A Skull of *Hemipsalodon* (Mammalia, Deltatheridia) From the Clarno Formation of Oregon

BY JAMES S. MELLETT[1]

INTRODUCTION

Hemipsalodon grandis was first described by Cope (1885) on the basis of a lower jaw fragment and partial femur that came from the Cypress Hills Formation (early Oligocene) of Saskatchewan. Cope believed the animal was an oxyaenid.

Some years later, Lambe (1908) illustrated a large canine fragment which he assigned to *Hemipsalodon.*

L. S. Russell (1934), in his revision of the Cypress Hills fauna, described and illustrated the presumed upper dentition of the genus and later (1938) described the anterior part of a skull and attempted a restoration of this large carnivorous mammal. Russell correctly depicted the bearlike appearance of the animal but underestimated the total length and width of the skull.

Schlaikjer (1935) discovered a lower jaw fragment and piece of humerus in the early Oligocene Yoder (? = Chadron) Formation[2] of southeastern Wyoming and referred it to a new species which he called *Hemipsalodon cooki.*

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[1] Department of Geology, Washington Square College, New York University.

[2] Schlaikjer (1935) based his Yoder Formation on what he interpreted to be an interval of channel cutting and filling in the early Oligocene that was later followed by deposition of the greenish-gray clays of the Chadron Formation. The Yoder channel

Evernden and others (1964), on the basis of an identification sup-plied by Malcolm C. McKenna, reported the presence of *Hemipsalodon* in the late Eocene Clarno Formation of Central Oregon. According to Hay (1963, p. 201), "The Clarno Formation consists largely of lave flows and volcanic breccias, but volcanic conglomerates and sandstones, clay-stones and vitric tuffs are common in some places. The various litho-logic units interfinger laterally, and no units have been found which are sufficiently widespread to subdivide the formation over a distance of more than 10 miles. The full thickness of the formation is about 5000 feet. . ." The fossil bearing horizon is in the uppermost few hundred feet of the section (see also Baldwin, 1964).

The specimen referred to in that paper (a complete, but partially crushed skull) was part of an extensive collection of mammals from the Clarno Formation which is now divided between the University of Oregon Museum of Natural History, Eugene, Oregon, and the Oregon Museum of Science and Industry, Portland. The present paper is a de-scription of that skull.

ACKNOWLEDGMENTS

ABBREVIATIONS

The following abbreviations are used to designate institutional collections in

fills, however, cannot be traced laterally and it is impossible to establish their strati-graphic relationships with the type area of the Chadron to the East. Clark and others (1967, fig. 24) treated the Yoder as a unit separate from the Chadron Formation, al-though they referred it to the Chadronian Stage. In the index of that same paper (p. 158) however, the Yoder is described as a member of the Chadron Formation.

vertebrate paleontology:

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

N.M.C., the National Museum of Natural Sciences, Ottawa, Ontario

O.M.S.I., the Oregon Museum of Science and Industry, Portland (A. S. Hancock Collection)

S.D.S.M., the South Dakota School of Mines, Rapid City

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

SYSTEMATICS

ORDER DELTATHERIDIA VAN VALEN, 1965

SUBORDER HYAENODONTA VAN VALEN, 1967

FAMILY HYAENODONTIDAE

HEMIPSALODON COPE, 1885

Hemipsalodon grandis COPE, 1885, p. 163.
Hemipsalodon cooki SCHLAIKJER, 1935.

HOLOTYPE: N.M.C. No. 6497 (A.M.N.H. No. 10636 is a cast of the holotype).

HYPODIGM: N.M.C. Nos. 8791 (fig. 7A), 8641, O.M.S.I. No. 619 (figs. 1–6, 7B, 8A, 9A, 10) and an unnumbered specimen (figs. 11, 12), S.D.S.M. No. 6333 (figs. 9B, C).

GEOLOGIC AND GEOGRAPHIC RANGE: late Eocene-early Oligocene of Saskatchewan, Oregon, Wyoming, and Texas.[1]

REVISED GENERIC DIAGNOSIS: Very large *Pterodon*-like hyaenodontid; skull length 450 mm.; dental formula 3-1-4-3/3-1-4-3; distinguished from *Hyaenodon* by the presence of M^3 and the absence of proximodis-

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[1] I prefer to avoid the problems involved in suggesting either a classical Lyellian age or a Land-Mammal age for the stratigraphic range of *Hemipsalodon*. Potassium-Argon dates on volcanic rocks deposited near sediments that produced *Hemipsalodon* show a five million year dispersion. Samples KA 818 (37.5×10^6 years) and KA 824A (36.5×10^6 years) are both from the Clarno Formation in Oregon (Evernden and others, 1964), but were collected about 20 miles from the locality that produced *Hemipsalodon* and according to Hay (*in* Evernden and others, 1964, p. 182), may be younger than the Clarno fauna. Swanson and Robinson (1968), however, have dated a rhyolite flow above what they referred to as "post-Clarno" rocks at 41 million years. If valid, this last date would clearly place the Clarno Formation in the latest Eocene (Uintan). Which of the Clarno dates (if any) is in error cannot be determined. The following dates have been obtained on the Bracks rhyolite, Vieja Group, Texas: KA 1010 (36.8×10^6 years) by Evernden and others (1964), and 36.5×10^6 years by Wilson and others (1968). The Bracks rhyolite is younger than the Porvenir Local Fauna, which includes *Hemipsalodon*. No dates have been obtained (or to my knowledge are they obtainable) from the Cypress Hills Formation, Saskatchewan, or from the "Yoder Formation" in Wyoming, both of which are now considered early Oligocene in age.
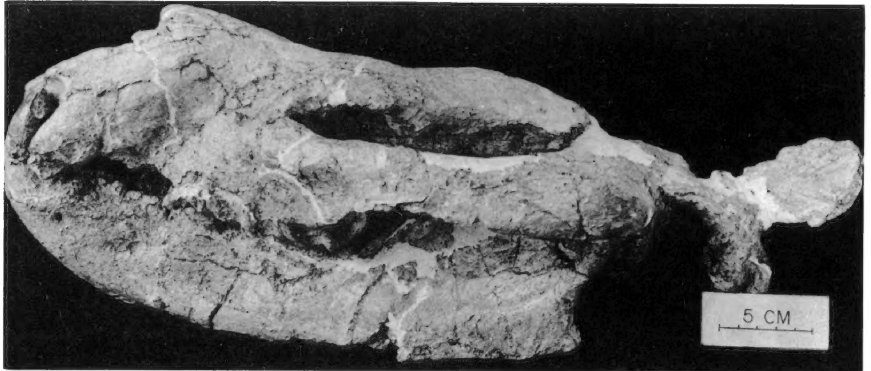
FIG. 1. *Hemipsalodon grandis,* O.M.S.I. No. 619, lateral view of skull and jaws.

tally oriented shear facets on M^{1-2}/M_{2-3}; distinguished from *Pterodon* by its much larger size, by the presence of widely separated paracone and metacone on M^2, by having a much larger M^3, distinct lingual cingula on the upper and lower teeth and by the presence of upper and lower molars that rotate during ontogeny along the proximodistal axis.

SPECIFIC DIAGNOSIS: Sole known species of the genus.

DESCRIPTION: The skull belonged to an old individual; it is extremely long and robust, with heavy, horizontal zygomatic arches (figs. 1–7), and exceeded in all proportions the size of *Pterodon africanus.* Although the sagittal crest has broken away, it is clear from the appression of the left and right frontal crests just above the orbits that the sagittal crest must have risen quite high above the braincase as it does in very old males of *Didelphis.* The skull of *Hemipsalodon* is very similar in many respects to the large mesonychid *Harpagolestes* of the Eocene of North America.

The nasal opening is quite large and the massive canines give an inflated appearance to the anterior part of the snout. The frontal area of the skull is broad anteriorly but narrows down considerably to the rear; the braincase is quite small.

Heavy zygomatic arches extend widely laterad. A crest rises from the dorsal portion of the arch and extends to the rear to meet the enormously expanded mastoid process. The postglenoid process is heavily built and is penetrated by a large postglenoid foramen. The nuchal crest is high and narrow and the occipital region of the skull is hourglass shaped when viewed from the rear (fig. 7B).

The palate is wide and concave in the frontal plane. A strong crest is developed along the midline of the palate and extends posteriorly to
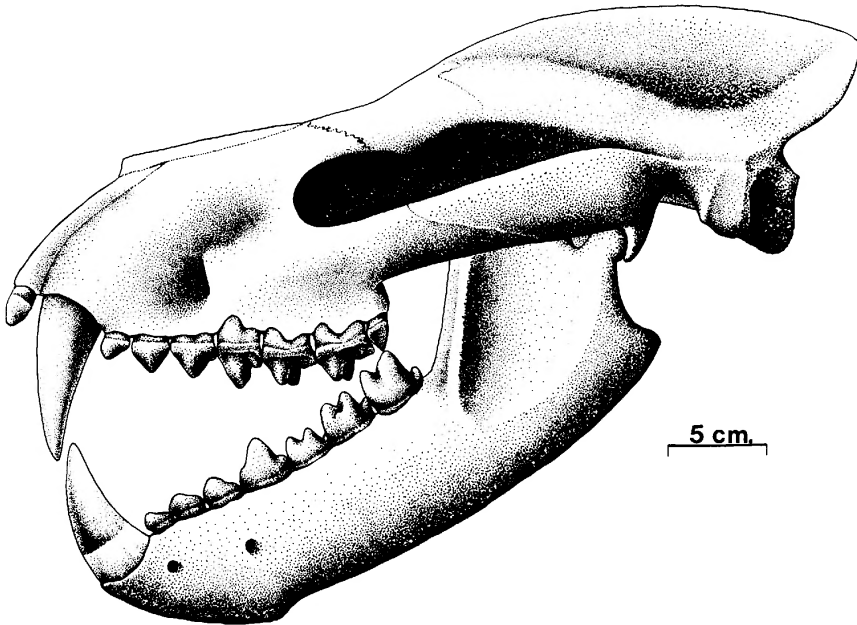
Fɪɢ. 2. *Hemipsalodon grandis,* reconstruction of skull and jaws.

merge with another (the postpalatine torus) that is developed trans-
versely, immediately behind the level of M^3.

A posterior palatine elongation exists in *Hemipsalodon,* although it is
not developed into the tubular extension that characterizes *Hyaenodon.*

The basicranium is moderately shortened; it does not appear to be
compressed anteroposteriorly to so great a degree as occurs in the larger
species of *Hyaenodon.* No details of basicranial structure can be ascer-
tained.

The lower jaw is quite deep, much more so than in *Pterodon africanus,*
but it is not so massive as it is in the type of *H. grandis.* The symphysis
is highly rugose and is inclined forward about 45 degrees (fig. 8C).
Two mental foramina penetrate the lateral side of the jaw; one occurs
below P_1 and the other ventral to the junction of P_3 and P_4. Most of
the coronoid process has been broken off but some detail can be seen.
The anterior border of the coronoid flares out laterally to form a dis-
tinct crest. A shallow masseteric fossa is developed on the lateral jaw
border; the lower portion of the fossa slopes off gradually onto the main
body of the ramus. The posteroventral portion of the fossa forms a faint
crest that rises dorsad and laterad onto the dentary condyle, which is
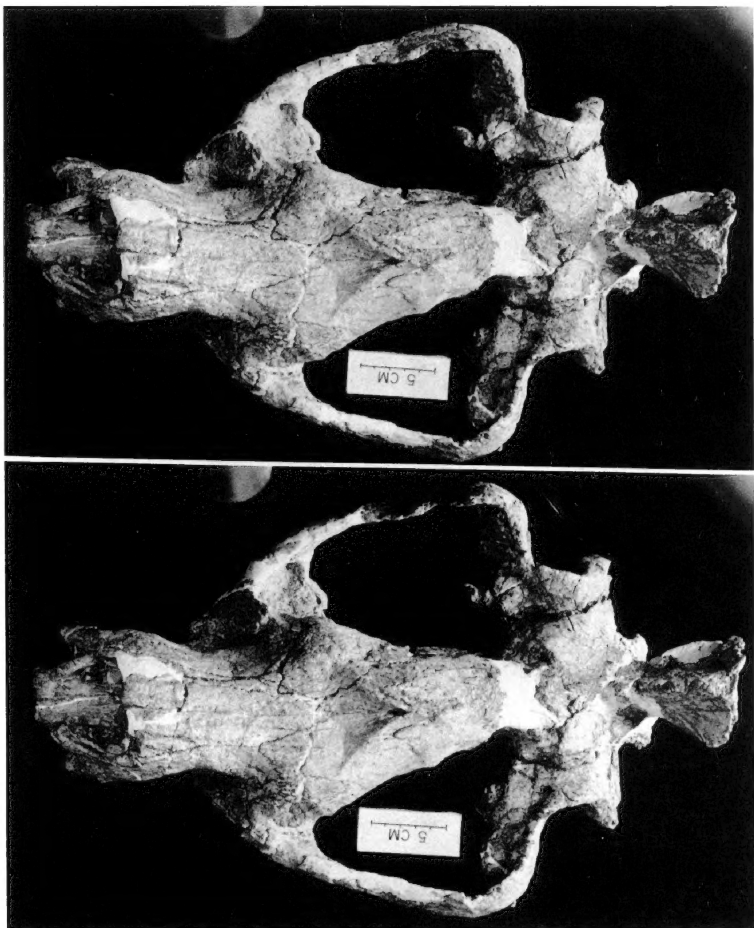
FIG. 3. *Hemipsalodon grandis*, O.M.S.I. No. 619, stereophotograph of skull in dorsal view.
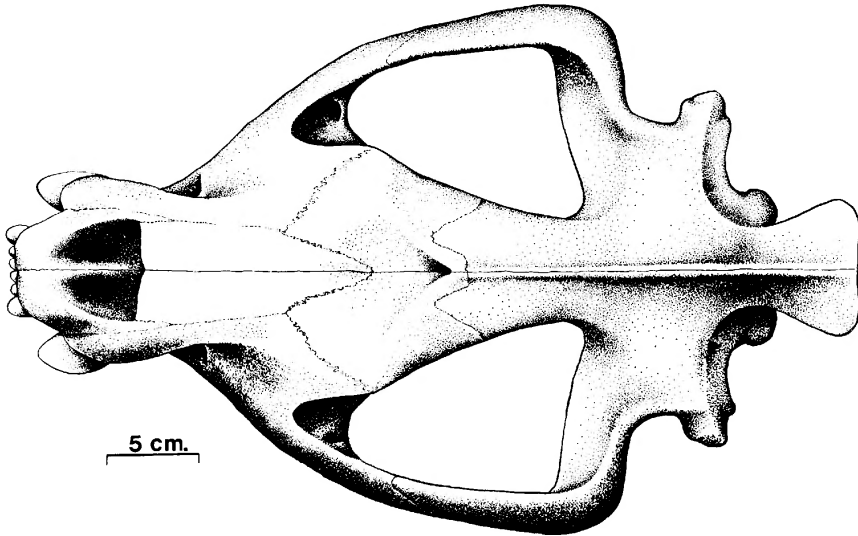
6

FIG. 4. *Hemipsalodon grandis,* reconstruction of skull, dorsal view.

extremely wide and heavy.

DENTITION (FIGS. 2, 5, 6, 8–12): The tooth formula of *Hemipsalodon* is 3-1-4-3/3-1-4-3 and not 3-1-3-3/ as Russell (1938) reported. The material he had to work with, however, made accurate determination of the formula difficult. Perhaps the most unusual aspect of the dentition is the rotation of the upper and lower molar tooth rows. Both sets are rotated along the proximodistal axes of the teeth; the uppers are rotated mediad and the lowers laterad. I had originally believed that the rotation was the result of postmortem crushing and, indeed, to some degree it is (figs. 5, 9A). However, if the teeth are restored to vertical positions within the jaw, the wear facets on the upper and lower molars

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF SKULL AND JAWS OF *Hemipsalodon grandis,* O.M.S.I. No. 619

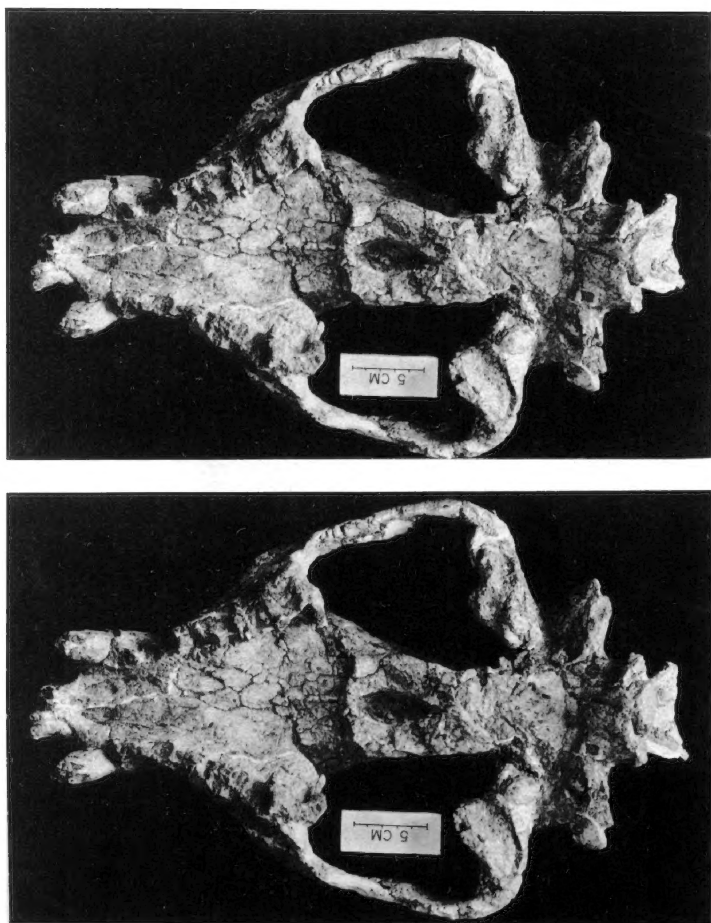|	
Total skull length	450
Maximum width across zygomas	290
Maximum width across mastoids	190
Width across orbits	130
Palatal width at level of M^{2-3}	160
Maximum length of lower jaw	340
Symphyseal length	90

Fɪɢ. 5. *Hemipsalodon grandis*, O.M.S.I. No. 619, stereophotograph of skull in ventral view.
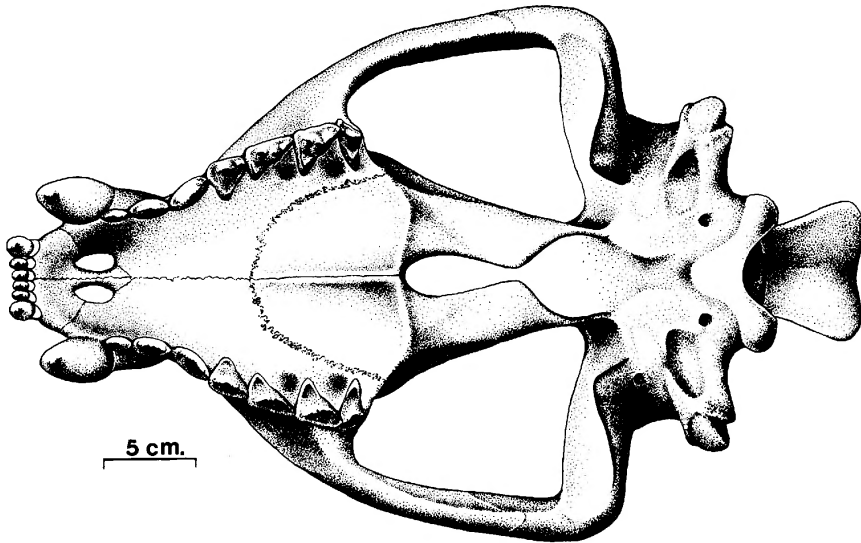
FIG. 6. *Hemipsalodon grandis,* reconstruction of skull, ventral view.

are arranged so as to make occlusion virtually impossible, short of dislocating the condyle from the glenoid fossa. It is significant that a similar kind of rotation during ontogeny occurs in a related hyaenodont, *Hyaenodon* (Mellett, [In Press]); it is also significant that rotation does not occur in any specimen of *Pterodon* that I have examined. The upper teeth of *Hemipsalodon* that were illustrated by Russell (1934, fig. 1) show a wear pattern similar to that observed in O.M.S.I. No. 619 and support the suggestion of molar rotation.

The upper incisors are arranged in a slightly convex row. I^3 is larger than the other two, which are subequal in size. A large diastema is developed between the incisors and the large upper canine to accommodate the massive lower canines. The upper canine is elliptical in cross section with the longer axis proximodistal. In a young individual, the canine enamel is rugose and a heavy enamel ridge runs down the distolingual border of the tooth.

P^1 and P^2 are double rooted; they are not preserved on the Clarno skull and little else can be said about them. P^3 has a small anterior and a large posterior root. A large, centrally situated cusp is developed on the tooth, but accessory cuspules cannot be recognized because of breakage. P^4 is very similar to that of *Hyaenodon;* it is a large, three-rooted tooth with a heavy cingulum developed around its periphery. The main

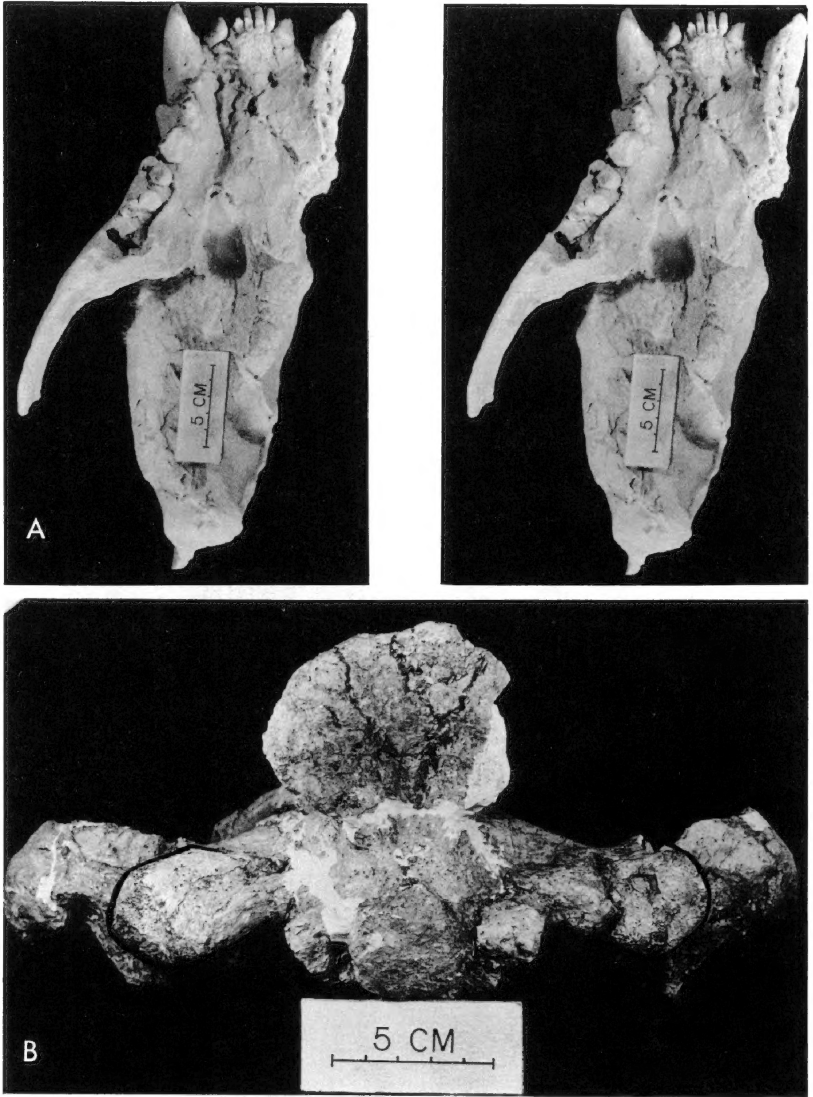Fig. 7. *Hemipsalodon grandis.* A. Cast of N.M.C. No. 8791, stereophotograph. B. O.M.S.I. No. 619, posterior view of skull.

labial cusp is high, laterally compressed, and central in position. An anterior crest runs from the apex of this tooth toward the cingulum; a posterior crest descends from the apex, but is interrupted by a large posterior basal cusp. Judging from the size of the medial root, the pro-
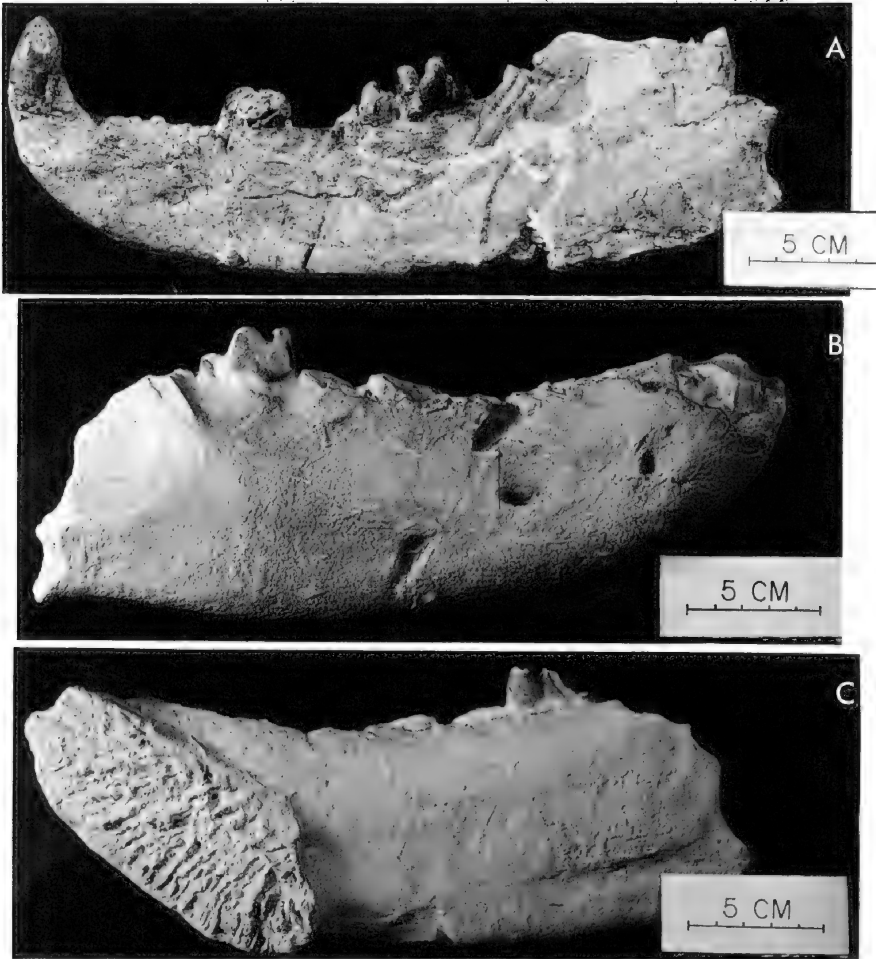
FIG. 8. *Hemipsalodon grandis*. A. O.M.S.I. No. 619, lateral view of lower jaw. B, C. A.M.N.H. No. 10636 (cast of holotype). B. Lateral view of lower jaw. C. Medial view of lower jaw.

tocone was an important cusp, but it is not preserved in any specimen at my disposal.

M^1 is a triangular tooth with distinct paracone, metacone, and protocone. The metacone is proximolingual to the paracone; both cusps are laterally compressed. A strong, bladelike metastyle extends proximobuccally from the rear portion of the tooth. M^2 is basically similar to M^1 except that it is much larger and the paracone and metacone are more strongly compressed. The protocone is low and sends a prepara-
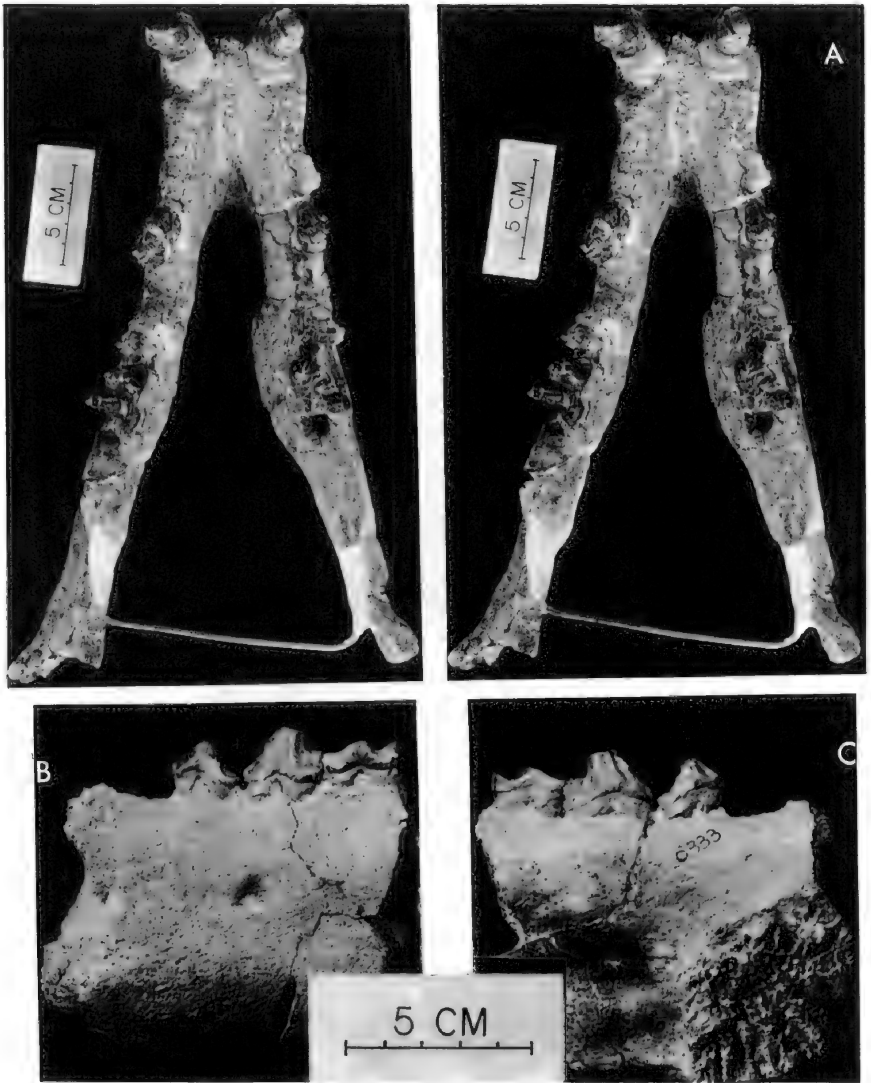
FIG. 9. *Hemipsalodon grandis*. A. O.M.S.I. No. 619, stereophotograph of lower jaws in dorsal view. B, C. S.D.S.M. No. 6333. B. Lateral view of lower jaw fragment. C. Medial view of lower jaw fragment.

crista and postparacrista buccally toward the base of the paracone and metacone respectively. M^3 is shaped like an isosceles triangle with a broad base. A single large parametacone occurs almost in the center of the tooth. A distinct preparacrista extends from the cusp apex disto-

FIG. 10. *Hemipsalodon grandis,* reconstruction of lower jaws in dorsal view.

buccally toward the margin of M^3. A postmetacrista is also developed but breakage prevents assessment of its extent. The protocone is much smaller than the parametacone and sends a preprotocrista buccally which merges against the base of the parametacone. A postprotocrista extends proximobuccally from the protocone toward the margin of the tooth, but breakage is too extensive to permit mapping of other details.
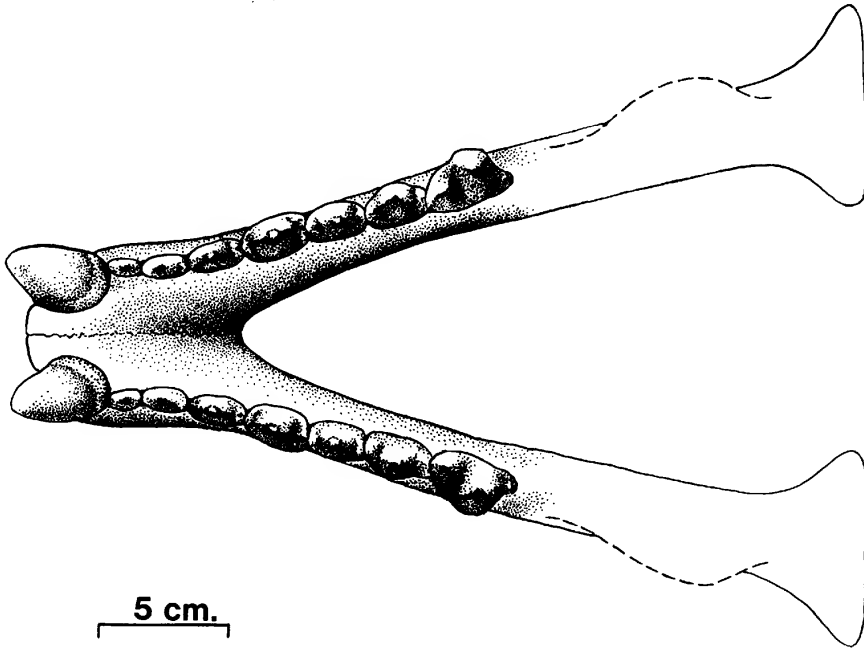
Deep sockets occur in the maxilla between M^{1-2} and M^{2-3} to accommodate the large trigonids of M_{2-3}.

The lower canine is large and is thickly covered with enamel. P_1 is single rooted and is rotated slightly buccad, out of the main axis of the tooth row. The crown is not preserved. P_2 is double rooted and is also missing the crown. P_3 is moderately high and relatively long, with a main cusp having anterior and posterior crests that run from the apex toward the base of the tooth. A small cuspule occurs at the base of the posterior crest. A distinct lingual cingulum appears on the tooth. P_4 is a large, robust tooth that is very similar to P_4 of *Hyaenodon.* A small cuspule occurs on the distolingual corner of the tooth, rises onto a high main cusp then drops off posteriorly to a large posterior basal cusp.
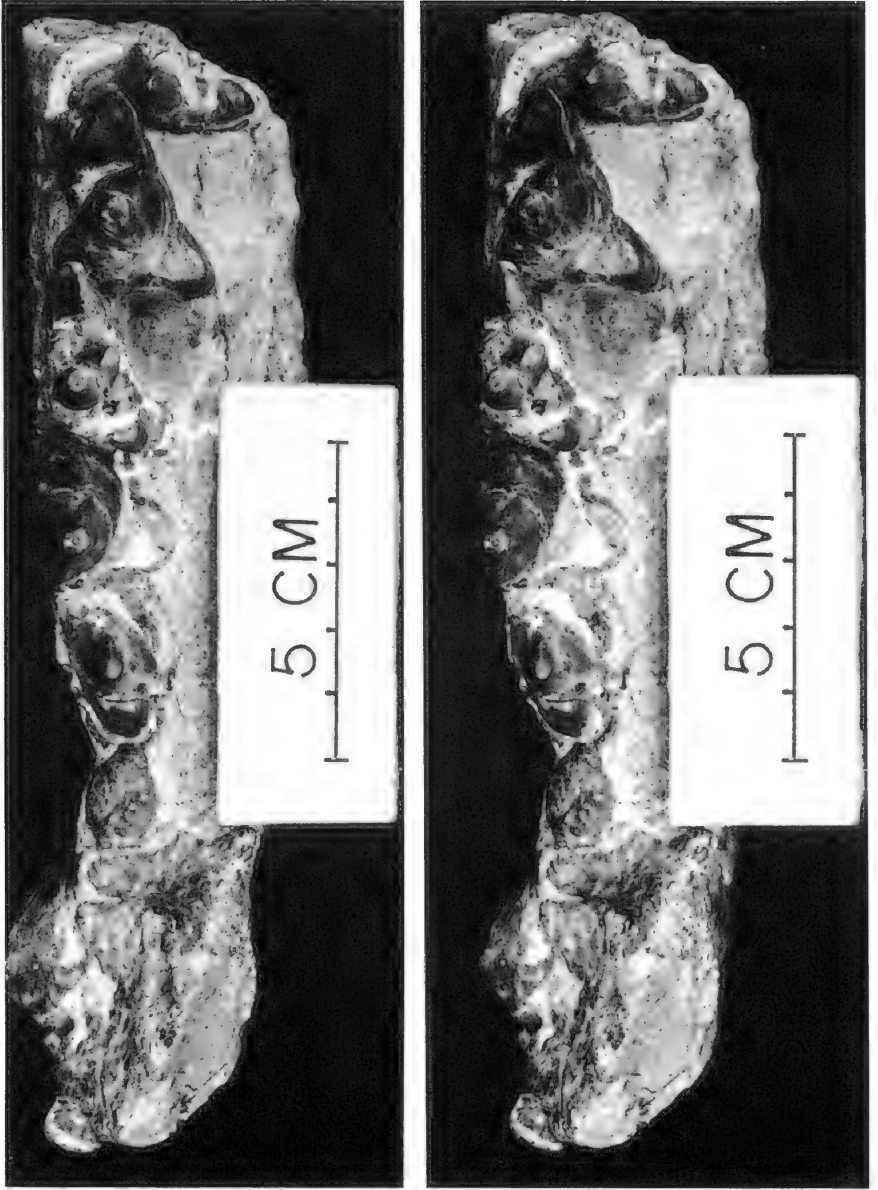
FIG. 11. *Hemipsalodon grandis*, O.M.S.I. No. (?), stereophotograph of left maxilla in ventral view.

14

M_1 is about as long as P_4 but is much narrower buccolingually and is developed as a carnassial. As in *Hyaenodon*, M_1 of *Hemipsalodon* probably occluded against a carnassial dP^4. No specimens I have seen show M_1 in its unworn condition and therefore little can be added to this description. M_2 is larger than M_1 and has a large carnassial blade that is made up of the enlarged paracristid. The protoconid is higher than the paraconid and there is no trace of a metaconid. A shearing face also occurs on the posterior portion of the protocristid. A rather large talonid is developed on the tooth. M_3 is the largest of the lower molar series and is similar to M_2 in all respects except for a slightly smaller talonid. Although breakage and distortion make it difficult to tell for certain, there appears to be no trace of a distolingual buttress on the prevallid of M_2 and M_3, as there is in *Pterodon*.
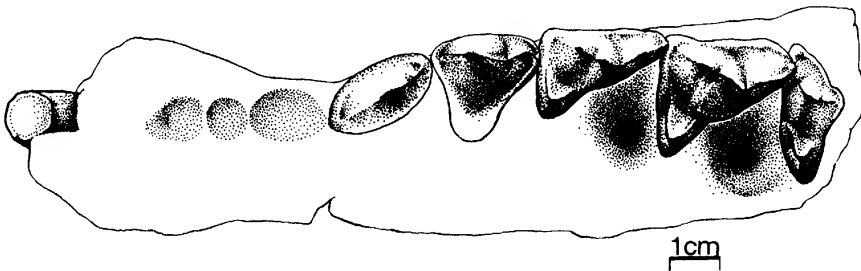

Fig. 12. *Hemipsalodon grandis*, reconstruction of P^3–M^3.

DISCUSSION: Russell (1938) thought that there were a number of species of *Hemipsalodon* in the Cypress Hills sediments because of a rather wide size range he had observed in the fossils available to him. The size differences among tooth and jaw measurements are no more than about 10 per cent, however, and differences of this magnitude can be ascribed easily to sexual dimorphism or intrapopulation variability. It is also difficult on ecologic grounds to argue for the coexistence of two carnivore species the size of *Hemipsalodon grandis* because competition between similar kinds of animals tends to become more severe the larger they are. For similar reasons, I believe that Schlaikjer's *Hemipsalodon cooki* is probably not valid. In fact the cast of Cope's type of *H. grandis* (a right mandible) and Schlaikjer's *H. cooki* (a left mandible) can be fitted together at their symphyses, which match each other quite well.

A number of authors, most recently Savage (1965) have stressed the great morphological similarity between *Pterodon* and *Hemipsalodon* and

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Hemipsalodon grandis*

	N.M.C. No. 8791[a]	N.M.C. No. 8641[b]	O.M.S.I. No. ?[c]	O.M.S.I. No. 619
Upper canine				
L	—	—	—	31
W	—	—	—	21
P1				
L	20[d]	—	—	—
W	—	—	—	—
P2				
L	18	—	—	—
W	10	—	—	—
P3				
L	20	—	—	—
W	15	—	—	—
P4				
L	15	—	—	—
W	—	—	23	—
M1				
L	—	24.4	26[d]	—
W	—	18.6	19	—
M2				
L	—	29.7	27	27
W	—	23.0	25	21
M3				
L	—	18.2	13	—
W	—	26.2	30	29
M1 3				
L	—	69.0	65	65
P1-M3				
L	130[d]	—	148	140

[a] Plaster cast of specimen.
[b] From Russell, 1934.
[c] Number apparently lost.
[d] Measured along alveoli or estimated.

have urged that both genera be lumped under the prior term *Pterodon*. Others, particularly Van Valen (1967) have urged separation of both forms. At the time of the most recent discussion, however, only fragmentary material of *Hemipsalodon* had been described and the evidence to support either viewpoint was insufficient. The skull described here (O.M.S.I. No. 619) provides additional information, which I believe supports continued separation of both taxa.

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Hemipsalodon grandis*

	A.M.N.H. No. 10636[a]	S.D.S.M. No. 6333	O.M.S.I. No. 619
Lower canine			
L	—	—	28
W	—	—	21
P_1			
L	20[b]	—	—
W	—	—	—
P_2			
L	23[b]	—	—
W	—	—	—
P_3			
L	—	19	—
W	—	10	—
P_4			
L	—	23	—
W	—	15	—
M_1			
L	—	21	—
W	—	11	—
M_2			
L	—	—	27
W	—	—	15
M_3			
L	35	—	34
W	22	—	22
$M_{1\ 3}$			
L	84	—	80
P_1–M_3			
L	165	—	160

[a] Cast of holotype.
[b] Measured along alveoli.

The salient differences between *Hemipsalodon* and *Pterodon* are listed in the diagnosis above. The most crucial difference is the appearance in *Hemipsalodon* of rotating upper and lower tooth rows, a condition that does not occur in any specimen of *Pterodon* that I have examined or seen illustrated. I conclude that *Pterodon* and *Hemipsalodon* represent independent parallel lineages that arose from some Old and New World proviverrines. Potential ancestors for both genera occur in Eocene sediments in both regions. *Arfia opisthotoma* (Van Valen, 1965) has a dental battery that with minor modifications (such as talonid reduction on M_{1-3})

could have given rise to *Hemipsalodon*. Similar kinds of proviverrines occur in Europe and were ancestral to *Pterodon*.

Hemipsalodon had a wide geographic range (from southern Canada to the Mexican border), although it was stratigraphically limited to sediments of late Eocene to early Oligocene age.

Fragmentary postcranial remains have been known for some time (Cope, 1885, Schlaikjer, 1935) and indicate that the animal was at least as large as a black bear. An astragalus (U.S.N.M. No. 7460), if it is correctly referred, suggests that the animal was plantigrade.

The heavy zygomatic arches indicate a well-developed masseteric muscle complex, unlike *Hyaenodon* in which the masseter group is reduced, and its function taken over by the internal pterygoids. The masseter complex of *Hemipsalodon* is much more like that of typical oxyaenids.

Hemipsalodon was the largest hyaenodontid to occur in North America.

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