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LATEST CRETACEOUS MAMMALS OF UPPER PART OF EDMONTON FORMATION OF ALBERTA, CANADA, AND REVIEW OF MARSUPIAL-PLACENTAL DICHOTOMY IN MAMMALIAN EVOLUTION

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JASON A. LILLEGRAVEN

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ABSTRACT

Multituberculate, marsupial, and placental mammals are described in detail from the upper part of the Edmonton Formation of Alberta, Canada, which is latest Cretaceous in age. Comparison of this fossil assemblage with assemblages of different ages from other geographic areas suggests that the Edmonton Formation was deposited at a critical period in the establishment of the modern mammalian fauna of North America. A definite taxonomic radiation of rapidly evolving placental mammals is documented, the two basal stocks of which appear to have been independently derived from Asiatic ancestors. Geological evidence suggests the possibility of faunal exchange across Bering Strait in Late Cretaceous time. Most lineages of Cretaceous marsupials, probably of North American origin, became extinct near the Mesozoic-Cenozoic boundary, immediately following the initiation of the placental radiation. The marsupials are abundantly represented in older rocks. No major climatic, floral, or physiographic changes have been recognized as having occurred at that time that would account for the taxonomically widespread extinction. The arrival of comparatively advanced (anatomically, physiologically, and behaviorally) placental mammals in North America in the Late Cretaceous was probably one major factor in the near extinction of marsupials on that continent.

The multituberculate fauna of the Edmonton Formation resembles that of the contemporaneous Lance Formation of Wyoming, but lacks *Meniscoessus* and *Essonodon*. A smaller new species of *Mesodma* can be separated from *M. formosa*. A new species of *Cimolomys* is larger than the previously described *C. gracilis*. A new species of *Cimexomys*, possessing several primitive features in its dentition, resembles multituberculates from older Cretaceous sediments of Asia and probably descended from an Asiatic migrant into North America.

All species of marsupials found in the Edmonton Formation have also been recorded in the Lance. However, several species commonly recovered from the Lance are rare or absent in the Edmonton. A new species of *Alphadon* can be separated from *A. marshi* on the basis of small size and dental proportions, but is present also in the Lance Formation.

The placentals from the Edmonton Formation represent two orders, Insectivora (Leptictidae) and Deltatheridia (Palaeoryctidae). *Gypsonictops* of the Leptictidae may be close to the ancestry of the Cenozoic leptictids, erinaceids, pantolestids, primates, and ultimately, the rodents. In the North American Cretaceous, *Cimolestes* (Palaeoryctidae) underwent a more profound radiation than did *Gypsonictops*. *Cimolestes magnus*, a large carnivorous species, may be a common ancestor for the hyaenodontid and oxyaenid carnivores. A smaller carnivorous species described as new of *Cimolestes* probably represents a primitive stage in the development of miacids, and subsequently fissiped and pinniped carnivores. An insectivorous species also described as new of *Cimolestes* is characterized by an early stage of development of the type of zalambdodont dentition observed in *Palaeoryctes* (Paleocene). *Batodon tenuis* probably will prove to be a species of *Cimolestes*. Detailed dental comparisons suggest that *Procerberus* (from the Hell Creek Formation, Montana) is a palaeoryctid deltatheridian, instead of a leptictid insectivore as has been supposed by others. It is suggested that the subfamily Procerberinae (Leptictidae) no longer be recognized. *Protungulatum*, the most primitive known condylarth, is not found in the Edmonton, but its affinities probably are greater with the palaeoryctids than with the leptictids.

Leptictids and palaeoryctids were genetically isolated from each other from the Campanian (about 75 million years before the present), but possess many common features not seen in the marsupials. A high degree of eutherian specialization probably already had been attained by Campanian time.

Most recent authors have stressed the point that living marsupials, especially in their urogenital system, lack the primitive characters to be expected in a therian ancestral to both marsupials and placentals, and are instead highly specialized. Nevertheless, a comparative analysis, character by character, of the urogenital system and of early embryonic development within the Amniota suggests that marsupials are less specialized than previously thought. The Early Cretaceous ancestral therian probably was rather "metatherian" in grade of development. No fundamental morphological feature, spatial relationship, or physiological mechanism in the urogenital system of living didelphid marsupials (probably excepting the pseudovaginal canal) is necessarily other than primitive for the Theria. Eutherian mammals, on the other hand, are profoundly specialized in many respects as compared with the typical amniote plan.

INTRODUCTION

Three basic purposes were kept in mind with the writing of this paper. The first was to describe in detail the assemblage of fossil mammals found in the upper part of the Late Cretaceous Edmonton Formation, Alberta, Canada, and to point out the evolutionary significance of the Edmonton fauna in comparison with fossils from other chronological sequences or geographic areas. The second purpose was to summarize the basic comparative anatomy and physiology of the reproductive systems of marsupial and placental mammals. This summarization led me to speculations upon the probable functional morphology of the common ancestor (primitive therian) of the two groups. The third purpose of this paper was to attempt a unification of the history of therian mammals in North America (as interpreted from the fossil record) with biological theory (based upon the comparative study of living mammals) concerned with problems of competition within the Theria.

It has previously been recognized that near the Mesozoic-Cenozoic time boundary, marsupial mammals became nearly extinct in North America after a profound Cretaceous radiation. Contemporaneously, however, the placentals underwent rapid evolution and taxonomic diversification. Specifically, the third purpose was to question factors related to the extinction of marsupials and to the adaptive radiation of placentals near the beginning of Cenozoic time in North America.

For the purposes of simplicity and usefulness to specific interests, the first two problems were discussed as separate units (Parts 1 and 2) with the final section (Part 3) serving as an integrated summary.

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This research project would not have been possible without the generous cooperation of the farmers and townspeople of Rumsey and Trochu, Alberta, Canada. Outstanding among these were the families of Messrs. Fred and John Griffith, Cyril (Bud) Nelson, Lloyd Heaton, Roy Ross, Roland Langshaw, and Thomas Lynch.

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The entire research project was conducted under the guidance of Dr. William A. Clemens, Jr., formerly of The University of Kansas, and now of the University of California at Berkeley. My appreciation of his professional assistance and personal interest is profound.

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PART 1

FOSSIL MAMMALS OF UPPER PART OF EDMONTON FORMATION

STRATIGRAPHY AND GEOLOGICAL SETTING OF EDMONTON FORMATION

The Edmonton Formation of Alberta, Canada, is widespread, covering most of the Province east of the foothills of the Rocky Mountains and south of 56 degrees North latitude (Allan & Sanderson, 1945, p. 61). It is composed of a complex intertonguing of marine and nonmarine sombre-colored clays and silts of Late Cretaceous (Maastrichtian) age with a total thickness of 1,300 feet (Russell & Chamney, 1967, p. 6, fig. 2). The sediments were deposited in flood plains, minor deltas, and marine tongues along the western coastal plain of the gradually eastwardly retreating Late Cretaceous epicontinental sea (see Haun & Kent, 1965, p. 1794, for comparisons with the United States). The formation as a whole correlates with part of the Bearpaw, Fox Hills, and Lance formations of the western United States (Tozer, 1956, fig. 2), thus representing a long interval of deposition. It is usually underlain in Alberta by the marine Bearpaw Shale, and is generally separated from it by a transitional zone of deposition. The Paleocene Paskapoo Formation overlies the Edmonton, generally with an erosional unconformity.

The area of study, accompanied by a diagrammatic generalized column of the Edmonton Formation as seen in the valley of the Red Deer River between Red Deer and Drumheller is shown in Figure 1. Measurements and detailed descriptions of the various members can be found in publications by Allan & Sanderson (1945), Ower (1960), Clemens & Russell (1965), and Russell & Chamney (1967). The Edmonton-Paskapoo contact is currently under detailed study by Robert Snead of the University of Alberta at Edmonton.

The Kneehills Tuff has been dated over a wide area by potassium-argon techniques at 65 to 66 million years before present. Potassium-argon analyses of biotite and sanidine in bentonites of the Bearpaw Formation indicate that the regression of the Bearpaw sea from southeastern Alberta occurred about 68 million years ago (see Baadsgaard *et al.*, 1964, p. 29). The Cretaceous-Tertiary boundary has been placed at 64 million years (all dates from Folinsbee *et al.*, 1965). Thus the Edmonton Formation may represent, at least in some areas, nearly four million years of deposition.

Previous paleontological studies on the Edmonton Formation have been diverse. Srivastava (1966, 1967), studying the pollen and spores, suggested several climatic changes through the period of deposition, varying from a tropical, humid regime with swampy vegetation to one of a warm-temperate aspect with woodlands. Foraminifera have been used as paleoecological indicators in the marine sequences (Russell & Chamney, 1967). Dinosaurs have been recovered from the Edmonton Formation since the 1880's by various collectors, principal among them being C. M. Sternberg (see Russell & Chamney, 1967, for historical survey and bibliography). The smaller lower vertebrates remain unstudied. Only scattered records of mammals from the Edmonton Formation have been published (see Russell, 1952, for review; Clemens & Russell, 1965).

The present study is concerned entirely with the mammalian remains found in the Edmonton Formation above the Kneehills Tuff, which has frequently been referred to as the "Upper Edmonton Formation." The use of "Upper" and "Lower" as formal parts of a formational name goes against generally accepted nomenclatural procedure; thus, "the upper part of the Edmonton Formation" is preferred terminology. This is used only as a temporary expedient until the nomenclature of the Edmonton Formation is formally reevaluated. The phrase "upper part of the Edmonton Formation" is, however, long and awkward. Following the custom of many geoscientists currently studying the area I have freely used "upper Edmonton Formation" as an informal term with full knowledge of the problem involved.

The area of study (Fig. 1) included a series of restricted exposures along the breaks of the Red Deer River (Fig. 2,*A*) northeast of the town of Trochu. The

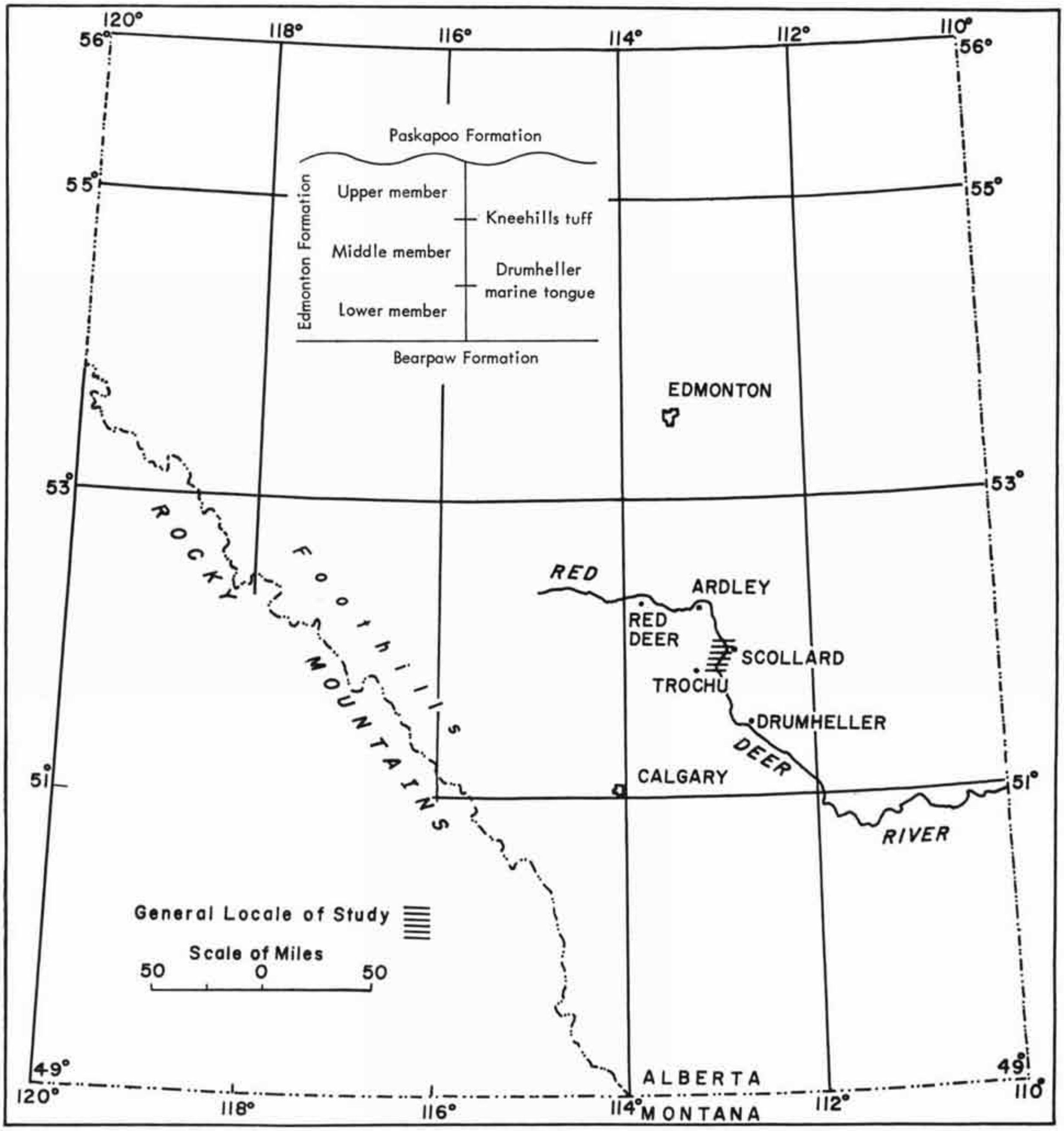

FIG. 1. Map of Alberta showing general locale of study, with diagrammatic generalized section of Edmonton Formation.

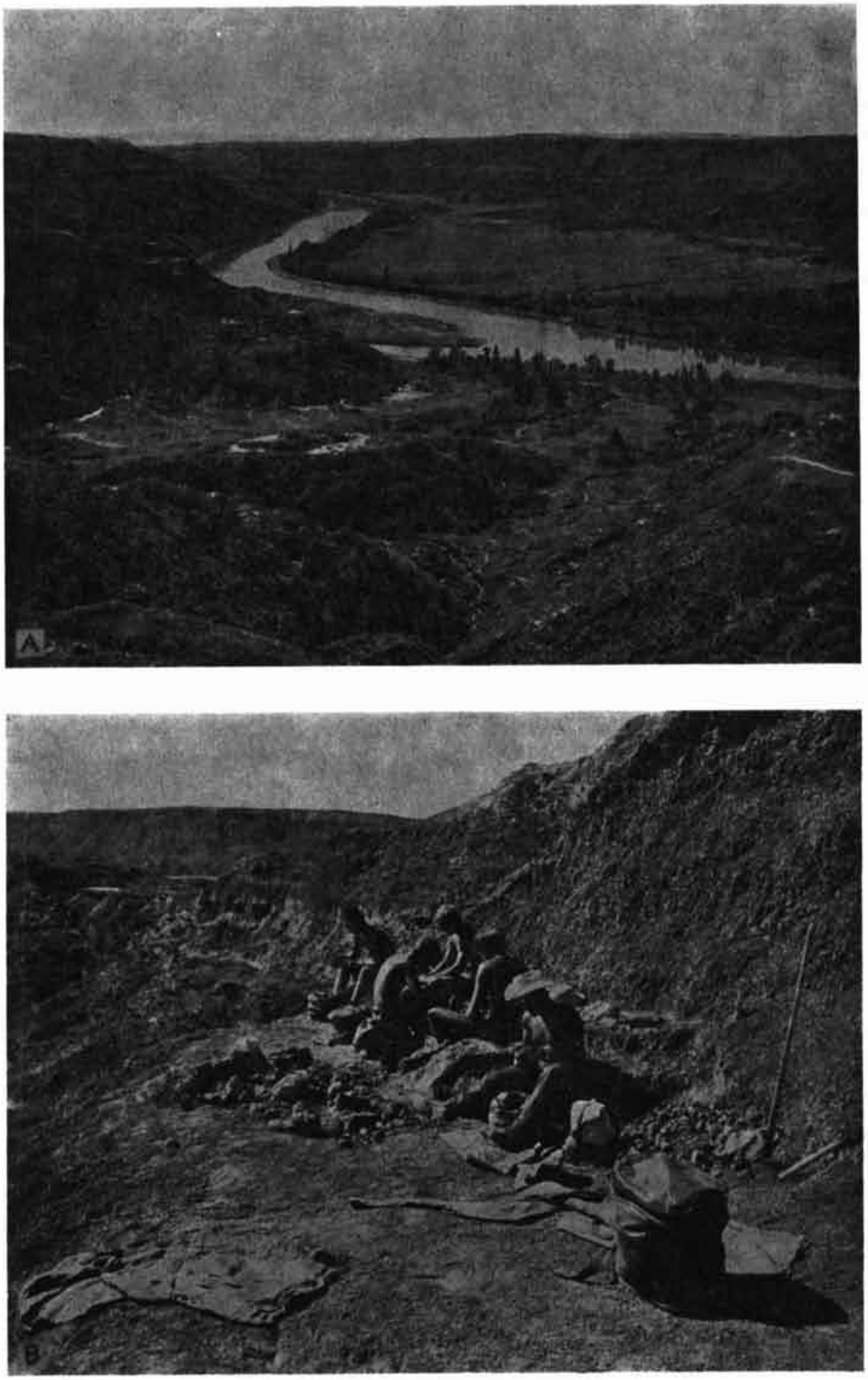

FIG. 2. Fossil localities in Red Deer River valley of Alberta northeast of Calgary.

A. View looking southwestward of Red Deer River from point above upper Edmonton Formation on Griffith farm **above locality** KUA-3.

B. View looking west at quarrying procedure at locality **KUA-1.**

upper Edmonton is generally rather unconsolidated with few competent layers, thus the exposures are frequently slumped.

LOCALITIES

Only those localities in the upper part of the Edmonton Formation which have yielded fossil mammals are here recorded. The base map used is the 1960 Alberta Department of Lands and Forests sheet 82 p/15. Some of the localities are recorded in SRIVASTAVA's (1967, p. 134, fig. 1) map. All of the localities are also precisely marked with pin-holes on aerial photographs deposited in the Museum of Natural History, The University of Kansas.

Loc. KUA-1

East-central edge of SW¼, SE¼, sec. 18, T. 34 N, R. 21 W. The locality is on the farm of Messrs. FRED and JOHN GRIFFITH, approximately two miles south and six miles west of Scollard. To the southeast is a wide bench, capped by the Kneehills Tuff, which leads to a small valley that has its head near the Griffith's farm house. The locality was discovered in 1963 by Dr. WILLIAM A. CLEMENS, JR., and was figured by CLEMENS & RUSSELL (1965, p. 37). KUA-1, about 43 feet above the Kneehills Tuff, is the most productive and heavily quarried locality yet found in the Edmonton Formation. Roughly 11 tons of matrix have been removed from a well-indurated clay and silt layer which varies laterally from less than 1 foot in thickness up to about 3 feet. The sediments composing the fossiliferous layer represent a muddy stratum which was thoroughly churned shortly after deposition. Practically no fossils were found in articulation, and long bones and jaws were found at all angles relative to the horizontal. Contorted bentonite streaks were abundant and bedding was strongly distorted. Prospect samples were removed in 1964 and full-fledged quarrying was carried out throughout much of the summers of 1965-67.

Loc. KUA-2

NE¼, SW¼, SE¼, sec. 18, T. 34 N, R. 21 W. The locality is on the Griffith farm on a bench 89 feet above the Kneehills Tuff on the first prominent ridge northwest of KUA-1, and separated from it by a wide, slumped area. Samples were taken from various levels and washed in 1964-66, but insufficient concentrations of fossil mammals were found to warrant large scale quarrying. Fish debris is abundant. The locality was discovered in 1964 by Mr. DONALD TAYLOR.

Loc. KUA-3

Center of NW¼, NW¼, SE¼, sec. 18, T. 34 N, R. 21 W. The fossiliferous strata are light gray clays about 82 feet above the Kneehills Tuff on the crest of the first major ridge to the northwest of the fence line extending west from Griffith's farm house. A wooden stake has been imbedded in the center of the 4-foot-thick layer. Samples were taken from various levels and washed in 1964 and 1967, but the concentration of fossil mammals was too small to warrant continued work. The locality was discovered in 1964 by Dr. RICHARD C. FOX.

Loc. KUA-17

SW¼, sec. 36, T. 33 N, R. 22 W. This number was given to mammalian fossils found in the area of "Prospect 2" of Mr. T. POTTER CHAMNEY (pers. comm. between CLEMENS and CHAMNEY). The exact site at which earlier collections were made could not be relocated, but the collection area is a broad cove of badlands on the Griffith farm within the quarter-section indicated.

Loc. KUA-18

East-central edge of NE¼, SW¼, sec. 20, T. 34 N, R. 21 E. The locality is 12 feet above the Kneehills Tuff on the crest of a prominent ridge and just west of a deep coulee, the head of which has cut far south across Griffith's north pasture. The productive stratum is only 4 to 6 inches in thickness and is composed of clay and silt with iron-cemented blocks. The deposit may be the filling of a Cretaceous channel cut into the Black Mud. Samples were taken in 1964 and 1965, but quarrying probably would not be profitable. It was referred to as "Prospect 1" by Mr. T. POTTER CHAMNEY, and rediscovered by Dr. CHARLES STELCK in 1964.

Although SRIVASTAVA (1967, p. 135, fig. 2) noted "upper" and "lower" mammal horizons at Scollard locality 18, there is, as far as I am aware, only a single horizon.

Loc. KUA-22

Center of NE¼, SW¼, NW¼, sec. 36, T. 33 N, R. 22 W. The locality is in a slump block roughly 20 feet above the Kneehills Tuff west of the steep erosional face below the farmed plateau. It is just north of a small swampy coulee and south of a semi-permanent pond. The locality is divided into two sublocalities by a fault running north-south within the slump block. The southern sublocality has been completely eliminated and washed for fossils, but it previously capped the southern third of the slump block. The more northerly sublocality is a 2-foot-thick layer of light clay immediately above the white outwash plain on the western edge of the slump block. Although fossils are not abundant in the locality, the proportion of multituberculates is high and its study should be continued. It was discovered by me in 1967.

Loc. KUA-23

NE¼, NW¼, SW¼, sec. 36, T. 33 N, R. 22 W. The locality is a 1-foot-thick black, bentonitic layer 30 feet above the Kneehills Tuff. It is on a nondescript badly creeping slope at the northern mouth of a small coulee which runs northwest-southeast. Samples were taken for washing in 1967 with little success. The locality holds little promise for future work. It was discovered by Mr. DOUGLAS L. EASTCOTT in 1967.

Loc. KUA-25

Center of NE¼, SW¼, sec. 20, T. 34 N, R. 21 E. The locality is just above the Kneehills Tuff in light-colored silty clays on the first substantial ridge due west of KUA-18 across the zone of slumping. Although no samples have been removed for washing, repeated prospecting gives little hope for the finding of mammals. It was discovered by Mr. JAMES P. CARRELL in 1966.

Loc. UA-2

SW¼, SE¼, sec. 35, T. 33 N, R. 22 W. UA-2 refers to a complex of several distinct localities, each of which is less than 10 feet above the Kneehills Tuff. All are on the southern flank of the large, circular, isolated butte included in the map coordinates. None is rich in mammals. They were discovered by Mr. TIMOTHY SCHOWALTER in 1966.

Loc. UA-3

Center of NE¼, NE¼, NW¼, sec. 29, T. 34 N, R. 21 W. The locality is in a 5-foot-thick layer of white-weathering clayey silt, with thin coal interbeds, seven feet above the Kneehills Tuff on the northern slope of a prominent knob. The layer has not been sampled for washing, but is not particularly promising for mammalian remains. It was discovered by SCHOWALTER in 1966.

As shown by the above descriptions, localities for fossil mammals in the upper part of the Edmonton Formation are hard-won indeed. Despite extensive prospecting, no definite mammal localities have yet been discovered in the sediments below the Kneehills Tuff.

TECHNIQUES OF COLLECTING

Most localities were quarried in at least an exploratory fashion after their discovery by prospecting. The rock of Loc. KUA-1 (Fig. 2,*B*), the most intensively quarried locality, was hard and had to be broken into walnut-sized or smaller pieces before any underwater screening operation was effective. However, the induration of the rock was also its beauty. Many delicate jaws that surely would have been demolished in collection from some more easily-worked sediment were securely encased and thus preserved. The rocks were examined for fossil material (which was wrapped individually) on a clod by clod basis and put into gunnysacks for removal from the quarry. This time-consuming quarrying technique was well worthwhile as many fine jaws were saved from the rigors of the washing process Each bag was numbered and its position in the quarry mapped. All specimens found have their respective bag numbers catalogued, thus their position in the quarry can be determined. I have found this method to be effective and worthwhile since different pieces of broken specimens can later be put back together.

Quarry KUA-1 was on a steep slope approximately 100 vertical feet below the level to which the field vehicles could be driven. The late Mr. RUSSELL R. CAMP invented the labor-saving "Red Mare" shown in Figure 3,*C* to get matrix out of the quarry. It is nothing more than a skid made from an inverted truck hood with welded seams, an oak 4- by 4-inch beam in the front (for cable attachment), a pine 4-by-4 beam in the rear (to keep bags of matrix from falling out backwards), and ¼-inch steel cable with two swivels along its length running to the vehicle. The vehicle was simply put into a low gear and driven away until the "Red Mare" reached the top of the cleared slope. As many as six fully-loaded bags have been brought up together using this method. Where conditions do not permit vehicle maneuverability, a power take-off unit could well be used.

The underwater screening techniques basically follow those described by MCKENNA (1965) and CLEMENS (1965) but several innovations were made. The Red Deer River, in which all washing was done, may fluctuate in depth several feet overnight. To keep the 150 washing boxes in use from being carried downstream by an unexpected rise of the water, a special device had to be invented. Mr. THOMAS H. RICH and I conceived of the apparatus ("playpen") shown in Figure 3,*B*. It is simply a large floating "bag" constructed from two air-filled 50-gallon drums interconnected by two, 20-foot, 2- by 4-inch boards upon which was stapled galvanized fencing to form an underwater floor; 24 washing-boxes of the type shown in Figure 4,*A* could be placed at a time in each "playpen" (Fig. 3,*A*) and three "playpens" were kept active at a time. The "playpens" were restrained by two 10-foot long cables running upstream to flat wooden-frame anchors covered with fencing, then piled high with large rocks. The "playpens" were thus free to rise and fall with changes in the water-level of the river. It was useful to have a large floating log anchored diagonally upstream from the "playpens" to act as a protective bumper to deflect flotsam (e.g., trees), which regularly drifted down the river.

Because of the high clay content of the matrix, the current of the river was ineffective in washing the matrix through the screening, and physical agitation was necessary. The washing boxes (Fig. 4,*A*) had bronze screening bottoms with 17 by 13 openings to the inch. Although such a grid size lends itself well to efficient washing, it is too coarse for collecting isolated teeth of the very small mammals represented in the fauna. Thus a double-screen system was devised with a fine screen (40 openings per inch) catching materials that passed through the washing-box screen. Figure 4,*A* illustrates construction of the lower box ("silt-catcher") and Figure 4,*B* shows how the two boxes were used in practice. The silt-catching box is large enough for each of two people to agitate a washing box simultaneously. The major difficulty with the double screen method is that the association of quarry bag number with specimens is lost for the small teeth that pass into the "siltcatcher" and thus are mixed with fossils from other quarry bags. Physical problems make processing of the fine concentrate of each quarry bag individually with the double screen system impractical.

Following the washing process, the concentrate was sun-dried and wrapped individually according to quarry bag number. The concentrate was returned to the Museum of Natural History at The University of Kansas where all of it was put into gallon plastic bleach containers having the tops sawed off, soaked in water with Alconox detergent, and individually rewashed using a double-screen system. The resulting superconcentrate was then picked for fossils, generally under a dissecting microscope.

TECHNIQUES OF STUDY

The fundamental similarity between the fauna of the Lance Formation of Wyoming and that of the upper Edmonton Formation allows considerable brevity in my systematic treatment due to overlaps with those of CLEMENS (1963, 1966). For example, repetition of synonymies here would be superfluous. The type is mentioned in each instance but its locality is not. Lists of referred specimens and localities include only those of

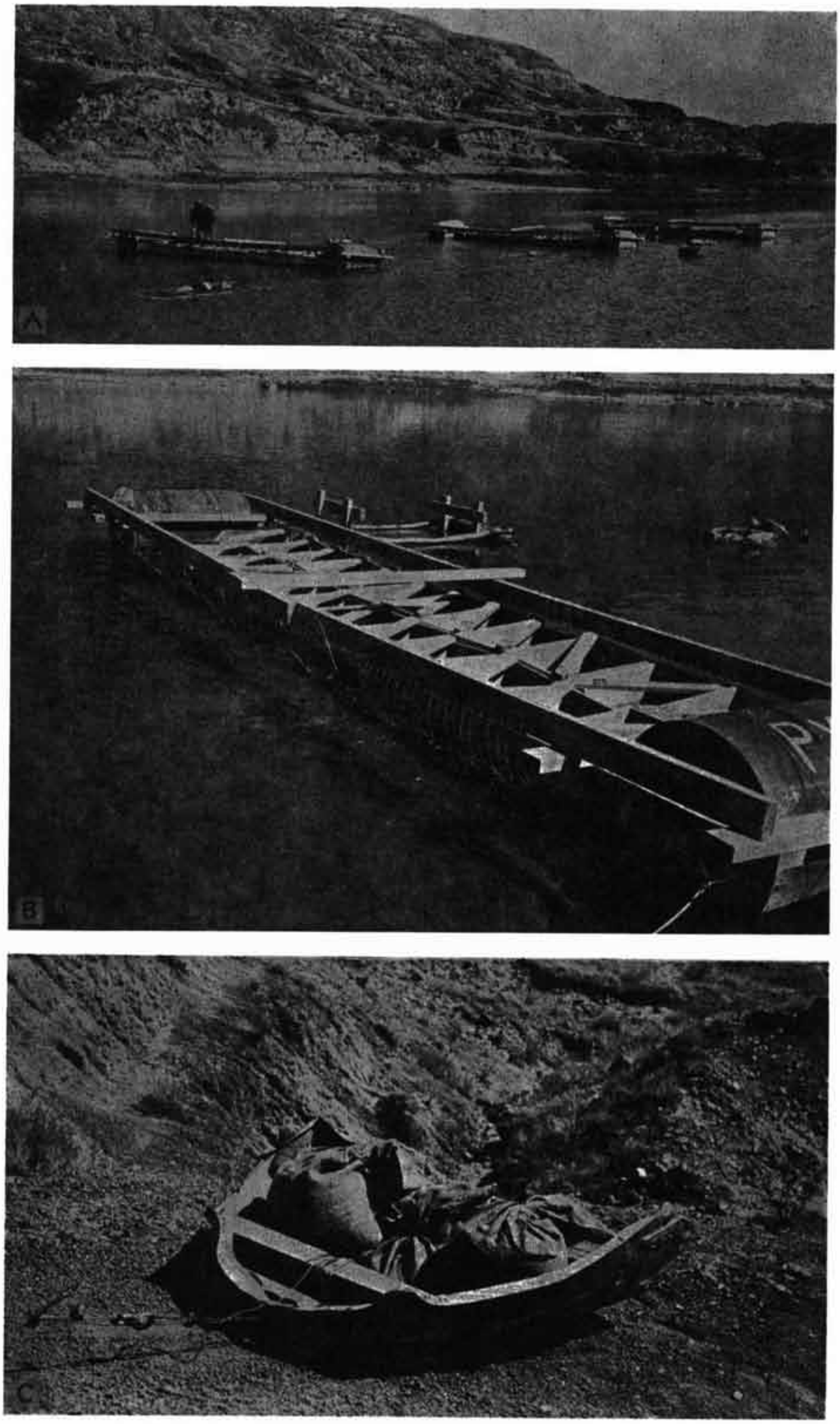

FIG. 3. Equipment for washing and moving fossil-bearing Edmonton deposits.

A. View of Red Deer River looking downstream showing array of three "playpens." A total of 72 washing boxes can be processed at a time in the three units.

B. Close-up view showing the construction of one of three "playpens" used for holding washing boxes in place in current of river.

C. Front view of "Red Mare," a skid device used in pulling bags of matrix from quarries up steep slopes to a field vehicle.

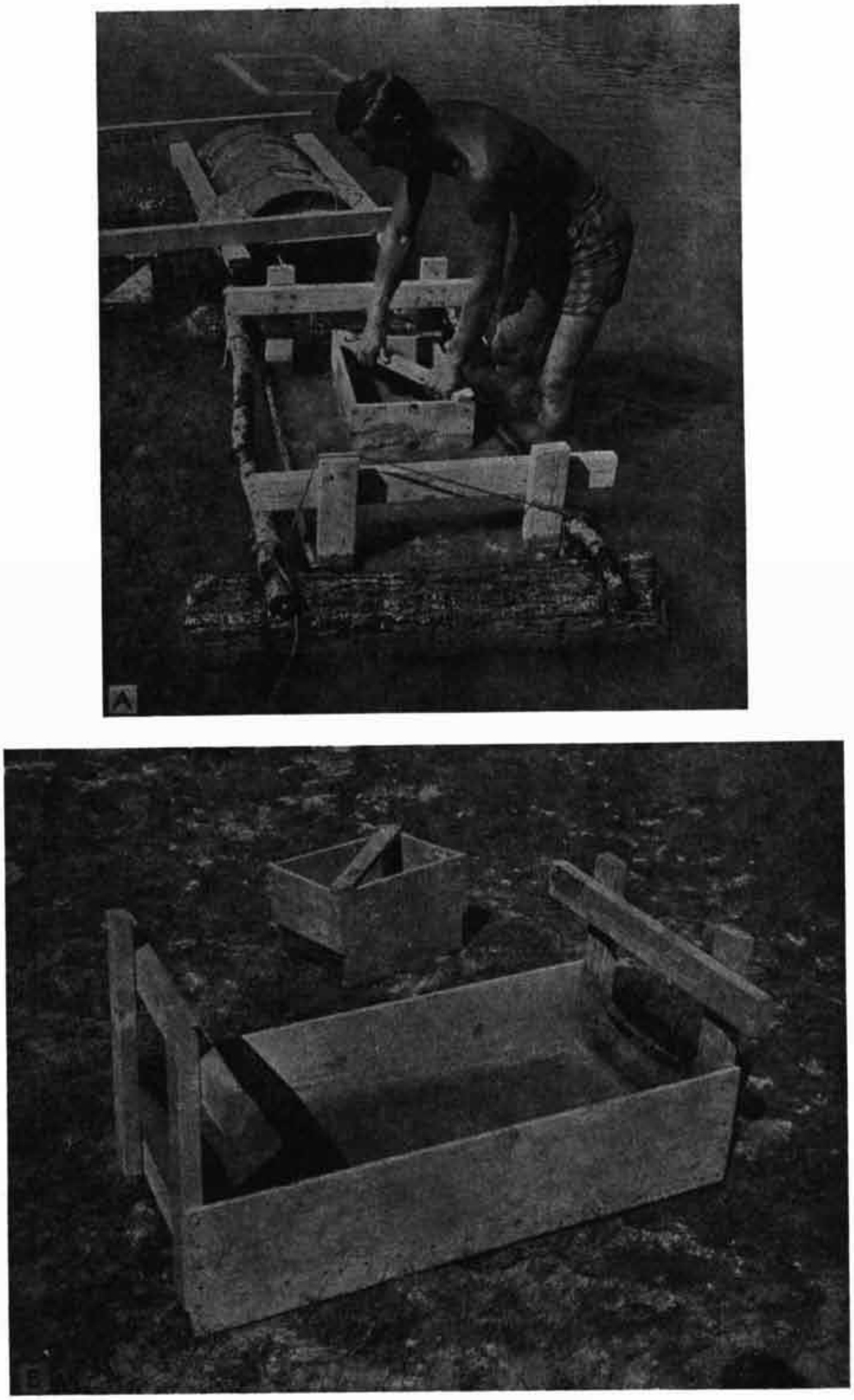

FIG. 4. Equipment for washing fossil-bearing Edmonton deposits.

A. Close-up of washing box one-fourth filled with quarry matrix being agitated in fine-screened "silt-catcher." The "silt-catcher" is supported above river-bottom by two logs connected by smaller branches.

B. Close-up photo showing construction of coarse-screened washing box (upper) and fine-screened "silt-catcher" (below).

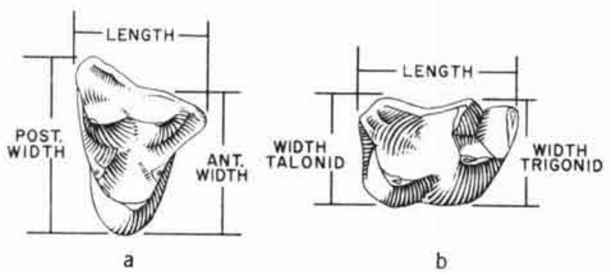

FIG. 5. Occlusal views of therian molars (*5a*, upper; *5b*, lower) showing orientation of measurements.

the upper Edmonton Formation, but the statement of known distribution is complete. Agreements in description and diagnosis with those of CLEMENS generally are not repeated and only differences or additions are emphasized. Terminology of dental morphology is a combination of that employed by CLEMENS (1963, p. 30; 1966, p. 3) and that of VAN VALEN (1966, p. 7-9). The locality of all figured specimens is KUA-1 unless otherwise specified in the legend.

The citations for authors of taxa are presented in the manner utilized by VAN VALEN (1967, p. 258).

All measurements are in millimeters and were obtained on the same microscope using an eyepiece grid. A mechanical stage was found to be effective in orienting specimens for measurements. Unless otherwise noted, all tables contain data lumped from all localities. Measurements of therian molars were done as indicated in Figure 5. In all cases a line drawn through the apices of the paracone and metacone of the upper molars and through the metaconid and entoconid of the lower molars was assumed to be the anteroposterior line of measurement. Width measurements were always taken at right angles to the anteroposterior line.

The terminology and techniques of measuring multituberculate teeth follow those of SIMPSON (1937b) and JEPSEN (1940).

ABBREVIATIONS

For conservation of space, abbreviations are used in the text, captions for figures, and tables of measurements, explained as follows.

A-P	anteroposterior length
Ant-W	anterior width
C	canine
CV	coefficient of variation
D	tooth of deciduous (milk) series
I	incisor
M	molar
N	number of specimens (sample size)
O R	observed range of variation
P	premolar
Post-W	posterior width
SD	standard deviation
W	width
W-Tal	width of talonid
W-Tri	width of trigonid
$\overline{X}$	mean

The following abbreviations are used for specimens from institutional collections.

AMNH	American Museum of Natural History
CMCVF	Carnegie Museum Catalog of Vertebrate Fossils
KU	The University of Kansas, Museum of Natural History
LACM	Los Angeles County Museum
UCMP	University of California, Berkeley, Museum of Paleontology
UMVP	University of Minnesota, Vertebrate Paleontology
USNM	United States National Museum, Smithsonian Institution
YPM	Yale Peabody Museum

All specimens not thus designated belong to the University of Alberta Paleontological Collection.

A considerable amount of skeletal material has been recovered, but none was found in articulation and most is fragmentary. Identifications have not been attempted.

SYSTEMATIC DESCRIPTIONS AND EVOLUTIONARY RELATIONSHIPS

Class MAMMALIA

Subclass ALLOTHERIA

Order MULTITUBERCULATA

Suborder PTILODONTOIDEA Sloan & Van Valen, 1965

Family ECTYPODONTIDAE Sloan & Van Valen, 1965

[original name emended, VAN VALEN & SLOAN, 1966]

Genus MESODMA Jepsen, 1940

MESODMA HENSLEIGHI Lillegraven, new species

Figures 6,*1-5*, 7,*1-2*

Separated from *Mesodma formosa* (MARSH), 1889 b.

Etymology.—Named for Mr. Hugh C. Hensleigh of Lawrence, Kansas, who was instrumental in making the 1966 field season a success.

Type.—3596, isolated left P_4 (Fig. 6,*1a-b*). Paratypes: 3762, left mandible fragment with M_1 (Fig. 6,*3a-c*); 3250, left mandible fragment with M_2 (Fig. 6,*5a-c*); 3852, isolated right P^4 (Fig. 6,*2a-c*); 3844, isolated left M^1 (Fig. 7,*1a-c*); 3335, isolated left M^2 (Fig. 6,*4a-c*).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—P_4's, 2886, 3337, 3916; M_1's, 3320, 3505, 3850, 3856, 4006; M_2, 3972; P^3, 3838; P^4's, 3388, 3984, 4026; M^1's, 3334, 3833, 3843, 3855, 3881, 3883, 3887, 3888; M^2's, 3546, 3834, 3835, 3845, 3847, 3858, 3889, 3971.

Localities.—KUA-1, 3, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; possibly type Lance Formation, Wyoming.

TABLE 1. *Measurements (in mm.) of Teeth Referable to* Mesodma *spp.*

Tooth	Taxon	Length					Width				
		N	O R	$\overline{X}$	S D	C V	N	O R	$\overline{X}$	S D	C V
DP^2	Mesodma sp.	2	1.30-1.40	1.35	----	----	2	0.95-1.00	0.97	----	----
	Mesodma sp.	1	1.70	----	----	----	1	1.05	----	----	----
P^1	M. formosa?	7	1.20-1.40	1.32	----	----	7	1.00-1.10	1.06	----	----
P^3	M. hensleighi?	1	1.10	----	----	----	1	0.80	----	----	----
	M. formosa?	3	1.25-1.35	1.30	----	----	3	0.85-0.90	0.87	----	----
P^4	M. hensleighi	3	1.60-1.90	1.77	----	----	3	0.70-0.90	0.80	----	----
	M. formosa	1	2.05	----	----	----	9	0.80-1.25	1.01	----	----
M^1	M. hensleighi	3	2.10-2.30	2.20	----	----	9	1.00-1.10	1.02	----	----
	M. formosa	2	3.10-3.15	3.13	----	----	7	1.25-1.40	1.36	----	----
	M. thompsoni	0	----	----	----	----	4	1.45-1.60	1.51	----	----
M^2	M. hensleighi	9	1.00-1.15	1.09	----	----	9	1.00-1.15	1.08	----	----
	M. formosa	17	1.30-1.60	1.44	0.10	6.94	17	1.25-1.50	1.37	0.09	6.93
	M. thompsoni	2	1.85-1.90	1.87	----	----	2	1.65-1.80	1.72	----	----
P_4	M. hensleighi	1	2.70	----	----	----	4	0.95-1.10	1.00	----	----
	M. formosa	2	3.05-3.10	3.08	----	----	13	1.10-1.35	1.18	----	----
	M. thompsoni	1	4.30	----	----	----	11	1.25-1.50	1.41	----	----
M_1	M. hensleighi	5	1.70-1.95	1.80	----	----	6	0.75-0.85	0.78	----	----
	M. formosa	3	2.10-2.50	2.30	----	----	11	0.90-1.15	1.07	----	----
	M. thompsoni	1	2.85	----	----	----	1	1.25	----	----	----
M_2	M. hensleighi	2	0.95-1.10	1.02	----	----	2	0.80-0.90	0.85	----	----
	M. formosa	16	1.25-1.60	1.41	0.14	9.79	17	1.00-1.40	1.18	0.15	13.13
	M. thompsoni	2	1.90-2.00	1.95	----	----	2	1.50-1.60	1.55	----	----

For abbreviations see end of Introduction.

Diagnosis.—Nearly identical morphologically with *Mesodma formosa* but significantly smaller, separable from it only on basis of size (Table 1); cusp formulae generally lowest for genus.

Discussion.—A few comments concerning the taxonomic division of *Mesodma* are necessary before attempting to describe *M. hensleighi.* Since essentially all materials referable to the genus are isolated teeth, most associations are open to question. None of the Edmonton specimens has been found in association. However, *Mesodma* is a rather tightly knit genus morphologically and it has no known close relatives in the Edmonton local fauna to confuse generic identification. Thus one can be relatively sure that observed size groupings or consistent morphological differences are either a result of intraspecific variation, such as that related to sexual dimorphism, or of involvement of distinct taxa. No 50-50 character frequency distributions have been found; thus, sexual differences probably are negligible.

Sufficient differences in the structure of the $P^4/_4$ have been found in the past within the genus to allow its division into two groups, *Mesodma formosa, s.l.* (see below) and *M. thompsoni* (CLEMENS, 1963, p. 39). Although CLEMENS could find no morphological differences between molars of the two species, he did find some bimodality in dimensions and assumed that the larger group represented *M. thompsoni.* I also have failed to find characteristics of molar construction distinctive as to species within the Edmonton specimens of *Mesodma,* but on the basis of molar measurements I agree fully with the distinctness of *M. thompsoni.* It should be pointed out here that *"M. formosa"* as diagnosed by CLEMENS (1963, p. 31) probably is a composite species, including representatives of *M. formosa, s.s., Cimexomys minor* (SLOAN & VAN VALEN, 1965, p. 221), and *M. hensleighi* as diagnosed in this paper. My interpretation of the observed size ranges of dentition of the Edmonton species of *Mesodma* is presented in Table 1.

Throughout his field work, CLEMENS used washing boxes built with ordinary window screening, the grid of which (17 by 13 openings per inch) is large enough to allow the passage of surprisingly large teeth. The finer grid screen (see "Techniques of Collecting") used in Alberta was instrumental in obtaining tiny specimens of *Mesodma* (especially upper premolars and $M^2/_2$) that otherwise would have been lost. This seems particularly clear when the low ends of the size ranges in Table 1 are compared with those of CLEMENS' (1963, tables 2, p. 43, and 3, p. 49). I suggest that CLEMENS' sample of the range of size variation of *M. formosa* was incomplete for

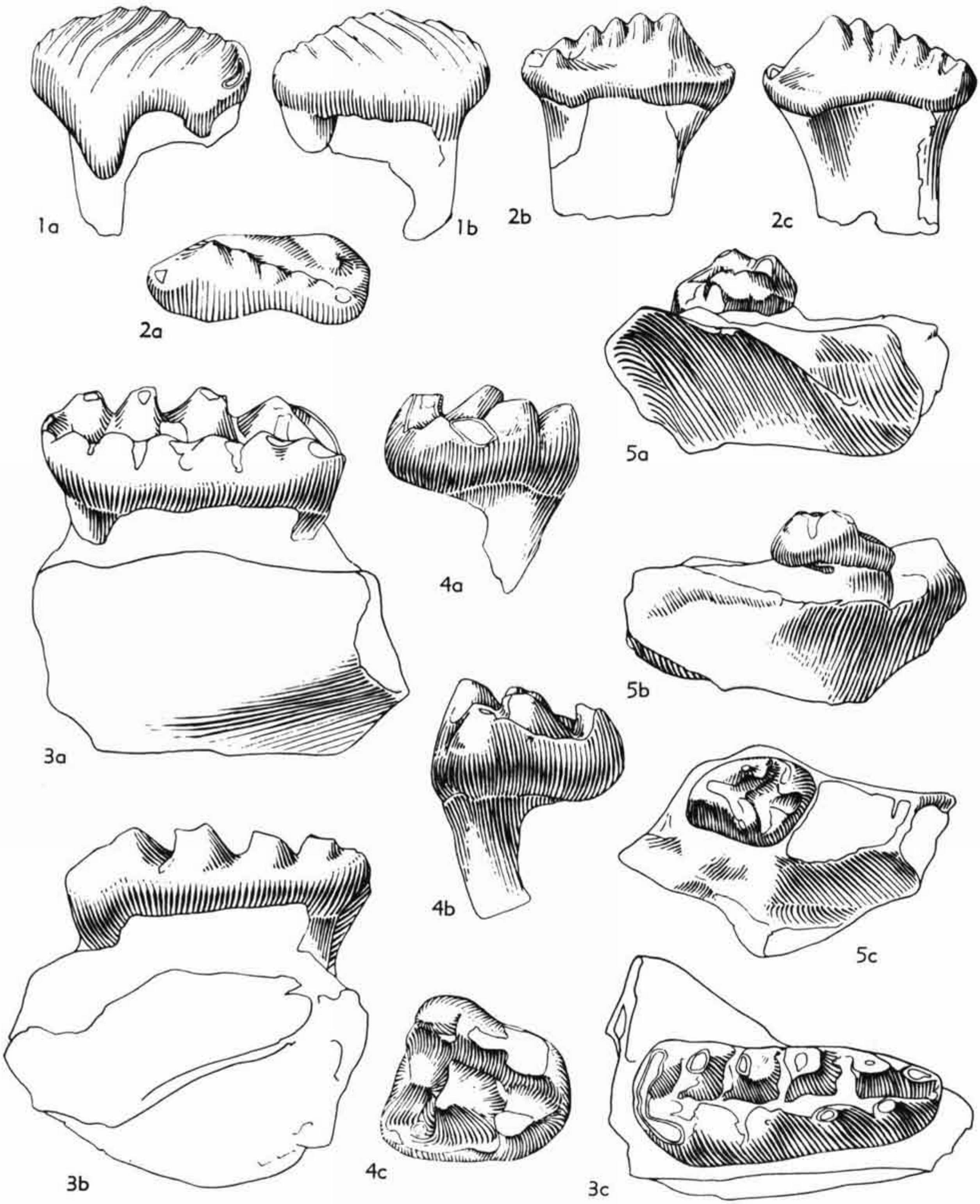

FIG. 6. *Mesodma hensleighi* LILLEGRAVEN, n. sp. *(continued on facing page).*

some teeth in the series, hence making size groupings especially difficult.

Clemens (1963, p. 53) questioned the homogeneity of *Mesodma formosa* on the basis of high coefficients of variation of posterior premolar measurements, but chose to maintain the integrity of the taxon until further evidence became available. I also question the homogeneity of *M. formosa,* and on the basis of a somewhat better sampling of the range of size variation suggest that it may be satisfactorily split into two species, one significantly larger than the other. The holotype of *M. formosa* (YPM 11812) is a P_4, the measurements of which fit the higher end of variation of *M. formosa, s.l.* as diagnosed by Clemens (1963, p. 31). I suggest that the smaller group be raised to the status of a distinct species, *M. hensleighi,* with 3596 (Fig. 6,*1*), an isolated P_4, as the holotype.

The decision to erect a new species in this case is based upon tenuous grounds. The material is scarce, frequently fragmentary, never in association, and I can find only meager evidence for consistent morphological differences from *Mesodma formosa, s.s.* The main defense for the reality of *M. hensleighi* rests in the size of distributions of $M^2/_2$ for *Mesodma* as a whole (*see* Fig. 9). These are the most abundant types of teeth collected and are morphologically the least variable. The low morphological variability is a function of simplicity of the teeth themselves in that normal genetic variation probably had little recognizable expression. However, it is likely that the sizes of molars were closely controlled to maintain efficient occlusal relationships with their complementary teeth in the upper or lower jaws. Three distinct clusters of measurements are evident with the medium-dimensioned cluster most abundant. Although other teeth in the jaw series are less abundant and more fragmentary, similar size-frequency relationships are observed (Table 1). The paleontologist is forced to work entirely with morphospecies and cannot know the biological nature of the extinct animals with which he works. Even though one may argue that the taxonomic formation of a new species so closely related to *M. formosa* is at this time premature, I can demonstrate differences from *M. formosa s.s.* and can thus emphasize the complexity within the genus by the addition of *M. hensleighi* to the faunal list.

Traditionally, P_4's have been chosen as the holotypes for multituberculate taxa, especially where only isolated teeth are available. I have chosen 3596 (Fig. 6,*1a,b*), and have also selected several paratypes from the same locality. These include an isolated M_1 (3762, Fig. 6,*3a,b*), M_2 (3250, Fig. 6,*5a-c*), P^4 (3852, Fig. 6,*2a-c*), M^1 (3844, Fig. 7,*1a-c*), and M^2 (3335, Fig. 6,*4a-c*). I should emphasize once again that few morphological characters other than size distinguish *Mesodma hensleighi* from *M. formosa.*

Clemens' (1963) descriptions of *Mesodma formosa* and *M. thompsoni* are perfectly adequate to cover the Edmonton specimens, thus detailed repetition here is unnecessary. The few necessary additions or comments about each tooth in the series will be discussed simultaneously for all three species of *Mesodma* following the preface for *M. thompsoni.*

MESODMA FORMOSA (Marsh), 1889b

Figures 7,*3-9*, 8,*1,2*

Type.—YPM 11812, left P_4 (Marsh, 1889b, pl. 8, fig. 36-39).

Referred specimens.—Fragmentary mandible with P_{3-4}, 3234; P_4's, 2297, 2380, 2450, 2506, 2601, 2804, 3379, 3472, 3901, 3903, 3909, 3982, 3996, 4027, 4037; M_1's, 3338, 3340, 3434, 3470, 3574, 3929, 3880, 3886, 3893, 3894, 3897, 3899, 3921, 4029; M_2's, 2756, 3321, 3341, 3380, 3396, 3606, 3832, 3836, 3840, 3841, 3846, 3853, 3860, 3862, 3922, 3931, 3934, 4033; P^1's, 2243, 3319, 3331, 3471, 3530, 3854, 3962; P^3's, 2438, 3842, 3939; P^4's, 2248, 2339, 2890, 3332, 3479, 3895, 3896, 3902, 3904, 3905, 3906, 3907, 3908, 3910, 3912, 3913; M^1's, 2802, 2870, 3128, 3264, 3318, 3333, 3861, 3882, 3884, 3900, 3961, 3967, 3973; M^2's, 2352, 2714, 2788, 2803, 3168, 3188, 3254, 3336, 3540, 3544, 3550, 3837, 3839, 3848, 3925, 3940, 3943, 3970.

Localities.—KUA-1, 3, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana, and (unpublished) South Dakota; possibly Kirtland and Fruitland formations, New Mexico (unpublished).

Comments.—*Mesodma formosa* is the most common multituberculate species in the sample of the upper Edmonton fauna, in contrast to the dominance of *M. thompsoni* in the type Lance and Hell Creek collections.

A revised diagnosis of the species is unnecessary. It is sufficient to say that only the specimens in the higher size ranges of Clemens' (1963, p. 31) revised diagnosis are now included in the taxon.

MESODMA THOMPSONI Clemens, 1963

Figures 7,*7*; 8,*3-6*

Type.—UCMP 47217, isolated P_4 (Clemens, 1963, fig. 10, p. 41).

Referred specimens.—P_3, 3131; P_4's, 657, 2249, 2348, 2401, 2412, 2507, 2865, 3038, 3144, 3234, 3255, 3691, 3695, 3734, 3926, 3974, 3975; M_1, 3654; M_2's, 3536, 3616; M^1's, 2360, 3110, 3303, 3383, 3790, 3885; M^2's, 2563, 3687.

Localities.—KUA-1, 22; UA-3.

Distribution.—Upper part of Edmonton Formation, Alberta;

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1. Holotype, left P_4 (3596); *1a,b,* labial and lingual views, ×14; meas. (mm.), A-P 2.70, W 1.00.

2. Paratype, right P^4 (3852); *2a-c,* occlusal, labial, and lingual views, ×20; meas. (mm.) A-P 1.80, W 0.80.

3. Paratype, left M_1 (3762); *3a-c,* labial, lingual, and occlusal views, ×30; meas. (mm.), A-P 1.75, W 0.75.

4. Paratype, right M^2 (3335); *4a-c,* lingual, labial, and occlusal views, ×30; meas. (mm.), A-P 1.00, W 1.00.

5. Paratype, fragment of right mandible with M_2 (3250); *5a-c,* labial, lingual, and occlusal views, ×20; meas. (mm.), A-P 0.95, W 0.80.

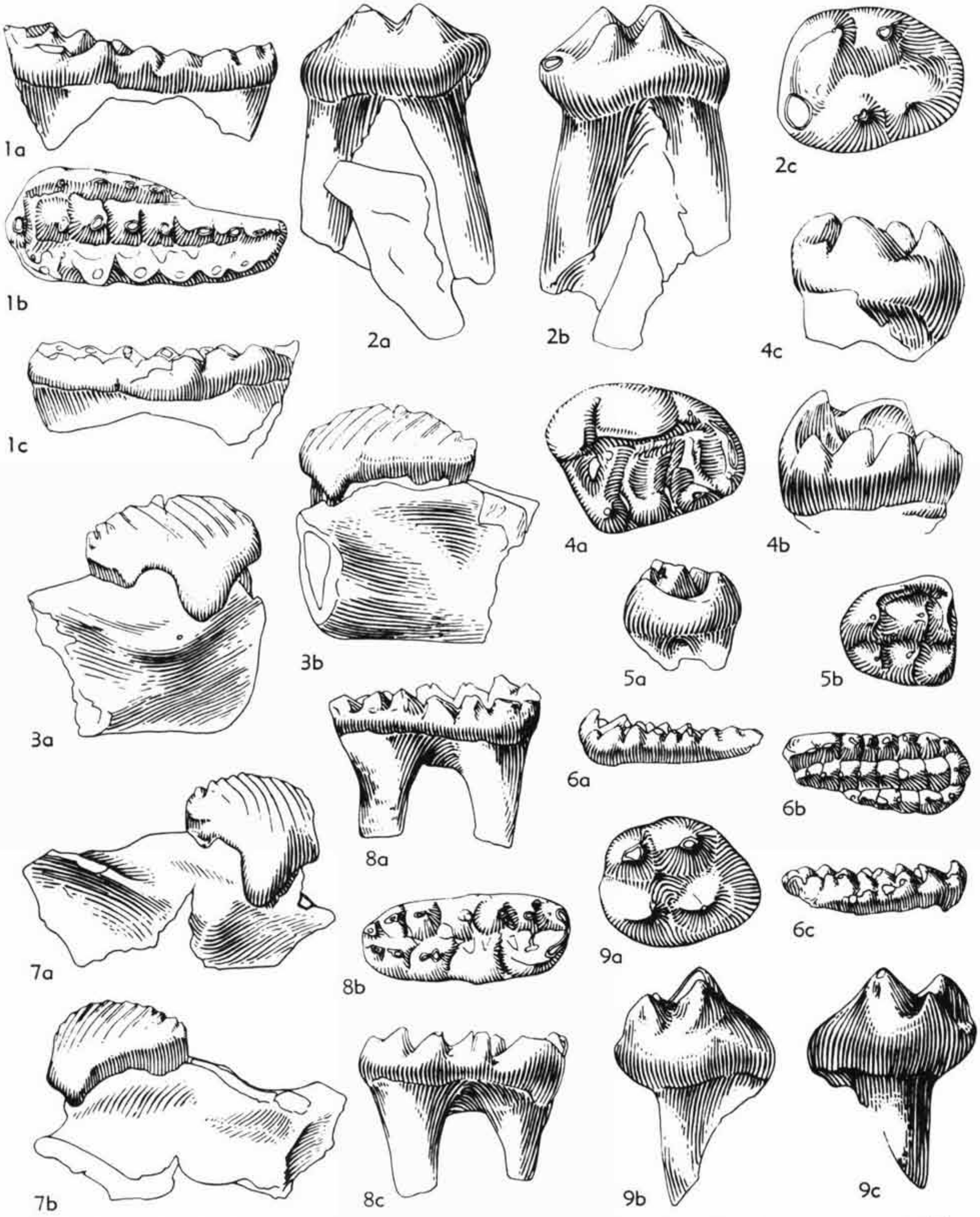

FIG. 7. *Mesodma hensleighi* LILLEGRAVEN, n. sp. *(1-2)*, *M. formosa* (MARSH) *(3-6, 8-9)* and *M. thompsoni* (CLEMENS) *(7)*

1-2. Mesodma hensleighi LILLEGRAVEN, n. sp.——*1.* Paratype, left M^1 (3844); *1a-c,* labial, occlusal, and lingual views, ×20; meas. (mm.), A-P 2.30, W 1.00.——2. Left P^3 (3838); *2a-c,* labial, lingual, and occlusal views, ×30; meas. (mm.), A-P 1.10, W 0.80.

(continued on facing page.)

type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota.

Comments and descriptions.—Specimens referable to *Mesodma thompsoni* are comparatively rare in the upper Edmonton localities.

The following is a series of miscellaneous comments upon or comparisons of the tooth series of all three Edmonton species of *Mesodma.* The fossils agree with the descriptions by CLEMENS (1963) in all other regards.

Information pertaining to the upper and lower incisors of all three species is lacking.

1) P_3. Only one specimen of a P_3 of *Mesodma formosa* (2273) has been found and none is known of *M. hensleighi.* Although none has been found that can be undoubtedly referred to *M. thompsoni,* a distinct alveolus is present in 3234 (Fig. 7,*7a,b*) and the specimen 3131, a mandible fragment with P_3 and the base of P_4, is about the right size for the species. If 3131 is a member of *M. thompsoni,* the description of the P_3 of *M. formosa* (CLEMENS, 1963, p. 33) holds perfectly for both species.

2) P_4. Due to the difficulty of breaking down the hard rocks from KUA-1, complete blades of small multituberculates are rare; most were broken during the washing process and fragments are common. The holotype (and only complete P_4) of *Mesodma hensleighi* (3596, Fig. 6,*1a,b*) has 11 serrations, eight external ridges, and nine internal ridges. The characteristics of the origin of the first and second external and internal ridges are variable and not diagnostic. The crest of the tooth has a rather low profile with the highest point at the fifth and sixth serrations. The last serration lacks an internal ridge, the penultimate has a short one. I have been able to find no morphological differences, other than size, between P_4's referable to *M. hensleighi* and *M. formosa.*

The specimen 2273 (Fig. 7,*3a,b*) is similar to the holotype of *Mesodma formosa* (YPM 11812), but is about a fourth smaller. Specimen 3234 (Fig. 7,*7a,b*) compares well with the holotype of *M. thompsoni* (UCMP 47217) but is slightly more convex dorsally.

3) M_1. A cusp formula of 6:4 was found on all specimens referable to *Mesodma hensleighi* (e.g., 3762, Fig. 6,*3a,b*). There is some tendency for the development of a tiny new cusp on the anterior end of the internal row. Specimens referable to *M. formosa* (e.g., 3897, Fig. 7,*8a-c*) have observed cusp formulae of 6-7:4-5. The only specimen referable to *M. thompsoni* (3654, Fig. 8,*5a-c*) has a cusp formula of 7:4.

4) M_2. Both specimens referred to *Mesodma hensleighi* (e.g., 3250, Fig. 6,*5a-c*) have a cusp formula of 3:2. The same is true for most of the specimens referred to *M. formosa.* However, on four of the 15 least worn specimens (e.g., 3841, Fig. 7,*4a-c*), the vertical groove on the lingual side of the third external cusp is deep enough to divide it into two distinct cusps, thus making the formula 4:2. The same variable condition (3-4:2) is seen in the two specimens referable to *M. thompsoni* (e.g., 3536, Fig. 8,*3a-c*). Measurements are plotted in Figure 9.

5) P^4. All three teeth referred to *Mesodma hensleighi* (e.g., 3852, Fig. 6,*2a-c*) have a cusp formula of 1:6:0. Only one complete P^4 referable to *M. formosa* (2248, Fig. 8,*1a-c*) was found (cusp formula 2:6:0) but 15 other fragments are catalogued. Among the fragments showing the anteroexternal cusp row, eight showed two cusps and two showed three. No teeth definitely referable to *M. thompsoni* were found although the species may be represented among the fragments tentatively referred to *M. formosa.*

6) M^1. The cusp formula for the specimens referred to *Mesodma hensleighi* (e.g., 3844, Fig. 7,*1a-c*) is 6-7:8-9:4-5 (modal 7:8:5). That observed in the Edmonton specimens referred to *M. formosa* (e.g., 3264, Fig. 7,*6a-c*) is 8-9:9:6-7. No complete M^1's have yet been found of *M. thompsoni.* Most of the specimens referred to *M. thompsoni* have a short internal cusp row (e.g., 3110, Fig. 8,*4a-c*), which terminates on the fourth or fifth cusp from the rear in the middle row. The internal row terminates on the fifth or sixth cusps from the rear in the middle row in *M. hensleighi* and on the sixth or seventh in *M. formosa.* Although much smaller, the morphology of the M^1 of *M. thompsoni* is strikingly similar to the eucosmodontid *Stygimys kuzmauli* (SLOAN & VAN VALEN, 1965, p. 224) from the Hell Creek Formation of Montana. However, other teeth in the upper Edmonton fauna do not strongly suggest this similarity and no eucosmodontid incisors have been found. The relationship is thus doubtful.

7) M^2. The cusp formula of specimens referred to *Mesodma hensleighi* (e.g., 3335, Fig. 6,*4a-c*) and *M. formosa* (e.g., 2803, Fig. 7,*5a,b*) is invariably 1:3:3. That of *M. thompsoni,* however, appears to be 1:3:3-4 (e.g., 2563, Fig. 8,*6a,b*). Measurements are plotted in Figure 9.

3-6. Mesodma formosa (MARSH).——*3.* Fragment of right mandible with P_4 (2273, loc. KUA-3); *3a,b,* labial and lingual views, ×10; meas. (mm.), A-P 3.05, W 1.15.——*4.* Left M_2 (3841); *4a-c,* occlusal, labial, and lingual views, ×24; meas. (mm.), A-P 1.60, W 1.40.——*5.* Right M^2 (2803); *5a,b,* labial and occlusal views, ×14; meas. (mm.), A-P 1.55, W 1.50.——*6.* Left M^1 (3264); *6a-c,* labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 3.15, W 1.40.

7. *Mesodma thompsoni* CLEMENS, fragment of right mandible with P_4 (3234); *7a-b,* labial and lingual views; ×6; meas. (mm.), A-P, 4.30, W 1.50.

8-9. Mesodma formosa (MARSH).——*8.* Right M_1 (3897), *8a-c,* labial, occlusal, and lingual views; ×14; meas. (mm.), A-P 2.50, W 1.10.——9. Left P^1 (2243); *9a-c,* occlusal, lingual and labial views, ×20; meas. (mm.), A-P, 1.35, W 1.10.

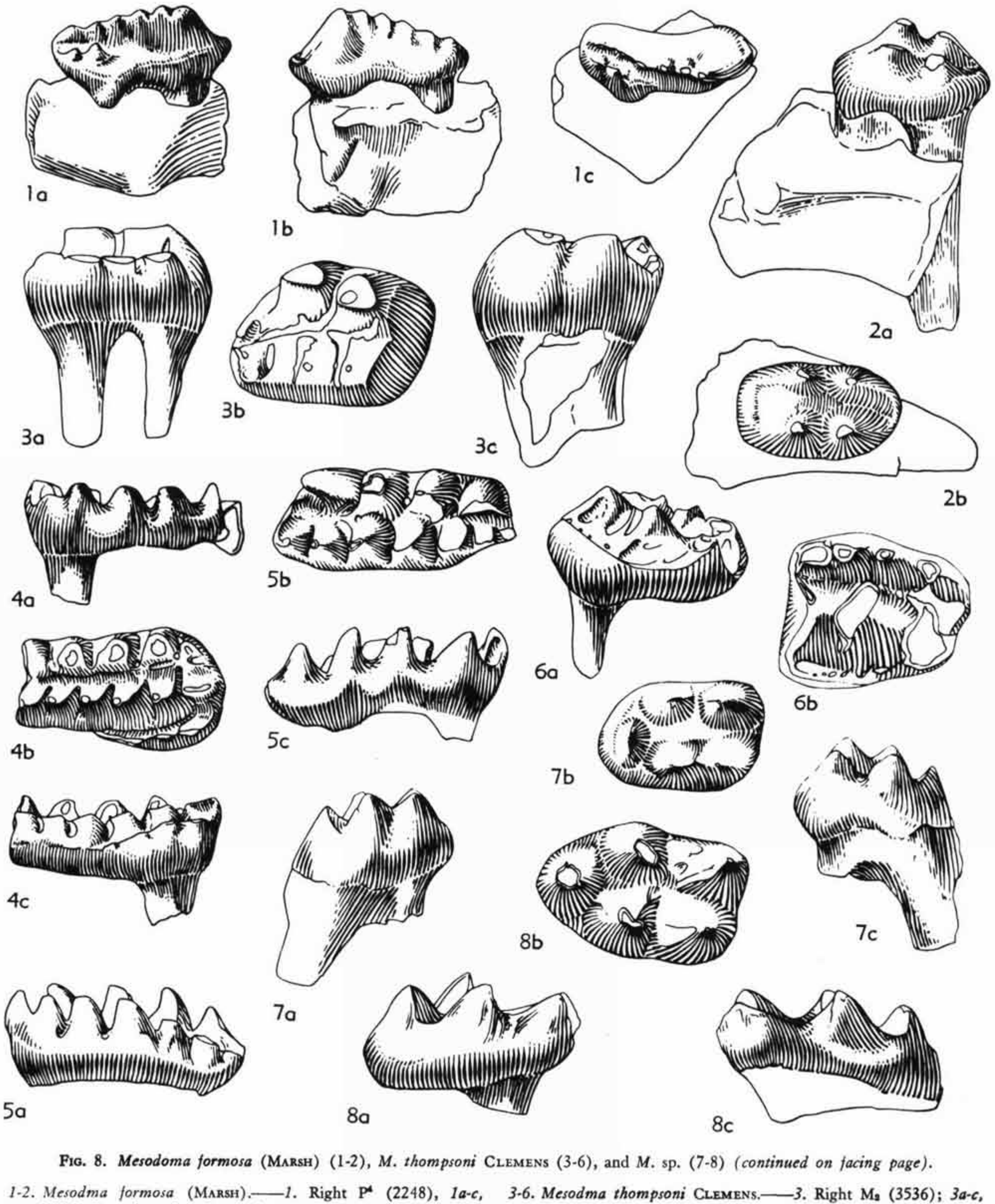

Fig. 8. ***Mesodoma formosa*** **(Marsh)** (1-2), *M. thompsoni* Clemens (3-6), and *M.* sp. (7-8) *(continued on facing page).*

1-2. Mesodma formosa (Marsh).——*1.* Right P^4 (2248), *1a-c,* labial, lingual, and occlusal views, ×14; meas. (mm.), A-P 2.05, W 0.95).——*2.* Left P^3 (2438); *2a-b,* labial and occlusal views, ×20; meas. (mm.), A-P 1.30, W 0.85.

3-6. ***Mesodma thompsoni*** **Clemens.**——*3.* Right M_2 (3536); *3a-c,* labial, occlusal, and lingual views, ×16; meas. (mm.), A-P 2.00, W 1.50.——*4.* Left M^1 (3110); *4a-c,* labial, occlusal, and lingual views, ×14; meas. (mm.), W 1.60.——*5.* Right M_1

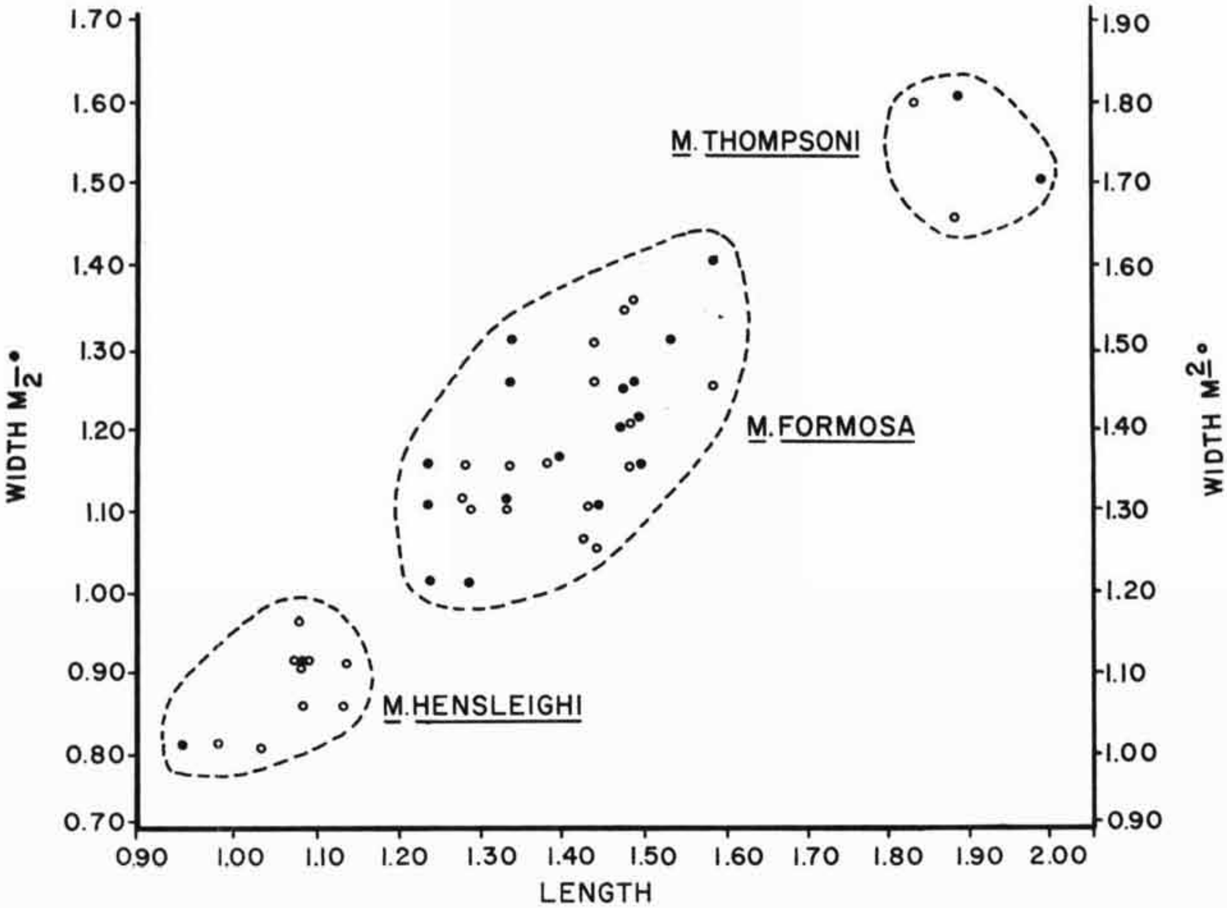

FIG. 9. Scatter diagram showing distribution of $M^2/_2$ measurements of three species of *Mesodma*.

8) Anterior upper premolars. The identification of isolated anterior premolars of multituberculates is difficult. However, groupings of size, morphology, and relative abundance large enough to hazard some guesses at specific identifications have been found.

8a) P^1. A group of seven isolated teeth (e.g., 2243, Fig. 7,*9a-c*) that are similar in size (Table 1) and morphology are tentatively referred to P^1's of *Mesodma formosa*. The measurements are somewhat larger than those recorded by CLEMENS (1963, p. 52, table 4). No specimens have yet been found that can be referred to *M. hensleighi* or *M. thompsoni*.

8b) P^2. A variety of small P^2's has been found in the upper Edmonton strata. Variations in morphology and size are bewildering and no attempt is made at identification. Some deciduous teeth may be represented.

8c) P^3. Only two kinds of small P^3's have been discovered. The smaller (3838, Fig. 7,*2*) is tentatively referred to *Mesodma hensleighi,* the larger (e.g., 2438, Fig. 8,*2*) to *M. formosa*. One specimen referred to *M. formosa* (3939) has a small third external cusp added anteriorly.

8d) DP^2. Two sizes of upper premolars referable to DP^2's have been found. The reasons for considering the teeth to be deciduous are discussed in the description of *Cimolodon nitidus*. Knowledge of multituberculate deciduous dentition is at this time inadequate to relate them with known permanent teeth. Thus, the species to which the specimens belong is unclear. Both types are similar in construction (3935, Fig. 8,*7*; 3859, Fig. 8,*8*) with two roots and five conical cusps. The teeth are anteroposteriorly elongated with the apices of four cusps

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3654, loc. KUA-22); *5a-c,* labial, occlusal, and lingual views, ×14; meas. (mm.), A-P 2.85, W 1.25.——*6.* Right M^2 (2563); *6a-b,* labial and occlusal views, ×16; meas. (mm.), A-P, 1.90, W 1.65.

7-8. Mesodma sp., DP^2 (3935); *7a,c,* side views; *7b,* occlusal view (anterior to right); ×20; meas. (mm.), A-P 1.30, W 1.00. ——*8.* DP^2 (3859); *8a,c,* side views; *8b,* occlusal view (anterior to right), ×20; meas. (mm.), A-P, 1.70, W 1.05.

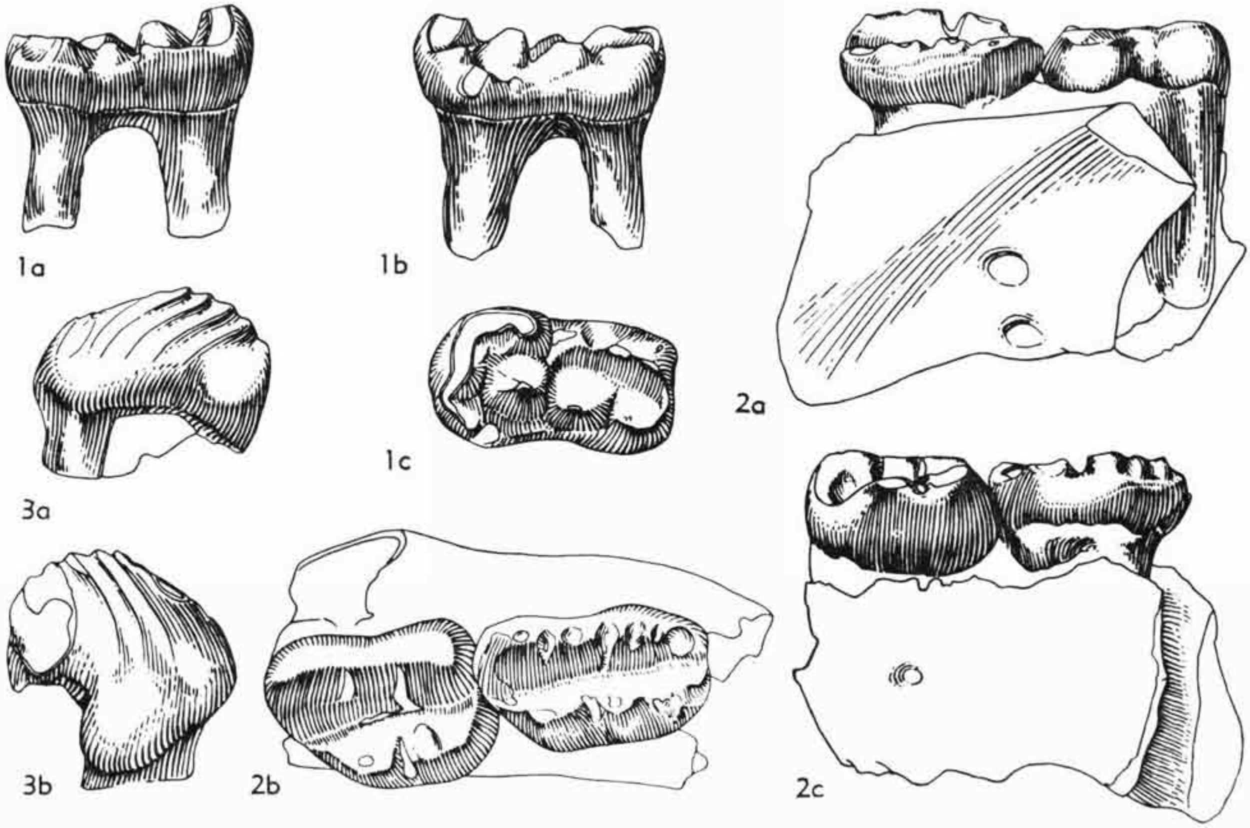

FIG. 10. *Cimexomys priscus* LILLEGRAVEN, n. sp.

1. Holotype, right M^1 (3231); *1a-c,* labial, lingual, and occlusal views, ×10; meas. (mm.), A-P 3.20, W 1.90.
2. Fragment of left mandible with M_{1-2} (3238); *2a-c,* labial, occlusal, and lingual views, ×10; meas. (mm.), M_1, A-P 2.60, W 1.60; M_2, A-P 2.40, W 1.85.
3. Right P_4 (second, third serrations broken off) (2862, loc. KUA-2); *3a-b,* lingual and labial views, ×8; meas. (mm.), A-P 3.80, W 1.80.

forming nearly a square. The fifth cusp is posterior and set slightly to one side of the mid-line of the tooth. As yet I have no evidence to indicate which side of the teeth is lingual. The posterior cusp is significantly the lowest of the five, and the anterior pair is slightly higher than the more posterior pair. A distinct depression is found on the anterobasal part of the teeth where contact probably was strong with the erupting P^2.

Genus CIMEXOMYS Sloan & Van Valen, 1965

CIMEXOMYS PRISCUS Lillegraven, new species
Figure 10,*1-3*

Etymology.—Latin, of former times, ancient.

Type.—3231, isolated right M^1 (Fig. 10,*1*).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—P_4's, 2312, 2862, 3249; fragmentary mandible with M_{1-2}, 3238; M_1, 3675; M^1's, 3287, 4021; M^2, 3239.

Localities.—KUA-1, 2, 3.

Distribution.—Upper part of Edmonton Formation, Alberta; possibly Kirtland and Fruitland formations, New Mexico (unpublished).

Diagnosis.—Teeth larger than *Cimexomys minor;* molars with low cusp formula (M^1, 4:4:2; M_1, 4:3); molar cusps low, quadrate, and show no tendency toward crescentic form; M^1 with short internal row terminating on anterior end of third cusp of middle row; $M^1/_1$ with distinct waist as seen from occlusal view.

Description.—No evidence is yet available for the structure of the incisors or upper premolars.

1) M^1. The holotype (3231, Fig. 10,*1*) has the low cusp formula of 4:4:2. There is a definite constriction on both sides of the middle of the tooth forming a distinct waist. The cusps are low and quadrate, giving a bunodont appearance. The internal cusp row is short and terminates on the anterior end of the third cusp of the middle row. The more anterior cusp of the internal row is much smaller (broken in the holotype) than the posterior cusp. Although the cusps of the external row increase in height only slightly from front to back, those of the middle row increase markedly posteriorly. The anterior faces of the cusps are steeper than the posterior, but they do not overhang and there is no tendency

toward a crescentic formation. The longitudinal valley between the external and middle cusp rows is sharply V-shaped posteriorly, but widens to a broad U-shape anteriorly. The transverse valley separating the first and second cusps on the middle row is shallow. The first cusp of the external row has two anteroposteriorly aligned expansions, but only the slightest depression separates them. The third and fourth cusps of the external row merge early in wear due to the shallow transverse groove separating them. The teeth are two-rooted.

The other two specimens of M^1's referred to *Cimexomys priscus* are considerably smaller than the type (e.g., 4021, length 2.60, width 1.60). If they are indeed members of the same species, size is quite variable.

2) M^2. Only one unmeasurable fragment can questionably be referred to *Cimexomys priscus* (3239). The cusps are robust and quadrate with no tendency toward a crescentic form. Only the posterior half of the tooth has been recovered, but it is definitely two-rooted.

3) P_4. No P_4's have yet been found in definite association with molars of *Cimexomys priscus,* but three teeth of the morphology shown in Figure 10,*3* are tentatively assigned to the species. The assignments are done on the basis of size and by a process of elimination—they do not belong to anything else yet described and are about the expected size. One specimen (3249) was found in matrix mined from a location in the quarry immediately adjacent to the spot from which specimen 3238 (Fig. 10,*2*) was derived, and may even belong to the same individual. However, the association cannot be proven and should be viewed cautiously.

The profile of the crest is rather high and symmetrical with the highest point at about the fourth serration. A range of ?8-10 serrations is observed. The internal (range of 6-8) and external (range of 7-8) ridges are significantly curved with an anterodorsal convexity. The anterolabial lobe is strong and pendulous with a symmetrically rounded bottom. A distinct anterobasal concavity is present for the reception of a small P_3 internally to the mid-plane of the blade. A strong wear-facet is present on the posterolabial surface of the tooth, which accompanies a gradual wearing off of a horizontally elongated cup. An accessory root is present between the two main roots on two of the three specimens.

4) M_1. Both the specimens (e.g., 3238, Fig. 10,*2*) show the low cusp formula of 4:3. The cusps are low and quadrate with those of the internal row being somewhat higher than those of the external. The transverse valleys separating the cusps are shallow except for that which separates the second and third cusps of the internal row. The slopes of the anterior and posterior faces of the cusps are of approximately the same angle. As with the M^1, there is a constriction on both sides of the middle of the tooth forming a waist. The teeth are two-rooted.

5) M_2. The only known specimen (3238, Fig. 10,*2*) is considerably wider than the M_1 and is almost as long. The cusp formula is 3:2 and the two cusp rows are about equal in height. The three external cusps are only weakly separated by transverse valleys which are evident only on the lingual surface of the cusps due to moderate wear on the apices. The labial surface of the third cusp of the external row is slightly inflated. The tooth is two-rooted.

Comments.—SLOAN & VAN VALEN (1965, p. 221) proposed a new genus and species of multituberculate, *Cimexomys minor,* based on teeth found in the Hell Creek Formation of Montana. CLEMENS (1963, p. 47) described but did not name a series of isolated M^1's that differed from those of *Mesodma* sp. These teeth were referred to *C. minor* by SLOAN & VAN VALEN. Another larger species, as yet unnamed, of *Cimexomys* is present in the Hell Creek Formation (SLOAN & VAN VALEN, 1965, p. 222); it is similar except in size to *C. minor. Cimexomys* "B" is shown by VAN VALEN & SLOAN (1966, p. 270, fig. 5) in the early Puercan. This probably represents the unnamed larger species that also is found in the Hell Creek Formation and the line should be continued downward to cross the Cretaceous-Paleocene boundary. Neither the larger unnamed species nor *C. minor* have yet been discovered in the upper Edmonton strata, but the above-described series of teeth is here referred to still another species, *C. priscus,* of the genus. *C. priscus* is more distantly related to *C. minor* and the larger unnamed species from the Hell Creek than the latter two are to each other, and may indeed ultimately be referred to a distinct genus.

Cimexomys priscus is significantly larger than *C. minor* and about the same size as the unnamed Hell Creek species, but may be distinguished from both by the lower cusp formula of the molars and the lack of a tendency toward crescentic molar cusp development.

The rudimentary development of the internal cusp row on the M^1, the simple molar cusp construction in general, the low number of molar cusps, and the subequal lengths of M_1 and M_2 suggest a primitive condition. In fact, the observed pattern is exactly what would be expected as a transitional development between the typically Jurassic plagiaulacids and the Early Cretaceous ptilodontids. On the basis of molar morphology, *Cimexomys priscus* is the most primitive multituberculate yet described from the Late Cretaceous of North America, and ancestral or descendant species on that continent are as yet unknown. However, unpublished information concerning recent finds from the Djadochta beds of the early (?) part of the Late Cretaceous (*see* LEFELD, 1965) of Mongolia show the past existence there of animals with a dental morphology strikingly similar to that of *C. priscus* (KIELAN-JAWOROWSKA, pers. comm.). Thus the existence of *C. priscus* in North America may well represent a Late Cretaceous migration of a surviving

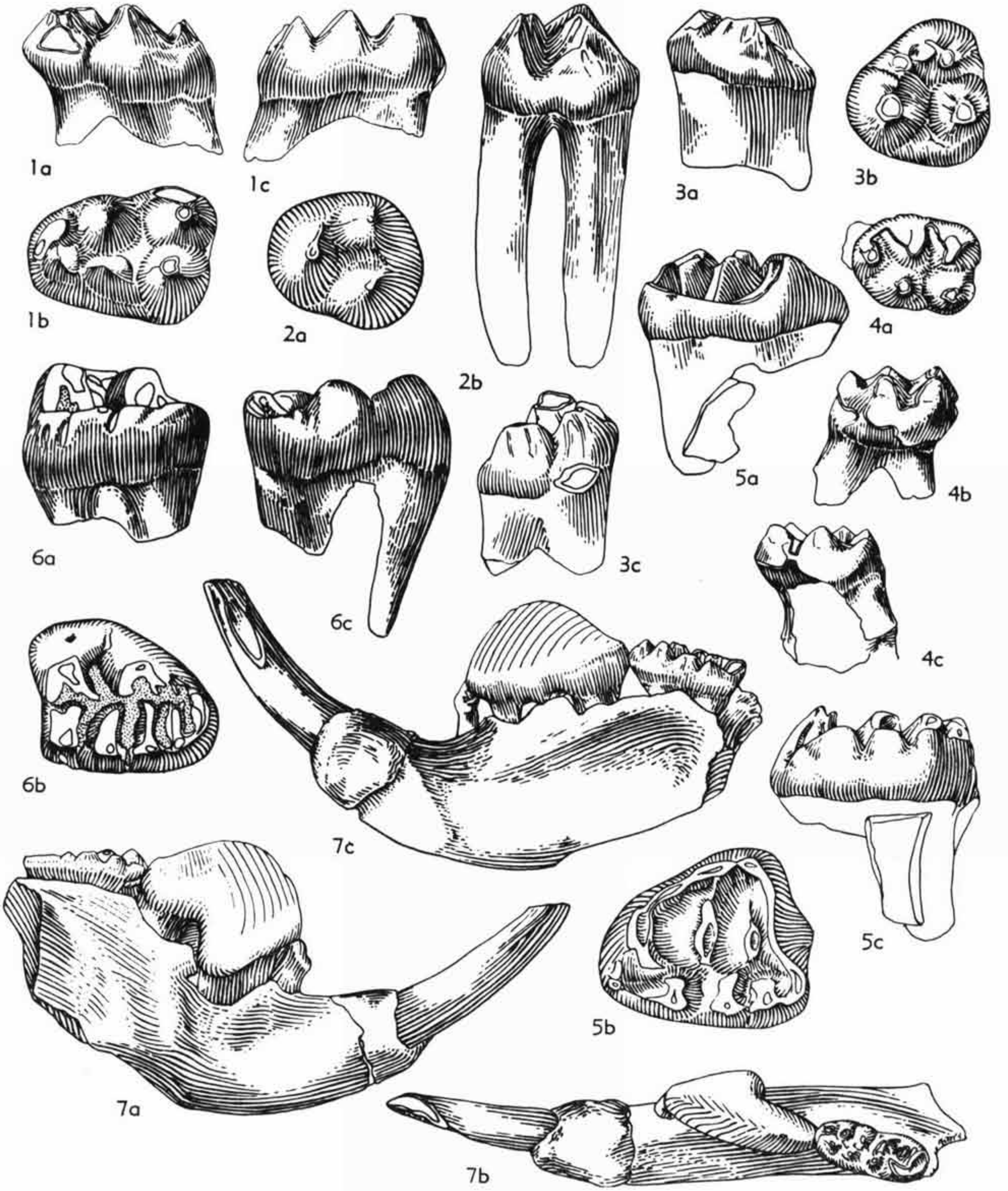

FIG. 11. *Cimolodon nitidus* MARSH *(continued on facing page).*

1. DP^2 (?side) (2499); *1a,c,* side views; *1b,* occlusal view (anterior to right); ×14; meas. (mm.), A-P 2.40, W 1.70.

2. Left P^1 (2411); *2a-b,* occlusal and lingual views, ×10; meas. (mm.), A-P 2.60, W 2.30.

primitive ptilodontid from Asia, a sterile line which soon became extinct.

Family CIMOLODONTIDAE Van Valen & Sloan, 1966

Genus CIMOLODON Marsh, 1889a

CIMOLODON NITIDUS Marsh, 1889a

Figures 11,*1-7*, 12,*3*

Type.—YPM 11776, left M_1 (Marsh, 1889a, pl. 2, fig. 5-8).

Referred specimens.—Fragmentary mandible with $I_1P_{3-4}M_1$, 2333; P_3, 3595; fragmentary mandible with P_4M_{1-2}, 3115; P_4's, 2562, 3187; fragmentary mandible with M_{1-2}, 3784; M_1's, 2298, 2595, 2666, 2757, 2852, 3141, 3148, 3220, 3297, 3737, 3963; M_2's, 2244, 2251, 2252, 3208, 3728, 3966; DP^2's, 2499, 2980, 3610; P^1's, 2246, 2411, 2492, 2992, 3018, 3738, 3958; fragmentary maxilla with P^{2-3}, 3700; P^2, 2974; fragmentary maxilla with $P^{3-4}M^1$, 3792; P^3's, 2247, 2382, 3299, 3300; P^4's, 2245, 2314, 2960, 3029, 3056, 3123, 3301, 3523, 3603, 3658; fragmentary maxilla with M^{1-2}, 2868; M^1's, 2599, 2600, 3017, 3084, 3086, 3124, 3594, 3749; M^2's, 2250, 2299, 2300, 2561, 2638, 3026, 3085.

Localities.—KUA-1, 3, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and possibly (unpublished) South Dakota; Kirtland and Fruitland formations, New Mexico (unpublished).

Description.—The specimens referred to *Cimolodon nitidus* generally agree with descriptions by CLEMENS (1963, p. 56), and only differences from or additions to his work will be covered here. All measurements of the Edmonton specimens are presented in Table 2 and drawings representing the known members of the dental series are included with the text (Fig. 11,*1-7*).

1) I_1. The I_1 (Fig. 11,*7*) has a pronounced wear-facet which is superior-lingually placed at the tip of the tooth, but adproximally it becomes entirely lingual in position. The wear-facet extends along half the extra-alveolar length of the tooth. Except for the interruption by the wear-facet, the tooth is completely enamel-covered. However, the enamel on the superior surface is very thin, providing a "pseudo-eucosmodontid" adaptation. A pronounced ridge runs along the distal half of the extra-alveolar tooth on the lingual side of the inferior border. The enamel is thickest on this ridge and a groove runs the same distance just superior to it on the lingual side. A weak ridge, flanked on both sides by shallow grooves, is present along half the distal extra-alveolar length of the superior-labial surface of the tooth. The cross section of the proximal end of the extra-alveolar tooth is ovoid with a height-width ratio of 1.20.

2) P_3. The two known P_3's are similar to CLEMENS' (1963, p. 59) description, but neither show the extra cusps on the ridge anterior to the apical cusp.

TABLE 2. *Measurements (in mm.) of Teeth Referable to* Cimolodon nitidus *Marsh.*

Tooth	Length			Width		
	N	OR	$\overline{X}$	N	OR	$\overline{X}$
DP^2	3	2.10-2.40	2.30	2	1.65-1.70	1.67
P^1	6	2.00-2.70	2.32	7	2.00-2.50	2.22
P^2	2	2.35-2.40	2.37	2	2.35-2.50	2.42
P^3	6	1.95-2.50	2.31	6	1.80-2.20	2.02
P^4	5	4.35-5.00	4.71	6	1.85-2.70	2.37
M^1	6	4.70-6.15	5.28	8	2.80-3.20	2.96
M^2	4	3.00-3.60	3.32	7	2.80-3.15	2.98
P_4	3	6.00-6.80	6.42	4	2.50-3.00	2.79
M_1	3	4.70-5.05	4.88	10	2.10-2.40	2.20
M_2	7	3.10-3.80	3.47	7	2.20-2.85	2.57

For abbreviations see end of Introduction.

3) DP^2. A variety of unidentified isolated anterior upper premolars was described and figured by CLEMENS (1963, p. 97-98) from the Lance Formation. Subsequent to that study, SZALAY (1965) described the replacement of the deciduous P^2 by its permanent equivalent in *Cimolodon* sp. (smaller than *C. nitidus*) from the Hell Creek Formation of South Dakota. I believe that the DP^2 shown by SZALAY (1965, fig. 4-6, p. 9-11) is morphologically equivalent to CLEMENS' anterior premolar "type F." It should be emphasized here that I am using CLEMENS' various "type *x*" designations in a morphological, not a taxonomic sense, and am not necessarily assigning the Lance specimens to any specific taxa. Two isolated teeth like "type F" have been found in the upper Edmonton Formation (e.g., Fig. 11,*4*), which I refer to DP^2's of *Cimolodon nitidus*. The teeth are anteroposteriorly elongated and composed of five rather low conical cusps. The apices of four of the cusps form a nearly perfect square; the fifth is posterior to the square and sets exactly on the midline of the tooth. The teeth are symmetrical and I cannot determine which is the internal side. The paired cusps are equal in height from one side to the other, but all cusps decrease in height uniformly from anterior to posterior. The teeth are two-rooted with the posterior root being the stronger.

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3. Right P^2 (2974); *3a-c*, labial, occlusal, and lingual views; ×10, meas. (mm.), A-P 2.40, W 2.50.

4. DP^2 (?side) (2980); *4a*, occlusal view (anterior to right); *4b-c*, side views; ×10; meas. (mm.), A-P 2.10, W 1.65.

5. Right M^2 (2638); *5a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 3.40, W 2.95.

6. Left M_2 (2252); *6a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 3.35, W 2.50.

7. Fragment of right mandible with $I_1P_{3-4}M_1$ (2333); *7a-c*, labial, occlusal, and lingual views, ×4; meas. (mm.), P_4, A-P 6.80, W 3.00; M_1, A-P 4.90, W 2.25.

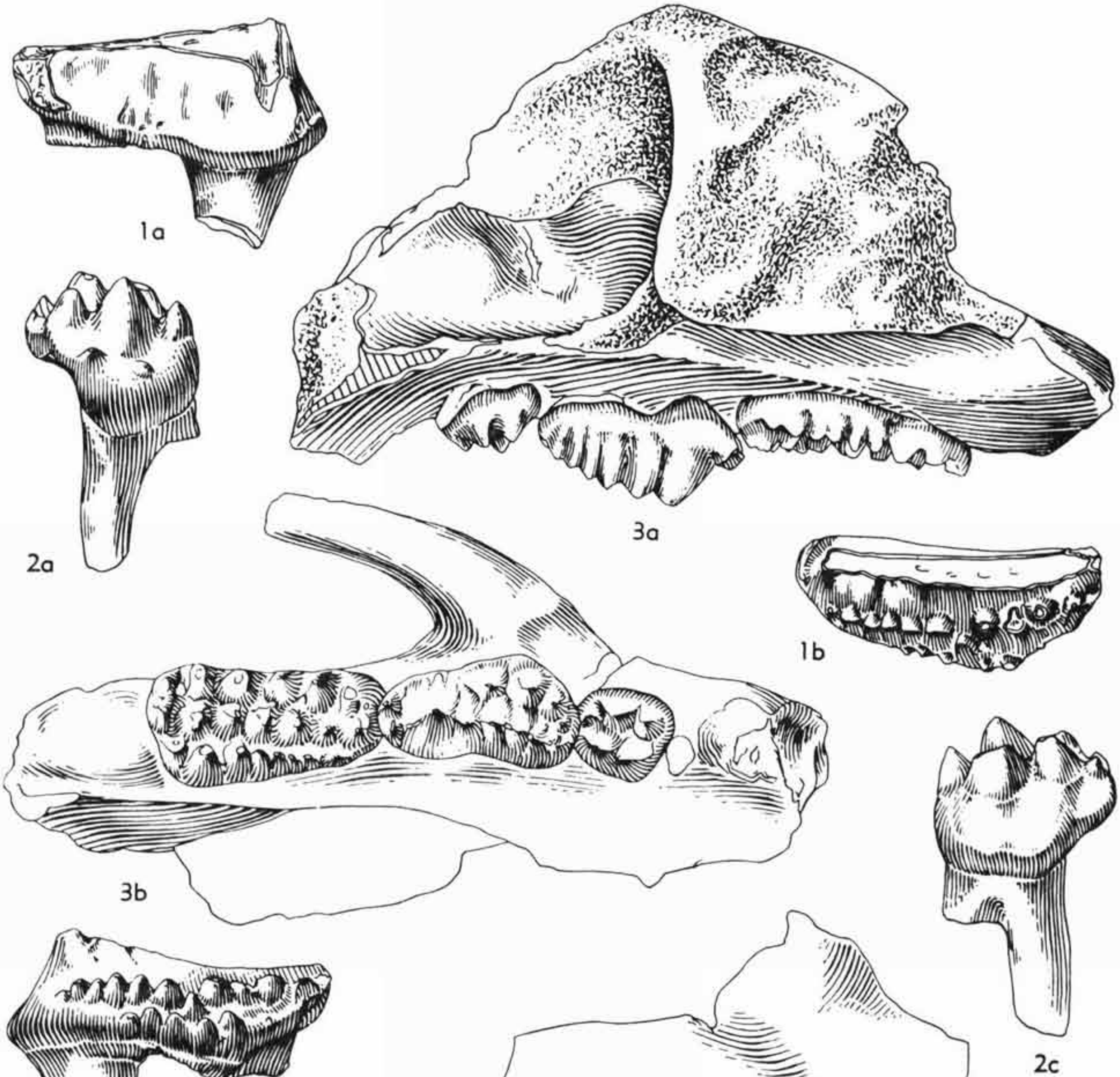

FIG. 12. Ptilodontidae, gen. et sp. indet. *(1-2)* and *Cimolodon nitidus* MARSH *(3) (continued on facing page).*

A similar tooth (Fig. 11,*1*) from the upper Edmonton Formation resembles Clemens' anterior premolar "type I" except that the latter is about one-third larger. The Edmonton specimen is probably a variation of a DP^2 of *Cimolodon nitidus* that has six conical cusps arranged in two anteroposterior rows of three. The cusps of the posterior pair are significantly the lowest and are set more closely to the mid-line than the other two pairs. The cusps of the anterior pair are the only ones that show obvious wear. Again, it cannot be determined certainly which side is internal, but one side is longer than the other with slightly more robust and higher cusps. This type of deciduous tooth is considerably more molariform than the first-described kind, and both possibly did serve as functional molars during the early youth of the animals.

Several of the isolated anterior upper premolars described by Clemens will probably eventually be referred to deciduous multituberculate teeth.

4) P^4. The observed cusp formula variation was 3-4:5-7. No specimens were found in which the length of the external cusp row approached that of the main medial row.

5) M^1. The observed cusp formula variation was 6-7:7-8:6-8 (usually three to five large cusps in the internal row). The M^1's are tightly knit morphologically and conform well with those of the Lance Formation.

Comments.—Morphologically, the members of *Cimolodon nitidus* from the upper Edmonton Formation of Alberta form a closely knit group, more so than those from the Lance Formation of Wyoming. The teeth of the Alberta group are slightly larger than those of the Wyoming sample and are less variable in size. A tooth-by-tooth comparison of the size ranges in Table 2 with those of Clemens' table 7 (1963, p. 68) indicates that the Edmonton specimens are consistently at the higher end of the Lance scale or exceed it. The differences are too slight, however, to suggest that distinct species are represented.

The Alberta localities are roughly 600 miles north of those of Wyoming. It is at least a possibility that "Bergmann's rule" (Mayr, 1963, p. 319) applies here, indirectly suggesting a cooler climate to the north. A period of relative cooling during the deposition of the mammal localities in the upper Edmonton Formation is indicated by palynological studies (Srivastava, 1967). It is also possible that, as Clemens suggested (1963, p. 69), *Cimolodon nitidus* of the Lance Formation is actually a composite of two closely related species. Perhaps only the larger of these has been found in the upper Edmonton Formation. The evidence is still insufficient to choose the first, the second, or a combination of alternatives to explain the observed differences between the northern and southern population samples.

Family PTILODONTIDAE Gregory & Simpson, 1926

Genus and Species UNDETERMINED

Two teeth of unusual construction have been found that probably are referable to the family Ptilodontidae, but whose generic affinities are unknown.

Figure 12,*1* shows an isolated P^4 (3739) with two roots and three well-developed rows of cusps. Although the cusps of the main crest are completely worn away, influences of the pulp cavity on the dentine indicate nine or 10 were originally present. The middle row is composed of 11 irregularly spaced, small, sharply conical cusps, the first four of which are worn. The external row has one tiny anterior cusp separated by a short gap from five additional evenly spaced, small, sharply conical cusps. The central axes of all the cusps of the two external rows project ventrolabially. There is no lingual cusp row and the entire lingual surface of the tooth shows wear from shearing with the P_4. A pronounced depression is present on the anterior end of the tooth where contact was made with the P^3. The crest of the main ridge in the unworn condition was probably fairly high in contrast to that in *Ptilodus* (Jepsen, 1940, p. 335, pl. 2) and the cusp formula and general morphology differs greatly from either *Kimbetohia* (Simpson, 1936, p. 2) or *Ptilodus*. The tooth probably represents a previously undescribed genus of multituberculate, but I would prefer to leave it unnamed until more evidence as to its affinities is accumulated.

Figure 12,*2* shows an isolated tooth (3304) with three cusp rows that may be a peculiar P^3 or perhaps a member of a deciduous series. The two roots are closely applied and are restricted to the posterior half of the tooth. The anterior half overhangs sharply and looks deformed as if the enamel organ was compressed by another erupting tooth. The middle row is composed of four sharply conical cusps of which the most anterior is the smallest and the penultimate the largest. The lateral orientation of the tooth cannot be determined. One external row has two tiny, subequal, conical cusps set low on the side of the tooth. The other external row has three cusps, the most anterior of which is the smallest. The remaining two are large and the more posterior cusp is slightly more robust. The tooth is about the right size to be a P^3 of the same species represented in Figure 12,*1*, but such a reference at this time would be only a guess.

1-2. Ptilodontidae, gen. et sp. indet.——*1.* Left P^4 (3739, loc. KUA-22); *1a-c*, lingual, occlusal, and labial views, ×14; meas. (mm.), A-P 3.50, W 1.43.——*2.* ?P^3 (?side) (3304); *2a,c*, side views; *2b*, occlusal view (anterior to left); ×20; meas. (mm.), A-P 1.30, W 1.20.

3. *Cimolodon nitidus* Marsh. Skull fragment with right $P^{3-4}M^1$ (3792); *3a-c*, lingual, occlusal, and labial views, ×6; meas. (mm.), P^3, A-P 2.50, W 2.15; P^4, A-P 5.00, W 2.70; M^1, A-P 5.55, W 3.00.

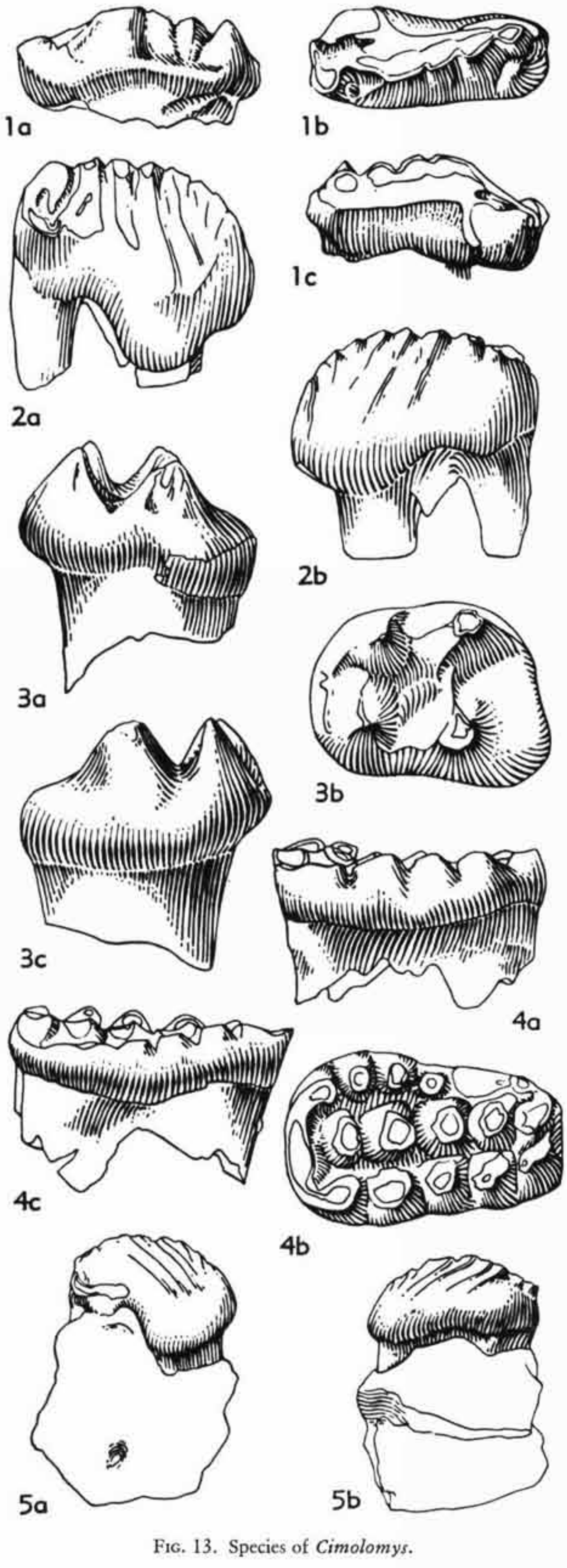

FIG. 13. Species of *Cimolomys*.

1-2. *Cimolomys gracilis* MARSH.——*1*. Left P^4 (2519); *1a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 3.20, W 1.45.——*2*. Right P_4 (3694, loc. KUA-22); *2a-b*, labial and lingual views, ×8; meas. (mm.), A-P 4.35, W 1.60.

3. ?*Cimolomys gracilis* MARSH. Right P^3 (3597); *3a-c*, labial, occlusal, and lingual views, ×20; meas. (mm.), A-P 1.65, W 1.25.

4-5. *Cimolomys trochuus* LILLEGRAVEN, n. sp.——*4*. Left M^1 (3086); *4a-c*, labial, occlusal, and lingual views, ×8; meas. (mm.), A-P 4.70, W 2.90.——*5*. Holotype, fragment of right mandible with P_4 (2353); *5a-b*, labial and lingual views, ×4; meas. (mm.), A-P 5.85, W 2.45.

Suborder TAENIOLABIDOIDEA Granger & Simpson, 1929

[*emend*. SLOAN & VAN VALEN, 1965]

Family CIMOLOMYIDAE Marsh, 1889a

[*emend*. SLOAN & VAN VALEN, 1965]

Genus CIMOLOMYS Marsh, 1889a

CIMOLOMYS GRACILIS Marsh, 1889a

Figure 13,*1-3*

Type.—YPM 11835, right M^1 (Marsh, 1889a, pl. 2, fig. 1-4).

Referred specimens.—P_4's, 2371, 3670, 3694, 3965; P^3's, 3597, 3683; P^4, 2519.

Localities.—KUA-1, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota.

Comments.—*Cimolomys gracilis* is rare in locality KUA-1, but is apparently more common in KUA-22. The known specimens agree well with CLEMENS' (1963, p. 76) descriptions of material from the Lance Formation except that the Edmonton P^4 (2519, Fig. 13,*1*) slightly exceeds the observed range of variation in length and all the Edmonton P_4's (e.g., 3694, Fig. 13,*2*) have an accessory root just behind the anterior main root. The range of size variation of the Edmonton P_4's is: length, 4.35-4.65; width 1.50-1.85.

Two small isolated P^3's (e.g., 3597, Fig. 13,*3*) have been found that are about the right expected size for *Cimolomys gracilis* and are tentatively referred to that taxon. The measurements are as follows: length, 1.65; width, 1.25-1.40. Except for the smaller size, the morphology is identical with that of *Cimolodon nitidus*.

CIMOLOMYS TROCHUUS Lillegraven, new species

Figure 13,*4,5*

Etymology.—Named in honor of the town of Trochu, Alberta, west of the upper Edmonton Formation collecting localities.

Type.—2353, fragmentary right mandible with P_4 (Fig. 13,*5*).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—M^1's, 3086, 3594.

Locality.—KUA-1.

Distribution.—Upper part of Edmonton Formation, Alberta.

Diagnosis.—P_4 similar to *Cimolomys gracilis* but larger, with four internal ridges, more subdued serrations, less vertical anterior edge of crest, and slightly more robust anterolabial lobe; P_3 lacking.

Description and comments.—The holotype, 2353 (Fig. 13,*5*), is a P_4 with nine serrations, four external ridges, four internal ridges, and a low symmetrically-arched crest. A distinct cuplike protuberance is present on the posterolabial side of the tooth. Although nearly obliterated by wear, two vertical grooves extend ventrally toward the cup from the notches separating the last three serrations. The first external and internal ridges originate on the fourth serration, and the others arise from the more posterior serrations in succession. Short aborted ridges on both sides also originate from the first three serrations. All ridges are rather straight and extend anteroventrally from their points of origin. If an accessory root is present, it is hidden by the mandible itself. The anterior root is much larger than the posterior. The P_3 is lacking.

Nearly all of the characters mentioned above fit the description of *Cimolomys gracilis* as described by CLEMENS (1963, p. 76). However, 2353 is significantly larger than any known P_4's of *C. gracilis*. A few minor differences other than size are evident. The anterior face of the crown is less vertical in *C. trochuus* than in *C. gracilis*. Four internal ridges are present in contrast to two or three in *C. gracilis* and all serrations are more subdued. The anterolabial lobe is slightly more robust than that seen in *C. gracilis*. The presence or absence of the P_3 in *C. gracilis* is unknown.

RUSSELL (1936, p. 75) described *Cimolomys major* as a new species from the Oldman Formation of Alberta; the holotype is a mandibular fragment with the root of the incisor, the alveolus for a P_3, the roots of P_4, and a complete M_{1-2}. A complete P_4 from another locality in the same formation was later referred to the same species on the basis of size and probable morphology (RUSSELL, 1952, p. 111). Assuming that the association is correct, *C. major* differs from *C. trochuus* in the possession of a P_3, in having a P_4 serration count of 11, being considerably larger, and having lived in a significantly more ancient period. It is quite possible, however, that *C. major* is directly ancestral to *C. trochuus*. The evidence is too meager to be conclusive.

Two isolated M^1's (e.g., 3086, Fig. 13,*4*) have been found in the upper Edmonton Formation which are similar to those of *Cimolodon nitidus*, but differ from it in several respects and may be referable to *Cimolomys trochuus*. The reference, however, is made with caution as the molars of *Cimolodon* and *Cimolomys* must be similar (CLEMENS, 1963, p. 69). The cusp formula of both teeth is 5:6:7. The middle row cusp count of six is lower than that observed in Lance specimens of *Cimolodon nitidus* (CLEMENS, 1963, p. 79). Both are shorter (length 4.70-4.80) than the Edmonton *Cimolodon* (Table 2) and are near the lower end of the range of width measurements (both 2.90). The cusps are more rounded, less crescentic, and less ornamented than those of *Cimolodon nitidus*. Unfortunately, the M^1's of *Cimolomys major* are unknown. One would expect, however, that the cusps would be more crescentic than those teeth referred to *C. trochuus*. The cusps of the M_{1-2} of *C. major* are only slightly less crescentic than in those teeth referred to *C. gracilis* (CLEMENS, 1963, p. 82).

ZOOGEOGRAPHIC CONSIDERATIONS OF EDMONTON FORMATION MULTITUBERCULATES

The list of multituberculate taxa discovered in the upper part of the Edmonton Formation is as follows:

Multituberculate Taxa in Upper Part of Edmonton Formation

Subclass ALLOTHERIA
  Order MULTITUBERCULATA
    Suborder PTILODONTOIDEA
      Family ECTYPODONTIDAE
        Mesodma hensleighi LILLEGRAVEN, n. sp.
        Mesodma formosa (MARSH, 1889b)
        Mesodma thompsoni CLEMENS, 1963
        Cimexomys priscus LILLEGRAVEN, n. sp.
      Family CIMOLODONTIDAE
        Cimolodon nitidus MARSH, 1889a
      Family PTILODONTIDAE
        Gen. et sp. indet.
    Suborder TAENIOLABIDOIDEA
      Family CIMOLOMYIDAE
        Cimolomys gracilis MARSH, 1889a
        Cimolomys trochuus LILLEGRAVEN, n. sp.

Of the eight species listed above, only *Cimexomys priscus*, the unnamed ptilodontid, and *Cimolomys trochuus* are peculiar to the local fauna. All the others (probably including *Mesodma hensleighi*) are also present in the type Lance (CLEMENS, 1963) and Hell Creek (SLOAN & VAN VALEN, 1965) formations. *Essonodon* has not yet been discovered in the upper Edmonton Formation. It is rare in both the Lance and Hell Creek formations, and its absence in Alberta may be an artifact resulting from insufficient collecting. The absence of *Meniscoessus*, specimens of which are physically large and common in other deposits, is an unexplained surprise. Not a scrap referable to this genus has yet been discovered from the Edmonton Formation.

The upper part of the Hell Creek Formation of Montana remains unique with the species of *Stygimys* and *Catopsalis* and the large unnamed species of *Cimexomys*. *Cimexomys minor* is now recognized in the Hell Creek and Lance formations, but has not been found in the Edmonton. The presence of *Cimexomys priscus* in the Edmonton Formation probably reflects a migration from an Asiatic stock. Its possible presence in the Kirtland and Fruitland formations of New Mexico and absence in

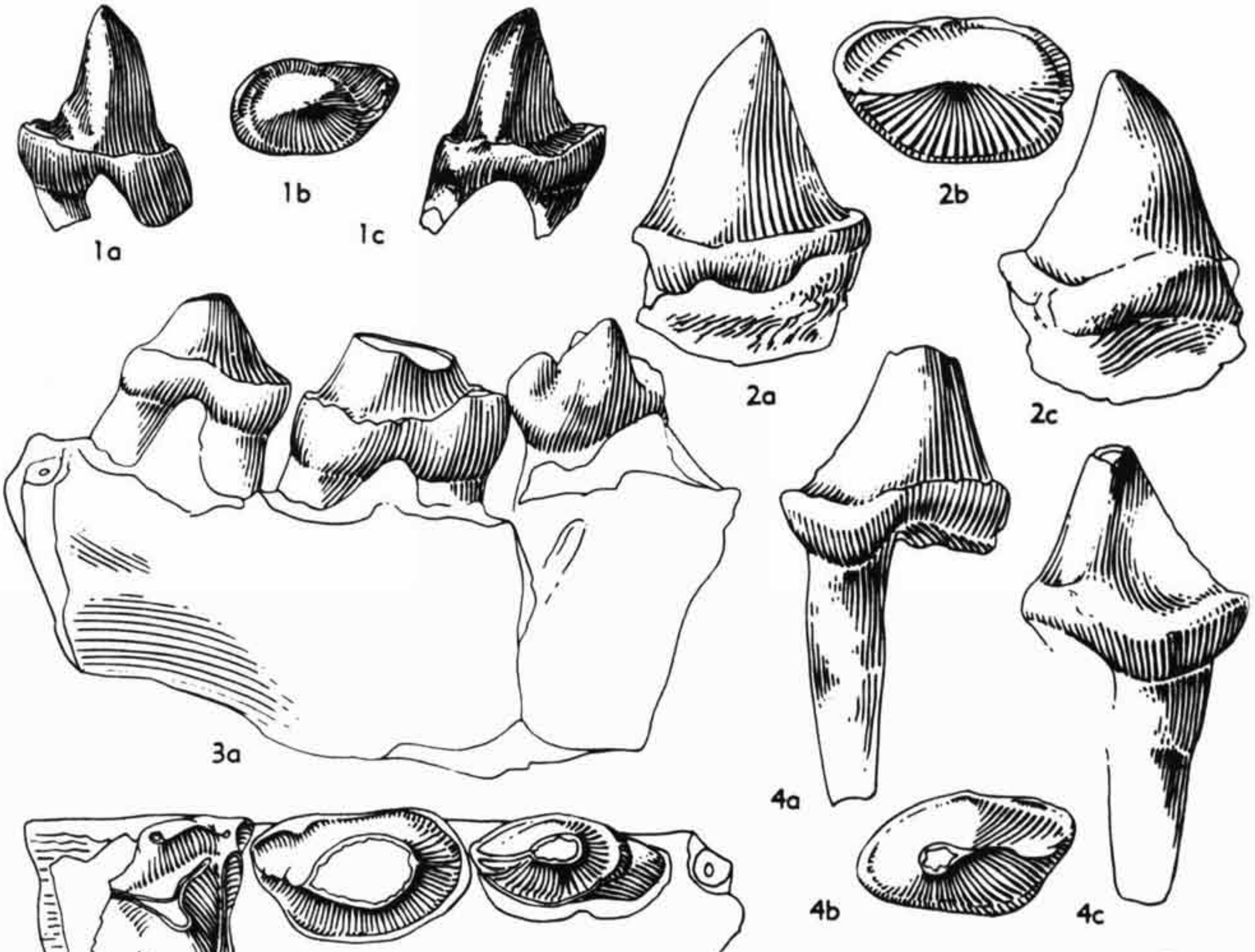

FIG. 14. *Alphadon marshi* SIMPSON (*continued on facing page*).

the eastern Montana and Wyoming deposits presents a puzzling zoogeographic problem.

I have found no indication of a significant difference in the ages of the type Lance Formation and the upper part of the Edmonton Formation on the basis of the multituberculate fauna. I agree with the conclusion of Van Valen & Sloan (1966, p. 265, fig. 1) that the Bug Creek Anthills locality and those stratigraphically above it in the Hell Creek Formation are slightly younger than the upper part of the Edmonton Formation.

Subclass THERIA Parker & Haswell, 1897

Infraclass METATHERIA Huxley, 1880

Order MARSUPIALIA Illiger, 1811

Family DIDELPHIDAE Gray, 1821

Genus ALPHADON Simpson, 1927a

ALPHADON MARSHI Simpson, 1927a

Figures 14,*1-6*; 15,*1-3*

Type.—YPM 13659, right M^3, not M^2 (Clemens, 1966, p. 5), (Simpson, 1929, fig. 45F).

Referred specimens.—One isolated P^1; fragmentary maxillae with $P^{2-3}M^1$ (2389), M^{1-4} (2846), and M^{2-3} (2232); five P^2's; 21 P^3's; 10 M^1's; five M^2's; three M^3's; four M^4's; eight P_2's; fragmentary mandibles with P_3M_1 (2477, 2912), P_3M_{1-2} (2742, 3796), P_3M_{1-4} (2846), P_3M_2 (2373), P_3M_{2-3} (2498), M_{1-3} (2851), M_{2-3} (2185, 2753), and M_{3-4} (2849, 3066, 3794); seven P_3's; nine M_1's; nine M_2's; six M_3's; seven M_4's.

Localities.—KUA-1, 3, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana; Kirtland and Fruitland formations, New Mexico (unpublished).

Revised diagnosis.—After Clemens (1966, p. 5) with following additions: P^3 with strong complete lingual and labial cingula; M^3 with stylar cusp D larger than C; P_2 distinctly smaller than P_3, and with proportionately lower main cusp, anterior border of main cusp strongly convex anteriorly, and labial and lingual cingula present; P_3 with sharp anterior and posterior borders of main cusp, anterior border of main cusp less convex than P_2, lingual and posterior half of labial cingulum present; M_4 significantly smaller than M_{2-3}. Measurements are recorded in Table 3.

Description of upper premolars.—The only known specimen in which the upper premolars have been found in association with molars is illustrated in Figure 14,*3*. Unfortunately, however, the apices of the P^2 and P^3 on the specimen are missing. A complete P^2 (3179, Fig. 14,*2*) and a complete P^3 (2590, Fig. 14,*1*) are also figured. The measurements for premolars referred to the two small species of *Alphadon* are presented in Table 4.

1) P^3. The two-rooted P^3 is a robust trenchant unicuspid tooth with a strong, completely encircling basal cingulum. The rounded anterior border of the main cusp bends sharply posteriorly for the ventral third of its height. The posterior border is sharper, slightly concave, and generally unworn. Nearly all teeth show a small wear facet on the apex of the cusp. The strong cingulum is a consistent feature distinctive of the species. It is variably expanded on the posterolabial corner of the tooth, nearly to the point of forming a definite cusp. The cingulum then passes horizontally on the labial side with a variable series of undulations to the anterior border of the tooth. A vertical, weakly defined ridge on

Table 3. *Dental Measurements (in mm.) of* Alphadon marshi *Simpson (specimen 2846).*

Tooth	Length	Width	
P_3	1.80	1.15	
		W-Tri	W-Tal
M_1	2.30	1.50	1.60 (est.)
M_2	2.65	1.90	2.00
M_3	2.75	1.90	1.70
M_4	2.50	1.60 (est.)	1.20
		Ant-W	Post-W
M^1	2.70	2.70	2.90
M^2	2.85	3.30	3.30
M^3	2.55	3.40	3.35
M^4	1.75	3.05	2.10
P_3-M_4	11.95		
M_1-M_4	10.25		
M^1-M^4	8.50		

For abbreviations see end of Introduction.

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1. Left P^3 (2590); *1a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 2.15, W 1.30.

2. Right P^2 (3179); *2a-c*, labial, occlusal, and lingual views, ×20; meas. (mm.), A-P 1.55, W 0.90.

3. Fragment of right maxilla with $P^{2-3}M^1$ (2389); *3a-c*, labial, occlusal, and lingual views, ×14; meas. (mm.), P^2, A-P 1.60, W 0.90; P^3, A-P 2.00, W 1.30; M^1, Ant-W 2.50.

4. Left P^1 (3350); *4a-c*, labial, occlusal, and lingual views, ×24; meas. (mm.), A-P 1.20, W 0.75.

5. Right P_2 (3349); *5a-c*, labial, occlusal, and lingual views, ×16; meas. (mm.), A-P 1.50, W 0.80.

6. Right P_3 (2376); *6a-c*, labial, occlusal, and lingual views, ×16; meas. (mm.), A-P 1.60, W 0.85.

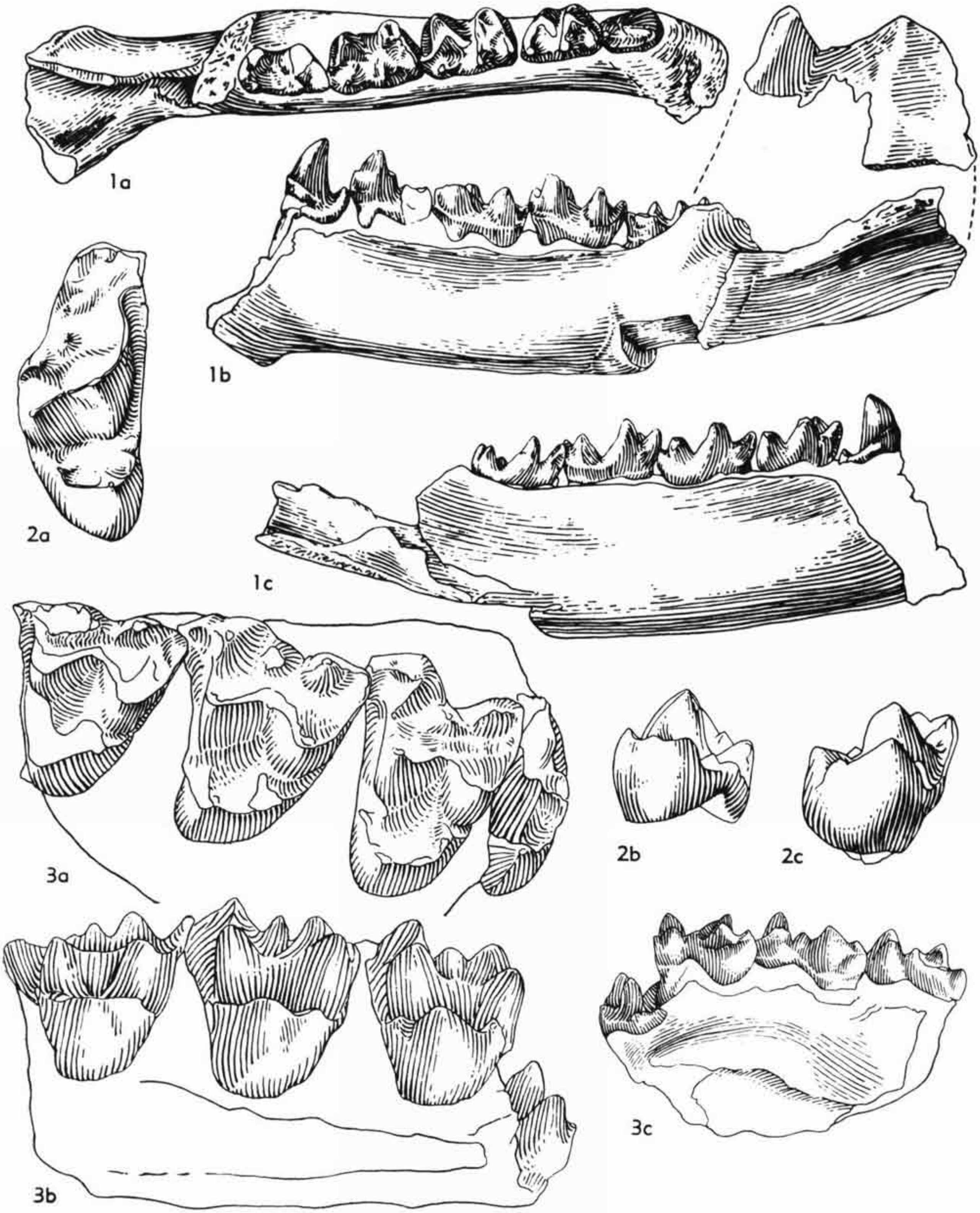

FIG. 15. *Alphadon marshi* SIMPSON (*continued on facing page*).

TABLE 4. *Measurements (in mm.) of Premolars Referable to* Alphadon *spp.*

Tooth	Taxon	Length					Width				
		N	OR	X̄	SD	CV	N	OR	X̄	SD	CV
P_1	A. wilsoni	2	0.80-1.00	0.90	----	----	2	0.55	0.55	----	----
	A. marshi	2	1.25-1.35	1.30	----	----	3	0.70-0.80	0.75	----	----
P_2	A. wilsoni	1	1.20	----	----	----	1	0.65	----	----	----
	A. marshi	8	1.30-2.00	1.62	----	----	8	0.75-1.05	0.89	----	----
P_3	A. wilsoni	5	1.15-1.35	1.26	----	----	4	0.65-0.90	0.74	----	----
	A. marshi	11	1.60-2.10	1.82	0.18	9.83	13	0.85-1.40	1.11	0.16	14.32
P^1	A. marshi	1	1.20	----	----	----	1	0.75	----	----	----
P^2	A. marshi	6	1.50-1.75	1.62	----	----	6	0.90-1.10	0.94	----	----
P^3	A. wilsoni	5	1.30-1.50	1.38	----	----	5	0.70-0.95	0.83	----	----
	A. marshi	19	1.80-2.25	2.01	0.12	6.14	22	1.05-1.45	1.25	0.10	7.85

For abbreviations see end of Introduction.

the lingual side of the main cusp extends from the apex to the cingulum. That part of the cingulum extending from the anterior border of the tooth to the lingual ridge is convex toward the roots. Consistently the cingulum continues posterially from the lingual ridge to a point about one-third the distance from the posterior end of the tooth, where it turns sharply posteroventrally to connect with the termination of the posterior ridge of the main cusp. Obvious normal wear on the cingulum has been detected only on the steeply descending posterolingual part just described. One specimen (3203) has a deep but narrow wear-gully on the anterolingual corner of the tooth that obliterates that part of the cingulum. Wear extends less distinctly about half way to the apex of the main cusp on its anterior border. The animal represented by this tooth probably suffered a malocclusion between the P^3 and the apex of a lower premolar.

2) P^2. The P^2 (e.g., 3179, Fig. 14,*2*) is a variation on the theme of P^3 except for its smaller size and somewhat weaker production of the posterolabial shelf of the cingulum. One unusually heavily worn specimen (3475) shows a continuous wear-facet extending from the apex of the tooth down the posterolingual edge of the cusp and connecting with the obliterated, steep posterolingual part of the cingulum. The cingulum of the specimen is elsewhere unworn.

3) P^1. Although no P^1's have been found in association with other known teeth, 3350 (Fig. 14,*4*) is here identified as a P^1 of *Alphadon marshi*. It is two-rooted and morphologically similar to both P^2 and P^3, but is considerably smaller. The wear on the cingulum is the same as that in P^{2-3}. The base of the slightly worn posterior border of the main cusp extends proportionately more posteriorly onto the cingulum than on the P^{2-3}.

Description of lower premolars.—The upper Edmonton specimen (2846, Fig. 15,*1,3*), which includes associated upper and lower dentitions, shows that Clemens (1966, p. 87) correctly identified the lower jaws that he referred to *Alphadon ?marshi.*

4) P_2. The height of the main cusp and the length of the entire P_2 (e.g., 3349, Fig. 14,*5*) are about equal. The anterior border of the main cusp is sharp and strongly convex anteriorly. The labial and lingual cingula are invariably present, but are generally weak anteriorly. The wear pattern is well illustrated by Figure 14,*5*.

5) P_3. The structure of the P_3 (e.g., 2376, Fig. 14,6) is similar to that of the P_2 except that it is significantly larger (Table 4), the height of the main cusp obviously exceeds the length of the tooth, and the anterior border of the main cusp is less convex anteriorly. Although the lingual cingulum is invariably present, the anterior half of the labial cingulum is either weak or absent. The wear-pattern is identical with that of the P_2.

Description of upper molars.—The upper Edmonton specimen 2846 (Fig. 15,*1,3*) of *A. marshi* includes upper and lower dentitions found in definite occlusion. The pertinent dental measurements of the specimen are included in Table 3. With this excellent reference specimen in hand it was my distinct impression upon examining the type of *A. marshi* (YPM 13659) that it is an isolated M^3, not an M^2 as proposed by Clemens (1966,

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1. Fragment of left mandible with P_3M_{1-4} (2846); found in occlusion with maxilla shown in *3*; *1a-c*, occlusal, labial, and lingual views, ×6; (measurements in Table 3).

2. Right M^4 (3376); *2a-c*, occlusal, labial, and lingual views, ×16; meas. (mm.), A-P 2.05, Ant-W 2.90, Post-W 2.15.

3. Fragment of left maxilla with M^{1-4} (2846); found in occlusion with mandible shown in *1*; *3a-c*, occlusal, lingual, and labial views, ×12; meas. (mm.) (measurements in Table 3).

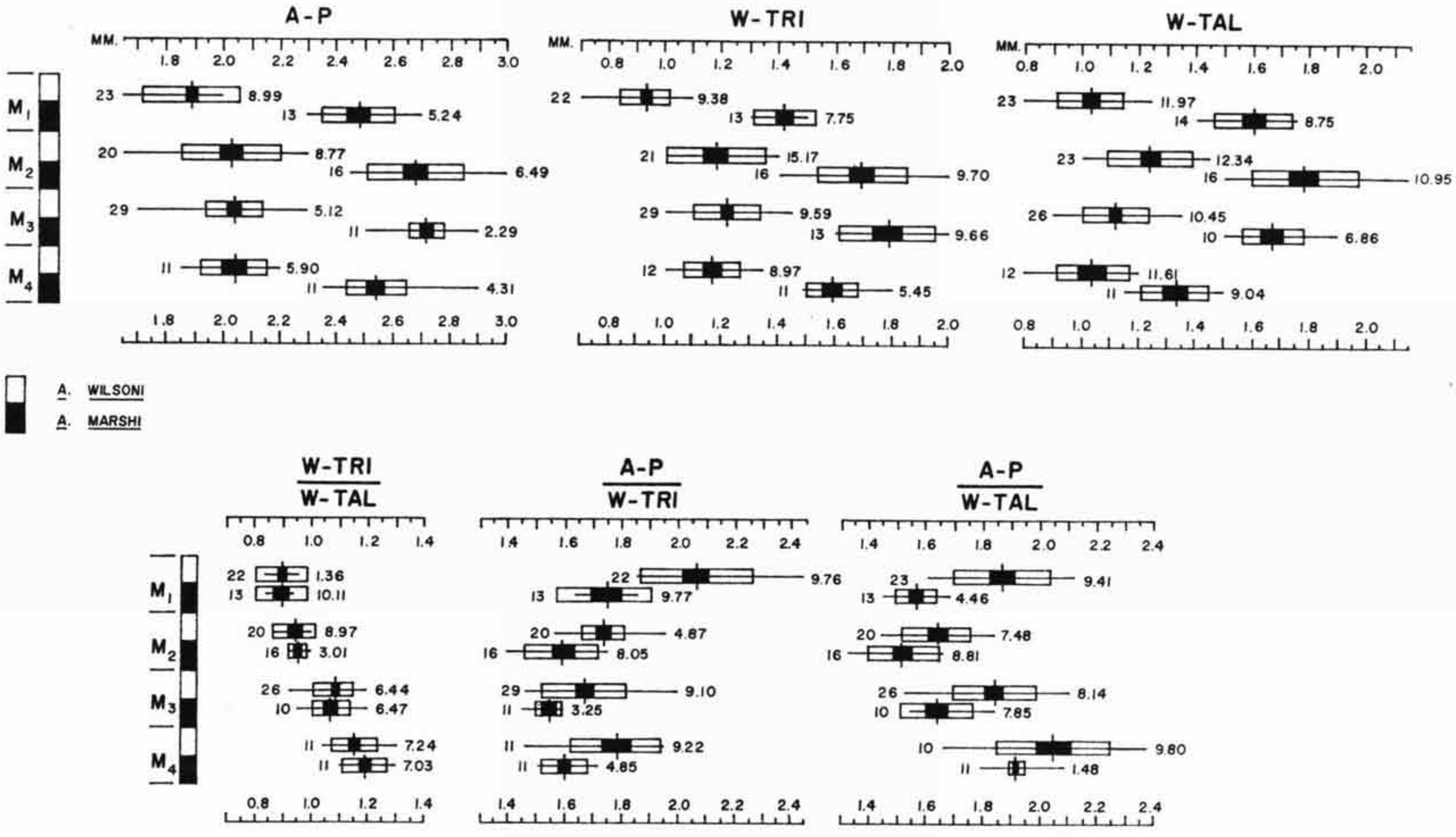

FIG. 16. Bar diagram showing statistical comparisons of lower molars of *Alphadon marshi* and *A. wilsoni*.

Horizontal line indicates range of variation of a given sample; vertical line, the mean; open bar, one standard deviation on either side of mean; black bar, one standard error of mean on either side of mean; left number, size of sample; right number, coefficient of variation.

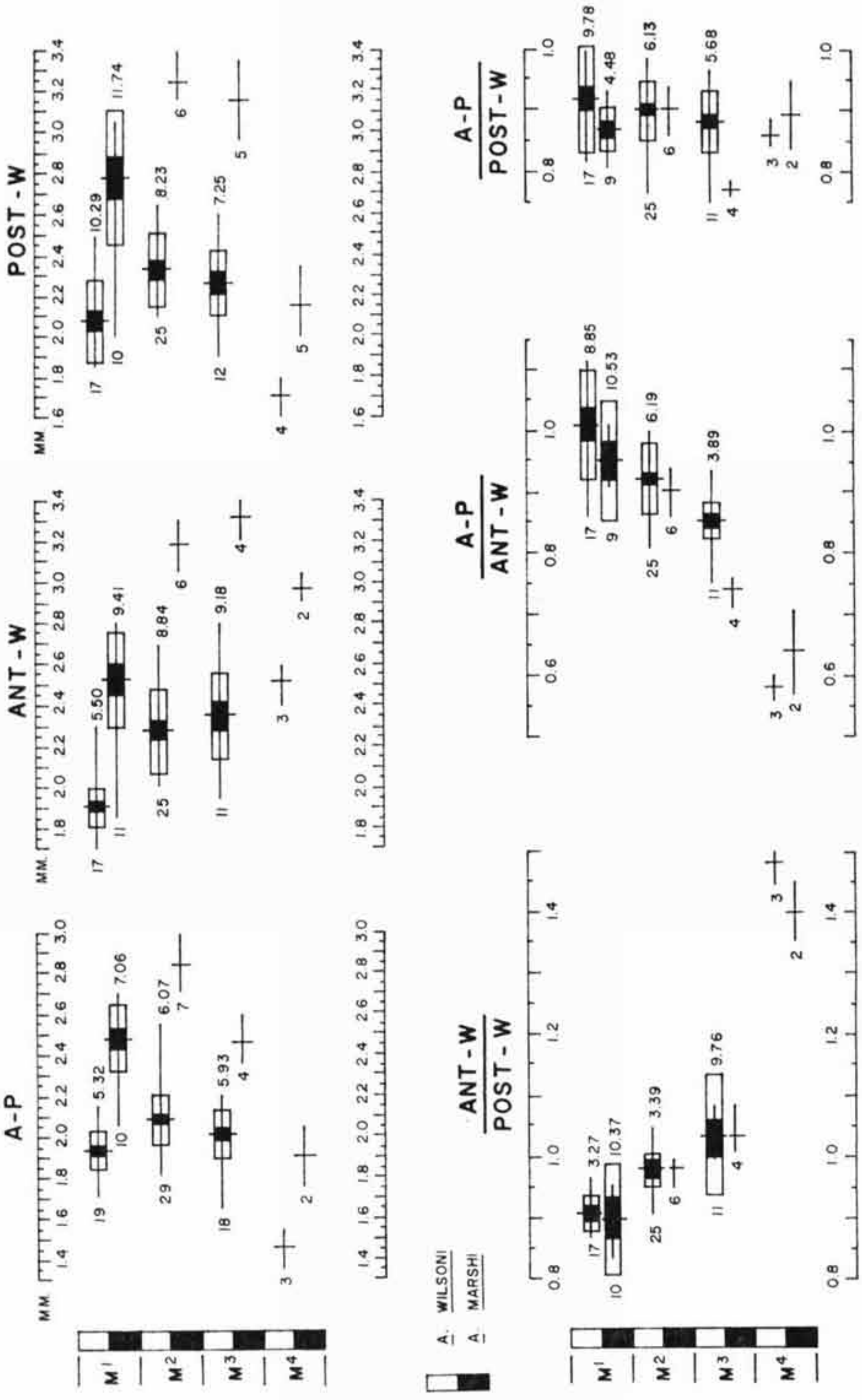

FIG. 17. Bar diagram showing statistical comparisons of upper molars of *Alphadon marshi* and *A. wilsoni*. Symbols are explained in Fig. 16.

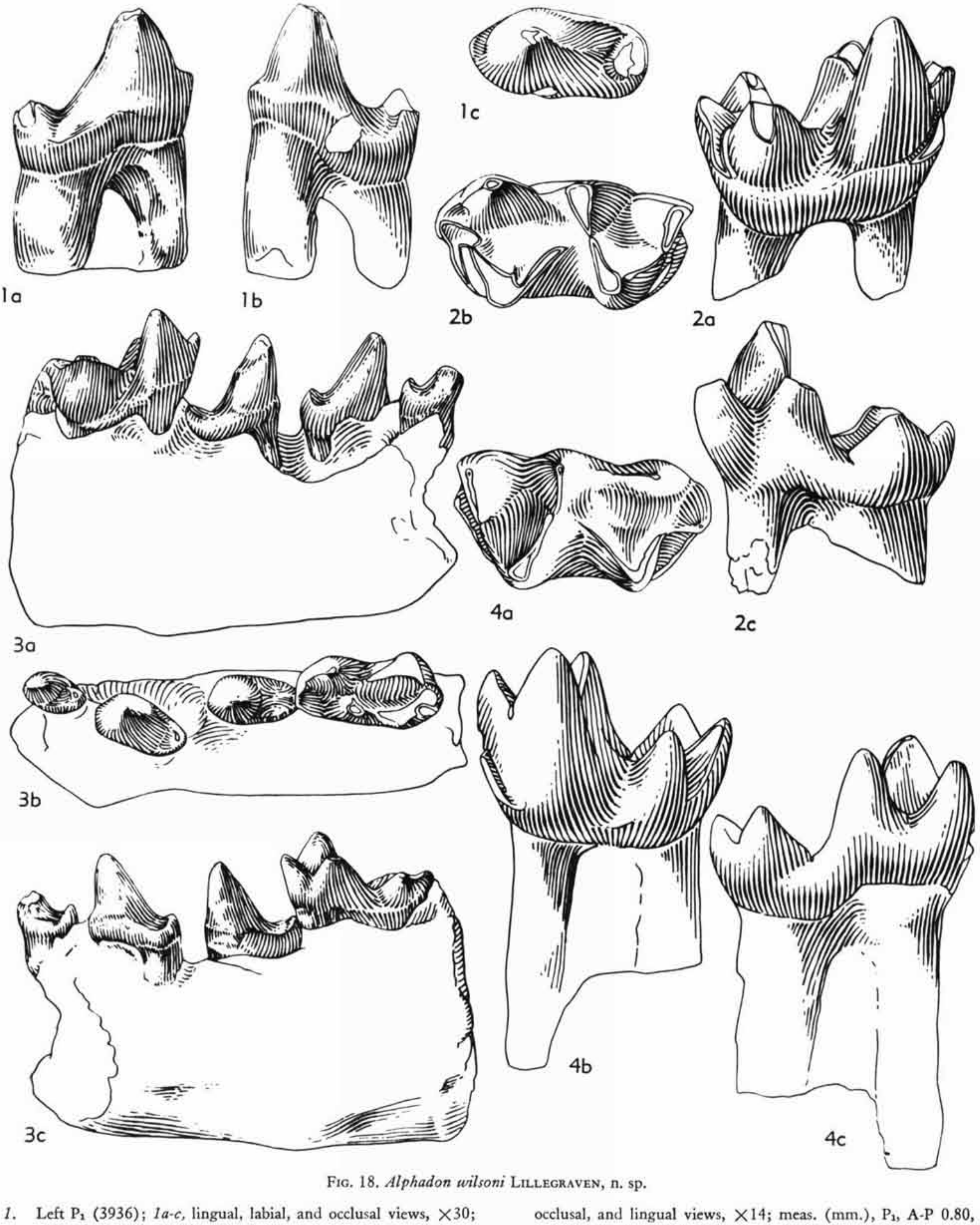

FIG. 18. *Alphadon wilsoni* LILLEGRAVEN, n. sp.

1. Left P_1 (3936); *1a-c,* lingual, labial, and occlusal views, ×30; meas. (mm.), A-P 1.00, W 0.55.

2. Right M_2 (3385); *2a-c,* labial, occlusal, and lingual views; ×20, meas. (mm.), A-P 2.10, W-Tri 1.10, W-Tal 1.15.

3. Fragment of right mandible with $P_{1-3}M_1$ (2230); *3a-c,* labial, occlusal, and lingual views, ×14; meas. (mm.), P_1, A-P 0.80, W 0.55; P_2, A-P 1.20, W 0.65; P_3, A-P 1.15, W 0.70; M_1, A-P 1.85, W-Tri 1.00, W-Tal 1.10.

4. Left M_3 (2338); *4a-c,* occlusal, labial, and lingual views, ×20; meas. (mm.), A-P 2.20, W-Tri 1.30, W-Tal 1.10.

p. 5). The type is somewhat smaller than 2846, but would fit within the smaller end of the size range of *A. marshi*.

Clemens' descriptions (1966, p. 5) of the upper dentition of *Alphadon marshi* are adequate and only a few additional remarks are necessary. Considerations of tooth proportions within the entire molar series will be discussed beyond in the description of a new species of *Alphadon*. It is sufficient here only to mention that the upper and lower molars of *A. marshi* are proportionately slightly shorter anteroposteriorly than those of the new species. All measurements are found in Figures 16 and 17.

All four M^3's referable to *Alphadon marshi* have the stylar cusp D somewhat larger than C.

The M^4 (e.g., 3376, Fig. 15,*2*) is a distinctive tooth with the paracone greatly exceeding the height and development of the metacone. The paracone is centrally placed in a transverse line and has a strongly developed stylar shelf. The stylar shelf is essentially nonexistent opposite the metacone. The strong crest that runs directly adlabially from the front border of the paracone weakens near its variable termination at stylar cusps A or B. Usually the stylar cusps are not strong, but are represented by low bumps. Stylar cusp C is always present at the termination of the valley separating the paracone and metacone. Stylar cusp D is present only on one of the five teeth, and cusp E is absent. The conules are well developed, but the internal crests leading to the valley between the paracone and metacone are absent or weak. The development of the protocone, although narrower, is nearly comparable to that of the other molars. Except for the presence of conules, a larger protocone, and somewhat more defined stylar cusps, the M^4 of *Alphadon* is strikingly similar to the terminal molar of the Early Cretaceous therian *Pappotherium pattersoni* Slaughter (1965, p. 5, fig. 1).

Description of lower molars.—Examination of specimen 2846 (Fig 15,*1*) shows Clemens to have been correct in his interpretation that the crista obliqua of *Alphadon* lower molars "intersects the back of the trigonid at a point ventral to the lowest point in the ridge linking the protoconid and metaconid" (Clemens, 1966, p. 83). This is in contrast to the condition seen in the species of *Pediomys*. Other than that, little information gleaned from the Edmonton specimens outside of size ranges and tooth proportions (Fig. 16, 17) can be added to Clemens' (1966, p. 87) original discussion. Tooth proportions will be considered in the description of the new species of *Alphadon*.

ALPHADON WILSONI Lillegraven, new species

Figures 18,*1-4*; 19,*1-5*; 20,*1-2*

Separated from *Alphadon marshi* Simpson, 1927a.

Etymology.—Named in honor of Professor Robert W. Wilson, vertebrate paleontologist and teacher.

Type.—3681, fragmentary right maxilla with M^{2-3} (Fig. 19,*4*).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—Five isolated P^3's; fragmentary maxillae with P^3M^{1-4} (3774) and M^{1-2} (3741); 18 M^1's; 26 M^2's; 17 M^3's; three M^4's; fragmentary mandibles with $P_{1-3}M_1$ (2230), P_3M_{1-3} (3748), M_{2-3} (2186, 2908, 2220, 3747, 3759), M_{3-4} (2944, 3442, 3952); one P_1; three P_3's; 21 M_1's; 18 M_2's; 20 M_3's; 10 M_4's.

Localities.—KUA-1, 2, 3, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Kirtland and Fruitland formations, New Mexico (unpublished).

Diagnosis.—Smallest species of *Alphadon* yet described; P^3 with apex of main cusp posteriorly recurved, anterior two-thirds of lingual cingulum absent, pronounced vertical ridge present on lingual side of main cusp extending from apex to anterior part of posterior root; M^3 with stylar cusp D smaller than C; upper and lower molars proportionately longer than those of *A. marshi* but otherwise morphologically similar; P_2 and P_3 morphologically similar and nearly equal in size, labial cingulum lacking, anterior and posterior borders of main cusps rounded.

Description of lower dentition and comparisons with Alphadon marshi.—The sample size of the lower dentition is larger and statistically more dependable than the upper, thus it will be discussed first.

1) P_1. The two-rooted P_1 (Fig. 18,*1,3*) has a rather weak main cusp, both the anterior and posterior borders of which are rounded. A posterolingual cingulum extends half the length of the tooth from the rather strong posterior accessory cusp. An anterior accessory cuspule is variably present.

2) P_2. The two-rooted P_2 (Fig. 18,*3*) is larger and has a proportionately higher main cusp than the P_1. The anterior border of the main cusp is rounded, but the posterior border is sharper than that of the P_1 and slightly less cutting than that of the P_3. A labial cingulum is lacking, but a weak continuous lingual cingulum is present. A tiny expansion of the cingulum is present at the base of the anterior border of the main cusp.

3) P_3. The P_2 and P_3 (Fig. 18,*2*) are nearly identical in size, morphology, and proportion. The lingual cingulum of the P_3 is slightly more pronounced and an anterior accessory cuspule is occasionally well developed. Although the shape of the P_3 is fundamentally like that of *Alphadon marshi*, its anterior and posterior borders are significantly more rounded and less secant.

The lower premolars of *Alphadon wilsoni* thus differ from those of *A. marshi* in that they are smaller, less secant, have less pronounced cingular development, and in that the P_2 and P_3 are nearly identical.

Lower molars. The measurements and standard statistics for all lower molars can be seen in Figure 16. As in *Alphadon marshi*, the paraconid and metaconid of the M_1 (Fig. 18,*3*) are proportionately more distantly separated than are the homologous cusps of the M_{2-4}. It thus

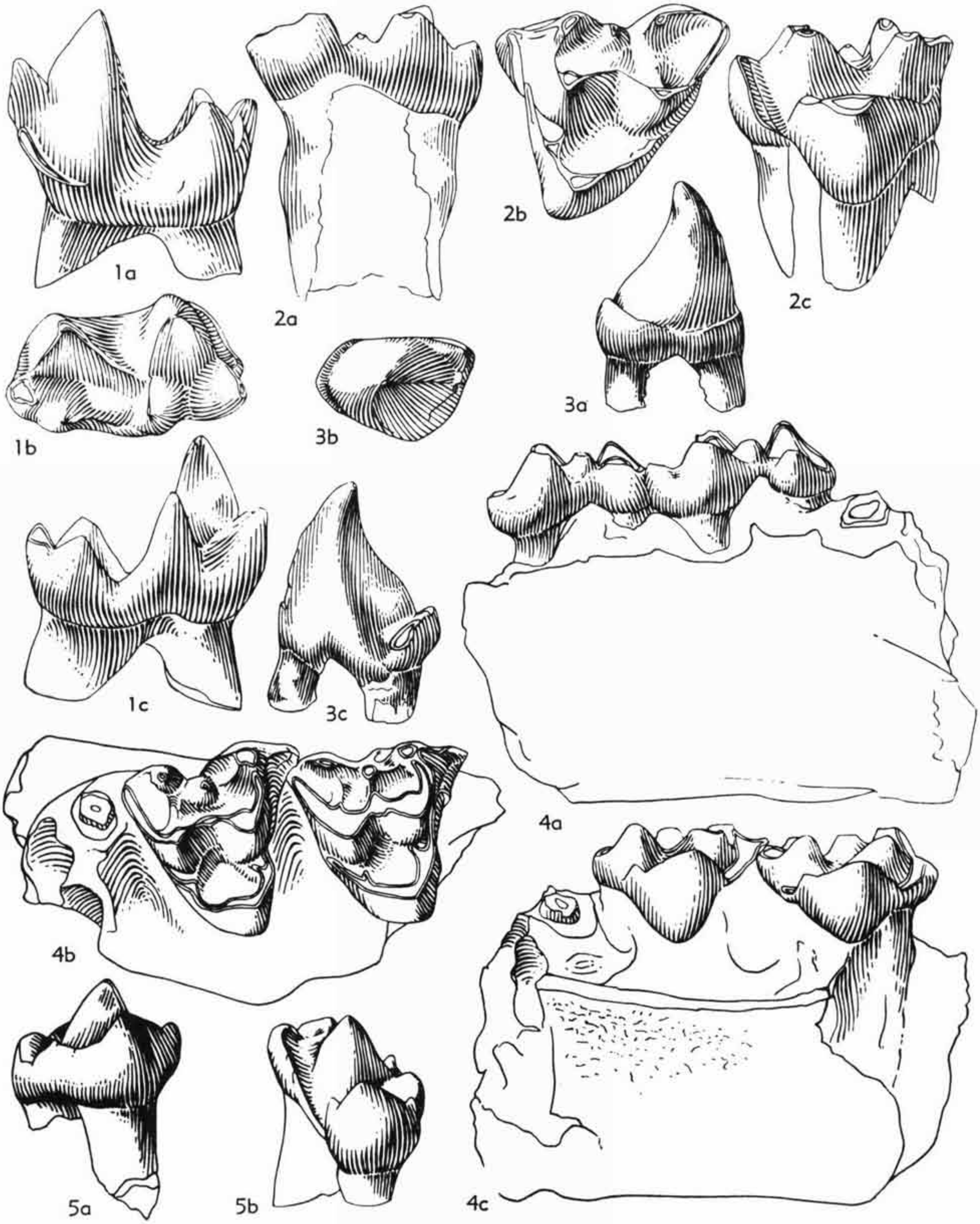

FIG. 19. *Alphadon wilsoni* LILLEGRAVEN, n. sp. *(continued on facing page)*.

differs from the proportions found in *A. lulli* (Clemens, 1966, p. 86). Except for slight differences in the length-width ratios, the M_1's, M_2's (e.g., 3385, Fig. 18,*2*), M_3's (e.g., 2338, Fig. 18,*4*), and M_4's (e.g., 3707, Fig. 19,*1*) are morphologically identical to those of *A. marshi*.

An inspection of Figure 16 brings out some interesting points concerning intraspecific and interspecific comparisons of tooth proportions. Unless otherwise stated, all differences discussed are significant at the 95 percent level or greater on Student's *t* distribution. The means of all direct measurements are larger in *Alphadon marshi* than in *A. wilsoni*. The M_1 in both species is the shortest molar of the series. The M_{2-4} are nearly equal in length in *A. wilsoni*, but the M_4 in *A. marshi* is significantly shorter than the M_{2-3}. The coefficients of variation of the length measurements are generally lower than those of the width measurements.

The trigonid of the M_1 of both species is the narrowest of the molar series and that of the M_3 is the widest. The widths of the trigonids of M_{2-4} do not differ greatly in *Alphadon wilsoni*, but the M_4 is significantly narrower than the M_{2-3} in *A. marshi*.

The widths of the talonids of M_1 and M_4 in *Alphadon wilsoni* are the narrowest of the molar series and the means do not obviously differ from each other. In *A. marshi*, however, the width of the talonid of the M_4 is significantly narrower than that of the M_1. The M_2 has the widest talonids in both species, followed in breadth by the M_3.

Comparisons of the ratios of the length of the teeth to the widths of the trigonids and talonids between the two species show that in all cases the molars of *Alphadon wilsoni* are significantly proportionately longer than those of *A. marshi* despite their smaller actual size.

Therian tuberculo-sectorial molars are characterized by a complexity of shearing function made possible by the precision of occlusion of many distinct surfaces. One would intuitively expect the development of the tooth to be strictly controlled genetically, an idea pursued by Butler (1939, 1956). The function of the broad stylar shelf in mastication is unclear at present (it is being studied in *Didelphis* by Sylvia Fagan Graham of the American Museum of Natural History and A. W. Crompton of the Yale Peabody Museum), but essentially every other line shown in Figure 21 represents a shearing surface that must have a precise alignment to be effective.

The precision of the control of molar morphology is, I believe, indirectly shown by a comparison of the ratios of the widths of the trigonids to the widths of talonids between the two species. The talonid becomes progressively narrower than the trigonid from the M_1 through the M_4 in both species. The narrow ranges of variation, the means, standard deviations, and coefficients of variation are strikingly similar for homologous teeth between the two species. This is true despite the fact that the lower molars of *Alphadon wilsoni* are proportionately longer than those of *A. marshi*. Identical relationships are observed in the upper molars (Fig. 17). The apparently critical nature of the various width ratios would seem to indicate strong selection for the maintenance of stable occlusal relationships between the upper and lower molars. Superimposed upon the necessity for the maintenance of precise occlusion, selection has favored alterations in the relative lengths of the teeth between the two species, probably a reflection of dietary differences. Of course changing the relative length of a tooth also changes its occlusal relationships, but apparently in this case morphological compensations for length were more easily accomplished than those for width. The selective pressures that acted upon the two species remain unknown.

The differences of the means between the widths of the trigonid of the M_{2-3} and M_{3-4} of *Alphadon wilsoni* are significant only at the 65 and 75 percent confidence levels respectively. However, the close correspondence of the ratios of the width of the trigonid to the width of the talonid between *A. marshi* and *A. wilsoni* for homologous teeth leads me to suspect that the differences between the means are indeed significant.

Description of upper dentition and comparisons with Alphadon marshi.—P^3. Although no P^1's, P^2's, or usable P^3's have been found in association with upper molars of *Alphadon wilsoni*, five teeth (e.g., 3920, Fig. 19,*3*) have been recovered that may be P^3's of the taxon. The mean length of the teeth is precisely that expected, assuming equivalent proportions between the lengths of the P^3 and M^1 in *A. marshi* and *A. wilsoni*. Although one would expect the teeth to be more abundant, they are small and have been recovered only from fine-screen samples.

The anterior border of the main cusp is rounded, but a weak keel is present on about half the specimens. The posterior border of the main cusp is sharp, and the apex of the cusp is posteriorly recurved. A pronounced ridge on the lingual side of the main cusp extends from the tip of the tooth posterodorsal to the base of the enamel near the anterior part of the posterior root. The axis of the ridge is slightly convex anteriorly. A similar but less pronounced structure is found on the P^3 of *Alphadon marshi*. Variably developed wear-facets are seen on the

---

1. Left M_4 (3707, loc. KUA-22); *1a-c*, labial, occlusal, and lingual views, ×20; meas. (mm.), A-P 2.05, W-Tri 1.20, W-Tal 1.00.

2. Left M^1 (2624); *2a-c*, labial, occlusal, lingual views, ×20; meas. (mm.), A-P 1.90, Ant-W 1.80, Post-W 2.00.

3. Left P^3 (3920, loc. KUA-22); *3a-c*, labial, occlusal, and lingual views, ×20; meas. (mm.), A-P 1.30, W 0.95.

4. Holotype, fragment of right maxilla with M^{2-3} (3681); *4a-c*, labial, occlusal, and lingual views, ×14; meas. (mm.), M^2, A-P 2.15, Ant-W 2.25, Post-W 2.40; M^3, A-P 2.20, Ant-W 2.45, Post-W 2.40.

5. Left M^4 (3811); *5a-b*, labial and lingual views, ×20; meas. (mm.), A-P 1.35, Ant-W 2.40, Post-W 1.60.

[*See* Fig. 20,*2* for occlusal view.]

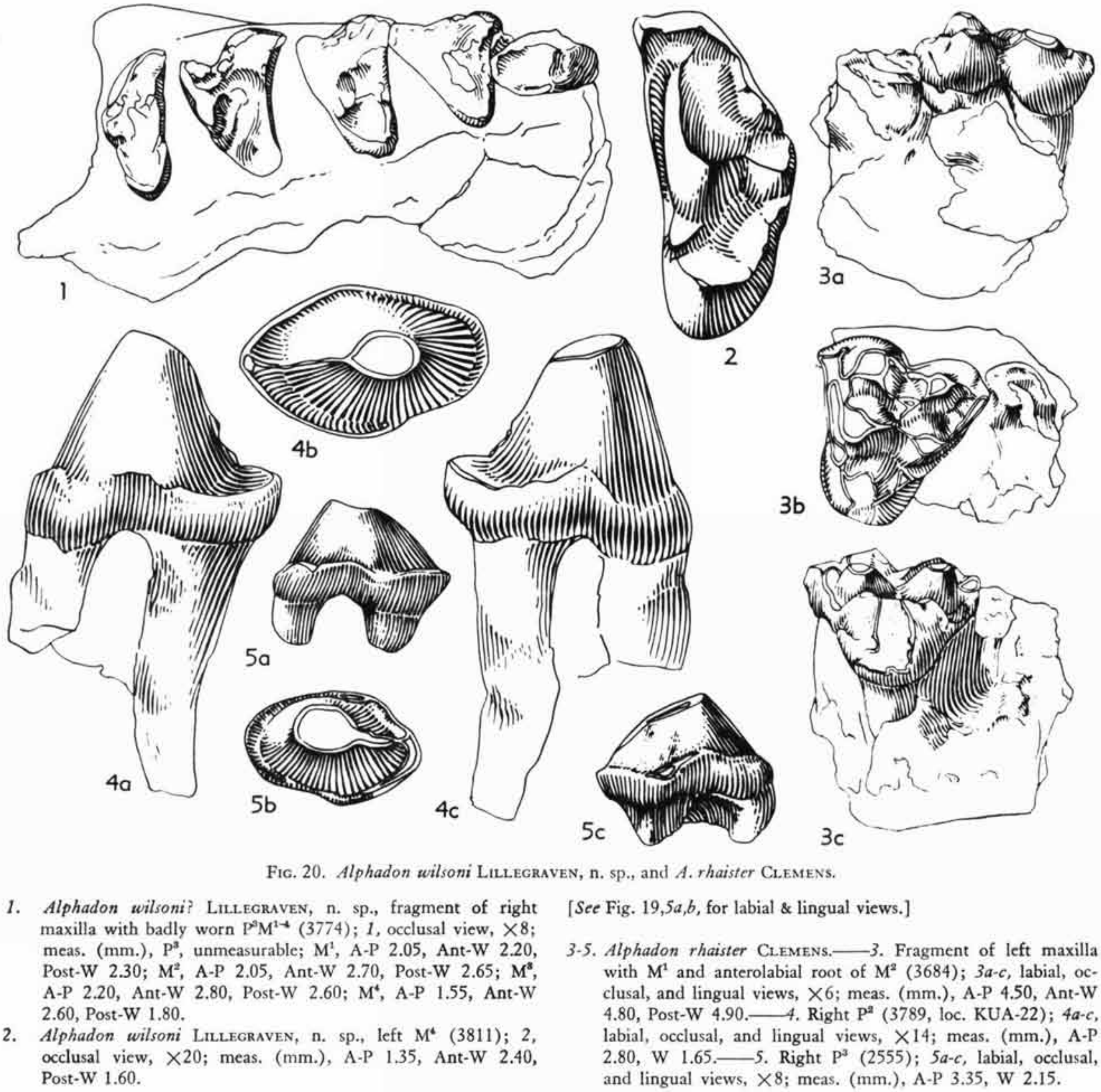

FIG. 20. *Alphadon wilsoni* LILLEGRAVEN, n. sp., and *A. rhaister* CLEMENS.

1. Alphadon wilsoni? LILLEGRAVEN, n. sp., fragment of right maxilla with badly worn P^3M^{1-4} (3774); *1*, occlusal view, ×8; meas. (mm.), P^3, unmeasurable; M^1, A-P 2.05, Ant-W 2.20, Post-W 2.30; M^2, A-P 2.05, Ant-W 2.70, Post-W 2.65; M^3, A-P 2.20, Ant-W 2.80, Post-W 2.60; M^4, A-P 1.55, Ant-W 2.60, Post-W 1.80.

2. *Alphadon wilsoni* LILLEGRAVEN, n. sp., left M^4 (3811); *2*, occlusal view, ×20; meas. (mm.), A-P 1.35, Ant-W 2.40, Post-W 1.60.

[*See* Fig. 19,*5a,b*, for labial & lingual views.]

3-5. Alphadon rhaister CLEMENS.——*3*. Fragment of left maxilla with M^1 and anterolabial root of M^2 (3684); *3a-c*, labial, occlusal, and lingual views, ×6; meas. (mm.), A-P 4.50, Ant-W 4.80, Post-W 4.90.——*4*. Right P^2 (3789, loc. KUA-22); *4a-c*, labial, occlusal, and lingual views, ×14; meas. (mm.), A-P 2.80, W 1.65.——*5*. Right P^3 (2555); *5a-c*, labial, occlusal, and lingual views, ×8; meas. (mm.), A-P 3.35, W 2.15.

posterior border of the main cusp and on the posterolingual side of the border. A labial cingulum is present and expanded on the posterolabial corner into an accessory cusp. The cingulum is weak across the anterior half of the tooth and is sometimes absent, but generally forms a tiny accessory cuspule at the anterior base of the main cusp. The lingual cingulum is absent except for one steep section extending from the termination of the posterior border of the main cusp to the base of the enamel near the middle of the posterior root. As in *A. marshi,* this is the only part of the cingulum that shows wear. The tooth shares a basic structure with the P^3 of *A. marshi,* but has several deletions or exaggerations. It is also similar to the P^3 of *Pediomys krejcii* figured by CLEMENS (1966, p. 43). That of *A. wilsoni* differs principally in having a proportionately higher main cusp with a posteriorly recurved apex.

Upper molars. Disregarding general proportions, the only consistent morphological difference between the upper molars of *Alphadon marshi* and *A. wilsoni* is the fact that in the latter, stylar cusp D is smaller than C in the M^3 (e.g., 3681, Fig. 19,*4*). All the upper Edmonton specimens of *A. marshi* (e.g., 2846, Fig. 15,*3*) have stylar cusp D exceeding the development of C.

An M^1 (2624) is illustrated in Figure 19,*2*, an M^4 (3811) in Figures 19,*5*; 20,*2* and a maxilla with badly worn P^3M^{1-4} (3774) is shown in Figure 20,*1*. The last shows the changes in molar outline along the series, but is useless for cusp morphology. Certain identification is impossible, and the animal may well have been a small individual of *Alphadon marshi*.

Examination of Figure 20,*2* again shows the means of all measurements of upper molars to be larger in *Alphadon marshi* than in *A. wilsoni*. Unfortunately the sample size of M^2's, M^3's, and M^4's of *A. marshi* and of M^4's for *A. wilsoni* are too small to be adequately handled statistically. The M^4 in both species is the shortest tooth in the molar series and the M^2 the longest. The M^1 and M^3 are approximately equal in length. The mean of the length of the M^3 of *A. wilsoni* is shorter than the M^2 at the 85 percent confidence level.

The anterior width in both species along the molar series is probably greatest in the M^3 and least in the M^1 (despite the high mean based on a low sample for the M^4 in *Alphadon wilsoni*). The anterior width of the M^2 in *A. wilsoni* is significantly greater than that of the M^1, and the M^3 is wider than the M^2 at the 65 percent confidence level.

The posterior width in both species along the molar series is probably greatest in the M^2 and least in the M^4. The mean of the width of the M^2 in *Alphadon wilsoni* is significantly greater than that of the M^1 and is greater than that of the M^3 at the 65 percent confidence level.

The ratio of the length of the tooth to the anterior width decreases progressively from the M^1 through the M^4 in both species. With the exception of the low sample of M^4's, the means of this ratio are consistently lower in *Alphadon marshi* than in *A. wilsoni*. The difference between the two species is significant at the 85 percent confidence level in the M^1's. The greater value of the ratios in *A. wilsoni* is consistent with the observation on the lower molars that the teeth of *A. wilsoni* are proportionately longer than those of *A. marshi*.

The ratio of the length of the tooth to its posterior width appears to be more stable within the molar series of each species than is the ratio of length to the anterior width. The progressive decrease between the means of the M^{1-2} and M^{2-3} of *Alphadon wilsoni* are significant to the 65 and 75 percent confidence levels respectively. The small sample size permits interspecific comparison only in the M^1, and the mean of *A. marshi* is smaller than that of *A. wilsoni* (significant to the 85 percent confidence level), again indicating a proportionately shorter tooth in *A. marshi*.

The ratios of the anterior width to the posterior width indicate that the posterior halves of the teeth progressively become proportionately narrower from the M^1 through the M^4 in both species. The mean values for both species are essentially identical for homologous teeth despite the fact that the upper molars of *Alphadon wilsoni* are proportionately longer teeth. The probable significance of this observation is discussed in the section describing the lower molars of *A. wilsoni*.

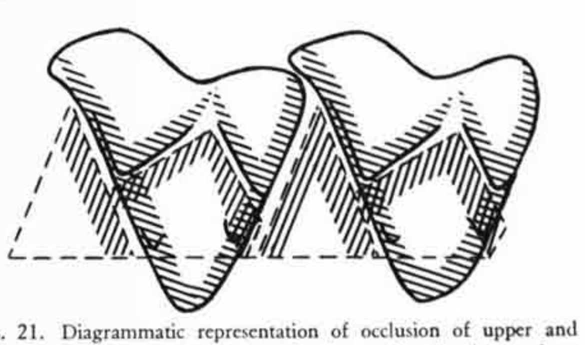

FIG. 21. Diagrammatic representation of occlusion of upper and lower tuberculosectorial dentitions showing major shearing surfaces (hatched lines).

Comments.—CLEMENS (1966, p. 8) noticed a bimodality in some molar dimensions of *Alphadon marshi* and suggested that more than one species might be included in his sample of the taxon. On the basis of size differences and premolar and molar morphology, I suggest that the species as previously understood may be divided into *A. marshi, s.s.*, and *A. wilsoni*, n. sp. *A. wilsoni* is significantly smaller than *A. marshi* and is the most common element of the marsupial fauna of the upper Edmonton Formation.

ALPHADON RHAISTER Clemens, 1966

Figure 20,*3-5*

Type.—UCMP 50292, fragment of left maxilla with M^{1-3} (CLEMENS, 1966, fig. 9).

Referred specimens.—P^2's, 2969, 3789; P^3's, 2555, 3258; fragmentary maxilla with M^1, 3684; fragmentary $M^{1?}$, 3265; M_4, 3709; fragmentary lower molar, 3302.

Localities.—KUA-1, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; possibly Kirtland and Fruitland formations, New Mexico (unpublished).

Comments.—Specimens representing *Alphadon rhaister* are rare in the upper Edmonton Formation.

The M^1 (3684, Fig. 20,*3*) which clearly illustrates the complexity of wear pattern on the upper molar, agrees well with CLEMENS' description (1966, p. 12). Essentially all of the areas of wear are connected. Both 3684 and 3265 are larger than the observed range of variation from the type Lance Formation (CLEMENS, 1966, p. 14, table 3), but both samples are small and the true range of variation of the species probably remains unknown.

Both lower molars recovered are of the proper size for *Alphadon rhaister*, but the M_4 (3709) shows morphological peculiarities worthy of note. It is a worn and battered tooth, but it appears that the metaconid is slightly lower than the paraconid, a character generally restricted to *Didelphodon* and *Eodelphis*. The nature of the crista obliqua is typical for that of *Alphadon*, but the

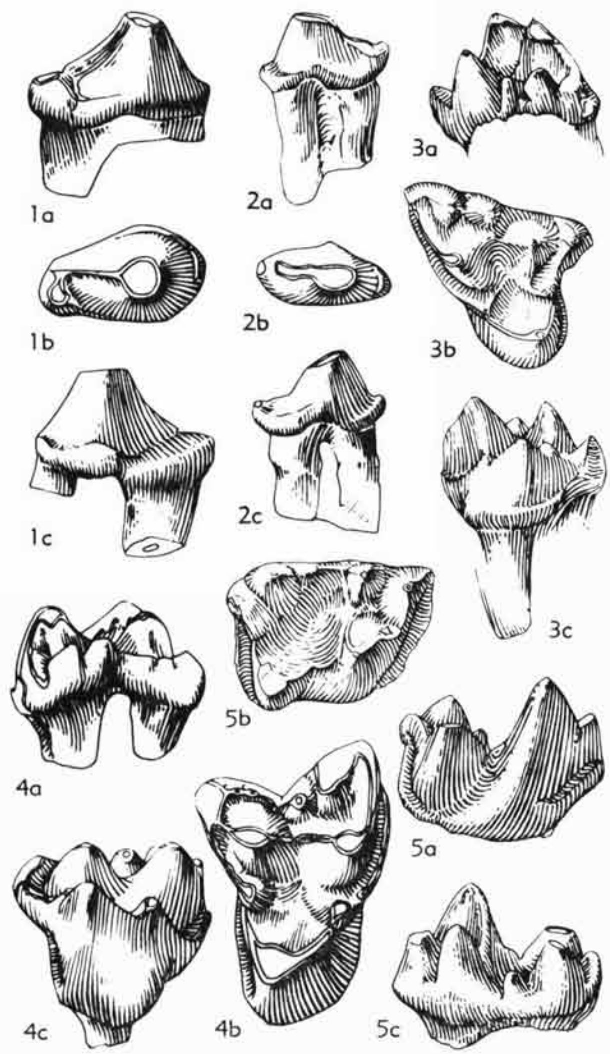

FIG. 22. *Pediomys elegans* MARSH.

1. Left P^3 (3342); *1a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 1.80, W 1.00.
2. Right P^2 (3869); *2a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 1.50, W 0.70.
3. Right, M^1 (2227); *3a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 1.90, Ant-W 1.90, Post-W 2.50.
4. Left M^3 (3706, loc. KUA-22); *4a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 2.10, Ant-W 2.70, Post-W 3.10.
5. Right M$_2$ (2365); *5a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 2.30, W-Tri 1.50, W-Tal 1.60.

talonid seems significantly narrower than in the Lance specimen figured by CLEMENS (1966, p. 92, fig. 64). The measurements of 3709 are as follows: A-P, 4.00 mm., W-Tal, 1.75 mm., W-Tri, 2.45 mm. The specimen is considerably smaller than the observed size range of *Didelphodon vorax* from the type Lance Formation (CLEMENS, 1966, p. 82, table 13). *Eodelphis* has not been recovered from post-Campanian rocks, and its presence in the upper Edmonton Formation seems unlikely.

The upper premolars of *Alphadon rhaister* have not been described and none has been found in association with upper molars from the upper Edmonton Formation. However, four premolars have been recovered that probably are referable to the species on the basis of size and expected morphology.

The two probable P^3's (e.g., 2555, Fig. 20,*5*) are robust unicuspid teeth with a strong basal cingulum completely encircling the tooth. The cingulum is similar in its configuration to that of *Alphadon marshi* except that in *A. rhaister* the dorsoventral variations in elevation are more subdued and the cingulum is unworn only along its anterolingual part. The main cusp is broadly rounded anteriorly but sharper on its posterior border. This cusp is bluntly worn on its apex and posterior edge.

The two probable P^2's (e.g., 3789, Fig. 20,*4*) are similar to the P^3's except for their smaller size, slightly narrower proportions, slightly better developed posterior accessory cusp, and less continuous cingulum. The cingulum is weak at the anterolabial corner of the tooth and absent at the anterolingual corner.

Family PEDIOMYIDAE Clemens, 1966

Genus PEDIOMYS Marsh, 1889a

PEDIOMYS ELEGANS Marsh, 1889a

Figure 22,*1-5*

Type.—CMCVF 1186, fragmentary maxilla with M$^{3-4}$, designated as a neotype by SIMPSON (1929, p. 111) to replace YPM 11866, the original type.

Referred specimens.—P^2's, 3869, 3545; P^3, 3342; M^1, 2227; M^3, 3706; M$_1$, 3946; M$_2$'s, 2365, 2816, 4056.

Localities.—KUA-1, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota.

Description and comments.—The single tooth identifiable as a P^3 (3342, Fig. 22,*1*) of *Pediomys elegans* from the upper Edmonton Formation matches morphologically with KU 14945, an unfigured Lance specimen with associated P^{3}M^1. The cingulum completely encircles the tooth and shows wear along its posterolingual two-thirds. It is weak along the anterolabial quarter of the tooth, but is strong on the posterolabial quarter and expanded into a distinct accessory cusp. The cusp is placed labial to the termination of the posterior crest of the main cusp and shows wear.

P^2's of *Pediomys elegans* are not known in association with upper molars, but two teeth (e.g., 3869, Fig. 22,*2*) are morphologically similar to known P^3's, are significantly smaller, and probably referable to the taxon. The posterolabial accessory cusp is weak or absent and the teeth are proportionately narrower than the P^3. The anterior border of the main cusp is broadly rounded, the posterior sharper and worn on its lingual border. The apex of the main cusp is bluntly worn.

The known upper and lower molars agree in all respects with CLEMENS' (1966, p. 37, 96) descriptions, and the representative specimens 2227, 3706, and 2365 are illustrated in Figure 22,*3-5*.

The measurements of the lower molars are presented in Table 5.

TABLE 5. *Measurements (in mm.) of Lower Molars Referable to* Pediomys elegans *Marsh.*

Tooth	Length		W-Tri		W-Tal	
	N	O R	N	O R	N	O R
M_1	----	----	1	1.15	----	----
M_2	3	1.95-2.30	3	1.45-1.55	3	1.45-1.60

For abbreviations see end of Introduction.

PEDIOMYS KREJCII Clemens, 1966

Figure 23,*1-7*

Type.—UCMP 51390, fragmentary left maxilla with P^3M^{1-3} (CLEMENS, 1966, fig. 26).

Referred specimens.—DP^3, 2872; fragmentary maxillae with M^{1-3} (2225) and M^{2-4} (2410); M^1's, 3804, 3939; M^2, 3227; M^3's, 3083, 3097, 3660, 4059; M^4's, 3347, 3375, 3812; fragmentary mandibles with $C_1P_1M_{2-3}$ (3671), $P_{2-3}M_{1-4}$ (3761), and M_{1-4} (2789); P_3, 4003; M_1's, 2553, 3659, 3717, 3813, 3917; M_2's, 2538, 3482, 3822; M_3, 2237.

Localities.—KUA-1, 22.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; possibly Kirtland and Fruitland formations, New Mexico (unpublished).

Description and comments.—The upper Edmonton specimens referable to *Pediomys krejcii* agree with CLEMENS' (1966, p. 43) descriptions, and only additions are necessary. Dental measurements are presented in Table 6.

Specimen 2410 (Fig. 23,*7*) is essentially identical with the holotype for the species. CLEMENS (1966, p. 43) noted that precingula and postcingula have not been observed in upper molars of *Pediomys krejcii*. However, specimens 2225 (Fig. 23,*4*) and 3375 (Fig. 23,*2*) show distinct cingula on both sides of the M^4 and on the anterolingual sides of the M^{1-3}. The development of lingual cingula is thus shown to be highly variable, and probably not necessarily of taxonomic significance in this instance.

Stylar cusp C has not been observed in the upper molars from the sample.

The previously undescribed M^4's (e.g., 3375, Fig. 23,*2*) have a strong metaconule that is sometimes as large as the metacone. A strong ridge extends from the protoconule labiad to be the large stylar cusp A and the ridge's

TABLE 6. *Measurements (in mm.) of Teeth Referable to* Pediomys krejcii *Clemens.*

Tooth	Length			Ant-W			Post-W		
	N	O R	$\bar{X}$	N	O R	$\bar{X}$	N	O R	$\bar{X}$
DP^3	1	1.20	----	1	0.90	----	1	1.10	----
M^1	3	1.60-1.75	1.68	3	1.65-1.70	1.63	3	2.05-2.15	2.08
M^2	3	1.60-1.80	1.67	2	1.85-2.00	1.92	2	2.30-2.45	2.37
M^3	5	1.30-1.70	1.49	5	1.60-2.30	1.88	5	2.00-2.80	2.32
M^4	2	1.25-1.30	1.27	2	1.75-2.05	1.90	3	1.35-1.50	1.42
				Width					
				N	O R	$\bar{X}$			
P_1	1	0.90	----	1	0.50	----			
P_2	1	1.15	----	1	0.50	----			
P_3	2	1.35	1.35	2	0.65-0.70	0.67			
				W-Tri			W-Tal		
				N	O R	$\bar{X}$	N	O R	$\bar{X}$
M_1	7	1.35-1.70	1.49	7	0.70-1.05	0.91	7	0.90-1.10	0.96
M_2	6	1.50-1.70	1.63	6	1.05-1.20	1.12	6	1.10-1.25	1.17
M_3	3	1.50-1.80	1.65	4	1.05-1.20	1.11	3	0.95-1.15	1.07
M_4	2	1.60	1.60	2	0.95-1.05	1.00	2	0.85-0.90	0.87

For abbreviations see end of Introduction.

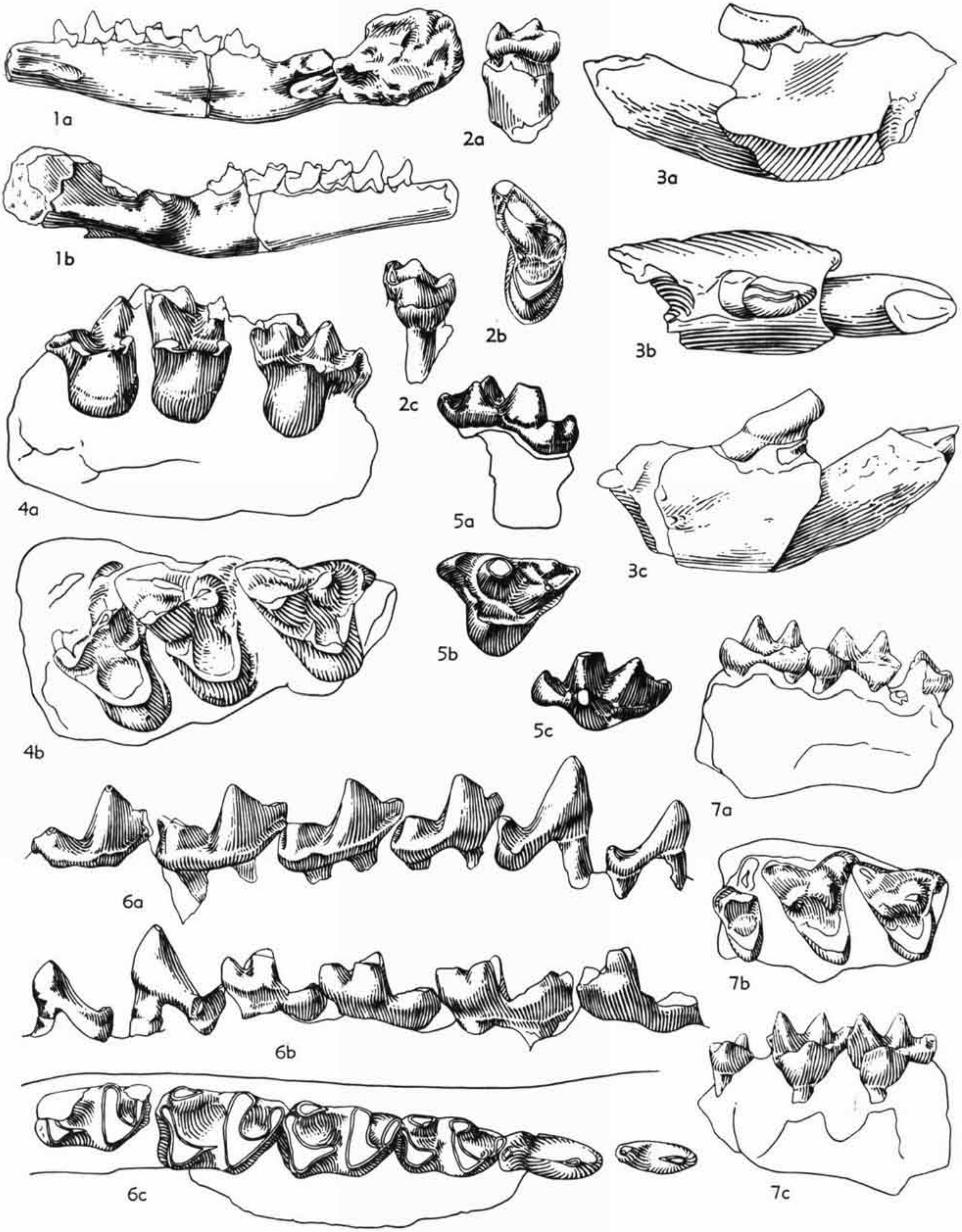

FIG. 23. *Pediomys krejcii* CLEMENS (*continued on facing page*).

separation from the paracone is more pronounced than in M^4's of *Alphadon* (Fig. 15,*2*). The ridge from the anterior crest of the paracone runs anterolabiad to stylar cusp A rather than directly labiad as in *Alphadon.* Stylar cusp B is small or lacking, and C, D, and E are absent. In contrast to the centrally placed paracone on a transverse line in *Alphadon,* that of *Pediomys krejcii* is less than one-third of the distance from the labial edge of the crown. The stylar shelf in general is less well developed than that in *Alphadon.* The anterior border of the tooth is convex posteriorly in occlusal view as opposed to the straight anterior border of *Alphadon.* The precingula and postcingula are usually absent, but are sometimes strong.

One tooth (2872, Fig. 23,*5*) has been recovered that has been identified as a DP^3. It is smaller (Table 6) than any similar specimens reported by CLEMENS (1966, p. 49). It is here referred to *Pediomys krejcii* on the basis of its tiny size and basic similarity with permanent upper molars of *Pediomys.* The apex of stylar cusp A is slightly lingual to a line drawn through the apices of the metacone and paracone. The stylar shelf is essentially nonexistent labial to the paracone, and stylar cusps B, C, and E are absent. Stylar cusp D is distinct, symmetrically conical, and nearly as high as the metacone. The conical paracone is the most robust cusp on the tooth and its labial surface is slightly steeper than its lingual surface. The metacone, though nearly as high as the paracone is weaker with a flat posterolingual surface that is continuous with a strong, sharp, posterior metacrista running to the posterolabial corner of the tooth. A weak ridge runs from the apex of the metacone down its labial surface to stylar cusp D. Another weak ridge connects the apices of the paracone and metacone. The protocone is weak and much lower than the paracone and metacone with its apex lingual to the center of the paracone. Both conules are weakly developed.

Specimen 3761 (Fig. 23,*1*,*6*; Table 7)fits perfectly the description of the dentition referred by CLEMENS (1966, p. 92) to *Pediomys krejcii.* Specimens representing upper and lower dentitions of *P. krejcii* and *P. elegans* still have not been found in articulation. However, the similarity of specimens discovered from the type Lance and upper Edmonton formations, the lack of *P. cooki* (the closest known relative to *P. krejcii*) in the Edmonton, and the relative abundances of specimens recovered lends, I think, considerable positive weight to CLEMENS' (1966) association of upper and lower dentitions of both *P. krejcii* and *P. elegans.*

TABLE 7. *Dental Measurements (in mm.) of* Pediomys krejcii *Clemens (Specimen 3761).*

Tooth	Length	Width	
P_2	1.15	0.50	
P_3	1.35	0.65	
		W-Tri	W-Tal
M_1	1.40	0.85	0.90
M_2	1.70	1.05	1.10
M_3	1.80	1.10	1.10
M_4	1.60	1.05	0.85 (est.)

For abbrev. see end of Introduction.

The previously undescribed P_1 of *Pediomys krejcii* is shown in Figure 23,*3.* It is strongly recumbent anteriorly with its apex ahead of the more anterior of the two roots. A broad wear-facet is evident along its entire posterior border.

PEDIOMYS HATCHERI (Osborn), 1898

Figure 24,*1-2*

Type.—AMNH 2202, fragmentary maxilla with M^3, designated as a lectotype by CLEMENS (1966, p. 45) with AMNH 2203, an isolated M^2, as the syntype.

Referred specimens.—Fragmentary mandible with roots of $P_{1-3}M_{1-4}$, 3690; isolated M_3, 3960.

Locality.—KUA-1.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota; North Horn Formation, Utah (Clemens, 1961).

Description and comments.—*Pediomys hatcheri* is a rare species in the upper Edmonton localities. The M_3 (3960, Fig. 24,*2*) fits the size ranges and description (CLEMENS, 1966, p. 101) for the taxon from the type Lance Formation.

The crowns of the dentition of the mandible shown in Figure 24,*1* were probably weathered and battered before the burial of the specimen. Identification cannot be certain between *Pediomys hatcheri* and *Alphadon rhaister,* but the size match between the well-preserved, isolated

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1. Large scale view of right mandible (3761), teeth of which are detailed in Fig. 23,*6*; *1a-b,* lingual and labial views, ×3.6.

2. Left M^4 (3375); *2a-c,* labial, occlusal, and lingual views, ×12.5; meas. (mm.), A-P 1.25, Ant-W 2.05, Post-W 1.50.

3. Fragment of right mandible showing base of canine and P_1 (3671, loc. KUA-22); *3a-c,* lingual, occlusal, and labial views, ×14.5; meas. (mm.), P_1, A-P 0.90, W 0.50.

4. Fragment of right maxilla with M^{1-3} (2225); *4a-b,* lingual and occlusal views, ×12.5; meas. (mm.), M^1, A-P 1.75, Ant-W 1.65, Post-W 2.15; M^2, A-P 1.60, Ant-W 2.00, Post-W 2.45; M^3, unmeasurable.

5. Left DP^3 (2872); identification doubtful; *5a-c,* labial, occlusal, and lingual views, ×18; meas. (mm.), A-P 1.20, Ant-W 0.90, Post-W 1.10.

6. Detail of $P_{2-3}M_{1-4}$ of right mandible shown in Fig. 23,*1* (3761); *6a-c,* labial, lingual, and occlusal views, ×12.5; meas. (mm.) (given in Table 7).

7. Fragment of right maxilla with M^{2-4} (2410); *7a-c,* labial, occlusal, and lingual views, ×9; meas. (mm.), M^2, A-P 1.60, Ant-W 1.85, Post-W 2.30; M^3, A-P 1.70, Ant-W 2.05, Post-W 2.40; M^4, Post-W 1.35.

TABLE 8. *Measurements (in mm.) of Teeth Referable to* Didelphodon vorax *Marsh.*

*Measured at base of enamel in canines at right angles to long axis of tooth.

Tooth	* Depth		* Width			
	N	O R	N	O R		
C_1	3	6.00-6.20	3	4.00-4.70		
	Length					
	N	O R				
P^1	1	4.65	1	5.40		
P^3	1	6.00	1	7.20		
P_3	2	5.60-6.15	2	4.35-4.60		
			W-Tri		W-Tal	
			N	O R	N	O R
DP_3	1	3.50	1	2.40	1	2.55
M_1	1	4.25	1	3.20	1	3.30
M_2	2	4.60-5.70	2	3.60-4.30	2	3.80-4.40
M_3	1	5.50	1	4.15	1	3.80

For abbreviations see end of Introduction.

M_3 and the remnants of the homologous tooth in the mandible is so close that the reference seems likely. A crista obliqua is not preserved intact. As in *P. hatcheri* from the Lance Formation (CLEMENS, 1966, p. 103, fig. 72), a mental foramen is located ventral to the anterior root of the M_1. Another is found ventral to the more posterior root of the P_1. The mandibular foramen is strong. The coronoid process is nearly as long as the postcanine tooth row. The angular process is inflected medially and reflected laterally.

Family STAGODONTIDAE Marsh, 1889b

Genus DIDELPHODON Marsh, 1889a

DIDELPHODON VORAX Marsh, 1889a

Figure 25,*1-6*

Type.—YPM 11827, left M^2 (MARSH, 1889a, pl. 4, fig. 1-3; SIMPSON, 1929, fig. 45A).

Referred specimens.—P^1, 648; P^3, 1987; fragmentary mandible with C_1 and M_2, 1985; C_1's, 3731, 3787; DP_3, 649; P_3's, 1986A, 1991; M_1, 2301; M_2, 1986B; M_3, 2893.

Localities.—KUA-2, 18, 23; UA-2, 3.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota.

Description and comments.—The lone tooth referable to a P^1 of *Didelphodon vorax* (648, Fig. 25,*1*) differs from those described by CLEMENS (1966, p. 69, 82) in that the accessory lobe is not demarcated from the main cusp by a distinct groove and the tooth is proportionately wider transversely than long (Table 8). Although upper premolars of *D. vorax* still have not been found in a maxilla, CLEMENS (1968b, p. 5) suggested that the orientation of the teeth is probably reversed 180 degrees from his earlier interpretation (1966, p. 68). The accessory lobe probably is developed medial to the main cusp.

The single P^3 (1987, Fig. 25,*3*) recovered from the upper Edmonton Formation does not differ from known specimens from the Lance Formation (CLEMENS, 1966, p. 69). Figure 25,*3d* shows the complicated root system of the tooth. It possesses only two roots, but the more posterior is greatly expanded transversely to support the posterior part of the main cusp plus the accessory lobe. Although the posterior root is constricted at its midpoint, the pulp cavity remains continuous.

One DP_3 (649, Fig. 25,*2*) has been recovered that agrees in all respects with those from the Lance sample.

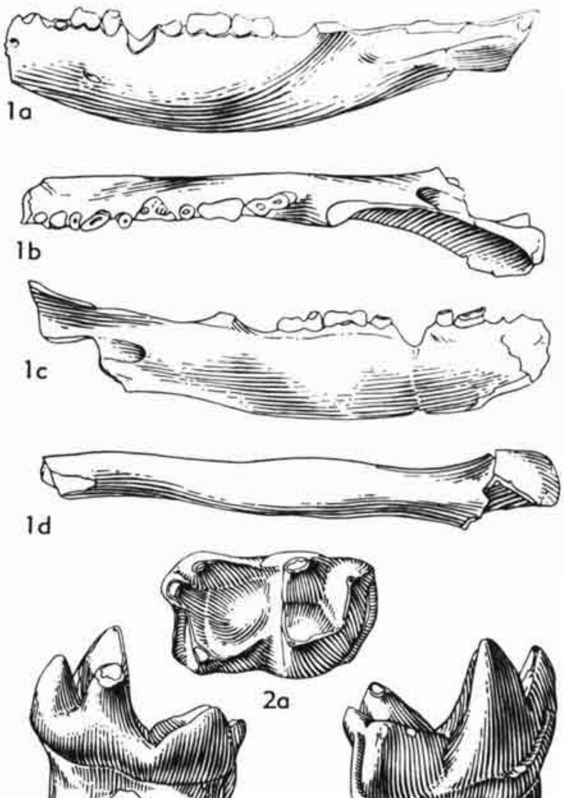

FIG. 24. *Pediomys hatcheri* (OSBORN).

1. Fragment of left mandible with roots of $P_{1-3}M_{1-4}$ (3690), identification doubtful; *1a-d,* labial, occlusal, lingual, and ventral views, ×1.5.
2. Right M_3 (3690); *2a-c,* occlusal, lingual, and labial views, ×8; meas. (mm.), A-P 3.70, W-Tri 2.25, W-Tal 2.30.

Although the measurements of the P_3's (Table 8) are slightly smaller than those observed in Lance specimens, they (e.g., 1991, Fig. 25,*6*) are morphologically identical and the size differences are probably not significant. The M_1, M_2's, and M_3 (2893, Fig. 25,*4*) agree in all described characters with the Wyoming specimens.

Three specimens of the previously undescribed lower canine of *Didelphodon vorax* have been recovered from

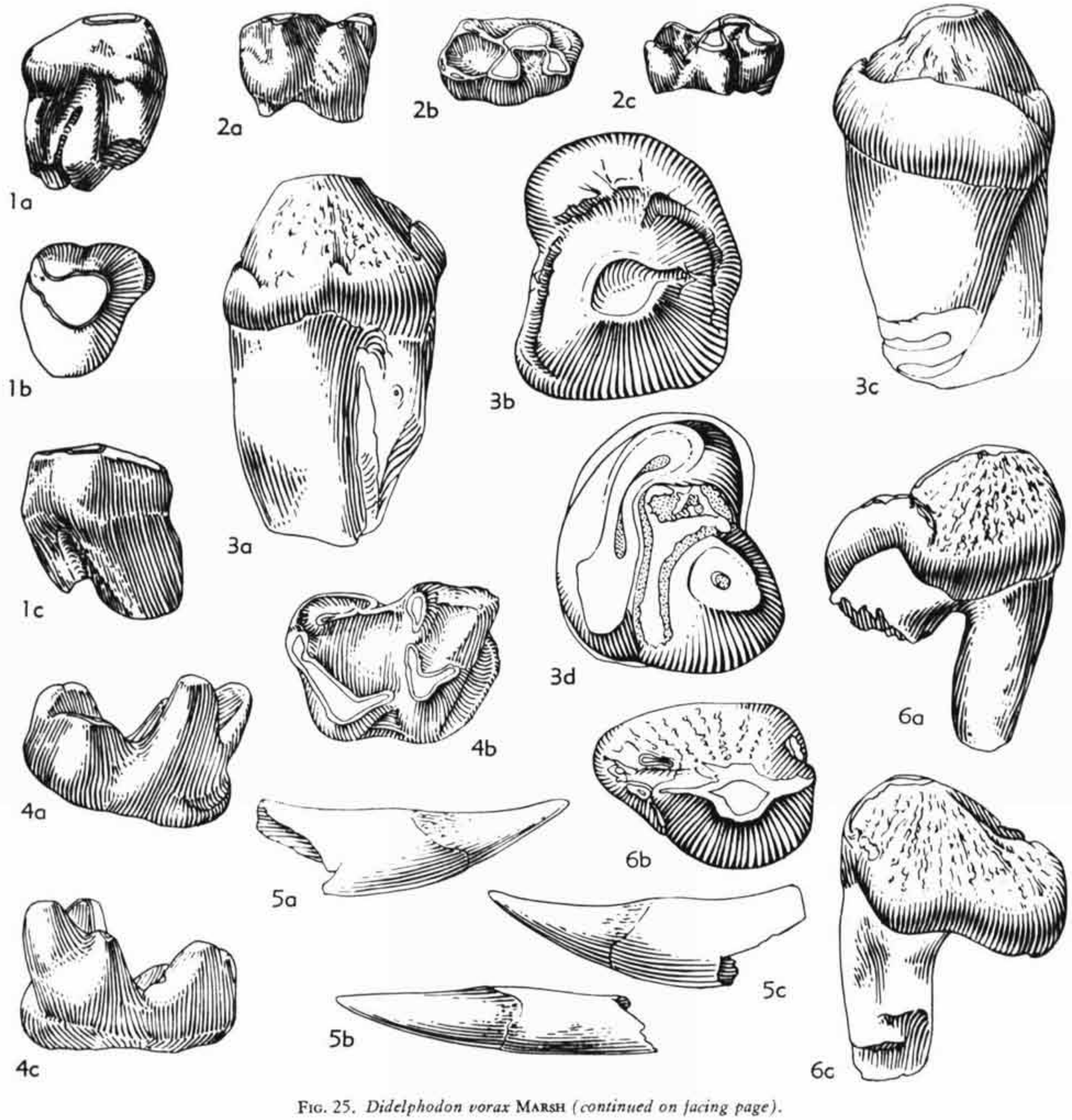

FIG. 25. *Didelphodon vorax* MARSH *(continued on facing page).*

1. Right ?P^1 (648, loc. UA-2); *1a-c*, anterior, occlusal, and posterior views, ×4; meas. (mm.), A-P 4.65, W 5.40.
2. Left DP_3 (649, loc. UA-2); *2a-c*, labial, occlusal and lingual views, ×6; meas. (mm.), A-P 3.50, W-Tri 2.40, W-Tal 2.55.
3. Right P^3 (1987, loc. UA-3); *3a-d*, labial, occlusal, lingual, and view of roots (anterior to right, labial down), ×6; meas. (mm.), A-P 6.00, W 7.20.
4. Right M_3 (2893, loc. KUA-18); *4a-c*, labial, occlusal, and lingual views, ×6; meas. (mm.), A-P 5.50, W-Tri 4.15, W-Tal 3.80.
5. ?Right C_1 (3787, loc. KUA-22); *5a-c*, ?labial, superior, and ?lingual views, ×2.67; meas. (mm.), at base of enamel, depth 6.05, width 4.00.
6. Right P_3 (1991, loc. UA-2); *6a-c*, labial, occlusal, and lingual views, ×6; meas. (mm.), A-P 5.60, W 4.35.

the upper Edmonton Formation (fragment figured by Marsh, 1892, pl. 8, fig. 6). The base of the most complete specimen (3787, Fig. 25,*5*) agrees well with depth and width measurements (Table 8) and ratios of incomplete specimens (1985 from the Edmonton; LACM 15433 described by Clemens, 1968b) found in jaws. The complete specimen is unworn and remarkably symmetrical, thus making the side designation difficult. The base of the tooth at the termination of the enamel is robust, but the crown itself tapers dorsoventrally, rapidly at first, then continues to its apex with a more gradual taper. The depth-width ratio at the base of the enamel is 1.51, but the tooth becomes perfectly circular in cross section near its apex. The enamel is smooth near the apex, but is lightly crenulated around its entire circumference near the base. The root is massive and extends within the mandible to a point ventral to the anterior root of the P_3. The crown of the lower canine probably pointed somewhat more anteriorly than is shown in Clemens' (1968b, p. 5, fig. 2) partial restoration.

ZOOGEOGRAPHIC CONSIDERATIONS OF EDMONTON FORMATION MARSUPIALS

Clemens (1968a) has carefully reviewed the early evolution of the marsupials and has suggested a North American origin for the group probably being derived from members of the Family Pappotheriidae (Slaughter, 1965).

The following marsupial taxa were in the upper Edmonton Formation:

Marsupials Present in Upper Edmonton Strata

- Subclass Theria
  - Infraclass Metatheria
    - Order Marsupialia
      - Family Didelphidae
        - *Alphadon marshi* Simpson, 1927
        - *Alphadon wilsoni* Lillegraven, n. sp.
        - *Alphadon rhaister* Clemens, 1966
      - Family Pediomyidae
        - *Pediomys elegans* Marsh, 1889a
        - *Pediomys krejcii* Clemens, 1966
        - *Pediomys hatcheri* (Osborn), 1898
      - Family Stagodontidae
        - *Didelphodon vorax* Marsh, 1889a

None of the taxa listed above are unique to the Edmonton Formation and all (including *Alphadon wilsoni*) are represented in the type Lance Formation of Wyoming. I can cite no evidence based upon elements of the marsupial fauna that suggests a significant temporal difference between the upper Edmonton and the type Lance formations. In fact the distinguishing characteristic of the Edmonton fauna is the absence of several taxa found in more southerly assemblages. Absent from the list are *Alphadon lulli, Glasbius intricatus, Pediomys cooki,* and *P. florencae.* With the exception of *Alphadon wilsoni* and *A. marshi,* all marsupial taxa are rare in the upper Edmonton localities. Although negative evidence is always dangerous and must be used with caution, the absence of several taxa and rarity of occurrence of several others may eventually be shown to be of significance. The upper part of the Edmonton Formation is the oldest known rock unit in North America that bears a mammalian fauna in which the eutherians challenge the abundance, taxonomically and numerically, of the metatherians. The local fauna of the Lance Formation, located 600 miles south of the Red Deer Valley, is, by both criteria, dominated by the marsupials. The local fauna of the probably slightly younger rocks represented by the Bug Creek Anthills of the upper part of the Hell Creek Formation (Sloan & Van Valen, 1965) is dominated by eutherians. Marsupials became all but extinct in North America by early Paleocene time (Clemens, 1968a). The problem of marsupial-placental competition in the Cretaceous of North America will be discussed in the final section of this paper. Suffice it here only to mention the possibility that the time in which the upper Edmonton Formation was deposited was a critical period in the evolution of the dominance of the eutherian fauna in North America.

A summary of the phylogenetic relationships of Cretaceous marsupials of North America is presented in Figure 26.

Infraclass EUTHERIA Gill, 1872

Order INSECTIVORA Illiger, 1811

Family LEPTICTIDAE Gill, 1872

Subfamily GYPSONICTOPINAE Van Valen, 1967

Genus GYPSONICTOPS Simpson, 1927b

GYPSONICTOPS HYPOCONUS Simpson, 1927b

Figure 27,*3*

Type.—YPM 13662, right M^2 (Simpson, 1927b, pl. 32, fig. 3-5; Slaughter, 1965, p. 15, fig. 6d).

Referred specimens.—P^4, 3994; upper molar fragments, 3048, 3465; M_2's, 2466, 3237; lower molar fragments, 2876, 2978, 3178.

Locality.—KUA-1.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming; Hell Creek Formation, Montana and (unpublished) South Dakota; possibly Kirtland and Fruitland formations, New Mexico (unpublished).

Diagnosis.—A revised diagnosis of the species, based upon more complete material than is available from the Edmonton Formation, is currently being compiled by Clemens (pers. comm.).

Comments.—*Gypsonictops hypoconus* is a rare member of the known fauna of the upper Edmonton Formation. Only two complete measurable teeth, both of which are M_2's (e.g., 2466, Fig. 27,*3*), have as yet been recovered. Their range of measurements is as follows: A-P 1.85-1.95, W-Tri 1.45-1.50, W-Tal 1.20-1.30. *G. hypoconus* is common in the type Lance Formation.

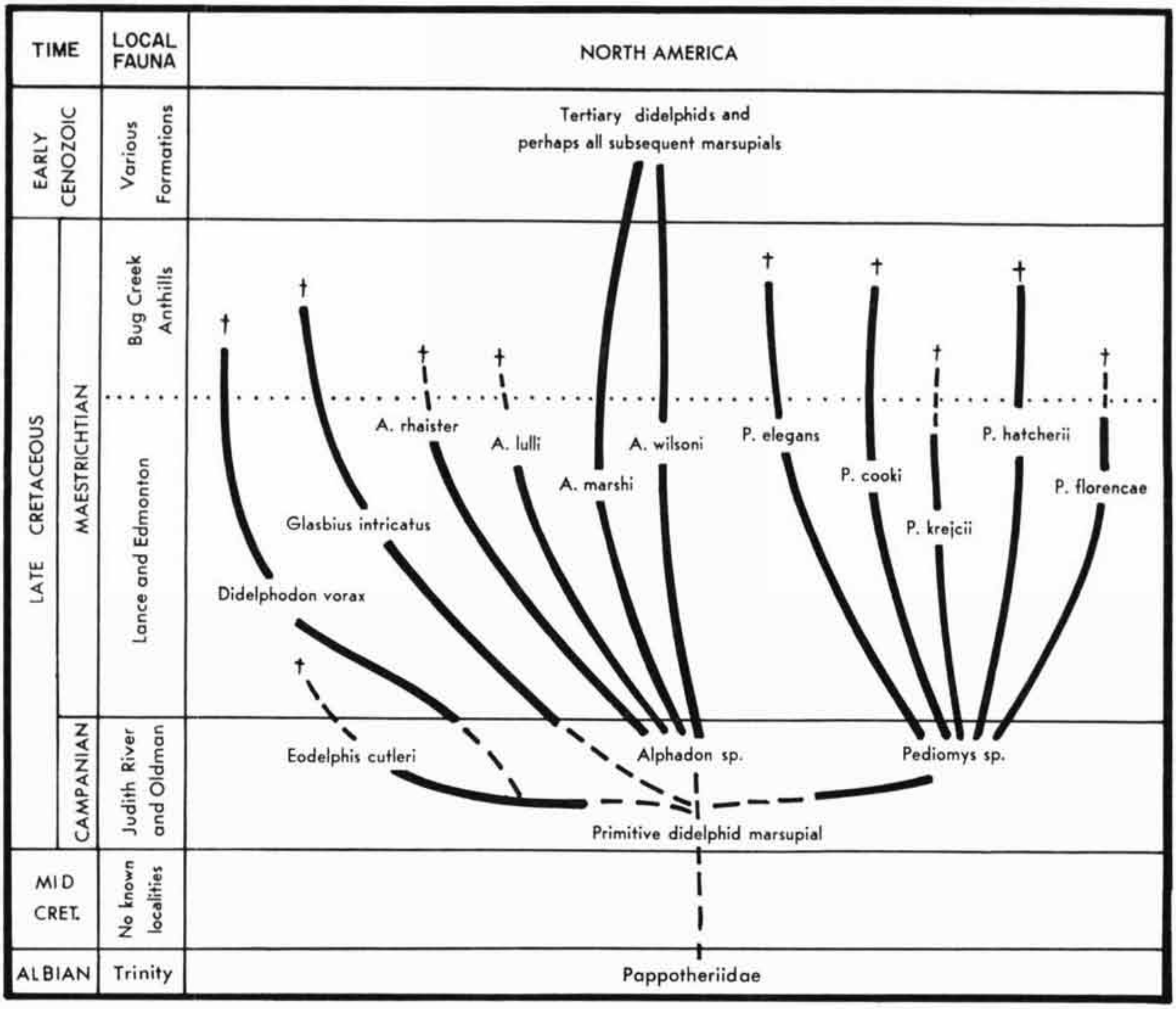

FIG. 26. Assumed phylogenetic relationships of known North American Cretaceous marsupials (adapted and modified from CLEMENS, 1966, p. 114, fig. 77).

GYPSONICTOPS ILLUMINATUS Lillegraven, new species

Figures, 27,*1,2,4-6*, 29,*1-5*

Etymology.—Latin, illumino, to light up, shed light.

Type.—2447, right maxillary fragment with $P^{3-4}M^{1-3}$ (Fig. 27,6).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—DP^3, 3216; fragmentary maxillae with P^3M^{1-2} (2951), P^4M^{1-3} (4045), P^4M^{1-2} (2966), and M^{1-2} (2470); eight P^3's; 11 P^4's; seven M^1's; five M^2's; two M^3's; DP_4's, 3538, 3927; six P_2's; fragmentary mandibles with P_eM_1 (2859), $P_{3-4}M_{1-3}$ (3210), P_3M_1 (3693), P_4M_{1-3} (3373), P_4M_{1-2} (2634), M_{1-2} (3715), and M_{2-3} (4046); nine P_3's; 12 P_4's; nine M_1's; 12 M_2's; six M_3's.

Localities.—KUA-1, 3, 22; UA-2.

Distribution.—Upper part of Edmonton Formation, Alberta.

Diagnosis.—Similar in most respects with *Gypsonictops hypoconus* but significantly larger with precingulum occasionally present on P^3, metacone on P^3 occasionally lacking, P^4 and upper molars more anteriorly recumbent, and trigonids of lower molars proportionately slightly lower.

Introductory notes.—SLOAN & VAN VALEN (1965, p. 225) described *Procerberus*, a new genus of placental mammal from the latest Cretaceous and earliest Paleocene sediments of Montana. They tentatively referred the genus to the family Leptictidae, and VAN VALEN (1967, p. 231) later did so with certainty. *Gypsonictops* and *Leptictis* (*Ictops* was relegated to the synonymy of *Leptictis* by VAN VALEN, 1967, p. 235) were assumed to have been independently derived from *Procerberus*, with *Gypsonictops* being a specialized, phylogenetically sterile offshoot. The newly discovered material from the upper Edmonton Formation allows the alternative interpretation that *Procerberus* is not a member of the Leptictidae,

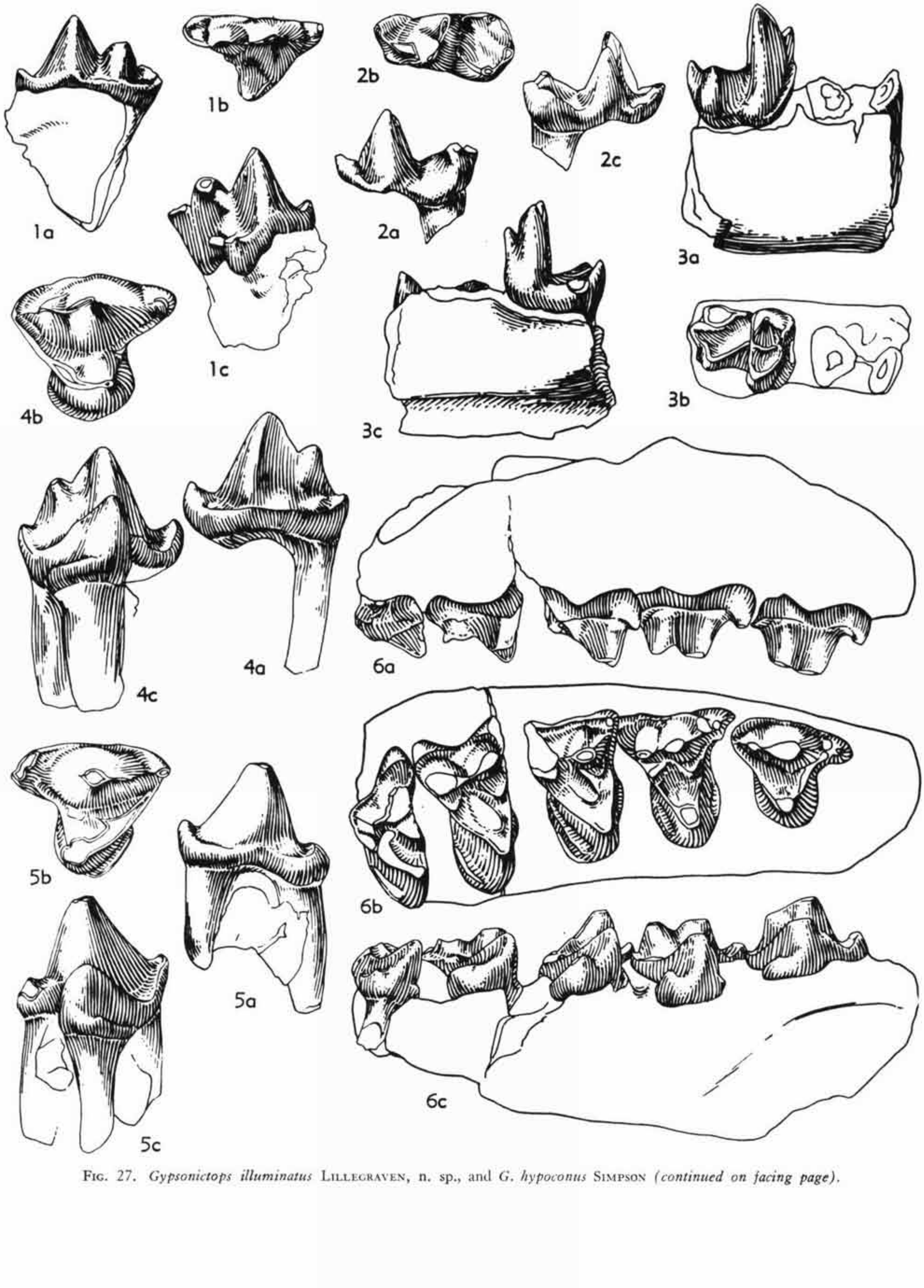

FIG. 27. *Gypsonictops illuminatus* LILLEGRAVEN, n. sp., and *G. hypoconus* SIMPSON *(continued on facing page).*

TABLE 9. *Measurements (in mm.) of Upper Dentition of* Gypsonictops illuminatus *Lillegraven, n. sp.*

Tooth	Length			Width		
	N	OR	$\overline{X}$	N	OR	$\overline{X}$
DP^3	1	3.20	----	1	1.85	----
P^3	8	2.35-2.90	2.70	8	2.10-2.95	2.45

Tooth	Length					Ant-W					Post-W				
	N	OR	$\overline{X}$	SD	CV	N	OR	$\overline{X}$	SD	CV	N	OR	$\overline{X}$	SD	CV
P^4	11	2.40-3.00	2.77	0.16	5.78	10	2.95-3.70	3.41	0.23	6.86	10	2.65-3.70	3.44	0.32	9.30
M^1	11	2.35-2.70	2.53	0.13	5.14	9	3.20-4.25	3.65	0.30	8.22	10	3.25-4.25	3.76	0.28	7.18
M^2	10	2.20-2.70	2.47	0.16	6.48	9	3.60-4.50	4.07	0.27	6.63	10	3.65-4.40	4.04	0.23	5.69
M^3	4	1.70-2.40	2.12	----	----	4	3.40-3.75	3.60	----	----	4	2.70-3.10	2.89	----	----

For abbreviations see end of Introduction.

order Insectivora, but rather a representative of the Palaeoryctidae, order Deltatheridia (of VAN VALEN, 1966). It is my interpretation that *Procerberus* was probably ancestral neither to *Gypsonictops* nor *Leptictis*. In defense of this interpretation, a point-for-point comparison of the dentition of *Leptictis*, the genus upon which the family Leptictidae is diagnosed, is included with the description of *G. illuminatus*. A comparable series of contrasts and comparisons between *Procerberus*, *Leptictis*, and the first-described species of *Cimolestes*, an unequivocal deltatheridian is given later (p. 65).

Description of upper dentition and comparisons with Leptictis.—The summarized measurements of the upper dentition of *Gypsonictops illuminatus* are shown in Tables 9 and 10.

1) DP^3. Although no deciduous teeth have yet been found in jaws of *Gypsonictops*, one tooth (3216, Fig. 27,*1*) is here regarded as a DP^3 of the genus. The assignment is based upon its size and a basic similarity with the previously undescribed DP^3 of *Leptictis* (Fig. 28,*1*). It may or may not be referable to *G. illuminatus*. An anterior accessory cusp, the paracone, metacone, and a posterior accessory blade are aligned close to the straight labial border. The weak protocone lacks conules, and a hypocone is absent. The paracone, the strongest cusp of the tooth, is rounded anteriorly and sharp posteriorly. The metacone is laterally compressed and has sharp anterior and posterior borders. It is separated from the posterior accessory blade by a distinct notch. Wear facets are found on the lingual half of the conical anterior accessory cusp, on the posterior border of the paracone, the entire crest of the metacone, the lingual border of the posterior accessory blade, and the entire protocone. Other than size, the structure differs from that of *Leptictis* in lacking a hypocone, a protoconule, and in the possession of a posterior accessory blade distinct from the metacone.

TABLE 10. *Dental Measurements (in mm.) of* Gypsonictops illuminatus *Lillegraven, n. sp. (Specimen 2447, holotype).*

Tooth	Length	Width	
P^3	2.75	2.50	
		Ant-W	Post-W
P^4	2.70	2.95	3.45
M^1	2.65 (est.)	3.50	3.65 (est.)
M^2	2.20 (est.)	4.00	3.85
M^3	1.70	3.75	2.70
P^3-M^3	11.40		
M^1-M^3	6.30		

For abbreviations see end of Introduction.

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1. *Gypsonictops* sp. cf. *G. illuninatus* LILLEGRAVEN, n. sp., right DP^3 (3216); *1a-c*, labial, occlusal, and lingual views, ×8; meas. (mm.), A-P 3.20, W 1.85.

2,4-6. *Gypsonictops illuminatus* LILLEGRAVEN, n. sp.,——2. Left DP$_4$ (3538); *2a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 2.50, W-Tri 1.00, W-Tal 1.20.——*4*. Right P^3 (3240); *4a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 2.85, W 2.60.——*5*. Left P^3 (3257); *5a-c*, **labial**, occlusal, and lingual views, ×10; meas. (mm.), A-P 2.70, W 2.35.——*6*. Holotype, fragment of right maxilla with P$^{3\text{-}4}$M$^{1\text{-}3}$ (2447); *6a-c*, labial, occlusal, and lingual views, ×8 (meas. in Table 10).

3. *Gypsonictops hypoconus* SIMPSON, fragment of right mandible with M$_2$ (2466); *3a-c*, labial, occlusal, and lingual views, ×10; meas. (mm.), A-P 1.85, W-Tri 1.45, W-Tal 1.20.

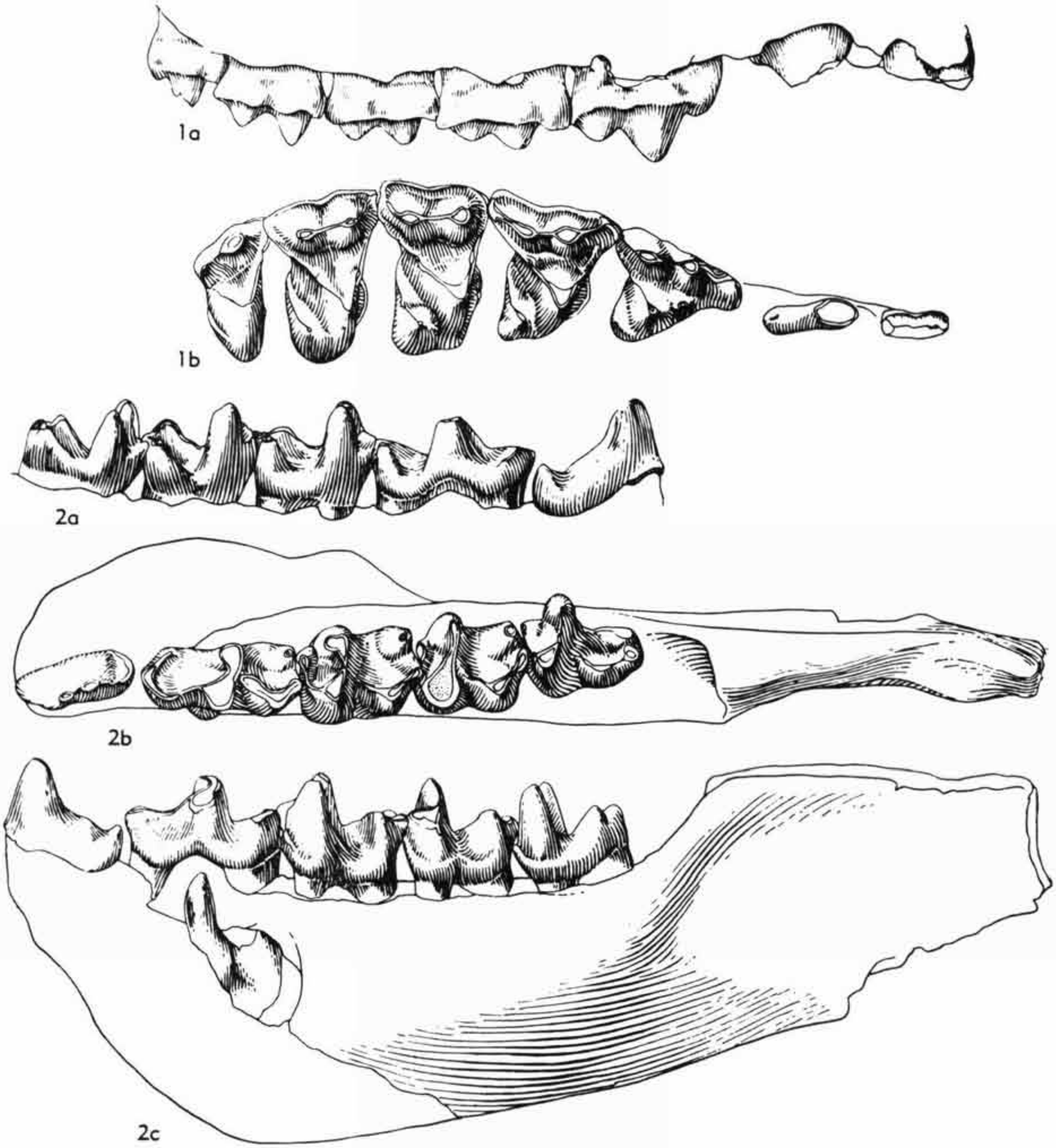

FIG. 28. *Leptictis haydeni* LEIDY.

1. Skull showing detail of right $DP^{3-4}M^{1-3}$ (AMNH, Frick 74963); mid. Oligocene, Converse County, Wyoming (same individual as Fig. 28,*2*); *1a-b,* labial and occlusal views, ×5.

2. Left mandible showing $DP_{3-4}M_{1-3}$ and erupting P_4 (same individual as Fig. 28,*1*); *2a-c,* lingual, occlusal, and labial views, ×5.

The proportions of the teeth and patterns of wear are otherwise identical.

CLEMENS will describe the DP^{3-4} of *Gypsonictops hypoconus.* Specimens referable to DP^4's of *G. illuminatus* have not yet been recovered, but they are probably fully molariform as in *Leptictis* (Fig. 28,*1*) and *G. hypoconus.*

2) P^3. The P^3 is submolariform (Fig. 27,*6*). A metacone is usually present (Fig. 27,*4*) but is totally absent in one specimen out of nine (Fig. 27,*5*). The protocone is strong, has an occlusal surface that usually is flat, and has a variably developed but generally strong postcingulum. Weak precingula are occasionally present. Conules are usually absent, but both protoconules and meta-

TABLE 11. *Measurements (in mm.) of Lower Dentition of* Gypsonictops illuminatus *Lillegraven, n. sp.*

Tooth	Length					Width									
	N	OR	$\bar{X}$	SD	CV	N	OR	$\bar{X}$	SD	CV					
P_2	6	1.40-1.70	1.54	----	----	6	0.75-0.90	0.82	----	----					
P_3	9	2.50-2.65	2.55	0.06	2.35	11	1.30-1.55	1.40	0.08	5.71					
						W-Tri					W-Tal				
						N	OR	$\bar{X}$	SD	CV	N	OR	$\bar{X}$	SD	CV
DP_4	1	2.50	----	----	----	2	0.95-1.00	0.97	----	----	1	1.20	----	----	----
P_4	10	2.20-2.75	2.50	0.16	6.40	14	1.45-1.70	1.55	0.08	5.15	12	1.15-1.60	1.47	0.12	8.16
M_1	14	2.15-2.70	2.40	0.17	7.08	14	1.65-2.00	1.84	0.11	5.98	15	1.60-2.00	1.82	0.12	6.59
M_2	15	2.15-2.70	2.44	0.18	7.38	16	1.70-2.10	1.95	0.12	6.15	16	1.50-1.90	1.74	0.11	6.32
M_3	8	2.20-2.60	2.43	----	----	8	1.55-1.90	1.73	----	----	9	1.30-1.60	1.45	----	----

For abbreviations see end of Introduction.

conules are occasionally weakly developed. The outline of the base of the labial border is generally slightly convex laterally, and has a continuous weak cingulum running from the anterior accessory cusp to the posterior corner of the tooth. Distinct wear-facets are found on the lingual side of the anterior accessory cusp, the entire crest of the tooth from the apex of the paracone posteriorly, and along the posterior border of the protocone and its cingulum.

The P^3 of *Leptictis* differs in that the labial cingulum is reduced or absent, the postcingulum is slightly weaker, and the protocone is conical. Some specimens of *Gypsonictops illuminatus* (e.g., 2951) approximate the condition seen in *Leptictis* in that the postcingulum is reduced and the protocone is more conical. The significance of these comparisons will be discussed later with the description of the P_{3-4}.

3) P^4 and upper molars. The P^4 of *Gypsonictops illuminatus* is fully molariform (Fig. 27,*6*) with a protocone equally as developed in form and function as the true molars. The protocone of the P^4 through M^3 becomes progressively more recumbent anteriorly. Short precingula and strong postcingula are always present on the P^4 and on all molars. Conules are well developed on the P^4 and on all molars are set close to the bases of the paracone and metacone. The crests of the internal wings of the conules are sharp. The P^4 through M^3 are rather low teeth with blunt wear-facets covering much of the occlusal surface area of the paracone, metacone, protocone, and postcingulum. The molars probably had a grinding function that differed significantly from the more precise shearing seen in the various species of *Cimolestes.* The P^4 has a strong anterior accessory cusp, the apex of which is slightly labial to a line drawn through the apices of the metacone and paracone. A weak stylar shelf, little better developed than that of the P^3, usually passes uninterrupted along the entire labial border of the tooth. The stylar shelf is reduced in comparison with most known Cretaceous therians, but increases in development from the P^4 through M^2. It is essentially absent labial to the metacone of the M^3 but is strong opposite the paracone.

The upper molars of *Leptictis* (Fig. 28,*1*) differ morphologically from those of *Gypsonictops illuminatus* only in minor details. The stylar shelf of *Leptictis* is slightly narrower (especially in the M^3), the posterolingual cingulum terminates in elevation closer to the occlusal surface of the protocone, and the internal wings of the conules are more rounded. Each of the contrasts seen in *Leptictis* is probably a specialization from a more primitive condition. All are also approximated or achieved in atypical specimens of *Gypsonictops.*

Description of lower dentition and comparisons with Leptictis.—The summarized measurements of the lower dentition of *Gypsonictops illuminatus* are given in Table 11.

1) DP_4. Two teeth (e.g., 3538, Fig. 27,*2*) have been recovered that are referred to DP_4's of *Gypsonictops illuminatus* on the basis of size and a basic similarity with the homologous tooth in *Leptictis* (Fig. 28,*2*). The protoconid is slightly higher than the metaconid but the entire tooth is rather low-crowned. The hypoconulid is centrally placed between the hypoconid and entoconid. The crista obliqua encounters the trigonid directly between the protoconid and metaconid. The paraconid is centrally placed between the protoconid and metaconid and juts strongly anteriorly. On one of the two specimens, a ridge runs down the anterior border of the protoconid and, after an interruption by a weak notch, continues up the labial border of the paraconid then down its lingual border. A short cingulum connects the bases of the paraconid and protoconid on both specimens. The

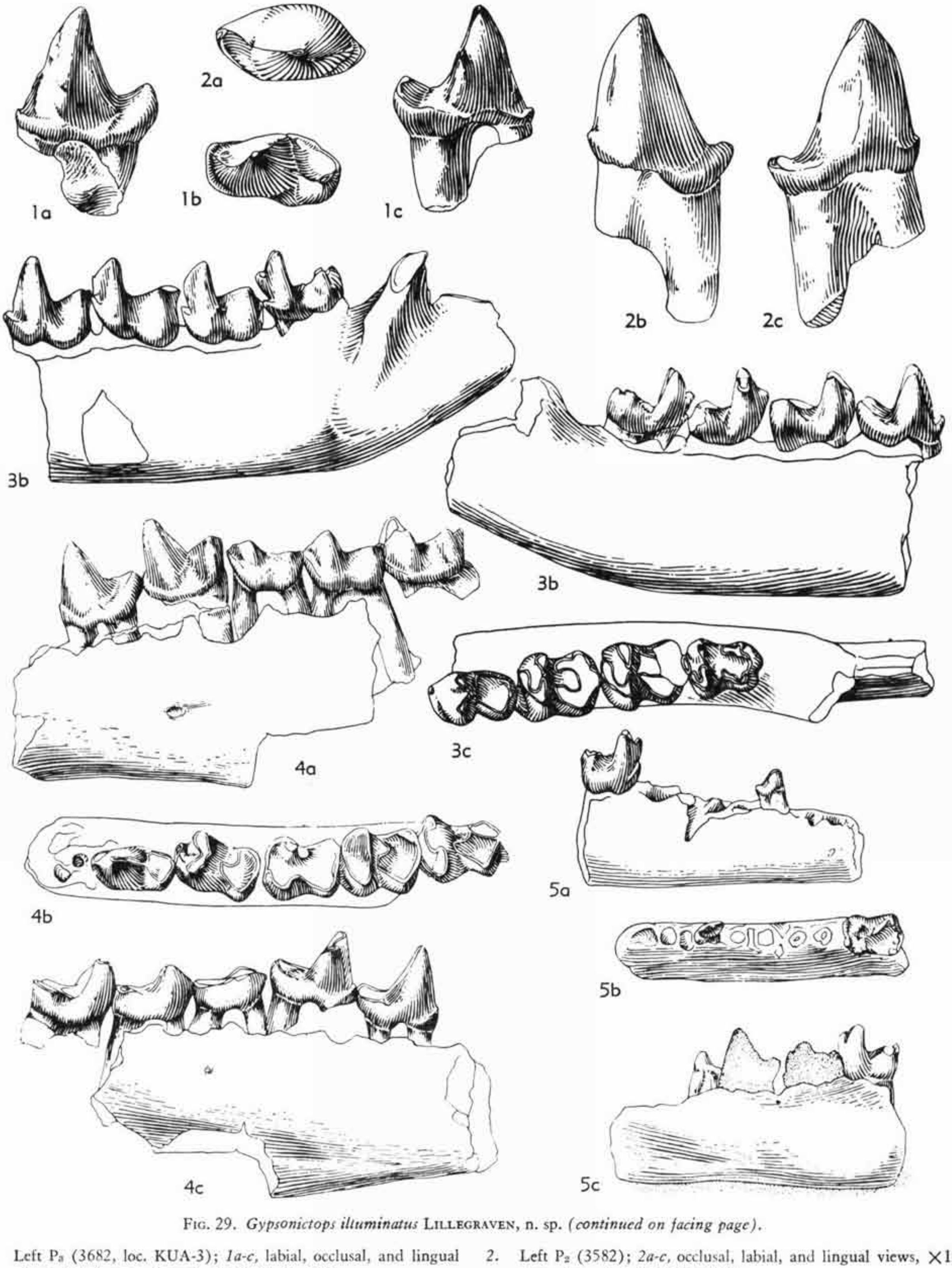

FIG. 29. *Gypsonictops illuminatus* LILLEGRAVEN, n. sp. (*continued on facing page*).

1. Left P_3 (3682, loc. KUA-3); *1a-c*, labial, occlusal, and lingual views, ×9.3; meas. (mm.), A-P 2.60, W 1.30.

2. Left P_2 (3582); *2a-c*, occlusal, labial, and lingual views, ×15; meas. (mm.), A-P 1.70, W 0.90.

tooth gradually narrows in occlusal view from posterior to anterior.

The DP_4 of *Leptictis* (Fig. 28,*2*) differs in that the width of the paraconid is as great as the width at the level of the protoconid and metaconid. The paraconid of *Leptictis* is as long anteroposteriorly as is the talonid. The permanent P_4 of *Leptictis* is proportionately broader and has essentially equal widths at the talonid and at the levels of the paraconid and the protoconid-metaconid. Other than those differences of proportion, the DP_4 of *Gypsonictops illuminatus* and the P_4 of *Leptictis* are morphologically similar.

2) P_2. No P_2's have yet been found in association with more posterior teeth definitely referable to *Gypsonictops*. However, several lines of evidence lead me to believe teeth of the type shown in Figure 29,*2* represent the P_2 of *G. illuminatus*. Members of the species had five lower premolars and the middle one (P_c) is reduced in size (Fig. 29,*5*). The alveoli for the P_2 in specimen 2859 match perfectly the size of the roots for the proposed P_2's. Secondly, specimen 3261 is a mandibular fragment with a complete ?P_2 followed posteriorly by two closely spaced alveoli, the diameters of which are smaller than those of the preceding premolar, and probably housed the P_c. Finally, the teeth are rather common and differ from anything referable to the species of *Cimolestes*. The two-rooted tooth has a tall main cusp, usually with a tiny anterior accessory cusp, and always with a small posterior accessory cusp. There is no indication of an incipient metaconid. Wear facets are found on the dorsal third of the anterior border of the main cusp and along the entire posterolabial border of the main and posterior accessory cusps.

3) P_c. As stated above, members of *Gypsonictops illuminatus* have five lower premolars, the central one of which is the smallest (Fig. 29,*5*). The usual eutherian condition of four lower (and upper) premolars is thus exceeded. CLEMENS (pers. comm.) has noted the same condition in *G. hypoconus*, but also observed a jaw with a short diastema between the P_2 and P_3, which probably means that *Gypsonictops* was in the process of losing its extra premolar in the Late Cretaceous. It is interesting to note the probable loss of a tooth from the middle of the premolar series rather than at its anterior end as occurred independently in many groups of mammals. The presence of an unusually large number of premolars quite possibly is to be expected in several groups of Cretaceous therians as primitive holdovers from the large number present in some of the known Jurassic and Early Cretaceous eupantotheres.

The P_c is two-rooted with a low main cusp and a broad posterior accessory cusp. The tooth is well worn from its apex down the posterior border of the main cusp and onto the accessory cusp. A vertical ridge marks the anterior border of the main cusp.

4) P_3. The P_3 (e.g., 3210, Fig. 29,*4*) of *Gypsonictops illuminatus* shows interesting transitions between the essentially unicuspid condition seen in the P_2 and the molariformity of the P_4. The main cusp is proportionately lower in relation to its length than is the P_2, and is slightly higher than the P_4. The posterior accessory cusp is strong, nearly to the point of forming a distinct talonid, but is not as well developed as that of the P_4. The talonid usually has only one distinct cuspule, equivalent in position to the hypoconid of the molars, but sometimes (e.g., 3133) has a second cuspule, equivalent to the hypoconulid. Although a third cuspule equivalent to the entoconid has not been observed in *G. illuminatus*, it is sometimes present in the P_3 of *G. hypoconus* (CLEMENS, pers. comm.). The talonid of the P_3 of *G. illuminatus* slopes sharply ventrally in the lingual direction from its labial crest and the enamel of the slope is thin and soon worn away by occlusion with the protocone of the P^3. Some minor wear is observed on the labial side of the talonid of the P_3 from contact with the lingual surface of the paracone of the P^3.

A variably developed narrow ridge follows an undulating path down the anterior border of the main cusp to a distinct cingulum present at the anterior base of both sides of the main cusp. The cingulum is not, however, developed into a weak paraconid as in the P_4. A distinct metaconid has not been observed. All known P_3's of *Gypsonictops illuminatus* do, however, have a definite bump on the center of the posterolingual border of the main cusp (e.g., 3682, Fig. 29,*1*) which does suggest that a potentiality for the formation of a metaconid or a steplike cusp such as is found in Cenozoic leptictids (e.g., *Palaeictops*) was present in the genotype of the animal. Whether the quasi-metaconid represents a reduction from or an addition to a primitive condition is an open question. The wear pattern on the posterior border of the main cusp starts at the apex of the tooth, passes linguoventrad to the quasi-metaconid, then labioventrad

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3. Fragment of left mandible with $P_4M_{1\text{-}3}$ (3373); *3a-c*, labial, lingual, and occlusal views, ×5.5; meas. (mm.), P_4, A-P 2.70, W-Tri 1.65, W-Tal 1.50; M_1, A-P 2.60, W-Tri 1.95, W-Tal 2.00; M_2, A-P 2.50, W-Tri 2.10, W-Tal 1.90; M_3, A-P 2.50, W-Tri 1.80, W-Tal 1.50.

4. Fragment of left mandible with $P_{3\text{-}4}$ and heavily worn $M_{1\text{-}3}$ (3210); *4a-c*, labial, occlusal, and lingual views, ×5.5; meas. (mm.), P_3, A-P 2.65, W 1.40; P_4, A-P 2.75, W-Tri 1.60, W-Tal 1.60; M_1, A-P 2.40, W-Tri 1.75, W-Tal 1.80; M_2, A-P 2.50, W-Tri 1.90, W-Tal 1.80; M_3, A-P 2.60, W-Tri 1.90, W-Tal 1.60.

5. Fragment of right mandible with P_c, M_1, and alveoli for $P_{1\text{-}2,\ 3\text{-}4}$, shading represents impressions of lost teeth preserved in enclosing rock (2859); *5a-c*, labial, occlusal, and lingual views, ×3.7; meas. (mm.), P_c, A-P 1.20, W 0.70; M_1, A-P 2.70, W-Tri 1.95, W-Tal 1.90.

to become confluent with the large wear surface on the lingual side of the talonid.

The structure of the P_3 of *Leptictis,* which is a simple cusp with no anterior cingulum, no trace of a metaconid, and with only a small posterior accessory cusp, shows the greatest differences from the known dentition of *Gypsonictops.* The significance of these differences will be discussed upon completion of the description of the P_4 of *G. illuminatus.*

5) P_4. The P_4 of *Gypsonictops illuminatus* (e.g., Fig. 29,*3,4*) shows nearly complete molariformity. The protoconid is only slightly stronger and higher than the metaconid, and a full sized talonid is present. The teeth fall short of total molariformity only in two respects. First, the paraconid is low and weak, and secondly, only talonid cuspules equivalent to the hypoconid and hypoconulid of the true molars are usually present. Some specimens, however, also have a fully developed entoconid (e.g., 2214). Usually the region where the entoconid would be expected is reduced and significantly lower than the lowest point on the crista obliqua. The crista obliqua contacts the trigonid directly below the notch separating the protoconid and metaconid. The talonid is fully half the height of the trigonid and the entire tooth is proportionately rather low. The protoconid is slightly anterior to the metaconid. A variably developed ridge usually runs anteroventrad from the apex of the protoconid to the small paraconid that is an elaboration of an anterior cingulum. The paraconid varies in development from no more than a cingulum (e.g., 2214) to a small but distinct conical cusp (e.g., 2805), and is variably placed from opposite the metaconid to a central position between the bases of the protoconid and metaconid. The anterior cingulum descends from the paraconid steeply to the lingual side of the base of the metaconid. The paraconid is usually worn. A broad, posteriorly sloping wear-facet connects the apices of the protoconid and metaconid. A weaker surface of wear is often seen on the anterior slope of the protoconid. Wear is sustained on the crista obliqua and hypoconulid long before it is on the lingual border of the talonid.

The P_4 of *Leptictis* differs from that of **Gypsonictops** only in that the paraconid is produced anteriorly into a strong but low cusp. A summary of the most significant contrasts of the P^3 and P_{3-4} of *Gypsonictops* and *Leptictis* is reported in Table 12. It is known from specimens of *Leptictis* with upper and lower dentitions preserved in occlusion (KU 2589 and KU 10982) that the paraconid of the P_4 had strong contact with the protocone of the P^3 and actually overlapped its anterior margin. On the other hand, the paraconid of *Gypsonictops* is small, and it was undoubtedly the talonid of the P_3 that functioned in occlusion with the protocone of the P^3. It is my interpretation that the posterolingual cingulum of the P^3 of *Gypsonictops* functioned, at least in part, in concert with the paraconid of the P_4 as a stopper device to protect the gingiva from being cut by the protoconid and metaconid of the P_4. No such device was "necessary" in *Leptictis* since the paraconid of the P_4 was large and overlapped the protocone of the P^3. By this method, the P_4 had solid abutments at both of its ends against the upper dentition, and the protoconid and metaconid posed little threat of damage to the gingiva posterior to the P^3. I believe the basic difference in the function of the protocone of the P^3 between *Gypsonictops* and *Leptictis* could have been easily bridged by a gradual concommitant increase in the size of the paraconid of the P_4 and the reduction of the posterior accessory cusp of the P_3. It is interesting to keep in mind at this point that the paraconids of the teeth regarded as DP_4's of *G. illuminatus* (e.g., 3538, Fig. 27,*2*) are significantly larger than those of the permanent P_4's. The significance of this observation is, however, unclear.

TABLE 12. *Structural Contrasts of P^3P_{3-4} Between* Gypsonictops *and* Leptictis.

Gypsonictops	*Leptictis*
P^3	P^3
1. Protocone with flat occlusal surface	1. Protocone conical
2. Posterolingual cingulum usually strong	2. Posterolingual cingulum usually reduced
P_3	P_3
1. Posterior accessory cusp developed into a talonid	1. Posterior accessory cusp weak
P_4	P_4
1. Paraconid weak	1. Paraconid strong

6) Lower molars. The lower molars of *Gypsonictops illuminatus* (e.g., Fig. 29,*3,4*) are proportionately low-crowned when compared to those of the various species of *Cimolestes.* The talonid is approximately half the height of the trigonid. The talonid accounts for about three-fifths the length of the tooth as the trigonid is anteroposteriorly compressed. The apex of the low paraconid is set significantly more labially than that of the metaconid. The paraconid and metaconid are closely appressed with only a slight gap between them in all three molars. The metaconid sometimes slightly exceeds the height of the protoconid in an unworn condition. Usually the two cusps are subequal in height, but the protoconid in the worn condition is almost always lower than the metaconid. A cingulum is present along the entire anterior bases of the teeth. The relative width of the talonid decreases from M_1 through M_3. The hypoconulid of the M_3 is not strongly produced posteriorly. Wear-facets on the paraconid, protoconid, and metaconid become broadly confluent early in the stages of wear (Fig. 29,*3*). The same is true for the crista obliqua and the three talonid cuspules. Broad wear-surfaces obliterating the apices of the cusps (e.g., Fig. 29,*4*) are developed much more frequently in *Gypsonictops* than in the species of *Cimolestes.* As stated

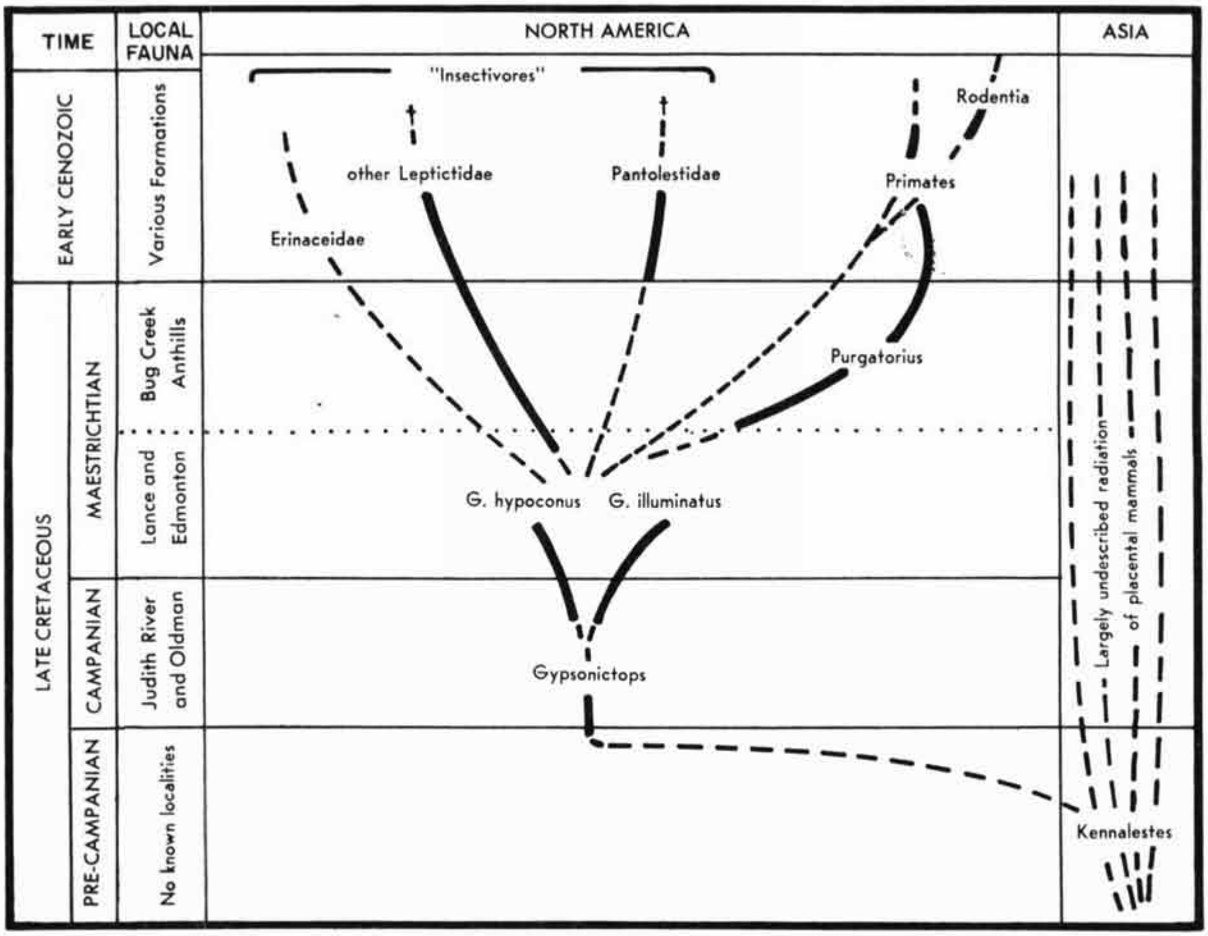

FIG. 30. Possible phylogenetic arrangement of Late Cretaceous leptictids and their likely descendants.

in the description of the upper molars of *G. illuminatus*, the molars probably emphasized a grinding function rather than the more complex shearing of the tuberculosectorial type.

The metaconid in *Leptictis* usually exceeds the height of the protoconid in the unworn condition. There are no other significant differences, disregarding size, between the lower molars of *Leptictis* and *Gypsonictops*. Tooth proportions, morphology, and surfaces of wear are otherwise identical.

Mandible. As in *Leptictis*, mental foramina are located ventral to the anterior root of the P_4 or posterior root of the P_3 and ventral to the anterior root of the P_2. Although no specimens of *Gypsonictops illuminatus* have yet been discovered with the angular process intact, CLEMENS (pers. comm.) has noted a definite inflection of the process in *G. hypoconus*. The same may have been true in *G. illuminatus*. The ventral border of the mandible is usually smoothly rounded. The mandibular symphysis extends to a point ventral to the anterior root of the P_3.

Affinities.—CLEMENS currently is preparing a discussion of the phylogenetic significance of *Gypsonictops*, thus only a few comments are necessary here. Following the above description of the dentition of *G. illuminatus* and its comparisons with *Leptictis*, I believe there is no doubt as to the membership of the former in the family Leptictidae. Furthermore, I can cite no dental characters that would bar *G. illuminatus* from a direct ancestry to most Cenozoic leptictids, *Leptictis* included. Of course this does not imply that *G. illuminatus* itself, biologically speaking, was the actual ancestor, but the species was not far removed from such a position. The relationship of *Gypsonictops* to *Procerberus* will be discussed following the description of the first species of *Cimolestes*.

The possible phylogenetic relationships of *Gypsonictops* are diagrammed in Figure 30. VAN VALEN & SLOAN (1965, p. 743) described *Purgatorius*, a new genus of paromomyid primates. Both the upper and lower dentitions are similar to those observed in *Gypsonictops*, and a close affinity may be inferred. Other paromomyids, such as *Plesiolestes problematicus* with its molariform P^4, are

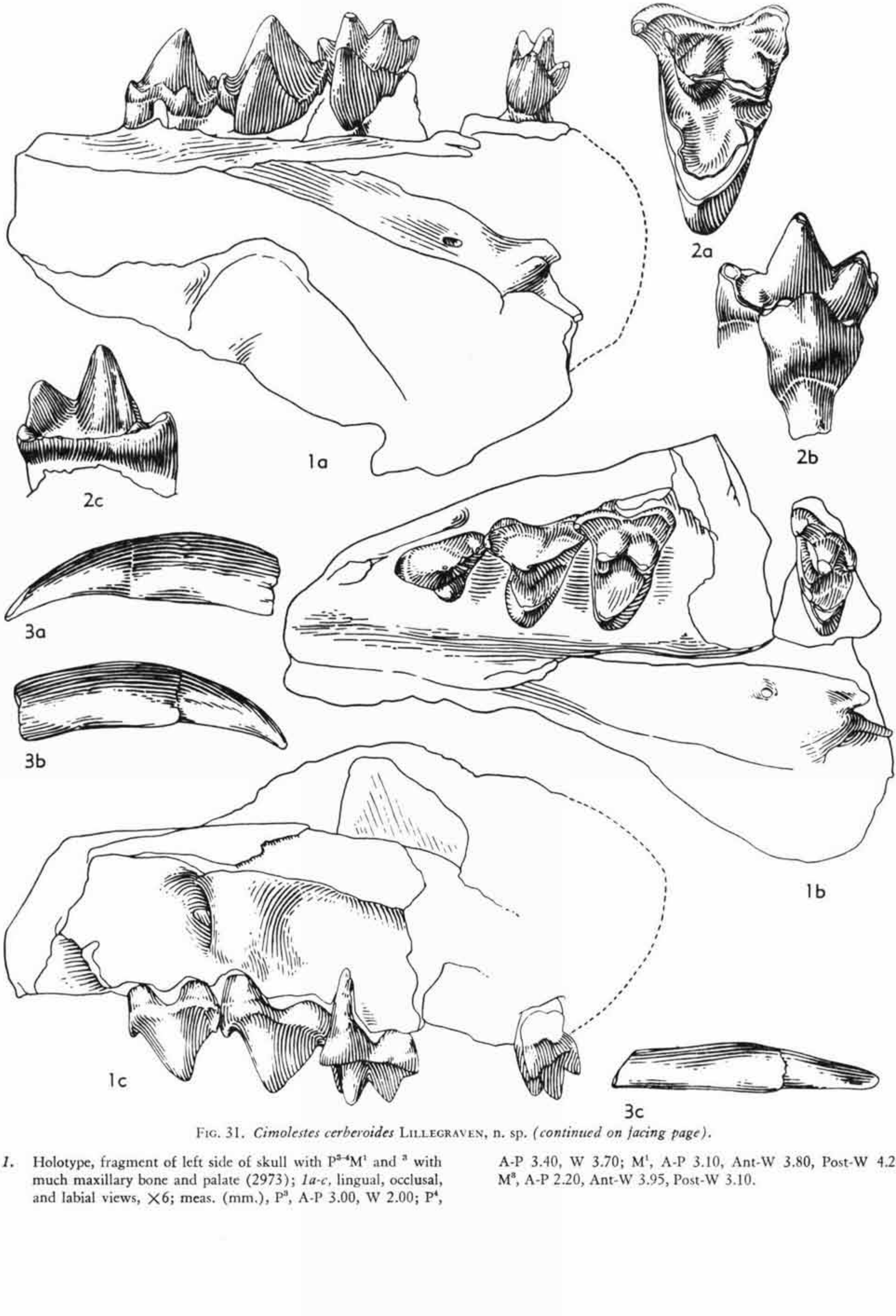

FIG. 31. *Cimolestes cerberoides* LILLEGRAVEN, n. sp. *(continued on facing page).*

1. Holotype, fragment of left side of skull with $P^{3-4}M^1$ and ^{3} with much maxillary bone and palate (2973); *1a-c,* lingual, occlusal, and labial views, ×6; meas. (mm.), P^3, A-P 3.00, W 2.00; P^4, A-P 3.40, W 3.70; M^1, A-P 3.10, Ant-W 3.80, Post-W 4.20; M^3, A-P 2.20, Ant-W 3.95, Post-W 3.10.

also strikingly similar to *Gypsonictops*. McKenna (1966, p. 11) presented evidence for a relationship between primitive primates and leptictids based upon details of the ear region. As pointed out by Szalay (1968, p. 34), the earliest primate radiation probably involved behavioral modifications, in several distinct groups, from predominantly insectivorous diets to those preferring fruits and leaves. Such dietary changes were accompanied by changes in the dentition with a deemphasis on the primitive eutherian shearing mechanism. He stated:

> As prevallid-postvallum and postvallid-prevallum shear lost relative importance the trigonid became less transverse and less tall, and the talonid gained functional importance.

The dentition of *Gypsonictops* seems a likely early stage in such evolution. McKenna has, in turn, recognized a possible origin for paramyid rodents from ". . . certain insectivores *(sensu lato)* related to primates" (1961, p. 4).

Gypsonictops is probably also related to the ancestry of the family Pantolestidae, especially to *Propalaeosinopa* (or *Bessoecetor*). The $P^4/_4$ of the pantolestines (Simpson, 1937b, p. 122-123, fig. 20, 21; Van Valen, 1967, pl. 6, fig. 3) are not molariform, but the molars are closely similar to those of *Gypsonictops*. A shift of the field of molarization posteriorly by one tooth in the upper and lower dentitions is the major condition necessary to derive the dental morphology of pantolestines from *Gypsonictops*.

Primitive erinaceids are poorly known (McKenna, 1960, p. 155), but are currently under study by McKenna. It is likely, however, that the ancestry of the group eventually goes back to *Gypsonictops* or to a rather closely related, as yet undiscovered genus. Assuming that *Gypsonictops* itself was the erinaceid ancestor, it would have been necessary to secondarily reduce and finally lose the metacone on both the P^3 and P^4.

Gypsonictops is also known from the Campanian rocks of the Judith River Formation of Montana and from the Oldman Formation of Alberta. Species from the two areas the being studied by Sahni and by Colwell and Fox, respectively. The Campanian species do not differ greatly from those of the Maastrichtian, and it is interesting to note the antiquity of the family Leptictidae. The known geological range in North America extends at least from the Campanian of the Cretaceous to the Whitneyan (Lillegraven, 1964, p. 51) of the Oligocene.

The ancestry of *Gypsonictops* is a still more interesting problem. Dr. Zofia Kielan-Jaworowska has kindly sent to me prepublication copies of photographs and drawings of several species of eutherian mammals from the Late Cretaceous Djadochta Formation of the Gobi Desert, Mongolia (*see* Lefeld, 1965). Her preliminary paper describing the fauna is in press, but she has allowed me to cite information contained on the plates, for which I most sincerely acknowledge her generosity. A new genus and species, *Kennalestes gobiensis,* is described that would, in my opinion based upon similarities of dentition, make a tantalizingly close structural ancestor for *Gypsonictops*. *Kennalestes* shows several tendencies toward a leptictid specialization in that: 1) the $P^4/_4$'s are submolariform; 2) lingual cingula are present on the P^4M^{1-3}; 3) conules are present on P^4M^{1-3} and are rather closely set to the paracone and metacone; 4) the paraconid and metaconid are closely approximated on the lower molars. As in *Gypsonictops,* a posterior accessory cusp is present on the P_3. *Kennalestes,* however, shows several characters which are probably more primitive than those of *Gypsonictops* in that: 1) the paracone of the P^3 is very strong and shows no trace of a metacone; 2) the metacone of the P^4 is distinctly weaker than the paracone; 3) the stylar shelf is broader in the upper molars; 4) the P_4 lacks an anterior accessory cusp (paraconid) and a metaconid; 5) the protoconid of the lower molars is taller than the metaconid and the entire trigonid is proportionately higher; and 6) a shearing function of the molars seems to have dominated over a grinding action. The upper and lower teeth labelled "canine" by Kielan-Jaworowska are double-rooted. Her reconstruction given in text-figure 3 shows the premaxillary-maxillary suture to be anterior to the upper "canine." The canine of most eutherian mammals is single-rooted and set between the two bones. Clemens has noted (pers. comm.) the presence of five lower premolars in *Gypsonictops hypoconus* and suggested the presence of five in the upper dentition as well. *G. illuminatus* (Fig. 29,*5*) also has five lower premolars, though the count of the uppers is unknown. It seems at least a possibility that the "canine" of *Kennalestes* is in actuality an initial premolar, giving a total of five.

An Asiatic origin of *Gypsonictops* seems likely.

Order DELTATHERIDIA Van Valen, 1966

Family PALAEORYCTIDAE (Winge, 1917), Simpson, 1931

Subfamily DIDELPHODONTINAE Matthew, 1918

Genus CIMOLESTES Marsh, 1889a

CIMOLESTES CERBEROIDES Lillegraven, new species

Figures 31,*1-3*, 32,*4*, 33,*1-6*

Etymology.—Latin, *cerberus,* doglike monster that guarded the gates of Hades; -oid, having the form of; to emphasize a similarity with *Procerberus.*

Type.—2973, fragment of left side of skull with $P^{3-4}M^{1-3}$ and with much of maxillary bone and palate (Fig. 31,*1*).

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2. Left M^2 (3296); *2a-c,* occlusal, lingual, and labial views, ×10; meas. (mm.), A-P 2.90, Ant-W 3.90, Post-W 4.40.

3. ?Left upper canine (3959); *3a-c,* ?labial, ?lingual, and dorsal views, ×4.

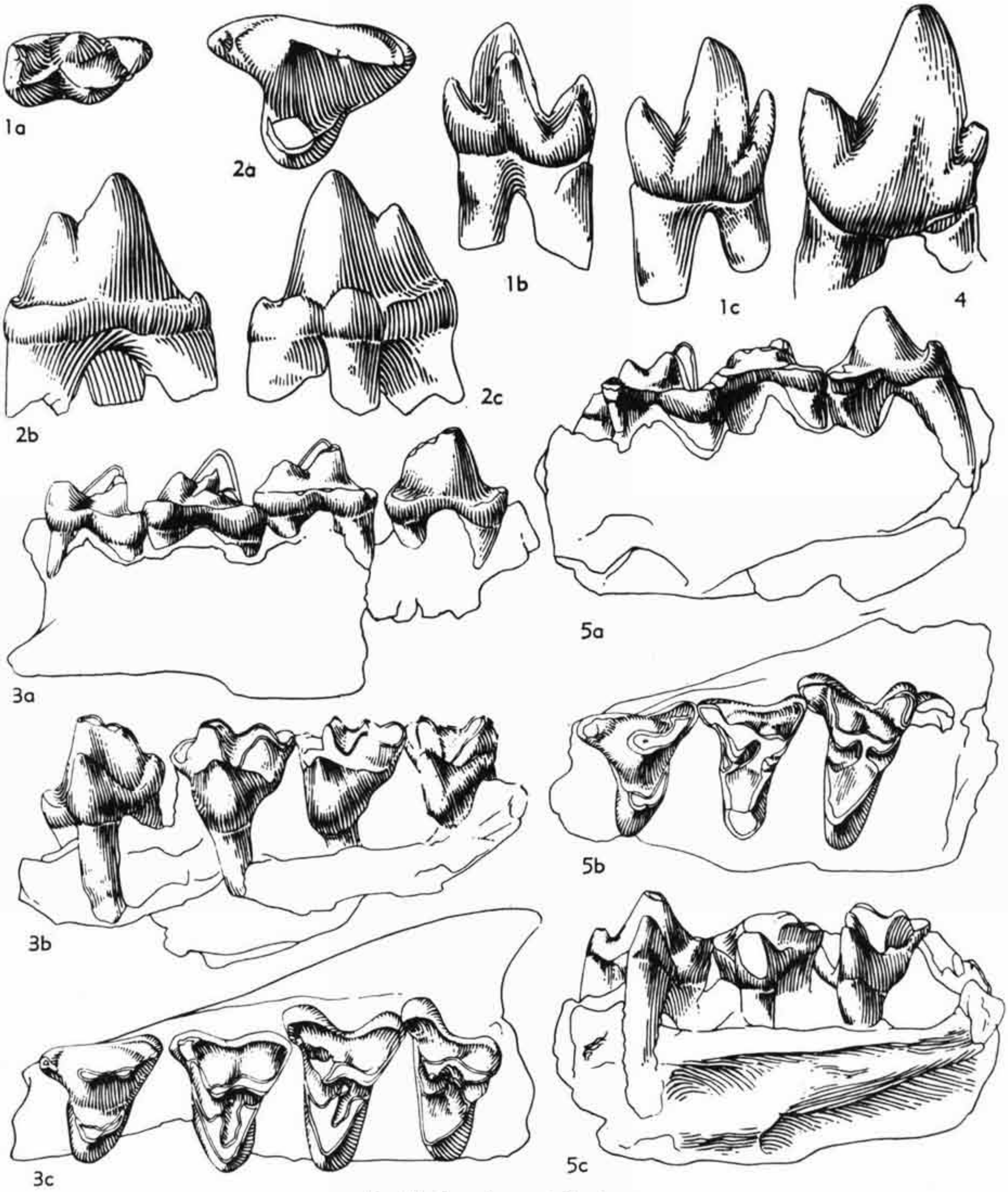

FIG. 32. *Procerberus* and *Cimolestes.*

1-3. Procerberus formicarum SLOAN & VAN VALEN.——*1.* Unworn right P$_4$ (KU 16079), Bug Creek Anthills, Hell Creek Formation, Montana; *1a-c,* occlusal, lingual, and labial views, ×9.3; meas. (mm.), A-P 2.55, W-Tri 1.25, W-Tal 1.25.——*2.* Left P^3 (KU 16078), Bug Creek Anthills, Hell Creek Formation, Montana; *2a-c,* occlusal, labial, and lingual views, ×13; meas. (mm.), A-P 2.50, W 1.95.——*3.* Fragment of left maxilla with P^{4}M$^{1-3}$ (UMVP 2310), Bug Creek Anthills, Hell Creek Formation, Montana; *3a-c,* labial, lingual, and occlusal views, ×7.5.

4. Cimolestes cerberoides LILLEGRAVEN, n. sp., labial view of moderately worn right P$_4$ (2190); ×9.3; meas. (mm.), A-P 3.20, W 1.75.

5. Cimolestes incisus MARSH, fragment of left maxilla with P^{4}M$^{1-2}$ (UCMP loc. V-5711), type Lance Formation, Wyoming (UMVP 1594); *5a-c,* labial, occlusal, lingual views, ×5.5.

TABLE 13. *Measurements (in mm.) of Upper Dentition of* Cimolestes cerberoides *Lillegraven, n. sp.*

Tooth	Length			Width					
	N	OR	X̄	N	OR	X̄			
P^3	9	2.50-3.00	2.80	10	1.75-2.20	1.88			
P^4	11	2.40-3.60	2.96	9	2.90-3.70	3.37			
				Ant-W			Post-W		
				N	OR	X̄	N	OR	X̄
M^1	7	2.60-3.10	2.88	4	3.80-4.10	3.94	5	3.20-4.30	4.01
M^2	4	2.65-3.10	2.86	3	3.80-4.30	4.00	4	4.00-4.65	4.30
M^3	8	2.10-2.90	2.49	2	3.95	3.95	5	2.90-3.45	3.10

For abbreviations see end of Introduction.

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—C^1's, 3600, 3959; fragmentary maxilla with P^{4}M^1, 3733; nine P^3's; 11 P^4's; five M^1's; five M^2's; nine M^3's; C$_1$'s, 2304, 3672, 3674; four P$_2$'s; fragmentary mandibles with P$_{2-4}$ (2190, 3054), P$_{3-4}$M$_1$ (3011), M$_{1-3}$ (2255), and M$_{1-2}$ (2240); two P$_2$'s; three P$_3$'s; five P$_4$'s; seven M$_1$'s; six M$_2$'s; 10 M$_3$'s.

Localities.—KUA-1, 3, 18, 22, 25; UA-2.

Distribution.—Upper part of Edmonton Formation, Alberta.

Diagnosis.—Similar to *Cimolestes incisus* in most details (currently being rediagnosed by CLEMENS), but P^{4}M$^{1-3}$ slightly less compressed anteroposteriorly and protocone less extended transversely; mandibular depth variable and angular process inflected.

Introductory note.—As stated in the introduction to the description of *Gypsonictops illuminatus,* the new material from the upper Edmonton Formation sheds some doubt upon the interpretation that *Procerberus* (VAN VALEN, 1967, p. 233) is a member of the Leptictidae and was ancestral to Cenozoic leptictids. Included with the description of *Cimolestes cerberoides* is a point-for-point comparison with equivalent characters in *Procerberus, Gypsonictops,* and *Leptictis* (=*Ictops*).

Description of upper dentition and comparisons.—Summarized measurements of the upper dentition of *Cimolestes cerberoides* can be found in Table 13.

1) P^2. No P^2's have yet been found in association with other known teeth of the species, but alveoli in specimen 3170 show that it was two-rooted.

2) P^3. The three-rooted P^3 of *Cimolestes cerberoides* (e.g., 2973, Fig. 31,*1*) has a small, low protocone jutting lingual from the middle of the base of the paracone. Anterior and posterior accessory cusps border either end of the paracone. The paracone is tall, but laterally compressed, with a rounded anterior border and a bladelike posterior border. The posterior border varies in development from an unswerving line (e.g., 3291) to a condition wherein a distinct incipient metacone is present (e.g., 2918). The anterior accessory cusp is weak, and in some teeth is nothing more than a gently sloping shoulder off the anterior base of the paracone. The posterior accessory cusp is a small blade that runs posterolabially at an angle from the posterior margin of the paracone. A weak ridge connects the apices of the anterior accessory cusp, protocone, and posterior accessory cusp. Lingual cingula and conules have not been observed on the protocone. A weak cingulum generally runs from the posterior-most part of the posterior accessory blade dorsal then anterior nearly to the center of the labial base of the paracone. A short, weak, transverse ridge frequently connects the apex of the protocone with the lingual base of the paracone. Wear-facets are found on the entire posterior border of the paracone, incipient metacone, and lingual side of the posterior accessory blade. The apex of the protocone, the ridges on either side, and the apex of the anterior accessory cusp show less severe wear.

The P^3 of *Cimolestes cerberoides,* which frequently exhibits an incipient metacone, differs from that of *Procerberus* (Fig. 32,*2*) in that *Procerberus* generally has a distinct metacone and lacks a posterior accessory blade. The teeth are essentially identical in all other respects. The P^3 of *Procerberus* agrees in structure with the usual condition of *Gypsonictops* and *Leptictis* in the presence of a distinct metacone and the lack of a posterior accessory blade, but differs in the lack of lingual cingula, all vestige of conules, and in the reduced size of the protocone.

3) P^4. Lingual cingula have not been observed on the P^4 of *Cimolestes cerberoides.* Conules are usually absent but a metaconule is sometimes present. It is generally represented by a low bump situated at the mid-point on the ridge that connects the apex of the protocone with the anterior base of the posterior accessory blade. A second ridge connects the apex of the protocone with the front of the anterior accessory cusp. A third ridge, generally weaker, connects the apex of the protocone with the lingual base of the paracone. This ridge is a common

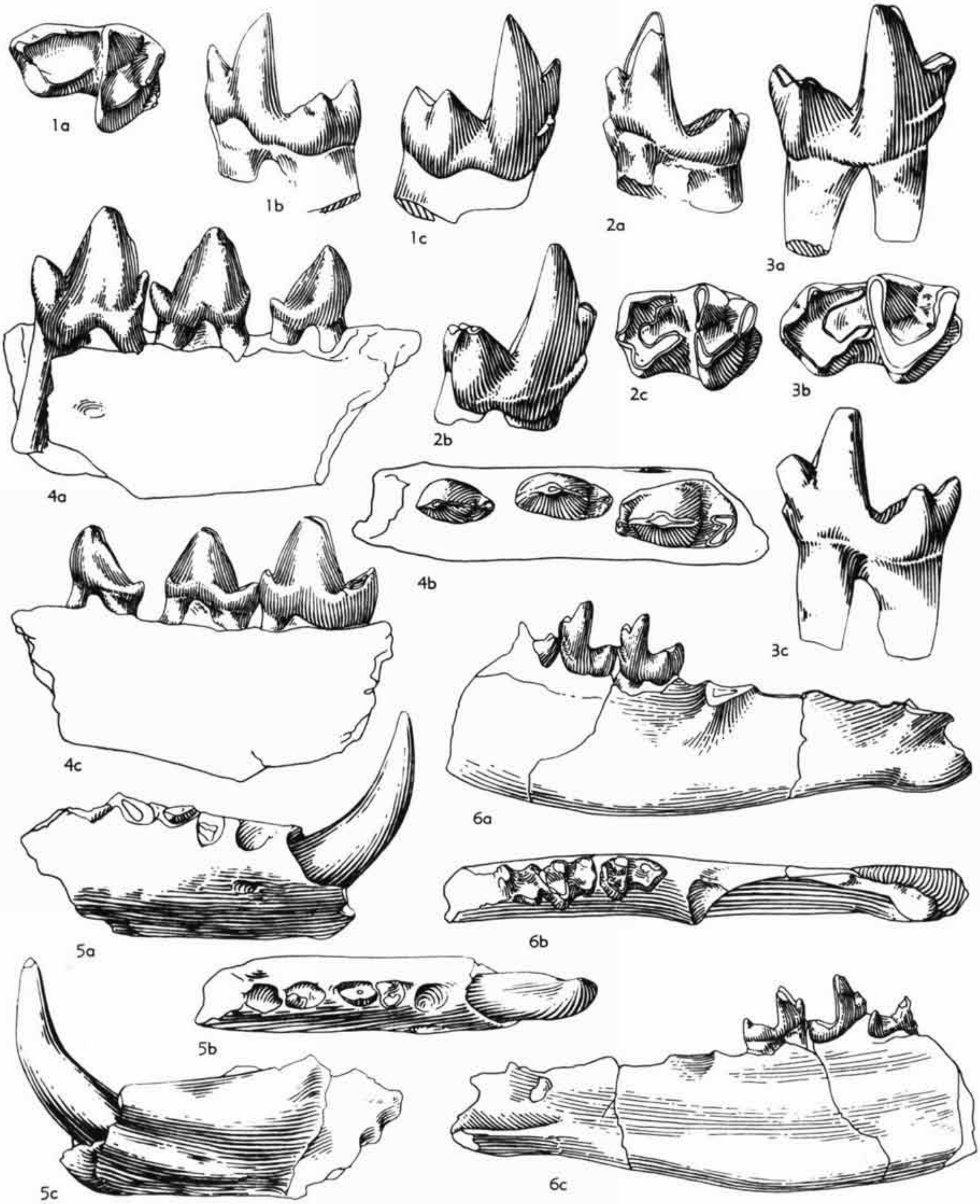

FIG. 33. *Cimolestes cerberoides* LILLEGRAVEN, n. sp. *(continued on facing page)*.

1. Right M_3 (2993); *1a-c*, occlusal, lingual, and labial views, ×8; meas. (mm.), A-P 3.10, W-Tri 2.20, W-Tal 1.60.
2. Right M_2 (3372); *2a-c*, lingual, labial, and occlusal views, ×8; meas. (mm.), A-P 2.90, W-Tri 2.25, W-Tal 1.85.
3. Right M_1 (3680, loc. KUA-3); *3a-c*, labial, occlusal, and lingual views, ×8; meas. (mm.), A-P 3.80, W-Tri 2.30, W-Tal 1.95.
4. Fragment of right mandible with P_{2-4} (3054); *4a-c*, labial, occlusal, and lingual views, ×6.4; meas. (mm.), P_2, A-P 2.00, W 1.00; P_3, A-P 2.55, W 1.20; P_4, A-P 3.15, W 1.65.

feature among primitive members of the order Deltatheridia (VAN VALEN, 1966). The labial and lingual surfaces of the protocone are steep, nearly to the point of being vertical. The anterior accessory cusp is small, low, and sharply conical. The paracone is tall, laterally compressed, has a rounded anterior border, and secant posterior border. A definite expansion of the posterior ridge of the paracone indicates the presence of an incipient metacone. The metacone area is worn down quickly, but probably is sometimes a distinct cuspule in the unworn condition (e.g., 2752). As in the P^3, the posterior accessory blade diverges posterolabially at an angle from the posterior margin of the paracone. A cingulum generally traverses the entire labial border of the tooth. The most pronounced wear occurs on the posterior border of the paracone, lingual surface of the posterior accessory blade, and on the ridge connecting the blade and the apex of the protocone. A strong shearing function with the M_1 is suggested. Lesser wear occurs on the apex of the protocone, its anterior ridge, and on the anterior accessory cusp.

Differences between the P^4 of *Cimolestes cerberoides* and *Procerberus* (Fig. 32,*3*) are minor. That of *C. cerberoides* is proportionately slightly more extended transversely than that of *Procerberus*. The shearing function was more pronounced in *C. cerberoides*, though the wear-facets are identically placed, and the cusps and ridges are sharper in the unworn condition. The metacone is larger, though not greatly so, in *Procerberus*. Although SLOAN & VAN VALEN (1965, p. 225) stated that conules are lacking in the P^4 of *Procerberus*, I have observed several specimens (e.g., KU 16080) that show distinct bumps representing metaconules developed in the same fashion and position as those of *C. cerberoides*. In any case, conules are weak or absent in both species. The P^4's of *C. cerberoides* and *Procerberus* are identical in all other characters.

The contrasts of the P^4 between *Procerberus-Cimolestes cerberoides* and *Gypsonictops-Leptictis* are, on the other hand, striking. The latter two genera have a strong protoconule and metaconule which are set close to the paracone and metacone, respectively. *Gypsonictops* and *Leptictis* have precingula and postcingula that are consistently present and strong. Both genera have a more distinctly developed metacone than found in *Procerberus* and *C. cerberoides* and the labial and lingual surfaces of the protocone slope significantly more gently. The entire tooth is proportionately lower in the leptictids. The occlusal surface of the protocone is concave at the base of the paracone and metacone of *Gypsonictops* and *Leptictis*, whereas it is strongly convex at that area in *Procerberus* and *C. cerberoides*. Finally, *Gypsonictops* and *Leptictis* lack the posterior accessory blade, and the wear is concentrated on the main occlusal surface of the tooth, not on its edges as a principally shearing (carnassial-like) function. As noted above, the P^4 of *Procerberus* probably had a lesser shearing function than that of *C. cerberoides*. It was not, however, developed as a grinder to the extent seen in the definite leptictids.

The upper dentition of *Cimolestes incisus* is similar to that of *C. cerberoides*, and the P^4M^{1-2} of the former are illustrated in Figure 32,*5*.

4) Upper molars. The upper molars of *Cimolestes cerberoides* (Fig. 31,*1*,*2*) have moderately wide stylar shelves and tall cusps. The paracone is the highest cusp on the teeth. The metacone is only slightly lower than the paracone on the M^1, but becomes proportionately lower on the M^{2-3} and is lower than the protocone on the M^3. The central axes of the paracone and metacone diverge sharply ventrally. Definite lingual cingula are lacking although weak ridges are occasionally present. Lingual cingula often function as protective devices against abrasion of the gingiva by the cusps of the lower molars. The lack of lingual cingula on the molars of *C. cerberoides* has apparently been compensated for by the presence of rather deep interdental embrasures. The conules are strong, but their internal wings are generally rounded. The apex of the protoconule is placed half way between the apices of the protocone and the paracone, and that of the metaconule is slightly more labially situated. A strong posterior metacrista diverges posterolabiad from the metacone of the M^{1-2} and is separated from the metacone by a distinct notch. The posterior metacrista and stylar shelf are lacking in the M^3 at the region of the metacone. A weak anterior paracrista runs anterolabially from the base of the anterior ridge of the paracone to the edge of the stylar shelf on M^{1-3}. The posterior halves of the stylar shelves are equally developed in M^{1-2} into distinct lobes, but the anterior half is reduced in the M^1. The earliest and most pronounced wear is found on the entire anterior protoconular ridge, the occlusal surface of the protocone, the posterior surfaces of the posterior metacrista and metacone, and the sides of the valley separating the apices of the paracone and metacone. Later stages of wear erode the anterolingual corner of the stylar shelf, anterior crest of the paracone, and posterior ridge of the metaconule.

The upper molars of *Cimolestes cerberoides* differ from those of *Procerberus* in the following ways. The stylar shelf of *Procerberus* is somewhat reduced in comparison, especially in the M^1. Their development in the M^{2-3} are rather comparable. *Procerberus* generally, though by no means always, has lingual cingula; they

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5. Fragment of right mandible with canine and alveoli or roots for P_{1-3} (3672); *5a-c*, labial, dorsal, and lingual views, ×4.8.
6. Fragment of left mandible with talonid of M_1, complete M_{2-3}, and inflected angular process (2255); *6a-c*, labial, occlusal, and lingual views, ×3.2; meas. (mm.), M_1, W-Tal 2.10; M_2, A-P 3.00, W-Tri 2.50, W-Tal 2.00; M_3, A-P 3.20, W-Tri 2.25, W-Tal 1.80.

are totally lacking on some molars (e.g., Fig. 32,*3*). The cingula, when present, show great variability of development. The conules of *Procerberus* are less strongly developed than those of *C. cerberoides*, but their placement is comparable. The molars of *Procerberus* are generally less broad transversely than those of *C. cerberoides*, but the range of the ratios of length to width overlap considerably. The posterior metacrista, though present, is reduced in *Procerberus* and the notch separating it from the metacone is weaker. The apices of cusps and crests of ridges are less acute in *Procerberus* than in *C. cerberoides*. The interdental embrasures are deeper in *C. cerberoides*. *Procerberus* did not have the carnassial shearing function developed to the degree seen in *C. cerberoides*. However, the basic wear pattern, which reflects an early emphasis upon shearing functions along the anterior crest of the protoconule, is the same. The upper molars of *C. cerberoides* and *Procerberus* are identical in all other respects.

Comparisons between the upper molars of *Cimolestes cerberoides-Procerberus* and *Gypsonictops-Leptictis* are important. *Procerberus* is similar to the definite leptictids in possessing a comparatively narrow stylar shelf. Nearly all post-Cretaceous eutherians had reduced stylar shelves, a character independently acquired in several groups. *Procerberus* and *C. cerberoides* differ from *Gypsonictops* and *Leptictis* in: 1) lack or irregular development of lingual cingula; 2) lingual position of the conules; 3) presence of a posterior metacrista on the M^{1-2}; 4) predominance of a carnassial style of shearing function over one of grinding; 5) comparative elevation of the cusps; and 6) comparative erectness of the protocone of M^{1-3}.

Skull.—Nothing is known of the skull of *Cimolestes cerberoides* other than that part represented by the holotype (2973, Fig. 31,*1*). The palate shows no major perforations, but has a definitely raised rim on the ventral side of its posterior border giving the appearance of a reduced marsupial-like "flange palate." A similar condition is present in *Didymictis simpsoni* (KU 7800), a Middle Paleocene miacid. A single posterior palatine foramen is present. The infraorbital canal opens just dorsal to the posterior root of the P^3.

Upper and lower canines.—Canines have yet to be found in jaws associated with known teeth of *Cimolestes cerberoides*. However, there is good reason to believe that the specimens illustrated in Figures 31,*3* and 33,*5* are representative of the species. Specimen 6411 shows that the P_1 is single-rooted, the more anterior mental foramen is ventral to the alveolus of the P_1, and that the root of the canine is strong and laterally compressed. Specimen 3672 (Fig. 33,*5*) lacks postcanine teeth, but shows a single alevolus for the first premolar, a mental foramen directly below it, and a strong complete canine. The base of the tooth at the point of exit from the alevolus measures 2.35 in depth and 1.53 in width measured at right angles to the longitudinal axis. It is posteriorly recurved with the axis of the tip being at about a right angle to the long axis of the mandible. The enamel is largely weathered away thus obliterating wear facets. The apex of the tooth is pulled in medially. The medial side is flat and lateral side broadly rounded. The lower canine of *Procerberus* has been described as "moderate" (VAN VALEN, 1967, p. 241, table 5).

The putative upper canines are straighter in all planes and have deep wear along the anterior surface resulting from abrasion with the tip and posterior side of the lower canines. Specimen 3959 (Fig. 31,*3*) measures 2.75 in depth and 1.90 in width at the beginning of the distal taper measured at right angles to the long axis of the tooth.

Description of lower dentition and comparisons.—The summarized measurements of the lower dentition of *Cimolestes cerberoides* can be found in Table 14.

1) Lower premolars. As in the most primitive known miacids (MACINTYRE, 1966), the P_1 of *Cimolestes cerberoides* is a small single-rooted tooth. The structure of its crown, however, is as yet unknown. The P_{2-4} (Fig. 33,*4*) are variations upon a theme. They are well separated from each other in the jaw and all are premolariform with a strong main cusp and no trace of a metaconid. The posterior roots are stronger than the anterior roots. The teeth have a posterior accessory cusp that is weak in the P_2 but becomes progressively stronger posteriorly. Two weak cusps, equivalent in position to the hypoconid and hypoconulid are sometimes (e.g., 3011) present on the talonid of the P_4. Usually, however, the talonid has a structure similar to that of the P_3 of *Gypsonictops illuminatus*. A ridge, which is strongest in the P_4, traverses from the posterior end of the crest of the posterior accessory cusp anterolingual to the lingual base of the paraconid. The anterior and posterior borders of all three teeth are sharp. The teeth increase in all dimensions rather uniformly from the P_2 through the P_4 and the apex of the main cusp shifts proportionately posteriorly. The P_4 has a distinct but low anterior accessory cusp. The P_3 lacks such a cusp, but a weak short cingulum is present on either side of the main cusp at the equivalent position. The P_2 lacks even a hint of an anterior accessory cusp. Wear on the P_2 has been observed only down the posterior border of the main cusp and on the apex of the posterior accessory cusp. The major wear on the P_3 occurs on the apex and posterior border of the main cusp and on the lingual side of the posterior accessory cusp. A light wear-facet is also present on the anterolabial side of the tip of the main cusp of the P_{3-4}. Wear on the P_4 always exceeds that of the P_{2-3}. Initial wear occurs on the apex of the anterior accessory cusp, the apex and posterior border of the main cusp, and the main crest and lingual ridge of the talonid. Continued wear abrades the basin and labial side of the talonid, and

TABLE 14. *Measurements (in mm.) of Lower Dentition of* Cimolestes cerberoides *Lillegraven, n. sp.*

Tooth	Length			Width					
	N	O R	$\overline{X}$	N	O R	$\overline{X}$			
P_2	4	2.00-2.10	2.04	4	1.00-1.15	1.05			
P_3	5	2.50-2.70	2.60	5	1.20-1.40	1.31			
P_4	7	3.05-3.20	3.15	8	1.45-1.80	1.61			
				W-Tri			W-Tal		
				N	O R	$\overline{X}$	N	O R	$\overline{X}$
M_1	5	3.00-3.80	3.27	9	1.90-2.30	2.07	7	1.70-2.10	1.93
M_2	7	2.80-3.15	3.01	8	2.25-2.50	2.34	7	1.75-2.00	1.90
M_3	2	3.10-3.20	3.15	4	2.05-2.25	2.16	9	1.45-1.80	1.62

For abbreviations see end of Introduction.

the anterior borders of the main cusp and anterior accessory cusp.

The P_{1-2} of *Procerberus* have not yet been described. Although VAN VALEN (1967, p. 241, table 5) stated that a posterior accessory cusp is absent on the P_3, SLOAN & VAN VALEN (1965, p. 225) described the tooth as "simple, with paraconid and one-cusped talonid." Specimen UMVP 1460 shows the latter description to be correct. The P_3 of *Procerberus* differs from that of *Cimolestes cerberoides* only in the possession of a distinct anterior accessory cusp ("paraconid").

The P_4 of *Procerberus* (Fig. 32,*1*) and *Cimolestes cerberoides* show the greatest differences of any parts of their known dentition. The P_4 of *Procerberus* is quite molariform with a distinct paraconid, metaconid, and a talonid with two or three cuspules. It is in many respects similar to the P_4 of Cenozoic leptictids for with the possession of a fully developed paraconid, it exceeds the degree of molariformity seen in *Gypsonictops.* It was probably largely on the basis of the structure of the P_4 that SLOAN & VAN VALEN (1965, p. 226) referred *Procerberus* to the family Leptictidae. It should be pointed out here, however, that the presence of a metaconid and semimolariform P_4 is no rarity among species of Cretaceous North American eutherians which have no close relationship with the leptictids. This point will be expanded later in the paper.

A comparison of the characteristics of the P_4 between *Cimolestes cerberoides, P. formicarum,* and *Gypsonictops-Leptictis* is presented in Table 15. One can see that *Procerberus* agrees structurally with the definite leptictids in the presence of a metaconid, a well-developed talonid, and, with *Leptictis,* in the presence of a strong paraconid. It differs from the leptictids, however, in characters 1, 3-8. The P_4 of *Procerberus* differs from that of *C. cerberoides* in the possession of a metaconid, strong paraconid, and a nearly complete talonid. It agrees, however, in characters 1, 3, 5, 7, and 8. Agreement is partial in character 9 because *C. cerberoides* occasionally has two talonid cuspules. It is my contention that although the P_4 of *Procerberus* is similar to that of definite leptictids, the similarity is superficial, and the fundamental structure of the tooth is more closely allied to typical deltatheridians such as *C. cerberoides.* This morphological similarity is especially well illustrated in Figure 32,*1c,4.* The question of whether the presence of a metaconid in *Procerberus* is a primitive or a specialized character awaits more paleontological evidence for its answer.

2) Lower molars. The lower molars of *Cimolestes cerberoides* have comparatively high trigonids, the paraconid of which is well separated from the metaconid. The separation is greater in the M_1 (Fig. 33,*3*) than in the M_{2-3} (Figs. 33,*1,2*). The paraconid is placed nearly as lingually as the metaconid. The protoconid is equal in height or slightly higher than the metaconid in an unworn condition. The lowest part of the talonid touches the trigonid at a point significantly lower than half the height of the protoconid. The hypoconulid of the M_3 is produced posteriorly much more than that of the M_{1-2}. Short anterior cingula slope ventrally from the center of the base of the paraconid to the anterolabial corner of the protoconid. The cusps of the trigonid remain high and well separated even after considerable wear. Wear is typical for that of primitive eutherian molars, and strong shear facets are found on the anterior surface of the protoconid, the entire posterior surface of the trigonid, and the lingual surface of the talonid ventral to the crista obliqua. The protoconid is worn more rapidly than the metaconid.

The above description of the lower molars of *Cimolestes cerberoides* holds equally well for those of *Procerberus* with only minor emendations. The shearing function of the molars of *Procerberus* was not as effective as that of *C. cerberoides.* The crests of the cusps of *Procerberus* are slightly duller in the unworn condition and were blunted earlier during the process of wear. A

TABLE 15. *Comparative Characteristics of* P_4 *in* Procerberus formicarum, Cimolestes cerberoides, *and* Gypsonictops-Leptictis.
(Numbers refer to equivalent characters.)

Procerberus formicarum

1. Protoconid laterally compressed.
2. Paraconid large.
3. Anterior cingulum absent.
4. Metaconid much smaller than protoconid and posteriorly set.
5. Tooth proportionately narrow (average length/width = 2.06).
6. Ridge from apex of metaconid to notch separating metaconid and protoconid frequently absent.
7. Posterior ridge of protoconid usually continuous with crista obliqua.
8. Distinct notch present between crista obliqua and base of posterior ridge of protoconid.
9. Talonid with two or three cuspules.

Cimolestes cerberoides

1. Main cusp (protoconid) laterally compressed.
2. Anterior accessory cusp (paraconid) small.
3. Anterior cingulum absent.
4. Metaconid lacking.
5. Proportions similar to *Procerberus formicarum* (average length/width = 1.96).
6. No equivalent character.
7. Posterior ridge of main cusp (protoconid) always continuous with main crest of posterior accessory cusp (crista obliqua).
8. Distinct notch present between anterior end of main crest (crista obliqua) of posterior accessory cusp and base of posterior ridge of main cusp (protoconid).
9. Posterior accessory cusp (talonid) with one or two cuspules.

Gypsonictops-Leptictis

1. Protoconid broadly rounded.
2. Paraconid absent or small in *Gypsonictops*, large in *Leptictis*.
3. Anterior cingulum present.
4. Metaconid only slightly smaller than protoconid.
5. Tooth proportionately wide (average length/width = 1.61).
6. Ridge always present.
7. Posterior ridge of protoconid lacking.
8. Crista obliqua in broad contact with posterior wall of trigonid.
9. Talonid with two or three cuspules.

distinct bump is almost always present on the crista obliqua half way between the hypoconulid and the point of contact with the talonid. Such a bump has not been observed in *C. cerberoides* or *Gypsonictops,* but is occasionally found on lower molars of *C. incisus* (e.g., KU 12888).

SLOAN & VAN VALEN (1965, p. 225) stated that the protoconid is not higher than the metaconid in *Procerberus*. It has been my experience, however, that in an unworn condition, the protoconid is equal or slightly greater (e.g., KU 16081) in height than the metaconid, as is the case in *Cimolestes cerberoides*. The protoconid simply was worn down more rapidly than the metaconid.

Rather strong contrasts, on the other hand, are observed between the lower molars of *Procerberus-Cimolestes cerberoides* and *Gypsonictops-Leptictis*. The latter pair differs from the former pair in that: 1) the trigonid is significantly proportionately lower; 2) the paraconid is more labially placed and appressed against the anterior face of the metaconid, even in the M_1; 3) the metaconid in *Leptictis* and some specimens of *Gypsonictops* slightly exceeds the height of the protoconid in the unworn condition; 4) the hypoconulid is not greatly extended posteriorly on the M_3; and 5) a grinding rather than a basically shearing function was emphasized.

Mandible.—Mental foramina are located ventral to the P_1 (Fig. 33,*5*) and the center of the P_4 (Fig. 33,*4*). The angular process (Fig. 33,*6*) is distinctly inflected medially, a characteristic previously thought to have been restricted, as a general feature, to the marsupials (e.g., Fig. 24,*1*). The mandibular foramen is rather small and posteriorly set just dorsal and slightly posterior to the beginning of the inflection of the angular process. The mandibular symphysis extends posteriorly to a point ventral to the anterior root of the P_3. Mandibular fragments vary rather strikingly in depth from specimen to specimen. Either this was a highly variable characteristic from one individual to another, or the mandibles themselves continued growth throughout life as in certain marsupials and possibly (CLEMENS, pers. comm.) *Gypsonictops*. Data correlating relative tooth wear to mandibular depth are insufficient at present to resolve the answer.

Affinities.—As suggested in the diagnosis, *Cimolestes cerberoides* is very closely related to *C. incisus* which is currently being described in detail by CLEMENS. There is no doubt as to the membership of these two species in the family Palaeoryctidae, order Deltatheridia.

The description of the canines, secant premolars, and shearing molars suggests a carnivorous mode of life for *Cimolestes cerberoides*. GILES T. MACINTYRE has pointed out to me that the species has all the characters which would be expected in an animal on the "main line" of evolution toward the family Miacidae, and eventually all of the order Carnivora, *s.s. C. cerberoides* does not show diagnostic miacid characters, but represents the best possibility for a basal stock yet known. A link showing miacid reduction of the $M^{2-3}/_{2-3}$ and increased functional emphasis on the P^4M_1 carnassial pair is still missing. It can be seen, however, that the structure of *C. cerberoides* is not impossibly removed from that of *Ictidopappus* (MACINTYRE, 1966, p. 142-143, fig. 10, 11). RUSSELL (1962) tentatively referred isolated teeth fragments from the Late Cretaceous St. Mary River Formation to the Miacidae, but CLEMENS (1966, p. 95) suggested that their affinities more likely were with the marsupial *Alphadon ?rhaister*.

The detailed comparisons of *Cimolestes cerberoides* and *Gypsonictops-Leptictis* indicate very different dental morphologies and functions between members of the Leptictidae and Palaeoryctidae. Descriptions of the remaining species of *Cimolestes* in the upper Edmonton fauna will point out the essential dental uniformity among the North American Cretaceous palaeoryctids. The comparison of the dentitions of *Procerberus* and *C. cerberoides* demonstrated a community of characters held in common between the two genera which are at variance with equivalent characters found in leptictids. I can only conclude that *Procerberus* is not a member of the Leptictidae, order Insectivora (VAN VALEN, 1967, p. 231) but on the contrary shows characters that relate the genus much more closely with the Palaeoryctidae, order Deltatheridia. Keeping this in mind, the diagnosis of the Procerberinae (SLOAN & VAN VALEN, 1965, p. 225) is no longer meaningful in context either with the Leptictidae or Palaeoryctidae and should no longer be recognized.

VAN VALEN (1967, p. 233, fig. 3) suggested that *Procerberus* was ancestral to several different lines of leptictids. *Gypsonictops* and *Leptictis* were thought to have been ultimately derived independently from *Procerberus*. Such an interpretation is not impossible since all known Cretaceous eutherians have a dental structure with many common characteristics. However, the independent derivation of *Gypsonictops* and *Leptictis* from *Procerberus* would require such a degree of parallel evolution in so many characters that the probabilities of such an occurrence seem low. As shown in Figure 30, *Gypsonictops* was present in North America at least since the Campanian. *Procerberus* has not yet been recovered from rocks older than the youngest part of the Maastrichtian and palaeoryctids are rare at best in rocks older than Maastrichtian (*see* Fig. 40). Such negative evidence is dangerous to weight too heavily, but makes the probability that *Procerberus* was ancestral to *Gypsonictops* seem still less likely.

A second species of *Procerberus* is found in the early Paleocene Tullock Formation of Montana (SLOAN & VAN VALEN, 1965, p. 225). GLENN L. JEPSEN has generously allowed me to cite the presence of species of *Procerberus* in the Mantua lentil of the Polecat Bench Formation of Wyoming. One of the probably two species present in this deposit is about one third larger than *P. formicarum*. The nearly equal length-width proportions of the molars of this larger species and its increased grinding function would make it a likely candidate for the origin of the stylinodontine taeniodonts (PATTERSON, 1949), a possibility suggested to me both by MALCOLM C. MCKENNA and LEIGH VAN VALEN. A detailed comparison of *Procerberus* with *Onychodectes*, the most primitive known taeniodont, has yet to be made and the proposed phylogeny is far from certain.

CIMOLESTES PROPALAEORYCTES Lillegraven, new species

Figure 34,*1-4*

Etymology.—Latin, *pro*, before; to emphasize a probable ancestry for *Palaeoryctes*.

Type.—3756, right mandible with two incisors and otherwise complete dentition (Fig. 34,*4*).

Type locality.—Loc. KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—P^4, 2706; fragmentary maxilla with M^{1-2}, 3111; M^1, 4092; upper molar fragments, 2476, 2896, 3012, 3270, 3315, 4072; P_1, 4065; P_4, 3829; fragmentary mandible with M_{1-3}, 3266; M_1's, 3305, 3458, 3801; M_3, 2368; lower molar fragments, 2267, 3098.

Locality.—KUA-1.

Distribution.—Upper part of Edmonton Formation, Alberta.

Diagnosis.—P^4 with small anterior accessory cusp, anteriorly keeled and laterally compressed paracone with an incipient metacone, bladelike posterior accessory cusp, and anteriorly placed, anteroposteriorly compressed protocone; upper molars anteroposteriorly compressed and separated by deep interdental embrasures; lingual cingula lacking; stylar shelf broad (especially opposite paracone) and strongly bilobate; apices of paracone and metacone well separated, but cusps fused throughout most of height; well-developed stylar cusp on or just posterior to labial termination of anterior paracrista; mandible shallow; lower incisors long, thin, anteriorly directed, and spatulate at tips; lower canine slender but fully developed; lower premolars reduced and well separated in jaw; P_{1-2} greatly reduced, unicuspid with small posterior heel, anteriorly recumbent, and single-rooted; P_1 larger than P_2; P_{3-4} double-rooted with trenchant main cusp and posterior accessory cusp; lower molars with high trigonid and narrow anteroposteriorly shortened talonid; protoconid and metaconid fused through most of height; paraconid placed low on trigonid; hypoconulid of M_3 not strongly produced posteriorly.

Description of lower dentition.—The summarized dental measurements for *Cimolestes propalaeoryctes* are given in Tables 16 and 17.

1) Incisors. Only two lower incisors are preserved in the holotype (Fig. 34,*4*). It could not be determined externally from the specimen if a third was represented. The jaw was not x-rayed. The incisors are thin in diameter, laterally compressed, elongated, and the long axes follow the curvature of the longitudinal axis of the mandible. The more medial incisor is longer and somewhat thicker than the more lateral, and the tips of both are slightly spatulate. The structure of the lower incisors of *Palaeoryctes* are unknown.

2) Canine. Except for its smaller size and more slender diameter, the lower canine of *Cimolestes propalaeoryctes* is structurally identical with that of *C. cerberoides*. Wear is observed only on the distal half of the posteromedial border. The lower canines of *Palaeoryctes* are undescribed.

3) Premolars. All four lower premolars are reduced in size. The P_1 and P_2 are single-rooted and greatly reduced. Their roots and crowns are anteriorly recumbent. The crowns of the P_1 (Fig. 34,*3*) and P_2 in an unworn

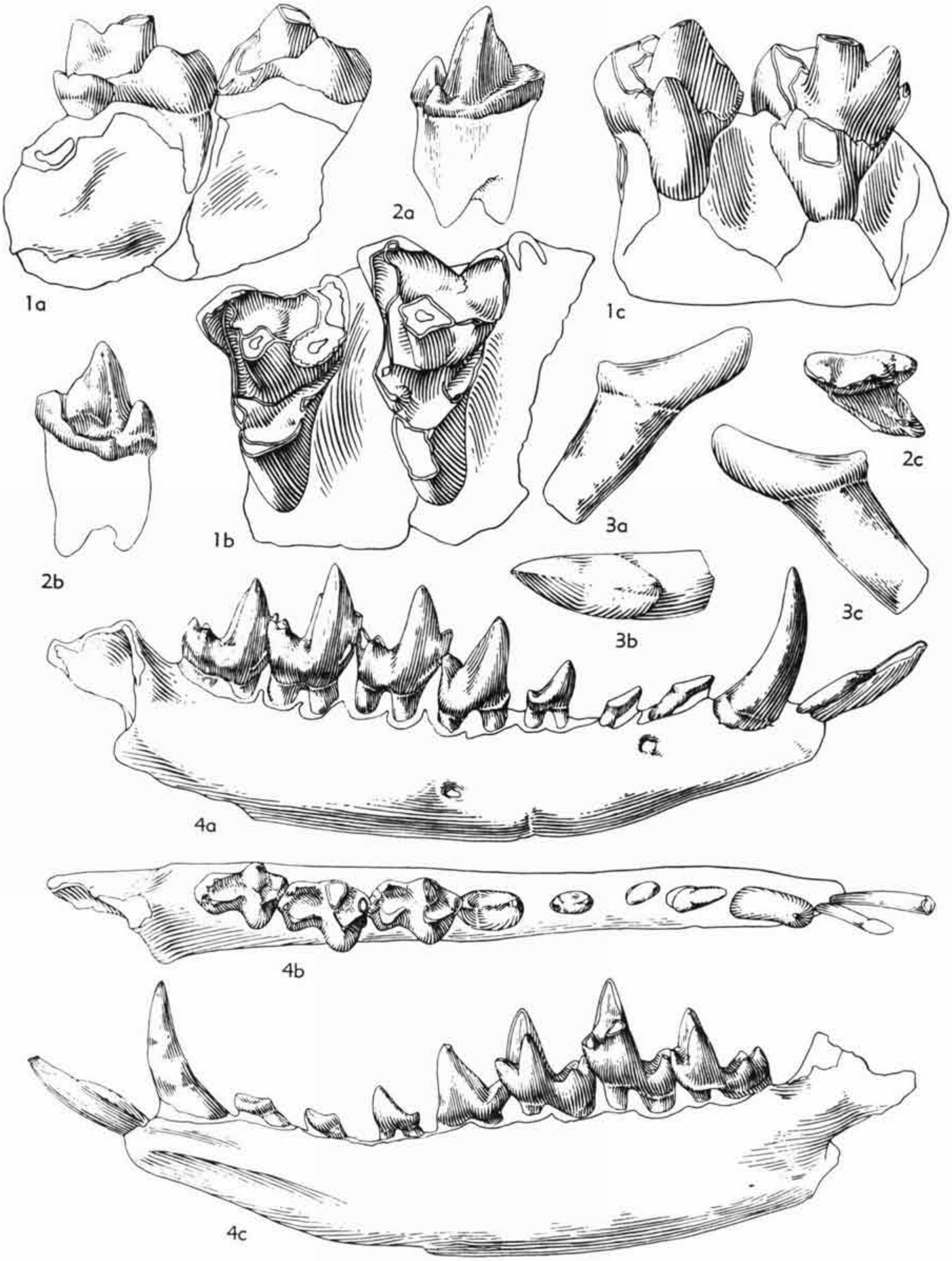

FIG. 34. *Cimolestes propalaeoryctes* LILLEGRAVEN, n. sp. *(continued on facing page)*.

1. Fragment of left maxilla with M^{1-2} (3111); *1a-c,* labial, occlusal, and lingual views, ×11; meas. (mm.), M^1, A-P 2.35 (est.), Ant-W 3.50, Post-W 3.45; M^2, A-P 2.55, Ant-W 4.00, Post-W 3.90.

TABLE 16. *Measurements (in mm.) of Dentition of* Cimolestes propalaeoryctes *Lillegraven, n. sp.*
[See Table 17 for C_1,P_{2-3}.]

Tooth	Length			Width					
	N	O R	$\bar{X}$	N	O R	$\bar{X}$			
P^4	1	2.40	----	1	2.50	----			
					Ant-W			Post-W	
				N	O R	$\bar{X}$	N	O R	$\bar{X}$
M^1	1	2.35	----	1	3.50	----	2	3.00-3.45	3.22
M^2	1	2.55	----	1	4.00	----	1	3.90	----
					Width				
				N	O R	$\bar{X}$			
P_1	2	1.05-1.15	1.10	2	0.40-0.50	0.45			
P_4	1	1.80	----	2	1.00	1.00			
					W-Tri			W-Tal	
				N	O R	$\bar{X}$	N	O R	$\bar{X}$
M_1	2	2.40-2.50	2.45	5	1.25-1.75	1.60	2	1.25-1.40	1.32
M_2	2	2.35-2.50	2.42	2	1.70-1.80	1.75	2	1.20-1.25	1.22
M_3	2	2.30-2.50	2.40	2	1.40-1.75	1.57	2	1.00-1.15	1.07

For abbreviations see end of Introduction.

state have a single main cusp with a posterior continuation as a heel. The anterior border and posterior ridge of the main cusp are sharp. A slight amount of wear occurs on the entire lingual side of the dorsal part of the main cusp. The P_1 is larger than the P_2. All the lower premolars are rather widely separated in the jaw. Those of *Palaeoryctes* are closely packed and the snout length of the animal is relatively shortened. The P_2 of *Palaeoryctes* is minute, anteriorly recumbent, and single-rooted. MATTHEW (1913, p. 309, fig. 2) attempted a reconstruction of the anterior dentition of *P. puercensis.* He noted the probable absence of a P_1 and assumed the root and partial crown anterior to the P_2 to be a canine "with a small heel-cusp." Anterior to the presumed "canine" he noted a root for a "large procumbent or semi-procumbent tooth presumably I_2." I suggest, on the basis of the newly discovered mandible of *Cimolestes propalaeoryctes,* that the partial tooth labelled "canine" by MATTHEW on *Palaeoryctes* is in actuality a P_1, which is larger than the P_2. The large root just anterior to the P_1 in *Palaeoryctes* thus may be homologized with the canine of *C. propalaeoryctes.* The argument is strengthened by the fact that a mental foramen is present

TABLE 17. *Dental Measurements (in mm.) of* Cimolestes propalaeoryctes *Lillegraven, n. sp. (specimen 3756, holotype).*

Tooth	*Depth	*Width	
C_1	1.15	1.00	
	Length	Width	
P_1	1.05	0.50	
P_2	0.90	0.45	
P_3	1.20	0.65	
P_4	1.80	1.00	
		W-Tri	W-Tal
M_1	2.50	1.70	1.25
M_2	2.50	1.90	1.25
M_3	2.50	1.75	1.00

*Measured at point of exit from alveolus at right angles to long axis of tooth.

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2. Right P^4 (2706); *2a-c,* labial, lingual, and occlusal views, ×8; meas. (mm.), A-P 2.40, W 2.50.
3. Right P_1 (4065); *3a-c,* labial, occlusal, and lingual views, ×24; meas. (mm.), A-P 1.15, W 0.40.
4. Holotype, right mandible with two incisors and otherwise complete dentition (3756); *4a-c,* labial, occlusal, and lingual views, ×6.4; meas. in Table 17.

below the P_1 on *C. propalaeoryctes, C. cerberoides, C. incisus, C. magnus,* and below MATTHEWS' "canine" on *Paleoryctes.* Thus it seems that the development of the canine, P_1, and P_2 of *C. propalaeoryctes* and *Palaeoryctes* is comparable.

The two-rooted P_3 and P_4 have trenchant main cusps with posterior accessory cusps. Both have rounded anterior borders on the main cusp and sharp posterior borders. A faint vertical keel is present on the anterior border of the main cusp of the P_4. The posterior roots are stronger than the anterior roots. The apex of the main cusp is lower and more anteriorly set on the P_3 than on the P_4, and the tip of the cusp is slightly posteriorly recurved on the P_4. The posterior accessory cusp of the P_3 is a simple low heel, little more developed than that of the P_1. The accessory cusp on the P_4, on the other hand, is complex and identical in construction with the talonid of the P_4 of *Cimolestes cerberoides* (Fig. 33,*4*). In fact, the homologous tooth in the two species differs mainly in proportions; the P_4 of *C. propalaeoryctes* is anteroposteriorly shortened, taller, yet proportionately reduced overall. Distinct anterior accessory cusps are lacking on the P_3 and P_4 of *C. propalaeoryctes,* but a small protuberance is present on the anterior base of the main cusp of the P_4 formed by short cingula. Wear is seen on the P_{3-4} only on the posterior border of the main cusp and crest of the posterior accessory cusp, but the specimens recovered are essentially unworn. The P_{3-4} of *C. propalaeoryctes* differ from those of *Palaeoryctes* only in that the main cusps are proportionately slightly lower in the former. An anterior accessory cusp on the P_4 is lacking on the specimens figured by MATTHEW (1913, pl. 61), but a small distinct cusp is present on the tooth in KU 7748, an undescribed skull with lower jaws in occlusion.

4) Lower molars. The structure of the lower molars of *Cimolestes propalaeoryctes* closely approximates that of *C. cerberoides* and differs from the latter only in that: 1) the protoconid and metaconid are proportionately higher with the protoconid distinctly exceeding the height of the metaconid; 2) the paraconid is reduced in some specimens, is set proportionately lower, and, in addition, the bodies of the protoconid and metaconid are more closely fused so that the notch separating the two cusps is much higher than the notch separating the paraconid and metaconid; 3) the width and length of the talonid is reduced with respect to the proportion of the trigonid; and 4) the hypoconulid of the M_3 is not as protuberant posteriorly. The wear-patterns are similar to those of *C. cerberoides.*

The lower molars of *Palaeoryctes* differ from those of *Cimolestes propalaeoryctes* principally in that the differences from *C. cerberoides* listed above are carried still further; the paraconid is still lower and more reduced, the protoconid and metaconid are still taller and more united, and the talonid is still narrower and proportionately shorter.

5) Mandible. As in *Palaeoryctes,* the mandible is shallow dorsoventrally with mental foramina ventral to the P_1 and the posterior root of the P_4. The mandibular symphysis extends to a point ventral to the P_3. The part of the mandible bearing the premolars is considerably elongated compared to the foreshortened condition seen in *Palaeoryctes.* Unfortunately, no information is yet available concerning the structure of the angular process of *Cimolestes propalaeoryctes.*

Description of upper dentition.—1) P^4. The only specimen referable to a P^4 (2706, Fig. 34,*2*) has a somewhat crushed protocone and lingual surface of the paracone. The roots are imbedded in a maxillary fragment and show that distortion due to crushing is negligible. The tooth is smaller but similar in construction with P^4's of *Cimolestes cerberoides* (Fig. 31,*1*). A low anterior accessory cusp is followed by the paracone, which has a rib on its anterior border and a bump representing a metacone on its posterior border. A strong posterior accessory blade extends at an angle posterolabially from termination of the posterior border of the paracone. The partly crushed paracone apparently was not inflated on its lingual side. The protocone lacks conules and lingual cingula, has a ridge on the anterior and posterior edges of the occlusal surface, and has a median ridge extending from the apex of the protocone labial toward the base of the paracone. The apex of the protocone appears to have been shifted slightly more anteriorly in proportion to that of *C. cerberoides.* The entire protocone is also somewhat narrower anteroposteriorly. Although the specimen is nearly unworn, the little wear exhibited is identical with that seen in *C. cerberoides.*

The P^4 of *Palaeoryctes* differs from *Cimolestes propalaeoryctes* in that: 1) the anterior accessory cusp is smaller; 2) the paracone is transversely thicker; 3) the paracone lacks an anterior rib and all trace of a metacone; 4) the protocone lacks the median ridge (common to many deltatheridians) extending from its apex toward the paracone; and 5) the protocone is more compressed anteroposteriorly.

2) Upper molars. The two teeth illustrated in Figure 34,*1* were somewhat crushed during the process of fossilization, but the distortion was not severe. The structure of the upper molars is basically similar to that found in *Cimolestes cerberoides,* but the molars are more specialized in several respects. The following description is based only upon the structure of the M^{1-2}; the M^3 is unknown. The protocone and the entire tooth is compressed anteroposteriorly. The protocone is somewhat recumbent anteriorly. The lingually placed conules are strong and the crests of their internal wings are rounded. Lingual cingula are absent, but the interdental embrasures of the maxilla are the deepest of any North American Cretaceous mammal yet described. The paracone and metacone are tall and fused throughout most of their height, but their apices are distinctly separated. The

labial surfaces of the paracone and metacone each bear a vertical rib. The stylar shelf is broad and strongly bilobate. A well-developed anterior paracrista extends labially from the base of the anterior border of the paracone to the edge of the stylar shelf. A distinct stylar cusp is variably located on, or just posterior to, the labial termination of the anterior paracrista. The anterior and posterior lobes of the stylar shelf are stronger than those of *C. cerberoides*, especially on the M^1. The development of the posterior metacrista is comparable to that of *C. cerberoides*. Shearing wear is heavy on the stylar shelf anterior to the anterior paracrista and along the length of the anterior crista of the protoconule. It is lighter, on the other hand, on the anterior surface of the stylar cusp, the apices and crests of the paracone and metacone, the posterior edge of the posterior metacrista, and the occlusal surface of the protocone. The most important part of the bite was apparently a shear between the posterior sides of the crests of the protoconid-metaconid of the lower molars and the anterior edges of the upper molars. Wear was more evenly distributed on the molars of more generalized animals such as *C. cerberoides*.

As is the case with the lower molars, the upper molars of *Palaeoryctes* continue the specializations seen in *Cimolestes propalaeoryctes* even further; the teeth are still narrower anteroposteriorly, the paracone and metacone are almost completely united, and the cusps are still higher.

Affinities.—I think there is little doubt, considering the above comparative dental description, that *Cimolestes propalaeoryctes* is an ideal structural ancestor for the North American Paleocene genus *Palaeoryctes* (*see* Fig. 40). *C. propalaeoryctes* shows close affinities with *C. cerberoides* and *C. incisus*, yet has every character expected in the early stages of a specialization toward the type of zalambdodonty seen in *Palaeoryctes*. I am in full agreement with VAN VALEN's (1966, p. 109, fig. 17) suggested relationship between *Cimolestes* and *Palaeoryctes* and I further suggest that the evolution of the specializations distinguishing *Palaeoryctes* occurred in North America.

The intermediacy of specialization observed in *Cimolestes propalaeoryctes* brings out an interesting nomenclatorial problem. All but the most ardent "splitters" would place the new species in the genus *Cimolestes* following an analysis of molar construction. The development of the premolars, however, is essentially that seen in *Palaeoryctes*. It would be possible to erect a new genus with a diagnosis based upon the difference in the evolutionary rate of change between the development of the molar series and the premolar series. Such a move, however, would be without scientific or practical value. Although the binominal system of nomenclature certainly has disadvantages (MICHENER, 1963), it also has distinct advantages, as in the case of *Cimolestes propalaeoryctes*. Such a phylogenetically based name emphasizes a common origin with other species of *Cimolestes*, yet points out its probable descendant. The name is thus both phylogenetically sound and useful to a nonspecialist.

CIMOLESTES MAGNUS Clemens & Russell, 1965

Figures 35,*1-6*; 36,*1-3*; 37,*1-3*

Type.—UA 622, fragmentary left mandible with P_4M_{1-3} (CLEMENS & RUSSELL, 1965, p. 34, fig. 5).

Type locality.—KUA-1, upper part of Edmonton Formation, Alberta.

Referred specimens.—Fragmentary maxillae with DP^{3-4} (4085), C^1 (3795), $P^{3-4}M^{1-3}$ (3793), $P^{3-4}M^1$ (2712), P^4M^1 (3689); DP^4, 3298; P^4's, 2997, 3199, 3370, 3781; M^1, 661; M^2's, 2464, 2905, 3267; M^3's, 3374, 3732, 3736; upper molar fragments, 2893, 2198, 3193, 4019; C_1, 2948, 3676, 3678; fragmentary mandibles with P_1 and $_{3-4}M_{1-3}$ (3754), alveoli or roots of $P_{1-4}M_{1-3}$ and talonid of M_2 (3653), $P_{3-4}M_{1-3}$ (3791), P_4M_{1-3} (3791), P_4M_{1-3} (3661), M_{1-2} (3692); P_1's, 2396, 2488, 2860, 3152; P_3, 625; P_4's, 624, 2446, 3661; M_1's, 658, 2201, 2332, 3247, 3274; M_2's, 623, 2577, 3777; M_3's, 2208, 2857, 3119, 3760; lower molar fragments, 2282, 2292, 2486, 2726, 2775, 2811, 2971, 2977, 3109, 3779.

Localities.—KUA-1, 18, 23; UA-2.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming (unpublished).

Revised diagnosis.—DP^{3-4} each with three strong roots, broad stylar shelf, strong paracone and metacone, small protocone, weak conules, and no lingual cingula; C^1 strongly developed; P^3 incompletely known, but three-rooted and probably with weak, posteriorly set protocone; paracone strong with no metacone; P^4 variable, but with strong protocone lacking lingual cingula; conules and central ridge of protocone present or absent; paracone strong, rounded anteriorly, keeled posteriorly (some with an incipient metacone); posterior accessory cusp either rounded or weakly bladelike; upper molars with lingual cingula strong, weak, or lacking; stylar shelf broad and moderately bilobate; posterior metacrista strong, and entire molar series specialized for strong shearing function; "accessory conules" frequently developed; crests of most cusps separated by deep notches (upper and lower molars); interdental embrasures deep; lower canine strong; P_{1-3-4} (P_2 unknown) two-rooted, robust, closely set in jaw, and with anterior surface of main cusp rounded; posterior surface of main cusp rounded in P_1, but sharply keeled in P_{3-4}; anterior accessory cusp present only in P_4 (weak); posterior accessory cusp progressively strengthened from P_1 through P_4; lower molars robust with tall trigonid; lengths of trigonid and talonid subequal; accessory cuspule present on crest linking entoconid to metaconid; mandible variable in depth; angular process inflected.

Introductory note.—Until now, *Cimolestes magnus* has been known only from its lower dentition (CLEMENS & RUSSELL, 1965). A much better dental series of both upper and lower teeth is now available from the upper Edmonton Formation. The variability of structure and size exhibited by the specimens is high, and I suspect that the taxon is a composite consisting of two species. Inter-

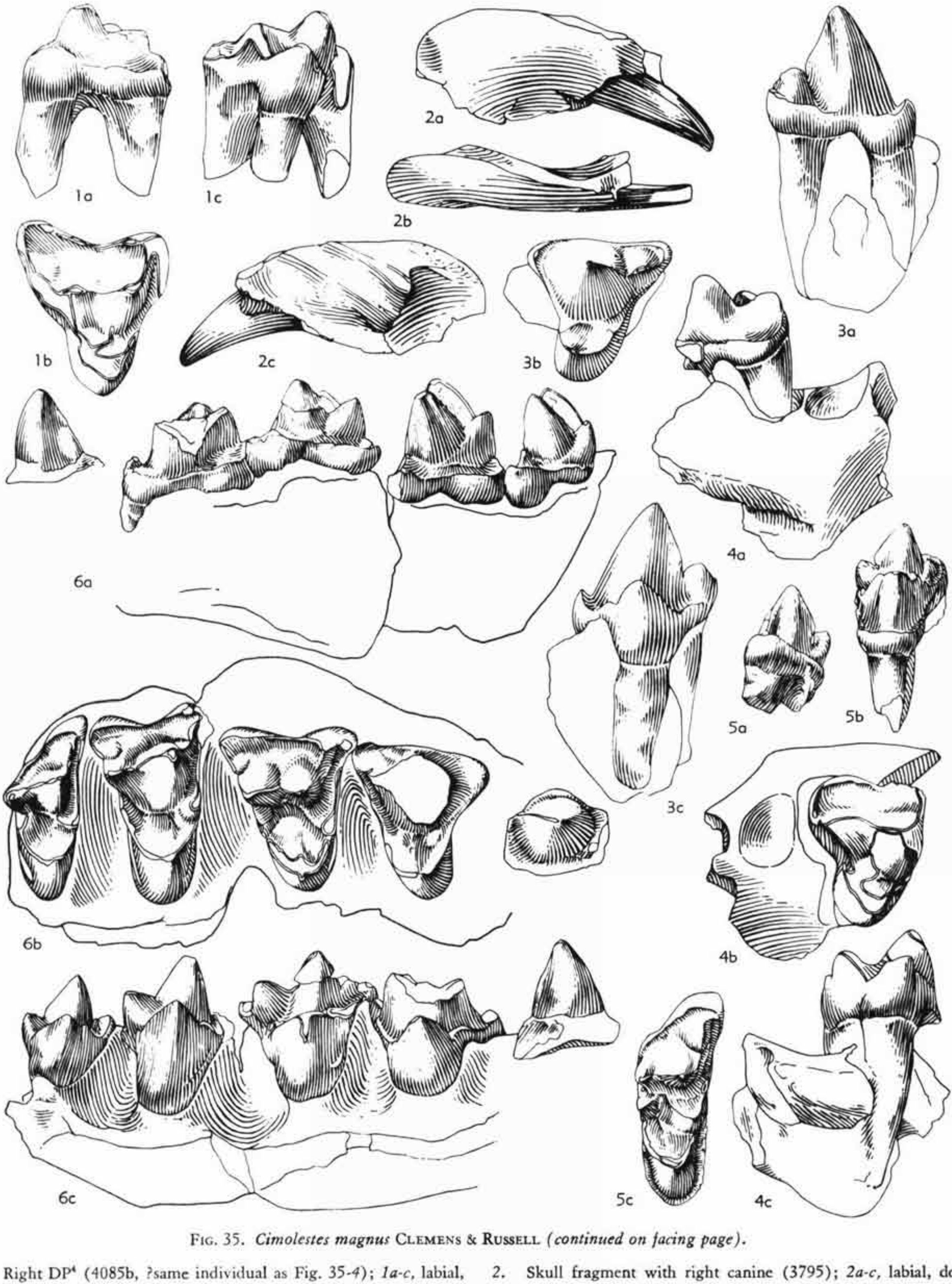

FIG. 35. *Cimolestes magnus* CLEMENS & RUSSELL *(continued on facing page)*.

1. Right DP^4 (4085b, ?same individual as Fig. 35-*4*); *1a-c,* labial, occlusal, and lingual views, ×6.4; meas. (mm.), A-P 3.95, Ant-W 4.30, Post-W 4.60.

2. Skull fragment with right canine (3795); *2a-c,* labial, dorsal, and lingual views, ×1.6; meas. taken at point of exit from alveolus at right angles to long axis to tooth; depth 4.50, width 2.85.

TABLE 18. *Measurements (in mm.) of Upper Dentition of* Cimolestes magnus *Clemens & Russell.*

Tooth	Length			Width					
	N	O R	$\bar{X}$	N	O R	$\bar{X}$			
P^3	1	4.00	----	1	3.15	----			
P^4	7	4.80-6.40	5.65	6	5.40-5.90	5.70			
				Ant-W			Post-W		
				N	O R	$\bar{X}$	N	O R	$\bar{X}$
DP^3	--	----	----	1	3.30 (est.)	----	1	3.25	----
DP^4	2	3.85-3.95	3.90	1	4.30	----	1	4.60	----
M^1	4	4.70-5.75	5.06	3	6.10-7.00	6.48	3	6.50-7.50	6.88
M^2	2	4.30-4.70	4.50	2	6.80-7.00	6.90	4	7.10-7.50	7.31
M^3	4	3.30-4.00	3.62	4	6.10-7.50	6.80	4	4.40-6.40	5.01

For abbreviations see end of Introduction.

grades, however, are noted between the extremes of most characters, and the sample is too small to show any statistical significance in observed bimodality of measurements. Thus accurate diagnoses for two species cannot be made, and all the specimens are described as representative of a single species until a better sample is obtained.

Description of upper dentition.—The summarized measurements of the upper dentition of *Cimolestes magnus* can be found in Table 18.

1) DP^{3-4}. Sediment-filled alveoli for a three-rooted tooth are located posterior to the intact tooth of specimen 4085a (Fig. 35,*4*). The second tooth apparently fell out of the maxillary fragment before burial. Specimen 4085b (Fig. 35,*1*) was retrieved during the washing process from the same quarry-bag as 4085a and is also a representative of the right side of the dentition. The roots of 4085b match the configuration of the empty alveoli of 4085a. The maxillary fragment is rounded posterior to these alveoli and they definitely represent the termination of the tooth row. Neither tooth is referable to any known permanent molar morphology, and both are interpreted as being deciduous. It seems likely that the two teeth were derived from the same individual and probably represent the DP^3 and DP^4. Their large size and obvious carnassial-like shearing function make their reference to *Cimolestes magnus* the most probable.

The DP^3 (Fig. 35,*4*) is three-rooted, has a broad, labially sloping stylar shelf, a paracone, metacone, and protocone. The anterior third of the stylar shelf is partly broken and partly worn away. The shelf is distinctly bilobate. The labial margin of the posterior lobe of the shelf has a weakly raised border terminated by a rounded notch at the posterior base of the metacone. The paracone is the highest cusp of the tooth, has a flat labial and rounded lingual surface, and a sharp posterior ridge. The lingual surface of the metacone is largely worn away, but its labial surface is flat. The protocone is small considering the probable unworn length of the labial side of the tooth, is rounded lingually, and lacks lingual cingula. Only suggestions of both conules are present. The tooth is heavily worn. The anterior end of the stylar shelf and paracone are so severely worn that the pulp cavity of the anterolabial root is broadly opened. The root itself is gone, probably due to postdepositional breakage. Although the posterior ridge and posterolingual base of the paracone are only slightly worn, the apex and anterolingual surface of the metacone is obliterated by wear. The protocone is lightly worn, and then only on its conules and posterior half of the occlusal surface. The remainder of the stylar shelf and entire posterior border of the tooth are unworn.

The DP^4 (Fig. 35,*1*) is considerably larger than the DP^3, but the structure is basically the same, and the size increase is mainly due to an exaggerated development of the stylar shelf. The protocone, paracone, and metacone are nearly the same size in the DP^3 and DP^4. The stylar shelf is lobed as in the DP^3, but the posterior lobe is strongly produced posterolabially. A raised rim borders the entire shelf. The wear-pattern differs significantly from that of the DP^3. A strong wear-surface is

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3. Left P^4 (2997); *3a-c*, labial, occlusal, and lingual views, ×4.8; meas. (mm.), A-P 5.30, W 5.40.

4. Fragment of right maxilla with worn DP^3 and alveoli for DP^4 (4085a, ?same individual as Fig. 35,*1*); *4a-c*, labial, occlusal, and lingual views, ×8; meas. (mm.), A-P unmeasurable, Ant-W 3.30 (est.), Post-W 3.25.

5. Right M^3 (3736); *5a-c*, labial, lingual, and occlusal views, ×4.8; meas. (mm.), A-P 3.55, Ant-W 7.50, Post-W 6.40.

6. Fragment of right maxilla with paracone of P^3 and P^4M^{1-3} (3793); *6a-c*, labial, occlusal, and lingual views, ×4.8; (meas. in Table 19A).

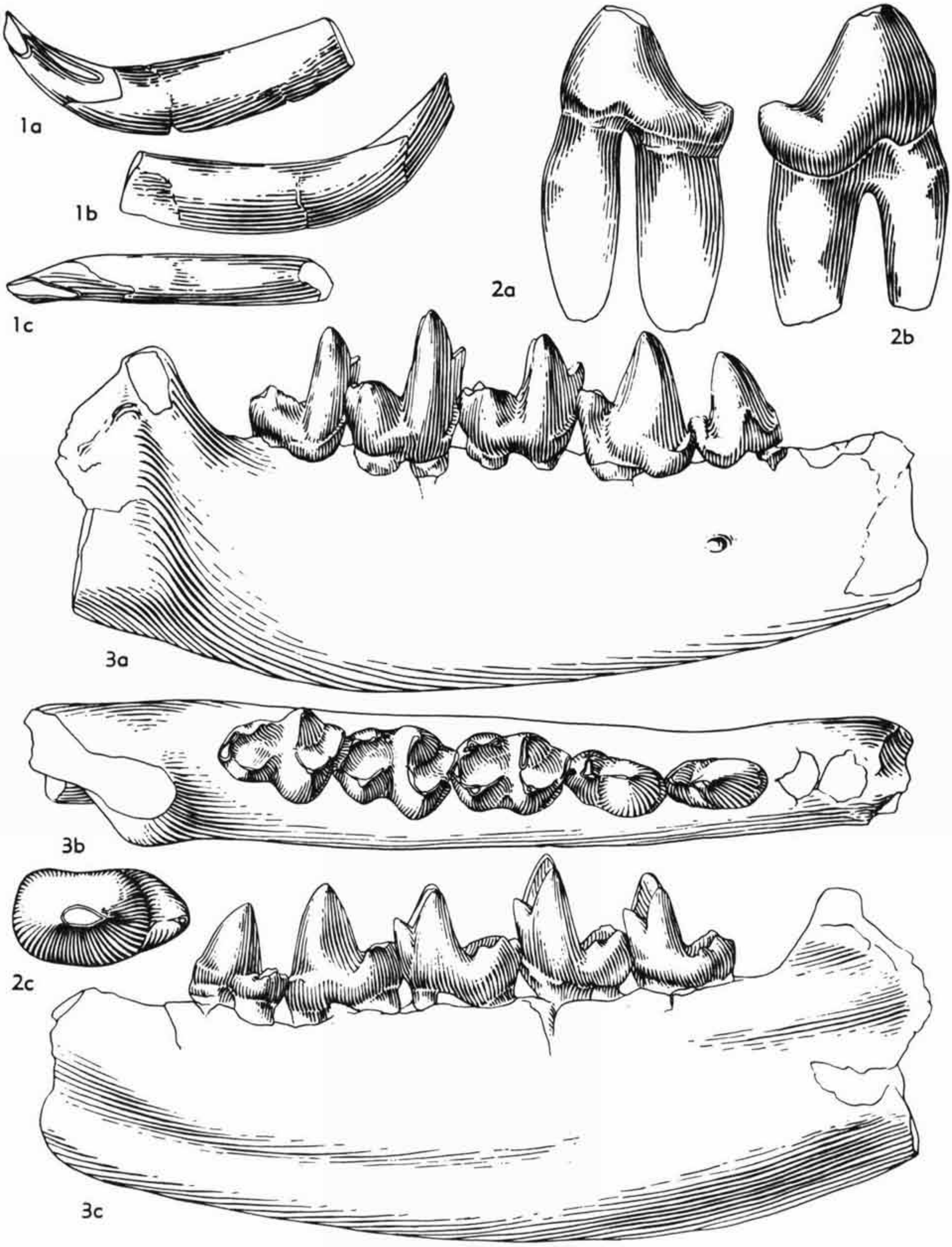

Fig. 36. *Cimolestes magnus* Clemens & Russell *(continued on facing page).*

seen along the posterior edge of the stylar shelf and on the posterior side of the metacone, probably due to a shearing function with the paraconid and metaconid of the permanent M_1. As in the DP^3, strong wear occurred on the anterior surface of the paraconid, stylar shelf, and the top part of the anterolabial root. Wear is also present on the labial surface of the metacone and posterolingual surface of the paracone, but it is less severe than that of the DP^3. The protocone is worn along its anterior and posterior occlusal borders. A weak ridge, partially worn, extends from the apex of the protocone to the lingual base of the paracone. Light discontinuous wear is observable along the entire crest of the border of the stylar shelf.

The roots of the DP^{3-4} are developed equally as well as those of the adult. One might expect weaker roots in deciduous teeth, but the wear patterns show that even as a "pup," the animal had a strongly shearing masticatory function and was probably carnivorous. Strong support for the teeth was thus a necessity.

The DP^4 of *Cimolestes magnus* is smaller but morphologically similar to the specimen labelled "?DP^4, cf. *Prolimnocyon atavus*" by VAN VALEN (1966, pl. 7, fig. 10).

2) Canine. The skull fragment and canine illustrated in Figure 35,*2* is referred to *Cimolestes magnus* principally on the basis of size. The tooth is more robust, but similar in construction to upper canines referred to *C. cerberoides* (e.g., Fig. 31,*3*). Dentine is exposed along the entire anterior surface of the tooth, apparently due to wear with the tip and posterior surface of the lower canine. However, the apparent wear extends well up the surface of the tooth into the alveolus, an impossible situation unless the canine had been jammed up into its alveolus before, during, or after burial. Such a possibility seems likely since one would expect the distal tip of the tooth to point somewhat more ventrally.

3) P^3. A complete P^3 of *Cimolestes magnus* has yet to be found. The subcrown base and the apex of the tooth are, however, represented by specimens 2712 and 3793 (Table 19,*A*) (Fig. 35,*6*) respectively. Specimen 2712 shows the P^3 to be three-rooted, and probably with a weak anterior accessory cusp and a small, posteriorly set protocone. In occlusal view, a line drawn through the centers of the anterolabial and posterolabial roots intersects at an angle of about 30 degrees with an equivalent line drawn through the P^4. The base of the tooth measures 4.00 in length and 3.15 in width. Specimen 3793 shows a tall conical paracone with no hint of a metacone. The paracone was probably subequal in height with that of the P^4. The anterior surface of the paracone is round, and the posterior border is sharply keeled with wear along the crest of the keel.

TABLE 19. *Dental Measurements (in mm.) of* Cimolestes magnus *Clemens & Russell—A, Specimen 3793.—B, Specimen 3791.—C, Specimen 3754.*

A Tooth	Length	Width	
P^4	4.80	5.70	
		Ant-W	Post-W
M^1	4.80	6.10	6.50
M^2	4.30	6.80	7.10
M^3	3.65	6.10	4.40

B Tooth	Length	Width	
P_3	4.20	2.25	
P_4	5.30	2.80	
		W-Tri	W-Tal
M_1	5.25	3.50	3.30
M_2	4.80	4.00	3.10
M_3	4.30	3.40	2.45

C Tooth	Length	Width	
P_1	2.85	1.70	
P_3	4.30 (est.)	2.40	
P_4	4.90	2.85	
		W-Tri	W-Tal
M_1	5.10 (est.)	3.40	3.20
M_2	5.50 (est.)	4.40	3.10
M_3	5.00	3.70	2.40

For abbreviations see end of Introduction.

4) P^4. The P^4 of *Cimolestes magnus* (Fig. 35,*3*,*6*, 37,*2*) has a small anterior accessory cusp, tall paracone, a variably developed posterior accessory cusp, and a strongly produced protocone. Lingual cingula have not been observed. The protocone is slightly recumbent posteriorly. The occlusal surface of the protocone shows considerable

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1. Left lower canine (3676); *1a-c*, labial, lingual, and dorsal views, ×2; (meas. taken at beginning of taper at right angles to long axis of tooth; depth 6.25, width 3.35.

2. Left P_1 (3152); *2a-c*, labial, lingual, and occlusal views, ×10; meas. (mm.), A-P 2.80, W 1.60.

3. Right mandible with alveoli of P_2, and $P_{3-4}M_{1-3}$ (3791); *3a-c*, labial, occlusal, and lingual views, ×6; (meas. in Table 19*B*).

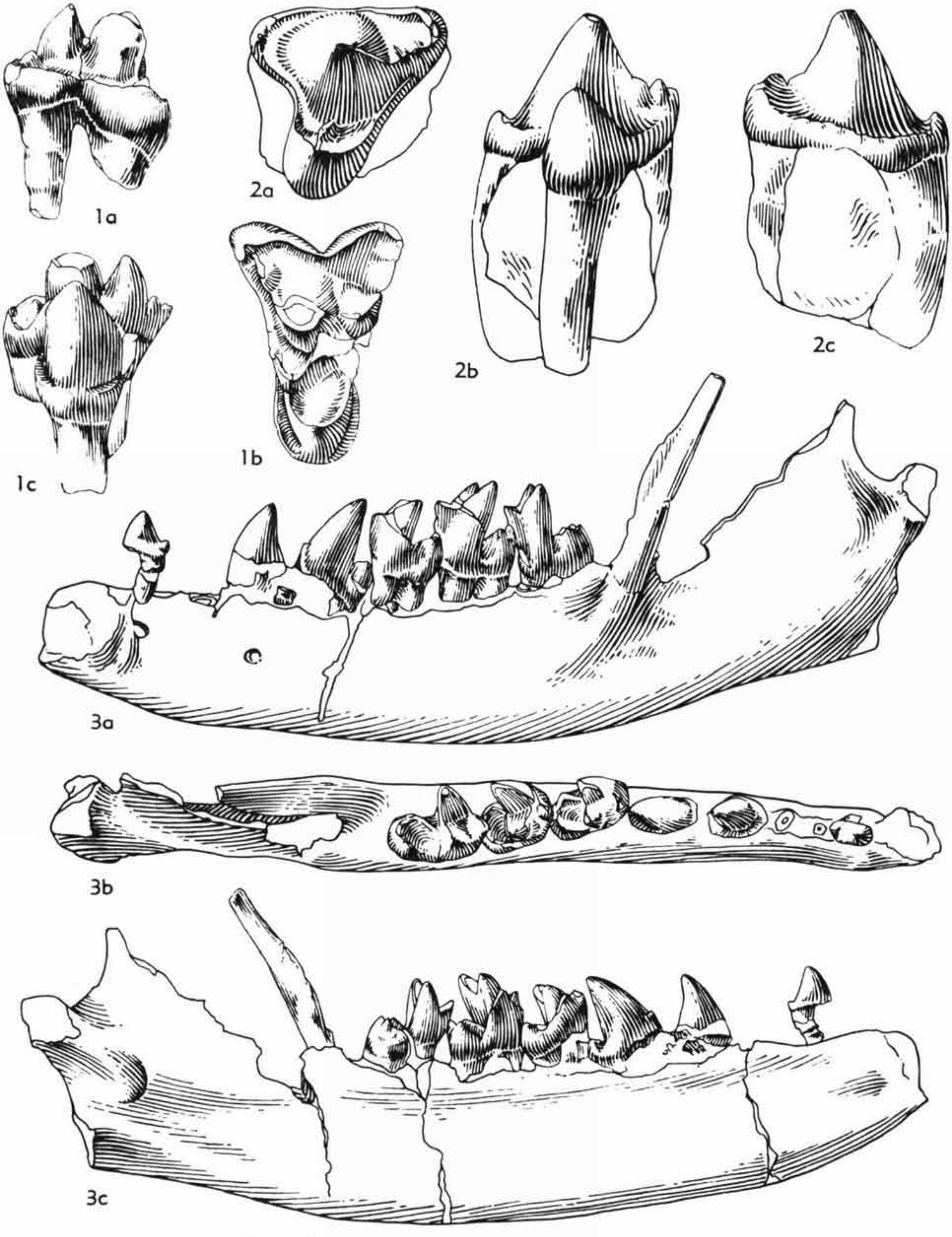

FIG. 37. *Cimolestes magnus* CLEMENS & RUSSELL *(continued on facing page).*

variability, the extremes of which are illustrated by specimens 2997 (Fig. 35,*3*) and 3781 (Fig. 37,*2*). Both a protoconule and a metaconule are present on 2997, and only a weakly rounded ridge extends from the apex of the protocone to the lingual base of the paracone. Specimen 3781, on the other hand, lacks all evidence of conules and a strongly developed central ridge is present. All combinations of presence or absence and degree of development of the central ridge, protoconule, and metaconule are observed. The anterior and posterior edges of the protocone are bordered by raised ridges. The anterior ridge runs to the apex of the anterior accessory cusp. The posterior ridge terminates on the lingual base of the posterior accessory cusp. A usually continuous, variably undulating cingulum runs posterially along the labial side of the tooth from the apex of the anterior accessory cusp to the posterolabial corner of the tooth. Sometimes, however, the labial cingulum is interrupted at the base of the widest part of the paracone (e.g., 2997, Fig. 35,*3*).

The anterior border of the paracone is rounded and the posterior border keeled. Although a distinct metacone is not present, several specimens (e.g., 3689) show a definite expansion on the lower half of the posterior border of the paracone. The posterior accessory cusp is sometimes strongly inflated (e.g., Fig. 35,*3*), sometimes only a weak blade (e.g., Fig. 35,*6*), and all intergrades exist. A deep notch separates the termination of the posterior border of the paracone from the posterior accessory cusp. Wear is most pronounced on the lingual side of the anterior accessory cusp, the apex and posterior border of the paracone, the posterolingual border of the posterior accessory cusp, and the apex of the protocone. Shearing wear along the posterior ridge of the protocone is less pronounced than that exhibited in *Cimolestes cerberoides.*

The above variations in morphology are independently developed on the P^4 itself, and specific variations cannot yet be correlated with peculiarities of molar morphology.

5) Upper molars. The upper molars of *Cimolestes magnus* (Fig. 35,*6*) are characterized by a broad stylar shelf and a morphology specialized for a strongly shearing function. The paracone is much higher than the metacone, and the disparity in height increases markedly from M^1 through M^3. The apices of the two cusps are well separated, and a notch between them progressively deepens from M^1 through M^3. Their anterior borders on M$^{1-3}$ and their posterior borders on M$^{1-2}$ are keeled. Lingual cingula may be absent (e.g., 3374), weak (e.g., 3793, Fig. 35,*6*), or strong (e.g., 3267, Fig. 37,*1*; 3736, Fig. 35,*5*). As shown by the last two specimens, the cingula may be restricted to the anterior and posterior sides of the teeth or they may be connected across the lingual base of the protocone. The interdental embrasures are deep. The conules are strong and the crests of their internal wings are usually sharp but are sometimes rounded. Frequently (e.g., 3736, Fig. 35,*5*) accessory conule-like protuberances are located labial to the true conules on the external cristae of the conules. They were probably functionally useful in increasing the length of the shearing surface, as in pinking shears. A low ridge usually extends from the apex of the protocone to the labial base of the paracone. The stylar shelf is bilobate in the M$^{1-2}$ but is weak or absent opposite the metacone of the M^3. The entire labial border has a slightly raised rim. As in *Cimolestes cerberoides,* the anterior lobe is somewhat reduced on the M^1. The posterior metacrista is absent on the M^3 but strongly bladelike on the M$^{1-2}$. It is separated by a deep notch from the termination of the posterior keel of the metacone. The anterior paracrista is strong and is separated from the termination of the anterior ridge of the paracone by a notch.

The wear surfaces reflect a strong molar specialization for shearing, similar to that seen among the hyaenodontids and oxyaenids. The heaviest wear occurs along the length of the anterior crista of the protoconule and anterior edge of the protocone. Equivalent but lesser wear is present along the posterior edge of the protocone and the posterior crista of the metaconule. Obvious shearing wear is present on the posterior surface of the metacone and posterior metacrista, but wear is not profound on the anterior ridge of the metacone and posterior ridge of the paracone. Wear is usually minor on the anterior ridge of the paracone and anterior paracrista. Minor wear is sometimes present on the transverse central ridge of the protocone.

Description of lower dentition.—The summarized measurements for the lower dentition of *Cimolestes magnus* are recorded in Tables 19 and 20.

1) Canine. The lower canine (e.g., 3676, Fig. 36,*1*) of *Cimolestes magnus* is similar in construction to that of *C. cerberoides* (Fig. 33,*5*), but much larger and more robust. The root is stout and laterally compressed. After emergence from the alveolus, the tooth bends laterally, then near the tip bends back medially. The enamel extends proximally from the tip much farther on the labial side than on the lingual side. A deeply worn groove extends from the superior surface of the tip down the labial side of the tooth, presumably caused by abrasion with the anterior border of the upper canine. Another strong surface of wear is present on the anterolabial side

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1. Left M^2 (3267); *1a-c,* labial, occlusal, and lingual views, ×6; meas. (mm.), A-P 4.70, Ant-W 7.00, Post-W 7.35.

2. Left P^4 (3781); *2a-c,* occlusal, lingual, and labial views, ×6; meas. (mm.), A-P 5.70, W 5.70.

3. Left mandible with P$_1$, alveoli of P$_2$, and P$_{3-4}$ M$_{1-3}$, teeth somewhat crushed during fossilization (3754); *3a-c,* labial, occlusal, and lingual views, ×2.67; (meas. in Table 19*C*).

of the tip, probably caused by action against the posterior edge of the terminal upper incisor.

2) Lower premolars. The lower premolars of *Cimolestes magnus* are of a more massive construction than those of *C. cerberoides,* and are more closely appressed in the mandible. The two-rooted P_1 (Figs. 36,*2*, 37,*3*) has a robust, rounded, rather low main cusp with a small posterior accessory cusp and no anterior accessory cusp. Only suggestions of anterior and posterior keels are present on the main cusp. Wear occurs principally on the apex and upper part of the posterior ridge of the main cusp and on the apex and labial side of the posterior accessory cusp. Small but distinct oval wear facets are present on the labial base on the main cusp. Minor wear is also seen on the lower part of the anterior border of the main cusp.

Tooth P_2 has not yet been recovered, but alveoli (Figs. 36,*3*, 37,*3*) show that it was two-rooted and probably intermediate in size between the P_1 and P_3.

The P_3 and P_4 are morphologically similar to each other (Fig. 36,*3*) and to the homologous teeth of *Cimolestes cerberoides* (Fig. 33,*4*). The teeth are robust with a strong main cusp and a posterior accessory cusp. A weak anterior accessory cusp is present on the P_4 of the type, but usually it is only the highest point of the sloping anterior cingulum. The cingulum is short on the lingual side of the main cusp but on the opposite side extends to the anterolabial base of the tooth. Equivalent but weaker cingula are present on the P_3. As in the P_1, the anterior surface of the main cusp of the P_{3-4} is rounded with only a hint of a vertical ridge. The posterior border of the P_{3-4}, on the other hand, is strongly keeled. A distinct notch always separates the termination of the posterior ridge of the main cusp of the P_{3-4} from the main crest of the posterior accessory cusp. A ridge on the P_{3-4} usually extends anterolingually from the posterior end of the main crest of the posterior accessory cusp to the base of the main cusp, decreasing in height throughout its extent. An extra cuspule may be present behind the termination of the main crest of the posterior accessory cusp (e.g., 3791, Table 19,*B*, Fig. 36,*3*). Wear is pronounced only on the posterior crest of the main cusp and on the crests of the posterior accessory cusp.

3) Lower molars. The lower molars of *Cimolestes magnus* (e.g., 3791, Table 19,*B*, Fig. 36,*3*) are robustly developed with a tall trigonid, the protoconid of which is significantly the highest cusp. The paraconid is lingually placed and well separated from the metaconid. The separation is greatest in the M_1. Notches, much deeper than those seen in *C. cerberoides,* separate the crests of the paraconid and metaconid from those of the protoconid. The relative anteroposterior lengths of the trigonid and talonid are subequal. An accessory cuspule is usually present on the crest linking the entoconid with the posterolingual base of the metaconid. The hypoconulid of the M_3 is not strongly produced posteriorly. A labially sloping anterior cingulum is always present.

As emphasized in the description of the upper molars, the molar series of *Cimolestes magnus* was effectively specialized for a principally shearing function. The wear-patterns are well illustrated in Figures 36,*3*, but it should be pointed out that wear on the apices of the cusps was probably minimal until rather late in the life of the animal. Strikingly developed abrasions due to shear are seen on the anterior surface of the protoconid and paraconid, entire posterior surface of the protoconid and metaconid, and labial side of the talonid ventral to the crista obliqua. This is true even when the apices of the cusps are essentially unworn.

4) Mandible. As with *Cimolestes cerberoides,* a great variability is observed in the depth of the mandibles of *C. magnus.* It is as yet unknown whether this represents simple individual variation, continued growth of the bone throughout life, or perhaps a species-restricted character within a composite taxon. The mandibular symphysis extends to a point ventral to the anterior root of the P_4 and, considering the weak development of rugosities, was probably flexible during life as in some other carnivorous mammals (Scapino, 1965). Mental foramina are located ventral to the posterior root of the P_2 and usually ventral to the posterior root of the P_3 or the anterior root of the P_4. As in *C. cerberoides,* the angular process is distinctly inflected (e.g., 3754, Table 19,*C*, Fig. 37,*3* and 3653), but less so than most marsupials. The mandibular foramen is proportionately somewhat stronger than that of *C. cerberoides.* It is posteriorly set, just dorsal to the beginning of the inflection of the angular process. The articular process is considerably damaged on specimen 3754, but its upper surface is at a level slightly more ventral than the apices of the trigonids of the lower molars (Table 20).

Affinities.—Following the original description of *Cimolestes magnus,* Clemens & Russell (1965, p. 36) suggested that upon collection of further material, a comparison with members of the Pantolestidae should be considered. Now that a nearly complete dental series of *C. magnus* is available for study, pantolestid affinities seem remote. As suggested following the description of *Gypsonictops,* the pantolestids show structural similarities with that genus.

Comparison of the descriptions of *Cimolestes magnus* with those of *C. cerberoides* and *C. incisus,* on a point-by-point basis, shows a strikingly similar morphology common to them all. *C. magnus* is much larger than the other two species. Size differences often loom important in the eyes of taxonomists, especially to those with a tendency toward "splitting." Several colleagues have suggested to me that *C. magnus* should be referred to a new genus. *C. magnus,* with its comparatively large size and minor differences of dental morphology, could quite

TABLE 20. *Measurements (in mm.) of Lower Dentition of* Cimolestes magnus *Clemens & Russell.*

Tooth	Length			Width					
	N	OR	$\overline{X}$	N	OR	$\overline{X}$			
P_1	3	2.80-3.00	2.88	5	1.60-2.05	1.77			
P_3	3	4.20-4.30	4.25	3	2.25-2.40	2.33			
P_4	3	4.90-5.70	5.30	6	2.80-3.20	2.96			
				W-Tri			W-Tal		
				N	OR	$\overline{X}$	N	OR	$\overline{X}$
M_1	5	4.60-5.45	5.09	8	3.10-3.55	3.34	7	2.70-3.60	3.19
M_2	7	4.75-5.65	5.20	7	3.80-4.40	4.09	8	2.80-3.45	3.16
M_3	5	4.05-5.30	4.73	4	3.30-3.70	3.47	7	2.35-2.80	2.49

For abbreviations see end of Introduction.

simply be diagnosed as a distinct genus. However, the basic similarities with the other species of *Cimolestes* are incontrovertible. The use of a common generic name serves a definite function in pointing out a phylogenetic unity, especially to students who are nonspecialists. The specific name indicates satisfactorily that significant differences between species exist. All species named from the fossil record are morphospecies and no information exists as to their biological reality. Thus there is no scientific reason or necessity for the establishment of a complex system of nomenclature based upon a series of monotypic or near-monotypic genera. I therefore support the maintenance of *C. magnus* within the genus *Cimolestes.*

VAN VALEN (1966, p. 109, fig. 17) suggested a common ancestry of the archaic carnivorous families Hyaenodontidae and Oxyaenidae from a stock basal to *Cimolestes.* I thoroughly agree with this interpretation. He also suggested that some fragmentary teeth from the earliest Paleocene, tentatively referred to as "genus B," may have been a link in the lineage. My knowledge of the nature of "genus B" is inadequate for comment, but I suggest that *C. magnus,* though generalized, would make an ideal structural ancestor for the hyaenodontids and oxyaenids (*see* Fig. 40). The animal was obviously specialized for a carnivorous way of life, but the carnassial function was distributed evenly throughout the molar series rather than being concentrated at the level of the M^1M_2 as in the oxyaenids or at the M^2M_3 as in the hyaenodontids. I believe a distribution of carnassial function as seen in *C. magnus* would be expected in a primitive stock common to the hyaenodontids and oxyaenids.

Genus BATODON Marsh, 1892

BATODON TENUIS Marsh, 1892

Figures 38,*1*; 39,*1-4*

Type.—USNM 2139, fragmentary right mandible with P_{2-4} (MARSH, 1892, pl. 11, fig. 5).

Referred specimens.—P^4, 3147 (destroyed); fragmentary maxilla with partial M^1 and complete M^2, 4081; M^2, 3802; fragmentary mandibles with P_4 (3714), M_{2-3} (3721), M_2 (3688); ?P_2, 4083; P_4, 4047; M_2, 3688.

Localities.—KUA-1, 3.

Distribution.—Upper part of Edmonton Formation, Alberta; type Lance Formation, Wyoming.

Comments.—The reference of the small, rare specimens from the upper Edmonton Formation ascribed below to *Batodon tenuis* is questionable. The original description given by MARSH (1892, p. 258) and the drawings of the type are insufficient for purposes of identification. I have not seen the holotype. CLEMENS is currently describing a mandible (AMNH 58777) referable to the species from the type Lance Formation that has a complete P_2 and M_1 and fragmentary P_{3-4} and M_2. Unfortunately, complete homologous teeth have not yet been recovered from the Alberta and Wyoming localities, and thus my identification is definitely tentative. For this reason, I refrain from presenting a revised diagnosis of the species.

The summarized measurements of the dentition of *Batodon tenuis* can be found in Table 21.

Description of upper dentition.—The only known P^4 referable to the species (3147, Fig. 39,*4*) was accidentally destroyed before this description was written. Measurements and drawings were, however, taken from the specimen, the construction of which was basically similar to the known Cretaceous species of *Cimolestes.* The anterior accessory cusp was small and the paracone strong with a posterior accessory blade angled posterolabiad from the posterior ridge of the paracone. A distinct cingulum extended across the entire labial base of the tooth. The anterior surface of the paracone was rounded, but the posterior surface was keeled with a distinct elevation at about its mid-point as an incipient metacone. The protocone was strongly produced but somewhat compressed anteroposteriorly. It lacked conules and cingula, but had

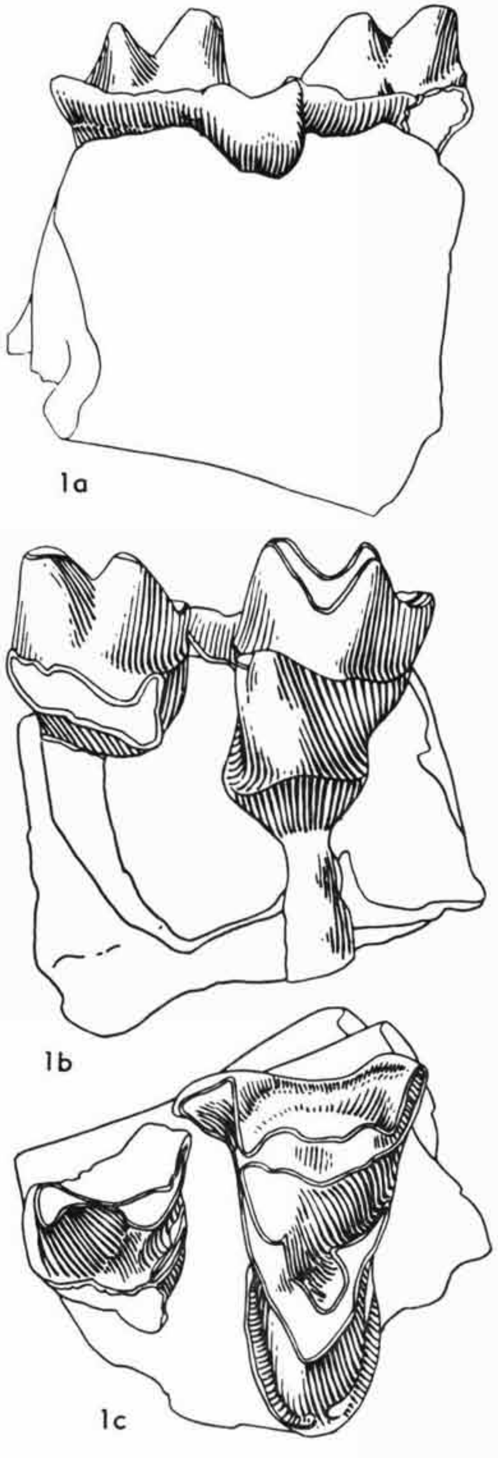

FIG. 38. *Batodon tenuis* MARSH, fragment of left maxilla with fragmentary M^1 and complete M^2 (4081); *1a-c,* labial, lingual, and occlusal views, ×30; meas. (mm.), M^1, unmeasurable; M^2, A-P 1.10, Ant-W 1.65, Post-W 1.60.

a distinct ridge running from its apex to the lingual base of the paracone. The tooth was essentially unworn, but slight wear was present on the apices of the protocone and anterior accessory cusp and on the posterior ridge of the paracone and crest of the posterior accessory blade.

The structure of most of the M^1 and all of the M^3 is still unknown. The M^2 (e.g., 4081, Fig. 38) is basically similar in construction with that of *Cimolestes cerberoides,* but is transversely extended, principally due to an exaggeration of the protocone. Although the stylar shelf at first glance looks narrow, it is nearly equivalent in proportions with that of *C. cerberoides.* Precingula and postcingula are strong and variable in construction. They are connected across the lingual base of the protocone in 4081, but are separated in 3802. The conules are strong, well separated from the base of the paracone and metacone, and have rounded crests on their internal wings. The protocone leans slightly anteriorly. The posterior metacrista is strong and the anterior paracrista weak. The interdental embrasures seem to be slightly proportionately deeper than those of *C. cerberoides.* The patterns of wear are identical with those of *C. cerberoides* except for the presence of distinct wear on the precingula and postcingula.

The fragment of the M^1 present on 4081 shows no special peculiarities. Specimen 3802 has a small piece of the anterolabial corner of the M^3 preserved. It extended distinctly anterior to the posterolabial corner of the M^2 and was closely appressed to its labial side.

Description of lower dentition.—The identification of specimen 4083 (Fig. 39,*2*) as a ?P_2 of *Batodon tenuis* may be incorrect. It differs from the P_2 in AMNH 58777 in its larger size, higher main cusp, and higher posterior accessory cusp. However, the teeth are similar in that they are laterally compressed, have the apex of the main cusp situated far anteriorly, and have the anterior border of the main cusp inclined anterodorsally. The labial side of the main cusp is shallowly rounded but the lingual side is flat. A ridge extends from the apex of the main cusp down its anterior border to the base of the crown, where it bends sharply backward and continues along the entire lingual base of the tooth. Upon reaching the posterolingual base of the posterior accessory cusp, it turns sharply dorsal to join the hinder end of the crest of the accessory cusp. Wear is most obvious on the lingual side of the posterior border of the main crest and posterior accessory cusp. Lesser wear is observed broadly along the center of the lingual base of the tooth and on the labial side of the crest of the posterior accessory cusp. A small round wear-facet is present just below the apex of the main cusp on its anterolabial side.

The P_4's (e.g., 3714, Fig. 39,*1*) referred to *Batodon tenuis* are interesting in that they have a low paraconid (anterior accessory cusp), a tall protoconid, a distinct but much weaker metaconid, and a strong posterior accessory

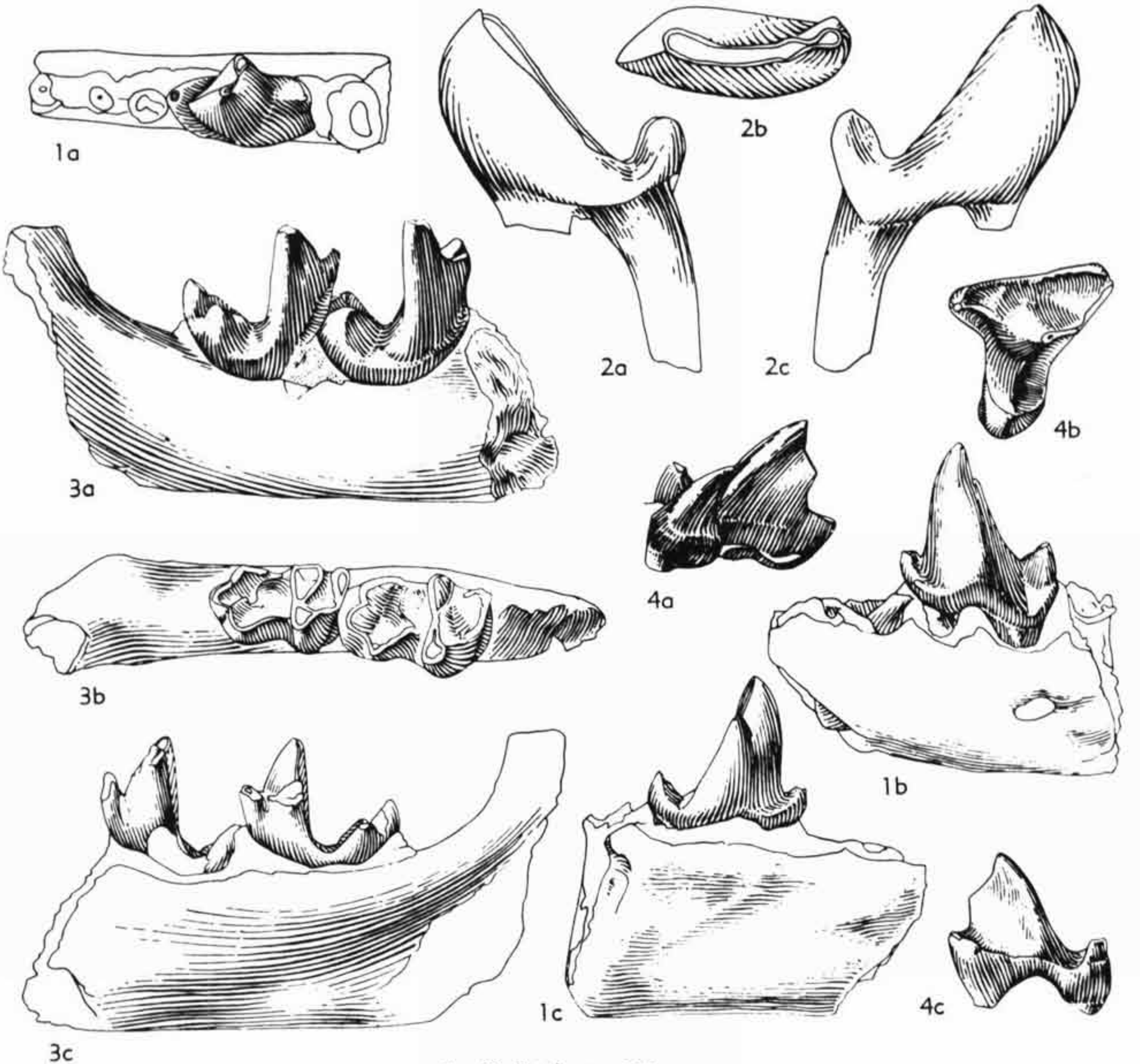

FIG. 39. *Batodon tenuis* MARSH.

1. Fragment of left mandible with P_4 (3714); *1a-c*, occlusal, labial, and lingual views, ×20; meas. (mm.), A-P 1.10, W 0.55.
2. Right ?P_3 (4083, identification of species doubtful); *2a-c*, lingual, occlusal, and labial views, ×30; meas. (mm.), A-P 1.15, W 0.50.
3. Fragment of right mandible with M_{2-3} (3721); *3a-c*, labial, occlusal, and lingual views, ×20; meas. (mm.), M_2, A-P 1.10, W-Tri 0.80, W-Tal 0.70; M_3, A-P 1.10, W-Tri 0.70, W-Tal 0.60.
4. Left, P^4 (3147); *4a-c*, lingual, occlusal, and labial views, ×20; meas. (mm.), A-P 1.20, W 1.20.

cusp. It cannot be determined from AMNH 58777 if a metaconid was present, but the remainder of the tooth is morphologically identical to the upper Edmonton specimens. The posterior mental foramen is ventral to the posterior root of the P_4 both in 3714 and AMNH 58777. The protoconid and metaconid are tall and united throughout most of their height. The posterior surface of the protoconid-metaconid pillar is flat. The anterior and lingual sides of the metaconid are rounded. The anterior border of the paraconid is laterally compressed and has a dull anterior keel that connects with the short anteroposterior crest of the paraconid. A distinct notch separates the two ridges in specimen 4047. The protoconid-metaconid pillar as viewed posteriorly, is curved lingually toward the apex. Cingula extend posterolingual and posterolabial from the apex of the conical paraconid

Table 21. *Measurements (in mm.) of Dentition of* Batodon tenuis *Marsh.*

Tooth	Length			Width					
	N	O R		N	O R				
P^4	1	1.20		1	1.20				
	Length			Ant-W			Post-W		
	N	O R	$\overline{X}$	N	O R	$\overline{X}$	N	O R	$\overline{X}$
M^2	2	1.10-1.20	1.15	2	1.55-1.65	1.60	2	1.60	1.60
				Width					
				N	O R	$\overline{X}$			
P_2	1	1.15	----	1	0.50	----			
P_4	2	1.10-1.25	1.17	2	0.55-1.60	0.57			
				W-Tri			W-Tal		
				N	O R	$\overline{X}$	N	O R	$\overline{X}$
M_2	2	1.10-1.15	1.12	2	0.80	0.80	2	0.70	0.70
M3	1	1.10	----	1	0.70	----	1	0.60	----

For abbreviations see end of Introduction.

to their terminations dorsal to the middle of the anterior root. The posterior accessory cusp is similar in construction to those of *Cimolestes cerberoides* and *C. magnus.* It has a high central ridge, which, at its posterior end, turns sharply anterolingual toward the base of the protoconid-metaconid pillar, gradually decreasing in height. A weak notch separates the front end of the central crest of the posterior accessory cusp from the back of the base of the metaconid on specimen 4047.

Strong wear is observed only on the crests connecting the apices of the protoconid and metaconid. Broad shearing abrasions are also observed on the entire posterior surface of the protoconid-metaconid pillar, labial side of the posterior accessory cusp, anterior surface of the metaconid, and anterolingual surface of the protoconid. The apex of the paraconid shows a small round wear-facet.

The M_2 and M_3 (e.g., 3721, Fig. 39,*3*) have a tall trigonid, the protoconid of which exceeds the height of the metaconid. The paraconid is distinctly separated from the metaconid, much lower, and lingually placed. A labially sloping cingulum is present at the anterior base of the tooth. The hypoconulid of the M_3 is rather strongly produced posteriorly. Except for their minute size, the M_{2-3} are structurally identical with those of *Cimolestes cerberoides.* The patterns of wear also are identical. The mandible is shallow, and the posterior mental foramen is ventral to the posterior P_4 root (Fig. 39,*1*).

Affinities.—Assuming that all or most of the above-described specimens are derived from the same species, I think there can be little doubt as to the affinities of the species with the Palaeoryctidae, and its close relationship to *Cimolestes cerberoides* and *C. incisus.* This is true whether or not the specimens described actually are referable to *Batodon tenuis.* Certainty of identification awaits the collection of more material. If the identification and above association of material is later shown to be correct, I would suggest that *Batodon* be considered a junior synonym of *Cimolestes.*

The latest classification (Van Valen, 1967, p. 267) placed *Batodon* in the subfamily Deltatheridiinae (family Palaeoryctidae) along with the Asian genera *Deltatheridium* and *Hyotheridium.* The newly discovered upper Edmonton material shows, I believe, a closer relationship of *Batodon* (assuming the identification to be correct) to the various species of *Cimolestes,* and thus the genus should be included with the didelphodontines. I know of no specific Paleocene descendant of *Batodon tenuis.*

The presence of a metaconid on the P_4 and an incipient metacone on the P^4 further emphasizes the point that such structures are not necessarily restricted in the Cretaceous to the family Leptictidae, but are also to be found among palaeoryctids such as *Batodon tenuis* and *Procerberus.*

ZOOGEOGRAPHIC AND EVOLUTIONARY CONSIDERATIONS OF EDMONTON FORMATION EUTHERIANS

The list of the eutherian taxa discovered in the upper Edmonton Formation is as follows:

Eutherian Mammals of Upper Part of Edmonton Formation

Infraclass EUTHERIA
  Order INSECTIVORA
    Family Leptictidae
      Subfamily Gypsonictopinae
        Gypsonictops hypoconus Simpson, 1927
        Gypsonictops illuminatus Lillegraven, n. sp.
  Order DELTATHERIDIA
    Family Palaeoryctidae
      Subfamily Didelphodontinae
        Cimolestes cerberoides Lillegraven, n. sp.
        Cimolestes propalaeoryctes Lillegraven, n. sp.
        Cimolestes magnus Clemens & Russell, 1965
        Batodon tenuis Marsh, 1892

The smaller Maastrichtian species of *Gypsonictops* (*G. hypoconus*) was geographically widespread, at least from New Mexico to Alberta. It is a rare member of the known Alberta fauna. *G. illuminatus*, a larger species, is common in the upper Edmonton Formation but is as yet unreported from type Lance Formation of Wyoming and the Hell Creek Formation of Montana and South Dakota. As already discussed following the description of *G. illuminatus*, *Gypsonictops* had been present in North America since at least the Campanian (Fig. 30), and probably had an Asiatic origin from a stock similar to *Kennalestes* (unpublished as of this writing).

The species of *Cimolestes*, on the other hand, have been commonly found only in sediments of post-Campanian age. ASHOK SAHNI found no evidence for the presence of palaeoryctids in the Campanian Judith River Formation of Montana, although multituberculates and marsupials were abundant and *Gypsonictops lewisi* (SAHNI, 1968) was common. COLWELL and FOX (pers. comm.), who collected in the Campanian Oldman Formation of Alberta, have also found abundant multituberculates, marsupials, and *Gypsonictops lewisi*, but have recovered only a single tooth that is possibly referable to a palaeoryctid. The specimen (670) is probably an M^3, with the stylar shelf, paracone, and metacone. It was my impression that its affinities were near *Cimolestes magnus*.

As can be seen in Figure 40, a definite radiation of palaeoryctids in North America occurred during latest Cretaceous (Maastrichtian) time. VAN VALEN (1967, p. 257, fig. 7) considered the family Leptictidae to be a central stock from which many mammalian lines, including palaeoryctids and arctocyonids, could have been derived. His thought was largely based on the concept that *Procerberus* represented a structurally and probably phylogenetically basal leptictid. I challenged this concept in the description of *Cimolestes cerberoides* and suggested that *Procerberus* is in actuality a specialized palaeoryctid having nothing to do with the origin of *Gypsonictops* or the family Leptictidae. It is, I believe, most unlikely that palaeoryctids could have been derived from *Gypsonictops* or similar, as yet unknown, North American leptictids. *Gypsonictops* shows many dental characters that are probably specializations from a primitive therian condition (*see* PATTERSON, 1956; SLAUGHTER, 1965). Teeth of the species of *Cimolestes*, on the other hand, are more similar to those of the probable primitive therian morphology. A series of reversals of evolutionary trends must be postulated to derive *Cimolestes* from *Gypsonictops*. It is simpler to assume independent derivation of the two genera from a more generalized eutherian stock.

Although the fossil record of North America gives little indication of a suitable ancestor for *Cimolestes*, that of the Late Cretaceous Djadochta Formation of Mongolia currently being described by KIELAN-JAWOROWSKA is more promising. The Djadochta Formation is now presumed to represent a lower part of the Upper Cretaceous (LEFELD, 1965, p. 81) and is thus probably older than the known Late Cretaceous mammal localities of North America. I have seen photographs of the skull and lower jaws of a placental mammal from the Djadochta simply labelled "MgMI-1," which would seem, at least on the basis of dental morphology, to be related to the palaeoryctids.

Endotherium, a Lower Cretaceous mammal possibly referable to the Eutheria, is reported from South Manchuria (SHIKAMA, 1947, p. 78). Incontrovertible eutherian remains have not yet been recovered from pre-Campanian sediments in North America, although members of the Pappotheriidae (SLAUGHTER, 1965) from the Lower Cretaceous (Albian) of Texas show primitive dental features that could be primitive for all subsequent therians. Both *Endotherium* and the pappotheriids could have been derived from such an animal as *Aegialodon* which has been found in the Late Jurassic of Wales (KERMACK *et al.*, 1965). It should be emphasized here that negative evidence suggesting the absence of eutherians in North America between the top of the Albian and base of the Campanian is not reliable since mammal-bearing localities simply have not been found.

As mentioned in the zoogeographic considerations of the upper Edmonton marsupials, the metatherians probably had a North American origin from the pappotheriids. It now seems likely, on the other hand, that the placental mammals were of Asiatic origin. They probably invaded North America in the Late Cretaceous at least twice; earlier for the stock ancestral to *Gypsonictops*, and later for that of *Cimolestes* and *Procerberus*. The evidence for mammalian migrations from Asia to North America

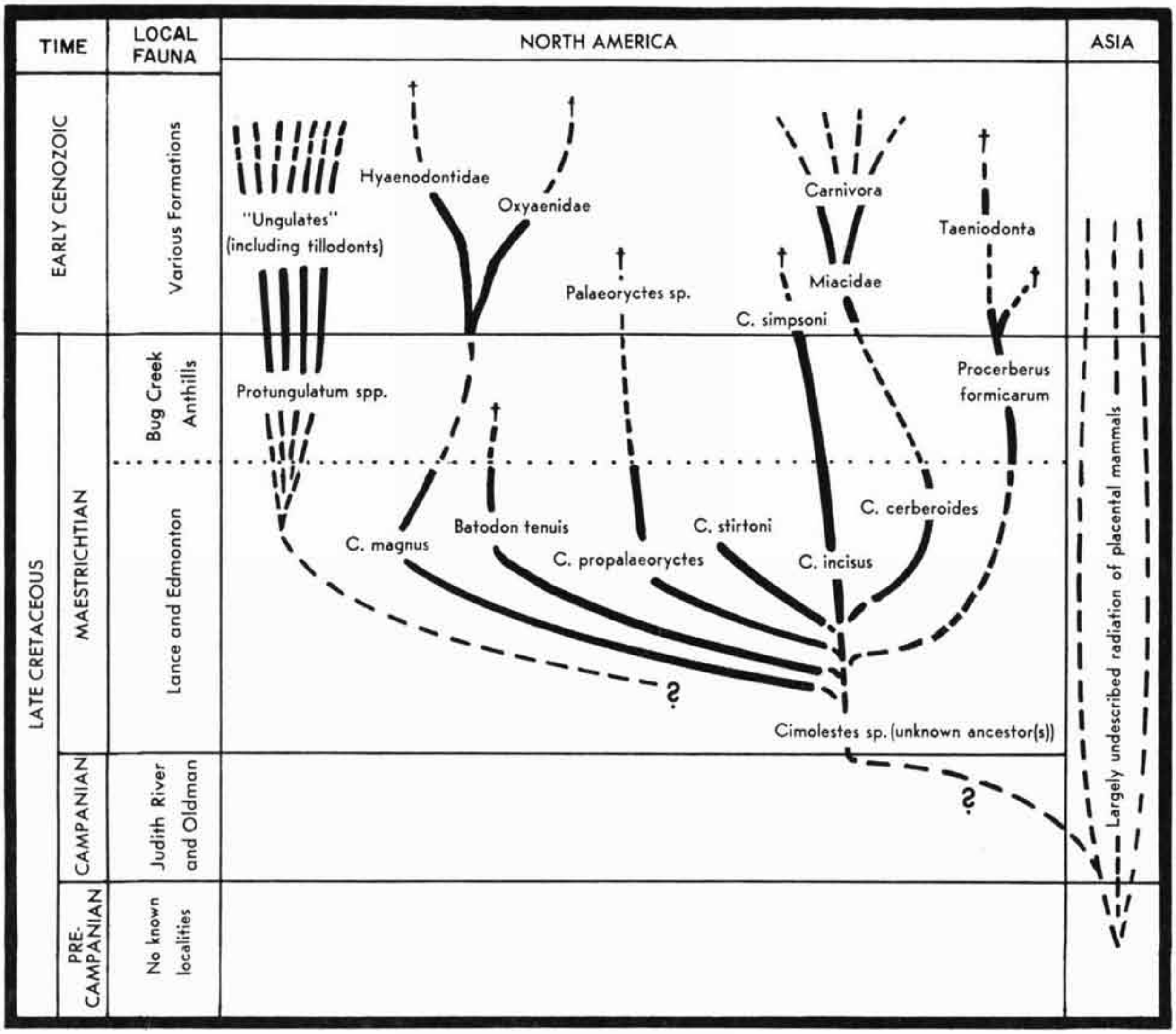

FIG. 40. Possible phylogenetic arrangement of Late Cretaceous and Early Tertiary eutherians (leptictids and their descendants excluded).

in the Late Cretaceous is strengthened by the presence of the multituberculate *Cimexomys priscus* in the upper Edmonton Formation. North American ancestors for *C. priscus* are unknown, but similar species are abundant in the Djadochta Formation of Mongolia (KIELAN-JAWOROWSKA, pers. comm.). An origin for North American Paleocene eutherian mammals from some other area was suggested long ago by SIMPSON (1937a).

Gypsonictops apparently did not diversify greatly in the Late Cretaceous of North America. The radiation within the genus *Cimolestes,* however, seems to have been more profound. The structural contrasts with *Gypsonictops* and the essential similarity of structure between the species of *Cimolestes* was emphasized in their descriptions. Although it cannot yet be proved, it is my opinion that all the known Late Cretaceous palaeoryctids of North America could have been derived from a single invading species that underwent rapid speciation and evolution during the Maastrichtian. At any rate, intercontinental faunal exchange between Asia and North America during the Late Cretaceous was probably a highly selective process. Using SIMPSON's (1962, p. 21) classification, the kind of interchange probably more closely resembled a "sweepstakes route" or "filter" than a full-fledged "corridor."

A few specific comments concerning Figure 40 are necessary as they are not discussed elsewhere in this paper. CLEMENS (pers. comm.) will assign the early Paleocene species *Puercolestes simpsoni* to the genus *Cimolestes.* He believes the species to be a direct descendant of *C. incisus.* CLEMENS is currently describing a new large species of *Cimolestes* from the type Lance Formation (unpublished at this writing). He believes this species to have been closely related to *C. incisus*.

The affinities of ***Protungulatum*** (Sloan & Van Valen, 1965, p. 226), the oldest known arctocyonid condylarth, are vague. Several species are present in the upper part of the Hell Creek Formation of Montana (Sloan & Van Valen, 1965, p. 221, table 1) and a closely related ancestral species in North America has yet to be discovered. The dentition is leptictid-like in that: 1) the cusps are comparatively low; 2) the precingula and postcingula are strong and consistently developed on the upper molars; 3) the stylar shelf and posterior metacrista on the upper molars are reduced; and 4) the P_4 has a metaconid. However, none of these characters is restricted to the leptictids. The dentition is more palaeoryctid-like in that: 1) the P^{3-4} are not molariform, lack conules, and are constructed much like those of the species of *Cimolestes*; 2) the conules of the upper molars are lingually placed; 3) a shearing function, rather than grinding, dominated in the early stages of wear; 4) the paraconid is well separated from the metaconid, especially on the M_1, and is lingually placed; 5) the protoconid is higher than the metaconid; and 6) the hypoconulid of the M_3 is produced posteriorly. The origin of ***Protungulatum*** may have been Asian or North American, but I suggest its affinities were closer to the palaeoryctids than to the leptictids. Such an interpretation is paleontologically plausible because there has long been recognized a rather close affinity between the eutherian carnivores and ungulates (cohort Ferungulata, Simpson, 1945). As Van Valen (1963, p. 372) suggested, the tillodonts probably represented a specialized line of condylarths.

Mossman (1937, p. 191, fig. 7) attempted to construct a phylogenetic tree of the Mammalia based solely upon the characters of the fetal membranes. It is interesting to note that he suggested a fundamental taxonomic dichotomy from an ancestral eutherian stock. An "insectivore-primate-rodent" group represented one trunk, and a "carnivore-ungulate" group represented the other. Such an interpretation is fully compatible with the fossil record.

Part 2

REVIEW OF MARSUPIAL-PLACENTAL DICHOTOMY IN MAMMALIAN EVOLUTION

INTRODUCTORY COMMENTS

Huxley (1880) divided the class Mammalia into three groups called Prototheria, Metatheria, and Eutheria. The prototherians supposedly represented a basal mammalian stock from which the monotremes have survived as a specialized offshoot. He thought that the prototherians also gave rise to the metatherian group, highly specialized descendants of which are the living marsupials. Kermack (1967, p. 247, fig. 1) has suggested that the monotremes and several extinct groups of nontherian mammals have probably been isolated from the therians since at least early in the Jurassic. The reptilian ancestors of the therians are as yet unknown (Kermack, 1967, p. 248) or unrecognized. Thus Huxley's concept of the "Prototheria" is, perhaps, less correct and useful than previously thought. Huxley suggested that the Metatheria, in turn, provided the ancestry for a eutherian stem from which all the living placental mammals, specialized though they are, could have been derived. Huxley strongly emphasized the point that marsupials, as we know them today, do not represent a primitive morphology from which placental mammals descended.

Huxley's conclusion that modern marsupial anatomy is specialized and not prototypal has been vigorously defended and challenged many times since its publication (McCrady, 1938, p. 206, for brief summary). Recently, some outstanding students of vertebrate morphology have defended the concept of profound marsupial specialization. For example, Grassé (1955, p. 142) stated:

> Les caractères révélés par le squelette et la denture mettent en évidence de profondes différences entre Marsupiaux et Placentaires; . . . L'anatomie cérébrale et génitale, ainsi que le mode de développement de l'embryon attestent qu'il s'agit de deux types réellement distincts. Deux types qui ne dérivent très probablement pas l'un de l'autre, mais s'insèrent, en des points distincts, sur l'arbre généalogique des Mammifères.

Also, Romer (1965, p. 151) stated:

> It has often been assumed that the placentals arose from the marsupials. This theory is now discredited, but the two groups are certainly related. . . .

The purpose of this part of my paper is to reopen the question of the significance of the anatomy and physiology of living marsupials to their own evolutionary history and to that of the placental mammals. I have followed the long-standing and widely used nomenclatural practice of using the terms "metatherians" and "marsupials" synonymously, as contrasted with the terms "eutherians" and "placentals." Kermack (1967, p. 245) suggested that the term "Eutheria" should be used to include both the marsupial and placental mammals and that "Marsupialia" and "Placentalia" should be used, respectively, in the places of "Metatheria" and "Eutheria" as arranged by Simpson (1945). Although Kermack's suggestions have some historical validity, such a basic nomenclatural revision would, in my opinion, cause unnecessary confusion.

The use of the term "eutherian" as being synonymous with "placental mammal" is deeply entrenched in the literature of paleontology and neozoology and in the minds of specialists and nonspecialists alike.

Frequently, those workers most familiar with the fossil record of a given group of organisms are not specially trained in the biological characteristics of its living representatives. I have attempted, in writing this section, to

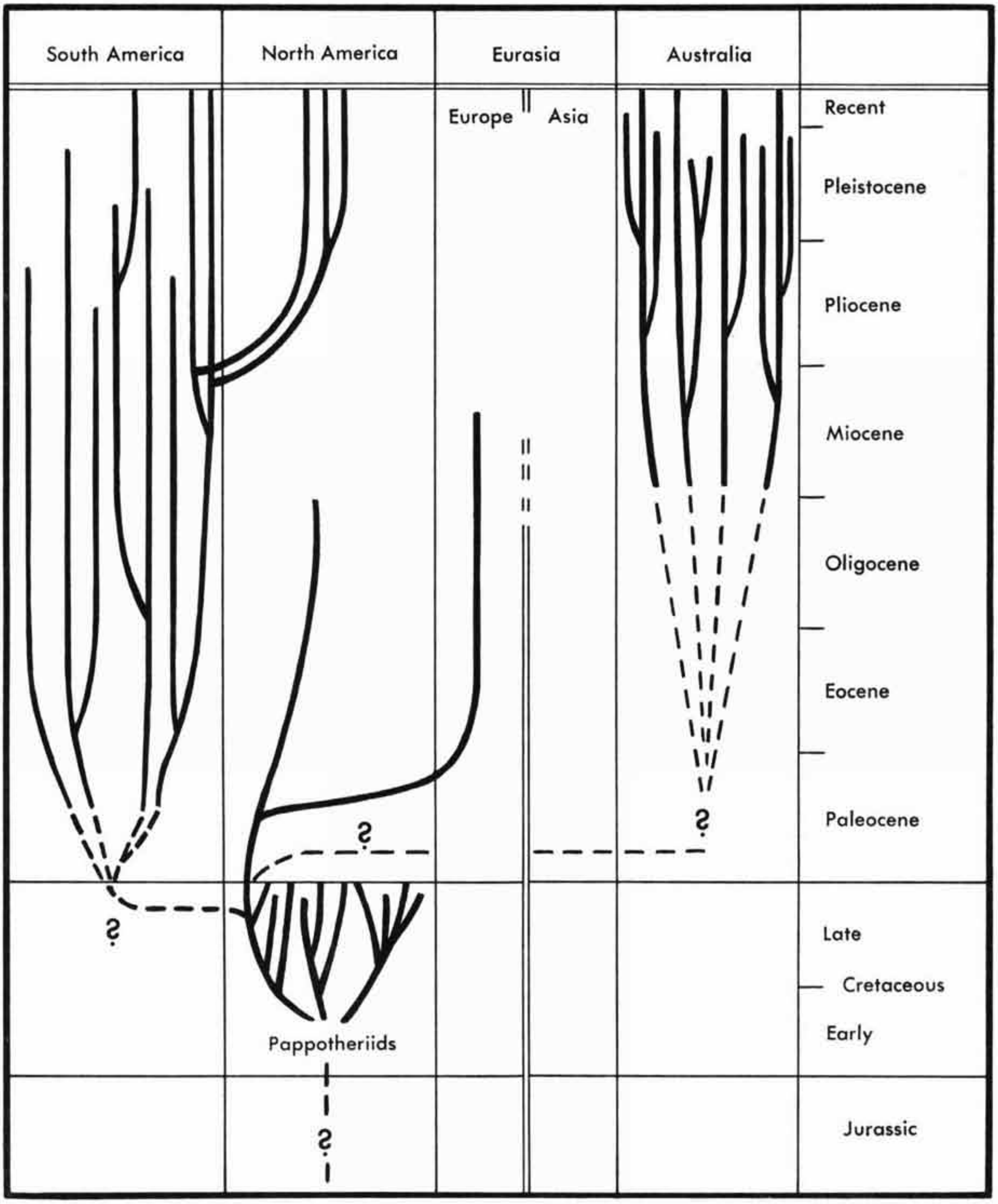

FIG. 41. Zoogeographic summary of Marsupialia.

remain at the level of fundamentals that are of interest to the paleontologist. The references cited are far from comprehensive, but sufficient to introduce an interested reader to the vast literature on marsupial mammals.

Speculations concerning the phylogenesis of characters derived only from living animals are fraught with many dangers, a problem succinctly considered by Edinger (1949). However, the standard procedures of comparative anatomy were employed in the study. That is, if a suite of detailed characters was found to be held in common between all known marsupials and placentals, it was concluded that the characters were present in the common ancestor and probably were not independently derived. Conversely, if a suite of characters was found to be unique either to marsupials or to placentals, two possibilities were considered: 1) the characters were evolved from a simpler, more primitive condition in only one of the groups, or 2) the characters were present in the common ancestor, but were secondarily lost in one of the two groups. Decisions concerning the latter pair of choices could only be made following comparisons with monotremes and living reptiles. The most parsimonious explanation was usually accepted. The phylogenetic significance of any one given character derived from a modern animal should be treated with suspicion. However, when many characters, more or less independent from one another, all point to a common interpretation of significance, the probabilities are good that such an inference is valid.

FOSSIL RECORD OF MARSUPIALS

Information pertaining to the early evolution of placental mammals is summarized in Figures 30 and 40. As proposed there, an Asiatic origin for placental mammals seems likely. A zoogeographic summary of marsupial evolution can be found in Figure 41, based upon the more complete summary by Clemens (1968a).

A mixture of negative and positive evidence suggests a North American origin for the Marsupialia as we know it. Mesozoic marsupials are abundant in North America, at least from Alberta to New Mexico, but are unknown from other parts of the world where various terrestrial vertebrates are common. Rare mammalian teeth have been recovered from the latest part of the Early Cretaceous (Albian) of Texas. Some of these represent members of the extinct therian family Pappotheriidae (Slaughter, 1965, p. 1). The dentitions of the pappotheriids show many characters thought to be primitive for the Theria. The dental structures of both the Cretaceous eutherians and metatherians are derivable from that of the pappotheriids (Fig. 42), and Slaughter (1965, p. 17) suggested that they represented, or were close to representing, the common ancestor for the Theria. Such an interpretation is certainly possible, and I agree with the probable ancestry for the Marsupialia. However, for biological reasons explained later, I suggest that the pappotheriids *sensu stricto* lived too late in the history of the earth to be ancestral to the placentals, and that we must look in still older rocks, perhaps in the earliest Cretaceous, to find the ancestral stock for the Eutheria.

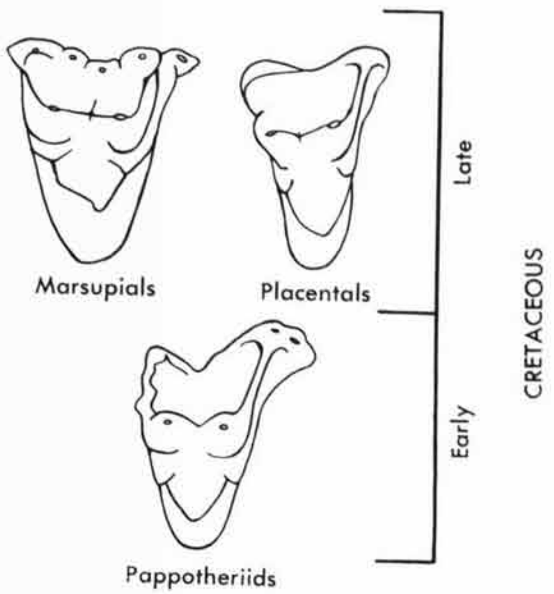

Fig. 42. Outline drawings of upper molars showing basic similarity of primitive therian dentitions.

Marsupials became nearly extinct at the end of the Cretaceous in North America (Fig. 26, 41). The fossil record of marsupials in South America begins in the late Paleocene with the sudden appearance of four characteristically South American families. Their specialized nature suggests they had existed in South America for some time previously, and probably arrived on the continent from North American didelphid ancestors in the early Paleocene or Late Cretaceous. A therian mammal, *Perutherium,* is recorded from the Lake Titicaca area from rocks supposedly of Late Cretaceous age (Grambast *et al.,* 1967). The rocks are dated on the basis of charophytes. *Perutherium* is of uncertain affinities, but is dentally similar to primitive arctocyonids and probably is not a didelphid. At any rate, the marsupials diversified greatly during the Cenozoic of South America, largely in the absence of eutherian insectivorous and carnivorous stocks. Many marsupial stocks became extinct in South America, and a few migrated into North America when the land connection was reestablished between the two continents near the end of the Pliocene. A great wave of eutherian stocks entered South America at that time. The marsupial migrants into North America were of minor importance in the late Cenozoic.

The evolution of marsupials in Australia is more mysterious because no fossils have yet been recorded from rocks older than the early Miocene or late Oligocene.

Again, at their first appearance there were four distinct groups characteristic of Australia. It is thus assumed that the arrival of marsupials in Australia was considerably earlier, perhaps as remote as the Paleocene or Late Cretaceous (SIMPSON, 1961, p. 443).

Figure 41 brings out an important point that is frequently overlooked. The American group of marsupials has probably been genetically isolated from the Australian group since at least the early Paleocene, and quite possibly since the end of the Cretaceous. Thus any character found in common between the two groups has either been independently derived, or is truly ancient, probably dating back to the Mesozoic. Serological investigations, as far as they have been taken, agree with the long-time separation of the American and Australian marsupials (KIRSCH, 1968). The ectoparasites of the South American and Australian marsupials are said to be related only at the family level (VANZOLINI & GUIMARÃES, 1955).

Another point well worth keeping in mind concerns the gymnosperm to angiosperm terrestrial floral revolution that occurred during the Cretaceous (AXELROD, 1960). As pointed out by CLEMENS (1966, p. 115), the floral change undoubtedly had a great influence on the evolution of terrestrial herbivores, and additionally on insects and insect-eating vertebrates (OLSON, 1966).

COMMENTS ON COMPARATIVE ANATOMY AND PHYSIOLOGY OF THERIA

The literature dealing with the anatomy of marsupial mammals is truly vast, greatly scattered, and largely unsynthesized. Although this discussion is concerned principally with aspects of the reproductive system and reproduction, a few miscellaneous characteristics should be considered to illustrate the morphological complexity of marsupial mammals. Four somewhat arbitrarily chosen categories of anatomical or physiological characteristics are employed:

Anatomical or Physiological Characteristics of Marsupialia

Type 1. Features more characteristic of the reptilian grade than the typically therian grade.
Type 2. Features that are composite in nature, showing a combination of reptilian and therian features.
Type 3. Features more characteristic of the typically therian grade.
Type 4. Features restricted to the Marsupialia.

Type 1 characteristics are not uncommon. For example, the structure of the accessory optic tract of the marsupial brain is in basic agreement with that of reptiles and birds, and suggests a condition considerably more primitive than that seen in placental mammals (GIOLLI, 1965). The vascularization of the tissues of most of the brain of marsupials is not by complex capillary networks as in eutherians, but as true end-arteries (WISLOCKI, 1940; BUBIS & LUSE, 1964) as are widely distributed among the amphibians and reptiles (SCHARRER, 1940). It is interesting, and somewhat perplexing, to note that the brain tissue of monotremes follows the plexiform capillary arrangement characteristic of eutherians (SUNDERLAND, 1941). However, several distinct groups of reptiles also have brain capillary networks, and the character may have been independently derived several times in vertebrate evolution.

Characters of Type 2 are abundantly represented in essentially every organ or tissue of the marsupial body. For example, although the marsupial eyeball as a whole is thoroughly mammalian, its retina has many features in common with that of the monotremes. The monotreme retina could easily be confused with the retina of a nocturnal reptile (WALLS, 1963, p. 670, 674). The development of the marsupial lung is interesting in that at birth its level of histological development is reptilian in several features (SOROKIN, 1962), and gradually becomes transformed to a more typically mammalian structure. Literature concerning the structure of the central nervous system of marsupials (especially *Didelphis*) is rich (ARIËNS-KAPPERS *et al.*, 1960). The brain, though showing many rather primitive features, is of the generalized construction expected in a primitive therian. Perhaps the most significant primitive difference from the eutherians is in the lack of the corpus callosum (ABBIE, 1939). This interhemispherical commissure is apparently of major functional importance in eutherians in allowing information interchange between the right and left cerebral hemispheres (SPERRY, 1964). The link between the hemispheres in marsupials is weak, but present in the form of an anterior commissure (MANNING & MEGIRIAN, 1963; NELSON & LENDE, 1965). A final example of a Type 2 character is the fact that marsupials, in contrast to most reptiles, have epiphyses on the ends of the long bones, but in many cases the union is delayed into old age and sometimes the fusion is never completed (WASHBURN, 1946). Thus growth can be continued well into the adulthood of the animal, a common reptilian feature.

Type 3 characters are also abundantly represented in marsupials. For example, the structure and function of the inner ear show no fundamental differences between marsupials and placentals (FERNANDEZ & SCHMIDT, 1963), but are quite different from the reptile-monotreme condition. Certain kinds of cutaneous nerve endings are held in common between marsupials and placentals, but frequently show specializations in eutherians (WINKELMANN, 1964). Facial vibrissae are similar in innervation (HUBER, 1930) and distribution (LYNE, 1959) within the Theria, but are absent in monotremes and reptiles. Milk is considered a mammalian character, and the structure of the mammary glands and teats (LINZELL, 1959) and the constitutents of marsupial milk (SLOAN *et al.*, 1961) do not differ greatly from those found in eutherians. It is well to point out here that echidna milk is similar in composition to that of the therians and the young echidna actively sucks the milk rather than lapping it from the mother's hair as is commonly believed (GRIFFITHS, 1965). The presence of an inflected angle on the lower jaw was previously thought to be a character peculiar, as a general feature, to the marsupials. However, Late Cretaceous placentals such as *Gypsonictops hypoconus* (CLEMENS, pers. comm.), *Cimolestes cerberoides* (Fig. 33,6), and *C. magnus* (Fig. 37,3) all have angular processes that are reduced, but distinctly inflected. It is probable that an inflected angle was a primitive character for the Theria and was secondarily lost in several different lines of eutherians.

Those specialized characters restricted to the marsupials (Type 4) are also abundant. This, of course, is to be expected since the marsupials and placentals probably have been distinct from each other for at least 100 million years. Interpretations become controversial, however, when one attempts to determine whether the characters represent specializations derived since the marsupial-placental dichotomy or whether the characters were present in the therian stem but were lost or altered in the eutherians. SHRIVASTAVA (1962) reported that marsupials show specializations in the deltoid musculature different from either monotremes or placentals, and favored the placement of marsupials in a natural subclass. HAINES (1958) suggested that the musculature involved in closing the hand and foot of *Didelphis* represents a structural specialization from a more primitive condition that points to a terrestrial, rather than arboreal, ancestry for the Theria. I have found differences such as these (disregarding the reproductive system) that are distinct, important, and widespread throughout the marsupials to be uncommon. The majority of specializations are rather minor in nature or of discontinuous distribution through the marsupials, indicating intra-group evolution following the marsupial-placental divergence. For example, a structure functionally analogous to the corpus callosum (the "fasciculus aberrans") has appeared in the brain of the "diprotodonts" of Australia (ABBIE, 1937). Kangaroos *(Macropus)* have been shown to have a higher level of intelligence than *Didelphis* (NEUMANN, 1961). Undoubtedly a multitude of factors were involved in the increase of intelligence above the didelphid level, but the majority of the evolution probably occurred within the marsupials in parallel with changes in the eutherians. It seems unlikely that *Didelphis* has decreased significantly in cerebral function from a more advanced level of intelligence.

In summary, I was able to find few fundamental characters (again, disregarding the reproductive system) that could bar even living didelphine marsupials from being satisfactory "ancestral" therians, either structurally or physiologically. Characters such as the pouch on the male and the webbed feet and bulbous molars of *Chironectes* and reduced paracones and conules of all didelphines appear to be products of a limited post-Cretaceous evolutionary radiation of the didelphines.

Although the above series of examples tends to emphasize differences from placentals and the relatively primitive nature of marsupials, the latter in most considerations are structurally quite close to the placentals and show a high degree of anatomical advancement. This would seem to indicate either profound parallelism in evolution between marsupials and placentals, or the presence of most characters in the common ancestral stock, which probably existed well back in the Cretaceous. The latter interpretation seems the more reasonable.

The marsupials thus show a curious mosaic of reptilian and typically therian characters. The most profound differences between metatherians and eutherians are concerned with reproductive structures and processes, and the remainder of this discussion shall be devoted to aspects of reproduction.

COMPARATIVE ANATOMY AND PHYSIOLOGY OF REPRODUCTION

INTRODUCTORY NOTES

A brief introduction to the fundamental contrasts of the monotreme, marsupial, and placental reproductive systems is presented here to set the stage for later more detailed discussion.

All monotremes lay eggs that are proportionately small compared with most reptiles (HARTMAN, 1929) and that are retained during much of the period of development in the oviduct of the mother. The female echidna has a transitory pouch (incubatorium), which is simply constructed of folds of skin pulled together by contraction of the dermal panniculus carnosus muscle of the skin (GRASSÉ, 1955, p. 52).

Marsupials are all viviparous, but the gestation period is almost always significantly shorter than the total duration of a nonpregnant estrous cycle and the young are born in an extremely immature state (SHARMAN, 1965). For example, the mass of a newborn young of *Didelphis virginiana* is only 1/10,750 that of its mother (HAMILTON, 1963) in contrast to a 1/20 value in the human. A pouch is usually, but not always present (depending on species), and most "embryonic" development occurs outside the body of the female while the young animals are semipermanently attached to a teat. The nipple expands within the mouth of the young, thus holding it rigidly in place, but the maternal and fetal tissues remain distinct (McCRADY, 1938, p. 184, fig. 57). Although licking of the fur between the vulva and the teat may be an essential act by the mother in some species, the newborn must find its own way to the teat without additional aid (McCRADY, 1938, p. 181). Olfaction may aid the neonate in locating a teat once in the area (HILL & HILL, 1955).

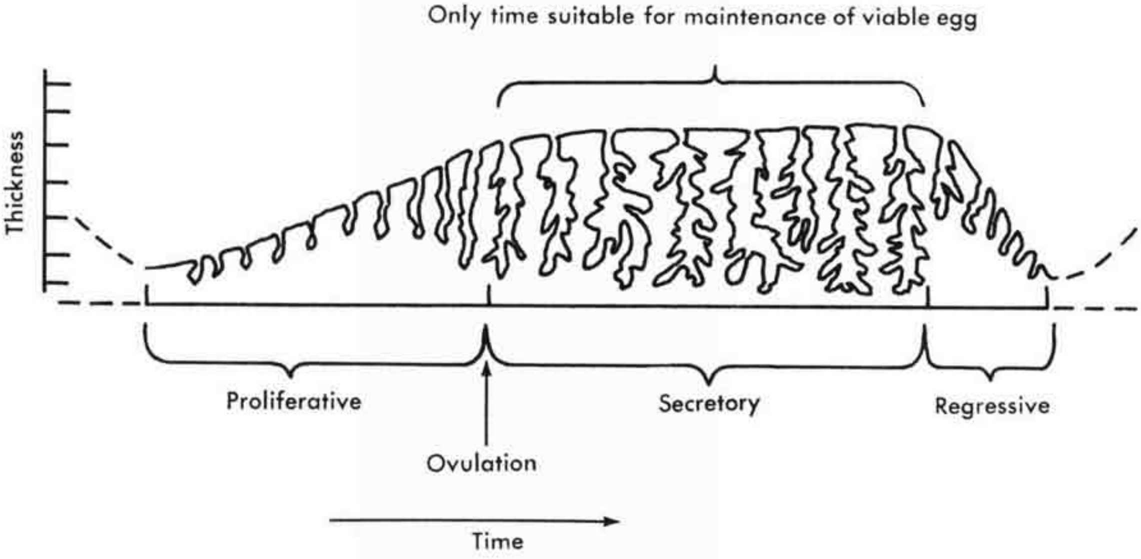

FIG. 43. Diagrammatic interpretation of changes in uterine (endometrial) wall during nonpregnant estrous cycle of therian (marsupial or placental) mammal (modified from Arey, 1954, p. 155, fig. 123).

Placental mammals are all viviparous and commonly have gestation periods that significantly exceed the duration of the nonpregnant estrous cycle. Thus placentals are usually born at an anatomically much more advanced stage than are marsupials. Pouches are unknown, and the young do not permanently attach to the teats.

IMPORTANCE OF THE UTERINE WALL

Egg development in birds, monotremes, and most reptiles follows cyclic hormonal control and upon completion of its coverage by albumen and shell layers, is either discharged from the body or is retained as a more or less sealed unit within the oviduct. There is little dependence upon the histological condition of the oviduct by the shelled egg for development. Its nutrition is principally from the yolk and albumen. This is certainly a primitive amniote feature and is quite in contrast to the specialized therian condition in which the egg contains little yolk and the embryo has a high dependency upon nutritive secretions from the endometrial glands or a maternal blood supply.

The basic nonpregnant hormonal control of the estrous cycle is, as far as is known, equivalent between marsupials and placentals (SHARMAN, 1965, p. 24). The obvious changes of the uterine wall of a "typical" therian (marsupial or placental) during a nonpregnant estrous cycle are shown in Figure 43. Comparisons of rhythmicity in accessory organs and structures in *Didelphis* were graphically shown by HARTMAN (1923, p. 367, Chart 1). During the proliferative stage of the cycle, the uterine glands become progressively more elongated and complex. Active secretion of "uterine milk" (AMOROSO, 1952, p. 207, for composition) begins near the time of ovulation and this secretion supposedly aids in the support and nutrition of the ovum. If pregnancy does not occur, the corpus luteum of the ovary terminates the secretion of progesterone, and the secretory phase of the uterine cycle is thus ended (DEANESLY, 1966, for extended discussion) after a rather regular lapse of time (ASDELL, 1964, for systematic comparisons). The regressive phase occurs rapidly, and involves a reduction in size, complexity, and secretory capacity of the uterine glands. As pointed out in Figure 43, the only time suitable for the maintenance of a living egg within the uterus is during the short secretory phase of the estrous cycle. Following the termination of the phase, the egg is sloughed outside.

Figure 44 illustrates the changes in the uterine wall during the pregnant uterine cycle of a placental mammal. Fertilization follows shortly after ovulation, and the zygote soon proliferates into a free-floating blastocyst (WOLSTENHOLME & O'CONNOR, 1965, for examples). The blastocyst quite early becomes implanted on or in the uterine wall (BOYD & HAMILTON, 1952, p. 64). True implantation, involving endometrial erosion, is unknown among marsupials. When pregnancy occurs in eutherian mammals, the gestation period usually continues for a period significantly beyond the time of the normal end of the secretory phase. Uterine glands continue active secretion throughout the pregnancy and the regressive phase occurs only after the time of birth. Thus, during pregnancy, an environment within the uterus suitable for internal development is prolonged much longer than in the nonpregnant cycle.

Comparative studies concerning the hormonal controls for the maintenance of the secretory phase are in their infancy and have not been investigated in most

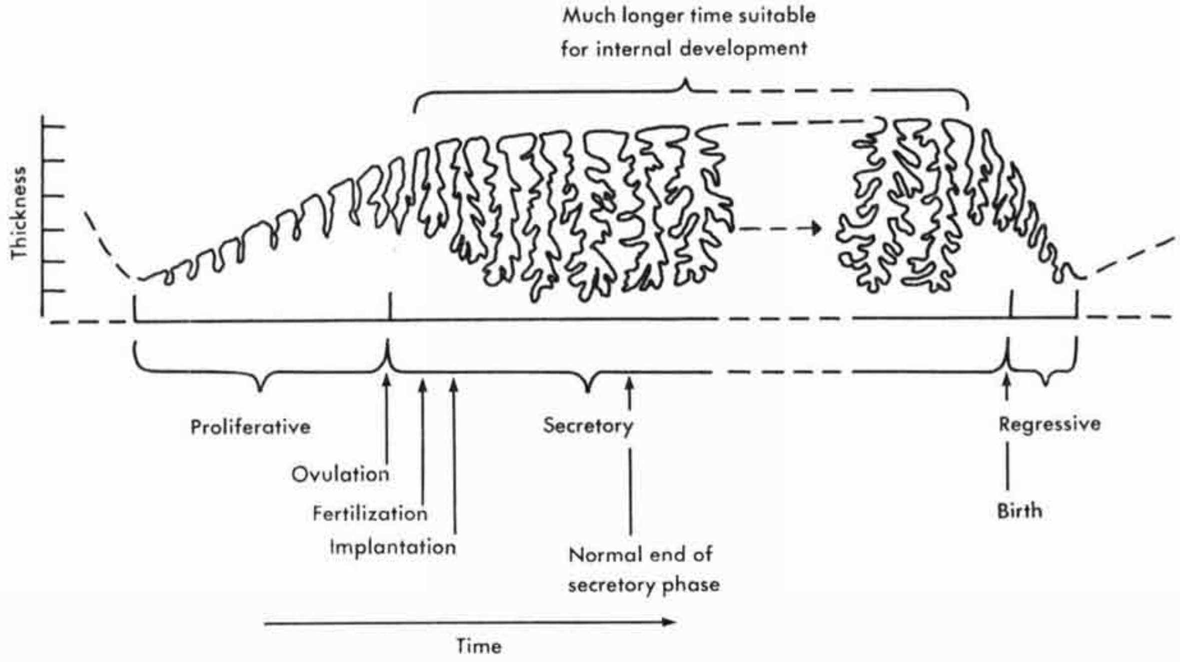

FIG. 44. Diagrammatic interpretation of changes in uterine (endometrial wall during eutherian pregnant estrous cycle (modified from Arey, 1954, p. 155, fig. 123).

placental mammals (DEANESLY, 1966, p. 930, for historical review). Most evidence now points to the fact that trophoblastic cells of the developing placenta act as an endocrine organ and secrete a hormone that somehow acts on the corpus luteum of the ovary to continue its secretion of progesterone. The hormone apparently differs from species to species (DEANESLY, 1966, p. 959) and is given the general term "chorionic gonadotropin" in at least the primates and the mare. Although the chemical nature of the hormone and its mode of action upon luteal cells seems to be diverse among placental mammals, it is probably a feature common within the infraclass. The placenta itself begins the secretion of progesterone after a given duration of pregnancy in several eutherian groups (ASDELL, 1966, p. 4). Thus the secretory importance of the corpus luteum is reduced and frequently it partly degenerates long before the termination of pregnancy. The distribution of this trait is taxonomically widespread among eutherians.

No evidence has yet been found to indicate the presence of chorionic gonadotropins or the secretion of progesterone by the placenta within the Marsupialia. As a consequence, the nonpregnant and pregnant estrous cycles are identical in marsupials, and only a few specialized mechanisms exist to successfully extend the duration of pregnancy beyond that of the uterine secretory phase. Some of the kangaroos have gestation periods that extend a few days into the beginning of the expected succeeding estrous cycle (SHARMAN *et al.*, 1966). Gestation in the Australian quokka *(Setonix)* is prolonged well beyond the termination of the secretory phase, but does not extend into the next estrous cycle (TYNDALE-BISCOE, 1963a). The quokka prolongs its gestation period by an increase in vascularization of its placenta and by more intimate approximation of the maternal and fetal tissues and apparently involves no fetal endocrine function (TYNDALE-BISCOE, 1963b). At any rate, no marsupial group has been particularly successful in devising mechanisms for a significant increase in the length of internal gestation. The net increase in time is minor when compared to that observed in many eutherian lineages. The physiological equivalence of the nonpregnant and pregnant estrous cycles in marsupials is dramatically emphasized by experiments involving transfer of developing blastocysts from a pregnant to a nonpregnant female. Transferred blastocysts are readily maintained in the uterus of a nonpregnant female during any part of the secretory phase. If the recipient and donor females are in equivalent stages of the estrous cycle, or if the donor is somewhat more advanced, the blastocyst will develop fully and undergo normal birth (TYNDALE-BISCOE, 1963b).

Within the amniotes, the presence of chorionic gonadotropins combined with the prolonged maintenance of pregnancy thus seems to be a unique feature of eutherians. It is my opinion that the importance of this feature cannot be overemphasized. All prenatal development must occur during a short gestation period in marsupials and the animal must be anatomically and functionally advanced to the point that it can crawl on its own to the teat at the time of birth. Many organs such as the lungs, forelimbs, claws (sometimes deciduous), and nervous system must be precociously developed. HUXLEY (1880, p.

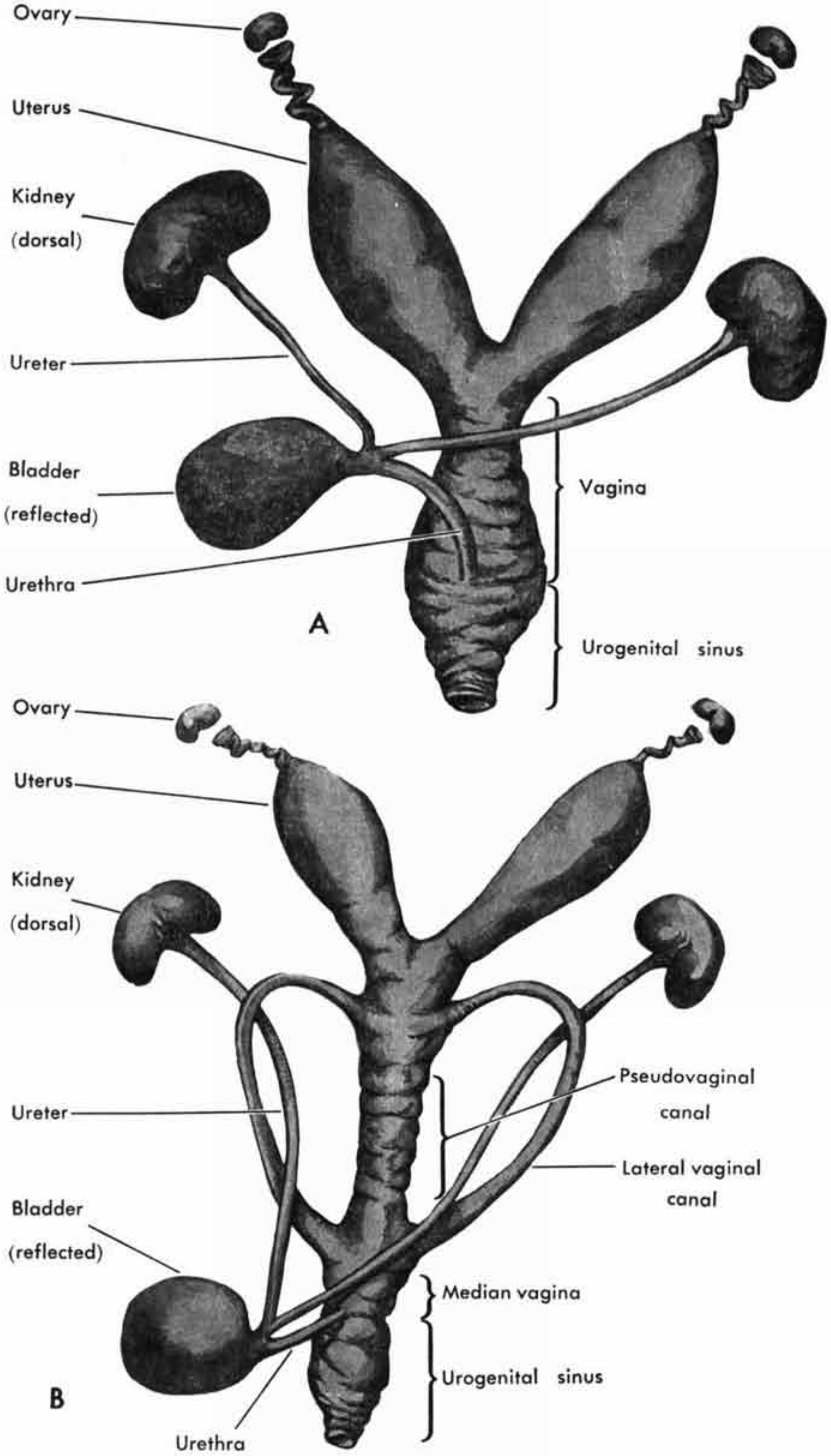

FIG. 45. Spatial relationships of female urogenital systems in ventral views, *(A)* "typical" eutherian (placental) and *(B)* "typical" metatherian (marsupial) mammals, the latter at time of parturition.

656) and several others since him have argued that the short gestation period is secondary, having been derived from a more primitive, longer period of gestation. Although such an interpretation cannot be completely disproven, I suggest that it is less likely than two alternate possibilities.

First, it is possible that viviparity was independently derived in marsupials and placentals from a primitive egg-laying state as exhibited today by the monotremes. This seems unlikely to me because of the striking similarity between marsupials and placentals of the histological structure and function of the uterus and the near identity of the hormonal control of reproduction. Such sophisticated structure and function would not be expected in an oviparous common ancestor (HILL, 1933, 1941; ECKSTEIN & ZUCKERMAN, 1956b, p. 544, for condition in monotremes). Rather profound parallel evolution would have to be postulated to account for the marsupial-placental similarities. Secondly, it is possible that the Early Cretaceous common ancestor was already viviparous in a primitively "marsupial" sense. That is, the animals were born alive and free from a shell after a short period of gestation. Placental hormones and the multitude of other modifications necessary for prolonged internal gestation could then have been evolved exclusively within the early "eutherian" stock.

I prefer to accept the second alternate described above because it is more parsimonious. Other arguments in favor of the marsupial condition being a logical transition between oviparity and viviparity in the eutherian sense shall be put forward with further development of this paper. The development of viviparity from a primitive oviparous condition undoubtedly underwent many early experiments involving egg retention and shell and yolk reduction (WEEKES, 1935). It is anatomically, physiologically, and paleontologically probable, however, that living marsupials and placentals were derived from a common stock.

COMPARATIVE ARCHITECTURE OF UROGENITAL DUCTS

The "typical" eutherian arrangement of urogenital ducts is illustrated in Figure 45,*A*. The uteri are usually paired, but various degrees of fusion are noted (ECKSTEIN & ZUCKERMAN, 1956a). A single median vagina is formed by the fusion of embryologically paired Müllerian ducts. The ureters drain the metanephric kidneys and open at or near the base of the urinary bladder. It is important to note that the ureters run lateral to the single median vagina. The bladder is drained by the cystic urethra which empties into the urogenital sinus.

The "typical" metatherian arrangement of urogenital ducts is illustrated in Figure 45,*B*. At first sight, the arrangement looks strange and quite "nonmammalian." As in the eutherians, the uteri are paired, but the vaginal complex differs in that three elements are present; paired "lateral vaginal canals" and a single median "pseudovaginal canal." As described below, the lateral vaginal canals are homologous with the vertebrate Müllerian ducts and the pseudovaginal canal is a specialization peculiar to marsupials. The ureters open at or near the base of the bladder, but in contrast to the eutherian plan, are medial to the true vaginae in marsupials. As in most eutherians, the urethra drains into a short urogenital sinus. Although the literature abounds with information concerning the "cloaca" of marsupials, MCCRADY (1940) convincingly showed that no such structure exists. The termination of the digestive and urogenital tracts are completely separated, and copulation in the opossum is accomplished by the insertion of a male phallus into a smaller but fully developed, malelike, female phallus. Although occasional embryos have been found in the lateral vaginal canals (FLYNN, 1923), birth is almost always by way of the pseudovaginal canal to the urogenital sinus (PEARSON, 1947).

The later stages in the embryogenesis of the marsupial urogenital tracts are semidiagrammatically shown in Figure 46 (BAXTER, 1935, for details). The paired Müllerian ducts, lateral to the ureters, differentiate along their lengths to form the uteri and lateral vaginae. The two Müllerian ducts become appressed about midway along their lengths, their lumina being separated by a double wall. The double wall breaks down in most marsupials, uniting the lumina of the two vaginae as a single cul-de-sac. The separating septum is retained, however, in a few species. Near the time of birth of the first litter from the adult, the median cul-de-sac is extended posteriorly to a contact with the median vagina. The walls of the median vagina and cul-de-sac rupture at the point of contact and the young pass through the opening to the exterior via the urogenital sinus (TYNDALE-BISCOE, 1966). The posterior part of the pseudovaginal canal is usually a network of connective tissue strands. Some evidence exists that the hormone relaxin may act specifically on softening the connective tissue for the process of birth (TYNDALE-BISCOE, 1963a). Relaxin in eutherians is also active in the birth process, working principally on the connective tissues of the various symphyses of the pelvic region (DEANESLY, 1966, p. 994). The pseudovaginal canal in most marsupials loses its direct connection with the urogenital sinus after birth, but remains permanently open in some species.

A second look at Figure 46 shows that although the urogenital ducts of the adult and reproductive stages appear to be peculiarly specialized, the condition in pouch young resembles that in reptiles. All birds, reptiles, and monotremes have the derivatives of the embryological Müllerian ducts completely separated along their lengths to the cloaca. The Müllerian ducts in all noneutherian amniotes are laterally placed with respect to the ureters (GRASSÉ, 1955, p. 75, fig. 69, for monotreme condition). Only two fundamental differences in the spatial arrange-

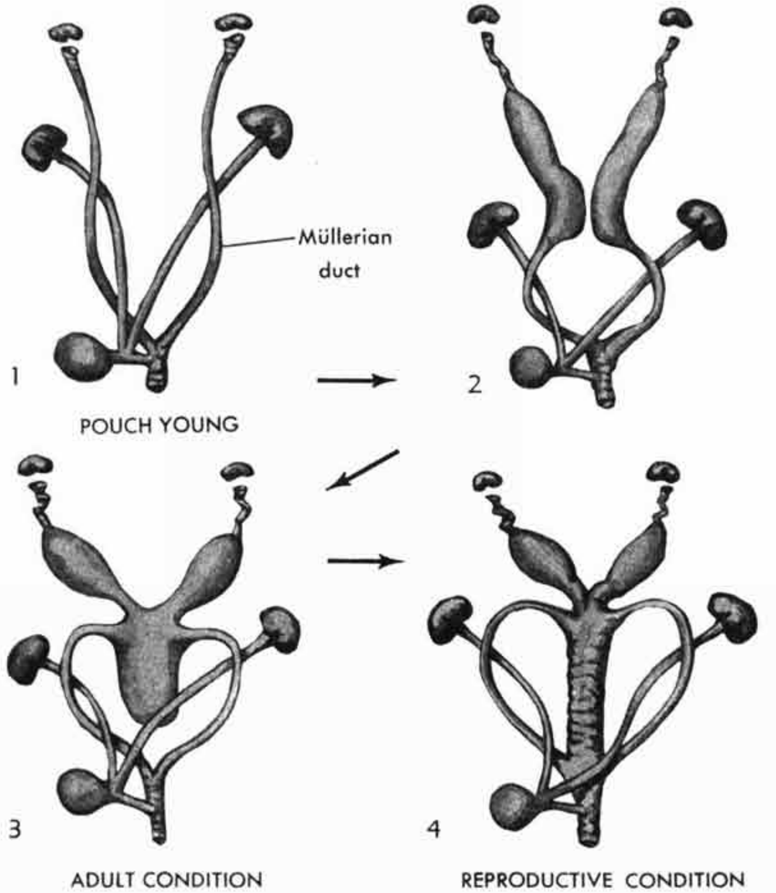

Fig. 46. Semidiagrammatic views showing embryological development of derivatives of Müllerian ducts in female marsupial.

ment of the urogenital ducts exist between the early pouch young marsupial and the other noneutherian amniotes. First, the ureters empty into the base of the bladder in the marsupials rather than into the anterodorsal wall of the cloaca as in the other groups. Secondly, the cloaca is developmentally modified into a urogenital sinus distinct from the termination of the digestive tract. Both these differences from noneutherian amniotes are held in common with the eutherians. Thus the female urogenital tract of marsupials, like so many other features of their morphology, shows a remarkable mixture of reptilian and typically mammalian characters. The only feature of the urogenital ducts specifically peculiar to the Marsupialia is the pseudovaginal canal. Thus it becomes clear that it is the eutherian condition that differs most significantly from the primitive amniote plan, and it is the placentals, not the marsupials, that are structurally unique.

It is of fundamental importance to understand how the basic difference in the spatial relationship between the ureters and genital ducts of eutherians and noneutherian amniotes comes about. A diagrammatic comparison is presented in Figure 47, the details of which have been derived principally from the work of Buchanan & Fraser (1919), McCrady (1940), Burns (1942, 1945b), Pearson (1947), and Arey (1954). It should be emphasized that the drawings are diagrammatic and were made principally to clarify the spatial relationships involved.

The mesonephric (Wolffian) ducts grow backward through the genital ridge to make contact with the dorsolateral wall of the cloaca (Fig. 47,*a*). The direction of growth taken by the ureteric buds from the mesonephric ducts is the key to the whole problem. The ureteric bud in all amniotes initially starts growth straight dorsally, and such a course is maintained in the nontherians. However, the bud quickly shifts to a dorsomediad course in the marsupials and a dorsolateral direction in the placentals (Fig. 47,*b*,*b*′). The Müllerian ducts grow rearward, closely paralleling the mesonephric ducts. The Müllerian ducts gradually shift their orientation along their length from a position lateral to the mesonephric duct, to a ventral, then to a medial position (Fig. 47,*c*,*c*′). Baxter (1935) suggested that the caudal part of the mesonephric duct contributes to the construction of the caudal part of the Müllerian duct. Meanwhile, the ureteric buds grow dorsally into developing tissue of

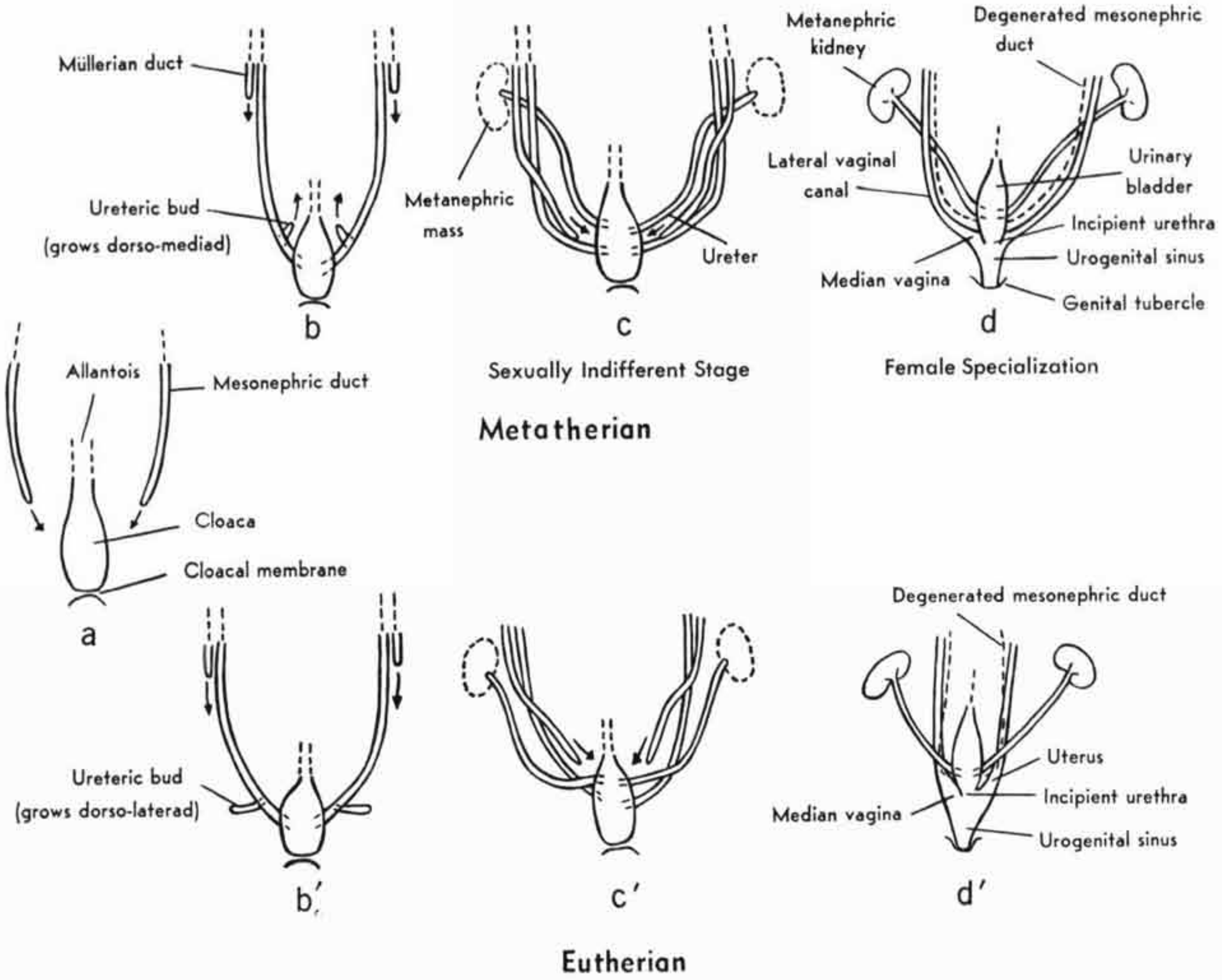

FIG. 47. Diagrammatic illustrations comparing development of differences in spatial relationships observed in female urogenital ducts between marsupial and placental mammals (ventral views).

the metanephros, medial to the Müllerian ducts in non-eutherians and lateral to them in the eutherians. The marsupial stage shown in Figure 47,*c* differs in no essential way from the adult condition in reptiles, birds, and monotremes. The equivalent eutherian stage (Fig. 47,*c′*), on the other hand, significantly differs from all other amniotes in that the ureters are lateral to the Müllerian ducts. The base of the ureteric bud becomes incorporated into the wall of the cloaca, thus losing its connection with the mesonephric duct, and, by differential growth of the cloacal wall, is moved somewhat anteriorly from the mesonephric duct. Finally, therian refinements of the basic structure occur (Fig. 47,*d,d′*) in that: 1) the cloaca becomes divided into a urogenital sinus distinct from the digestive tract; 2) the caudal end of the ureters become restricted to the base of the urinary bladder; 3) a distinct urethra is formed; and 4) the caudal ends of the Müllerian ducts fuse into a median vagina. Vaginal fusion is complete or nearly so in eutherians, but is only partial in marsupials. As PEARSON (1947, p. 74) emphasized, the presence of the ureters medial to the vaginae in marsupials does not "prohibit" the fusion of the vaginal walls, but rather is a phylogenetic holdover from a primitive developmental condition.

Generally, the majority of attention is given to the differences in the female urogenital tracts between marsupials and placentals. However, the mesonephric duct in the male becomes the vasa deferentia of the adult and, as PEARSON (1947, p. 73) pointed out, has the same spatial relationship as the Müllerian ducts with respect to the ureters between marsupials and placentals.

Considerations of the antiquity of that part of the urethra that drains the bladder are of critical importance to the study of the spatial relationships of the therian urogenital ducts. The presence of a true urethra with the ureters emptying into the base of the bladder is a character restricted to the Theria. Was the structure present in the common ancestor of the marsupials and placentals, or was it independently derived between the two groups? Although Cowper's glands are present in the monotremes (Grassé, 1955, p. 74), prostate and urethral glands are restricted to the therians. Chase (1939), in a detailed study of the male reproductive system of *Didelphis*, found that the development, histology, and basic structure of the prostate, urethral, and Cowper's glands are similar to those of eutherian mammals, but in several respects are of a more diffuse, probably more primitive, organization. The development and structure of the urethra itself shows no fundamental differences from eutherians. It seems unlikely that such similarities in development, structure, and function could have been independently derived between marsupials and placentals, and I suggest that the urethra, with its accessory glands, was a feature present in the common therian ancestor. As was pointed out following the comparative discussion of the spatial embryogensis of the therian urogenital ducts, the marsupials differ less significantly from the primitive amniote plan than the placentals. Only the eutherians among the amniotes have their ureters lateral to the genital ducts. Thus I find no conflict with the idea that the ancestral therian had a distinct urethra draining the bladder and ureters that were medial to the genital ducts and conveyed their urine into the base of the bladder—i.e., the condition seen in living marsupials.

The antiquity of the pseudovaginal canal can only be discussed in terms of speculation. Most workers agree that the primitive amniote path of birth was via completely separated right and left oviducts. The various types of oviductal fusion along the mid-line seen in therians undoubtedly represent specializations. The pseudovaginal canal is a feature held in common between Australian and American marsupials, and as shown in Figure 41, the two stocks probably have been genetically isolated from each other since the Late Cretaceous. Thus the psuedovaginal canal is probably an ancient structure, but no evidence is available to suggest its presence or absence in the most primitive Early Cretaceous therians. It is only my guess that birth in the primitive Theria was via a reptilian path with the pseudovaginal canal being a marsupial specialization. Birth is via medial pathways both in eutherians and metatherians. The advantages of such a path in placentals are obvious; the pelvic area of the body cavity is crowded, the embryos are large, must be wrenched free from intimate endometrial connections, and must be forced to the outside by strong contractions of the uterine musculature. Complete fusion of the Müllerian ducts to form a long median vagina can be easily accomplished only if the ureters are placed lateral to the genital ducts. This has been accomplished among the amniotes only in the eutherians by the unique path taken by the early growth of the ureteric bud (Fig. 47,*b'*).

The advantages of a median birth canal (the pseudovaginal canal) in a marsupial in which the offspring are small, on the other hand, are less obvious. It may simply be that it is the shortest path to the outside and thus facilitates speed in the birth process. The mechanics of the birth process in marsupials have not been adequately studied. At any rate, the pseudovaginal canal is universally present among marsupials, is almost always used during the birth process, and is assumed to be of some selective advantage over birth via the lateral vaginal canals.

It should be clear following the above series of comparisons that the spatial arrangement of the urogenital tubes of the metatherian is not as peculiarly specialized as one would assume at first glance. The ducts show an interesting mosaic of reptilian and typically mammalian characters in their arrangement. The only character in the marsupial plan that is unique among the amniotes is the presence of the pseudovaginal canal, the phylogenetic significance of which is unknown. Pearson (1947, p. 99), following a discussion concerning the difference between marsupials and placentals in the position of ureters and genital ducts, stated:

> This cardinal difference is such that it is inconceivable that the Metatheria gave rise to the Eutheria, as Abbie (1941) would have us believe, or that, on the contrary, the Metatheria arose from the Eutheria as Hubrecht (1909) supposed.

I certainly agree with Pearson in that metatherians were not derived from eutherians. However, I believe his position that eutherians cannot be derived from metatherians on the basis of the arrangement of their urogenital ducts is a little extreme. The differences between the marsupial and placental plans simply are not that profound. The necessary evolutionary alterations (Fig. 47) could easily have been made upon selection for a strongly muscular, single median birth canal to cope with increasingly large offspring in eutherians. Occasional pathological reversals to an essentially marsupial condition of the genital ducts ("uterus didelphys") have been noted in man (e.g., Meyer, 1941).

COMPARISONS OF EARLY DEVELOPMENT

NONTHERIAN AMNIOTES

The early stages of morphogenesis of birds, reptiles, and monotremes are diagrammatically illustrated in Figure 48. Details can be found in any book concerned with comparative embryology (e.g., Nelsen, 1953). The uncleaved fertilized eggs are characterized by shell membranes, copious layers of albumen, and a relatively enormous quantity of yolk. The cytoplasm of the zygote is flattened on the surface of the yolk (Fig. 48,*a*). The

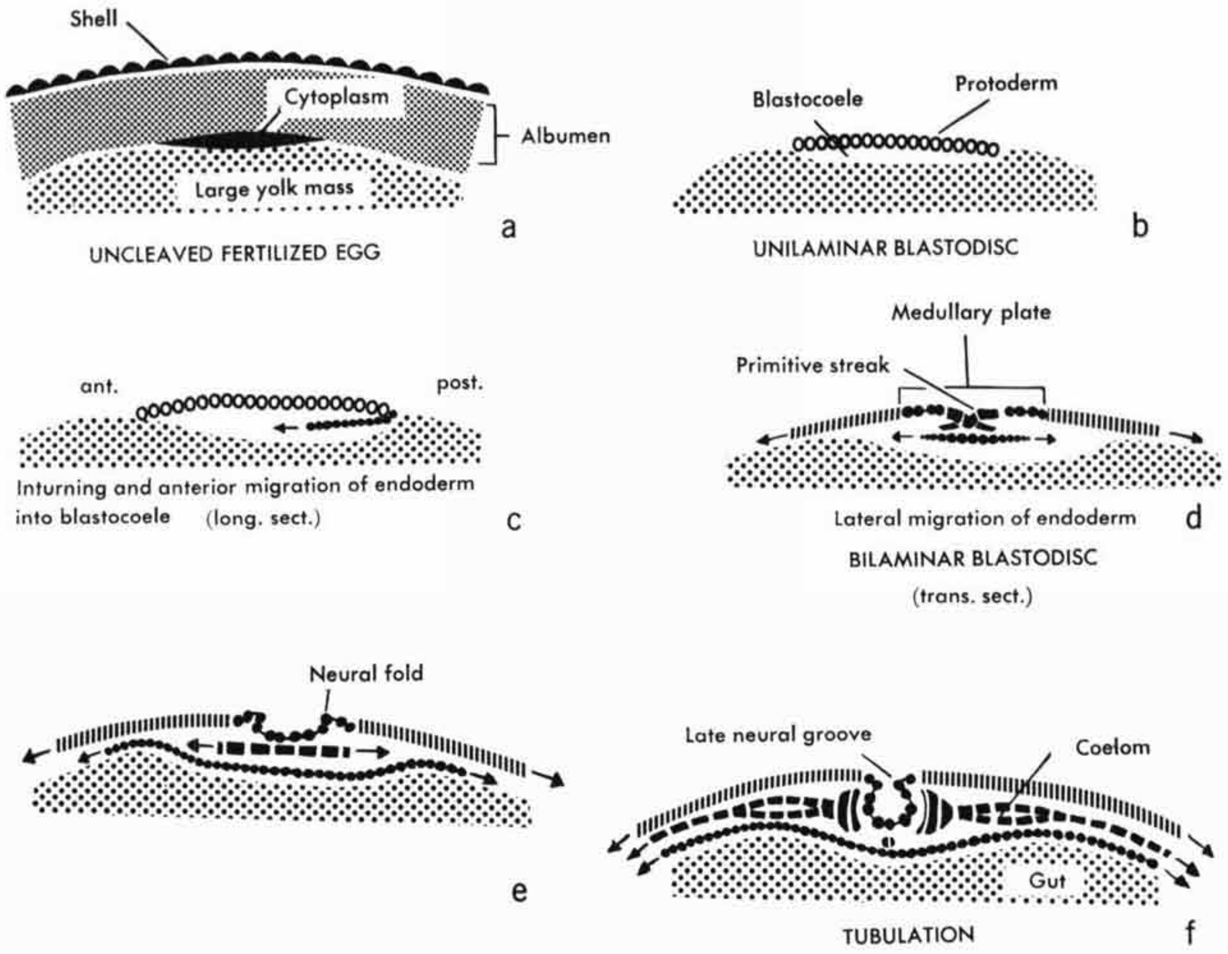

FIG. 48. Diagrammatic summary of early development of reptile, bird, or monotreme.

cytoplasm of the zygote rapidly proliferates mitotically (Fig. 48,*b*) to form a disc of cells (the unilaminar blastodisc), which is separated from the yolk by a space (the blastocoele). The cells of the unilaminar blastodisc are termed "protodermal" since they form the presumptive cells of the three primary germ layers. The unilaminar blastodisc becomes changed to a two-layered structure (the bilaminar blastodisc, Fig. 48,*d*) by an inturning, anterior migration, and proliferation of presumptive endoderm cells from the posterior part of the disc (Fig. 48,*c*). The bilaminar blastodisc is converted to a three-layered embryo (Fig. 48,*e*) by the migration of presumptive mesodermal cells from the primitive streak. The neural folds quickly close over to form the neural tube. Figure 48,*f* illustrates the formation of the three basic tubes of the body; the neural tube, the paired coelomic cavities, and the gut. The coelomic cavities are formed by a process of delamination of the lateral mesoderm. The gut is enormous early in development but soon becomes restricted by a variety of occurrences.

MARSUPIALS

The following summarizing description is based principally on the study of McCrady (1938) on *Didelphis*, an outstanding reference work that frequently has been overlooked by subsequent investigators. The fertilized egg (Fig. 49,*a*) is surrounded by a distinct leathery shell membrane and layers of albumen (Austin, 1961, p. 102). Yolk droplets, which are more or less peripherally arranged, are found within the cytoplasm of the zygote. The albumen layers thicken considerably upon the first cleavage (Fig. 49,*b*) by the addition of water. The yolk droplets begin to be extruded from the daughter cells upon the first cleavage. This phenomenon has not, to my knowledge, been studied by the use of an electron microscope and the exact mechanism is unknown. The daughter cells of the early and late four-cell stage of Figure 49,*c*,*d* are drawn to the same scale. It is noted that the cell volumes of the later stage are considerably reduced from the earlier stage, presumably due to the extrusion of

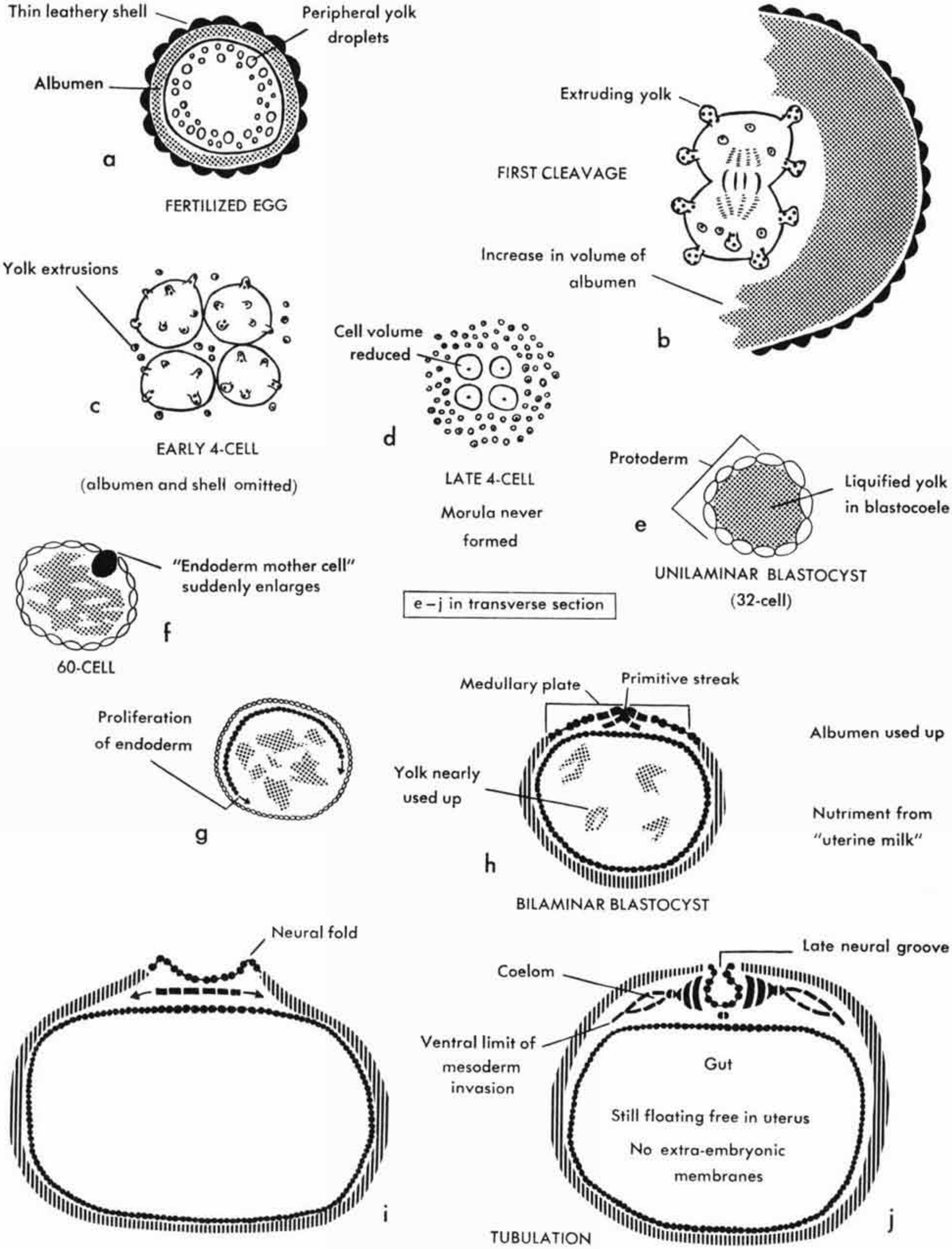

FIG. 49. Diagrammatic summary of early development of marsupial mammal (adapted from McCrady, 1938).

yolk. Yolk droplets are abundantly represented outside of the cells in the late four-cell stage. A solid mass of dividing cells (the morula) is not formed in marsupials, but the cells immediately become ordered into a hollow sphere (unilaminar blastocyst, Fig. 49,*e*). The yolk is somehow entrapped within the blastocoele of the unilaminar blastocyst and becomes liquified. Again, the cells of the unilaminar blastocyst are termed "protodermal" since they will differentiate into all three basic germ layers of the body.

It is important to note here that the relationships of the marsupial stage shown in Figure 49,*e* are comparable with the "reptilian" stage shown in Figure 48,*b*. The only difference is that the marsupial protoderm is arranged as a sphere ("-cyst") rather than as a relatively flat surface ("-disc"). It is most probable that the marsupial condition represents an adaptation to cope with a reduced yolk content from a primitively more heavily yolk-laden egg.

At about the 60-cell stage (Fig. 49,*f*) one cell (the "endoderm mother cell") suddenly enlarges and proliferates into presumptive endoderm cells (Fig. 49,*g*), thus changing the embryo from a single- to a double-layered structure (the bilaminar blastocyst, Fig. 49,*h*).

Yolk and albumen are practically used up for nourishment by the embryo by the time the bilaminar blastocyst is completed. From that stage (late in the sixth day of a 13-day gestation period in *Didelphis*) until birth, the embryo is entirely dependent upon the secretions of the uterine glands ("uterine milk") for its nutrition.

Migration of presumptive mesoderm from the primitive streak changes the embryo from a double- to a triple-layered structure (Fig. 49,*i*). Finally, the neural folds close over to form the neural tube and the lateral mesoderm delaminates to form the coelomic cavities. The elements of the gut were already present, thus the three basic tubes of the adult body are formed (Fig. 49,*j*).

Only one fundamental difference exists between the early development of a marsupial (Fig. 49) and that of the nontherian amniote (Fig. 48). The yolk content of marsupials is significantly reduced, thus the embryo early takes the form of a sphere rather than a disc. Dependence upon the uterine secretions for nutrition of the embryo is thus significantly greater in marsupials. FLYNN & HILL (1947) pointed out striking similarities between the early development of the monotremes and the marsupials. I believe it is justified to state that the early embryology of marsupials is fundamentally "reptilian" in contrast to the condition exhibited by the placental mammals.

The embryo remains floating free in the fluids of the uterus for some time following tubulation, but eventually become appressed against the uterine wall. Although the contact between fetal and maternal tissues may become quite intimate in some marsupials (TYNDALE-BISCOE, 1963a), true implantation by erosion of the maternal epithelium never occurs in marsupials. Although the rudiments of the embryo proper (Fig. 49,*j*) are well established by the middle of the gestation period in marsupials, the extra-embryonic membranes are poorly represented. The development of the amnion (*see* MAHLO, 1963, for fine structure), chorion, and allantois begins late in comparison with eutherians. The yolk sac, on the other hand, is large in early stages and the vitelline blood supply functions in the absorption of nutrients from the uterine milk. The yolk sac is, of course, devoid of yolk.

PLACENTALS

Early development within the eutherians is highly variable with many group-specific modifications (see MOSSMAN, 1937, for comparative discussion). However, all show common modifications not seen in other amniotes. The illustrations in Figure 50 are based principally upon development in primates as discussed by AREY (1954), but the descriptions apply to most eutherians.

Eutherian eggs have little or no albumen or yolk, and the shell membranes are lacking (AUSTIN, 1961). The comparative study of the detailed anatomy of preimplantation stages is in its infancy (WOLSTENHOLME & O'CONNOR, 1965). In contrast to the marsupials, a solid mass of cells (the morula) is formed after several divisions. Quickly, however, the morula begins to hollow out (Fig. 50,*b*) to form a cavity analogus to the blastocoele of other amniotes. The "blastocoele" of the eutherian is not, however, homologous with that of noneutherian amniotes.

Implantation of the embryo occurs early in the development of eutherians (BOYD & HAMILTON, 1952) and is often accompanied by erosion into the maternal epithelium. Erosion is accomplished by a combination of necrosis of the endometrium, due to a shutdown of maternal vascularization, and by the action of cytolytic enzymes derived from the membranes of the developing embryo (AREY, 1954, p. 125). As stated above, implantation involving endometrial erosion is restricted to the eutherians.

Further cellular proliferation results in the increase in volume of the "blastocoele" (Fig. 50,*c*). A differentiation can be seen at this time in that a clump of cells (the inner cell mass) is appressed against the inside of the cellular sphere (trophoblast). Contributions from the inner cell mass will eventually form the entire embryo proper and some of its extra-embryonic membranes. The trophoblast is involved solely with the formation of extra-embryonic membranes. The differentiation of an inner cell mass distinct from a trophoblast is not found in marsupials (SHARMAN, 1961, p. 203) and the phenomenon is thus peculiar to the eutherians among the amniotes.

The development of the extra-embryonic membranes occurs rapidly in eutherians. The amnion formation (Fig. 50,*d*) is accomplished either by a process of folding or a more specialized delamination (MOSSMAN, 1937, p. 139). The yolk sac is relatively large in the early stages of development (*see* plates in MOSSMAN, 1937, for comparative information). Recent studies have shown that the

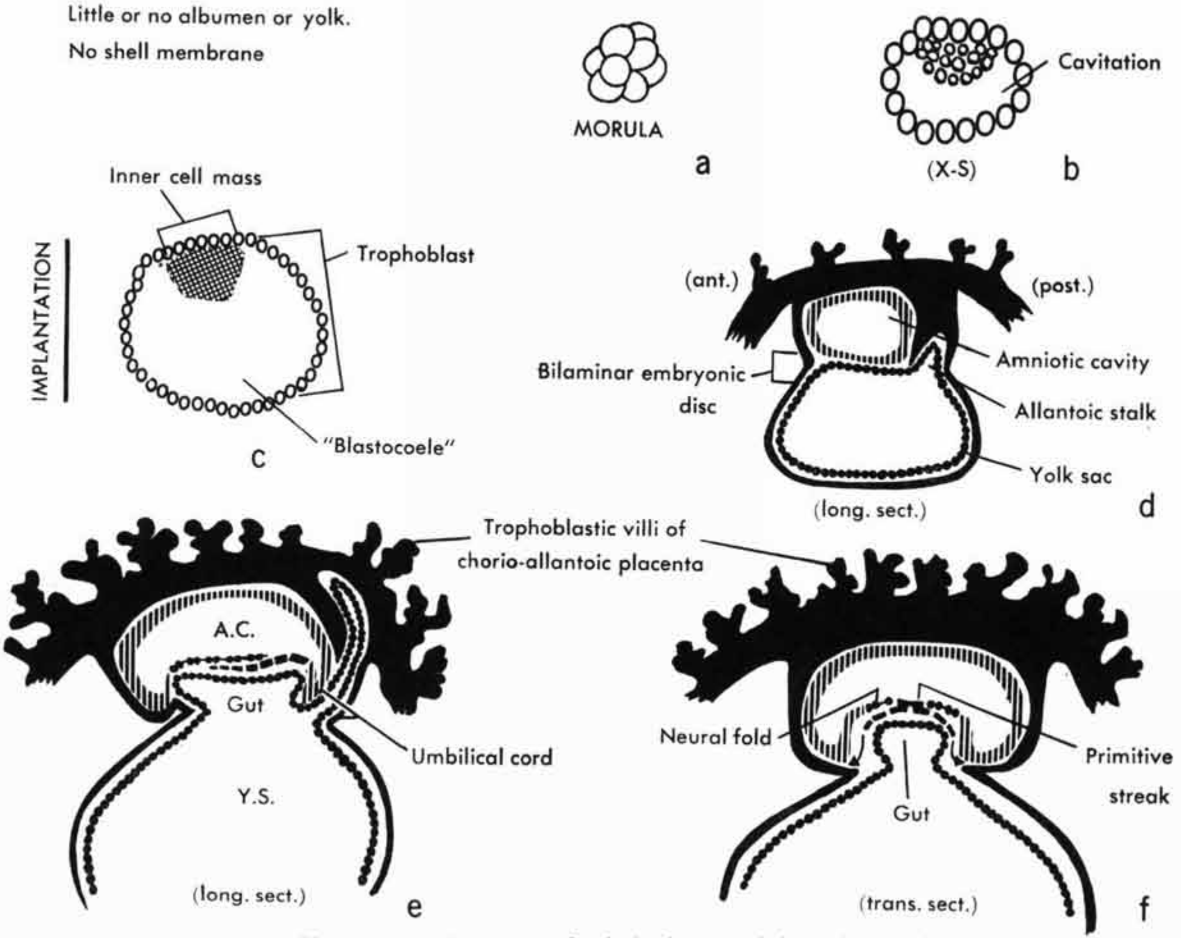

FIG. 50. Diagrammatic summary of early development of placental mammal.

yolk sac actively absorbs and transports nutrients from the surrounding medium (PADYKULA *et al.*, 1966; DEREN *et al.*, 1966a, 1966b) and thus is not merely a phylogenetic remnant. The yolk sac is also active, as in all other amniotes, in the early development of blood (AREY, 1954, p. 340). Although a semipermanent allantoic vesicle of the "reptilian" and marsupial (Fig. 51) type usually does not develop, an allantoic stalk quickly grows from the posterior part of the embryo proper to the trophoblast, carrying with it the important allantoic (umbilical) blood vessels (Fig. 50,*d*). The allantoic stalk itself usually atrophies, but the umbilical vessels remain and branch profusely within the trophoblast. Complex villi rapidly develop on the outer surface of the trophoblast to increase the area of contact between the fetal and maternal tissues. Thus the rudiments of the chorioallantoic placenta characteristic of the eutherian mammals is established remarkably rapidly. The yolk sac gradually decreases in size and becomes incorporated into the ventral wall of the gut.

Although the extra-embryonic membranes are developed quickly in eutherians, the organization of the embryo itself is usually delayed. For example, the stage of the poorly developed embryo shown in Figure 50,*e,f* is comparable to roughly two weeks of development in the human (AREY, 1954, opposite p. 106, reference table) and the pig (PATTEN, 1952, p. 53). The early developmental emphasis is placed on rapid construction of the chorioallantoic placenta. The yolk sac functions for the early nutrition of the embryo, but when the more effective vascularization of the chorioallantoic placenta is established, the yolk sac degenerates. Differentiation of the cells within the inner cell mass in eutherians is temporarily delayed until an effective nutritive source, the chorioallantoic placenta, is established. Early developmental emphasis in marsupials (Fig. 49), on the other hand, is placed on the construction of the embryo proper. The basic plan of the separation of the primary germ layers of the animal is complete in the stage shown in Figure 49,2*f* after only nine and one-third days of gestation in *Didelphis* (MCCRADY, 1938, p. 75). Only the nutritive yolk sac among the extra-embryonic membranes is strongly developed until rather late in the period of development.

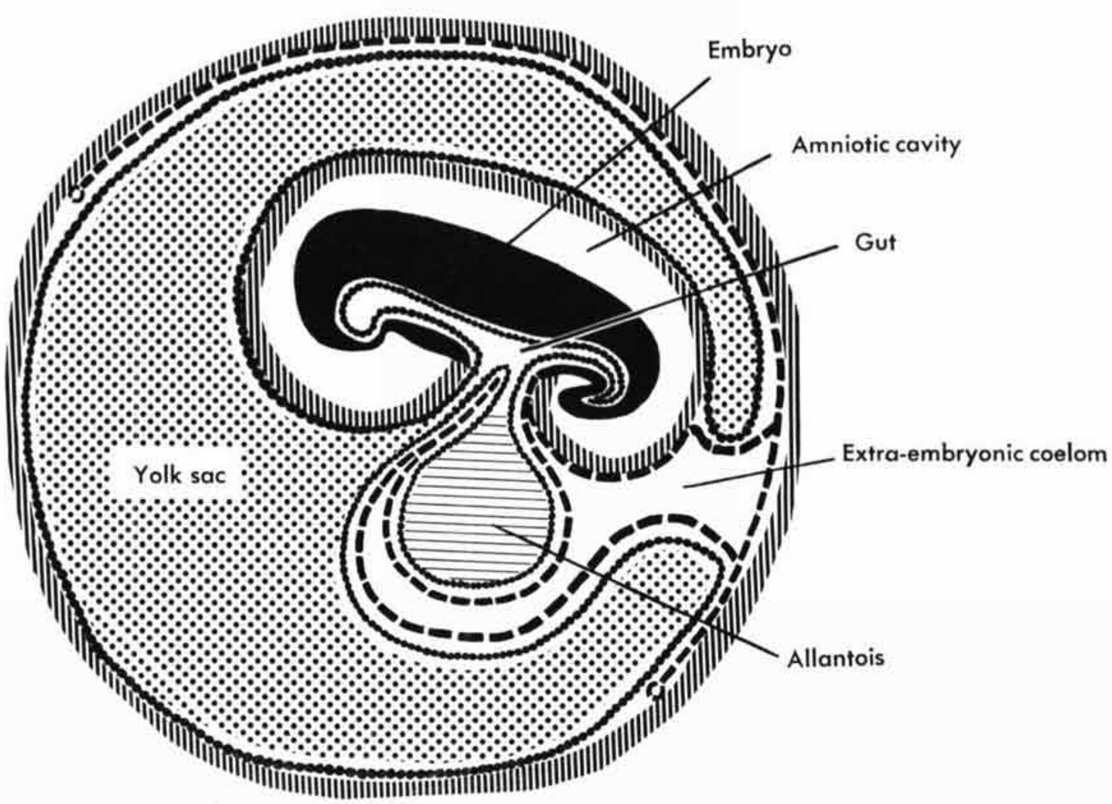

FIG. 51. Diagrammatic view of yolk sac placenta characteristic of *Didelphis* (after McCrady, 1938).

SUMMARY OF COMPARATIVE EARLY DEVELOPMENT OF THERIANS

Only four basic differences exist between the early development of marsupials and placentals. First, eutherians show an extreme reduction of the albumen and yolk, and the shell membranes. Second, eutherians usually have an intimate type of implantation, frequently with some endometrial erosion. Third, a specialization exists in eutherians in the differentiation of an inner cell mass and trophoblast. The "trophoblast" as used in the eutherian sense is a neomorphic structure peculiar to the group with no specific homologue in other amniotes. Finally, the development in eutherians emphasizes the early organization of the extra-embryonic membranes at the expense of the differentiation of the embryo proper. The reverse is true in marsupials.

The rapid development of effective placentation in the eutherians is associated with the lack of yolk and albumen. The delayed development of the embryo proper is tolerated because of the comparatively long time available for internal gestation due to the action of placental hormones, the continuation of progesterone secretion by the corpus luteum, and the prolongation of the endometrial secretory phase beyond its normal (nonpregnant) time of regression. Conversely, in marsupials, the embryonic animal must be developed to the point of being able to crawl by its own efforts from the vaginal orifice to the teat after a short period of gestation. Thus the embryo itself precociously develops at the expense of the extra-embryonic membranes—the embryo must be out of the uterus before the endometrial walls literally collapse around it.

The general marsupial plan of early development seems plainly reptilian with certain specializations for coping with reduced yolk and for viviparity. The eutherian plan, on the other hand, shows more profound specializations involved with a prolonged gestation period, including the precocious development of extra-embryonic (nutritive) membranes and the delayed development of embryonic tissues proper. It seems to me that the mechanisms seen in placental mammals could not have been developed within the Theria until after the evolution of the hormonal pathways leading to a prolongation of internal gestation. Thus again it seems the marsupial mode of reproduction seen today would be a logical half-way point in the evolution of viviparity from oviparous reptiles to the highly efficient processes seen in eutherians. I can find no reason to believe that marsupial early development is importantly specialized from a condition expected in an Early Cretaceous therian ancestral to both the marsupials and placentals.

COMPARISONS OF PLACENTATION

The vitelline circulation of the yolk sac of reptiles, birds, and monotremes acts in liquifying the yolk and carrying its nutrients to the cells of the developing embryo. The presence of a large yolk sac is certainly a primitive amniote feature. The allantois serves both as a storage place for nitrogenous wastes and as an organ of gaseous exchange to the atmosphere.

The term "placental" mammals for eutherians is indeed a misnomer since all marsupial mammals also have one of two basic kinds of placentae. The arrangement of extra-embryonic membranes of *Didelphis*, which is basically similar to that of most marsupials, is shown in Figure 51. The yolk sac is huge and has placental functions in the absorption of nutrients from the uterine milk. It is usually called a "yolk sac placenta." The allantois is small, does not make contact with the exterior surface of the extra-embryonic vesicle, and functions only as a urinary reservoir (McCrady, 1938, p. 116). However, functional chorioallantoic placentae similar in some respects to those seen in eutherians are present in at least two distinct lines of Australian marsupials (Sharman, 1961).

The yolk sac is also large (Mossman, 1937) and probably active in absorption of uterine secretions in the early stages of development in most eutherians (Padykula *et al.*, 1966; Deren *et al.*, 1966a, 1966b). However, the allantoic stalk grows to the trophoblast (Fig. 50,*e*), carrying with it the umbilical vessels, and the vessels divide quickly into the reticulate network characteristic of the eutherian chorioallantoic placenta.

It is the current consensus (e.g., Pearson, 1947, p. 85; Sharman, 1961, p. 214), with which I fully agree, that the yolk sac placenta seen in living didelphid marsupials is probably closely similar to the primitive therian condition. The chorioallantoic placenta was probably independently derived among perameloid marsupials, the primitive eutherian stock, and several distinct groups of viviparous reptiles (Weekes, 1935). With the increase in the length of the gestation period characteristic of eutherian mammals, the function of a simple yolk sac and restricted allantois would have become inadequate beyond early embryonic development. The increasing size of the embryo required a more efficient transport system of materials—nutrients and oxygen to the cells and waste products from the cells. Gas and nutrient exchange to and from the uterine milk via the vitelline circulation and the storage of nitrogenous wastes in the allantoic vesicle were inefficient processes compared to the continuous flow system provided by close contact between the umbilical capillaries and the maternal circulation (*see* Ramsey, 1967, for details of maternal vascularization). The development of effective placentation in eutherians must have been closely allied with the multitude of other physiological and anatomical modifications necessary for prolonged internal gestation.

Keeping the above considerations in mind, I can find no fundamental reason to assume that the placentation seen in living didelphid marsupials is far removed, anatomically or functionally, from a condition expected in an Early Cretaceous therian ancestral to both the marsupials and placentals.

SIGNIFICANCE OF EPIPUBIC BONES AND POUCH

A pouch (marsupium) is present in most, though certainly not all, adult female marsupials. The pouch is formed by elevations of the skin on either side of the mammary area that are thrown medially to form double-walled folds (Enders, 1937; *see* Burns, 1945a, pl. 6, for illustrations of early formation). The musculature of the pouch is always formed by the dermal superficial muscles of the skin, the panniculus carnosus. The musculature is usually developed in three units, and functions more in the closure of the pouch by an anterior pull than in its actual support. The gross structure of the pouch is highly variable from one species to the next. Sometimes it is a great pendulous bag as in the kangaroos, and sometimes it is absent as in the American genus *Marmosa*. However, *Marmosa* has the reduced muscular components necessary for pouch development. Although the pouch generally opens anteriorly, it may open posteriorly as in the fossorial Australian bandicoots. Males of *Notoryctes*, the Australian marsupial mole, like the eutherian moles, have undescended testes and lack a scrotum. However, the male has a small, though fully developed pouch (Sweet, 1907). Males of the American water-opossum, *Chironectes*, have a scrotum and a small pouch that encloses the scrotum during violent activity and swimming (Enders, 1937).

A pouch is lacking in the nest-building duck-billed platypus, but an "incubatorium" is present in the echidna as a transitory structure after the eggs are laid (Grassé, 1955, p. 52; *see* Griffiths, 1965, for photographs). The echidna's pouch, as that of the marsupials, has the panniculus carnosus as its musculature and is closed in the same manner. Although the pouch may have been independently derived between the monotremes and the marsupials, I feel they may be considered homologous structures despite frequent statements to the contrary (e.g., Hyman, 1959, p. 57). Pouches are, of course, lacking in all eutherians.

It appears that Hart (1909a, 1909b, 1909c) was the first to notice a developmental and functional similarity between the scrotum of the male and the pouch of the female marsupial. McCrady (1938, p. 201) noted a striking parallelism in the development of the lips of the pouch in the female and the scrotal anlagen of the male. He concluded that the pouch of the female marsupial is homologous to the labia majora of the vulva of the female eutherian, which in turn is the equivalent of the scrotum in the male (*see* Arey, 1954, p. 338, for tabulation of urogenital homologies). A series of experiments was carried out on the scrotum of Australian brush possums, *Trichosurus,* by **Bolliger** (1942) and **Bolliger** & **Tow** (1947). Adolescent males with descended testes were castrated and injected with estrogens. After a period of time the scrotum underwent complete involution and formed a small, though complete, "female" pouch. They concluded that the scrotum represents an evagination, and the pouch an invagination, of a "scroto-marsupial" area of the abdomen and that the two are, at least in part, homologous.

A paired muscle in the female, the iliomarsupialis, originates on the anterior superior iliac spine and inserts into the mass of the mammary gland deep to the lateral border of the pouch (**Barbour**, 1963, p. 558). The male homologue of the muscle, the cremaster, inserts in the tunica vaginalis of the scrotum. Thus another similarity of structure is seen between the scrotum and marsupium. As an aside, it has frequently been suggested that the iliomarsupialis acts in the ejection of milk from the mammary glands upon contraction, but as shown by **Hill** & **Hill** (1955), the newborn marsupial has several modifications for effective sucking and the muscle probably serves principally as a sling for the support of hypertrophied glandular tissue.

To my knowledge, **Sharman** (1959, p. 361) has been the only dissenter from the idea that the pouch and scrotum are partly homologous structures. His strongest criticism is based on the fact that occasional male marsupials (e.g., *Chironectes*) have both a scrotum and a pouch. Proof one way or the other in such a debate may never be possible. However, the arguments in favor of the homology of part of the "scroto-marsupial area" seem to me to be stronger than those in opposition. Variations in development of both the scrotum and the pouch seem to be related to the life habits of the species in which they are found. The construction is highly labile.

The scrotum is anterior to the penis in all marsupials, but is posterior to it in all placentals except the lagomorphs (**Young**, 1957, p. 664, fig. 272). The vasa deferentia (derived from the mesonephric ducts) are medial to the ureters in the marsupials but lateral to them in the placentals (Fig. 47). Except for the above two differences, the spatial relationships of the male genitalia and their ducts are identical in marsupials and placentals (**Eckstein** & **Zuckerman**, 1956a, p. 56, fig. 7). Despite the fact that the testes in eutherians usually descend into a scrotal sac posterior to the penis, the spermatic cords leave the abdominal cavity through the inguinal canals anterolateral to the penis as in marsupials (**Gray**, 1959, p. 1352, fig. 1135). The paired genital swellings (future scrotal swellings) early in the development of the male of most eutherians are present lateral to the genital tubercle (future penis) and move posteriorly during development to their position posterior to the penis (**Arey**, 1954, p. 333, fig. 294). There is no sound reason to assume that the scrota of the marsupials and placentals are not homologous structures. Regulation of testicular temperature is similar in marsupials and placentals (**Biggers**, 1966, p. 262). The genital swellings in the female eutherian embryo remain in a neutral position more or less surrounding the genital tubercle and become the labia majora of the adult. Labia majora as such are absent in marsupials, but as suggested by **McCrady** and **Bolliger** are probably represented by the lips of the pouch. Occasional pathological cases of a prepenile scrotum have been reported in placental mammals (e.g., **Francis**, 1940).

The significance of the prepenile scrotum in marsupials has suffered many speculations. Perhaps the most interesting was that by **Woodland** (1903), who assumed the ancestral marsupial to have been like a kangaroo. He thought the supporting ligaments of the testes were under severe strain due to the leaping of the animal, and were constantly being thrown anterodorsally to their eventual permanent anterior placement. Such an interpretation, however, seems unlikely today. The phylogenetic significance of the prepenile scrotum seems to hinge around two questions: 1) are the scrotum and pouch homologous, or at least partly homologous, structures? and 2) is the presence of a pouch a primitive therian or a specialized marsupial character? Both questions are complex and open to speculation, and my only purpose in this section is to suggest the probabilities involved.

The developmental comparisons of the pouch and scrotum, the actual transformation of a scrotum into a pouch under estrogen treatment (at least in some species), and the absence of labia majora in marsupials seems strong evidence indeed that the pouch and scrotum are at least partly equivalent structures between the female and male. Little doubt exists that the scrotum is a homologous structure between marsupials and placentals and that descended testes were present in the ancestral therian. Assuming, for the moment, that the pouch and scrotum (or "scroto-marsupial areas") are partly equivalent structures and have a similar ontogeny, it is quite expected that the scrotum should be anterior to the penis in marsupials. In placentals, as in marsupials, the abdominal connections of the spermatic cords are through the inguinal canals, which are anterolateral to the penis. The genital swellings migrate posteriorly with respect to the phallus during early development of the male eutherian to form the postpenile scrotum.

The selective advantages of a posteriorly placed scrotum are obscure, but perhaps such a position renders the testicles less vulnerable to traumatic concussions during the normal functions of life. The homology of the pouch of the echidna and of marsupials may certainly be debated. However, the muscle layers, mechanism of closure, and general function in the protection of young is the same. So whether the homology is true, or whether the pouch was independently derived in the two groups, the fact remains that the abdominal area anterior to the female genitalia in "primitive" mammals was receptive to modifications involving the formation of a pouchlike structure for the protection of young. As discussed at length in earlier sections, most evidence now points to the presence of viviparity after a short period of gestation in the ancestral therian stock. The young were probably born at an immature state, essentially incapable of thermoregulation (*see* PETAJAN *et al.*, 1962) and vulnerable to evaporative water loss through the thin skin, and to abrasions with the physical environment (ENDERS, 1966). Although several marsupial genera (e.g., *Marmosa*) quite successfully rear young without the aid of a pouch, one is present in the majority of genera and is presumably of selective value in protection or partial support of immature young, or both. Keeping the above considerations in mind, I judge that presence of a pouch and prepenile scrotum in the Early Cretaceous therians ancestral to both the marsupials and placentals was indeed a possibility. In fact, I would go so far as to say that it was likely.

Epipubic bones (also called "marsupial" or "prepubic" bones) are endochondral in development and are present in both sexes of the monotremes and in all marsupials except the extinct South American carnivorous borhyaenids and the now rare Australian thylacine carnivores. They are lacking as such in placentals, but JELLISON (1945) suggested the possibility that the baculum (os penis) of the male or the os clitoridis of the female are homologous to the epipubic bones of the marsupial. He based his idea on the facts that the bones: 1) are endochondral; 2) are taxonomically widespread throughout the eutherians; 3) are lacking in the monotremes and marsupials; and 4) develop in some species as paired centers of ossification, similar to that seen in the marsupials, which ultimately fuse into a single shaft. The epipubic bones are imbedded within the connective tissue of the external oblique muscle (ELFTMAN, 1929) and receive slips from various other muscles of the abdominal region (BARBOUR, 1963).

There is no direct connection between the muscles or connective tissue of the pouch and the epipubic bones. This observation has occasionally been used to suggest that the bones have no function in the support of the pouch. In addition, the bone is found subequally developed in both sexes and even in the platypus, which has no pouch at all. A comparative study of the pelvic musculature of living and fossil reptiles, monotremes, marsupials, and placentals was undertaken by VAUGHN (1956). He noted a posterior retreat in origin of the anterior margin of the gracilis muscle, one of the major muscles of the thigh, which was apparently correlated with a change from a primitive sprawling position of the hindlimbs to the therian condition in which the knees are tucked anteriorly under the body (*see* PARRINGTON, 1961, for comparisons of femora). The gracilis originates along the length of the puboischiadic symphysis in sprawling-gaited animals such as the modern lizards and probably the therapsid reptiles. The evolution of the mammalian pelvis from the therapsids involved architectural reduction in the size of the anterior part of the puboischiadic plate. VAUGHN argued strongly that the epipubic bones of the monotreme and marsupial represent a remnant or functional replacement of an anterior part of the reptilian puboischiadic plate. The epipubic bones thus represent a primitive feature for the Mammalia, not specializations restricted to peculiar evolutionary sidebranches. The posture of the hindlimbs of the monotremes is somewhat sprawling, and the gracilis muscle originates along all of the puboischiadic symphysis and much of the epipubic bones. The gracilis in marsupials, having a much improved mammalian type of posture, originates along most of the length of the puboischiadic plate but usually does not touch the epipubic bones. The origin of the muscle is still more restricted posteriorly in some eutherians.

What, then, is the function of epipubic bones in the marsupials? I believe VAUGHN (1956, p. 260) had the answer when he wrote:

> The retention of the prepubis by marsupials, in which it no longer functions as a surface of origin for the gracilis, may be due to the bone's having been early put to secondary uses—perhaps support of the marsupium, perhaps in some way in the connection with the actions of the trunk and pyramidalis muscles.

The embryos of eutherians (Fig. 52,*a*), which undergo prolonged internal gestation periods, are maintained within the uteri that are supported by strong mesometrial ligaments attached to the rigid inner wall of the lumbar region of the body cavity. Such a durable method of support is most effective. The young of marsupials, on the other hand, undergo most of their "embryonic" development suspended from the mother's teats outside of the body (Fig. 52,*b*). The belly region of mammals is soft with only thin sheets of abdominal musculature present for support. By the time the young's dependence upon the mother's milk or pouch is terminated, the offspring represent a considerable mass that must be supported by the thin abdominal muscle sheets alone. I agree with ELFTMAN (1929), who suggested that the epipubic bones, which are ligamentously attached to the pubis, act in conjunction with the belly musculature in increasing abdominal rigidity—so to speak, to reduce "swing and sway."

Should the above interpretations be correct, one must still explain the presence of the epipubic bones in the male marsupial. The bones in *Didelphis* are first seen in the embryo four weeks after birth (NESSLINGER, 1956, p. 391), well after the sex of the young becomes recognizable externally (MCCRADY, 1938, p. 199). Thus, perhaps, it can-

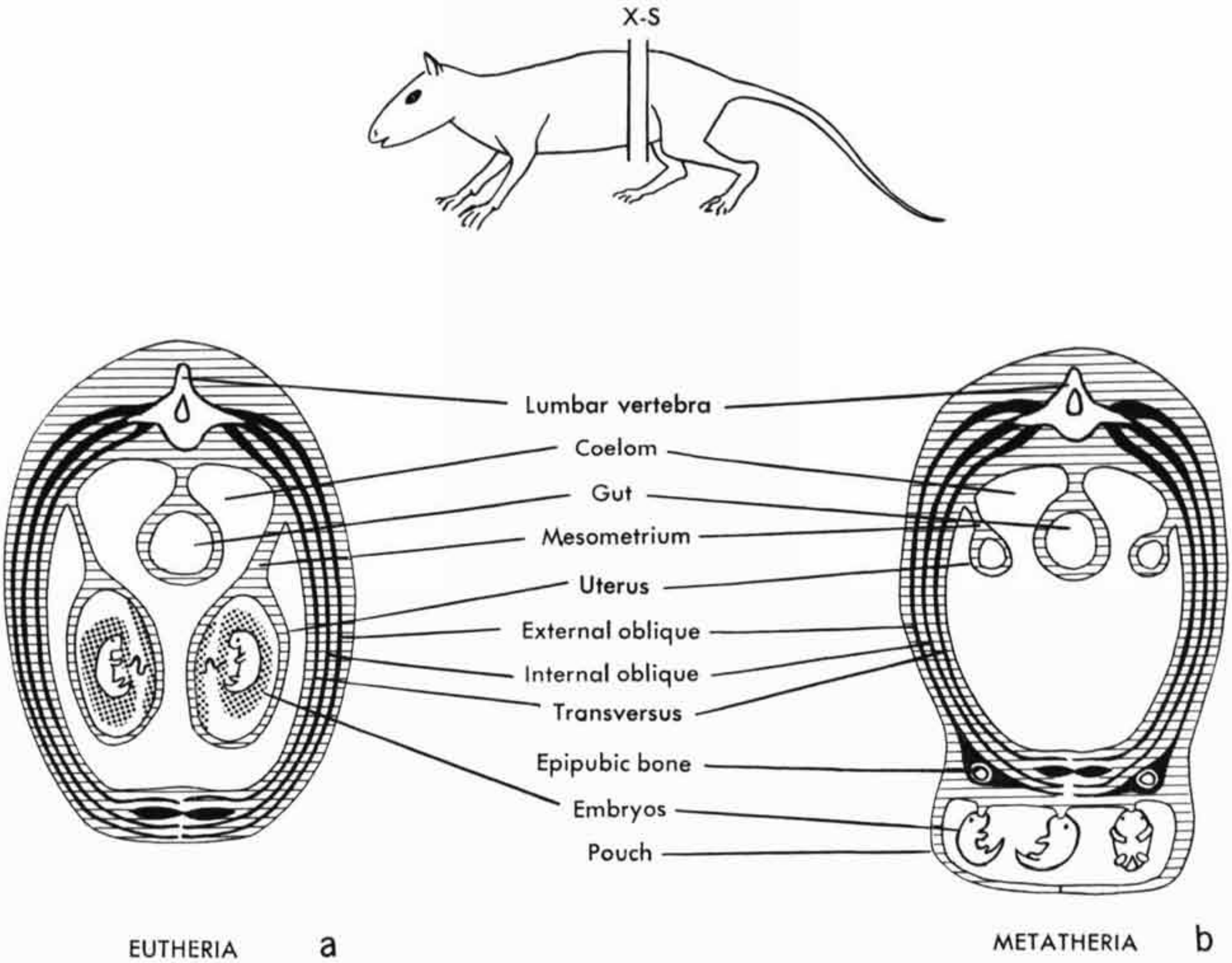

FIG. 52. Diagrammatic transverse sections of female therians to compare methods of support for developing young.

not necessarily be argued that the bones are merely neutral holdovers in the male from a sexually indifferent embryonic stage. However, the marsupial bones act as the point of insertion of the external oblique muscles and the point of origin for parts of the pyramidalis and rectus abdominis muscles (BARBOUR, 1963). Thus although the selective advantages to the possession of the bones in the male are probably fewer than in the female, they do serve as points of muscle attachment, and thus their presence would be expected in both sexes. I can think of no selective disadvantage in their presence in the male.

As the gradual evolution of prolonged internal gestation in eutherians occurred, the epipubic bones were lost, or perhaps put to a new use as the baculum. Prolonged internal gestation is invariably accompanied by distention of the abdominal body wall by the larger embryos. The presence of abdominal rigidity in such a situation would be of distinct disadvantage, and the epipubic bones probably suffered active negative selection.

CONCLUSION

As stated in the Introductory Comments, the purpose of this discussion was to reopen the question as to the extent of specialization exhibited by living marsupials from a putative primitive therian grade of evolution. Although a few characters not concerned with reproduction were briefly considered, the major emphasis was placed upon a point-by-point comparison of the morphology and function of the urogenital system of marsupials and placentals. It is in this system that the most profound differences are seen between the two infraclasses.

It would be naïve and incorrect to assume that living marsupials have descended without specialization from the Early Cretaceous ancestral therian, which probably lived at least 100 million years ago. However, as shown in the above analysis of the structures and functions that were popularly presumed to be specializations unique to the marsupials, one realizes that perhaps the existing characters are not so eccentric after all. I have found no fundamental morphological feature, spatial relationship, or physiological mechanism in the urogenital system of living didelphid marsupials (with the exception of the pseudovaginal canal) that could not be defended as being a primitive, rather than a divergent, character. I thoroughly disagree with statements to the effect that the urogenital system of marsupials is so profoundly modified that its fundamental design could not be primitive for that of the Theria. It is my opinion that if it were possible to study living specimens of the ancestral therian stock, most observers would not hesitate to assign them to the infraclass Metatheria, order Marsupialia. I would not, however, go so far as to propose a formal nomenclature involving "Marsupialia" for Early Cretaceous therians. The concept of "therians of eutherian-metatherian grade" (Patterson, 1956; Slaughter, 1965) is useful, instructive, and, I believe, desirable. My only point is that the animals, biologically speaking, were probably much more "metatherian" than "eutherian" than previously considered. From the biological point of view, it seems entirely possible that the differences between the ancestral therians and the living didelphids are comparable, for example, to those between living representatives of the orders Primates and Carnivora within the infraclass Eutheria.

The pappotheriids, or so-called "therians of eutherian-metatherian grade" (Slaughter, 1965) are found in the Albian deposits of Texas which represent the youngest part of the Early Cretaceous (about 100 million years before present, Casey, 1964, p. 195, table 1). As shown in Figures 30 and 40, the North American leptictids and palaeoryctids were probably already quite distinct by Campanian time (about 75 million years before present, Casey, 1964, p. 195, table 1). Comparative anatomical and physiological investigations on the probable living descendants of the lepticids and palaeoryctids indicate a rather close homogeneity, fully characteristic of the eutherians and divergent from the metatherians. Although profound parallelism in evolution between the descendants of the leptictids and palaeoryctids cannot be ruled out, it seems more likely that a rather high grade of eutherian specialization was already in existence by Campanian time. If it were assumed that the pappotheriids, *sensu stricto* were ancestral to both the marsupials and placentals, the evolution of innumerable features characteristic only of the eutherians would had to have occurred in a relatively short span of geologic time. It is my opinion that this is unlikely. It seems more probable that the marsupials and placentals have been distinct for a longer period of time, perhaps as remote as the earliest Cretaceous.

Part 3

SUMMARY OF THERIAN EVOLUTION IN LATE CRETACEOUS OF NORTH AMERICA

INTRODUCTORY NOTES

Clemens (1968a, p. 8) suggested a North American origin for marsupial mammals. Other evidence (p. 85) now points to an Asiatic origin for placental mammals. Both groups are commonly represented in latest Cretaceous (Maastrichtian) deposits of North America (Fig. 53). Marsupials and mutituberculates are abundantly represented in deposits of Campanian age, but to date only one species of placental (*Gypsonictops* n. sp.) has been described (but not published as of this writing) from these older sediments in North America. It seems likely that eutherian mammals invaded North America, probably by island-hopping or via a minor land connection across Bering Strait, in or shortly before Campanian time.

A definite taxonomic radiation of placental mammals in North America is now well documented by finds in latest Cretaceous and early Paleocene sediments. Concommitant with the eutherian radiation, the fossil record shows a nearly complete extinction of metatherians.

The remainder of this paper is concerned with the effects of ecological changes during the Late Cretaceous of Holarctica and their effects on the establishment of the modern mammalian fauna.

PALEOGEOGRAPHY, PALEOCLIMATOLOGY, AND MIGRATIONS

A generalized paleogeographic map of the Cretaceous of the world was presented by Kummel (1961, p. 253, fig. 9-9). Throughout most of the Mesozoic the entire eastern border of Asia acted as a mobile belt, the Pacific Ocean geosyncline (Nalivkin, 1960, p. 138). Marine sediments were deposited in abundance throughout the Cretaceous, but terrestrial deposits became common in

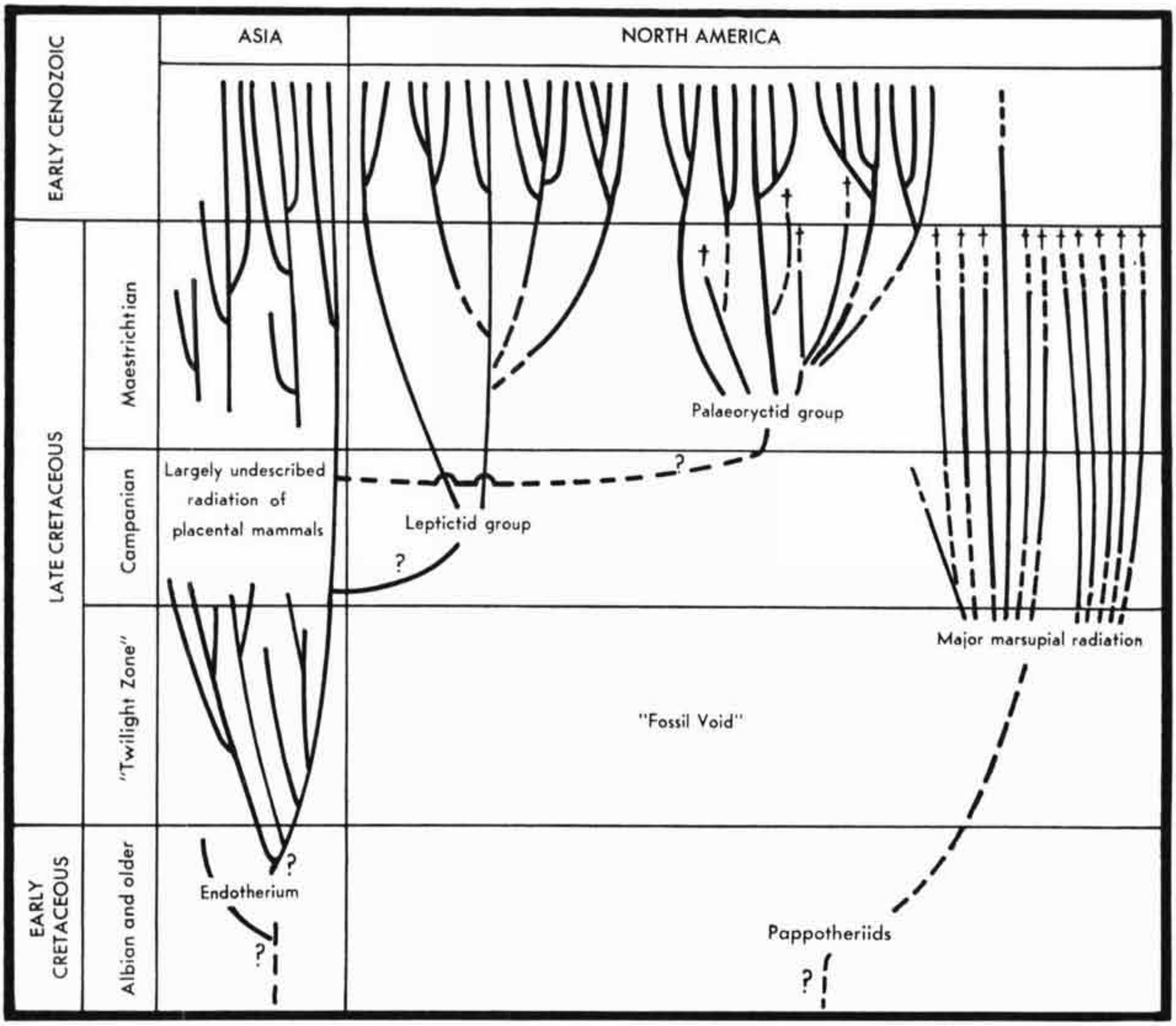

FIG. 53. Summary of possible phylogenetic relationships of North American Cretaceous therians (based on Fig. 26, 30, 40). The "Twilight Zone" refers to Cenomanian through Santonian geologic stages in which localities with fossil mammals have not yet been found in North America.

the upper parts (MINATO *et al.,* 1965, p. 166, fig. 14-2b). Thick Upper Cretaceous sediments with coal-bearing beds are known from the northeastern corner of Asia (NALIVKIN, 1960, p. 141).

Alaska was covered by the sea through most of the Early Cretaceous (MARTIN, 1926, p. 477). A regression of the sea began in the initial half of the Late Cretaceous and continued with numerous fluctuations throughout the remainder of the Cretaceous. The land masses of Asia and Alaska could have been joined or nearly so at that time. Finally, a widespread orogeny occurred at the end of the Cretaceous and beginning of the Tertiary in which the precursors of the present mountain ranges were established (GATES & GRYC, 1963, p. 273). Paleobotanical evidence from Arctic Alaska, covering a Late Cretaceous (late Cenomanian-early Turonian) time span of 30 million years, indicates a gradual cooling from a warm temperate to a cool temperate climate (SMILEY, 1966, p. 12). Associated with the cooling was a profound floral revolution changing from gymnosperm- to angiosperm-dominated assemblages. Climatic extremes could not have been considered a barrier to the distribution of mammals across Alaska or Bering Strait during the Cretaceous. Cretaceous mountain ranges probably did not form effective barriers to dispersal. Thus the broader physical record, as well as the record of fossil mammals, points to the possibility of faunal interchange between Asia and North America in the Late Cretaceous.

Comparative analysis of the Cretaceous dinosaurian faunas of Asia and North America suggest that intercontinental migrations did occur, but that the exchange was highly selective (LANGSTON, 1959, p. 12). The interchanges were restricted either to large dinosaurs which were presumably capable of wading through shallow water or to those which were at least partly adapted for an aquatic way of life.

NEAR EXTINCTION OF MARSUPIALS IN NORTH AMERICA

AXELROD (1967, p. 207) argued that with increasing continentality and the formation of new mountain ranges during the Late Cretaceous of North America, the climate became discontinuous with many isolated pockets of aridity placed within an overall monsoonal condition. Such discontinuity, he believes, was important in the isolation of populations of plants and animals, and thus allowing rapid speciation and adaptive radiation. The fossil record of Late Cretaceous and early Paleocene placental mammals in North America indicates a rapid evolutionary rate (SLOAN, 1964), and is quite consistent with AXELROD's ideas. Climatic and floral changes alone at the end of the Cretaceous probably were not radical or swift enough to cause the near extinction of the marsupials. If anything, the climatic discontinuities, along with the extinction of the dinosaurs, would have been expected to be effective in increasing the marsupial diversity still more than was already evident. Yet the fossil record clearly shows a profound termination of most metatherian lineages near the Cretaceous-Paleocene boundary (CLEMENS, 1966, p. 114, fig. 77).

Extinctions can only be described, not explained, by a study of the fossil record. All interpretations of ancient extinctions can only be speculations. It is tempting to try to explain the concommitant near extinction of the marsupials and adaptive radiation of placentals near the Cretaceous-Paleocene boundary of North America on the basis of competitive superiority of placentals over marsupials. However, as pointed out by BIRCH & EHRLICH (1967), few data exist concerning mechanisms of competitive exclusion for living animals, to say nothing of those long extinct.

The dentitions of the Cretaceous marsupial genera *Alphadon* and *Pediomys* and the placental genera *Gypsonictops* and *Cimolestes* suggest a largely insectivorous diet for most species. The sizes of the various animals were similar, and they are found together in fossil localities, suggesting that they lived near to each other in a common area. It is quite likely that they were in at least partial competition for habitats and for food.

Before discussing the extinction of marsupials, an analogous situation, the early Cenozoic extinction of the multituberculates, will be considered. The herbivorous multituberculates were derived from a primitive Jurassic mammalian stock and probably had been genetically isolated from the therian ancestors for some 70 million years before the marsupial-placental divergence occurred (HOPSON, 1967, p. 354). HOPSON believed it improbable that the multituberculates independently derived advanced mammalian specializations comparable to those of the therians and considered the multituberculates to be "submetatherian" in evolutionary grade. He stated (1967, p. 354):

> Though at first not as highly adapted in their teeth and jaws as were the multituberculates, the early placental herbivores were probably so superior in general biological efficiency (i.e., in such features as thermoregulation, reproduction, behavior, locomotion), that they immediately placed the multituberculates at a competitive disadvantage. With continued specialization of the placental groups as increasingly effective herbivores, the competitive pressure on the multituberculates would have increased.

VAN VALEN & SLOAN (1966, p. 277) compared the elements of progressively younger Late Cretaceous and Cenozoic faunal assemblages and concluded:

> . . . as far as now can be determined, the decline of the multituberculates was probably initiated by competition with condylarths, increased by primates, and completed by rodents.

Although such speculations may never be proven, I believe they are biologically sound. Surely the advent of placental mammals with similar herbivorous adaptations were at least one major factor in the extinction of the multituberculates.

Different genetically isolated mammalian groups have evolved at different rates, and various grades of mammalian specialization are seen in the living fauna. CARTER (1957, p. 204), in discussing the evolution of monotremes, stated:

> The evidence seems to indicate—and I believe the paleontological evidence supports the same view—that in the long course of mammalian evolution, the various structures and physiological functions were changed consecutively rather than simultaneously, and that this step-by-step evolution extended to small features within the major organs as well as to the organs as wholes.

It has long been recognized that among living mammals, the monotremes possess the greatest number of reptilian ("primitive") features with the marsupials following second. Placental mammals, of course, show the greatest number of specializations from their reptilian ancestors. Few would argue that the majority of these specializations (e.g., the corpus callosum, precise thermoregulation, advanced maternal behavior) are not of profound selective advantage to the animals.

Marsupial carnivores (the borhyaenids) flourished on the island continent of South America through most of the Tertiary. However, when the land connection between North and South America (LLOYD, 1963, p. 97, fig. 11) was reestablished during Pliocene time, Holarctic species of carnivores invaded South America and became abundant. The borhyaenids nearly simultaneously became extinct. SIMPSON (1950, p. 368) proposed that:

> . . . the extinction of South American and Australian marsupial carnivores in competition with placental carnivores gives evidence not particularly that placentals are superior to marsupials but that the late World Continent groups had become competitively superior to those of the island continents. In South America, the old native placental groups were also decimated when they came into contact with placentals from the World Continent. They fared no better than the marsupials of similar geographic history.

Mammalian interchange between Europe, Asia, and North America (KURTÉN, 1966; SIMPSON, 1962) occurred throughout the Tertiary. Thus new groups of animals were sporadically migrating into different areas and being put into association with other kinds of mammals. Selective pressures from competition for resources were probably frequently high, and in many cases resulted in a narrowing of specialization. Such a system of isolation of whole faunas followed by sporadic invasions occurred less easily within South America since few real barriers to distribution existed on the island continent during most of the Tertiary (*see* HARRINGTON, 1962, p. 1803). Thus it is not surprising that Holarctic placentals invading South America during the late Pliocene were apparently more effective when placed in competition with the "old native" South American marsupial and placental groups.

The situation of the Cretaceous of Holarctica is interesting in that the common stock ancestral to primitive marsupials and placentals had probably been zoogeographically isolated since sometime in the Early Cretaceous. The reuniting of the two stocks seems to have occurred through invasions of North America by at least two distinct lineages of placentals (the leptictids and paleoryctids), perhaps in Campanian time (Fig. 53). As suggested in Figures 30 and 40, the leptictids and palaeoryctids were either directly ancestral or closely related to several important Cenozoic groups of placental mammals. As discussed in the Conclusions of Part 2 of this paper, it is likely that a rather high grade of eutherian specialization was already in existence by Campanian time in both the leptictids and palaeoryctids. Thus it seems reasonable to assume that many advantageous specializations restricted to the placentals today were present, at least in rudimentary form, in the Late Cretaceous. Various aspects of the comparative anatomy, physiology, and development of marsupials and placentals were presented in Part 2 of this paper.

The marsupials are highly advanced mammals, and in the majority of characters are comparable to placentals with regard to the basic development of organs, tissues, and functions. The majority of differences are those of degree of development. For example, BODIAN (1939, p. 307), speaking of the brain of *Didelphis,* stated:

> Considered as a whole, this undoubtedly generalized mammalian diencephalon is remarkable not only for its primitive features, of which there are abundant examples, but also for its possession of most of the typical features of higher mammalian brains.

Examples of minor differences such as this are abundantly represented in marsupials.

Seemingly more important differences in degree of specialization are also seen between marsupials and placentals. For example, few would object to the generalization that placentals are overall more intelligent animals than marsupials. It seems to me that the degree of intelligence would be a highly critical consideration in most competitive situations. The importance of psychological aspects of behavior upon extinction was stressed by GILL (1955, p. 90) and by LESOUEF (1926).

Although some placental rodents have a gestation period shorter than some marsupials of comparable size (MARLOW, 1961, p. 216), most eutherians have internal gestation periods considerably exceeding the duration observed in similar marsupials. It is interesting to note that the macropods, the most highly specialized marsupials, as a group have the longest gestation periods within the order (SHARMAN, 1965). Several workers (e.g., DOLLO, 1899) have suggested that the short gestation period of marsupials represents a secondary reduction from a more primitive, placental condition. The placenta was thought to have been secondarily reduced in marsupials due to frequent accidents, such as premature birth, associated with an arboreal way of life. Such interpretations are surely incorrect, and prolonged internal gestation is, in general, of distinct selective advantage to therian mammals. Prolonged internal gestation seems to be especially prominent in placentals of moderate to large size and in those with aquatic adaptations.

It would seem that it is the sum of all the advantageous specializations seen in a particular group of animals that ultimately would determine the competitive success of the group when placed in association with other groups of animals with similar life habits over a long period of time and in varying environmental conditions. Many genera of marsupials, both in Australia and in Latin America, successfully live in association with advanced placental mammals. However, although many groups of placentals have invaded all habitats of Latin America from North America since the late Pliocene, only one genus of marsupial *(Didelphis)* has extended its range from the south beyond northern Mexico. Many Latin American marsupial extinctions occurred at about the same time as the original placental invasion. One may argue, as did SIMPSON (1950, p. 368), that marsupials as such were not necessarily "second-rate" mammals as compared to placentals as such, but rather that the faunas of the "World Continent" had become competitively superior to that of the "Island Continent." This is most certainly true, at least to a point. However, perhaps this is not the entire answer. Is it not possible that an analogous situation to the late Pliocene connection of the Americas occurred in the Late Cretaceous between Asia and North America? In the latter situation, placental insectivorous mammals were suddenly brought into association with marsupial insectivorous mammals. The two groups of animals had possibly been genetically isolated since their original divergence. One cannot think of the association as one of derivatives of "World Continent" with "Island Continent" faunas, but only as an association of "marsupials" and "placentals." As summarized in Figure 53, most marsupial lineages underwent rapid extinction at the time the leptictid and palaeoryctid placental mammals started a pronounced radiation. No major climatic, floral, or physiographic changes have yet been recognized as having occurred at that time that would suggest physical reasons for the near extinction of marsupials near the Cretaceous-Paleocene boundary.

It seems highly likely to me that the placental mammals invading North America in the Late Cretaceous were primarily competitive with the marsupials in their insectivorous-frugivorous diets. Secondarily, the placentals were probably more adroit in gaining and controlling favorable cover and denning or nesting sites, and were more intelligent in predation. Many a marsupial and multituberculate probably fell prey to *Cimolestes magnus, C. cerberoides,* and other Late Cretaceous placentals that had tendencies toward a predaceous way of life. Aside from these more obvious factors, a multitude of minor anatomical, physiological, or behavioral specializations restricted to the placentals probably acted in increasing the coefficients of selection within most marsupial species. The coefficients were gradually raised to points beyond which effective competition and survival with the rapidly evolving and diversifying placental groups was nearly impossible.

I believe the arrival into North America in the Late Cretaceous of placental mammals that were comparatively advanced anatomically, physiologically, and behaviorally was at least one major factor in effecting the near extinction of marsupials on that continent.

CONCLUDING NOTE

Authors concerned with comparative anatomy or physiology frequently contrast and cite characters in noneutherian mammals with equivalent characters in "higher mammals." Such an approach is often fully justified. However, as suggested in Figure 53, living descendants of the primitive leptictid and palaeoryctid placentals have probably been genetically isolated for some 75 million years (since at least the Campanian), and it is well to keep in mind and to state exactly in which "higher mammals" the characters are found. A great deal of geologic time for divergent or convergent evolution of specific characters has been available since the basic eutherian groups separated.

SUMMARY

Three fundamental problems were considered in this paper. The first was to describe in detail the assemblage of fossil mammals found in the upper part of the Late Cretaceous Edmonton Formation, Alberta, Canada, and to point out the evolutionary significance of the Edmonton fauna in comparison with fossils from other chronological sequences or geographic areas. The second was to reopen the question as to the probable functional anatomy of the urogenital system of the common ancestor of marsupial and placental mammals. The third was to attempt a unification of the early history of therian mammals in North America (as interpreted from the fossil record) with biological theory (based upon the study of living mammals) concerned with problems of competition and extinctions within the Theria.

The climate of North America during the Cretaceous was mild (tropical to cool temperate in Arctic regions) and the vegetation underwent a gradual shift from gymnosperm- to angiosperm-domination. Major geosynclines were present along the eastern coast of Asia and western coast of North America, but widespread terrestrial deposits are found in Upper Cretaceous sediments in adjacent parts of Alaska and Asia, indicating possible faunal migration routes between the two continents. The Edmonton Formation was deposited along the western coastal plain of the Late Cretaceous (Maastrichtian) interior epicontinental sea and represents about four million years of deposition (68 to 64 m. y. before present).

Fossils were recovered by quarrying, combined with large-scale underwater screening techniques using finer screens than previously attempted for the collection of Cretaceous mammals. Multituberculates, marsupials, and placentals were recovered, including several small species previously unknown or poorly represented. The dentition of each species, including patterns of wear, was described in some detail.

The multituberculate fauna has an overall similarity with that of the contemporaneous Lance Formation of Wyoming, but several differences are evident. Specimens representing *Meniscoessus* and *Essonodon* have not yet been found in the Edmonton. In addition to *Cimolomys gracilis,* a new, larger species, *C. trochuus,* is also present. Another new species, *Cimexomys priscus,* has several rather primitive features in its dentition, is similar to multituberculates in the Late Cretaceous Djadochta Formation of Mongolia, and probably represents an Asiatic migrant into the North American fauna. *Cimolodon nitidus* is commonly represented, but is at the large end of the size range or slightly larger than the specimens recovered from the Lance Formation. A new unnamed genus of ptilodontid, represented by two teeth, was described. Both *Mesodma thompsoni* and *M. formosa* are represented, and a small new species, *M. hensleighi,* was separated from *M. formosa* on the basis of size differences. *M. hensleighi* is probably also present in the Lance Formation.

No species of marsupial was found to be unique to the Edmonton Formation. The marsupial fauna is basically similar to that of the Lance. However, several species commonly found in the Lance are rare or absent in the Edmonton. A small new species, *Alphadon wilsoni,* was separated from *A. marshi* on the basis of size and dental proportions and is the most common marsupial represented. *A. wilsoni* is also present in the Lance Formation. *Alphadon rhaister, Pediomys elegans, P. krejcii, P. hatcheri,* and *Didelphodon vorax,* though present, are uncommon or rare elements of the fauna. The dentitions of most of the Cretaceous marsupials suggest an insectivorous diet.

The upper part of the Edmonton Formation is the oldest known rock unit in North America that bears a mammalian fauna in which eutherians challenge the abundance, taxonomically and numerically, of metatherians. *Gypsonictops hypoconus,* although common in the Lance Formation, is rare in the Edmonton. However, a larger new species, *G. illuminatus,* is abundantly represented. *Gypsonictops* was a primitive member of the North American family Leptictidae and was possibly close to the ancestry of Cenozoic leptictids, erinaceids, pantolestids, primates, and perhaps ultimately, the rodents. *Gypsonictops* has many similarities with the Late Cretaceous genus *Kennalestes* reported from Mongolia, and probably had an Asiatic origin. The dentition of *Gypsonictops* suggests a combined insectivorous-frugivorous diet.

Cimolestes cerberoides, a new placental species of palaeoryctid deltatheridian, is closely related to *C. incisus* of the Lance Formation. The dental structure and wear suggest a primitive grade in the development of a carnivorous diet from an ancestral insectivorous stage, and may well be an ancestor of the miacids and subsequently to the fissiped and pinniped carnivores. Another small new species, *C. propalaeoryctes,* is an ideal ancestor for the Paleocene genus *Palaeoryctes. C. propalaeoryctes* is closely related to *C. cerberoides* and the dentition of the former represents early stages in the evolution of one kind of zalambdodonty, probably associated with an insectivorous mode of life. *Cimolestes magnus,* originally described from the Edmonton Formation but also present in the Lance, was a large animal with a rather primitive dentition, but specialized for carnivorous habits. Carnassial-like shearing functions were distributed evenly along the entire molar row. *C. magnus,* on the basis of molar morphology, would make an ideal common ancestral stock for the hyaenodontid and oxyaenid carnivores of the early Cenozoic.

Additional material of a tiny placental mammal from the Edmonton probably referable to *Batodon tenuis* (originally described from the Lance Formation), suggests that the genus possibly will be found to be a junior synonym of *Cimolestes. B. tenuis,* along with the other species of *Cimolestes,* is classified here as a didelphodontine palaeoryctid deltatheridian. An insectivorous diet is suggested by the dentition.

Previous authors have assumed that *Procerberus,* a Late Cretaceous and early Paleocene North American placental mammal, was a leptictid and was ancestral (at least structurally) to several Cenozoic groups, the later leptictids included. Detailed comparative descriptions in this paper of *Cimolestes cerberoides* and *Gypsonictops-Leptictis* indicated strikingly different dental morphologies and functions between members of the Palaeoryctidae and the Leptictidae. The comparison of the dentitions of *Procerberus* and *C. cerberoides* demonstrated a community of characters held in common between the two genera that are at variance with equivalent characters found in definite leptictids. It was concluded that *Procerberus* is not a member of the Leptictidae, order Insectivora, but on the contrary shows characters which relate the genus much more closely to members of the Palaeoryctidae, order Deltatheridia. As a consequence, the subfamily Procerberinae, as currently diagnosed, no longer holds meaning in context either with the Leptictidae or Palaeoryctidae and should no longer be recognized.

The presence of an inflected angle on the lower jaw was previously thought to be a character peculiar, as a general feature, to the marsupials. However, Late Cretaceous placentals such as *Gypsonictops hypoconus, Cimolestes cerberoides,* and *C. magnus* all have angular processes that are reduced when compared with the typical marsupial condition, but are distinctly inflected. It is probable that an inflected angle was a primitive character for the Theria and was secondarily lost in several different lines of eutherians.

All the known species of *Cimolestes* (plus *Batodon* and *Procerberus*) in the Late Cretaceous are closely related and are quite distinct from contemporaneous species of *Gypsonictops. Cimolestes* probably could not be derived from *Gypsonictops* or vice versa. *Gypsonictops,* along with abundant multituberculates and marsupials, is known in rocks of Campanian and Maastrichtian age in North America. However, *Cimolestes* is rare or absent on the continent before the Maastrichtian. Remains of animals dentally similar to *Cimolestes* have been recovered from older Late Cretaceous rocks of Asia, thus an Asiatic origin for that genus also seems likely. It is probable that placental mammals invaded North America in two distinct groups; a Campanian or earlier leptictid migration and a somewhat later, late Campanian or early Maastrichtian migration of palaeoryctids. The palaeoryctids had the more profound Cretaceous radiation. It is suggested that *Protungulatum,* the oldest known condylarth, was more closely related to the palaeoryctids than to the leptictids, thus agreeing with the concept of the cohort Ferungulata.

Previous investigators have suggested a North American origin for marsupials, possibly from the Early Cretaceous pappotheriids. A profound radiation of the group is documented from North American Cretaceous rocks. However, near the Mesozoic-Cenozoic boundary, immediately following the beginning of the eutherian radiation in North America, the previously diverse marsupials became essentially extinct on that continent.

It would be naïve and incorrect to assume that living marsupials have descended without specialization from the Early Cretaceous ancestral therian, which probably lived at least 100 million years ago. Most recent authors have stressed the predominance of extreme specializations, especially with regard to characters observed in the urogenital system, of living marsupials from a condition probable in the putative therian ancestor of both the marsupials and placentals. It is my opinion, however, based upon an analysis of the comparative embryogenesis, morphologies, and functions of living marsupials and placentals that their common ancestor was probably much more "metatherian" than "eutherian" than has seriously been considered in recent years.

Marsupials are highly advanced mammals, and in the majority of characters are comparable to placentals with regard to the basic development of organs, tissues, and functions. The majority of differences are only those of degree of development. Australian and American marsupials have probably been genetically isolated since the Late Cretaceous. However, the fundamental structure of members of the two marsupial groups is highly similar in most respects. It seems more probable that the high degree of advancement seen among marsupials was already established in the Cretaceous than to assume profound parallel evolution between the Australian and American species. In addition, comparative anatomical and physiological investigations on the probable living descendants of the leptictids and palaeoryctids indicate a rather close homogeneity fully characteristic of the eutherians and divergent from the metatherians. Although profound parallelism in evolution between the descendants of the leptictids and palaeoryctids cannot be completely ruled out, it seems more likely that a rather high grade of eutherian specialization was already in existence by Campanian time.

The North American pappotheriids lived in Albian time (late Early Cretaceous) and have in the past been suggested as the common ancestor of marsupials and placentals. If it were assumed that the pappotheriids, *sensu stricto* were ancestral to both the groups, the evolution of innumerable features characteristic only of the eutherians would had to have occurred in a relatively short span of geologic time. It seems more probable that the marsupials and placentals have been distinct for a longer period of time, perhaps as remote as the earliest Cretaceous.

The main discussion of the marsupial-placental dichotomy in mammalian evolution centered upon comparisons and contrasts of features of reproduction, since it is there that the most profound differences between the two groups are observed. Although, as far as is known, the hormonal control of the estrous cycle and reactions of the uterine wall are identical in marsupials and placentals, only the eutherians have developed effective mechanisms for the prolongation of internal gestation. Trophoblastic and other placental hormones which are active in the maintenance of internal gestation are specializations restricted to the eutherians. It seems probable that the Early Cretaceous ancestral therian was viviparous in the sense that the young were born alive and free from a shell after a short period of gestation. Placental hormones and the multitude of other modifications necessary for prolonged internal gestation could then have been evolved exclusively within the early "eutherian" stock.

Although the arrangement of marsupial urogenital ducts appears peculiar at first sight, an analysis of their development and spatial relationships points out an interesting mosaic of reptilian and typically mammalian characters. The only feature in the marsupial plan that is unique among the amniotes is the presence of the pseudovaginal canal, the phylogenetic significance of which is unknown. The differences between the spatial relationships of marsupial and placental urogenital ducts are not profound, and it is the eutherian plan that is the more highly specialized, not that seen in metatherians as is usually stated. The necessary evolutionary alterations from a primitively marsupial condition could easily have been made in early eutherians by a unique direction of growth of the ureteric bud and by more complete fusion of the Müllerian ducts following selection favoring a strongly muscular, single median birth canal to cope with increasingly large offspring.

The general marsupial method of early embryogenesis seems plainly reptilian with certain specializations associated with reduced yolk and viviparity. The neonate must be developed to the point of being able to crawl by its own efforts from the vaginal orifice to the teat following a short period of gestation. The tissues of the embryo proper precociously develop at the expense of extra-embryonic membranes—the animal must be out of the uterus before the endometrial walls literally collapse around it. On the other hand, development in eutherians emphasizes the early organization of specialized extra-embryonic membranes (trophoblast and part of the inner cell mass) at the expense of the differentiation of the embryo proper. The rapid development of effective placentation in the eutherians is associated with the lack of yolk and albumen. The delayed development of the embryo proper is tolerated because of the comparatively long time available for internal gestation due to the action of placental hormones, the continuation of progesterone secretion by the corpus luteum, and the prolongation of the endometrial secretory phase beyond its normal (nonpregnant) time of regression. It seems the developmental processes seen in placental mammals could not have been developed within the Theria until the evolution of hormonal pathways leading to a prolongation of internal gestation. The eutherian early development is clearly unique among the amniotes. However, there is no reason to believe that the early embryology of marsupials is importantly specialized from that expected in an Early Cretaceous therian ancestral to both marsupials and placentals.

All therian mammals are endowed with some type of placenta during their development. Most marsupials absorb nutrients from the uterine milk through a large yolk sac placenta. The yolk sac is also large and functional in the early development of most eutherians and only later is its function taken over by the chorioallantoic placenta. Yolk sac placentation is probably a primitive feature, and the chorioallantoic placenta was independently derived in several groups of viviparous reptiles, the perameloid marsupials, and the eutherian mammals. With the increase in the length of the gestation period characteristic of eutherians, the function of a simple yolk sac and restricted allantois would have become inadequate. The increasing mass of the embryo required a more efficient transport system of materials—nutrients and oxygen to the cells and waste products from the cells. Gas and nutrient exchange to and from the uterine milk via the vitelline circulation and the storage of nitrogenous wastes in the allantoic vesicle were inefficient processes compared to the continuous flow system provided by close contact between the umbilical capillaries and maternal circulation.

The developmental comparisons of the pouch and scrotum in a marsupial, the transformation of a scrotum into a pouch under estrogen treatment (at least in the males of some species), and the absence of labia majora in female marsupials seems strong evidence that the pouch and scrotum are at least partly equivalent structures between the female and male. Little doubt exists that the scrotum is a homologous structure between marsupials and placentals and that descended testes were present in the ancestral therian. The scrotum of marsupials is positioned anterior to the penis, while in all placentals (except the lagomorphs) it is posterior to the penis. Assuming, for the moment, that the pouch and scrotum (or "scrotomarsupial area") are partly equivalent structures in marsupials and have a similar ontogeny, it is quite expected that the scrotum should be anterior to the penis. In the placental, as in marsupials, the abdominal connections of the spermatic cords are through the inguinal canals, anterolateral to the penis. The genital swellings migrate posteriorly with respect to the phallus during the early development of the male eutherians to form the postpenile scrotum.

Although the homology of the pouches of the echidna and marsupial may be questioned, their structure and mechanisms of closure are the same, and one may say that the area anterior to the female genitalia in "primitive" mammals was receptive to modifications involving the formation of pouchlike structures. The young of the ancestral therian stock were probably born at an immature state, essentially incapable of thermoregulation and vulnerable to evaporative water loss and to abrasions with the physical environment. A pouch is present in the vast majority of marsupial genera and is presumably of selective value in the protection of immature young. Keeping the considerations of the last two paragraphs in mind, the presence of a pouch and prepenile scrotum in the Early Cretaceous therians ancestral to both the marsupials and placentals seems indeed a possibility.

It has been suggested in the past that the marsupial (epipubic) bones represent a primitive, not specialized, feature for the Mammalia. They were originally functional in mammals with a sprawling gait as a point of origin, along with the puboischiadic plate, for the gracilis muscle of the thigh. As the knees became tucked under the body in the therians, the anterior border of the gracilis migrated posteriorly to originate only along the puboischiadic plate. However, the bones were retained in marsupials as points of origin and insertion for several abdominal muscles and probably are functional in increasing abdominal rigidity, especially in the female with attached or pouch young. Abdominal rigidity on the other hand, would be of selective disadvantage in placental mammals which have prolonged internal gestation associated with abdominal expansion during pregnancy. The internal support of embryos within the uterus attached to the lumbar body wall by strong ligaments in eutherians represents a much more secure system than that observed in the marsupials in which the majority of "embryonic" development occurs outside the body of the mother with the young being principally supported by the mother's thin abdominal muscle sheets. It has been suggested in the past that marsupial bones are represented in eutherians in the modified form of the baculum and os clitoridis.

The marsupials nearly became extinct at the end of the Cretaceous in North America after a major radiation. No major climatic, floral, or physiographic changes have yet been recognized as having occurred at that time that would suggest physical reasons for the near extinction. If anything, following the extinction of the dinosaurs, a continued radiation of marsupials would have been expected. The dentitions of the Cretaceous marsupial genera *Alphadon* and *Pediomys* and the placental genera *Gypsonictops* and *Cimolestes* suggest a largely insectivorous diet for most species. *Gypsonictops* and *Glasbius* (a marsupial) also probably had tendencies toward fruit- or leaf-eating habits. The sizes of the various animals are similar, and they are found together in fossil localities, suggesting they lived in a common area. It seems highly likely that the placental mammals invading North America from Asia in the Late Cretaceous were competitive with the marsupials in their insectivorous-frugivorous diets. Secondarily, the placentals were probably more adroit in gaining and controlling favorable cover and denning or nesting sites, and were more intelligent in predation.

Aside from the above more obvious factors, a multitude of minor but advantageous anatomical, physiological, or behavioral specializations restricted to the placentals probably acted in gradually increasing the coefficients of selection in most species of marsupials to points beyond which effective competition and survival with the rapidly evolving and diversifying placental groups was nearly impossible. It would seem that it is the sum of all the advantageous specializations seen in a particular group of animals which would ultimately determine its competitive success when put in association with other groups of animals with similar life habits over a long period of time and in varying environmental conditions. The arrival of comparatively advanced placental mammals in North America in the Late Cretaceous was probably at least one major factor in the near extinction of marsupials on that continent.

Modern descendants of the primitive leptictid and palaeoryctid placentals have probably been genetically isolated for some 75 million years (since at least the Campanian). Thus it is well for authors to keep in mind and to state exactly in which "higher mammals" specific characters under discussion are found. A great span of geologic time for the divergent or convergent evolution of specific characters has been available since the basic eutherian groups separated.

REFERENCES

Abbie, A. A., 1937, *Some observations on the major subdivisions of the Marsupialia with special reference to the position of the Peramelidae and Caenolestidae:* Jour. Anatomy, v. 71, p. 429-436, fig. 1-3.

———, 1939, *The origin of the corpus callosum and the fate of the structures related to it:* Jour. Comp. Neurology, v. 70, p. 9-44, fig. 1-15.

———, 1941, *Marsupials and the evolution of mammals:* Austral. Jour. Sci., v. 4, p. 77-92, fig. 1-3.

Allan, J. A. & Sanderson, J. O. G., 1945, *Geology of Red Deer and Rosebud sheets, Alberta:* Research Council of Alberta Rept. 13, 115 p., 37 fig., 2 pl., 2 map.

Amoroso, E. C., 1952, *Placentation:* in A. S. Parkes (ed.) Marshall's Physiology of Reproduction, v. 2, p. 127-311, 88 fig., 7 tables, Longmans, Green and Co., New York.

Arey, L. B., 1954, *Developmental anatomy:* xi + 680 p., 630 figs., W. B. Saunders Co., Philadelphia.

Ariëns-Kappers, C. U., Huber, G. C., & Crosby, E. C., 1960, *The comparative anatomy of the nervous system of vertebrates, including man:* 3 v., 1845 p., Hafner Publ. Co., New York.

Asdell, S. A., 1964, *Patterns of mammalian reproduction:* viii + 670 p., 17 tables, Cornell Univ. Press, Ithaca, New York.

———, 1966, *Evolutionary trends in physiology of reproduction:* in I. W. Rowlands (ed.) Comparative Biology of Reproduction in Mammals, Zool. Soc. London, Symposium 15, p. 1-13, Academic Press, New York.

Austin, C. R., 1961, *The mammalian egg:* 183 p., 75 fig., 7 table, Blackwell Scient. Publ., Oxford.

Axelrod, D. I., 1960, *The evolution of flowering plants:* in S. Tax (ed.) Evolution After Darwin, v. 1, The Evolution of Life, Its Origin, History, and Future, p. 227-305, 10 fig., 1 table, Univ. Chicago Press, Chicago.

———, 1967, *Drought, diastrophism, and quantum evolution:* Evolution, v. 21, p. 201-209, 1 fig.

Baadsgaard, H., Cumming, G. L., Folinsbee, R. E., & Godfrey, J. D., 1964, *Limitations of radiometric dating:* in F. F. Osborne (ed.) Geochronology in Canada, Roy. Soc. Canada Spec. Publ. 8, p. 20-38, 7 fig., 13 table, Univ. Toronto Press, Toronto.

Barbour, R. A., 1963, *The musculature and limb plexuses of* Trichosurus vulpecula: Austral. Jour. Zool., v. 11, p. 488-610, fig. 1-66, 2 pl.

Baxter, J. S., 1935, *Development of the female genital tract in the American opossum:* Contrib. Embryology, v. 25, no. 145 (Carnegie Inst. Washington Publ. 459), p. 15-35, 2 fig., 3 pl., 1 table.

Biggers, J. D., 1966, *Reproduction in male marsupials:* in I. W. Rowlands (ed.) Comparative Biology of Reproduction in Mammals, Zool. Soc. London, Symposium 15, p. 251-280, 17 fig., 6 table, Academic Press, New York.

Birch, L. C. & Ehrlich, P. R., 1967, *Evolutionary history and population biology:* Nature, v. 214, p. 349-352.

Bodian, D., 1939, *Studies on the diencephalon of the Virginia opossum. Part I. The nuclear pattern in the adult:* Jour. Comp. Neurology, v. 71, p. 259-323, 11 pl.

Bolliger, A., 1942, *Functional relations between scrotum and pouch and the experimental production of a pouch-like structure in the male of* Trichosurus vulpecula: Jour. and Proc. Roy. Soc. New South Wales, v. 76, p. 283-293, 6 pl.

———, & Tow, A. J., 1947, *Late effects of castration and administration of sex hormones on the male* Trichosurus vulpecula: Jour. Endocrinology, v. 5, p. 32-41, 4 pl.

Boyd, J. D. & Hamilton, W. J., 1952, *Cleavage, early development and implantation of the egg:* in A. S. Parkes (ed.) Marshall's Physiology of Reproduction, v. 2, p. 1-126, 57 fig., 5 table.

Bubis, J. J. & Luse, S. A., 1964, *An electron microscopic study of the cerebral blood vessels of the opossum:* Zeitschr. für Zellforsch. und mikroskop. Anatomie, v. 62, p. 16-25, 8 fig.

Buchanan, G. & Fraser, E. A., 1919, *The development of the urogenital system in the Marsupialia, with special reference to* Trichosurus vulpecula: *Parts I, II, and III:* Jour. Anatomy, v. 53, p. 35-129, 47 fig., 15 pl.

Burns, R. K., Jr., 1942, *The origin and differentiation of the epithelium of the urinogenital sinus in the opossum, with a study of the modifications induced by estrogens:* Contrib. Embryology, v. 30, no. 191 (Carnegie Inst. Washington Publ. 541), p. 63-83, 2 fig., 10 pl.

———, 1945a, *The differentiation of the phallus in the opossum and its reactions to sex hormones:* Contrib. Embryology, v. 31, no. 205 (Carnegie Inst. Washington Publ. 557), p. 147-162, 10 pl.

———, 1945b, *The effects of male hormone on the differentiation of the urinogenital sinus in young opossums:* Contrib. Embryology, v. 31, no. 206 (Carnegie Inst. Washington Publ. 557), p. 163-175, 4 fig., 3 pl.

Butler, P. M., 1939, *Studies of the mammalian dentition. Differentiation of the post-canine dentition:* Proc. Zool. Soc. London, v. 109, ser. B, p. 1-36, 28 fig., 4 table.

———, 1956, *The ontogeny of molar pattern:* Biol. Rev., v. 31, p. 30-70, 12 fig.

Carter, G. S., 1957, *The monotremes and the evolution of mammalian organization:* Proc. Zool. Soc. (India), Calcutta, Mookerjee Memorial Vol., p. 195-206, 5 fig.

Casey, R., 1964, *The Cretaceous period:* in W. B. Harland, A. G. Smith, and B. Wilcock (eds.) The Phanerozoic Time-scale, Quart. Jour. Geol. Soc. London, v. 120 (suppl.), p. 193-202, 2 table.

Chase, E. B., 1939, *The reproductive system of the male opossum,* Didelphis virginiana *Kerr and its experimental modification:* Jour. Morphology, v. 65, p. 215-239, 1 fig., 1 pl., 1 table.

Clemens, W. A., Jr., 1961, *A Late Cretaceous mammal from Dragon Canyon, Utah:* Jour. Paleontology, v. 35, p. 578-579, fig. 1.

———, 1963, *Fossil mammals of the type Lance Formation, Wyoming: Part I. Introduction and Multituberculata:* Univ. Calif. Publ. Geol. Sci., v. 48, 105 p., 51 fig., 10 table.

———, 1965, *Collecting Late Cretaceous mammals in Alberta:* 15th Ann. Field Conf. Guidebook of Alberta Soc. Petroleum Geologists, p. 137-141, 2 fig.

———, 1966, *Fossil mammals of the type Lance Formation, Wyoming: Part II. Marsupialia:* Univ. Calif. Publ. Geol. Sci., v. 66, 122 p., 77 fig., 24 table.

———, 1968a, *Origin and early evolution of marsupials:* Evolution, v. 22, p. 1-18, fig. 1-5.

———, 1968b, *A mandible of* Didelphodon vorax *(Marsupialia, Mammalia):* Los Angeles County Museum Contrib. Sci., no. 133, 11 p., 5 fig., 1 table.

———, & Russell, L. S., 1965, *Mammalian fossils from the upper Edmonton Formation:* in Vertebrate Paleontology in Alberta, Univ. Alberta Bull. Geol. 2, p. 32-40, 9 fig., 1 table.

Deanesly, R., 1966, *The endocrinology of pregnancy and foetal life:* in A. S. Parkes (ed.) Marshall's Physiology of Reproduction, v. 3, p. 891-1063, 33 fig., 8 table, Little, Brown & Co., Boston.

Deren, J. J., Padykula, H. A., & Wilson, T. H., 1966a, *Development of structure and function in the mammalian yolk sac. II. Vitamin B_{12} uptake by rabbit yolk sacs:* Developmental Biol., v. 13, p. 349-369, 7 fig., 7 table.

———, ———, & ———, 1966b, *Development of structure and function in the mammalian yolk sac. III. The development of amino acid transport by rabbit yolk sac:* Developmental Biol., v. 13, p. 370-384, 4 fig., 4 table.

Dollo, L., 1899, *Les ancêtres des Marsupiaux étaient-ils arboricoles?:* Trav. Station zool. Wimereux, v. 7, p. 188-203.

Eckstein, P. & Zuckerman, S., 1956a, *Morphology of the reproductive tract:* in A. S. Parkes (ed.) Marshall's Physiology of Reproduction, v. 1, pt. 1, p. 43-155, 34 fig., 5 table.

———, & ———, 1956b, *Changes in the accessory reproductive organs of the non-pregnant female:* in A. S. Parkes (ed.) Marshall's Physiology of Reproduction, v. 1, part 1, p. 543-654, 35 fig., 1 table.

Edinger, T., 1949, *Paleoneurology versus comparative brain anatomy:* Confina Neurologica, v. 9, p. 5-24, 3 fig.

Elftman, H. O., 1929, *Functional adaptations of the pelvis in marsupials:* Bull. Am. Museum Nat. History, v. 58, p. 189-232, 12 fig., 6 pl., 2 table.

Enders, R. K., 1937, Panniculus carnosus *and formation of the pouch in didelphids:* Jour. Morphology, v. 61, p. 1-26, 20 fig.

———, 1966, *Attachment, nursing and survival of young in some didelphids:* in I. W. Rowlands (ed.) Comparative Biology of Reproduction in Mammals, Zool. Soc. London Symposium 15, p. 195-203, Academic Press, New York.

Fernandez, C. & Schmidt, R. S., 1963, *The opossum ear and evolution of the coiled cochlea:* Jour. Comp. Neurology, v. 121, p. 151-159, 5 fig.

Flynn, T. T., 1923, *Photograph illustrating method of parturition in* Potorous tridactylus *exhibited at meeting Linn. Soc. N. S. W.,* 27th Sept. 1922: Proc. Linn. Soc. New South Wales, v. 47, p. xxviii.

———, & Hill, J. P., 1947, *The development of the Monotremata. Part VI. The later stages of cleavage and the formation of the primary germ layers:* Zool. Soc. London, Trans., v. 26, p. 1-178, 27 pl.

Folinsbee, R. E., Baadsgaard, H., Cumming, G. L., Nascimbene, J., & Shafiqullah, M., 1965, *Late Cretaceous radiometric dates from the Cypress Hills of western Canada:* Alberta Soc. Petroleum Geologists, 15th Ann. Field Conf. Guidebook (Part 1), Cypress Hills Plateau, p. 162-174, 3 fig., 1 table.

Francis, C. C., 1940, *A case of prepenial scrotum (marsupial type of genitalia) associated with absence of urinary system:* Anat. Rec., v. 76, p. 303-308, 1 fig.

Gates, G. O. & Gryc, G., 1963, *Structure and tectonic history of Alaska:* in O. E. Childs and B. W. Beebe (eds.) Backbone of the Americas, Am. Assoc. Petroleum Geologists, Mem. 2, p. 264-277, 10 fig.

Gill, E. D., 1955, *The problem of extinction, with special reference to Australian marsupials:* Evolution, v. 9, p. 87-92.

Giolli, R. A., 1965, *An experimental study of the accessory optic and system and of other optic fibers in the opossum,* Didelphis virginiana: Jour. Comp. Neurology, v. 124, p. 229-242, 1 fig., 1 pl., 3 table.

Grambast, L., Martinez, M., Mattauer, M., & Thaler, L., 1967, Perutherium altiplanese, *nov. gen., nov. sp., premier mammifère mésozoique d'Amérique du Sud:* Comp. Rend. Acad. Sci. Paris, v. 264, ser. D, p. 707-710, 1 fig., 1 pl.

Granger, W. & Simpson, G. G., 1929, *A revision of the Tertiary Multituberculata:* Bull. Am. Museum Nat. History, v. 56, p. 601-676, 43 fig.

Grassé, P. (ed.), *Traité de zoologie, anatomie, systematique, biology* (tome 17, fasc. 1, Mammifères): Ordre des Monotrèmes, p. 47-92, Ordre de Marsupiaux, p. 93-185, Masson et Cie Éditeurs, Paris.

Gray, H., 1959, *Anatomy of the human body:* 27th ed., C. M. Goss (ed.), 1458 p., 1174 fig.

Gregory, W. K. & Simpson, G. G., 1926, *Cretaceous mammal skulls from Mongolia:* Am. Museum Novitates, no. 225, 20 p., 19 fig.

Griffiths, M., 1965, *Rate of growth and intake of milk in a suckling echidna:* Comp. Biochem. Physiol., v. 16, p. 383-392, 10 fig., 3 table.

Haines, R. W., 1958, *Arboreal or terrestrial ancestry of placental mammals:* Quart. Rev. Biol., v. 33, p. 1-23, 16 fig.

Hamilton, W. J., Jr., 1963, *Success story of the opossum:* Nat. History, v. 72, p. 16-25, 15 pl.

Harrington, H. J., 1962, *Paleogeographic development of South America:* Bull. Am. Assoc. Petroleum Geologists, v. 46, p. 1773-1814, 34 fig.

Hart, D. B., 1909a, *The nature and cause of the physiological descent of the testes. Part 1. Descent in marsupials:* Jour. Anatomy, London, v. 43, p. 244-265, 19 fig.

———, 1909b, *The nature and cause of the physiological descent of the testes. Part 2. Descent in man:* Jour. Anatomy, London, v. 44, p. 4-26, 9 fig.

———, 1909c, *The physiological descent of the ovaries in the human foetus:* Jour. Anatomy, London, v. 44, p. 27-34, 4 fig.

Hartman, C. G., 1923, *The oestrous cycle in the opossum:* Am. Jour. Anatomy, v. 32, p. 353-421, 14 pl., 1 table, 1 chart.

———, 1929, *How large is the mammalian egg?:* Quart. Rev. Biology, v. 4, p. 373-388, 8 table.

Haun, J. D., & Kent, H. C., 1965, *Geologic history of Rocky Mountain region:* Bull. Am. Assoc. Petroleum Geologists, v. 49, p. 1781-1800, 25 fig.

Hill, C. J., 1933, *The development of Monotremata. Part I. The histology of the oviduct during gestation:* Zool. Soc. London, Trans., v. 21, p. 413-476, 10 pl.

———, 1941, *The development of the Monotremata. Part 5. Further observations on the histology and secretory activities of the oviduct prior to and during gestation:* Zool. Soc. London, Trans., v. 25, p. 1-31, 5 pl.

Hill, J. P. & Hill, W. C. O., 1955, *The growth-stages of the pouch-young of the native cat* (Dasyurus viverrinus) *together with observations on the anatomy of the new-born young:* Zool. Soc. London, Trans., v. 28, p. 349-452, 3 fig., 13 pl.

Hopson, J. A., 1967, *Comments on the competitive inferiority of the multituberculates:* Syst. Zoology, v. 16, p. 352-355.

Huber, E., 1930, *Evolution of facial musculature and cutaneous field of trigeminus:* Quart. Rev. Biology, v. 5, p. 133-188, 389-437, 46 fig.

Huxley, T. H., 1880, *On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia:* Zool. Soc. London, Proc., 1880, p. 649-662, 2 table.

Hyman, L. H., 1959, *Comparative vertebrate anatomy,* 2nd ed.: Univ. Chicago Press, Chicago, xx + 544 p., 136 fig.

Jellison, W. L., 1945, *A suggested homolog of the os penis or baculum of mammals:* Jour. Mammalogy, v. 26, p. 146-147.

Jepsen, G. L., 1940, *Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming:* Am. Philos. Soc., Proc., v. 83, p. 217-340, 22 fig., 5 pl., 20 table.

Kermack, K. A., 1967, *The interrelations of early mammals:* in C. Patterson and P. H. Greenwood (eds.) Fossil Vertebrates, Jour. Linnean Soc. London (Zoology), v. 47, no. 311, p. 241-249, 1 fig., Academic Press Inc., New York.

———, Lees, P. M., & Mussett, F., 1965, Aegialodon dawsoni, *a new trituberculosectorial tooth from the lower Wealden:* Roy. Soc., London, B, Proc., v. 162, p. 535-554, 6 fig., 4 pl.

Kielan-Jaworowska, Z., *Results of the Polish-Mongolian palaeontological expeditions, Part I:* Palaeontologia Polonica, no. 19, Warsaw (in press).

———, *Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert:* Same (in press).

Kirsch, J. A. W., 1968, *Prodromus of the comparative serology of Marsupialia:* Nature, v. 217, p. 418-420, 1 fig.

Kummel, B., 1961, *History of the earth:* W. H. Freeman and Co., San Francisco, xii + 610 p.

Kurtén, B., 1966, *Holarctic land connexions in the early Tertiary:* Commentationes Biologicae, Societas Scientiarum Fennica, v. 29, p. 1-5, 1 fig.

Langston, W., Jr., 1959, *Alberta and fossil vertebrates:* Alberta Soc. Petroleum Geologists, 9th Ann. Field Conf. Guidebook, p. 8-19, fig. 1-5.

Lefeld, J., 1965, *The age of mammal-containing beds at Bain-Dzak northern Gobi Desert:* Acad. Polonaise Sciences, Bull. (série des sci. géol. et géogr.), v. 13, p. 81-83.

LeSouef, A. S., 1926, *Notes on the habits of certain families of the order Marsupialia:* Zool. Soc. London, Proc., 1926, p. 935-937.

Lillegraven, J. A., 1964, *The stratigraphy, structural geology, vertebrate paleontology, and paleoecology of the Brule Formation, Slim Buttes, South Dakota:* Unpubl. M.S. thesis, South Dakota School of Mines and Tech., 71 p., 7 fig., 15 pl., 5 table.

Linzell, J. L., 1959, *Physiology of the mammary glands:* Physiol. Rev., v. 39, p. 534-576.

Lloyd, J. J., 1963, *Tectonic history of the south Central-American orogen:* in O. E. Childs and B. W. Beebe (eds.) Backbone of the Americas, Am. Assoc. Petroleum Geologists, Mem. 2, p. 88-100, fig. 1-12.

Lyne, A. G., 1959, *The systematic and adaptive significance of the vibrissae in the Marsupialia:* Zool. Soc. London, Proc., v. 133, p. 79-133, fig. 1-26, 5 pl., 7 table.

MacIntyre, G. T., 1966, *The Miacidae (Mammalia, Carnivora). Part 1. The systematics of* Ictidopappus *and* Protictis: Am. Museum Nat. History, Bull., v. 131, p. 115-210, fig. 1-21, 20 pl., 12 table.

Mahlo, J., 1963, *Vergleichende Studien über Bau und Funktion des Amnions: Das Säugeramnion am Beispiel des Beuteltieramnions (*Didelphys marsupialis virginiana *Kerr):* Zeitschr. für Zellforsch. und mikroskop. Anatomie, v. 60, p. 237-248, fig. 1-9.

Manning, J. W., & Magirian, D., 1963, *An evoked interhemispheric response in opossum:* Federation Proc., v. 22, p. 457 (abs.).

Marlow, B. J., 1961, *Reproductive behavior of the marsupial mouse,* Antechinus flavipes *(Waterhouse) (Marsupialia) and the development of the pouch young:* Australian Jour. Zoology, v. 9, p. 203-218, fig. 1-3, 2 pl., 1 table.

Marsh, O. C., 1889a, *Discovery of Cretaceous Mammalia:* Am. Jour. Sci., ser. 3, v. 38, p. 81-92, 4 pl.

———, 1889b, *Discovery of Cretaceous Mammalia, Part 2;* Same, v. 38, p. 177-180, 2 pl.

———, 1892, *Discovery of Cretaceous Mammalia. Part 3;* Same, v. 43, p. 249-262, 7 pl.

Martin, G. C., 1926, *The Mesozoic stratigraphy of Alaska:* U. S. Geol. Survey, Bull. 776, xii + 493 p., 13 fig., 4 correlation charts.

Matthew, W. D., 1913, *A zalambdodont insectivore from the basal Eocene:* Am. Museum Nat. History, Bull., v. 32, p. 307-314, fig. 1-6, 2 pl.

Mayr, E., 1963, *Animal species and evolution:* Belknap Press of Harvard Univ. Press, Cambridge, Mass., xiv + 797 p., 62 fig., 43 table.

McCrady, E., Jr., 1938, *The embryology of the opossum:* Am. Anat. Mem., no. 16, Wistar Inst. Anat. and Biol., Philadelphia, 234 p., 66 fig., 3 pl.

———, 1940, *The development and fate of the urinogenital sinus in the opossum,* Didelphys virginiana: Jour. Morphology, v. 66, p. 131-154, fig. 1-15.

McKenna, M. C., 1960, *The Geolabidinae, a new subfamily of early Cenozoic erinaceoid insectivores:* Univ. Calif. Publ. Geol. Sci., v. 37, p. 131-164, fig. 1-6, 2 table.

———, 1961, *A note on the origin of rodents:* Am. Museum Nat. History, Novitates, no. 2037, 5 p., 1 fig.

———, 1965, *Collecting microvertebrate fossils by washing and screening:* in B. Kummel and D. Raup (eds.) Handbook of paleontological techniques, W. H. Freeman and Co., San Francisco, p. 193-203.

———, 1966, *Paleontology and the origin of the primates:* Folia Primat., v. 4, p. 1-25, fig. 1-10.

Meyer, R., 1941, *Dislocation of the phallus, penis and clitoris following pelvic malformations in the human fetus:* Anat. Rec., v. 79, p. 231-241, 2 pl.

Michener, C. D., 1963, *Some future developments in taxonomy:* Syst. Zoology, v. 12, p. 151-172, fig. 1, 2 table.

Minato, M., Gorai, M., Hunahashi, M. (eds), 1965, *The geologic development of the Japanese islands:* Tsukiji Shokan Co., Ltd., Tokyo, xxv + 442 p., 137 fig., 44 table, 30 map.

Mossman, H. W., 1937, *Comparative morphogenesis of the fetal membranes and accessory uterine structures:* Contrib. Embryology, v. 26, no. 158 (Carnegie Inst. Washington Publ. 479), p. 129-246, fig. 1-12, 24 pl., 3 table.

Nalivkin, D. V., 1960, *The geology of the U. S. S. R., A short outline:* Pergamon Press, xii + 170 p., 2 map.

Nelsen, O. E., 1953, *Comparative embryology of the vertebrates:* McGraw-Hill Book Co., New York, xxiii + 982 p., 380 fig.

Nelson, L. R. & Lende, R. A., 1965, *Interhemispheric responses in the opossum:* Jour. Neurophysiology, v. 28, p. 189-199, fig. 1-6.

Nesslinger, C. L., 1956, *Ossification centers and skeletal development in the postnatal Virginia opossum:* Jour. Mammalogy, v. 37, p. 382-394, fig. 1-7, 1 table.

Neumann, V. G. H., 1961, *Die visuelle Lernfähigkeit primitiver Säugetiere:* Zeitschr. für Tierpsychologie, v. 18, p. 71-83, fig. 1-7, 2 table.

Olson, E. C., 1966, *Community evolution and the origin of mammals:* Ecology, v. 47, p. 291-302, fig. 1-5.

Ower, J. R., 1960, *The Edmonton Formation:* Alberta Soc. Petroleum Geologists, Jour., v. 8, p. 309-323.

Padykula, H. A., Deren, J. J., & Wilson, T. H., 1966, *Development of structure and function in the mammalian yolk sac. I. Developmental morphology and vitamin B_{12} uptake of the rat yolk sac:* Developmental Biology, v. 13, p. 311-348, fig. 1-19, 2 table.

Parrington, F. R., 1961, *The evolution of the mammalian femur:* Zool. Soc. London, Proc., v. 137, p. 285-298, fig. 1-9.

Patten, B. M., 1952, *Embryology of the pig:* Blakiston Co., New York, 3rd edit., xiii + 352 p., 186 fig.

Patterson, B., 1949, *Rates of evolution in taeniodonts:* in G. L. Jepsen *et al.* (eds.), Genetics, Paleontology and Evolution, Princeton Univ. Press, p. 243-278, fig. 1-7, 1 table.

———, 1956, *Early Cretaceous mammals and the evolution of mammalian molar teeth:* Fieldiana, Geology, v. 13, p. 1-105, fig. 1-17.

Pearson, J., 1947, *Some problems of marsupial phylogeny:* Rept. 25th Meeting, Australian-New Zealand Assoc. Adv. Sci., Sec. D, Zoology, Adelaide, p. 71-102, fig. 1-3.

Petajan, J. H., Morrison, P., & Akert, K., 1962, *Localization of central nervous control of temperature regulation in the opossum:* Jour. Expt. Zoology, v. 150, p. 225-231, fig. 1-3.

Ramsey, E. M., 1967, *Vascular anatomy of the uterus:* in R. M. Wynn (ed.) Cellular biology of the uterus, Meredith Publ. Co., New York, p. 33-52, fig. 1-14.

Romer, A. S., 1965, *Possible polyphylety of the vertebrate classes:* Zool. Jahrb. Syst., v. 92, p. 143-156.

Russell, D. A., & Chamney, T. P., 1967, *Notes on the biostratigraphy of dinosaurian and microfossil faunas in the Edmonton Formation (Cretaceous), Alberta:* Nat. History Papers, Natl. Museum Canada, no. 35, 22 p., 7 fig.

Russell L. S., 1936, *New and interesting mammalian fossils from western Canada:* Roy. Soc. Canada, Trans., ser. 3, v. 30, p. 75-80, 1 pl.

———, 1952, *Cretaceous mammals of Alberta:* Ann. Rept. Nat. Mus. Canada, Bull. 126, p. 110-119, 2 pl.

———, 1962, *Mammal teeth from the St. Mary River Formation (Upper Cretaceous) at Scabby Butte, Alberta:* Nat. History Papers, Natl. Museum Canada, no. 14, 4 p., 6 fig.

Sahni, A., 1968, *The vertebrate fauna of the Judith River Formation, Montana:* Unpubl. Ph.D. dissertation, Univ. Minnesota, iii + 241 p., 9 pl.

Scapino, R. P., 1965, *The third joint of the canine jaw:* Jour. Morphology, v. 116, p. 23-50, fig. 1-22.

Scharrer, E., 1940, *Arteries and veins in the mammalian brain:* Anat. Rec., v. 78, p. 173-196, fig. 1-14.

Sharman, G. B., 1959, *Marsupial reproduction:* in A. Keast, R. L. Crocker, & C. S. Christian (eds.) Biogeography and ecology in Australia, Monographiae Biologicae, v. 8, p. 332-368, fig. 1-8.

———, 1961, *The embryonic membranes and placentation in five genera of diprotodont marsupials:* Zool. Soc. London, Proc., v. 137, p. 197-220, fig. 1-4, 4 pl.

———, 1965, *Marsupials and the evolution of viviparity:* in J. D. Carthy & C. L. Duddington (eds.) Viewpoints in biology, v. 4, Butterworth and Co., Ltd., London, p. 1-28, fig. 1-4, 3 table.

———, Calaby, J. H., & Poole, W. E., 1966, *Patterns of reproduction in female diprotodont marsupials:* in I. W. Rowlands (ed.) Comparative biology of reproduction in mammals, Zool. Soc. Lond. Symposium 15, p. 205-232, fig. 1-4, 3 table. *(Albian) of Texas:* Postilla, no. 93, 18 p., 6 fig.

Shikama, T., 1947, Teilhardosaurus *and* Endotherium, *new Jurassic Reptilia and Mammalia from the Husin coal-field, South Manchuria:* Japan. Acad., Proc., v. 23, p. 76-84, fig. 1-5.

Shrivastava, R. K., 1962, *The deltoid musculature of the Marsupialia:* Am. Midland Naturalist, v. 67, p. 305-320, fig. 1-14.

Simpson, G. G., 1927a, *Mesozoic Mammalia. VIII: Genera of Lance mammals other than multituberculates:* Am. Jour. Sci., ser. 5, v. 14, p. 121-130.

———, 1927b, *Mammalian fauna of the Hell Creek Formation of Montana:* Am. Museum Nat. History, Novitates, no. 267, 7 p., 6 fig.

———, 1929, *Some Cretaceous mammals from the Lance Formation:* Ann. Carnegie Museum, v. 19, p. 107-113, fig. 1-6.

———, 1931, *A new classification of mammals:* Am. Museum Nat. History, Bull., v. 59, p. 259-293.

———, 1936, *Additions to the Puerco fauna, lower Paleocene:* Am. Museum Nat. History, Novitates, no. 849, 11 p., 6 fig.

———, 1937a, *The beginning of the age of mammals:* Biol. Rev., v. 12, p. 1-48, fig. 1-11.

———, 1937b, *The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas:* U.S. Natl. Museum, Bull., v. 169, x + 287 p., 80 fig., 10 pl.

———, 1945, *The principles of classification and a classification of mammals:* Am. Mus. Nat. History, Bull., v. 85, xvi + 350 p.

———, 1950, *History of the fauna of Latin America:* Am. Jour. Sci., v. 38, p. 361-389, fig. 1-10, 3 table.

———, 1961, *Historical zoogeography of Australian mammals:* Evolution, v. 15, p. 431-446, fig. 1, 5 table.

———, 1962, *Evolution and geography:* Condon Lecture, Univ. Oregon Press, Eugene, 64 p., 30 fig., 10 table.

Slaughter, B. H., 1965, *A therian from the Lower Cretaceous (Albian) of Texas:* Postilla, no. 93, 18 p., 6 figs.

Sloan, R. E., 1964, *Paleoecology of the Cretaceous-Tertiary transition in Montana:* Science, v. 146, p. 430.

———, Jenness, R., Kenyon, A. L., & Regehr, E. A., 1961, *Comparative biochemical studies of milks—I. Electrophoretic analysis of milk proteins:* Comp. Biochem. Physiol., v. 4, p. 47-62, fig. 1-9, 2 table.

——— & Van Valen, L., 1965, *Cretaceous mammals from Montana:* Science, v. 148, p. 220-227, fig. 1-6, 1 table.

Smiley, C. J., 1966, *Cretaceous floras from Kuk River area, Alaska: Stratigraphic and climatic interpretations:* Geol. Soc. America, Bull., v. 77, p. 1-14, fig. 1, pl. 1.

Sorokin, S., 1962, *A note on the histochemistry of the opossum's lung:* Acta Anatomica, v. 50, p. 13-21, fig. 1-7.

Sperry, R. W., 1964, *The great cerebral commissure:* Scientific American, v. 210, no. 1, p. 42-52, fig. 1-9.

Srivastava, S. K., 1966, *Upper Cretaceous microflora (Maastrichtian) from Scollard, Alberta, Canada:* Pollen et Spores, v. 8, p. 497-552, fig. 1-2, 11 pl.

———, 1967, *Palynology of Late Cretaceous mammal beds, Scollard, Alberta (Canada):* Palaeogeography, Palaeoclimatol., Palaeoecol., v. 3, p. 133-150, fig. 1-2, 3 pl.

Sunderland, S., 1941, *The vascular pattern in the central nervous system of the monotremes and Australian marsupials:* Jour. Comp. Neurology, v. 75, p. 123-129, fig. 1-2.

Sweet, G., 1907, *The skin, hair, and reproductive organs of* Notoryctes: Quart. Jour. Micros. Sci., New Ser., v. 51, p. 325-342, fig. 1-3, 2 table.

Szalay, F. S., 1965, *First evidence of tooth replacement in the subclass Allotheria (Mammalia):* Am. Museum Nat. History, Novitates, no. 2226, 12 p., 6 fig. 1 table.

———, 1968, *The beginnings of primates:* Evolution, v. 22, p. 19-36, fig. 1-5.

Tozer, E. T., 1956, *Uppermost Cretaceous and Paleocene nonmarine molluscan faunas of western Alberta:* Geol. Survey Canada, Mem. 280, v + 125 p., 8 fig., 9 pl., 6 table.

Tyndale-Biscoe, C. H., 1963a, *Effects of ovariectomy in the marsupial* Setonix brachyurus: Jour. Reprod. Fert., v. 6, p. 25-40, fig. 1, 1 pl., 5 table.

———, 1963b, *Blastocyst transfer in the marsupial* Setonix brachyurus: Same, v. 6, p. 41-48, 1 pl., 1 table.

———, 1966, *The marsupial birth canal:* in I. W. Rowlands (ed.) Comparative biology of reproduction in mammals, Zool. Soc. London Symp. no. 15, Academic Press, New York, p. 233-250, fig. 1-8, 2 table.

Van Valen, L., 1963, *The origin and status of the mammalian order Tillodontia:* Jour. Mammalogy, v. 44, p. 364-373, 2 pl.

———, 1966, *Deltatheridia, a new order of mammals:* Am. Museum Nat. History, Bull., v. 132, p. 1-126, fig. 1-17, 8 pl., 26 table.

———, 1967, *New Paleocene insectivores and insectivore classification:* Same, v. 135, p. 217-284, fig. 1-7, 2 pl., 7 table.

———, & Sloan, R. E., 1965, *The earliest primates:* Science, v. 150, p. 743-745, fig. 1, 1 table.

———, & ———, 1966, *The extinction of the multituberculates:* Syst. Zoology, v. 15, p. 261-278, fig. 1-5, 2 table.

Vanzolini, P. E., & Guimarães, L. R., 1955, *South American land mammals and their lice:* Evolution, v. 9, p. 345-347.

Vaughn, P. P., 1956, *The phylogenetic migrations of the ambiens muscle:* Jour. Elisha Mitchell Sci. Soc., v. 72, p. 243-262, fig. 1-10.

Walls, G. L., 1963, *The vertebrate eye and its adaptive radiation:* Hafner Publ. Co., New York, xiv + 785 p.

Washburn, S. L., 1946, *The sequence of epiphyseal union in the opossum:* Anat. Record, v. 95, p. 353-363, 2 table.

Weekes, H. C., 1935, *A review of placentation among reptiles with particular regard to the function and evolution of the placenta:* Zool. Soc. London, Proc., 1935, p. 625-645, 6 pl.

Winge, H., 1917, *Udsigt over Insektaedernes indbyrdes Slaegtskab.:* Vidensk. Meddel. Dansk Naturh. Foren., v. 68, p. 83-203.

Winkelmann, R. K., 1964, *Nerve endings of the North American opossum* (Didelphis virginiana): Am. Jour. Physical Anthropology, v. 22, ser. 2, p. 253-258, fig. 1-7.

Wislocki, G. B., 1940, *Peculiarities of the cerebral blood vessels of the opossum: Diencephalon, area postrema and retina:* Anat. Record, v. 78, p. 119-137, fig. 1-2, 3 pl.

Wolstenholme, G. E. W., & O'Connor, M. (eds.), 1965, *Preimplantation stages of pregnancy:* CIBA Foundation Symposium, Little, Brown & Co., Boston, 430 p.

Woodland, W., 1903, *On the phylogenetic cause of the transposition of the testes in Mammalia: With remarks on the evolution of the diaphragm and the metanephric kidney:* Zool. Soc. London, Proc., 1903, p. 319-340, fig. 1.

Young, J. Z., 1957, *The life of mammals:* Clarendon Press, Oxford, 820 p., 338 fig.

ADDENDUM

Since the submission of materials for this article, four papers pertinent to the subject have come to my attention.

Martin (1966) reported that the testes in the rather primitive living tree shrews (Tupaiidae, Eutheria) are, in common with the lagomorphs and marsupials, prepenial in position.

Fourie (1963) showed that well-developed paired marsupial bones were present in tritylodontid mammal-like reptiles. This observation strengthens Vaughn's (1956) conclusion as to the antiquity of epipubic bones in mammalian evolution.

Slaughter (1968a) recognized a new genus and species of therian mammal *(Clemensia texana)* from Albian deposits of north-central Texas. He separated *Clemensia* from the family Pappotheriidae and placed it in the Didelphidae, order Marsupialia, thus indicating it as the oldest recognized marsupial. Slaughter (1968b) also suggested the presence of placental mammals in contemporaneous deposits of Texas on the basis of two submolariform premolars, a specialization as yet unknown in marsupials. He thus presumed the marsupial-placental dichotomy in mammalian evolution to have been pre-Albian, a concept with which I fully agree. However, weighing the evidence now available, I still hold to the idea of an Asiatic origin for North American leptictid and palaeoryctid eutherians.

REFERENCES

Fourie, S., 1963, *A new tritylodontid from the Cave Sandstone of South Africa:* Nature; v. 198, p. 201.

Martin, R. D., 1966, *Tree shrews: Unique reproductive mechanism of systematic importance:* Science, v. 152, p. 1402-1404, 3 fig.

Slaughter, B. H., 1968a, *Earliest known marsupials:* Science, v. 162, p. 254-255, 1 fig.

———, 1968b, *Earliest known eutherian mammals and the evolution of premolar occlusion:* Texas Jour. Sci., v. 20, p. 1-12, 2 fig.

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