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DESMATOCHOERINAE, A NEW SUBFAMILY OF OREODONTES

C. BERTRAND SCHULTZ AND
CHARLES H. FALKENBACH



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DESMATOCHEERINAE, A NEW SUBFAMILY OF OREODONTES

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INTRODUCTION

THE PRESENT REPORT on the Desmatochoerinae constitutes the sixth in a series contributing to a revision of the oreodonts (Merycoidodontidae). Previous publications of the sequence include subfamilies 1, Merycochoerinae¹; 2, Ticholeptinae²; 3, Merychyinae³; 4, Promerycochoerinae⁴; and 5, Phenacocoelinae.⁵

The new subfamily 6, Desmatochoerinae, includes six closely related genera and one subgenus: *Megoreodon*, new genus; *Desmatochoerus* Thorpe; *D.* (*Paradesmatochoerus*), new subgenus; *Pseudodesmatochoerus*, new genus; *Superdesmatochoerus*, new genus; *Subdesmatochoerus*, new genus; and *Prodesmatochoerus*, new genus. The subfamily embraces forms with medium- to large-sized skulls [the two smallest, *Subdesmatochoerus socialis* and *Prodesmatochoerus meekae*, are approximately equal in size to examples of *Ticholeptus hypsodus* and *T. tooheyi*, and the largest, *Megoreodon grandis*, is slightly larger than examples of *Promerycochoerus* (*Pseudopromerycochoerus*) *inflatus*].

The main phylogenetic succession, *Prodesmatochoerus-Subdesmatochoerus-Desmatochoerus*, represents the longest known continuous line of oreodonts, ranging from early Oligocene to possibly late Miocene. (See chart 1, p. 156.)

The Desmatochoerinae are represented by the 237 numbered skulls, mandibular rami, and skeletal elements described in the following lists. The 25 text figures illustrate 33 of these specimens which include seven refigured types and embrace 22 species and six subspecies (of which 12 species and three subspecies are new). The drawings are reproduced at one-third and one-half natural size. Figures 1, 4, and 16 are reproduced at one-half natural size for comparison with figures of the same scale in this and previous reports.

The figures show the range in size, shape, and proportions of the skulls, mandibular rami, and skeletal elements. Illustrations of

Megoreodon and *Desmatochoerus* when compared with those of *Promerycochoerus*, *P.* (*Parapromerycochoerus*), and *P.* (*Pseudopromerycochoerus*)⁶ indicate the characters by which the writers divided these genera and subgenera into two subfamilies, Promerycochoerinae and Desmatochoerinae.

The writers are grateful to all who have helped make this revision possible: in addition to those⁷ whose continued aid and encouragement have been previously acknowledged, thanks are expressed also to Dr. L. S. Cressman and Dr. W. D. Smith of the University of Oregon and Dr. Joseph T. Gregory of the Yale Peabody Museum, who kindly arranged for the examination of various specimens in the collections of their respective institutions, and Mrs. Kay Stockman and Miss M. Kathleen McMullen, who aided with the typing of the manuscript.

The following is a list of abbreviations of institutions cited:

A.C., Amherst College
A.M., the American Museum of Natural History
C.C., Condon Collection
C.I.T., California Institute of Technology
C.M., Carnegie Museum
C.N.H.M., Chicago Natural History Museum
F.A.M., Frick Collection American Mammals
M.C.Z., Museum of Comparative Zoölogy
U.C., University of California
U.N.S.M., University of Nebraska State Museum
U.O., University of Oregon
W.M.C.U., Woodwardian Museum, Cambridge University
Y.P.M., Yale University, Peabody Museum

STRATIGRAPHIC RELATIONSHIPS

It should be noted that the correlations of the Brule sediments in Nebraska, South Dakota, and Wyoming are very complicated. The faunal evidence does not always correspond to the lithologic. The consensus of the members of the Frick Laboratory field parties and the University of Nebraska State Museum collectors is that until geologic correlations are definitely established the terms Orella and Whitney should not be applied

¹ Schultz, C. Bertrand, and Charles H. Falkenbach, 1940, Bull. Amer. Mus. Nat. Hist., vol. 77, art. 5, p. 213.

² *Ibid.*, 1941, vol. 79, art. 1, p. 1.

³ *Ibid.*, 1947, vol. 88, art. 4, p. 161.

⁴ *Ibid.*, 1949, vol. 93, art. 3, p. 73.

⁵ *Ibid.*, 1950, vol. 95, art. 3, p. 91.

⁶ *Idem*, 1949.

⁷ *Idem*, 1940, p. 216; 1941, p. 4; 1947, p. 165; 1949, p. 79; 1950, p. 95.

to the South Dakota region. As a means of convenience, the writers tentatively use the letters "A," "B," "C," and "D" to represent the faunal zones of the Brule formation until the regional correlation is better understood and a standard terminology has been adopted.

Recent studies of Oligocene paleosols tend to indicate that the breaks between these faunal zones are marked by buried soil zones. Schultz, Tanner, and Harvey¹ have reported the following: "Preliminary studies show that major faunal breaks coincide with important buried soil zones, which indicate that these paleosols actually represent unconformities. The major soils were developed on old land surfaces where deposition was practically at a stand-still for long periods of time."

The Brule terminology of Wanless,² the collecting zones³ of Morris F. Skinner and Ralph Mefferd, and the provisionally lettered faunal zones used by the writers are shown in chart 1 (p. 156).

The discrepancies which seem to exist in the various geologic correlations between the Brule localities in Nebraska, South Dakota, and Wyoming became apparent as the study of the oreodont collections progressed. Although the lithologic correlations have not been determined regionally, the writers believe that the stratigraphic sequences of the oreodonts are the same in the various areas.

The Frick Laboratory oreodonts from South Dakota were collected by Morris F. Skinner and associates, and those from eastern Wyoming and the Hat Creek region of Nebraska by Charles H. Falkenbach and associates. In Nebraska the University of Nebraska State Museum field parties under the direction of E. L. Blue, Thompson M. Stout, Lloyd Tanner, Loren Toohey, C. Bertrand Schultz, and associates have made extensive collections from the Brule (including the type locality). The majority of the specimens were carefully documented in the field with geologic data.

¹ 1953, Bull. Geol. Soc. Amer., vol. 64, no. 12, pt. 2, p. 1471.

² Wanless, Harold R., 1923, Proc. Amer. Phil. Soc., vol. 62, no. 4, pp. 190-269.

³ Although these collecting zones represent somewhat different divisions than those of Wanless, they appear to indicate prominent faunal breaks. (See chart 2, p. 158, for comparison of bullae from these zones.)

Within the South Dakota collections are oreodonts from the high "ash" or "white" layer and the deposits immediately above, as exposed at the top of Sheep Mountain, Cedar Pass, and other localities. These specimens suggest an age approximately equivalent to that of the basal part of the Gering formation. Various workers have considered these high deposits as part of the "*Leptauchenia* beds." Wanless,⁴ however, reported that these same deposits were a part of the "Rosebud,"⁵ and stated: "The White Ash layer is one of the most persistent and interesting elements in the White River area. It rests upon the upper division of the *Leptauchenia* beds and is clearly recognizable at all points through the region where the higher beds are exposed, the best sections being on top of Sheep Mountain, the Cedar Butte near the mouth of Cottonwood Creek, the Cedar Pass section at Interior. . . ."

"In the section at Sheep Mountain and Cedar Pass, Interior, the beds above the White Ash layer closely resemble those immediately below it . . . the similarity of these Rosebud ash beds to those of those of *Leptauchenia* age and the presence of channels in them resembling the *Protoceras* Channels indicates that, though these beds may be classed as Miocene on faunal grounds, the depositional conditions were not greatly changed."

The writers, basing their decision on independent geologic data and faunal evidence, agree with Wanless.

Further complications in regard to the Brule terminology have resulted in the use of the names Orella and Whitney in South Dakota (see chart 1, p. 156). In an abstract concerning the original description of the Orella and Whitney members of the Brule formation in Nebraska, Schultz and Stout⁶ stated: "A lithologic break and in places a significant and pronounced disconformity divide the Brule formation into two widespread lithologic units which, it is suggested, should be considered as stratigraphic members. For the lower or *Oreodon* zone portion

⁴ 1923, pp. 231, 235.

⁵ See Schultz and Falkenbach, 1949, chart 3, p. 83, for age assignment of "Rosebud."

⁶ 1938, Bull. Geol. Soc. Amer., vol. 49, no. 12, pt. 2, p. 1921.

of the Brule formation as it occurs in northwestern Nebraska the name Orella member is proposed. . . . Here the Orella member is disconformably overlain by the massive clays of the upper or *Leptauchenia* zone of the Brule formation for which the name Whitney member is proposed."

In 1941, the Committee (Wood, Chaney, Clark, Colbert, Jepsen, Reeside, and Stock) on Nomenclature and Correlation of the North American Continental Tertiary¹ published the following correlation:

"Orella member of Brule formation, Orellan, Nebraska, South Dakota and Wyoming (Schultz and Stout, 1938) . . .

"Oreodon beds = middle White River = lower Brule = Orella member . . ."

No mention had been made by Schultz and Stout concerning the correlation of Nebraska Brule deposits with those of South Dakota. It should be pointed out that the type locality of the Brule is in Nebraska; therefore, it seemed logical that the members should be named from the same locality. Undoubtedly the names "*Oreodon* zone" and "*Leptauchenia* zone" should not have been applied to the Nebraska area by Schultz and Stout because there is a certain implication of correlation.

Chart 1 (p. 156) also demonstrates the stratigraphic distribution of the Phenacocoelinae² and the Desmatochoerinae,³ and indicates the apparent relationship between the Phenacocoelinae and the Merycochoerinae.⁴ The chart further includes the faunal zones shown in relationship to the Orella and Whitney members of the Brule formation heretofore discussed.

CHARACTERS IN AUDITORY BULLAE

The Desmatochoerinae include the first oreodonts possessing small (minute) bullae to be discussed by the writers. In chart 2 (p. 158) examples of the bullae of the genera and the subgenus included in this subfamily are illustrated. For comparison, the outline (cross section) of the bulla is placed at its proper position on a horizontal line, which represents the basal length of the particular

skull. The bullae actually may be divided into three groups: (1) small⁵ (minute) and slightly inflated bullae as exemplified in *Prodesmatochoerus*; (2) large and inflated bullae with various degrees of grooving for the hyoid as in *Subdesmatochoerus* (from "Zone B" of Brule); and (3) large and inflated bullae, lacking the hyoid groove as in *Subdesmatochoerus* (from "Zone D" of Brule), *Desmatochoerus*, *D.* (*Paradesmatochoerus*), *Pseudodesmatochoerus*, *Superdesmatochoerus*, and *Megoreodon*.

In a discussion of the bullae, Thorpe⁶ reported: "Scott has long maintained that the presence of the inflated bullae is a primitive condition and that the development of small bullae is a secondary development. Van der Klaauw (1931) has also shown this to be true, but in somewhat different sense. The Uinta forms show the small bullae, together with *Oreonetes* and some species of *Merycoidodon*, and these have been put in a separate phylum by Loomis (1924) and earlier by Douglass. The size of the bulla in proportion to the size of the skull varies greatly in different genera. While it is a fact that the inflated bulla is generally present in all forms above the middle Oligocene, yet it is proportionally as small in relation to size of the skull in some of these genera as it is in *Merycoidodon culbertsonii*. In *Merycoidodon gracilis*, a true member of this genus, the bulla is relatively as large as in *Eporeodon*. . . ."

The evidence does not support the theory that the presence of the inflated bullae is a primitive condition but suggests the reverse—that the small (minute) bullae were primitive, as exemplified in *Prodesmatochoerus meekae* (from "Zone A" of Brule) with a small bulla, which presumably gave rise to *Subdesmatochoerus socialis* ("Zone B") with a large bulla (see chart 2, p. 158; figs. 21–22). Apparently the bullae of the oreodonts originally were small or minute and later evolved into well-inflated forms (of different shapes). In some instances the bullae, after reaching the inflated stage, developed still further into

⁵ The terms "small" and "large" refer to the actual size of the bulla to differentiate between the sizes of the various bullae in each phylogenetic line. See discussion of bullae (Schultz and Falkenbach, 1950, p. 96).

⁶ Thorpe, Malcolm R., 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 26.

¹ 1941, Bull. Geol. Soc. Amer., vol. 52, p. 27, pl. 1.

² Schultz and Falkenbach, 1950.

³ Present report.

⁴ *Idem*, 1940, pp. 213–306, and 1949, p. 80.

EPOCHS	GROUPS	FORMATIONS West-central Great Plains				
MIOCENE	HEMINGFORD	"Lower Snake Creek"	↑	↑	↑	Subfamily 6 DESMATOCOEERINAE
		"Sheep Creek"	↑	↑	↑	Subfamily 1' MERYCOCHOERINAE
		Marland	↑	↑	↑	Subfamily 5 PHENACOCOEELINAE
	ARIKAREE	Harrison	1 3	10, 4 1, 2	1 3, 5	I. <i>Phenacocoelus</i>
		Monroe Creek	1 3	10, 4 1, 2	1 3, 5	II. <i>Hypslops</i>
OLIGOCENE	WHITE RIVER	Schultz and Stout ⁵ [Nebraska]	CORRELATIONS OF FAUNAL ZONES IN S. DAK.			
			Wentz ³	Shiner and Mettler ⁴		
			"Upper Division of Leptauchenia Beds"	"Leptauchenia Beds"		
	Brule	Whitney	"Middle Division of Leptauchenia Beds"	"Leptauchenia Beds"		
			"Lower Division of Leptauchenia Beds"	"Leptauchenia Beds"		
	Orellia		"Upper Oredon Red Clays"	"Upper Oredon Beds"		
			"Middle Oredon Green Sandstone"	"Middle Oredon Beds"		
			"Lower Oredon Banded Sills"	"Lower Oredon Beds"		
	Chadron		"Upper Nodular Layer"	"Upper Oredon Beds"		
			"Lower Nodular Layer"	"Lower Oredon Beds"		

CHART 1. Stratigraphic distribution of two subfamilies of oreodonts: Phenacocoelinae (subfamily 5, Schultz and Falkenbach, 1950, pp. 91-149); and Desmatochoerinae (subfamily 6, present report).

EXPLANATION OF CHART 1. The known geologic limitations of 10 genera and one subgenus of the Phenacocoelinae and Desmatochoerinae 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 geologic scale. The limited meanings of the "Lower Snake Creek" and "Sheep Creek" are here used (Schultz and Falkenbach, 1949, p. 83). The arrows connecting *Submerycochoerus*, a genus in the Phenacocoelinae (subfamily 5), with the Merycochoerinae (subfamily 1) indicate the apparent relationship between these two subfamilies.

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

Subfamily 5. Phenacocoelinae

I. *Phenacocoelus* Peterson

1. *P. kayi* Schultz and Falkenbach
2. *P. stouli* Schultz and Falkenbach
3. *P. typus* Peterson

II. *Hypslops* Schultz and Falkenbach

1. *H. brachymelis* (Douglass)
2. *H. breviceps* (Douglass)
3. *H. erythroceps* (Stock)
4. *H. luskensis* Schultz and Falkenbach
5. *H. johndayensis* Schultz and Falkenbach

III. *Submerycochoerus* Schultz and Falkenbach

1. *S. bannackensis* (Douglass)

IV. *Pseudomesoreodon* Schultz and Falkenbach

1. *P. rooseyi* Schultz and Falkenbach
2. *P. rolli* Schultz and Falkenbach
3. ?*P. boulderensis* Schultz and Falkenbach

Subfamily 6. Desmatochoerinae

I. *Megoreodon*, new genus

1. *M. fricki*, new species
2. *M. grandis* (Douglass)

II. *Desmatochoerus* Thorpe

1. *D. curvidens* (Thorpe)
- 1a. *D. curvidens gregoryi* (Loomis)
2. *D. leiayi* (Bettany)
3. *D. hatcheri* (Douglass)

- 3a. *D. hatcheri geringensis*, new subspecies
- 3b. *D. hatcheri grinnelli* (Koerner)
- 3c. *D. hatcheri niobrarensis*, new subspecies
4. *D. newchicogoensis*, new species

IIIA. *Desmatochoerus* (*Paradesmatochoerus*), new subgenus

1. *D. (P.) grangeri*, new species
2. *D. (P.) montocreekensis*, new species
3. *D. (P.) sanfordi*, new species; 3a, geologic variety
4. *D. (P.) wyomingensis*, new species

III. *Pseudodesmatochoerus*, new genus

1. *P. hoffmani*, new species
2. *P. longiceps* (Douglass)
3. *P. milleri*, new species
4. *P. wascoensis*, new species
5. ?*P. paragonus* (Cope)

IV. *Superdesmatochoerus*, new genus

1. *S. lulli* (Thorpe)
2. *S. microcephalus* (Thorpe)

V. *Subdesmatochoerus*, new genus

1. *S. montanus* (Douglass)
2. *S. socialis* (Marsh)
- 2a. *S. socialis dakotensis*, new subspecies
3. *S. shannonensis*, new species

VI. *Prodesmatochoerus*, new genus

1. *P. meekae*, new species
2. *P. natronensis*, new species

¹ Apparent relationship of Merycochoerinae, subfamily 1.

² Faunal zones used by writers until definite geologic correlations can be established in the Nebraska-South Dakota-Wyoming region. See Falkenbach and Schultz, 1951, Guide Book, Fifth Field Confer., Soc. Vert. Paleont., p. 47; also see discussion, p. 153 present report.

³ After Wanless, Harold R., 1923, *loc. cit.*

⁴ As used by Morris F. Skinner and Ralph Mefferd of the Frick Laboratory in the collecting of fossils in South Dakota. The uppermost "*Leptanchenia* Beds" (of some writers), which are considered to be Miocene in age, are not included here. See discussion, p. 154.

⁵ Members of Brule in Nebraska.

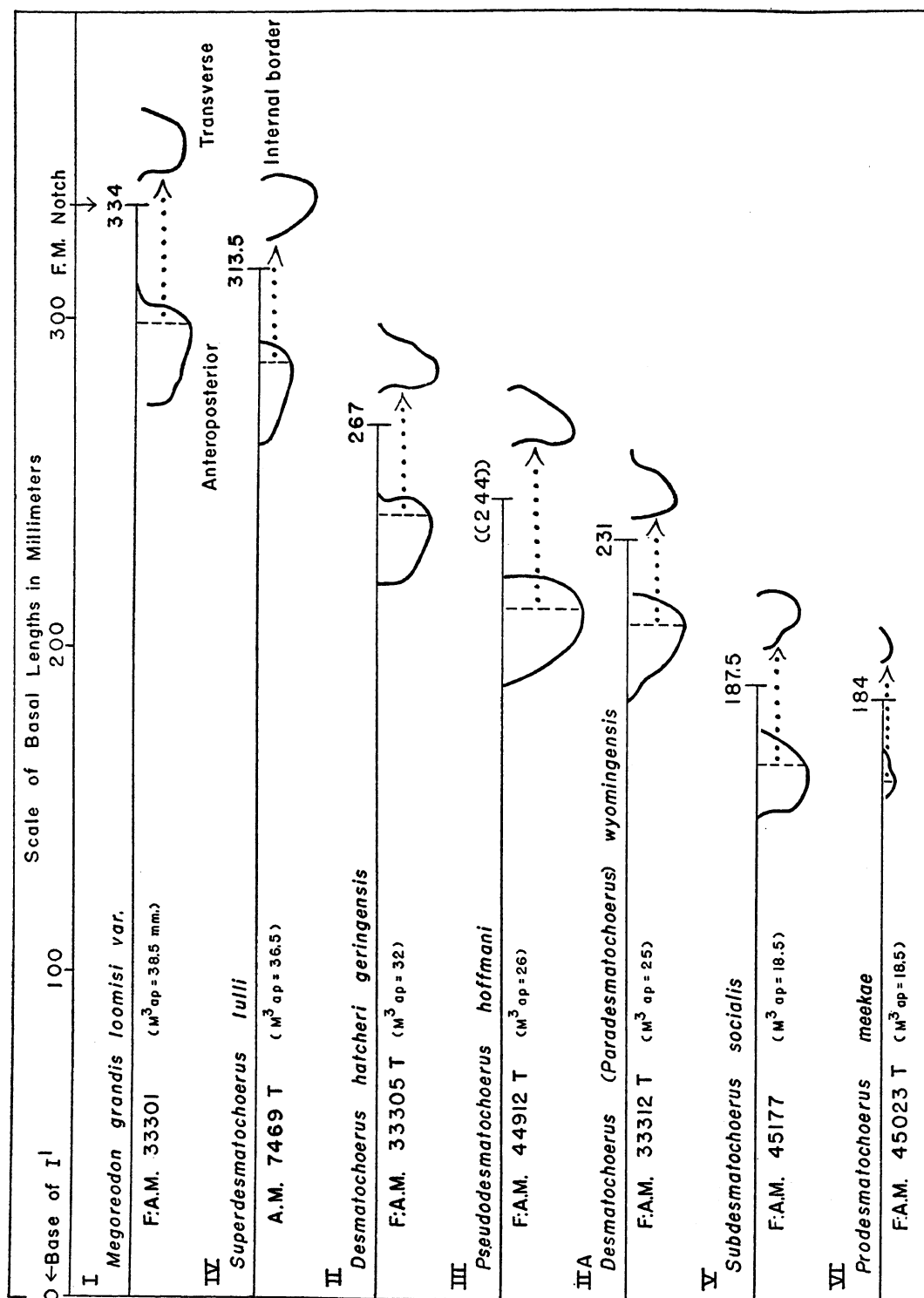


CHART 2. Comparative basal lengths of skulls and cross sections of auditory bullae in the Desmatochoerinae. Anteroposterior cross section taken through bulla at highest point (parallel to longitudinal axis of skull), and is placed in relative position on lines representing basal lengths of skulls (from posterior base of I³ to anterior edge of foramen magnum notch). Transverse section drawn through bulla at widest point (perpendicular to longitudinal axis of skull). (Compare with chart 1 in Schultz and Falkenbach, 1950, p. 97.)

depressed but expanded forms as in *Ustatochoerus*¹ and *Pseudomesoreodon*.²

Thorpe stated that the inflated (large) bullae are generally present in all forms above the middle Oligocene. This is true in the Desmatochoerinae: all examples from above "Zone A" of the Brule have large bullae. It is of interest that in the available material there is no overlapping in occurrences of the small and large bullae—a circumstance suggesting that the two faunal zones ("A" and "B") may have been separated by a significant time lapse (see discussion of stratigraphic relationships, p. 153). It should be noted, however, that in the Chadron formation well-inflated bullae are present which have been observed in examples of *Limnenetes* and *Oreo-*

netes which may well represent end members of their respective phyla. The holotype of *O. anceps* has been considered by Loomis³ and Thorpe⁴ as having "tiny" bullae; Scott,⁵ however, pointed out that the bullae of the holotype of *O. anceps* were absent but probably inflated. The conflicting evidence will be discussed in a forthcoming report.

RANGE OF VARIATION

Comparisons of the size range in the different species, emphasizing apparent individual variation in basal lengths, superior and inferior dentitions, are given in chart 3 (p. 160).

¹ Schultz and Falkenbach, 1941, p. 10, figs. 2-9.

² *Idem*, 1950, p. 128, chart 1 (p. 97).

³ 1924, Ann. Carnegie Mus., vol. 15, p. 370.

⁴ 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 42.

⁵ 1940, Trans. Amer. Phil. Soc., Philadelphia, new ser., vol. 28, pt. 4, p. 651.

CHART 3

RANGE OF VARIATION IN THE DESMATOCHOERINAE

	No. of Ex-amples	SKULL		DENTITION							
		Basal Length ¹		P ¹ -M ³		P ₁ -M ₃		M ³ AP ³		M ₃ AP	
		Range	Mean ²	Range	Mean	Range	Mean	Range	Mean	Range	Mean
I. <i>Megoreodon</i>											
<i>M. fricki</i> , Monroe Creek (Wyo.)	3	246	246	151	151	155	155	36	36	42	42
<i>M. grandis</i> , Gering equivalent(Mont.)	5	312-327	321	155-176	167	173-191	182	36-43	40	47	47
<i>M. grandis loomisi</i> , Gering (Wyo.)	7	335-351	341	166-174	170	177-193	185	39-41	40	42-48	45
<i>M. g. loomisi</i> , geol. var., Monroe Creek (Nebr., Wyo.)	40	322-357	333	156-177	166	169-194	184	37-43	40	41-48	44
II. <i>Desmatochoerus</i>											
<i>D. curvidens</i> , Harrison equivalent (Oreg.)	1	265	265	125	125	136	136	33	33	37	37
<i>D. c. gregoryi</i> , Harrison (Nebr., S. Dak., Wyo.)	7	255-270	265	121-135	130	130-150	142	31-37	33	32-39	37
<i>D. leidyi</i> , Harrison equivalent (Oreg.)	8	280-285	282	131-139	134	148	148	31-38	33	38-39	38
<i>D. hatcheri</i> , Gering equivalent(Mont.)	3	261	261	122-137	130	146	146	31-35	33	—	—
<i>D. hatcheri geringensis</i> , Gering(Nebr., S. Dak., Wyo.)	27	233-268	253	116-138	127	129-149	140	29-34	32	33-38	36
<i>D. h. grinnelli</i> , Gering equivalent(Mont.)	3	256-268	262	120-128	123	130-135	133	31	31	37	37
<i>D. h. niobrarensis</i> , Monroe Creek (Nebr., S. Dak., Wyo.)	13	251-265	261	122-138	130	129-150	143	29-35	31	32-37	35
<i>D. newchicagoensis</i> Sheep Creek equiv- alent (Mont.)	1	—	—	—	—	141	141	—	—	36	36
IIA. <i>D. (Paradesmatochoerus)</i>											
<i>D. (P.) grangeri</i> , Gering (Wyo.)	1	236	236	105	105	122	122	23	23	29	29
<i>D. (P.) monroecreekensis</i> , Monroe Creek (Wyo.)	11	215-230	225	108-127	117	117-134	124	25-31	29	31-35	33
<i>D. (P.) sanfordi</i> , Gering (S. Dak., Wyo.)	4	—	—	93-100	97	100-103	101	17-23	21	25-26	25
<i>D. (P.) wyomingensis</i> , Gering (Nebr., S. Dak., Wyo.)	25	231-234	232	109-120	116	122-140	129	24-30	27	29-32	31

CHART 3—Continued

	No. of Ex-amples	SKULL		DENTITION							
		Basal Length		P ¹ -M ³		P ₁ -M ₃		M ³ AP ³		M ₃ AP	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
III. <i>Pseudodesmatochoerus</i>											
<i>P. hoffmani</i> , Monroe Creek, (Wyo.)	10	244	244	112-125	122	124-134	131	26-31	29	31-35	33
<i>P. longiceps</i> , Harrison equivalent (Mont.)	3	233	233	100	100	105-108	107	25	25	28-29	29
<i>P. milleri</i> , Gering (Wyo.)	5	240	240	115	115	126	126	29	29	35	35
<i>P. wascoënsis</i> , Harrison equivalent (Oreg.)	2	250-257	254	106-108	107	—	—	23	23	—	—
IV. <i>Superdesmatochoerus</i>											
<i>S. lulli</i> , Harrison equivalent (Oreg.)	4	313-320	317	148-157	153	166-174	170	33-36	35	41-43	42
<i>S. microcephalus</i> , Harrison equivalent (Oreg.)	3	306-312	309	141-153	146	153-157	155	31-37	34	38	38
V. <i>Subdesmatochoerus</i>											
<i>S. montanus</i> , approximately equal to "Zone D" Brule (Mont.)	1	209	209	101	101	107	107	24	24	26	26
<i>S. socialis</i> , "Zone B" Brule (Nebr., S. Dak.)	10	180-186	184	81-91	86	90-100	95	17-20	18	21-25	23
<i>S. s. dakotensis</i> , "Zone B" Brule (S. Dak.)	1	175	175	81	81	87	87	17	17	20	20
<i>S. shannonensis</i> , "Zone D" Brule (Nebr., S. Dak.)	8	193-215	205	91-100	94	106	106	20-22	21	25-26	25
VI. <i>Prodesmatochoerus</i>											
<i>P. meekae</i> , "Zone A" Brule (S. Dak., Wyo.)	23	173-190	178	78-90	85	85-94	90	15-20	18	20-25	23

¹ All measurements in millimeters.² Weighted mean.³ AP, anterior-posterior.

PROPORTIONS OF LENGTHS OF LIMBS TO BASAL LENGTHS OF SKULLS

Chart 4 is based on the measurements¹ of the various limb elements compared to the basal length of the skull of the same individual. In *Megoreodon*, with the exception of *M. fricki*, it is evident that the genus has proportionately shorter limbs than the other members of the subfamily. *M. fricki* has a comparatively small skull, but the limb ele-

¹ See table 3 (p. 170) for types of measurements (articular or maximum).

ments are equal in length to those of other species and subspecies of the genus, and in the over-all picture it has the longest limb proportions within the subfamily. In instances where more than one individual of a species are shown in the chart, some proportions show a comparatively constant range, but in others considerable individual variation is noted. It may be concluded that the proportions of the limb elements to the basal lengths of the skulls in associated individuals are apparently of no value in a systematic division within the subfamily.

CHART 4

PROPORTIONS OF LENGTHS OF LIMBS TO BASAL LENGTHS OF ASSOCIATED SKULLS
IN DESMATOCHOERINAE

	Humerus Skull	Radius Skull	Ulna Skull	Mc. III Skull	Femur Skull	Tibia Skull	Mt. III Skull	Calc. Skull
I. <i>Megoreodon</i>								
<i>M. fricki</i>	.80	.68	.95	.35	.88	.78	.36	.34
<i>M. grandis</i>	.67	—	—	.26	.80	.62	.26	.27
<i>M. grandis loomisi</i>	.63	.51, .54	.69, .73	.26	.71	.59, .60	.26	.25
<i>M. grandis loomisi</i> , geol. var.	.61, .62	.57	.76	.26	.73	.60	.25	.24
II. <i>Desmatochoerus</i>								
<i>D. curvidens gregoryi</i>	.70	.57	.84	.30	.81	.63	.26	.27
<i>D. hatcheri niobrarensis</i>	—	—	.84	—	.77, .78	.66, .66	.29	.27
<i>D. hatcheri geringensis</i>	.72	.63	.85	.32	.81	.71	.33	.27
IIA. <i>D. (Paradesmatochoerus)</i>								
<i>D. (P.) grangeri</i>	—	—	—	—	.87	.75	.33	—
<i>D. (P.) monroecreekensis</i>	.77, .77	.67	.88	.32	.77, .81, .89	.70, .89	.33	.26
III. <i>Pseudodesmatochoerus</i>								
<i>P. hoffmani</i>	—	—	—	—	.77	—	—	—
<i>P. longiceps</i>	—	.60	—	—	.82	.71	.35	.28
V. <i>Subdesmatochoerus</i>								
<i>S. socialis</i>	.73	.65	—	—	.88, .93	.78, .82	.38	.31
VI. <i>Prodesmatochoerus</i>								
<i>P. meekae</i>	—	.64	.86	—	.89	.78	—	.30
<i>P. natronensis</i>	—	—	—	—	—	—	—	.31
Range	.61-.80	.51-.68	.69-.95	.26-.35	.71-.93	.59-.89	.25-.38	.24-.34

DESCRIPTION OF DESMATOCHOERINAE, NEW SUBFAMILY 6¹

MEDIUM TO VERY LARGE skulls (including the longest known oreodont skulls); dolichocephalic to brachycephalic; supraoccipital wings not widely spread, produced posteriorly beyond the occipital condyles; moderately deep lacrimal fossa; bullae from very small (minute) to large inflated, and laterally compressed; apophysis on posterior border of ramus projecting well behind condyle; dentition from medium to very large size, brachyodont; molars deeply trenched.

Remains of *Megoreodon* are known from the Gering and Monroe Creek formations or their approximate equivalents; *Desmatochoerus* from the Gering, Monroe Creek, Harrison, and questionably Sheep Creek formations or their approximate equivalents; *D. (Paradesmatochoerus)* from the Gering and Monroe Creek formations; *Pseudodesmatochoerus* from the Gering, Monroe Creek, and Harrison formations or their approximate equivalents; *Superdesmatochoerus* from the John Day (in part equal to the Harrison formation); *Subdesmatochoerus* from the Brule formation (faunal "Zone B" and "Zone D"); and *Prodesmatochoerus* from the Chadron and Brule ("Zone A") formations. (See chart 1, p. 156.)

I. MEGOREODON,² NEW GENUS

GENOTYPE: *Megoreodon grandis* (Douglass).

DESCRIPTION

SKULL: Large (including largest known oreodont skulls), basal length ranging from 246 to 357 mm., width from 142 to 245 mm.; dolichocephalic to brachycephalic; supraoccipital wings small, not widely spread, produced posteriorly beyond occipital condyles (similar to examples of *Promerycochoerus*); elongated foramina in large, deep depression on each side of midline of exoccipital; sagittal crest high, rising posteriorly, comparatively thin for size of skull, similar to examples of *Desmatochoerus* (not robust as in examples of

Promerycochoerus); brain case long and narrow to inflated and depressed (in contrast to rounded brain case of *Promerycochoerus*); frontals moderately wide with oblong protuberance usually present along midline above posterior border of orbits; nasals moderately long with slight anterior retractions; anterior nasal-maxilla contact in area above P¹; orbit roundish, looking mostly forward and slightly upward, postorbital pillar massive; zygomatic arch moderately robust (not so massive as in examples of *Promerycochoerus*); squamosal extending posteriorly to point above posterior border of postglenoid process (not extending upward so far as in examples of *Promerycochoerus*), somewhat U-shaped in outline from side view; malar very deep below orbit; infraorbital foramen above P⁴; lacrimal fossa moderately deep, but comparatively small for size of skull; elongated facial depression bounded by inflated ridge above and by alveolar border of premolars below (suggesting extension of anterior malar ridge to region above P¹); premaxillae joined for short distance; occipital condyles large; paroccipital process wide at base, long and comparatively light; bulla small and inflated, elongated anteroposteriorly, laterally compressed; postglenoid process small but robust; posterior palate projecting posteriorly beyond M³.

MANDIBLE: Moderately robust; postsymphysis below P₃; ramus shallow; inferior border of ramus increasing in depth posteriorly to a point below second lobe of M₃, with a moderately abrupt downward curve posterior to this point; coronoid process robust; condyle light with longitudinal axis set at approximately right angle to dental series.

DENTITION: Brachyodont; heavy (more so than in *Promerycochoerus*); series extending posteriorly almost to rear border of orbit (decidedly farther than in examples of *Promerycochoerus*); incisors spatulate-shaped; C/ and P₁ large and moderately long; /C two to three times size of I₃; external styles of superior molars robust and prominent, more so than in examples of *Promerycochoerus*; P² and P³ each set somewhat obliquely to alveolar border; P¹-P³ each with anterior inter-

¹ *Idem*, 1940 (subfamily 1, Merycochoerinae); 1941 (subfamily 2, Ticholeptinae); 1947 (subfamily 3, Merychyinae); 1949 (subfamily 4, Promerycochoerinae); 1950 (subfamily 5, Phenacocoelinae).

² *Megoreodon* = large mountain teeth.

DISTINCTIVE CHARACTERS

	I. <i>Megoreodon</i> (P. 163, figs. 1-3, 18, 23-25)	II. <i>Desmatochoerus</i> (P. 177, figs. 4-7, 18, 23-25)	IIA. <i>D. (Paradesmatochoerus)</i> (P. 193, figs. 8-11, 18, 24-25)
Skull (see chart 2, p. 158)	Very large	Medium	Slightly smaller than in <i>Desmatochoerus</i>
Sagittal crest	High	Long and high	Not so high as in <i>Desmatochoerus</i>
Infraorbital foramen above (see chart 5, p. 181)	P ⁴	P ³ -M ¹	P ³ -P ⁴
Bulla (see chart 2, p. 158)	Inflated, and elongated anteroposteriorly (small)	Inflated, laterally compressed, long anteroposteriorly	Inflated, similar to that of <i>Desmatochoerus</i>
Zygomatic arch	Moderately robust	Moderately light	Moderately light
Downward curve of inferior border of ramus below M ₃	Moderately abrupt	Noticeably abrupt	Less than in <i>Desmatochoerus</i>
Dentition	Brachyodont, heavy	More brachyodont and lighter than in <i>Megoreodon</i>	More brachyodont than in <i>Desmatochoerus</i>
Anterior intermediate crest on	P ¹ -P ³	P ¹ -P ³	P ¹ -P ³ , moderately prominent
Posterior intermediate crest on	P ₃	P ₂ -P ₃	P ₃
Limbs	Moderately long and robust	Shorter and lighter than in <i>Megoreodon</i>	Shorter (tendency only) and lighter than in <i>Desmatochoerus</i>

mediate crest; P₃ with posterior intermediate crest.

LIMBS: Moderately long and robust (approximately same length, but lighter than examples of *Promerycochoerus carrikeri*; approximately same length as those of *Pseudodesmatochoerus*; longer and more robust than in other genera of Desmatochoerinae).

MEASUREMENTS: Tables 1-4 (pp. 166, 167, 170, and 173).

ILLUSTRATIONS: Figures 1-3, 18 (skulls, rami, and dentitions); 23-25 (limbs).

DISCUSSION

The proposed new genus, *Megoreodon*, includes some large oreodonts which have previously been considered to be *Promerycochoerus*, but which differ from *Promerycochoerus* in having a long and narrow skull, an elongated facial region, a strong facial ridge, and a more robust dentition. The earliest oc-

currences of *Megoreodon* are found in the Gering formation (or its approximate equivalents). The characters of the unusually large skulls referred to this genus show affinities to those of *Desmatochoerus* from the Gering and Monroe Creek formations. No evidence of *Megoreodon* has been reported from below the Gering or above the Monroe Creek in the west-central Great Plains area. The examples from Montana seem to have come from deposits of an age similar to that of the specimens from Nebraska and Wyoming. (See p. 172.)

The Gering *Megoreodon* was considerably larger than *Mesoreodon*,¹ which represented the *Promerycochoerinae* during the earliest Miocene (Gering and Monroe Creek). Examples of *Promerycochoerus* are restricted to the Harrison formation or to deposits approximately equivalent in age.

¹ *Idem*, 1949, p. 131.

OF THE DESMATOCHOERINAE¹

III. <i>Pseudodesmatochoerus</i> (P. 203, figs. 12-15, 18, 23-25)	IV. <i>Superdesmatochoerus</i> , (P. 213, figs. 16-18, 23, 25)	V. <i>Subdesmatochoerus</i> (P. 217, figs. 18-21)	VI. <i>Prodesmatochoerus</i> (P. 225, figs. 18, 22, 24-35)
Medium, smaller than in <i>Desmatochoerus</i>	Large	Medium	Medium, slightly smaller than in <i>Subdesmato-</i> <i>choerus</i>
Very low, depressed in medial region P ³	High, more massive than in <i>Desmatochoerus</i> P ³ -P ⁴	Moderately high P ³	Moderately high and light P ³ , slightly more for- ward than in <i>Prodes-</i> <i>matochoerus</i>
Inflated (medium to large size with some lateral compression)	Inflated, laterally com- pressed	Inflated, laterally com- pressed	Slightly inflated (minute)
Moderately light to some- what robust	Light	Light	Light
Gradual	Gradual	Gradual with tendency for arching	Gradual
Brachyodont, similar to that of <i>D.</i> (<i>Parades-</i> <i>matochoerus</i>)	Brachyodont, slightly more so than in <i>Meg-</i> <i>oreodon</i>	Brachyodont, more so than in <i>Desmatochoerus</i>	Brachyodont, similar to that of <i>Subdesmato-</i> <i>choerus</i>
P ¹ -P ³ , moderately prom- inent	P ¹ -P ³ , suggestion only	P ¹ -P ³	P ¹ -P ³ (weak)
P ₂ -P ₃ (weak)	P ₃	P ₃ (weak)	P ₃ (weak)
Equal to those of <i>D.</i> (<i>Paradesmatochoerus</i>)	Questionably larger than in <i>Desmatochoerus</i>	Shorter and lighter than in <i>Desmatochoerus</i>	Shorter and lighter than in <i>Subdesmatochoerus</i>

¹ Compare with Schulz and Falkenbach, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85; 1950, p. 100.

Either *Prodesmatochoerus* or *Subdesmatochoerus* was evidently ancestral to *Megoreodon*, as well as to the remaining genera of the Desmatochoerinae. The conspicuous size difference between examples of *Megoreodon* of the Gering compared with those of *Subdesmatochoerus* from the upper Brule suggests a definite faunal gap between the forms of the upper Brule and those of the lower Gering in the Great Plains.

It is of interest to note that formations which have yielded specimens referable to *Megoreodon* have also produced examples of *Mesoreodon*² and leptauchenids, not only in the Great Plains but also in Montana. In the same formations, however, examples of *Promerycochoerus* are absent. It is also noteworthy that no examples of *Megoreodon*, *Mesoreodon*, *Leptauchenia*, or *Cyclopidius* have been reported from the John Day Valley of Oregon

² *Idem*, 1949, p. 131.

where examples of *Promerycochoerus* are so common.

The available remains of *Megoreodon* exhibit very little change in characters or size with respect to either their geographic or geologic distribution. Considerable individual variation within a species is apparent, especially in the width of the skulls and in the dentition. The presence of both comparatively wide and narrow skulls in the same formations or faunal zones undoubtedly can be attributed to sexual variation, the narrow skulls representing the females. In some examples the premolar and molar series are of equal length, in others the premolars are slightly longer, while in the majority the molars are longer. These variations are given in table 4 (p. 173).

A specialized form, *M. fricki*, occurs in the same location and formation (Monroe Creek) as examples of *M. grandis loomisi*, geologic

variety. The skeletons of the two forms are alike, but the skull and mandible of *M. fricki* are conspicuously foreshortened, although the majority of other characters are similar. *M. fricki* may represent a new genus or subgenus, but until additional material is available the species is included under *Megoreodon*.

DISTRIBUTION

Two species and one subspecies of *Megoreodon* are known from the lower Miocene (Gering and Monroe Creek formations or their approximate equivalents) of Montana, Nebraska, and Wyoming. (See geologic distribution, chart 1, p. 156.)

TABLE 1

Megoreodon, NEW GENUS. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND MANDIBULAR RAMI

SKULL	<i>M. fricki</i> , new species	<i>M. grandis</i> (Douglass)		<i>M. grandis loomisi</i> (Schlaikjer)		<i>M. grandis loomisi</i> (Schlaikjer), geologic variety	
	Holotype F:A.M. 33308	Holotype C.M. 990	Referred C.M. 1194 ²	Holotype M.C.Z. 2820	Referred F:A.M. 42320	Example F:A.M. 33301	Referred F:A.M. 37244
Stage of wear of teeth	(w)	(w+)	(w $\frac{1}{2}$)	(w)	(w)	(w+)	(w $\frac{1}{2}$)
Length (including supraoccipital crest and incisors)	285	391	—	403	387.5	378	374
Basal length (from anterior notch of foramen magnum to posterior base of I ¹)	246	327	327	335	336	334	322
Width (max.)	212.5	189	243	175	(240)	214	178
Width of brain case (max.)	85	73	92	74	91	82	84.5
Width, interorbital (min.)	89.5	83	99	76	—	87	72
Distance from anterior rim of orbit to anterior base of canine	130	171	157	180.5	175	163	166
Distance from anterior rim of orbit to supraoccipital crest	155	207	—	219	212.5	207.5	200
Length of nasals	126.5	—	—	—	—	(156)	160
Width of muzzle at infraorbital foramina	84	89	96	74	104	97.5	84
Width across canines	79.5	71	97	79	90	92.5	71.5
Length, C—M ³ incl.	168	199	191.5	205	194.5	195	186.5
Length, P ¹ —M ³ incl.	151	176	162.5	171	166	167.5	159
Length, P ¹ —P ⁴ incl.	68.5	83	78	87	80	81	76
Length, M ¹ —M ³ incl.	88	96	88.5	88	90	88	87
Width of M ³ (max.)	33.5	34	31	31	32.5	31.5	29
Depth of malar below orbit.	41.5	—	—	—	45.5	42	42.5
MANDIBULAR RAMUS							
Length (max., including incisors) .	241	306	282	310	309	311.5	—
Length, /C—condyle incl.	202.5	292	275	301.5	293	287	—
Depth of jaw under coronoid	140	142	146.5	148	—	126	—
Depth of jaw below anterior edge of M ₃	54.5	56	62	63	50	56	—
Length, /C—M ₃	169	204	189.5	208.5	193	208	—
Length, P ₁ —M ₃ incl.	155	191	174	193	177	189	—
Length, P ₁ —P ₄ incl.	70	90	81.5	98	86	89	—
Length, M ₁ —M ₃ incl.	89	102.5	93	97	98	100.5	—

¹ (), Approximate. All measurements in millimeters.

² Holotype of "*P. hollandi*."

TABLE 2

Megoreodon, NEW GENUS. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

	<i>M. fricki</i> , new species	<i>M. grandis</i> (Douglass)		<i>M. grandis loomisi</i> (Schlaikjer)		<i>M. grandis loomisi</i> (Schlaikjer), geologic variety
	Holotype F:A.M. 33308	Holotype C.M. 990	Referred C.M. 1194	Holotype M.C.Z. 2820	Referred F:A.M. 42320	Example F:A.M. 33301
Length of humerus (articular) . .	(198)	—	220	—	(212)	206
Length of radius (articular) . . .	168	—	—	172	182	192
Length of ulna (max.)	((235))	—	—	232	247	254.5
Length of metacarpal III (max.) .	85.5	—	86	—	90	89
Length of femur (articular) . . .	(217)	250	262	—	239.5	245
Length of tibia (articular)	192	—	204	203	200	202
Length of metatarsal III (max.) .	89.5	—	86	86	82	85.5
Length of calcaneum (max.) . . .	84.5	—	91	—	—	81.5

¹ (), Approximate. All measurements in millimeters.

SUMMARY OF SPECIES AND TYPES

Two species and one subspecies of *Megoreodon* from four lower Miocene localities are here recorded:

1. *Megoreodon fricki*, new species, from Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Skull, mandible, and skeleton, F:A.M. 33308. Figures 1-3, 23-25.

2. *Megoreodon grandis* (Douglass), from Lewis and Clark County, Montana. (Approximate Gering equivalent.)

HOLOTYPE: Skull, mandible, and skeletal elements, C.M. 990.

2a. *Megoreodon grandis loomisi* (Schlaikjer), from Goshen County, Wyoming; referred remains from Niobrara County, Wyoming. (Gering.)

HOLOTYPE: Skull, mandible, and skeletal elements, M.C.Z. 2820.

2b. *Megoreodon grandis loomisi* (Schlaikjer), geologic variety, from Niobrara County, Wyoming, and Morrill and Sioux counties, Nebraska. (Monroe Creek.)

EXAMPLE: Skull, mandible, and skeleton, F:A.M. 33301. Figures 1-3, 18, 23-25.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MEGOREODON

TOTAL AVAILABLE SPECIMENS: 56²

1. *Megoreodon fricki*,³ new species

From the Monroe Creek formation,
Niobrara County, Wyoming

DESCRIPTION

SKULL: Smallest known of genus (considerably shorter than examples of *M. grandis*

² Includes 47 F:A.M. and three U.N.S.M. specimens.

³ Named in honor of Mr. Childs Frick who has made possible the present revision of the oreodonts.

loomisi, geologic variety, from the same formation); brachycephalic; facial region short (considerably shorter than other species or subspecies of genus); supraoccipital wings with less posterior projection than in other forms of genus; nasals unusually broad and flaring in region of anterior nasal-maxilla contact (nasals long and narrow in other examples of genus with gradual posterior reduction in width from nasal-maxilla contact); infraorbital foramen⁴ above anterior portion

⁴ The holotype possesses a second foramen near the nasals (see fig. 1, p. 232).

of P⁴; lacrimal fossa pronounced; depression above premolar region very noticeable; occipital condyles light but widely spread; bulla more inflated than in other species of genus; postglenoid process higher and lighter than in average examples of genus.

MANDIBLE: More robust and shorter than in other species of genus; symphysis shorter than that of *M. grandis loomisi*; ascending ramus high and unusually narrow (anteroposteriorly); condyle lighter and smaller than found in other species of genus.

DENTITION: Less brachyodont than in other species of genus; series shorter than in other forms of the genus (series long for length of skull, extending posteriorly beyond orbit); short diastema between C/ and P¹; premolars very crowded and overlapping.

LIMBS: Approximately of same lengths and characters as in other examples of genus.

MEASUREMENTS: Tables 1 and 2 (pp. 166–167).

ILLUSTRATIONS: Figures 1–3, 23–25.

DISCUSSION

The new species is considered to be a specialized form (see discussion, p. 165), found in the same locality and formation (Monroe Creek) as examples of *M. grandis loomisi*, geologic variety. The foreshortened skull and mandible of *M. fricki* might suggest a dwarfed form, but the size of the limb elements is the same as in *M. grandis loomisi*, geologic variety. The dental series of *M. fricki* are not reduced in length in proportion to the skull and mandible but are approximately the same as in the geologic variety.

The skull and mandible of the holotype of *M. fricki* have been crushed somewhat, but, with a generous allowance for this deformation, the length of the skull is considerably less than that of other forms of the genus.

The material referred to this species was collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933–1934.

Three specimens are here recorded:

HOLOTYPE

Skull with I¹–M³, mandible with I¹–M³, and most of skeleton. (w)¹

F:A.M. 33308

From Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933

Figures 1–3, 23–25

REFERRED FROM TYPE LOCALITY, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

2 ASSOCIATED INDIVIDUALS

Partial skull with P¹–dP²–M² (erupt.²) and mandible with I¹–C alv. and P¹(br.)–dP³–M¹ (i)

F:A.M.

44885

2 femora, tibia, astragalus, calcaneum, and pelvis

44885A

The above skeletal elements were found associated in the field with the immature skull and mandible. The skeletal elements, however, seem to be from a mature individual and are slightly longer than those of the holotype. This difference in length is well within the expected individual variation of a species.

2. *Megoreodon grandis* (Douglass)

From lower Miocene deposits (approximately equal in age to the Gering formation of the central Great Plains), Lewis and Clark County, Montana

Promerycochoerus grandis DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, p. 104, pl. 27.

Promerycochoerus montanus grandis (Douglass),

THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 139, figs. 4, 96; pl. 18.

Promerycochoerus hollandi DOUGLASS, 1907, *ibid.*, p. 106, pl. 28. THORPE, 1937, *ibid.*, p. 124, fig. 81; pl. 10, fig. 2; pl. 15, figs. 4–5.

CHARACTERS

SKULL: Large and massive (larger than ex-

¹ Stage of wear of teeth: (i), immature; (m), mature; (w), worn.

² Abbreviations used in description: alv., alveolus or alveoli; br., broken; erupt., erupting; rt., root or roots.

amples of *M. fricki*, tendency to be smaller than those of *M. grandis loomisi*; infraorbital foramen above posterior portion of P⁴.

MANDIBLE: Smaller than in average examples of *M. grandis loomisi*.

DENTITION: Series similar to those of examples of *M. grandis loomisi*.

LIMBS: Approximately equal to those of other forms of genus.

MEASUREMENTS: Tables 1, 2, and 3 (pp. 166, 167, and 170).

ILLUSTRATIONS: See Douglass, 1907, plate 27.

DISCUSSION

Megoreodon grandis, the genotypic species, does not differ from the examples of *M. grandis loomisi* except for the slightly smaller average size. The holotype has an opening on the skull in the position where a facial vacuity would be. It is questionable, however, if this does represent a true vacuity; perhaps it is merely a break in the surface of the skull. In the oreodonts, even within a single species, a facial vacuity may be absent in one example and present in another. Hence vacuities are not considered diagnostic in this genus (see discussion of vacuities in the Phenacocoelinae, Schultz and Falkenbach, 1950, p. 105).

At the time Douglass¹ described "*Promerycochoerus*" *grandis* and "*P. hollandi*" there were four specimens of this group in the Carnegie Museum's collection, all from the Canyon Ferry area of Montana. Douglass established his specific divisions of the two forms in question on the width of the skulls. He based his description of "*P.*" *grandis* on a narrow skull, C.M. 990, and "*P. hollandi*" on a wide skull, C.M. 1194. In table 3 (p. 170 of present report), the measurements of the four specimens are given, and it is evident that the two skulls in question are approximately the same length but differ in width. The holotype of the former species has slightly more massive teeth than the latter. Douglass considered the limb elements of "*P. hollandi*" (the wider skull) as being more robust than those of "*P.*" *grandis* (the narrower skull).

The writers believe that "*P. hollandi*" is synonymous with *M. grandis* based on the following comparisons

1. The difference in the widths of the two skulls appears to be due to sex variation, the narrower one representing a female (see discussion of sex variation in *Ustatochoerus profectus*² and *Promerycochoerus carrikeri*³). In Nebraska and Wyoming wide and narrow skulls with characters otherwise identical are found associated in the same deposits, thus strongly suggesting sexual differences.

2. The lighter and heavier dentitions are also found to vary in individuals, which may or may not be attributed to sex variation. (See table 4, page 173, for individual variation.)

3. The variation in the limb elements mentioned by Douglass are well within individual variation within a species. The lighter limbs,⁴ however, may indicate female examples. The writers have found that limb elements of a species show as much, if not more, individual size variation than do the skulls.

A comparison of tables 3 and 4 (pp. 170-173) demonstrates that the four Carnegie Museum skulls of *M. grandis* are on the average smaller than material listed under *M. grandis loomisi* (Schlaikjer), geologic variety.

In describing "*P.*" *grandis*, Douglass⁵ noted several characters which strengthen the writers' contention that this species and related forms do not belong to the genus *Promerycochoerus*. Douglass reported: "The species [*M. grandis*] is one of the largest of the family. The skull is of the long and narrow type; the face is long and narrow; the upper line of the skull is nearly straight; the sagittal crest is quite high, but not heavy; . . . the brain case is comparatively small; . . ."

In *Promerycochoerus*⁶ the skull is wide; the "upper line" of the skull is not straight; the sagittal crest is comparatively robust; and the brain case is inflated.

Thorpe⁷ considered *M. grandis* as a subspecies of "*P.*" *montanus* and stated: "The skull is among the longer ones in the genus [*Promerycochoerus*] and is dolichocephalic, with a long, narrow face and with the superior contour nearly straight. . . ."

² Schultz and Falkenbach, 1941, p. 36.

³ *Idem*, 1949, p. 94.

⁴ *Idem*, 1941, p. 11.

⁵ 1907, p. 105.

⁶ Schultz and Falkenbach, 1949, p. 84.

⁷ 1937, pp. 139-141.

¹ 1907, pp. 104-106

TABLE 3

Megoreodon grandis (DOUGLASS). COMPARATIVE MEASUREMENTS¹ OF FOUR SPECIMENS FROM CANYON FERRY AREA OF MONTANA

	C.M. 990 ²	C.M. 1194 ³	C.M. 1305	C.M. 851	Percent- age of Variation
SKULL					
Stage of wear of teeth	(w+)	(w‡)	(w+)	(w‡)	
Length	391	—	370	359	8
Basal length.	327	327	317	312	4
Width (max.)	189	243	196	236	22
Length, C/-M ³ incl.	199	191.5	188.5	189	5
Length, P ¹ -M ³ incl.	176	162.5	160	155	11
Length, P ¹ -P ⁴ incl.	83	78	79	71	14
Length, M ¹ -M ³ incl.	96	88.5	87.5	87	9
Width, P ¹	13	9.5	10.5	9	30
Width, P ⁴	23.5	20	21	21	14
Width, M ³	34	31	30	31	11
MANDIBULAR RAMI					
Length, /C-M ₃ incl.	204	189.5	191	190	7

¹ All measurements in millimeters.

² Holotype of "*Promerycochoerus*" *grandis* = *Megoreodon grandis*.

³ Holotype of "*P. hollandi*" = *M. grandis*.

"DISCUSSION: This subspecies is certainly closely related to *P. montanus*, although by no means synonymous."

The writers considered the species *montanus* under the subgenus *P. (Pseudopromerycochoerus)*⁴ on the basis of its having a wide skull, a well-inflated brain case, a small, light, brachyodont dentition, and a light, specialized, zygomatic arch.

Thorpe considered the lower Miocene beds

in the Canyon Ferry area of Montana as equal to the "lower" Harrison (=Harrison) of the Great Plains, but the present writers consider these deposits as approximately equal to the Gering. (See discussion, p. 172.)

The holotype of *M. grandis* is not refigured in this report since it differs only slightly from examples of *M. grandis loomisi* which is figured (fig. 1-3, 18.)

Six specimens are here recorded:

HOLOTYPE

Skull with I¹-M³, partial scapula, humerus, radius, femur, tibia, pelvis, and vertebrae. (w+)

C.M. 990

From Canyon Ferry, Lewis and Clark County, Montana; collected by Earl Douglass, 1902

Figured by Douglass, 1907, pl. 27; Thorpe, 1937, figs. 4, 96; pl. 18

REFERRED FROM TYPE AREA, CANYON FERRY, LEWIS AND CLARK COUNTY, MONTANA

(Carnegie Museum specimens collected by Earl Douglass; F:A.M. material by Charles H. Falkenbach, 1936)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with I¹-M³, mandible with /C-M₃, humerus, femur, tibia, manus and pes elements, pelvis, and vertebrae (w‡)

C.M.
1194

⁴ Schultz and Falkenbach, 1949, p. 121.

The above specimen is the holotype of "*Promerycochoerus hollandi*" Douglass. Figured by Douglass, 1907, p. 28; Thorpe, 1937, fig. 81; pl. 10, fig. 2; pl. 15, figs. 4-5.

3 SKULLS AND MANDIBLES		C. M.
Skull with I ¹ -M ³ and mandible with I ¹ -M ³	(w ⁺)	851
Skull and mandible	(w ⁺)	1305
Partial skull with C/-M ³ and partial mandible with P ¹ -M ³	(w ⁺)	F:A.M. 42326
MAXILLA		
Maxilla (2 pieces) with I ³ -C/ and P ¹ -M ³	(M ⁺)	49641

2a. *Megoreodon grandis loomisi* (Schlaikjer)

From the Gering formation, Goshen County, Wyoming; referred remains from Niobrara County, Wyoming; and 2b, a geologic variety from the Monroe Creek formation, Niobrara County, Wyoming, and Morrill and Sioux counties, Nebraska

Promerycochoerus loomisi SCHLAIKJER, 1934, Proc. Boston Soc. Nat. Hist., vol. 40, no. 3, p. 225 (preliminary report); 1935, Bull. Mus. Comp. Zool., vol. 76, no. 4, p. 172, pls. 33-35.

Promerycochoerus gregoryi loomisi (Schlaikjer), THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 122, pl. 13, figs. 1-2; pl. 46, fig. 2.

CHARACTERS

SKULL: Characters similar to those of *M. grandis*; basal lengths longer on average than examples of latter species; infraorbital foramen above posterior portion of P⁴.

MANDIBLE: Similar to that of *M. grandis*; postsymphysis below anterior portion of P³.

DENTITION: Similar to that of *M. grandis*; series of greater length than in examples of *M. fricki*; small diastema between P¹ and P².

LIMBS: Similar to those of examples of *M. grandis* and *M. fricki*.

MEASUREMENTS: Tables 1, 2, 4 (pp. 166, 167, and 173).

ILLUSTRATIONS: Figures 1-3, 18, 23-25.

DISCUSSION

The subspecies *Megoreodon grandis loomisi* apparently is little more than a geographic variety of the species, and the subspecific name is held for convenience only, since the name is already available. The amount of material at hand from Montana is insufficient to establish the amount of individual variation present in *M. grandis*. Perhaps fur-

ther examples from the Montana locality will show that the subspecies is synonymous with the species, or that it is specifically different. The only noticeable difference between the two forms is that the skulls of *M. grandis* are smaller on the average than those of the subspecies.

The holotypes of both *M. grandis* and *M. grandis loomisi* are here considered as representing skulls of females. Examples of what is considered to be male and female skulls are evident in table 4 (p. 173; wider skull = male).

Schlaikjer,¹ who reported the holotype of *M. grandis* as coming from the "Lower Miocene, Lower Harrison formation, approximately 200' above the Brule-lower Harrison contact," considered all deposits in this area (above the Brule contact) as Harrison in age. Field parties of the Frick Laboratory and the University of Nebraska State Museum, however, have collected from this same area. The deposits have been measured and studied by the writers, who consider the sediments to be chiefly Gering. The fauna from the Goshen County locality of Schlaikjer includes *Mesoreodon*,² *Desmatochoerus*,³ and leptachenids, all of which are typical Gering and Monroe Creek. Leptachenids are index fossils in the Gering and Monroe Creek or their approximate equivalents. No remains of *Promerycochoerus* have been found in the Gering or Monroe Creek formations of Nebraska or Wyoming.

Thorpe⁴ considered *M. grandis loomisi* as a subspecies of "*Promerycochoerus*" *gregoryi* (here considered as *Desmatochoerus curvidens gregoryi*, p. 183) and stated: "On the basis of

¹ 1934, p. 225; 1935, p. 172.

² Schultz and Falkenbach, 1949, p. 131.

³ Present report (p. 177).

⁴ 1937, p. 123.

the skeleton, the proportions of this species are exceedingly close to those of *P. gregoryi*, and I shall ally it with that form [*P. gregoryi loomisi*]."

The holotype of *Desmatochoerus curvidens gregoryi* (p. 184) consists of a skull and mandible only and lacks any skeletal elements. Loomis,¹ however, referred a skull, mandible, and skeletal elements, A.C. 1931-109, to "*Hypselchoerus*" *gregoryi* (= *Desmatochoerus curvidens gregoryi*, p. 183). This partial skeleton and not the holotype must have been the basis for Thorpe's conclusions, i.e., in considering *Megoreodon grandis loomisi* as a subspecies of *D. c. gregoryi*. The referred specimen of Loomis has a skull which is decidedly different from examples of *Megoreodon* and *Desmatochoerus*, and the present writers have referred it to *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*.² It is true that the holotype of *Desmatochoerus curvidens gregoryi* has many characters in common with those of the genus *Megoreodon*, and both genera are here considered under the *Desmatochoerinae* (pp. 163 and 177). The outstanding differences between *Desmatochoerus* and *Megoreodon* are apparent in the larger skull size and the more massive dentition of the latter. (See tables 1 and 5.)

In the original description of "*Promerycochoerus*" *loomisi* by Schlaikjer,³ *Megoreodon grandis* and *M. g. loomisi* were compared as follows:

"1. Skull [*M. g. loomisi*] somewhat longer and narrower. [*M. g. loomisi* skull (M.C.Z. 2820)=403 mm. long and 174 mm. wide; *M. grandis* skull (C.M. 990)=391 mm. long and 189 mm. wide.]

"2. Antorbital region proportionately deeper and more elongated. [The depth of the face of the holotype of *M. g. loomisi* is greater than in the holotype of *M. grandis*, but the more "elongated antorbital region" in the former is not apparent. In *M. grandis loomisi* the distance from anterior rim of orbit to anterior base of canine is 180.5 mm. and in *M. grandis*, 171 mm.]

"3. P^1-P^4 almost equals M^1-M^3 in length. [*M. g. loomisi*, $P^1-P^4=87$ mm.; $M^1-M^3=88$

mm. *M. grandis*, $P^1-P^4=83$ mm.; $M^1-M^3=96$ mm. Some differences in the dentition are apparent, but within the genus *Megoreodon* considerable individual variation is present in the proportions of the molar to the premolar series, as demonstrated in table 4, p. 173, of the present report.]

"4. Incisors, especially I^3 proportionately larger. [Some variation is present but within the individual variation of one species.]

"5. Premaxillaries less protruded anteriorly. [Within individual variation.]

"6. Diastema between P^1 and P^2 . [This is usually true in all large oreodont skulls. Some individuals have a more pronounced diastema than others within a single species. The holotype of *M. grandis* seems to lack this diastema.]

"7. Style on molars more developed. [Slightly more prominent.]

"8. Longer limbed and body seemingly of lighter construction. [Douglass⁴ gave only the length of the femur in his description of *Megoreodon grandis* and failed to mention the limb elements of "*P. hollandi*," except to state that the limbs of both forms were approximately equal. "*P. hollandi*" is here considered synonymous with *M. grandis*. The skeletal measurements of all three specimens in question have been made by the present writers and they compare favorably (see table 2).]"

The comparisons made by Schlaikjer were based on the holotypes only, evidently without allowances for individual variation which is a prime factor in considering specific characters in the oreodonts. The individual variation within a single subspecies of *Megoreodon* is demonstrated in table 4 (p. 173).

Schlaikjer in further comparisons of the two forms stated, "Although the two species occur at approximately the same geological level, *P. grandis*, so far as known, forms a splendid ancestral stage, structurally at least, for *P. loomisi*."

The writers see very little evidence in the possibility that either form is ancestral to the other. We do agree, however, that both forms came from deposits of approximately the same age, i.e., the Gering (not Harrison as suggested by Schlaikjer).

⁴ 1907, pp. 104 and 106.

¹ Loomis, Frederic B., 1933, Bull. Geol. Soc. Amer., vol. 44, p. 728, fig. 9.

² Schultz and Falkenbach, 1949, p. 128.

³ 1934, p. 227.

TABLE 4

Megoreodon grandis loomisi (SCHLAIKJER), GEOLOGIC VARIETY, FROM THE MONROE CREEK FORMATION.
COMPARATIVE MEASUREMENTS¹ OF INDIVIDUALS WITHIN ONE SUBSPECIES

F:A.M.	Skull				Dentition						
	State of Wear	Length	Basal Length	Width	Length				Width	Length	AP ²
					C/-M ³	P ¹ -M ³	P ¹ -P ⁴	M ¹ -M ³	M ³	/C-M ₃	M ₃
33300	(w ⁺)	(400)	—	(170)	207	177	87	92	30	—	(50)
33301	(w ⁺)	378	334	214	195	167.5	81	88.5	31.5	208	46.5
33302	(w)	((365))	322	(245)	192	162	78	85.5	28	—	—
33328A	(w)	—	—	((187))	188	160.5	80	86.5	—	—	—
33328B	(w)	—	—	—	192.5	(165)	87	86	—	—	—
33330	(-M)	((360))	((313))	—	183	160	76	86	29	—	—
33332	(w ⁺⁺)	—	—	((210))	188	166.5	83	87	33	190	47.5
33333	(w ⁺⁺)	—	—	—	201.5	172.5	88	89	32.5	206.5	46.5
33334	(w ⁺)	—	—	((185))	193	165.5	82	87	30	197	45.5
33358	(w ⁺)	—	—	—	185	162.5	76	87.5	31	—	—
37244	(w ⁺)	374	322	178	189	161	74.5	88	29	—	—
42321	(w)	396	334	—	194	168.5	82.5	92.5	32	186.5	45
42322	(w)	—	—	—	190.5	164.5	79	90	—	—	44
44888	(w ⁺)	—	—	—	200	171	88	86.5	—	—	—
44890	(w ⁺)	—	—	(180)	—	156	80	(84)	33	—	46.5
44891	(w)	—	—	—	183.5	162	83	88	—	—	42
44893	(w)	—	—	—	195.5	168	81.5	89	32	—	—
45433	(w ⁺)	((400))	((330))	203	—	(162)	(77)	89	32	—	43.5
45436	(w ⁺)	431	357	142	209	176	84.5	97.5	30	211	45.5
45437	(w ⁺⁺)	377	329	(225)	194	163	83	81.5	30	194	43

¹ (), Approximate; (()), estimated. All measurements in millimeters.

² AP, anterior-posterior length.

In his conclusions, Schlaikjer³ stated, "*Pro-merycochoerus loomisi* is an end member of a phylum of narrow-skulled forms and is a splendid example of gigantism among oreodonts."

It is here considered that *M. grandis* and *M. grandis loomisi* are the earliest (geologically) known forms of the genus *Megoreodon* and that the subspecies continued to survive

through Gering and Monroe Creek times with very little, if any, change. The writers agree with Schlaikjer that this genus is a good example of gigantism, at least in size of skulls.

The F:A.M. specimens were collected by Gene Roll, John Lynch, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1931-41.

Seven specimens are here recorded:

HOLOTYPE

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

M.C.Z. 2820

From upper part of Gering formation, Bear Mountain, Goshen County, Wyoming; collected by Erich M. Schlaikjer

Figured by Schlaikjer, 1935, pls. 33-35; Thorpe, 1937, pl. 13, figs. 1-2; pl. 46, fig. 2

³ 1934, p. 229.

REFERRED FROM GERING FORMATION, LITTLE MUDDY CREEK,
NIOBRARA COUNTY, WYOMING

SKULL, MANDIBLE, AND 2 ASSOCIATED SKELETONS

Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , partial scapula, 2 partial humeri, 2 radii (1 partial), 2 ulnae (1 partial), 2 partial femora, 2 tibiae (1 partial), manus and pes elements, pelvis, and ribs. Figures 2-3	(w)	F:A.M. 42320
2 partial humeri, 2 radii (1 partial), 2 ulnae (1 partial), 2 partial femora, 2 tibiae (1 partial), manus and pes elements, and partial pelvis.	(I)	42320A
The above two specimens were found associated in the field.		
The mature skeletal elements are considered to belong to the same individual as the skull and mandible.		

3 SKULLS

Partial skull with P ¹ (br.)-M ³	(w ⁺)	33331
Partial skull with I ¹ (alv.)-M ³	(w ⁺)	42324
Partial skull with I ¹ -dP ² -M ²	(I)	44886

MANDIBLE

Partial mandible with P ₁ -P ₃ rt. and P ₄ -M ₃	(M ⁺)	42323
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2b. Geologic Variety from the Monroe Creek formation, (A) Niobrara County, Wyoming, and (B) Morrill and (C) Sioux counties, Nebraska

and does not differ noticeably from examples of *M. grandis loomisi* from the Gering. In most instances of phylogenetic lines of the oreodonts, at least a size change is evident between material from two different formations in one general locality. Table 4 (p. 173) demonstrates individual variation of the geologic variety.

Forty specimens are here recorded:

DISCUSSION

The following listed material is here considered as a geologic variety of *M. grandis loomisi* from the Monroe Creek formation,

A. FROM MUDDY CREEK, NIOBRARA COUNTY, WYOMING

EXAMPLE

Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ and most of skeleton. (w ⁺)	F:A.M. 33301	From below the "white layer," ¹ Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1934 Figures 1-3, 18, 23-25
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FROM BELOW THE "WHITE LAYER":

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with C/-M ³ , partial mandible with I ₁ -I ₃ rt. and /C-M ₃ , partial scapula, and partial humerus	(w)	F:A.M. 42322
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2 SKULLS AND MANDIBLES

Crushed anterior portion of skull with I ² -M ³ and partial mandible with /C-M ₃	(w ⁺)	44888
The premolar series of the above specimen is longer than the molar series.		

¹ In the area from which most of the listed material was collected, a "white layer" is present near the top of the exposures on Muddy Creek, Wyoming. The specimens from above the "white layer" show no observable differences in size or characters from those below the "white layer." In the field this layer makes a good "marker," and the following listing of material states the relationship of occurrence in respect to the layer, wherever possible.

Anterior portion of skull with C/-dP²-dP⁴(rt.) and partial mandible with I₁-dP₂-M₂ (I) F:A.M. 44951

MANDIBLE

Mandible with I₁-M₃ (M+) 42325

FROM ABOVE THE "WHITE LAYER":

2 ASSOCIATED SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Partial skull with I¹-M³ and mandible with I₁-M₃. (W) 33328A
 Poorly preserved partial skull with I¹-M³ and partial right ramus with P₁-M₃ (P₂ and P₄ absent) (W) 33328B
 Fragmentary limb elements, manus and pes elements, vertebrae, and ribs of two individuals 33328A-B

2 ASSOCIATED SKULLS, MANDIBLES, AND SKELETAL ELEMENTS, IMMATURE

Partial skull with I²-dP⁴-M²(germ) (P¹-P³ alv.) and mandible with I₃-dP₂-M₁ (mandible attached to skull) (I) 44889A
 Partial skull with I¹-dP²-M²(germ) and partial mandible with I₁-dP₂-M₁. . . (I) 44889B
 Partial humerus, manus, fragmentary limbs, vertebrae, and ribs. 44889A-B

The above two skulls, mandibles, and skeletal elements were found associated in the field. The skeletal elements may belong to either skull.

4 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Partial skull with I¹-M³, mandible with I₁-M₃, 2 partial scapulae, 2 partial humeri, and fragments (W) 42321
 Partial skull with P¹(br.)-M³, partial mandible with P₂-M₃, and most of skeleton (still in field block) (W+) 45433
 Partial skull with M²(br.)-M³, partial left ramus with M₂(br.)-M₃, and most of skeleton (still in field block) (W⁺) 45434
 Skull and C/(br.)-dP²-M³, mandible (attached) with I₁-C/ rt. and P₁-dP₄-M₃(erupt.), 2 partial scapulae, 2 partial humeri, partial radius, partial ulna, and vertebrae. (I) 45444

SKULL

Skull with I¹-I³ alv. and C/-M³ (lacking supraoccipital region, brain case, and left zygomatic arch) (W) 33302

SKELETAL ELEMENTS

2 femora, 2 tibiae, 2 pedes, and pelvis 44897

FROM DEPOSITS EQUAL TO THOSE ABOVE "WHITE LAYER":

SKULL, MANDIBLE, AND 2 SKELETONS (ASSOCIATED)

Anterior portion of skull with I²-M³, partial mandible with I₁-M₃, 2 radii (1 partial), 2 ulnae (1 partial), manus, 2 femora, 2 tibiae, 2 pedes, and pelvis . . (W⁺) 33332
 Partial scapula, partial humerus, 2 partial femora, partial tibia, astragalus, calcaneum, pes, partial pelvis, vertebrae, ribs 33332A

The above two specimens were found associated in the field. The division of the skeletal elements (above) is based on the position of the elements in relation to the skull. It is possible that the association may actually be reversed.

SKULL, MANDIBLE, AND 2 SKELETONS (ASSOCIATED)

Anterior, inferior portion of skull with I¹-M³, mandible with I₁-M₃, and most of the skeleton (still in field block) (W⁺) 33333
 Partial manus 33333A

The above two individuals were found associated in the field. The premolar series are subequal in length to the molar series in the skull. The manus of the second individual is smaller than that of the first specimen.

SKULL, MANDIBLE, AND SKELETON, IMMATURE

Partial skull with dP^4-M^3 , partial mandible with P_3 (erupt.)- M_3 (P_4 erupt.), and most of the skeleton (I)	F:A.M. 45435
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The above specimen was found in the higher portion of the exposures.

3 SKULLS AND MANDIBLES

Skull with $I^2-C/rt.$ and P^1-M^3 (lacking zygomatic arches and anterior of nasals), and mandible with P_1-M_3 (P_3-P_4 br.) (w_1^+)	33300
Partial skull with I^1-M^3 and partial mandible with I_1-M_3 (w_1^+)	33334
Inferior, anterior portion of skull with I^2-M^3 and partial mandible with I_1-M_3 (w)	33358

3 SKULLS

Partial skull with $C/-M^3$ (-m)	33330
Complete skull with I^1-M^3 . Figure 3. (w_1^+)	37244
The above specimen was found in the higher portion of the exposures. Considered a female example of the subspecies.	
Right side of skull with $C/-dP^2-M^3$ (I)	44887

2 PARTIAL SKELETONS (ASSOCIATED)

Radius, ulna, astragalus, calcaneum, and partial manus	33329A
Deciduous teeth, 2 partial radii, ulna, tibia, astragalus, and foot bones	33329B
The above two specimens were found associated in the higher portion of the exposures.	

B. MORRILL COUNTY, NEBRASKA

FROM 5 MI. N. AND 2 MI. E. OF BRIDGEPORT, COLLECTED BY S. R. SWEET AND A. C. G. KAEMPFFER, BRIDGEPORT, 1931:

SKULL AND MANDIBLE

Partial skull with $C/-M^3$ and partial mandible with I_2-M_3 (w_+)	C.N.H.M. PM14771
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SKULL

Anterior portion of skull with P^2-M^3 (w_+)	U.N.S.M. 28017
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MAXILLAE

Partial left and right maxillae with M^2-M^3 (w_1^{++})	1073
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The above three specimens were found associated in one field block.

FROM $\frac{1}{4}$ MI. E. OF REDINGTON GAP, COLLECTED BY E. L. BLUE, FRANK CRABILL, LOREN C. EISELEY, AND C. BERTRAND SCHULTZ, 1931:

SKULL

Anterior portion of skull with I^1-I^3 alv. and $C/-M^3$ (P^1-P^4 alv.) (w_1^+)	U.N.S.M. 28019
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C. FROM SIOUX COUNTY, NEBRASKA

FROM LEDINGHAM RANCH, COLLECTED BY MORRIS F. SKINNER AND PARTY, 1941:

5 SKULLS AND MANDIBLES

Skull with $C/-P^3$ rt. and P^4-M^3 (lacking premaxillae) and partial mandible with $P_3(rt.)-M_3$ (P_4 br.) (w_1^+)	F:A.M. 44890
Anterior portion of skull with $C/-M^3$ and mandible with I_1-M_3 (P_1 alv.) (w)	44891
Anterior, inferior portion of skull with $P^1(br.)-M^3(br.)$ (P^2 br.) and partial mandible with $P_2(br.)-M_3$ (w)	44892
Skull with I^1-M^3 and mandible with $I_3(br.)-M_3$ (w_+)	45436
Skull with $I^1(alv.)-M^3$ and mandible (attached) with I_1-M_3 (w_1^{++})	45437

The superior premolar series of the above specimen is longer than the molar.

SKULL		F:A.M.
Partial skull with I ¹ -M ³ alv. and C/-M ³ (P ² -P ³ alv.)	(w)	44893
MAXILLA		
Partial right maxilla with P ⁴ -M ³	(w)	44894
MANDIBULAR RAMUS		
Partial right ramus with I ₂ /C alv. and P ₁ (rt.)-M ₂ (P ₂ br.)	(w†)	44895

II. DESMATOCHOERUS THORPE

Promerycochoerus (*Desmatochoerus*) THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 1, art. 14, p. 241.

Promerycochoerus Douglass, HAY (in part only), 1930, Carnegie Inst. Washington Publ., no. 390, vol. 2, p. 784. THORPE (in part only), 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 104.

Hypselochoerus LOOMIS, 1933, Bull. Geol. Soc. Amer., vol. 44, p. 728.

Hypselochoerus Loomis = *Promerycochoerus* Douglass, THORPE, 1937, loc. cit.

GENOTYPE: *Desmatochoerus curvidens* (Thorpe).

SKULL: Medium size, basal lengths ranging from 233 to 285 mm., widths from 136 to 196 mm.; dolichocephalic to mesocephalic; supra-occipital wings posteriorly extended beyond occipital condyles, but not widely spread; vacuities present on either side of midline of exoccipital above occipital condyles; sagittal crest long and high [higher than in *D. (Paradesmatochoerus)*, decidedly higher than in *Pseudodesmatochoerus*]; brain case long and narrow, (not inflated to the degree found in *Promerycochoerus*); frontals comparatively narrow with prominent protuberance at midline above the orbits (protuberance varying in size within a single species, usually present in all individuals); nasals long and narrow; anterior nasal-maxilla contact above area of P¹; orbit moderately large, looking mostly outward and forward, oval vertically, with long axis sloping upward anteroposteriorly; squamosal moderately light to robust (lighter zygomatic arch usually designates a female example of species); zygomatic arch with noticeable inward curve or notch just posterior of the orbit; malar moderately deep below orbit; infraorbital foramen above P²-M¹; lacrimal fossa prominent; facial vacuity usually present; depression present on side of face above premolar region (similar to other

genera of Desmatochoerinae); muzzle slightly inflated; premaxillae joined for short distance; occipital condyles of moderate size; paroccipital process long vertically, wide at base, and laterally compressed (differing from examples of *Merycochoerus*, *Brachycrus*, *Ustattochoerus*, *Ticholeptus*, and *Promerycochoerus*, in which paroccipital process is laterally expanded); bulla inflated, laterally compressed, long anteroposteriorly; postglenoid process robust.

MANDIBLE: Moderately light, postsymphysis below P₂-P₄; symphysis elongated; ramus moderately shallow; muzzle slightly inflated; inferior border of ramus almost parallel to alveolar border (P₁-M₂) with a noticeable downward curve posterior to M₂; ascending ramus moderately high; condyle moderately large and robust, set at less than right angle to axis of dental series, with external border of condyle farther forward and higher than internal border.

DENTITION: Brachyodont (more so than in examples of *Megoreodon*, but similar to that of other examples of Desmatochoerinae from Miocene, less so than in *Prodesmatochoerus* from Oligocene); C/ and P₁ large; /C approximately three times the size of I₃; superior premolars almost parallel to alveolar border, not overlapping; superior molars with moderately prominent external styles; P¹-P³ each with anterior intermediate crest; P₂ and P₃ each with posterior intermediate crest.

LIMBS: Moderately robust (similar to those of other genera of Desmatochoerinae, except for shorter examples of *Megoreodon* and shorter and lighter ones of *Prodesmatochoerus*).

MEASUREMENTS: Tables 5 and 6 (pp. 180-181).

ILLUSTRATIONS: Figures 4-7, 18 (skulls, rami, and dentitions), 23-25 (limbs).

DISCUSSION

Desmatochoerus was originally proposed as a new subgenus of *Promerycochoerus* by Thorpe,¹ with *P. (D.) curvidens* as the subgenotype. Thorpe concluded that *Desmatochoerus* was the link between *Eporeodon* and *Promerycochoerus*.² The writers do not agree with this relationship and endeavor to demonstrate that the phylum of *Desmatochoerus* is a distinct line from that of *Promerycochoerus* and also that of *Eporeodon*, which had no close relationship with either of the two former genera. The *Desmatochoerus* line is continuous from the Chadron on through the Harrison and has a questionable form from the Upper Miocene (Sheep Creek equivalent). The line is represented in the Chadron and "Zone A" of the Brule by *Prodesmatochoerus*; in "Zone B" and "Zone D" of the Brule by *Subdesmatochoerus*; in the Gering, Monroe Creek, Harrison, and deposits of questionable Sheep Creek age by *Desmatochoerus*. The *Promerycochoerus* line had a somewhat shorter geologic history in that it is represented in "Zone D" of the Brule by *Promesoreodon*; in the Gering and Monroe Creek by *Mesoreodon*; and in the Harrison by *Promerycochoerus*.

Concerning *Eporeodon*, it should be pointed out that this genus is based on the holotypic species, *E. occidentalis*, from the John Day of Oregon. Schultz and Falkenbach³ have discussed the age of the John Day deposits and considered them to be approximately equal in age to the Harrison of the Great Plains. *Eporeodon occidentalis* has a small skull, which is decidedly smaller than in *Mesoreodon* from the Gering and smaller than many forms referred to *Eporeodon*, which come from much older geologic deposits. The *Eporeodontinae* will be discussed in detail in a later report on the oreodonts, but the genus *Eporeodon* is mentioned here in order that the problem may be considered along with Thorpe's statement as to the relationship of the three genera.

Thorpe compared the long and narrow skulls of *Desmatochoerus* with the wide and

massive skulls of *Promerycochoerus*. Later, Loomis⁴ proposed a new genus, "*Hypselochoerus*," with "*H. gregoryi*" as the genotype, for oreodonts with long and slender limbs. The holotype of this species, however, consists of a skull and mandible only, and it is difficult to separate it specifically from *D. curvidens* (Thorpe). The new genus (*Hypselochoerus*) proposed by Loomis was based on the holotype of "*H. gregoryi*" and a second referred individual (A.C. 1931-109) which had long limbs. Schultz and Falkenbach⁵ listed Loomis' referred skeleton as an example of *Promerycochoerus* (*Pseudopromerycochoerus*) *montanus pinensis*. In regard to "*H. gregoryi*," it must be included in the same genus as *D. curvidens*, thus giving Thorpe's *Desmatochoerus* priority.

Thorpe⁶ in the following statement considered both *Desmatochoerus* Thorpe and "*Hypselochoerus*" Loomis as synonyms of *Promerycochoerus*: "It was the discovery of a specimen of this species [*gregoryi*] in the holotype locality, possessing a short-bodied, long-limbed skeleton, which led Loomis (1933) to erect the genus *Hypselochoerus* for its reception. . . .

"The holotype of *P. gregoryi* and that of *P. curvidens* are exceedingly close to each other in general characters. If Loomis' species should warrant a subgeneric rank on further evidence, then I believe that it should be placed in my *Desmatochoerus*, which was proposed twelve years earlier, rather than in the later *Hypselochoerus*. It is true that there is no skeleton of *Desmatochoerus* known, but the type skulls are certainly no more than specifically distinct.

"The validity of Loomis' reference to *P. gregoryi* of the skeleton found at a later date has been questioned. It is true that the accompanying skull differs in several respects from that of the holotype, but it seems to me that these differences are not of sufficient importance to invalidate the reference."

Thorpe's statement in reference to the validity of Loomis' referred skeleton presumably was based on a conversation which the writers had with Thorpe before his report was

¹ 1921, p. 241.

² For comparison of geologic distribution of *Promerycochoerus* and *Desmatochoerus* see Schultz and Falkenbach, 1949, chart 1 (p. 80); present report, chart 1 (p. 156).

³ 1949, pp. 89-93 and chart 3 (p. 83).

⁴ 1933, p. 728.

⁵ 1949, p. 130.

⁶ 1937, p. 121.

issued. At that time it was agreed that the holotypes of *D. curvidens* and *D. c. gregoryi* were very much alike, and the referred skeleton was questioned as to genus and species. Thorpe, in an oral statement to the writers, said that the limb elements of *D. curvidens* were unknown, but that the referred skeleton did possess limb elements, and that he preferred to place both genera as synonyms of *Promerycochoerus*.

The reason that the present writers questioned Loomis' identification of the Amherst skeleton (A.C. 1931-109) was based primarily on the following comparisons:

	<i>D. curvidens</i> <i>gregoryi</i> (Loomis)	<i>P. (Pseudo- promerycochoerus)</i> <i>montanus pinensis</i> Schultz and Falkenbach
	Holotype A.M. 12964	Referred A.C. 1931-109
Over-all length of skull	309 mm.	((375)) mm.
Basal length of skull	268	(320)
Width of skull	150	256
Interorbital width of skull.	67	122
Length of C/-M ³ incl.	149	186

The skull (A.C. 1931-109) is much restored, and the restoration of the occipital region does not allow for any posterior protrusion of the occipital wings.

The available examples of *Desmatochoerus* from various geologic levels and from widely separated geographic localities differ mainly in size. One important change found in this phylogenetic line, however, is the posterior migration of the infraorbital foramen (see chart 5, p. 181).

DISTRIBUTION

Four species and four subspecies of *Desmatochoerus* are known from the Miocene (Gering, Monroe Creek, Harrison, and ?Sheep Creek formations or their approximate equivalents), of Montana, Nebraska, Oregon, South Dakota, and Wyoming. (See geologic distribution chart 1, p. 156).

SUMMARY OF SPECIES AND TYPES

Four species and four subspecies of *Desmatochoerus* from seven lower Miocene localities

and one species from an upper Miocene locality are here recorded (of these, three species are from west of the Continental Divide):

1. *Desmatochoerus curvidens* (Thorpe), from the John Day Valley, Oregon. (?Middle John Day=in part to Harrison.)

HOLOTYPE: Partial skull and mandible, Y.P.M. 10997. Figures 4-7.

1a. *Desmatochoerus curvidens gregoryi* (Loomis), from Shannon County, South Dakota; referred remains from Niobrara County, Wyoming, and Sioux County, Nebraska; and tentatively referred from Shannon County, South Dakota. (Harrison.)

HOLOTYPE: Skull and mandible, A.M. 12964. Figures 4-7.

2. *Desmatochoerus leidy* (Bettany), from the John Day Valley, Oregon. (Upper John Day=in part to Harrison.)

HOLOTYPE: Partial skull and mandible, W.M.C.V. 3299.

3. *Desmatochoerus hatcheri* (Douglass), from Canyon Ferry, Lewis and Clark County, Montana. (Approximate Gering equivalent.)

HOLOTYPE: Skull and mandible, C.M. 1303.

3a. *Desmatochoerus hatcheri geringensis*, new subspecies, from Niobrara County, Wyoming; referred remains from Goshen County, Wyoming, Morrill County, Nebraska, and Shannon County, South Dakota. (Gering.)

HOLOTYPE: Skull and mandible, F:A.M. 33305. Figures 5-7.

3b. *Desmatochoerus hatcheri grinnelli* (Koerner), from Meagher County, Montana. (Gering equivalent.)

HOLOTYPE: Skull, mandible, and skeletal elements, Y.P.M. 13957. Figures 5-7.

3c. *Desmatochoerus hatcheri niobrarensis*,

TABLE 5

Desmatochoerus THORPE. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND MANDIBULAR RAMI

	<i>D. curvidens</i> (Thorpe)	<i>D. c. gregoryi</i> (Loomis)	<i>D. leidy</i> (Bettany)		<i>D. hatcheri</i> (Douglass)	<i>D. h. niobrarensis</i> , new sub-species	<i>D. h. ger- ingensis</i> , new sub-species	<i>D. h. grinnelli</i> (Koerner)	<i>D. newchi- cagoensis</i> , new species
SKULL	Holotype Y.P.M. 10997	Holotype A.M. 12964	Holotype ² W.M.C.U. 3299	Referred A.M. 7466	Holotype C.M. 1303	Holotype F:A.M. 33344	Holotype F:A.M. 33305	Holotype Y.P.M. 13957	Holotype F:A.M. 34480
Stage of wear of teeth .	(w ⁺)	(w ⁺)	(w)	(w ⁺)	(w)	(w ⁺)	(w)	(w ⁺)	(w)
Length (including supraoccipital crest and incisors)	((305))	309	(340)	(324)	306	313	315	297	((336))
Basal length (from anterior notch of foramen magnum to posterior base of I ¹) .	265	268	((285))	—	261.5	251	267	263.5	—
Width (max.)	(152)	150	—	((175))	152	179	165.5	161.5	((225))
Width of brain case (max.)	69	62	73	—	62.5	—	56	74.5	81.5
Width, interorbital (min.)	66	67	—	—	64	71	69	77.5	(94)
Distance from anterior rim of orbit to anterior base of canine .	122	133	—	—	128	124	122	122	—
Distance from anterior rim of orbit to supraoccipital crest . .	((177))	171	—	—	170	191	183	177	—
Length of nasals . . .	—	133.5	—	—	—	—	—	106.5	—
Width of muzzle at infraorbital foramina .	70	64	—	—	59	(67)	60	—	—
Width across canines .	(64)	69	—	—	54.5	55	58.5	62	—
Length, C-M ³ incl. .	145	149	(159)	157.5	155.5	152	147.5	140	—
Length, P ¹ -M ³ incl. .	125	127.5	(136)	131	137	132.5	126.5	120.5	—
Length, P ¹ -P ⁴ incl. .	57	59	(64.5)	60	66	64	60	55	—
Length, M ¹ -M ³ incl. .	70	70.5	(75)	72	76.5	70	66.5	68.5	—
Width of M ³ (max.) . .	25.5	25.5	—	27	24.5	26	22	26.5	—
Depth of malar below orbit	30.5	31	(39.5)	32	—	36.5	33	26.5	—
MANDIBULAR RAMUS		Referred A.M. 12962 (w)							
Stage of wear of teeth .									
Length (max., including incisors)	—	((231))	(253.5)	—	244	234	241.5	229	(244)
Length, /C-condyle incl.	—	((214))	—	—	224	212	220	—	236
Depth of jaw under coronoid	—	105	—	—	121	107	130	—	113.5
Depth of jaw under anterior edge of M ₃ .	39	56	—	—	53	50	49	46	50
Length, /C-M ₃ incl. . .	(145)	—	—	—	157	154	154	145	152
Length, P ₁ -M ₃ incl. . .	136	130	—	—	146.5	145	139	135	141.5
Length, P ₁ -P ₄ incl. . .	63	61	—	—	71	70	65.5	60.5	64
Length, M ₁ -M ₃ incl. . .	73	70	—	—	77	76	73.5	74.5	78.5

¹ (), Approximate; (()), estimated. All measurements in millimeters.² Measurements after Bettany, 1876.

TABLE 6

Desmatochoerus THORPE. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

	<i>D. c. gregoryi</i> (Loomis)	<i>D. h. niobrarensis</i> , new subspecies		<i>D. h. geringensis</i> , new subspecies
	Tentatively Referred A.M. 12949	Holotype F:A.M. 33344	Referred F:A.M. 44936	Referred F:A.M. 45451
Length of humerus (articular)	190	—	—	176
Length of radius (articular)	155	—	—	154.5
Length of ulna (max.)	226	—	225	208
Length of metacarpal III (max.)	82.5	—	—	77
Length of femur (articular)	220	(198)	204	199
Length of tibia (articular)	170	168	176	175
Length of metatarsal III (max.)	71	—	77	81
Length of calcaneum (max.)	73.5	—	72	66.5

¹ () Approximate. All measurements in millimeters.

CHART 5

COMPARATIVE POSITION OF INFRAORBITAL FORAMINA² IN *Desmatochoerus* THORPE

	Number of Specimens	Infraorbital Foramina Above					
		Posterior Portion of P ³	Between P ³ -P ⁴	Anterior Portion of P ⁴	Midline of P ⁴	Posterior Portion of P ⁴	Anterior Portion of M ¹
<i>D. curvidens</i> ?Middle John Day = Harrison in part (Oreg.)	1	1					
<i>D. curvidens gregoryi</i> Harrison (Nebr., S. Dak., Wyo.)	6				1	3	2
<i>D. leidyi</i> ?Upper John Day = Harrison in part (Oreg.)	7			1	4	1	1
<i>D. hatcheri</i> Gering equivalent (Montana)	2	1		1			
<i>D. hatcheri niobrarensis</i> Monroe Creek (Nebr., S. Dak., Wyo.)	8	1		7			
<i>D. hatcheri geringensis</i> Gering (Nebr., S. Dak., Wyo.)	14	2		12			
<i>D. hatcheri grinnelli</i> Gering equivalent (Montana)	3		3				

² See p. 164.

new subspecies, from Niobrara County, Wyoming; referred remains from Morrill County, Nebraska, Washabaugh County, South Dakota; and tentatively referred from Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Skull, mandible, and skeletal

elements, F: A.M. 33344. Figures 5-7, 24-25.

4. *Desmatochoerus newchicagoensis*, new species, from Granite County, Montana. (?Sheep Creek equivalent.)

HOLOTYPE: Partial skull and mandible, F: A.M. 34480. Figures 5, 7.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

DESMATOCHOERUS

TOTAL AVAILABLE SPECIMENS: 63¹

1. *Desmatochoerus curvidens* (Thorpe)

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

Promerycochoerus (*Desmatochoerus*) *curvidens* THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 1, art. 14, p. 241, figs. 6a-6b.

Promerycochoerus curvidens (Thorpe), HAY, 1930, Carnegie Inst. Washington Publ., no. 390, vol. 2, p. 784. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 117, figs. 77-78.

CHARACTERS

SKULL: Medium size; approximate size of examples of *D. hatcheri*, smaller than in *D. leidy*; anterior nasal-maxilla contact approximately above P¹; infraorbital foramen above posterior portion of P³; muzzle narrower than in *D. hatcheri*; postglenoid process wide transversely, rounded in *D. hatcheri*.

MANDIBLE: Approximately same size as examples of *D. hatcheri*; postsymphysis below P₂ (below P₂ in *D. hatcheri*); inferior border of ramus with more abrupt downward curve posterior to M₂ than usually found in this genus.

DENTITION: Series shorter than in *D. leidy*, slightly shorter than in *D. hatcheri*.

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 180).

ILLUSTRATIONS: Figures 4-7.

DISCUSSION

Thorpe² originally established *Desma-*

tochoerus as a subgenus of *Promerycochoerus*, basing his description on the species under discussion. Hay,³ however, considered the subgenus to be synonymous with *Promerycochoerus*. Loomis⁴ later erected a new genus, "*Hypselochoerus*," with "*H.*" *gregoryi* as the genotypic species. He apparently failed to compare the holotype of *D. curvidens* with the material he was describing. Thorpe,⁵ however, considered both genera, *Desmatochoerus* and "*Hypselochoerus*," as synonymous with *Promerycochoerus*. (See p. 178 for a more complete discussion.)

Thorpe was the first to suggest that forms with long narrow skulls as in *D. curvidens* should be separated from *Promerycochoerus*, but later he dropped the subgeneric standing of *Desmatochoerus*. The present writers here consider *Desmatochoerus* Thorpe as a separate and valid genus, with "*Hypselochoerus*" Loomis as a synonym.

Desmatochoerus curvidens from the ?middle John Day appears to have given rise to *D. leidy* from the upper John Day. The geologic occurrence of the holotype of *D. curvidens* is questionable, as is the case with many of the oreodont specimens collected from the John Day deposits.⁶

Desmatochoerus curvidens is known only from the holotype, an incomplete skull. Additional material, when found, may demonstrate greater differences from *D. hatcheri* and *D. curvidens gregoryi* than are noted in the present paper.

One specimen is here recorded:

¹ 1930, p. 784.

² 1933, Bull. Geol. Soc. Amer., vol. 44, p. 728.

³ 1937, p. 117.

⁴ For discussion and correlation of John Day deposits, see Schultz and Falkenbach, 1949, pp. 83, 89-93.

¹ Includes 50 F:A.M. and 5 U.N.S.M. specimens.

² 1921, p. 241.

HOLOTYPE

Partial skull with I¹(br.)-M³ (I², C/, and P¹-P² br.) and partial mandible with I₁-M₃ (I₂ rt. and P₁-P₂ br.). (w†)

Y.P.M. 10997

From ?middle John Day deposits, North Fork, John Day River, John Day Valley, Oregon; collected by L. S. Davis, 1875

Figured by Thorpe, 1921, figs. 6a-6b; 1937, figs. 77-78

This report, figs. 4-7

1a. *Desmatochoerus curvidens gregoryi*
(Loomis)

From the Harrison formation, Shannon County, South Dakota; referred remains from Niobrara County, Wyoming, and Sioux County, Nebraska; and tentatively referred from Shannon County, South Dakota

Promerycochoerus gregoryi LOOMIS, 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 23, fig. 12. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 119, fig. 79; pl. 12.

Hypselochoerus gregoryi (Loomis), LOOMIS, 1933, Bull. Geol. Soc. Amer., vol. 44, p. 728.

CHARACTERS

SKULL: Similar to that of holotype of *D. curvidens*, within size variation of examples of *D. hatcheri* and *D. hatcheri grinnelli*; tendency to be smaller than examples of *D. leidy*, from approximate size to larger than examples of *D. hatcheri niobrarensis* and *D. hatcheri geringensis*; anterior nasal-maxilla contact above P¹; infraorbital foramen above P⁴ to anterior portion of M¹ (above posterior of P³ in *D. curvidens*); facial vacuity present (see discussion below); postglenoid process wide transversely; tendency for bulla to be smaller and more compressed laterally than in examples of the two last-mentioned subspecies; posterior palate projected farther posteriorly than in *D. h. niobrarensis* and *D. h. geringensis*.

MANDIBLE: Same size as examples of *D. curvidens*; postsymphysis below posterior portion of P₃; inferior border of ramus with less downward curve posterior to M₂ than in *D. curvidens*.

DENTITION: Dental series longer on average than in holotype of *D. curvidens*; average examples smaller than those of *D. leidy*.

LIMBS: Slightly longer than examples of *D. hatcheri niobrarensis*.

MEASUREMENTS: Tables 5 and 6 (pp. 180-181).

ILLUSTRATIONS: Figures 4-7

DISCUSSION

The subspecies *D. curvidens gregoryi* has a complicated history. Originally Loomis¹ described the form as a species of *Promerycochoerus* and referred a specimen (A.M. 13816; misprinted in Loomis' report as A.M. 12816), as a male example of the species. The present writers have referred Loomis' "male example" to *Promerycochoerus* (*Parapromerycochoerus*) *barbouri*.² Later Loomis³ proposed a new genus, "*Hypselochoerus*," with "*H. gregoryi*" as the genotypic species. Loomis' re-description of the species *gregoryi* was based on a referred skeleton (A.C. 1931-109) which he considered to be a male example. The major reason for Loomis' separation of *D. curvidens gregoryi* from the genus *Promerycochoerus* was the comparatively long limbs of the referred skeleton. (See more detailed discussion, p. 178). The present writers have referred this same skeleton to *P. (Pseudopromerycochoerus) montanus pinensis*.⁴

Loomis⁵ stated that the skeleton in question (A.C. 1931-109) was found in the same locality as the holotype of *D. c. gregoryi*. In a conversation with the present writers Dr. Loomis stated that the skeleton (A.C. 1931-109) was found "within fifty feet above the concretionary layer" (prominent marker in the Harrison formation). There is no evidence, however, that both the holotype of *D. c. gregoryi* and the referred skeleton (A.C. 1931-109) were found at the same geologic level, but the present writers consider both specimens as coming from the Harrison formation.

A referred example (F:A.M. 37211) of *D.*

¹ 1924, p. 23.

² Schultz and Falkenbach, 1949, p. 118.

³ 1933, p. 728.

⁴ Schultz and Falkenbach, 1949, p. 130.

⁵ 1933, p. 728.

c. gregoryi deserves special consideration because of the presence of unusual vacuities. On the right side of the skull there is a well-defined facial vacuity with a rounded surface along the border. A bony plate is present about a quarter of an inch below the surrounding surface. This plate-like structure undoubtedly is directly associated with the vacuity. On the left side of the skull, which is somewhat crushed, the vacuity actually appears to be absent. This would suggest that in some instances the plate may become fused with the border of the vacuity, and thus all

indication of the opening would be lost.¹

The subspecies *D. curvidens gregoryi* appears to be little more than a geographic variety of the species. Perhaps additional material of *D. curvidens* will show that the two forms are definitely distinct from each other.

The A.M. specimens were collected by William D. Matthew and Albert Thomson, 1906, and the F:A.M. material by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1936.

Seven specimens are here recorded:

HOLOTYPE

Skull with I ¹ -M ³ and partial mandible with I ₁ -M ₃ (br.). (w+)	A.M. 12964	From upper portion of "Lower Rosebud" = Harrison, on divide E. of Porcupine Creek, Shannon County, South Dakota; collected by Albert Thomson, 1906
? Female example		Figured by Loomis, 1924, fig. 12; Thorpe, 1937, fig. 79; pl. 12
		This report, figs. 4-7

REFERRED FROM (A) SHANNON COUNTY, SOUTH DAKOTA; (B) SIOUX COUNTY, NEBRASKA; (C) NIOBRARA COUNTY, WYOMING; AND (D) TENTATIVELY REFERRED FROM SHANNON COUNTY, SOUTH DAKOTA

A. FROM PORCUPINE CREEK AREA, SHANNON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE	A.M.
Skull with I ¹ -M ³ and partial mandible with P ₁ -M ₃ (w)	12962
SKULL	
Partial skull with C/-M ³ (M ¹ br.) (w+)	12947

B. FROM SOUTH OF HARRISON, SIOUX COUNTY, NEBRASKA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS	F:A.M.
Partial skull with I ¹ -M ³ , partial mandible with I ₃ (br.)-M ₃ , and partial scapula . (w††)	42308

C. FROM NORTH OF KEELINE, NIOBRARA COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS	
Skull with I ¹ (alv.)-M ³ , mandible with I ₁ -M ₃ , and vertebrae. Figures 4-7 . . (w)	37211
Considered as a male example of the species and illustrated for comparison with the holotype (a female example).	

D. TENTATIVELY REFERRED FROM 4 MI. N./N.W. OF PORCUPINE POST OFFICE, PORCUPINE CREEK, SHANNON COUNTY, SOUTH DAKOTA

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS	A.M.
Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and most of skeleton (w†)	12949
The above skeleton is mounted in a plaster plaque and, as far as can be ob-	

¹ See discussion of facial vacuities in the Phenacocoelinae, Schultz and Falkenbach, 1950, p. 105.

served, the supraoccipital region differs from other examples of the subspecies in not extending posteriorly as far as usual. This, of course, may be due to crushing.

Partial skull with I^1 (alv.)-dP²-M³, mandible with P₁-dP₂-M₃ (P₃-P₄ erupt. on left side), and partial humerus (1) A.M. 12941

Immature and incomplete, but larger than other examples of the subspecies. The characters present, however, compare favorably with those of the subspecies.

2. *Desmatochoerus leidyi* (Bettany)

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

Merycochoerus leidyi BETTANY, 1876, Quart. Jour. Geol. Soc. London, vol. 32, p. 270, pl. 18.

Promerycochoerus leidyi (Bettany), DOUGLASS, 1901, Amer. Jour. Sci., vol. 11, art. 6, p. 82. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 128, fig. 84.

CHARACTERS

SKULL: Largest and most robust of genus; longer and wider than in holotype of *D. curvidens*; brain case more inflated than in *D. curvidens*; nasals moderately robust, with slight anterior retraction; anterior nasal-maxilla contact above diastema between C/ and P¹; infraorbital foramen above anterior portion of P⁴ to anterior portion of M¹; squamosal more robust than in other examples of the genus; malar deep below orbit; postglenoid process wide transversely.

MANDIBLE: Largest of genus; postsymphysis below P₃; inferior border of ramus with less downward curve than in examples of *D. curvidens*.

DENTITION: Series longer than in *D. curvidens*.

LIMBS: Approximately equal to examples of *D. hatcheri geringensis*. (Known from fragmentary remains only.)

MEASUREMENTS: Table 5 (p. 180).

ILLUSTRATIONS: Figures 5-6.

DISCUSSION

With the exception of the unavailable holotype of *Promerycochoerus superbus*, the holotype of *D. leidyi* is the only type specimen of the oreodonts not studied and measured by the writers. Most of the above characters are based on Bettany's original description and illustration. Some additional information, however, has been added from the here-listed referred specimens.

This species is the largest known of the genus, but is readily separated from the still larger examples of the genus *Superdesmatochoerus* from the same deposits in the John Day Valley. *Desmatochoerus leidyi* appears to be from the upper John Day, as Bettany reported, and it seems to have evolved from the smaller and less massive *D. curvidens*, which is here considered as coming from the middle John Day.

Eight specimens are here recorded:

HOLOTYPE

Partial skull with I^1 -M ³ and partial mandible with I_1 -P ₄ (br.). (w)	W.M.C.V. 3299	From upper John Day, John Day Valley, Oregon; collected by Lord Walsingham, 1871-1872 Figured by Bettany, 1876, pl. 18; Thorpe, 1937, fig. 84
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REFERRED FROM THE JOHN DAY VALLEY, OREGON

3 SKULLS AND MANDIBLES

Anterior portion of skull with C/-M ³ and mandible (attached) with P ₁ -M ₃ . (w+).	U.O. 686	From Bridge Creek, John Day Valley, Oregon; collected by Rev. Thomas Condon
Anterior portion of skull with C/(rt.)-M ³ and partial right ramus with P ₂ -M ₃ (P ₃ -P ₄ br.). (w+)	A.M. 7432	From the Cove, John Day Valley, Grant County, Oregon; collected by Charles H. Sternberg, 1878

- Partial skull with C/(rt.)-M³ (P¹ br.), Y.P.M. 10965 From Bridge Creek, John Day Valley;
mandible with I₁-P₁ rt. and P₂(br.)-
M₃, and atlas. (w+)
collected by S. H. Snook, 1874

2 SKULLS AND ASSOCIATED SKELETAL ELEMENTS

- Partial skull with I¹(rt.)-M³ (C/-P¹ and A.M. 7468 From the John Day Valley, Oregon
P³ br.), partial radius, and partial
ulna. (w+)
Partial skull with I¹-I³ rt. and C/(br.)- A.M. 7479 From the John Day Valley, Oregon
M¹(br.), and vertebrae. (w)

2 SKULLS

- Crushed skull with C/(br.)-M³. (w+) A.M. 7466 From the Cove, John Day Valley, Grant
County, Oregon; collected by Day and
Warfield, 1877
Figures 5-6
Partial skull with M¹(br.)-M³. (w+) U.C. 2249 From Butler's Basin, upper end of the
Cove; collected by Davis and Osmont,
1900

3. *Desmatochoerus hatcheri* (Douglass)

From lower Miocene deposits (approximately
equal in age to the Gering formation of the
central Great Plains), Lewis and Clark
County, Montana

Promerycochoerus hatcheri DOUGLASS, 1907,
Ann. Carnegie Mus., vol. 4, no. 2, p. 104, pl. 26.

Promerycochoerus hollandi hatcheri (Douglass),
THORPE, 1937, Mem. Peabody Mus., vol. 3, pt.
4, p. 125, fig. 82; pl. 14.

CHARACTERS

SKULL: Approximately same size and char-
acters as in *D. curvidens*; anterior nasal-
maxilla contact above region of P¹; infra-
orbital foramen above posterior portion of P³
to anterior portion of P⁴; facial vacuity pres-
ent; muzzle slightly wider than in *D. curvi-
dens*; postglenoid process rounded, as wide
laterally as anteroposteriorly (differing from
laterally compressed process in *D. curvidens*).

MANDIBLE: Approximately equal to that
of *D. curvidens*; postsymphysis below P₂.

DENTITION: Approximately equal in length
to examples of *D. hatcheri geringensis*, tend-
ency to be slightly smaller than in *D.
hatcheri niobrarensis*, slightly larger than in
D. curvidens and *D. hatcheri grinnelli*.

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 180).

ILLUSTRATIONS: Figure 6. (See Thorpe,
1937, fig. 82; pl. 14.)

DISCUSSION

The number of examples of this form now

available is insufficient to suggest the limits
of individual variation within the species. The
writers noted very little evidence of charac-
ter changes except size differences between
this species and the following subspecies, *D.
hatcheri geringensis*, *D. h. niobrarensis*, and
D. h. grinnelli. In *D. hatcheri*, however, the
postglenoid process is rounded, while in the
two subspecies it is wide transversely.

Desmatochoerus hatcheri was first reported
to be associated in the same geologic deposits
with *Megoreodon grandis* by Douglass¹: "The
type [*Desmatochoerus hatcheri*] . . . was col-
lected by the writer in 1902 from the same
deposits and same locality as the types of
Promerycochoerus grandis [*Megoreodon
grandis*], *P. hollandi* [also = *M. grandis*], and
the species of *Merycoides* [*cursor*] described
in this paper." Douglass further stated, in a
discussion of *D. hatcheri*, "The general form
and proportions of the skull are very much
like those of *Promerycochoerus grandis* but is
much smaller and the teeth are decidedly less
heavy than in that species."

It is evident that Douglass did not compare
D. hatcheri with a typical species of the genus
Promerycochoerus, but rather with *M. grandis*,
which at that time was considered under the
genus *Promerycochoerus*. As stated by Doug-
lass, the two species have many characters in
common, and the present writers have in-
cluded both forms under the subfamily Des-
matochoerinae. (See *Megoreodon grandis*, p.
168.)

¹ 1907, p. 104.

Thorpe¹ included *D. hatcheri* as a subspecies of "*P. hollandi*" (= *M. grandis*), presumably basing his conclusions on the similar characters of the two forms, which are here considered to be of diagnostic value in estab-

lishing the subfamily.

The two referred F:A.M. specimens were collected by Everett De Groot and Charles H. Falkenbach, 1936.

Three specimens are here recorded:

HOLOTYPE

Skull with I¹-M³ and mandible with I₁-M₃. (w)

C.M. 1303

From lower Miocene deposits, Canyon Ferry area, Lewis and Clark County, Montana; collected by Earl Douglass, 1902

Figured by Douglass, 1907, pl. 26; Thorpe, 1937, fig. 82; pl. 14

REFERRED FROM TYPE AREA, CANYON FERRY, LEWIS AND CLARK COUNTY, MONTANA

2 SKULLS

F:A.M.

Anterior portion of skull with I ¹ -M ³ . Fig. 6.	(w $\frac{1}{2}$)	42327
Posterior portion of skull with M ² -M ³	(w $\frac{1}{4}$ +)	42328

The crushing of the partial skull has increased its total width.

3a. *Desmatochoerus hatcheri geringensis*,² new subspecies

From the Gering formation, Niobrara County, Wyoming; referred remains from Goshen County, Wyoming; Morrill County, Nebraska; and Shannon County, South Dakota

DESCRIPTION

SKULL: Average examples slightly shorter than those of *D. hatcheri* and *D. hatcheri niobrarensis*; average width greater than in holotype of *D. hatcheri*, less than in examples of *D. hatcheri niobrarensis*; anterior nasal-maxilla contact above region of P¹; malar deep below orbit; infraorbital foramen above posterior portion of P³ to anterior portion of P⁴; facial vacuity frequently present; postglenoid process wide transversely; posterior palate projected posteriorly for less distance than in *D. curvidens gregoryi*.

MANDIBLE: Average size slightly smaller than in holotype of *D. hatcheri*; postsymphysis below P₃-P₄; ramus with less depth below

anterior of M₃ than in holotype of *D. hatcheri*, slightly less depth than in examples of *D. hatcheri niobrarensis*.

DENTITION: Approximately equal to examples of *D. hatcheri* and *D. hatcheri niobrarensis*; shorter than in examples of *D. curvidens gregoryi*.

LIMBS: Approximately equal to examples of *D. hatcheri niobrarensis*.

MEASUREMENTS: Tables 5 and 6 (pp. 180-181).

ILLUSTRATIONS: Figures 5-7, 18.

DISCUSSION

This subspecies from the Gering differs from *D. hatcheri niobrarensis* from the Monroe Creek only in the characters above mentioned.

The F:A.M. specimens were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1932-1941.

Twenty-seven specimens are here recorded:

HOLOTYPE

Skull with I¹(rt.)-M³ and mandible with I₁-M₃. (w)

F:A.M. 33305

From Gering formation, Little Muddy Creek, Niobrara County, Wyoming;

¹ 1937, p. 125.

² Named after the Gering formation, the source of the holotype and referred specimens of this subspecies.

collected by John Lynch, Everett De
Groot, and Charles H. Falkenbach.
1933

Figures 5-7, 18

REFERRED FROM (A) NIOBRARA AND (B) GOSHEN COUNTIES, WYOMING;
(C) MORRILL COUNTY, NEBRASKA; AND (D) SHANNON COUNTY,
SOUTH DAKOTA

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

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

F:A.M.

Partial skull with I²-M³, mandible with I₂-M₃, humerus, radius, ulna, manus,
partial femur, partial tibia, astragalus, 2 pedes, pelvis, and fragments . . . (w₊⁺) 42307

The above skull is considerably crushed and is wider than other examples of
the subspecies. The M³ on either side of the above skull has a cervid-like style
similar to that of an example of *Brachycrus siouense*.¹ This has no diagnostic
value and in both instances the occurrences are unique.

Skull with I²-M³, mandible (attached) with I₁-M₃, atlas and cervical vertebrae
(attached), and limb fragments . . . (w₊⁺) 45450

Skull with I¹-I³ alv. and C/-dP³-M³, partial mandible with /C(alv.)-dP₃-M₃
(P₁ br.), 2 humeri (1 partial), partial radius, 2 partial ulnae, and partial femur. (I) 33306

The above skull, although immature, is the second largest example of the
subspecies.

7 SKULLS AND MANDIBLES

7 partial skulls and associated mandibles with:

I¹-M³, and P₂-M₃ . . . (w₊⁺) 33341

I¹-M³ (P₁ br.), and I₁-M₃ . . . (w) 33340

P⁴-M³, and P₄-P₃ (mandible attached to skull) . . . (w₊⁺) 44932

C/-M³, and /C-M₃ (mandible attached to skull) . . . (w₊⁺) 45446

I²-M³, and I₂-M₃ . . . (w) 45447

I¹-M³, and I₁-M₃ . . . (w+) 45448

C/-dP²-M³, and mandibular fragments . . . (I) 44935

3 SKULLS

3 partial skulls with:

I¹-M³ (I¹ and P₁ br.) . . . (w) 37209

C/(br.)-M³ (M²-M³ br.) . . . (w₊⁺) 44931

I¹-M³ (I²-I³ absent) . . . (M+) 43316

A'. FROM WILLOW CREEK, NIOBRARA COUNTY, WYOMING

2 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

F:A.M.

Skull with I²-M³, mandible with I₁-M₃, and pelvis . . . (w₊⁺) 37598

Partial skull with I²-M³, left ramus with I₂-M₃ (P₂-P₄ absent, M₁-M₂ br.),
partial radius, partial ulna, and partial femur . . . (w) 45449

2 SKULLS

F:A.M.

Anterior portion of skull with I¹(alv.)-C/-dP⁴ (br.) and M¹-M³(erupt.) . . . (I) 43348

Partial skull with C/-M³(br.) . . . (w₊⁺) 44945

MANDIBLE

Partial mandible with I₃-M₃ . . . (w) 37599

B. FROM THE HORSE CREEK BASIN, GOSHEN COUNTY, WYOMING
FROM 2-3 MI. E. OF TREMAIN:

¹ Schultz and Falkenbach, 1940, p. 235, fig. 9.

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

F:A.M.

Partial skull with I¹-M³, mandible with I₁-M₃, scapula, humerus, radius, ulna, manus, femur, 2 tibiae, fibula, astragalus, calcaneum, pes, vertebrae, pelvis, and ribs. Figures 23-25 (in part) (w) 45451

SKULL

Inferior, anterior portion of skull with C/(br.)-M³. (w+) 45452

FROM SOUTH SIDE OF 66 MOUNTAIN:

SKULL AND MANDIBLE

Partial skull with I¹-M³(br.) and symphysis of mandible with I₁-C (w) 45453

C. FROM MORRILL COUNTY, NEBRASKA

(Collected by E. L. Blue, Frank Crabill, Eugene Vanderpool, C. Bertrand Schultz, and Associates)

FROM U.N.S.M. COL. LOC. MO-109, BLACK HANK'S CANYON, 2 MI. N.W. OF REDINGTON GAP, 1932, 1934:

2 SKULLS

U.N.S.M.

Crushed skull with I¹-I² alv. and I³-M³ (-M) 28016

Posterior portion of skull with P⁴-M³. (w) 28021

FROM U.N.S.M. COL. LOC. MO-107, $\frac{1}{4}$ MI. E. OF REDINGTON GAP, 1931:

SKULL

Crushed skull with I¹-M³. (w) 28018

D. FROM PORCUPINE CREEK CANYON, SHANNON COUNTY, SOUTH DAKOTA

(Collected By Morris F. Skinner, Charles H. Falkenbach and Party, 1950)

SKULL AND SKELETAL ELEMENTS

F:A.M.

Crushed skull with I²-M³, partial scapula, radius, vertebrae and fragments . . . (w₊⁺) 49632

MANDIBULAR RAMUS

Partial right ramus with P₃-M₃ (w₊⁺) 49633

The above two specimens, which came from $1\frac{1}{2}$ mi. S. of the large exposures at the mouth of Porcupine Creek Canyon, were found in a pink clay with small nodules that underlies the high exposures.

3b. *Desmatochoerus hatcheri grinnelli*
(Koerner)

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

Promerycochoerus grinnelli KOERNER, 1940, Amer. Jour. Sci., vol. 238, p. 850, pl. 6.

Promerycochoerus thorpei KOERNER, *ibid.*, p. 853, pl. 7, fig. 2.

CHARACTERS

SKULL: Average size slightly smaller than in holotypes of *D. hatcheri* and *D. curvidens*; anterior nasal-maxilla contact above P¹; infraorbital foramen above region between P³ and P⁴; squamosal lighter, malar below

orbit of less depth and occipital condyles more robust than in above-mentioned species; postglenoid process wide laterally.

MANDIBLE: Postsymphysis below P₃ (slightly more posterior than in holotype of *D. curvidens*); less depth of ramus below anterior of M₃ than in *D. curvidens*.

DENTITION: Average length of dental series less than in other known forms of genus.

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 180).

ILLUSTRATIONS: Figures 5-7.

DISCUSSION

In the original description of "*Promerycochoerus thorpei*," Koerner¹ stated that the

¹ 1940, p. 850.

species may be distinguished from his "*P.*" *grinnelli* by the length of the superior dental series. In the table of measurements accompanying his description, the difference is cited as 5 mm., which is well within the variation found in any one species of the oreodonts. The holotype of *D. hatcheri grinnelli* (Koerner) and that of "*P. thorpei*" are from the same locality and formation.

The width of the holotype skull of *D. hatcheri grinnelli* is 161 mm., while a referred skull of Koerner (Y.P.M. 13958) has a width of 195 mm. Concerning this measurement, Koerner evidently did consider individual variation. A similar amount of variation has been noted in *D. hatcheri geringensis* (p. 187).

Koerner further noted that *D. hatcheri grinnelli* may be distinguished from *D. hatcheri* by the following characters: wider palate of the former (the holotype of the latter is crushed laterally and would be considerably wider in a normal skull); greater distance between supraorbital foramina; lack of internal cingula on the molars; and absence of a diastema between P^1 and P^2 . All these differences are here considered to be within the limits of individual variation, as demonstrated by the large assemblages of the vari-

ous species of oreodonts in the Frick Laboratory.

In the description of his species *grinnelli*, Koerner¹ pointed out that one of the characters that differed from *D. hatcheri* is the absence of the antero-external pit on P^4 . This character also varies in individuals and is not present on a worn tooth. The writers have tried to consider diagnostic characters which are present through the life span of an individual.

Although *D. hatcheri grinnelli* is here considered a subspecies, additional specimens of *D. hatcheri* may demonstrate that both forms are synonymous.

The White Sulphur Springs area of Montana, from which the holotype and referred specimens of this subspecies were collected, is of special geologic interest. Deposits are equivalent in age to the Gering, Harrison, and Sheep Creek formations of the central Great Plains. The geologic evidence is supported by the presence of leptachenids (forms restricted to Gering and Monroe Creek formations), *Promerycochoerus* (Harrison), and *Brachycrus*² (Sheep Creek) in the area.

Three specimens are here recorded:

HOLOTYPE

Skull with I^1 - M^3 and partial mandible with I_1 - M_3 . (w+)

Y.P.M. 13957

From lower Miocene deposits, White Sulphur Springs area, Meagher County, Montana; collected by Harold E. Koerner
Figured by Koerner, 1940, pl. 6
This report, figs. 5-7

REFERRED FROM TYPE AREA, MEAGHER COUNTY, MONTANA

SKULL AND MANDIBLE

Y.P.M.

Skull with I^1 - M^3 , mandible with I_1 - I_2 alv. and I_2 - M_3 , atlas, and partial axis . . (w+) 13958
Koerner's "paratype" of "*Promerycochoerus*" *grinnelli*.

SKULL

Skull with I^1 - I^3 alv. and C - M^3 . Figured by Koerner, 1940, pl. 7, fig. 2 . . . (w) 13959
The holotype of "*Promerycochoerus thorpei*."

¹ 1940, p. 851.

² Schultz and Falkenbach, 1949, p. 105. There is also evidence of Pleistocene deposits in the White Sulphur Springs area.

3c. *Desmatochoerus hatcheri niobrarensis*,¹
new subspecies

From the Monroe Creek formation, Niobrara County, Wyoming; referred remains from Morrill County, Nebraska, and Washabaugh County, South Dakota; and tentatively referred from Niobrara County, Wyoming

DESCRIPTION

SKULL: Slightly longer on average than those of *D. hatcheri geringensis*, similar to holotype of *D. hatcheri* in size; average width greater than in above-mentioned forms; anterior nasal-maxilla contact above posterior portion of P¹; infraorbital foramen above posterior portion of P³ to anterior portion of P⁴; facial vacuity frequently present; postglenoid process peg-like, almost as wide as long; posterior palate not extended posteriorly as in *D. curvidens gregoryi*.

MANDIBLE: Slightly larger on average than examples of *D. hatcheri geringensis*; post-

symphysis below P₃-P₄; ramus slightly deeper below the anterior border of M₃ than in either *D. hatcheri* or *D. hatcheri geringensis*.

DENTITION: Tendency for series to be slightly longer than in *D. hatcheri geringensis*.

LIMBS: Approximately equal to examples of *D. hatcheri geringensis*; slightly smaller than tentatively referred example of *D. curvidens gregoryi*.

MEASUREMENTS: Tables 5 and 6 (pp. 180-181).

ILLUSTRATIONS: Figures 5-7, 24-25.

DISCUSSION

The proposed new subspecies, *Desmatochoerus hatcheri niobrarensis*, is here considered to have developed directly from *D. hatcheri geringensis* from the Gering formation.

The F:A.M. specimens here recorded were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1933-1936.

Thirteen specimens are here recorded:

HOLOTYPE

Skull with I¹-M³, mandible with I₁-M₃,
2 partial femora, and tibia. (w+)

F:A.M. 33344

From Monroe Creek formation above the "white layer," Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933

Figures 5-7, 24-25

The specimen is of interest in that both the left and right P⁴ have an infolded internal surface, which may indicate a tendency of the premolars to become molariform. This character, however, is not considered to be of diagnostic value as it also occurs in other genera and species of oreodonts.²

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; (B) MORRILL COUNTY, NEBRASKA; (C) WASHABAUGH COUNTY, SOUTH DAKOTA; AND (D) TENTATIVELY REFERRED FROM NIOBRARA COUNTY, WYOMING

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

SKULL, MANDIBLE, AND SKELETAL ELEMENTS	F:A.M.
Partial skull with I ² -M ³ , partial mandible with I ₁ -M ₃ , partial humerus, radius, ulna, femur, tibia, calcaneum, partial pes, vertebrae, and fragments. (w+)	44936

4 SKULLS AND MANDIBLES

Partial skull with I ¹ -I ² rt. and I ³ -M ³ and partial mandible with I ₂ -M ₃ (w+)	33346
Partial skull with I ¹ -M ³ and partial mandible (attached) with /C-M ₃ (P ₁ br.) (w)	43213
Partial skull with I ¹ -M ³ and partial mandible (attached) with /C-M ₃ (w ⁺)	44944
Partial skull with I ² -M ³ and inferior dentition crushed on palate (w)	45461

¹ Named after Niobrara County, Wyoming, the area from which the holotype and most of the referred specimens of this subspecies were collected.

² Schultz and Falkenbach, 1949, fig. 4 (example: *Promerycochoerus carrikeri*).

2 SKULLS		F:A.M.
Partial skull with I ¹ -M ³	(w+)	43315
Anterior portion of skull with C/-M ³	(M+)	43327

MANDIBLE

Partial mandible with I ₂ (br.)-M ₃	(M+)	43314
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B. FROM LOWER MONROE CREEK DEPOSITS, MORRILL COUNTY, NEBRASKA

(Collected by E. L. Blue, Frank Crabill, Robert Long, T. M. Stout, and C. Bertrand Schultz)

SKULL AND MANDIBLE

Partial skull with C/-M ³ and mandible (attached) with P ₁ -M ₃ . (w+)	U.N.S.M. 28020	From Col. Loc. Mo-105, ½ mi S.E. of Bird Cage Gap, 1933
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SKULL

Anterior portion of skull with I ¹ -I ³ alv. and C/-M ³ . (w+)	28022	From Col. Loc. Mo-109, Black Hank's Canyon, 2 mi. N.W. of Redington Gap, 1934
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C. FROM QUIVER HILL AREA, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBULAR RAMUS

F:A.M.

Anterior inferior portion of skull with C/(rt.)-M ³ (P ¹ -P ³ mutilated), partial right ramus with M ₃ and fragments	(w+)	49634
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D. TENTATIVELY REFERRED FROM MUDDY CREEK, NIOBRARA COUNTY, WYOMING

SKULL AND MANDIBLE

F:A.M.

Skull with I ² -M ³ and partial mandible with I ₁ -M ₃	(w++)	33309
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The specimen is tentatively referred because of the great width across the zygomatic arches. Other characters, however, are readily comparable with those of other examples of the subspecies.

4. *Desmatochoerus newchicagoensis*,¹
new species

From upper Miocene deposits (approximately equal in age to the Sheep Creek formation of the Central Great Plains), Granite County, Montana

DENTITION: Inferior premolars lighter and more laterally compressed than in other species of genus. (Superior series unknown.)

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 180).

ILLUSTRATIONS: Figures 5, 7.

DESCRIPTION

SKULL: Moderately large, larger than in other species of genus, but not so large as examples of *Superdesmatochoerus*; brain case long, inflated more than usual in genus; frontals wide with the usual midline protuberance of genus; nasals comparatively long and narrow; orbits small; malar deep below orbit; paroccipital process with less anterior twist to shaft than in other species of genus. (Bulla unknown.)

MANDIBLE: Similar to examples of *D. hatcheri niobrarenensis*; postsymphysis below P₂.

¹ Named after the town of New Chicago, Granite County, Montana, which is northwest of the locality from which the holotype was collected.

DISCUSSION

The generic reference of the proposed new species might well be questioned, as the holotype (only known specimen of the species) consists of a poorly preserved skull, which lacks the superior dentition. The mandible with dentition, however, is well preserved. The skull, although crushed, is definitely the largest found in this genus. The mandible can be readily compared with other examples of the genus, except for the lighter premolars. The New Chicago area, from which the type specimen came, seems to be equivalent to the Sheep Creek formation of the central Great Plains. The holotype and referred specimens of *Brachycrus laticeps*,² as

² Schultz and Falkenbach, 1940, p. 231.

well as the holotype of *Ticholeptus zygomaticus smithi*,¹ also came from these same deposits. Both of these latter forms, as far as known, are restricted to the Sheep Creek for-

mation or to beds of equivalent age. This is the only evidence that the line of *Desmatochoerus* extends into the upper Miocene.

One specimen is here recorded:

HOLOTYPE

Crushed partial skull (lacking dentition)
and partial mandible with I₁-I₃ alv.
and /C(br.)-M₃. (w)

F:A.M. 34480

From upper Miocene deposits, at the north end of the exposures southeast of New Chicago, Granite County, Montana; collected by Everett De Groot and Charles H. Falkenbach, 1936

Figures 5, 7

IIA. DESMATOCHOERUS (PARADESMATOCHOERUS), NEW SUBGENUS

DESCRIPTION

SKULL: Medium size, basal length ranging from 215 to 236 mm., width from 105 to 174 mm.; smaller than in species of *Desmatochoerus*; dolichocephalic to submesocephalic; sagittal crest high, but not so high as in *Desmatochoerus*, considerably higher than in *Pseudodesmatochoerus*; supraoccipital wings small and not widely spread, protruding posteriorly for short distance (less than in *Desmatochoerus*); large exoccipital vacuities present; brain case long and narrow; frontals narrow, with oblong protuberance usually present along midline above orbits; nasals long and narrow; anterior nasal-maxilla contact above P¹; orbit moderately large, looking mostly outward and forward, oval vertically, with long axis sloping upward anteroposteriorly; squamosal light to moderately heavy (lighter in the supposed female examples); zygomatic arch with prominent inward curve just posterior to orbit; malar moderately deep below orbit; lacrimal fossa small but deep; infraorbital foramen above posterior portion of P³ to anterior portion of P⁴; facial vacuity usually present; shallow depression above premolar region; premaxillae joined for short distance; occipital condyles lighter than in *Desmatochoerus*; paraoccipital process wide at base but more peg-shaped and with less lateral compression than in *Desmatochoerus*; postglenoid process robust, almost round in cross section; bulla laterally compressed (similar to examples of *Desmatochoerus*); posterior

palate produced posteriorly beyond M³.

MANDIBLE: Moderately light; smaller than in *Desmatochoerus*; postsymphysis below P₃; ramus shallow, increasing in depth posteriorly; inferior border of ramus with slight downward trend to a point below posterior lobe of M₃, and an abrupt downward curve posterior to M₃; ascending ramus moderately high; condyle light, set at less than right angle to longitudinal axis of dentition and with external border farther forward and higher than internal border.

DENTITION: More brachyodont than in *Desmatochoerus*; series of less length and lighter than in examples of *Desmatochoerus*; /C approximately three times as large as I₃; premolars not crowded, but P¹-P³ and P₂-P₃ each set at slight angle to alveolar border; external styles on superior molars moderately prominent; P¹-P³ each with anterior intermediate crest; P₃ with posterior intermediate crest.

LIMBS: Moderately light, lighter and with tendency to be shorter than examples of *Desmatochoerus*.

MEASUREMENTS: Tables 7 and 8 (pp. 198-199).

ILLUSTRATIONS: Figures 8-11, 18 (skulls, rami, and dentition), 24-25 (limbs).

DISCUSSION

Desmatochoerus (*Paradesmatochoerus*), new subgenus, includes forms that are found in the same formations and localities as examples of *Desmatochoerus* and *Pseudodesmatochoerus*. It is distinguished from the former by its smaller size and shallower sagittal crest, as well as its lighter dentition, and from the latter by its comparatively

¹ *Idem*, 1941, p. 86.

higher sagittal crest and lighter dentition. *D. (Paradesmatochoerus)* represents a line which has the same geologic distribution as *Desmatochoerus* and *Pseudodesmatochoerus*.

The two following species of the new subgenus do not differ greatly from each other, except for certain minor distinctions already mentioned above, chiefly size. *Desmatochoerus (Paradesmatochoerus) wyomingensis* is known from the Gering formation and *D. (P.) monroecreekensis* from the Monroe Creek. Phylogenetic lines in other subfamilies of the oreodonts also show a definite size change from the Gering to the Monroe Creek, as is evident in the genus *Mesoreodon*.¹ In the *Megoreodon* line, however, there is little evidence of size change (p. 165). This provides additional evidence that development in the oreodonts did not take place at the same rate in all lines.

DISTRIBUTION

Four species of *Desmatochoerus (Paradesmatochoerus)* are known from the lower Miocene (Gering and Monroe Creek formations) of Nebraska and Wyoming. (See geologic distribution chart 1, p. 156).

SUMMARY OF SPECIES AND TYPES

Four species of *D. (Paradesmatochoerus)* from nine lower Miocene localities are here recorded (all from the west central Great Plains):

1. *Desmatochoerus (Paradesmatochoerus) grangeri*, new species, from Niobrara County,

Wyoming; referred remains from Morrill County, Nebraska. (Gering.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 33303. Figures 8-11, 24-25.

2. *Desmatochoerus (Paradesmatochoerus) monroecreekensis*, new species, from Niobrara County, Wyoming; referred remains from Converse County, Wyoming. (Monroe Creek.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 37551. Figures 8-11.

3. *Desmatochoerus (Paradesmatochoerus) sanfordi*, new species, from Sioux County, Nebraska; referred remains from Niobrara County, Wyoming; and tentatively referred from Pennington County, South Dakota. (Gering.)

HOLOTYPE: Skull and ramus, F:A.M. 45443. Figures 8-11.

- 3a. *Desmatochoerus (Paradesmatochoerus) sanfordi*, geologic variety, from Washabaugh County, South Dakota. (Monroe Creek.)

EXAMPLE: Partial skull and mandible, F:A.M. 49635.

4. *Desmatochoerus (Paradesmatochoerus) wyomingensis*, new species, from Niobrara County, Wyoming; referred remains from Goshen County, Wyoming, Banner County, Nebraska, Pennington, Shannon, and Washabaugh counties, South Dakota. (Gering.)

HOLOTYPE: Skull and mandible, F:A.M. 33312. Figures 8-11, 18.

5. ?*Desmatochoerus (Paradesmatochoerus) thurstoni* (Stock), from Ventura County, California. (Sespe=in part to Gering.)

HOLOTYPE: Partial skull and most of skeleton, C.I.T. 1566.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

DESMATOCHOERUS (PARADESMATOCHOERUS)

TOTAL AVAILABLE SPECIMENS: 43²

1. *Desmatochoerus (Paradesmatochoerus) grangeri*,³ new species

From the Gering formation, Niobrara County, Wyoming; referred specimen from Morrill County, Nebraska

DESCRIPTION

SKULL: Medium size; longest known of sub-

genus; width similar to examples of *D. (P.) monroecreekensis* and *D. (P.) wyomingensis*, wider than those of *D. sanfordi*; submesocephalic; facial region longer than other examples of subgenus; sagittal crest slightly higher than in other species of subgenus (not so high as examples of *Desmatochoerus*); exoccipital vacuities smaller and nasals with more anterior retraction than in other species of subgenus; posterior portion of zygomatic

² Includes 39 F:A.M. and 4 U.N.S.M. specimens.

³ Named in honor of the late Dr. Walter Granger of the American Museum of Natural History.

¹ Schultz and Falkenbach, 1949, p. 131.

arch robust, more so than in examples of *D. (P.) monroecreekensis*; infraorbital foramen above anterior portion of P^3 ; bulla with more lateral compression and posterior palate projecting more posteriorly than in other forms of subgenus.

MANDIBLE: Similar to those of other species of subgenus; postsymphysis below P_3 ; ascending ramus higher than in examples of *D. (P.) wyomingensis*.

DENTITION: Lighter than in other species of subgenus; superior series extending to the midline of orbit, not so far posteriorly as in other forms of subgenus.

LIMBS: Longer but similar to other examples of subgenus.

MEASUREMENTS: Tables 7 and 8 (pp. 198-199).

ILLUSTRATIONS: Figures 8-11, 24-25.

DISCUSSION

Desmatochoerus (Paradesmatochoerus) grangeri, the proposed new species, has been recognized only from the holotype and one referred specimen. The robust zygomatic arch of the holotype suggests a male example of the species. A facial vacuity is present on the right side of the holotypic skull but absent on the left. The outstanding specific characters which make this form distinct from the other species of the subgenus are: elongated facial region, light dentition, comparatively short dental series, robust zygomatic arch, and longer limb elements. The sagittal crest is high, but not so high as found in examples of *Desmatochoerus*, although slightly higher than in *D. (P.) monroecreekensis* and *D. (P.) wyomingensis*.

Two specimens are here recorded:

HOLOTYPE

Skull with I^1-M^3 , mandible with I_1-M_3 , 2 femora (1 partial), 2 tibiae, partial pes, and vertebrae. (w+)

F:A.M. 33303

From Gering formation, Little Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933

Figures 8-11, 24-25

REFERRED FROM U.N.S.M. COL. LOC. MO-108, WEST OF REDINGTON GAP, WILDCAT RIDGE, MORRILL COUNTY, NEBRASKA

(Collected by E. L. Blue, Frank Crabill, Robert Long, T. M. Stout, and C. Bertrand Schultz, 1934)

SKULL

U.N.S.M.

Skull with I^1-M^3 (C/- P^2 br.) (w+) 28500

2. *Desmatochoerus (Paradesmatochoerus) monroecreekensis*,¹ new species

From the Monroe Creek formation, Niobrara County, Wyoming; referred remains from Converse County, Wyoming

DESCRIPTION

SKULL: Medium size [average examples equal in length to those of *D. (P.) wyomingensis*, slightly shorter than in *D. (P.) grangeri*]; more robust and wider than *D. (P.) wyomingensis*; submesocephalic; exoccipital vacuities intermediate in size between examples of *D. (P.) wyomingensis* and *D. (P.) grangeri*; anterior nasal-maxilla contact

above P^1 ; zygomatic arch moderately robust (lighter in female examples); infraorbital foramen above posterior portion of P^3 to anterior portion of P^4 ; paroccipital process more robust, bulla with less vertical height, and postglenoid process more massive and wider laterally than in *D. (P.) wyomingensis*.

MANDIBLE: Slightly more robust than in examples of *D. (P.) wyomingensis*; postsymphysis below posterior portion of P_3 ; ramus with tendency to be deeper below the anterior edge of M_3 than later species.

DENTITION: Similar to examples of *D. (P.) wyomingensis*, lighter than in *D. (P.) grangeri*.

LIMBS: Similar to examples of *D. (P.) wyomingensis*; shorter than those of *D. (P.) grangeri*.

¹ Named after the Monroe Creek formation from which the holotype and referred specimens were collected.

MEASUREMENTS: Tables 7 and 8 (pp. 198-199).

ILLUSTRATIONS: Figures 8-11.

DISCUSSION

Desmatochoerus (Paradesmatochoerus) monroecreekensis, new species, from the Monroe Creek formation does not differ greatly except for size from *D. (P.) wyomingensis* from

the Gering. The characters mentioned above and the difference in geologic occurrence distinguish the two forms. It is here considered that *D. (P.) monroecreekensis* evolved directly from *D. (P.) wyomingensis*.

The F.A.M. specimens were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1932-1940.

Eleven specimens are here recorded:

HOLOTYPE

Skull with I ¹ (br.)-M ³ , mandible with I ₁ -M ₃ , partial femur, partial tibia, vertebrae, and pelvis. (w†)	F:A.M. 37551	From Monroe Creek formation, Muddy Creek, Niobrara County Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1937
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Figures 8-11

REFERRED FROM (A) TYPE AREA, NIOBRARA AND (B) CONVERSE COUNTIES WYOMING

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

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Partial skull with I ¹ (rt.)-M ³ (C/br.) and mandible with I ₁ -M ₃ (w†)	F:A.M. 44915
2 partial femora, 3 tibiae (1 partial), 3 partial manus, vertebrae, and pelvis.	44915A
The above two specimens were found associated in one field block, and represent two individuals.	
Skull with I ¹ -M ³ (I ² alv.), mandible with I ₁ -M ₃ , partial scapula, humerus, 2 partial radii, 2 partial ulnae, 2 femora, 2 tibiae, astragalus, calcaneum, and pes elements. Figures 10-11 (M+)	45439
The above specimen was found about 50 feet above the "white layer" which is used as a field marker in the Muddy Creek area.	

Skull with I ¹ -M ³ , mandible with /C-M ₃ , and most of skeleton (w+)	A.C. 1922-541 or 22-638
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The skeleton was figured by Loomis,¹ and considered as referable to *Mesoreodon megalodon*. The skull and mandible of this specimen resemble examples of *Mesoreodon* only superficially and are definitely distinct from *M. megalodon*.²

The skull, a long, narrow form, is typical of the subgenus, *D. (Paradesmatochoerus)*.

4 SKULLS AND MANDIBLES

Partial skull with C/(br.)-M ³ and mandible (attached) with M ₂ -M ₃ (w†+)	F:A.M. 33582
Anterior portion of skull with I ² -M ³ and partial mandible with /C-M ₃ (w†+)	34456
Partial skull with I ¹ -M ³ and mandible with I ₁ -M ₃ (w)	45438
Partial skull with I ¹ -I ³ br. and C/-M ³ and partial mandible with I ₁ -I ₃ rt. and /C(br.)-M ₃ (br.) (w†)	45457

PARTIAL SKULL

Partial skull with P ³ (br.)-M ³ (w†)	33643
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B. FROM 3 MI. SOUTH OF DOUGLAS, CONVERSE COUNTY, WYOMING

MANDIBULAR RAMUS

Left ramus with I ₁ -M ₃ (w†)	F:A.M. 33682
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¹ 1933, Bull. Geol. Soc. Amer., vol. 44, p. 727, fig. 6.

² Schultz and Falkenbach, 1949, p. 145.

3. *Desmatochoerus* (*Paradesmatochoerus*)
sanfordi,¹ new species

From the Gering formation, Sioux County, Nebraska; referred remains from Niobrara County, Wyoming; tentatively referred remains from Pennington County, South Dakota; and (3a) a geologic variety from Monroe Creek formation, Washabaugh County, South Dakota

DESCRIPTION

SKULL: Small size (smallest known of subgenus); no facial vacuity; anterior nasal-maxilla contact above the posterior portion of P^1 ; infraorbital foramen above P^3 ; postglenoid process comparably robust, higher and with less steeply sloping external border than in examples of *D. (P.) wyomingensis*. (Occipital region, bulla, zygomatic arch, and nasals unknown.)

MANDIBLE: Similar to examples of *D. (P.) wyomingensis* except for smaller size; post-symphysis below anterior portion of P_3 .

DENTITION: Smallest known series of subgenus.

LIMBS: Long and slender; shortest examples of subgenus.

MEASUREMENTS: Table 7 (p. 198).

ILLUSTRATIONS: Figures 8-11.

DISCUSSION

The available material of the proposed new species, while incomplete, is sufficient to show that the species is referable to this subgenus. The known characters are similar to those of *D. (P.) wyomingensis* except for the smaller size. It may well represent a dwarf form of the subgenus. The lack of facial vacuity is not considered as diagnostic. Additional specimens may have the vacuity present. As has been pointed out in other species of the oreodonts where vacuities are present, they may be observed in some examples and may be absent in others of the same species.

The holotype of this species is a very old individual and the wear of the dentition (w_{++}) is such that very little of the enamel is present. The individual teeth have spread laterally, and P^4 is worn so as to have a triangular outline. The superior premolars are slightly longer than the molar series, a non-diagnostic character in the *Desmatochoerinae*.

Four specimens are here recorded:

HOLOTYPE

Partial skull with I^1 - M^3 and right ramus with I_1 (alv.)- M_3 (I_3 rt., /C alv., and P_1 br.). (w_{++})

F:A.M. 45443

From Gering formation, Joe Sanford Ranch, Sioux County, Nebraska; collected by Morris F. Skinner and party, 1941

Figures 8-11

REFERRED FROM (A) SIOUX COUNTY, NEBRASKA; (B) NIOBRARA COUNTY, WYOMING; AND (C) TENTATIVELY REFERRED FROM PENNINGTON COUNTY, SOUTH DAKOTA

A. FROM TYPE LOCALITY, JOE SANFORD RANCH, SIOUX COUNTY, NEBRASKA
(Collected By Morris F. Skinner and Party, 1942)

SKULL, RAMUS, AND SKELETAL ELEMENTS

Partial skull with P^4 (rt.)- M^3 (M^1 alv.), partial right ramus without dentition, partial tibia, astragalus, calcaneum, and foot bones

(w_{++}) F:A.M. 45445

B. FROM GERING FORMATION, EAST OF MUDDY CREEK BRIDGE, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

(Collected By John Lynch, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1937)

SKULL AND MANDIBLE

Partial skull with I^1 - M^3 (P^1 br.) and partial mandible with I_1 - M_3 . Figures 10-11 (w_{++})

F:A.M.

37580

The figured dentition illustrates a series with less wear than in the holotype.

¹ Named in honor of Mr. Joe Sanford, the owner of the ranch on which the holotype was collected.

TENTATIVELY REFERRED

C. FROM VICINITY OF PINNACALS, PENNINGTON COUNTY, SOUTH DAKOTA

SKULL

F:A.M.

Right anterior portion of skull with P¹(rt.)-M³ (P²-M³ br.) (w+) 49636

The specimen is tentatively referred owing to its fragmentary condition,
but it seems to compare very favorably with other examples of this species.

TABLE 7

Desmatochoerus (*Paradesmatochoerus*), NEW SUBGENUS. COMPARATIVE MEASUREMENTS¹
OF SKULLS AND MANDIBULAR RAMI

	<i>D. (P.) grangeri, new species</i>	<i>D. (P.) monroe- creekensis, new species</i>	<i>D. (P.) sanfordi, new species</i>	<i>D. (P.) sanfordi, geologic variety</i>	<i>D. (P.) wyoming- ensis, new species</i>
SKULL	Holotype F:A.M. 33303	Holotype F:A.M. 37551	Holotype F:A.M. 45443	Example F:A.M. 49635	Holotype F:A.M. 33312
Stage of wear of teeth	(w+)	(w $\frac{+}{+}$)	(w $\frac{++}{++}$)	(w $\frac{++}{+}$)	(w $\frac{+}{+}$)
Length (including supraoccipital crest and incisors)	296.5	276	((230))	—	279
Basal length (from anterior notch of foramen magnum to posterior base of I ¹)	236	228	—	—	231
Width (max.)	165.5	174	(105)	—	122
Width of brain case (max.)	57.5	63	(44)	—	54
Width, interorbital (min.)	71	64	50.5	—	58
Distance from anterior rim of orbit to anterior base of canine	114.5	106	99	—	108
Distance from anterior rim of orbit to supraoccipital crest	177	176	—	—	166
Length of nasals	102	101.5	—	—	106
Width of muzzle at infraorbital foramina	57	65	50.5	—	50
Width across canines	55	54	38	—	42
Length, C/-M ³ incl.	125.5	134.5	105.5	—	130
Length, P ¹ -M ³ incl.	105.5	114	93	—	113.5
Length, P ¹ -P ⁴ incl.	50	53.5	48	53	55.5
Length, M ¹ -M ³ incl.	55	63	45	—	60
Width of M ³ (max.)	18.5	25	20	—	22
Depth of malar below orbit.	24.5	26	20.5	—	22
MANDIBULAR RAMUS					
Length (max., including incisors) . .	223	217	190	—	208
Length, /C—condyle incl.	208	197	172.5	—	194
Depth of jaw under coronoid	121	109	(87)	—	114
Depth of jaw below anterior edge of M ₃	42	47.5	35.5	—	43
Length, /C-M ₃ incl.	135.5	129.5	(108)	(115.5)	131
Length, P ₁ -M ₃ incl.	122	121	100.5	(106.5)	122
Length, P ₁ -P ₄ incl.	61	54.5	48	48	58
Length, M ₁ -M ₃ incl.	61	68.5	52.5	(59.5)	65

¹ (), Approximate; (()), estimated. All measurements in millimeters.

TABLE 8

Desmatochoerus (*Paradesmatochoerus*), NEW SUBGENUS. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

	<i>D. (P.) grangeri</i> , new species	<i>D. (P.) monroe-creekensis</i> , new species	<i>D. (P.) wyomingensis</i> , new species	<i>D. (P.) sanfordi</i> , new species	? <i>D. (P.) thurstoni</i> , (Stock)
	Holotype F:A.M. 33303	Referred A.C. 1922-541	Referred F:A.M.	Referred F:A.M. 45445	Holotype ² C.I.T. 1566
Length of humerus (articular) . . .	—	((172))	—	—	((142))
Length of radius (articular) . . .	—	149	134.5-44906A	—	126.5
Length of ulna (max.) . . .	—	197	—	—	151.5
Length of metacarpal III (max.) . .	—	72	68.5-44906A	—	—
Length of femur (articular) . . .	206	200	—	—	154
Length of tibia (articular) . . .	177.5	172	—	—	153
Length of metatarsal III (max.) . .	78.5	73	81-42311	—	—
Length of calcaneum (max.) . . .	—	—	—	(54)	—

¹ (), Approximate; (()), estimated. All measurements in millimeters.

² Measurements after Thorpe, 1937 (questionable whether measurements are articular or max.).

3a. Geologic Variety from Monroe Creek Formation, Washabaugh County, South Dakota

DISCUSSION

The fragmentary specimen with well-worn dentition listed below is of interest in that it was collected from deposits here considered to be equal in age to the Monroe Creek formation. (Morris F. Skinner secured an example of *Desmatochoerus hatcheri niobrarensis*

from this same locality and geologic level, see p. 192.)

The partial skull and the dentition, especially M¹ and M², are slightly larger than in the Gering form *D. (P.) sanfordi* (the possible ancestor of this geologic variety). If additional future material should substantiate this suggested relationship, *D. (P.) sanfordi* and the geologic variety may represent a new subgenus of *Desmatochoerus*.

EXAMPLE

Inferior, anterior portion of skull with I¹-M² and partial mandible with I₁-M₃. (w₁⁺)

F:A.M. 49635

From the Monroe Creek formation, "upper part of the deposits," 1 mi. W. of Quiver Hill, Washabaugh County, South Dakota; collected by Morris F. Skinner and party, 1950.

4. *Desmatochoerus* (*Paradesmatochoerus*) *wyomingensis*, new species

From the Gering formation, Niobrara County, Wyoming; referred remains from Niobrara and Goshen counties, Wyoming; Banner and Morrill counties, Nebraska; Washabaugh, Pennington, and Shannon counties, South Dakota; and tentatively referred remains from Goshen County, Wyoming

DESCRIPTION

SKULL: Approximately same length but

narrower and lighter than examples of *D. (P.) monroecreekensis*, smaller than in the holotype of *D. (P.) grangeri*, larger than in *D. (P.) sanfordi*; dolichocephalic; exoccipital vacuities larger than in other known forms of subgenus; anterior nasal-maxilla contact above middle of P¹; infraorbital foramen above P²; base of paroccipital process heavier, postglenoid process more robust, and bulla with greater vertical length than in examples of *D. (P.) monroecreekensis*.

MANDIBLE: Similar to examples of *D. (P.) monroecreekensis*, but lighter and with less depth below M₃; postsymphysis below P₃.

DENTITION: Approximate size of examples of *D. (P.) monroecreekensis*; greater length and more robust than in *D. (P.) grangeri* and *D. (P.) sanfordi*.

LIMBS: Similar in size and form to examples of *D. (P.) monroecreekensis*.

MEASUREMENTS: Tables 7 and 8 (pp. 198-199).

ILLUSTRATIONS: Figures 8-11, 18.

DISCUSSION

Desmatochoerus (Paradesmatochoerus) wyo-

mingensis, the subgenotypic species, is similar to examples of *D. (P.) monroecreekensis*, except for the characters mentioned above. It is here considered that *D. (P.) wyomingensis* from the Gering formation gave rise to *D. (P.) monroecreekensis* from the Monroe Creek.

The F:A.M. specimens were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1932-1938.

Twenty-five specimens are here recorded:

HOLOTYPE

Skull with I¹-M³ and mandible with I₁-M₃. (w⁺)
Female example

F:A.M. 33312

From Gering formation, Willow Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1932
Figures 8-11, 18

REFERRED FROM (A), (A') AND (A'') NIOBRARA AND (B) GOSHEN COUNTIES, WYOMING; (C) BANNER AND (D) MORRILL COUNTIES, NEBRASKA; (E) WASHABAUGH, (F) PENNINGTON, AND (G) SHANNON COUNTIES, SOUTH DAKOTA

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

	SKULL	F:A.M.
Partial skull with I ³ -C/ rt. and P ¹ -M ³	(w ⁺)	44922

A'. FROM LITTLE MUDDY CREEK, NIOBRARA COUNTY, WYOMING

2 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Partial skull with P ⁴ -M ³ , partial left ramus with M ₃ br., partial humerus, partial tibia, partial manus, vertebrae, ribs, and pelvis	(w ⁺)	42310
Partial skull with P ³ -M ³ , partial right ramus with P ₃ -M ₃ , 2 partial femora, 2 partial tibiae, 2 astragali, 2 partial calcanea, 2 partial pedes, vertebrae, and fragments	(w ⁺)	42311

SKULL, MANDIBLE, AND SKELETAL ELEMENTS, IMMATURE

Skull with I ² -I ³ rt. and C/-dP ² -M ³ (germ), mandible (attached) with /C(rt.)-dP ₂ -M ₃ (germ), partial scapula, 2 partial humeri, 2 radii (1 partial), 2 partial ulnae, 2 partial manus, pelvis, and fragments	(i)	33343
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2 SKULLS AND MANDIBLES

Partial skull with I ¹ -I ² rt. and I ³ -M ³ (P ¹ -P ² br.) and partial mandible with I ₂ -I ₃ (br.) and /C-M ₃	(w ⁺)	43114
Partial skull with I ³ (br.)-M ³ (br.) (P ¹ absent) and partial mandible with I ₁ -C (rt.) and P ₁ (br.)-M ₃	(w)	44910

SKULL

Partial skull with C/(rt.)-M ² (br.) (P ¹ rt. and M ¹ br.)	(M ⁺)	44911
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A". FROM GERING FORMATION, EAST OF MUDDY CREEK BRIDGE, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

3 ASSOCIATED PARTIAL SKELETONS

F:A.M.

Partial muzzle of skull with I ¹ (alv.)-P ² (br.) (I ³ alv.), partial right ramus with P ₄ (br.)-M ₃ , radius, ulna, partial femur, 2 partial manus, atlas, and partial pelvis	(w ₊ ⁺)	44906A
Right and left maxillae with C/-dP ² -M ²	(i)	44906B
Partial right maxilla with P ¹ -dP ² -M ¹	(i)	44906C
Partial frontals of skull with brain case, 2 partial scapulae, partial humerus, partial radius, 2 partial tibiae, pes elements, and vertebrae		44906B-C

The above three specimens were found associated in one field block. The frontals and the brain case may belong to any of the three individuals, while the skeletal elements B-C may belong to either of the immature individuals.

SKULL, IMMATURE

Partial skull with I ¹ -dP ² -M ² (br.)	(i)	45454
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B. FROM THE HORSE CREEK AREA, GOSHEN COUNTY, WYOMING

SKULL AND MANDIBLE, IMMATURE

F:A.M.

Partial skull with I ³ -dP ² -M ² (germ) (P ¹ br., M ¹ absent) and partial mandible with /C(germ)-P ₁ (erupt.)-dP ₂ -M ₂ (germ).	(i)	44914
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MAXILLA

Partial right maxilla with P ³ -M ³ (br.)	(w ₊ ⁺)	44913
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2 MANDIBLES

Partial mandible with I ₂ -M ₃ (br.)	(w ₊ ⁺)	44950
Partial mandible with I ₁ -P ₁ (erupt.)-dP ₂ -M ₂ (germ) and partial scapula.	(i)	42314

C. FROM THE HORSE CREEK AREA, BANNER COUNTY, NEBRASKA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

F:A.M.

Skull with I ¹ -M ³ (lacking right zygomatic arch), mandible with I ₁ -M ₃ , partial scapula, partial humerus, 2 partial femora, vertebrae, and pelvis	(w+)	37571
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Male example.

D. FROM MORRILL COUNTY, NEBRASKA

FROM ROUNDHOUSE ROCK, WILDCAT RIDGE; COLLECTED BY A. C. G. KAEMPFER OF BRIDGEPORT, NEBRASKA, 1933:

SKULL AND MANDIBLE

Skull with C/(br.)-M ³ and mandible with I ₁ -I ₃ roots and /C-M ₃	(w ₊ ⁺)	28339
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The above skull is more robust than average examples of this species and may represent a male example. In size, the specimen approaches *D. (P.) monroecreekensis*.

FROM U.N.S.M. COL. LOC. MO-107:

SKULL AND MANDIBLE

Skull with I ¹ -M ³ and mandible with I ₁ -M ₃	(w ₊ ⁺)	28343
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Not included in chart 3.

FROM U.N.S.M. COL. LOC. MO-108:

SKULL

Partial skull with I ¹ -M ³ (C/and P ² -P ³ rt.)	(w+)	28342
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Not included in chart 3.

E. FROM LOWER PART OF DEPOSITS, QUIVA HILL AREA,
WASHABAUGH COUNTY, SOUTH DAKOTA

(Collected by Morris F. Skinner and Party, 1950)

SKULL AND SKELETAL ELEMENTS, IMMATURE

F:A.M.

Partial skull with dP⁴-M³ br., 2 partial humeri, 2 partial radii, 2 partial ulnae,
partial manus, 2 partial femora, 2 tibiae (1 partial), and 2 partial pedes . . . (i) 49639

F. FROM VICINITY OF THE PINNACALS, PENNINGTON COUNTY, SOUTH DAKOTA

(Collected by Morris F. Skinner and Party, 1950)

SKULL, 2 MANDIBLES AND SKELETAL ELEMENTS

F:A.M.

Anterior portion of skull with I¹-M³(br.) and partial mandible with I¹-M₃ . . . (w+) 49637A
Symphysis of mandible with I₁ and I₂-P₂ rt. (w+) 49637B
Partial ulna, partial manus, partial femur, 2 tibiae (1 partial), and 2 pedes . . . 49637A-B

The above two specimens were found associated in the field. The skeletal elements may belong to either dentition.

G. FROM MOUTH OF PORCUPINE CREEK CANYON, SHANNON COUNTY,
SOUTH DAKOTA

(Collected by Morris F. Skinner, Charles H. Falkenbach, And Party, 1950)

SKULL

F:A.M.

Partial skull with C/-M³. (w) 49638

The above skull, which is badly crushed, is the smallest recorded example of the species. It was secured in the pink clay with small nodules that underlies the high exposures in this area.

TENTATIVELY REFERRED

H. FROM 66 MOUNTAIN, GOSHEN COUNTY, WYOMING

(Collected By Erich Schlaikjer, 1930-1933)

SKULL

M.C.Z.

Skull with I¹-I³ alv. and C/-M³. (w+) 2815

The specimen is tentatively referred to this species because the skull is wider and the molar series longer than are usually found in the referred material. Schlaikjer¹ referred the specimen to "*Promerycochoerus*" *hatcheri* = *Desmatochoerus hatcheri* (this report, p. 186).

5. ?*Desmatochoerus* (*Paradesmatochoerus*)
thurstoni (Stock)

From Sespe deposits (equal in part to the
Gering of the Great Plains), Willard
Canyon, South Mountain, Ventura
County, California

Eporeodon thurstoni STOCK, 1934, Proc. Natl.
Acad. Sci., vol. 20, no. 9, p. 518, pl. 2. THORPE,
1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 96,
pl. 43, fig. 1.

MANDIBLE: (See discussion below).

DENTITION: Superior series estimated to
be shorter than examples of *D. (P.) sanfordi*,
slightly longer than those of *M. cursor*.

LIMBS: Resembling examples of *Subdesma-
tochoerus socialis*.

MEASUREMENTS: Table 8 (p. 199).

ILLUSTRATIONS: (See Stock, 1934, and
Thorpe, 1937).

CHARACTERS

SKULL: Smaller than skulls of *D. (P.)
sanfordi* and *Merycoides cursor*; prelacrima
fossa present; bulla large.

DISCUSSION

The holotype of this species was not ex-
amined by the present writers. At the time of
their visit to the California Institute of Tech-
nology, the part of the building that housed

¹ 1935, Bull. Mus. Comp. Zool., vol. 76, no. 4, p. 172, pls. 36-37.

the type was "out of bounds" for all except those engaged in the war effort. The present discussion is based on Stock's original description (lacking measurements) and the measurements given by Thorpe.¹

Stock's² and Thorpe's³ illustrations indicate that the mandible is largely restored, which is the reason, perhaps, why neither author mentioned the mandible in his description.

Thorpe's measurements indicate a form approaching the size of *D. (P.) sanfordi*⁴ as well as that of *Merycoides cursor*⁵ from Montana. Stock⁶ reported: "In presence of the large bulla and in the characters displayed by the premolar teeth, the Sespe form is more like *Eporeodon* than like *Merycoidodon*. The skeleton is of an individual resembling *Eporeodon socialis* in size." (The latter is considered as *Subdesmatochoerus socialis* in

the present report, p. 220.)

Stock's geologic section was discussed by Schultz and Falkenbach⁷ under *?Mesoreodon hesperus* (Stock), also from the Sespe deposits, and it was suggested that the occurrence of this species would indicate that the upper portion of the Sespe formation was approximately equal in age to the Monroe Creek formation of the Great Plains. The species *?D. (P.) thurstoni* occurred "approximately 1500 feet lower stratigraphically than ... *?M. hesperus*," which portion of the Sespe includes the range of the leptauchenids.

The present writers here suggest that perhaps the part of the Sespe beds which produced *?D. (P.) thurstoni* and the leptauchenids is approximately equal in age to the Gering of the Great Plains.

One specimen is here recorded:

HOLOTYPE

Partial skull and most of skeleton

C.I.T. 1566

From Loc. 157, Calif. Inst. Tech. Vert. Pal. Coll., Willard Canyon, South Mountain, Ventura County, California

Figured by Stock, 1934, pl. 2; Thorpe, 1937, pl. 43, fig. 1

III. PSEUDODESMATOCHOERUS,

NEW GENUS

GENOTYPE: *Pseudodesmatochoerus hoffmani*, new species.

DESCRIPTION

SKULL: Medium size; basal length ranging from 233 to 257 mm., width from 125 to 176 mm.; dolichocephalic to mesocephalic; supra-occipital wings small, not widely spread, produced posteriorly beyond the occipital condyles, similar to examples of *Desmatochoerus* and *D. (Paradesmatochoerus)*; small exoccipital vacuities in deep pits, above condyles; sagittal crest exceptionally low, depressed in medial region; brain case long and narrow; frontals with slight protuberance at midline (not so pronounced as in average examples

of *Desmatochoerus*); frontals usually with a convex surface; nasals with slight anterior retraction; anterior nasal-maxilla contact above P¹; orbit directed mostly outward and forward; malar moderately deep below orbit; posterior border of zygomatic arch light to moderately robust, with inward curve posterior to orbit; infraorbital foramen above P³; lacrimal fossa small, but deep; facial vacuity usually absent; depression above P¹-P³ very shallow; premaxillae joined for short distance; occipital condyles similar to those of *Desmatochoerus*; paroccipital process wide at base, laterally compressed, tapering to an oval-shaped inferior border; bulla inflated, from medium to large size, with some lateral compression; postglenoid process usually lighter than in examples of *Desmatochoerus*; posterior palate projecting posteriorly beyond M³.

MANDIBLE: Medium size; moderately robust; ramus below dentition shallow; post-

¹ 1937, p. 282.

² 1934, pl. 2.

³ 1937, pl. 43, fig. 1.

⁴ This report, p. 197.

⁵ Schultz and Falkenbach, 1949, p. 157.

⁶ 1934, p. 520.

⁷ 1949, p. 151.

symphysis below area between P_2 and P_3 ; ramus increasing gradually in depth posteriorly, with a more pronounced downward curve of inferior border posterior to M_3 ; ascending ramus moderately high; condyle light, wide laterally, set at less than right angle to axis of dentition, with external border of condyle farther forward and higher than internal border.

DENTITION: Brachyodont; series approximately same size as examples of *D. (Paradesmatochoerus)*, shorter than those of *Desmatochoerus*, but nearly as robust; $C/$ and P_1 moderately large; external styles of superior molars weak to moderately prominent; premolars not crowded (set approximately parallel to alveolar border); P^1-P^3 each with anterior intermediate crest, not so strong as in examples of *Desmatochoerus* or *D. (Paradesmatochoerus)*; P_2 and P_3 with weak posterior intermediate crest.

LIMBS: Similar in size and form to examples of *D. (Paradesmatochoerus)*, but with tendency to be longer.

MEASUREMENTS: Tables 9-10 (pp. 205-206).

ILLUSTRATIONS: Figures 12-15, 18 (skulls, rami, and dentitions), 23-25 (limbs).

DISCUSSION

Pseudodesmatochoerus, the proposed new genus, differs from the other genera of the Desmatochoerinae in that the sagittal crest of the skull is depressed rather than being prominent. The lack of a prominent sagittal crest on the skull, however, does not exclude this genus from the subfamily. A similar case is found in the Promerycochoerinae, where *Mesoreodon*¹ has a prominent crest and *Merycoides*² lacks it. The absence of a facial vacuity is not considered diagnostic. All the material listed under this genus does lack the facial vacuity with the exception of *P. longi-*

ceps in which case the writers question the presence or absence of the vacuity (see footnote, p. 207). The limb elements show a tendency to be longer than in other examples of the subfamily with the exception of *Megoreodon*.

DISTRIBUTION

Five species of *Pseudodesmatochoerus* are known from the lower Miocene (Gering, Monroe Creek, and Harrison formations or their approximate equivalents) of Montana, Oregon, and Wyoming. (See geologic distribution chart 1, p. 156.)

SUMMARY OF SPECIES AND TYPES

Five species of *Pseudodesmatochoerus* from six lower Miocene localities are here recorded:

1. *Pseudodesmatochoerus hoffmani*, new species, from Niobrara County, Wyoming. (Monroe Creek.)

HOLOTYPE: Skull, mandible, and femur, F:A.M. 44912. Figures 12-15, 24.

2. *Pseudodesmatochoerus longiceps* (Douglass), from Jefferson County, Montana. (Approximately equal in age to the Harrison.)

HOLOTYPE: Skull, mandible, and skeletal elements, A.M. 9732. Figures 12-15, 23-25.

3. *Pseudodesmatochoerus milleri*, new species, from Niobrara County, Wyoming; referred remains from Goshen County, Wyoming. (Gering.)

HOLOTYPE: Skull and mandible, F:A.M. 33304. Figures 12-15, 18.

4. *Pseudodesmatochoerus wascoensis*, new species, from Wasco County, Oregon. (Approximately equal in age to the Harrison.)

HOLOTYPE: Skull, A.M. 7827. Figures 12-14.

5. *?Pseudodesmatochoerus pariogonus* (Cope), from Montana; referred from Meagher County, Montana; and tentatively referred from Montana, and Lewis and Clark County, Montana. (Approximately equal in age to Gering.)

HOLOTYPE: Partial skull and partial mandible, A.M. 8113.

¹ Schultz and Falkenbach, 1949, p. 131.

² *Idem*, p. 153.

TABLE 9

Pseudodesmatochoerus AND *Superdesmatochoerus*, NEW GENERA. COMPARATIVE MEASUREMENTS¹ OF SKULLS AND MANDIBULAR RAMI

	<i>P. hoffmani</i> , new species	<i>P. longiceps</i> (Douglass)	<i>P. milleri</i> , new species	<i>P. wascoensis</i> , new species	? <i>P. parigonus</i> (Cope)	<i>S. lulli</i> (Thorpe)	<i>S. microcephalus</i> (Thorpe)
	Holotype F:A.M. 44912	Holotype A.M. 9732	Holotype F:A.M. 33304	Holotype A.M. 7827	Holotype A.M. 8113	Holotype Y.P.M. 10234	Holotype Y.P.M. 10998
SKULL							
Stage of wear of teeth . . .	(w ₊)	(w)	(w ₊)	(w+)	(w)	(w)	(w+)
Length (including supraoccipital crest and incisors)	280	262	280	(281)	—	375	((356))
Basal length (from anterior notch of foramen magnum to posterior base of I ¹)	((244))	233	240	257	—	—	((303))
Width (max.)	(140)	(125)	141.5	(176)	((100))	194.5	153
Width of brain case (max.)	66	63.5	58	69	54	70.5	56.5
Width, interorbital (min.)	66.5	60	68	69	((50))	78.5	—
Distance from anterior rim of orbit to anterior base of canine	110	110	115	118	—	163	((143))
Distance from anterior rim of orbit to supraoccipital crest	(170)	161.5	165	172	((140))	215	((198))
Length of nasal	99	87.5	—	116	—	—	146
Width of muzzle at infraorbital foramina	61	59.5	56	—	—	((68))	73
Width across canines	44.5	43.5	51	—	—	76	—
Length, C/-M ³ incl.	127	114	133	(124)	—	187	—
Length, P ¹ -M ³ incl.	112	100.5	115	108	—	157	147.5
Length, P ¹ -P ⁴ incl.	53.5	47	53	53	—	77	69.5
Length, M ¹ -M ³ incl.	61.5	55	64	(58)	—	84.5	80
Width of M ³ (max.)	24.5	21.5	24	20.5	16.5	27	28.5
Depth of malar below orbit	25.5	23.5	23	24.5	14	41.5	42.5
MANDIBULAR RAMUS							
Length (max., including incisors)	—	211.5	220	—	—	297	—
Length, /C-condyle incl.	—	181.5	204	—	—	276	—
Depth of jaw under coronoid	—	102	109	—	71	143.5	133
Depth of jaw below anterior edge of M ₃	46	40	45	—	30	61	65
Length, /C-M ₃ incl.	133.5	116	139	—	—	190	— ²
Length, P ₁ -M ₃ incl.	124	108.5	126.5	—	—	174.5	—
Length, P ₁ -P ₄ incl.	58	49	55.5	—	—	82	—
Length, M ₁ -M ₃ incl.	66.5	60.5	72	—	—	93	82

¹ (), Approximate; (()), estimated. All measurements in millimeters.

² P₁-P₃=138.5; P₂-P₄=57.5.

TABLE 10

Pseudodesmatochoerus AND *Superdesmatochoerus*, NEW GENERA. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

	<i>P. hoffmani</i> , new species		<i>P. longiceps</i> (Douglass)	<i>S. lulli</i> (Thorpe)	
	Holotype F:A.M. 44912	Referred F:A.M. 44947	Holotype A.M. 9732	Tentatively	Referred
				A.M. 7482	A.M. 7906
Length of humerus (articular)	—	—	—	223	—
Length of radius (articular)	—	153	140	190	—
Length of ulna (max.)	—	—	—	256	—
Length of femur (articular)	184	—	(192)	—	—
Length of tibia (articular)	—	—	167	—	—
Length of metatarsal III (max.) . . .	—	—	82	—	96
Length of calcaneum (max.)	—	—	66.5	—	—

¹ (), Approximate. All measurements in millimeters.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PSEUDODESMATOCHOERUS

TOTAL AVAILABLE SPECIMENS: 25²

1. *Pseudodesmatochoerus hoffmani*,³ new species

From the Monroe Creek formation,
Niobrara County, Wyoming

DESCRIPTION

SKULL: Tendency to be slightly longer, but of approximately same width as examples of *P. milleri*; medial depression on sagittal crest more pronounced and nasals with greater anterior retraction than in examples of *P. milleri*; anterior nasal-maxilla contact above posterior portion of P¹; infraorbital foramen above posterior portion of P³ to anterior portion of P⁴; bulla larger and higher than in *P. milleri* (more like *P. wascoënsis* in this respect); postglenoid process more robust than in *P. milleri*.

MANDIBLE: Approximately equal in size and form to examples of *P. milleri*; post-

symphysis below anterior portion of P₃; condyle more robust than in *P. milleri*.

DENTITION: Series similar to examples of *P. milleri*, slightly longer and heavier than examples of *P. wascoënsis*, definitely larger than those of *P. longiceps*.

LIMBS: Longer than examples of *P. longiceps*.

MEASUREMENTS: Tables 9 and 10 (pp. 205–206).

ILLUSTRATIONS: Figures 12–15, 24.

DISCUSSION

The proposed new species, *P. hoffmani*, from the Monroe Creek formation differs from examples of *P. milleri*, the ancestral form from the Gering, in possessing a greater medial depression on the sagittal crest, a larger bulla, and a more massive postglenoid process. The anterior nasal-maxilla contact, which is located farther posteriorly than in *P. milleri*, may indicate a tendency for a retraction of the nasals.

The F:A.M. specimens were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1934–1940.

Ten specimens are here recorded:

² Includes 18 F:A.M. specimens.

³ Named in honor of the late Mr. Charles Hoffman, who for many years as a member of the Frick Laboratory aided in the preparation of oreodont specimens used by the writers.

HOLOTYPE

Partial skull with I¹-M³, partial mandible with I₁-M₃, and femur. (w⁺)

F:A.M. 44912

From the Monroe Creek formation, the "high brown sand," 2 mi. west of Bridge, Muddy Creek, Niobrara County, Wyoming; collected by Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1940

Figures 12-15, 24

REFERRED FROM TYPE AREA, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

4 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Partial skull with I ¹ -M ³ (C/br.), partial mandible with I ₁ -M ₃ , radius, partial ulna, and fragments	(w ⁺)	F:A.M. 44947
Partial skull with P ¹ (erupt.)-dP ² -M ² (germ), mandible with I ₁ -dP ₂ -M ₂ (germ), partial manus, vertebrae, pelvis, and fragments	(i)	45441
Partial skull with C/-dP ² -M ² , partial mandible with I ₁ -C rt. and P ₁ (br.)-dP ₂ -M ₂ (germ), atlas, and fragments	(i)	45455
Partial skull with I ¹ -M ³ , partial tibia, and partial fibula	(M+)	45456

SKULL AND MANDIBLE

Partial skull with I ¹ -M ³ and mandible (attached) with I ₁ -M ₃	(w ⁺)	44946
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4 SKULLS

Four partial skulls with		
P ¹ (br.)-M ³	(w+)	44920
P ¹ -M ³ (br.)	(w ⁺⁺)	44952
M ¹ (rt.)-M ³	(w ⁺⁺)	45440
I ¹ -dP ² -M ²	(i)	44927

2. *Pseudodesmatochoerus longiceps*

(Douglass)

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

Mesoreodon longiceps DOUGLASS, 1907, Bull. Amer. Mus. Nat. Hist., vol. 23, art. 32, p. 811, figs. 1-5.

Merycoides longiceps (Douglass), THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 174, figs. 5, 126-128.

CHARACTERS

SKULL: Medium size; smallest known form of the genus; supraoccipital wings comparatively small, more widely spread than in examples of *P. hoffmani* and *P. milleri*; sagittal crest similar to examples of *P. milleri*, medial depression on sagittal crest less pronounced than in *P. hoffmani*; brain case more inflated, rounder, and shorter than in latter two species; nasals shorter and wider than in other species of genus (anterior nasal-maxilla contact farther down on the side of the face than in other forms of genus), anterior retraction less than in *P. hoffmani*,

more so than in *P. wascoensis*; anterior nasal-maxilla contact above posterior portion of P¹; posterior portion of zygomatic arch comparatively light (similar to supposed female examples of *P. hoffmani* and *P. milleri*), lighter than in holotype of *P. wascoensis*, posterior border with less posterior rise than in two former species (more like *P. wascoensis* in this respect); infraorbital foramen above posterior portion of P³; lacrima fossa larger and deeper than in other species of the genus; facial vacuity questionable¹; occipital condyles similar to examples of *P. hoffmani* and *P. milleri*, lighter than *P.*

¹ The holotypic skull of *P. longiceps*, the only known skull representing the species, is damaged in the area of the vacuity on the right side. On the left side of the face, however, there is a triangular opening that may well represent a vacuity, but the area is badly cracked and part of the surface is wanting. The presence or absence of a facial vacuity appears to be of no special diagnostic value (see discussion, p. 204).

In the genus *Ustatchoerus* Schultz and Falkenbach (1941, pp. 16, 23), *U. medius* from the Valentine possesses a vacuity, but *U. major* from the higher Ash Hollow deposits lacks one.

wascoënsis; paroccipital process similar to that of *P. milleri*; bulla suggesting a form similar to that of *P. hoffmani* (large and with some lateral compression); postglenoid process peg-shaped, light, and high; posterior palate projecting posteriorly for longer distance beyond M^3 than in examples of other species of this genus.

MANDIBLE: Postsymphysis below P_3 ; posterior border of ascending ramus comparatively robust; condyle larger than in *P. milleri*, approximately equal to that of *P. hoffmani*.

DENTITION: Smallest known series of genus; lighter than examples of *P. hoffmani* and *P. milleri* (similar to those of *P. wascoënsis* in this respect); diastema between P^1 and P^2 shorter than in other examples of the genus.

LIMBS: Within size range of examples of *P. hoffmani*.

MEASUREMENTS: Tables 9 and 10 (pp. 205–206).

ILLUSTRATIONS: Figures 12–15, 23–25.

DISCUSSION

Douglass¹ described this species as "*Mesoreodon*" *longiceps* and stated: "The characters which distinguish this species from the type of *Mesoreodon* are numerous, and in some respects considerable in degree." Among the characters which Douglass listed are many that do separate this species from the genus *Mesoreodon* and are sufficient to demonstrate affinity to the new genus *Pseudodesmatochoerus*.

Loomis² was the first to suggest that this species belonged to the genus *Merycoides* and stated: "The type of the genus *Merycoides* is *M. cursor*, and I should associate with this such species as has been known as *Mesoreodon longiceps* and *Mesoreodon laticeps* [misprint for *latidens*]."

Thorpe³ considered *P. longiceps* under the genus *Merycoides* and stated: "In most respects this species conforms to the genus

Merycoides, but in facial vacuities, the greater length of the palate, the posterior obtuse shape of the nasal bones, and the lengthening of the posterior part of the skull there are marked differences, as well as the higher geological horizon. It is indeed an extreme type of *Merycoides* and almost entitled to subgeneric rank."

From the foregoing quotations, it is clear that neither Douglass nor Thorpe, although each placed this species in different genera, was satisfied with his conclusions. The holotypic skull of *P. longiceps* is different from the comparatively low and broad skulls of *Mesoreodon*⁴ and *Merycoides*.⁵ The skulls of *Mesoreodon* have very prominent sagittal crests, while those of *Merycoides* and *Pseudodesmatochoerus* almost lack a sagittal crest; the latter, however, shows a rise of the posterior portion of the crest.

As to Thorpe's reference to the geologic occurrences, it should be pointed out that *Mesoreodon* remains are restricted to the Gering and Monroe Creek formations (or equivalents), while *Promerycochoerus* is restricted to the Harrison. *Merycoides* also is known from the Gering and Monroe Creek formations, but there is no evidence of this genus in the Harrison or its equivalents.

The holotype and referred specimens of *P. longiceps* are here considered as coming from beds⁶ approximately equal in age to the Harrison of the Great Plains. The skull of this species, however, is actually smaller than examples of *P. milleri* from the Gering. It is of interest that the dentition of *P. longiceps* is lighter than in either *P. milleri* or *P. hoffmani*, and is closer in this respect to dentitions of *P. wascoënsis* from Oregon, yet the skull characters are closer to those of forms from the Great Plains than to the Oregon species.

Three specimens are here recorded:

⁴ Schultz and Falkenbach, 1949, p. 131. (Also, p. 140, *Mesoreodon latidens* = *M. chelonys*.)

⁵ *Idem*, p. 153.

⁶ *Hypsiops brachymelis* remains are also reported from these deposits; *idem*, 1950, p. 116.

¹ 1907, p. 811.

² Loomis, Frederic B., 1924, Bull. Amer. Mus. Nat. Hist., vol. 51, art. 1, p. 12.

³ 1937, p. 177.

HOLOTYPE

Skull with I¹-M³, mandible with I₂-M₃, partial scapula, partial humerus, radius, partial femur, tibia, partial pes, astragalus, 2 calcanea (1 partial), and vertebrae. (w)

A.M. 9732

From lower Miocene deposits, east side of North Boulder Valley, near Cold Springs Post Office, Jefferson County, Montana; collected by Albert Thomson, 1902

Figured by Douglass, 1907, figs. 1-5; Thorpe, 1937, figs. 5, 126-128

This report, figs. 12-15, 23-25

REFERRED FROM TYPE AREA, NORTH BOULDER VALLEY,
JEFFERSON COUNTY, MONTANA

(Collected by Everett De Groot, N. Z. Ward, Nelson J. Vaughan, and Charles H. Falkenbach, 1936 and 1942)

SKULL AND MANDIBULAR RAMUS

Muzzle of skull with C/-P³(br.) (P¹ br.) and partial left ramus with I₁-M₃(br.) (P₁-P₂ br.) (w)

F:A.M.
44953

MANDIBLE

Mandible with I₁-M₃ (w) 34474

3. *Pseudodesmatochoerus milleri*,¹
new species

From the Gering formation, Niobrara County,
Wyoming; referred remains from Goshen
County, Wyoming

DESCRIPTION

SKULL: Medium size; tendency to be slightly smaller than examples of *P. hoffmani*, larger than in *P. longiceps*; supraoccipital wings with less spread than in *P. longiceps*; sagittal crest with slightly depressed medial region, not so pronounced as in examples of *P. hoffmani*; nasals long and light, with slight anterior retraction, less retraction than in latter species; anterior nasal-maxilla contact above P¹, slightly more anterior than in examples of *P. hoffmani*; infraorbital foramen above P³-P⁴; bulla of moderate size, smaller than other examples of genus; postglenoid process more peg-shaped than in examples of *P. hoffmani* (closer to that of *P. longiceps* in this respect, but with less height).

MANDIBLE: Postsymphysis below anterior

¹ Named in honor of Mr. Frank G. Miller, member of the Frick Laboratory, who has contributed much to the revision of the oreodonts by his careful preparation of many of the specimens.

portion of P₃; posterior border of ascending ramus lighter than in *P. longiceps*.

DENTITION: Series approximately same size as examples of *P. hoffmani*, larger than in *P. longiceps*, slightly longer than in *P. wascoensis*; more robust than in latter two species.

LIMBS: (Unknown).

MEASUREMENTS: Table 9 (p. 205).

ILLUSTRATIONS: Figures 12-15, 18.

DISCUSSION

The remains of the here-proposed new species, *P. milleri*, come from the Gering formation and occur lower in the geologic section than those of other species of the genus. *P. milleri* apparently gave rise to *P. hoffmani* from the Monroe Creek formation. The former species differs from the latter in having a less marked medial depression of the sagittal crest, a lighter postglenoid process, and a smaller bulla. It also differs from *P. longiceps* in its larger size and more robust dentition. The heavier dentition of *P. milleri* is distinguishable from the lighter dental series of *P. wascoensis*.

Five specimens are here recorded:

HOLOTYPE

Skull with I¹-M³ and mandible with I¹-M³. (w†)

F:A.M. 33304

From Gering formation, Little Muddy Creek, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1932

Figures 12-15, 18

REFERRED FROM (A) NIOBRARA AND (B) GOSHEN COUNTIES, WYOMING

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

(Collected by John Lynch, Everett De Groot and Charles H. Falkenbach, 1931-1932)

	SKULL	F:A.M.
Skull with I ¹ -M ³	(-M)	33339
2 SKULLS, IMMATURE		
Skull with I ¹ -dP ³ -M ³ (erupt.)	(I)	33350
Partial skull with C/-P ¹ erupt. and dP ² -M ¹	(I)	44926

B. FROM THE HORSE CREEK BASIN, GOSHEN COUNTY, WYOMING

	SKULL, IMMATURE	
Partial skull with C/(erupt.)-dP ² -M ¹ (P ¹ alv.)	(I)	45422

4. *Pseudodesmatochoerus wascoënsis*,¹
new species

From middle or upper John Day (approximately equal in age to the Harrison formation of the central Great Plains), Wasco County, Oregon

DESCRIPTION

SKULL: Approximately same length as examples of *P. hoffmani* and *P. milleri*, larger than that of *P. longiceps*; mesocephalic, wider than other examples of genus; lower than in other species of genus, but not so low as examples of *Mesoreodon* (some of vertical compression of skull may be due to crushing); supraoccipital wings larger and with more lateral spread than in other species of genus; brain case inflated but slightly depressed; frontals wide; nasals more robust than usual in this genus, less anterior retraction than in *P. hoffmani*; anterior nasal-maxilla contact above anterior portion of P¹; less posterior rise of zygomatic arch than in other species of genus (arch incomplete); malar moderately deep below orbit; lacrimal fossa comparatively small but deep; occipital condyles

more widely spread than in other species of genus; paroccipital process more massive and with less lateral compression than usual in this genus; bulla large, larger than in *P. milleri*, similar to that of *P. hoffmani* except for less lateral compression; postglenoid process robust; posterior palate projecting posteriorly beyond M³, not to extent found in the holotype of *P. longiceps*.

MANDIBLE: (Unknown).

DENTITION: Series lighter than in examples of *P. hoffmani* and *P. milleri*, approximately equal to those of *P. longiceps*; series of less length than in two former species and longer than in latter.

LIMBS: (Unknown).

MEASUREMENTS: Table 9 (p. 205).

ILLUSTRATIONS: Figures 12-14.

DISCUSSION

The proposed new species, *Pseudodesmatochoerus wascoënsis*, from the John Day of Oregon differs considerably (as do most oreodonts from this area) from forms of apparently the same genus from the Great Plains. It may be that some of the John Day forms evolved locally. A better understanding of the stratigraphic occurrences of the oreodonts of the John Day region would un-

¹ Named after Wasco County, Oregon, where the holotype was collected.

doubtedly clarify the phylogenetic picture in Oregon. The present collections from the John Day area embrace specimens that usually are far from complete, and considerable crushing is evident. This adds to the difficulties of differentiating species. In this report, the John Day area is considered as

approximately equal (in part) to the Harrison of the Great Plains.¹

The more massive and wider skull and the lighter dentition of *P. wascoensis* distinguish it from the other species of the genus from the Great Plains.

Two specimens are here recorded:

HOLOTYPE

Partial skull with I¹-I³ alv. and C/(rt.)-M³. (w⁺)

A.M. 7827

From middle or upper John Day, Bridge Creek, Wasco County, John Day Valley, Oregon; collected by Day and Sternberg party, 1878
Figures 12-14

REFERRED FROM THE JOHN DAY VALLEY, OREGON

(Collected by L. E. Davis, 1879)

SKULL

A.M.

Partial skull with C/-P¹ rt. and P²-M³. (w⁺) 7634

5. ?*Pseudodesmatochoerus pariogonus* (Cope)

From the Deep River formation,² Deep River area, Montana; referred specimens from Meagher County, Montana, and tentatively referred from Montana, and Lewis and Clark County, Montana

Merychys pariogonus COPE, 1884, Proc. Amer. Phil. Soc., vol. 21, pp. 536 and 542. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 231, pl. 34, figs. 7-9. KOERNER, 1940, Amer. Jour. Sci., vol. 238, no. 12, p. 854.

CHARACTERS

SKULL: Medium size; light; dolichocephalic; supraoccipital wings not widely spread, extending short distance posterior to condyles; sagittal crest very low and depressed in medial region; brain case inflated, elongated; frontals moderately wide, slight protrusion at midline; supraorbital foramen with anterior groove; orbit large, suggests being longer vertically than wide anteroposteriorly; zygomatic arch very light, slight inward curve or notch posterior to orbit; malar shallow below orbit, but robust for size of zygomatic arch; occipital condyles moderately large;

paroccipital process wide at base, tapering rapidly to inferior border, long axis anteroposteriorly to length of skull; bulla inflated, high, longer anteroposteriorly than wide laterally; postglenoid process moderately robust, wider laterally than anteroposteriorly.

MANDIBLE: Moderately light; inferior border with noticeable downward curve posterior to M₃; ascending ramus wide anteroposteriorly; condyle of moderate size, external border higher and slightly more anterior than internal border.

DENTITION: Moderately light.

LIMBS: Light. (Known from tentatively referred fragments only.)

MEASUREMENTS: Table 9. (p. 205).

ILLUSTRATIONS: (See Thorpe, 1937, figs. 7-9).

DISCUSSION

The holotype of ?*Pseudodesmatochoerus pariogonus* has narrowly spread supraoccipital wings, which are deeply notched at the sides, differing considerably from either the semi- or completely fan-shaped occipital region of the Merychyinae.³ The very low sagittal crest and posterior rise to the supraoccipital wings of the holotype of ?*P. pariogonus* are similar to examples of *Pseudodesmatochoerus*.

¹ See Schultz and Falkenbach, 1949, p. 89, chart 3 (p. 83).

² See discussion, p. 212.

³ Schultz and Falkenbach, 1947.

Thorpe¹ questioned the placing of the species *pariogonus* under the genus *Merychys* in the following statement: "... a barely perceptible sagittal crest up to a point above the posttympanic process, whence the crest gradually rises, thus giving a saddleback profile, ...

"For the present I shall consider the species as referable to *Merychys* but keep an open mind. In most of the characters now known it is nearest to that genus, but the long brain case, the slender, low, and angulate zygomatic arch, the presumably larger size, the superior contour, ... are all at least specific differences from the normal seen in *Merychys*." To this may be added that the skull in question is higher than any examples of the *Merychyinae*. Thorpe² also considered a second specimen (A.M. 8114) as a paratype, although this partial skull exhibits a well-defined and rather high sagittal crest (see the following discussion). The sagittal crest of oreodonts have proved, so far, to be fairly constant in their outline; the amount of difference present in the holotype (A.M. 8113) and the here tentatively referred A.M. 8114 cannot be attributed either to age or to individual variation.

The age of the deposits from which the holotype and the tentatively referred specimens were collected is questionable. It is not known whether both specimens came from the same horizon, nor has that level been identified. The Deep River formation, to the present writers at least, seems to represent a group of formations. Schultz and Falkenbach³ have previously stated: "The ... 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 here tentatively referred specimen F:A.M. 42330, which is fragmentary, came

from the Canyon Ferry area of Montana and is considered approximately equal in age to the Gering of the central Great Plains.

All of the material here considered under the species *pariogonus* is fragmentary. The holotype (A.M. 8113) consists of the posterior portion of a skull with M² and M³ and the posterior portion of the mandible with M₂-M₃. Thorpe⁴ considered that the partial mandible belonged to specimen A.M. 8114, rather than to the holotype (A.M. 8113). The American Museum catalogue indicates that the partial mandible belongs to the holotype; furthermore, the wear of the teeth is similar to that of the superior teeth of the holotype and does not resemble the very well-worn superior teeth of A.M. 8114.

Specimen A.M. 8114, here tentatively referred to *?P. pariogonus*, differs somewhat from the holotype. The portions present seem to be about the same size as the holotype, but the sagittal crest is more prominent, the bullae are seemingly larger, the dentition is of a more aged individual, and the M² is noticeably smaller.

The second tentatively referred specimen (F:A.M. 45330 from the Canyon Ferry area of Montana) also is fragmentary, consisting of the posterior portion of a crushed skull with M³, a distorted posterior portion of the right ramus, and fragmentary limb elements. The skull seems to lack a prominent sagittal crest and is like the holotype in this respect. The malar, however, is decidedly deeper than in the holotype; the paroccipital process differs in having its long axis more or less perpendicular to the long axis of the skull; the bulla is more like that of A.M. 8114; M³ is slightly longer than in the holotype; and the limb elements are moderately light.

Scott⁵ referred a partial skull (P.U. 10477) from the Smith River Valley, Deep River beds, Montana, to "*Merychys pariogonus?*." The specimen consists of the anterior portion of skull, which the writers would tentatively refer to *Ticholeptus zygomaticus smithi*,⁶ rather than to *?Pseudodesmatochoerus pariogonus*.

Five specimens are here recorded:

¹ 1937, p. 232.

² 1937, p. 231.

³ 1949, p. 105.

⁴ 1937, p. 231.

⁵ 1895, Trans. Amer. Phil. Soc., vol. 18, p. 148.

⁶ Schultz and Falkenbach, 1941, p. 86.

HOLOTYPE

Posterior portion of skull with M^2-M^3 A.M. 8113 From "Ticholeptus beds," Deep River,
and partial mandible with M_2-M_3 Montana; collected by J. C. Isaac,
(w) 1877
Figured by Thorpe, 1937, pl. 34, figs. 7-9

REFERRED FROM (A) MEAGHER COUNTY, MONTANA; TENTATIVELY REFERRED
FROM (B) MONTANA, AND (C) LEWIS AND CLARK COUNTY, MONTANA

A. FROM MEAGHER COUNTY, MONTANA

(Collected by H. E. Koerner, 1935 and 1937)

2 MANDIBULAR RAMI

Y.P.M.

Right ramus with I_1-C alv. and P_1-M_3 (M+) 13969
Partial right ramus with I_3-M_2 (W+) 13970

The above two specimens are here considered as coming from the portions
of the beds in this area that are approximately equal in age to the Gering of
the central Great Plains.

TENTATIVELY REFERRED

B. FROM "TICHOLEPTUS BEDS," DEEP RIVER, MONTANA

(Collected by J. C. Isaac, 1877)

PARTIAL SKULL

A.M.

Posterior portion of skull, right maxilla with P^1-M^3 and fragments (W $^{++}$) 8114

C. FROM CANYON FERRY AREA, LEWIS AND CLARK COUNTY, MONTANA

(Collected by Charles H. Falkenbach, 1936)

PARTIAL SKULL, MANDIBULAR RAMUS, AND LIMB FRAGMENTS

Posterior portion of skull with M^3 , partial right ramus with M_3 br., partial radius,
partial ulna, and fragments. (w) F:A.M. 42330

IV. SUPERDESMATOCHOERUS, NEW GENUS

GENOTYPE: *Superdesmatochoerus lulli*
(Thorpe).

DESCRIPTION

SKULL: Large size; basal length ranging from 306 to 320 mm., width from 153 to 220 mm.; dolichocephalic to submesocephalic; supraoccipital wings produced posteriorly beyond occipital condyles, not so widely spread as in examples of *Promerycochoerus*; exoccipital vacuities large, similar to examples of *Desmatochoerus*; sagittal crest prominent; brain case long and narrow, not inflated to extent found in *Promerycochoerus*, similar to examples of *Desmatochoerus*; frontals moderately wide, comparable with examples of *Desmatochoerus*; nasals long and comparatively robust; anterior nasal-maxilla contact above P^1 ; orbits looking mostly outward; posterior portion of zygomatic arch

light for size of skull, lighter than in examples of *Promerycochoerus*, posterior border not so high as in *Promerycochoerus*, more U-shaped in outline from lateral view than in *Megoreodon* (similar to examples of *Desmatochoerus* in this respect); malar very deep below the orbit in comparison with examples of *Desmatochoerus*; infraorbital foramen above P^3 to P^4 ; no facial vacuity; lacrimal fossa pronounced and deep; slight depression above the premolar region, not so deep or so extensive as in examples of *Megoreodon* (lacking prominent facial ridge above depression as present in *Megoreodon*); premaxillae joined for slightly longer distance than in *Megoreodon*; occipital condyles large, approaching size of those of *Megoreodon*; paroccipital process wide at base, compressed, with longitudinal axis approximately 45 degrees from long axis of skull; bulla inflated, laterally compressed, considerably less steep anterior

slope to inferior border than in *Megoreodon* (bullae much more rounded in *Promerycochoerus* than in *Superdesmatochoerus*); postglenoid process robust (more robust than in examples of *Megoreodon*), wide laterally.

MANDIBLE: Moderately robust; ramus deeper than in *Megoreodon*; inferior border of ramus slightly increasing in depth posteriorly, with a more pronounced downward curve posterior to M_3 ; ascending ramus high, higher than in examples of *Megoreodon grandis*; condyle moderately large, set approximately at right angle to dental series, with external border higher than internal; smaller than in *Megoreodon grandis*.

DENTITION: Slightly more brachyodont than in examples of *Megoreodon*; lighter than average examples of that genus; $/C$ approximately twice the size of I_3 ; premolars decidedly smaller than those of *Megoreodon*; $C/$ and P_1 large; diastema between P^1 and P^2 , and frequently between P^2 and P^3 ; external styles of superior molars less prominent than in *Megoreodon*; suggestion of anterior intermediate crest on P^2 and P^3 ; posterior intermediate crest on P_3 .

LIMBS: (Fragments questionably associated with specimen Y.P.M. 10956, referred to *Superdesmatochoerus microcephalus*, indicate limb elements of smaller size than in *Megoreodon*; in the tentatively referred examples of *S. lulli*, the limb elements are slightly larger than in the last-mentioned genus.)

MEASUREMENTS: Tables 9 and 10 (pp. 205–206).

ILLUSTRATIONS: Figures 16–18 (skulls, rami, and dentitions), 23, 25 (limbs).

DISCUSSION

The proposed new genus, *Superdesmatochoerus*, embraces forms that have long and narrow skulls, which were previously considered as *Promerycochoerus*. They are smaller than the forms here referred to *Megoreodon* with the exception of *M. fricki*, and definitely larger than other genera of the Desmatochoerinae. The long and narrow skulls are considerably different from the comparatively short-faced and wide skulls of *Promerycochoerus*. Examples of *Superdesmatochoerus* differ from those of *Megoreodon* in the higher and U-shaped zygomatic arch, the less steep anterior slope to the inferior border of the

bullae, the smaller premolars, and the lack of the facial ridge above the premolar region. The specimens appear to be oversized examples of *Desmatochoerus*, occurring in a geologic formation (John Day, approximately equal in age to the Harrison of the Great Plains) which also yields examples of *Desmatochoerus* and *Promerycochoerus*. No examples of *Megoreodon* are known to have survived into the Harrison formation.

Thorpe,¹ in discussing *Superdesmatochoerus microcephalus*, stated: "It is one of the three dolichocephalic skulls in the genus [*Promerycochoerus*]." Presumably Thorpe was referring to "*P.* *lulli*," "*P.* *microcephalus*," and "*P.* *leidy*." The first two species are here referred to *Superdesmatochoerus* and the last to *Desmatochoerus*. The writers agree with Thorpe's indication that the three mentioned species were different from a true *Promerycochoerus*.

As discussed on page 182, the geologic occurrence of the John Day specimens are in question. It is here considered that the smaller form, *S. microcephalus*, came from the middle John Day, and the larger, *S. lulli*, came from the upper John Day,² with the former species giving rise to the latter.

DISTRIBUTION

Two species of *Superdesmatochoerus* are known only from the lower Miocene (John Day deposits, equal in part to the Harrison of the Great Plains) of Oregon. (See geologic distribution chart 1, p. 156.)

SUMMARY OF SPECIES AND TYPES

Two species of *Superdesmatochoerus* from one lower Miocene locality are here recorded:

1. *Superdesmatochoerus lulli* (Thorpe), from the John Day Valley, Oregon. (Approximately equal in age to the Harrison.)

HOLOTYPE: Skull and mandible, Y.P.M. 10234. Figures 16–18.

2. *Superdesmatochoerus microcephalus* (Thorpe), from the John Day Valley, Oregon. (Approximately equal in age to the Harrison.)

HOLOTYPE: Skull and mandible, Y.P.M. 10998. Figures 16–17.

¹ 1937, p. 137.

² See a correlation of the John Day deposits with those of the Great Plains, Schultz and Falkenbach, 1949, p. 83, chart 3.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS AND SYNONYMY

SUPERDESMATOCHOERUS

TOTAL AVAILABLE SPECIMENS: 10

1. *Superdesmatochoerus lulli* (Thorpe)

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

Promerycochoerus lulli THORPE, 1921, Amer.
Jour. Sci., ser. 5, vol. 1, art. 14, p. 231, figs. 1a-1b;
1937, Mem. Peabody Mus. vol. 3, pt. 4, p. 130,
figs. 85-88.

CHARACTERS

SKULL: Larger than examples of *S. microcephalus*; anterior nasal-maxilla contact above P¹; infraorbital foramen above posterior portion of P⁴.

MANDIBLE: Larger than examples of *S.*

microcephalus; postsymphysis below P₃.

DENTITION: Series longer than examples of *S. microcephalus*.

LIMBS: Within the size range of *Megoreodon*. (Known from tentatively referred specimens only.)

MEASUREMENTS: Tables 9 and 10 (pp. 205-206).

ILLUSTRATIONS: Figures 16-18, 23, 25.

DISCUSSION

The species *Superdesmatochoerus lulli* is here considered as coming from the upper John Day and as having evolved from *S. microcephalus* from the middle John Day. There is little that distinguishes these two forms, except for the larger size of the skull of *S. lulli*.

Four specimens are here recorded:

HOLOTYPE

Crushed skull with I²-M³ and mandible
with I₁-M₃. (w)

Y.P.M. 10234

From questionably upper John Day,
Turtle Cove, John Day Valley, Oregon;
collected by William Day, 1875
Figured by Thorpe, 1921, figs. 1a-1b;
1937, figs. 85-88
This report, figs. 16-18

REFERRED FROM THE JOHN DAY VALLEY, OREGON

SKULL AND MANDIBLE

A.M.

Partial skull with I¹-I³ alv. and C/-M³, and mandible with I₁-M₃ (w+)

7469

TENTATIVELY REFERRED FROM THE JOHN DAY VALLEY, OREGON

SKELETAL ELEMENTS

A.M.

Humerus, radius, ulna, and fragments. Figure 23

7482

Partial tibia, astragalus, partial calcaneum, and pes elements. Figure 25 . . .

7906

2. *Superdesmatochoerus microcephalus*
(Thorpe)

From questionably middle John Day (ap-
proximately equal in age to the Harrison
formation of the central Great
Plains), John Day Valley,
Oregon

Promerycochoerus microcephalus THORPE, 1921,
Amer. Jour. Sci., ser. 5, vol. 1, art. 14, p. 239, figs.
5a-5b; 1937, Mem. Peabody Mus., vol. 3, pt. 4,
p. 137, figs. 94-95.

CHARACTERS

SKULL: Smaller than examples of *S. lulli*; brain case slightly smaller for size of skull than in that species; anterior nasal-maxilla contact above area posterior to P¹; infraorbital foramen above posterior portion of P³ to posterior portion of P⁴; lacrimal fossa smaller than in *S. lulli*.

MANDIBLE: Smaller than examples of *S. lulli*; postsymphysis below P₃; inferior border

of ramus slightly more arched than last-mentioned species.

DENTITION: Similar to examples of *S. lulli* except for smaller size of series.

LIMBS: (Unknown).¹

MEASUREMENTS: Table 9 (p. 205).

ILLUSTRATIONS: Figures 16-17.

DISCUSSION

The geologic occurrence of this species is questionable. The species is here considered as coming from the middle John Day, giving rise to *S. lulli*.

The holotypic skull of this species is badly crushed, especially in the region of the brain case. Thorpe² stated that the type had an "... extremely small brain chamber," and

later³ he further reported: "The extremely small, narrow brain case is one of the remarkable features of this peculiar skull and suggested the specific name [*microcephalus*]."

The writers consider the crushed brain case of the holotype to be slightly smaller than that of the holotype of *S. lulli*, but similar in form (long and narrow). It is of interest that Thorpe⁴ compared these same species and came to the following conclusion: "*P. macrostegus* appears to be similar in many ways to *P. montanus grandis*. . . ." The writers agree with Thorpe and have placed both forms under the same subfamily, the Desmatochoerinae (see *Megoreodon grandis*, p. 168).

Six specimens are here recorded:

HOLOTYPE

Skull with P ¹ -M ³ and mandible with P ² -M ³ . (w+)	Y.P.M. 10998	From questionably upper John Day, Turtle Cove, John Day Valley, Oregon; collected by William Day, 1875 Figured by Thorpe, 1921, figs. 5a-5b; 1937, figs. 94-95 This report, figs. 16-17
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REFERRED FROM THE JOHN DAY VALLEY, OREGON

SKULL, MANDIBLE, AND QUESTIONED ASSOCIATED LIMB ELEMENTS

Skull with I ¹ (alv.)-M ³ , mandible with I ¹ -M ³ , partial tibia, astragalus, calcaneum, and fragments. (w)	Y.P.M. 10956	From Hay Stack Valley, John Day Area, Oregon; collected by William Day, 1876
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The above specimen was considered as a plesiotype of the species *leidy* by Thorpe.⁵ The writers, however, consider that the skull is too large and the teeth too robust for that species. Whether the limb elements associated with the skull actually belonged to the same individual as the skull is questionable. They seem exceptionally small for the size of the skull, in comparison with other associated specimens representing this subfamily.

2 SKULLS AND MANDIBLES

Skull with I ¹ -M ³ and mandible (attached) with I ¹ -I ² rt. and I ³ -M ³ . (w)	U.C. 2240	Collected by University of California field party, 1899
Skull and mandible (attached). (w+)	U.O. 511	From North Fork, John Day River, Oregon; collected by Rev. Dr. Thomas Condon

The above specimen is in the collection of the University of Oregon, but has been lent to the Oregon State College at Corvallis, Oregon.

2 SKULLS

Anterior portion of skull with I ² -M ³ . (w+)	U.O. F709	Condon collection, C.C. 660
Anterior portion of skull with I ¹ -M ² . (w)	A.M. 7461	From the Cove, John Day Valley, Oregon; collected by J. L. Wortman, 1879

¹ See discussion of associated limb elements of specimen Y.P.M. 10956 (this page).

² 1921, p. 239.

³ 1937, p. 138.

⁴ 1937, p. 106.

⁵ 1937, p. 128.

V. SUBDESMATOCHOERUS, NEW GENUS

GENOTYPE: *Subdesmatochoerus socialis* (Marsh).

DESCRIPTION

SKULL: Small to medium size; basal length ranging from 175 to 215 mm., width from 94 to 125 mm.; dolichocephalic to submesocephalic; supraoccipital wings not widely spread, produced posteriorly beyond the occipital condyles; exoccipital vacuities present; sagittal crest moderately high; brain case elongated; frontals narrow; nasals with noticeable tapering posteriorly, also anteriorly, slight anterior retraction; anterior nasal-maxilla contact above P^1 ; orbits slightly oval vertically, with long axis sloping upward anteroposteriorly; zygomatic arch with moderately abrupt rise posteriorly from below the orbit, with inward notch posterior to orbit; squamosal moderately light; malar moderately deep below the orbit; infraorbital foramen above P^3 ; lacrimal fossa moderately large and deep; slight facial depression in area above P^1 to midline of P^3 (anterior to infraorbital foramen); muzzle narrow; premaxillae touching, but not definitely fused; occipital condyles of medium size; paroccipital process wide at base, with noticeable external notch, triangular in outline at contact with bulla; bulla inflated, laterally compressed; postglenoid process robust, with tendency to be wide laterally as it is anteroposteriorly, steep slope to external border; posterior palate even with last lobe of M^3 to slightly posterior of M^3 .

MANDIBLE: Medium size; postsymphysis in region below P_2 and P_3 ; inferior border of ramus parallel to alveolar border, with gradual downward curve posterior to M_3 ; ascending ramus moderately high, posterior border robust; condyle set at less than right angle to axis of dentition, with external border of condyle farther forward and higher than internal border.

DENTITION: Brachyodont, more so than in examples of *Desmatochoerus*; series longer than examples of *Prodesmatochoerus* (with exception of those of *P. socialis dakotensis*) and shorter than in *Desmatochoerus*; C/ and P_1 moderately large; /C two to three times the size of I_3 ; premolars large, usually crowded, P^1 - P^2 and P_2 set at slight angle to

alveolar border; external styles of superior molars prominent; P^1 - P^3 each with anterior intermediate crest; P_3 with posterior intermediate crest.

LIMBS: Tendency to be slightly longer than examples of *Prodesmatochoerus meekae*; lighter and shorter than examples of *Desmatochoerus* and *D. (Paradesmatochoerus)*.

MEASUREMENTS: Tables 11 and 12 (pp. 218-219).

ILLUSTRATIONS: Figures 18-21 (skulls, rami, and dentitions).

DISCUSSION

The new genus *Subdesmatochoerus* represents an intermediate stage in the phylogenetic line of the Desmatochoerinae between *Desmatochoerus* (examples of which are larger, with more inflated bullae and more hypsodont dentitions) of the Gering and *Prodesmatochoerus* [examples of which have smaller (minute) bullae] of the Chadron and the Brule (faunal "Zone A"). At this writing *Subdesmatochoerus* is not known from "Zone C" of the Brule, but future collecting will no doubt give evidence of the presence of this genus in that zone.

The genotypic species, *S. socialis* (Marsh), previously has been considered under the genus *Eporeodon* (see discussion, p. 221).

DISTRIBUTION

Three species and one subspecies of *Subdesmatochoerus* are known from the Oligocene (faunal "Zone B" and "Zone D" of the Brule) of Montana, Nebraska, and South Dakota. (See geologic distribution chart 1, p. 156).

SUMMARY OF SPECIES AND TYPES

Three species and one subspecies of *Subdesmatochoerus* from five Oligocene localities are here recorded:

1. *Subdesmatochoerus montanus* (Douglass), from Lewis and Clark County, Montana. (Approximately equal to "Zone D" of Brule.)

HOLOTYPE: Skull and mandible, pelvis and vertebrae, C. M. 907. Figures 19-21.

2. *Subdesmatochoerus socialis* (Marsh), from Scotts Bluff County, Nebraska; referred remains from Pennington and Shan-

TABLE 11

Subdesmatochoerus AND *Prodesmatochoerus*, NEW GENERA. COMPARATIVE
MEASUREMENTS¹ OF SKULLS AND MANDIBULAR RAMI

	<i>S. montanus</i> (Douglass)	<i>S. socialis</i> (Marsh)		<i>S. s. dakotensis</i> , new sub- species	<i>S. shan- nonensis</i> , new species	<i>P. meekae</i> , new species	<i>P. natro- nensis</i> , new species
SKULL	Holotype C.M. 907	Holotype Y.P.M. 13318	Referred F:A.M. 45177	Holotype F:A.M. 45351	Holotype A.M. 1310	Holotype F:A.M. 45023	Holotype F:A.M. 45194
Stage of wear of teeth . . .	(w†)	(w+)	(w)	(w+)	(-M)	(M+)	(w††)
Length (including supraoc- cipital crest and incisors)	258	((212))	((212))	—	(227)	(209)	—
Basal length (from anterior notch of foramen mag- num to posterior base of I ¹)	209	((184.5))	187.5	((175))	195	((184))	((155))
Width (max.)	125	94	((98))	—	(108)	((85))	—
Width of brain case (max.)	52.5	48	50	48.5	51	40	—
Width, interorbital (min.)	58	52	(45)	43	(47)	44	—
Distance from anterior rim of orbit to anterior base of canine	101	79.5	81.5	78.5	88.5	78	—
Distance from anterior rim of orbit to supraoccipital crest	157	131.5	131	—	—	((125))	—
Length of nasals	91.5	—	80	—	—	79	—
Width of muzzle at infra- orbital foramina	59.5	54	47	42	49	36	—
Width across canines	46.5	43	42	(40)	57	31.5	—
Length, C/-M ³ incl.	116	103.5	103	95	111	99.5	(87)
Length, P ¹ -M ³ incl.	101	90.5	88.5	81.5	96	88.5	(80)
Length, P ¹ -P ⁴ incl.	49	44	44	41.5	44	43.5	38.5
Length, M ¹ -M ³ incl.	56.5	49	49	42	54	47.5	(42)
Width of M ³ (max.)	22	19.5	19.5	16.5	19	19.5	—
Depth of malar below orbit	24	18	21.5	16.5	18	21	—
MANDIBULAR RAMUS					Referred F:A.M. 49550 (w)		
Stage of wear of teeth . . .							
Length (max., including in- cisors)	205	171.5	165.5	—	194	—	—
Length, /C-condyle incl.	169	(153)	153	—	178	—	—
Depth of jaw under coron- oid	105	((74))	—	—	—	—	—
Depth of jaw under ante- rior edge of M ₃	41.5	35.5	—	33.5	35.5	33	—
Length, /C-M ₃ incl.	118.5	(105.5)	102	—	115	—	—
Length, P ₁ -M ₃ incl.	107.5	96.5	94	87	106	(92)	—
Length, P ₁ -P ₄ incl.	47	45.5	43.5	39.5	52	(38)	(33)
Length, M ₁ -M ₃ incl.	59.5	53	51.5	46.5	54	52	—

¹ (), Approximate; (()), estimated. All measurements in millimeters.

TABLE 12

Subdesmatochoerus AND *Prodesmatochoerus*, NEW GENERA. COMPARATIVE MEASUREMENTS¹ OF SKELETAL ELEMENTS

	<i>S. socialis</i> (Marsh)		<i>P. meekae</i> , new species	<i>P.</i> <i>natronensis</i> , new species
	Cotype Y.P.M. 13118	Referred F:A.M.	Referred F:A.M. 45331	Holotype F:A.M. 45194
Length of humerus (articular)	133.5	148-45182	—	—
Length of radius (articular)	—	120-45333	114	—
Length of ulna (max.)	—	—	153	—
Length of femur (articular)	161	—	159	—
Length of tibia (articular)	143	—	139	—
Length of metatarsal III (max.)	—	(70)-45333	—	—
Length of calcaneum (max.)	57.5	56-45182	54.5	48

¹ (), Approximate. All measurements in millimeters.

non counties, South Dakota. ("Zone B" of Brule.)

COTYPES: Two skeletons, Y.P.M. 13118 and 13119.

2a. *Subdesmatochoerus socialis dakotensis* new subspecies, from Shannon County, South Dakota. ("Zone B" of Brule.)

HOLOTYPE: Partial skull and mandible, F:A.M. 45351. Figures 19-21.

3. *Subdesmatochoerus shannonensis*, new species, from Shannon County, South Dakota; referred remains from Jackson County, South Dakota, and Sioux County, Nebraska; and tentatively referred from Shannon County, South Dakota, and Sioux County, Nebraska. ("Zone D" of Brule.)

HOLOTYPE: Skull, A.M. 1310. Figures 19-21.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

SUBDESMATOCHOERUS

TOTAL AVAILABLE SPECIMENS: 20*

1. *Subdesmatochoerus montanus* (Douglass)

From Oligocene deposits (approximately equal to "Zone D" of the Brule formation in the central Great Plains), Lewis and Clark County, Montana

Eucrotaphus montanus DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, no. 2, p. 100, pl. 23. HAY, 1930, Carnegie Inst. Washington Publ., no. 390, vol. 2, p. 781.

Eporeodon montanus (Douglass), THORPE, 1924, Amer. Jour. Sci., ser. 5, vol. 7, art. 15, p. 222; 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 80, fig. 40, pl. 9, figs. 1-3. SCOTT, 1940, Trans. Amer. Phil. Soc., new ser., vol. 28, pt. 4, p. 686.

* Includes 15 F:A.M. specimens.

CHARACTERS

SKULL: Largest known form of genus; smaller than examples of *Desmatochoerus* and *Pseudodesmatochoerus*, larger than those of *Prodesmatochoerus*; sagittal crest light, high, and arched (more so than in examples of *S. shannonensis*), posterior portion slightly depressed; exoccipital vacuities larger than in *S. socialis*; nasals moderately light; zygomatic arch with more abrupt posterior rise than examples of *S. shannonensis*, more like those in *S. socialis*; malar deeper below orbit than in *S. shannonensis*; infraorbital foramen above P⁴; lacrimal fossa moderately large, very deep; slight depression posterior to infraorbital foramen; paroccipital process moderately light at base, with moderately down-

ward tapering, long axis of base paralleling longitudinal axis of skull; paroccipital process on external side of posterior portion of bulla (not directly posterior to bulla as in other examples of genus); bulla inflated, compressed laterally (similar, but larger than in examples of *S. socialis dakotensis*); postglenoid process robust, wider than that in last-mentioned subspecies; posterior palate projecting farther posteriorly than in other forms of genus (palatal area partially restored in holotype).

MANDIBLE: More robust and deeper than in examples of *S. shannonensis* (more like examples of *Desmatochoerus* from the Gering); inferior border of ramus arched, somewhat like those of *Brachycrus* but shallower anteriorly; ascending ramus high, wide anteroposteriorly; condyle large and moderately robust.

DENTITION: Series more robust and of greater length than in examples of *S. shannonensis*; premolars crowded; P^1 - P^3 and P_2 - P_3 each set at angle to alveolar border; posterior external style of M^3 more prominent than in other species of genus; P^2 and P^3 with anterior intermediate crest (P^1 may have crest, but not present on well-worn P^1 of holotype).

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 218).

ILLUSTRATIONS: Figures 19-21.

Skull with I^2 (br.)- M^3 , mandible with I_1 (alv.)- M_3 , pelvis, and vertebrae. (w†)

2. *Subdesmatochoerus socialis* (Marsh)

From "Zone B" of the Brule formation, Scotts Bluff County, Nebraska; referred remains from Pennington, Shannon, and Washabaugh counties, South Dakota

Eporeodon socialis MARSH, 1884, Monogr., U. S. Geol. Surv., vol. 10, figs. 73, 162-163 (no description); 1885, Fifth Rept. U. S. Geol. Surv., figs.

DISCUSSION

Concerning geology in the original description of this species Douglass¹ stated, "... the beds evidently overlie the Lower White River." In 1924, Thorpe² gave the horizon as "... at the top of the Middle Oligocene." Hay³ questioned the horizon and considered it as "Miocene (lower) or Oligocene (upper)."

The skull of the holotype of this species is larger than in any known forms of the *Desmatochoerinae* from the Oligocene. The dentition, however, is similar to the forms from the Oligocene and more brachyodont than those from the Gering or from deposits higher in the geologic sequence. It is here considered that the beds yielding the holotype are approximately equal to faunal "Zone D" of the Brule formation of the Great Plains.

Thorpe⁴ referred to this species a specimen (Y.P.M. 12446) which was collected at "Scotts Bluff [Monument], Nebraska, on the north side of the Platte River, in the same geological horizon as the type [of *S. montanus*], and shows no important variation." The specimen in question, however, is distinct from this species and will be considered in another subfamily of the oreodonts.

The over-all length (measurements by writers) of the holotypic skull of *S. montanus* (table 11) is greater than that given by Douglass,⁵ Thorpe,⁶ or Scott.⁷

One specimen is here recorded:

HOLOTYPE

C.M. 907

From Oligocene deposits, near Stubb's Ferry, on the Missouri River, about 11 mi. N.E. of Helena, Lewis and Clark County, Montana; collected by Earl Douglass, 1903

Figured by Douglass, 1907, pl. 23; Thorpe, 1937, fig. 40, pl. 9, figs. 1-3

This report, figs. 19-21

128-129 (no description). THORPE, 1921, Amer. Jour. Sci., ser. 5, vol. 2, p. 309, figs. 1-4; 1931,

¹ 1907, p. 101.

² P. 222.

³ 1930, p. 781.

⁴ 1924, p. 222; 1937, p. 81.

⁵ 1907, p. 101.

⁶ 1937, p. 282, table 4.

⁷ 1940, p. 687.

Bull. Peabody Mus., no. 2, p. 5, figs. 1-3, 5, 7-23; 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 86, figs. 46-64, 186, pl. 42, pl. 50, figs. 1-2. Scott, 1940, Trans. Amer. Phil. Soc., new ser., vol. 28, pt. 4, p. 683.

CHARACTERS

SKULL: Slightly larger than in holotype of *S. socialis dakotensis* and average examples of *Prodesmatochoerus meekae*, smaller than in holotype of *S. montanus* and examples of *S. shannonensis*; exoccipital with elongated vacuities, smaller than in *S. montanus* and *S. shannonensis*; orbit smaller than in *S. shannonensis*; paroccipital process wide at base, adhering to the bulla; bulla well inflated, pit for hyoid attachment more prominent than in *S. shannonensis* (paroccipital process placed posterior to bulla, differing from *S. montanus* in which it is more laterally placed).

MANDIBLE: Postsymphysis below anterior portion of P_3 ; ramus of less depth than in the holotype of *S. montanus*; inferior border of ramus with gradual downward curve; ascending ramus moderately high.

DENTITION: Series slightly larger than in examples of *P. meekae*; approximately equal to those of *S. shannonensis*.

LIMBS: More robust and longer than examples of *P. meekae*.

MEASUREMENTS: Tables 11 and 12 (pp. 218-219).

ILLUSTRATIONS: Figures 18-21.

DISCUSSION

The first publication of the name "*Eporeodon*" *socialis* was by Marsh¹ in 1884, at which time he gave three illustrations of the material but failed to provide a description. Later, Marsh² referred the specimens to the same species and presented two figures, but he still gave neither a description nor information concerning the geologic or geographic occurrences. The first description of this material was by Thorpe³ in 1921, who reported that the cotypes came from "Scotts Bluff [Monument], Nebraska." Thorpe gave the horizon of the cotypes as "... the Upper Oligocene (Protoceras Beds)"—here considered as "Zone D" of the Brule—but the pres-

ent writers believe instead that the cotypes were derived from "Zone B" of the Brule.

Prior to 1921 Matthew,⁴ Hay,⁵ and Merriam and Sinclair⁶ all reported that the cotypes came from the John Day of Oregon, which at that time was considered by many workers to be Oligocene, at least in part. (The present writers regard the middle and upper John Day as approximately equal in age to the Harrison of the Great Plains.⁷)

The additional material of this species for which geologic data have been carefully recorded indicates that it came from faunal "Zone B" of the Brule, and further geologic evidence is at hand in regard to *S. shannonensis*, from "Zone D" of the Brule, a larger species than *S. socialis*. The bullae of these two forms differ, as do those of most oreodonts from these horizons, in that the species from "Zone B" of the Brule exhibit bullae which have a deep pit or groove for the hyoid attachment, while those from "Zone D" of the Brule possess bullae which are more inflated and lack the pit or groove.

Scott⁸ referred *S. socialis* to the genus *Eporeodon*, but noted outstanding differences between this species and *E. major*: "So striking are the differences between *Eporeodon socialis* and *E. major*, as to suggest the propriety of referring them to separate genera. Be that as it may, the two species clearly indicate the existence of two distinct phylogenetic series within the genus, as now constituted. One of these, exemplified by *E. socialis*, continues the central line of the family through the John Day species to the Miocene and Pliocene genera and ends in *Metoreodon*, the other leading from *E. major* to *Promerycochoerus*, *Merycochoerus* and *Pronomothe-rium*."

The writers agree with Scott that the two species in question are definitely different, and therefore have separated the forms into two different genera (*E. major* will be discussed in a forthcoming report). As to Scott's contention in regard to *Metoreodon*, *Promery-*

¹ 1884, fig. 73.

² 1885, figs. 128-129.

³ 1921, p. 309.

⁴ 1889, Bull. Amer. Mus. Nat. Hist., vol. 12, art. 3, p. 64.

⁵ 1902, Bull. U. S. Geol. Surv., no. 179, p. 667.

⁶ 1907, Bull. Dept. Geol. Univ. California, vol. 5, p. 187.

⁷ Schultz and Falkenbach, 1949, p. 83, chart 3.

⁸ 1940, pp. 683-684.

cochoerus, *Merycochoerus*, and *Pronomothe-rium*, see the writers' reports¹ on these genera.

It is here considered that *S. socialis* developed directly from *P. meekae*; the outstanding difference is the small (minute) bulla of the latter compared with the in-

flated one in the former.

The F:A.M. material was collected by Ralph Mefferd, Morris F. Skinner, and associates, 1938.

Ten specimens are here recorded:

COTYPES

Skull with I ¹ -M ³ , mandible with I ₁ -M ₃ , and most of skeleton. (w+)	Y.P.M. 13118	From "Zone B" of the Brule formation, Scotts Bluff (Monument), Scotts Bluff County, Nebraska; collected by M. H. Clifford and A. S. Shelly, 1884. Figured by Marsh, 1884, fig. 73 (in part); 1885, 128-129; Thorpe, 1921, fig. 1 (in part); 1931, figs. 1-2 (in part), 3, 5, 7, and 15; 1937, figs. 47-48 (in part); pl. 42 (in part).
Skull with I ¹ (rt.)-M ³ (C/rt.), mandible with I ₁ -M ₃ , and partial skeleton. (w)	13119	Figured by Marsh, 1884, figs. 162-163 (in part); 1885, figs. 128-129 (in part); Thorpe, 1921, figs. 1-2 (in part), 3-4; 1931, figs. 1-2 (in part), 8-14, 16-23; 1937, figs. 49-64; pl. 42 (in part).

The above two specimens were found associated in the field. The mounted skeleton on the Yale Peabody Museum consists of the skull, Y.P.M. 13118, and the skeleton of 13119. The two skulls do not vary greatly in measurements. In reference to the two skeletons, Thorpe² stated: "Cat. No. 13118 is slightly smaller and somewhat more slenderly constructed than the other skeleton. Both animals are fully adult, and it is possible that the larger specimen, Cat. No. 13119 may have been the male and the other a female."

REFERRED FROM (A) PENNINGTON, (B) SHANNON, AND (C) WASHABAUGH COUNTIES, SOUTH DAKOTA

A. FROM PENNINGTON COUNTY, SOUTH DAKOTA

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Partial skull with C/(rt.)-M ³ (P ¹ rt.) (poor state of preservation), partial mandible with P ₂ -M ₃ (P ₄ br.), partial scapula, 2 humeri (1 partial), partial radius, partial femur, 2 partial tibiae, manus and pes elements, vertebrae, and ribs. (w†††)	F:A.M.	45182
Partial skull with C/-P ³ rt. and P ⁴ -M ³ , partial mandible with /C-P ₂ rt. and P ₃ -M ₃ , 2 radii (1 partial), 2 partial ulnae, 2 partial femora, 2 tibiae, and partial pes (w†)		45333

2 SKULLS AND MANDIBULAR RAMI

Partial skull with P ¹ (rt.)-M ³ and left ramus with I ₂ (rt.)-M ₃ (I ₃ -C alv. and P ₁ -P ₂ rt.) (w†)		45179
Skull with I ¹ -dP ₂ -M ² and mandible (attached) with I ₁ (br.)-dP ₂ -M ₂ (i)		45180

B. FROM SHANNON COUNTY, SOUTH DAKOTA

2 SKULLS, MANDIBLES AND SKELETAL ELEMENTS

Skull with C/-M ³ , partial mandible with P ₁ -M ₃ , 2 femora (1 partial), 2 partial tibiae, and vertebrae. (m+)	F:A.M.	45181
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¹ Schultz and Falkenbach, 1940, p. 218 (*Pronomothe-rium*=*Brachycrus*), p. 277 (*Merycochoerus*); 1941, p. 10 ("Metoreodon"=in part to *Ustatochoerus*); 1947, p. 232 [*Metoreodon*=*Merychys* (*Metoreodon*)]; 1949, p. 84 (*Promerycochoerus*).

² 1937, p. 95.

Partial skull with P^1 - dP^2 - M^2 , partial mandible with P_2 (br.)- dP_3 - M_3 (germ),
partial ulna, and partial radius (1) F:A.M. 45178

SKULL AND MANDIBLE

Skull with I^1 - M^2 and mandible with I_1 - M_2 . Figures 18-21 (w) 45177

C. FROM QUIVER HILL AREA, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL

F:A.M.

Crushed skull with I^2 - M^2 (I^3 absent) (w) 49640

The skull has the longest basal length of any of the referred specimens of this species; this elongation, however, may be due to crushing. Morris Skinner, the collector of this specimen, considers its occurrence as in the "upper Oreodon" and he may be correct, which would extend the geologic range of the species.

2a. *Subdesmatochoerus socialis dakotensis*,
new subspecies

From "Zone B" of the Brule formation,
Shannon County, South Dakota

molars not so prominent; weaker posterior
intermediate crest on P_3 .

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 218).

ILLUSTRATIONS: Figures 19-21.

DESCRIPTION

SKULL: Differing from that of *S. socialis* in: smaller size; bulla decidedly smaller; postglenoid process lighter.

MANDIBLE: Similar to examples of *S. socialis* except for smaller size; postsymphysis below P_2 .

DENTITION: Differing from *S. socialis* in: shorter series; anterior intermediate crests on superior premolars weaker; external styles of

DISCUSSION

The new subspecies is based on the holotype only. Although the skull is incomplete, the identifiable characters differ from *S. socialis* as observed above. The bulla of the subspecies is smaller than in *S. socialis*, but has the same laterally compressed outline, and the pit for the hyoid attachment on the bulla is similar.

One specimen is here recorded:

HOLOTYPE

Partial skull with I^1 - I^2 rt. and I^3 - M^2 and
partial mandible with I_1 - I_2 (br.) and
 I_3 - M_3 (/C and P_1 rt.). (w+)

F:A.M. 45351

From "Zone B" of the Brule formation,
E. side of Harney Springs Range, on
Spring Creek, Shannon County, South
Dakota; collected by Ralph Mefferd
and Morris F. Skinner, 1938

Figures 19-21

3. *Subdesmatochoerus shannonensis*,¹
new species

From "Zone D" of the Brule formation,
Shannon County, South Dakota; referred
remains from Jackson County, South
Dakota, and Sioux County, Nebraska;
and tentatively referred from Sioux
County, Nebraska, and Shannon
County, South Dakota

DESCRIPTION

SKULL: Slightly larger than in *S. socialis*,

smaller than that of holotype of *S. montanus*; exoccipital vacuities moderately large, smaller than those in *S. montanus*; zygomatic arch with less abrupt posterior rise and inward notch below posterior aspect of orbit more pronounced than in *S. socialis*; paroccipital process heavier at base than in that species; bulla similar to that in *S. socialis* except for less prominent external posterior groove and pit for hyoid attachment.

MANDIBLE: Slightly smaller than in holotype of *S. montanus*; larger than other forms of the genus.

DENTITION: Series with average length

¹ Named after Shannon County, South Dakota, where the holotype was secured.

greater than that in *S. socialis*; anterior intermediate crests on P^1-P^3 each well developed (a remnant of an analogous crest indicated in unworn $C/$).

LIMBS: Slightly larger and more robust than in *S. socialis*. (Known from fragmentary specimens only.)

MEASUREMENTS: Table 11 (p. 218).

ILLUSTRATIONS: Figures 19-21.

DISCUSSION

This species represents *Subdesmatochoerus* in "Zone D" of the Brule. The genus is not

yet known from "Zone C." *S. socialis* from "Zone B" has a smaller skull and a larger pit for the hyoid attachment on the bulla than in *S. shannonensis*. The size difference in the skulls of the two forms in question is less than is usually observed in species of the same genus from different geologic horizons.

The F:A.M. material from South Dakota was collected by Ralph Mefferd, Morris F. Skinner, and associates, 1938 and 1940; the specimens from Nebraska by George Sternberg, John C. Blick, and Charles H. Falkenbach, 1944.

Eight specimens are here recorded:

HOLOTYPE

Partial skull with I^1-M^3 (I^3 rt., dP^4 present on right side, P^4 erupt. on left side). (-m)

A.M. 1310

From "Zone D" of the Brule formation, Cheyenne River, Shannon County, South Dakota; collected by American Museum Expedition of 1894
Figures 19-21

REFERRED FROM (A) SHANNON AND (B) JACKSON COUNTIES, SOUTH DAKOTA, AND (C) SIOUX COUNTY, NEBRASKA

A. FROM SHANNON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

Parts of skull with $I^1-C/$ rt. and P^1 (br.)- M^3 (P^3 absent) and partial mandible with P_1-P_2 rt. and P_3 (br.)- M_3 (P_4 br.) (w) F:A.M. 45184

2 SKULLS

Two partial skulls with
 I^1-P^1 rt. and P^2-M^3 (w+) 45183
 $I^1-C/$ br. and P^1-M^3 (w_1^+) 45327

B. FROM N.W. OF INTERIOR, JACKSON COUNTY, SOUTH DAKOTA

SKULL

Partial skull with P^1-M^3 (m+) F:A.M. 45328

C. FROM 10 MI. N. OF HARRISON, SIOUX COUNTY, NEBRASKA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^1-M^3 , mandible (attached) with I_1-M_3 (I_2 alv.), partial humerus, partial ulna, partial pes, and fragments (w) F:A.M. 49550

TENTATIVELY REFERRED FROM (D) SIOUX COUNTY, NEBRASKA, AND (E) SHANNON COUNTY, SOUTH DAKOTA

D. FROM SAND CREEK, SIOUX COUNTY, NEBRASKA

(Collected by H. F. Wells and J. W. Gidley, 1896)

SKULL AND MANDIBLE (ATTACHED) WITH SKELETAL ELEMENTS

Skull with I^1-M^3 , mandible with I_1-M_3 , partial scapula, vertebrae, pelvis, and fragments. (The exhibit in the Princeton Museum includes a partial hind foot made up of elements from specimens nos. 11441, 10204, and 10521). (w_1^+) P.U. 11441

The above specimen was referred to *Merycoidodon culbertsonii* by Scott¹ and illustrated under that species. The skull and mandible are still attached in the matrix. The skull is long and narrow, like that of *Subdesmatochoerus shannonensis*. All the exposed characters compare with that species. (The bulla has not been exposed.) The size of the skull suggests derivation from faunal "Zone D" of the Brule formation. The skull is longer and narrower than examples of *Merycoidodon culbertsonii*—larger, in fact, than any known oreodont from "Zone A" of the Brule.

E. FROM SHANNON COUNTY, SOUTH DAKOTA

SKULL

F:A.M.

Skull with I¹–I³ alv. and C/–M³. Figure 21 (in part). (w+) 45460

The illustration shows the difference between the bulla of this skull as compared with that of the holotype. The bulla of skull F:A.M. 45460 is considerably smaller and is more like the minute bulla found in *Prodesmatochoerus*. This reduction may be evidence of a reversion to the ancestral form.

VI. PRODESMATOCHOERUS, NEW GENUS

GENOTYPE: *Prodesmatochoerus meekae*, new species.

DESCRIPTION

SKULL: Medium size; basal length ranging from 155 to 184 mm., width from 80 to 100 mm.; dolichocephalic; supraoccipital high and narrow, lateral wings not widely spread, produced posteriorly beyond occipital condyles; exoccipital foramina small and oblong in outline (no vacuities in prominent pit as in *Subdesmatochoerus*); sagittal crest moderately high and light; brain case elongated; frontals narrow; nasals long and narrow, with pointed to rounded posterior border and with slight anterior retraction; anterior nasal-maxilla contact above C/; orbits rounded, moderately large, looking mostly outward; zygomatic arch with abrupt posterior rise; malar moderately deep below the orbit, deepest point below middle of orbit; infra-orbital foramen above anterior portion of P³; lacrimal fossa large and moderately deep; small facial depression in area above P¹–P³; muzzle narrow; premaxillae touching but not definitely fused; occipital condyles of medium size, widely spaced; paroccipital process with excavated external surface; bulla very small (minute in contrast to those of *Subdesmatochoerus*); postglenoid process light, wide laterally, with moderately steep slope on external border; glenoid surface arched; posterior palate projecting posteriorly for slight distance beyond M³.

MANDIBLE: Medium size; ramus shallow; postsymphysis in region below P₃; inferior border with gradual downward curve below and posterior to M₃; ascending ramus moderately high, robust posterior border; condyle light, set at less than right angle to axis of dentition, external border farther forward and slightly higher than internal border.

DENTITION: Brachyodont, approximately equal to examples of *Subdesmatochoerus*, definitely more brachyodont than in *Desmatochoerus*; dental series shorter than in the latter genus, approximately equal to those of *S. socialis*, and long in relation to length of skull; inferior and superior premolars rather large, not crowded, set approximately parallel to alveolar border; external styles of superior molars moderately prominent; C/ and P₁ varying in size from comparatively small to large (similar to those of *Merychys*); P¹–P³ each usually with weak anterior intermediate crest; P⁴ may or may not have an external anterior pit; P₃ with weak posterior intermediate crest.

LIMBS: Moderate length; smaller and lighter than in *Subdesmatochoerus*.

MEASUREMENTS: Tables 11 and 12 (pp. 218–219).

ILLUSTRATIONS: Figures 18, 22 (skulls, rami, and dentitions), 24–25 (limbs).

DISCUSSION

The proposed new genus *Prodesmatochoerus* (with a geologic distribution from the Chadron to lower Brule, faunal "Zone A") includes

¹ 1940, Trans. Amer. Phil. Soc., vol. 28, pt. 4, p. 671, pl. 69, fig. 1; pl. 73, fig. 2.

the first examples of oreodonts with minute bullae to be discussed by the writers. (See discussion, p. 155). It is of interest to note that in the skulls of this phylogenetic line the minute bullae do not appear in any horizon higher than "Zone A." In faunal "Zone B" examples of *Subdesmatochoerus*, representing the same phylogenetic line, have inflated bullae.

The bullae of modern sheep have been dissected by Charles H. Falkenbach, under the supervision of the late Henry C. Raven, in order to discover, if possible, whether the minute bullae of *Prodesmatochoerus* fulfill the same functions as the inflated bullae of other forms. The construction of the bullae and of the various foramina seems to be the same in both the minute and inflated bullae.

The writers have considered the possibility that the skulls with minute bullae were associated with short limbs so that additional sound vibrations could be received from the ground. This theory cannot be substantiated, however, since *Subdesmatochoerus socialis* (from "Zone B") possesses inflated bullae, but has only slightly longer limb elements than *Prodesmatochoerus meekae* (from "Zone A").

The material at hand shows no gradation between the minute bullae of *Prodesmatochoerus* and the inflated ones of *Subdesmatochoerus*. The seemingly abrupt change in

size of the bullae from minute in "Zone A" to inflated in "Zone B" suggests that a hiatus exists. In the Merycoidodontinae, as in the *Prodesmatochoerus-Subdesmatochoerus* line, the bullae are minute in "Zone A" and inflated above this zone. Other oreodont lines (yet to be reported upon) continue through these same faunal zones but retain the minute bullae.

DISTRIBUTION

Two species of *Prodesmatochoerus* are known from the Oligocene (Chadron and faunal "Zone A" of the Brule or approximate equivalents) of South Dakota and Wyoming. (See geologic distribution, chart 1, p. 156.)

SUMMARY OF SPECIES AND TYPES

Two species of *Prodesmatochoerus* from four Oligocene localities are here recorded:

1. *Prodesmatochoerus meekae*, new species, from Niobrara County, Wyoming; referred remains from Converse County, Wyoming, and Pennington County, South Dakota. ("Zone A" of the Brule.)

HOLOTYPE: Skull and mandible, F:A.M. 45023. Figures 18, 22.

2. *Prodesmatochoerus natronensis*, new species, from Natrona County, Wyoming. (Chadron.)

HOLOTYPE: Partial skull, mandible, and calcaneum (F:A.M. 45194). Figures 22, 25.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS

PRODESMATOCHOERUS

TOTAL AVAILABLE SPECIMENS: 24¹

1. *Prodesmatochoerus meekae*,² new species

From "Zone A" of the Brule formation, Niobrara County, Wyoming; referred remains from Converse County, Wyoming, and Pennington County, South Dakota

DESCRIPTION

SKULL: Slightly larger than in holotype of *P. natronensis*, slightly smaller than in co-types of *Subdesmatochoerus socialis*; exoccipi-

¹ Includes 22 F:A.M. specimens.

² Named in honor of Miss Harriett E. Meek of the Frick Laboratory.

tal foramina elongated; infraorbital foramen above P³.

MANDIBLE: Postsymphysis below anterior portion of P₃.

DENTITION: Series longer than those of the holotype of *P. natronensis*.

LIMBS: Larger than in *P. natronensis*.

MEASUREMENTS: Tables 11 and 12 (pp. 218-219).

ILLUSTRATIONS: Figures 18, 22, 24-25.

DISCUSSION

The proposed new species from faunal "Zone A" of the Brule is the first of the oreodonts with a minute bulla to be discussed by the writers (see discussion, p. 155). *Prodesmatochoerus meekae* is presumed to have given

rise to *Subdesmatochoerus socialis* from "Zone B." The slight size difference between the two species lies within the range of individual variation generally found within one oreodont species, but the minute bulla of *P. meekae* is regarded as generically distinct from the inflated bulla of *S. socialis* (see discussion, p. 221).

The examples of *P. meekae* are larger than the holotype of its ancestor, *P. natronensis*

from the Chadron. The limb elements, in common with those of other species of oreodonts from "Zone A," are not well represented in the collection.

The F:A.M. specimens were collected by Gene Roll, Everett De Groot, George Sternberg, John C. Blick, and Charles H. Falkenbach, 1938, 1943-1945.

Twenty-three specimens are here recorded:

HOLOTYPE

Skull with I ¹ -M ³ and mandible with P ₁ (rt.)-M ₃ . (M+)	F:A.M. 45023	From "Zone A" of the Brule formation, Old Woman Creek, Niobrara County, Wyoming; collected by Gene Roll, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1938
		Figures 18, 22

REFERRED FROM (A) NIOBRARA AND (B) CONVERSE COUNTIES, WYOMING, AND (C) PENNINGTON COUNTY, SOUTH DAKOTA

A. FROM HAT CREEK BASIN AREA, NIOBRARA COUNTY, WYOMING

2 SKULLS AND SKELETAL ELEMENTS

Skull with I ³ (br.)-M ³ , partial humerus, radius, ulna, 2 femora, tibia, calcaneum, and partial pelvis. Figures 24-25 (in part)	(M+)	F:A.M. 45331
Skull with I ¹ -dP ³ -M ² , radius, ulna, and partial manus	(I)	45193

10 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Partial skull with I ¹ -I ³ rt. and C/-M ³ and mandible with P ₁ -M ₃	(W+)	45024
Partial skull with I ¹ -M ³ and mandible with I ₁ -M ₃	(W)	45025
Partial skull with I ¹ -P ² rt. and P ³ -M ³ , and mandible with I ₁ -I ₃ alv. and /C-M ₃	(W+)	45026
Partial skull with C/(rt.)-M ³ and mandible with P ₁ (rt.)-M ₃ (P ₂ br.)	(W+)	45187
Partial skull with I ¹ -C. (rt.) and P ¹ -M ³ and mandible with I ₁ (rt.)-M ₃	(W)	45332
Partial skull with I ¹ -M ³ and mandible (attached) with I ₁ -M ₃	(W+)	45458
Partial skull with I ¹ -M ³ and mandible (attached) with I ₁ (rt.)-M ₃ (/C and P ₁ br.)	(W)	49548
Partial skull with I ¹ -M ³ , partial right ramus with P ₂ -M ₃ , and partial atlas	(W)	49549
Partial skull with C/-dP ² -M ² , mandible (attached) with /C-dP ₂ -M ₂ , and limb fragments	(I)	49587
Partial skull with I ¹ -dP ² -M ³ (germ) and mandible with I ₃ -dP ₂ -M ₃ (germ)	(I)	49589

3 SKULLS

Anterior portion of skull with I ¹ -I ² alv. and I ³ (rt.)-M ³ (C/rt.)	(W+)	45064
Partial skull with P ⁴ -M ³	(W+)	45185
Partial skull with I ² -I ³ rt. and C/(br.)-dP ² -M ³ (P ₁ br., right P ³ erupt.)	(I)	49588

B. FROM 8 MI. SOUTHEAST OF DOUGLAS, CONVERSE COUNTY, WYOMING

3 SKULLS AND MANDIBLES

Partial skull with I ¹ -M ³ and mandible (attached) with I ₁ -M ₃	(M+)	F:A.M. 45098
Skull with I ¹ -M ¹ br. and M ² -M ³ and mandible (attached) with I ₁ -M ₃ (I ₂ -I ₃ br.)	(W)	45186
Skull with I ¹ -dP ² -M ² (erupt.) and mandible (attached) with I ₁ -P ₁ (erupt.)-M ₂	(I)	49590

2 SKULLS

Skull with I ¹ -M ³	(W+)	45459
Partial skull with I ¹ -P ² br. and dP ³ -M ³ (erupt.)	(I)	49591

C. FROM NEAR SCENIC, PENNINGTON COUNTY, SOUTH DAKOTA

(Collected by Walter Granger and Albert Thomson, 1940)

2 SKULLS AND MANDIBLES, IMMATURE

Complete skull with I^1 -dP ² -M ² and mandible (attached) with I_1 -dP ₂ -M ₃ (P ₄ germ)	(1)	A.M. 39119
Partial skull with I^1 (alv.)-dP ² -M ² and mandible with I_1 -dP ₂ -M ₃ (germ).	(1)	39429

2. *Prodesmatochoerus natronensis*,¹
new speciesFrom the lower part of the Chadron formation,
Natrona County, Wyoming

DESCRIPTION

SKULL: Smaller than in examples of *P. meekae*; brain case suggests slightly more rounded contour than in that species (only available specimen incomplete); infraorbital foramen above anterior portion of P⁴; occipital condyles more widely spread than in *P. meekae*; bulla very small (minute), similar to examples of *P. meekae*; postglenoid process more robust than in *P. meekae*.

MANDIBLE: Light; postsymphysis below anterior portion of P₄. (Known from incomplete holotype only.)

DENTITION: Series shorter than in *P. meekae*.

LIMBS: Smaller than in *P. meekae*. (Known from calcaneum only.)

MEASUREMENTS: Tables 11 and 12 (pp. 218-219).

ILLUSTRATIONS: Figures 22, 25.

DISCUSSION

The proposed new species is founded on a fragmentary skull and ramus, too incomplete for a detailed description, and a calcaneum.

This form has characters similar to those of *P. meekae* from faunal "Zone A" of the Brule, but it is of smaller size. The importance of this species lies particularly in its geologic occurrence, in the Chadron. It thus completes the phylogenetic line of *Prodesmatochoerus* from the Chadron and "Zone A" of the Brule, through *Subdesmatochoerus* from "Zone B" and "Zone D," to *Desmatochoerus* from the Gering through the Harrison, and perhaps also to a Sheep Creek equivalent in Montana. (See chart 1, p. 156.)

The holotype was found in the same area as a referred specimen of *Bathygenys alpha* Douglass (to be discussed in a forthcoming paper by the writers). Under the discussion of *Limninetes* sp., Matthew² mentioned a number of lower rami, not identified by catalog numbers, but considered by him to represent more than one species and, perhaps, more than one genus. In the collection of the American Museum of Natural History a small tray of partial rami, teeth, and skeletal elements from Pipestone Springs, Montana—an area equal in age to the collecting site of the holotype of *P. natronensis*—may answer the description of the material referred to by Matthew. The rami are referable to *Oreonetes*, but a larger tooth (A.M. 9768) may well represent *P. natronensis*.

One specimen is here recorded:

HOLOTYPE

Partial skull with C/-P² (rt.) and P³-M³,
partial mandible with P₂-M₃(br.) and
calcaneum. (w††)

F:A.M. 45194

From Chadron, Bates Hole, Natrona
County, Wyoming; collected by Gene
Roll and Charles H. Falkenbach, 1941
Figures 22, 25

¹ Named after Natrona County, Wyoming, the area from which the holotype was collected.

² Matthew, W. D., 1903, Bull. Amer. Mus. Nat. Hist., vol. 19, art. 6, p. 222.

EXPLANATION OF TEXT FIGURES¹

FIG. 1. Lateral views of skulls: *Megoreodon fricki*, new species, holotype, F:A.M. 33308 (nasals restored from opposite side), from Monroe Creek formation, Niobrara County, Wyoming (see ramus, fig. 3); *M. grandis loomisi* (Schlaikjer), geologic variety, example, F:A.M. 33301, from Monroe Creek formation, Niobrara County, Wyoming (see ramus, fig. 3). $\times \frac{1}{2}$. IF, infraorbital foramen; MA, external auditory meatus; PG, postglenoid process; PP, paroccipital process.

FIG. 2. Lateral and dorsal views of skulls: *Megoreodon grandis loomisi* (Schlaikjer), referred, F:A.M. 42320 (C/ from opposite side), from Gering formation, Niobrara County, Wyoming (see ramus, fig. 3); also dorsal views of *M. fricki*, new species, and *M. grandis loomisi* (Schlaikjer), geologic variety (see explanation, fig. 1). $\times \frac{1}{2}$. NF, nasal-frontal contact; MA, external auditory meatus; PG, postglenoid process; SOF, supraorbital foramen.

FIG. 3. Ventral views of skulls (see explanation, figs. 1 and 2); also mandibular rami and inferior dentitions: *Megoreodon fricki*, new species, holotype, F:A.M. 33308, from Monroe Creek formation, Niobrara County, Wyoming (see skull, figs. 1 and 2); *M. grandis loomisi* (Schlaikjer), geologic variety, example F:A.M. 33301, from Monroe Creek formation, Niobrara County, Wyoming (see skull, figs. 1 and 2); *M. grandis loomisi* (Schlaikjer), referred, F:A.M. 42320, from Gering formation, Niobrara County, Wyoming (see skull, fig. 2). $\times \frac{1}{2}$. APF, anterior palatine foramen; B, bulla; MA, external auditory meatus; PP, paroccipital process; PPF, posterior palatine foramen; 5, lacerated foramen; 6, glenoid foramina; 7), condylar foramen.

FIG. 4. Lateral views of skulls: *Desmatochoerus curvidens* (Thorpe), holotype, Y.P.M. 10997, from ?middle John Day (approximately equal to Harrison formation), Oregon (see ramus, fig. 7); *D. curvidens gregoryi* (Loomis), holotype, A.M. 12964, from Harrison formation, Shannon County, South Dakota (see ramus, fig. 7); and referred, F:A.M. 37211 (I¹ from opposite side), from Harrison formation, Niobrara County, Wyoming (see ramus, fig. 7). $\times \frac{1}{2}$.

FIG. 5. Dorsal views of skulls: *Desmatochoerus curvidens* (Thorpe), holotype Y.P.M. 10997, from ?middle John Day (approximately equal to Harrison formation), Oregon (see ramus, fig. 7); *D. curvidens gregoryi* (Loomis), holotype, A.M. 12964, from Harrison formation, Shannon Coun-

ty, South Dakota (see ramus, fig. 7); and referred, F:A.M. 37211 (I¹ from opposite side), from Harrison formation, Niobrara County, Wyoming (see ramus, fig. 7); *D. leidy* (Bettany), referred, A.M. 7466 (P⁴ from opposite side), from ?upper John Day (approximately equal to Harrison formation), Oregon; *D. hatcheri geringensis*, new subspecies, holotype, F:A.M. 33305, from Gering formation, Niobrara County, Wyoming (see ramus, fig. 7); *D. hatcheri grinnelli* (Koerner), holotype, Y.P.M. 13957, from deposits approximately equal to Gering formation, Meagher County, Montana (see ramus, fig. 7); *D. hatcheri niobrarensis*, new subspecies, holotype, F:A.M. 33344, from Monroe Creek formation, Niobrara County, Wyoming (see ramus, fig. 7); *D. newchicagoensis*, new species, holotype, F:A.M. 34480, from deposits approximately equal to Sheep Creek, Granite County, Montana (see ramus, fig. 7). $\times \frac{1}{2}$.

FIG. 6. Lateral views of skulls: *Desmatochoerus leidy* (Bettany); *D. hatcheri geringensis*, new subspecies; *D. hatcheri grinnelli* (Koerner); *D. hatcheri niobrarensis*, new subspecies; also ventral views of *D. curvidens* (Thorpe); *D. curvidens gregoryi* (Loomis); *D. leidy* (Bettany) (see explanation, fig. 5); also superior dentition, *D. hatcheri* (Douglass), referred, F:A.M. 42327, from deposits approximately equal to Gering formation, Lewis and Clark County, Montana. $\times \frac{1}{2}$.

FIG. 7. Ventral views of skulls: *Desmatochoerus curvidens geringensis*, new subspecies; *D. hatcheri niobrarensis*, new subspecies; *D. hatcheri grinnelli* (Koerner) (see explanation, fig. 5); also mandibular rami and inferior dentitions, *D. curvidens* (Thorpe), holotype, Y.P.M. 10997, from ?middle John Day (approximately equal to Harrison formation), Oregon (see skull, figs. 4-6); *D. curvidens gregoryi* (Loomis), holotype, A.M. 12964, from Harrison formation, Shannon County, South Dakota (see skull, figs. 4-6), and referred, F:A.M. 37211, from Harrison formation, Niobrara County, Wyoming (see skull, figs. 4-6); *D. hatcheri niobrarensis*, new subspecies, holotype, F:A.M. 33344 (P₁ from opposite side), from Monroe Creek formation, Niobrara County, Wyoming (see skull, figs. 5-7); *D. hatcheri geringensis*, new subspecies, holotype, F:A.M. 33305 (I₁ and P₁ from opposite side), from Gering formation, Niobrara County, Wyoming (see skull, figs. 5-7); *D. hatcheri grinnelli* (Koerner), holotype, Y.P.M. 13957, from deposits approximately equal to Gering formation, Meagher County, Montana (see skull, figs. 5-7); *D. newchicagoensis*, new species, holo-

¹ T following specimen number indicates holotype.

type, F:A.M. 34480, from deposits approximately equal to Sheep Creek, Granite County, Montana (see skull, fig. 5). $\times \frac{1}{2}$.

FIG. 8. Lateral views of skulls: *Desmatochoerus* (*Paradesmatochoerus*) *sanfordi*, new species, holotype, F:A.M. 45443, from Gering formation, Sioux County, Nebraska (see ramus, fig. 11); *D. (P.) wyomingensis*, new species, holotype, F:A.M. 33312 (facial vacuity restored from opposite side, I³ and C/ from opposite side), from Gering formation, Niobrara County, Wyoming (see ramus, fig. 11); *D. (P.) monroecreekensis*, new species, holotype, F:A.M. 37551 (C/ from opposite side), from Monroe Creek formation, Niobrara County, Wyoming (see ramus, fig. 11); *D. (P.) grangeri*, new species, holotype, F:A.M. 33303, from Gering formation, Niobrara County, Wyoming (see ramus, fig. 11). $\times \frac{1}{2}$. EV, exoccipital vacuity.

FIG. 9. Dorsal views of skulls (see explanation, fig. 8). $\times \frac{1}{2}$.

FIG. 10. Ventral views of skulls (see explanation, fig. 8); also superior dentition, *D. (P.) sanfordi*, new species, referred, F:A.M. 37580, from Gering formation, Niobrara County, Wyoming (see inferior dentition, fig. 11); *D. (P.) monroecreekensis*, new species, referred, F:A.M. 45439, from Monroe Creek formation, Niobrara County, Wyoming (see inferior dentition, fig. 11). $\times \frac{1}{2}$.

FIG. 11. Inferior dentitions and mandibular rami: *Desmatochoerus* (*Paradesmatochoerus*) *sanfordi*, new species, holotype, F:A.M. 45443, from Gering formation, Sioux County, Nebraska (see skull, figs. 8-10), and referred, F:A.M. 37580, from Gering formation, Niobrara County, Wyoming (see superior dentition, fig. 10); *D. (P.) wyomingensis*, new species, holotype, F:A.M. 33312, from Gering formation, Niobrara County, Wyoming (see skull, figs. 8-10); *D. (P.) monroecreekensis*, new species, holotype, F:A.M. 37551 (foramen from opposite side), and referred, F:A.M. 45439, both from Monroe Creek formation, Niobrara County, Wyoming (see skull, figs. 8-10, superior dentition, fig. 10); *D. (P.) grangeri*, new species, holotype, F:A.M. 33303 (P₃ from opposite side), from Gering formation, Niobrara County, Wyoming (see skull, figs. 8-10). $\times \frac{1}{2}$.

FIG. 12. Lateral views of skulls: *Pseudodesmatochoerus longiceps* (Douglass), holotype, A.M. 9732, from deposits approximately equal to Harrison formation, Jefferson County, Montana (see ramus, fig. 15); *P. milleri*, new species, holotype, F:A.M. 33304 (orbit restored from opposite side), from Gering formation, Niobrara County, Wy-

oming (see ramus, fig. 15); *P. hoffmani*, new species, holotype, F:A.M. 44912 (C/ from opposite side), from Monroe Creek formation, Niobrara County, Wyoming (see ramus, fig. 15); *P. wascoensis*, new species, holotype, A.M. 7827, from John Day (approximately equal to Harrison formation), Oregon. $\times \frac{1}{2}$.

FIG. 13. Dorsal views of skulls (see explanation, fig. 12). $\times \frac{1}{2}$.

FIG. 14. Ventral views of skulls (see explanation, fig. 12). $\times \frac{1}{2}$.

FIG. 15. Mandibular rami and inferior dentitions: *Pseudodesmatochoerus longiceps* (Douglass), holotype, A.M. 9732 (I₁-P₁ and foramina from opposite side), from deposits approximately equal to Harrison formation, Jefferson County, Montana (see skull, figs. 12-14); *P. milleri*, new species, holotype, F:A.M. 33304 (I₁-I₂ from opposite side), from Gering formation, Niobrara County, Wyoming (see skull, figs. 12-14); *P. hoffmani*, new species, holotype, F:A.M. 44912, from Monroe Creek formation, Niobrara County, Wyoming (see skull, figs. 12-14). $\times \frac{1}{2}$.

FIG. 16. Lateral views of skulls: *Superdesmatochoerus microcephalus* (Thorpe), holotype, Y.P.M. 10998, from ?middle John Day (approximately equal to Harrison formation), Oregon (see ramus, fig. 17); *S. lulli* (Thorpe), holotype, Y.P.M. 10234 (bulla from opposite side), from ?upper John Day (approximately equal to Harrison formation), Oregon (see ramus, fig. 17). (The atlas is attached in both type specimens, thus preventing a detailed drawing of the posterior portion of the skulls.) $\times \frac{1}{2}$.

FIG. 17. Dorsal and ventral views of skulls (see explanation, fig. 16); also mandibular rami and inferior dentitions: *Superdesmatochoerus microcephalus* (Thorpe), holotype, Y.P.M. 10998, from ?middle John Day (approximately equal to Harrison formation), Oregon (see skull, fig. 16); *S. lulli* (Thorpe), holotype, Y.P.M. 10234 (P₂ combination of both sides), from ?upper John Day (approximately equal to Harrison formation), Oregon (see skull, fig. 16). $\times \frac{1}{2}$.

FIG. 18. Examples of occipital regions of skulls, representing species of *Prodesmatochoerus*, *Subdesmatochoerus*, *Desmatochoerus* (*Paradesmatochoerus*), *Pseudodesmatochoerus*, *Desmatochoerus*, *Superdesmatochoerus*, and *Megoreodon*. $\times \frac{1}{2}$. EF, exoccipital foramen; EV, exoccipital vacuity.

FIG. 19. Lateral views of skulls: *Subdesmatochoerus socialis dakotensis*, new subspecies, holotype, F:A.M. 45351 (I³ from opposite side), from

"Zone B," Brule formation, Shannon County, South Dakota (see ramus and inferior dentition, figs. 20-21); *S. socialis* (Marsh), referred, F:A.M. 45177 (C/ from opposite side), from "Zone B," Brule formation, Shannon County, South Dakota (see ramus and inferior dentition, figs. 20-21); *S. shannonensis*, new species, holotype, A.M. 1310 (P⁴ from opposite side), from "Zone D," Brule formation, Shannon County, South Dakota; *S. montanus* (Douglass), holotype, C.M. 907 (combination of both sides), from deposits approximately equal to "Zone D," Brule formation, Lewis and Clark County, Montana (see ramus and inferior dentition, figs. 20-21). $\times \frac{1}{2}$.

FIG. 20. Dorsal views of skulls (see explanation, fig. 19); also mandibular rami: *Subdesmatochoerus socialis dakotensis*, new subspecies, holotype, F:A.M. 45351 (M₂ from opposite side), from "Zone B," Brule formation, Shannon County, South Dakota; *S. socialis* (Marsh), referred, F:A.M. 45177, from "Zone B," Brule formation, Shannon County, South Dakota; *S. montanus* (Douglass), holotype, C.M. 907, from deposits approximately equal to "Zone D," Brule formation, Lewis and Clark County, Montana. $\times \frac{1}{2}$.

FIG. 21. Ventral views of skulls (see explanation, fig. 19), also *Subdesmatochoerus shannonensis*, new species, referred, F:A.M. 45460, from "Zone D," Brule formation, Shannon County, South Dakota; and inferior dentitions (see explanation, fig. 20). $\times \frac{1}{2}$.

FIG. 22. *Prodesmatochoerus*, new genus, skulls, mandibular rami, and inferior dentitions: *P. natronensis*, new species, holotype, F:A.M. 45194, from Chadron formation, Natrona County, Wyoming; *P. meekae*, new species, holotype, F:A.M. 45023 (C/ and P₃ from opposite side), from "Zone A," Brule formation, Niobrara County, Wyoming. $\times \frac{1}{2}$.

FIG. 23. *Superdesmatochoerus*, new genus, *Megoreodon*, new genus, *Desmatochoerus* Thorpe, *D. (Paradesmatochoerus)*, new subgenus, *Pseudodesmatochoerus*, new genus, *Prodesmatochoerus*, new genus: comparison of skeletal elements. A, *Superdesmatochoerus lulli* (Thorpe); B, *Megoreodon grandis loomisi* (Schlaikjer), geologic variety; C, *M. fricki*, new species; D, *Desmatochoerus hatcheri geringensis*, new subspecies; E, *D. (Paradesmatochoerus) grangeri*, new species (see figs. 24-25); F, *D. hatcheri niobrarenensis*, new subspecies (see figs. 24-25); G, *Pseudodesmatochoerus longiceps* (Douglass); H, *P. hoffmani*, new species (see fig. 24); I, *Prodesmatochoerus meekae*, new species (see figs. 24-25); J, *P. natronensis*, new species (see fig. 25). $\times \frac{1}{2}$.

FIG. 24. Comparison of skeletal elements (see explanation, fig. 23; A and J not illustrated). $\times \frac{1}{2}$.

FIG. 25. Comparison of skeletal elements (see explanation, fig. 23; H not illustrated). $\times \frac{1}{2}$.

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 (Merycoidontidae)."

Hypselochoerus, 177, 182
hollandi, 168
thorpei, 189

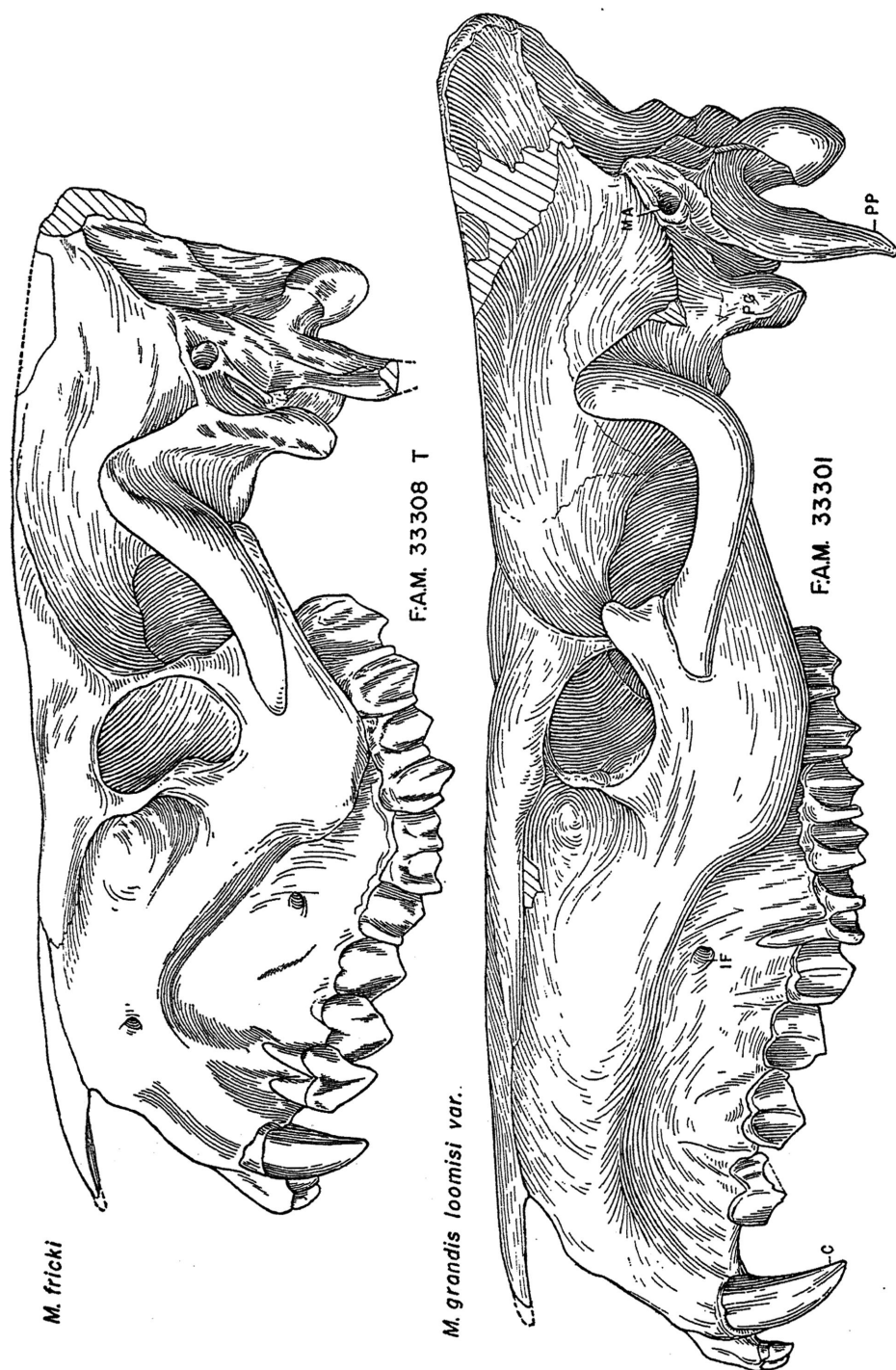
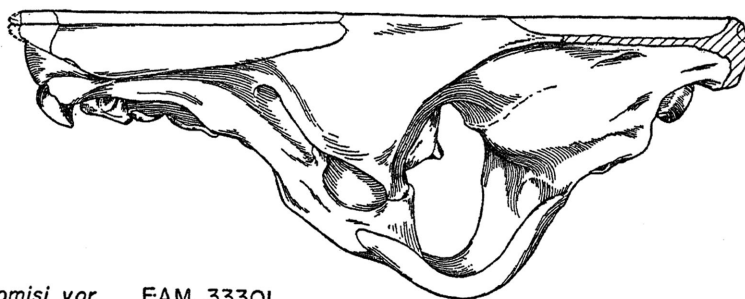


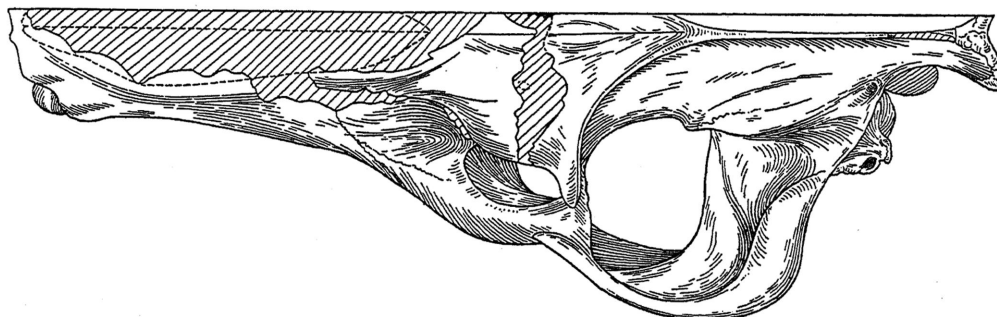
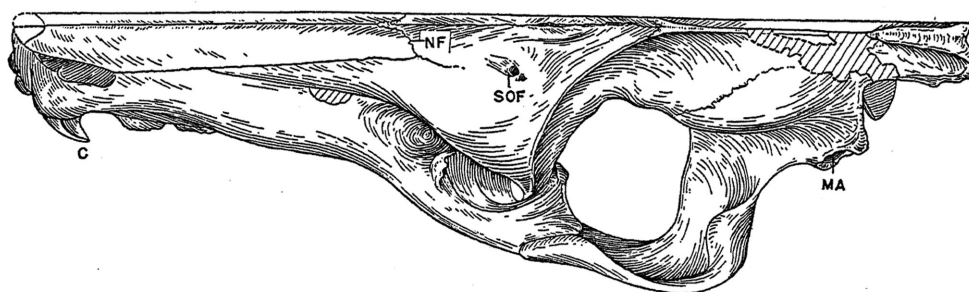
FIG. 1. *Megalonycteris*, one species, and one geologic variety, holotype, F:A.M. 33308, and one example, F:A.M. 33301. (See p. 229.) $\times \frac{1}{2}$.

M. fricki

F.A.M. 33308 T

*M. grandis loomisi* var.

F.A.M. 33301

*M. grandis loomisi*

F.A.M. 42320

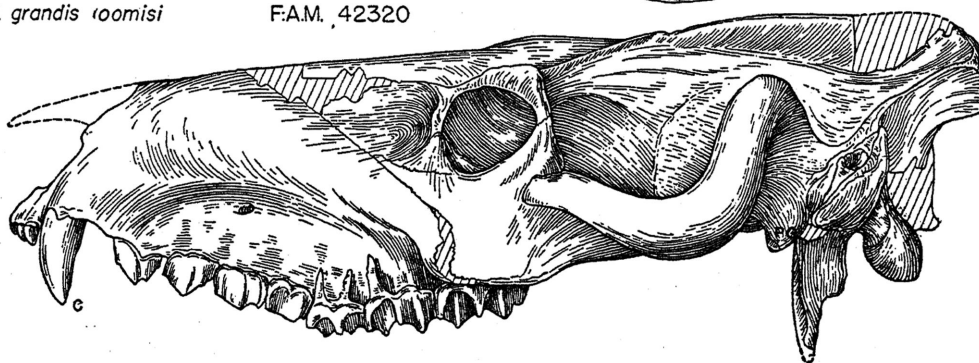


FIG. 2. *Megoreodon*, one species, one subspecies, and one geologic variety, holotype, F:A.M. 33308, and referred, F:A.M. 33301 and 42320. (See p. 229.) $\times \frac{1}{3}$.

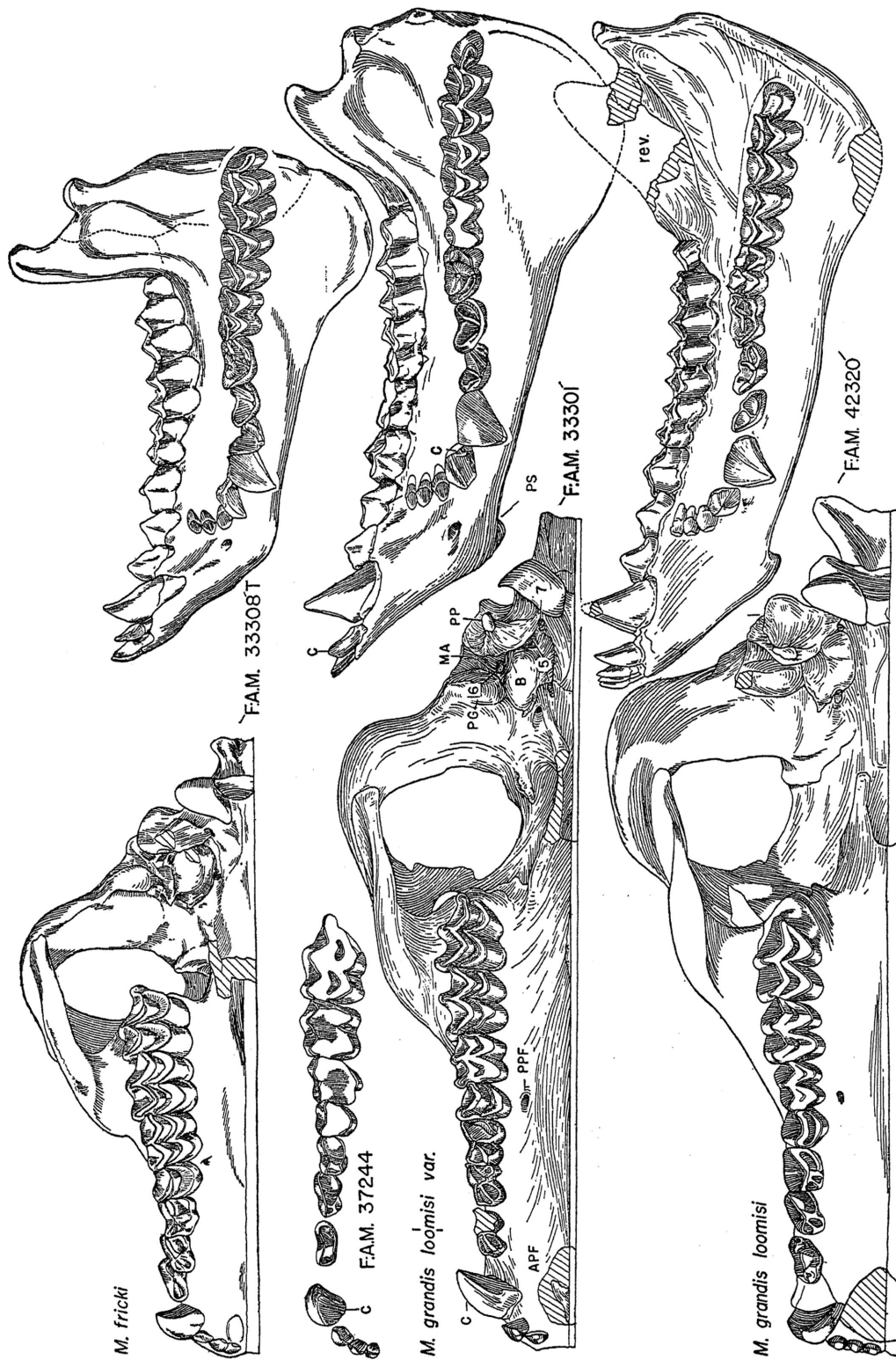


FIG. 3. *Megoreodon*, one species, one subspecies, and one geologic variety, holotype, F:A.M. 33308, and referred, F:A.M. 37244, 33301, and 42320. (See p. 229.) $\times \frac{1}{3}$.

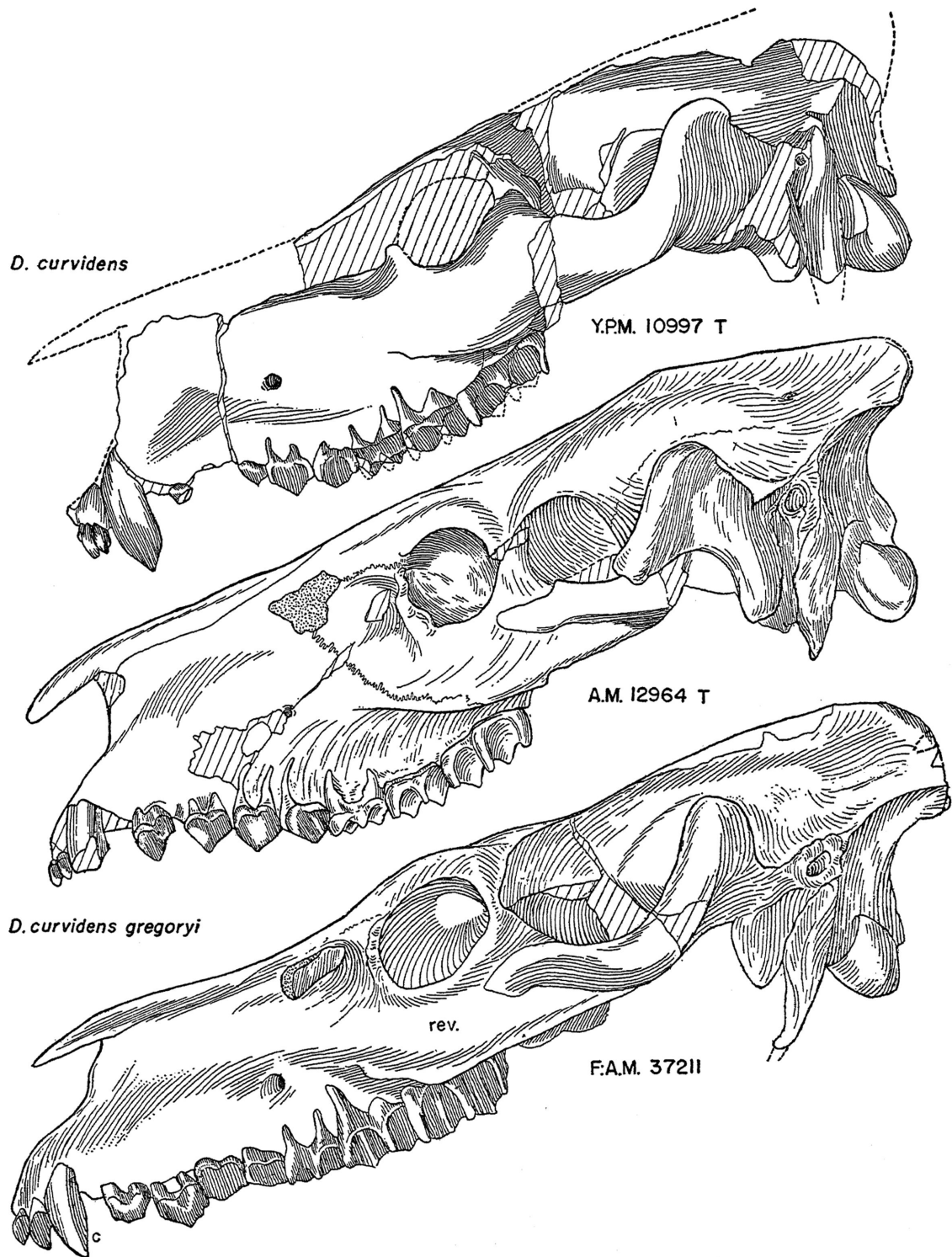


FIG. 4. *Desmatochoerus*, species and subspecies, holotypes, Y.P.M. 10997, and A.M. 12964, and referred, F:A.M. 37211. (See p. 229.) $\times \frac{1}{2}$.

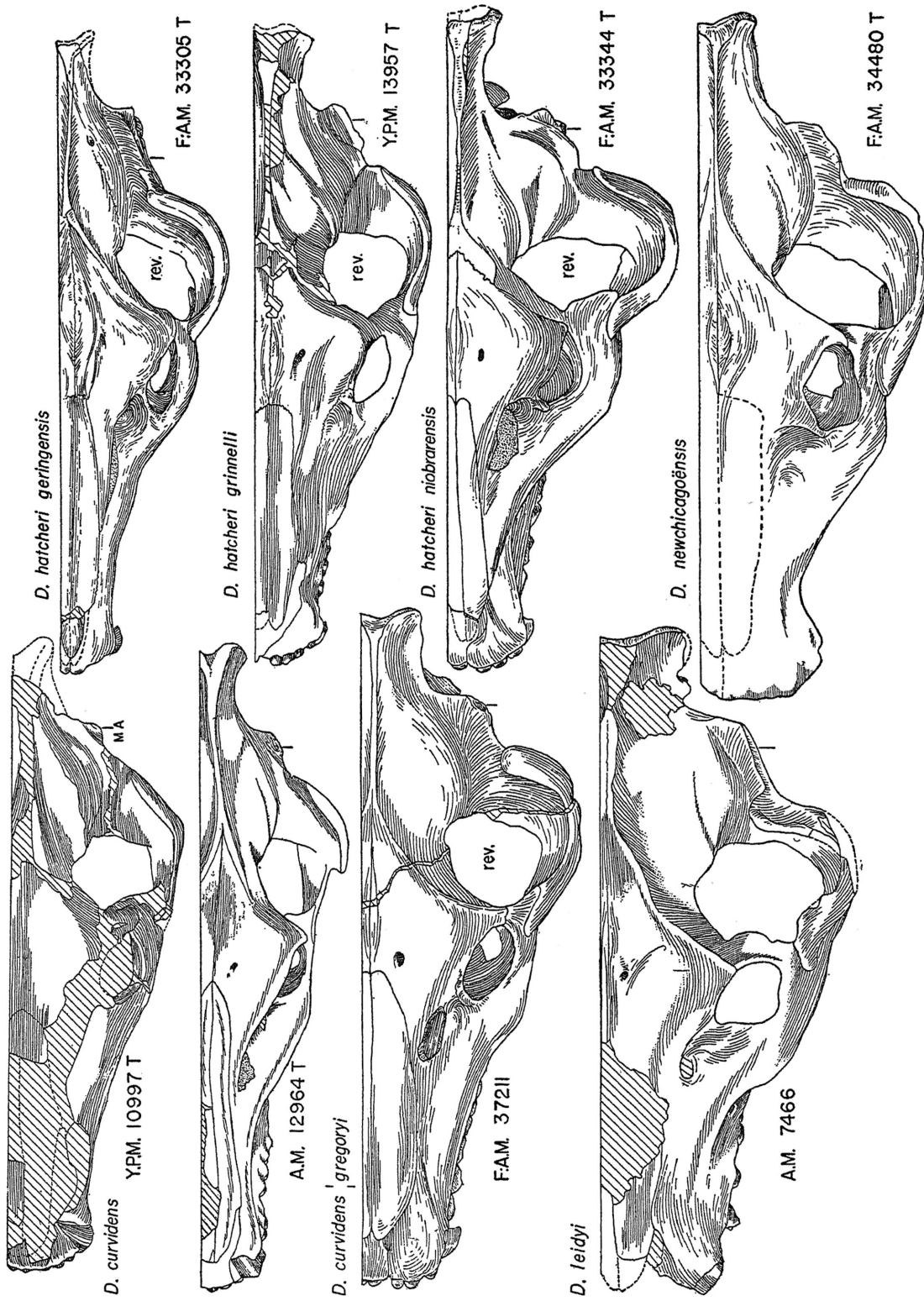


FIG. 5. *Desmatochoerus*, three species and four subspecies, holotypes, Y.P.M. 10997, A.M. 12964, F.A.M. 33305, Y.P.M. 13957, F.A.M. 33344 and 34480, and referred, F.A.M. 37211 and A.M. 7466. (See p. 229.) $\times \frac{1}{3}$.



FIG. 6. *Desmatochoerus*, three species and four subspecies, holotypes, F:A.M. 33305, Y.P.M. 13957, F:A.M. 33344, Y.P.M. 10997, and A.M. 12964, and referred, A.M. 7466, and F:A.M. 37211 and 42327. (See p. 229.) $\times \frac{1}{3}$.

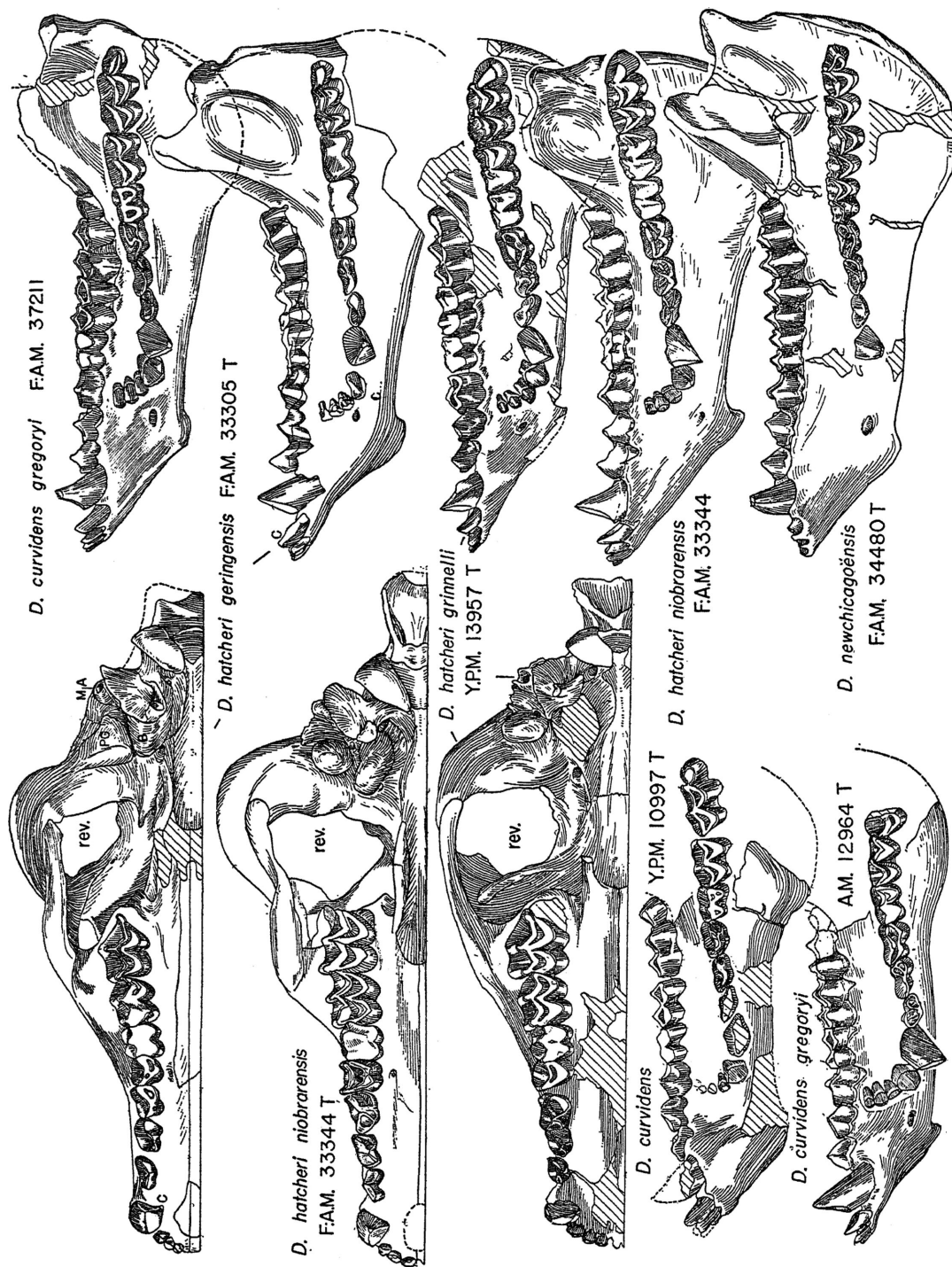


FIG. 7. *Desmatochoerus*, two species and four subspecies, holotypes, Y.P.M. 10997 and 13957, A.M. 12964, F.A.M. 33344, 33305, and 34480, and referred, F.A.M. 37211. (See p. 229.) $\times \frac{1}{3}$.

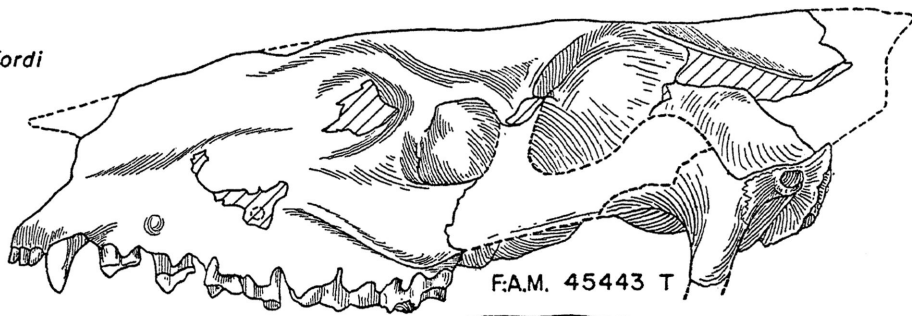
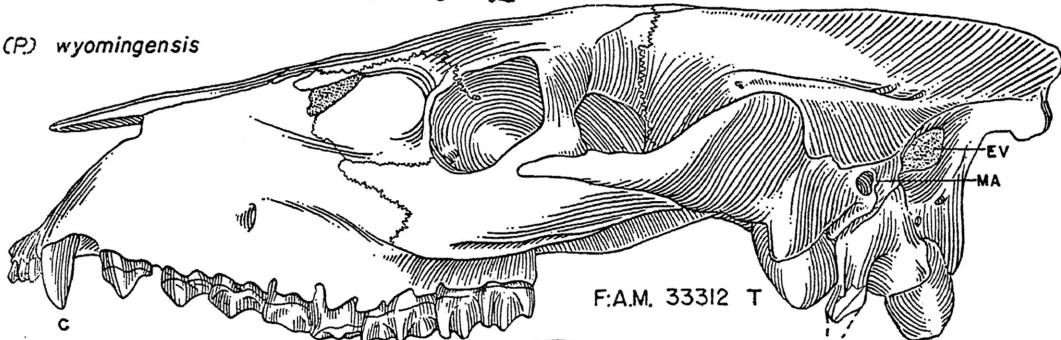
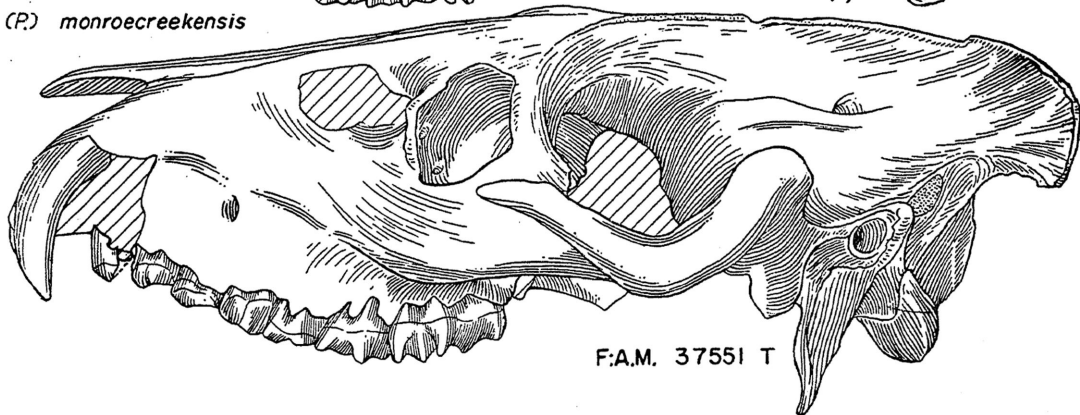
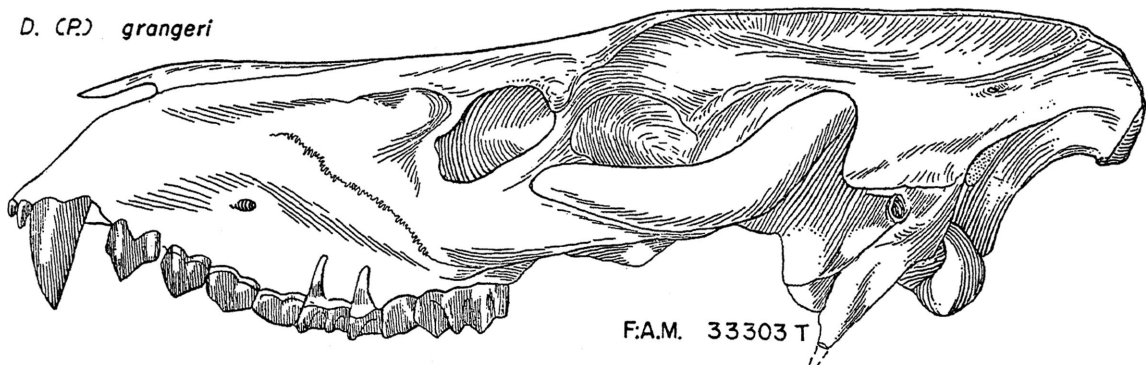
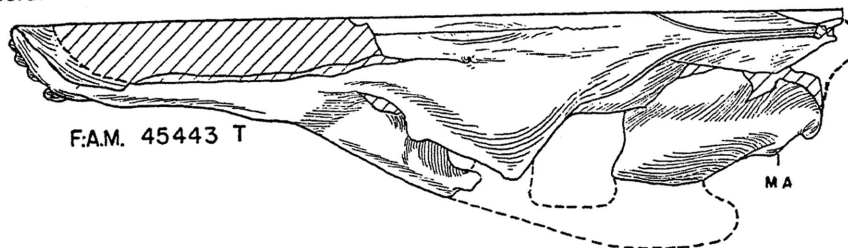
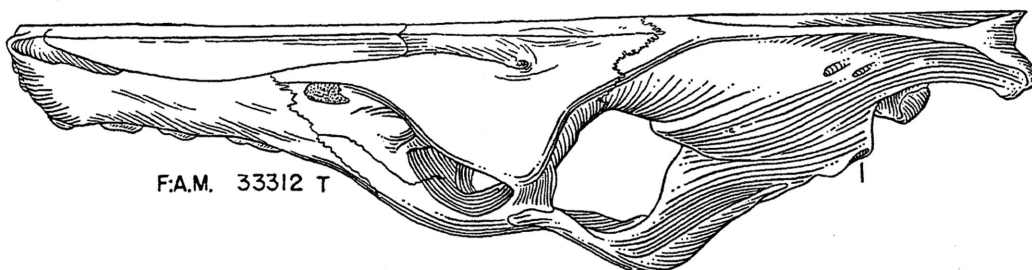
D. (P.) sanfordi*D. (P.) wyomingensis**D. (P.) monroecreekensis**D. (P.) grangeri*

FIG. 8. *Desmatochoerus* (*Paradesmatochoerus*), four species, holotypes, F:A.M. 45433, 33312, 37551, and 33303. (See p. 230.) $\times \frac{1}{2}$.

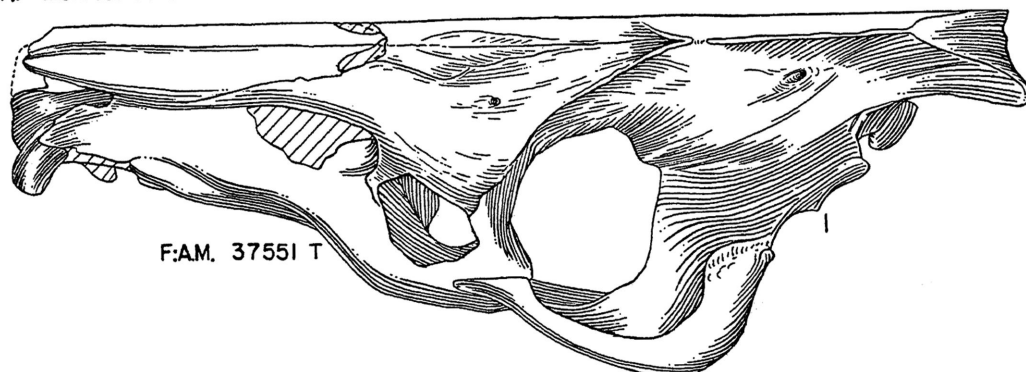
D. (P.) sanfordi



D. (P.) wyomingensis



D. (P.) monroecreekensis



D. (P.) grangeri

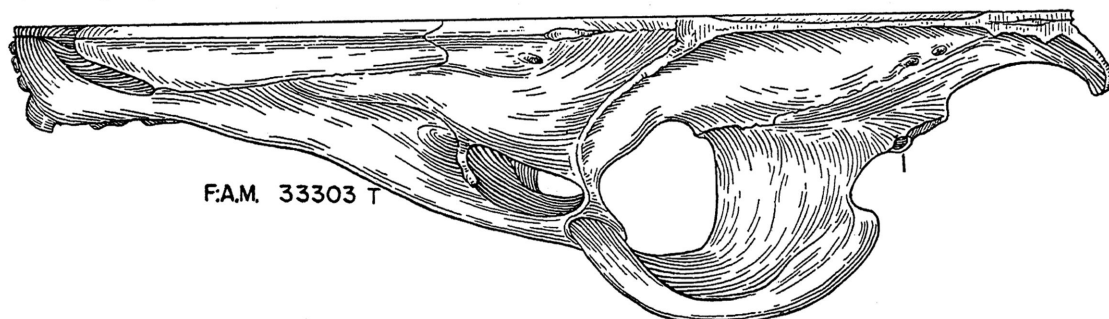


FIG. 9. *Desmatochoerus* (*Paradesmatochoerus*), four species, holotypes, F:A.M. 45443, 3312, 37551, and 33303. (See p. 230.) $\times \frac{1}{2}$.

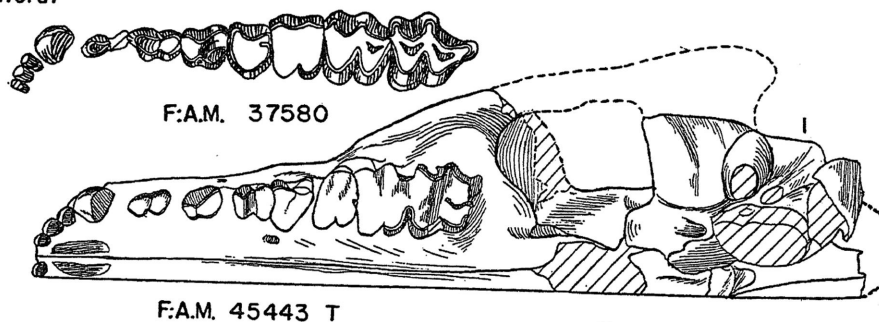
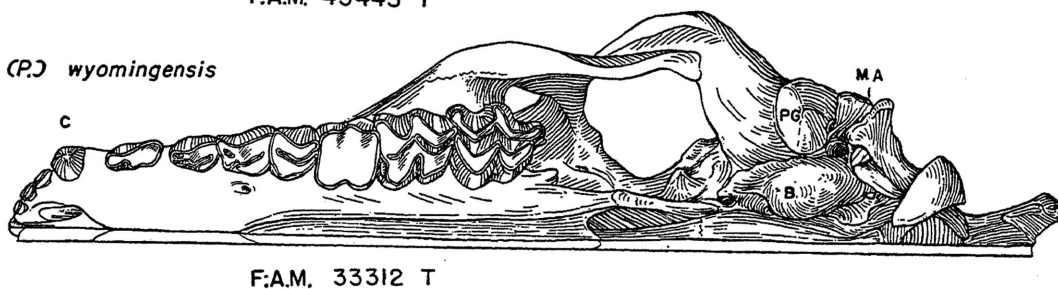
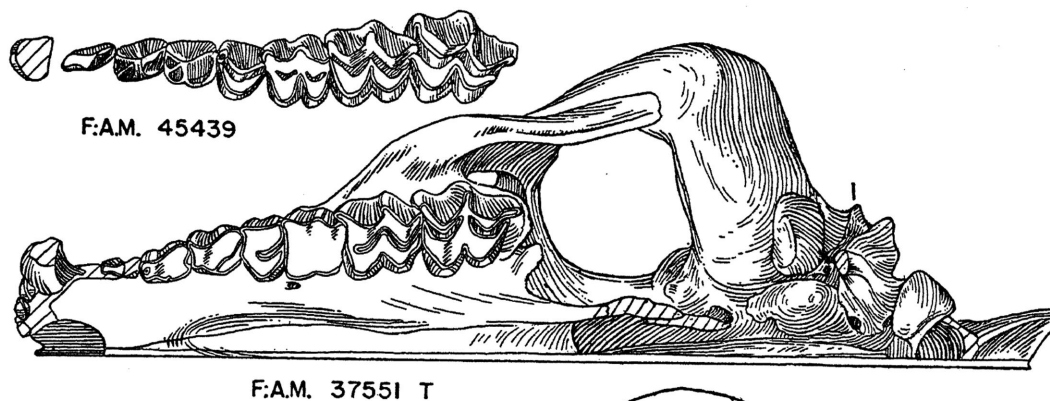
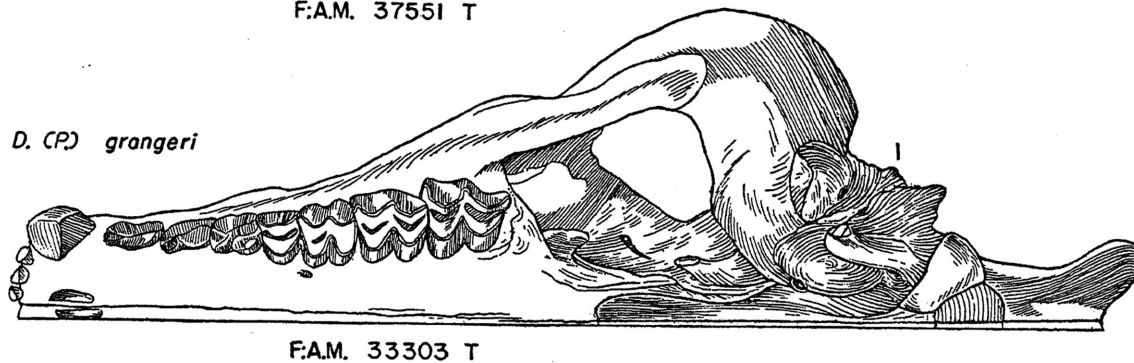
D. (P.) sanfordi*D. (P.) wyomingensis**D. (CP) monroecreekensis**D. (P.) grangeri*

FIG. 10. *Desmatochoerus* (*Paradesmatochoerus*), four species, holotypes, F:A.M. 45443, 33312, 37551, and 33303, and referred, F:A.M. 37580 and 45439. (See p. 230.) $\times \frac{1}{2}$.

D. (P.) sanfordi

F.A.M. 37580

F.A.M. 45443 T rev.

D. (P.) wyomingensis

F.A.M. 33312 T rev.

D. (P.) monroecreekensis

F.A.M. 45439

F.A.M. 37551 T rev.

D. (P.) grangeri

F.A.M. 33303 T rev.

FIG. 11. *Desmatochoerus* (*Paradesmatochoerus*), four species, holotypes, F:A.M. 45443, 33312, 37551, and 33303, and referred, F:A.M. 37580 and 45439. (See p. 230.) $\times \frac{1}{2}$.

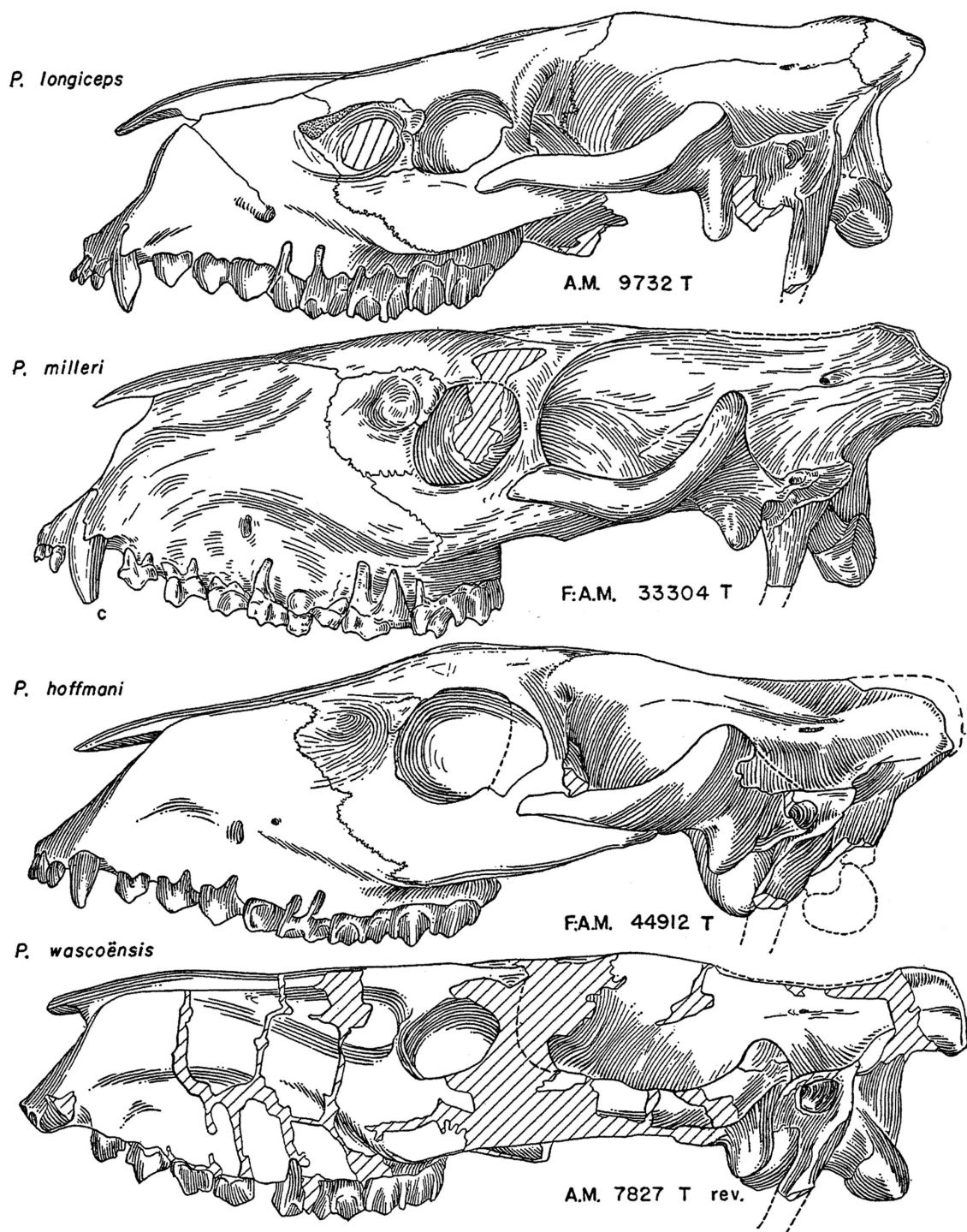
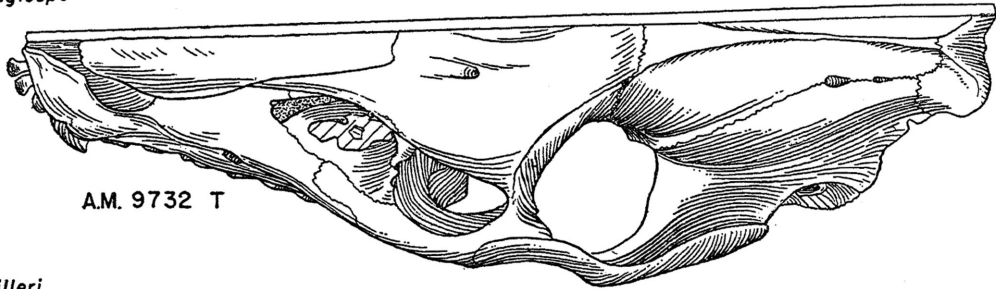


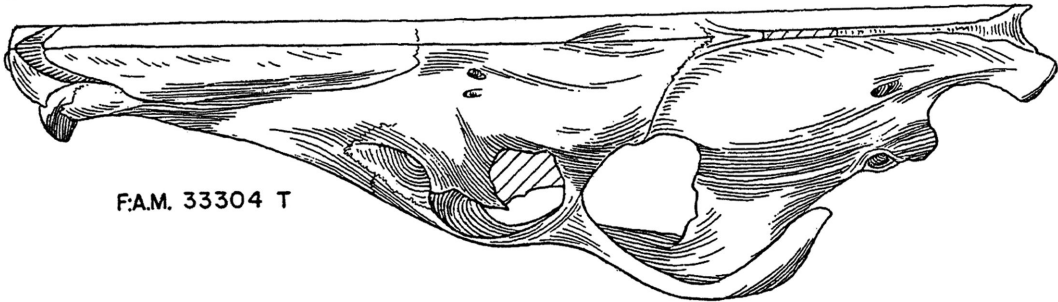
FIG. 12. *Pseudodesmatochoerus*, four species, holotypes, A.M. 9732 and 7827, and F.A.M. 3304 and 44912. (See p. 230.) $\times \frac{1}{2}$.

P. longiceps



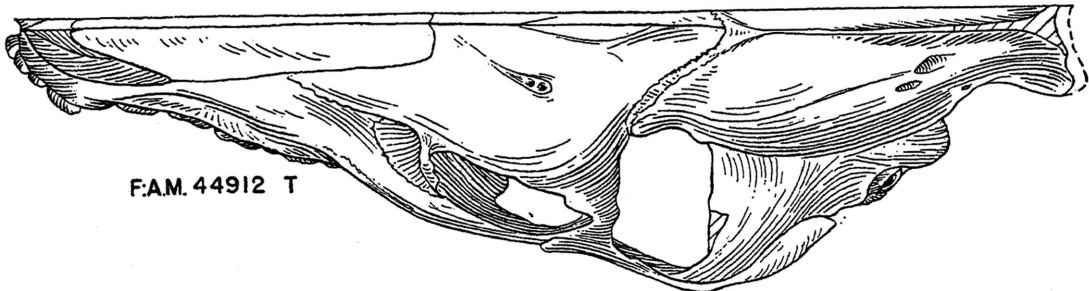
A.M. 9732 T

P. milleri



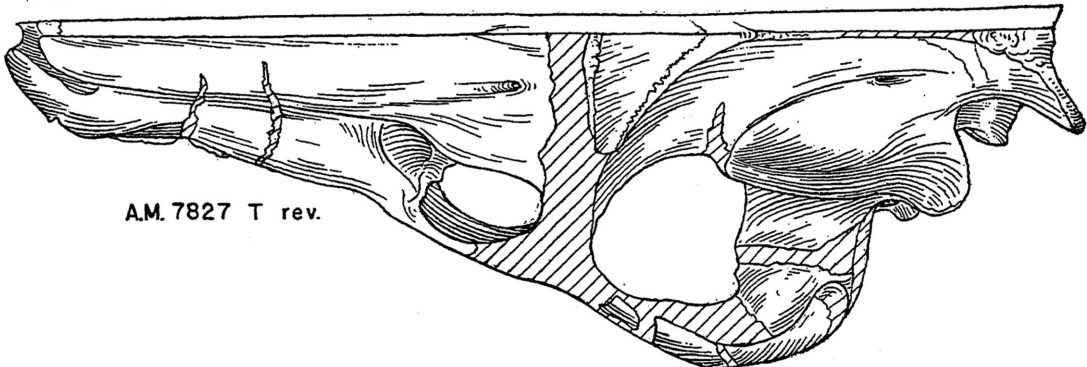
F.A.M. 33304 T

P. hoffmani



F.A.M. 44912 T

P. wascoënsis



A.M. 7827 T rev.

FIG. 13. *Pseudodesmatochoerus*, four species, holotypes, A.M. 9732 and 7827, and F.A.M. 33304 and 44912. (See p. 230.) $\times \frac{1}{2}$.

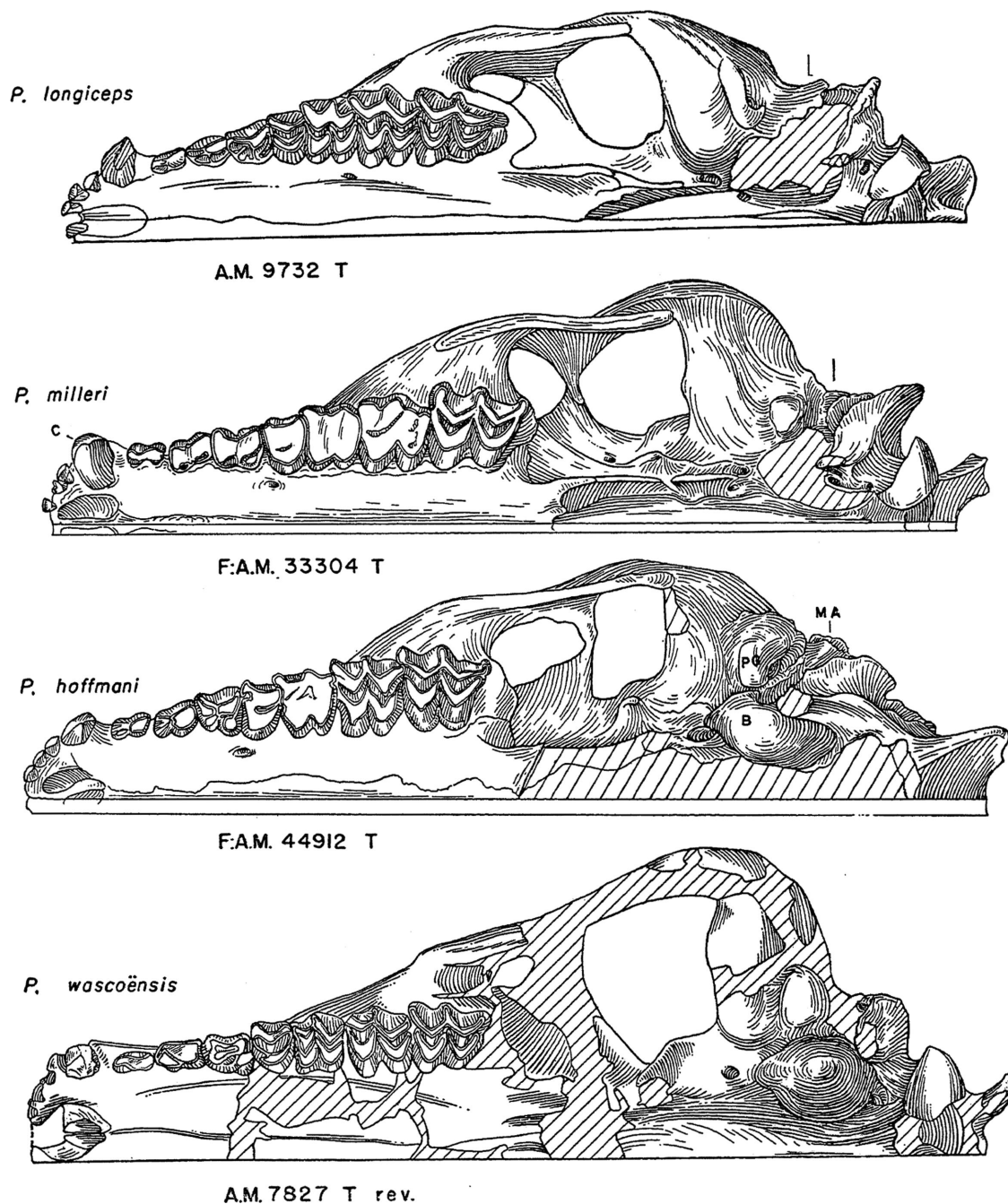
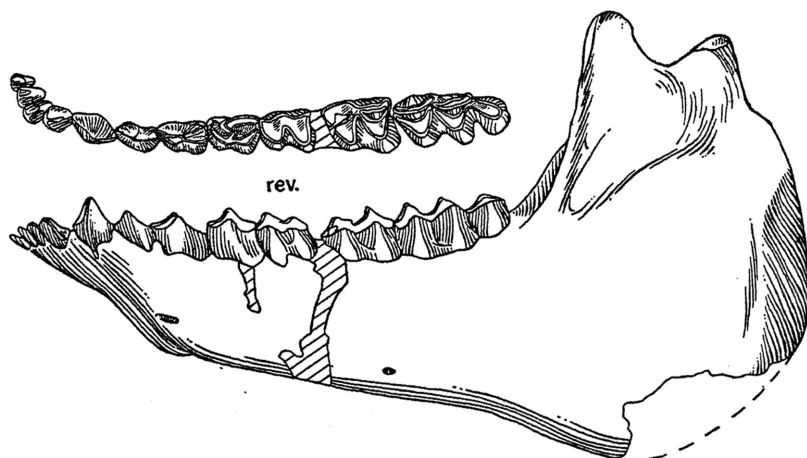


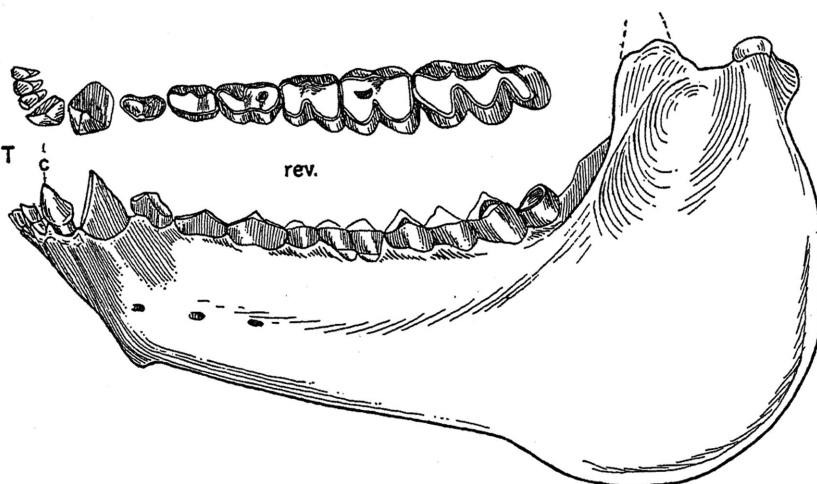
FIG. 14. *Pseudodesmatochoerus*, four species, holotypes, A.M. 9732, and 7827, and F:A.M. 33304 and 44912. (See p. 230.) $\times \frac{1}{2}$.

P. longiceps

A.M. 9732 T

*P. milleri*

F.A.M. 33304 T

*P. hoffmani*

F.A.M. 44912 T

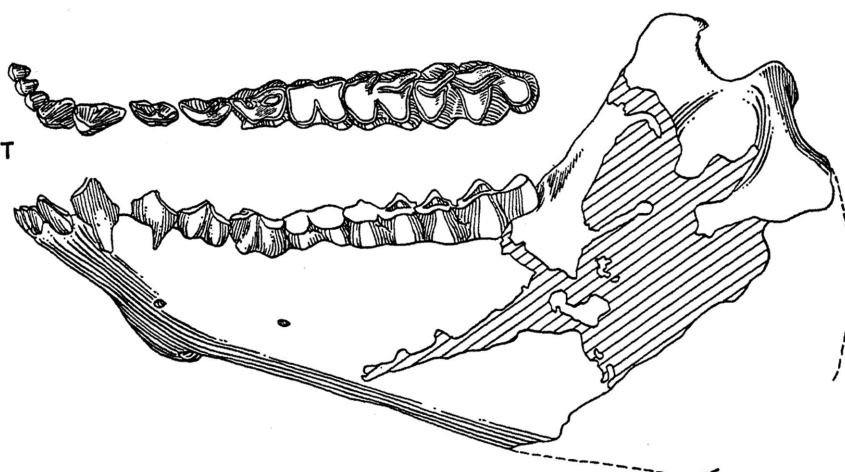


FIG. 15. *Pseudodesmatochoerus*, three species, holotypes, A.M. 9732, and F.A.M. 33304 and 44912. (See p. 230.) $\times \frac{1}{2}$.

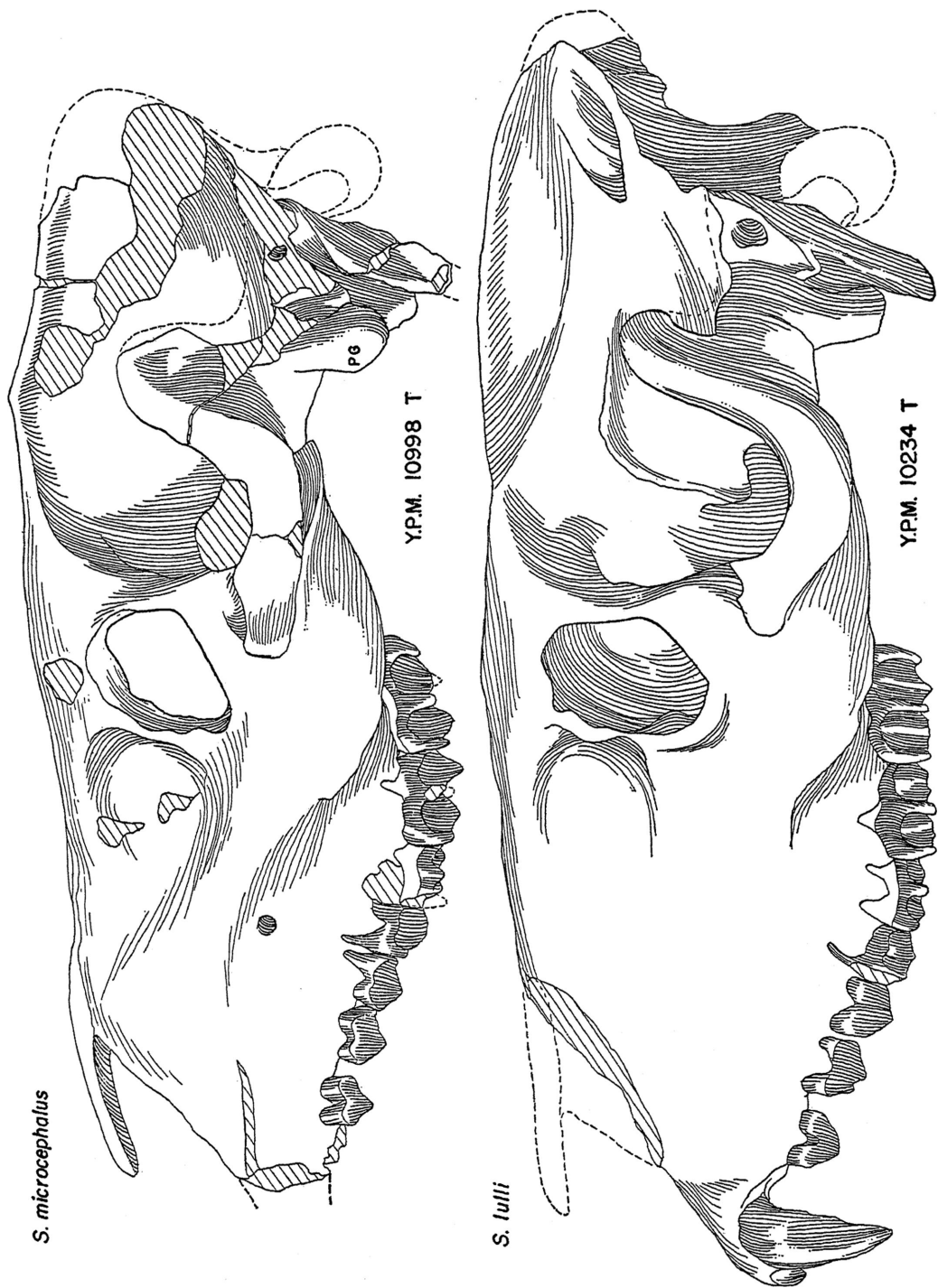


FIG. 16. *Superdesmatochoerus*, two species, holotypes, Y.P.M. 10998 and 10234. (See p. 230.) $\times \frac{1}{2}$.

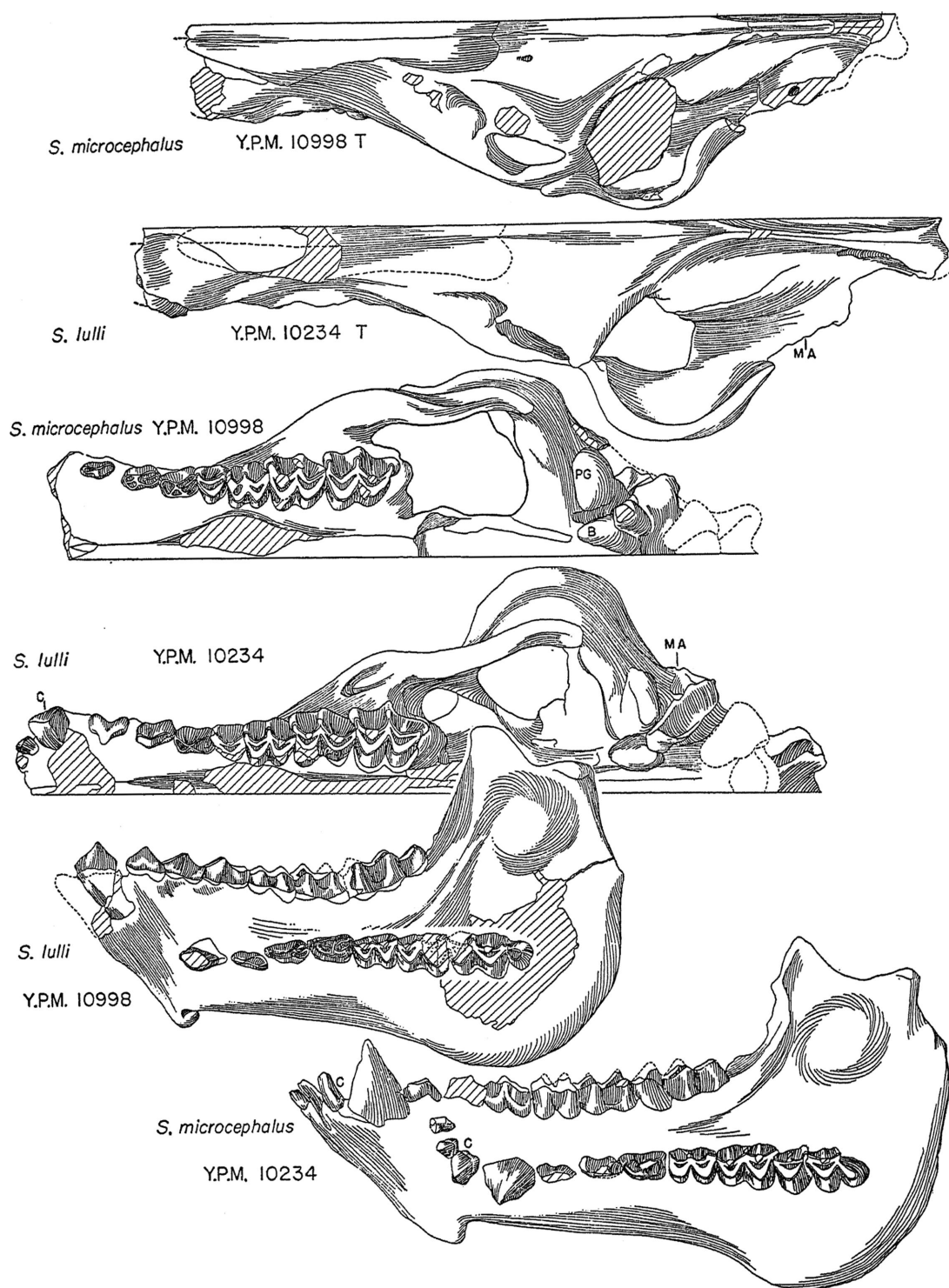


FIG. 17. *Superdesmatochoerus*, two species, holotypes, Y.P.M. 10998 and 10234. (See p. 230.) $\times \frac{1}{2}$.

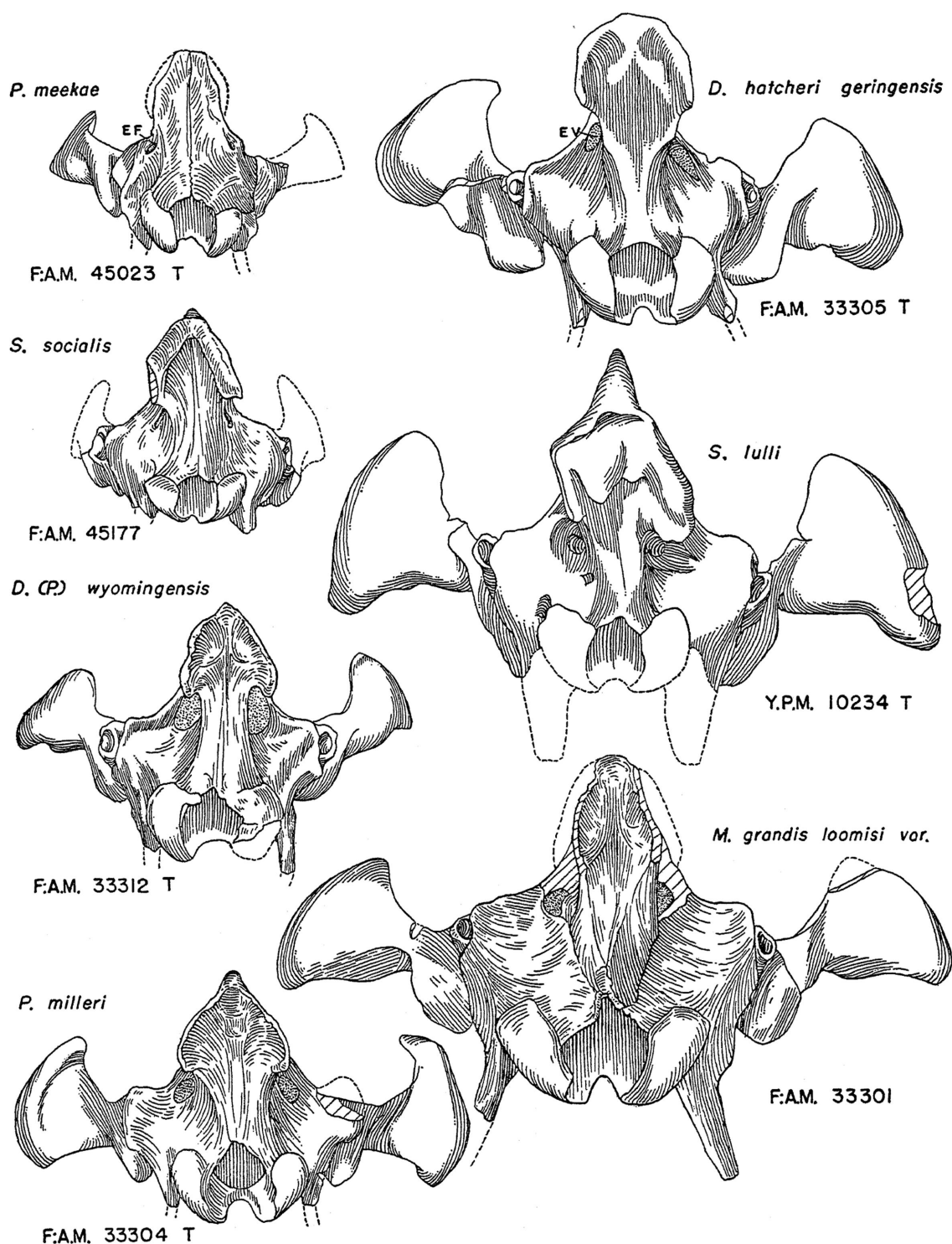


FIG. 18. *Prodesmatochoerus*, *Subdesmatochoerus*, *Desmatochoerus* (*Paradesmatochoerus*), *Pseudodesmatochoerus*, *Desmatochoerus*, *Superdesmatochoerus*, and *Megoreodon*, holotypes, F:A.M. 45023, 33312, 33304, 33305, and Y.P.M. 10234, and referred, F:A.M. 45177 and 33301. (See p. 230.) $\times \frac{1}{2}$.

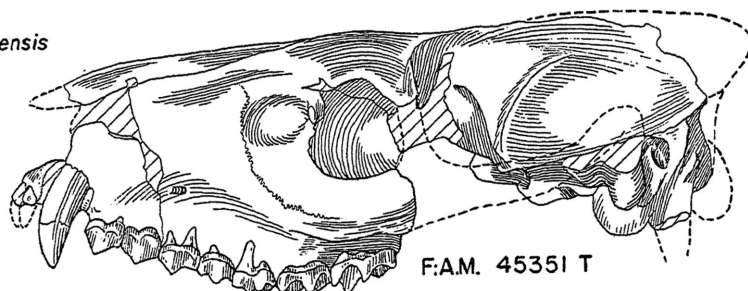
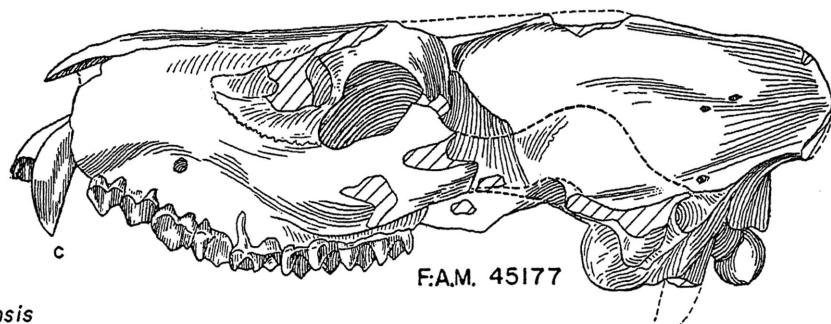
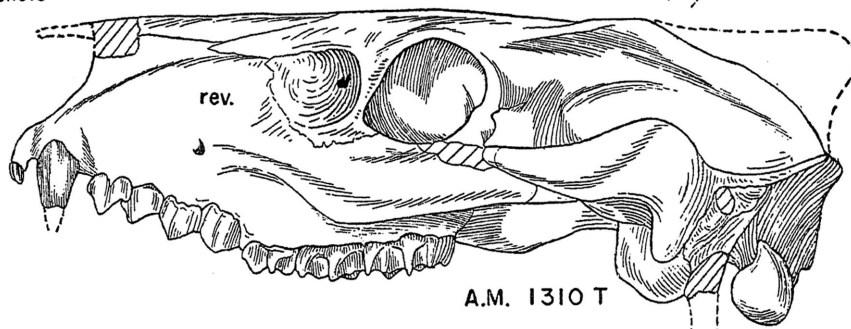
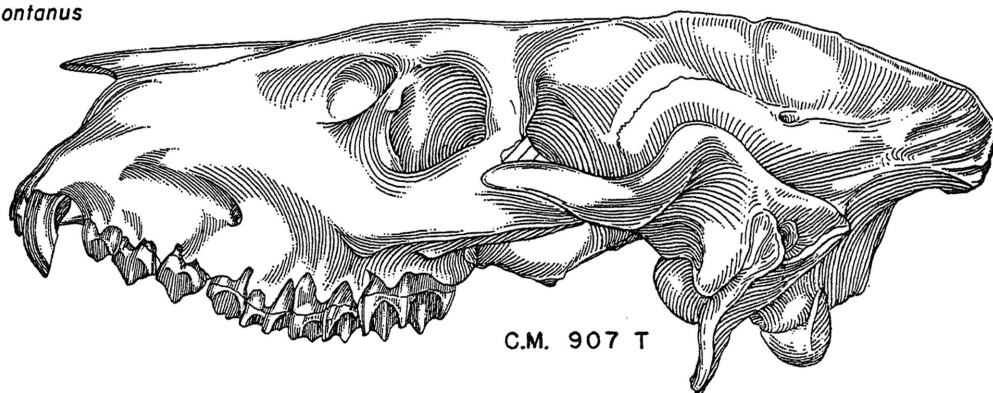
S. socialis dakotensis*S. socialis**S. shannonensis**S. montanus*

FIG. 19. *Subdesmatochoerus*, three species and one subspecies, holotypes, F:A.M. 45331, A.M. 1310, and C.M. 907, and referred, F:A.M. 45177. (See p. 230.) $\times \frac{1}{2}$.

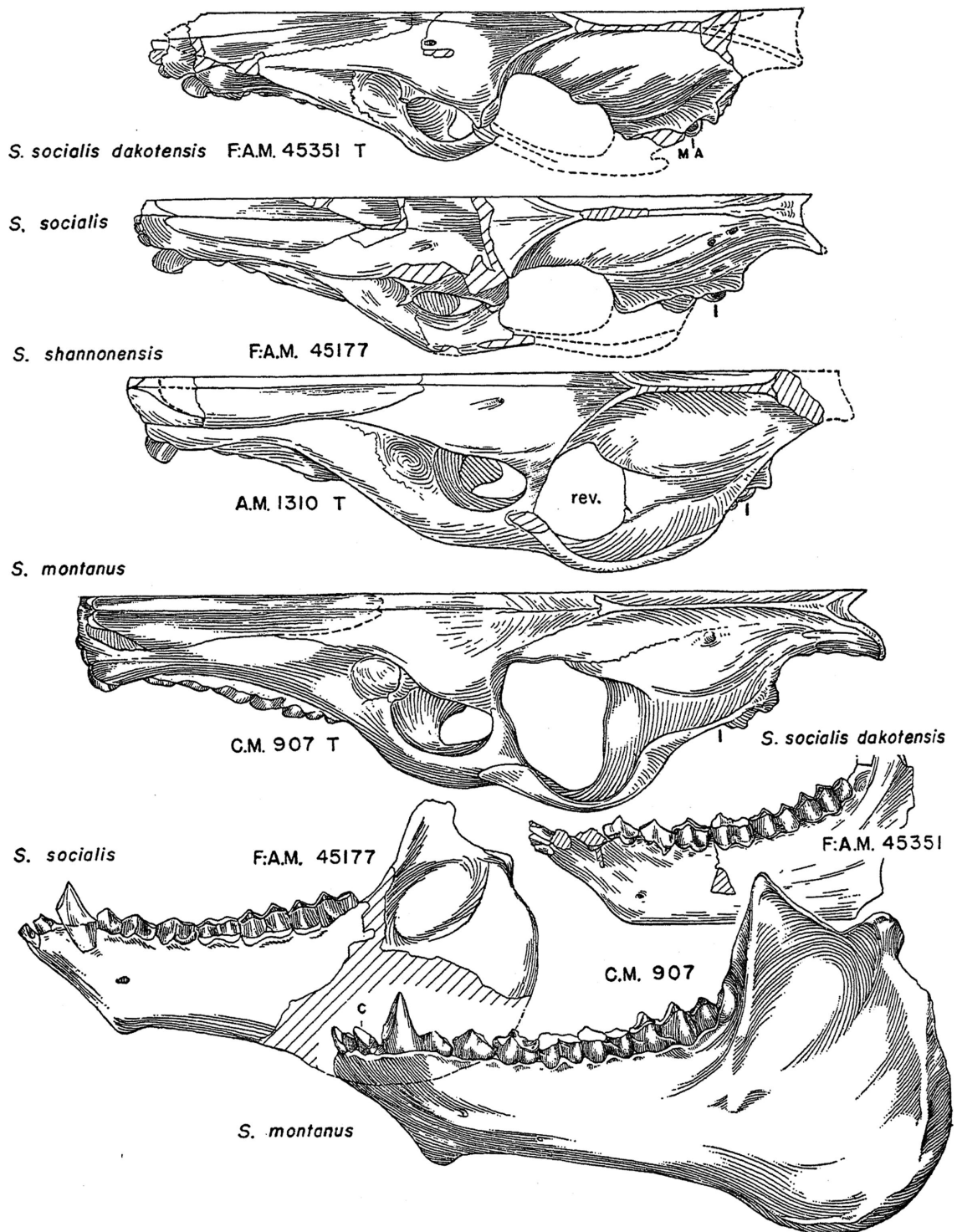


FIG. 20. *Subdesmatochoerus*, three species and one subspecies, holotypes, F:A.M. 45351, A.M. 1310, and C.M. 907, and referred, F:A.M. 45177. (See p. 231.) $\times \frac{1}{2}$.

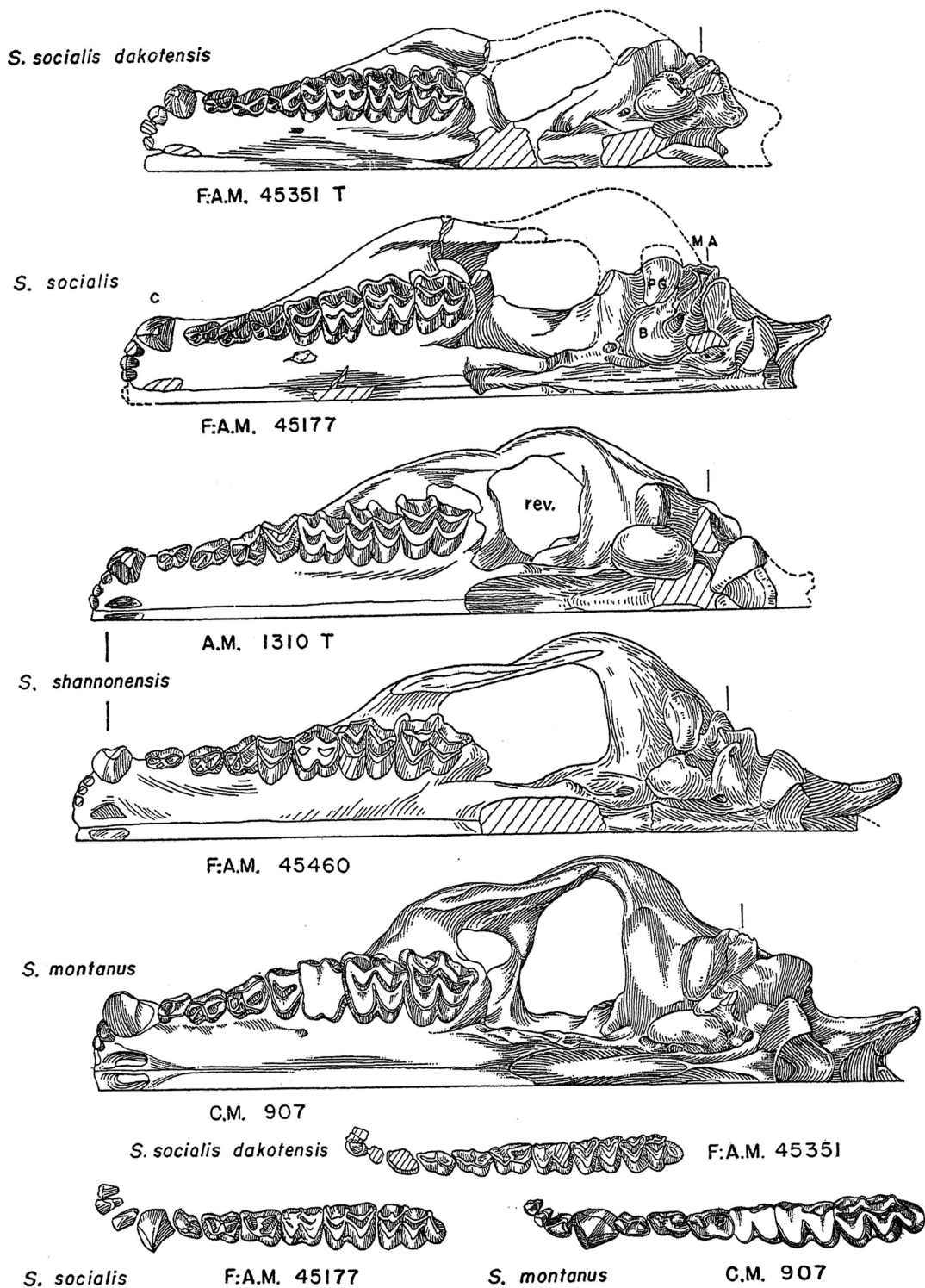


FIG. 21. *Subdesmatochoerus*, three species and one subspecies, holotypes, F:A.M. 45351, A.M. 1310, and C.M. 907, and referred, F:A.M. 45177 and 45460. (See p. 231.) $\times \frac{1}{2}$.

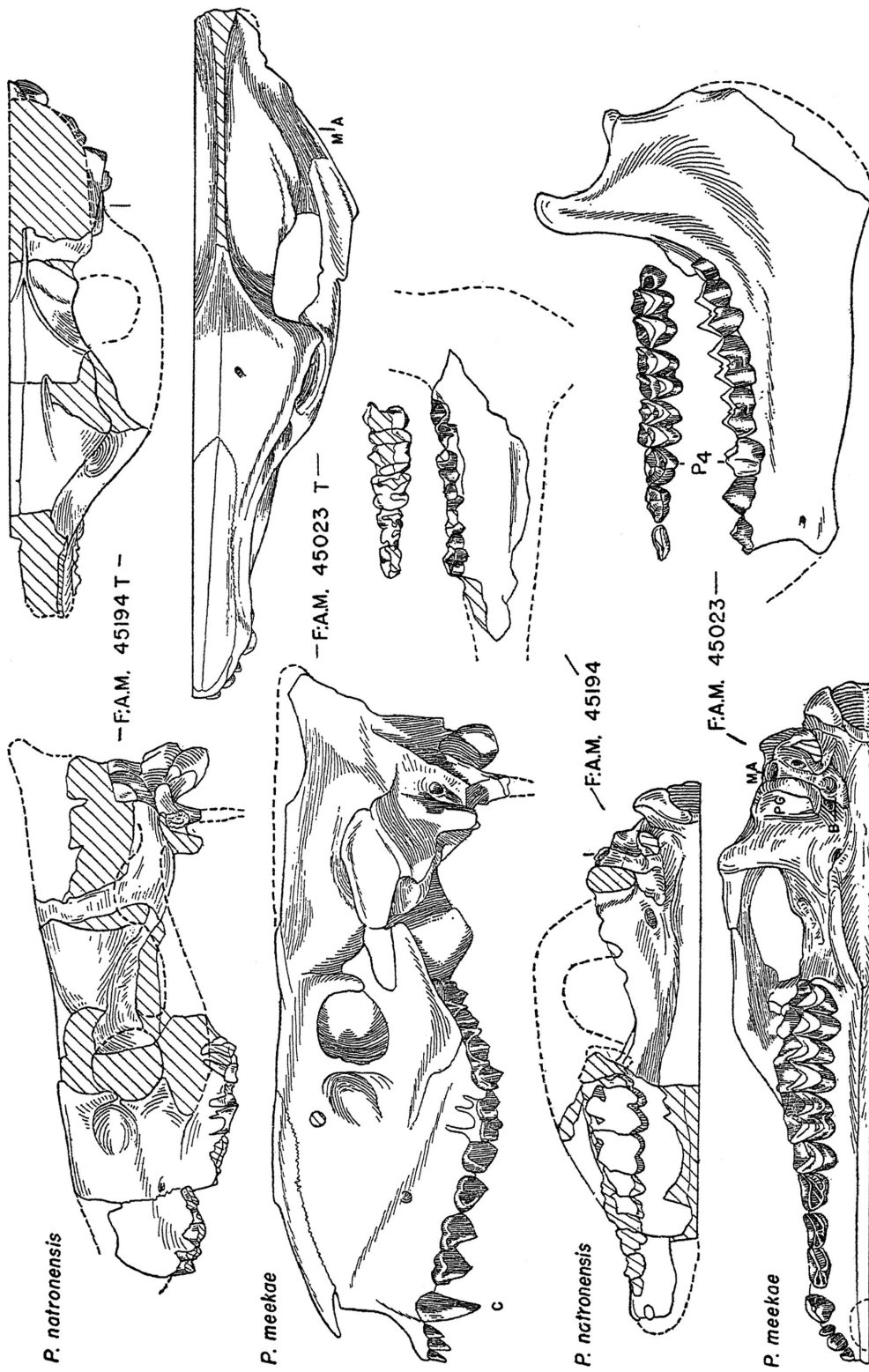


FIG. 22. *Prodesmatochoerus*, two species, holotypes, F.A.M. 45194 and 45023. (See p. 231.) $\times \frac{1}{2}$.

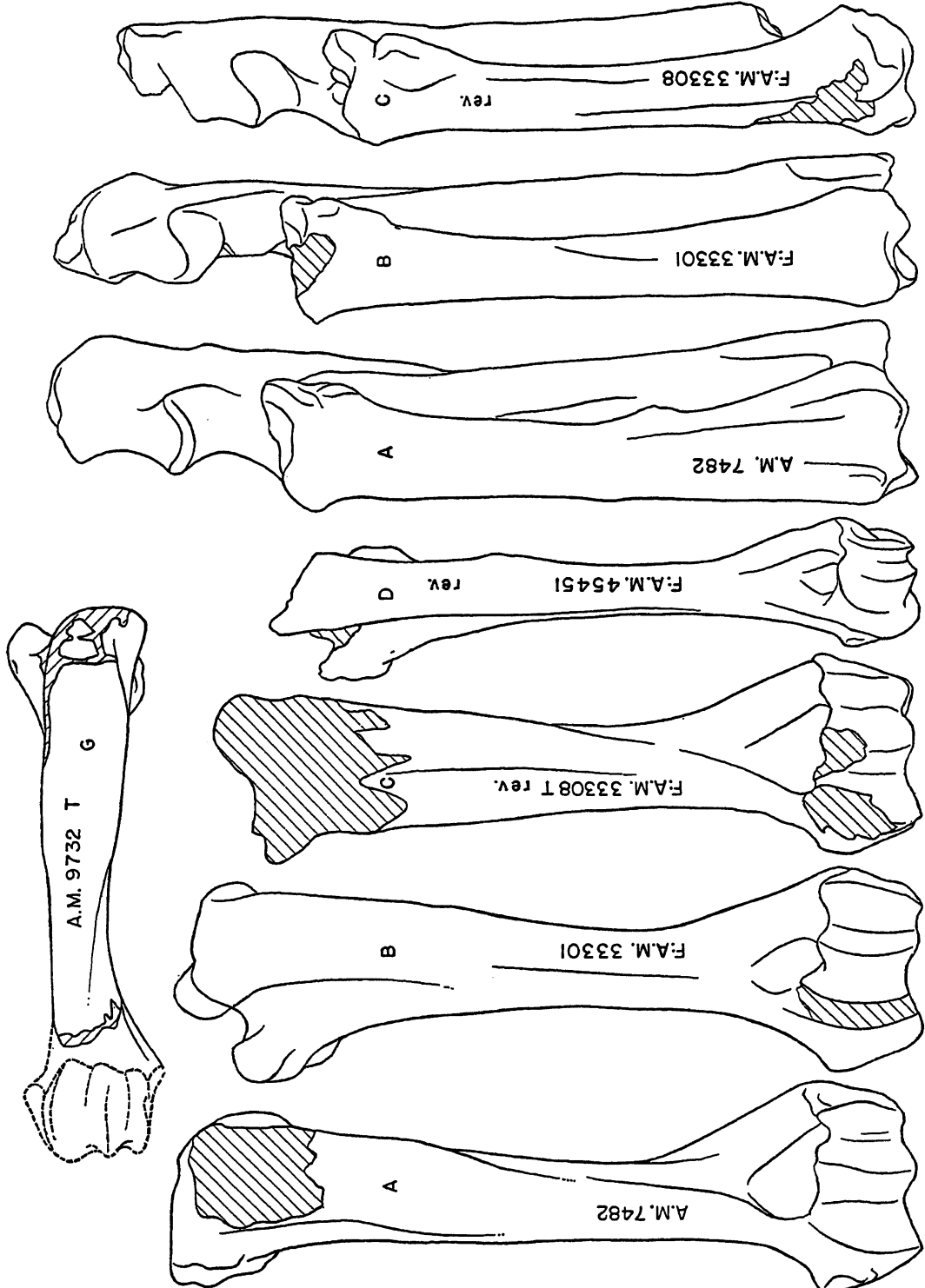


FIG. 23. *Desmatochoerinae*. (See p. 231, and legend, fig. 25.) $\times \frac{1}{2}$.

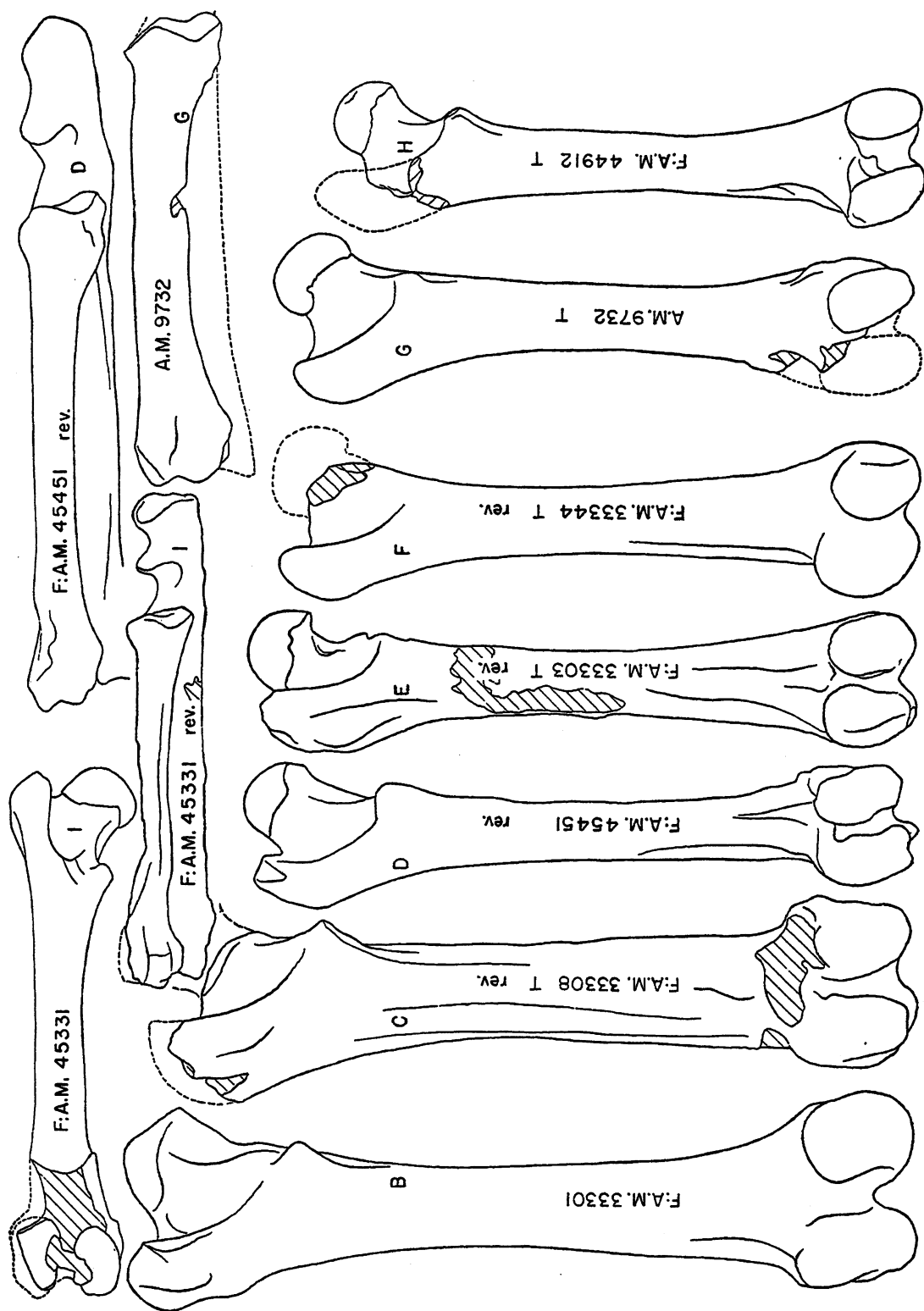


FIG. 24. Desmatochoerinae. (See p. 231, and legend, fig. 25.) $\times 4$.

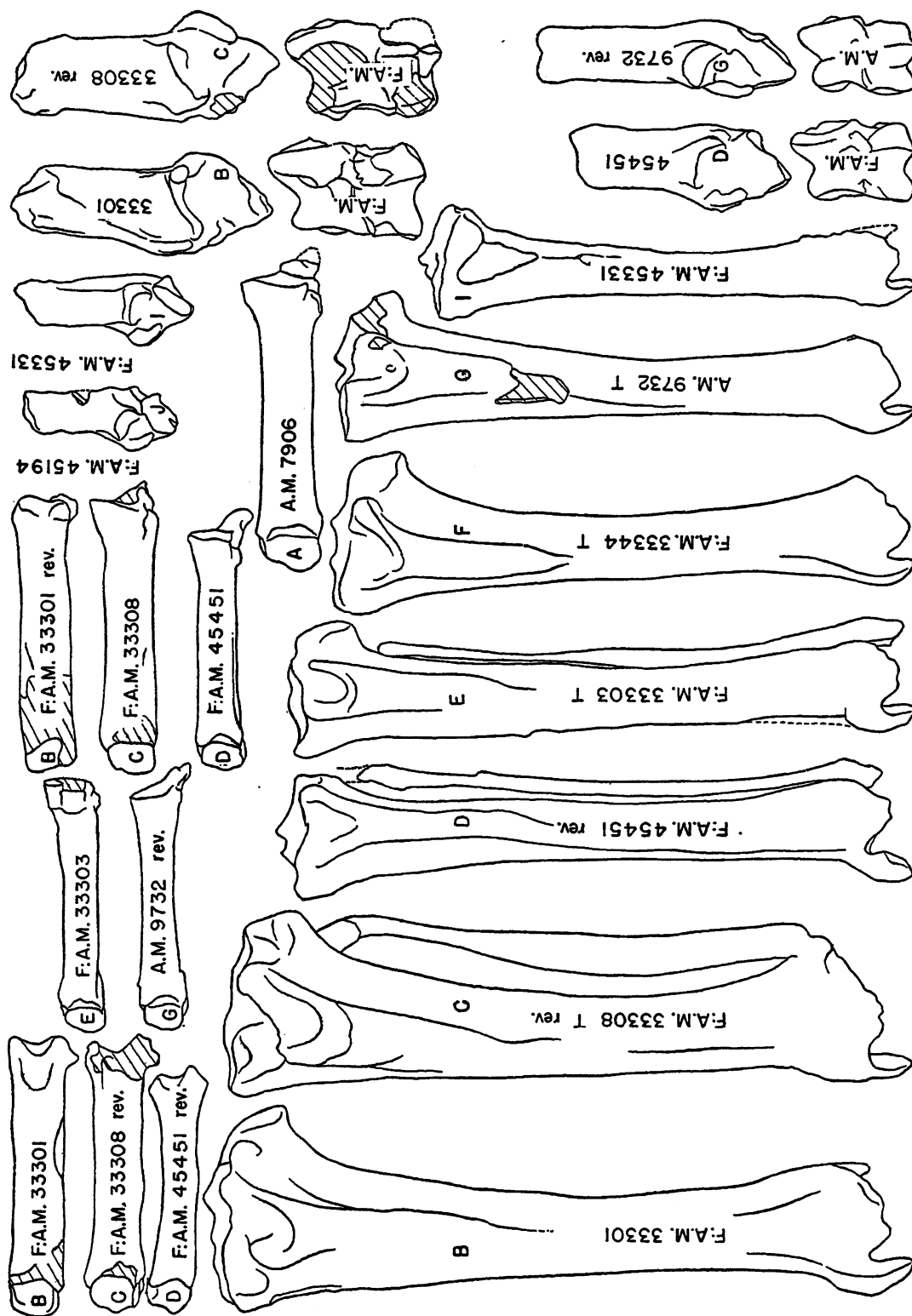


FIG. 25. A, *Superdesmatochoerus lullii*; B, *Megareodon grandis loomisi*, geologic variety; C, *M. fricki*; D, *Desmatochoerus hatcheri grangeri*; E, D. (*Paradesmatochoerus*) *grangeri*; F, D. *hatcheri niobrarenis*; G, *Pseudodesmatochoerus longiceps*; H, *P. hoffmani*; I, *Prodesmatochoerus meekae*; J, *P. natronensis*. (See p. 231.) $\times \frac{1}{2}$.