PHENACOCOELINAE, A NEW SUBFAMILY OF OREODONTS

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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 95 : ARTICLE 3 NEW YORK : 1950

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C. BERTRAND SCHULTZ

Director of the University of Nebraska State Museum and Associate Professor of Geology

CHARLES H. FALKENBACH

Field Associate, Frick Laboratory The American Museum of Natural History

CONTRIBUTION TO THE REVISION OF THE OREODONTS (MERYCOIDODONTIDAE), NUMBER 5

PUBLICATION OF THE FRICK LABORATORY
DEPARTMENT OF MAMMALS
THE AMERICAN MUSEUM OF NATURAL HISTORY

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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Issued November 13, 1950

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INTRODUCTION

THE PRESENT REPORT is the fifth in a series dealing with a revision of the oreodonts (Merycoidodontidae). Previous reports cover subfamily 1, Merycochoerinae[1]; subfamily 2, Ticholeptinae[2]; subfamily 3, Merychyinae[3]; and subfamily 4, Promerycochoerinae.[4]

The new subfamily 5, Phenacocoelinae, includes four genera: *Phenacocoelus* Peterson; *Hypsiops*, new genus; *Submerycochoerus*, new genus; and *Pseudomesoreodon*, new genus. The subfamily is now represented by 85 specimens, ranging from small to large. The small *Phenacocoelus typus* Peterson has a skull comparable in length with that of *Merychyus siouxensis* Loomis, and the large *?Pseudomesoreodon boulderensis*, new species, a skull that compares in length with that of *Ustatochoerus profectus* (Matthew and Cook). In the Phenacocoelinae the length of the limb elements relative to the over-all cranial dimension tends to be proportionately greater in the shorter-skulled forms. *Submerycochoerus* presumably gave rise to *Merycochoerus* of the Merycochoerinae (see discussion, p. 127).

The remains of Phenacocoelinae are so far known only from the lower Miocene deposits (Harrison or its equivalent)—except for the occurrence of *Phenacocoelus stouti* in the middle Miocene (lower Marsland)—of California, Montana, Nebraska, Oregon, South Dakota, and Wyoming. The geographical and geological distribution is shown in chart 3 (p. 102). The distribution of the four previously discussed subfamilies has been treated in the Promerycochoerinae bulletin.[5]

In the study of the Phenacocoelinae the writers have used the same method of approach[6] as previously, with emphasis on morphologic characters, phylogeny, and variation, coordinating these with geological distribution. The new subfamily includes the only known species of oreodonts possessing frontal vacuities (*Phenacocoelus typus* and indicated in *P. kayi*).

[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] *Idem*, 1949, pp. 80, 81, 86.
[6] *Idem*, 1947, p. 166.

In the following pages, 85 numbered skulls, mandibular rami, and skeletal elements are listed or described under four named genera (of which three are new). Twenty-five of these specimens (including two refigured holotypes), representing 12 species (of which seven are new) and one subspecies, are illustrated in detail in the 15 text figures. The drawings are reproduced at one-half natural size.

The illustrations of Phenacocoelinae show the range in size, shape, and proportions of the skulls, mandibular rami, and limb elements. Diagnostic characters include height of skulls, anterior retraction of nasals, shape of supraoccipital regions, and size and shape of tympanic bullae.

The writers[7] reiterate their appreciation of the aid and encouragement of the various associates to whom acknowledgments have been previously made[8] and to Mr. Wesley Echolm and Mrs. Helen Ziska of the Frick Laboratory for illustrations which were drawn under the supervision of Miss Hazel de Berard; Miss Mary Louise Hanson of the University of Nebraska State Museum for preliminary editorial assistance; and Miss Dawn Daggett for aid in typing. To all these and others the writers are grateful.

The following is a list of abbreviations of institutions cited:

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

[7] Statement by C. Bertrand Schultz: Owing to additional duties at the University of Nebraska, it has been impracticable for me to spend as much time during the past seven years with the oreodont studies as during the period 1933 to 1942. Hence it has been necessary for Charles H. Falkenbach to do the major portion of the detailed work with the collections in our revision of the family. In recognition of this fact I have suggested to him that the sequence of the writers' names be Falkenbach and Schultz for this and certain future reports. Falkenbach, however, has considered it best to leave the order the same as in the past for bibliographical reasons.—C. B. S.

[8] *Idem*, 1940, p. 216; 1941, p. 4; 1947, p. 165; 1949, p. 79.

CHARACTERS IN AUDITORY BULLAE OF CERTAIN OREODONTS

Among the large available series of oreodont skulls the bullae are frequently incomplete and badly crushed. The bullae, however, are well enough known to be of diagnostic value in the division of the 18 genera and subgenera so far reported on by the writers, and, in certain instances, of species. Considerable variation is exhibited in size and in the external profile of the bullae within the family. In chart 1 (p. 97), the bullae representing the five subfamilies so far reported upon are illustrated with cross sections to show shape and relative size. The noted variation may be considered as follows:

1. For a species: the bullae are usually constant in shape, but with some size variation.

2. For a genus: the bullae usually have the same general shape, but vary greatly in size; for example, if the bullae of a genus tend to have a flattened ventral surface, the species from the lower geologic zone may show this character less markedly than the species from a higher zone, but there is a gradation in the bulla's shape from one species to another in the same phylogenetic line.

3. For a subfamily: the bullae usually show a trend towards a particular form; for example, if the general tendency is for the bullae to be high and round, there may be some that are high and completely round, others high and subround, while the remainder may be high and oval.

The auditory bullae of the Merycoidodontidae differ considerably, depressed but large in *Ustatochoerus*, high and round in *Promerycochoerus*, and very small (minute) in some Oligocene forms (these last to be discussed in a forthcoming report).

The five subfamilies used as the basis for chart 1 are as follows:

Merycochoerinae (1940), subfamily 1, includes *Brachycrus* Matthew and *Merycochoerus* Leidy, in which the bullae tend to be high with a small diameter.

Ticholeptinae (1941), subfamily 2, includes *Ustatochoerus* Schultz and Falkenbach, *Ticholeptus* Cope, and *Mediochoerus* Schultz and Falkenbach, the former two with bullae that are depressed but enlarged in the basal region. The bullae of *Mediochoerus* are unknown.

Merychyinae (1947), subfamily 3, includes *Merychyus* Leidy, *Merychyus* (*Metoreodon*) (Matthew and Cook), *Paramerychyus* Schultz and Falkenbach, *Oreodontoides* Thorpe, and *Oreodontoides* (*Paroreodon*) (Thorpe), in which the ventral surface of the bullae has various degrees of flatness, sloping internally to the basioccipital ridge.

Promerycochoerinae (1949), subfamily 4, includes *Promerycochoerus* Douglass, *Promerycochoerus* (*Parapromerycochoerus*) Schultz and Falkenbach, *Promerycochoerus* (*Pseudopromerycochoerus*) Schultz and Falkenbach, *Mesoreodon* Scott, *Promesoreodon* Schultz and Falkenbach, and *Merycoides* Douglass, in which the bullae tend to be high and round (or oval or suboval).

Phenacocoelinae (this report), subfamily 5, includes *Phenacocoelus* Peterson, and *Hypsiops*, *Submerycochoerus*, and *Pseudomesoreodon*, new genera, which have bullae that tend to have a flattened ventral surface and an internal slope. The uniform internal slope (of approximately 45°) is especially evident in *Hypsiops* and *Pseudomesoreodon*. The bullae of *Submerycochoerus* are unknown.

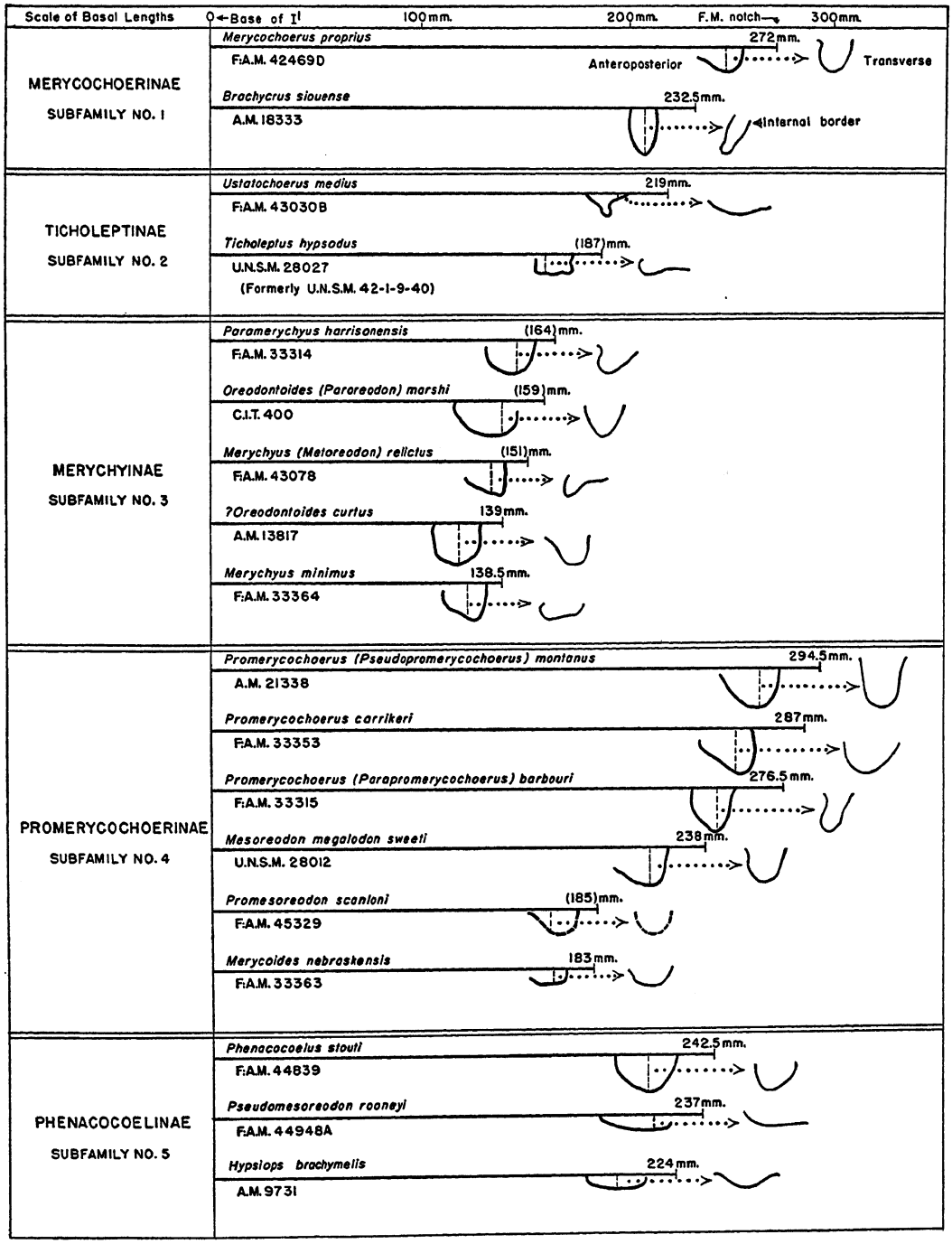


CHART 1. Comparative basal lengths of skulls and cross sections of auditory bullae in five subfamilies of oreodonts. The anteroposterior cross section was taken through the bulla at its highest point (parallel to the longitudinal axis of the skull), and is placed in its relative position on lines representing the basal lengths of the skulls (from the posterior base of I^1 to the anterior edge of the foramen magnum notch). The transverse section was drawn through the bulla at its widest point (perpendicular to the longitudinal axis of the skull). Apparently there is no relationship between the length of the skull and the size of the bulla, a fact especially well illustrated in a skull of *?Oreodontoides curtus*, with a basal length of only 139 mm., but with a bulla larger than in an example of *Merycochoerus proprius*, with a basal length of 272 mm.

CHART 2

RANGE OF VARIATION IN *Phenacocoelus, Hypsiops, Submerycochoerus,* AND *Pseudomesoreodon*

Comparison of species, emphasizing individual and age variation in basal lengths, superior and inferior dentitions

	Skull				Dentition					
	Basal Length				P^1–M^3			P_1–M_3		
	State of Wear	No. of Examples	Range	Mean	No. of Examples	Range	Mean	No. of Examples	Range	Mean
Phenacocoelus kayi Harrison 2 specimens	M	—	—		—	—		—	—	
	M+	—	—		—	—		—	—	
	W	—	—		—	—		—	—	
	W+	2	190–198	194	2	88– 91	89	2	100–101	100
	W‡	—	—		—	—		—	—	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	
P. stouti Lower Marsland 40 specimens	M	—	—		—	—		—	—	
	M+	1	254		1	106		—	—	
	W	—	—		—	—		—	—	
	W+	2	229–243	241	2	103	105	—	—	107
	W‡	5	232–255		5	100–111		6	109–123	
	W‡+	2	240–248		4	100–108		6	111–119	
	W‡‡	2	230–240		3	102–114		4	105–118	
P. typus Harrison 5 specimens	M	—	—		—	—		—	—	
	M+	1	162		1	81		1	90	
	W	1	155		1	72		—	—	
	W+	—	—	162	—	—	78	—	—	86
	W‡	1	167		1	80		—	—	
	W‡+	1	165		1	79		1	82	
	W‡‡	—	—		—	—		—	—	
Hypsiops brachymyelis Approx. Harrison equivalent 4 specimens	M	—	—		—	—		—	—	
	M+	—	—		—	—		—	—	
	W	—	—		1	98		—	—	
	W+	1	224	222	1	105	102	1	113	113
	W‡	1	220		1	103		—	—	
	W‡+	—	—		1	105		—	—	
	W‡‡	—	—		—	—		—	—	
H. brachymelis petersoni Harrison 11 specimens	M	—	—		—	—		—	—	
	M+	—	—		—	—		—	—	
	W	—	—		2	105		1	111	
	W+	2	211–227	216	3	96–106	103	3	103–111	111
	W‡	1	219		2	105–111		2	118	
	W‡+	1	209		1	96		2	102–112	
	W‡‡	—	—		—	—		—	—	

CHART 2—*Continued*

	Skull				Dentition					
	Basal Length				P^1–M^3			P_1–M_3		
	State of Wear	No. of Examples	Range	Mean	No. of Examples	Range	Mean	No. of Examples	Range	Mean
H. breviceps	M	—	—		—	—		—	—	
Approx. Harrison	M+	—	—		—	—		—	—	
equivalent	W	1	183		1	100		1	104	
1 specimen	W+	—	—	183	—	—	100	—	—	104
	W‡	—	—		—	—		—	—	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	
H. luskensis	M	—	—		—	—		—	—	
Harrison	M+	—	—		—	—		—	—	
6 specimens	W	—	—		—	—		1	95	
	W+	1	182	180	1	88	85	1	93	92
	W‡	—	—		—	—		—	—	
	W‡+	1	178		1	82		1	87	
	W‡‡	—	—		—	—		—	—	
H. johndayensis	M	—	—		—	—		—	—	
Approx. Harrison	M+	—	—		—	—		—	—	
equivalent	W	—	—		—	—		—	—	
2 specimens	W+	—	—	229	—	—	108	—	—	
	W‡	1	229		1	108		—	—	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	
Submerycochoerus	M	—	—		—	—		—	—	
bannackensis	M+	—	—		—	—		—	—	
Approx. Harrison	W	—	—		—	—		1	127	
equivalent	W+	—	—	250	—	—	117	—	—	127
3 specimens	W‡	1	250		1	117		1	128	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	
Pseudomesoreodon	M	1	237		1	110		—	—	
rooneyi	M+	—	—		—	—		—	—	
Approx. Harrison	W	—	—		—	—		—	—	
equivalent	W+	—	—	237	—	—	110	—	—	
1 specimen	W‡	—	—		—	—		—	—	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	
?P. boulderensis	M	—	—		—	—		—	—	
Approx. Harrison	M+	—	—		—	—		—	—	
equivalent	W	—	—		—	—		—	—	
1 specimen	W+	1	287	287	1	118	118	1	129	129
	W‡	—	—		—	—		—	—	
	W‡+	—	—		—	—		—	—	
	W‡‡	—	—		—	—		—	—	

DESCRIPTION OF PHENACOCOELINAE, NEW SUBFAMILY 5[1]

THE NEW SUBFAMILY Phenacocoelinae includes the afore-mentioned *Phenacocoelus* Peterson, and *Hypsiops*, *Submerycochoerus*, and *Pseudomesoreodon*, new genera. Small to large size; skulls submesocephalic to brachycephalic; occipital region with widely spread supraoccipital wings, deeply notched at sides; deep exoccipital pits; orbits oblong in outline; tendency to anterior retraction of nasals; deep lacrimal fossae; facial vacuities usually present; ventral surface of tympanic bullae flattened to depressed; dentition small to moderately large, brachyodont to subhypsodont; P^1–P^3 usually with anterior intermediate crest; P_3 with posterior intermediate crest.

Remains of *Phenacocoelus* are known from the Harrison formation and the lower part of the Marsland; *Hypsiops*, *Submerycochoerus*, and *Pseudomesoreodon* only from the Harrison formation or from deposits of approximately the same geologic age. (See geological and geographical distribution, chart 3, p. 102.)

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

DISTINCTIVE CHARACTERS[2]

	Phenacocoelus (P. 101, figs. 1–3, 11, 13–15)	*Hypsiops* (P. 113, figs. 4–7, 9, 11–15)	*Submerycochoerus* (P. 124, figs. 8–10, 12, 13)	*Pseudomesoreodon* (P. 128, figs. 8–10, 12–15)
Anterior tip of nasals retracted to region above	Incisors to P^1	C/–P^1	P^2	?
Infraorbital foramen above	P^3–P^4	Posterior portion of P^3 to anterior portion of P^4	Anterior portion of P^4	P^4
Anterior nasal-maxilla contact above	P^1–P^3	P^2	P^3	P^2–P^3
Facial vacuity	Present and absent	Present	Present	?
Inferior border of ramus with a downward curve posterior to M_3	Slightly abrupt	Gradual	Slight	Abrupt
Limbs	Moderately robust	Moderately light	Robust	Moderately robust
Comparison of species (based on skulls)	1. *P. kayi:* larger than *P. typus;* smaller than *P. stouti;* elongated supraorbital slot-like depression	1. *H. brachymelis:* smaller than *H. johndayensis;* larger than other known forms of genus	1. *S. bannackensis:* greatly retracted nasals	1. *P. rooneyi:* smallest known form of genus
	2. *P. stouti:* largest known form of genus; true supraorbital foramen	1a. *H. brachymelis petersoni:* approximate size of *H. brachymelis*		2. *P. rolli:* slightly larger than *P. rooneyi*

[2] *Idem*, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85.

DISTINCTIVE CHARACTERS—*Continued*

Phenacocoelus (P. 101, figs. 1–3, 11, 13–15)	*Hypsiops* (P. 113, figs. 4–7, 9, 11–15)	*Submerycochoerus* (P. 124, figs. 8–10, 12, 13)	*Pseudomesoreodon* (P. 128, figs. 8–10, 12–15
3. *P. typus:* smallest known form of genus; supraorbital vacuity	2. *H. breviceps:* dwarf form; smallest known form of genus; approaching size of *H. luskensis*		3. *?P. boulderensis:* skull longer and higher than other known forms of genus
	3. *H. erythroceps:* largest known dentition of genus		
	4. *H. luskensis:* dwarf form; slightly larger than *H. breviceps*		
	5. *H. johndayensis:* most robust and largest form of genus		

I. PHENACOCOELUS[1] PETERSON

Phenacocoelus PETERSON, 1906, Ann. Carnegie Mus., vol. 4, no. 1, p. 29; 1928, Mem. Carnegie Mus., vol. 11, no. 3, p. 131. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 180.

GENOTYPE: *Phenacocoelus typus* Peterson.

CHARACTERS

SKULL: Small to medium size, basal lengths ranging from 155 to 250 mm., widths from 90 to 169 mm.; mesocephalic; low to moderately high; supraoccipital wings widely spread, protruding posteriorly, deeply notched on sides [not fan shaped as in *Brachycrus*, *Ustatochoerus*, or *Merychyus* (*Metoreodon*), but more widely spread and with less posterior projection than in *Promerycochoerus*]; deep pit on each side of medial line in exoccipital above base of paroccipital process; sagittal crest low; brain case inflated, rounded laterally, and slightly elongated anteroposteriorly; frontals moderately wide, flat to convex laterally; supraorbital foramina vary in form (see discussion following); orbit roundish to oblong in outline, looking outward and upward; zygomatic arch moderately light (see specific variation); malar moderately shallow below the orbit; lacrimal fossa large and deep, with a shelflike area below and extending anteriorly (see discussion, p. 104); muzzle slightly inflated; premaxillae joined for short distance, more so in large species; occipital condyle of moderate size; paroccipital process moderately wide at base, tapering rapidly to inferior border; bulla inflated, elongated anteroposteriorly, with flattened surface sloping from high external border to low internal border (adjacent to basioccipital region), similar to examples of *Merychyus* (*Metoreodon*); postglenoid process from moderately light to robust; posterior palate projects for short distance posterior to M^3.

MANDIBLE: Small to medium size; moderately robust (in comparison with examples of *Ticholeptus* and *Merychyus*); postsymphysis in area below anterior portion of P_3; inferior

[1] The genus *Phenacocoelus* was included under the subfamily Merycoidodontinae by Simpson, 1945, Bull. Amer. Mus. Nat. Hist., vol. 85, p. 149.

CHART 3

GEOGRAPHICAL AND GEOLOGICAL DISTRIBUTION OF *Phenacocoelus*, *Hypsiops*, *Submerycochoerus*, AND *Pseudomesoreodon*

	Harrison							Lower Marsland				
	Calif.	Mont.			Nebr.	Oreg.	Wyo.	Nebr.	S.D.	Wyo.		
	Kern Co.	Beaverhead Co.	Jefferson Co.	Silver Bow Co.	Sioux Co.	John Day Area	Niobrara Co.	Sioux Co.	Shannon Co.	Goshen Co.	Niobrara Co.	Platte Co.
Phenacocoelus kayi (1)							T[1]					
P. stouti (2)								X	X	X	X	T
P. typus (3)					T		X					
Hypsiops brachymelis (1)		X	T									
H. brachymelis petersoni (1a)					X		T					
H. breviceps (2)				T								
H. erythroceps (3)	T											
H. luskensis (4)							T					
H. johndayensis (5)						T						
Submerycochoerus bannackensis (1)		T										
Pseudomesoreodon rooneyi (1)		T										
P. rolli (2)			T									
?P. boulderensis (3)			T									

[1] T, locality of holotype (and referred specimens when known); X, referred specimens only.

border of ramus increasing gradually in depth from symphysis to a point below M_3, with a marked downward and inward curve just posterior to M_3; ascending ramus moderately high; condyle set at approximate right angle to dental series, with an internal downward slope.

DENTITION: Brachyodont (slightly more brachyodont than in *Hypsiops*); external styles of superior molars moderately prominent; superior molars have a squarish appearance from crown views; premolars slightly crowded; P^1–P^3 with anterior intermediate crest; C/ and P_1 moderately large to large.

LIMBS: Moderately robust, more so than in *Hypsiops* and *Merychyus* but less than in *Submerycochoerus* and *Merycochoerus*.

MEASUREMENTS: Tables 1 and 2; chart 4.

ILLUSTRATIONS: Figures 1–3, 11 (skulls, mandibles, and dentitions); 13 (occipital regions of skulls); 13–15 (limbs).

DISCUSSION

The genus *Phenacocoelus* was established by Peterson with *P. typus* as the genotypic species and "*P. monroensis*" as a referred

TABLE 1

Phenacocoelus PETERSON. COMPARATIVE MEASUREMENTS[1] OF SKULLS AND RAMI

	P. kayi, new species	*P. stouti*, new species	*P. typus* Peterson	
SKULL	Holotype F:A.M. 33660A	Holotype F:A.M. 44839	Holotype C.M. 1263	Referred F:A.M. 33397
Stage of wear of teeth	(w+)	(w‡)	(w)	(w‡⁺⁺)
Length (including supraoccipital crest and incisors)	218	264.5	((181))	((193))
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	198	242.5	((155))	((165))
Width (max.)	125	144.5	((90))	((123))
Width of brain case (max.)	60	73	47	55
Width, interorbital (min.)	(58)	78	((44))	52
Distance from anterior rim of orbit to anterior base of canine	91	112	—	(67)
Distance from anterior rim of orbit to supraoccipital crest	132	156	114.5	125
Length of nasal	73	92	—	(66)
Width of muzzle at infraorbital foramina	56	73	—	55
Width across canines	53	59	—	—
Length, C/–M^3 incl.	103.5	121	—	—
Length, P^1–M^3 incl.	88.5	104.5	—	79.5
Length, P^1–P^4 incl.	42.5	46	—	37.5
Length, M^1–M^3 incl.	48.5	59.5	49	45
Width of M^3 (max.)	18	22.5	—	17.5
Depth of malar below orbit	17	24	16.5	17
RAMUS		Referred F:A.M. 33361		
Stage of wear of teeth		(w‡⁺⁺)		
Length (max., including incisors)	—	217	—	(153)
Length, /C to condyle incl.	—	209	—	135
Depth of jaw under coronoid	—	100	—	—
Depth of jaw below anterior edge of M_3	(36)	38.5	—	36.5
Length, /C–M_3 incl.	107	131	—	90
Length, P_1–M_3 incl.	100	119	—	82.5
Length, P_1–P_4 incl.	45	51	—	36.5
Length, M_1–M_3 incl.	55	68	—	46.5

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

species. Only forms which had a frontal or supraorbital vacuity were to be included in the genus. The referred species, however, was known only from a mandible and limb. Schultz and Falkenbach[1] with supplementary evidence at hand, referred the holotype of "*P. monroensis*" to *Merychyus siouxensis*.

[1] 1947, p. 223, figs. 7, 16.

Additional material in the Frick collection indicates the presence of two new undescribed species of *Phenacocoelus*. The three forms apparently belong to a single phylogenetic line and differ from one another chiefly as follows: *P. typus* Peterson (from the Harrison formation), small size with a definite oblong supraorbital vacuity; *P. kayi*, new species (Harrison), medium size with a supraorbital fora-

TABLE 2

Phenacocoelus PETERSON. COMPARATIVE MEASUREMENTS[1] OF SKELETAL ELEMENTS

	P. kayi, new species	*P. stouti*, new species	*P. typus* Peterson	
	Referred F:A.M. 33660A–B	Referred F:A.M. 34473	Holotype C.M. 1263	Referred F:A.M. 33397
Length of humerus (articular)	149	159	127	—
Length of radius (articular)	128	132.5	107.5	—
Length of ulna (max.)	—	184.5	140	—
Length of metacarpal III (max.)	61	65	55.5	—
Length of femur (articular)	166.5	—	—	—
Length of tibia (articular)	152.5	(184)	—	111.5
Length of metatarsal III (max.)	—	69	57	—
Length of calcaneum (max.)	55.5	62	47	(44)

[1] ( ), Approximate. All measurements in millimeters.

men at posterior end of an elongated slot-like depression, and a suggestion of a groove extending forward and downward from it to the facial vacuity; *P. stouti*, new species (lower Marsland), large size with a round supraorbital foramen with a prominent groove extending forward and downward on the side of the face to approximately the anterior border of the large lacrimal fossa.

The close relationship of the three species and the evident progressive changes in the frontal vacuity, as well as the size gradation, necessitate a redescription of the generic characters.

An outstanding point of interest is the apparent affinities of *Phenacocoelus* and the new genus *Hypsiops* (p. 113). The small species of both genera have important characters in common.

Phenacocoelus typus has a zygomatic arch which differs from that of the other two species of *Phenococoelus* but which is similar to the arch of the various species of *Hypsiops*, excepting *H. luskensis*. The arch of the latter form differs from that of other species of its genus, but is similar to that of *P. kayi* and of *P. stouti* (see figs. 1–3). This may indicate that the two small species (*P. typus* and *H. luskensis*) lived at a time that followed closely the branching of the ancestral stock into two separate lines. Perhaps both species represent dwarf forms of their respective genera.

In *Phenacocoelus* the large lacrimal fossa is included in a shelf-like surface anterior to the orbit and above the cheek teeth. In *P. typus* and *P. kayi* a facial vacuity also is included in this area but is lacking in *P. stouti*. The shelf-like area seems to have been caused by the enlargement of the lacrimal fossa, and somewhat resembles a like area on examples of *Brachycrus*.[2] In the latter genus, however, the infraorbital foramen is incorporated in the shelf-like area, whereas in *Phenacocoelus* the foramen is below the shelf.

Peterson[3] in the original description of *Phenacocoelus* stated: "The genus belongs to the family Agriochoeridae, revealing affinities to *Leptauchenia* and *Cyclopidius*."

This conclusion was based, perhaps, on the presence of the frontal vacuities in *Phenacocoelus typus* and the large facial vacuities of *Leptauchenia* and *Cyclopidius*, as well as the large inflated bullae of all three genera. It is true that all three forms possess large bullae, but the bullae of *Phenacocoelus* are distinct from those of the other two genera. (See discussion of the bullae, p. 96.)

At a later date, Peterson[4] further stated concerning the genus *Phenacocoelus:* ". . . the external border of the frontal opening is partly preserved. This opening is an extraordinary feature of this genus and most nearly recalls that of *Leptauchenia* and *Cyclo-*

[2] Schultz and Falkenbach, 1940, p. 218.
[3] 1906, p. 30.
[4] 1928, p. 134.

pidius. The vacuity extends farther back than in *Leptauchenia* and is equally as far back as in the latter genus, but does not, however, extend so far anteriorly, and is very much smaller in size. Its function was no doubt the same as that in the genera mentioned. "

The present writers doubt that the frontal vacuity of *P. typus* had the same function as the large facial vacuities of *Leptauchenia* and *Cyclopidius*, but rather had the same special purpose as the supraorbital foramen of other oreodonts. The facial vacuity of *P. typus* is comparatively small and is confined to the lacrimal region, while in *Leptauchenia* and *Cyclopidius* the facial vacuities are large and invade the frontal and nasal bones.

The vacuities of *Phenacocoelus typus* are best described by Thorpe[1]: "The facial vacuities are much smaller than in *Leptauchenia* and lie mainly in the lacrimal and maxillary bones. They do not invade the nasal bones and probably affect the frontals very little, if at all. They are narrow, and their main axis is anteroposterior. There are also narrow, elongate frontal vacuities, one on either side of the sagittal suture, extending from a point just in advance of the supraorbital foramina to the nasofrontal suture."

In additional comparisons of *Phenacocoelus* and its possible relationship with *Merycoidodon*, *Leptauchenia*, and *Cyclopidius*, Peterson[2] wrote: "At the present time it is, however, difficult to point out the phylogenetic ancestry of *Phenacocoelus* with any degree of certainty. In many respects the Oligocene genus *Merycoidodon* is sufficiently closely related to be regarded as in the line leading to *Phenacocoelus* . . . a critical and detailed comparison of the bony structure of these two genera points rather to parallelism than to direct phylogenetic relationship. . . .

"*Phenacocoelus* and the phylum of *Leptauchenia-Cylcopidius* have no especially close relationship, but parallel one another more closely. This is indicated by the many cranial similarities; *i.e.*, the fronto-nasal vacuities, the position of the orbit, the size of the tympanic bulla. . . .

"Many features displayed in the osteology of *Phenacocoelus*, especially those of the cranium, point to relationship with *Leptauchenia* and *Cyclopidius*, but the specialization of the latter genera shows, on the whole, a greater separation from the earlier types of the family than is the case in *Phenacocoelus*."

One might conceive the idea that the frontal and facial vacuities of *P. typus* could have evolved into the large facial vacuities found in the *Leptauchenia-Cyclopidius* group, but of course the geological occurrences of the forms in question do not support this theory. The remains of *Leptauchenia* and *Cyclopidius* are restricted to deposits (Brule to Monroe Creek) which are earlier in age than those (Harrison) containing examples of *P. typus*.

The small frontal vacuities present in *P. typus* appear to have no relationship to the large facial vacuities of *Leptauchenia* and *Cyclopidius*. In the latter two genera, the vacuities have the same shape and comparative size in all species, while in *Phenacocoelus* the frontal vacuities vary (completely lacking in *P. stouti*). It is obvious that species from one line would have some important characters in common with species belonging to other lines within the same family. These characters, however, may appear at different geological periods but would not necessarily indicate close affinities between the groups.

The bullae of *Phenacocoelus* and those of the *Leptauchenia-Cyclopidius* group have some characteristics in common. In the former, however, the bullae are high, narrow, and elongated anteroposteriorly, showing some change in development from the Harrison species (*P. kayi*) to those (*P. stouti*) from the lower Marsland. In the *Leptauchenia-Cyclopidius* line the bullae are high and round, and no noticeable change, except for size, is apparent from the first appearance of this group in the Brule deposits to the last known occurrence in the Monroe Creek. In other words the bullae of *Leptauchenia* and *Cyclopidius* had already reached an advanced point of specialization at the time of their first known appearance. In other oreodont phyla there are examples where the bullae developed from a very small type, gradually becoming inflated, and finally very large and almost spherical in shape (see discussion of the bullae, p. 96).

[1] 1937, p. 182.
[2] 1928, pp. 165–166.

In the genus *Phenacocoelus*, the rate of development appears to have been very rapid from the first appearance of *P. kayi* during the Harrison to the time of extinction of *P. stouti* during the lower Marsland. This development was most noticeable in the increase in size, and in the changes from the elongated, narrow, slot-like, supraorbital foramen and a prominent facial vacuity (in *P. kayi*) to the normal, round, supraorbital foramen and the absence of the facial vacuity (in *P. stouti*).

Distribution

Three species of *Phenacocoelus* are known from the lower and middle Miocene (Harrison and lower Marsland formations) of Nebraska, South Dakota, and Wyoming. (See geological and geographical distribution, chart 3, p. 102.)

Summary of Species and Types

Three species of *Phenacocoelus* from five lower and middle Miocene localities are here recorded:

1. *Phenacocoelus kayi*, new species, from Niobrara County, Wyoming. (Harrison.)

Holotype: Skull and mandible, F:A.M. 33660A. Figures 1–3, 11.

2. *Phenacocoelus stouti*, new species, from Platte County, Wyoming; referred remains from Goshen and Niobrara counties, Wyoming, Sioux County, Nebraska, and Shannon County, South Dakota. (Lower Marsland.)

Holotype: Skull, F:A.M. 44839. Figures 1–3, 13.

3. *Phenacocoelus typus* Peterson, from Sioux County, Nebraska; referred remains from Niobrara County, Wyoming. (Harrison.)

Hololype: Partial skull and skeleton, C.M. 1263. Figures 1–3, 13.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PHENACOCOELUS

Total available specimens: 48

1. Phenacocoelus kayi,[1] new species

From the Harrison formation, Niobrara County, Wyoming

Description

Skull: Intermediate in size between *P. typus* and *P. stouti*; frontals slightly rounded laterally; nasals retracted anteriorly to a point above posterior portion of P^1, with greater retraction than in examples of *P. typus;* anterior nasal-maxilla contact above the posterior portion of P^2; supraorbital foramen at posterior end of a deep, narrow, elongated, slot-like depression (not an oblong vacuity as in *P. typus* or a round foramen as in *P. stouti*), with suggestion of a groove extending forward and downward from it to facial vacuity; zygomatic arch with a gradual rise posteriorly, extending to a point above posterior border of postglenoid process; infraorbital foramen above posterior portion of P^3; facial vacuity[2]; bulla with inferior surface more depressed towards basioccipital than in *P. typus;* postglenoid process moderately heavy with sloping external border.

Mandible: Intermediate in size between examples of *P. typus* and *P. stouti;* approximately equal in size to examples of *Hypsiops luskensis.*

Dentition: Superior and inferior series intermediate in over-all length between *P. typus* and *P. stouti*, approximately equal in size to examples of *H. luskensis;* C/ and P_1 large; axis of P^1–P^3 parallel to alveolar border; P_2 and P_3 set at slight angle to alveolar border; P_2 with weak posterior intermediate crest; P_3 and P_4 each with moderately prominent posterior intermediate crest.

Limbs: Decidely longer than examples of *P. typus;* lighter, but approximately same length as examples of *P. stouti.*

Measurements: Tables 1 and 2.

Illustrations: Figures 1–3, 11, 13–15.

[1] Named in honor of Dr. J. LeRoy Kay, Curator of Paleontology, Carnegie Museum of Pittsburgh.

[2] The known specimens of this species are damaged in the area of the facial vacuity, but the rounded surface of the edge of the break strongly suggests the presence of the vacuity.

Discussion

The proposed new species appears to have given rise to *P. stouti* from the lower Marsland. It differs from that species in its smaller size, and in having a supraorbital foramen at the posterior end of a long, narrow, slot-like depression, as well as in possessing a facial vacuity. *Phenacocoelus kayi* differs from *P. typus* in that it is larger in size, possesses a different type of zygomatic arch, and lacks the oblong supraorbital vacuity.

Phenacocoelus kayi is known from two associated specimens (F:A.M. 33660A-B) found in one field block. The holotype (F:A.M. 33660A) is well preserved, while the referred individual (F:A.M. 33660B) is badly crushed and does not add any information to the description of the species. The limbs found with the two individuals were not articulated, and it is impossible to tell which limbs may belong to the holotype.

Phenacocoelus kayi and *P. typus* are both found in the same formation (Harrison), but the latter appears to have been a dwarf form while *P. kayi*, the larger species, seems to have given rise to *P. stouti*. While the remains of the two species have been recorded from the same formation, they have not been found directly associated in the same local areas. It is possible that the known examples of *P. typus* came from a different zone in the Harrison than did those of *P. kayi*. Unfortunately the locality where the *P. kayi* specimens were found is a small, isolated exposure without enough stratigraphic evidence present to warrant detailed correlation.

Two specimens are here recorded:

HOLOTYPE

Skull with I^2–M^3 and partial mandible with I_1–I_3 alv.[1] and /C–M_3. (W+)[2] — F:A.M. 33660A — From the Harrison formation, 4 mi. E. and 2 mi. S. of Lusk, Niobrara County, Wyoming; collected by Everett De Groot, 1935. Figs. 1–3, 11

REFERRED, ASSOCIATED WITH HOLOTYPE

Partial skull with I^3–M^3 (P^3 br., P^4–M^1 absent and M^2 br.) and partial mandible with I_3–M_3 . . . . . (W+) — F:A.M. 33660B

SKELETAL ELEMENTS

3 partial scapulae, 4 partial humeri, 3 radii (1 partial), 3 partial ulnae, partial manus, 4 femora (2 partial), 4 tibiae (2 partial), 3 partial pedes, astragalus, pelvis, vertebrae, and ribs. Figs. 13–15 . . . . . — F:A.M. 33660A–B

The limb and skeletal elements were found associated with both the holotype and referred skulls and mandibles. There was no articulation, so there is a question as to which specimen the limbs belong.

[1] Abbreviations used in descriptions: alv., alveolus or alveoli; br., broken; erupt., erupting; rt., root or roots.
[2] Stage of wear of teeth; (I) immature; (M), mature; (W), worn.

2. **Phenacocoelus stouti**,[3] new species

From the lower Marsland formation, Platte County, Wyoming; referred specimens from Goshen and Niobrara counties, Wyoming, Sioux County, Nebraska, and Shannon County, South Dakota

Description

Skull: Largest known form of the genus; frontals rounded laterally; nasal retracted anteriorly to a point above anterior portion of P^1; anterior nasal-maxilla contact in region above P^2; typical round supraorbital foramen present (not an oblong vacuity as in *P. typus* or elongated slot-like depression as in *P. kayi*), with prominent groove extending forward and downward on side of face to approximately the anterior border of large lacrimal fossa; zygomatic arch moderately heavy, with gradual rise posteriorly, extending to and above posterior border of postglenoid process (similar to arch of *P. kayi*, not U-shaped in outline as in *P. typus*);

[3] Named in honor of Thompson M. Stout, Research Associate of the University of Nebraska State Museum and Instructor, Department of Geology.

CHART 4

VARIATION IN *Phenacocoelus stouti*

Comparison of skull measurements,[1] of associated individuals of a single species

F:A.M.	Stage of Wear of Teeth	Skull				Dentition			
		Basal Length of Skull	Width of Skull	Depth of Malar Below Orbit	Length of Nasal	Length C/–M^3	Length P^1–M^3	Length P^1–P^4	Length M^1–M^3
44835	W+	(257)	144	25	—	118	103	46.5	58.5
44836	W‡+	((274))	167.5	29.5	96	124.5	108.5	44.5	63.5
44837	W‡	271.5	153	28.5	89	119.5	104.5	46	62.5
44838	M+	—	(153)	27.5	92.5	122	106.5	45.5	63
44839	W‡	264.5	144.5	24	92	121	104.5	46	59.5
Mean[2]		267	152	27	92	121	105	45	61

[1] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[2] The mean is weighted.

malar deeper than in other species of genus; infraorbital foramen above P^4, enlarged; bulla similar to that of *P. kayi*, with inferior surface more depressed towards basioccipital than in *P. typus;* postglenoid process robust, wide transversely.

MANDIBLE: Largest of genus; similar in shape to that of *P. kayi*; ramus shallower than examples of *P. typus;* inferior border with more downward curve below M_3 than in other species of genus.

DENTITION: Superior and inferior series longer and more robust than in other species of *Phenacocoelus;* C/ and P_1 moderately large and heavy; premolars not crowded, tendency to slight diastema between P^1 and P^2; P^1 usually set at slight angle to alveolar border; P_1–P_3 each set at slight angle to alveolar border; weak posterior intermediate crest developed on P_2.

LIMBS: Approximately same length as examples of *P. kayi;* considerably longer than those of *P. typus*; more robust than in either of these two species.

MEASUREMENTS: Tables 1 and 2; chart 4.

ILLUSTRATIONS: Figures 1–3, 11, 13–15.

DISCUSSION

The proposed new species, the largest known of the genus, differs from *P. kayi* and *P. typus* chiefly in size, and also in the presence of a round supraorbital foramen and in the absence of a facial vacuity. In *P. kayi* the supraorbital foramen is at the posterior end of a long, deep, slot-like depression, while in *P. typus* an oblong supraorbital vacuity is present, and in both of the latter species a facial vacuity is evidenced. It is here considered that *P. kayi* gave rise to *P. stouti.*

Of the three known species of *Phenococoelus*, *P. stouti* is the best represented in the collections. The associated material from the Roll Quarry[3] gives some evidence of the individual variation within the species. (See chart 4.)

Examples of *P. stouti* have been found only in the lower Marsland, and there is no evidence of *Phenacocoelus* in deposits of later age.

The F:A.M. material was collected by Gene Roll, John Lynch, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1931–1941.

Forty specimens are here recorded:

[3] Named in honor of Gene Roll who was a member of the various Frick Laboratory field parties from 1936 to 1941. Roll lost his life during World War II in the service of his country in the South Pacific.

HOLOTYPE

Skull with I^1–I^2 alv. and I^3–M^3. (w‡) F:A.M. 44839 From the lower part of the Marsland formation, Roll Quarry, 2 mi. S. of Guernsey, Platte County, Wyoming; collected by Gene Roll, 1940
Figs. 1–3, 13

REFERRED FROM (A) TYPE LOCALITY, PLATTE COUNTY, (B) GOSHEN, AND (C) NIOBRARA COUNTIES, WYOMING; (D) SIOUX COUNTY, NEBRASKA; AND (E) SHANNON COUNTY, SOUTH DAKOTA

A. FROM TYPE LOCALITY, PLATTE COUNTY, WYOMING, 1940

4 SKULLS

		F:A.M.
3 skulls with		
I^1–I^3 alv. and C/–M^3 (lacking anterior of nasals)	(w+)	44835
I^1–M^3	(w‡+)	44836
I^1–M^3	(w‡)	44837
Partial skull with I^2–I^3 alv. and C/–M^3	(M+)	44838

MANDIBLE

		F:A.M.
Partial mandible with I_1–P_1 alv. and P_2–M_3	(w‡+)	44899

8 PARTIAL MANDIBULAR RAMI

4 partial right rami with		
P_3(alv.)–M_3(br.) (P_4 br.)	(w+)	44841A
The above specimen may belong to the same individual as F:A.M. 44841B.		
I_1–M_3 (/C alv.)	(w‡)	44842
P_1–P_4	(M+)	44843
P_1 is much wider anteroposteriorly than average examples of this species, and except for size, is similar in structure to P_2.		
M_1–M_3	(w+)	44844
4 partial left rami with		
P_4–M_3	(w‡)	44841B
The above specimen may belong to the same individual as F:A.M. 44841A.		
/C(alv.)–M_3	(w‡)	44845
P_1(br.)–M_3	(w‡+)	44846
P_2–M_3	(w‡)	44847

3 SKELETAL ELEMENTS

Radius		44848
Calcaneum		44849
Partial pes		44850

FROM 28 FEET ABOVE ROLL QUARRY:

SKULL AND RAMUS

Partial skull with C/(rt.)–M^3 (P^4 rt.) and partial right ramus with I_2–M_3(br.) (I_3 alv. and P_1 br.)	(w‡‡)	44840

FROM 2 MILES WEST OF GUERNSEY:

PARTIAL MANDIBLE

Partial mandible with P_1(br.)–M_3	(w‡+)	44879

B. FROM GOSHEN COUNTY, WYOMING, 1931–1940

FROM JAY EM AREA (INCLUDES AREAS FROM 16 MI. TO 22 MI. S. E. OF LUSK, EAST SIDE OF U. S. HIGHWAY NO. 85):

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

		F:A.M.
Skull with I^1–M^3, mandible with I_1–M_3, partial scapula, partial humerus, 2 radii, 2 partial ulnae, 2 partial manus and partial pes. Fig. 11 (in part)	(w‡⁺)	33361
Anterior inferior portion of skull with I^1–M^3, partial mandible with I_1–M_3, 2 partial scapulae, partial humerus, radius, ulna, partial manus, tibia, astragalus, calcaneum, 2 pedes, partial pelvis, vertebrae, ribs, and skeletal fragments. Figs. 13–15 (in part)	(w‡⁺)	34473
Skull with I^1–M^3 (P^2 alv.), partial mandible with I_1(rt.)–M_3 (P_1 br.), atlas, and skeletal fragments	(w‡‡)	37581

SKULL AND MANDIBLE

Anterior portion of skull with I^1–M^3(br.) and partial mandible with I_1–M_3	(w‡‡)	44898

SKULL

Skull with I^1–M^3	(w‡⁺)	33319

2 MAXILLAE

Partial right maxilla with P^4–M^2	(w+)	44903
Partial left maxilla with M^1–M^2	(w)	44881

MANDIBLE

		F.A.M.
Partial mandible with I_1–M_3	(w+)	44901

FROM JAY EM CREEK, COLLECTED BY T. F. OLCOTT, 1906:

SKULL AND MANDIBULAR RAMUS

		C.N.H.M.
Skull with I^1–I^2 alv. and I^3–M^3 and partial left ramus with I_1–M_3 (/C br.)	(w‡)	P12229

FROM RAWHIDE CREEK, COLLECTED BY J. B. ABBOT, 1906:

PARTIAL SKULL AND MANDIBLE

Partial skull with P^2–M^3 and mandible with I_2–M_3	(w‡⁺)	P12251

B′. FROM SAND GULCH (NEAR WOLF RANCH), GOSHEN COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with I^1(alv.)–M^3 (I^2 rt. and P^2–P^4 erupt.), partial mandible with I_1–M_2 (P_2–P_4 erupt.), and partial manus. Fig. 11 (in part)	(–M)	44900

MANDIBULAR RAMUS

Partial right ramus with P_1(alv.)–M_2(br.)	(w+)	44856

C. FROM NIOBRARA COUNTY, WYOMING, 1933–1935

FROM ROYAL VALLEY, 9 MI. S. OF LUSK:

2 ASSOCIATED INDIVIDUALS

		F:A.M.
Partial skull with I^3–M^3, mandible with I_3–M_3, partial scapula, radius, partial ulna, 2 partial tibiae, astragalus, 2 calcanea, and atlas	(w‡)	33646
Immature, partial mandible with dI_1–dP_4–M_1 (P_1 germ), and atlas	(I)	33646A

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

SKULL, MANDIBLE, AND VERTEBRAE

Partial skull with M^1(alv.)–M^3, partial mandible with M_1(br.)–M_3, and vertebrae	(w‡⁺)	44834

FROM NEAR VAN TASSEL:

MANDIBLE

		F:A.M.
Partial mandible with I_1–/C alv. and P_1–M_3	(w‡)	44831

The exact location of the above specimen is unknown, but the matrix is typical of the Marsland beds southeast of Van Tassel.

D. FROM SOUTH OF HARRISON, SIOUX COUNTY, NEBRASKA, 1937

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Anterior portion of skull with I^1–M^3, partial mandible with I_1–M_3, partial scapula, partial radius, partial ulna, partial tibia, and astragalus	(w‡)	44851

2 PARTIAL SKULLS

Posterior portion of skull with M^2–M^3	(w‡‡)	44832
Anterior right side of skull with C/–M^2(br.)	(w+)	44902

MAXILLA AND MANDIBLE

Left maxilla with P^2(br.)–M^3 and partial mandible with /C(rt.)–M_3 (P_2 rt.) .	(w‡‡)	44877

E. FROM PORCUPINE CREEK, SHANNON COUNTY, SOUTH DAKOTA

(Collected by Albert Thomson, 1906)

SKULL		A.M.
Skull with I^1–I^3 alv. and C/–M^3.	(w+)	12969

3. **Phenacocoelus typus** Peterson

From the Harrison formation, Sioux County, Nebraska; and referred specimens from Niobrara County, Wyoming

Phenacocoelus typus PETERSON, 1906, Ann. Carnegie Mus., vol. 4, no. 1, p. 29, figs. 4–5; 1928, Mem. Carnegie Mus., vol. 11, no. 3, p. 131, pls. 16–19. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 182, figs. 132–136; pl. 43, fig. 2.

CHARACTERS

SKULL: Smaller than those of other species of genus; frontals rather flat with depressed area in supraorbital vacuity region; nasals not noticeably retracted; anterior nasal-maxilla contact in area above P^1, oblong supraorbital vacuity same position as elongated slot-like depression in *P. kayi* and the supraorbital foramen in *P. stouti;* zygomatic arch light, with slight inward curve below posterior border of orbit (more U-shaped from side view than in *P. kayi* or *P. stouti*, more like *Hypsiops brachymelis petersoni* in this respect); posterior border of zygomatic arch above anterior border of postglenoid process, not extending so far posteriorly as in other species of genus; infraorbital foramen above middle of P^3; facial vacuity present; bulla more inflated in *P. kayi* and *P. stouti;* palate more oval in outline than other known forms of genus; postglenoid process moderately heavy but lighter and with steeper incline on external border than in other two species of genus.

MANDIBLE: Smaller than those of other species of genus; ramus deep for size of skull (deeper than in examples of *P. kayi* and *P. stouti*); inferior border with less suggestion of downward curve below and posterior to M_3 than in latter species.

DENTITION: Series shorter than in other species of genus; C/ and P_1 moderately large and heavy; premolars crowded; P^1 and P^2 set at slight angle to alveolar border; P_1–P_3 less crowded than in other two species but slightly overlapping and nearly parallel to the alveolar border; slight suggestion of posterior intermediate crest on P_2 (P_3 worn in available material, and posterior intermediate crest not present).

LIMBS: Short and comparatively robust; considerably smaller than examples of *P. kayi* and *Merychyus siouxensis.*

MEASUREMENTS: Tables 1 and 2.

ILLUSTRATIONS: Figures 1–3, 11, 13, 15.

DISCUSSION

Phenacocoelus typus, the genotypic species, has been thoroughly discussed and described by Peterson.[1] The skull lengths of this form approximate those of *Merychyus siouxensis*, from the Harrison, but the skull of *P. typus* differs from those of *Merychyus* in having less height and in possessing a supraorbital vacuity and a very large, deep, lacrimal fossa. The ramus of *P. typus* is considerably heavier and deeper than in *Merychyus*, while the limbs are approximately the same length as the smallest examples of the latter genus, but decidedly more robust.

Peterson, in his 1906 and 1928 reports, considered that both *P. typus* and "*P. mon-*

[1] 1906; 1928.

roensis" were restricted to the "upper Monroe Creek Beds." The latter species, however, was placed in synonymy with *Merychyus siouxensis* by Schultz and Falkenbach (see discussion, p. 103), and the cited "upper Monroe Creek Beds" were considered as part of the Harrison formation. The difference of opinion between Peterson and the writers concerning the geologic occurrence of *P. typus* may be due to the fact that Peterson considered that the lower part of the Harrison was part of the Monroe Creek. At the time that Peterson published concerning *P. typus* there was much confusion as to what actually constituted the Harrison.[1] Most workers unfortunately did not follow Hatcher's[2] original description of the Harrison when they were in the field. The present writers consider that *P. typus*, *M. siouxensis* (including "*P. monroensis*"), and *Hypsiops luskensis* are all restricted to the Harrison and that none of these species has actually been collected from the Monroe Creek.

The field location of the *P. typus* material in the Carnegie Museum was given by Peterson (1906) as "at the head of Squaw Creek" and (1928) "near the head of Squaw Creek." According to the catalogue of the Carnegie Museum, the holotype and a referred specimen came from the "Head of Warbonnet Creek," and other referred specimens from "Squaw Butte" and "Squaw Creek." This, perhaps, is of little importance since the various localities are along the same escarpment, but the fact that "*P. monroensis*" Peterson (=*Merychyus siouxensis*) also came from the same area and beds strengthens the conclusion that the deposits are Harrison. The latter species is known only from the Harrison.

Peterson[3] in the original description stated that the nasals greatly overhang in front. In the illustration, the nasals of the holotype do extend anteriorly beyond the incisors, but it should be noted that the nasal region of the skull is entirely restored.

Later, Peterson[4] gave a thorough description of the species and stated concerning the nasals: "From the illustration (Pl. XVII, fig. 11) it is seen that they greatly extend in front, more or less as in *Promerycochoerus carrikeri* . . . "

In a discussion of the same species, Thorpe[5] added: "The nasal bones are unreduced, extending forward nearly to a point above the incisors."

The present writers agree with Thorpe that the nasals have slight, if any, retraction.

Peterson's[6] illustration of the skull, C.M. 1276, shows a supraorbital foramen as well as a supraorbital vacuity. The holotype and other referred specimens, however, lack the additional foramen.

The F:A.M. specimen was collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1931. The specimen came from the Harrison formation north of Keeline, Niobrara County, Wyoming, along the same escarpment (Pine Ridge) from which Peterson's material was collected (in Nebraska). In the Nebraska area the Monroe Creek formation is present, but very little material has been secured from it because of the almost perpendicular exposures. Along this same ridge in the Lusk, Wyoming, area, the Monroe Creek formation is absent.

Five specimens are here recorded:

HOLOTYPE

Partial skull with C/(rt.)–M^3 (P^1 absent, only external portions of P^2–M^2) and most of skeleton. (w)

C.M. 1263

From the Harrison formation, head of Warbonnet Creek, Sioux County, Nebraska; collected by O. A. Peterson, 1904

Figured by Peterson, 1906, figs. 4–5; 1928, pl. 16, figs. 1–30 and 32–39; pl. 17, figs. 5–10; pl. 19; Thorpe, 1937, fig. 132; pl. 43, fig. 2

This report, figs. 1–3, 13

[1] Schultz, 1938, Amer. Jour. Sci., ser. 5, vol. 35, p. 441.

[2] 1902, Proc. Amer. Phil. Soc. vol. 41, p. 113.

[3] 1906, p. 30, fig. 4.

[4] 1928, p. 136, pl. 17, fig. 11.

[5] 1937, p. 182.

[6] 1928, pl. 17, fig. 11.

REFERRED FROM (A) SIOUX COUNTY, NEBRASKA; AND (B) NIOBRARA COUNTY, WYOMING

A. FROM SIOUX COUNTY, NEBRASKA

(Collected by O. A. Peterson, 1904)

2 SKULLS AND MANDIBULAR RAMI

Partial, crushed skull with C/–M^3 and partial ramus with P_3–M_3. (w)	C.M. 1278	From the head of Squaw Creek Figured by Peterson, 1928, pl. 18, figs. 12–13
Partial skull with I^3–M^3 and mandible with P_1–M_3. (M+)	1335	From the head of Warbonnet Creek Figured by Peterson, 1928, pl. 16, fig. 31; pl. 17, figs. 1–2; Thorpe, 1937, figs. 135–136

SKULL

Skull with I^2–I^3 alv. and C–M^3. (w+)	C.M. 1276	From Squaw Butte Figured by Peterson, 1928, pl. 17, figs. 11–12; Thorpe, 1937, figs. 133–134

Supraorbital foramen, as well as supraorbital vacuity, present. This specimen was one of Peterson's paratypes of *P. typus*.

B. FROM NORTH OF KEELINE, NIOBRARA COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull (lacking premaxillae) with C/(alv.)–M^3, partial mandible with I_1(alv.)–M_3, tibia, and calcaneum. Figs. 1–3, 11, 15	(w‡⁺⁺)	F:A.M. 33397

II. HYPSIOPS, NEW GENUS

GENOTYPE: *Hypsiops brachymelis* (Douglass).

DESCRIPTION

SKULL: Size medium, basal lengths ranging from 199 to 265 mm., widths from 111 to 161 mm.; mesocephalic to brachycephalic; high; supraoccipital wings widely spread and protruding posteriorly, notched on sides; supraoccipital wings not fan shaped as in *Brachycrus*, *Merycochoerus*, *Ustatochoerus*, *Ticholeptus*, and *Merychyus* (*Metoreodon*), similar to *Phenacocoelus*, but with less lateral spread; deep pit on each side of medial line in exoccipital above base of paroccipital process; sagittal crest moderately prominent, higher than in examples of *Phenacocoelus;* brain case inflated, narrow posteriorly; frontals moderately wide above orbits, laterally rounded as in *Phenacocoelus;* nasals moderately robust, with anterior retraction; supraorbital foramen with slight to moderately prominent groove extending anteriorly; orbit oblong vertically in outline; zygomatic arch moderately light; zygomatic arch with slight notch (or inward curve) on external surface below and posterior to orbit; malar moderately deep to deep below orbit with an angular protuberance on anterior, inferior border (less prominent than in *Submerycochoerus);* lacrimal fossa large and deep (similar to examples of *Phenacocoelus);* facial vacuity present (see following discussion); small depressed area above premolar region; premaxillae joined for short distance; occipital condyle of moderate size; paroccipital process wide at base with a marked tapering to a flattened tip; bulla inflated but semi-depressed (more so than in examples of *Phenacocoelus*, less so than in *Pseudomesoreodon);* postglenoid process moderately high and robust; posterior palate projecting posteriorly beyond M^3 for a greater distance than in *Phenacocoelus*.

MANDIBLE: Moderately heavy; postsymphysis usually below P_3; ramus moderately shallow for height of skull, increasing gradually in depth from symphysis to point below M_3, with gradual downward and inward curve extending posteriorly from M_3; condyle set approximately at right angle to axis of dental series with slight downward internal slope (latter not so great as in *Phenacocoelus*).

DENTITION: Brachyodont to subhypsodont

TABLE 3

Hypsiops, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKULLS AND RAMI

	H. brachymelis (Douglass)	*H. brachymelis petersoni* (Loomis)		*H. breviceps* (Douglass)	*H. erythroceps* (Stock)	*H. luskensis*, new species	*H. johndayensis*, new species
SKULL	Holotype A.M. 9731	Holotype A.C. 22–656	Referred F:A.M. 33313	Holotype C.M. 1191	Holotype C.I.T. 486	Holotype F:A.M. 44853A	Holotype C.I.T. 3503
Stage of wear of teeth	(w+)	(w+)	(w+)	(w)	(w+)	(w+)	(w‡)
Length (including supraoccipital crest of incisors)	253	234	246	199	—	206	(265)
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	224	227	211	183.5	—	182	229.5
Width (max.)	138.5	(160)	142	138.5	—	111	161
Width of brain case (max.)	62	(66)	61	56.5	—	58.5	74
Width, interorbital (min.)	70	—	71	65	—	49.5	79.5
Distance from anterior rim of orbit to anterior base of canine	107	(103)	102	81	—	81	104
Distance from anterior rim of orbit to supraoccipital crest	152	145.5	147	122	—	133	(173)
Length of nasal	81.5	83	85.5	—	—	71.5	(98)
Width of muzzle at infraorbital foramina	63	—	61	55.5	—	55.5	78
Width across canines	49	—	(52)	44	—	37.5	—
Length, C/–M^3 incl.	122.5	122	115.5	110	—	100	125
Length, P^1–M^3 incl.	105	106	100	100	—	88.5	108
Length, P^1–P^4 incl.	48	46.5	43.5	41.5	61	38.5	48
Length, M^1–M^3 incl.	62	60.5	58.5	62.5	—	51.5	60
Width of M^3 (max.)	22.5	—	24	22	—	20	24.5
Depth of malar below orbit	32	23.5	29	21.5	—	21	27.5
RAMUS							
Length (max., including incisors)	208	198	194	186	—	172.5	—
Length, /C to condyle incl.	193	183	184	166	—	150.5	—
Depth of jaw under coronoid	104.5	(102)	96	98	—	86	117.5
Depth of jaw below anterior edge of M_3	40	41	44	38	—	36	48
Length, /C–M_3 incl.	124.5	(120)	119	112.5	—	102	—
Length, P_1–M_3 incl.	113	111.5	110	104	—	93.5	—
Length, P_1–P_4 incl.	49.5	50	46	43.5	—	40	—
Length, M_1–M_3 incl.	64.5	61.5	65	62.5	—	53.5	67.5

[1] ( ), Approximate. All measurements in millimeters.

TABLE 4

Hypsiops, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKELETAL ELEMENTS

	H. brachymelis (Douglass)	*H. brachymelis petersoni* (Loomis)	*H. breviceps* (Douglass)	*H. luskensis*, new species	
	Holotype C.M. 9731	Holotype A.C. 22–656	Holotype C.M. 1191	Referred F:A.M. 44853C	Referred F:A.M. 44853D
Length of humerus (articular)	157	(152)	143	162	—
Length of radius (articular)	126	(120)	115.5	131.5	—
Length of ulna (max.)	((152))	154	—	—	—
Length of metacarpal III (max.)	66	(61)	—	66.5	54.5
Length of femur (articular)	177	(163)	—	179	—
Length of tibia (articular)	—	((156))	148.5	151	135
Length of metatarsal III (max.)	62.5	((69))	—	74	54
Length of calcaneum (max.)	62.5	55	59.5	59.5	—

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

(slightly longer crowned than in examples of *Phenacocoelus*); external styles of superior molars moderately prominent, premolars slightly crowded; C/ and P_1 large; P^1 and P^2 usually set at slight angle to alveolar border; P^1–P^3 usually with anterior intermediate crest.

LIMBS: Moderately light, but less so than in *Merychyus;* approximately equal in length to, to longer than in, *Phenacocoelus*, and somewhat lighter.

MEASUREMENTS: Tables 3 and 4.

ILLUSTRATIONS: Figures 4–7, 9, 11, 12 (skulls, mandibles, and dentitions); 13 (occipital region of skull); 13–15 (limbs).

DISCUSSION

The proposed new genus includes forms with comparatively high skulls, some of which previously have been referred to *Ticholeptus*. This latter misidentification was due to the fact that the holotype of the genotypic species of *Ticholeptus* (*T. zygomaticus*) is a badly crushed skull and mandible, which were not completely prepared and separated until recently.[2] Due to crushing, the skull seemed to be high, but with further preparation and allowance made for the crushing, it became evident that the skull actually was rather low. The supraoccipital region of *Ticholeptus* is fan shaped and definitely different from the posteriorly produced supraoccipital wings of *Hypsiops*. The latter genus is known from the Harrison formation or its equivalent, while *Ticholeptus* is reported from the "Sheep Creek," the "Lower Snake Creek," and the Valentine, or their equivalents.

The species *bannackensis* was also described as *Ticholeptus* by Douglass, but the present writers consider that this species belongs to a new genus; it is here discussed under *Submerycochoerus bannackensis* on page 127.

There appears to be very little variation in the size of the various species of *Hypsiops* except for *H. breviceps* and *H. luskensis*, which are smaller in size, and *H. johndayensis*, which is more robust than any of the remainder of the species.

There is apparently a close relationship between *Phenacocoelus* and *Hypsiops*. The species *H. luskensis* especially shows affinities to *Phenacocoelus* and *Hypsiops*. *P. typus* and *H. luskensis* are here considered as dwarf forms. (See discussion, p. 104.)

In the available specimens of *Hypsiops*, the area of the skull that included the lac-

[2] Schultz and Falkenbach, 1941, p. 72, discussion concerning the preparation of this specimen.

rimal fossa and the facial vacuity is depressed. This area, unfortunately, is not always preserved, and in some instances the facial vacuity appears to be enlarged owing to the loss of additional bone surface, as is shown in figure 4. The bone in the above-mentioned depression is unusually thin, and some of it apparently has been lost in the process of fossilization. In some skulls this thin bone is preserved on one side and not on the other, as is demonstrated by an example (F:A.M. 33313) of *H. brachymelis petersoni*. Thus the exact size and shape of the facial vacuities are usually questionable.

Distribution

Five species and one subspecies of *Hypsiops* are here recorded from lower Miocene deposits (Harrison formation or its approximate equivalent) of Montana, Nebraska, and Wyoming. (See geological and geographical distribution, chart 3, p. 102.)

Summary of Species and Types

Five species and one subspecies of *Hypsiops* from five lower Miocene localities are here recorded:

1. *Hypsiops brachymelis* (Douglass), 1907, from Jefferson County, Montana. (Approximate Harrison equivalent.)

Holotype: Skull, mandible, and most of skeleton, A.M. 9731. Figures 4–6, 13–15.

1a. *Hypsiops brachymelis petersoni* (Loomis), 1923, from Niobrara County, Wyoming; referred remains from Sioux County, Nebraska. (Harrison.)

Holotype: Skull, mandible, and most of skeleton, A.C. 22–656.

2. *Hypsiops breviceps* (Douglass), 1907, from Silver Bow County, Montana. (Approximate Harrison equivalent.)

Holotype: Skull, mandible, and skeletal elements, C.M. 1191. Figures 4–6, 12–15.

3. *Hypsiops erythroceps* (Stock), 1932, from Kern County, California. (Approximate Harrison equivalent.)

Holotype: Anterior portion of skull, C.I.T. 486. Figure 9.

4. *Hypsiops luskensis*, new species, from Niobrara County, Wyoming. (Harrison.)

Holotype: Skull and mandible, F:A.M. 44853A. Figures 4–6, 11.

5. *Hypsiops johndayensis*, new species, from John Day Valley, Oregon. (John Day = in part to Harrison.)

Holotype: Skull, C.I.T. 3503. Figures 4–6, 12.

6. *Hypsiops* species (Peterson), 1928, from questionable locality.[1]

Example: Partial mandible, C.M. 11391.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

HYPSIOPS

Total available specimens: 28

1. Hypsiops brachymelis (Douglass)

From lower Miocene deposits (approximately equal in age to the Harrison of the central Great Plains), Jefferson County, Montana; referred remains from Beaverhead County, Montana

Ticholeptus brachymelis Douglass, 1907, Bull. Amer. Mus. Nat. Hist., vol. 23, art. 32, p. 815, figs. 6–7. Thorpe, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 188, fig. 138; pl. 29, figs. 3–4.

Characters

Skull: Larger than those of *Hypsiops breviceps* and *H. luskensis*, slightly larger than average examples of *H. brachymelis petersoni*, somewhat smaller and less massive than those of *H. johndayensis;* mesocephalic; nasals retracted anteriorly to area above anterior of P^1; anterior nasal-maxilla contact above P^2; posterior portion of arch somewhat U-shaped in outline from side view, with sharp rise of inferior border; posterior border of arch extending posteriorly to anterior border of postglenoid process; malar deep below orbit; infraorbital foramen above anterior border of P^4.

Mandible: Same size comparisons as in skull; postsymphysis below midline of P_3.

Dentition: C/ large; /C approximately twice the size of I_3, spatulate shape in outline; premolars crowded (worn in holotype, but suggesting presence of anterior intermediate crest on P^2 and P^3); P_3 with suggestion of posterior intermediate crest.

Limbs: Slightly longer than known examples of other species of genus (*H. john-*

[1] See discussion, page 124.

dayensis known from fragmentary examples only).

MEASUREMENTS: Tables 3 and 4.

ILLUSTRATIONS: Figures 4–6, 11, 13–15.

DISCUSSION

The holotype is the only example of this species known from North Boulder Valley, Montana. The three referred specimens from north of Bannack, Montana, are definitely smaller than the holotype, but within the possible range of individual variation within a single species. It may be that the holotype is a small example of the forms typical of the North Boulder Valley area and therefore may represent a distinct species or subspecies. The writers believe, however, that there may be a slight difference in geologic age of the deposits of the North Boulder Valley and the locality north of Bannack, and that the former may be slightly younger than the latter, but both are considered to be Harrison equivalents. Remains of *Pseudomesoreodon rooneyi* from north of Bannack and the holotype of *P. rolli*, a larger species from the North Boulder Valley, also seem to substantiate this age assignment. (See discussion, p. 132.)

The size and characters of *Hypsiops brachymelis* are similar to those of *H. brachymelis petersoni* from the central Great Plains. Perhaps the subspecies represents nothing more than a geographic variant. However, until more examples of *H. brachymelis* are available and a better idea of the individual variation within this species is known, the writers prefer to consider *petersoni* as a subspecies.

In the holotype of *H. brachymelis*, the only known example of this species, the posterior border of the zygomatic arch is light, but this specimen may represent a female. Both light and comparatively heavy posterior borders are present in examples of *H. brachymelis petersoni*.

Although the holotype of *H. brachymelis* was described by Douglass in 1907, the skull and mandible remained attached in the matrix until 1946, thus obscuring some of the skull characters.

Five specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, scapula, 2 humeri (1 partial), 2 radii, 2 partial ulnae, femur, 2 partial tibiae, partial manus, partial pes, vertebrae, and pelvis. (w+)	A.M. 9731	From lower Miocene deposits, opposite Cold Springs post office (North Boulder Valley), Jefferson County, Montana; collected by Albert Thomson, 1902 Figured by Douglass, 1907, figs. 6–7; Thorpe, 1937, fig. 138; pl. 29, figs. 3–4 This report, figs. 4–6, 11, 13–15

REFERRED[1] FROM NORTH OF BANNACK, BEAVERHEAD COUNTY, MONTANA

(Collected by N. Z. Ward, Nelson J. Vaughan, and Charles H. Falkenbach)

3 PARTIAL SKULLS AND ASSOCIATED MATERIAL

		F:A.M.
Partial skull with C/(rt.)–M^3, partial right ramus with I_1–P_3 (/C alv. and P_2 br.), partial femur, partial tibia, astragalus, and calcaneum. Fig. 6 (in part). . .	(w)	34335
Partial skull with I^1–M^3 (C/br., P^1 br., and P^2 rt.) and manus	(w‡)	34401
Right side of skull (nasals complete) with I^2–M^3, partial radius, and partial pes. Fig. 13 (in part)	(w‡+)	44882
The above radius may belong to a second individual since it appears to be immature.		

PARTIAL SKULL, IMMATURE

		F:A.M.
Anterior portion of skull with C/(germ)–dP^2–M^1(erupt.)	(i)	49581
The P^1 and M^1 of the above specimen seem large for this species.		

[1] See discussion of possible horizon of this material, this page.

1a. Hypsiops brachymelis petersoni (Loomis)

From the Harrison formation, Niobrara County, Wyoming; referred remains from Sioux County, Nebraska

Ticholeptus petersoni LOOMIS, 1923, Amer. Jour. Sci., ser. 5, vol. 6, p. 225, figs. 2–4. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 193, figs. 5, 141; pl. 47, fig. 2.

CHARACTERS

SKULL: Larger than examples of *H. breviceps* and *H. luskensis*, approximately same size as that of *H. brachymelis* (average examples shorter than holotype of latter species, but within the expected individual variation); nasals approximately same length and shape as in *H. brachymelis*, retracted anteriorly to region above P^1; anterior nasal-maxilla contact above P^2; malar of less depth below orbit than in *H. brachymelis*.

MANDIBLE: Similar to that of *H. brachymelis* in size and outline; postsymphysis below P_3.

DENTITION: Similar to examples of *H. brachymelis*.

LIMBS: Slightly less in length than examples of *H. brachymelis*.

MEASUREMENTS: Tables 3 and 4.

ILLUSTRATIONS: Figures 7, 11, 14, 15.

DISCUSSION

In his original description Loomis[1] failed to make comparisons with the holotype of *H. brachymelis* (at that time considered as *Ticholeptus*) but did make the statement: "However, there is no other *Ticholeptus* anywhere near this size."

The present writers have not been able to find any characters, except for the shorter limb elements (which may well be within individual variation), that distinguish this subspecies from *H. brachymelis*. Perhaps when additional material representing the species is available, distinctive characters separating the two forms may become evident.

Hypsiops brachymelis petersoni is definitely larger than examples of *H. luskensis* and *H. breviceps*. In Montana there are large (*H. brachymelis*) and small (*H. breviceps*) species; in Nebraska, *H. brachymelis petersoni* is large and *H. luskensis* is small. The two large forms are not separable, while the two small species are recognized by the differences in the shapes of the zygomatic arches. The arch of *H. breviceps* is typical of the genus *Hypsiops*, while the arch of *H. luskensis* is similar to that of *Phenacocoelus*. (See discussion, p. 104.)

Thorpe,[2] in a discussion of this subspecies, stated: "The skull is about the size of that of *T. brachymelis* but of somewhat less depth facially. . . . The squamosal part of the arch is not so widely expanded as in *T. brachymelis* and does not rise so abruptly posteriorly."

As to the depth of the face, the present writers see very little difference in the two forms in question. It is true that the line-cut illustrations by Loomis[3] and Thorpe[4] (after Loomis) show a rather low skull for the subspecies, but the photographs of Loomis[5] and Thorpe[6] show a somewhat higher facial region. The photographs also indicate a slightly higher posterior border to the zygomatic arch (more U-shaped in outline).

The holotype of *H. brachymelis petersoni* (Loomis) is a mounted skeleton which is partially embedded in a plaster plaque, thus making it difficult, if not impossible, to measure the specimen accurately. There are considerable differences between the measurements cited by Loomis and Thorpe and those given in this report, especially in the limb elements.

An example of *H. brachymelis petersoni* (skull, mandible, and skeletal elements, C.N.H.M. U.C. 1478) was collected near Van Tassel, Niobrara County, Wyoming, by the late Paul Miller and was found in direct association with a skeleton of *Promerycochoerus carrikeri*.

The F:A.M. specimens were collected by John Lynch, Everett De Groot, Nelson J. Vaughan, and Charles H. Falkenbach, 1931, 1933, 1937, and 1938. The U.N.S.M. material was collected by various University of Nebraska State Museum parties, 1924 and 1937.

Fourteen specimens are here recorded:

[1] 1923, p. 226.

[2] 1937, p. 193.

[3] 1923, fig. 3.

[4] 1937, fig. 141.

[5] 1923, fig. 2.

[6] 1937, pl. 47, fig. 2.

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, and mounted skeleton. (w+)	A.C. 22–656	From the Harrison formation, "directly behind the village of Van Tassel," Niobrara County, Wyoming Figured by Loomis, 1923, figs. 2–4; Thorpe, 1937, figs. 5 and 141; pl. 47, fig. 2

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; (B) SIOUX COUNTY, NEBRASKA

A. FROM NIOBRARA COUNTY, WYOMING

FROM TYPE AREA NEAR VAN TASSEL:

3 SKULLS AND ASSOCIATED MATERIAL		C.N.H.M.
Skull with C/–M^3 and mandible with I_1–M_3	(w‡)	UC1383
Skull with I^1–M^3, mandible with I_1–M_3, and skeletal elements	(w+)	UC1478
The above specimen was found associated with *Promerycochoerus carrikeri* by Paul Miller.		
		A.M.
Partial skull with C/–M^3	(w)	13803
PARTIAL MANDIBLE		F:A.M.
Partial mandible with M_2–M_3	(w)	44878

FROM S.E. OF LUSK:

SKULL AND MANDIBLE		
Skull with I^1(alv.)–M^3 (I^2 rt.) and mandible with I_1(alv.)–M_3. Figs. 7, 11	(w+)	33313
MAXILLA AND MANDIBLE		
Partial left maxilla with I^1–M^2 and partial mandible with I_1–M_3	(w‡)	34432

FROM S.E. OF VAN TASSEL:

SKULL AND SKELETAL ELEMENTS		
Inferior portion of skull with C/(alv.)–M^3, 2 partial scapulae, 2 partial humeri, 2 radii, 2 ulnae, partial femur, partial tibia, astragalus, calcaneum, metapodials, and vertebrae. Figs. 14–15	(w)	F:A.M. 44905
PARTIAL MANDIBLE		
Partial mandible with I_1–M_3	(w)	44904

B. FROM COLLECTING LOCALITY SX-70, 3 MI. S., 1 MI. W. OF ANDREWS, SIOUX COUNTY, NEBRASKA

(Collected By E. L. Blue, Frank Crabill, Thomas Gerzic, Gordon Graham, Thompson M. Stout, and C. Bertrand Schultz)

3 PARTIAL SKULLS AND MANDIBLES		U.N.S.M.
Skull with I^1–I^3 alv. and C/–M^3 and partial mandible with /C–M_3 (P_1 br.)	(w‡+)	28023
Anterior portion of skull with C/–M^3 and partial mandible with I_3–M_3	(w+)	28024
Partial skull with P^3–M^3 and partial mandible with I_1–M_3	(w‡+)	28025
PARTIAL MANDIBLE		
Partial mandible with P_3–M_3	(w‡)	28026

C. FROM ALONG THE NIOBRARA RIVER, NEAR HARRISON

PARTIAL SKULL		C.N.H.M.
Partial skull (crushed) with I^1–M^3	(w‡)	PM12270

2. Hypsiops breviceps (Douglass)

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

Ticholeptus breviceps DOUGLASS, 1907, Ann. Carnegie Mus. Nat. Hist., vol. 4, no. 2, p. 107, pl. 29. OSBORN, 1901, The age of mammals in Europe, Asia, and North America, fig. 142. ABEL, 1919, Die Stamme der Wirbeltiere, fig. 609. WEBER AND ABEL, 1928, Die Säugetiere, fig. 404. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 190, fig. 139; pl. 28, figs. 3–5.

CHARACTERS

SKULL: Smaller than examples of *H. brachymelis*, approximately same length but wider than *H. luskensis;* brachycephalic, more so than in other species of genus; supraoccipital wings (damaged in holotype, only known specimen) suggesting less posterior extension than in *H. luskensis;* anterior nasal-maxilla contact above middle of P^2; infraorbital foramen above posterior portion of P^3; deep lacrimal fossa.

MANDIBLE: Similar to *H. brachymelis*, but of smaller size; postsymphysis below P_3.

DENTITION: More hypsodont than in other species of genus; series almost as long as those of *H. brachymelis;* cheek teeth considerably heavier than in *H. luskensis* and similar to those of *H. brachymelis;* superior and inferior premolars crowded; P^1–P^3 each set at an angle to alveolar border; anterior ntermediate crest on P^1–P^3 close to external border of teeth; P_1–P_3 each set at an angle to alveloar border; P_3 with posterior intermediate crest.

LIMBS: Similar to examples of *H. luskensis;* smaller than those of holotype of *H. brachymelis.*

MEASUREMENTS: Tables 3 and 4.

ILLUSTRATIONS: Figures 4–6, 12–15.

DISCUSSION

This species seems to represent a dwarf form comparable with *H. luskensis* of Nebraska, i.e., its relationship in size to *H. brachymelis* seems to be similar to the size difference between *H. luskensis* and *H. brachymelis petersoni.* In *H. breviceps*, however, the zygomatic arch is about the same as the arch of *H. brachymelis*, but in *H. luskensis* the arch is different from that of *H. brachymelis petersoni* (see discussion, p. 118). The dentition is comparatively hypsodont and heavy for the size of the skull.

The collecting area of the holotype of this species has yielded very little fossil material to date. Schultz and Falkenbach[1] referred some fragmentary material from this same area to *Merychyus siouxensis.* The writers consider this locality as equal in part to the Harrison formation of the central Great Plains, and perhaps slightly older than the Harrison equivalent in the North Boulder Valley of Montana. (See discussion under *H. brachymelis*, p. 117.)

One specimen is here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, and skeletal parts. (W)	C.M. 1191	From lower Miocene deposits, 1 mi. S.E. of Woodin, Silver Bow County, Montana; collected by Douglass, 1903 Figured by Douglass, 1907, pl. 29; Osborn, 1901, fig. 142; Abel, 1919, fig. 609; Weber and Abel, 1928, fig. 404; Thorpe, 1937, fig. 139; pl. 28, figs. 3–5 This report, figs. 4–6, 12–15

[1] 1947, p. 227.

3. Hypsiops erythroceps (Stock)

From lower Miocene deposits (approximately equal in age to the Harrison of the central Great Plains), Tecuya Canyon, Kern County, California

Promerycochoerus erythroceps STOCK, 1932, Carnegie Inst. Washington Publ., no. 418, p. 89, pl. 1, figs. 1, 1a, 1b. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 119, pl. 15, figs. 1–3.

CHARACTERS

SKULL: Larger (known from anterior portion of skull only) than other species of genus, approaching *Promerycochoerus* in size; nasals moderately heavy and pointed, anteriorly retracted to area above posterior portion of C/ (similar to the holotype of *H. johndayensis*); anterior nasal-maxilla contact above P^1.

MANDIBLE: Unknown.

DENTITION: P^3 and P^4 with anterior intermediate crest (see discussion following). (Dentition incomplete and poorly preserved.)

LIMBS: Unknown

MEASUREMENTS: Table 3.

ILLUSTRATIONS: Figure 9.

DISCUSSION

In the original description, Stock placed this species, perhaps correctly, under the genus *Promerycochoerus*. The holotype, the only known example of the species, is very incomplete. The present writers have examined the holotype and have observed characters similar to those of *Hypsiops*, such as the high muzzle and the retraction and shape of the anterior portion of the nasals. Stock stated that P^3 had an anterior intermediate crest and that P^2 completely lacked the crest. From Stock's illustration, however, there is a suggestion of an anterior intermediate crest on P^2. One of the characters of *Hypsiops* appears to be that the premolars wear much more rapidly than do the molars in comparison with most genera of the oreodonts. The stage of wear of the molars in an example of this genus may be judged to be W+, but when compared with a W+ specimen of *Promerycochoerus*, the premolars of *Hypsiops* will show much more wear.

The holotype of *H. erythroceps* is larger than any known species of the genus and approaches *Promerycochoerus* in size. On the evidence given here, the writers prefer to consider *erythroceps* as belonging to *Hypsiops*.

Both *Promerycochoerus* and *Hypsiops*, as known, are restricted to the Harrison or its approximate equivalent, hence the reference of the species to either genera is not affected by the geologic occurrence. Schultz and Falkenbach,[1] in a discussion of the John Day beds, considered the middle and upper John Day as equivalent to the Harrison of the central Great Plains. On page 123 of the present report under *Hypsiops*, a new species, *H. johndayensis* from the John Day is proposed. It is possible that this new form comes from the middle John Day and that *H. erythroceps* may represent a form similar to what may be expected from the upper John Day. This would account for the size difference here mentioned.

One specimen is here recorded:

HOLOTYPE

Anterior portion of skull with I^1–I^3 rt. and C(br.)–M^1(br.) (P^1–P^3 br.). (W+)	C.I.T. 486	From lower Miocene deposits, C.I.T. Coll. Loc. no. 116, Tecuya Canyon, Kern County, California; collected by Wesley L. Bliss, 1930 Figured by Stock, 1932, pl. 1, figs. 1, 1a, and 1b; Thorpe, 1937, pl. 15, figs. 1–3 This report, fig. 9

[1] 1949, p. 89.

4. **Hypsiops luskensis,**[1] new species

From the Harrison formation, Niobrara County, Wyoming

Ticholeptus harrisonensis (Peterson) LOOMIS, referred, 1923, Amer. Jour. Sci., ser. 5, vol. 6, p. 227, fig. 5 (see following discussion).

DESCRIPTION

SKULL: Approximately same length but narrower than *H. breviceps*, smaller than other species of genus; nasals retracted to area above P^1; anterior nasal-maxilla contact above anterior portion of P^2; zygomatic arch elongated posteriorly and not extending upward as high as in other species of this genus, but similar to those of *Phenacocoelus kayi* and *P. stouti* (see discussion, p. 104); infraorbital foramen above anterior portion of P^4; small, round, facial vacuity; other characters similar to those of *H. brachymelis* and *H. brachymelis petersoni.*

MANDIBLE: Characters and outline typical of genus; postsymphysis below P_3.

DENTITION: Shorter and lighter than in *H. breviceps*; smaller than examples of other known species of genus; P^1–P^3 each with anterior intermediate crest; P_2–P_3 each with posterior intermediate crest.

LIMBS: Similar to those of *H. brachymelis*; considerable individual variation in length but within the expected variation of a species.

MEASUREMENTS: Tables 3 and 4.

ILLUSTRATIONS: Figures 4–6, 11, 13–15.

DISCUSSION

The holotype was found associated with a ramus representing a second specimen with disarticulated limb elements of two individuals. The second ramus compares favorably with that of the holotype, but the two sets of limbs demonstrate a considerable amount of individual variation.

The new species seems to duplicate most of the characters found in *H. brachymelis* and *H. brachymelis petersoni* except for size and the above-mentioned difference in the zygomatic arch. (See discussion of size comparisons, p. 118.)

The two referred Amherst College specimens were considered by Loomis[2] as "*Ticholeptus harrisonensis.*" Schultz and Falkenbach,[3] however, discussed these two specimens under *Paramerychyus harrisonensis* and stated: "Loomis reported two skulls of this species [*P. harrisonensis*] in the Amherst Collection. Basing his decision on these two skulls, he placed this species [*P. harrisonensis*] under the genus *Ticholeptus.* Loomis also illustrated one of the skulls, an immature individual, and identified it in the caption as *Ticholeptus* (*Merychyus*) *harrisonensis.* He considered this species too large and too heavy for *Merychyus*, but evidently used the two referred specimens for his basis of comparison. These two skulls, however, are not referable to *P. harrisonensis* but to a genus and species to be discussed in a later paper [this report]. Presumably Loomis used the type of '*Ticholeptus petersoni*' [*Hypsiops brachymelis petersoni*] for his basis of generic comparison and was correct in noting the likeness of the two skulls in question and the larger '*T. petersoni*' but neither form belongs to the genus *Ticholeptus* [but rather to *Hypsiops*]."

Six specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3 and mandible with I_1–M_3. (W+) F:A.M. 44853A

From the Harrison formation, 2½ mi. S.W. of Van Tassel (or 18 mi. E. and S. of Lusk), Niobrara County, Wyoming; collected by Nelson J. Vaughan, Everett De Groot, and Charles H. Falkenbach, 1942

Figs. 4, 6, 11

[1] Named after the town of Lusk (headquarters for Frick Laboratory field parties, 1930–1949), Niobrara County, Wyoming, the locality of the holotype.

[2] 1923, p. 227.

[3] 1947, p. 248.

REFERRED FROM TYPE AREA, ASSOCIATED WITH HOLOTYPE

		F:A.M.
MANDIBULAR RAMUS		
Right ramus with I_1–P_1 alv. and P_2–M_3	(w)	44853B
SKELETAL ELEMENTS		
2 humeri (1 partial), radius, partial ulna, partial manus, femur, 2 tibiae, 2 astragali, 2 calcanea, partial pes, and vertebrae. Figs. 13–15		44853C
The above limb elements are the larger examples.		
Partial radius, partial ulna, 2 tibiae (1 partial), 2 astragali, 2 calcanea, and partial manus. Figs. 13, 15		44853D
The above limb elements are smaller than the examples listed with F:A.M. 44853C. The size difference between the two sets of limbs is shown in figures 13 and 15.		
FROM VAN TASSEL AREA, AMHERST COLLEGE COLLECTION:		
SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Crushed skull with C/–M^3, mandible with I_1–I_3 alv. and /C–M_3, partial humerus, partial radius, 2 partial ulnae, and partial manus	(w‡⁺⁺)	A.C. 646
SKULL, IMMATURE		
Skull with I^1–I^3 alv. and C/(br.)–dP^3–M^2. Figured by Loomis, 1923, fig. 5	(r)	A.C.
The above two specimens were on exhibit in the Amherst College Museum at the time the present writers studied the collection and were labeled "*Tricholeptus harrisonensis*," so it is assumed that these are the two individuals mentioned by Loomis in 1923.		

5. **Hypsiops johndayensis,**[1] new species

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

DESCRIPTION

SKULL: Slightly longer and wider than examples of *H. brachymelis*, definitely larger than those of *H. breviceps* and *H. luskensis;* more robust than those of other known species of genus; wider across frontals than in other species of genus; nasals with slight anterior retraction, less than in other species of genus; anterior nasal-maxilla contact above posterior portion of P^1; zygomatic arch similar to that of *H. brachymelis* (light posterior border which may represent a female); malar not so deep below orbit as in last-named species, similar to that of *H. brachymelis petersoni;* lacrimal fossa deep and large; infraorbital foramen above anterior portion of P^4; occipital condyles much larger than in other known species of genus; bulla more inflated and extending farther downward than in *H. brachymelis;* postglenoid process more massive and with external border less steep than in other species of genus.

MANDIBLE: Similar to that of *H. brachymelis* in size; inferior border of ramus with more marked downward curve posterior to first lobe of M_3 than in *H. brachymelis;* ascending ramus very high with sharp inward curve of inferior border and with prominent fold on internal, inferior border (apparently for attachment of muscles). (Postsymphysis unknown.)

DENTITION: Series approximately same length as those of *H. brachymelis;* P^2 and P^3 with anterior intermediate crest; inferior series similar to those of *H. brachymelis.* (Inferior series known from P_3–M_3 only.)

LIMBS: Similar to examples of *H. brachymelis.* (Known from referred fragmentary examples only.)

MEASUREMENTS: Table 3.

ILLUSTRATIONS: Figures 4–6, 12.

DISCUSSION

The skull of the proposed new species may be easily recognized by its more robust appearance, the large occipital condyles, the larger and more inflated bulla, and the more massive postglenoid processes in comparison

[1] Named for the John Day Valley, Oregon, the locality of the holotype.

with those of other species of the genus. The mandible may be distinguished by the high ascending ramus and the deep, sharply downward-curving inferior border.

It is uncertain whether the holotype and referred specimen came from the middle or upper John Day. Both of these horizons, however, are considered by the writers to be approximately equal in age to the Harrison of the Great Plains. (See discussion [1] of the John Day beds.)

Two specimens are here recorded:

HOLOTYPE

Skull with I^1(alv.)–M^3, partial left ramus with P_3–M_3, and atlas. (w‡)	C.I.T. 3503	From middle or upper John Day deposits, C.I.T. Coll. Loc. no. 372, John Day Valley, Oregon Figs. 4–6, 12

REFERRED FROM TYPE AREA, JOHN DAY VALLEY, OREGON

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		A.M.
Partial skull (in 2 pieces) with I^1–I^2 rt. and I^3–M^3 br., partial mandible with fragmentary teeth, 2 partial humeri, and fragments	(w‡)	7787

The bullae preserved in the above specimen have a vertical height which is greater than that in the holotype, but this may be due to lateral crushing.

6. Hypsiops, species undetermined

From questionable Miocene deposits and locality

Ticholeptus? PETERSON, 1928, Mem. Carnegie Mus., vol. 11, no. 2, p. 99, fig. 8.

Peterson published the following report concerning a partial ramus (C.M. 11391) of *Ticholeptus* in the collection of the Carnegie Museum: "The specimen is reported by Mr. Haslem of Vernal Valley, Utah, to have been found on top of a butte close to the camp of the Emma (Gilsonite) Mine near the bluff of the White River canyon in Utah. If this is the locality at which this specimen was found[29] we have perhaps at last located the contact between the true Brown's Park formation and the horizons A, B, and C of the upper Eocene sediments in the Uinta Basin." In footnote 29 Peterson continued: "There does not now seem to be any reason for doubt as to the accuracy of Mr. Haslem's report."

There does seem to be considerable doubt concerning the collecting locality of the ramus in question. Dr. J. LeRoy Kay, Curator of Paleontology in the Carnegie Museum, has assured the present writers that the specimen definitely did not come from the Utah locality, but probably from Wyoming.

The partial ramus, with P_4–M_1 present, is of no diagnostic value, but as stated by Peterson, the teeth compare favorably in size with those of *H. breviceps* and *H. brachymelis petersoni*. The skull and mandible of the holotype of *H. brachymelis* have recently been separated, and the writers have had the opportunity to make detailed comparisons. The ramus in question seems to belong to the genus *Hypsiops*, and probably to the subspecies *H. brachymelis petersoni*.

One specimen is here recorded:

Partial right ramus with P_4–M_1. (w‡)	C.M. 11391	Locality unknown; collected by W. Haslem Figured by Peterson, 1928, fig. 8

III. SUBMERYCOCHOERUS, NEW GENUS

GENOTYPE: *Submerycochoerus bannackensis* (Douglass).

DESCRIPTION

SKULL: Large size; high; frontals wide; nasals moderately heavy with slight lateral curve to superior surface, greatly retracted anteriorly (more so than in *Hypsiops* and *Promerycochoerus*, but not to extent found in examples of *Merycochoerus* or *Brachycrus*); anterior nasal-maxilla contact above P^4 [in *Hypsiops* above P^1 and P^2, in *P.* (*Paraprо-*

[1] Schultz and Falkenbach, 1949, p. 89, and chart 3, p. 83.

TABLE 5

Submerycochoerus, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKULLS AND RAMI

	S. bannackensis (Douglass)	
SKULL	Holotype C.M. 995	Referred F:A.M. 34317
Stage of wear of teeth	(w)	(w‡)
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	—	((250))
Width (max.)	—	187
Width, interorbital (min.)	—	92
Distance from anterior rim of orbit to anterior base of canine	(116.5)	130
Length of nasal	—	94
Width of muzzle at infraorbital foramina	—	91
Width across canines	—	70
Length, C/–M^3 incl.	—	141
Length, P^1–M^3 incl.	—	117.5
Length, P^1–P^4 incl.	—	53
Length, M^1–M^3 incl.	—	55
Width M^3 (max.)	—	26
Length of malar below orbit	—	36
RAMUS		
Length (max., including incisors)	220	232
Length, /C to condyle incl.	204.5	227
Depth of jaw under coronoid	114	124.5
Depth of jaw below anterior edge of M_3	50	55
Length, /C–M_3 incl.	138	140.5
Length, P_1–M_3 incl.	127	128
Length, P_1–P_4 incl.	56	56
Length, M_1–M_3 incl.	73	73

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

merycochoerus) *macrostegus* above P^1, and in *M. matthewi* above M^1]; orbit oval vertically, with long axis sloping upward anteroposteriorly, looking chiefly outward; zygomatic arch moderately heavy, squamosal U-shaped in outline; malar moderately deep below orbit, with a prominent angular protuberance present on anterior, inferior border, similar to that found in examples of *Hypsiops* and *Merycochoerus*; infraorbital foramen above anterior portion of P^4; lacrimal fossa large and deep; small facial vacuity just anterior to and above the lacrimal fossa; muzzle broad, similar to that of *Hypsiops* and *Merycochoerus*, not protruding beyond the side of the face as in examples of *Promerycochoerus;* premaxillae joined for about same distance as in *Hypsiops*, for longer distance than in examples of *Promerycochoerus*, but less than in *Merycochoerus;* postglenoid process moderately robust, wide transversely, with steeply sloping internal and external borders; posterior palate noticeably projecting beyond M^3, comparable with examples of *Hypsiops*, but not to the extent found in *Merycochoerus*. (Sagittal crest and occipital region including bulla unknown.)

MANDIBLE: Moderately heavy; postsymphysis below posterior portion of P_3; ramus increasing in depth posteriorly, inferior border with a slight downward curve below and posterior to M_3, similar to examples of *Hypsiops;* ascending ramus high, similar to examples of *H. brachymelis*, but higher than

TABLE 6

Submerycochoerus, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKELETAL ELEMENTS

	S. bannackensis (Douglass)		
	Holotype C.M. 995	Referred F:A.M. 34317	Referred C.M. 1185
Length of radius (articular)	145	145	—
Length of ulna (max.)	—	((178))	—
Length of metacarpal III (max.)	71	—	—
Length of femur (articular)	—	—	208.5
Length of tibia (articular)	162.5	—	170
Length of metatarsal III (max.)	80	—	81
Length of calcaneum (max.)	66	—	70.5

[1] (( )), Estimated. All measurements in millimeters.

in examples of *Promerycochoerus* or *Merycochoerus*; condyle wide transversely, set at less than right angle to axis of dental series with external border of condyle noticeably farther forward than internal border.

DENTITION: Series slightly heavier than in *Hypsiops*, lighter than in average examples of *Promerycochoerus* and *Merycochoerus;* less crowding of the premolars than in *Merycochoerus*, more like examples of *Hypsiops* and *Promerycochoerus;* P^2 with anterior intermediate crest, somewhat stronger on P^3.

LIMBS: Robust, slightly longer and heavier than examples of *H. brachymelis*, definitely lighter and shorter than in examples of *Promerycochoerus* and *Merycochoerus*.

MEASUREMENTS: Tables 5 and 6.

ILLUSTRATIONS: Figures 8–10, 12 (skull, ramus, and dentition); 13 (limb).

DISCUSSION

The proposed new genus is based on one species which is known from three specimens. Knowledge of the occipital region is completely lacking. It is unfortunate that the supraoccipital region and the bullae are unknown, since both usually are of diagnostic value. The high skull, the retracted nasals, and the facial vacuity, however, seem to indicate relationships with the subfamily Phenacocoelinae rather than with either Promerycochoerinae or Merycochoerinae. Many characters of the three preceding subfamilies are evident in *Submerycochoerus*, but the writers believe that a closer relationship exists with Phenacocoelinae. It is very possible that this genus (*Submerycochoerus*) gave rise to *Merycochoerus*.

DISTRIBUTION

The remains of *Submerycochoerus* are known only from one lower Miocene locality (approximately equal in age to the Harrison of the central Great Plains) in Montana. (See geological and geographical distribution, chart 3, p. 102.)

SUMMARY OF SPECIES AND TYPE

One species of *Submerycochoerus*, new genus, from one lower Miocene locality is here recorded:

1. *Submerycochoerus bannackensis* (Douglass) from Beaverhead County, Montana. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull (lacking dentition), mandible, and skeletal elements, C.M. 995.

DETAILED LISTS OF SPECIMENS AND SYNONYMY

SUBMERYCOCHOERUS

TOTAL AVAILABLE SPECIMENS: 3

1. Submerycochoerus bannackensis (Douglass)

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

Ticholeptus bannackensis DOUGLASS, 1907, Ann. Carnegie Mus., vol. 4, no. 2, p. 108, pl. 30. THORPE, 1937, Mem. Peabody Mus., vol. 3, pt. 4, p. 187, fig. 137; pl. 27, fig. 3.

CHARACTERS

SKULL: Size large (approaching size of *Merycochoerus matthewi*); nasals greatly retracted to anterior portion of P^2; anterior nasal-maxilla contact above P^3; zygomatic arch extending posteriorly to a point above the posterior border of the postglenoid process; large and deep lacrimal fossa; small facial vacuity. (See generic description.)

MANDIBLE: Similar to examples of *Hypsiops*. (See generic description.)

DENTITION: Series longer than any known examples of *Hypsiops;* smaller than in examples of *Merycochoerus*. (See generic description.)

LIMBS: Robust, somewhat longer and heavier than examples of *H. brachymelis;* lighter and shorter than examples of *Promerycochoerus* or *Merycochoerus*.

MEASUREMENTS: Tables 5 and 6.

ILLUSTRATIONS: Figures 8–10, 12, 13.

DISCUSSION

Douglass[1] based his original description on incomplete material which consisted of a partial skull (lacking dentition), a mandible, and skeletal elements. Douglass noted that the nasal of the skull, although incomplete, was somewhat like that of *Merycochoerus:* "The portion of the skull which is preserved shows the anterior nares were large, broad, and well rounded above. They are situated far back. This imparts to the face an appearance somewhat similar to that of *Merycochoerus*. It is uncertain whether or not the nasals were much shortened anteriorly."

Thorpe[2] accepted Douglass' reference of this species to the genus *Ticholeptus*. The misinterpretation of the generic characters of *Ticholeptus*, as has been mentioned by the present writers on page 115, was due to the fact that the holotype of *T. zygomaticus*, the genotypic species, was not completely prepared, or the skull and jaws separated, until 1940.

Additional material of this species now available in the Frick Laboratory collection includes a more complete skull with superior dentition. An enlarged description of the species is therefore possible, which makes it evident that this form cannot be referred to *Ticholeptus*, or even to *Hypsiops*. (See discussion, p. 115.)

Submerycochoerus bannackensis appears to be the most likely ancestral form for the genus *Merycochoerus*. Schultz and Falkenbach[3] have already pointed out that *Promerycochoerus* undoubtedly did not give rise to *Merycochoerus*. Until the occipital region and the bullae are known no further connection between *Submerycochoerus* and *Merycochoerus* can be established.

Three specimens are here recorded:

HOLOTYPE

C.M. 995 — From lower Miocene deposits, Grasshopper Creek, 10 mi. N. of Bannack, Beaverhead County, Montana; collected by Douglass, 1903

Anterior portion of skull, lacking dentition, mandible with I_1–M_3, partial scapula, 2 partial humeri, 2 partial ulnae, 2 radii, manus elements, tibia, fibula, astragalus, calcaneum, pes elements, vertebrae, and ribs. (W)

Figured by Douglass, 1907, pl. 30; Thorpe, 1937, fig. 137; pl. 27, fig. 3

[1] 1907, p. 108.

[2] 1937, p. 187.

[3] 1949, p. 88.

REFERRED FROM TYPE AREA, GRASSHOPPER CREEK, 10 MI. N. OF BANNACK, BEAVERHEAD COUNTY, MONTANA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Anterior portion of skull with I^1–M^3, mandible with I_1–M_3, humerus fragments, radius, partial ulna, and partial manus. (w‡)	F:A.M. 34317	Collected by Everett DeGroot and Charles H. Falkenbach, 1936 Figs. 8–10, 12, 13

SKELETAL ELEMENTS

2 partial scapulae, 2 femora (1 partial), 2 tibiae (1 partial), partial fibula, astragalus, calcaneum, pes elements, vertebrae, and ribs.	C.M. 1185	Collected by Douglass, 1903

The above limb elements seem to be within the expected size variation of this species.

IV. PSEUDOMESOREODON, NEW GENUS

GENOTYPE: *Pseudomesoreodon rooneyi*, new species.

DESCRIPTION

SKULL: Size medium, basal lengths ranging from 237 to 287 mm., widths from 140 to 178 mm. (approximately same size as large examples of *Mesoreodon*); submesocephalic to brachycephalic; supraoccipital wings widely spread and protruding posteriorly, deeply notched at sides, similar to examples of *Phenacocoelus* and *Hypsiops*, but definitely differing from the narrow, posteriorly protruding wings of *Mesoreodon;* sagittal crest moderately prominent, less so than in *Hypsiops;* brain case well inflated but depressed posteriorly; frontals from moderately wide to wide; orbits oval in outline with an almost vertical axis, looking mostly outward and upward; squamosal portion of zygomatic arch light, extending posteriorly to above postglenoid process, superior border not very high; malar deep below orbit; infraorbital foramen above P^4; lacrimal fossa large and deep; premaxillae joined for about the same distance as in examples of *Hypsiops*, less than in *Mesoreodon*; occipital condyles medium to large in size; paroccipital process wide laterally at base; bulla large and inflated, with depressed inferior surface (similar to that of *Hypsiops*, but not to degree noted in examples of *Ustatochoerus);* postglenoid process moderately robust, long vertically; posterior palate projects posteriorly beyond M^3.

MANDIBLE: Moderately robust; postsymphysis below P_3; inferior border of ramus almost parallel to dental series from symphysis to a point below the last lobe of M_3, with a sharp downward curve extending posteriorly from M_3 (more abrupt than in examples of *Hypsiops* or *Mesoreodon);* ascending ramus high, higher than in *Hypsiops* or *Mesoreodon;* condyles set at less than right angle to axis of dental series with external border of condyle noticeably farther forward than internal border; (characters of mandible based on holotype of *?Pseudomesoreodon boulderensis*).

DENTITION: Brachyodont to subhypsodont; series longer than in examples of *Hypsiops* or *Phenacocoelus*, approximately same length as small examples of *Mesoreodon;* slight crowding of premolars; C/ moderately light; P^1–P^3 each with prominent anterior intermediate crest; external styles of superior molars light; P_1 moderately heavy; P_3 with suggestion of the posterior intermediate crest.

LIMBS: Robust, approximately same length as examples of *H. brachymelis* and *P. stouti;* heavier and somewhat shorter than examples of *Mesoreodon* (from the Gering formation).

MEASUREMENTS: Tables 7 and 8.

ILLUSTRATIONS: Figures 8–10, 12 (skulls, mandibles, and dentitions); 13 (occipital region of skull); 13–15 (limbs).

DISCUSSION

Pseudomesoreodon, new genus, is not well represented in the collections, and so far as known is confined to two localities in Montana. A complete nasal from either species is wanting, but the approximate nasal-maxilla contact suggests an anterior retraction, similar to *Hypsiops*. The bullae of the specimens

TABLE 7

Pseudomesoreodon, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKULLS AND RAMI

	P. rooneyi, new species	*P. rolli*, new species	*?P. boulderensis*, new species
SKULL	Holotype F:A.M. 44948A	Holotype F:A.M. 34481	Holotype F:A.M. 44883
Stage of wear of teeth	(M)	(M+)	(W+)
Length (including supraoccipital crest and incisors)	270	((280))	((299))
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	237	—	287
Width (max.)	150	178	(140)
Width of brain case (max.)	(73)	80	—
Width, interorbital (min.)	—	93	((57))
Distance from anterior rim of orbit to anterior base of canine	111	—	122.5
Distance from anterior rim of orbit to supraoccipital crest	162	161	—
Width of muzzle at infraorbital foramina	(72)	—	74
Width across canines	50	—	51
Length, C/–M^3 incl.	122.5	—	137
Length, P^1–M^3 incl.	110	—	118
Length, P^1–P^4 incl.	50	—	47.5
Length, M^1–M^3 incl.	65	72	74
Width of M^3 (max.)	24.5	26.5	—
Depth of malar below orbit	29	29.5	38
RAMUS			
Length (max., including incisors)	—	—	(218)
Length, /C to condyle incl.	—	—	208.5
Depth of jaw below anterior edge of M_3	—	—	50.5
Length, /C–M_3 incl.	—	—	140.5
Length, P_1–M_3 incl.	—	—	129
Length, P_1–P_4 incl.	—	—[2]	50
Length, M_1–M_3 incl.	—	—	62.5

[1] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[2] P_2–P_4=44.

at hand have flattish or depressed ventral surfaces, not to the extent found in *Ustatochoerus*, but more so than in *Hypsiops* (in *Mesoreodon* the bullae are well inflated). The supraoccipital wings of the skulls of *Pseudomesoreodon* are widely spread and project posteriorly for a short distance. This character is decidedly different from the narrower wings and longer posterior projection evident in examples of *Mesoreodon*.

Pseudomesoreodon has some characters in common with *Mesoreodon*, but possesses others which suggest closer affinities to *Hypsiops*. The depressed bulla of *Pseudomesoreodon* indicates that the genus is more advanced than either of the two latter genera. The bullae of *Pseudomosoreodon*, however, are much more like those of *Hypsiops* than of *Mesoreodon* (see discussion of bullae, p. 96, and chart 1, p. 97).

DISTRIBUTION

The remains of *Pseudomesoreodon* are rare and so far are restricted to two lower Miocene localities (approximately equal in age to the Harrison of the central Great Plains) in

TABLE 8

Pseudomesoreodon, NEW GENUS. COMPARATIVE MEASUREMENTS[1] OF SKELETAL ELEMENTS

	?P. boulderensis, new species
	Referred F:A.M. 44948A–B
Length of radius (articular)	123.5
Length of ulna (max.)	(170)
Length of metacarpal III (max.)	63
Length of metatarsal III (max.)	62
Length of calcaneum (max.)	61.5

[1] ( ), Approximate. All measurements in millimeters.

Montana. Two species and one tentatively referred species are here recorded. (See geological and geographical distribution, chart 3, p. 102.)

SUMMARY OF SPECIES AND TYPES

1. *Pseudomesoreodon rooneyi*, new species, from Beaverhead County, Montana. (Approximate Harrison equivalent.)

HOLOTYPE: Skull, F:A.M. 44948A. Figures 8–10.

2. *Pseudomesoreodon rolli*, new species, from Jefferson County, Montana. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull, F:A.M. 34481. Figures 8–10, 13.

3. *?Pseudomesoreodon boulderensis*, new species, from Jefferson County, Montana. (Approximate Harrison equivalent.)

HOLOTYPE: Partial skull and mandible, F:A.M. 44883. Figures 8, 10, 12.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS

PSEUDOMESOREODON

TOTAL AVAILABLE SPECIMENS: 5

1. Pseudomesoreodon rooneyi,[1] new species

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

DESCRIPTION

SKULL: Smallest of the genus; approximately same height as holotype of *P. rolli*, lower and wider than type of *?P. boulderensis;* mesocephalic; sagittal crest comparatively short anteroposteriorly but prominent; brain case slightly elongated; anterior nasal-maxilla contact above P^3; malar moderately deep below orbit, approximately equal to depth in *P. rolli*, decidedly less than in *?P. boulderensis;* paroccipital process more slender than in *P. rolli* or *?P. boulderensis*.

MANDIBLE: (Known from fragment of ramus only).

DENTITION: Smallest known series of genus; superior incisors graduating in size with I^3 approximately twice the size of I^2; P^1–P^3 each set at slight angle to alveolar border; C/ with anterior internal vertical groove. (Inferior dentition known from worn P_2–P_3 only.)

LIMBS: Moderately robust, similar in length to examples of *Hypsiops brachymelis*.

MEASUREMENTS: Tables 7 and 8.

ILLUSTRATIONS: Figures 8–10, 13–15.

DISCUSSION

The holotype skull of *Pseudomesoreodon rooneyi*, new species, is shorter and narrower than the holotype of *P. rolli*. It is also shorter but wider than the holotype of *?P. boulderen-*

[1] Named in honor of Joseph Rooney, Chief Preparator of the Frick Laboratory, the American Museum of Natural History.

sis. In general it resembles examples of *Mesoreodon cheeki sweeti*, but differs from the latter in having a shorter and less prominent sagittal crest, a posterior border of a zygomatic arch which does not extend so far upward, and a depressed bulla. The presence of the anterior intermediate crest on P^1–P^3 is of little generic value as this same character is also noted in *Submerycochoerus*, *Hypsiops*, and *Mesoreodon*.

The holotype of this new species comes from the same location as the holotype of *Submerycochoerus bannackensis* and referred examples of *H. brachymelis*. (See discussion of geological data of *Hypsiops*, p. 117.)

Two specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3. (M) F:A.M. 44948A From lower Miocene deposits, Grasshopper Creek, 10 mi. N. of Bannack, Beaverhead County, Montana; collected by N. Z. Ward, Nelson J. Vaughan, and Charles H. Falkenbach, 1942

Figs. 8–10

REFERRED, ASSOCIATED WITH HOLOTYPE

MANDIBULAR RAMUS

Partial right ramus with P_1(rt.)–P_4(rt.) . . . . . (W+) F:A.M. 44948B

SKELETAL ELEMENTS

3 partial humeri, 3 radii (1 partial), 2 ulnae (1 partial), 2 manus, partial femur, 3 partial tibiae, 2 calcanea, partial astragalus, 2 partial pedes, pelvis, vertebrae, and fragments. Figs. 13–15 (in part) 44948A-B

The holotype and the referred specimens were found associated in one field block. The limb elements indicate very little individual size variation, and, since there was no articulation, it is impossible to determine which limbs belong to the holotype.

2. **Pseudomesoreodon rolli,**[1] new species

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

Characters

Skull: Intermediate in length between that of *P. rooneyi* and of *?P. boulderensis;* brachycephalic; low; frontals very wide; posterior border of nasals extending posteriorly beyond anterior border of orbit (nasals not preserved in holotype); posterior superior border of squamosal of zygomatic arch extending posteriorly to a point above middle of postglenoid process; malar deep below orbit, equal to that of *P. rooneyi*, but considerably less than in *?P. boulderensis;* paroccipital process wider at base than in other two species of genus; postglenoid process more massive than in *P. rooneyi.*

Mandible: (Unknown).

Dentition: Subhypsodont; premolars [known from P^2(br.)–P^4 only] larger than in other two species of this genus; molar series longer and heavier than in type of *P. rooneyi* and slightly heavier but approximately same length as in holotype of *?P. boulderensis.*

Limbs: (Unknown).

Measurements: Table 7.

Illustrations: Figures 8–10, 13.

Discussion

The proposed new species, *Pseudomesoreodon rolli*, has characters similar to those of *P. rooneyi.* In comparison with the latter species, the skull is longer and wider, the dentition is heavier, with a greater over-all length, and the premolar series (known from P^2–P^4) are definitely larger. The skull of *P. rolli* differs from that of *?P. boulderensis* in having less length, less height, considerably

[1] Named in memory of the late Gene Roll, a collector for the Frick Laboratory.

more width, a more robust paroccipital process, and larger premolars.

The writers consider that the collecting locality of the holotype of this species and that of *?P. boulderensis* may possibly represent a slightly higher geological level than the deposits from which the holotype of *P. rooneyi* was obtained (see discussion, p. 117).

It is of interest to note that the holotype of *P. rolli* is similar in general appearance to large examples of *Ustatochoerus*, but in the latter genus the occipital region is fan shaped and the premolars have additional anterior cusps.[1]

One specimen is here recorded:

HOLOTYPE

Partial skull with P^2–M^3. (M+)	F:A.M. 34481	From lower Miocene deposits, E. side of North Boulder Valley, Jefferson County, Montana; collected by Everett De Groot and Charles H. Falkenbach, 1936 Figs. 8–10, 13

3. ?Pseudomesoreodon boulderensis,[2] new species

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

Description

SKULL: Longest of genus; submesocephalic; narrower and higher than that of *P. rooneyi* and of *P. rolli;* anterior nasal-maxilla contact in area above P^3; anterior maxilla border with abrupt rise to nasals starting above posterior of P^2 on maxilla (more abrupt than in *Hypsiops*); malar exceptionally deep below orbit; paroccipital process heavier at base than in *P. rooneyi*, but slightly lighter at base than in *P. rolli;* postglenoid process more robust than in two above-mentioned species.

MANDIBLE: (See generic description).

DENTITION: Series longer than in *P. rooneyi;* molar series slightly longer than in *P. rolli;* individual premolars approximately same size as those in former species, smaller and lighter than in latter; P^1–P^3 each set at slight angle to alveolar border; P_3 with posterior intermediate crest; P_2 set at slight angle to alveolar border.

LIMBS: (Unknown).

MEASUREMENTS: Table 8.

ILLUSTRATIONS: Figures 8, 10, 12.

Discussion

The new species, *?Pseudomesoreodon boulderensis*, is tentatively placed in this genus. The characters of the skull in general indicate affinities to *Pseudomesoreodon*, but the unusually high skull and the very deep malar below the orbit differ from examples of the other two species of this genus. Unfortunately, the holotype of *?P. boulderensis* lacks most of the superior surface of the skull, thus adding to the difficulties in definitely placing this species. This specimen was found at the same locality as the type of *P. rolli* (see discussion concerning geological occurrence, p. 117 and this page).

One specimen is here recorded:

HOLOTYPE

Partial skull with I^1–M^3(br.) and mandible with /C–M_3. (W+)	F:A.M. 44883	From lower Miocene deposits, North Boulder Valley, Jefferson County, Montana; collected by N. Z. Ward, Nelson J. Vaughan, and Charles H. Falkenbach, 1942 Figs. 8, 10, 12

[1] Schultz and Falkenbach, 1941, p. 10, fig. 17C.

[2] Named after North Boulder Valley, Jefferson County, Montana, the location of the holotype.

EXPLANATION OF TEXT FIGURES

FIG. 1. Lateral views of skulls: *Phenacocoelus typus* Peterson, referred, F:A.M. 33397, from Harrison formation, Niobrara County, Wyoming (see ramus, fig. 11), and holotype, C.M. 1263, from Harrison formation, Sioux County, Nebraska; *P. kayi*, new species, holotype, F:A.M. 33660A, from Harrison formation, Niobrara County, Wyoming (see ramus, fig. 11); *P. stouti*, new species, holotype, F:A.M. 44839 (I^3 from opposite side), from lower Marsland formation, Platte County, Wyoming. ×½.

FIG. 2. Same as fig. 1. Dorsal views. ×½.

FIG. 3. Same as fig. 1. Ventral views. ×½.

FIG. 4. Lateral views of skulls: *Hypsiops luskensis*, new species, holotype, F:A.M. 44853A, Niobrara County, Wyoming (see ramus, fig. 11); *H. breviceps* (Douglass), holotype, C.M. 1191 (C/ and paroccipital process from opposite side), Silver Bow County, Montana (see ramus, fig. 12); *H. brachymelis* (Douglass), holotype, A.M. 9731 (combination of both sides), Jefferson County, Montana (see ramus, fig. 11); *H. johndayensis*, new species, holotype, C.I.T. 3503 (facial vacuity from opposite side), John Day Valley, Oregon (see ramus, fig. 12). All from Harrison formation or its approximate equivalent. ×½.

FIG. 5. Same as fig. 4. Dorsal views. ×½.

FIG. 6. Same as fig. 4. Ventral views; also *H. brachymelis* (Douglass), referred, F:A.M. 34335, superior dentition, from deposits approximately equal to Harrison formation, Beaverhead County, Montana. ×½.

FIG. 7. *Hypsiops brachymelis petersoni* (Loomis), referred, skull, F:A.M. 33313 (paroccipital process from opposite side), from Harrison formation, Niobrara County, Wyoming (see ramus, fig. 11). APF, anterior palatine foramen; B, auditory bulla; IF, infraorbital foramen; MA, external auditory meatus; NF, nasal-frontal contact; PP, paroccipital process; PPF, posterior palatine foramen; SOF, supraorbital foramen; 5, lacerated foramina; 6, glenoid foramina; 7, condylar foramen. ×½.

FIG. 8. Lateral views of skulls: *Pseudomesoreodon rooneyi*, new species, holotype, F:A.M. 44948A (combination of both sides), Beaverhead County, Montana; *P. rolli*, new species, holotype, F:A.M. 34481 (P^2 and P^3 from opposite side), Jefferson County, Montana; *?P. boulderensis*, new species, holotype, F:A.M. 44883 (C/, paroccipital process, and external auditory meatus from opposite side), Jefferson County, Montana (see ramus, fig. 12); *Submerycochoerus bannackensis* (Douglass), referred, F:A.M. 34317 (P^2 from opposite side), Beaverhead County, Montana (see ramus, fig. 12). All from deposits approximately equal to the Harrison formation. ×½.

FIG. 9. Dorsal views of skulls: *Pseudomesoreodon rooneyi*, *P. rolli*, and *Submerycochoerus bannackensis*, same as fig. 8; also dorsal and ventral views of *Hypsiops erythroceps* (Stock), holotype, C.I.T. 486, skull fragment (after Stock), from deposits approximately equal to the Harrison formation, Kern County, California. ×½.

FIG. 10. Same as fig. 8. Ventral views. ×½.

FIG. 11. Lower dentitions and mandibular rami: *Phenacocoelus typus* Peterson, referred, F:A.M. 33397 (I_3 from opposite side), from Harrison formation, Niobrara County, Wyoming (see skull, figs. 1–3); *P. kayi*, new species, holotype, F:A.M. 33660A (M_3 from opposite side), from Harrison formation, Niobrara County, Wyoming (see skull, figs. 1–3); *P. stouti*, new species, referred, F:A.M. 33361 (ascending ramus from opposite side), from lower Marsland formation, Platte County, Wyoming, and F:A.M. 44900, from lower Marsland formation, Goshen County, Wyoming; *Hypsiops luskensis*, new species, holotype, F:A.M. 44853A, from Harrison formation, Niobrara County, Wyoming (see skull, figs. 4–6); *H. brachymelis petersoni* (Loomis), referred, F:A.M. 33313, from Harrison formation, Niobrara County, Wyoming (see skull, fig. 7); *H. brachymelis* (Douglass), holotype, A.M. 9731 (I_3 from opposite side), from deposits approximately equal to Harrison formation, Jefferson County, Montana (see skull, figs. 4–6). PS, posterior border of symphysis. ×½.

FIG. 12. Lower dentitions and mandibular rami: *Hypsiops breviceps* (Douglass), holotype, C.M. 1191 (I_1, I_2, and /C from opposite side), Silver Bow County, Montana (see skull, figs. 4–6); *H. johndayensis*, new species, holotype, C.I.T. 3503, John Day Valley, Oregon (see skull, figs. 4–6); *?Pseudomesoreodon boulderensis*, new species, holotype, F:A.M. 44883 (/C from opposite side), Jefferson County, Montana (see skull, figs. 8, 10); *Submerycochoerus bannackensis* (Douglass), referred F:A.M. 34317 (I_1 from opposite side), Beaverhead County, Montana (see skull, figs. 8–10). All from deposits approximately equal to Harrison formation. ×½.

FIG. 13. Examples of occipital regions of skulls representing species of *Phenacocoelus*, *Hypsiops*, and *Pseudomesoreodon*. Comparisons of skeletal elements: A. *Phenacocoelus kayi*, new species; B. *P. stouti*, new species; C. *P. typus* Peterson (see fig. 15); D. *Hypsiops brachymelis* (Douglass); E. *H. breviceps* (Douglass); F. *H. brachymelis petersoni* (Loomis) (see figs. 14, 15); G. *H. luskensis*, new species; H. *Pseudomesoreodon rooneyi*, new species; I. *Submerycochoerus bannackensis* (Douglass). $\times\frac{1}{2}$.

FIG. 14. Comparison of skeletal elements, same as fig. 13. $\times\frac{1}{2}$.

FIG. 15. Comparison of skeletal elements, same as fig. 13. $\times\frac{1}{2}$.

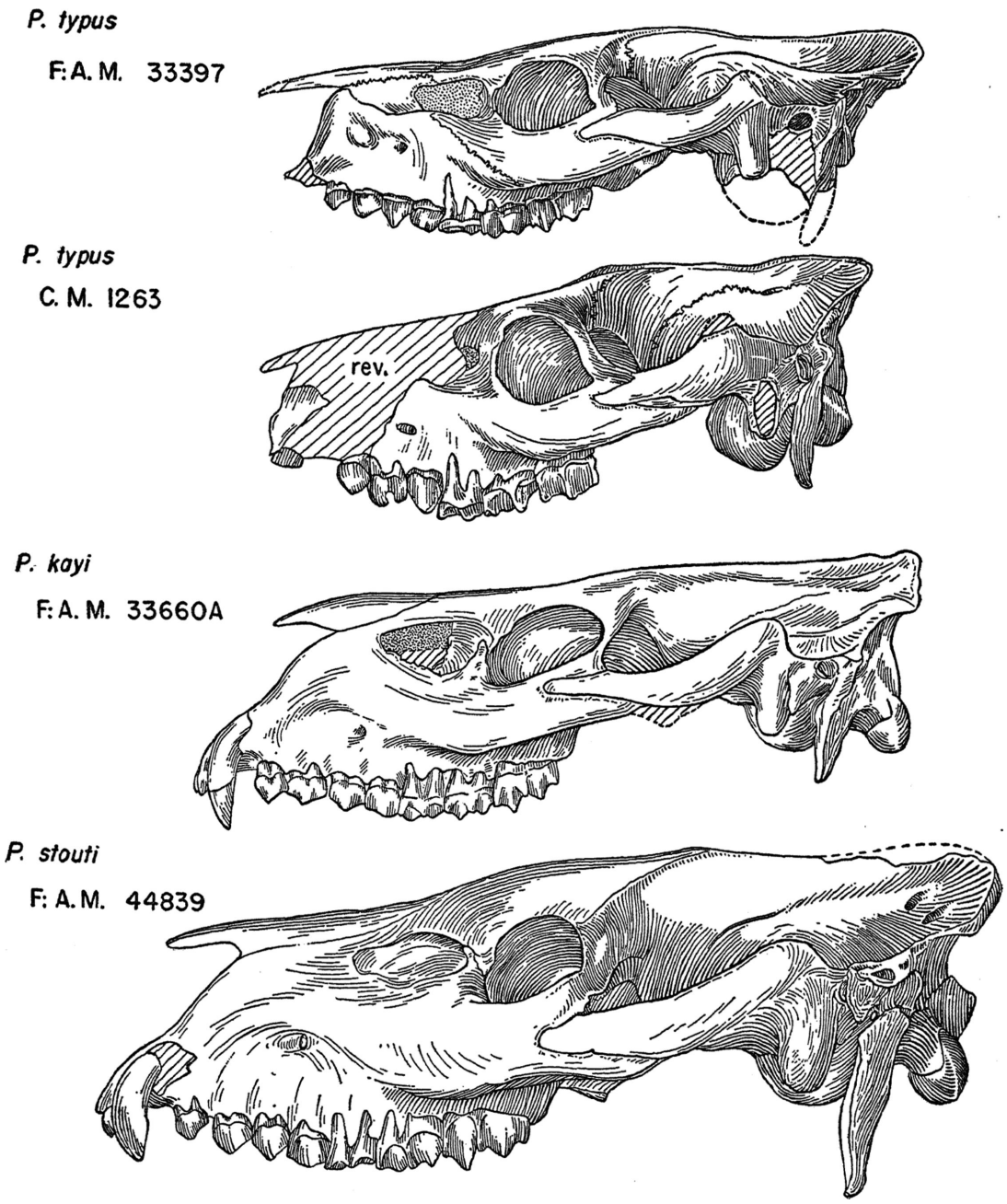


FIG. 1. *Phenacocoelus*, three species, holotypes, C.M. 1263, F:A.M. 33660A, and F:A.M. 44839, and referred, F:A.M. 33397. (See p. 133.) ×⅓. (See figs. 2, 3, 11.)

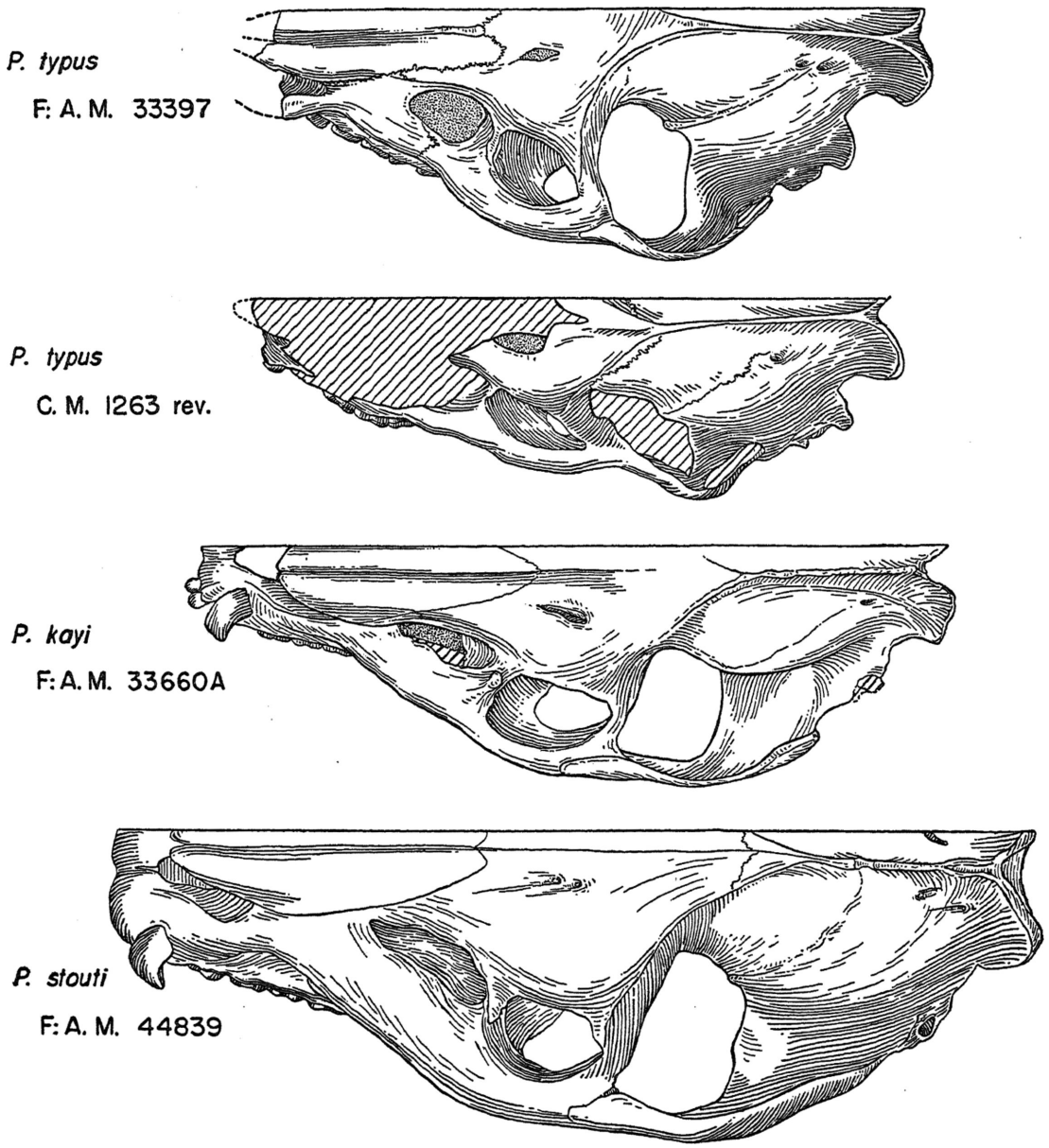


FIG. 2. *Phenacocoelus*, three species, holotypes, C.M. 1263, F:A.M. 33660A, and F:A.M. 44839, and referred, F:A.M. 33397. (See p. 133.) ×½. (See figs. 1, 3, 11.)

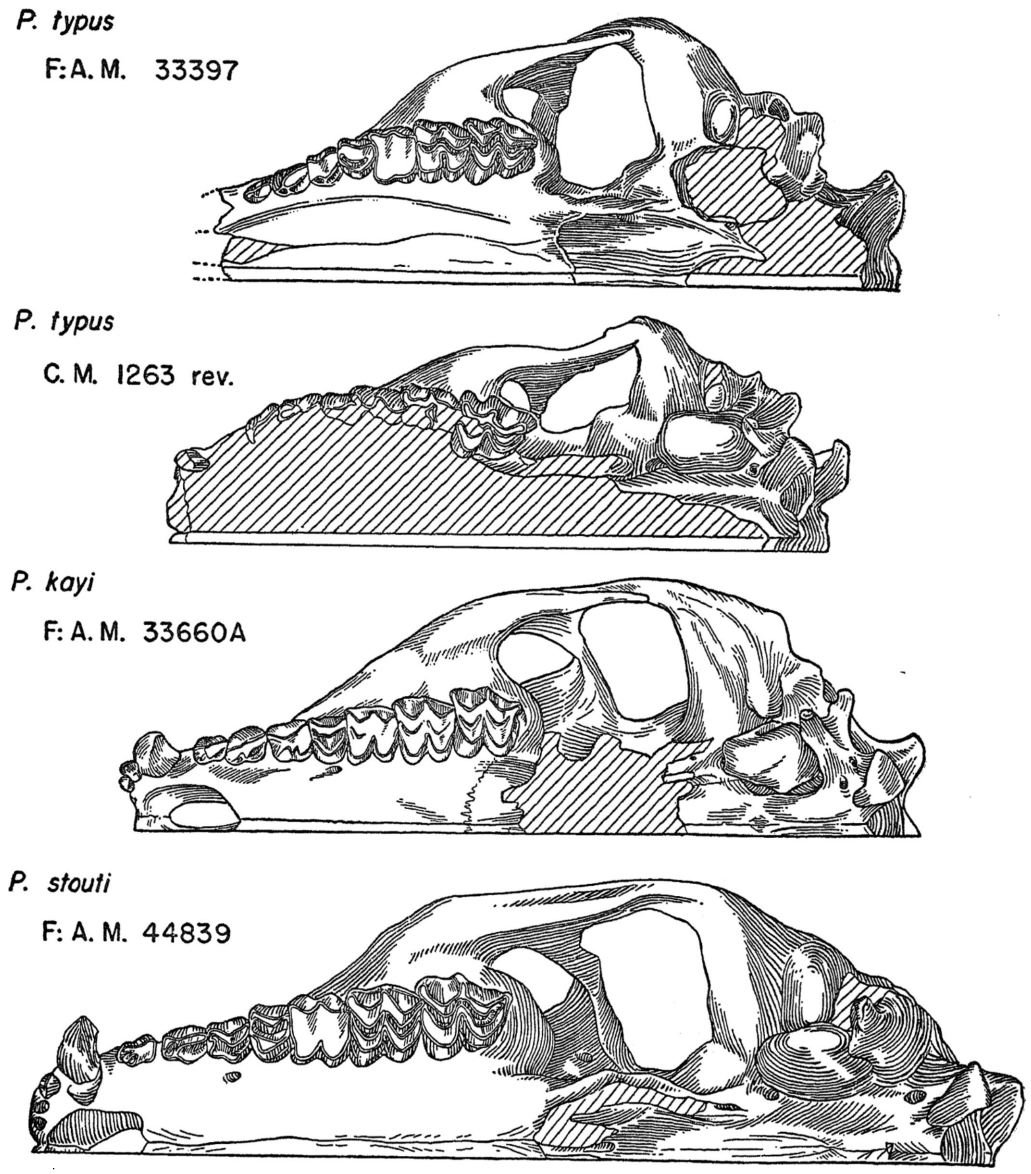


FIG. 3. *Phenacocoelus*, three species, holotypes, C.M. 1263, F:A.M. 33660A, and F:A.M. 44839, and referred, F:A.M. 33397. (See p. 133.) $\times\frac{1}{2}$. (See figs. 1, 2, 11.)

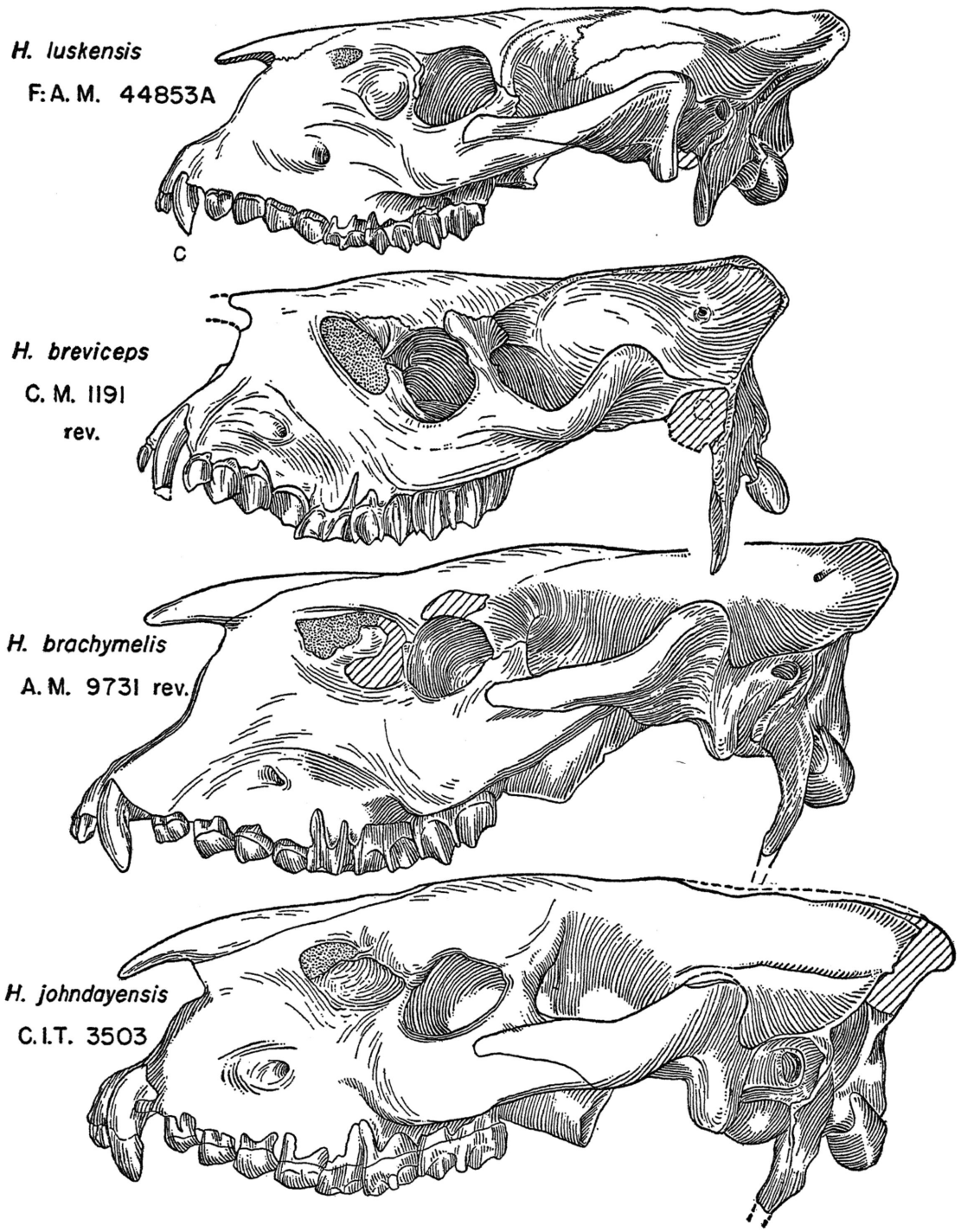


FIG. 4. *Hypsiops*, four species, holotypes, F:A.M. 44853A, C.M. 1191, A.M. 9731, and C.I.T. 3503. (See p. 133.) ×½. (See figs. 5, 6, 11, 12.)

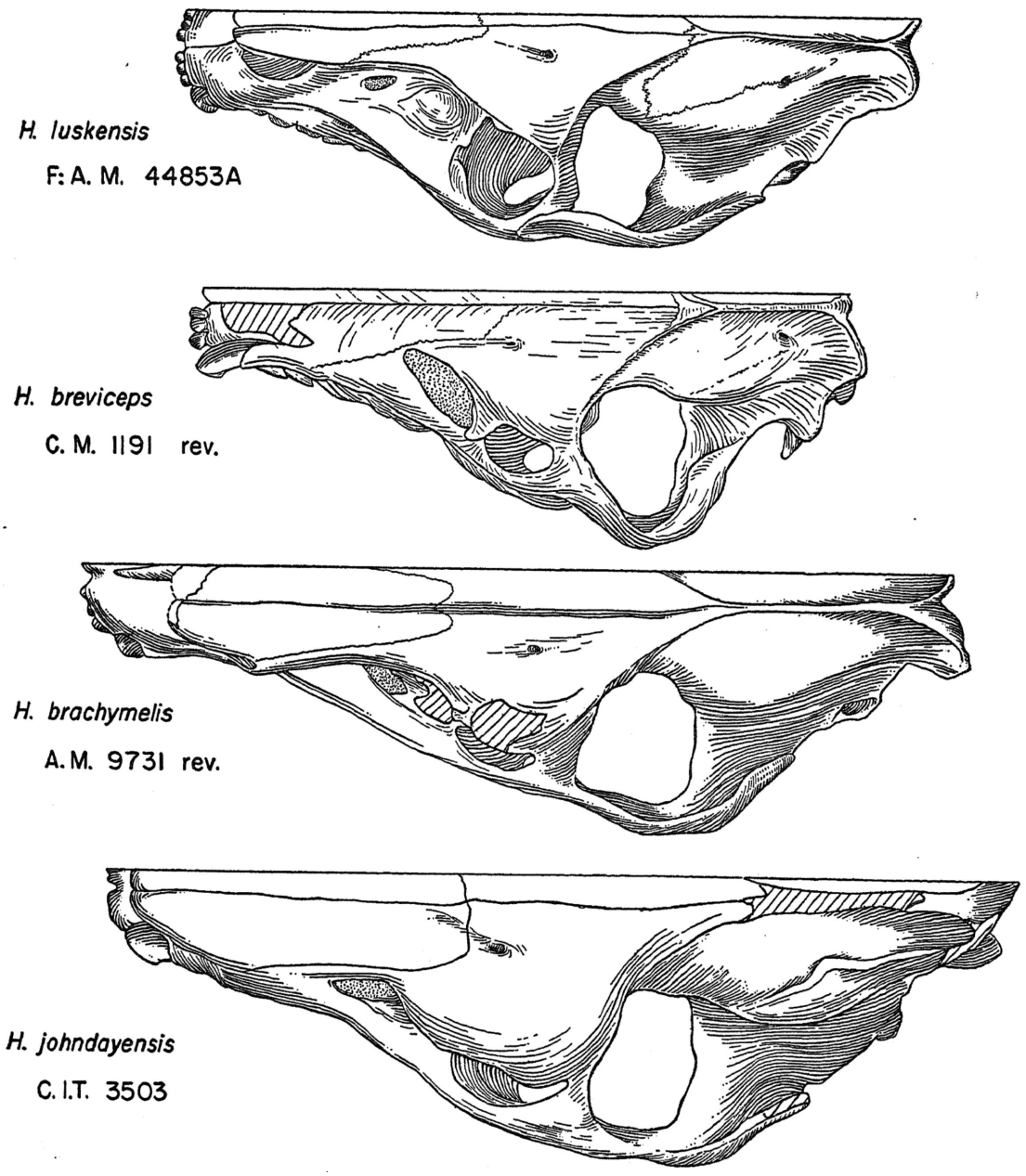


FIG. 5. *Hypsiops*, four species, holotypes, F:A.M. 44853A, C.M. 1191, A.M. 9731, and C.I.T. 3503. (See p. 133). ×½. (See figs. 4, 6, 11, 12.)

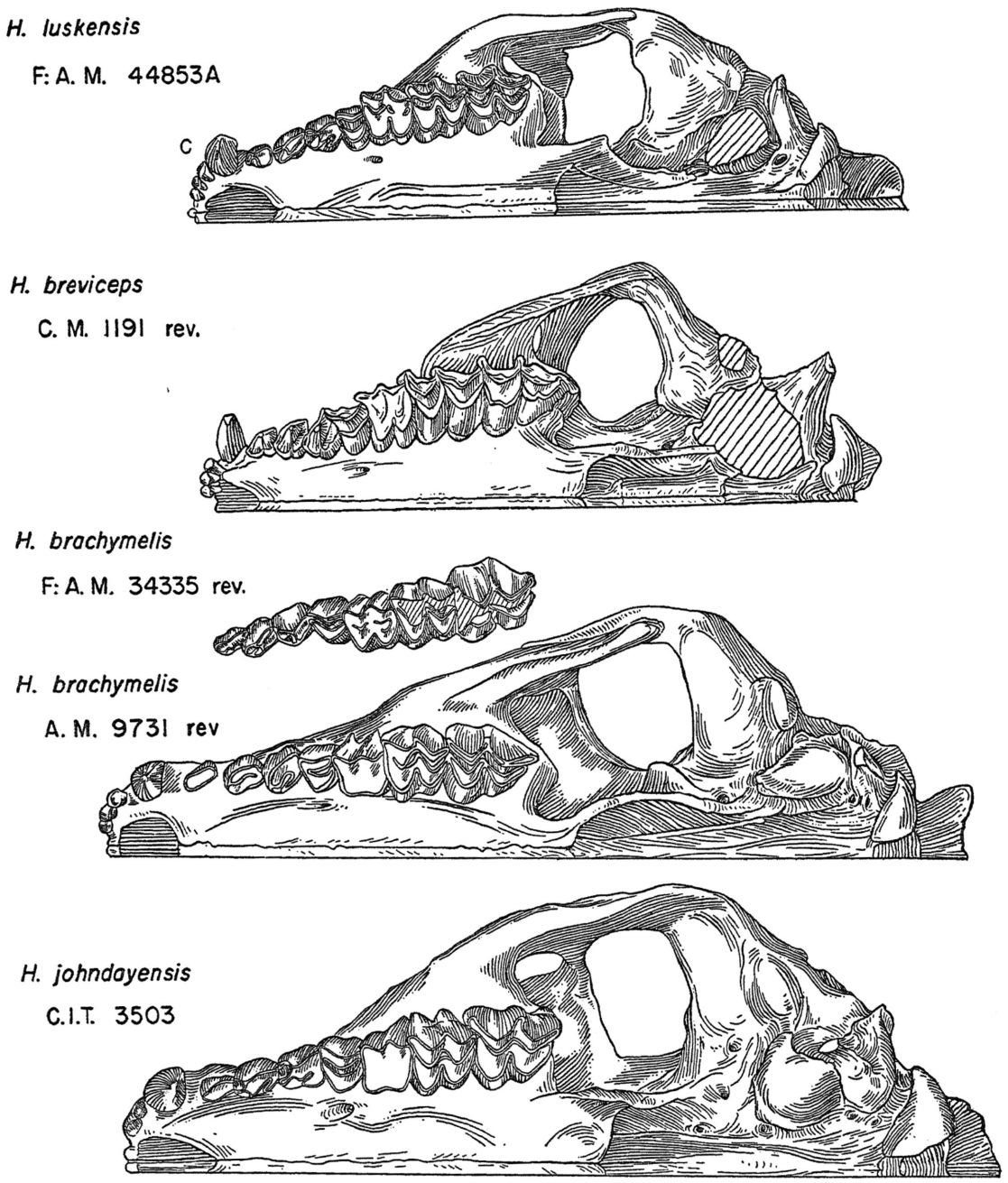
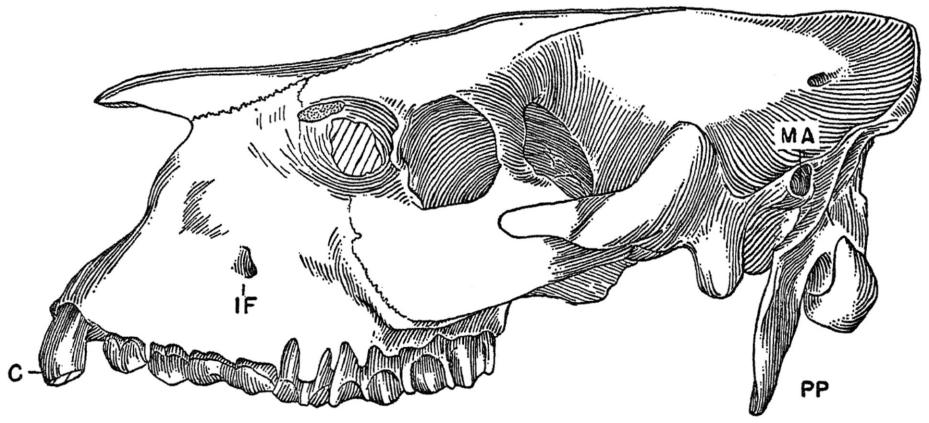


FIG. 6. *Hypsiops*, four species, holotypes, F:A.M. 44853A, C.M. 1191, A.M. 9731, and C.I.T. 3503, and referred, F:A.M. 34335. (See p. 133.) $\times\frac{1}{2}$. (See figs. 4, 5, 11, 12.)



H. brachymelis petersoni

F: A.M. 33313 rev.

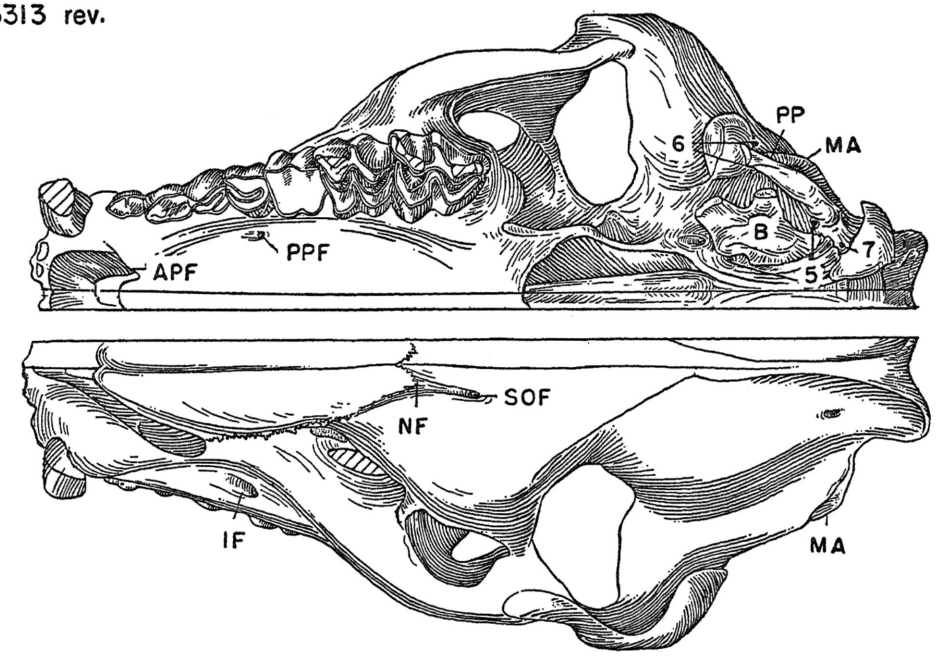


FIG. 7. *Hypsiops brachymelis petersoni* (Loomis), referred, F:A.M. 33313. (See p. 133.) ×½. (See fig. 11.)

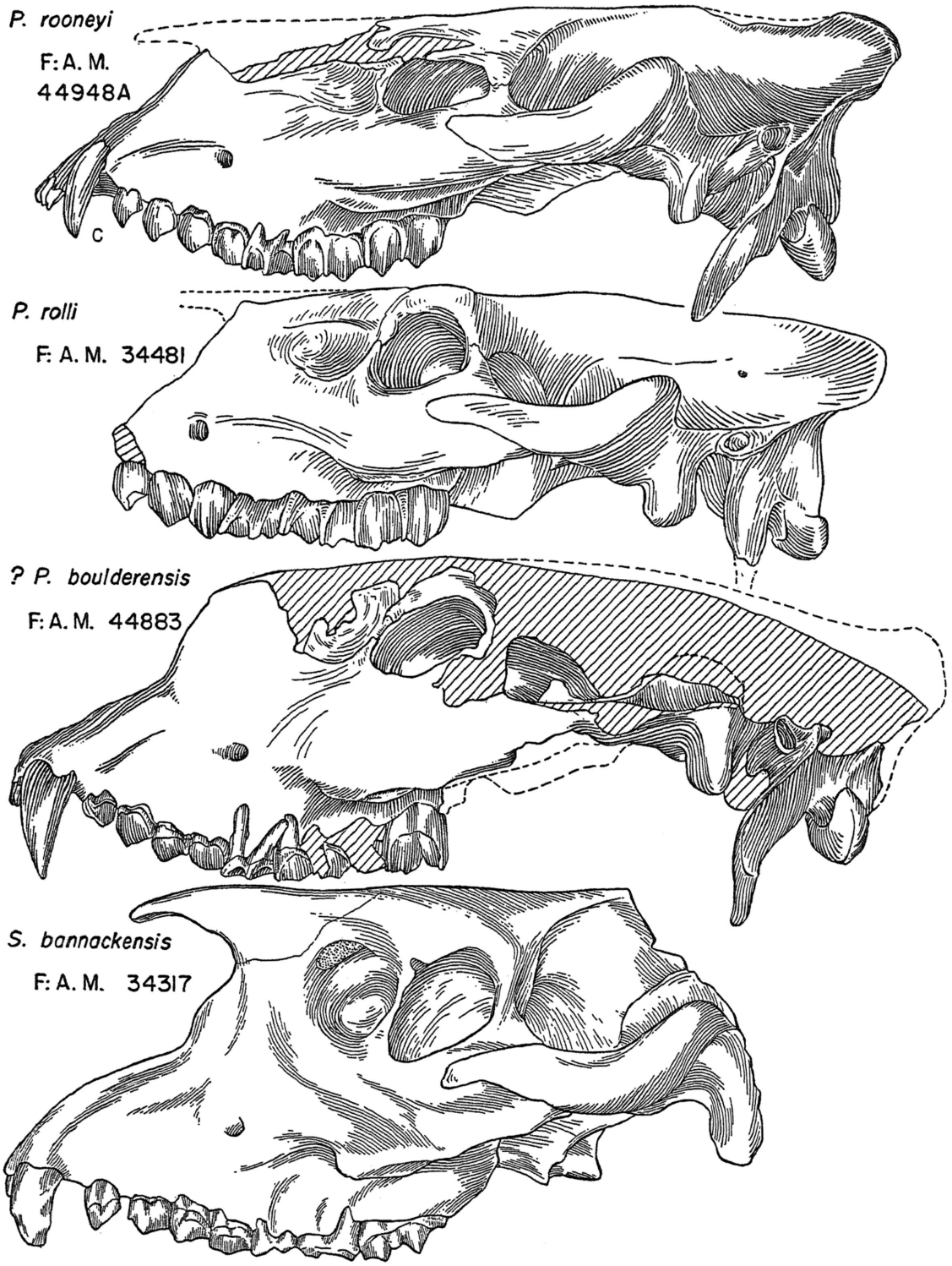


FIG. 8. *Pseudomesoreodon*, three species holotypes, F:A.M. 44948A, F:A.M. 34481, and F:A.M. 44883; *Submerycochoerus*, one species, referred, F:A.M. 34317. (See p. 133.) ×½. (See figs. 9, 10, 12.)

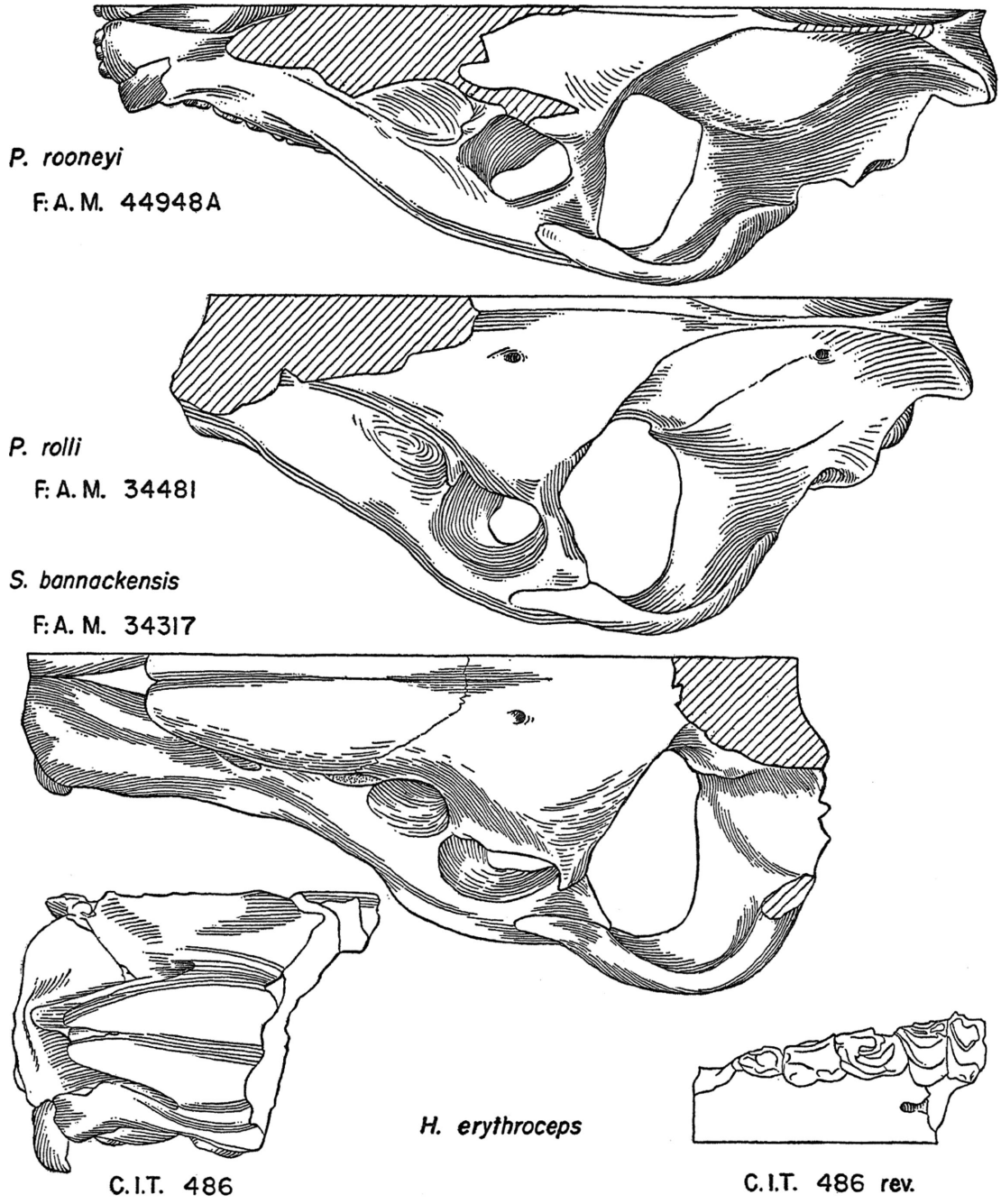


FIG. 9. *Pseudomesoreodon*, two species, holotypes, F:A.M. 44948A and F:A.M. 34481; *Submerycochoerus*, one species, referred, F:A.M. 34317; *Hypsiops*, one species, holotype, C.I.T. 486. (See p. 133.) ×½. (See figs. 8, 10, 12.)

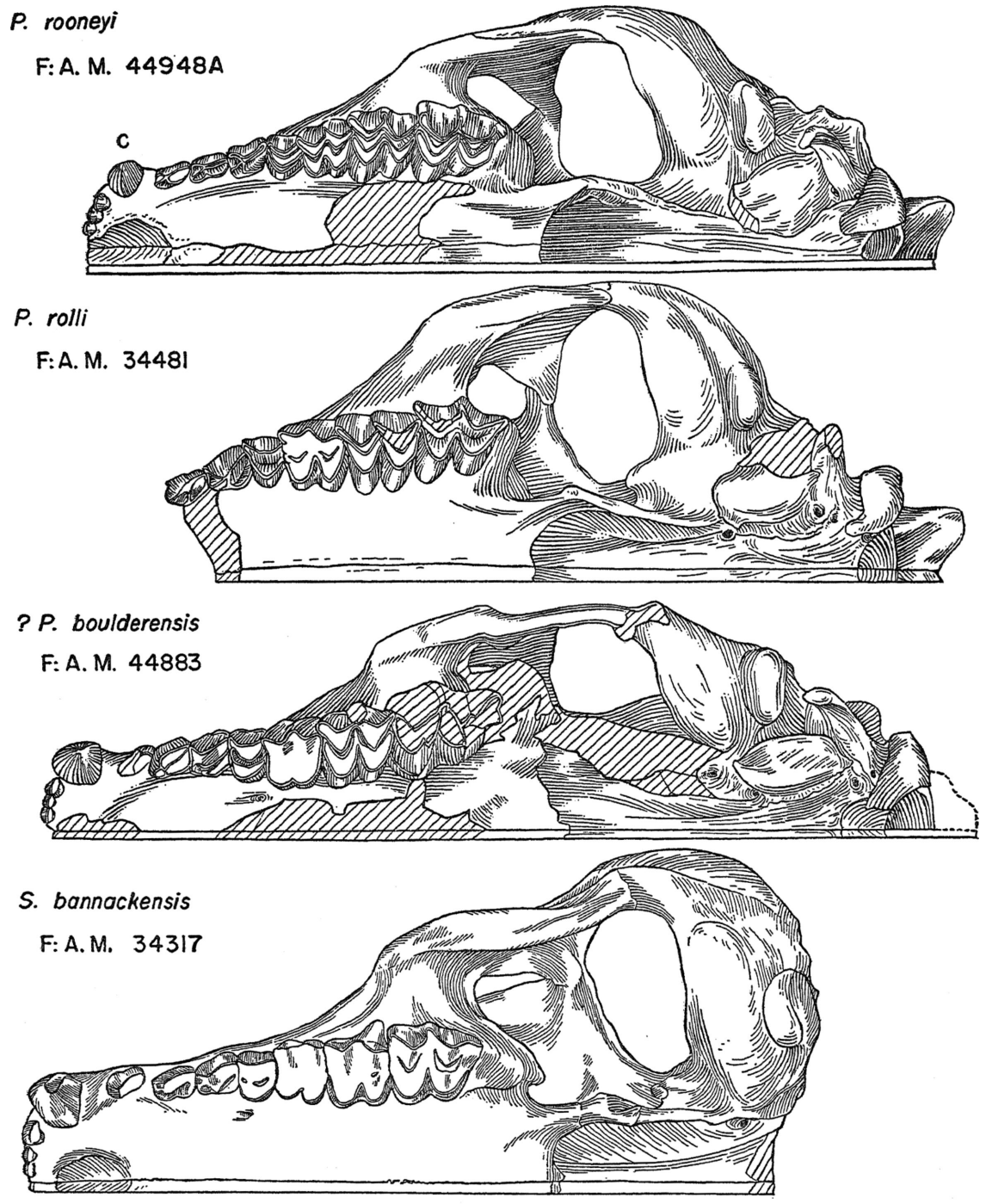


FIG. 10. *Pseudomesoreodon*, three species, holotypes, F:A.M. 44948A, F:A.M. 34481, and F:A.M. 44883; *Submerycochoerus*, one species, referred, F:A.M. 34317. (See p. 133.) ×⅓. (See figs. 8, 9, 12.)

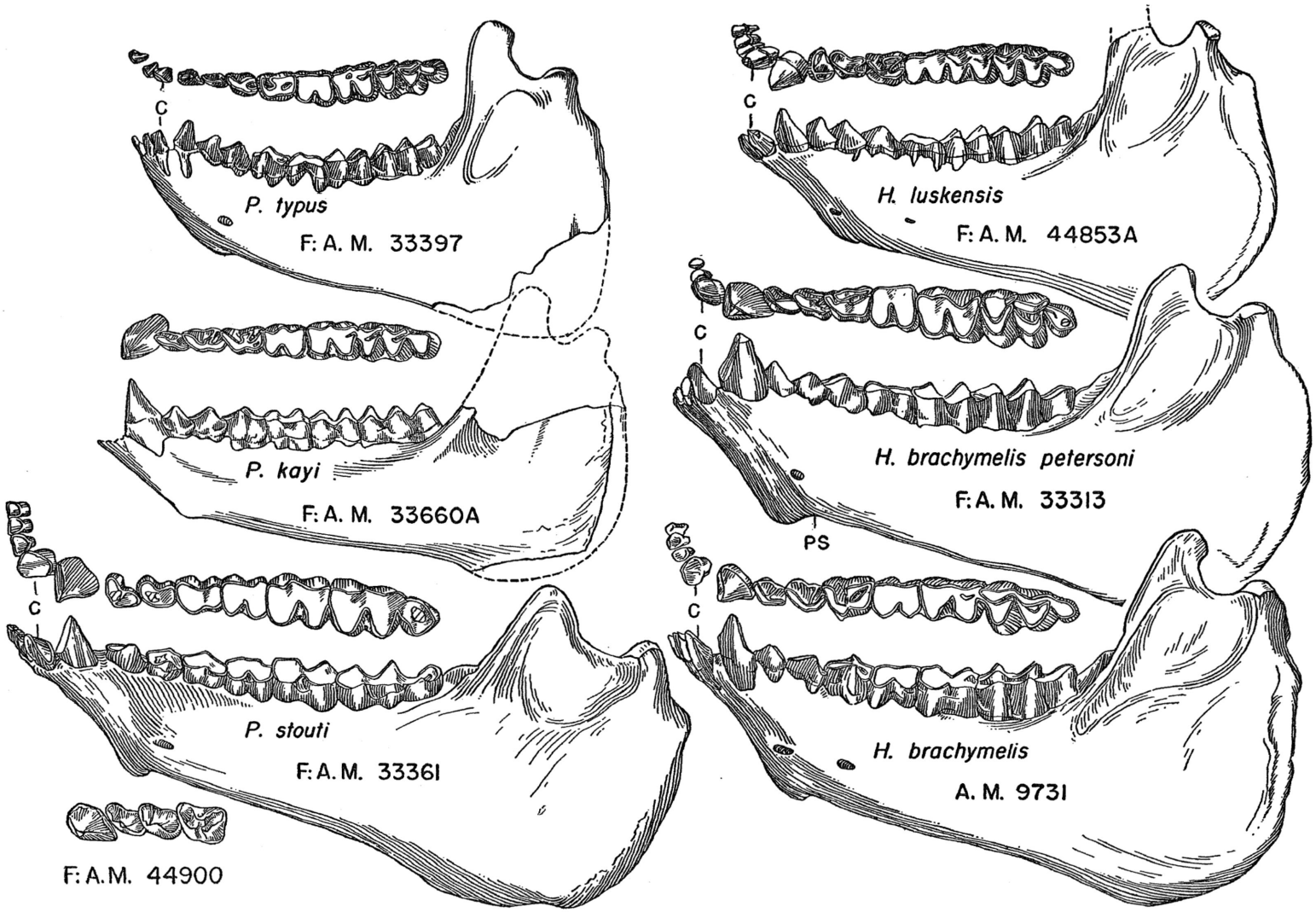


FIG. 11. *Phenacocoelus*, three species, holotype, F:A.M. 33660A, and referred, F:A.M. 33397, F:A.M. 33361, and F:A.M. 44900; *Hypsiops*, three species, holotypes, F:A.M. 44853A and A.M. 9731, and referred, F:A.M. 33313. (See p. 133.) ×½. (See skulls, figs. 1–7.)

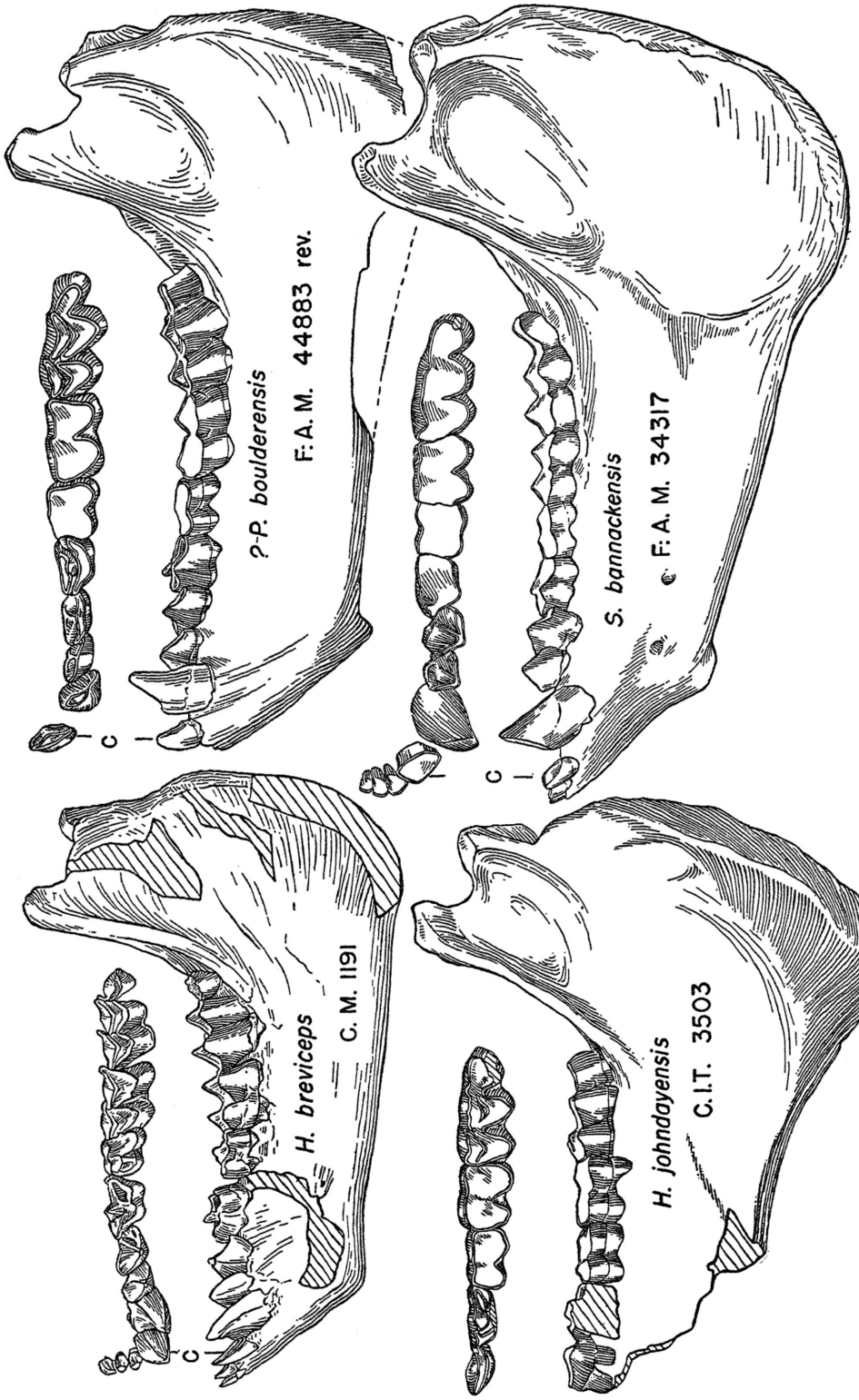


FIG. 12. *Hypsiops*, two species, holotypes, C.M. 1191 and C.I.T. 3503; *Pseudomesoreodon*, one species, holotype, F:A.M. 44883; *Submerycochoerus*, one species, referred, F:A.M. 34317. (See p. 133.) ×½. (See skulls, figs. 4–6, 8–10.)

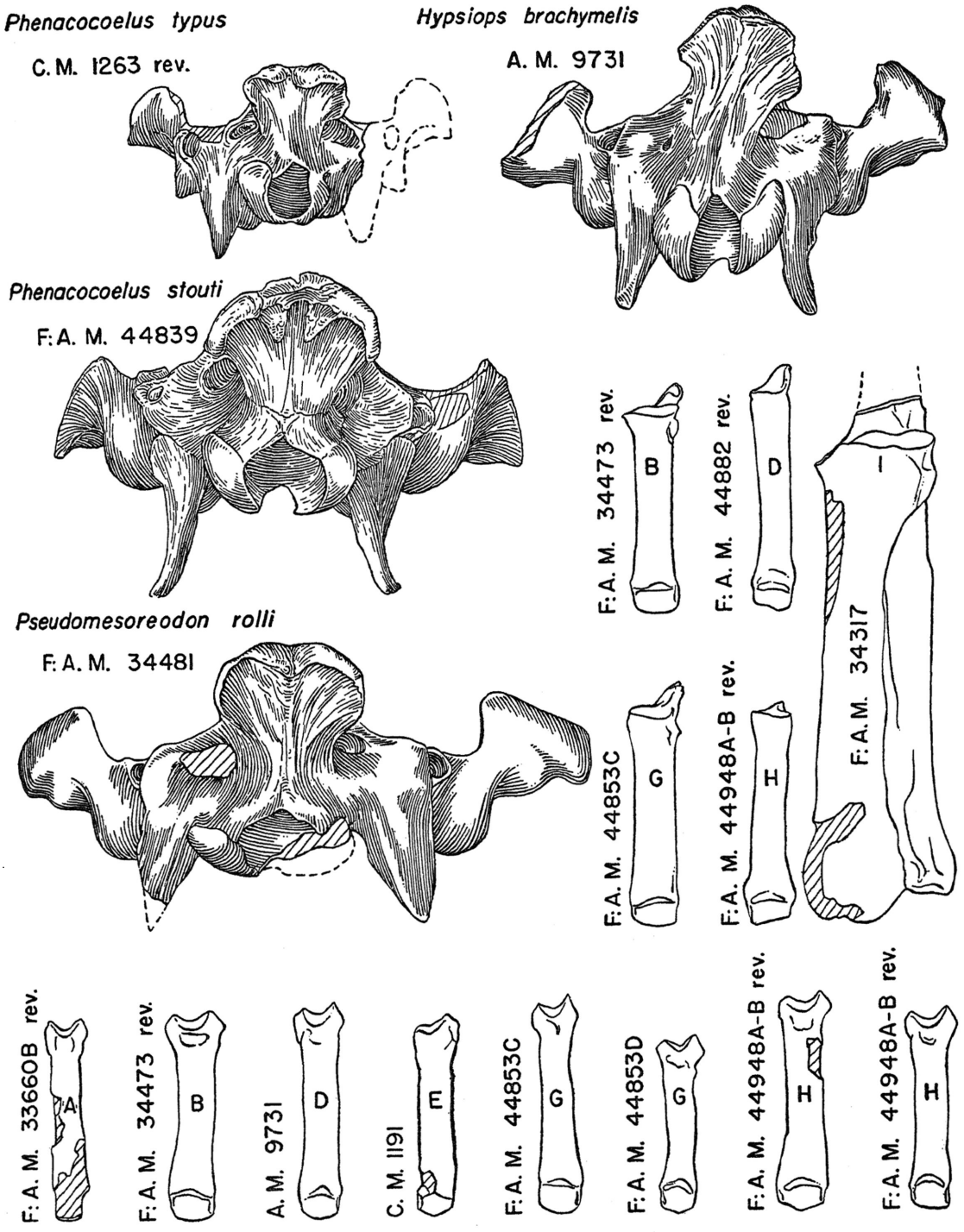


FIG. 13. *Phenacocoelus*, two species, holotypes, C.M. 1263 and F:A.M. 44839; *Hypsiops*, one species, holotype, A.M. 9731; *Pseudomesoreodon*, one species, holotype, F:A.M. 34481. Comparison of limb elements: *A. Phenacocoelus kayi*. B. *P. stouti*. C. *P. typus* (see fig. 15). D. *Hypsiops brachymelis*. E. *H. breviceps*. F. *H. brachymelis petersoni* (see figs. 14, 15). G. *H. luskensis*. H. *Pseudomesoreodon rooneyi*. I. *Submerycochoerus bannackensis*. (See p. 134.) ×⅓.

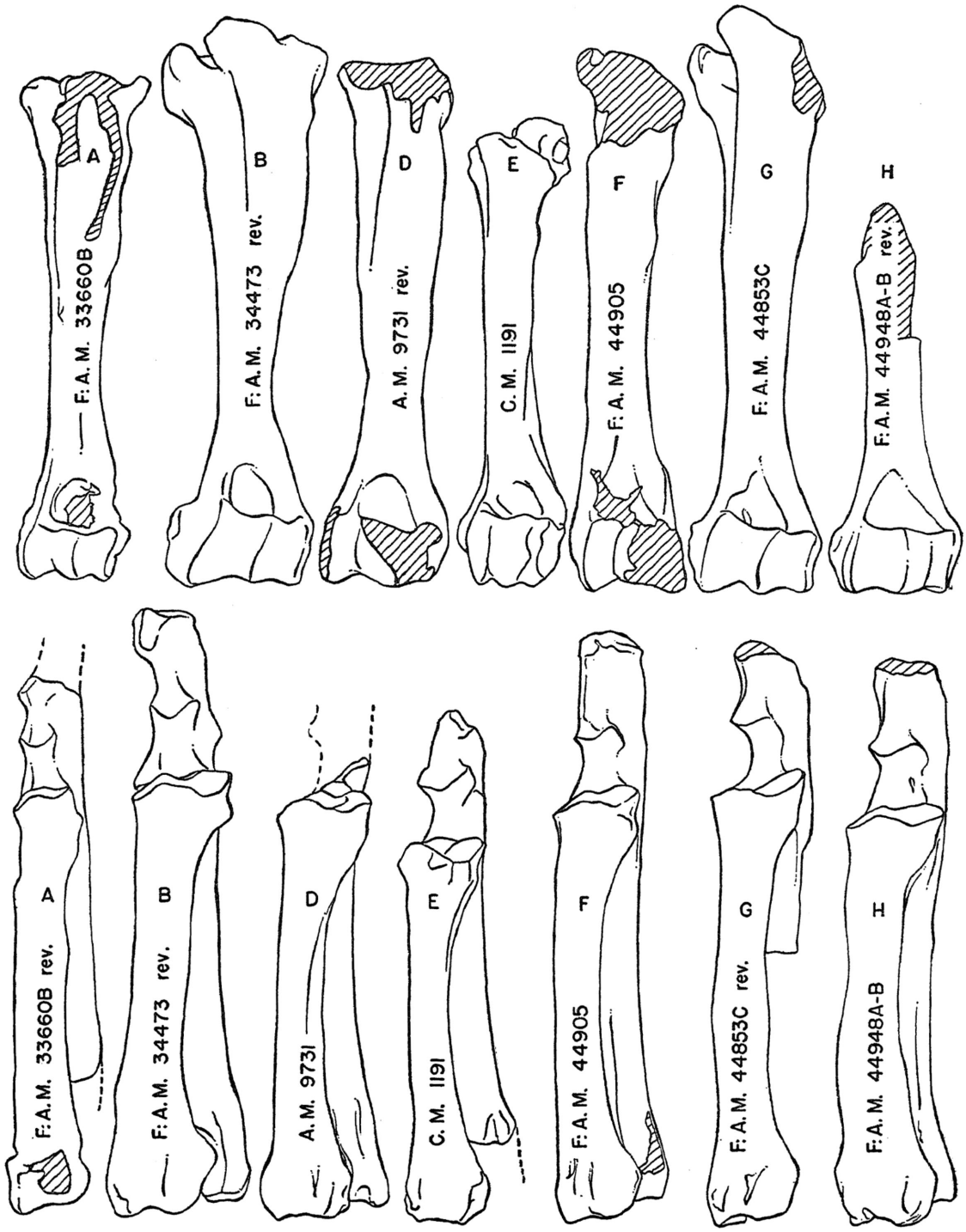


FIG. 14. See legend, fig. 13, and p. 134.

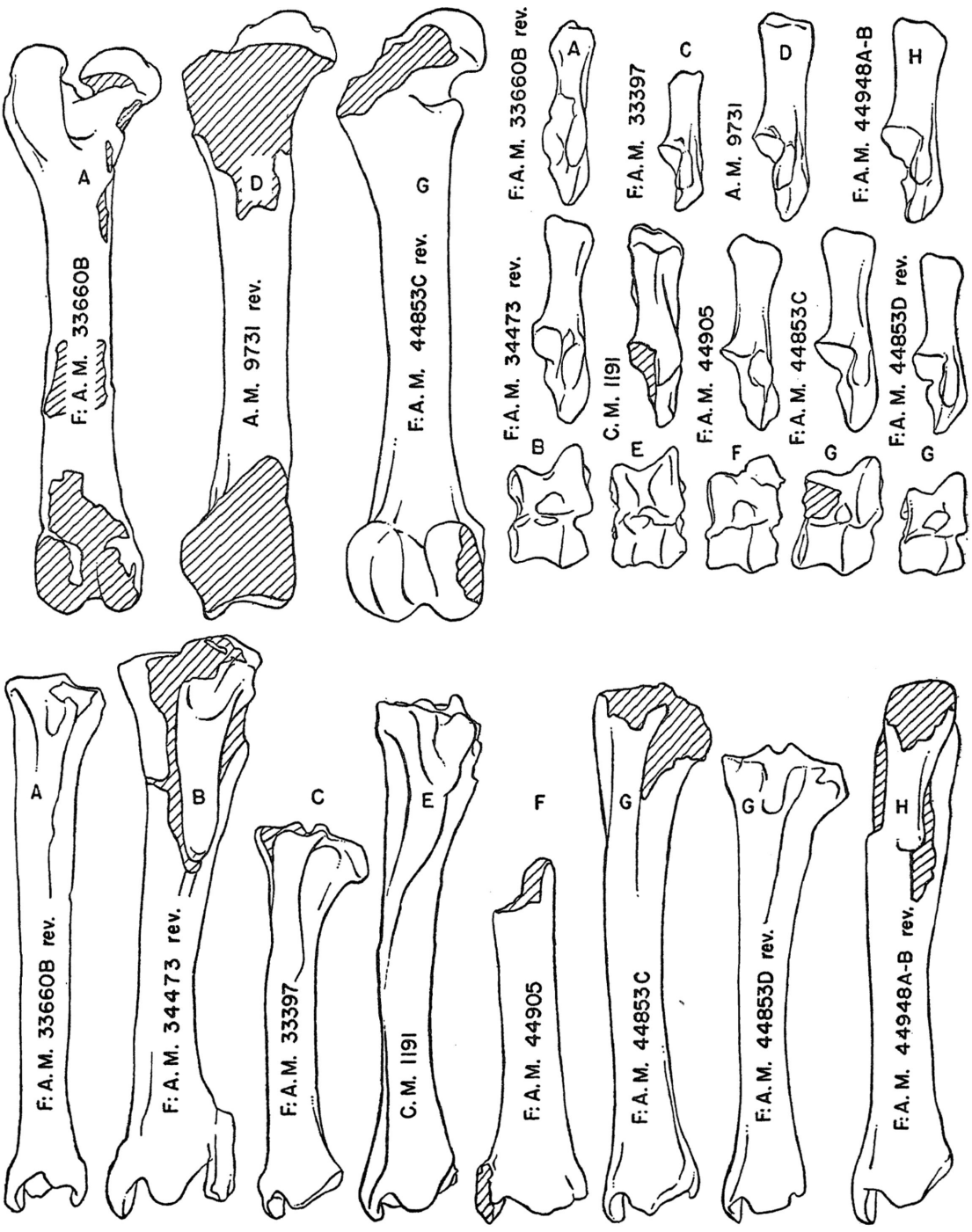


FIG. 15. See legend, fig. 13, and p. 134.