*. The present writers do not consider the skeleton to be referable to *Mesoreodon* and will consider it under another genus in a forthcoming paper.

The holotype of *M. megalodon* is a poorly preserved skull, and comparisons have been difficult. Figures 7, 16, 17, 19, and 20 illustrate a partial skull and mandible, F:A.M. 33318, from the same formation as the holotype. This F:A.M. specimen duplicates the preserved portions of the holotype as closely as one may expect to find.

Fourteen specimens are here recorded:

HOLOTYPE

Partial skull with I¹-M³ and partial mandible with I₁-P₄. (w)

C.M. 1325

From near Squaw Butte, head of Warbonnet Creek, Sioux County, Nebraska

Figured by Peterson, 1906, figs. 2-3; Thorpe, 1937, figs. 66-67, pl. 10, figs. 3-5

This paper, figs. 19, 20 (in part)

REFERRED FROM (A) SIOUX AND (B) MORRILL COUNTIES, NEBRASKA, AND (C) NIOBRARA COUNTY, WYOMING

A. FROM 8 MI. W. OF MARSLAND, SIOUX COUNTY, NEBRASKA

(Collected by Morris Skinner and Associates, 1941-1942)

SKULL AND MANDIBLE

F:A.M.

Anterior portion of skull with I¹-M³ and partial mandible with I₁-M₃ (w⁺⁺)

44940

MAXILLA

Partial left maxilla with P⁴-M³(br.) (w⁺⁺)

44941

B. FROM MORRILL COUNTY, NEBRASKA

(Collected by University of Nebraska State Museum field parties)

FROM 2½ MI. S. OF CHIMNEY ROCK:

¹ Loomis, Frederic B., 1933, Bull. Geol. Soc. Amer., vol. 44, p. 727, figs. 4-6.

² Thorpe, Malcolm R., 1937, *ibid.*, vol. 3, pt. 4, pl. 44, fig. 1.

³ Scott, W. B., 1895, Trans. Amer. Phil. Soc., Philadelphia, vol. 18, pl. 4, figs. 33-34, pl. 5, figs. 37-42, pl. 6, figs. 46-47.

SKULL AND MANDIBLE

U.N.S.M.

Skull with I²-I³ alv. and C/(br.)-M³ and mandible with /C-M₃ (w⁺) 28003
 ?Male example

C. FROM NIOBRARA COUNTY, WYOMING

(Collected by John Lynch, Everett De Groot, Nelson J. Vaughan, Gene Roll,
 and Charles H. Falkenbach, 1933-1939)

FROM MUDDY CREEK:

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Left anterior portion of skull with C/-M³, mandible with I₁-M₃, partial tibia, calcaneum, and partial pes (w⁺) F:A.M. 37578
 Partial skull with P¹-P² rt. and P³(br.)-M³(br.) (M¹-M² br.), partial mandible with I₁-P₃ rt. and P₄-M₃(br.) (M₁ br.), partial humerus, partial radius, partial ulna, and fragments (M+) 44949
 Crushed skull with C/-M³, mandible (attached) with I₁-M₃, radius, and partial ulna (w+) 44954
 ?Male example

2 ASSOCIATED SKULLS, MANDIBLES, AND LIMBS

Skull with C/-M³ and mandible with I₁-M₃. Fig. 19 (w) 33336
 ?Female example
 Skull with I¹-M³. Fig. 19 (w) 33337
 ?Female example
 Fragmentary limbs associated with F:A.M. 33336 and 33337.

The above two specimens were collected in one field block.

2 SKULLS AND MANDIBLES

Partial skull with P¹-M³ and partial mandible with P₁-M₃. Figs. 7, 16, 17, 19, 20 (w⁺) 33318
 ?Male example
 Anterior portion of skull with P²-M³ and partial mandible with P₂-M₃ . . . (w+) 44943

2 SKULLS

Anterior portion of skull with I¹-M³ (w⁺) 37579
 Partial skull with P¹-dP⁴-M³(erupt.) (I) 45429

FROM NEAR SPANISH DIGGINGS:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with I²-M³ (P³ alv.), mandible with I₁-C alv. and P₁-M₃, partial scapula, 2 humeri (1 partial), 2 radii, partial ulna, 2 femora, 2 tibiae, partial pes, astragalus, calcaneum, vertebrae, and ribs. Figs. 25, 26 (in part) (w+) 33349
 ?Female example

3a. *Mesoreodon megalodon sweeti*,¹
 new subspecies

From the Gering of Morrill County, Nebraska;
 referred examples from Goshen and
 Niobrara counties, Wyoming

DESCRIPTION

SKULL: Differing from typical examples of

¹ Named in honor of Mr. and Mrs. S. R. Sweet, who aided the University of Nebraska State Museum in collecting examples of this subspecies and many other fossils from the Bridgeport area (1931-1942).

M. megalodon in the following respects: smaller and narrower; tendency for sagittal crest to be lighter and lower; zygomatic arch lighter; bulla smaller; postglenoid process not so robust.

MANDIBLE: Similar to examples of *M. megalodon*, but with a tendency towards being smaller and lighter than in that species.

DENTITION: Similar to that of *M. megalodon*, but with tendency towards being lighter than in that species; average length of series less than average of *M. megalodon*.

LIMBS: Similar to those of *M. megalodon* but with tendency towards being lighter than in that species.

MEASUREMENTS: Tables 6 and 7.

ILLUSTRATIONS: Figures 16-18, 20, 25, 26.

DISCUSSION

The examples of skulls of the new subspecies from the lower part of the Gering are smaller and the zygomatic arches are noticeably lighter than those specimens from the upper part of the formation. The individuals from the lower geologic level have much in common with *M. cheeki*, while those occurring higher in the section resemble examples

of *M. megalodon*. This type of geologic variation in a species within a formation should be expected, of course, in any phylogenetic line. It is considered here that *M. megalodon sweeti* is closely related to *M. cheeki* and that the two forms developed from a common ancestral species of *Promesoreodon*, probably during late Oligocene time. *M. megalodon sweeti* developed rapidly to a larger size and gave rise to *M. megalodon* of the Monroe Creek. *M. cheeki* remained more conservative and smaller, and became the form recognized here as *M. cheeki scotti* (from the Monroe Creek).

Forty-seven specimens are here recorded:

HOLOTYPE

Skull with I¹(alv.)-M³ (I² rt.), mandible with I₁-M₃, humerus, radius, ulna, and partial pes. (w)
?Male example

U.N.S.M. 28012

From 3 mi. S. of Chimney Rock, Wild Cat Range, Morrill County, Nebraska; collected by South Field Party, 1935
Figs. 16-18, 20

REFERRED FROM (A) MORRILL COUNTY, NEBRASKA, (B) GOSHEN AND (C) NIOBRARA COUNTIES, WYOMING

A. FROM WILD CAT RANGE, MORRILL COUNTY, NEBRASKA (Collected by University of Nebraska State Museum field parties)

FROM ½ TO 3 MI. S. OF CHIMNEY ROCK:

| | SKULL | U.N.S.M. |
|---|---------------------|----------|
| Partial skull (in two parts) with C/-M ³ (w) | | 28013 |
| Associated with holotype. | | |
| | 2 ASSOCIATED SKULLS | |
| Skull with C/-M ³ rt. | | 28004 |
| ?Male example | | |
| Skull with C/(rt.)-dP ² -M ³ (erupt.) (i) | | 28005 |
| ?Female example | | |

These specimens are larger than typical examples of this subspecies. They were collected at a higher level than most material listed here.

FROM W. SIDE OF BIRDCAGE GAP:

| | 2 ASSOCIATED SKELETONS | |
|--|------------------------|--------|
| Skull with P ¹ -M ³ , mandible with I ₁ -M ₃ , and skeleton (w†) | | 28000A |
| ?Female example | | |
| Skull with I ² -C/(erupt.)-dP ⁴ -M ¹ , mandible with I ₁ -P ₁ (erupt.)-dP ₄ -M ₁ , and skeleton (i) | | 28000B |

These specimens have been left articulated in the original matrix and are exhibited as a panel mount in the University of Nebraska State Museum (figured by Barbour, Erwin H., and C. Bertrand Schultz, 1932, Bull. Univ. Nebraska State Mus., vol. 1, no. 31, fig. 162).

FROM VARIOUS WILD CAT RANGE LOCALITIES:

2 SKULLS AND MANDIBULAR RAMI

| | | |
|--|----------------|------------------------------|
| Skull with C/-M ³ and mandible with I ₁ -I ₃ rt. and /C-M ₃ . (w+) | U.N.S.M. 28006 | From Round House Rock |
| Skull with I ² -M ³ and mandible with P ₄ -M ₃ . (w+) | 28002 | From 2 mi. W. of Hubbard Gap |

4 SKULLS

| | | |
|--|-------|--|
| Skull with I ³ -M ³ . (w+) | 28001 | From 4 mi. W. of Redington Gap |
| Partial skull with C/(rt.)-M ³ . (w $\frac{1}{2}$) | 28010 | From E. side of Redington Gap (collected by S. R. Sweet, 1933) |
| Skull with I ¹ -M ³ (C/,P ³ -M ³ br.). (w) | 28008 | From Black Hank Canyon |
| Skull with I ¹ -M ³ . (w+) | 28009 | From Round House Rock |
| ?Female example | | |

B. FROM HORSE CREEK AREA, GOSHEN COUNTY, WYOMING

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

| | |
|---|--------------|
| Skull with I ¹ -M ³ (I ³ alv.) mandible with I ₁ -M ₃ , partial scapula, partial manus, vertebrae, ribs, and limb fragments (w) | F:A.M. 37566 |
| ?Female example | |
| Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , partial scapula, 2 humeri (1 partial), 2 radii, 2 ulnae, 2 partial manus, 2 femora, 2 tibiae, 2 astragali, 2 calcanea, partial pes, vertebrae, and ribs. Figs. 25, 26 (in part) (w+) | 45431 |

The size of the skull approaches examples of *M. megalodon*. The bullae are exceptionally well inflated, more so than average examples of the subspecies.

SKULL AND SKELETAL ELEMENTS

| | |
|--|-------|
| Skull with I ¹ -I ³ alv. and C/-M ³ , 2 partial scapulae, partial humerus, radius, ulna, partial manus, femur, 2 tibiae, fibula, partial pes, 2 astragali, calcaneum, vertebra, and ribs (w $\frac{1}{2}$) | 45432 |
|--|-------|

2 SKULLS AND MANDIBULAR RAMI

| | |
|--|-------|
| Skull with I ¹ -M ³ and partial left ramus with M ₁ -M ₃ (w+) | 37565 |
| ?Male example | |
| Skull with I ¹ -M ³ , partial mandible with M ₃ (br.), atlas, and partial axis . . . (w $\frac{1}{2}$) | 37568 |
| ?Male example | |

SKULL

| | |
|---|-------|
| Skull with C/-M ³ (P ² erupt., P ³ alv., and P ⁴ erupt.) (-m) | 37564 |
| ?Male example | |

2 SKULLS, IMMATURE

| | |
|--|-------|
| Skull with I ¹ -I ³ alv. and C/-dP ² -M ³ (erupt.) (I) | 37569 |
| ?Female example | |
| Skull with C/-dP ² -M ³ (erupt.) (I) | 37570 |

MAXILLA

| | |
|--|-------|
| Left maxilla with dP ¹ -M ³ (erupt.) (I) | 45414 |
|--|-------|

LIMB ELEMENTS

| | |
|---|-------|
| Partial humerus, radius, 2 femora, tibia, 2 calcanea, and partial pes | 45413 |
|---|-------|

Limbs heavier than in other examples.

C. FROM LITTLE MUDDY CREEK, NIOBRARA COUNTY, WYOMING

| 2 ASSOCIATED INDIVIDUALS | | F:A.M. |
|---|--------------------------------|----------|
| Skull with I ¹ -M ³ (I ² -I ³ alv.), partial mandible with I ₁ (alv.)-M ₃ (/C rt.) . . . | (w ₊ ⁺) | 33307A |
| ?Male example | | |
| Partial mandible with I ₂ -M ₃ (br.) | (w) | 33307B |
| Scapula and skeletal fragments | | 33307A-B |
| 2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS | | |
| Skull with I ¹ -I ³ alv. and C/-M ³ , mandible with I ₁ -/C alv. and P ₁ -M ₃ , 2 scapulae, humerus, radius, ulna, carpal bones, and atlas | (w) | 33320 |
| ?Female example | | |
| Anterior portion of skull with I ¹ -M ³ (br.), partial mandible with I ₁ -M ₃ (br.), scapula, 2 humeri, 2 radii, 2 ulnae, partial manus, partial tibia, calcaneum, partial pes, vertebrae, and ribs | (w ₊ ⁺) | 33360 |
| 13 SKULLS AND MANDIBULAR RAMI | | |
| Skull with I ¹ -M ³ and mandible with I ₁ -I ₃ alv. and /C-M ₃ | (w ₊ ⁺) | 33311 |
| ?Male example | | |
| Exceptionally heavy zygomatic arch. | | |
| Skull with C/-M ³ and mandible with /C(alv.)-M ₃ | (w ₊ ⁺) | 33342 |
| ?Male example | | |
| Partial skull with I ¹ -M ³ (C/ br.) and mandible with I ₁ -M ₃ (I ₂ -/C rt.) | (w ₊ ⁺) | 33348 |
| ?Female example | | |
| The skull is quite high, but is also crushed laterally. | | |
| Partial skull with I ¹ -C/ rt. and P ¹ -M ³ and mandible with I ₁ -I ₃ alv. and /C(rt.)-M ₃ (P ₁ alv.) | (w ₊ ⁺) | 33362 |
| The skull is slightly higher than average examples. | | |
| Anterior inferior portion of skull with I ¹ -M ³ and partial mandible with I ₁ (rt.)-M ₃ | (w ₊ ⁺) | 33509 |
| Skull with C/(rt.)-M ³ and partial mandible (attached) with M ₁ -M ₃ | (w) | 37572 |
| ?Male example | | |
| Skull with I ¹ -M ³ and partial mandible with I ₁ -M ₃ | (w) | 37573 |
| ?Female example | | |
| Partial skull with I ¹ (alv.)-M ³ (C/ br.) and partial mandible with P ₄ -M ₃ | (w) | 37574 |
| ?Female example | | |
| Partial skull with I ¹ -M ³ and partial mandible with /C-M ₃ (rt.) | (w) | 37575 |
| ?Male example | | |
| Right side of skull with C/(rt.)-M ³ and partial right ramus with P ₁ (br.)-M ₃ . . . | (w ₊ ⁺) | 37576 |
| Anterior portion of skull with C/(rt.)-M ³ and partial mandible with P ₄ (br.)-M ₃ . | (-M) | 44942 |
| Anterior portion of skull with I ² -M ³ (C/ br.) and partial mandible with I ₁ -I ₂ rt. and I ₃ -M ₃ | (w) | 45412 |
| Partial skull with I ¹ -dP ² -M ³ (germ) and partial right ramus with dP ₄ -M ₂ . . . | (I) | 45425 |
| 7 SKULLS | | |
| Skull with I ¹ -M ³ (I ³ alv.) | (w) | 33338 |
| ?Female example | | |
| Skull with C/-dP ² -M ³ | (I) | 33345 |
| ?Female example | | |
| On the left side there appear to be two canines. | | |
| Skull with I ¹ -I ³ rt. and C/-dP ³ -M ³ (erupt.) | (I) | 33351 |
| ?Female example | | |
| Partial skull with P ³ (rt.)-M ³ | (M+) | 44929 |
| Partial skull with I ³ (br.)-M ³ | (M+) | 44930 |
| ?Female example | | |
| Inferior, anterior portion of skull with dP ³ -M ³ (erupt.) | (I) | 44934 |
| Partial skull with C/-dP ² -M ³ | (I) | 45426 |

4. *?Mesoreodon hesperus* (Stock)

From Sespe deposits (equal in part to the Monroe Creek of the Great Plains), Ventura County, California

Promerycochoerus ? hesperus STOCK, 1930, Carnegie Inst. Washington Publ., no. 404, p. 39, fig. 2.

Promerycochoerus hesperus (Stock), THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 123, fig. 80.

CHARACTERS

SKULL: Unknown.

MANDIBLE: Approximate size and construction of large examples of *Mesoreodon megalodon*; larger than in average examples of *M. cheeki*.

DENTITION: Superior series unknown; inferior series similar to large examples of *M. megalodon*; P_3 with posterior intermediate crest.

LIMBS: Unknown.

MEASUREMENTS: Table 6.

ILLUSTRATIONS: Figure 20.

DISCUSSION

In the original description, Stock compares the premolars of this species with those of *Mesoreodon* and *Promerycochoerus* as designated by Loomis.¹ The present writers, however, at various times in the discussion of oreodont dentitions, have attempted to demonstrate that some of these characters may vary with the age of an individual. The posterior intermediate crest on P_3 is a consistently appearing character when individual wear allows this points to be observed. In *Promerycochoerus* P_3 has a weak posterior intermediate crest and in *Mesoreodon* the crest of P_3 is somewhat stronger.

The size and construction of the ramus of *?M. hesperus* are similar to those of *M. megalodon*, and decidedly smaller than in any known species of *Promerycochoerus*. It is larger than examples of *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* or *P. (P.) minor pygmyus*.

Stock² states that *?M. hesperus* occurred 600 to 650 feet below the top of the Sespe, that a specimen of a leptachenid occurred approximately 2000 feet below the top of the Sespe, and that a second possible leptachenid occurred approximately 100 feet below the position of *?M. hesperus*. In the west-central Great Plains, the leptachenids occur in the Whitney member of the Brule and throughout the Gering and Monroe Creek formations. *Promerycochoerus* and subgenera are known only from the Harrison or its approximate equivalent. To date there are no records of the association of *Promerycochoerus* and leptachenids at the same horizon in the Great Plains. The Sespe beds have yielded very little oreodont material, and it is possible that a leptachenid may be found at the same horizon as *?M. hesperus*. If so, this would strengthen the opinion that *?M. hesperus* belongs to the genus *Mesoreodon*.

The part of the Sespe in which *?M. hesperus* occurs is here considered approximately equal to the Monroe Creek of the Great Plains. This, of course, is based entirely on the size and characters of the mandible, and the comparisons of the occurrences of the leptachenids.

Unfortunately the holotype, a partial mandible, has very few characters which aid in identification. In a complete mandible, there are usually such diagnostic characters as the height of the ascending ramus, the contour of the inferior border, the point of descent of the downward curve, and the degree of slope of the downward curve.

One specimen is here recorded:

HOLOTYPE

Partial mandible with P_1 - M_3 (P_3 , P_4 and M_1 - M_2 br.). (w+)

U.C. 27003

From U.C. coll. loc. no. A725, South Mountain, Ventura County, California

Figured by Stock, 1930, fig. 2; Thorpe, 1937, fig. 80

This paper, fig. 20

¹ Loomis, Frederic B., 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 9, fig. 5.

² Stock, Chester, 1930, *ibid.*, no. 404, p. 30.

III. PROMESOREODON, NEW GENUS

GENOTYPE: *Promesoreodon scanloni*, new species.

DESCRIPTION

SKULL: Small, decidedly smaller than in any known species of *Mesoreodon*, ranging in basal length from 185 to 194 mm., in width from 112 to 132 mm.; low and wide; supraoccipital produced posteriorly; lateral wings not widely spread; exoccipital foramina present; sagittal crest light and high; brain case well inflated; frontals wide; nasals moderately robust; anterior nasal-maxilla contact above P^1 ; malar moderately deep below the orbit; zygomatic arch light, with inward notch posterior of the orbit; infraorbital foramen above P^3 ; lacrimal fossa of moderate size, moderately deep (deeper than in examples of *Mesoreodon*); slight depression on side of face above P^1 - P^2 ; muzzle robust; occipital condyles medium sized; paroccipital process wide at base; bulla well inflated and high; postglenoid process from moderately robust to robust, peg-like in outline; posterior palate projecting slightly beyond M^3 .

MANDIBLE: Light; ramus increasing in depth rapidly posteriorly; inferior border of ramus straight with rapid downward curve below anterior of M^3 ; ascending ramus high.

DENTITION: Lighter and more brachyodont than in *Mesoreodon*.

LIMBS: Short and light.

MEASUREMENTS: Table 6.

ILLUSTRATIONS: Figures 21-24 (skull, mandible, and dentitions); 25 (limbs).

DISCUSSION

The proposed new genus includes forms somewhat similar to *Mesoreodon*, but differing from that genus in having comparatively smaller skulls and skeletal elements, and more brachyodont dentition.

DISTRIBUTION

Promesoreodon remains are known from one new species, in Washabaugh, Washington, and Jackson counties, South Dakota (see distribution chart, p. 87).

SUMMARY OF SPECIES AND TYPES

One species of *Promesoreodon* from one upper Oligocene locality is here recorded:

1. *Promesoreodon scanloni*, new species, from Washabaugh County, South Dakota; referred remains from Washington County, South Dakota; and tentatively referred from Jackson and Washington counties, South Dakota. (Whitney member of Brule.)

HOLOTYPE: Partial skull and mandible, F:A.M. 45329. Figures 21-24.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS

PROMESOREODON

TOTAL AVAILABLE SPECIMENS: 5

1. *Promesoreodon scanloni*, new species

From the Whitney member of the Brule, Washabaugh County, South Dakota; referred specimens from Washington County, South Dakota; tentatively referred remains from Jackson and Washington counties, South Dakota

DESCRIPTION

SKULL: Small; see generic characters.

MANDIBLE: Light; see generic characters.

DENTITION: Brachyodont; series of less length than that in known species of *Mesoreodon*; P^3 with anterior internal pits and P^4 with external anterior pit (not observable in well-worn specimens).

LIMBS: Short and light, equal to small examples of *Merycoidodon culbertsonii*.

MEASUREMENTS: Table 6.

ILLUSTRATIONS: Figures 21-25.

DISCUSSION

The new species is established on the basis of the holotype along with an immature individual and several tentatively referred specimens. As acknowledged in various places in this report, a new species and especially a new genus are always questionable when based on scanty material. In the present case the material in question is definitely different from other known specimens found in the Whitney member ("Leptauchenia beds") of the Brule formation. The form seems to have been ancestral to *Mesoreodon*. The outstanding differences between *Promesoreodon* and *Mesoreodon* are the comparatively smaller size and more brachyodont teeth of the former.

Five specimens are here recorded:

HOLOTYPE

Partial skull with C/-P¹ rt. and P²(br.)-M³ and partial mandible with I₁-P₂ rt. and P₃-M₃. (w₊)

F:A.M. 45329

From the Whitney member of the Brule ("Leptauchenia beds"), Washabaugh County, South Dakota; collected by Ralph Mefferd and Morris Skinner, 1939

Figs. 21-24

REFERRED FROM (A) WASHABAUGH AND (B) WASHINGTON COUNTIES, SOUTH DAKOTA

A. FROM REDWATER CREEK, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL

F:A.M.

Partial skull with C/(br.)-M³ (P¹ rt. and P²-P⁴ erupt.) (-M) 45354

B. FROM SHEEP MOUNTAIN, WASHINGTON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE, IMMATURE

F:A.M.

Skull with P¹-dP²-M³ and mandible (attached) with /C-dP₂-M₃(erupt.) . . . (I) 45355

TENTATIVELY REFERRED FROM (C) JACKSON AND (D) WASHINGTON COUNTIES, SOUTH DAKOTA

C. FROM NORTHWEST OF INTERIOR, JACKSON COUNTY, SOUTH DAKOTA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I¹(rt.)-M³, partial mandible with I₁-M₃ (P₁ rt.), partial radius, and partial ulna. Fig. 25 (w₊₊) F:A.M. 45357

D. FROM COTTONWOOD PASS, WASHINGTON COUNTY, SOUTH DAKOTA

SKULL

F:A.M.

Partial skull with I¹-C/ alv. and P¹-M³ (w₊₊) 45356

The above two tentatively referred skulls differ from the holotype in that they are somewhat higher. The limb fragments of F:A.M. 45357 are very light and suggest that the complete bones are shorter than in typical examples of *Mesoreodon*. They are approximately equal in size to those of small examples of *Merycoidodon culbertsonii*.

IV. MERYCOIDES DOUGLASS

Merycoides DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, art. 6, p. 101. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 171.

GENOTYPE: *Merycoides cursor* Douglass.

CHARACTERS

SKULL: Small to medium sized, ranging in basal length from 176 to 247 mm. and in width from 116 to 161 mm. (ranging from size of examples of *Promesoreodon* to large specimens of *Mesoreodon*); postoccipital wings moderately spread, more so than in examples of *Mesoreodon* and less so than in *Promesoreodon*; supraoccipital region protruding posteriorly beyond condyles; deep exoccipital pits; sagittal crest short and low; brain case broad and inflated; frontals wide; tendency

for anterior retraction of nasals; anterior nasal-maxilla contact above P²; malar moderately shallow below the orbit; zygomatic arch light and low, with exterior notch below the posterior border of the orbit, posterior border rising for short distance, extending posteriorly to a point above the posterior border of the postglenoid process; infraorbital foramen above posterior portion of P³ and anterior portion of P⁴; lacrimal fossa small but moderately deep; small depression on side of face above P²; muzzle joined for short distance; paroccipital process moderately wide at base and perpendicular to the longitudinal axis of skull, process also incorporated in the somewhat semifan-shaped occipital region, tapering rapidly to a three-sided inferior tip, and adhering to the bulla; bulla small but inflated, suboval in outline; post-

TABLE 6

Mesoreodon SCOTT AND *Promesoreodon*, NEW GENUS. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND RAMI

| SKULL | <i>M. cheeki</i> (Schlaikjer) | | <i>M. cheeki scotti</i> (Schlaikjer) | | <i>M. chelonys</i> Scott | | |
|---|----------------------------------|-----------------------------|---|-----------------------------|---------------------------|--------------------------|------------------------------|
| | Holotype M.C.Z. 17765 | Referred F:A.M. 45430 | Holotype M.C.Z. 17480 | Referred F:A.M. 44921 | Holotype P.U. 10425 | Referred | |
| | | | | | | C.M. 908 ² | Y.P.M. 13949 ³ |
| Stage of wear of teeth | (w) | (w ⁺) | (w+) | (m) | (w+) | (w ⁺⁺) | (w+) |
| Length (max., including supraoccipital crest and incisors). | 258 | 244 | 259 | 254 | ((250)) | 252 | — |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | 219 | 217 | (219) | — | (215) | 220 | — |
| Condylbasal length | 228 | 225 | 229 | — | (225) | 229 | — |
| Width (max.) | 149 | 166 | (180) | 140 | ((131)) | 140 | — |
| Width of brain case (max.) | 66 | 69 | — | 65 | 64 | 62 | 58.5 |
| Width, interorbital (min.) | 69 | 70 | 68 | 69 | 64.5 | 72 | 58 |
| Distance from anterior rim of orbit to anterior base of canine | 93 | 100 | 95 | 101 | 97 | 94 | 90 |
| Distance from anterior rim of orbit to supraoccipital crest | 162.5 | 156 | 163 | — | ((150)) | 156 | — |
| Distance from ventral portion of occipital condyles to top of supraoccipital | — | — | 80 | — | ((89)) | 70 | — |
| Width of muzzle at infraorbital foramina | 67 | 65 | 70 | 69.5 | 63 | 65 | 53 |
| Width across canines (max.) | 54 | 61 | 58 | — | ((45)) | 46.5 | 51 |
| Width of palate between fourth superior premolars | 39 | 35 | — | 37.5 | — | 32 | 23 |
| Width of palate between canines | 28 | 27.5 | 25 | — | (24) | 22 | 23 |
| Length, C-M ³ incl. | 125 | 124.5 | 128 | 124 | 117 | 127 | 116.5 |
| Length, P ¹ -M ³ incl. | 110 | 105.5 | 110 | 110 | — | 110.5 | 100 |
| Length, P ¹ -P ⁴ incl. | 54 | 49 | 51 | 50 | — | 51 | 49.5 |
| Length, M ¹ -M ³ incl. | 60 | 59 | 61.5 | 61 | 56.5 | 60 | 53.5 |
| Width of M ³ (max.) | 22 | 20.5 | — | 20.5 | — | 24 | 21 |
| Width across condyles | — | 45 | — | — | 41 | 44.5 | — |
| Depth of malar below orbit | — | 22 | — | 20 | — | — | 19.5 |
| RAMUS | | | | | | | |
| Length (max., including incisors) | 205 | 196 | 208 | 197 | ((188)) | 204 | — |
| Length, /C to condyle incl. | 185 | 172 | 188 | 186.5 | ((175)) | 187 | — |
| Depth of jaw under coronoid | 91 | 93.5 | 82 | — | 89 | — | — |
| Depth of jaw below anterior edge of M ₃ | 43 | 37 | 39 | 38 | 36 | 44 | — |
| Length, /C-M ₃ incl. | 131 | 124 | — | 124 | — | — | — |
| Length, P ₁ -M ₃ incl. | 120 | 115.5 | — | 117 | 108 | 127 | — |
| Length, P ₁ -P ₄ incl. | 55 | 53 | 54 | 55 | 49 | 57 | — |
| Length, M ₁ -M ₃ incl. | 65 | 62 | — | 62 | 59 | 70 | 68 |

¹ Measurements in millimeters; (), approximate; (()), estimated.

² Holotype of "*Mesoreodon* (?) *latidens*" Douglass.

³ Holotype of "*Mesoreodon danai*" Koerner.

TABLE 6—Continued

| | <i>M. chelonys wheeleri</i> (Koerner) | | <i>M. megalodon</i> Peterson | | <i>M. megalodon sweeti</i> , new sub-species | ? <i>M. hesperus</i> (Stock) | <i>P. scanloni</i> , new species |
|---|--|-----------------------------|---------------------------------|-----------------------------|---|---------------------------------|-------------------------------------|
| SKULL | Holotype Y.P.M. 13950 | Referred F:A.M. 45423 | Holotype C.M. 1325 | Referred F:A.M. 33318 | Holotype U.N.S.M. 28012 | Holotype U.C. 27003 | Holotype F:A.M. 45329 |
| Stage of wear of teeth | (w†) | (w†) | (w) | (w†) | (w) | (w+) | (w†) |
| Length (max., including supraoccipital crest and incisors). | (285) | 283 | — | ((300)) | (277) | — | ((211)) |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | 239 | 227.5 | — | ((255)) | 238 | — | (185) |
| Condylbasal length | 251.5 | 244.5 | — | ((265)) | 248 | — | — |
| Width (max.). | 167 | ((145)) | — | 199 | (162) | — | 122 |
| Width of brain case (max.) | 74 | (70) | — | 73 | 71 | — | 55.5 |
| Width, interorbital (min.) | 76 | (72) | — | 82 | 71 | — | (60) |
| Distance from anterior rim of orbit to anterior base of canine | 104.5 | 110 | 113 | ((120)) | 111 | — | 86 |
| Distance from anterior rim of orbit to supraoccipital crest | 182.5 | (167) | — | 177 | — | — | (137) |
| Distance from ventral portion of occipital condyles to top of supraoccipital | 88.5 | 93.5 | — | 80 | — | — | — |
| Width of muzzle at infraorbital foramina | 76.5 | 68.5 | — | 76 | 62 | — | 54.5 |
| Width across canines (max.) | (52) | 63 | 66 | — | 60 | — | — |
| Width of palate between fourth superior premolars | 41 | 37 | — | 40 | 41 | — | 34 |
| Width of palate between canines | (30) | 41 | 34.5 | 22 | 30 | — | (20) |
| Length, C/M ³ incl. | (134.5) | 137 | — | ((150)) | 140 | — | (106) |
| Length, P ¹ –M ³ incl. | 116 | 117 | — | 125.5 | 120 | — | 93.5 |
| Length, P ¹ –P ⁴ incl. | 57.5 | 58 | 60 | 59 | 55 | — | 48 |
| Length, M ¹ –M ³ incl. | 61.5 | 62 | — | 70 | 68 | — | 49 |
| Width of M ³ (max.) | 25.5 | 23 | — | 27.5 | 25 | — | 19.5 |
| Width across condyles | 46 | (45) | — | 49 | 54 | — | — |
| Depth of malar below orbit | 23.5 | 28.5 | — | 32 | 29.5 | — | 18 |
| RAMUS | | | | | | | |
| Length (max., including incisors) | — | (204) | — | ((215)) | 215 | — | — |
| Length, /C to condyle incl. | — | (184) | — | ((211)) | 206 | — | — |
| Depth of jaw under coronoid | — | 106 | — | 110 | 100 | — | — |
| Depth of jaw below anterior edge of M ₃ | — | 41.5 | — | 45 | 48 | — | 38 |
| Length, /C–M ₃ incl. | — | — | — | ((143)) | 144 | — | 108 |
| Length, P ₁ –M ₃ incl. | — | — | — | 136 | 131 | 142 | 101 |
| Length, P ₁ –P ₄ incl. | — | — | 60 | 59 | 59 | 66 | 47 |
| Length, M ₁ –M ₃ incl. | — | 63.5 | — | 78 | 72 | (76) | 54 |

TABLE 7

Mesoreodon SCOTT. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

| | <i>M. cheeki</i> (Schlaikjer) | | <i>M. cheeki</i> <i>scotti</i> (Schlaikjer) | <i>M. chelonys</i> Scott | |
|---|----------------------------------|-----------------------------|---|-----------------------------|--------------|
| | Holotype M.C.Z. 17765 | Referred F:A.M. 45430 | Holotype M.C.Z. 17480 | Referred | |
| | | | | P.U. | C.M. 1234 |
| Length of scapula (max.) | ((127)) | — | — | — | — |
| Length of humerus (articular) | ((167)) | 156 | — | 148 | 11373 |
| Length of radius (articular) | 140 | 137 | 134 | 135 | 11373 |
| Length of ulna (max.) | 189 | 184 | 172 | ((180)) | 11373 |
| Length of metacarpal III (max.) | — | — | 63 | 69.5 | 10414 |
| Length of femur (articular) | 190 | — | 175 | 185 | 11374 |
| Length of tibia (articular) | 165 | — | — | 164 | 11374 |
| Length of metatarsal III (max.) | 77 | — | 65 | — | — |
| Length of calcaneum (max.) | 61 | — | 54 | 61 | 10470 |

TABLE 7—Continued

| | <i>M. megalodon</i> Peterson | <i>M. megalodon sweeti</i> , new subspecies | |
|---|---------------------------------|--|-----------------------------|
| | Referred F:A.M. 33349 | Holotype U.N.S.M. 28012 | Referred F:A.M. 45431 |
| Length of scapula (max.) | — | — | — |
| Length of humerus (articular) | 170 | 149 | 172.5 |
| Length of radius (articular) | 146 | 151 | 149 |
| Length of ulna (max.) | — | 212 | 200.5 |
| Length of metacarpal III (max.) | — | 80 | 72.5 |
| Length of femur (articular) | 194 | — | 203 |
| Length of tibia (articular) | 163 | — | 175 |
| Length of metatarsal III (max.) | — | — | 75 |
| Length of calcaneum (max.) | 63 | — | 68 |

¹ Measurements in millimeters; (()), estimated.

glenoid process moderately high and rather peg shaped; posterior palate projecting slightly beyond M³.

MANDIBLE: Light and comparatively shallow; postsymphysis below P₃; ramus increasing slightly in depth posteriorly to a point below the posterior lobe of M₃, then curving decidedly downward; ascending ramus moderately high.

DENTITION: More brachyodont than that in *Mesoreodon*, but comparable to the dentition of *Promesoreodon* in this respect; C/ and

P₁ moderately large; premolars not overcrowded and set almost straight with alveoli border; external style of M¹ weak, M² more prominent, M³ well developed; P¹–P³ with anterior intermediate crest, and P₃ with posterior intermediate crest.

LIMBS: Slender but less so than in examples of *Merychyus*; lighter than in *Mesoreodon*.

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 7, 21–24 (skulls, mandibles, and dentitions).

DISCUSSION

The genus *Merycoides* is similar to *Mesoreodon* in that the skull is comparatively low and broad, the zygomatic arch has an inward curve, and the bulla is suboval. It differs in having a shorter and lower sagittal crest, a lower occipital region, a tendency towards a more semifan-shaped occipital region, and more brachyodont teeth.

Material referred to the genus *Merycoides* is of a size comparable with the dentition of *Promesoreodon* and *Mesoreodon*. Apparently *Merycoides* evolved from *Promesoreodon*, as did *Mesoreodon*, but retained the same degree of brachyodonty as found in the ancestral form.

DISTRIBUTION

Three species of *Merycoides* are known from the Gering and Monroe Creek formations, or their equivalent, from Nebraska, Montana, and Wyoming. (See distribution chart, p. 87.)

SUMMARY OF SPECIES AND TYPES

Three species and one subspecies of *Merycoides* from three lower Miocene localities are here recorded:

1. *Merycoides cursor* Douglass, 1907, Jefferson County, Montana. (Approximate Gering equivalent.)

HOLOTYPE: Skull, mandible, and skeletal fragments, C.M. 1222. Figures 21-24.

2. *Merycoides giganteus*, new species, from Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Skull, F:A.M. 33316. Figures 21-23.

3. *Merycoides nebraskensis*, new species, from Scotts Bluff County, Nebraska. (Gering.)

HOLOTYPE: Skull and mandible, F:A.M. 33363. Figures 7, 21-24.

3a. *Merycoides nebraskensis blairi*, new subspecies, from Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Partial skull, F:A.M. 42306. Figures 22, 23.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MERYCOIDES

TOTAL AVAILABLE SPECIMENS: 6

1. *Merycoides cursor* Douglass

From lower Miocene deposits (approximately equal in age to the Gering of the Great Plains), Jefferson County, Montana

Merycoides cursor DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, art. 6, p. 101, pl. 24. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 171, fig. 124, pl. 25.

CHARACTERS

SKULL: Slightly smaller than that of *M. nebraskensis*; lacrimal fossa deeper and larger than that of *M. nebraskensis*.

MANDIBLE: Smaller than that of *M. nebraskensis*.

DENTITION: Length of dental series less than that of *M. nebraskensis*.

LIMBS: Smaller than those of other species of genus.

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 21-24.

DISCUSSION

The holotype of the genotypic species, *Merycoides cursor*, came from the same location and formation in Montana as the holotype of "*Mesoreodon latidens*," here recorded as synonymous with *Mesoreodon chelonys* (see p. 140). The age of the Canyon Ferry locality is here considered to be approximately equivalent to the Gering of Nebraska and Wyoming. This demonstrates the close geological relationship of the deposits containing the remains of *Mesoreodon chelonys* and *Mesoreodon cheeki* and also *Merycoides cursor* and *Merycoides nebraskensis*. The size difference in the former two species is proportionately the same as in the latter two species, i.e., *Merycoides cursor* is smaller than *M. nebraskensis* and *Mesoreodon chelonys* is smaller than *M. cheeki*.

One specimen is here recorded:

HOLOTYPE

Skull with I¹-M³, mandible with I₁-M₂, partial scapula, partial humerus, partial radius, partial femur, 2 partial tibiae, tarsus, and partial pes. (w+)

C.M. 1222

From Canyon Ferry, Jefferson County, Montana; collected by Douglass, 1902
Figured by Douglass, 1907, pl. 24;
Thorpe, 1937, fig. 124, pl. 25
This paper, figs. 21-24

2. *Merycoides giganteus*, new species

From the Monroe Creek formation, Muddy Creek, Niobrara County, Wyoming

DESCRIPTION

SKULL: Medium size, considerably larger than in *M. nebraskensis* or *M. cursor*; infra-orbital foramen above anterior P⁴.

MANDIBLE: Larger than that of *M. nebraskensis* and *M. cursor*.

DENTITION: Longer and heavier than that of *M. nebraskensis* and *M. cursor*.

LIMBS: Unknown.

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 21-24.

DISCUSSION

The characters of this species are typical

of the genus and differ from those of *M. cursor*, *M. nebraskensis*, and *M. nebraskensis blairi* in size only. The large skull, however, has a small type of bulla similar to that found in *P. (Parapromerycoherus)*. This species is found in the same formation as *M. nebraskensis blairi*, and perhaps represents gigantism within a line of development. It is also possible that the form may represent a separate subgeneric line.

Merycoides giganteus occurs in the same beds (Monroe Creek) as examples of *M. megalodon* but differs from that species in possessing a low occipital region, short and low sagittal crest, and small bulla.

Two specimens are here recorded:

HOLOTYPE

Skull with C/-M³. (w+)

F:A.M. 33316

From Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1932
Figs. 21-23

REFERRED FROM TYPE AREA

(Collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1931)

SKULL AND MANDIBLE

F:A.M.

Partial skull with C/(br.)-M³ and mandible with P₂-M₂. Fig. 24 (in part) . . (w+) 44923

The teeth of this specimen are slightly heavier than those of the holotype. This may indicate that the holotype is an example of a female and the referred individual that of a male. The malar below the orbit is of less depth in the referred specimen.

3. *Merycoides nebraskensis*, new species

From the Gering formation, Scotts Bluff County, Nebraska

DESCRIPTION

SKULL: Slightly larger than in *M. cursor*; infra-orbital foramen above posterior portion of P³; lacrimal fossa smaller than in *M. cursor*.

MANDIBLE: Slightly longer and heavier than in *M. cursor*.

DENTITION: Series somewhat heavier than that in *M. cursor*.

LIMBS: Unknown.

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 7, 21-24.

DISCUSSION

The new species is known from the holo-

type only. The specimen is somewhat larger than the holotype of *M. cursor* from Montana. When both species are represented by additional material, the writers believe the

size variation will be similar to that existing between *Mesoreodon chelonys* from Montana and *Mesoreodon cheeki* from Wyoming.

One specimen is here recorded:

HOLOTYPE

Partial skull with I¹-M³ and mandible with I₁-M₃ (P₂-P₄ br.). (w⁺)

F:A.M. 33363

From near Signal Butte, Scotts Bluff County, Nebraska; collected by Jack Wilson, 1934
Figs. 7, 21-24

3a. *Merycoides nebraskensis blairi*,¹ new subspecies

From the Monroe Creek formation,
Niobrara County, Wyoming

LIMBS: Unknown.

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 21-23.

DESCRIPTION

SKULL: Larger than in *M. nebraskensis* but decidedly smaller than in *M. giganteus*; supraoccipital region protruding posteriorly for less distance than in *M. nebraskensis*; bulla larger than in that species, and the condyle more widely spread.

MANDIBLE: Known from immature example only.

DENTITION: Larger, more robust, and slightly less brachyodont than in *M. nebraskensis*.

DISCUSSION

The holotype of *M. nebraskensis blairi* is fragmentary and is the only mature specimen known of the species at this time. It occurs in the Monroe Creek formation and apparently evolved from *M. nebraskensis* from the Gering. It is important because it demonstrates that the small conservative size group of *Merycoides* persisted into the Monroe Creek times along with a large species, *M. giganteus*.

Two specimens are here recorded:

HOLOTYPE

Fragmentary skull with M²-M³. (w⁺)

F:A.M. 42306

From Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1938
Figs. 22, 23

REFERRED FROM TYPE AREA

IMMATURE SKULL AND MANDIBLE

F:A.M.

Skull with C/-dP²-M³(germ), mandible with I₁-dP₂-M₃(germ), and pelvic fragments. Fig. 21 (1)

45424

¹ Named in honor of Mr. Floyd Blair, Registrar, Frick Laboratory, the American Museum of Natural History.

TABLE 8

Merycoides DOUGLASS. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND RAMI

| | <i>M. cursor</i> Douglass | <i>M. giganteus</i> , new species | <i>M. nebrascensis</i> , new species | <i>M. nebrascensis blairi</i> , new subspecies |
|---|------------------------------|--------------------------------------|---|---|
| SKULL | Holotype C.M. 1282 | Holotype F:A.M. 33316 | Holotype F:A.M. 33363 | Holotype F:A.M. 42306 |
| Stage of wear of teeth | (w+) | (w+) | (w‡) | (w‡) |
| Length (max., including supraoccipital crest and incisors) | 209 | (285) | 215 | — |
| Basal length (from anterior notch of foramen magnum to posterior base of I ¹) | 176 | (247) | 183 | — |
| Condylobasal length | 186 | (258) | 191 | — |
| Width (max.) | 116.5 | 161 | 123 | — |
| Width of brain case (max.) | 57 | 72 | 56 | 60 |
| Width, interorbital (min.) | 60 | 82 | ((53)) | — |
| Distance from anterior rim of orbit to anterior base of canine | 78 | 124 | 84 | — |
| Distance from anterior rim of orbit to supraoccipital crest | 131 | (165) | 131 | 131.5 |
| Distance from ventral portion of occipital condyles to top of supraoccipital | 61 | 76 | 56 | — |
| Width of muzzle at infraorbital foramina | 53.5 | 69 | 49 | — |
| Width across canines (max.) | 33 | (53) | 42 | — |
| Width of palate between fourth premolars | 25 | 37 | 29 | — |
| Width of palate between canines | 17 | 27 | 23 | — |
| Length, C-M ³ incl. | 95.5 | 144 | 104 | — |
| Length, P ¹ -M ³ incl. | 85 | 123 | 90 | — |
| Length, P ¹ -P ⁴ incl. | 40 | 59 | 42 | — |
| Length, M ¹ -M ³ incl. | 46 | 66.5 | 51 | ((51)) |
| Width of M ³ (max.) | 17 | 24 | 19 | — |
| Width across condyles | — | 47.5 | 33.5 | 37 |
| Depth of malar below orbit | — | 24 | 12 | — |
| RAMUS | | Referred F:A.M. 44923 | | |
| Stage of wear of teeth | | (w+) | | |
| Length (max., including incisors) | 155 | — | — | — |
| Length, /C to condyle incl. | 150 | — | 155 | — |
| Depth of jaw under coronoid | 75 | — | — | — |
| Depth of jaw below anterior edge of M ₃ | 32.5 | 37.5 | 32 | — |
| Length, /C-M ₃ incl. | 99.5 | — | 100 | — |
| Length, P ₁ -M ₃ incl. | 92 | — | 98 | — |
| Length, P ₁ -P ₄ incl. | 42 | — | 45 | — |
| Length, M ₁ -M ₃ incl. | 51 | 75 | 53 | — |

¹ Measurements in millimeters; (), approximate; (()), estimated.

CHART 5

ASPECTS OF VARIATION AND RANGE IN *Promerycochoerus*, *P. (Parapromerycochoerus)*,
AND *P. (Pseudopromerycochoerus)*Comparisons of species, emphasizing apparent individual variation in basal lengths,
superior and inferior dentitions

| | Skull | | | | Dentition | | | | | |
|--|--|---------------------------------|---|-------------------|----------------------------------|---|------|----------------------------------|---|------|
| | Basal Length ¹ | | | | P ¹ -M ³ | | | P ₁ -M ₂ | | |
| | Wear | No. of Ex-amples | Range | Mean ² | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean |
| <i>Promerycochoerus carrikeri</i> Harrison 83 specimens | M M+ W W+ W ⁺ ₁ W ⁺ ₁ + W ⁺ ₁ + ₁ | 1 1 8 9 7 4 1 | 292 274 266-306 273-325 282-310 271-322 312 | 294 | 2 1 9 12 7 4 1 | 133-143 140 133-152 135-159 135-150 137-149 145 | 144 | — 2 10 9 6 5 2 | — 161-162 150-181 149-182 151-170 163-174 157-162 | 160 |
| <i>P. latidens</i> Approx. Harrison equivalent 36 specimens | M M+ W W+ W ⁺ ₁ W ⁺ ₁ + W ⁺ ₁ + ₁ | — — 3 4 2 1 — | — — 312-328 324-336 338 350 — | 330 | — 1 5 6 3 1 — | — 143 142-154 151-163 152-160 147 — | 154 | — 2 3 5 — — — | — 151-164 159-166 162-175 — — — | 165 |
| <i>P. superbus</i> Approx. Harrison equivalent 30 specimens | M M+ W W+ W ⁺ ₁ W ⁺ ₁ + W ⁺ ₁ + ₁ | — — 3 — — 1 — | — — 275-309 — — 309 — | 296 | 1 — 4 1 — 1 — | 131 — 139-149 143 — 143 — | 141 | — 1 1 — — — — | — 144 151 — — — — | 147 |
| <i>P. superbus chelydra</i> Approx. Harrison equivalent 5 specimens | M M+ W W+ W ⁺ ₁ W ⁺ ₁ + W ⁺ ₁ + ₁ | — — — 1 1 — — | — — — 287 296 — — | 291 | — — — 2 1 — — | — — — 131-144 143 — — | 139 | — — — — 1 — — | — — — — 158 — — | 158 |
| <i>P. (Parapromerycochoerus) barbouri</i> Harrison 6 specimens | M M+ W W+ W ⁺ ₁ W ⁺ ₁ + W ⁺ ₁ + ₁ | 1 — — 2 — — — | 285 — — 276 — — — | 279 | 1 — — 2 1 — — | 127 — — 133-136 132 — — | 132 | 1 — — 1 — — — | 132 — — 138 — — — | 135 |

¹ All measurements in millimeters.² Weighted mean.

CHART 5—*Continued*

| | Skull | | | | Dentition | | | | | |
|---|------------------|------------------|---------|------|--------------------------------|---------|------|--------------------------------|---------|------|
| | Basal Length | | | | P ¹ -M ³ | | | P ₁ -M ₃ | | |
| | Wear | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean |
| <i>P. (P.) macrostegus</i> Approx. Harrison equivalent 14 specimens | M | — | — | 317 | — | — | 147 | — | — | 164 |
| | M+ | — | — | | — | — | | — | — | |
| | W | 1 | 306 | | 1 | 143 | | 1 | 147 | |
| | W+ | 3 | 307-325 | | 4 | 140-149 | | 4 | 157-179 | |
| | W ⁺ | 2 | 325 | | 2 | 150-155 | | 1 | 172 | |
| | W ⁺⁺ | 1 | 320 | | 1 | 152 | | 1 | 167 | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>P. (P.) macrostegus furlongi</i> Approx. Harrison equivalent 1 specimen | M | — | — | 287 | — | — | 134 | — | — | — |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | — | — | | — | — | | — | — | |
| | W ⁺ | 1 | 287 | | 1 | 134 | | — | — | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>P. (Pseudopromerycochoerus) inflatus</i> Approx. Harrison equivalent 1 specimen | M | — | — | 355 | — | — | 173 | — | — | — |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | 1 | 355 | | 1 | 173 | | — | — | |
| | W ⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>P. (P.) minor</i> Approx. Harrison equivalent 1 specimen | M | — | — | — | — | — | 104 | — | — | 117 |
| | M+ | — | — | | 1 | 104 | | 1 | 117 | |
| | W | — | — | | — | — | | — | — | |
| | W+ | — | — | | — | — | | — | — | |
| | W ⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>P. (P.) minor pygmyus</i> Harrison 4 specimens | M | — | — | 226 | — | — | 105 | — | — | 115 |
| | M+ | — | — | | — | — | | — | — | |
| | W | 2 | 221-224 | | 2 | 104-118 | | 1 | 123 | |
| | W+ | 1 | 224 | | 1 | 102 | | 1 | 115 | |
| | W ⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺ | 1 | 237 | | 1 | 96 | | 1 | 106 | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |

CHART 5—*Continued*

| | Skull | | | | Dentition | | | | | |
|---|-----------------------------|------------------|---------|------|--------------------------------|---------|------|--------------------------------|---------|------|
| | Basal Length | | | | P ¹ -M ³ | | | P ₁ -M ₃ | | |
| | Wear | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean |
| <i>P. (P.) montanus</i> Approx. Harrison equivalent 14 specimens | M | — | — | 297 | — | — | 147 | — | — | 157 |
| | M+ | — | — | | — | — | | — | — | |
| | w | 4 | 290-315 | | 5 | 142-151 | | 2 | 155-164 | |
| | w+ | 1 | 295 | | 1 | 151 | | 2 | 147-164 | |
| | w ⁺ ₁ | — | — | | — | — | | — | — | |
| | w ⁺ ₂ | — | — | | — | — | | — | — | |
| | w ⁺ ₃ | — | — | | — | — | | — | — | |
| <i>P. (P.) montanus</i> <i>pinensis</i> Harrison 15 specimens | M | — | — | 307 | — | — | 153 | — | — | 163 |
| | M+ | — | — | | — | — | | — | — | |
| | w | — | — | | 2 | 148-160 | | 2 | 162-171 | |
| | w+ | 3 | 304-316 | | 3 | 149-160 | | 3 | 159-167 | |
| | w ⁺ ₁ | 2 | 295-304 | | 3 | 146-155 | | 4 | 156-163 | |
| | w ⁺ ₂ | — | — | | — | — | | — | — | |
| | w ⁺ ₃ | — | — | | — | — | | — | — | |

CHART 6

ASPECTS OF VARIATION IN *Mesoreodon*, *Promesoreodon*, AND *Merycoides*
 Comparisons of species, emphasizing apparent individual variation in basal
 lengths, superior and inferior dentitions

| | Skull | | | | Dentition | | | | | |
|--|---|---------------------------------|---|-----------------------------------|---------------------------------|---|-----------------------------------|--------------------------------------|--|-----------------------------------|
| | Basal Length ¹ | | | | P ¹ -M ³ | | | P ₁ -M ₃ | | |
| | Wear | No. of Ex-amples | Range | Mean ² | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean |
| <i>Mesoreodon cheeki</i> Gering 10 specimens | M M+ W W+ W ⁺ W ⁺⁺ W ⁺⁺⁺ | — — 1 — 2 — — | — — 219 — 211-217 — — | — — 216 — — — — | — — 1 1 3 — — | — — 110 110 105-111 — — | — — 109 — — — — | — — 1 — 1 — — | — — 120 — 115 — — | — — 118 — — — — |
| <i>M. cheeki scottii</i> Monroe Creek 11 specimens | M M+ W W+ W ⁺ W ⁺⁺ W ⁺⁺⁺ | — — — 1 — — — | — — — 219 — — — | — — — 219 — — — | 1 — — 1 4 — — | 110 — — 110 109-119 — — | — — — 112 — — — | 1 — — — 2 1 — | 117 — — — 123-125 135 — | — — — 125 — — — |
| <i>M. chelonys</i> Approx. Gering equivalent 25 specimens | M M+ W W+ W ⁺ W ⁺⁺ W ⁺⁺⁺ | — — — 2 2 2 — | — — — 215 222-225 200-220 — | — — — 216 — — — | — — 2 2 2 2 — | — — 95-109 100-116 100-106 97-110 — | — — — 104 — — — | — — — 1 1 1 1 — | — — — 100 108 110 127 — | — — — 111 — — — |
| <i>M. chelonys wheeleri</i> Approx. Gering equivalent 2 specimens | M M+ W W+ W ⁺ W ⁺⁺ W ⁺⁺⁺ | — — — — 2 — — | — — — — 227-239 — — | — — — 233 — — — | — — — — 2 — — | — — — — 116-117 — — | — — — 116 — — — | — — — — — — — | — — — — — — — | — — — — — — — |
| <i>M. megalodon</i> Monroe Creek 14 specimens | M M+ W W+ W ⁺ W ⁺⁺ W ⁺⁺⁺ | — — 1 — 3 — — | — — 259 — 226-255 — — | — — 249 — — — — | — 1 2 1 6 — — | — 120 117-130 124 115-135 — — | — — 124 — — — — | — — 1 1 5 — — | — — 143 137 125-137 — — | — — 135 — — — — |

¹ All measurements in millimeters.² Weighted mean.

CHART 6—Continued

| | Skull | | | | Dentition | | | | | |
|--|------------------|------------------|---------|------|--------------------------------|---------|------|--------------------------------|---------|------|
| | Basal Length | | | | P ¹ -M ³ | | | P ₁ -M ₃ | | |
| | Wear | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean | No. of Ex-amples | Range | Mean |
| <i>M. megalodon sweeti</i> Gering 47 specimens | M | 1 | 233 | 235 | 1 | 124 | 118 | — | — | 128 |
| | M+ | — | — | | 1 | 113 | | — | — | |
| | W | 5 | 225-238 | | 10 | 114-121 | | 6 | 124-146 | |
| | W+ | 8 | 220-255 | | 8 | 113-124 | | 2 | 126-133 | |
| | W ⁺ | 6 | 228-245 | | 9 | 115-125 | | 5 | 122-135 | |
| | W ⁺⁺ | 1 | 232 | | 4 | 112-122 | | 3 | 118-128 | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>Promesoreodon scanloni</i> Whitney 5 specimens | M | — | — | 190 | — | — | 94 | — | — | 99 |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | — | — | | — | — | | — | — | |
| | W ⁺ | 1 | 185 | | 1 | 93 | | 1 | 101 | |
| | W ⁺⁺ | 1 | 195 | | 1 | 96 | | 1 | 97 | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>Merycoides cursor</i> Approx. Gering equivalent 1 specimen | M | — | — | 176 | — | — | 85 | — | — | 92 |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | 1 | 176 | | 1 | 85 | | 1 | 92 | |
| | W ⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>M. giganteus</i> Monroe Creek 2 specimens | M | — | — | 247 | — | — | 121 | — | — | — |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | 1 | 247 | | 2 | 118-123 | | — | — | |
| | W ⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |
| <i>M. nebraskensis</i> Gering 1 specimen | M | — | — | 183 | — | — | 90 | — | — | 98 |
| | M+ | — | — | | — | — | | — | — | |
| | W | — | — | | — | — | | — | — | |
| | W+ | — | — | | — | — | | — | — | |
| | W ⁺ | 1 | 183 | | 1 | 90 | | 1 | 98 | |
| | W ⁺⁺ | — | — | | — | — | | — | — | |
| | W ⁺⁺⁺ | — | — | | — | — | | — | — | |

EXPLANATION OF TEXT FIGURES

FIG. 1. *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352, skull and ramus, lateral view (in outline), drawn at $\frac{1}{2}$ scale for size comparison with other figures reproduced at same scale in this and previous papers (the shaded drawings of the larger forms in the present paper are at a scale of $\frac{1}{3}$). $\times \frac{1}{2}$.

FIG. 2. Lateral views of skulls of *Promerycochoerus superbus chelydra* (Cope), holotype, A.M. 7430 (P², P³, M², and M³ from opposite side), John Day Valley, Oregon; *Promerycochoerus superbus* (Leidy), referred, A.M. 7431, John Day Valley, Oregon; *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus latidens* Thorpe, referred, A.M. 7442 (P¹, P³, P⁴, and M³ from opposite side), John Day Valley, Oregon. $\times \frac{1}{3}$. C, canine; IF, infraorbital foramen; MA, external auditory meatus; PP, paroccipital process.

FIG. 3. Dorsal views of skulls of *Promerycochoerus superbus chelydra* (Cope), holotype, A.M. 7430, John Day Valley, Oregon; *Promerycochoerus superbus* (Leidy), referred, A.M. 7431, John Day Valley, Oregon; *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus latidens* Thorpe, referred, A.M. 7442, John Day Valley, Oregon. $\times \frac{1}{3}$. IF, infraorbital foramen; MA, external auditory meatus; NF, nasal-frontal contact; SOF, supraorbital foramen.

FIG. 4. Ventral views of skulls of *Promerycochoerus superbus chelydra* (Cope), holotype, A.M. 7430 (P², P³, M², and M³ from opposite side), John Day Valley, Oregon; *Promerycochoerus superbus* (Leidy), referred, A.M. 7431, John Day Valley, Oregon; *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352 and F:A.M. 33353 (superior dentition only), Harrison formation, Niobrara County, Wyoming; *Promerycochoerus latidens* Thorpe, referred, A.M. 7442 (P¹, P³, P⁴, and M³ from opposite side), John Day Valley, Oregon. $\times \frac{1}{3}$. APF, anterior palatine foramen; B, auditory bulla; FO, foramen ovale; MA, external auditory meatus; PP, paroccipital process; PPF, anterior palatine foramen; PPR, posterior palatine projection; Z, depression for tympanohyal; 5, lacerated foramina; 6, glenoid foramina; 7, condylar foramen.

FIG. 5. Lateral views of skulls of *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, holotype, F:A.M. 33315, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus*

(*Parapromerycochoerus*) *macrostegus furlongi*, new subspecies, holotype, C.I.T. 1727, John Day Valley, Oregon; *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444, John Day Valley, Oregon. Occipital regions of skulls of *Promerycochoerus superbus chelydra* (Cope), holotype, A.M. 7430, John Day Valley, Oregon; *Promerycochoerus superbus* (Leidy), referred, A.M. 7431, John Day Valley, Oregon; *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352 and 33355, Harrison formation, Niobrara County, Wyoming. $\times \frac{1}{3}$.

FIG. 6. Dorsal views of skulls of *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, holotype, F:A.M. 33315, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus furlongi*, new subspecies, holotype, C.I.T. 1727, John Day Valley, Oregon; *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444, John Day Valley, Oregon. Occipital regions of skulls of *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus furlongi*, new subspecies, holotype, C.I.T. 1727, John Day Valley, Oregon; *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, holotype, F:A.M. 33315, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota. $\times \frac{1}{3}$.

FIG. 7. Ventral views of skulls of *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, holotype, F:A.M. 33315, Harrison formation, Niobrara County, Wyoming; *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus furlongi*, new subspecies, holotype, C.I.T. 1727, John Day Valley, Oregon; *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444, John Day Valley, Oregon. Occipital regions of skulls of *Mesoreodon megalodon* Peterson, referred, F:A.M. 33318, Monroe Creek formation, Niobrara County, Wyoming; *Mesoreodon cheeki* (Schlaikjer), referred, F:A.M. 45430, Gering formation, Goshen County, Wyoming; *Merycoides nebraskensis*, new species, holotype, F:A.M. 33363, Gering formation, Scotts Bluff County, Nebraska. $\times \frac{1}{3}$.

FIG. 8. Lateral views of skulls of *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), holotype, A.M. 12967, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope),

referred, A.M. 7452 (P^1 and M^1 from opposite side), John Day Valley, Oregon, and A.M. 21338, Meagher County, Montana; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *inflatus* (Thorpe), holotype, Y.P.M. 10233, John Day Valley, Oregon. $\times \frac{1}{3}$.

FIG. 9. Dorsal views of skulls of *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), holotype, A.M. 12967, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), referred, A.M. 7452, John Day Valley, Oregon, and A.M. 21338, Meagher County, Montana; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *inflatus* (Thorpe), holotype, Y.P.M. 10233, John Day Valley, Oregon. $\times \frac{1}{3}$.

FIG. 10. Ventral views of skulls of *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), holotype, A.M. 12967, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass), holotype, C.M. 769 (superior dentition only), Granite County, Montana; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), holotype, A.M. 8107 (superior dentition only), Montana, and referred, A.M. 7452 (P^1 and M^1 from opposite side), John Day Valley, Oregon, and A.M. 21338 (bulla from opposite side), Meagher County, Montana; *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota; *Promerycochoerus* (*Pseudopromerycochoerus*) *inflatus* (Thorpe), holotype, Y.P.M. 10233, John Day Valley, Oregon. $\times \frac{1}{3}$.

FIG. 11. Mandibular rami. A. *Promerycochoerus superbus* (Leidy), referred, A.M. 7431 (I_2 and P_2 from opposite side, and M_2 and M_3 combination of both sides), John Day Valley, Oregon. B. *Promerycochoerus superbus chelydra* (Cope), referred, A.M. 7901 (I_3 , P_1 , and P_2 from opposite side), John Day Valley, Oregon. C, D. *Promerycochoerus carrikeri* Peterson (C not illustrated), referred, F:A.M. 33352, Harrison formation, Niobrara County, Wyoming. E. *Promerycochoerus latidens* Thorpe, referred, A.M. 8108, Meagher County, Montana. F. *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, referred, F:A.M. 45417 (I_3 from opposite side), Harrison formation, Niobrara County, Wyoming. G. *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444, John Day Valley, Oregon. H. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass), holotype, C.M. 769, Granite County, Montana. I. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), referred, A.M. 12968, Harrison formation, Shannon County, South Dakota. J. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota. K. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), holotype, A.M. 8107, ?Meagher County, Montana. L. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), referred, F:A.M. 45422A, Meagher County, Montana. $\times \frac{1}{3}$.

merlycochoerus (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444 (P_2 from opposite side), John Day Valley, Oregon. H. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass), not illustrated. I. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), referred, A.M. 12968, Harrison formation, Shannon County, South Dakota. J. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota. K. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), not illustrated. L. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), referred, F:A.M. 45422A, Meagher County, Montana. $\times \frac{1}{3}$.

FIG. 12. Inferior dentitions. A. *Promerycochoerus superbus* (Leidy), referred, A.M. 7431 (I_2 and P_2 from opposite side, and M_2 and M_3 combination of both sides), John Day Valley, Oregon. B. *Promerycochoerus superbus chelydra* (Cope), referred, A.M. 7901 (I_3 , P_1 , and P_2 from opposite side), John Day Valley, Oregon. C, D. *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33353 and 33352, Harrison formation, Niobrara County, Wyoming. E. *Promerycochoerus latidens* Thorpe, referred, A.M. 8108, Meagher County, Montana. F. *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*, new species, F:A.M. 45417, Harrison formation, Niobrara County, Wyoming. G. *Promerycochoerus* (*Parapromerycochoerus*) *macrostegus* (Cope), holotype, A.M. 7444, John Day Valley, Oregon. H. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass), holotype, C.M. 769, Granite County, Montana. I. *Promerycochoerus* (*Pseudopromerycochoerus*) *minor pygmyus* (Loomis), referred, A.M. 12968, Harrison formation, Shannon County, South Dakota. J. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*, new subspecies, holotype, A.M. 12948, Harrison formation, Shannon County, South Dakota. K. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), holotype, A.M. 8107, ?Meagher County, Montana. L. *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus* (Cope), referred, F:A.M. 45422A, Meagher County, Montana. $\times \frac{1}{3}$.

FIG. 13. *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33353, 33354, and 33355, three associated skulls, dorsal views (in outline), showing age variation, Harrison formation, Niobrara County, Wyoming. $\times \frac{1}{3}$.

FIG. 14. *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352, 33353, 33354, 33355, 33356, 33357, and 33357A, seven associated skeletons (dotted lines indicate limits of field blocks as

collected), Harrison formation, Niobrara County, Wyoming.

FIG. 15. Lateral views of skulls of *Mesoreodon chelonys* Scott, holotype, P.U. 10425 (combination of both sides of skull), Meagher County, Montana; *Mesoreodon cheeki scotti* (Schlaikjer), referred, F:A.M. 44921, Monroe Creek formation, Niobrara County, Wyoming; *Mesoreodon cheeki* (Schlaikjer), referred, F:A.M. 45430, Gering formation, Goshen County, Wyoming; *Mesoreodon chelonys wheeleri* (Koerner), referred, F:A.M. 45423, Meagher County, Montana. $\times \frac{1}{2}$.

FIG. 16. Lateral views of skulls of *Mesoreodon megalodon sweeti*, new subspecies, holotype, U.N.S.M. 28012, Gering formation, Morrill County, Nebraska; *Mesoreodon megalodon* Peterson, referred, F:A.M. 33318, Monroe Creek formation, Niobrara County, Wyoming. Dorsal views of skulls of *Mesoreodon cheeki scotti* (Schlaikjer), referred, F:A.M. 44921, Monroe Creek formation, Niobrara County, Wyoming; *Mesoreodon chelonys* Scott, holotype, P.U. 10425 (combination of both sides of skull), Meagher County, Montana. $\times \frac{1}{2}$.

FIG. 17. Dorsal views of skulls of *Mesoreodon cheeki* (Schlaikjer), referred, F:A.M. 45430, Gering formation, Goshen County, Wyoming; *Mesoreodon chelonys wheeleri* (Koerner), referred, F:A.M. 45423, Meagher County, Montana; *Mesoreodon megalodon sweeti*, new subspecies, holotype, U.N.S.M. 28012, Gering formation, Morrill County, Nebraska; *Mesoreodon megalodon* Peterson, referred, F:A.M. 33318, Monroe Creek formation, Niobrara County, Wyoming. $\times \frac{1}{2}$.

FIG. 18. Ventral views of skulls of *Mesoreodon chelonys* Scott, holotype, P.U. 10425 (combination of both sides of skull), Meagher County, Montana; *Mesoreodon cheeki scotti* (Schlaikjer), referred, F:A.M. 44921, Monroe Creek formation, Niobrara County, Wyoming; *Mesoreodon cheeki* (Schlaikjer), referred, F:A.M. 45430, Gering formation, Goshen County, Wyoming; *Mesoreodon chelonys wheeleri* (Koerner), referred, F:A.M. 45423, Meagher County, Montana; *Mesoreodon megalodon sweeti*, new subspecies, holotype, U.N.S.M. 28012, Gering formation, Morrill County, Nebraska. Superior dentitions of *Mesoreodon chelonys* Scott, referred, C.M. 908, Jefferson County, Montana, and F:A.M. 44955, Meagher County, Montana. $\times \frac{1}{2}$.

FIG. 19. *Mesoreodon megalodon* Peterson, holotype, C.M. 1325, superior dentition, Monroe Creek formation, Sioux County, Nebraska, and referred, F:A.M. 33318, skull, and F:A.M. 33336 and 33337, superior dentitions, Monroe Creek formation, Niobrara County, Wyoming; *Mesoreo-*

don chelonys Scott, holotype, P.U. 10425, ramus (combination of both sides); *Mesoreodon cheeki scotti* (Schlaikjer), referred, F:A.M. 44921, ramus (I₁ and I₂ from opposite side), Monroe Creek formation, Niobrara County, Wyoming; *Mesoreodon cheeki* (Schlaikjer), referred, F:A.M. 45430, ramus, Gering formation, Goshen County, Wyoming. $\times \frac{1}{2}$.

FIG. 20. Mandibular rami of *Mesoreodon chelonys wheeleri* (Koerner), referred, F:A.M. 45423, ramus, Meagher County, Montana; *Mesoreodon megalodon sweeti*, new subspecies, holotype, U.N.S.M. 28012, Gering Formation, Morrill County, Nebraska; *Mesoreodon megalodon* Peterson, holotype, C.M. 1325, inferior dentition, Monroe Creek formation, Sioux County, Nebraska, and referred, F:A.M. 33318, ramus, Monroe Creek formation, Niobrara County, Wyoming; ?*Mesoreodon hesperus* (Stock), holotype, U.C. 27003, ramus, Sespe deposits, Ventura County, California. $\times \frac{1}{2}$.

FIG. 21. Lateral views of skulls of *Merycoides cursor* Douglass, holotype, C.M. 1222, Jefferson County, Montana; *Merycoides nebraskensis blairi*, new subspecies, referred, F:A.M. 45424 (P¹ from opposite side), Monroe Creek formation, Niobrara County, Wyoming; *Merycoides nebraskensis*, new species, holotype, F:A.M. 33363 (I¹ and I² from opposite side), Gering formation, Scotts Bluff County, Nebraska; *Merycoides giganteus*, new species, holotype, F:A.M. 33316, Monroe Creek formation, Niobrara County, Wyoming; *Promesoreodon scanloni*, new species, holotype, F:A.M. 45329 (zygomatic arch, posterior pillar of orbit, and M³ from opposite side), Whitney member of Brule formation, Washabaugh County, South Dakota. $\times \frac{1}{2}$.

FIG. 22. Dorsal views of skulls of *Merycoides cursor* Douglass, holotype, C.M. 1222, Jefferson County, Montana; *Merycoides nebraskensis blairi*, new subspecies, holotype, F:A.M. 42306, Monroe Creek formation, Niobrara County, Wyoming; *Merycoides nebraskensis*, new species, holotype, F:A.M. 33363, Gering formation, Scotts Bluff County, Nebraska; *Merycoides giganteus*, new species, holotype, F:A.M. 33316, Monroe Creek formation, Niobrara County, Wyoming; *Promesoreodon scanloni*, new species, holotype, F:A.M. 45329 (zygomatic arch and posterior pillar of orbit from opposite side), Whitney member of Brule formation, Washabaugh County, South Dakota. $\times \frac{1}{2}$.

FIG. 23. Ventral views of skulls of *Merycoides cursor* Douglass, holotype, C.M. 1222, Jefferson County, Montana; *Merycoides nebraskensis blairi*, new subspecies, holotype, F:A.M. 42306 (P¹ from opposite side), Monroe Creek formation, Niobrara

County, Wyoming; *Merycoides nebraskensis*, new species, holotype, F:A.M. 33363 (I¹ and I² from opposite side), Gering formation, Scotts Bluff County, Nebraska; *Merycoides giganteus*, new species, holotype, F:A.M. 33316, Monroe Creek formation, Niobrara County, Wyoming; *Promesoreodon scanloni*, new species, holotype, F:A.M. 45329 (zygomatic arch, posterior pillar of orbit, and M³ from opposite side), Whitney member of Brule formation, Washabaugh County, South Dakota. $\times \frac{1}{2}$.

FIG. 24. Mandibular rami of *Merycoides cursor* Douglass, holotype, C.M. 1222, Jefferson County, Montana; *Merycoides nebraskensis*, new species, holotype, F:A.M. 33363 (I₁ from opposite side), Gering formation, Scotts Bluff County, Nebraska; *Merycoides giganteus*, new species, referred, F:A.M. 44923, Monroe Creek formation, Niobrara County, Wyoming; *Promesoreodon scanloni*, new species, holotype, F:A.M. 45329 (M₂ and posterior of ramus from opposite side), Whitney member of Brule formation, Washabaugh County, South Dakota. $\times \frac{1}{2}$.

FIG. 25. *Promerycochoerus* Douglass, *Promerycochoerus* (*Pseudopromerycochoerus*), new subgenus, *Mesoreodon* Scott, and *Promesoreodon*, new genus, comparison of humeri, radii, ulnae, and metacarpals. A. *Promerycochoerus carrikeri* (Peterson). B. *P. latidens* Thorpe. C. *P. superbus* (Leidy). D. *P. (P.) montanus* (Cope). E. *P. (P.) minor pygmyus* (Loomis). F. *Mesoreodon chelonys* Scott, not illustrated. G. *M. cheeki* (Schlaikjer). H. *M. cheeki scotti* (Schlaikjer). I. *M. megalodon* Peterson. J. *M. megalodon sweeti*, new subspecies. K. *Promesoreodon scanloni*, new species. $\times \frac{1}{2}$.

FIG. 26. *Promerycochoerus* Douglass, *Promerycochoerus* (*Pseudopromerycochoerus*), new subgenus, and *Mesoreodon* Scott, comparison of femora, tibiae, calcanea, astragali, and metatarsals. A. *Promerycochoerus carrikeri* Peterson. B. *P. latidens* Thorpe. C. *P. superbus* (Leidy). D. *P. (P.) montanus* (Cope). E. *P. (P.) minor pygmyus* (Loomis). F. *Mesoreodon chelonys* Scott. G. *M. cheeki* (Schlaikjer), not illustrated. H. *M. cheeki scotti* (Schlaikjer). I. *M. megalodon* Peterson. J. *M. megalodon sweeti*, new subspecies. $\times \frac{1}{2}$.

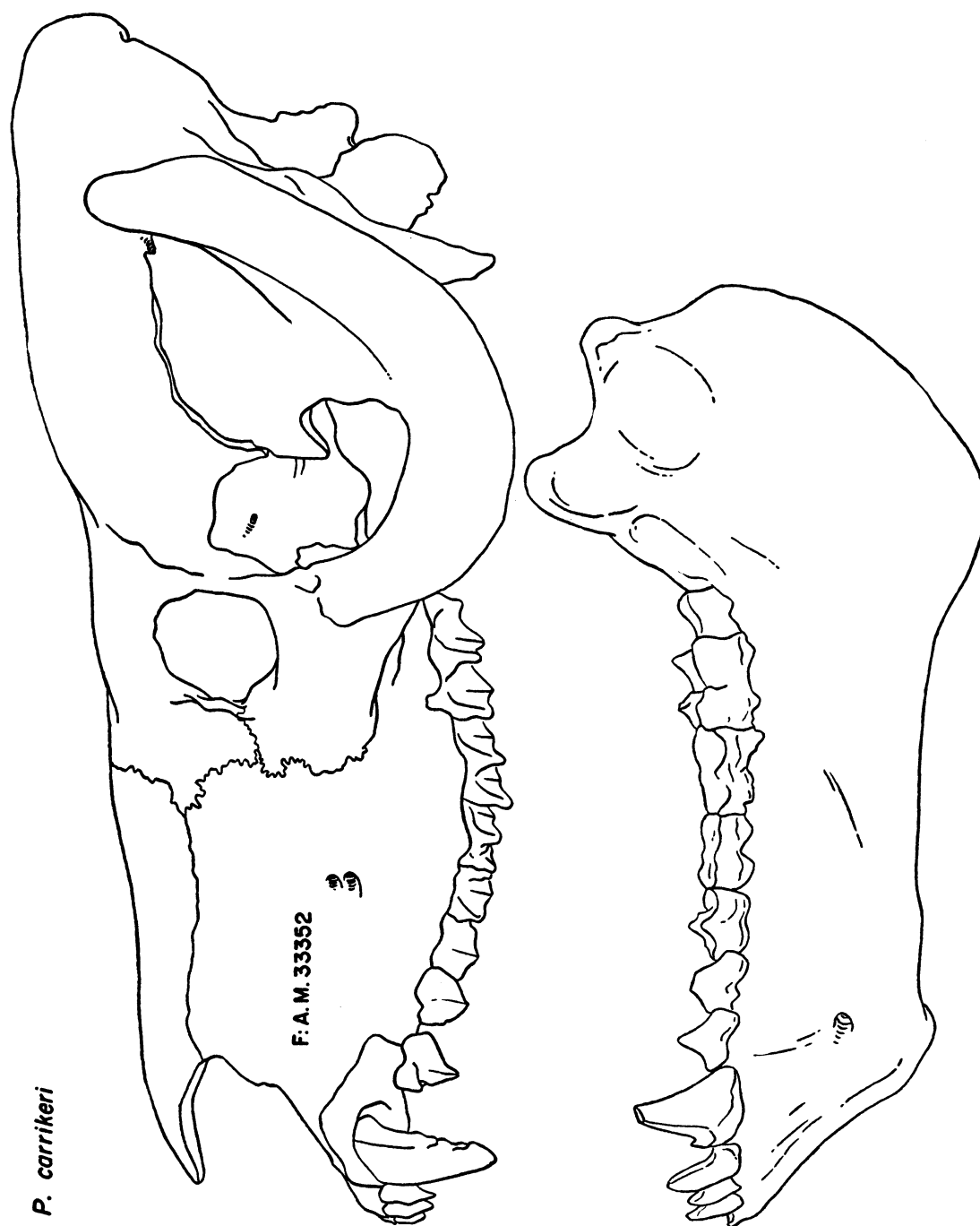
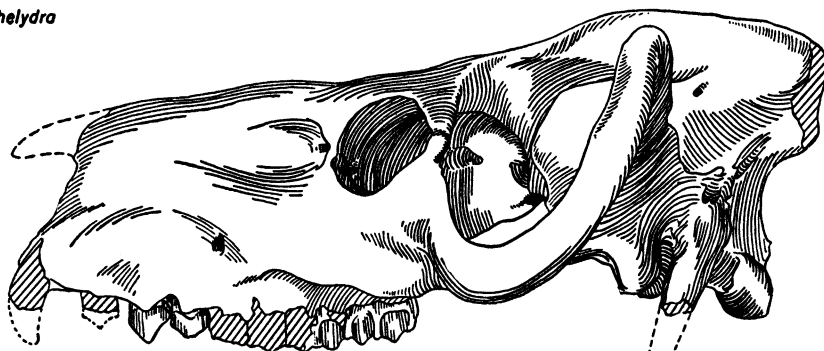


FIG. 1. *Promerycochoerus carrikeri* Peterson, referred, F.A.M. 33352. (See p. 166.) $\times \frac{1}{2}$.

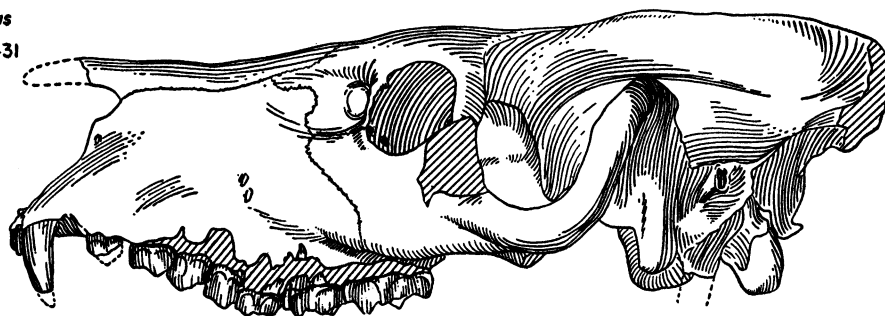
P. superbus chelydra

A. M. 7430



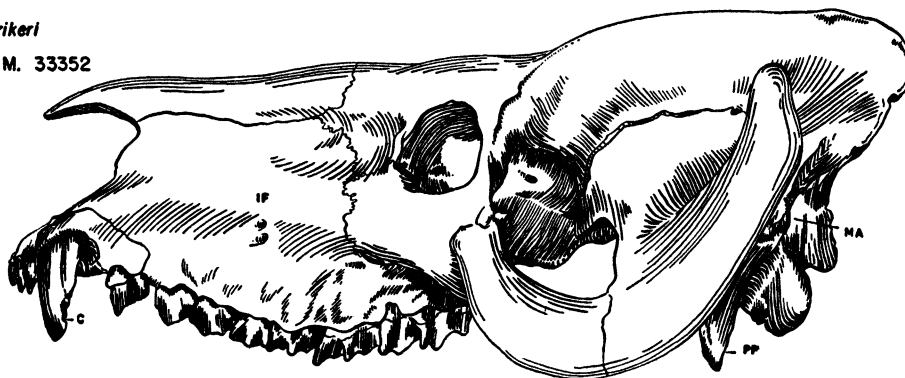
P. superbus

A. M. 7431



P. carrikeri

F. A. M. 33352



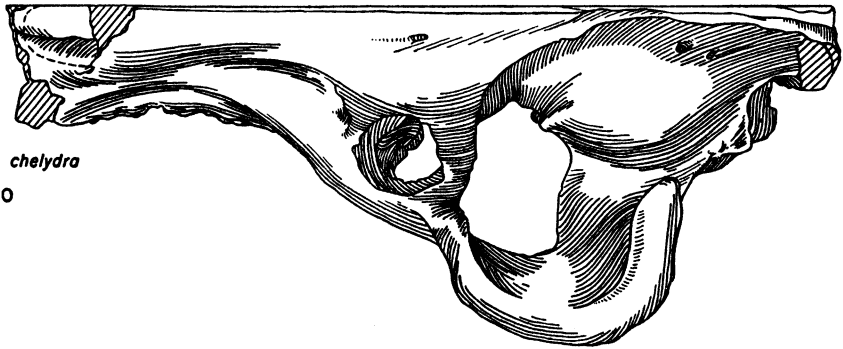
P. latidens

A. M. 7442

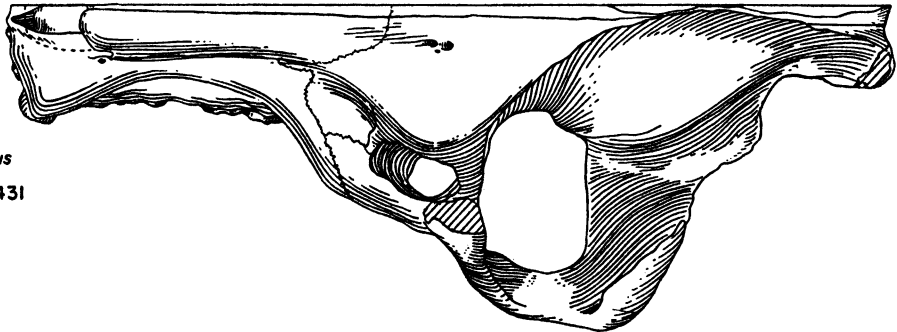


FIG. 2. *Promerycochoerus*, three species and one subspecies, holotype, A.M. 7430, and referred, A.M. 7431, F:A.M. 33352, and A.M. 7442. (See p. 166.) $\times \frac{1}{2}$.

P. superbus chelydra
A. M. 7430



P. superbus
A. M. 7431



P. carrikeri
F:A.M. 33352



P. latidens
A. M. 7442

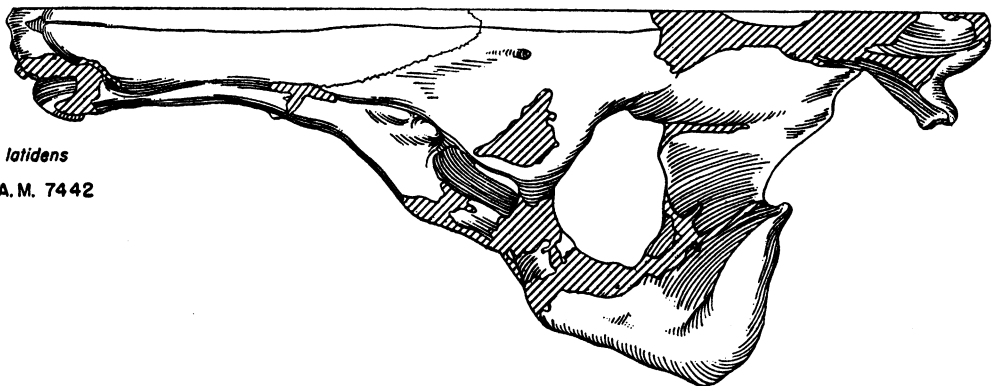
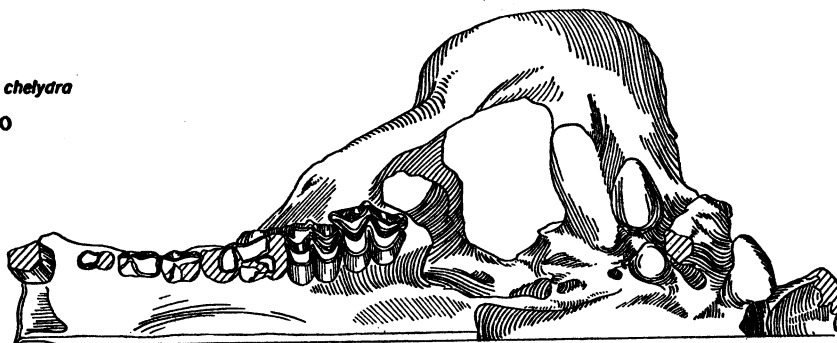


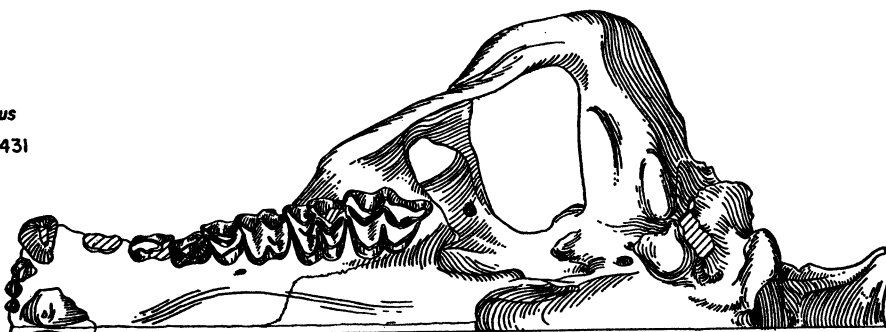
FIG. 3. *Promerychochoerus*, three species and one subspecies, holotype, A.M. 7430, and referred, A.M. 7431, F:A.M. 33352, and A.M. 7442. (See p. 166.) $\times \frac{1}{3}$.

P. superbus chelydra

A.M. 7430

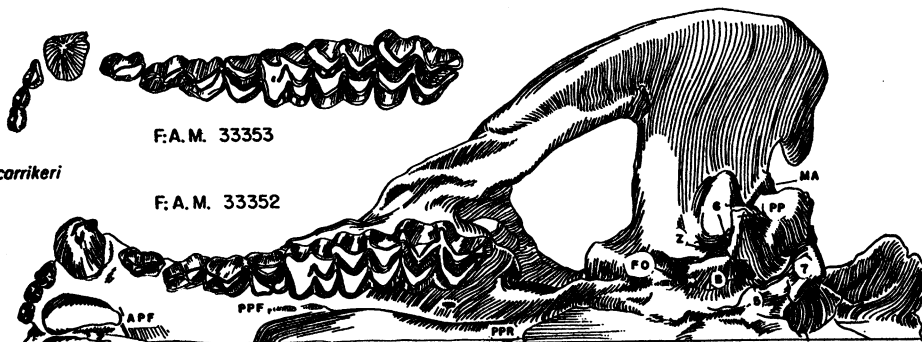
*P. superbus*

A.M. 7431

*P. corrikeri*

F.A.M. 33353

F.A.M. 33352

*P. latidens*

A.M. 7442

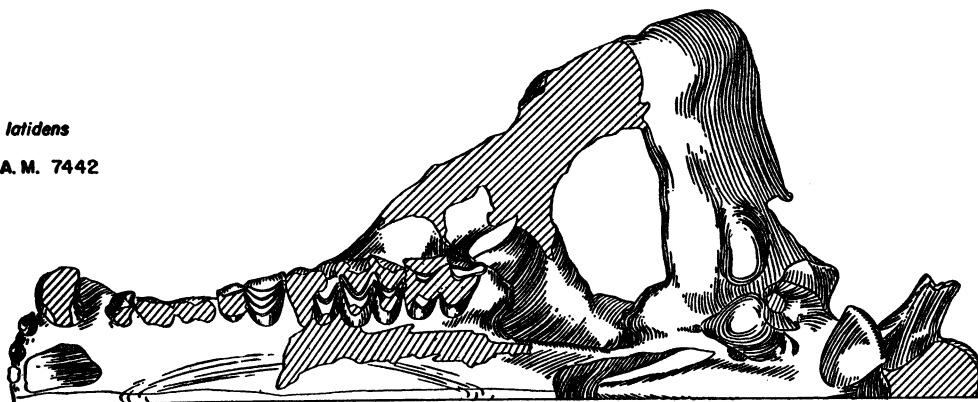
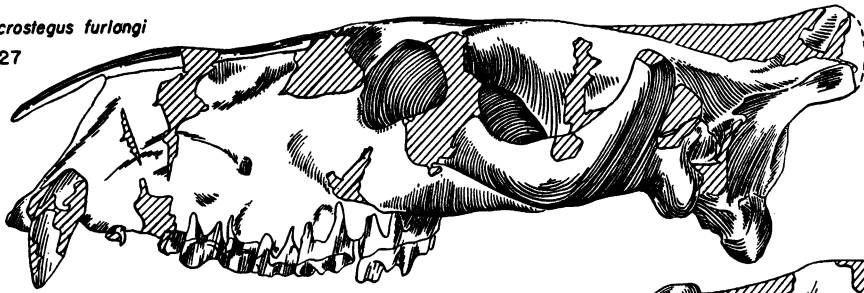


FIG. 4. *Promerycochoerus*, three species and one subspecies, holotype, A.M. 7430, and referred, A.M. 7431, F.A.M. 33352 and 33353, and A.M. 7442. (See p. 166.) $\times \frac{1}{3}$.

P. (Parapromerycochoerus) barbouri
F. A. M. 33315



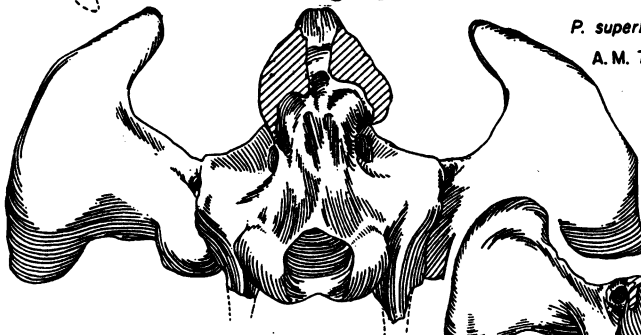
P. (P.) macrostegus furlongi
C. I. T. 1727



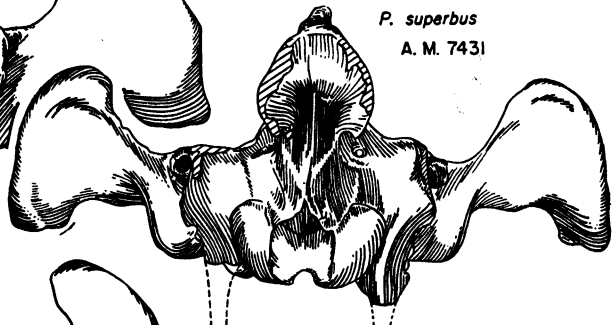
P. (P.) macrostegus
A. M. 7444



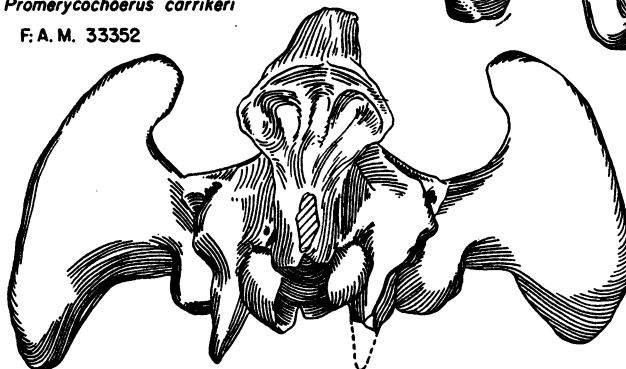
P. superbus chelydra
A. M. 7430



P. superbus
A. M. 7431



Promerycochoerus carrikeri
F. A. M. 33352



P. carrikeri
F. A. M. 33355

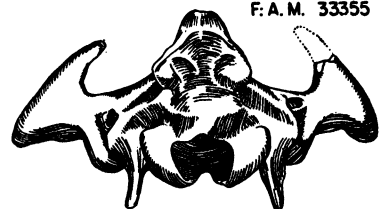


FIG. 5. *Promerycochoerus* (*Parapromerycochoerus*), two species and one subspecies, holotypes, F:A.M. 33315, C.I.T. 1727, and A.M. 7444; *Promerycochoerus*, two species and one subspecies, holotype, A.M. 7430, and referred, A.M. 7431, and F:A.M. 33352 and 33355. (See p. 166.) $\times \frac{1}{2}$.

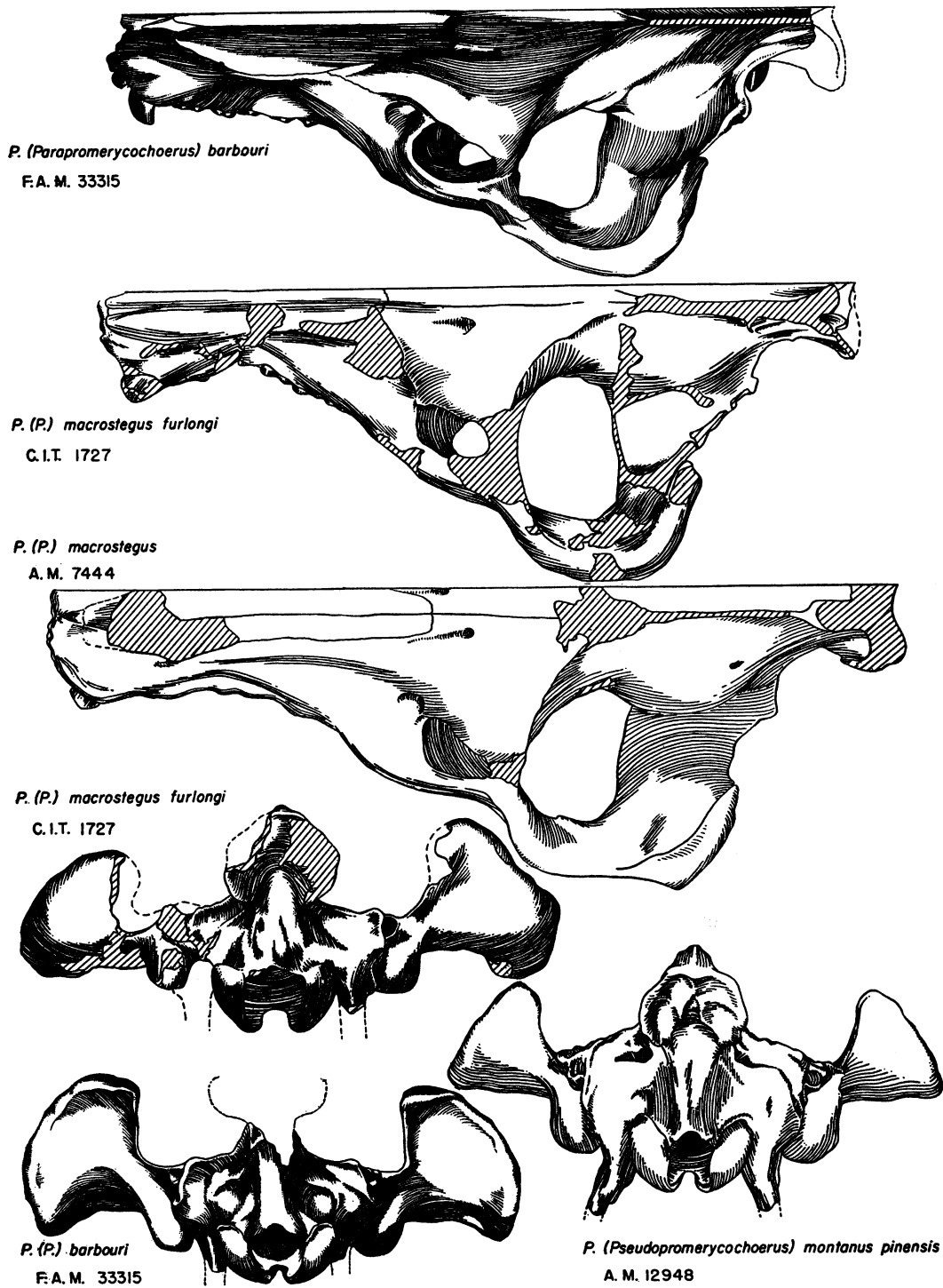
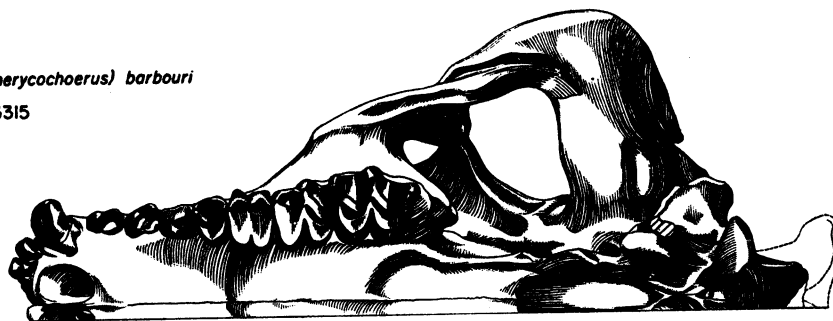
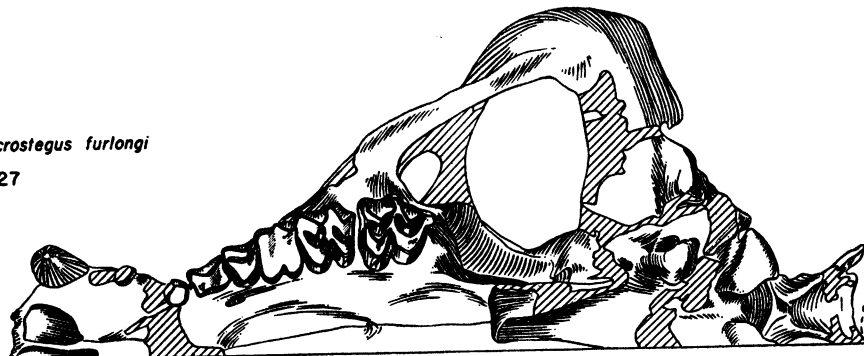


FIG. 6. *Promerycochoerus* (*Parapromerycochoerus*), two species and one subspecies, holotypes, F.A.M. 33315, C.I.T. 1727, and A.M. 7444; *Promerycochoerus* (*Pseudopromerycochoerus*), one subspecies, holotype, A.M. 12948. (See p. 166.) $\times \frac{1}{3}$.

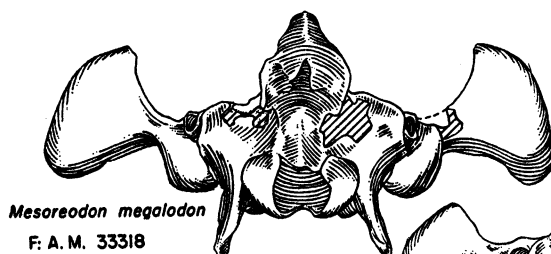
P. (Parapromerycochoerus) barbouri
F. A. M. 33315



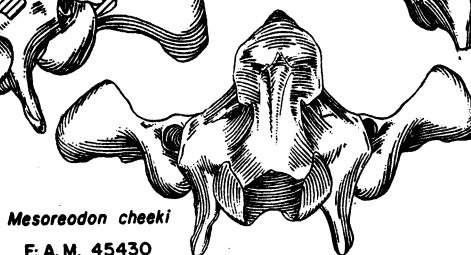
P. (P.) macrostegus furlongi
C. I. T. 1727



P. (P.) macrostegus
A. M. 7444



Mesoreodon megalodon
F. A. M. 33318



Mesoreodon cheeki
F. A. M. 45430



Merycoides nebraskensis
F. A. M. 33363

FIG. 7. *Promerycochoerus* (*Parapromerycochoerus*), two species and one subspecies, holotypes, F:A.M. 33315, C.I.T. 1727, and A.M. 7444; *Mesoreodon*, two species, referred, F:A.M. 33318 and 45430; *Merycoides*, one species, holotype, F:A.M. 33363. (See p. 166.) $\times \frac{1}{2}$.

P. (Pseudopromerycochoerus) minor pygmyus

A. M. 12967

P. (P.) montanus

A. M. 7452 rev.

P. (P.) montanus

A. M. 21338 rev.

P. (P.) montanus pinensis

A. M. 12948

P. (P.) inflatus

Y. P. M. 10233 rev.

FIG. 8. *Promerycochoerus* (*Pseudopromerycochoerus*), three species and two subspecies, holotypes, A.M. 12967 and 12948, and Y.P.M. 10233, and referred, A.M. 7452 and 21338. (See p. 166.) $\times \frac{1}{2}$.

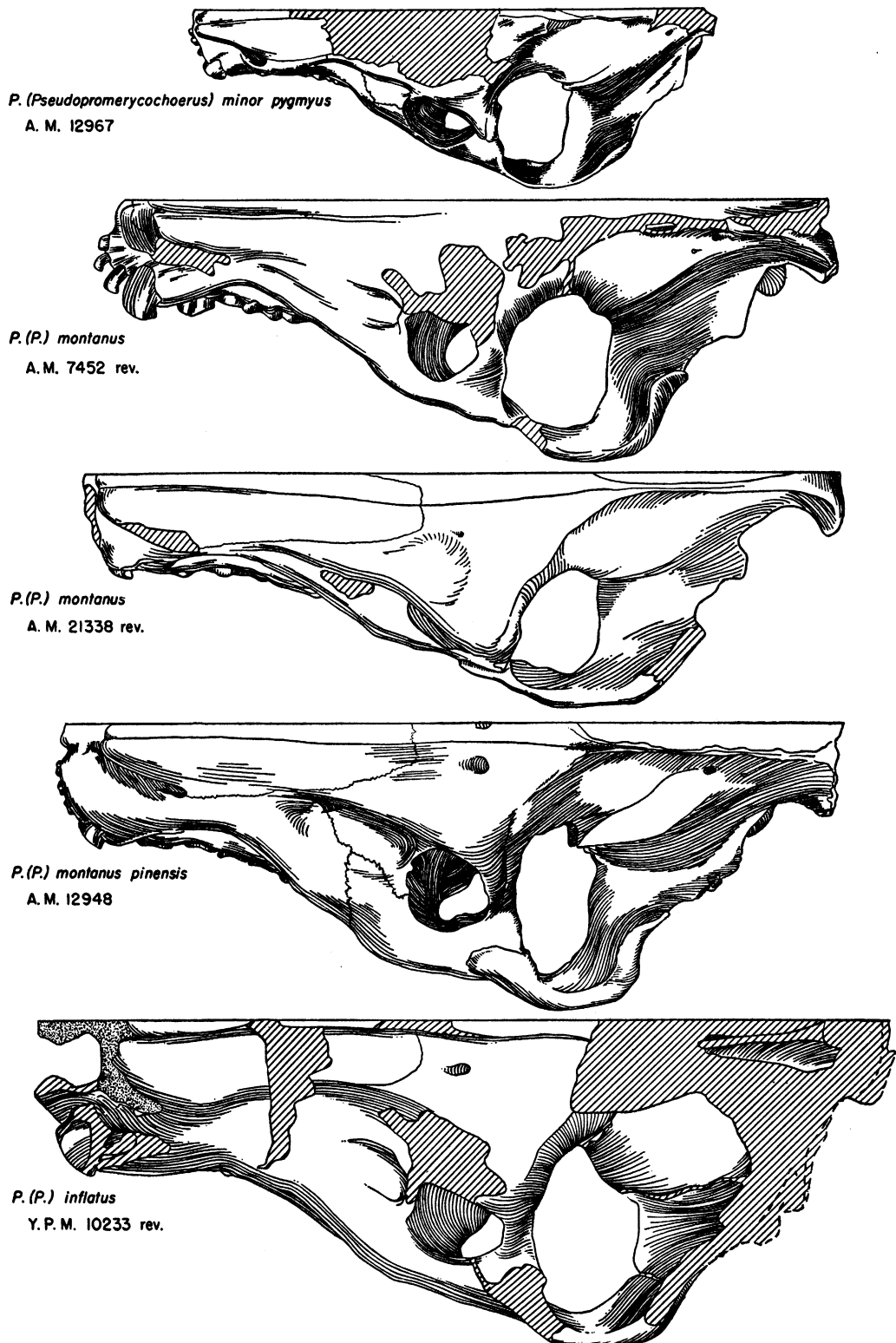
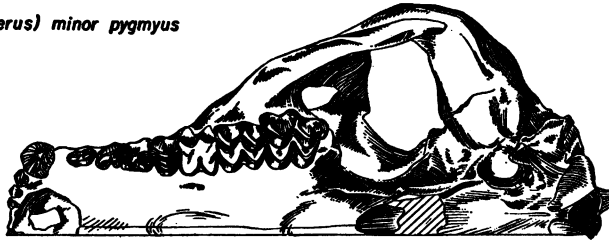


FIG. 9. *Promerycochoerus* (*Pseudopromerycochoerus*), three species and two subspecies, holotypes, A.M. 12967 and 12948, and Y.P.M. 10233, and referred, A.M. 7452 and 21338. (See p. 167.) $\times \frac{1}{3}$.

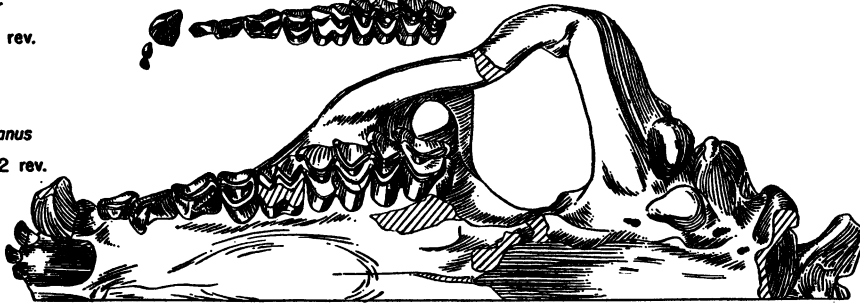
P. (Pseudopromerycochoerus) minor pygmyus
A. M. 12967



P. (P.) minor
C. M. 769 rev.



P. (P.) montanus
A. M. 7452 rev.



A. M. 8107

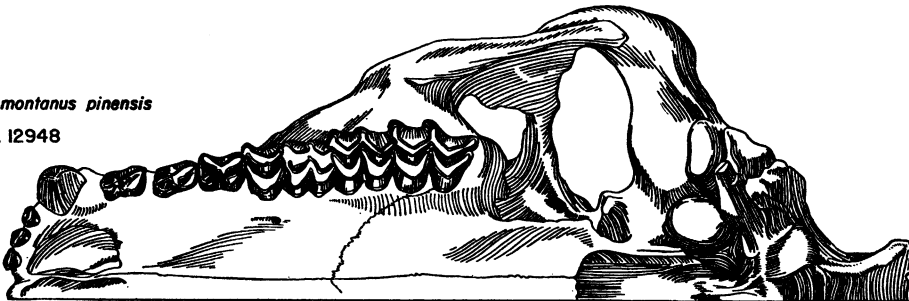


P. (P.) montanus

A. M. 21338 rev.



P. (P.) montanus pinensis
A. M. 12948



P. (P.) inflatus
Y. P. M. 10233 rev.

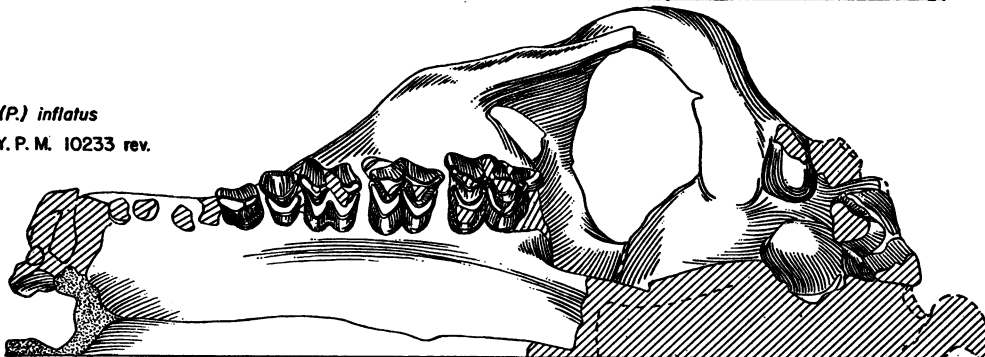


FIG. 10. *Promerycochoerus* (*Pseudopromerycochoerus*), four species and two subspecies, holotypes, A.M. 12967, C.M. 769, A.M. 8107 and 12948, and Y.P.M. 10233, and referred, A.M. 7452 and 21338. (See p. 167.) $\times \frac{1}{3}$.

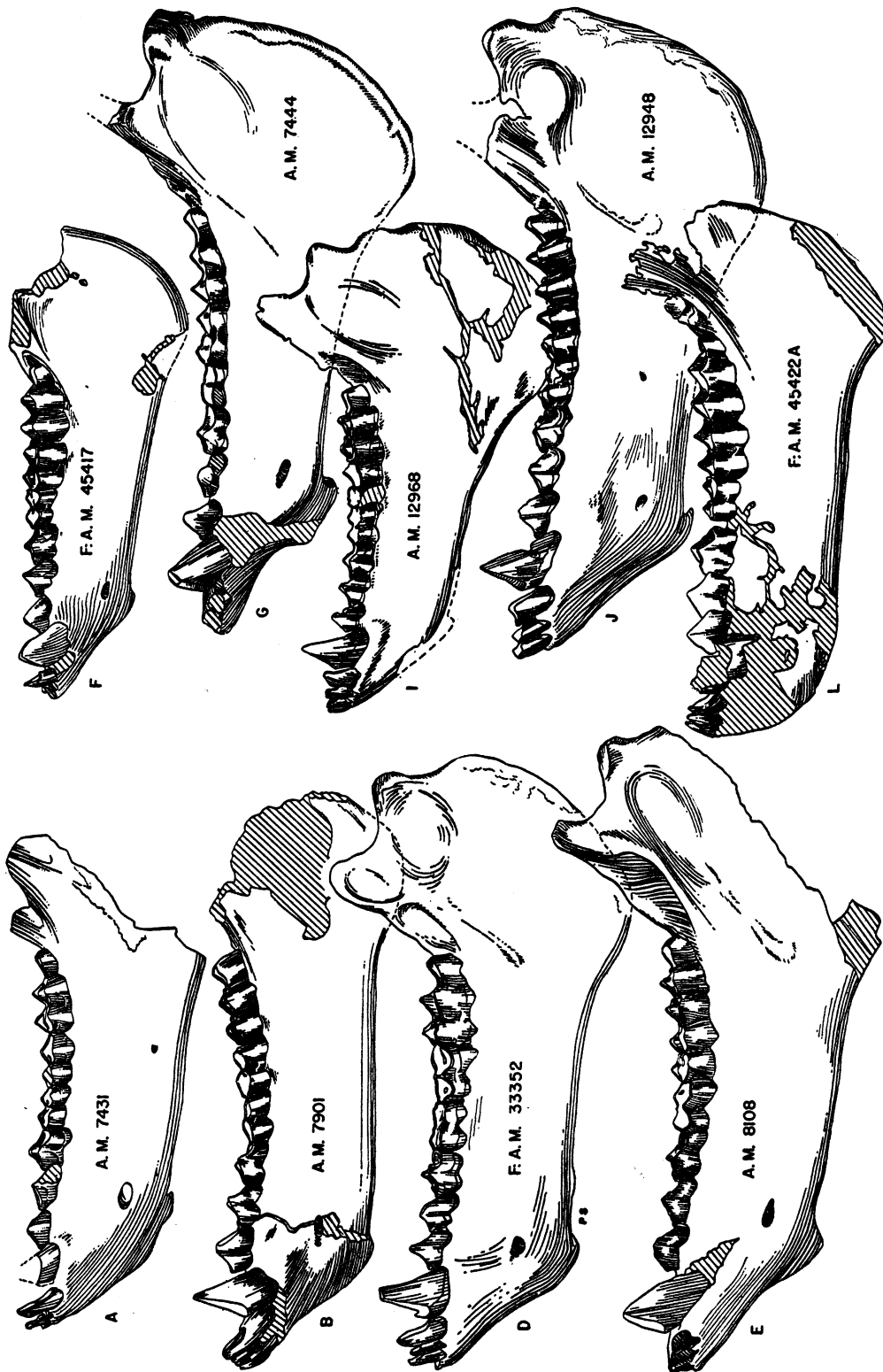


FIG. 11. *Promerycochoerus*, three species and one subspecies, referred, A.M. 7431 (A, *P. superbus*), A.M. 7901 (B, *P. superbus chelydra*), and F.A.M. 33352 (D, *P. carrikeri*); *Promerycochoerus* (*Parapromerycochoerus*), two species, holotype, A.M. 7444 (G, *P. (P.) macrostegus*) and referred, F.A.M. 45417 (F, *P. (P.) barbouri*); *Promerycochoerus* (*Pseudopromerycochoerus*), one species and two subspecies, holotype, A.M. 12948 (J, *P. (P.) monatanus pinensis*), and referred, A.M. 12968 (I, *P. (P.) minor pygmyus*) and F.A.M. 45422A (L, *P. (P.) montanus*). (See p. 167.) $\times \frac{1}{2}$.

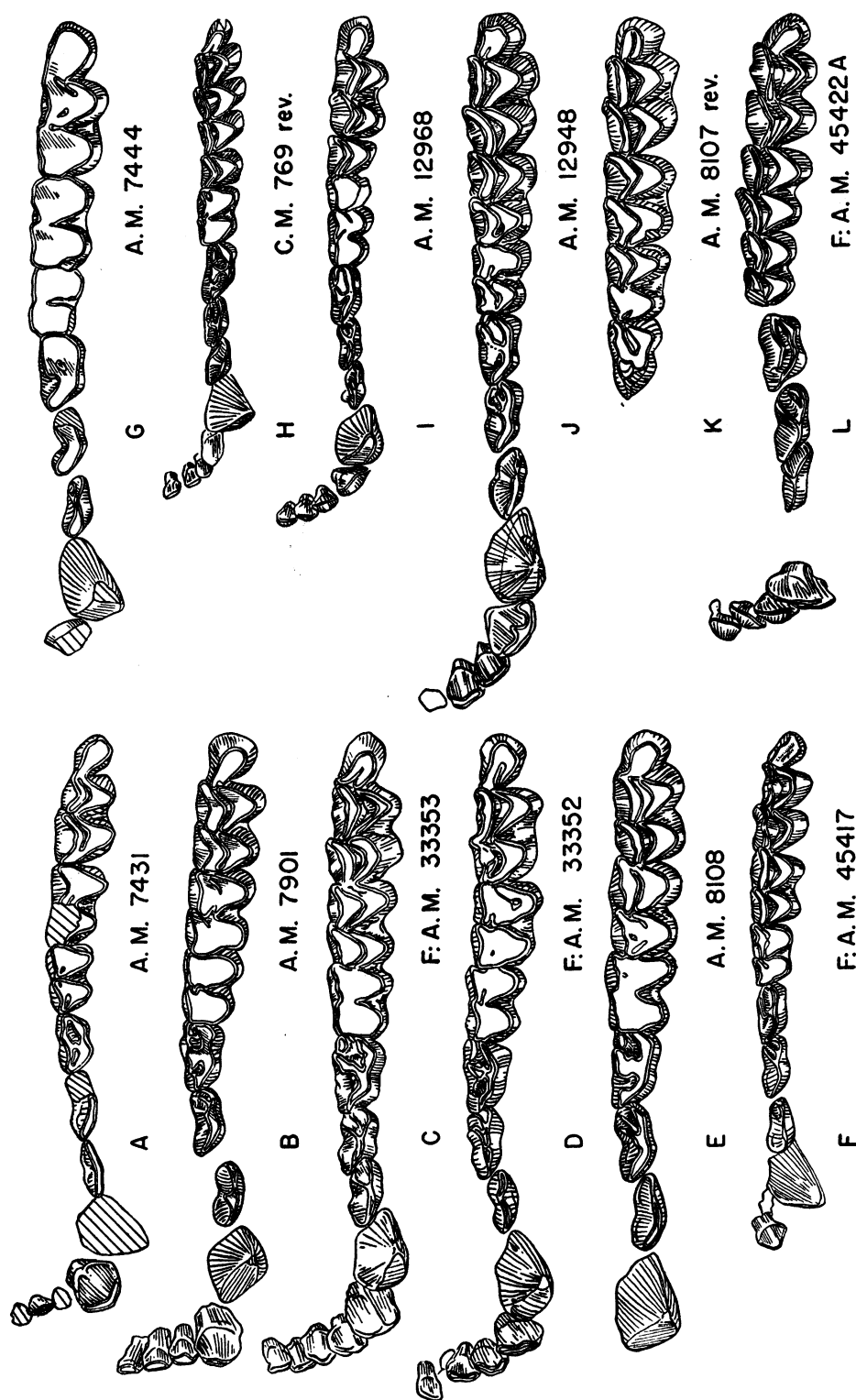


FIG. 12. *Promerycochoerus*, three species and one subspecies, referred, A.M. 7431 (A, *P. superbus*), A.M. 7901 (B, *P. superbus chelydra*), and F.A.M. 33353 and 33352 (C and D, *P. carrikeri*); *Promerycochoerus* (*Parapromerycochoerus*), two species, holotype, A.M. 7444 (G, *P. (P.) macrostegus*) and referred, F.A.M. 45417 (F, *P. (P.) barbouri*); *Promerycochoerus* (*Pseudopromerycochoerus*), two species and two subspecies, holotypes, C.M. 769 (H, *P. (P.) minor*), A.M. 8107 (K, *P. (P.) montanus*), and A.M. 12948 (J, *P. (P.) montanus pinensis*), and referred, A.M. 12968 (I, *P. (P.) minor pygmyus*) and F.A.M. 45422A (L, *P. (P.) montanus*). (See p. 167.) $\times \frac{1}{2}$.

P. carrikeri

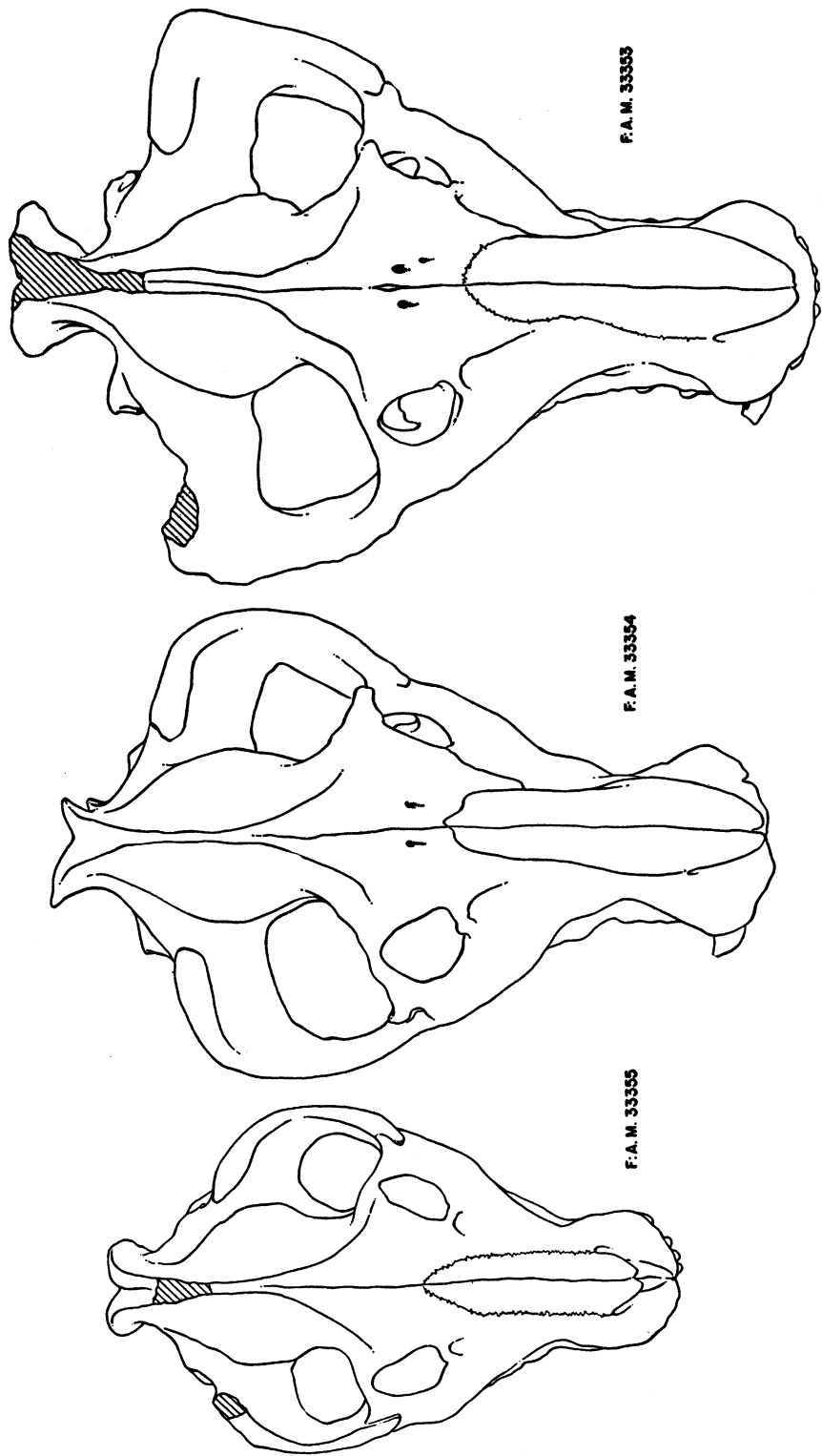


FIG. 13. *Promerycochoerus carrikeri* Peterson, referred, F.A.M. 33353, 33354, and 33355. (See p. 167.) $\times \frac{1}{4}$.

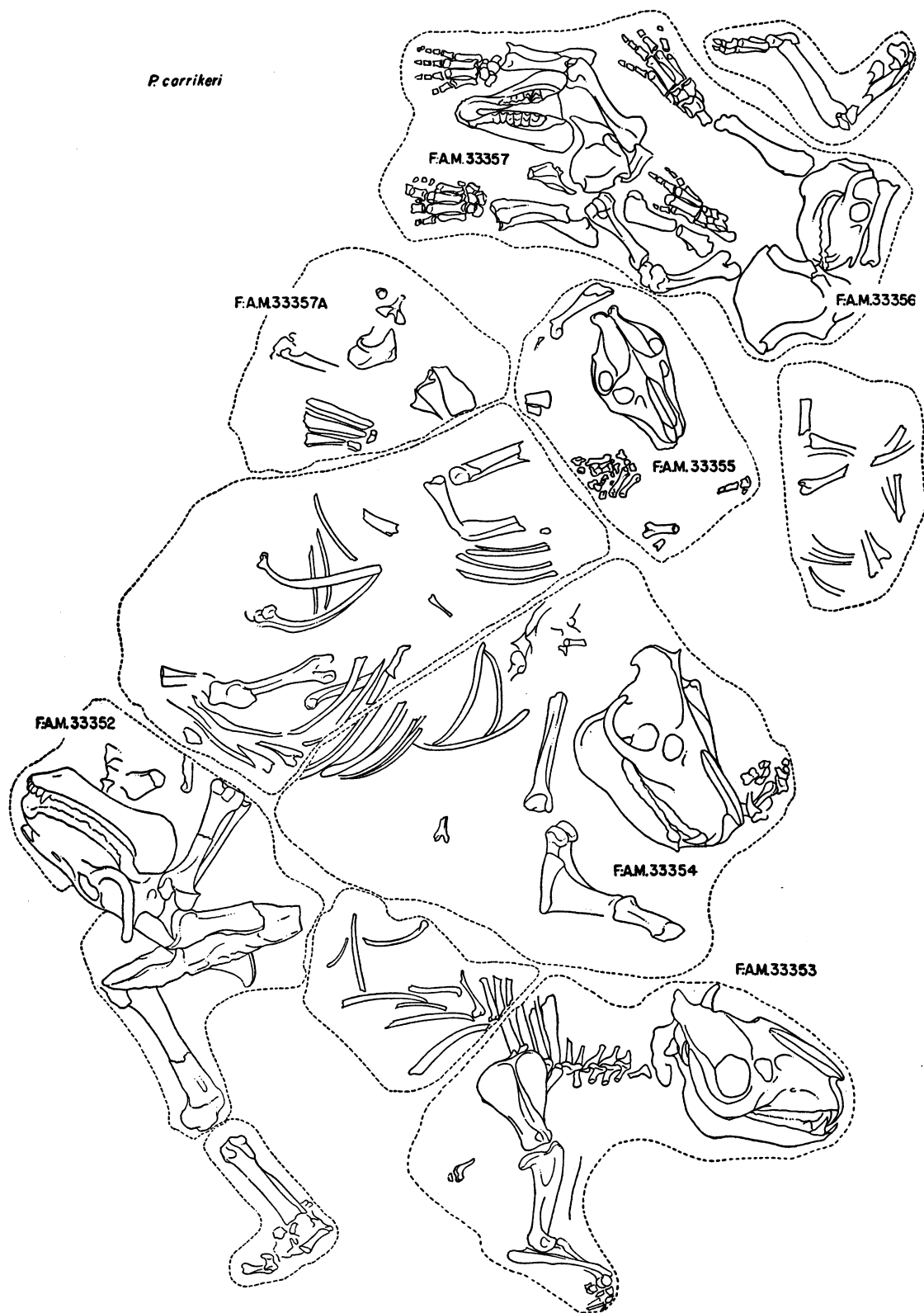
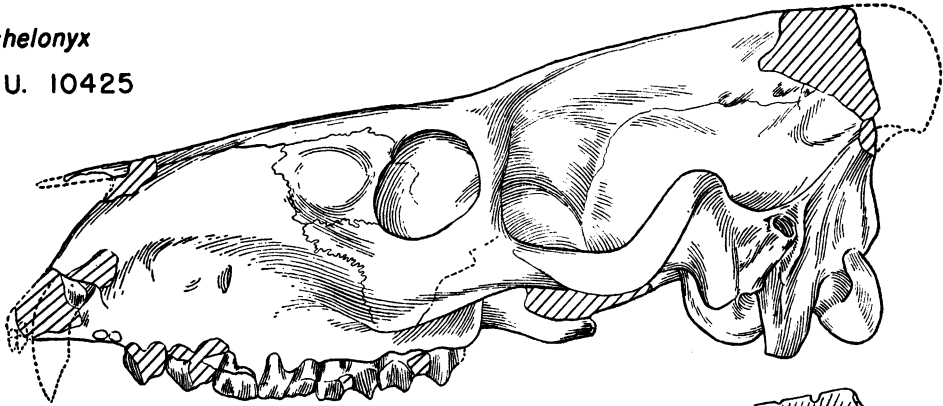


FIG. 14. *Promerycochoerus carrikeri* Peterson, referred, F:A.M. 33352, 33353, 33354, 33355, 33356, 33357, and 33357A. (See p. 167.)

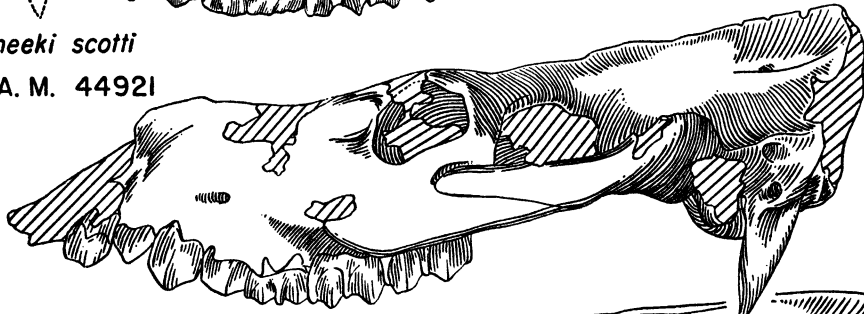
M. chelonyx

P. U. 10425



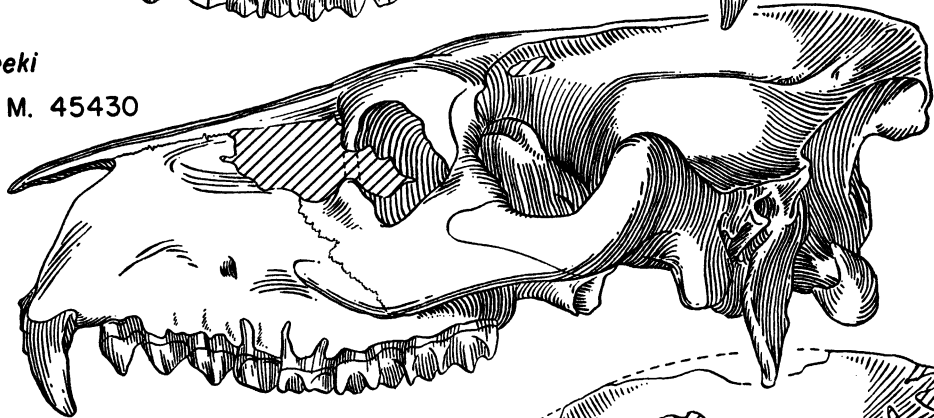
M. cheeki scotti

F: A. M. 44921



M. cheeki

F: A. M. 45430

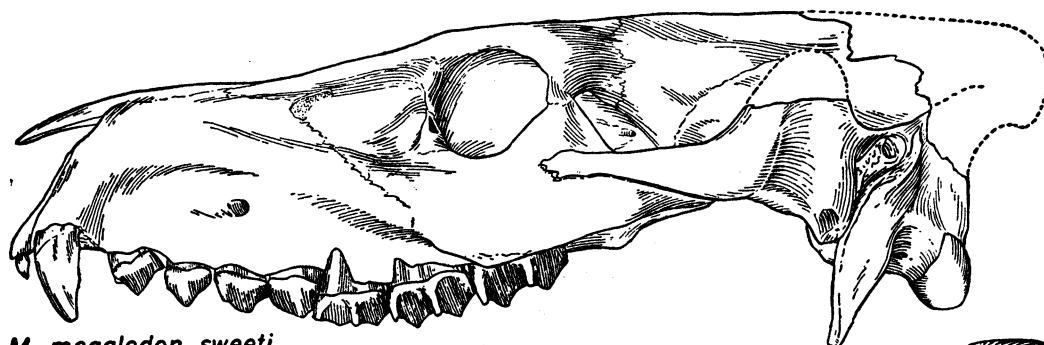


M. chelonyx wheeleri

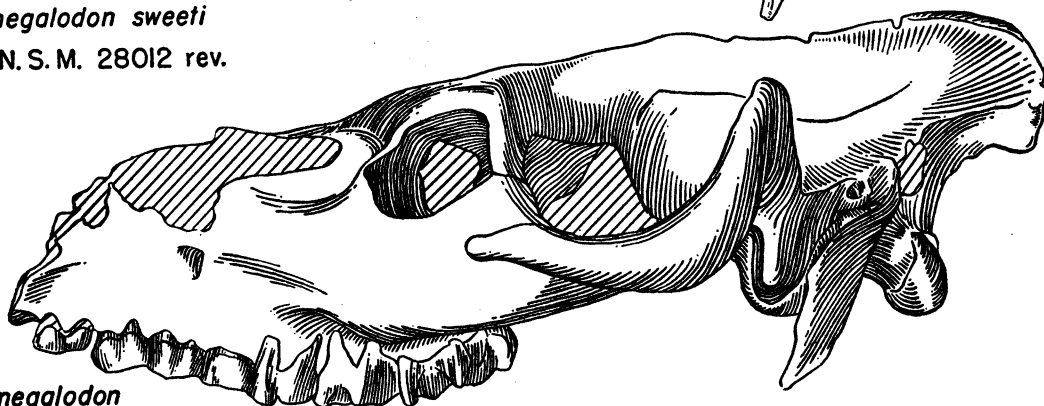
F: A. M. 45423



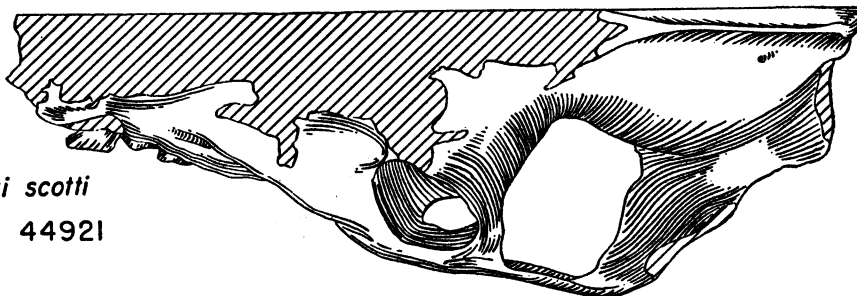
FIG. 15. *Mesoreodon*, two species and two subspecies, holotype. P.U. 10425, and referred, F:A.M. 44921, 45430, and 45423. (See p. 168.) $\times \frac{1}{2}$.



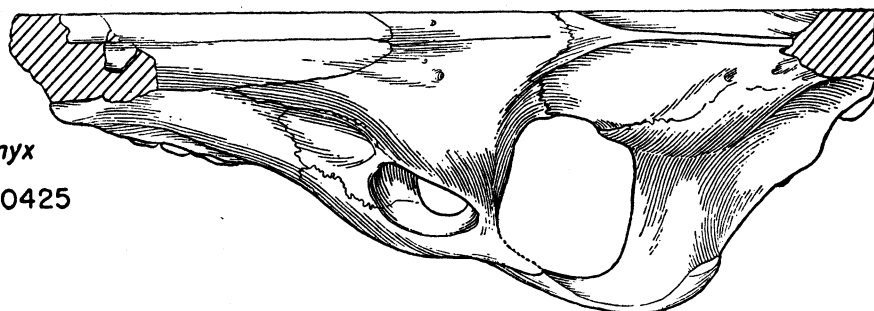
M. megalodon sweeti
U. N. S. M. 28012 rev.



M. megalodon
F: A. M. 33318



M. cheeki scotti
F: A. M. 44921



M. chelonyx
P. U. 10425

FIG. 16. *Mesoreodon*, two species and two subspecies, holotypes, U.N.S.M. 28012 and P.U. 10425, and referred, F:A.M. 33318 and 44921. (See p. 168.) $\times \frac{1}{2}$.

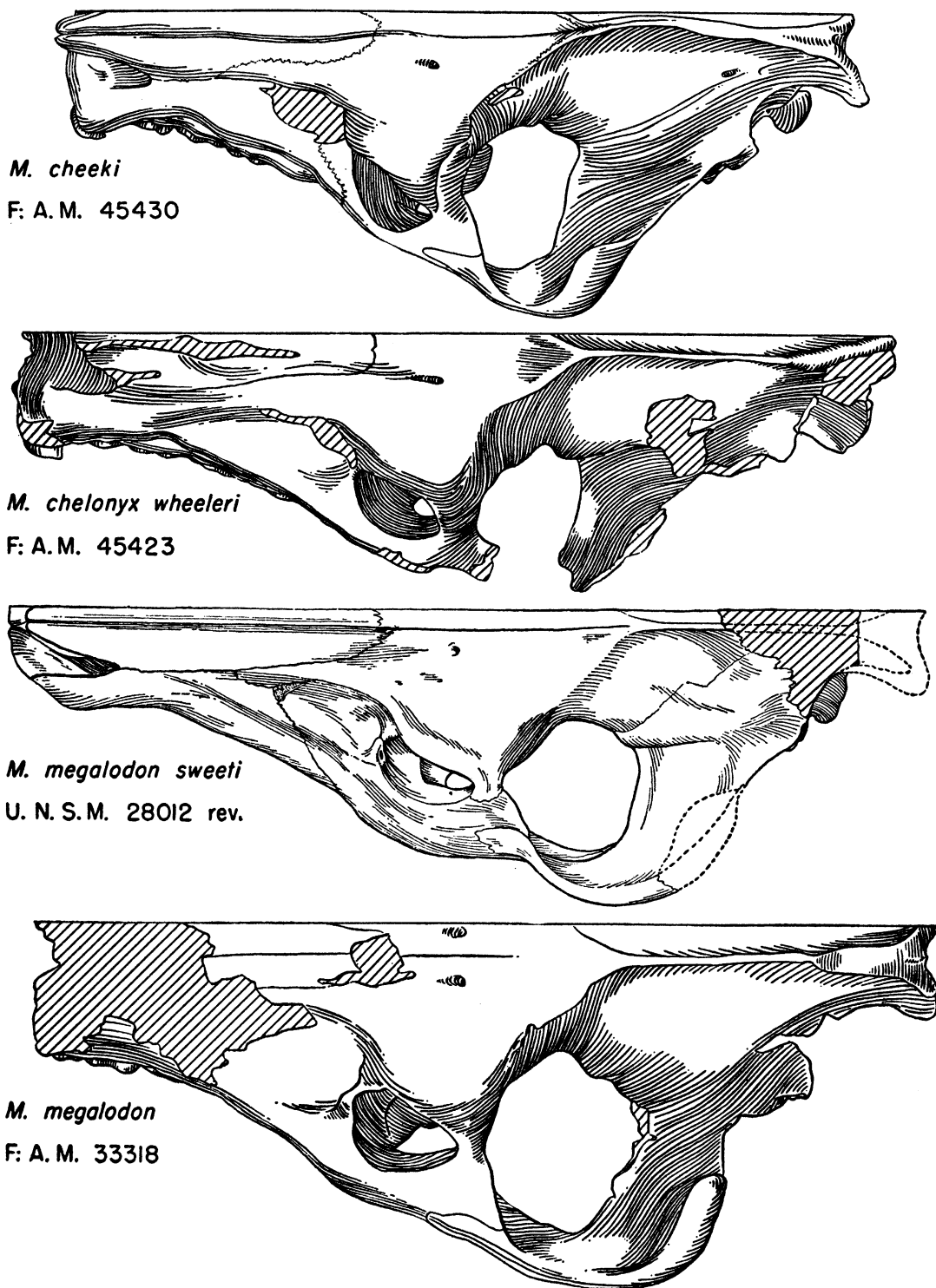


FIG. 17. *Mesoreodon*, two species and two subspecies, holotype, U.N.S.M. 28012, and referred, F:A.M. 45430, 45423, and 33318. (See p. 168.) $\times \frac{1}{2}$.

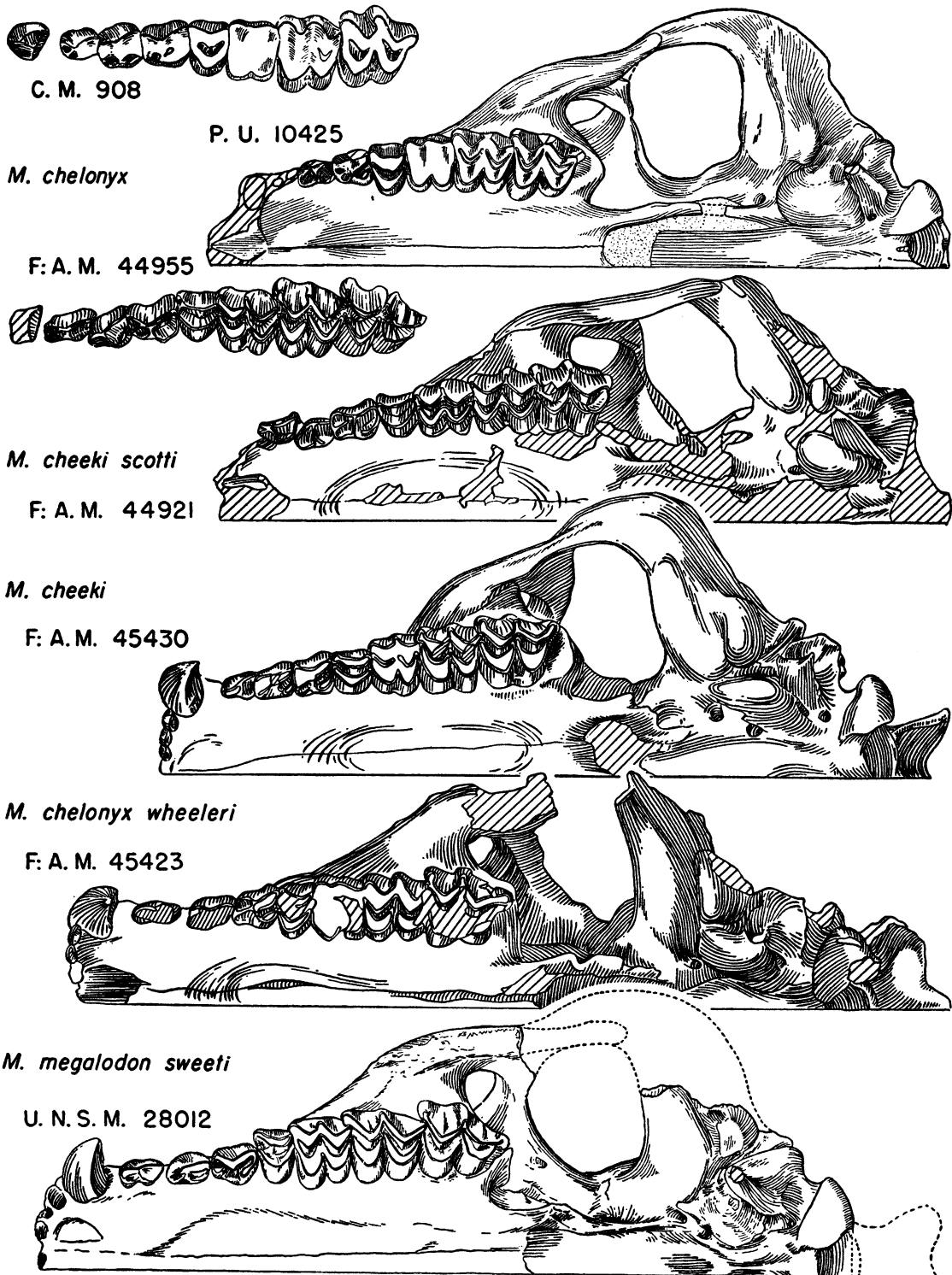


FIG. 18. *Mesoreodon*, two species and three subspecies, holotypes, P.U. 10425 and U.N.S.M. 28012, and referred, C.M. 908, F:A.M. 44955, 44921, 45430, and 45423. (See. p. 168.) $\times \frac{1}{2}$.

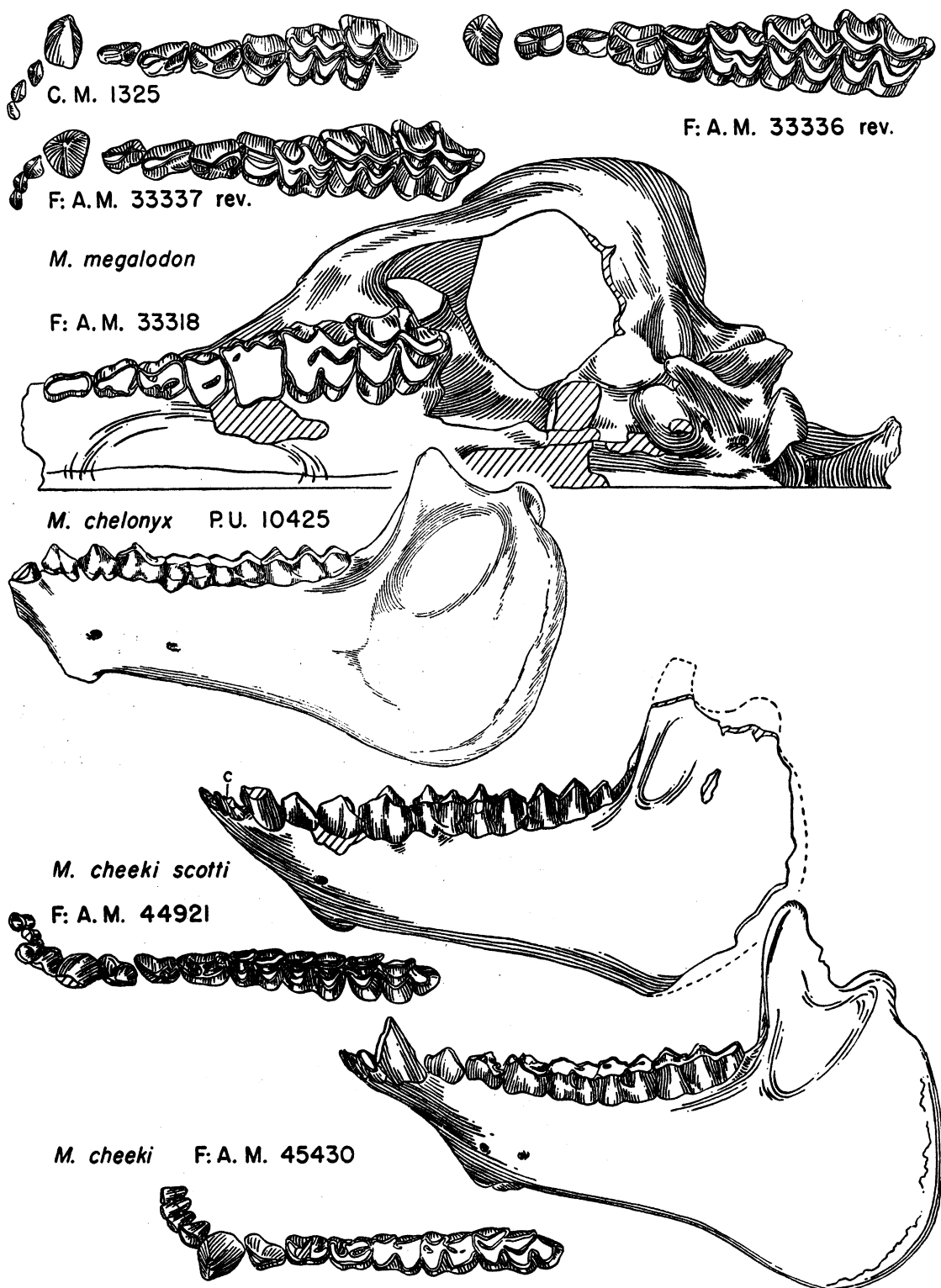
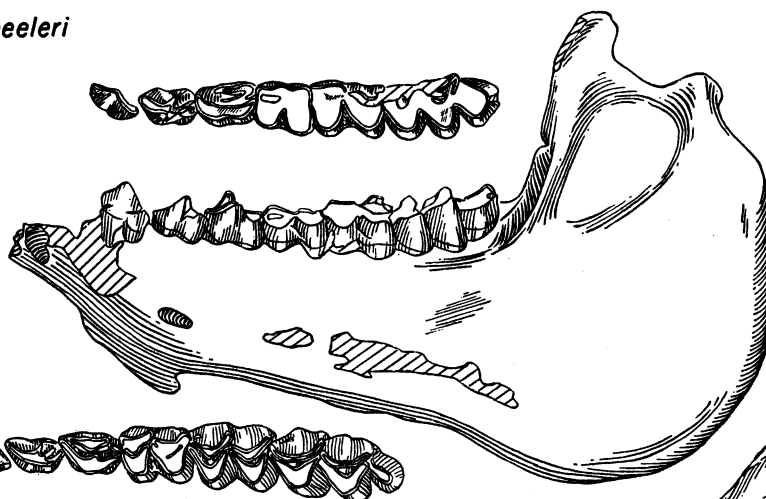


FIG. 19. *Mesoreodon*, three species and one subspecies, holotypes, C.M. 1325 and P.U. 10425, and referred, F:A.M. 33336, 33337, 33318, 44921, and 45430. (See p. 168.) $\times \frac{1}{2}$.

M. chelonyx wheeleri

F: A. M. 45423



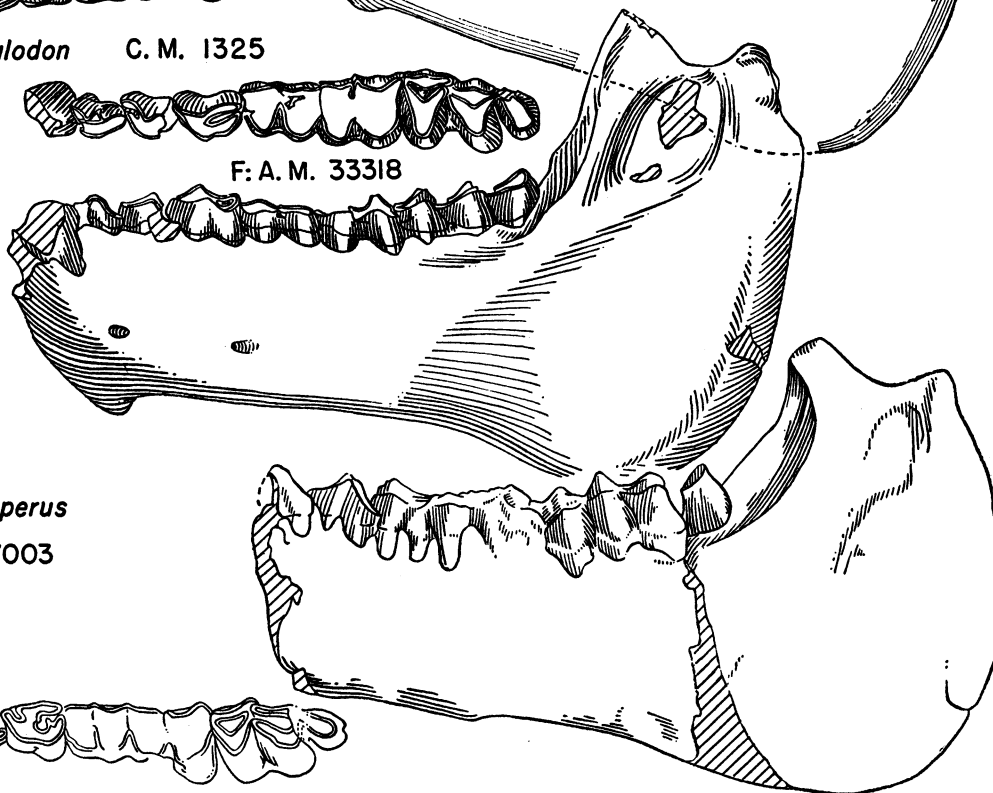
M. megalodon sweeti

U. N. S. M. 28012 rev.



M. megalodon C. M. 1325

F: A. M. 33318



?*M. hesperus*

U. C. 27003

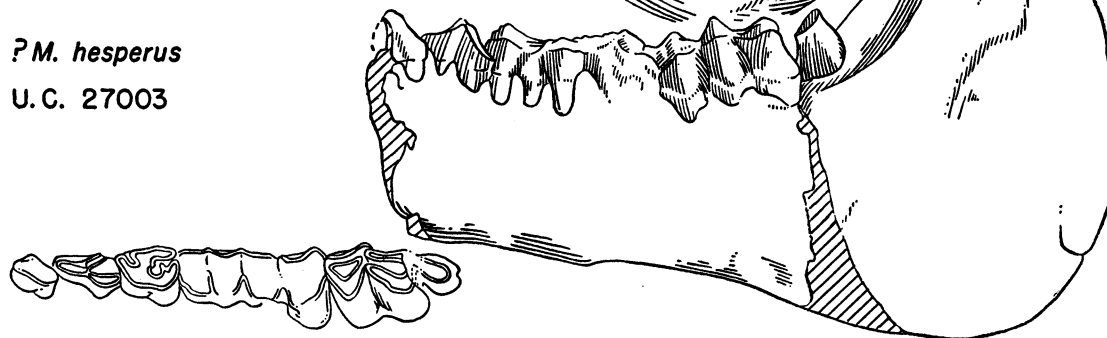
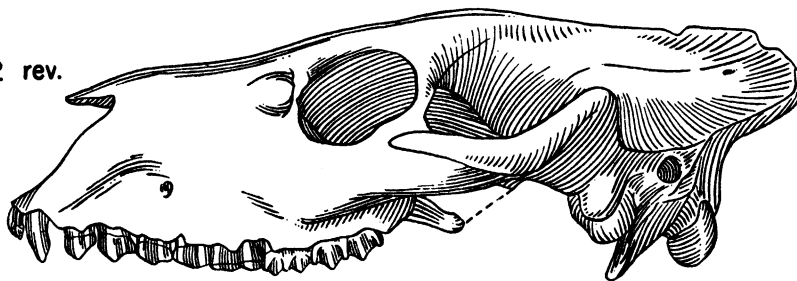


FIG. 20. *Mesoreodon*, two species and two subspecies, holotypes, U. N. S. M. 28012, C. M. 1325, and U. C. 27003, and referred, F: A. M. 45423 and 33318. (See p. 168.) $\times \frac{1}{2}$.

M. cursor

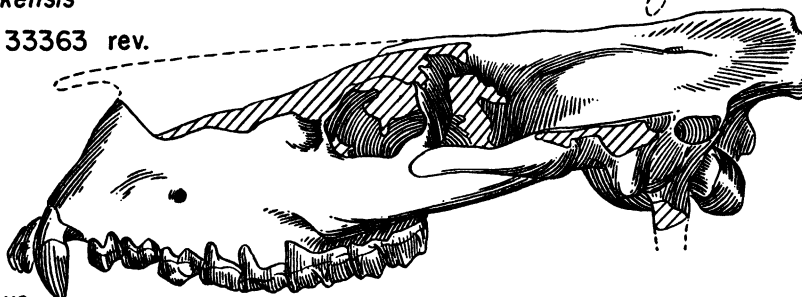
C. M. 1222 rev.

*M. nebraskensis blairi*

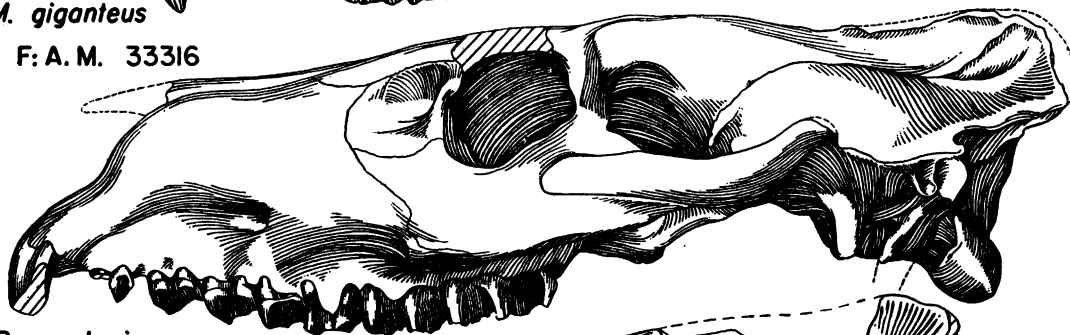
F:A.M. 45424

*M. nebraskensis*

F: A. M. 33363 rev.

*M. giganteus*

F: A. M. 33316

*P. scanloni*

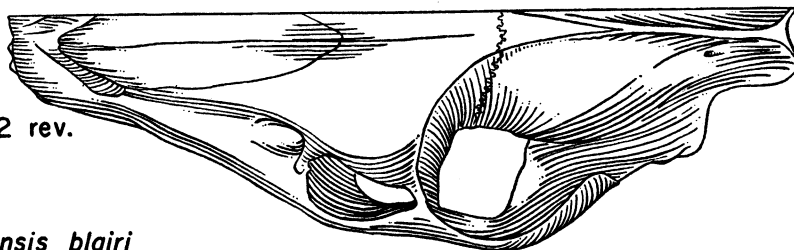
F: A. M. 45329



FIG. 21. *Merycoides*, three species and one subspecies, holotypes, C.M. 1222 and F:A.M. 33363 and 33316, and referred, F:A.M. 45424; *Promesoreodon*, one species, holotype, F:A.M. 45329. (See p. 168.) $\times \frac{1}{2}$.

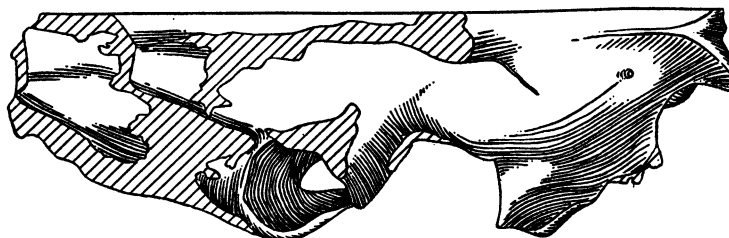
M. cursor

C.M. 1222 rev.

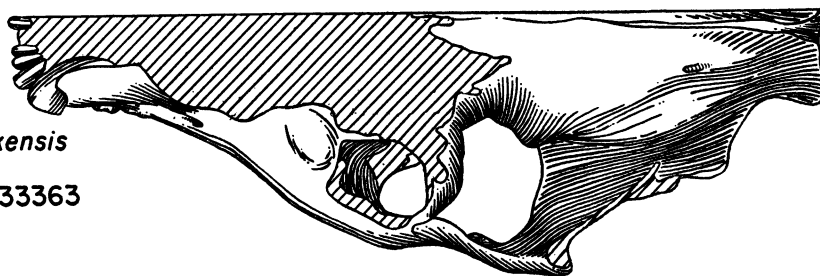
*M. nebraskensis blairi*

F: A.M. 42306

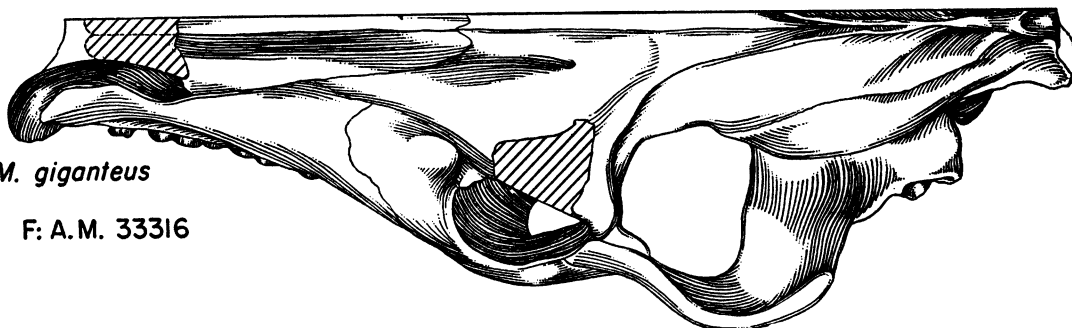
rev.

*M. nebraskensis*

F: A.M. 33363

*M. giganteus*

F: A.M. 33316

*P. scanloni*

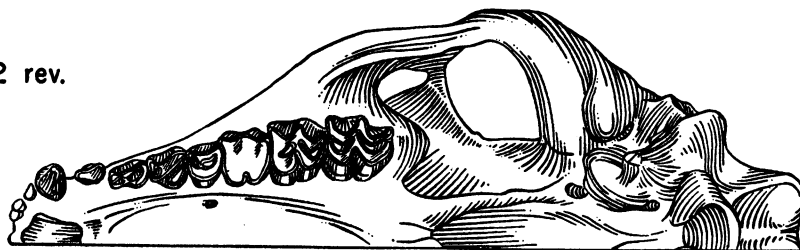
F: A.M. 45329



FIG. 22. *Merycoides*, three species and one subspecies, holotypes, C.M. 1222 and F:A.M. 42306, 33363, and 33316; *Promesoreodon*, one species, holotype, F:A.M. 45329. (See p. 168.) $\times \frac{1}{2}$.

M. cursor

C. M. 1222 rev.



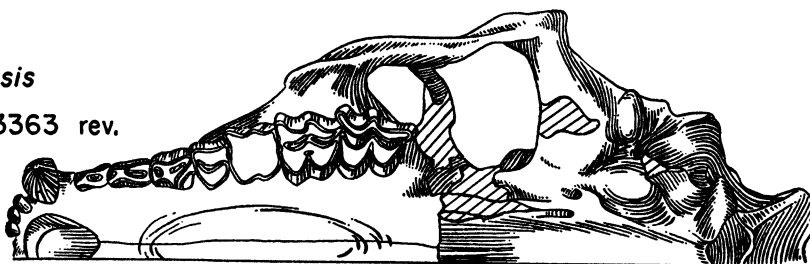
M. nebraskensis blairi

F: A. M. 42306 rev.



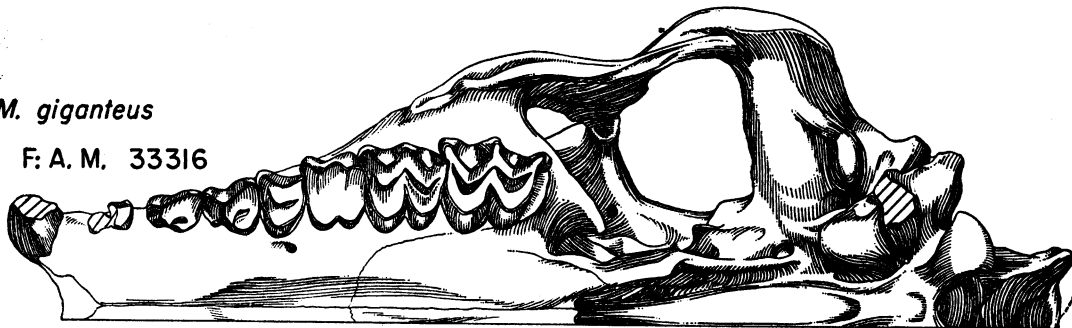
M. nebraskensis

F: A. M. 33363 rev.



M. giganteus

F: A. M. 33316



P. scanloni

F: A. M. 45329

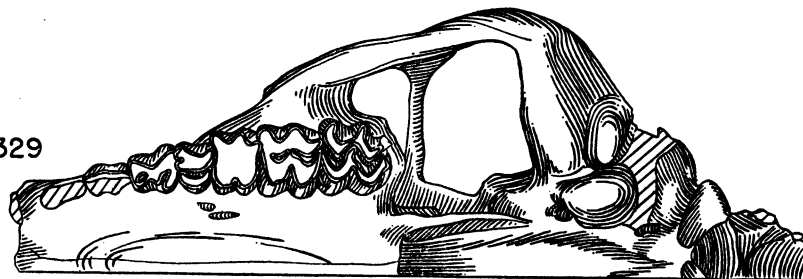
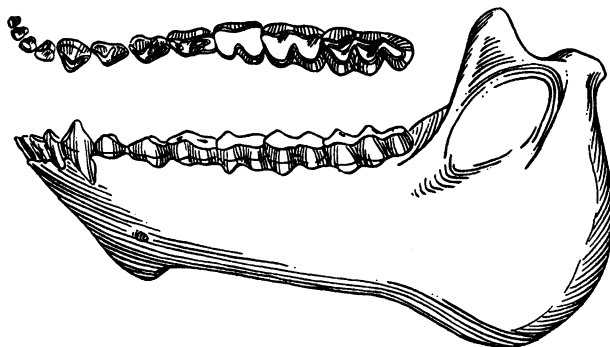


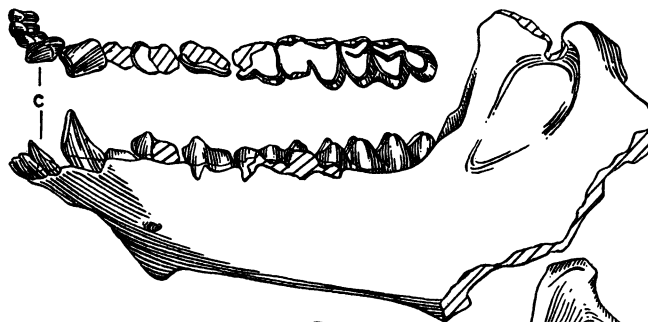
FIG. 23. *Merycoides*, three species and one subspecies, holotypes, C.M. 1222 and F:A.M. 42306, 33363, and 33316; *Promesoreodon*, one species, holotype, F:A.M. 45329. (See p. 168.) $\times \frac{1}{2}$.

M. cursor

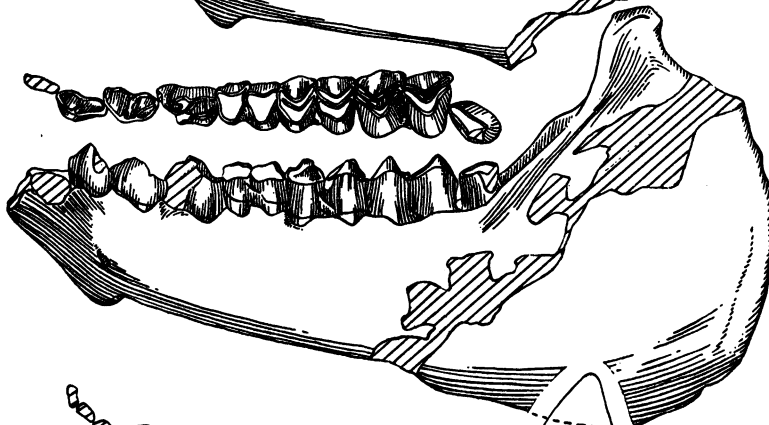
C.M. 1222 rev.

*M. nebraskensis*

F:A.M. 33363 rev.

*M. giganteus*

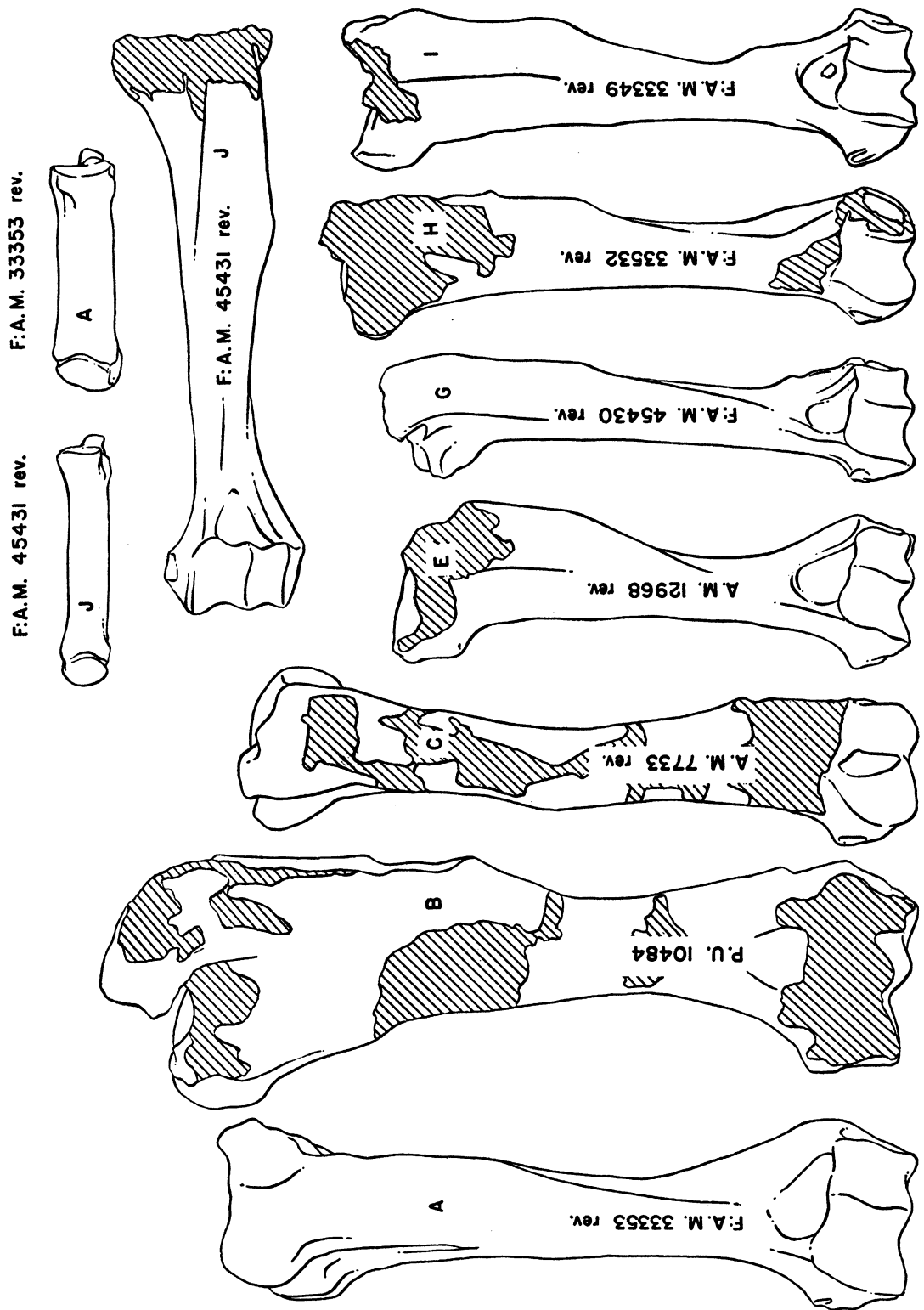
F:A.M. 44923

*P. scanloni*

F:A.M. 45329



FIG. 24. *Merycoides*, three species, holotypes, C.M. 1222 and F:A.M. 33363, and referred, F:A.M. 44923; *Promesoreodon*, one species, holotype, F:A.M. 45329. (See p. 169.) $\times \frac{1}{2}$.



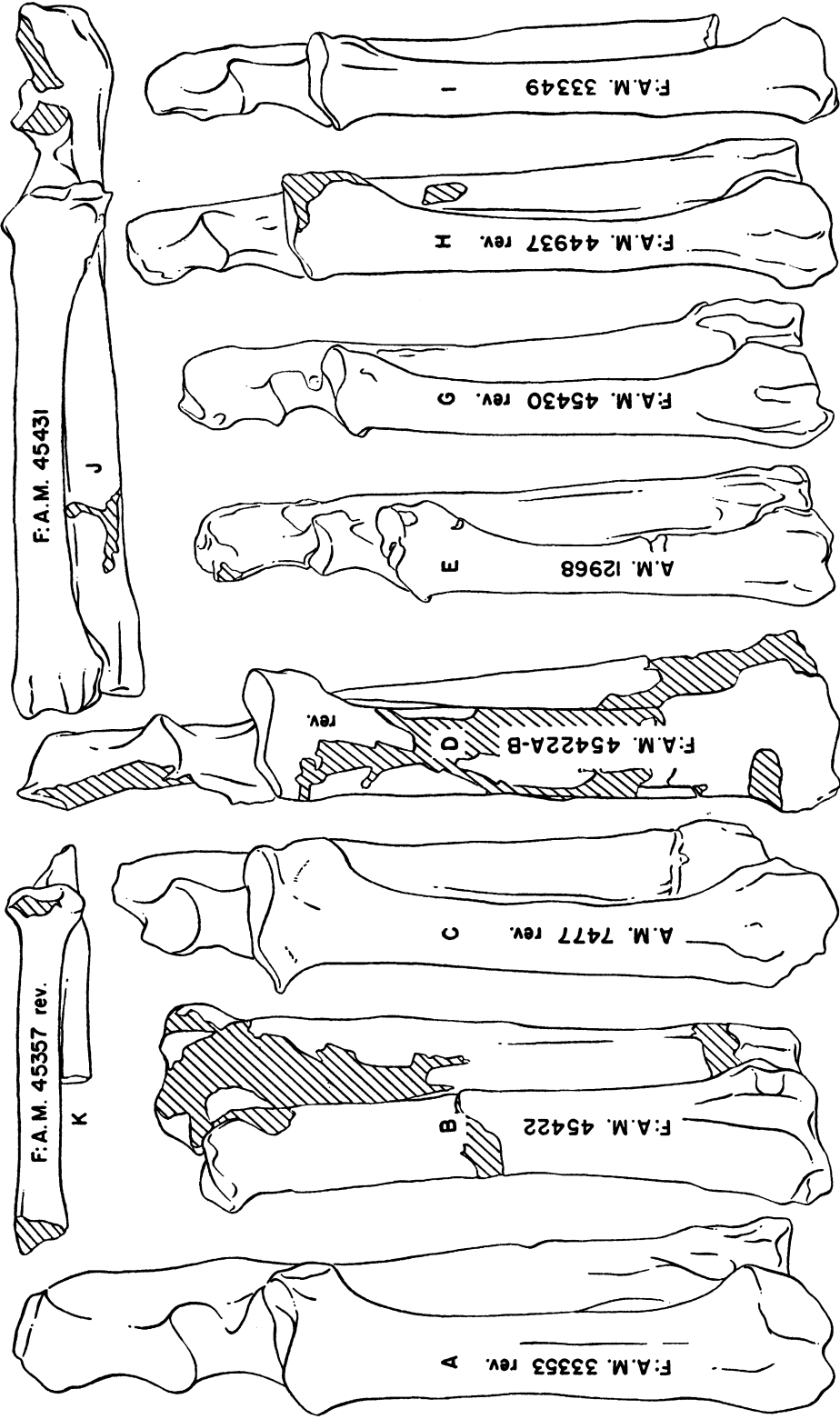
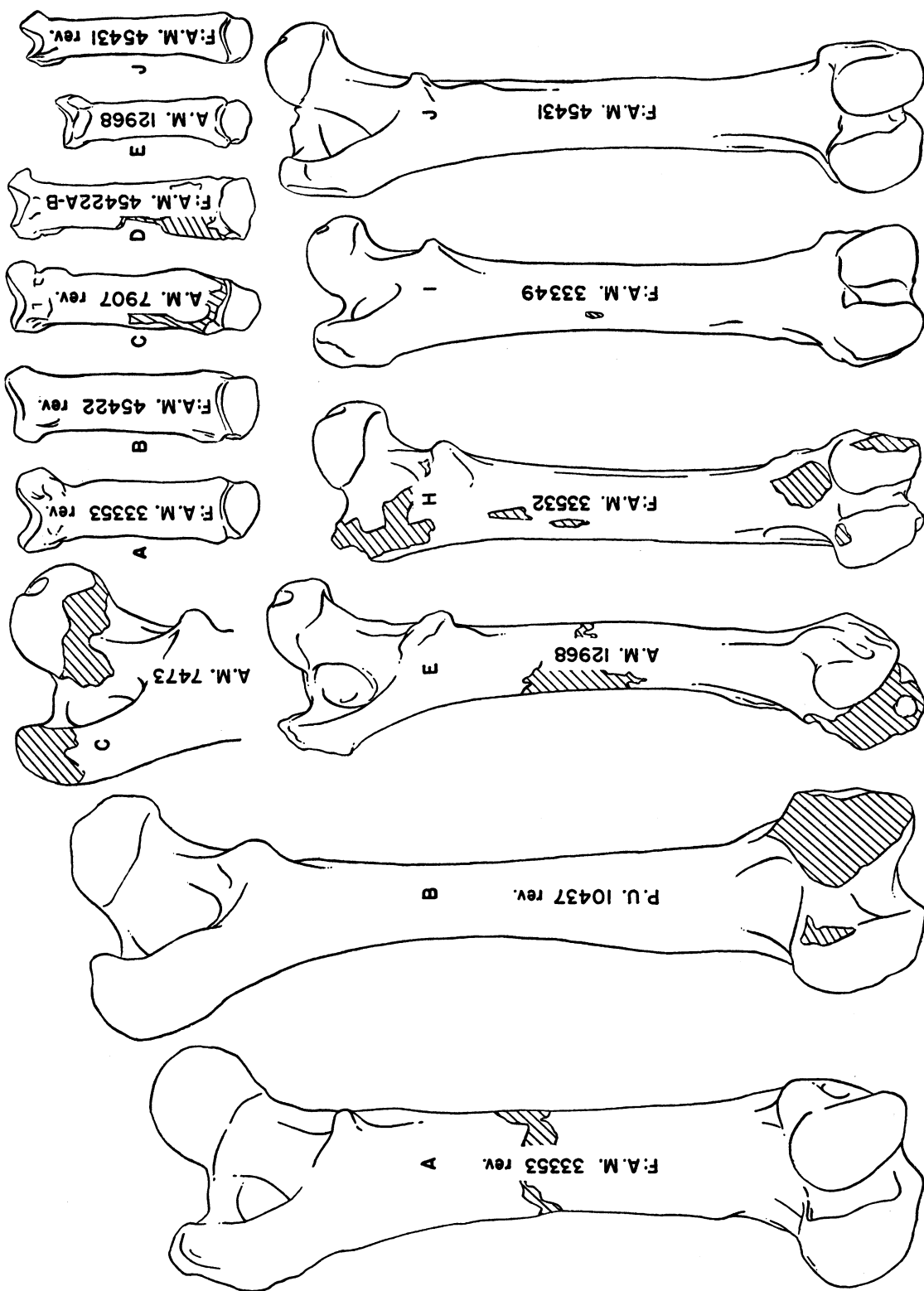


FIG. 25. *Promerycochoerus* Douglass, *Promerycochoerus* (*Pseudopromerycochoerus*), new subgenus, *Mesoreodon* Scott, and *Promesoreodon*, new genus, comparison of humeri, radii, ulnae, and metacarpals. A. *Promerycochoerus carrikeri* Peterson. B. *P. latidens* Thorpe. C. *P. Superbus* (Leidy). D. *P. (P.) montanus* (Cope). E. *P. (P.) minor pygmyus* (Loomis). G. *M. cheeki* (Schlaikjer). H. *M. cheeki scotti* (Schlaikjer). I. *M. megalodon* Peterson. J. *M. megalodon sweeti*, new subspecies. K. *Promesoreodon scanloni*, new species. (See p. 169.) $\times \frac{1}{2}$.



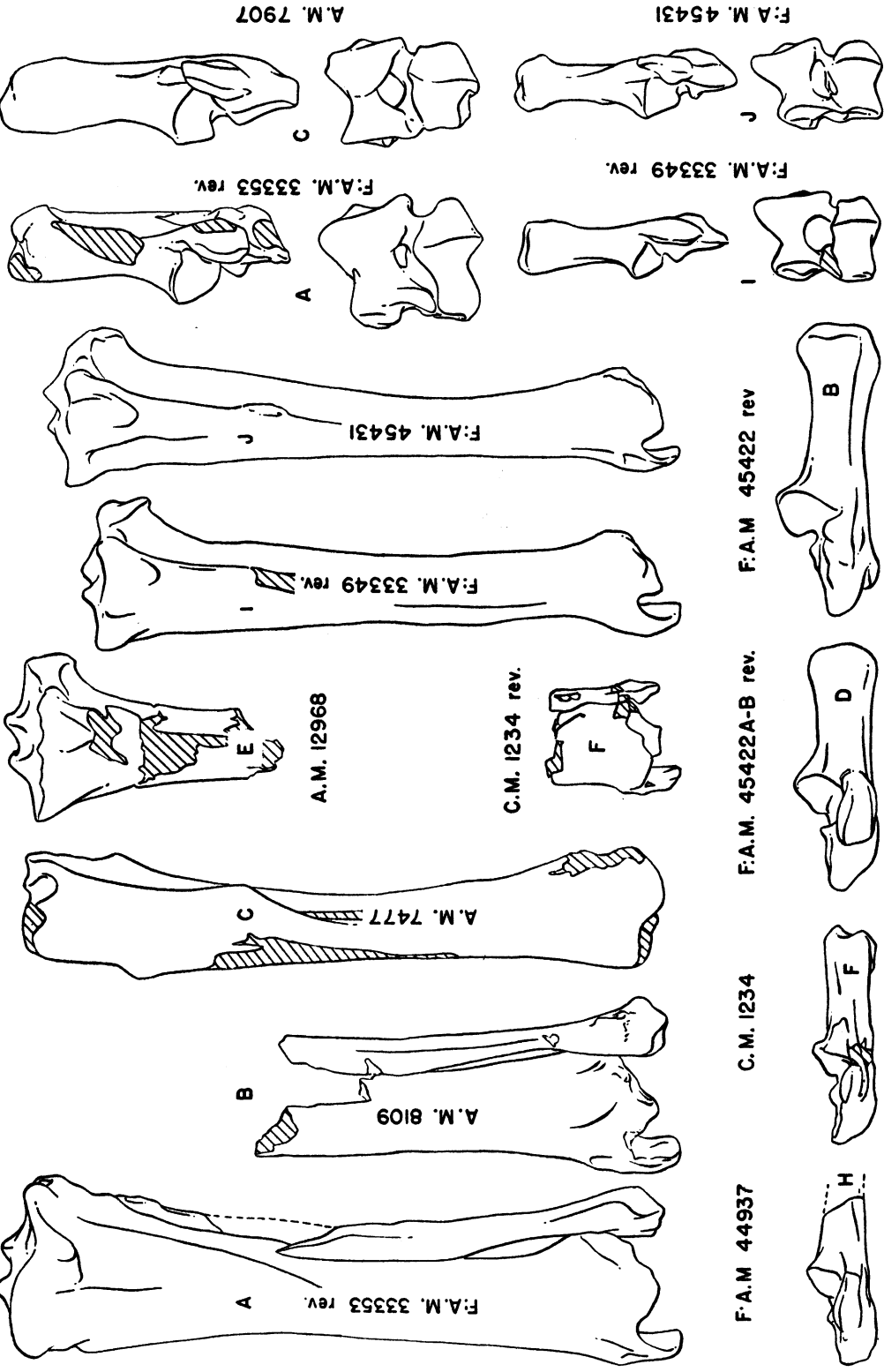


FIG. 26. *Promerycochoerus* Douglass, *Promerycochoerus* (*Pseudopromerycochoerus*), new subgenus, and *Mesoreodon* Scott, comparison of femora, tibiae, calcanea, astragali, and metatarsals. A. *Promerycochoerus carrikeri* Peterson. B. *P. latidens* Thorpe. C. *P. superbus* (Leidy). D. *P. (P.) montanus* (Cope). E. *P. (P.) minor pygmyus* (Loomis). F. *M. chelonys* Scott. H. *M. cheeki scotti* (Schlaikjer). I. *M. megalodon* Peterson. J. *M. megalodon sweeti*, new subspecies. (See p. 169.) $\times \frac{1}{2}$.

LIST OF SYNONYMS

The following list of synonyms is here recorded for the convenience of the reader. A formal and detailed index is planned for the final report on the "Contributions to the revision of the oreodonts (Merycoidodontidae)."

Paracotylops, 84
danai, 140
intermedius, 140
latidens, 140

marshi, 118
temporalis, 107
thomsoni, 93, 128
vantasselensis, 93

