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AND
THE EVOLUTION OF MAMMALIAN MOLAR TEETH

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EARLY CRETACEOUS MAMMALS
AND
THE EVOLUTION OF MAMMALIAN MOLAR TEETH

BRYAN PATTERSON
Research Associate, Fossil Vertebrates
Professor of Vertebrate Paleontology
Museum of Comparative Zoology, Harvard University

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CONTENTS

Early Cretaceous Mammals and The Evolution of Mammalian Molar Teeth

INTRODUCTION

The fortunate circumstances resulting in the discovery of Early Cretaceous mammals[1] at a locality in the Trinity Sand near Forestburg, Montague County, Texas, have been related in a previous publication (Patterson, 1951). A program of field and laboratory work by this Museum, in co-operation with the Texas Memorial Museum and the Bureau of Economic Geology of the University of Texas, was at once begun in the Forestburg area and is still in progress. Mr. Louis H. Bridwell of Forestburg, representing the Texas Memorial Museum, devoted the winter of 1949–50 to an intensive examination of the Trinity Sand exposures in Montague County and in the northern part of Wise County. His careful and painstaking work resulted in the discovery of two new localities yielding fragmentary materials similar to those found at the original locality, one to the northeast of Forestburg, in the valley of Willawalla Creek, and the other to the south, near the site of the abandoned settlement of Uz. Both these localities were worked during 1950–52, that in the Willawalla valley yielding mammalian remains, but most of the work so far has been done at the original locality. This consists of a series of exposures at the head of a short canyon that opens into Braden Branch, a tributary of Denton Creek, the exposures being almost exactly 2½ miles southwest of Forestburg as the crow flies. To this canyon the name Greenwood Canyon may be applied, after Mr. Virgil Greenwood, the owner of the land, and the area may be called the Greenwood Canyon locality.

In 1950, I accompanied Dr. and Mrs. Rainer Zangerl to northern Texas, they to prospect the various Cretaceous formations for fossil reptiles and I to camp at the Greenwood Canyon locality. Having determined the previous winter that the bone-bearing matrix broke down readily in water, washing operations in the field were decided upon. At the suggestion of Mr. Glen L. Evans, a number of empty 55-gallon oil drums were obtained, some of which were split lengthwise to serve as washing and soaking troughs. The rest were filled with water and set up at the edge of the bank of the main exposure. From there, the water was piped down to the

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[1] Early Cretaceous as employed in this paper follows North American usage, in which the period is divided into two parts. For those who recognize a three-fold division, these mammals are of Mid-Cretaceous age.

troughs, the matrix was then shoveled into the soaking troughs and, when sufficiently disintegrated, was washed through a graded series of screens placed in the washing troughs. The water in the drums was replenished through the kind co-operation of Mr. Greenwood. In this way, it was possible to extract the concentrate from perhaps five tons of matrix. During 1951, Mr. Orville L. Gilpin and I resumed operations. With transportation continuously available, we were able to dispense with the relatively inefficient drums and to take the matrix to the water instead of bringing the water to the matrix. A small platform was built over the margin of a nearby tank, or reservoir, and the screens were placed on this. The matrix was shoveled into sacks, which were taken to the tank and staked out to soak in the water. After about 24 hours of soaking, the matrix was sufficiently disintegrated to be placed in the screens, and the sand and clay were washed through by pouring water over the mass. The concentrates in each tray were then washed into a bag held at the end of a funnel, and the bags, when full, hung up to dry on an adjoining fence. With this improved technique, production was stepped up to a total of approximately 15 tons processed during the season. Mr. Gilpin and Mr. William D. Turnbull employed the same technique in 1952, processing some twenty tons. Mr. Gilpin and I, in 1954, processed approximately six tons, in addition to other work.

Back in the laboratory, the concentrates received a final washing in an ingenious machine, consisting of a series of revolving concentric drums of screening, designed by Dr. Zangerl and constructed by Mr. Stanley J. Kuczek. Mass production techniques unfortunately end here. Except for coarsest grade, the concentrates have to be sorted piece by piece and grain by grain under a binocular microscope. Our sympathies have frequently gone out across the years to Plieninger, who over a century ago faced a similar situation in the Rhaetic with only a hand lens to help him. There is a certain fascination about this laborious, time-consuming task, however, and in consequence everyone around the laboratory periodically tries his hand at finding a mammalian specimen; but the brunt of the work has been borne by Miss Nancy Robertson, whose devoted labors have been rewarded by the finding of over three-quarters of all the mammalian specimens thus far detected.

The question naturally arises as to whether the mechanical processes employed cause any damage to the specimens. This possibility has, of course, been a source of concern during the work, but the evidence appears to be in the negative. Careful examination of the breaks in the specimens indicates that although many are sharp they are not fresh, and alveoli in jaw fragments are filled with well-packed silt, showing that the teeth were lost prior to burial. That no breakage at all occurs is unlikely, but the amount is believed to be sufficiently low to justify the methods employed.

Approximately 300 specimens of mammals have been found, the great majority being isolated teeth, many of them imperfect. Of those determinable, 77 are triconodonts, 135 multituberculates, 4 symmetrodonts, and 34 therians of uncertain infraclass position but of metatherian–eutherian grade.

Since laboratory work on the concentrates is still actively in progress, and a great deal is yet to be sorted, no definitive account of these remains is yet possible, but the interest attaching to them is believed to be sufficiently great to warrant this interim study and a consideration of certain theoretical questions raised by it. The very fragmentary nature of most of the material precludes for the present the application of names to most of the specimens. The taxonomy of the Lance Mammalia, badly confused by Marsh's piecemeal naming of fragmentary specimens, is a decided warning against premature attempts to erect a formal nomenclature on the basis of such evidence. Of the various forms thus far discovered, only two—the triconodont described previously and a symmetrodont diagnosed more recently (Patterson, 1955)—are represented by material sufficiently unequivocal to warrant the bestowal of a name. For the rest, there is always the chance that a superior specimen may turn up; if it does not, nomenclatural decisions will be deferred until all evidence is in hand.

To the persons mentioned above and to Mr. Douglas Tibbetts, who prepared nearly all the illustrations, I wish to extend my most sincere thanks. Mr. and Mrs. Turnbull have been so kind as to further the progress of this paper during my absences in South America, Mr. Turnbull taking the measurements and working with Mr. Tibbetts during the preparation of the drawings. Several friends have read all or parts of the manuscript, and I am much indebted to them for comment and criticism: Mr. D. Dwight Davis, Dr. Robert H. Denison, Dr. E. Lloyd DuBrul, Dr. Robert F. Inger, Dr. Everett C. Olson, Dr. George Gaylord Simpson, Mr. Turnbull, and Dr. Zangerl.

This paper was to have been one of a series published in honor of my old friend, colleague and mentor, Dr. Karl Patterson Schmidt, on the occasion of his sixty-fifth birthday. It proved too long for inclusion in that volume and I accordingly take this opportunity for an affectionate personal dedication.

NOTES ON THE GEOLOGY AND ASSOCIATED FAUNA

It was stated previously that the mammal-bearing horizon occurs within the upper 100 feet of the Trinity Sand. A section run by Mr. Evans and myself in 1950 confirmed this, revealing that the Greenwood Canyon exposures are approximately 87 feet from the top of the Trinity. The Willawalla locality discovered by Mr. Bridwell is somewhat lower, approximately 140 feet from the top.

The brief visits to the Greenwood Canyon locality during November of 1949 led to the opinion that the fragmentary remains of mammals and other vertebrates were ". . . concentrated in small pockets, a yard or so across, all at essentially the same stratigraphic level" (Patterson, 1951, p. 44). During a subsequent visit to this locality, Mr. Evans noticed that the remains actually occurred in a bed, rather than being concentrated in pockets. This became obvious as soon as field work began in earnest during 1950. The bed is continuous around the head of Greenwood Canyon, being exposed in all the tributaries that have been cut down to a depth sufficient to reveal it. Late Pleistocene erosion has removed it from the immediate vicinity of the canyon (the present cycle of erosion, which has exposed the bed and further excavated the canyon, is twentieth century, initiated by over-cropping of cotton). At the other localities only a single exposure is available.

The bone bed is variable in composition and also in thickness, ranging up to some three feet, although it is probable that the original thickness has nowhere been preserved. Consisting predominantly of fine white sand and clay, it includes lenses of somewhat coarser, darker sand, channels of fine sand, and irregular deposits and some partings of green clay. Slight effervescence with dilute HCl may be noted here and there in the bed and some decidedly limy masses occur. Limonitic concretions, most of them small, although large masses are also encountered, are very numerous, and minute nodules of manganese oxide sometimes occur on the bone fragments. Numerous well-worn pebbles, a number of which are of dreikanter type, and a few smooth cobbles are present, both distributed at random through the bed. The deposit was laid down on the slightly irregular surface of a bed of fine, yellowish-white pack sand. It is overlain by fine, thin-bedded sands that frequently show decided depositional dips. These cut into the upper parts of the bed, which in a few places was eroded completely away.

Bone fragments occur throughout the stratum, in the clay and limy lenses as well as in the fine silt. The bed seems to vary slightly in richness from place to place, but bone is present everywhere in it. The condition of the fragments varies from much abraded to completely unworn, with clean, sharp breaks. No certain association of fragments has been noted.[1] Only one really large fragment, a portion of a dinosaur limb bone, has thus far been found wholly within the bed. This was badly disintegrated; it seems likely that it had lain in the open exposed to the elements for a considerable time prior to being washed into the deposit. In favorable spots, the fragments that weather out of the bed are concentrated on the slopes of the underlying pack sand. Collecting was limited to such spots during the brief visits paid to the Greenwood Canyon locality during 1949, and it was this circumstance, combined with the fact that the bed is difficult to detect under brilliant sunlight in dry weather, that led to the mistaken impression that the fossils occurred in pockets.

As stated previously, mammalian specimens constitute only a minute fraction of the vertebrate remains occurring in the bed. Small, undetermined fishes, represented by thousands (the number must run to the millions in the whole bed) of isolated, ganoin-covered scales, numerous vertebrae and teeth, and occasional jaw fragments, are numerically predominant. Isolated teeth of small sharks of *Acrodus* type are common, as are heavy, ganoin-covered scales resembling those of the Jurassic *Dapedius* in size. The rarest element among the fish fauna is *Ceratodus*, not hitherto reported in the North American Early Cretaceous, which is represented by a few isolated teeth. Frog remains (Leptodactylidae) are common, as are jaw fragments of various small lizards. Turtles, represented by isolated elements of the carapace and plastron, and fragments of crocodiles, both large and small, are numerous. Carnosaur and ornithopod dinosaur remains consist of isolated teeth with an occasional foot bone, and many fragments of ossified tendons of the ornithopods; the carnosaurs range from very small to large forms, while the ornithopods are all of approximately *Camptosaurus* size. No further traces of pterosaurs have been recovered since the first account was written, and no bone that could certainly be identified as avian

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[1] In 1952, Messrs. Gilpin and Turnbull found a nearly complete turtle resting on the underlying pack sand, and covered by the mammal-bearing bed. The top of the carapace had been crushed down, and this permitted escape of the gases of decomposition and thus prevented extrusion of the head and limbs. The body cavity above the crushed down portion was filled by fine, even-grained, unconsolidated sand of a type encountered in the bone bed. Embedding in the pack-sand substrate, decomposition and desiccation seem to have preceded deposition of the overlying stratum. The turtle thus does not appear to be an exception to the rule that all vertebrates deposited in the bed are fragmentary.

has yet turned up. The only determinable, autochthonous[1] invertebrate remains that have been encountered during the washing operations are referable to estheriid phyllopods with thin, delicately sculptured shells (determined by Dr. Fritz Haas and Dr. W. S. Adkins).

Under the impression that the bone fragments occurred in pockets, I previously stated (1951, p. 44) that the beds containing them had been laid down off shore and that the fossils had been concentrated by current action. It now appears that this was an incorrect interpretation. The evidence at present available suggests, on the contrary, deposition in quiet, confined, fresh or only slightly brackish water, and a fauna that lived partly in and partly very near the area of accumulation. We are dealing with a burial assemblage that was autochthonous, or nearly so, in origin. It seems likely that conditions were not very different from those reconstructed by Simpson (1926) for Quarry 9 in the Morrison formation.

One point remains for emphasis. The Forestburg stratum and the Rhaetic bone beds stress the fact that any Mesozoic deposit of continental or near shore origin that contains an appreciable quantity of fragmentary remains of small terrestrial vertebrates is a potential source of Mesozoic mammals, and as such is worthy of the most careful scrutiny.

DESCRIPTIONS

Class **Mammalia**

Subclass uncertain

Order **Triconodonta**

Family **Triconodontidae**

Subfamily **Triconodontinae**

Astroconodon[2] **denisoni** Patterson

Astroconodon denisoni Patterson, 1951, Amer. Jour. Sci., **249**: 31–41, figs. 1–2.

Triconodonts run second to multituberculates in numbers. In addition to the two jaw fragments on which *A. denisoni* was based, several additional

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[1] Occasional crinoid columnals and small fragments of bryozoans have been found. These have been derived from Paleozoic rocks (smooth pebbles and small cobbles of Paleozoic corals are not uncommon in the Trinity Sand). A few internal casts of a medium-sized, high-spired gastropod, probably *Tylostoma*, have been picked up on the surface at the Greenwood Canyon locality, but none have been found *in situ*. In the cotton-growing days, the area was traversed by various roads not now in existence, one of which ran close to if not over the exposures. Limestone from the nearby ridges of the Goodland was brought down for use as road metal and the casts may well have come from this source.

[2] ἀστήρ, a star (lone), + κῶνος, cone, + ὀδούς, tooth. The derivation was incorrectly given in the type description.

ramus fragments, a maxillary fragment or two and many isolated teeth representing nearly all parts of the dentition are now available.

Several of the ramus fragments and the teeth or alveoli that they bear combine to suggest that the cheek tooth formula of *Astroconodon* is P_4, M_4, as in the Purbeckian *Triconodon*. With one exception, the diagnostic characters given in the type description are confirmed. Cement is not always found on the necks of the cheek teeth and a posterior spur of this substance is not constant in the molars.[1] The anterior groove in the molars extends to the summit of the anterior face and, as would have been anticipated, is as well developed in the upper as in the lower series. In unworn lower molars, the three main cusps are of nearly equal size and height and are well separated; the posterior cingulum cusp is but little inferior to them in both respects. The main cusps of unworn upper molars, on the contrary, are united for the greater part of their heights and the posterior cingulum cusp is comparatively small. Seen in side view, the apex of the crown forms a wavy line. The external face is gently convex and the cingula are comparatively slight. The length of the crown decreases from apex to base and the roots converge at their tips.

It now seems likely that the incomplete humerus described in the earlier paper (CNHM no. PM 543) may actually be referable to this species. *A. denisoni* is the only form among the Forestburg mammals to which, on the basis of size, the humerus could at present be referred.

There is some indication that a second, smaller form is included among the material.

Subclass **Allotheria**

Order **Multituberculata**

Family **Plagiaulacidae**

Multituberculates are the commonest forms at Forestburg. The first of their kind thus far found in American Early Cretaceous deposits, they are represented by a ramus fragment with the roots of the last premolar and the alveoli of the molars, by very numerous single cheek teeth, and by some incisors.

All specimens found may be referred to the Plagiaulacidae. The last lower premolar[2] is very similar to that of *Plagiaulax* itself in outline, in the

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[1] It is, of course, conceivable that the cement may have been removed by weathering or by post-mortem abrasion.

[2] The Marsh-Simpson cheek tooth formula, P^{5}_{4-3}, M^{2}_{2}, is here followed, although, as pointed out in the concluding section, there is as yet no positive evidence in favor of this or of any other proposed formula.

eight oblique ridges on the crown and in the presence of small, external, basal cuspules. The lower molars resemble those of the Jurassic forms in cusp number and structure, being less advanced toward the crescentic cusps characteristic of the Ptilodontidae than is *Loxaulax* of the earlier Wealden (Simpson, 1928a). In the upper molars, a slight but positive advance toward the ptilodontid condition is to be seen. The incipient third row of cusps is more definite than in the Jurassic forms, consisting not only of a buttress but also of a cusp. The upper premolars, unfortunately poorly known, indicate the presence of at least two forms.

Subclass **Theria**

Infraclass **Pantotheria**

Order **Symmetrodonta**

Family **Spalacotheriidae**

Spalacotheroides bridwelli Patterson

Spalacotheroides bridwelli Patterson, 1955, Fieldiana, Zool., **37**: 690–692, fig. 145.

In addition to the type of this species, already sufficiently described, three other symmetrodont specimens have been recovered, all upper molars. These are clearly referable to the Spalacotheriidae and possibly, although of course not certainly, to *S. bridwelli*. Further discussion of the cusp terminology employed in the following descriptions may be found in a later section of the paper.

The most complete of these molars, a right (PM 1235, fig. 1), is approximately as long as wide. The internal cusp, the paracone, largest and highest element of the crown, is nearly vertical on its internal face and has its sharp apex inclined posteriorly and a little externally. Four stylar cusps are present, one pair anterior, the other posterior, the two pairs connected by a low cingulum that descends anteriorly; the external face is gently concave between them. The second and third of these cusps are the largest and the posterior the smallest. Crests run antero- and postero-externally from the apex of the paracone to the second and third stylar cusps respectively. The shorter, more transverse anterior crest is considerably the lower of the two and does not bear a cusp. The cusp near the center of the posterior crest, the metacone, is elongate, flat posteriorly, and only slightly convex anteriorly; it is bounded by a well-defined notch internally and a shallower one externally. The valley of the trigon is a nearly featureless concavity, deepest antero-medially. From the apex of the anterior stylar cusp a cingulum runs upward and inward for a short distance along the anterior face of the tooth. The root structure is unfortunately not clear. There appears to have been a large internal root and smaller antero- and postero-external ones, but the possibility that the internal and antero-external may have been joined cannot be excluded. The absence of a cusp on the anterior crest suggests that this tooth is an anterior molar, possibly M^2, Butler having shown (1939b, p. 341, fig. 7, *a*) that M$^{1-2}$ of *Peralestes* lack this element; if so, the angle enclosed by the crests is more acute than in the Jurassic form.

Fig. 1. Symmetrodonta, Spalacotheriidae. Right upper anterior molar; CNHM no. PM 1235, crown and external views; ×23. Drawn by John Pfiffner.

PM 1133, of the left side, is unfortunately very incomplete, lacking the whole of the external face and most of the posterior. The paracone is similar to that of PM 1235. The anterior crest bears a cusp that, for a symmetrodont, is comparatively large. It projects anteriorly and is thus set off from the paracone not only by the notch in the crest but also by a vertical depression on the anterior face. External to it there appears to have been a second, smaller cusp on the crest. The valley of the trigon bears a low, median transverse ridge flanked by a very shallow posterior and a deeper anterior depression. The posterior crest was evidently higher than the anterior. Judging from what is left of the posterior face, the trigon appears to have been shorter than in M^5 of *Peralestes*, the tooth which it most nearly resembles.

PM 1236 agrees rather well with M^6 of *Peralestes* and is evidently a last right molar; it is complete save for the antero-external portion and the roots. The paracone resembles those of the specimens just described. The crests are of nearly equal height, the anterior rising somewhat more in the external half. The posterior crest is featureless; the anterior bears two barely perceptible swellings suggestive of the two cuspules on this crest in the last molar of *Peralestes*. The postero-external corner of the tooth is better developed than in that form and bears a prominent posterior projection. The postero-external cingulum cusp is well developed. There is no cusp, as such, posterior to it, but the posterior projection clearly corresponds to the posterior stylar cusp of PM 1235. A short, well-defined notch in the external face separates this portion of the tooth from the missing but evidently larger antero-external corner. The external cingulum is low and the valley of the trigon a featureless depression.

DISCUSSION

These teeth are obviously very similar in structure to the molars of *Peralestes*. Two of them have shorter, more acute-angled trigons and in this they agree with the type molar of *Spalacotheroides bridwelli*, in which the paraconid and metaconid are closer to each other than is the case in *Spalacotherium*. Comparison of PM 1235 with any of the molars of *Peralestes* at once shows that two additional elements are present on the crown. These are the anterior and posterior stylar cusps, and their presence in this Albian symmetrodont is of the greatest interest. Butler supposed (and so did I prior to the finding of this tooth) that the antero-external cingulum cusp of *Peralestes* was homologous with the antero-external cingulum cusp, the parastyle, of pantotheres. If so, and if the symmetrodonts were broadly ancestral to the pantotheres, which seems likely, then the large second stylar cusp of the pantothere molar (the stylocone, p. 16) has to be regarded as a new element. Since the anterior crest in pantotheres runs toward this cusp and not to the parastyle, a shift in the relations of this crest has to be assumed. PM 1235 suggests another and a simpler explanation. Here the anterior crest runs to the second stylar cusp, which is clearly homologous with the antero-external cingulum cusp of *Peralestes*, and the anterior stylar cusp is as clearly a new element. This new element has all the attributes of the parastyle of pantotheres and later therians, being anterior to the stylocone and having the short anterior cingulum running to its apex. It now seems, therefore, that a parastyle was acquired independently by pantotheres and by the latest symmetrodonts, that the antero-external cingulum cusp of *Peralestes* is homologous with the stylocone of pantotheres, and that the anterior crest maintained the same cusp relations in the two groups. Fully comparable structures frequently appear independently in related lines. Acquisition of a parastyle may be regarded as one more item of evidence in favor of pantothere–symmetrodont relationships.

The identity of the posterior stylar cusp of PM 1235 remains for consideration. Since the third stylar cusp of this tooth is clearly homologous with the postero-external stylar cusp of *Peralestes*, it could be assumed that the new element is a metastyle. It may indeed be, but here a question arises as to which, if either, of the two cusps in the metastylar area of Late Jurassic pantotheres corresponds to the metastyle of eutherian and metatherian molars. One of those cusps is situated at the external extremity of the posterior crest and the other is external or even antero-external to the first (fig. 12, C). The former is certainly homologous with the postero-external cingulum cusp of *Peralestes* and with the third stylar cusp of PM 1235. The latter, like the posterior stylar cusp of PM 1235, is as certainly an addition to the crown. I am inclined to suspect that this latter cusp really is the homologue of the metastyle and that the homologue of the postero-external cingulum cusp of *Peralestes* did not persist beyond the pantothere stage, but this is very uncertain. The whole stylar area has been profoundly modified during the successive adaptive shifts from the symmetrodont to the pantothere and from this to the tribosphenic stages, and only further knowledge can settle this vexatious but really very minor question.

Therian Mammals of Uncertain Infraclass Affinities but of Metatherian–Eutherian Grade

The most interesting specimens yet found at Forestburg are the fragmentary remains now to be described. Despite their regrettable incompleteness, these clearly represent a stage in therian evolution advanced beyond that represented by the Jurassic pantotheres. They show that the great eutherian–metatherian radiation had its beginnings as far back as the Early Cretaceous, and the molar structure revealed by them contributes greatly to an understanding of the early course of therian molar evolution. Some jaw fragments, evidently not triconodont and too large for *Spalacotheroides*, are tentatively referred here.

In the hope of obtaining better material, it has been decided not to apply formal names to these specimens, but simply to describe them under their catalogue numbers. In the ensuing discussion of molar evolution, the molars are referred to either collectively as the Forestburg molars or by their numbers when occasion requires. The following are the more important specimens:

CNHM no. PM 931, right upper premolar, probably the last.
PM 884, left upper molar, incomplete internally and postero-externally.
PM 886, right upper molar, incomplete internally and antero-externally.
PM 999, right upper molar, incomplete internally and antero-externally.
PM 1075, last left upper molar, complete save for posterior and internal roots.
PM 1287, last left upper molar.
PM 1005, right lower molar, essentially complete.
PM 887, trigonid of right lower molar.
PM 965, right lower molar, essentially complete.
PM 948, right lower molar; most of metaconid, apices of paraconid and of talonid cusps, and anterior root missing.
PM 660, trigonid of right lower molar; most of metaconid missing.

PM 930, trigonid of right lower molar.
PM 966, trigonid of left lower molar; apex of paraconid damaged.
PM 922, right lower molar, complete save for apex of paraconid and posterior root.
PM 583, anterior portion of left mandibular ramus with alveoli of I_{1-4}, C, P_{1-4}.

All the above are from the Greenwood Canyon exposures.

MORPHOLOGY

Upper premolar (fig. 2, A).—The tooth is much longer than wide. The paracone is high, although not as high as the tooth is long, rather flat on the external face and rounded on the internal. The parastyle is a small but prominent cusp, projecting anteriorly and sharply separated from the anterior slope of the paracone. The metastyle is completely subordinated in a crest running from the apex of the paracone to the posterior margin of the tooth. A low external cingulum is present. Midway on the paracone–metastyle crest there is a well-defined metacone, its tip truncated by wear. A cingulum runs internally from the parastyle, thickens to a small but noticeable prominence at the base of the antero-internal slope of the paracone, continues around the base of this cusp, and ends at the base of its postero-internal slope. Wear on the crown is greatest between the apices of the paracone and metacone. In addition, there is a small wear surface, caused by shearing, above the metacone on the internal side of the paracone-metastyle crest, and another on the anterior slope of the paracone extending for a short distance above the apex. The tooth is implanted by two roots. Each consists of a rounded main portion with a bulbous extremity (cf. the bulbous alveoli in the ramus fragments described below), situated one anterior and the other posterior to a line drawn through the apex of the paracone. These two main portions are approximately subequal. The anterior root has an antero-external extension going forward beneath the parastyle, and the posterior has a long, thin extension running the length of the paracone-metastyle crest.

Upper molars.—Of these, PM 884 and PM 999 agree quite closely and differ in several respects from PM 886. PM 1075 and PM 1287, the complete last molars, cannot of course be identified at present with either type. In PM 884 (fig. 2, B), the paracone and metacone are well separated, occupy a nearly central position on the tooth and lie on the same anteroposterior line. The paracone is the higher and larger of the two, and has a steep anterior face. A crest runs posteriorly from its apex to meet, in a wide **V**, a crest running anteriorly from the apex of the metacone. The paracone also sends a crest externally from its apex, and the metacone a crest postero-externally. External to these two cusps is a long and broad stylar area that, in the part preserved, bears three cusps. The most anterior of these,

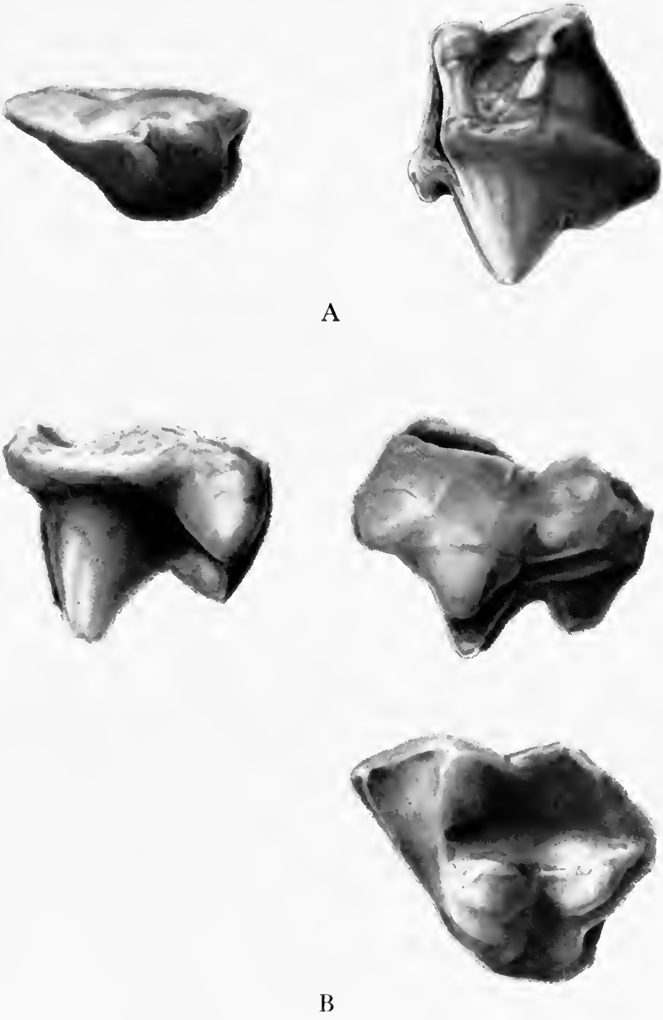

Fig. 2. A, Right upper premolar of therian mammal of uncertain infraclass affinities but of metatherian–eutherian grade; CNHM no. PM 931, crown and internal views. B, Incomplete left upper molar of therian; CNHM no. PM 884, anterior, external, and crown views. Both ×23.

the parastyle, is not hook-like, as in most pantothere molars, but small, low and poorly demarcated externally from the very large cusp that follows it. From its apex, a small but clearly defined cingulum runs internally along the anterior face of the tooth. The following cusp, which is homologous with the large centro-external cusp—the stylocone[1]—in pantothere upper molars, is relatively enormous, being approximately equal in size to and but slightly lower than the metacone. It is situated directly external to the paracone. A crest runs internally from its apex to meet the ridge running externally from the apex of the paracone. Very similar relations between stylocone and paracone obtain in pantotheres. The third stylar cusp is somewhat larger than the parastyle, although much smaller than the stylocone, and a crest runs posteriorly from its apex. This crest and the one running postero-externally from the metacone extend to the missing metastylar area, which was clearly well developed. There can be no doubt that a low protocone was present on the missing internal portion of the tooth, and that the anterior cingulum ran inward to it.

PM 999 (fig. 3, A) is a smaller tooth than PM 884 but agrees well with it in nearly all structures preserved in common. The only notable exception is that in PM 999 there is no appreciable third stylar cusp, only a small, poorly defined swelling. The metastylar area, here preserved, is prominent and extends well out postero-externally. It is much lower than the stylocone, obscurely divided into small cuspules, and connected to the apex of the metacone by a ridge.

In PM 886 (fig. 3, B), the paracone and metacone are farther apart than in PM 884, their apices are nearer the anterior and posterior edges of the tooth, and the metacone is somewhat larger relative to the paracone. The crest running externally from the apex of the paracone goes in the direction of the missing parastyle, or of an intermediate cuspule, and not to the base of the stylocone. This cusp is not as high as on PM 884 and there is only a

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[1] The term "stylocone" is proposed for this cusp, despite the fact that the terms "amphicone" and "eocone" have previously been applied to it by Simpson (1929a, fig. 2, p. 7) and by Bohlin (1945, p. 373), respectively. The former term refers to the belief that the cusp represented the combined para- and metacone of eutherian-metatherian molars and is synonymous in this sense with the earlier parametacone (Wood, 1927); the latter that it was the primary cusp of the crown. It would now appear that neither view is correct (see p. 36). Since neither term is deeply embedded in the literature, an alternative, non-committal name for this cusp, so important in early therian molar history, seems preferable to continued use of a name with a misleading connotation. Furthermore, "amphicone" has attained a certain currency in eutherian-metatherian dental terminology for the combined para- and metacone, and the original definition of "eocone" is somewhat ambiguous (see footnote, p. 36).

I believe that the large stylar cusp forming part of the anterior crest in the molars of zalambdodont insectivores is homologous with the stylocone in the pantotheres and in the Forestburg molars, but it is impossible at present to be sure which of the various stylar cusps in didelphids represents this ancestral structure. In *Didelphodon* and *Enacodon* (Simpson, 1929a, fig. 45, p. 121), it may possibly be stylar cusp B, but certainty on this point can only come with knowledge of the intermediate stages.

faint suggestion of a crest running for a short distance internally from its apex. It is somewhat more posterior in position relative to the paracone than in PM 884. The metastylar area is large and rather flat, marked only by faint groovings. A low protocone was also certainly present.

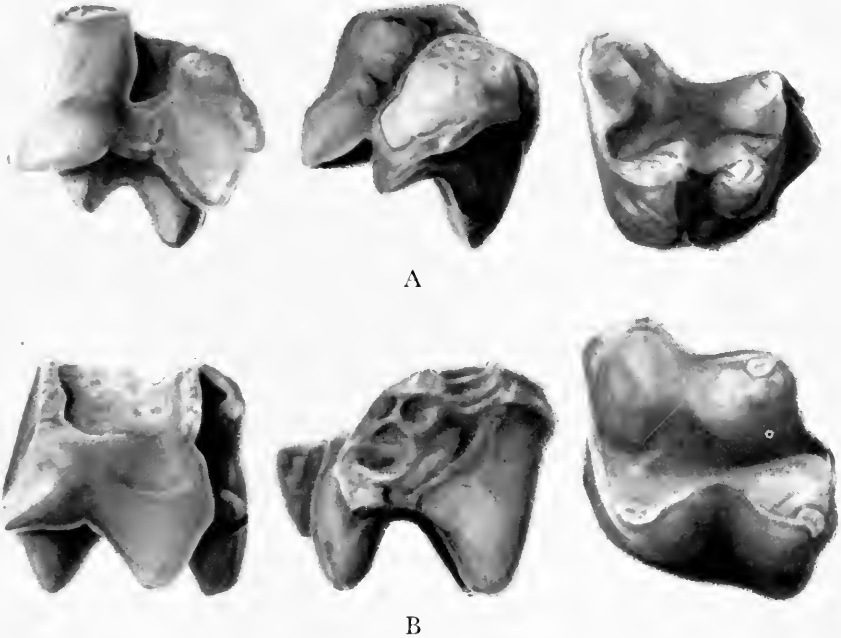

Fig. 3. A, Incomplete right upper molar of therian; CNHM no. PM 999, external, anterior, and crown views. B, Incomplete right upper molar of therian; CNHM no. PM 886, external, anterior, and crown views. Both ×23.

In neither molar is the root structure entirely clear. The indications, however, suggest that there were two external roots beneath the stylar area and a third beneath the internal half, as in the last molar.

Of the last molars, PM 1075 (fig. 4, A) is very short in proportion to its width. The paracone, the highest cusp, is situated almost exactly in the center of the tooth. The much smaller metacone is posterior and a little internal to it. From the paracone, a high ridge runs externally to the stylocone, which is only a little lower and smaller than the paracone. The parastyle is a distinct cusp, smaller than the stylocone and directly anterior to it. The rest of the stylar area is much reduced, as is usual in therian molars of this general construction. From the posterior slope of the stylocone the external margin of the tooth falls sharply away internally to the

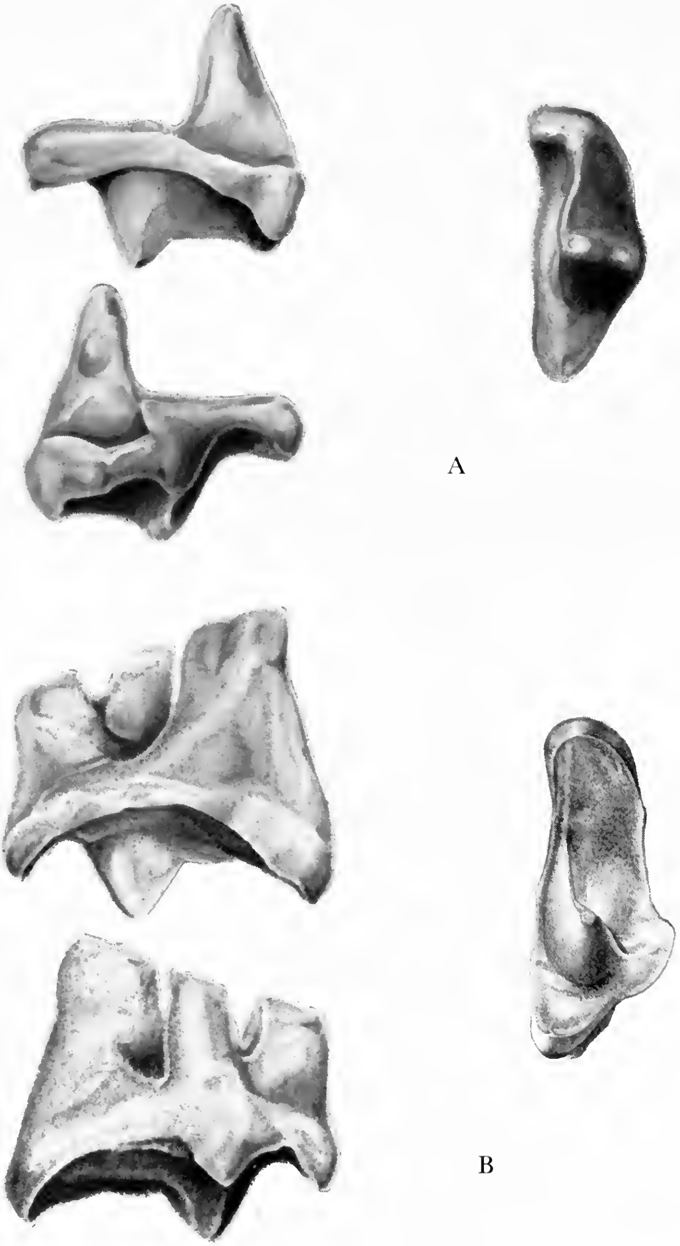

Fig. 4. A, Left upper last molar of therian; CNHM no. PM 1075, crown, anterior, and posterior views. B, Left upper last molar of therian; CNHM no. PM 1287, crown, anterior, and posterior views. Both ×23.

Fig. 5. Right lower molar of therian; CNHM no. PM 1005, crown, anterior, internal, and posterior views; ×23.

metacone. A poorly defined ridge bearing a slight elevation near the middle of its course connects these two cusps. The great importance of this and the following tooth is, of course, the fact that the structure and relative prominence of the protocone are revealed. This element is small and low—insignificant in comparison with the main portion of the crown—as may clearly be seen from the figures. Its apex is connected to the parastyle by a rather well-defined anterior cingulum, and to the base of the metacone by a slight ridge. There is no indication of a proto- or metaconule. It is possible, of course, that rudiments of these cusps may have been present on the more anterior molars. There are three roots, an external beneath the stylar area, a smaller posterior beneath the reduced metacone, and an internal mainly beneath the paracone but extending inward below the protocone; the size of the internal relative to the external cannot be determined.

PM 1287 (fig. 4, B) is a considerably larger tooth of the same general type, although differing in detail. Paracone and metacone are not on the midline but within the internal half of the crown, the stylar area being in consequence relatively larger. There is no separate parastyle, and the crest running externally from the apex of the paracone is lower and fades away before reaching the apex of the stylocone. The protocone is not only relatively but absolutely smaller. The three roots are similar in position to those of PM 1075, but the internal is here much smaller than the external, being but little larger than the posterior.

Lower molars.—Three structural types appear to be represented among available specimens, one by PM 1005 and PM 887, another by PM 965, PM 948, PM 660, PM 930 and PM 966, and a third by PM 922.

PM 1005 (fig. 5) is an almost perfect, unworn tooth. The trigonid and talonid are approximately equal in length, but the trigonid is much higher, more massive and wider than the talonid. The crown is higher on the labial than on the lingual side. The protoconid is the highest and largest cusp, curving inwardly and posteriorly toward its apex. The metaconid is but slightly lower and is considerably larger than the paraconid, which is the lowest and smallest of the three and does not extend as far inwardly as the metaconid. Sharply notched crests connect the apex of the protoconid with the apices of the para- and metaconid. The cusps are separate for less than half the height of the trigonid. Near the center of the anterior face there is a conspicuous basal cuspule. This cuspule is present in all three types of lower molars; nothing comparable has been reported for the Jurassic Theria. The trigonid, as a whole, is rather short. Of the three talonid cusps, the hypoconid is the largest, followed by the posteriorly projecting hypoconulid, with the entoconid the smallest. All are connected by notched crests. A prominent crest, the crista obliqua, runs from the hypoconid to the center of the posterior face of the trigonid, and another, less pronounced, connects the entoconid with the base of the metaconid; a well-defined talonid basin is thus enclosed. The anterior root is short and wide, the posterior elongate.

PM 887 (fig. 6) is similar in size and structure to PM 1005, the only notable differences being that the paraconid extends farther inward and an anterior basal cingulum, rather than a cuspule, appears to have been present. The tooth had been in use for some time; the apices of the cusps, the protoconid–metaconid crest, and the internal half of the posterior face of the trigonid all show considerable wear.

Fig. 6. Trigonid of right lower molar of therian; CNHM no. PM 887, crown, anterior, internal, and posterior views; ×23.

Molars of the second type (figs. 7, 8, 9, A) exhibit the same general structure but differ consistently in several features. The trigonid is longer. The protoconid is not as large, the metaconid not as high, and the paraconid notably larger, approximately equal in size to the metaconid. Paraconid and metaconid are better separated. In addition to the anterior basal cuspule, there is an antero-internal cuspule below the paraconid, similar to but smaller than that present in the Jurassic pantothere *Peramus;* it is possible that this may be a homologue of the antero-internal cingulum

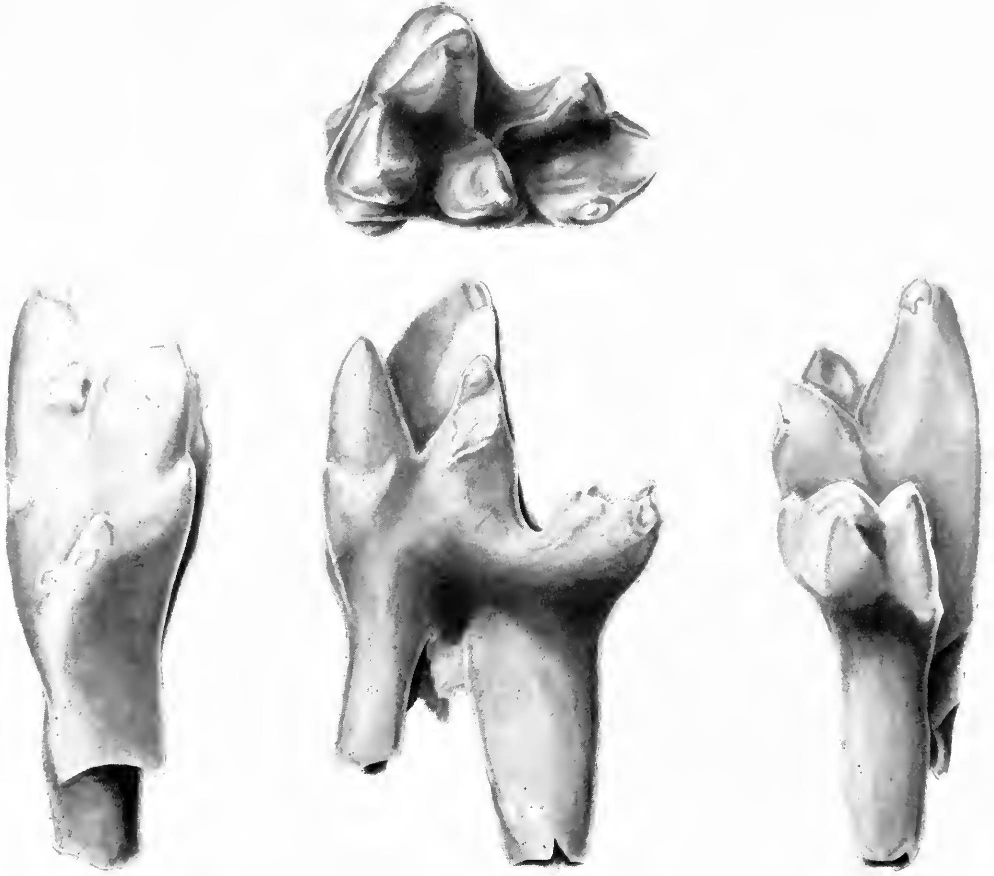

Fig. 7. Right lower molar of therian; CNHM no. PM 965, crown, anterior, internal, and posterior views; ×23.

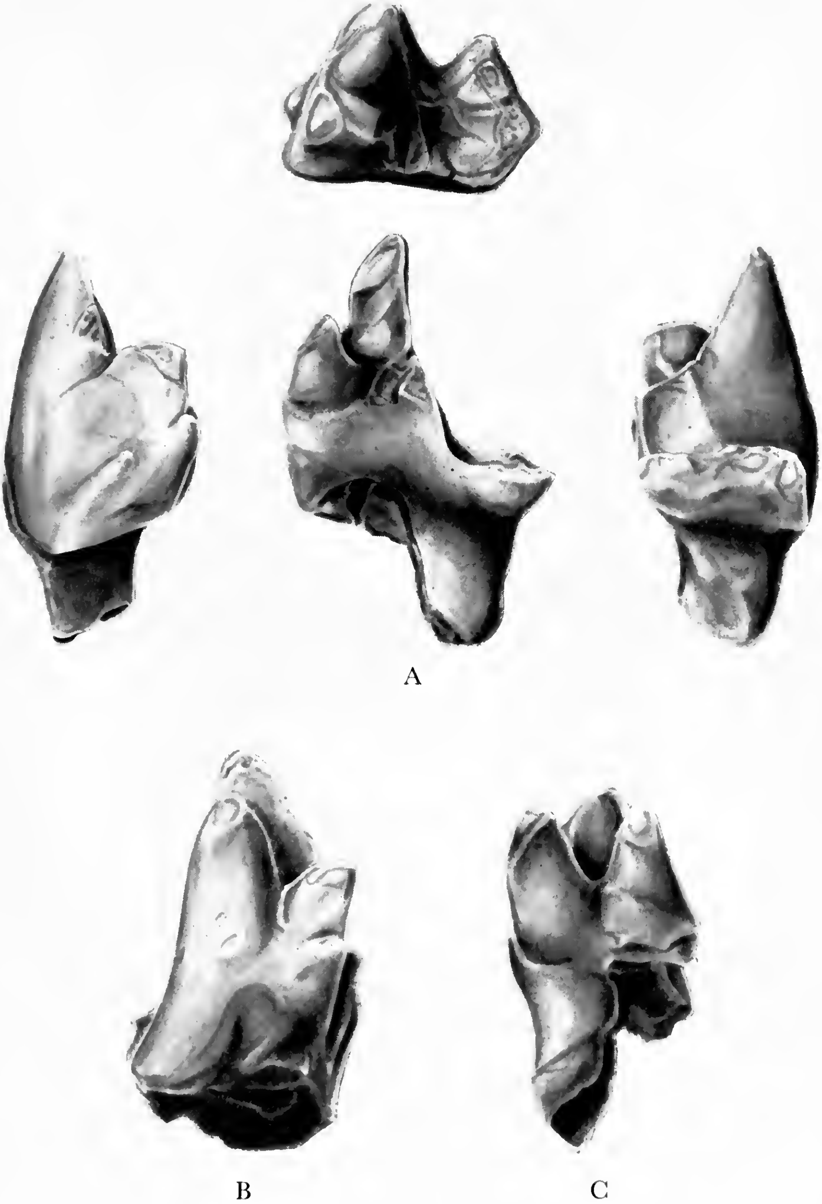

Fig. 8. A, Right lower molar of therian; CNHM no. PM 948, crown, anterior, internal, and posterior views. B, Trigonid of left lower molar of therian; CNHM no. PM 966, internal view. C, Trigonid of right lower molar of therian; CNHM no. PM 930, internal view. All ×23.

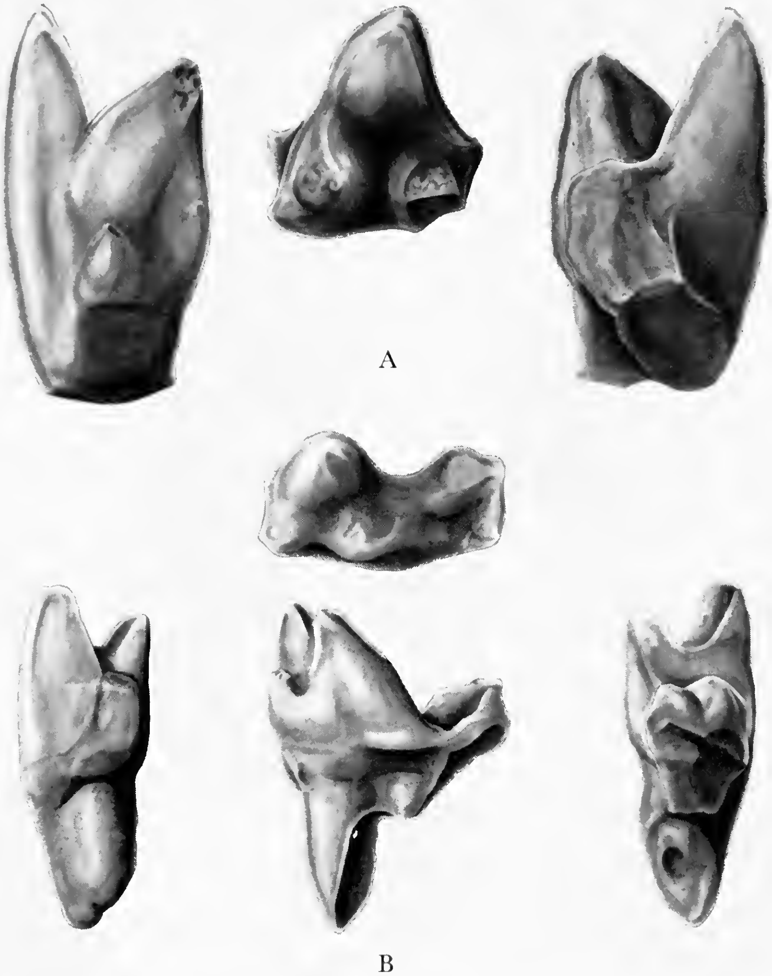

Fig. 9. A, Trigonid of right lower molar of therian; CNHM no. PM 660, anterior, crown, and posterior views. B, Right lower molar of therian; CNHM no. PM 922, crown, anterior, internal, and posterior views. Both ×23.

cuspule of symmetrodonts (see below). As regards the talonid cusps (at least in PM 965, the only tooth in which all details can be seen), the entoconid is slightly better developed, although still much smaller than either of the others, and the hypoconulid is rather larger and more projecting.

The third type, represented only by PM 922 (fig. 9, B), is quite distinctive. It is narrow in proportion to length, and the protoconid is very large in proportion to the other trigonid elements. The apex of the paraconid is missing, but despite this, it seems evident that the cusp was the lowest and smallest of the three, as in molars of the first type. The cleft between it and the protoconid extends much farther down than that between protoconid and metaconid, a difference from either of the other types. Paraconid and metaconid are separated to about the extent seen in the second type, but the metaconid is much longer than in either, sloping back into the talonid. The hypoconulid is more postero-external than postero-central in position and is not entirely separate from the larger hypoconid, the two cusps forming what is essentially a heavy ridge with two apices. A crest from the hypoconulid runs inward and then turns forward to the base of the metaconid. At the angle there is an elevation, the entoconid, again the smallest and lowest of the talonid cusps. In addition to the crista obliqua, here rather poorly defined, and the metaconid–entoconid crest, there is a third, faint crest running from the base of the metaconid into the talonid basin. This may perhaps be a vestige of the crest that runs to the talonid cusp in pantotheres. Wear on this tooth is present on the protoconid–metaconid crest and on the upper parts of the crests running posteriorly from the metaconid.

Mandibular fragment, PM 583.—There were clearly four incisors in this specimen (fig. 10). The alveolus of the first is the smallest of the series and that of the third the largest, the second and fourth being intermediate in, and of approximately the same, size. Relative to the alveoli of the other teeth, that of the canine is enormous. It is elongate-oval in outline and the tooth itself was single-rooted. The eight post-canine alveoli are nearly circular in outline, approximately equal in size, and evidently housed four two-rooted teeth. These are tentatively identified as premolars, the reasons being: (1) the decided break in size and structure between the premolar and molar series should surely be reflected in the alveolar structure, whereas these alveoli are all approximately equal in size; (2) none of the lower molars thus far recovered could have fitted into them.

Immersion in oil of anise has revealed nearly all details of the alveoli (fig. 11). That of the first incisor is very procumbent, the remainder becoming progressively more upright in position. The first and second taper evenly to a pointed extremity, the third is longer with a slightly bulbous expansion at the base, and the fourth is the shortest of the series, tapering but little and having a blunt termination. The alveolus for the canine extends ventrally for almost the entire depth of the ramus, tapers only slightly and curves posteriorly to terminate bluntly beneath P_1. The post-canine alveoli have slightly bulbous terminal expansions, similar to but larger than that seen in I_3. The alveoli of P_1 are somewhat shorter than

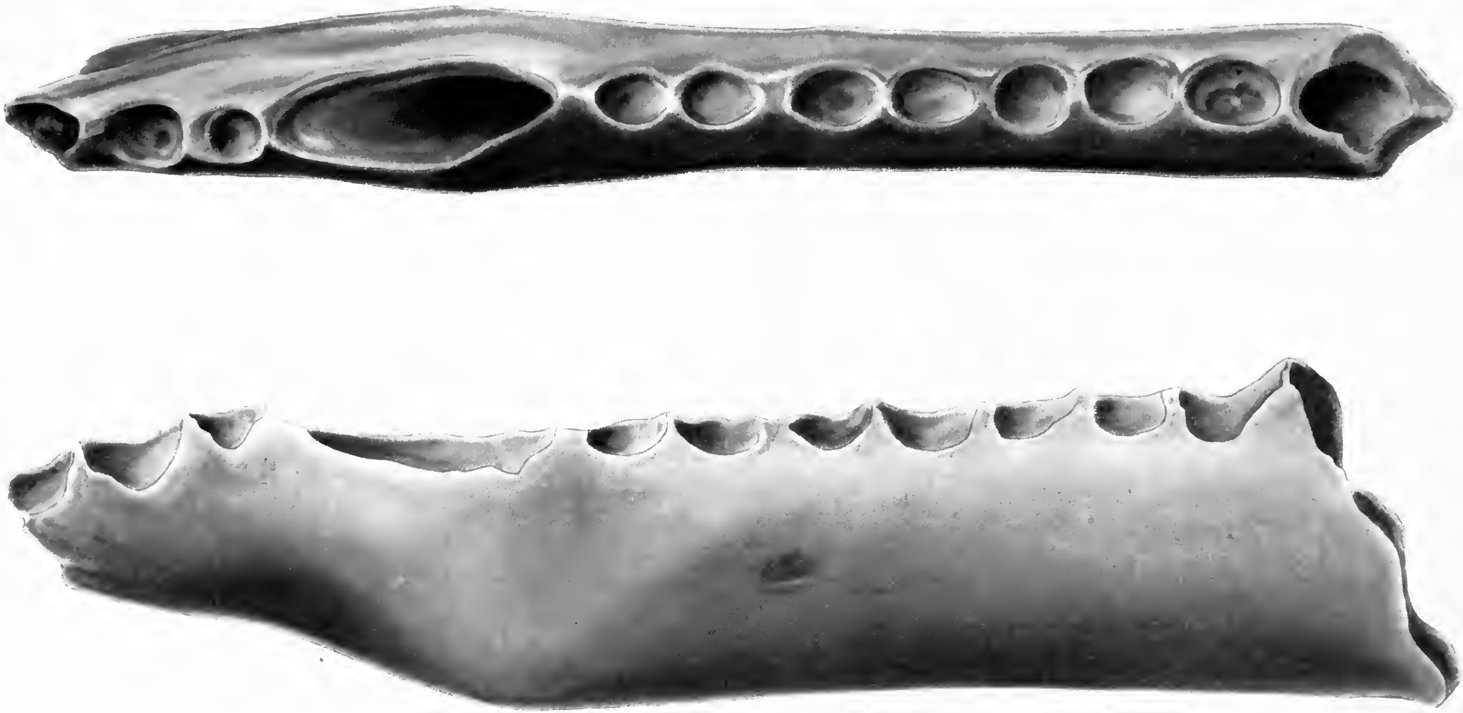

Fig. 10. Portion of left ramus of therian; CNHM no. PM 583, dorsal and external views; ×23.

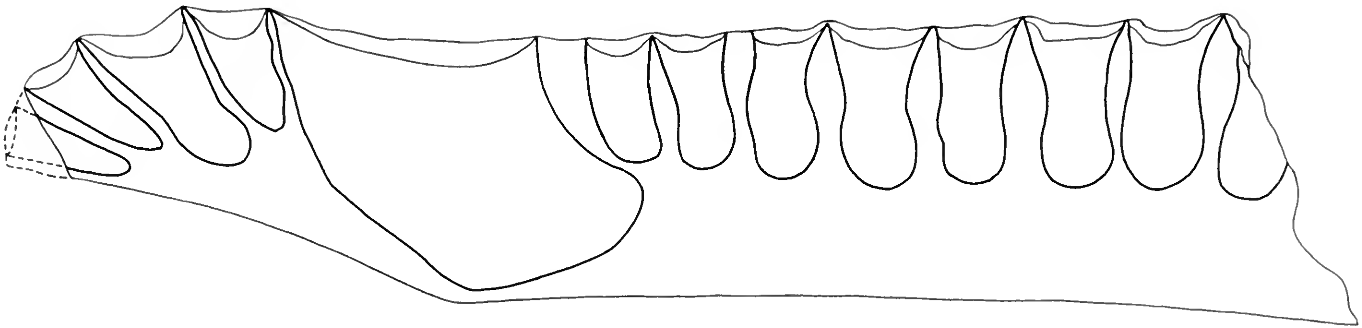

FIG. 11. Portion of left ramus of therian; CNHM no. PM 583, view of alveoli visible during immersion in oil of anise.

those of P_{2-4}, which extend ventrally for slightly over half the depth of the ramus.

The horizontal ramus, so far as preserved, is slender throughout, except in the region of the canine, where it is decidedly swollen on the external side. The ventral border is straight from the canine posteriorly, and gently concave beneath the incisors. A mental foramen is present below the anterior extremity of P_2. The ligamentous symphysis extends back to a point beneath P_1. No trace of an internal mandibular groove can be seen.

None of the other ramus fragments includes an alveolus certainly identifiable as to position.

PM 931: upper premolar, length 1.31 mm., width 0.73 mm.
PM 884: upper molar, length at paracone 1.29 mm.
PM 886: upper molar, length at paracone 1.26 mm.
PM 999: upper molar, length at paracone 1.09 mm.
PM 1075: upper molar (last), length at paracone 0.60 mm., width 1.46 mm.
PM 1005: lower molar, length 1.93 mm., width of trigonid 1.44 mm., width of talonid 1.05 mm.
PM 887: lower molar, width of trigonid 1.47 mm.
PM 965: lower molar, length 1.77 mm., width of trigonid 1.19 mm., width of talonid 0.86 mm.
PM 948: lower molar, length 1.40 mm., width of trigonid 1.00 mm., width of talonid 0.85 mm.
PM 660: lower molar, width of trigonid 1.20 mm.
PM 930: lower molar, width of trigonid 0.89 mm.
PM 966: lower molar, width of trigonid 1.39 mm.
PM 922: lower molar, length 1.28 mm., width of trigonid 0.72 mm., width of talonid 0.58 mm.

DISCUSSION

The association of the several types of upper and lower molars one with the other, not to mention the upper premolar, last upper molars and the mandibular fragments, is at present wholly uncertain. I do suspect, however, that three different animals may be represented. The numerous molars of dryolestid pantotheres show a considerable range in size and structure. If these Forestburg therians had an equally high number of molars, then it could, perhaps, be supposed that the range was sufficiently great for but one form to be represented by the material thus far found. This is highly improbable, however. The molars are much longer than those of any dryolestid, and it is therefore practically certain that no more than five molars were present, and indeed likely that the number was as low as three or four. In such series so wide a range as that shown by the material at hand does not seem likely.

The major taxonomy is as uncertain as the minor. It is evident that the molars are of eutherian–metatherian grade, but it is impossible to determine on this evidence alone whether the mammals that bore them were metatherians, eutherians, or neither. The ramus fragment, as far as it goes and if it is correctly referred, tends to support the last interpretation. The four incisors suggest pantotherian or metatherian affinities, the supposed four premolars pantotherian or eutherian. The molars definitely exclude the Forestburg forms from the order Pantotheria. The incisor and premolar formulae and the molar structure[1] present a combination such as must have occurred in the placental–marsupial ancestry. It is probable that the adaptive shift from the pantotherian to the eutherian–metatherian molar type preceded the divergence of these infraclasses, and possible that the radiation, which was to result in this divergence, was going on in Early Albian time. The order Pantotheria, under such a view, would not be directly ancestral to the marsupials and placentals but to the group from which these two infraclasses arose, a possibility admitted by Simpson (1936, p. 949). If future finds should confirm all this, it might become necessary to erect a new order for these Early Cretaceous therians, an order that would find its most logical place within the infraclass Pantotheria.

The uncertainty that prevails as to the taxonomy fortunately does not extend to the morphology. The homologies of the principal cusps present on the molars are not open to question, and the structure of these teeth casts a good deal of light on the early history of therian molars, a subject that is reviewed in some detail below. A discussion of the possible ancestry, within the Pantotheria, of the Forestburg forms is given in the concluding section.

NOTES ON THE MANCHURIAN MESOZOIC MAMMALS

Within the past twenty years, two mammals have been described from the Husin Series in southern Manchuria. One of these, *Manchurodon simplicidens* Yabe and Shikama (1938), is a symmetrodont of the family Amphidontidae, the type consisting of a lower jaw with eight post-canine teeth.[2] The second is a therian mammal, of eutherian–metatherian grade as regards molar structure, known from incomplete lower jaws. The last three molars of the right side are preserved. These are nearly equal in size, the first rather well worn and the second moderately so. Shikama (1947)[3] has named this specimen *Endotherium niinomii* and has erected for it a new family, Endotheriidae, named but not diagnosed, which he has referred to the

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[1] The central to centro-external position of the hypoconulid might perhaps be regarded as an indication of therian affinities, this cusp in Late Cretaceous didelphids being postero-internal (Simpson, 1951). This position is a specialized one, however, and there is, of course, no evidence that it was achieved by Albian time.

[2] The formula is given as P_3, M_5, but it seems possible that it could be P_4, M_4, as in *Amphidon*, since the measurements show a noticeable break in size between the first four and the last four teeth.

[3] A copy of this paper was not received in Chicago until 1951.

"order" Therictoidea.[1] He regards the animal as a placental, and believes that the three molars are M_{1-3}. This may very well be the case, but it is also conceivable that there may have been a molar or molars anterior to the first one preserved. The infraclass affinities of *Endotherium* cannot yet, I think, be regarded as positively established.

The Forestburg lower molars are distinguished from those of *Endotherium*, judging from Shikama's figures, in having the trigonid cusps somewhat better separated, the trigonid not pitched forward, a conspicuous external constriction present between trigonid and talonid, a smaller entoconid, and an anterior basal cuspule. As far as most of these characters are concerned, the Forestburg molars would appear to be somewhat less specialized than those of the Manchurian form.

A major question concerning *Manchurodon* and *Endotherium* is that of their age. Both Yabe and Shikama (1938) and Shikama (1947) regard the Husin coal-bearing beds as Late Jurassic. Shikama observes that, if this is the case, placentals appeared in eastern Asia much earlier than had previously been suspected and must have originated in Mid-, if not Early, Jurassic time. The evidence for a Late Jurassic age of the Husin beds is mainly paleobotanical. Shikama (1947, p. 77) states that, according to Maezima, the Husin flora is referable to the *Onychiopsis* floral series of Oishi (1940), which ranges in age from Late Jurassic through Early Cretaceous. Nine of the Husin species occur in the Rakuto, or Naktong, flora of Korea and eight each in the Tetori and Ryôseki floras of Japan. Oishi regarded the Naktong and Tetori as Late Jurassic and the Ryôseki as Early Cretaceous. Kobayashi (1939, pp. 90–92), however, regards the Naktong as Early Cretaceous and not improbably ". . . younger than Wealden," and mentions (p. 87) the possibility that the uppermost portion of the Tetori Series may be of Wealden age.[2] As regards paleobotanical evidence, it would seem that an Early Cretaceous age for the Husin flora is at least as likely as a Late Jurassic one.

On the basis of non-marine mollusks, Suzuki (1949, pp. 94, 116, 117) concludes that the Husin is a part of his Jehol faunal series, which he considers Late Jurassic. It may be noted, however, that none of the Husin species occurs in any of the other faunas regarded as Jehol.

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[1] Therictoidea, however, was proposed by Gregory (1910, p. 464) as a superorder for the reception of the orders Insectivora and "Ferae." It may be that Shikama intended to apply the name to the largely hypothetical "insectivore–creodont group" believed by many to lie at or near the base of the Eutheria, but so great a change in the meaning and content of the term would hardly seem justifiable from a nomenclatural viewpoint.

[2] In Arkell's monumental *Jurassic Geology of the World*, 1956, pp. 423–424 (Edinburgh: Oliver and Boyd), the Naktong and part of the Upper Tetori are considered to be Early Cretaceous, following Japanese authorities.

The Husin beds overlie the Shahai shale, which contains an undetermined lycopterid fish. The lycopterid-bearing formations are usually referred to the Cretaceous (e.g., Young, 1945). Takai (1940) has regarded them, again partly on paleobotanical evidence, as Mid- to Late Jurassic, but in so doing he has had to regard the Djadochta as Early Cretaceous. On vertebrate evidence, however, the Djadochta is surely of Late Cretaceous age.

The tetrapods from the Husin Series include, in addition to the mammals, *Yabeinosaurus* Endo and Shikama, *Manchurochelys* Endo and Shikama and *Teilhardosaurus* Shikama. *Yabeinosaurus* and *Teilhardosaurus* are of little help in correlation, but *Manchurochelys*, as Shikama remarks, "represents a somewhat advanced type for Jurassic Chelonia." Of the mammals, *Manchurodon*, an amphidontid symmetrodont, would suggest Jurassic rather than Cretaceous age were it not for the fact that *Spalacotheroides* shows that spalacotheriid symmetrodonts survived until Albian time at least. In view of this, it would not be surprising if the amphidontids had a comparable range in time. *Endotherium* is far more advanced than any therian known from the Purbeck and Morrison faunas and is comparable to, perhaps somewhat more advanced than, the Albian Forestburg forms. As such, it very definitely suggests an Early Cretaceous age for the Husin Series. The Purbeck and Morrison faunas are widely separated yet remarkably similar.[1] The Husin area is between them and if the three were in reality nearly contemporaneous, it would be most surprising that so advanced a form as *Endotherium* should occur in one and not in the others.

More evidence is clearly needed, but I nevertheless strongly suspect that the Husin Series is of Early Cretaceous age. The great potential importance of the Husin area, the second locality for Mesozoic mammals in Asia, is obvious, and it is to be hoped that the paleontologists of eastern Asia will be able to give to it the attention that it deserves.

THE HISTORY OF THE THERIAN MOLARS

It has long been recognized that evidence from Early Cretaceous deposits would be of crucial importance for an understanding of therian molar evolution. Such evidence is now at hand. It is neither as complete nor as extensive as could be desired, but it nevertheless seems sufficient for the purpose. From this vantage point in time, it is now possible to look forward to later developments or backward to earlier ones and, in either direction, to throw light on questions hitherto shrouded in uncertainty or clouded by dispute.

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[1] Imlay has recently (1952) stated that the Morrison is in great part of Kimeridgean age, hence earlier than the Purbeck. Be this as it may, the two mammalian faunas are at an almost exactly comparable evolutionary level.

THE TRIBOSPHENIC STAGE

As regards the Forestburg molars themselves, there can be no doubt concerning either the homologies of the major cusps they bear or the type of tooth they represent. Although primitive in their retention of a large stylocone, they are definitely tribosphenic[1] molars of the general type almost universal among latest Cretaceous and earliest Tertiary Theria. As such, they bring additional supporting evidence to the first part of the Cope–Osborn theory, namely, that from molars of this sort arose all the varied kinds evolved among marsupials and placentals during the Cenozoic. This view, proposed by Cope and supported, modified and extended by Osborn, Gregory, Matthew, Simpson and many others (for an extensive review see Gregory, 1934), is about as well documented as an historical evolutionary theory can be and is opposed today only by those who willfully ignore the supporting evidence. Indeed, emphasis on this part of the Cope–Osborn theory or on the support contributed to it by the Early Cretaceous material would scarcely be necessary were it not for the fact that Butler (1939a, 1941) has, it seems to me, confused the issue somewhat by setting up arbitrary definitions for primitive types of tribosphenic molars. By operating within the framework thus set up, he has made what appear at first glance to be important modifications of the theory, but the modifications are in reality results of the definitions. He lists "tritubercular," "dilambdodont" and "zalambdodont" types, arbitrarily limits the Cope–Osborn or "tritubercular" theory to the first of these (i.e., molars with paracone and metacone external and protocone internal in position, and stylar area small), and then proceeds to demonstrate that the other two types have not passed through a "tritubercular" stage. This restriction of the term "tritubercular" is a retrogression to some of the earliest literal statements of the Cope–Osborn theory and ignores the contributions of later authors (e.g., Gregory, 1916, 1922; Simpson, 1928b, 1936), who had so amply demonstrated the importance of the stylar, or external shelf, area in primitive therian molars that their findings had become an integral part of the theory by 1941.[2] Butler mentions these contributions in his introduction, yet disregards them in his thesis. By so doing, he is able inferentially to

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[1] A term coined by Simpson (1936, p. 797) to replace the cumbersome tritubercular–tubercular–sectorial circumlocution previously in use for upper and lower molars, respectively, of this type. Of these, as he pointed out, the first was in a strict sense inaccurate and the second inadequate. The word was intended to be ". . . suggestive of the mortar and pestle, opposing action of protocone and talonid and of the wedge-like, alternating and shearing action of trigon and trigonid." The desirability and usefulness of the term cannot be too strongly emphasized.

[2] There is thus no justification for Butler's statement (1941, p. 444) that the "usual view" upheld by proponents of the theory is that the primitive position of the paracone and metacone was external.

label as "non-tritubercular" molar types that other authors, working within the framework of the developing Cope–Osborn theory, had long regarded as "primitive tritubercular." Use of the term "tribosphenic," to which Butler only alludes in passing, avoids such purely verbal confusion.

It is not to be denied that "tritubercular," "dilambdodont" and "zalambdodont" molars are readily recognizable in their typical, specialized form. To stretch the terms to include teeth that have not attained these typical forms is not helpful, however. "Primitive zalambdodont" and "primitive dilambdodont" (Butler, 1941, fig. 8, p. 441), for example, approach a common structural and functional type, and the same would be true of a "tritubercular" tooth with an external shelf of moderate dimensions. Application of different, and not precisely definable, descriptive terms to such generalized teeth tends to distract attention from their basic similarity. To borrow a simile from music, such incipient divergences in crown structure are merely variations on an original theme; it is the theme —the tribosphenic molar—and not the variations that is the important thing. Each of Butler's three types is directly derivable, structurally, from the Forestburg molars: the "zalambdodont" by retention of the stylocone, shortening of the tooth accompanied by reduction and eventual complete subordination of the metacone in a crest, and broadening of the stylar area with progressive reduction of the protocone and talonid; the "dilambdodont" by reduction of the stylocone and development of a W-shaped ectoloph through acquisition of a mesostyle; and the "tritubercular" by reduction of the entire stylar area (the Late Cretaceous *Zalambdalestes* is, I suspect, an example of this). Early stages in any one of these three processes would readily be reversible or capable of transformation into either of the others.[1]

The primitive nature of the Forestburg molars—especially the presence of a large stylocone—suggests that the adaptive shift to the tribosphenic from the earlier pantothere molar stage had occurred not very long prior to Early Albian time. The further fact that differences in structure are to be seen among these molars shows that divergence followed hard upon the shift. If this be granted, and I think it must, then it follows that the eutherian–metatherian radiation began between 50 and 60 million years prior to the Cenozoic. In a reptilian-dominated world, this must have been an exceedingly slow and halting process, as the Paleocene flowering in fact shows, but it is nevertheless virtually certain that the basic characters that

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[1] Butler (1941, p. 444) indeed states that "tritubercular" types probably evolved independently in several groups from a "dilambdodont" base. He has further tentatively hinted (e.g., 1939b, p. 333; 1941, p. 437, figs. 8–9) that the therian "tritubercular" pattern could also have evolved directly from the docodont molar. With this, I am unable to agree; the docodonts are not therians (see p. 71).

underlay the later, rapid adaptive diversification of the Eutheria became established during this prolonged dawning of the mammalian era, and that the divergence of the Metatheria from the primitive Eutheria took place at a very early date, at the beginning of the Late Cretaceous, at least. So much for the forward look; the backward look is equally fascinating—and even more informative.

THE PANTOTHERE STAGE

The preceding section dealt very briefly with the well-documented first part of the Cope–Osborn theory—the origin of the highly varied metatherian and eutherian molars from a common tribosphenic type, Osborn's "First Principle" (1907, pp. 2–4).[1] We now pass to what may loosely be termed the second part of this theory—the origin of the tribosphenic type. This is a much more difficult, because less documented, subject, and its core is the interpretation of the upper molars of the Jurassic Pantotheria.[2] The structure of these teeth is now well known (Simpson, 1928a, 1929a; Butler, 1939b). In upper molars, there is a large, high internal cusp and a more or less centro-external cusp, which is large in some forms, the two frequently joined by a transverse median ridge. Two notched crests lead from the internal cusp, one in an antero-external, and the other in a postero-external direction, to form the anterior and posterior borders of the crown. The anterior of these crests terminates at the centro-external cusp and may very exceptionally (e.g., M^4 on *Melanodon oweni*) bear a small cuspule or swelling.[3] The posterior crest rises to a medium-sized cuspule

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[1] Simpson (1936, p. 794) would restrict the term "Cope–Osborn theory" to this first part, or Osborn's First Principle. The evidence presented in this paper shows, however, that the main point of Osborn's Fourth Principle, that upper and lower molars were originally reversed triangles, is true. The Third Principle, that tooth complication came about by budding or outgrowth on a single crown and not by the concrescence of several crowns into one, is now almost universally admitted. Osborn's Second Principle (1907, p. 4) is a restatement of Cope's views on cusp rotation. Osborn himself (1907, pp. 7–9) was more cautious; rotation of the two subsidiary cusps to one side of the main cusp was his favored hypothesis, but he also clearly stated (1888b, p. 1075; 1907, pp. 7, 227) that the subsidiary cusps of triangular molars may have arisen *in situ*. The latter of these alternatives seems more likely, but the rotation hypothesis cannot yet be completely written off (see p. 45). For these reasons, it is, I think, permissible, even obligatory, to refer to the whole as the Cope–Osborn theory.

[2] Considered as comprising the families Amphitheriidae, Paurodontidae and Dryolestidae. The Docodontidae, hitherto regarded as pantotheres, are here placed in a distinct order, Docodonta (p. 76).

[3] Butler (1939b) neither mentions nor shows this cuspule, although his figure is based on the same specimen (Yale Peabody Museum no. 10663) as that shown in Simpson's stereoscopic photographs (1929a, pls. 13, 14), in which the cuspule seems evident. Dr. Joseph T. Gregory has very kindly examined the specimen and informed me that, although some breakage appears to have occurred since Simpson's figures were made, there is a swelling in this part of the crest.

about midway in its course and then continues on to the postero-external corner of the tooth, where it terminates in a small cusp; a prominent, almost always hook-like, antero-external cusp is present and there is a small cusp posterior to the centro-external one. In the majority of forms these teeth, apart from the most anterior ones, are much wider than they are long. The upper molars are three-rooted, the internal root beneath the internal cusp.

As may be seen from figure 12, B, C, there are two possible ways of homologizing the cusps on these teeth with those on a tribosphenic upper molar. Either of two cusps may be regarded as the primary one. These possibilities combine to present the following three interpretations: (1) the primary cusp is centro-external and the paracone (or "amphicone" or "eocone"[1]), (2) the primary cusp is internal and the protocone, or (3) the primary cusp is internal and the paracone. Identification of the remaining cusps follows more or less automatically upon the determination of the primary cusp, although it must be emphasized that all the authors mentioned below have not applied names to all cusps. Each interpretation has found adherents; for example, Gidley (1906), Gregory (1926), Roth (1927)[2] and Bohlin (1945) have favored the first; Osborn (1888a and b, 1904, 1907), Simpson (1927, p. 413; 1928a, p. 117; 1929a, p. 9, fig. 2; 1933, p. 144; 1935, p. 167)[3] and Gregory (1934) the second; and Gregory (1916, 1922), Matthew (1922) and Butler (1939b) the third.

The Forestburg molars permit a definitive choice among the three interpretations. In these teeth, a large stylar cusp is situated external to the

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[1] Although Bohlin did apply the term "eocone" to the pantothere stylar cusp, here called "stylocone," which he regarded as the primary one in this group, he evidently did not intend to restrict the name solely to this cusp. He defined it (1945, p. 373) as "a term designating the original cone without regard to where it has its place in the specialized mammalian molar. . . ." I gather from this that should he subsequently decide that a cusp other than the stylocone was the original one in pantotheres, then the name "eocone" would be transferred to it. In this sense, "eocone" and its lower equivalent, "eoconid," are synonymous with "paracone" and "protoconid" as used here.

[2] Roth called this cusp "protocone," the parastyle "paracone" and the large internal cusp "deuterocone." He believed that all teeth, incisors to molars inclusive, had passed through a triconodont stage, the "deuterocone" being a later addition to the molars. His theory, of some historical interest since he was ahead of his time in struggling with what later became the field concept, was published posthumously from manuscripts assembled by Fernández.

[3] Simpson's endorsements, or rather acceptances, of this interpretation have been made only in passing, and consist of one reference to a metaconule, one reference to the protocone shearing against the talonid, one figure and its caption, one reference to a protocone, and a reference to the internal upper cusp as the primary one. Cusp homologies of upper molars have not been an integral part of his magnificent work on Mesozoic mammals; in fact, he has consistently maintained that the available evidence has been insufficient to arrive at a conclusion on this score. Simpson's data, however, have profoundly influenced Gregory's thinking, leading him to abandon interpretation 3, which he had proposed and which now appears to be correct, and to accept in succession, although with seeming reluctance, 1 and 2.

paracone, to which it is connected by a crest in some (e.g., PM 884 and PM 1075). In pantothere upper molars, the centro-external cusp, the stylocone as defined above (p. 16), has almost exactly similar relations. It is clear, I think, that this cusp in these forms can be neither the primary cusp nor the paracone, but is, as Butler maintains, a stylar element. It follows, therefore, that the internal cusp can only be the paracone, that this is the primary cusp, and that there is no trace of a protocone in these molars. The third interpretation, that of Gregory (1916, 1922), Matthew, and Butler, is the correct one. The antero-external cusp is clearly the parastyle, but which of the two cusps in the metastylar area corresponds to the metastyle is uncertain. As noted above (p. 13), it may be the more external of the two, in which case the other, the homologue of the postero-external cingulum cusp of Jurassic symmetrodonts, did not persist beyond the pantothere stage.

The one cusp that remains to be discussed is situated near the middle of the posterior crest. To those who believed that the internal cusp was the protocone, determination of the cusp on this crest was simple: it was obviously the metaconule. Since the internal cusp is not the protocone but the paracone, this clearly will not do. Butler (1939b) has boldly stated that the cusp in question is the metacone. Prior to the discovery of the Forestburg molars, this had seemed to me unlikely. It is highly exceptional for the metacone to be postero-external to the paracone in later Theria, *Potamogale* (Butler, 1939a) being one of the very few forms in which it occupies this position. Further, the Late Cretaceous *Deltatheridium*, in which paracone and metacone are practically connate, seemed to indicate that the metacone had originated on the posterior slope of the paracone (Gregory, 1927). In view of these facts, it then appeared to me more likely that, if the third interpretation was correct, the cusp under discussion on pantothere upper molars would disappear, like its opposite number on the anterior crest of the upper molars of spalacotheriid symmetrodonts, and its function would be taken over by a metacone that would arise *de novo* on the posterior slope of the paracone. The Forestburg molars do not support such an idea, however. In these, the paracone and metacone are well separated, in fact far apart in some specimens, e.g., PM 886, and give no hint of having been connate in an earlier stage. From the tip of the metacone in PM 886 one crest runs to the metastylar area and another toward the base of the paracone, precisely as in the supposed metacone of pantothere molars. Butler, I therefore believe, was right in regarding these cusps as homologous. It now seems likely that the metacone shifted inwardly from the pantothere postero-external position to the tribosphenic position posterior to the paracone *pari passu* with the lengthening of the teeth, narrowing of the stylar area and

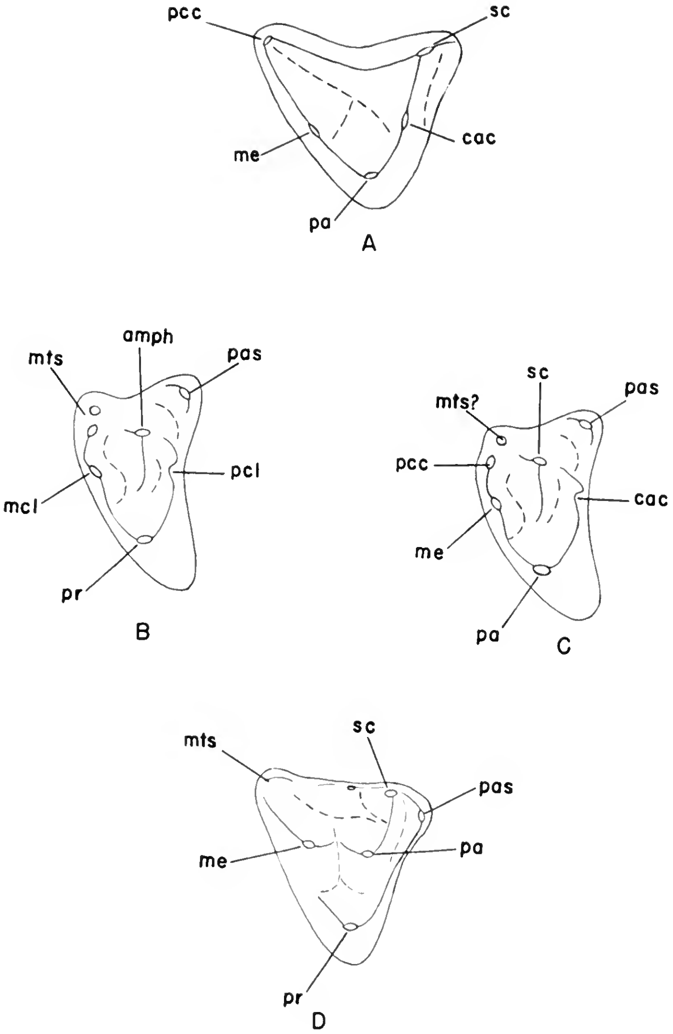

FIG. 12. Right upper molars of Mesozoic therians. A, M^4 of *Peralestes longirostris* Owen; B and C, M^4 of *Melanodon oweni* Simpson, showing differing interpretations of cusp homologies (those of C are here accepted); D, an intermediate upper molar of a Forestburg therian. A from Butler, B and C from Simpson; lettering in part original. D based on CNHM nos. PM 884 and PM 999, protocone restored to accord with that of last upper molars PM 1075 and PM 1287. Not to scale; greatly enlarged.

amph, amphicone (paracone + metacone); *cac*, cusp on anterior crest (only occasional vestiges of this cusp occur subsequent to the symmetrodont stage); *mcl*, metaconule; *me*, metacone; *mts*, metastyle; *pa*, paracone; *pas*, parastyle; *pcc*, postero-external cingulum cusp; *pcl*, protoconule; *pr*, protocone; *sc*, stylocone.

addition of the protocone and basined talonid. The close approximation of paracone and metacone in *Deltatheridium* and numerous other forms would appear to be secondary, brought about by a narrowing of this part of the crown.

The interpretation of the pantothere lower molar has never been a matter of controversy. The identity of the trigonid cusps with those of the tribosphenic trigonid and the identification of the protoconid as the primary cusp have not been in question. The antero-internal basal cuspule seen in some paurodontids occurs in the Forestburg molars. The only point that has been in doubt is the identity of the small cusp in the incipient, shelf-like talonid. Osborn regarded it as the hypoconid. Gregory has consistently described it as the entoconid. Simpson (1928a, p. 117) suspected that it might be the entoconid but suspended judgment as between this cusp and the hypoconulid, and Butler (1939b) has come out strongly for hypoconulid homology. In the Forestburg molars, the entoconid is the smallest of the talonid cusps, and gives the impression of having but recently come into existence on the crest connecting the hypoconulid and the base of the metaconid. In PM 948, PM 965 and PM 922, the hypoconid and hypoconulid are approximately equal in size, and in the last imperfectly differentiated, while in PM 1005 the hypoconid is the largest. So far as it goes, then, the Forestburg evidence favors either Osborn's or Butler's interpretation of the pantotherian talonid cusp, and of the two the latter is provisionally adopted here. Acquisition of the protocone and basined talonid involved so complete a remodeling of the posterior part of the lower molar, however, that the possibility exists that the only real homology is between the whole talonid areas of pantotheres and later therians. It is true, of course, that as the talonid becomes reduced in zalambdodonts the hypoconulid becomes the most prominent or the only remaining cusp, but it is not certain that the course of retrogression necessarily demonstrates the course of the original differentiation.

The unbasined, shelf-like pantotherian talonid is in itself the strongest evidence that the internal cusp of the upper molars is not the protocone, and this is further supported by the occlusal relationships of the upper and lower molars. Consideration of these matters is best postponed, however, until after the morphology of the earliest stage in therian molar history and certain questions connected with it have been discussed. Yet it now seems clear, and the point may be stressed here, that acquisition of the protocone and the basined talonid was a decisive factor in the shift from the pantothere to the tribosphenic stage. A relation between these elements was long ago pointed out by Gregory and Simpson (1926, p. 3).

THE SYMMETRODONT STAGE

Peralestes, *Spalacotherium* and the Forestburg specimens, the "acute-angled" symmetrodonts, are typical representatives of this stage. The upper and lower molars of these forms (Simpson, 1928a; Butler, 1939b; Patterson, 1955; this paper, above) are essentially reversed, although not identical, triangles, the uppers with a high internal cusp and the lowers with a high external one (figs. 1, 12, A, 15, B). From these main cusps notched crests run down to the other corners of the teeth, forming the anterior and posterior borders of the crown. In the central part of the upper molar series each crest bears a cusp near its center, the cusp on the posterior crest decreasing posteriorly, that on the anterior disappearing anteriorly. Toward the end of the series, a second cusp external to the first appears on the anterior crest. The crests of the lower molars terminate in internal cusps. The upper molars of the Jurassic *Peralestes* have an external cingulum that rises to antero-external and postero-external cusps connected to the ends of the crests running from the main cusp; the Cretaceous molar described above bears two additional cingulum cusps anterior and posterior, respectively, to these. The lower molars have a continuous or nearly continuous basal cingulum that bears a small postero-internal cusp and a still smaller antero-internal one (Simpson, 1928a, p. 101; Patterson, 1955). The upper molars are not as wide as is usually the case in pantotheres, the principal cusps, especially the upper, are much higher than the others, and the apices of the three main cusps of the lower molars are closer together.

As Butler has noted, these teeth are fundamentally very similar to those of the pantotheres. There can be no doubt as to the homologies of nearly all the cusps present. In the upper molars, the primary, internal cusp is the paracone and the cusp on the posterior crest is the homologue of that here regarded, following Butler, as the metacone in pantotheres (fig. 12, A). The cusp on the anterior crest becomes lost in later therians. The only subsequent traces of it are to be seen in the vestigial cuspule occupying this position in the Morrison pantothere *Melanodon oweni* and the occasional similar vestige occurring very rarely in insectivores (Butler, 1939b, p. 343). As discussed above (p. 12), the structure of the Forestburg symmetrodont PM 1235 suggests that the antero-external cingulum cusp in *Peralestes* is homologous with the second stylar cusp—the stylocone—of pantotheres, and that a parastyle was independently acquired in pantotheres and in the latest spalacotheriids. Under this view the anterior crest connected paracone and stylocone from the symmetrodont stage on to the early tribosphenic. As concerns the metastyle there is less assurance, although it is certain that an additional cusp in the metastylar area was also acquired independently in pantotheres and in the latest spalacotheriids. In the lower molars, the primary, external cusp is the protoconid and the cusps on the crests running from it are the paraconid and the metaconid, the whole thus corresponding exactly to the pantotherian trigonid. The small postero-internal cingulum cusp is clearly homologous with the similarly situated cusp in pantotheres, which is here tentatively regarded, again following Butler, as the hypoconulid. The only element of the pantothere molar crowns not present therefore in symmetrodonts is the talonid shelf. I thus agree completely with Butler's homologies on all points save two—the cusp here regarded as the metaconid is for him "the posterior accessory cusp," and he equated, as was natural, the pantothere parastyle, rather than the stylocone, with the antero-external cingulum cusp of *Peralestes*. Butler neither mentioned nor figured the antero-internal cingulum cuspule of *Spalacotherium* described by Simpson; a similar cuspule is present in *Spalacotheroides*. A possibly homologous, or at least similarly situated, cuspule occurs in some paurodontids among the Pantotheria, and among the Forestburg lower molars.

In view of the difference of opinion on the metaconid just referred to, some consideration of this element is necessary. Butler's argument against such an identification is threefold: (1) comparison of the last premolar and first molar in *Spalacotherium* suggests that the cusp in question is a "posterior accessory cusp," (2) in *Tinodon* (a form with relatively long, narrow molars) the cusp is on the posterior slope of the protoconid, whereas, (3) ". . . the true metaconid is always lingual or postero-lingual in origin." As regards the first of these points, the "posterior accessory cusp" of the last premolar is posterior in position, the metaconid of the first molar postero-internal. The second gives unwarranted emphasis to a difference in degree that is probably due to secondary elongation of the *Tinodon* molar (see p. 44). As written, the third seems irrelevant because the cusp in question actually *is* postero-lingual to the protoconid in *Tinodon* as well as in *Spalacotherium* and *Spalacotheroides*, so that this could almost be read as an argument in favor of the metaconid homology.[1] The fact of the matter is that the metaconid, as I regard it, has almost the same relation to the protoconid in symmetrodonts as it does in pantotheres and later therians. It is not quite as internal to the protoconid as it is in these forms, and the explanation of this is to be sought in the dentition as a whole. Simpson (1928a, p. 106) has observed that the interdental embrasures in the upper

[1] I gather from his next few sentences that what Butler means by the statement quoted is that on the lower *premolars* of much later therians the metaconid appears, as the molarization region extends forward, on the inner side of the protoconid and hence internal to the "posterior accessory cusp," when this is present (cf. his identification of a slight median elevation on the internal cingulum of the lower molar of *Tinodon* as a "metaconid"; 1939b, p. 342, fig. 7, *h, j*). Premolar analogy is not a safe guide to molar history, as I attempt to show in a later section, and dependence on it can, as in this case, lead to very questionable interpretations.

molars of *Peralestes* are widely open. It is hardly surprising, therefore, that the metaconid in *Spalacotherium* should occupy a slightly more posterior position relative to the protoconid than the somewhat more internally situated metaconid of pantotheres. In these forms not only are the interdental embrasures narrower but the anterior borders of the upper molars, against which the protoconid–metaconid crest shears, are rather more transverse than in *Peralestes*, in some cases even slightly inclined anteriorly. The slight difference in position of the metaconids in the two groups thus reflects function and does not indicate different origins. In *Spalacotheroides*, which has a shorter trigonid, the metaconid is farther postero-internal than in *Spalacotherium*.

Simpson (1928a, p. 177) noted the very considerable degree of resemblance between pantothere and symmetrodont molars, pointed out the differences alluded to above—no enlarged stylar cusp, more symmetrical outline, talonid not present as such in the latter—and emphasized the presence of internal cingula on the lower molars in symmetrodonts and their absence in pantotheres. This last feature led him to suspect, in agreement with Osborn (1888a, p. 245) and Gregory (1910, p. 174), that ". . . the accessory cusps [paraconid and metaconid of this paper] seem to be derived from the slopes of the main cusp, whereas the pantotheres never have internal cingula and the accessory cusps appear to be derived from the basal part of the tooth," i.e., the cingulum.[1] I am unable to accept this view. The internal cingulum is, of course, present in spalacotheriids (although not in amphidontids) and absent in pantotheres, but this fact hardly justifies such far-reaching conclusions on cusp origins. In *Amphitherium* and *Peramus*, the paraconid and metaconid arise high on the crown; in fact Simpson himself states (1928a, p. 123) that these cusps in *Peramus* do ". . . spring from the lower slope of the *prd*." The disappearance of the internal cingulum in pantothere lower molars is, I suspect, merely a minor specialization that may, like the differences in metaconid position just discussed, be correlated with other changes in trigonid proportions, such as the spreading of the cusp apices, that were involved in the further evolution of the masticatory function.[2]

[1] Earlier (1925c, p. 567), Simpson had stated that ". . . the main cusps of symmetrodont molars arise from quite different parts of the crown and hence are not even comparable. . . ." This more extreme view was evidently modified by subsequent first hand knowledge of *Spalacotherium* and *Peralestes*, which are more pantothere-like than the American Jurassic forms.

[2] In the lower molars of the docodontids, which Simpson and others regard as pantotheres but which I do not (see p. 71), the cusp postero-internal to the primary cusp evidently did arise from the internal cingulum. This fact may have contributed to Simpson's belief that the internal cusps of the pantotherian trigonid had such an origin, and perhaps also to Butler's identification of a part of the internal cingulum of *Tinodon* as an incipient metaconid (see above).

To sum up briefly, there is now, I believe, no reason to doubt that the symmetrodonts, pantotheres and earliest tribosphenic forms constitute a structural series so far as the morphology of their molars is concerned (see figs. 12, 15, A–D). As pointed out in a succeeding section, it is also probable that these three groups stand in an ancestor–descendant relationship.

THE REVERSED TRIANGLES OF EARLY THERIAN MOLARS AND RELATED PROBLEMS

As the Forestburg molars permitted a definitive determination of cusp homologies in pantothere molars, so the latter in their turn perform the same service for symmetrodont molars. It is now evident that in symmetrodonts and pantotheres the primary cusps are internal above and external below. Osborn (1907, p. 5) was therefore in large measure correct in his belief, his Fourth Principle, that "... the evolution and relation of both the upper and lower molars are those of a pair of reversed triangles. . . ." His mistake, of course, was that he regarded the original, internal cusp in these upper molars as homologous with the internal cusp in metatherian and eutherian upper molars. Evidence from the embryology and from the premolar structure of these later therians soon showed that the main antero-external cusp—the tribosphenic paracone—and not the internal cusp—the protocone—was the primary one on their upper molars, a fact that persuaded the advocates of what came to be known as the embryology and premolar analogy theories that their evidence discredited the conception of the original reversed triangles. It remained for Gregory (1916, 1922) to reconcile these opposing views, to show that each partook of a part of the truth, and to suggest that the therian upper molar was first a primary trigon with the paracone internal and that this was later replaced by a secondary trigon, in which a new internal cusp, the tribosphenic protocone, was added to the crown. This brilliant interpretation, one of the greatest of Gregory's many fundamental contributions, is completely confirmed by the evidence reported and reviewed here, and it is a matter for regret that this distinguished student saw fit to abandon it at a later date.

If we were to let quibbling over nomenclatural priority of morphological terms concern us, we would be in a pretty pickle at this point. Osborn, working with Mesozoic mammals, stated that "the primary cusp may be called the protocone" (1888a, p. 242). This term in its original usage thus clearly applies to the internal cusp of the primary trigon of symmetrodont and pantothere upper molars. With acquisition of the secondary, tribosphenic trigon, this primary cusp came to occupy a centro- to antero-external position on the tooth and a new cusp arose postero-internal to it. In the Osbornian nomenclature, as misapplied (by Osborn himself) to tribosphenic teeth, these cusps are called paracone and protocone, respectively. If the concept of rigid priority obtained in morphology as it has for so long in systematics,[1] we should be under the ridiculous necessity of abandoning the term "paracone," of transferring the term "protocone" to the cusp universally called paracone in tribosphenic nomenclature, and of adopting another term (Scott's deuterocone, 1892, would be the logical candidate—a step actually taken by Roth, although for different reasons) for the internal cusp universally called protocone in this nomenclature. Most fortunately, such absurdities are not required. It is the Osbornian nomenclature as used for tribosphenic teeth and their derivatives that has been in wide and daily use for over half a century, and it is this tribosphenic nomenclature that must be extended, as it was implicitly by Butler (1939b) and as it is explicitly here, to the earlier therian stages. The prior claims of the nomenclature based on Jurassic therians must yield to convenience and utility.

Recognition of the fact that therian molars were originally reversed triangles at once poses, or rather re-poses, three questions. Was this condition inherited by or did it evolve within the order Symmetrodonta? Did rotation from a cusp-in-line stage take place? To what, if any, extent are the cusps of upper and lower molars "equivalent"? These may be considered in turn.

Until very recently, the only known symmetrodonts were from the Late Jurassic Purbeck and Morrison formations. Two of these, *Spalacotherium* and *Peralestes* (the possibility exists that these may represent the lower and upper dentition, respectively, of the same form), have numerous molars, six above and seven below, that are sharply triangular and possibly three-rooted above. These and the Forestburg specimens are the "acute-angled" symmetrodonts (Patterson, 1955). The rest, *Tinodon*, *Eurylambda*, and *Amphidon*, have fewer molars, four below (*Eurylambda* is known only from a single upper), which are longer and narrower, perhaps two-rooted above and with more widely open triangles. The question of whether one of these two kinds was more primitive than the other, and if so which one, or whether both were about equally specialized, was difficult to decide on the basis of material that was all of the same age. Simpson (1925b, pp. 469–470) thought that *Amphidon* might represent the ancestral type, and this view has found further expression in Gregory's diagrams illustrating his later views on the early evolution of occlusal relationships in the Theria (1934, fig. 44, p. 249). Simpson regarded *Tinodon* and *Spalacotherium* as about equally but divergently specialized (1928a, pp. 98–99).

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[1] Since this was written, the decisions made at the International Zoological Congress held at Copenhagen, 1954, hold forth the promise of at least some measure of relief from absurdities committed in the name of priority.

The more recent discoveries have shed some light on this matter. *Spalacotherium*, certainly, and *Manchurodon*, very possibly, show that both kinds survived into the Early Cretaceous. More important than either of these, however, is the Rhaeto-Liassic molar, "Duchy 33,"[1] described by Kühne (1950). This is the earliest known tooth of therian type, and, as emphasized by Kühne, it has all the earmarks of a symmetrodont lower molar. Interpreted as such, it bears a high external cusp connected by notched crests to lower antero-internal and postero-internal cusps, the whole surrounded by a continuous basal cingulum. According to Kühne's figure and description, the cingulum does not bear antero-internal and postero-internal cuspules. The three cusps are, in this view, the protoconid, paraconid and metaconid, and we therefore have a trigonid with no indication of a talonid, other than the undifferentiated cingulum on which the hypoconulid later arose. Duchy 33, if really a lower molar, thus contradicts Butler's assertion (1941, p. 448) that "the talonid did not arise as an addition to a tooth that originally consisted of a trigonid only."[2] It must be emphasized, however, that this identification is based on the differences between the upper and lower molars of the much later *Peralestes–Spalacotherium*. Such differences may not have existed in the Rhaeto–Lias, and the possibility that Duchy 33 may be an upper molar should not be left out of account.[3] Regardless of its position, this tooth shows an angle of "approximately 100°" (Kühne) between the three cusps, and this is helpful in deciding the evolutionary status of the later forms. The angle is intermediate between that of *Peralestes–Spalacotherium*, "less than 90°," and that of *Amphidon* and *Eurylambda*, "approximately 135°" (Bohlin, 1945, p. 383), although closer to the former. This suggests, as Simpson has already intimated, that there was divergent specialization within the Symmetrodonta: *Peralestes–Spalacotherium* and *Spalacotheroides* of the Spalacotheriidae, the "acute-angled" forms, evolved narrower triangles that became three-rooted above, emphasizing the transverse, alternating shear and retaining a high number of molars; the amphidontids, and *Tinodon* and *Eurylambda* among the spalacotheriids, evolved more open triangles, trending toward a more antero-posterior shear, retaining the two-rooted condition and reducing the number of molars. The latter would appear to be somewhat the

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[1] From the name of the quarry, near Bridgend, Glamorgan, South Wales, in which the matrix containing this tooth and the equally important molar of *Morganucodon* was found. It is most gratifying that Dr. Kühne's painstaking work in the difficult field of fissure-filling investigation should have resulted in these major discoveries.

[2] This is in any event largely a matter of definition; from a functional point of view, a small cuspule on a basal cingulum hardly constitutes a talonid.

[3] If the upper and lower molars were essentially alike in this form and its contemporary relatives, a possibility which is not unlikely, then the earliest therian molars were very literally "tritubercular."

more specialized of the two types, particularly as regards molar reduction.[1] The source of the Pantotheria is clearly to be sought among the first of these types. Finally, and in answer to the first of the questions posed above, Duchy 33 strongly suggests, in view of its great age, that molars of the reversed triangle type were inherited by the Symmetrodonta.

This probability in turn suggests that if cusp rotation did take place, it occurred within the group of therapsid reptiles from which the therian mammals arose. Actually, the mode of origin of the reversed triangles is of minor significance in comparison with the importance of the triangles themselves. Tracing the controversy that has raged over the question of origin, much of it summarized in Osborn (1907), it becomes apparent that a great deal of the early furor stemmed from the fact that neither Osborn nor the proponents of the embryology and premolar analogy theories enjoyed a monopoly of the truth. Osborn was arguing in large part from conditions in Mesozoic therians, his opponents entirely from conditions in much later therians, and neither realized that different trigons were involved. By proving that the tribosphenic paracone was the primary cusp, Osborn's critics believed that they had demolished the reversed triangle theory, and with it the cusp rotation hypothesis, whereas in fact they had done nothing of the sort. The reversed triangles are real, and, contrary to these critics, their reality is in no way dependent upon hypotheses as to their origin. Now that the tumult and the shouting have largely died away, we can see that, as regards origin, we stand precisely where Osborn stood in 1888, when he stated that the triangles could have arisen either by rotation of the two subsidiary cusps (or, I would add, the crests on which they arose), or by the growth of these cusps *in situ*. My personal preference is for the *in situ* hypothesis—appearance of the cusps on crests that had extended outward from the paracone and inward from the protoconid—but the possibility of rotation can not at present be rejected entirely.[2] The necessary evidence for an answer to the second question is yet to come, and I believe that it must be sought within the Therapsida.

The third and most difficult question, to what extent are the cusps of upper and lower molars "equivalent," remains. A definite answer, as far as the symmetrodonts are concerned, unfortunately hinges upon resolution

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[1] The Jurassic mammals, multituberculates perhaps excepted, have in general a high number of molars. Triconodontines and paurodontids, exceptions to this rule, appear to be specialized groups within their respective orders.

[2] Butler apparently favors the rotation hypothesis; at least he speaks of the symmetrodonts differing from the triconodonts ". . . by a displacement of the paracone lingually and the protoconid buccally" (1939b, p. 353). If rotation did occur, I think it must have been the other way around; the paracone and protoconid have retained much the same position relative to each other from the beginning.

of the second question, but, despite this, some consideration of the problem is relevant to the present discussion.[1]

In his major publication on Mesozoic mammals, Osborn (1888a, p. 242) intimated that a definite relationship existed between the cusps of upper and lower molars. Very shortly thereafter (1888b), he presented his well-known scheme of "homologies" of upper and lower molar cusps, which may be arranged as follows:

Upper	*Lower*
Protocone	Protoconid
Paracone	Paraconid
Metacone	Metaconid
Hypocone[2]	Hypoconid
Protoconule	. . . .
Metaconule	. . . .
. . . .	Entoconid

Osborn, of course, believed that this scheme applied throughout the Theria, to the eutherians and metatherians as well as to the earlier Mesozoic forms. The convenient nomenclature met with a ready acceptance, but the supposed equivalents, as already noted, soon came under fire from the advocates of the embryology and premolar analogy theories, and no further inclusive attempts along this line were presented during the ensuing half century of doubt and confusion. Butler has recently returned to the subject (1939a and b, 1941) and has proposed the following:

Upper	*Lower*
Paracone	Protoconid
Metacone	Posterior accessory cusp
Anterior accessory cusp	Paraconid
Anterior cusp (parastyle)	Anterior cusp
Posterior cusp	Posterior cusp (hypoconulid)
Buccal cusp [stylocone]	Metaconid
Protocone	. . . .
. . . .	Hypoconid

This scheme is based primarily on all Jurassic mammals, except multituberculates, and therefore attempts to reconcile conditions in such quite different groups as therians, docodonts (regarded by Butler as pantotheres) and triconodonts. There is, however, no assurance that these groups had an immediate common ancestry (i.e., an origin from the same group of

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[1] The term "equivalent" is here applied in the sense in which Osborn, and recently Butler, have used the word homology—to indicate a "kind of serial homology between . . . cusps of the upper and lower teeth" (Osborn, 1907, p. 5). This is not "homology," as the word is currently restricted. The luxuriant terminology that has grown up around the homology concept apparently includes no term that precisely applies to this situation, and it is a pleasure to refrain from coining one. The quotation marks are omitted from "equivalent(s)" and "equivalence" in the following pages.

[2] The term "talon" was proposed by Osborn (1897) for the hypoconal area in the mistaken belief that it was in some degree equivalent ("exactly analogous") to the talonid.

therapsids) or that the main subsidiary molar cusps of non-therian mammals are homologous with those of therians; the reverse is in fact probable (see below). The assumption that the cusps are homologous, coupled with dependence upon the premolar analogy theory, led Butler astray and accounts for his equation of the metacone with the "posterior accessory cusp" and of the stylocone (his buccal cusp) with the metaconid, and for his failure to detect any equivalents for the protocone and hypoconid. Attempts at determining equivalents must, I think, be limited to each group. Thus, within the Theria, there can be no reasonable doubt that the metaconid has been present from the symmetrodont stage on, and the likelihood exists that it has some sort of relationship with either the antero-external cusp or the metacone, or with both. Also, in this group, it is probable that the addition of the parastyle (and perhaps of the metastyle) to the upper molars was not accompanied by the addition of any new cusp to the lowers, and virtually certain that the protocone above and the talonid basin below, possibly with the hypoconid and entoconid on its rim, were added concurrently as a functional unit.[1] It seems clear that some cusps are equivalent but that not all are, and quite evident, besides, that a sort of regional equivalence, sometimes involving several crown elements, may also exist. An answer to the third question must be sufficiently inclusive to account for all three.

Butler, and Osborn as well, if we may judge from the names he applied to cusps, in arriving at a scheme of equivalents started with the basic assumption that the labial side of the upper molars is equivalent to the lingual side of the lowers, and vice versa, the anterior and posterior ends being equivalent, each to each, in both. Parrington has recently countered by pointing out (1947, pp. 719–720) that if teeth "are regarded as serially homologous units developed from denticles which were originally arranged along a gill arch" then the anterior ends of the uppers would be equivalent to the posterior ends of the lowers, and vice versa, the lingual and labial sides being equivalent, each to each, in both series. The latter view would seem to be the more logical from a developmental viewpoint, while the former would seem to accord better with the reversed triangles of the earliest Theria. The fact is, however, that neither of them accords *in toto* with the great diversity of trends in mammalian dental evolution, and the same is true of a third view, Frechkop's "homodynamie renversée" (1933a and b, 1935), which attempts to combine them both. To give but one example, the concurrent addition of the protocone and the definitive talonid

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[1] In arriving at the conclusion that there was no sort of relationship between protocone and hypoconid, Butler may well have been misled by conditions in the docodonts. In these forms, there is a large internal cusp that resembles the tribosphenic protocone, but which has clearly had a different history (p. 74), and no cusp that is comparable to the therian hypoconid—nor, it may be added, even a talonid in the therian sense.

to the therian molars, involving as it does an internal cusp above and a posterior basin with two new cusps on its rim below, is really random with regard to any of these postulated axes. It is precisely this random element in molar as in all evolution that defeats at the outset attempts at interpretation along rigid lines. An answer to the third question is evidently not to be found in this direction, but at the same time no answer can be considered satisfactory that does not offer an explanation for trends in molar evolution that give an appearance of a controlling axis.

The search for this answer must take into account what is known, or rather what may reasonably be inferred, concerning the operation of genetic processes in the dental field. Genes affecting tooth structure appear to operate throughout the dentition or throughout parts of it, such as the molar region. This, the field concept, whose modern development as applied to teeth we owe to Butler (e.g., 1939a), does not now seem open to serious question. It follows then that any mutation affecting molar structure will operate in the lower and upper series simultaneously, but it does not follow that the phenotypic result will necessarily be the same or even similar in both. Phenotypic expression of a mutation depends, among other things, upon the amount and distribution of the embryonic material present in the dental field at the time of its appearance. Amount and distribution of material is a resultant of past history, which thus plays a major role in determining expression in the upper and lower series. Expression may accordingly range from practically identical to utterly dissimilar in the two, depending upon the nature of the adaptive trend under way and the degree of progress attained in it. The developmental paths followed by genetic factors resulting in molar differentiation at one stage in the history of a group may or may not follow the paths taken by factors that resulted in earlier differentiations.

A concrete example is provided by an undescribed Oligocene dog of the subfamily Caninae in the collections of the American Museum of Natural History (A.M. no. 38986), which illustrates, as well as one case can, the processes just outlined. In this specimen, or rather in the line represented by it, a genetic change operated to increase the sizes of the internal portions of M_{1-2}^{1-2} and P^4. The metaconids and entoconids of the lower molars are enlarged, the former particularly so on M_2, the latter on M_1; in the upper molars there is a correlated enlargement of the hypocone and of the internal cingula generally; and in P^4 the protocone is larger than in contemporary relatives, indicating that it too was involved.[1] The change thus affected an area involving a number of cusps, and imposed a new gradient upon it. Three things stand out. First, as regards amount and distribution

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[1] It is an interesting fact that similar tendencies may be seen if adequate series of small Recent members of the Caninae are examined.

of embryonic materials, the genetic changes seized, so to speak, on whatever material was handiest, i.e., most internal; the disposition of this material, unusual in the more internal position of the hypocone material in the molars (a character of the Caninae), was a result of the past history of the group to which the specimen belonged. Second, the cusps concerned were affected without regard either to their serial relationships, in the case of the protocone of P^4 and the hypocone of M^{1-2}, or to the order of their phylogenetic addition to the crowns; the developmental paths followed by the new factors controlling this differentiation were clearly independent of those followed by factors controlling earlier differentiations. Third, a functional area was affected; complementary parts of upper and lower teeth were involved and the degrees of expression on the various teeth involved were nicely adjusted to the maintenance of over-all functional efficiency.

Here again, as in the case of the protocone and the basined talonid, function is involved, and this provides the key to the problem. If complementary areas of upper and lower molars can come under the common control of genetic factors operating independently of the factors that earlier controlled these same areas, and it would seem that they can, then the random nature of molar evolution, its lack of relation to any postulated axis or axes, becomes readily understandable in terms of synthetic evolutionary theory. The wide range of phenotypic expression in upper and lower teeth of mutations affecting the molar series as a whole similarly becomes explicable as the results of selective control of opposing functional units, which naturally come to be as varied as the functions they fulfill. Finally, this same theory can also account satisfactorily for trends that give the appearance of a controlling axis. Adequate accounts of the synthetic theory exist[1] and I shall not attempt an outline of it here. Its core, the method of change, is, however, pertinent at this point and may be stated. In baldest outline, it is as follows: a mutation will become established in, and may spread from, a breeding population of appropriate structure if possession of it confers some degree of selective advantage upon the possessors. The population will, as a resultant of the past history of the group to which it belongs, be adapted to some particular way of life, and the new mutation will therefore have one of two effects—either it will render its possessors better adapted to this particular way of life, or it will be a factor in preparing them for another. Integration into a genetic system of a mutation having the first of these effects will result in further confirmation of the particular adaptive trend and the attainment of a new base for possible subsequent evolution along the same line. Integration of one having the second

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[1] For an excellent general presentation, see Simpson, 1949, especially chapters 10–16.

may, if all other factors are favorable, initiate a new adaptive trend that may lead to a thoroughgoing transformation of structure.

If we combine what may be inferred concerning the operation of genetic processes in the dental field with the method of change that is basic to the synthetic theory, it is possible to arrive at an answer to the third question that is in general satisfactory. Integration of mutations having the first of the two effects just mentioned is much more common than integration of those having the second, and this, as is now fully realized, is one of the principal factors responsible for the long-continued adaptive trends that are so striking a feature of the fossil record. No trend is ever self-perpetuating, however; at any time in its history, a threshold may be reached at which deflection of the trend by integration of a mutation having the second effect may occur. Such events are rare, but they nevertheless occur and have occurred in the past in sufficient number to account for the wonderful variety of trends in molar structure that characterizes the Theria. In the great majority of trends, the function of the dentition is such that the opposing molar series are dissimilar. In these, the amount and distribution of the embryonic materials are unlike, the phenotypic expression of new mutations affecting the dentition tends to be different in the two series, and the equivalence of new elements added to the crowns is usually difficult or impossible to recognize with any assurance. Among the variety of trends, however, there are a comparative few in which the upper and lower molars become progressively more alike in structure and function, shape and area. As the amount and distribution of the embryonic materials become progressively similar in the two series, the phenotypic expression of new mutations becomes progressively more alike in both. It is in these that the equivalent relationships of new elements added to the crowns are more readily recognizable, and it is in these that axial controls appear to operate. The reasons for the latter would seem to be evident. Once an adaptive trend toward similarity of structure and function of upper and lower molars is under way, mutations that maintain the trend will be those liable to be selected. These are the mutations that tend to follow the same developmental paths as those followed by earlier mutations, or at any rate to affect the same complementary areas. The results give the impression of an axial control that does not in reality exist. The "control" is nothing more than the maintenance of the trend, and this, as already stated, is at any time liable to deflection.

To summarize, it is the functional relationships between upper and lower teeth that are all-important in molar evolution. Complementary parts of the molars come under the control of common genetic factors. The developmental paths followed by mutations newly affecting such parts may be independent of the paths followed by mutations that earlier affected them. Maintenance and improvement or changes in the direction of functional trends may thus involve the addition or reduction of the same or of different elements in the two series, the establishment of gradients that occasionally do but usually do not give the appearance of axial controls, and the replacement of these gradients by others.

The trend that culminated in the reversed symmetry of the symmetrodont molars was one of the relatively rare type in which upper and lower teeth became to a considerable degree alike in structure and function. It is very possible, therefore, that in this group several crown elements are equivalent in the upper and lower molars, i.e., that they were added at various times as expressions of the same genetic changes. Aside from the paracone and protoconid, however, it is not now possible to state definitely which element in one series may be equivalent to which element in the other; this information can only come with much greater knowledge than we now possess.[1] The reversed symmetry evolved by the earliest symmetrodonts or by their ancestors profoundly influenced later evolutionary stages, but it did not "control" them. Additions to and modifications of crown structure involved in the successive adaptive shifts to the pantothere and tribosphenic stages occurred without regard to the maintenance of this symmetry and in the end obliterated it.

THE EVOLUTION OF FUNCTION

The preceding sections have of necessity been devoted to the structural evolution of the therian molars, to the establishment of the homologies of the various cusps, and to a consideration of certain related problems. This

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[1] I may indulge myself to the extent of a guess, however. The earliest therian molars probably consisted of the primary cusp with crests running from it, antero- and postero-externally above and antero- and postero-internally below, and a continuous basal cingulum, the upper and lower teeth alternating and shearing past each other. Given such structure and function, all four of the cusps on the crests may have originated as the phenotypic expressions of the same genetic change. Later, the first four cuspules on the cingula may have come into existence as the expression of another change. If so, and it is a big if, the equivalence of therian molar elements, to and including the earliest tribosphenic forms, would be as follows:

Upper	*Lower*
Paracone	Protoconid
Cusp on anterior crest Metacone	Paraconid Metaconid
Stylocone Original postero-external cingulum cusp (of symmetrodonts)	Antero-internal cingulum cusp Postero-internal cingulum cusp (talonid rudiment, = hypoconulid?)
Parastyle Metastyle	. . . .
Protocone	Talonid basin Hypoconid Entoconid

done, and the necessary groundwork laid, we can now turn to the more interesting and all-important dynamic aspects of the subject, to the occlusal relationships of the molars in successive structural—and broadly ancestral—stages, a field in which Simpson's contributions (1933, 1936) are of fundamental importance.

Symmetrodont molars, particularly those of *Peralestes–Spalacotherium* type, were primarily alternating, shearing teeth. The anterior and posterior edges of the lowers engaged the posterior and anterior edges of the uppers, and the lowers worked during active occlusion within the embrasures between the upper molars. This type of action may be termed *embrasure-shearing* to distinguish it from the open, antero-posteriorly aligned type of shearing action characteristic of such groups as felids and triconodonts, in which the cutting surfaces of the opposing cheek teeth are aligned in antero-posterior rows. No information concerning wear surfaces in symmetrodonts is available in the literature. The type specimen of *Spalacotheroides bridwelli* shows obliquely running scorings in the enamel of the posterior face of the lower molar that were presumably caused by the shearing of the tooth against its opponent in the upper dentition. In addition, there is a sharply defined wear surface that faces upward and backward on the crest between protoconid and metaconid, and also extends up on the inner face of the protoconid. Evidently, this crest worked against the opposing one of the upper molar before the tooth plunged upward to complete the shearing motion. In a discussion of the shearing action in pantotheres, Simpson (1933, pp. 141–142) has pointed out that the efficiency of the shear is increased by the presence of a cusp and a median notch on the crests. "Analogous to the action of a pair of scissors, although achieved in a different way, this increases the mechanical efficiency by making the apparent motion along the actual edge much faster than the actual motion of the jaw, and it also increases the length of the shearing edge. . . ." These remarks apply also to the symmetrodonts. The cusps surely arose as a part of this evolving functional complex, which emphasizes the fundamental importance of embrasure-shearing in the early history of the therian dentition. Occlusion in symmetrodonts was evidently a comparatively simple affair, but we may perhaps see in the engagement of crest on crest in *Spalacotheroides* some indication of a type of interaction that was characteristic of the next stage.

Active occlusion in pantotheres was a more complicated matter. The embrasure-shearing action of the trigonids was carried over, but new functions were added. The action of crest on crest assumed great importance, and the rudimentary talonid began to play a part. Our knowledge of wear surfaces during this stage of therian molar evolution is all due to Simpson

(1928a, p. 117, fig. 37, *a;* 1929a, pp. 80–81, fig. 33, pl. 16, figs. 1–2; 1933, p. 142, fig. 5, *b*). One specimen of *Amphitherium* has the outer face of the talonid deeply grooved, several dryolestid specimens show varying degrees of wear on the transverse crests, the surfaces being more horizontal than inclined, and at least one dryolestid has the trigonids deeply truncated. The groove on the talonid was obviously caused by the action of the internal cusp of the upper molar, but the explanation of the other surfaces, and especially of the deeply worn trigonid, is not so simple. Simpson (1933, 1936) believed that the occlusion was primarily of an embrasure-shearing type with the rudimentary talonid serving as a stopping device and also for pounding (his "simple opposition"). The deeply worn trigonid he regarded as having been caused by the abrasive action of the food consumed. With part of this I am unable to agree; the wear surfaces on the crests and the deeply worn trigonids were, I think, the results of crest on crest action, which was equally as important as shearing in pantothere occlusion and function. The evidence for this view is to be found in the zalambdodont insectivores,[1] and some consideration of the structure and function of the molars of these forms is accordingly necessary.

Molar cusp homologies in zalambdodonts are now well known, thanks to the efforts of a number of authors—Mivart (1868), Woodward (1896), Gidley (1906), Matthew (1913), Gregory (1916), Butler (1937, 1939a)—and it is evident that their peculiar molars were evolved from the tribosphenic type. In fact, as pointed out above, they are readily derivable, structurally, from molars of the sort occurring at Forestburg. Specialized zalambdodont upper molars are short and wide and have a large, high internal paracone and crests running antero-externally and postero-externally from it. There is usually an anteriorly hooked parastyle and almost invariably a large stylocone[2] that is frequently incorporated in the anterior crest. Lingually, the protocone varies; it is comparatively well developed in the less specialized forms and is totally absent in the most specialized; exceptionally (e.g., in *Solenodon*) a second small internal cusp is present. A distinct metacone occurs only in less specialized forms such as *Palaeoryctes* and *Potamogale*. Specialized lower molars consist of a high, short trigonid and a low, vestigial talonid (relatively large on M_3) consisting of a single cusp, the hypoconulid. In less specialized forms, vestiges of the talonid basin and of the hypoconid exist, their degree of

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[1] The term zalambdodont insectivores, or, simply, zalambdodonts, is used here for descriptive convenience. It applies to members of the superfamilies Tenrecoidea and Chrysochloroidea of current classification (e.g., Simpson, 1945), and has no taxonomic significance.

[2] The cusp called the parastyle by Schlaikjer (1933) in *Apternodus* is actually the stylocone, the smaller cusp anterior to it being the parastyle.

prominence correlated with the size of the protocone. The resemblance between the molars of pantotheres and of specialized zalambdodonts is extraordinarily close, amounting nearly to identity in almost all features of the crown (fig. 13, B, C). There can now be little doubt that the cusps that are so similar in structure, position, and relations in the two groups are actually homologous. Gregory (1916) and Butler (1939b) were, I think, entirely correct on this very important point. It would appear, therefore, that we are so fortunate as to have with us today a group of primitive eutherian mammals that in molar structure has largely reverted to the ancestral pantothere stage. In the upper molars, the primary trigon has thus been reinstated. Careful study of the dentition of zalambdodonts can hardly fail to contribute toward an understanding of that of pantotheres.

The first point that may be taken up concerns the relative positions of the upper and lower tooth rows in centric occlusion.[1] It is a commonplace observation that, in this position, the paracones and protoconids of therian molars fall along a more or less zigzag line. The zalambdodonts are no exception (fig. 13, C), but in the specialized forms, because of the great reduction of the protocones and talonids, the two rows barely touch, and the primary trigons, which constitute the bulk of the upper molars, lie wholly external to the trigonids. To those accustomed to orthodox eutherian or metatherian centric occlusion, this is an untidy-looking arrangement, but it is nevertheless the natural one. The very similar molar structure of pantotheres permits no doubt that in centric occlusion the relations of their upper and lower tooth rows were essentially as in zalambdodonts (fig. 13, B′), and the same was almost surely true of symmetrodonts (fig. 13, A′). However, diagrams of pantothere and symmetrodont occlusion in the literature (e.g., Simpson, 1933, fig. 2, B, p. 138; fig. 5, D, p. 142; and Gregory, 1934, fig. 44, p. 249) show the protoconids thrust far into the embrasures between the upper molars and, in pantotheres, almost on a line with the stylocones (fig. 13, A, B). These occlusal diagrams are of course entirely correct, but I believe them to illustrate not centric but active occlusion, the extreme lateral shearing position, to be exact. Did they truly

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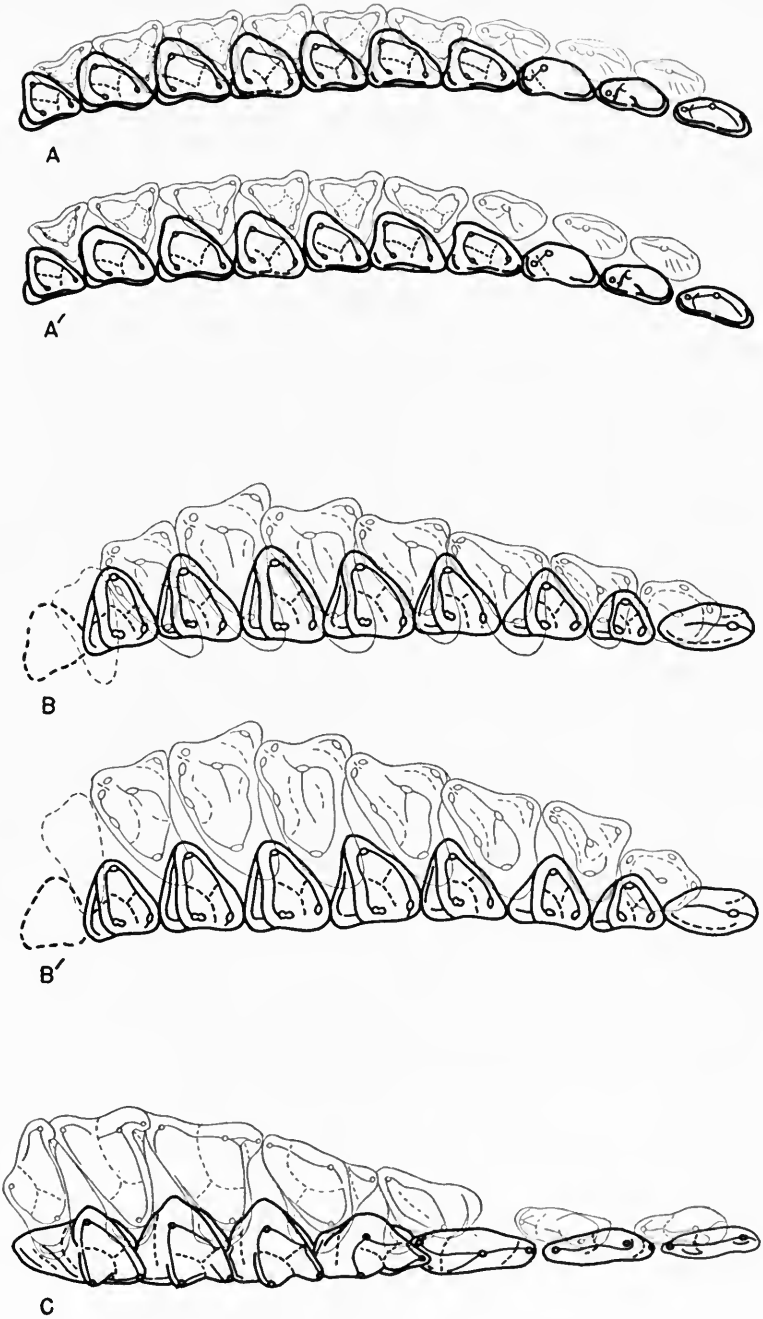
[1] Centric occlusion: the mutual relations of the tooth rows when the teeth and the temporo-mandibular joint are in the central position and the teeth are in contact, causing the midlines of the maxillaries and mandibles to coincide. I am indebted to Dr. E. Lloyd DuBrul for calling my attention to this term, long used in human dental anatomy.

FIG. 13. Occlusion in symmetrodonts, pantotheres, and zalambdodonts. A, active, A′, centric occlusion in acute-angled symmetrodonts (*Peralestes* upper, *Spalacotherium* lower molars). B, active, B′, centric occlusion in dryolestid pantotheres (*Melanodon* upper, *Laolestes* lower molars). C, centric occlusion in a tenrecid zalambdodont (*Microgale cowani* Thomas, CNHM no. 18865). A based on Gregory, B on Simpson. Not to scale; greatly enlarged.


A
A′
B
B′
C

represent centric occlusion, we would be driven to conclude that the stylocone was the primary upper cusp, since the apex of the primary upper is never far internal to the apex of the primary lower in this position. As it is, however, the relations of the tooth rows during centric occlusion in the specialized zalambdodonts, and inferentially in the pantotheres, in which the large internal cusp of the upper molars is on a zigzag line with the protoconid, provide strong supporting evidence that this cusp in both groups is the paracone and not the protocone.[1]

The close similarity in structure between pantothere and zalambdodont molars would appear to extend to function also, since every one of the wear surfaces described and illustrated by Simpson for the Jurassic forms is duplicated among the living. A groove exactly comparable to that seen on the outer side of the talonid in the old *Amphitherium* is produced in zalambdodonts by the action of the paracone. More important than this is the almost exact duplication of the wear surfaces on the crests of the molars, and the fact that old zalambdodonts have the trigonids truncated in the same manner as old dryolestids. If these surfaces are produced in the one group by the action of tooth against tooth, it is a reasonable assumption that they are so produced in the other. Manipulation of the zalambdodont skull and mandible reveals that a variety of jaw movements, not all of which can properly be understood from dry material, is possible in these forms. The lower jaw is certainly capable of wide lateral excursion, in the course of which the smaller trigonid works across the wider primary trigon, the crests of the upper and lower molars engage each other, and the teeth of one side only are in use at the same time. This appears to have been brought about to a considerable extent by a sort of rocking movement of the trigonid within the primary trigon. The muscle involved in such movement appears to be M. transversus mandibulae (M. mylohyoideus, pars ant.), which is well developed in certain zalambdodonts (Fiedler, 1953), acting in concert with the muscles of mastication. Loose union of the rami at the symphysis makes possible partially independent movement of each. It is the action of crest on crest that produces the wear surfaces on these

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[1] It is odd that Gidley, who regarded the internal cusp of zalambdodonts as the paracone (1906, p. 95) and noted—and fully appreciated—the fact that protocone and talonid increase or decrease as a unit (p. 104), should not have gone on to infer that the rudimentary talonid of the pantotheres was evidence that the internal upper cusp was homologous in the two groups. Instead, as noted above, he considered the pantotherian internal cusp to be homologous with the tribosphenic protocone and believed the centro-external cusp (stylocone) to be the primary one and the paracone. He arrived at this conclusion by analogy with the triconodonts and, especially, with the docodonts, in the latter of which the primary cusp is certainly external in position (although just as certainly not homologous with the therian stylocone). This is not the only time, as may be seen from several of the footnotes peppered through previous pages, that these troublesome non-therian mammals appear to have been at the bottom of some misunderstanding or other of early therian molars.

structures and leads eventually to the truncation of trigon and trigonid. As it is in the zalambdodonts, so I believe it was in the pantotheres, and in the latter, mandibular movements would have been facilitated by the small size of the canines,[1] as well as by the possibility of a good measure of independent movement of the two halves of the rami, union at the symphysis being loose in these forms also (Simpson, 1928c, p. 463). The abrasive action of the food no doubt contributed to the formation of the wear surfaces but it does not appear to have been the major factor in producing them. M. transversus mandibulae is insignificant as mammalian muscles go, yet it appears to have played an important although brief role in therian history.

Pantothere occlusion, then, involved not only alternation and shear, in which the talonid participated both as a stopping device (Simpson, 1933, p. 142) and as an additional shearing surface, but also a peculiar form of grinding, involving the opposed crested surfaces. Simpson (1936, p. 950) believed that opposition (his "simple opposition") occurred. This is partly a matter of definition, but pantothere molars were not truly opposing, having no cusp and basin relations, and were certainly not crushing teeth. Grinding evidently preceded crushing in therian molar evolution and in fact appears to have been a keynote in the shift from the symmetrodont to the pantothere adaptive type.

Jaw motion in symmetrodonts, with their mainly embrasure-shearing teeth, must have been largely orthal, but there was surely, particularly in the "acute-angled" forms, an ectental component as well, in order to bring the trigonids into the interdental embrasures from the centric occlusal position. This I believe to have been of fundamental importance in therian molar evolution. During the ectental movement, a brief engagement of the upper and lower crests evidently took place. This seems to be indicated by the type of *Spalacotheroides bridwelli*—the only "acute-angled" symmetrodont of whose wear surfaces we have any knowledge—in which the posterior crest of the trigonid is worn more or less horizontally. The dentition of these symmetrodonts thus appears to have reached a morphological threshold, a stage at which incorporation of mutations having the second of the two effects discussed above, with consequent deflection of the adaptive trend, became possible. The initial changes perhaps resulted merely in an increase of the ectental motion and the action of crest on crest, but this would have been enough to confer a selective advantage upon nearly all the characters in which pantothere molars differ from symmetrodont molars. The transverse widening of the upper molar and the more nearly

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[1] The enlarged anterior teeth of certain zalambdodonts interfere to some extent with movements of the mandible in the dried skull. In the living animals this may be compensated for by independence of movement of the two halves.

equal heights of its external and internal portions, the increase in size of the stylocone, the elimination of the cusp on the anterior crest of the upper molars, and the further separation of the trigonid cusps may all be interpreted as adaptations to the grinding action—changes that followed fast upon initiation of the new adaptive trend. The separation of the trigonid cusps achieved the maximum area consistent with retention of the shearing function, and the widening of the upper molars—in the external, not internal, direction—increased the area across which the talonid worked.[1] The more nearly equal heights of the external and internal portions of the molars brought the opposing areas closer to the horizontal. Enlargement of the stylocone provided an essential external element, and the height of this cusp rendered the cusp on the anterior crest, inherited from the symmetrodont molar, superfluous.

Jaw movements in pantotheres were clearly more complex than in symmetrodonts. The former possess an angular process of the mandible whereas the latter lack one—a difference that has been regarded as an obstacle to the view that there was a close relationship between the two groups (e.g., Simpson, 1936, pp. 948–949; Bohlin, 1945). I suggest that the angle arose as part and parcel of the changes in the jaw-muscle-joint-tooth complex that were involved in the shift from the one adaptive type to the other. In living therians the angle provides an area of insertion for part of M. masseter, laterally, and for M. pterygoideus internus, medially, the two acting synergistically; the same was no doubt true of the pantotheres. It seems likely (Adams, 1919; Parrington and Westoll, 1940) that the Mammalia inherited one pterygoid muscle, the posterior pterygoid, or capiti-mandibularis profundus, of reptiles. Monotremes lack M. pterygoideus internus and do not possess a true angle (see p. 76). The condyle is low on the mandible in Jurassic non-therians, all of which lack an angle, and a single pterygoid muscle may in these forms have fulfilled part at least of the functions performed by the two muscles in therians. *Amphitherium* and the dryolestid pantotheres have the condyle situated higher on the mandible (the relatively low position in *Peramus* is believed to be secondary), an obvious advantage if complex jaw movements are performed. The position of the condyle in *Spalacotherium*, higher than in contemporary non-therians, may be an indication that in the symmetrodont ancestry of the pantotheres some elevation of the condyle had already occurred. With the addition of more complex jaw movements, modification of the pterygoid musculature presumably occurred; acquisition of angle and of M. pterygoideus internus

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[1] A rapid widening of the upper molars was supposed by Gregory (1926) to have occurred at a very early stage in therian history—earlier than under the view here advanced.

may well have gone on hand in hand. The presence of two pterygoid muscles may be a purely therian character.

The eminently workable pantothere dentition—a reversion to which is still in use today—probably came into existence during late Early or early Mid-Jurassic time. Within less than a geologic period, however, it was undermined and largely transformed by a further adaptive shift, the keynote of which was the evolution of true opposition and of crushing.

Concurrently with the evolution of the grinding action, the shearing action of pantothere molars also underwent improvement. This took the form of an enlargement of the talonid, which, as noted above, came to serve both as a stopping device in the shear and as an additional shearing surface. As soon as this had taken place, another morphological threshold was reached, the inner surface of the upper molar and the heel of the lower now acted as a functional unit and the way was open for incorporation of mutations affecting this unit as a whole. Addition of an internal cusp (protocone) to the upper molars was presumably accompanied by a lengthening of the talonid, the outward movement of the ridge connecting the hypoconulid to the base of the metaconid, and the rise of a second ridge internal to it. The tip of the protocone worked within the incipient basin between these ridges. The evolution of the secondary trigon and of true opposition (Simpson's "double opposition") had begun. Further evolution of the upper and lower components of the functional unit went hand in hand, increase in size of the protocone being matched by widening and further lengthening of the talonid, deepening of the basin, and rise of the new cusps on its rim. Concurrently, the upper molars lengthened, the metacones shifted internally in line with the paracones, and the number of molars became of necessity reduced.[1] The functional emphasis changed from shearing and grinding to shearing and crushing, and the stylar area, the remnant of the primary trigon, declined in importance. The internal root of the upper molars presumably moved inward from beneath the paracone in step with the progressive increase of the protocone; this supposition presents no difficulty, the work of Orban and Müller having shown that a considerable measure of independence exists between crown and root (Butler, 1941).

The net result of the changes thus visualized, the tribosphenic molar, was attained in Early Cretaceous time, and one of the major structural requirements for the great eutherian–metatherian radiation was in readiness. It is a remarkable fact that the triangular trigonid persisted without any great change from the symmetrodont to the tribosphenic stage; it was

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[1] If the immediate common ancestors of the Eutheria and Metatheria descended from the paurodontid pantotheres, which does not seem likely, molar reduction preceded the shift.

universal or nearly so from the beginning of the Jurassic to the beginning of the Cenozoic and persists in some groups to the present day. The reason, of course, was that, while new parts and new functions were added to the molars, the embrasure-shearing action of the trigonids remained essentially unchanged, functioning as well with the secondary as with the primary trigon. Ectental motion, of course, was carried over from the pantothere to the tribosphenic stage, for such motion was very useful in crushing. It is probable, too, that the pantothere type of grinding action did not come to an abrupt end upon completion of the shift to the tribosphenic adaptive type. I have seen wear surfaces in later forms (e.g., in soricids)[1] that appear to have been produced by similar crest against crest movements. This retention of old functions and old structures, while radically new ones are being added, is of some interest. It is an example of what may perhaps be considered as a general evolutionary principle, namely, that there is no change so sudden and so drastic that old functions and structures are at a stroke replaced by new; there is always a period of transfer, of greater or lesser duration, during which the new progressively replace the old. The long retention of the shearing trigonid as an integral part of the therian molar series is an example of a very protracted period of transfer, one made possible by an increasing variety of functions accompanying increasing complexity of form. Structures that fulfill less varied functions may be expected to undergo more rapid periods of transfer when involved in adaptive shifts, some of them no doubt very rapid, geologically speaking.

THE PREMOLARS OF MESOZOIC THERIANS AND THE PREMOLAR ANALOGY THEORY

Premolar evolution in Mesozoic Theria is a subject that can be dealt with briefly—there was very little of it. During the symmetrodont and pantothere stages, those teeth consisted mainly of a single, high cusp, the paracone above and the protoconid below. The upper premolars of *Peralestes* have, in addition, an external cingulum, a rudimentary parastyle, and a small cusp low on the posterior slope of the paracone. The lowers of *Spalacotherium* possess a cusp on the posterior slope of the protoconid. The posterior upper premolars of dryolestid pantotheres have external and posterior cingula, which rise to rudimentary parastyles and metastyles and, in P^4 of *Melanodon oweni* (Simpson, 1929a, pl. 13, fig. 3; 1933, fig. 5; Butler, 1939b, fig. 4, *g–h*)[2] to a rudimentary stylocone. The paracones of the premolars are

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[1] In this connection it is interesting to note that the Soricidae have a well-developed M. transversus mandibulae (Fiedler, 1953).

[2] Butler (1939b, pp. 338, 354) regarded the posterior cingulum in this form as the probable homologue of the internal cusp of the docodont upper molar; this, I feel, is reading altogether too much into a simple cingulum that may well be nothing more than a premolar feature.

in line with the paracones of the molars, as in zalambdodonts (P^4 of *Melanodon oweni* has suffered post-mortem external displacement relative to M^1, as the photographic illustration in Simpson, 1929a, shows). Lower premolars have a rudimentary talonid, an internal cingulum and, in some cases, an anterior cingulum cuspule. Again as in zalambdodonts, the line of the premolar protoconids is more internal than that of the molar protoconids. The posterior cusps of the *Peralestes–Spalacotherium* premolars are not present. These appear to have been a symmetrodont specialization and had perhaps not been acquired by the forms ancestral to the Pantotheria. The Forestburg P^4 shows definite evidence in its root structure of recent phyletic lengthening. In addition, it has a rudimentary parastyle, a metastyle crest and a definite metacone. By Late Cretaceous time, the posterior premolars of certain insectivores were well on the way to acquiring molariform structure (e.g., *Gypsonictops–Euangelistes*, Simpson, 1951). It would seem, therefore, that molarization of the premolars in the Theria did not really get under way until Cretaceous time, i.e., not until after the tribosphenic stage had been reached. During the whole of the Jurassic, and apparently the earliest Cretaceous as well, while the molars were evolving from the symmetrodont to the pantothere stage and from the pantothere to the tribosphenic, the premolars remained essentially single-cusped teeth. The reason for this presumably lay in the high number of molars in "acute-angled" symmetrodonts and in most pantotheres, as well as in the functions performed by the premolars; there was simply no selective advantage for these insectivorous–omnivorous forms in increasing the number of molariform teeth. The reduction in molar number that accompanied, perhaps immediately preceded, the shift from the pantothere to the tribosphenic stage resulted in a dentition in which the comparatively few remaining molars stood in sharp structural contrast to the premolars. The two series thus had very different early histories, or, to put it more correctly, the premolars had almost no history while the molars had a very complex one; this has an important bearing on what is known as the premolar analogy theory.

Osborn, in his early development of the Cope–Osborn theory (1888a and b), paid little attention to the premolars. It remained for Scott (1892) to point out that, if Osborn's identification of the eutherian–metatherian protocone as the primary cusp was correct, the history of the upper premolars was very different from that of the molars. As he showed, the primary cusp in these teeth was clearly equivalent, in position at least, to Osborn's molar paracone. Since he accepted Osborn's identification, Scott applied the term "protocone" to the primary premolar cusp and coined new terms for other cusps equivalent in position to molar elements, e.g., tetartocone–metacone, deuterocone–protocone. Thus was born what Gregory has aptly called the premolar–molar paradox: cusps that were to all appearances serially homologous throughout the cheek teeth were supposed to be quite different in the premolar and molar series. This view did not long remain unchallenged. Wortman (1902, pp. 41–46), working on mesonychid creodonts, asserted that the paracone was the primary cusp and that this and all other cusps that occupied the same position on upper premolars and molars were serially homologous throughout the cheek teeth. From this, which was a matter of observation and in general accord with the evidence from eutherian and metatherian embryology, he went on to state that it was improbable that ". . . the premolars have had one history and the molars another," that the addition of secondary cusps to the molars had almost certainly come about in the same way as the addition of the comparable cusps to the premolars (". . . the evidence is *overwhelmingly* in favor of the view . . ."), and that the rotation, including the reversed triangle, theory was therefore incorrect. The premolar analogy theory, as thus originally stated, actually breaks down into five parts: (1) the paracone is the primary cusp in the upper molars; (2) cusps occupying similar positions on premolars and molars are serially homologous; (3) the progressive molarization of the premolars thus epitomizes molar history; therefore (4) premolars and molars have had similar histories; and (5) the molars have not passed through a reversed triangle stage. These five parts do not stand or fall as a unit. The first part is certainly correct and the second is largely although not entirely so, while the third and its corollaries (4 and 5) are certainly incorrect. Wortman was thus partly right and partly wrong. His errors were due to his having no inkling that Jurassic therians had one kind of trigon and metatherians and eutherians another, or that the premolars remained essentially unchanged during the adaptive shifts to the tribosphenic type. Scott, of course, was laboring under the same difficulty. Nevertheless, their work was of the greatest value in helping to focus attention on the possibility that the paracone might be the primary cusp.

More recent statements of the theory have tended to stress the third part. Thus, for Gregory (1922, p. 104) the main point is that ". . . the evolution of the molars during pre-Tertiary times probably followed the same general lines as the observed evolution of the premolars in many phyla during the Tertiary." Butler (1941, p. 444) states that "the Premolar Analogy Theory . . . is, I believe, essentially true. In the evolution of the dentition the teeth that are functionally the most important have been the most progressive, while the anterior premolars and milk molars, which are functionally the least important, have tended to retain archaic characters."

The most anterior cheek teeth of many Theria are, to be sure, very simple, consisting of little more than the primary cusps. They are not much advanced over the anterior cheek teeth of many therapsids in crown structure and in this sense do retain archaic characters. The reason is a functional one—they have remained simple, grasping and/or piercing teeth that play an essential part in the work of the dentition as a whole. The same is true of triconodonts and, to a lesser extent, of docodonts, and it is therefore not surprising that the anterior premolars are often very similar in the three groups. To proceed from this to the assumption that because the anterior cheek teeth are similar there must be a large measure of similarity in molar history is not justifiable, however. The view that premolar evolution epitomizes molar history is, in fact, completely fallacious.

Molarization of the premolars apparently comes about as a result of the anterior extension of genetic factors governing development in the molar region (Butler, 1939a; Patterson, 1949). It would seem to follow from this that *the structure assumed by molariform premolars largely depends upon the structure of the molars at the time the process of molarization begins.* The structures acquired by the premolars in the course of the molarization process are the results of a series of compromises between the anterior extension of the molar factors on the one hand and the structure of the base on which they have to operate—the amount and distribution of the embryonic premolar materials—and the pre-existing premolar functions on the other. Under these circumstances, then, it is hardly surprising that the order and the manner of cusp addition in the premolars may exhibit certain peculiarities. Once fully molariform, the premolars evolve as a unit with the molars. The process cannot in any sense, therefore, recapitulate the history of the molars *prior to* the anterior extension of the molarization region. For example: molariform upper premolars of eutherians and metatherians convey not a hint of the symmetrodont and pantothere[1] stages in molar evolution; those of mesonychids carry no suggestion of the wide stylar shelf of ancestral creodonts; the second internal cusp on P^3 of *Orohippus* was formed by enlargement of the protoconule, and thus was anterior and not posterior to the protocone (Granger, 1908); from the molariform premolars of highly specialized zalambdodonts it could not be inferred that a protocone had occurred on the molars of less specialized ancestral forms. In the first example the stages were over and done with, and in the second the shelf had been reduced before molarization of the premolars had really begun. The peculiar P^3 of *Orohippus* exemplifies the compromises that may result from interaction of molarization factors and the structure and function of

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[1] Zalambdodont premolars did not retain the pantothere molar structure; molars and molariform premolars reverted to it together.

premolars. In highly specialized zalambdodonts, the protocone was lost on molars and molariform premolars together.

Nor is this all. There are no good grounds for assuming, in the absence of positive evidence, that structures present on premolars but not on molars occurred on the molars of ancestral forms. The premolars are not simply a passive part of the dentition, but may, and often do, become specialized to varying degrees.[1] Premolar specialization may, at one stage in the history of a group, involve the addition of crown elements that do not extend to the molar series. Later in the history of the same group selection may favor the forward extension of the molarization region, with the result that previously acquired premolar elements may be lost in the process. As an example, the cusp on the posterior slope of the protoconid (Butler's posterior accessory cusp) may be cited. This is a common premolar adaptive structure, presumably useful in grasping, that occurs in triconodonts, docodonts, symmetrodonts (at least in the later forms) and a number of eutherians. In those placental groups that possess this cusp and in which molarization of the premolars takes place, the metaconid appears postero-internal or internal to the protoconid, and the cusp on the posterior slope disappears.[2] There is no evidence whatever that a serial homologue of this premolar cusp occurred in early tribosphenic lower molars. In the Eutheria, it was purely a premolar specialization that rose independently in a number of groups. The same was almost surely true of the Symmetrodonta, and probably, although not certainly, of the Docodonta and Triconodonta as well. It was this cusp, as noted above, that seems to have been a major factor in leading Butler to the mistaken conclusion that the postero-internal cusp of the symmetrodont trigonid was a "posterior accessory cusp" and not the metaconid.

Like so much that is fallacious, the view that premolar evolution recapitulates molar evolution is very seductive. I have myself swallowed it hook, line and sinker, reconstructing the lower molar history of the Typotheria on the basis of premolar structure in the Casamayoran interatherid *Notopithecus* (Riggs and Patterson, 1935).[3] As a description of the forward exten-

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[1] It would seem necessary to postulate a premolarization region in the morphogenetic field of the dentition in addition to the regions of incisivation, caninization, and molarization postulated by Butler (1939a, pp. 1–3). The region is usually not as important as the others, but premolars can become the most specialized of cheek teeth, with attendant modification of molars, e.g., P_3 of the Polydolopidae; or a premolar may combine with a molar to form a functional unit, e.g., P^4–M_1 of most fissiped carnivores.

[2] The equivalent cusp on the posterior slope of the paracone in eutherian upper premolars occupies much the same position as the metacone of the molars. It is possible therefore that, in some cases at least, the factors governing metacone development may simply "appropriate" this ready-made element.

[3] The personal pronoun is used because my former chief was not responsible for the preparation of this part of our joint paper.

sion of the molarization region to the premolars in interatherids, the account is no doubt reasonably accurate, but as a reconstruction of typotherian lower molar history it can only be described, and charitably at that, as so much solemn nonsense.

The milk molars have frequently been invoked as an aid in the reconstruction of molar history, the general impression apparently being that they are more "molariform" than the premolars. A voluminous literature on the deciduous dentition exists, but it seems to me that an all-important point in connection with it has not always been sufficiently stressed. This is simply that this dentition really *is* deciduous—that it is a temporary, ontogenetic feature adapted to tide its possessor over the critical growth period between weaning and the attainment of adult size. As such, it has to fulfill in a small space all, or at least the major part, of the functions fulfilled in a larger space by the permanent dentition. This requirement falls heaviest in the region of the deciduous cheek teeth, where, in the great majority of eutherian groups, the functions of a higher number of permanent premolars and molars are carried out by a lower number of milk molars. There is accordingly a structural "spread" in the milk molars, corresponding, so far as possible, to the structural diversity of the premolars and molars.[1] The need for maintenance of this "spread" is the key to the interpretation of deciduous cheek teeth. In forms in which the premolars and molars differ, there is one molariform milk molar and two or three that become progressively simpler anteriorly; more than one molariform tooth is not necessary, since the first permanent molar soon erupts to reinforce it. If the last premolar is specialized, its deciduous predecessor occurs one place farther forward. The last milk molar is always more "molariform" than the replacing premolar in such dentitions and the "spread" is thereby maintained; the morphogenetic explanation may be that, with growth, the premolarization region extends and the molarization region shifts a little posteriorly, so that the former comes to occupy the site of dm4–P4 after dm4 has been formed, although this is very uncertain. Molarization of the anterior milk molars keeps pace with and does not precede the molarization of the premolars.

During the process of molarization, compromises take place comparable to those occurring during the molarization of premolars. Like premolars, milk molars may themselves become specialized. The elongate dm2–4 of the later Equidae, and of other groups, provide an example of a rather common specialization in form; the peculiar six-cusped dm_4 of artiodactyls, which is unlike any of the molars, is an example of specialization in struc-

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[1] It is not intended to imply that there is anything novel in this view—indeed, it is one of several set forth in so standard a reference work as Tomes' Dental Anatomy—but it does appear to be in need of re-emphasis.

ture. The deciduous dentition is frequently considered to form a unit with the permanent molars; the permanent incisors, canines and premolars are regarded as the "replacing" dentition. It would seem more logical to regard, as various authorities have, the milk teeth as constituting one dentition and the permanent another. The fact that milk and permanent molars are in series in the jaws does not indicate that they necessarily belong to the same dentition. It is functionally advantageous that the permanent molars should supplement the milk series and progressively extend the dental battery during growth, and this is made possible by the fact that these teeth can develop one behind the other as the jaws enlarge.

Very little is known of the milk molars of Mesozoic therians. Butler (1939b, pp. 337, 340, figs. 4, *e–f*, 6, *g–h*) has interpreted the anterior of the two teeth preserved in *Malthacolestes* as dm^4, and the canine and the first four cheek teeth of "*Asthenodon*" as $dc–dm_4$. Both are Morrison dryolestids, the latter placed by Simpson in the synonymy of *Dryolestes*. The supposed dm^4 is narrower and longer than M^1, a specialization in form broadly comparable to the elongate milk molars of many placentals. Dm_{1-4} of "*Asthenodon*" exhibit a "spread" that is also comparable to that seen in many placentals. Dm_3 may have been molariform as well as dm_4, and if so this was perhaps a reflection of the high number of molars and the low number of premolars in the Dryolestidae. If Butler is correct in his identifications of these teeth, and this seems likely, it would appear highly probable that pantotheres had a deciduous dentition comparable to that of placentals, that this was the primitive condition, and that the reduced deciduous dentition of marsupials, over the significance of which there has been so much discussion, was a later specialization.

To reconstruct molar history by means of "milk molar analogy"—as I once did for the upper molars of notoungulates on the basis of dm^{2-4} of *Leontinia* (1934)—is as misleading as to do so by means of premolar analogy. The only trustworthy guides to molar history are the molars themselves.[1]

THE MOLARS OF NON-THERIAN MAMMALS

Therian mammals are completely dominant today, but this was not always the case. During their infancy, there were at least three other groups, one of which survived to Eocene time, and there is a still existing

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[1] Since this was written, two papers by Butler on the milk molars and premolars of perissodactyls (1952a and b) have come to hand. In these studies, he has receded somewhat from his earlier, unqualified acceptance of the premolar–milk molar analogy theory (1952a, p. 814), has very properly criticized my "reconstruction" of notoungulate upper molar history, and has raised a number of interesting points. With some of these I am unable to agree, but the subject cannot be pursued further here.

non-therian order whose ancestry certainly dates back to the Mesozoic. The molars of the known members of these have been very thoroughly described and illustrated, and it would serve no useful purpose to summarize this readily available information here. The point to be stressed in this brief section is that the Theria differed fundamentally from all of them in molar structure.

The molars of non-therian mammals never went through a reversed triangle stage, their two principal subsidiary cusps being in line with the primary ones. This is very obvious as far as triconodonts are concerned, these forms never having gone beyond the acquisition of a single row—the first row—of cusps. The multituberculates added a row, surely developed from a cingulum, parallel to the first one in both upper and lower molars, and followed this by the addition of another row to the uppers. Such evidence as *Ornithorhynchus* can offer suggests that in monotremes, also, a row parallel to the first one was added in both series. The Docodontidae have molars that are basically similar, although in detail they differ from those of the other groups.

If this be granted, it follows that the only molar cusps that can at present be regarded without reservation or qualification as completely homologous throughout the Mammalia are the primary ones, the paracone and the protoconid. In monotremes and, especially, multituberculates, there is uncertainty as to which cusps are the primary ones, a matter that is briefly discussed in the concluding section. In triconodonts (Butler, 1939b) these are the central of the three principal cusps—Simpson's cusp *b* (1925a) and my central main cusp (1951); and in docodonts[1] they are the large external cusps above (Butler, 1939b) and below (Simpson, 1929a; Butler, 1939b).

The two principal subsidiary cusps may well be homologous within the non-therian Mammalia. Such evidence as is available suggests that some, at least, of the non-therian groups arose independently from within the Therapsida. These reptiles do show a tendency toward the development of a subsidiary cusp on the anterior and posterior slopes of the primary ones, and these may have come into existence independently in the groups ancestral to the non-therian mammals. Even if so, it is permissible to regard them as homologous, in the sense that it is permissible to speak of the hypocone as being homologous (some would prefer to say homoplastic) within the Eutheria–Metatheria. However, unless rotation *of cusps* occurred in the group ancestral to the Theria, and I strongly doubt that it did, the principal subsidiary cusps of the earliest members of this subclass—antero-external cusp, metacone, paraconid, metaconid—are not homolo-

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[1] Here and elsewhere in this section, statements concerning the docodonts are based on the evidence reviewed and the conclusions reached in the following section.

gous with those of the non-therians. They arose external and internal to the primary cusps in therians, not in a fore and aft line with them, and as parts of a different functional complex. I am unable, therefore, to follow Butler (1939b) in his application of the terms "metacone" and "paraconid" to principal subsidiary cusps occurring in triconodonts and docodonts.

Additions to the triad formed by the primary cusp and the two principal subsidiary cusps arose from a primary basal cingulum in non-therian mammals and in therians as well until the tribosphenic stage had been reached. This primary cingulum may be homologous throughout the Mammalia, but the same cannot be said for all the elements that have developed from it in the various Mesozoic groups. The internal cusps of docodont upper and lower molars, the internal cuspules of some upper molars of the triconodont *Priacodon*, and the cusps of the additional rows in multituberculates have no homologues in the Theria. These elements, like the therian protocone, arose as parts of quite different functional complexes. I cannot, therefore, follow Simpson (1929a), who inferentially regards the internal upper cusp in *Docodon* as the protocone, or Butler (1939b), who definitely labels it as such, together with one of the internal cingulum cuspules of *Priacodon*. Neither can I agree with these authors in their identification of the main internal cingulum cusp of *Docodon* as the metaconid, this therian cusp having arisen, as one of the principal subsidiary cusps, on the postero-internal slope of the protoconid and not from the primary cingulum.

The problem of non-therian molar cusp nomenclature does not arise in descriptive work on multituberculates, in which nearly all the cusps in the several rows are of the same size and structure. It is certainly of no present practical significance for investigations on monotremes, but it does assume workaday importance in the study of triconodonts and docodonts. For the former, a simple nomenclature may be selected from among the terms used in the literature. The five antero-posteriorly aligned cusps in upper and lower molars may be designated, from front to back, the anterior cingulum cusp, cusp *a*, paracone or protoconid (cusp *b*), cusp *c* and posterior cingulum cusp (fig. 14, A, B). The cuspules on the internal cingulum of the upper molars of some triconodontines are neither sufficiently prominent nor sufficiently universal in the order to warrant special designation. The docodont molar is a far more complicated affair. The outer side of the uppers is comparable in general to nearly the whole of the triconodont upper molar, and the external cusps may be similarly called anterior cingulum cusp, cusp *a* (lost in *Docodon*, but presumably present in earlier forms), paracone, cusp *c* and posterior cingulum cusp (this last is not mentioned by Butler, but Simpson states that a minute one may be seen on quite unworn teeth). The large internal cusp, surely a cingulum derivate, may be named the main internal cingulum cusp, and the smaller one behind it the postero-internal cingulum cusp. The outer side of the lowers is also comparable in general to nearly the whole of the triconodont lower molar, and the external cusps may likewise be called anterior cingulum cusp (displaced internally in *Docodon*), cusp *a*, protoconid, cusp *c* (lost in *Docodon*, but presumably present earlier) and posterior cingulum cusp. The anterior cingulum cusp may in some specimens of *Docodon* be cut off from the internal cingulum, which then runs up to cusp *a*, but in others it is still connected to it (Butler, 1939b, fig. 2, *a*, *d*). The internal cusps are more numerous than in upper molars, and all were evidently developed from the primary cingulum. The largest, the main internal cingulum cusp, is internal and a little posterior to the protoconid. In front of it and behind it are two smaller ones that may be termed the antero-internal and postero-internal cingulum cusps respectively (fig. 14, C, D). This nomenclature is a little on the clumsy side, but it does seem preferable to the unwarranted, and I am sure incorrect, practice of applying therian terms to cusps other than the two primary ones.

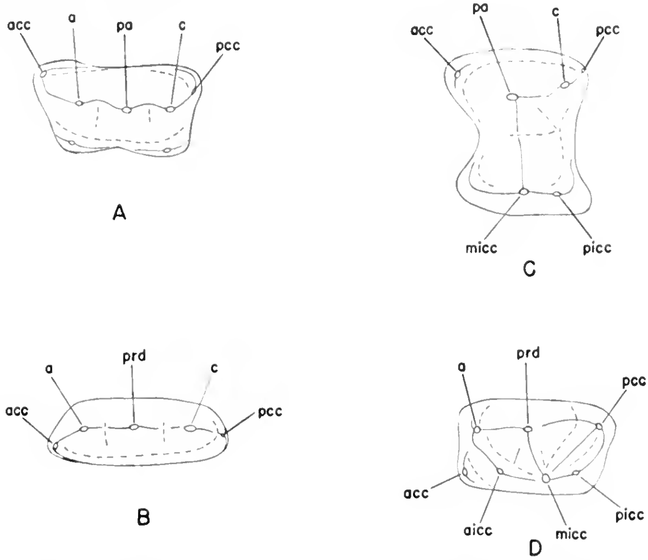

FIG. 14. Molar cusp terminology of triconodonts and docodonts. A, left upper molar of *Priacodon grandaevus* Simpson; B, right lower molar of *P. robustus* Marsh; C, left upper molar of *Docodon superus* Simpson; D, right lower molar of *Docodon* sp. Based on Butler; lettering in part original. Not to scale; greatly enlarged.

a, cusp *a; acc*, anterior cingulum cusp; *aicc*, antero-internal cingulum cusp; *c*, cusp *c; micc*, main internal cingulum cusp; *pa*, paracone; *pcc*, posterior cingulum cusp; *picc*, postero-internal cingulum cusp; *prd*, protoconid.

The striking difference between premolars and molars seen in Jurassic Theria does not exist to the same degree in triconodonts and, especially, in docodonts. Indeed, in *Docodon*, as Simpson (1929a, p. 96) has pointed out, the posterior premolars, especially P4, are well on the way to becoming molariform, and a number of the cusps present clearly seem to be serially homologous with those of the molars. The small median elevation on the external cingulum of one P^4, no. 13770 in the Yale collection, tentatively identified by Butler as a homologue of the therian stylocone, would almost certainly appear to be nothing more than a minor premolar feature. The cusp on the posterior slope of the protoconids in most specimens of *Docodon* also appears to be a premolar structure; it is variable in degree of development and is lacking entirely in some individuals (Simpson, 1929a, fig. 38, p. 88), presumably as a result of the molarization process. Multituberculate premolars, concerning which there is some uncertainty, are briefly considered in the concluding section.

One milk molar, dm_4, is known in *Triconodon* (Simpson, 1928a). If Butler (1939b, pp. 332–333, fig. 2, *e*, *f*) is correct in his identification of the four cheek teeth present in the Purbeck docodontid *Peraiocynodon* as $dm_{1\text{-}4}$—and I believe he is—we have good grounds for suspecting that there were two complete dentitions in this group. In fact, it seems likely that this condition was characteristic of the Mammalia generally, and that reduction or loss of the deciduous dentition is a secondary specialization. Dm_4 of *Triconodon* is molariform, as in other mammals. The milk molars of *Peraiocynodon* are rather narrow and elongate in comparison with the molars of *Docodon*, a specialization in form of a type rather frequently found among eutherians. As in eutherians and the dryolestid "*Asthenodon*," they show a structural "spread" between the simple dm_1 and the molariform dm_4. The high number of molariform teeth—dm_3 is almost wholly molariform and dm_2 largely so—is a reflection of the high number of molars, the low number of premolars and the tendency toward molarization of the latter that characterized the permanent dentition. These several resemblances to the deciduous cheek teeth of therians are of course to be expected, since in all mammals, be they therians or non-therians, milk molars have the function of maintaining the "spread."

None of the non-therian Mammalia evolved a true angle in the mandible. None of them passed through a reversed triangle stage in molar evolution; their first rows of cusps above and below were parallel and close together when in centric occlusion, and consequently none of them evolved the embrasure-shearing occlusion that was one of the basic characters of the earliest therians. These facts are possibly related. If the view advanced above—that the embrasure-shearing of "acute-angled" symmetrodonts provided the morphologic threshold for the adaptive shift to pantothere occlusion, during which evolution of the angle occurred—be correct, then the absence of a true angle in the non-therians becomes more readily understandable. The early mammals clearly differed in jaw mechanics and differences in bone-muscle relationships among the various groups are only to be expected. As noted (p. 58), it is conceivable that only one pterygoid muscle was present in non-therians, and the absence of M. pterygoideus internus in monotremes (Schulman, 1906; Adams, 1919, p. 112) may be significant in this connection. As discussed below, the ventrally directed process in the docodont mandible is not a true angle.

THE AFFINITIES OF THE DOCODONTIDAE

As has been made evident in the foregoing pages, the docodontids are believed to be fundamentally different from the pantotheres. The evidence for this view must now be presented.

The taxonomic history is brief. Marsh referred the family, under the invalid name Diplocynodontidae, to the Pantotheria, and with two exceptions all subsequent authors have concurred in this view of relationships, some, e.g., Gregory (1910), with implied reservations. One exception is Gidley, who stated (1906, p. 105) that the molars were derived from "the simple reptilian cone" independently of those of pantotheres and triconodonts. He did not place the family in any higher category and gave no reasons for his conclusion, which was rather illogical from the standpoint of his own work. In the same paper (pp. 96–100), he had argued that the primary cusp occupied the same central and external position in all three groups and that the internal cusps in both docodontids and pantotheres were additions to the external portions of the crowns. Since, in this view, the major cusps of the two latter were regarded either as homologous or as acquired in strictly similar ways, it is difficult to see what basis Gidley imagined he had for his view; he was saying, in effect, that although the cusps are similar, there is no relationship. Possibly it was, as Simpson has remarked, simply another instance of this author's "known extreme polyphyletic conception of mammalian evolution." The second exception is Kretzoi (1946), who proposed a new order for the reception of the family; his work is discussed below.

Our real knowledge of the Jurassic docodontids dates from Simpson's monographs, in which *Docodon* and *Peraiocynodon* are thoroughly figured and described. Simpson concluded (1929a, p. 85) that "all of the original pantothere cusps . . . are present and they retain their original relationships. . . . Superimposed on this . . . pantotherian inheritance . . . there is a specialization, confusing but not really profound." This was a consistent, logical view; the cusps were considered to be, in large measure, fully comparable and the docodontids were placed in the Pantotheria. The latest first-hand study of the group is by Butler (1939b), who presented evidence that the post-canine dentition was quite different from that of the Amphitheriidae, Paurodontidae or Dryolestidae. He believed that the primary cusp in the upper molars was centro-external, not internal, in position, and that a stylocone (his buccal cusp) was lacking. The large internal cusp of the upper molars was considered to be the protocone, and the remaining cusps, with the exception of the two small ones in lower molars anterior and posterior to the main internal cusp, were regarded as homologous with the pantotherian molar elements. In recognition of these differences, he stated (p. 353) that "among the Pantotheres, it is possible to distinguish (*a*) the Dryolestoidea . . . (*b*) the Docodontoidea. . . ."[1] My own view is that the molars are even less similar than Butler supposed, and that the two groups were much farther apart than he, not to mention Simpson, was prepared to admit. Although his reasoning was faulty and his conception of a haplodont reptilian ancestry extreme, Gidley, with his shot in the dark, came nearer the mark than his successors.

The evidence reviewed in the previous sections appears to confirm fully the beliefs of Gregory (1916, 1922), Matthew and Butler that the primary cusp of the pantothere upper molar is internal in position and homologous with the tribosphenic paracone. This cusp is the highest on the crown and is in line with what is obviously the primary cusp on the premolars. In the Docodontidae, on the other hand, the highest cusp is centro-external in position and is in line with what is obviously the primary cusp on the premolars. There can be no escape from Butler's conclusion (1939b, p. 331) that these cusps are serially homologous and that, as Gidley had earlier believed, the primary cusp is external in docodontid upper molars. This is indeed a major difference between the two groups, but it is far from being the only one. There is no evidence that the docodontids ever passed through a reversed triangle stage in their molar evolution. The stylar area, as Butler noted, is represented merely by a low cingulum, without any hint of an enlarged stylocone. Cusp *c* is in an antero-posterior line with the paracone. In the lower molars cusp *a* is in a similar line with the protoconid, the posterior part of the tooth is not set off from the anterior, and the main internal cusp, which is postero-internal to the protoconid, arose from the internal cingulum. In pantotheres, the principal subsidiary cusps are external and internal to the primary ones, not in line with them; the pos-

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[1] He did not formally state these divisions to be new, nor did he specify the rank assigned them. Presumably they were intended as superfamilies but the spelling does not exclude suborders. I must join with Simpson (1951) in protest against such offhand methods of proposing major taxonomic units.

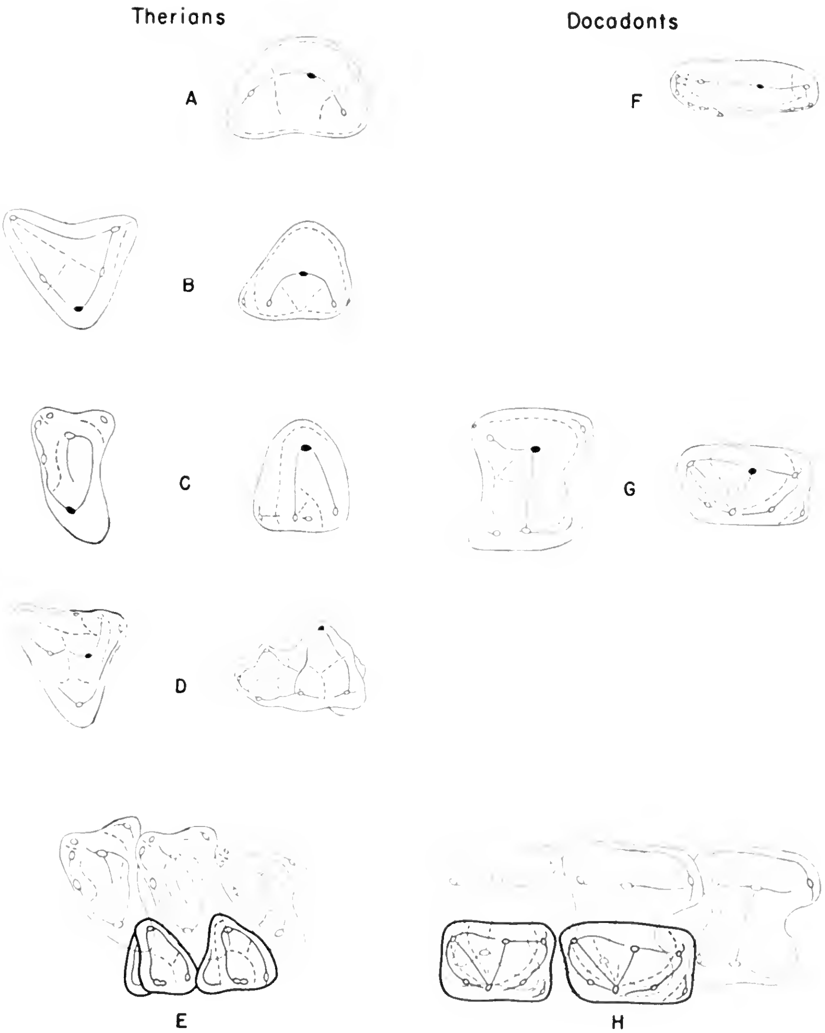

FIG. 15. Right upper and left lower molars of Mesozoic therians and of docodonts. A, "Duchy 33"; B, *Peralestes*, upper, and *Spalacotherium*, lower; C, *Melanodon*, upper, and *Laolestes*, lower; D, Forestburg therians; F, *Morganucodon;* G, *Docodon*. Black dots mark primary cusps. Centric occlusion: E, in dryolestid pantotheres, *Melanodon* and *Laolestes;* H, in *Docodon*. A and F based on Kühne, B, C, and G on Butler, C, E, and H on Simpson. Not to scale; greatly enlarged.

terior part of the lower molars, the talonid, is sharply set off from the anterior (continuing to be so, and to a greater degree, in tribosphenic molars); and the postero-internal metaconid arose on the slope of the protoconid. Apart, then, from the primary cusps and perhaps the cingulum, there is seemingly not an element in common between the two groups (fig. 15, A–G). The docodontids arose from ancestors in which the primary cusp and cusps *a* and *c* were in line, and evolved an opposing, crushing type of dentition through enlargement and differentiation of internal cingula. In the process, they lost cusps *a* above and *c* below (the slight elevation on the posterior slope of the protoconid in dm_4 of *Peraiocynodon* shown in Butler's figure suggests that vestiges of *c*, and hence possibly of *a* above as well, may have been present in the lower molars of this genus). The main internal cusp of the upper molars came into existence as a part of the enlargement and differentiation of the cingulum; it is merely analogous to and in no sense homologous with the tribosphenic protocone, which arose later in time as an addition to a trigon. The posterior part of the lower molars, vaguely analogous to the tribosphenic talonid, was likewise an integral part of the tooth from the beginning of the cingular differentiation; it cannot be regarded as homologous with the talonid, which was an addition to a tooth that at first consisted entirely or almost so of a trigonid. The docodontid adaptive type was very different from the pantothere, and the relations of the upper and lower molars during centric occlusion were utterly dissimilar in the two (fig. 15, E, H).

Kühne (1949) has recently described, as *Morganucodon watsoni*, a remarkable Rhaeto-Liassic tooth from the same quarry that shortly afterwards yielded "Duchy 33." He interpreted it, correctly I am sure, as a right lower molar. There is (fig. 15, F) a large protoconid situated slightly in advance of the center of the tooth. Anterior and posterior to and in a fore and aft line with it are the two principal subsidiary cusps, *a* being much smaller and somewhat lower than *c*. There is no external cingulum, but the internal is well developed and bears a number of small cusps. The posterior cingulum cusp is in line with *c*, and the anterior cingulum cusp is internal and a little anterior to *a*. Between these two are five others, of which the largest is postero-internal to the apex of the protoconid. Kühne at first referred the genus to the Triconodonta, but later, in his account of "Duchy 33" (1950), he abandoned this opinion and tended to regard it as a "pre-pantothere." He stated that "Dr. P. M. Butler has suggested to me that *Morganucodon* might be a 'pre-docodontid' and compared the specimen with M_4 [dm_4] of *Peraiocynodon inexpectatus*. . . . The disappearance of the rather large posterior accessory cusp [cusp *c*] of *Morganucodon* would make the two teeth agree in structure." I am in complete agreement; the resemblance between *Morganucodon* on the one hand and *Docodon* and *Peraiocynodon* on the other is striking.[1] With the exception of cusp *c* and of two cuspules internal to the posterior cingulum cusp, every element in the Rhaeto-Liassic molar is present in the Late Jurassic forms, and the similarity extends even to the antero-internal position of the anterior cingulum cusp; furthermore, in dm_4 of *Peraiocynodon*, as noted above, there is perhaps a faint suggestion of cusp *c*. *Morganucodon* is certainly a pre-docodontid—I would venture to say a docodontid—but it is very far from being a pre-pantothere. This form and "Duchy 33" clearly show how widely different the molar structure of docodonts and therians was at that remote time (fig. 15, A, F).

The mandible is fully known only in *Docodon*. A general resemblance to the pantothere mandible exists—and also to the symmetrodont and triconodont—coupled with certain differences. The pedunculate condyle is somewhat lower than in pantotheres, and the articular surface presents posteriorly. More important, a large triangular process is present on the ventral border of the ramus situated a little distance behind the last molar, and this seems to have no counterpart among the Pantotheria (fig. 16, A). It is concave externally, with a thickened ventral margin and, on the internal side, is demarcated from the ascending ramus by a conspicuous groove (Simpson, 1929a, 1933). Simpson has identified it as the angle and has published a restoration showing a part of M. pterygoideus inserting on its inner surface (1928c, fig. 7). I am unable to agree with this interpretation. The process is farther forward than the angle in pantotheres and later therians, and the lower border of the ramus curves gently upward beyond it, as a continuation of the curve anterior to it. If this structure is not an angle in the strict therian sense, the question arises as to what its function may have been. Similarly situated, ventrally directed, but smaller processes occur among the Theria in carnivores (*Melursus*) and in zalambdodonts (*Solenodon*). Toldt (1905, p. 42) has applied the name "processus marginis mandibulae" (abbreviated to "marginal process" by Davis, *in* MS) to them. Dobson (1882, p. 89) and Allen (1910, p. 16), for *Solenodon*, and Toldt, for *Melursus*, have shown that M. digastricus inserts wholly or in large part on this process.[2] It is conceivable that the docodont process is broadly com-

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[1] The contrast between the lower molar of *Morganucodon* and the specialized M_{5-6} of *Docodon* is considerable (see fig. 15), but the anterior molars of *Docodon* show a greater resemblance to that of the earlier form, being ". . . so narrow that the internal cusps appear like so many elevations of an internal cingulum plastered on the higher external cusps." (Simpson, 1929a, p. 92.)

[2] Toldt, evidently basing his opinion on Owen's figures (1871), considered that *Peramus* possessed a marginal process rather than an angle. This I doubt, believing that this genus, in common with other pantotheres, had a true angle.

parable to the therian marginal process, although evolved independently as part of a different functional complex and hence larger. M. digastricus, however, is a therian muscle; it is lacking in monotremes and this may have been the case in other non-therian groups as well. An alternative and perhaps more likely possibility thus suggests itself. The process in docodonts may be comparable to the "echidna-angle" of monotremes. In tachyglossids, but not in *Ornithorhyncus*, there is a rather small, ventrally directed process that is in a similar position. This has been regarded as a true angle —a view to which I cannot subscribe, since bone-muscle relationships should be taken into account in any such identification. As Schulman (1906, pp. 334, 384, 387; pls. 50, fig. 8, 56, fig. 36) showed, the apex of the process forms part of the area of insertion of M. detrahens mandibulae—a muscle peculiar to monotremes among living mammals—with M. masseter inserting near the base on the lateral side and a portion of the M. temporalis mass (the "M. pterygoideus internus" of Toldt and others) near the base on the medial side, the latter serving as a synergist of M. masseter in place of the absent M. pterygoideus internus. The functional complex is thus analogous to rather than strictly homologous with the therian one. The "echidna-angle" of monotremes and the angle of therians were surely evolved independently; the two reveal that more than one set of bone-muscle relationships arose in the masticatory apparatus during the transition from the reptilian to the mammalian level of organization. The similarity in position between the process in *Docodon* and in the tachyglossids at least suggests that a correspondence in function was not impossible, the greater size of the process in *Docodon* being of course correlated with the presence of a functional dentition. Whatever the case, conditions in docodonts appear to have been different from those obtaining in pantotheres. M. pterygoideus, which I believe to have been single, probably inserted wholly on the prominent ridge described by Simpson (1929a, p. 93) as running anteriorly from the condyle in *Docodon*.

The available evidence indicates that docodontid and pantothere evolution started from different bases, followed different paths, and resulted in wholly different end products. The Docodontidae represent a distinct, non-therian order, for which Kretzoi's (1946) name is available.

Docodonta

Diagnosis and definition.—Distinguished from all orders in subclass Theria by neither possessing nor deriving from ancestors possessing molars of reversed triangular type; from Triconodonta by evolution of opposing, crushing molars through enlargement and differentiation of internal cingula; from Multituberculata by retention of long mandibular ramus and canines, and by lack of specialized incisors and shearing post-canine teeth; from all Mesozoic orders by possession of large triangular descending process on ventral border of ramus.

Dentition of latest forms $I_{3+}^{?}$, C_{1}^{1}, $P_{3\text{-}4}^{3}$, $M_{7\text{-}8}^{6+?}$. Incisors small; canines double-rooted, piercing; premolars with high primary cusps, other cusps variable, tending to become molariform in later forms. Molars of early forms elongate, with primary cusps large, cusps *a* and *c* in line with them; prominent, cuspidate internal cingula; in later forms cusps *c* above and *a* below lost, and main internal cingulum cusps greatly enlarged, upper molars becoming irregularly hourglass-shaped in outline, lowers rectangular, both with strongly grooved enamel; molars opposing, crushing. Ramus long, slender, internal mandibular groove present; symphysis long, ligamentous; condyle at level of cheek teeth, articular surface presenting posteriorly; coronoid process large, sloping posteriorly; large triangular descending process on ventral border of ramus immediately behind molars, not homologous with therian angle.

Range.—Rhaeto-Lias to Late Jurassic, Europe; Late Jurassic, North America.

Docodontidae Simpson 1929

Sole known family of the order diagnosed and defined above. Includes the following genera: *Docodon* Marsh 1881, Morrison formation, Wyoming; *Peraiocynodon* Simpson 1928, Purbeck formation, England; *Morganucodon* Kühne 1949, Rhaeto-Liassic fissure filling, Wales.

Kretzoi proposed Docodonta on the following grounds: lower premolars "caniform," thus differing from the "primitive-undifferentiated" premolars of pantotheres and from the "feliform" ones of triconodonts and symmetrodonts; lower molars "caniform," "of pure symmetrodont structure, but more specialized"; upper molars more pantothere than symmetrodont-like; mandible with anteriorly situated ("oriental") angle.

Kretzoi evidently believed that the cusps of docodont (and triconodont) cheek teeth were comparable with those of pantotheres and symmetrodonts; as will be evident from the foregoing, I am quite unable to agree. For him, a "feliform" lower cheek tooth is one in which ". . . the primary para- and metaconid-cingula develop to regular cusps and become in final modernisation new basal cingula" (i.e., presumably, a new cingulum arises beneath these cusps). In a "caniform" lower cheek tooth ". . . the primary para- and metaconid-cingulum remains in this original form and notches, developing later to cusps on the (anterior and) posterior edge of the main cusp, become to definitive para- and protoconids [metaconids?]. In this final stage feliform and caniform cusp evolution becomes uniformised." There is no good evidence for these supposed distinctions, which Kretzoi appears to regard as of fundamental importance. The paraconid and metaconid of therian molars (and the anterior and posterior principal subsidiary cusps on the molars of non-therians) arose on the slopes of the protoconid and not from cingula; and premolar structure in the Eutheria is not a safe guide to molar history, as has been emphasized in a previous section. The position of the descending process on the mandible (his angle) is the only valid character given.

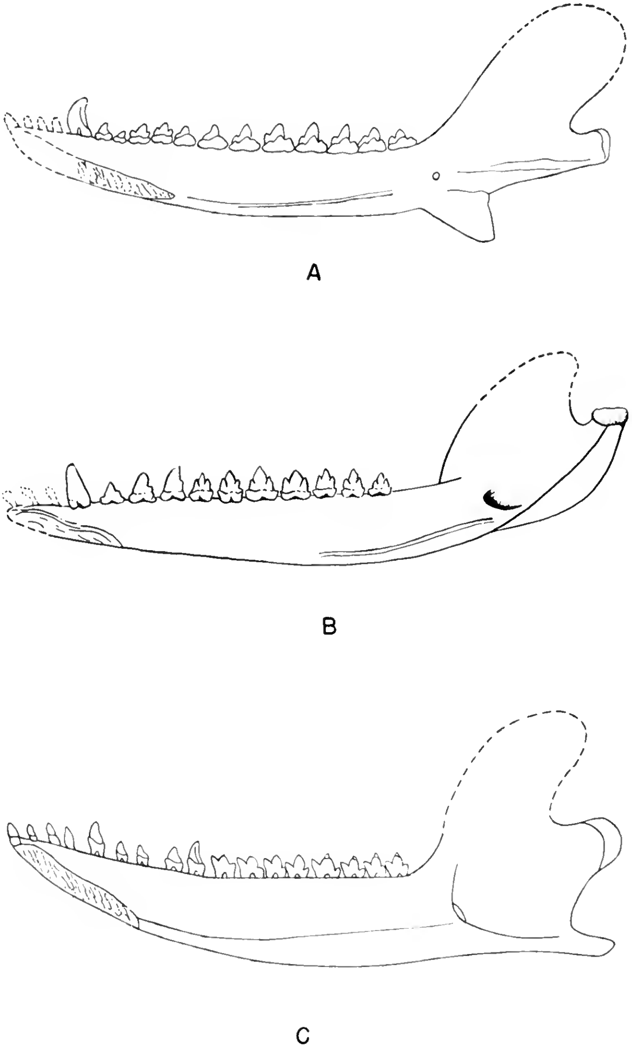

FIG. 16. Diagrammatic internal views of right lower jaws of A, *Docodon;* B, *Spalacotherium;* and C, *Laolestes.* From Simpson. Not to scale; enlarged.

Kretzoi included *Docodon*, *Peraiocynodon* and *Peramus* in his Docodonta, placing each of the two latter in undefined new families. *Peramus*, however, is unmistakably pantothere in molar structure, possesses a true angle, although one much less prominent than in the dryolestids, and thus has nothing to do with the other two forms. The genus is aberrant within the Paurodontidae, but separation of it is not helpful in the present state of our knowledge. The differences in structure between *Docodon* and *Peraiocynodon* are by no means profound, and since the latter is in all probability based on a milk dentition we cannot even compare the two forms directly. No reason exists for the recognition of Peraiocynodontidae.

THE RELATIONSHIPS OF MESOZOIC MAMMALS AND THE MAJOR DIVISIONS OF THE CLASS MAMMALIA

The evidence presented and the conclusions reached in the preceding pages have a bearing upon a number of problems concerning the Mesozoic mammals as a whole, such as the degree of affinity between the various orders, the group or groups of therapsids from which they descended, their relationship, or lack of it, to later mammals, and their taxonomic arrangement. This concluding section is devoted to a consideration of these questions.

The starting point for any general discussion of the Mesozoic Mammalia is Simpson's work on these forms as summed up in his two monographs (1928a, 1929a), for the existence of which, as Bohlin has justly remarked, "science is forever indebted to this author." In brief, he regarded the triconodonts and multituberculates as distinct groups going back to the therapsid reptiles, and the symmetrodonts and pantotheres as having had a possible common ancestry, this ancestry also going back independently to the Therapsida. The tritylodonts were placed in a suborder of the Multituberculata and the Microcleptidae (formerly Microlestidae and now Haramyidae) were questionably included, as incertae sedis, in the same order; the Docodontidae were referred to the Pantotheria. The Multituberculata were considered to represent a distinct subclass, Allotheria, and the Triconodonta were left incertae sedis as regards subclass allocation. The Monotremata were regarded as unrelated, or at least of unproven relationship, to any of the Mesozoic groups and as representing a subclass, Prototheria, of unknown history. All other mammals were placed in the subclass Theria, the Mesozoic Symmetrodonta and Pantotheria being united in the infraclass Pantotheria. Evidence was brought forward in support of the view that "the Order Pantotheria does represent the ancestry of both marsupials and placentals, without itself belonging to either group." This view, as Simpson pointed out, was hinted at by Owen (1871), proposed, although later abandoned, by Marsh (1880) and supported by Gregory (1922). Simpson's classification of 1945 maintains these opinions essentially unchanged, the only modification being the exclusion of the tritylodonts from the class and the transfer of the haramyids from Multituberculata? to Mammalia? inc. sed. The formal arrangement there set forth is:

Class MAMMALIA
  Subclass PROTOTHERIA
      Order MONOTREMATA
  Subclass ALLOTHERIA
      Order MULTITUBERCULATA
  ?Mammalia of uncertain subclass and order
        Family MICROCLEPTIDAE [= HARAMYIDAE]
  Mammalia of uncertain subclass
      Order TRICONODONTA
  Subclass THERIA
    Infraclass PANTOTHERIA
      Order PANTOTHERIA
      Order SYMMETRODONTA
    Infraclass METATHERIA
      Order MARSUPIALIA
    Infraclass EUTHERIA
      Order INSECTIVORA, etc., etc.

Removal of the Tritylodontoidea was, of course, due to Young's description (1940) of *Bienotherium*, and to the discussion of his paper by Watson (1942), which showed that the tritylodonts were therapsids and not mammals.[1] The continued inclusion of the Haramyidae, even as Mammalia? inc. sed., seems open to question. Parrington's study of new material (1947) has confirmed Simpson's earlier conclusion that the cheek teeth are unlike those of any of the Mesozoic groups whose mammalian status is established, and the tritylodonts reveal that cheek teeth with more than one root may occur among therapsids. Romer (1945) has placed the family in the therapsid suborder Ictidosauria, while Kühne (1949) has advocated listing it as Therapsida of uncertain suborder. I follow the latter course.

Since the publication of Simpson's monographs, and apart from various more or less supplementary papers by him, only a few studies based on new evidence or new interpretations dealing directly or indirectly with Mesozoic mammals have appeared. Butler's work (1939b, 1941) contains only incidental references to taxonomy. It has been extensively discussed above and is further referred to in the following pages. Parrington (1941, 1947) has described *Eozostrodon*, based on isolated, Rhaetic teeth of triconodont

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[1] Bohlin (1945), it should be noted, came to the same conclusion independently of Watson, whose work was unknown to him because of war-imposed isolation.

type. Olson (1944), on the basis of a thoroughgoing investigation of cranial structure in the various therapsid suborders, concluded that Simpson was essentially correct in his view that the various Mesozoic groups and the monotremes arose independently from therapsids. Bohlin's opinions on cusp homologies in pantotheres (1945) have been referred to above. On the basis of them, he concluded that the symmetrodonts had nothing to do with the pantotheres, but had descended either directly from primitive triconodonts or from the same ancestral stock, their crown structure being the result of rotation. He was inclined to consider the multituberculates as having arisen from unknown triconodonts with an external cingulum on the lower molars. The Jurassic Mammalia were thus considered by him to be essentially diphyletic, the Triconodonta, Symmetrodonta and Multituberculata having descended from one group of therapsids, the Pantotheria from another. Kretzoi (1946), as already noted, proposed a new order for the reception of the Docodontidae. In his introductory remarks he stated that he could not consider the multituberculates and monotremes as true mammals. Of the Mesozoic orders admitted to mammalian status, the Triconodonta were regarded as an isolated group, the Symmetrodonta and Pantotheria as lying ". . . in the direction of higher mammals." Gregory (1947) sought to show that the monotremes are not an isolated mammalian order but are derivatives from the marsupial stem. At the end of his paper, he proposed a new subclass, Marsupionta, for the reception of the orders Monotremata and Marsupialia, the placentals being placed in the subclass Monodelphia. No formal subclass allocation of the Mesozoic orders was made, but he concluded with the following statement: "The Multituberculata may be a very early side branch of the Marsupionta. The transition from the earlier Marsupionta to the Monodelphia may have occurred not by way of the Monotremes but through the Mesozoic orders Triconodonta, Symmetrodonta, Pantotheria. From the construction of their jaws and teeth, I infer that the first two were essentially marsupionts, the third, primitive placentals." It would seem from this that Gregory regarded the Pantotheria and the various placental orders, his subclass Monodelphia, as descended from symmetrodonts and these in turn from triconodonts, the mammals thus being monophyletic, rather than polyphyletic, in origin. In his view, the divergence between marsupials and placentals goes back to the symmetrodonts—not to the pantotheres or to a group descended from them. Kühne (1949) concluded that "*Eozostrodon* and its allies were certainly ancestral to the Jurassic Triconodonta and possibly ancestral to all mammals except the monotremes."

Considerable diversity of opinion thus exists. The available evidence is far from extensive but it nevertheless seems adequate to support or confirm some of the suggestions thus far advanced and to modify or reject others.

Three of the known Jurassic orders now appear to be represented, or at least closely approached, by material, unfortunately very scanty, from the Late Triassic or the Rhaeto-Lias: the Triconodonta by *Eozostrodon*,[1] the Docodonta by *Morganucodon* and the Symmetrodonta by "Duchy 33." As Kühne (1950) has remarked, it is true that we do not know if the animals that possessed these teeth had lower jaws composed of one or of several bones, i.e., whether they were technically mammals or not, but I would agree with his earlier statement (1949) that this is a relatively unimportant point, the dividing line between therapsids and mammals being an arbitrary one at that particular time in history. What is important is that these Rhaetic and Rhaeto-Liassic teeth show that animals possessing molars of the same type as those occurring in three of the Mesozoic orders were in existence at or before the beginning of the Jurassic Period. To this extent, therefore, they support the view that these orders had independent origins within the Therapsida.

The Triconodonta appear to occupy a central place in the thinking of several authors. Bohlin has definitely stated that he believes the symmetrodonts to be very closely related to primitive triconodonts, and the quotation from Gregory given above would seem to indicate that he holds essentially similar views. Butler's remark (1939b, p. 345) that ". . . there is no reason for supposing, with Simpson [1928a, p. 171], that the Triconodonta are not fairly closely related to the Symmetrodonta and Pantotheria," coupled with his implied approval of the rotation hypothesis, might perhaps be interpreted in much the same way. So long as our knowledge of the Symmetrodonta was confined to the Late Jurassic,[2] it was perhaps possible to hold such opinions, but Kühne's discovery of "Duchy 33" would seem to render them untenable. It is now evident that the reversed triangular molars that characterized the early Theria were at least as old as the cusp-in-line molars of the Triconodonta. Contrary to the views of some

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[1] Romer (1945) places this form in the Ictidosauria.

[2] Absence of symmetrodonts—and of multituberculates—at Stonesfield really has little meaning, except perhaps to suggest that they were not among the commoner faunal elements there. The Stonesfield mammalian "fauna," excluding the limb bones of uncertain ordinal position, and also of course the therapsid *Stereognathus*, consists of three species represented by eleven specimens. Two of these are triconodonts, *Amphilestes broderipi* and *Phascolotherium bucklandi*, represented by three and four specimens, respectively, and the third is a pantothere, *Amphitherium prevostii*, represented by four. It is an interesting coincidence that at Purbeck two triconodonts and a pantothere, *Triconodon mordax*, *Trioracodon ferox* and *Amblotherium pusillum*, are about equally common and together account for 45 per cent of all specimens determinable to order. Had the same offshore conditions of deposition obtained at Purbeck as at Stonesfield, it is conceivable that chance might have given us a sample of the mammalian fauna that would have been similar to the Stonesfield one, with no trace of symmetrodonts or of multituberculates. Neither of these groups is common at Purbeck, accounting only for 7 per cent and 11 per cent, respectively, of the total. (Data from Simpson's Catalogue, 1928a.)

authors, symmetrodont and pantothere molars are fully comparable, which is certainly more than can be said for symmetrodont and triconodont molars. The available evidence thus appears to be in favor of the view that the Triconodonta or their immediate predecessors were not ancestral to the Symmetrodonta and that the two groups arose independently from the Therapsida. Molars comparable in structure to those of triconodonts occur in the suborder Cynodontia.

The Multituberculata are regarded by Bohlin as descended from unknown triconodonts or ancestral triconodonts, and Simpson earlier admitted the possibility of such a relationship. The fact that the multituberculates were already highly specialized in the Late Jurassic, the time of their first appearance in the record, makes it impossible to come to any definite conclusion. The cheek teeth are so specialized that it is impossible even to identify the primary cusps with any assurance. The occlusal relationships appear to indicate that the original row, the three cusps in line, is internal in the two posterior lower cheek teeth, the external row of cusps being an addition from an outer cingulum, as Bohlin suggested. The primary cusp in plagiaulacids may perhaps be the central one, and the anterior and posterior *a* and *c*, respectively. The original row would appear to be internal in the penultimate upper cheek tooth and external in the last in plagiaulacids, central in both in ptilodontids. The third internal cusp of the penultimate and the antero-external of the last upper plagiaulacid cheek tooth may be the primary ones. This is very speculative, however.

The cheek tooth formula is equally dubious. Simpson, in agreement with Marsh, believed it to be P_{4-3}^{5}, M_{2}^{2} in plagiaulacids. Bohlin, perhaps seeking to ally them more closely with triconodonts, pointed out that the great difference in structure between the highly specialized cutting teeth and the grinding teeth behind them does not prove that the two types belonged to different series, and that there may well have been fewer premolars and more molars. His point is well taken; structural differences of this sort do not necessarily indicate that different series are involved. The marsupials of the superfamily Caenolestoidea provide an instructive example. In the Polydolopidae, the cutting, somewhat multituberculate-like tooth is P_3, in the *Abderites* group of the Caenolestidae it is M_1, and in the *Parabderites* group both P_3 and M_1 are involved in the formation of a serrated cutting edge. The small cuspules present in plagiaulacids on the outer side of the large, lower cutting tooth could be interpreted, as Bohlin intimates, as vestiges of an outer row of cusps, thus indicating derivation from ancestors in which this tooth resembled those behind it. Either Osborn's formula, P_{2-1}^{3}, M_{4}^{4}, which Simpson considered possible, or Broom's view that three, possibly four, molars were present could be correct. Unfortunately, it is not possible to come to a decision, and will not be until more is learned of multituberculate ancestry. Nothing whatever is known about tooth succession in the order, and all of the known forms may well have been monophyodont. This certainly seems to be true of the Tertiary ptilodontids. Jepsen, in his discussion of the Polecat Bench material (1940, p. 245), has stated that "not one specimen, of all the multitude collected, shows a deciduous tooth in the process of being replaced by a permanent one, although several jaws and skull fragments obviously belonged to young and small individuals with the teeth erupted less fully than in the adults."

Even if the premolar number was the same as in certain triconodonts, and it may well have been, this would not necessarily indicate close relationship. Comparing what is known of skull structure in the two groups, Simpson (1937) found ". . . nothing conclusive or even partially suggestive of triconodont-multituberculate affinities. . . ." What little resemblance exists in molar structure, and it is far from close, may well be due to nothing more than the possession of cusp-in-line molars common to all nontherian mammals. The available evidence, admittedly inconclusive, seems to point rather to independent derivation from the Therapsida than to descent from the Triconodonta, but it does not definitely rule out the latter possibility. The once rather widely prevalent opinion that multituberculates were marsupials has been thoroughly refuted by Simpson.

The Docodonta, here recognized as a distinct order, were regarded by Simpson as aberrant pantotheres that had nothing to do with the ancestry of either placentals or marsupials. Gidley, who believed them to be distinct from the Pantotheria, held similar views concerning their lack of relationship to later mammals. Butler (1939b, 1941), however, has hinted at an altogether different possibility, namely, that the "trituberculates" (in his sense) may have arisen from the docodontids, which he regarded as a superfamily (or suborder?) of pantotheres. He did not pursue the matter further, but it must be pointed out that the logical consequence of such a view would be a hypothesis of polyphyletic origin of different major groups of Eutheria—each of which would presumably be co-ordinate with the Metatheria—from the Pantotheria (in the old sense). The evidence presented above disposes, it seems to me, of any such possibility; docodont molars were fundamentally different from those of therians. The similarity in form that exists is nevertheless of great interest, since it shows that superficially therian-like molars could arise from the cusp-in-line type. Had the adaptive shift from the pantothere to the tribosphenic stage not taken place in the Theria, it is conceivable that a docodont radiation might have occurred, in which case mammalian history would have been a very different affair. Accepting *Morganucodon* as a member, the order appears to be at least as old as the Triconodonta and to have arisen independently from the Therapsida. There is no evidence that it was ancestral to the Multituberculata. Dr. Everett C. Olson has very kindly informed me that molars of *Morganucodon* type occur in the therapsid suborder Bauriamorpha.

Although not a Mesozoic or even a Tertiary order, the Monotremata demand consideration in any general discussion of the early Mammalia, with some of which, particularly the Multituberculata, various authors have attempted to link them. It is difficult to make adequate comparisons because of our ignorance concerning skull structure in the vast majority of Mesozoic mammals and the fact that only *Ornithorhynchus* among monotremes has teeth, and these ephemeral and degenerate. It may be stated at once that cranial and post-cranial characters oppose any hypothesis of multituberculate-monotreme relationships (Simpson, 1937), and that what little is known of the triconodont skull yields no positive evidence of close affinities between this order and the Recent one. The Forestburg humerus, which appears to be referable to *Astroconodon*, is decidedly different from the humerus of *Ornithorhyncus* or of the echidnas. The most recent studies of the *Ornithorhynchus* dentition (Simpson, 1929b; Green, 1937[1]) agree in identifying the main cusps, two in number, as internal in upper molars and external in lowers. In both uppers and lowers, the anterior of the two is the first to develop during ontogeny (Green). These, then, may be the primary cusps, the paracone and protoconid, and the posterior ones may be *c*. If so, the wide, crenulated shelves on the external sides of the uppers and on the internal sides of the lowers were derived from cingula, as Simpson suspected. Granting this, there is little resemblance to the plagiaulacids, in which, as noted above, the external row of the last upper and the internal rows of the last two lower cheek teeth may be the original ones, with the internal and external rows, respectively, derived from cingula—exactly the reverse of the apparent situation in *Ornithorhynchus*. The adaptive type is furthermore very different in the two, the multituberculates with anteroposteriorly running valleys and *Ornithorhynchus* with transverse valleys between the two main cusps. The molars thus seem to agree with the cranial characters in opposing the view that there is any close relationship between the two orders. As Simpson noted, there is a vague resemblance between platypus and triconodont molars but this again may be due to nothing more than that both are cusp-in-line types.

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[1] Green, who has made a most thorough study of the embryology of the platypus dentition, finds no support for Bolk's "Dimer Theory." This was a far-fetched view, based on questionable interpretations of embryonic material, that mammalian teeth are composed of outer and inner portions, each portion corresponding to one reptilian tooth. The hypothesis, if it may be dignified by such a name, is so completely at variance with the paleontological facts that it does not merit serious consideration.

Gregory (1947, p. 18) was inclined to see a resemblance between the molars of *Ornithorhynchus* and of certain marsupials, especially phalangeroids. Such similarity as exists is very slight and appears to be superficial. The primary cusp of phalangeroid upper molars, for example, is the antero-external paracone, whereas the primary cusp in *Ornithorhynchus* is evidently antero-internal in position. I must agree with Simpson and with Green that the platypus molars differ fundamentally from those of any of the Theria. Consideration of the other evidence brought forward by Gregory in support of monotreme-marsupial relationship is beyond the scope of this paper, but I may state my adherence to the consensus that the two groups have nothing in common beyond the fact that both are mammalian in the broad sense.

The upper molars of *Ornithorhyncus* appear to differ from those of *Docodon*, not only in form but in having the cingular expansion on their external rather than on their internal sides. Beyond this it is difficult to contrast the two groups. The tachyglossids among the monotremes agree with the docodontids in having a somewhat similar, although reduced, pseudo-angular process—the "echidna-angle"—and it is at least conceivable, as noted above, that this process may have furnished attachment to similar muscles in the two groups. To proceed from consideration of this possibility to an assumption of relationships would indeed be to compound speculation; the idea, however intriguing, is simply not testable at present. Derivation of the monotremes remains a mystery.

As already stated, there is no good evidence that the Symmetrodonta were derived from a triconodont ancestry. Only if cusp rotation actually occurred—and there are at present no real grounds for supposing that it did—could the order have arisen from therapsids with cusp-in-line molars. Simpson (1925c, fig. 3) has offered a tentative reconstruction of the ancestral molar. This is triangular and consists of a high main cusp, the apex of the triangle, with anterior and posterior ridges running externally from it above and internally below. "Duchy 33" shows that this reconstruction may well be very close to the truth. The symmetrodonts were rather tentatively included in the subclass Theria by Simpson in his earlier discussions of them. In a later paper (1936, p. 948) he put the case a little more strongly: "Structurally, the symmetrodonts represent a simpler and possible anterior term in the series [of therian molar types]. It is conceivable that they do represent an actual survival of the structural ancestry of the Pantotheria, but this is speculative. There is at present no satisfactory evidence bearing on the possible derivation of the markedly different pantothere upper molars from those of symmetrodonts." The situation now seems clearer. "Duchy 33" and the Forestburg molars combine to present evidence that is satisfactory and to lift the suggestion from the realm of the conceivable to that of the probable. The "acute-angled" symmetrodonts do represent, it seems to me, a survival—no doubt somewhat modified—of the structural ancestry of the pantotheres. The case for inclusion of the order in the Theria now seems to be securely grounded.[1] So far as I am aware, molars resembling those of symmetrodonts are as yet unknown among therapsids.

One or two problems within the Symmetrodonta are raised by the new evidence. Are the simple molars of the amphidontids, with their very small paraconids and metaconids, primitive or secondary? "Duchy 33" would suggest the latter, but more evidence is clearly needed. Is *Tinodon*, a form with only four molars and a long, wide-angled trigonid, really a member of the same family as *Spalacotherium*, which has a high number of lower molars, each with a short, acute-angled trigonid? May it not represent a distinct family of symmetrodonts, analogous in molar reduction to the Paurodontidae among the Pantotheria? This is possible; the Symmetrodonta may have undergone a small-scale radiation during the first half of the Jurassic, and the amphidontids, *Tinodon* and *Eurylambda*, and the "acute-angled" forms may be the representatives of lines that survived to or beyond the end of that period. The answers to such questions can only be supplied by future discoveries. Until these are forthcoming, no radical changes in the existing taxonomic arrangement would be justified, but it would, I think, be advisable to list *Tinodon* and *Eurylambda* as Spalacotheriidae? inc. sed.

The order Pantotheria makes its first appearance toward the end of Mid-Jurassic time, in the Stonesfield Slate of Bathonian age. If the views advanced in this paper are correct, the pantotheres arose from early "acute-angled" spalacotheriids, probably toward the end of Liassic or early in Bajocian time. As far as the relationships of the Pantotheria to later mammals are concerned, there are two main questions. Was the order ancestral to the Eutheria and Metatheria, and, if so, from which of its divisions did these later forms, or the group immediately ancestral to them, arise? The thesis that pantotheres were broadly ancestral to both

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[1] Kühne has remarked (1950) that with molars of triconodont, docodont, and symmetrodont type known from earliest Jurassic or pre-Jurassic time, ". . . the question . . . arises . . . whether we may expect even pantotherian teeth in the Rhaeto-Lias. At the moment, we do not possess such a tooth and we are still at liberty to build sequences of 'grades' or phylogenies and similar schemes without being encumbered by it." Dr. Kühne will have noted that very full advantage of this liberty has been taken here. As should be evident from the foregoing pages, I do not believe that the pantotheres had evolved at this early date. However, even if one should turn up in the Rhaeto-Lias, thus demonstrating that I have grossly overstated the case for a symmetrodont stage in therian molar history, the reference of the Symmetrodonta to the Theria would not be affected. Such a discovery would only demonstrate that pantotheres and symmetrodonts had diverged early from a common ancestry, and this community of origin would be sufficient justification for placing them in the same subclass.

marsupials and placentals has been rather generally accepted since Simpson restated it and brought forward new supporting evidence. Gregory's latest opinion, as noted above, is very different, however. For him, pantotherians and eutherians form one major group, metatherians another, each derived independently, it would seem, from symmetrodonts. The evidence is flatly opposed to this. The hypothesis postulates that tribosphenic molars and mandibular angles of strictly therian type arose twice. Primitive marsupial and primitive placental molars are far too similar to be due to anything but community of origin. As Simpson (1936, p. 797) has stated: "The tribosphenic dentition must have been typically developed at the time when the marsupial and placental stocks separated, for the earliest marsupial and insectivore or creodont molars agree in so many and such minute details that it is almost inconceivable that this can be the result of parallelism or convergence." This is not putting it too strongly. The tribosphenic dentition is two stages removed from the symmetrodont and each stage seems to have been due to one of those rare events, an adaptive shift in the direction of evolution. That two such shifts should have occurred twice and resulted in essentially identical end products is hardly credible. It is virtually certain that both eutherians and metatherians had a common ancestry and that this ancestry was once pantotherian. Simpson's classification, in which all three groups are regarded as infraclasses of the subclass Theria, is the only one that adequately expresses available data.

The primitive structure of the Forestburg molars suggests, as already noted, that the tribosphenic dentition came into existence not long before Albian time, probably during the Neocomian. This is also suggested by the nature of the associated mammalian fauna. During the later Jurassic, the Pantotheria was but one of five mammalian orders that played their parts in the vertebrate microfauna of a dinosaur-dominated world. This microfauna continued to the Albian with only one major change—the role of the pantotheres was taken by the tribosphenic forms. Triconodonts and plagiaulacid multituberculates were common at Forestburg, and symmetrodonts still survived. Docodonts are perhaps to be expected, and it would not be too surprising were some lingering pantotheres to be found. In the Late Cretaceous, the picture is entirely different. Save for the multituberculates, the Jurassic mammalian orders had disappeared, evidently swamped by the rising tribosphenic tide.[1] The inference to be drawn is that

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[1] The long survival of multituberculates was of course due to their early occupation of a highly specialized adaptive zone. They were the "rodents" of the later Mesozoic and earliest Cenozoic, and as such more than held their own; the fate that overtook triconodonts, docodonts, symmetrodonts, and pantotheres was long postponed for the multituberculates. Survival of the Monotremata, perhaps the oldest of all mammalian orders, is presumably due to extreme specialization combined with isolation in a region where placental competition was not a factor.

in the Albian this tide was just entering upon the flood. Simpson (1936, p. 798) suspected that the tribosphenic dentition had not yet come into existence in the Late Jurassic. The relative abundance of pantotheres in the Morrison and Purbeck suggests that this was indeed the case.

The tribosphenic dentition appears to have been the result of an adaptive shift, an event that surely occurred but once (i.e., within one group of pantotheres). It is therefore likely, as pointed out on a previous page, that marsupials and placentals did not arise independently from the order Pantotheria, but that their common ancestry did, with divergence following soon after. There is even a hint, but no more, that representatives of this ancestral group may have been living at Forestburg during the Albian. Assuming that but one of the pantothere divisions gave rise to this ancestry, the question arises as to which, if any, of the known families is most likely to have done so. The Amphitheriidae are known only from lower jaws of the Mid-Jurassic *Amphitherium*, considered by Simpson as an almost ideally generalized therian. This form, or forms like it, almost surely did participate in the metatherian–eutherian ancestry, but whether this was direct or through an intermediate group is uncertain. The upper molars being unknown, we are in ignorance concerning the size of the stylocone, the extent of transverse widening, and other points. If the family survived as such into the Late Jurassic, it may very well have been directly ancestral, otherwise not. The known Late Jurassic families, the Paurodontidae and the Dryolestidae, were presumably descended from amphitheriids. Paurodontids have a low number of molars (3–4), which is a definite approach to the eutherian–metatherian formula, and some of them show a vestige of the anterior cingulum cusp, such as occurs in the Forestburg lower molars, but those resemblances are accompanied by marked differences. With one exception, the premolar formula is reduced below the eutherian–metatherian number. The trigonids are longer and narrower than in the Forestburg molars, and the paraconids and metaconids farther apart. The only form with four premolars, *Peramus*, seems to be an aberrant type with paraconids and metaconids absent (M_1) or reduced, which may indicate that it was a member of a phylum whose molars were undergoing secondary simplification. Upper molars are not certainly known, but both Simpson and Butler suggest that the Morrison *Pelicopsis* may be referable to the family. If so and if this form is typical, the stylocone was relatively small and the teeth comparatively narrow transversely. The Forestburg molars strongly suggest descent from forms with short, wide trigonids and wide upper molars with large stylocones, characters that the paurodontids seemingly did not possess. Despite the low molar number, this family would appear to be the least likely of the pantothere groups to have given rise to the tribosphenic dentition.[1] The Dryolestidae possess a high number of molars and are advanced over the ancestral amphitheriids in their more antero-posteriorly compressed trigonids and somewhat shorter, wider talonids. These characters do not necessarily bar them from the tribosphenic ancestry; in fact, a short, wide trigonid and a wide talonid rudiment are features that surely occurred in this ancestry, and the same is true of the wide upper molars and large stylocones of the dryolestids. Two cusps, both small and minor, present in the trigonids of the Forestburg molars are not known in the family. These are the anterior basal cusp, thus far not known in any Jurassic therian, and the vestige of the anterior cingulum cusp of the symmetrodont stage, present in some paurodontids. Neither is important, and it is conceivable that the former cusp may exist in some Jurassic forms. Many of them are known from mandibular fragments with molars in place, and it would be very difficult—and risky—to attempt to expose the anterior faces of these molars to view. A definite answer to the question—from which pantothere family did the tribosphenic dentition arise—cannot now be given, but there would seem to be three possibilities: surviving, unknown amphitheriids, an unknown family, or the Dryolestidae. Appeals to the unknown are very easy in paleontology, and paleontologists have been perhaps a little too prone to make them. Of the families we know, only the dryolestids combine a type of structure that could have given rise to the tribosphenic with existence (and comparative abundance) in Late Jurassic time, and they deserve serious consideration in this connection. It is not intended to imply that any of the known forms is in the direct line—it would indeed be remarkable if the actual ancestors of the earliest tribosphenic forms had been living around the pond in central Wyoming and the lagoon in southern England that preserved our only real glimpses to date of Late Jurassic mammalian life—but the possibility would seem to exist that somewhere in the world the genetic changes that were to result in the eutherian-metatherian radiation took place in a population of latest Jurassic or earliest Cretaceous dryolestids.

To summarize to this point, the available evidence appears to indicate that, with the exception of the Symmetrodonta and the Pantotheria, none

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[1] Butler (1939b, pp. 346–349), on the basis of an examination of certain quantitative relations between the lengths of the molar series, of the jaw, and of that part of the jaw posterior to P_4, believes that zalambdodonts and paurodontids differ from other mammals in their departure from the normal relation between length of molar series and length of jaw posterior to P_4 and has suggested a direct relationship between the two groups. "In that case they [the zalambdodonts] would be independent of the other Insectivores and of the Marsupials, and would have to be regarded as a distinct order [infraclass?] of mammals." (p. 348.) Other evidence is not in accord. The zalambdodonst are certainly unguiculate placentals and as such have descended from tribosphenic ancestors. It is highly unlikely, as stated above, that this dentition arose more than once and improbable that it arose within the Paurodontidae.

of the Jurassic orders is sufficiently close structurally to any of the others to warrant a hypothesis of close relationship. Triconodonts, docodonts, and symmetrodonts all seem to have arisen independently from therapsid reptiles, and the same may be true of the multituberculates. The class Mammalia is thus considered to have been polyphyletic in origin, although in a very narrow sense, each of the early divisions having arisen within the same reptilian order.[1] Symmetrodonts and pantotheres appear to stand in an ancestor-descendant relationship, the latter having perhaps come into existence toward the end of Early or the beginning of Middle Jurassic time. The tribosphenic dentition arose from the pantotherian, probably during the earliest Cretaceous (Neocomian). Among known Late Jurassic pantotheres, the dryolestids are the most likely ancestral group. The earliest tribosphenic forms were in all probability neither marsupials nor placentals but members of a group ancestral to both. It will be evident that these opinions differ little in essentials from those expressed earlier by Simpson, the only major difference being the recognition of a new order for the reception of the Docodontidae. The new evidence that has become available in recent years, however, has made it possible to express somewhat more positive views on problems of molar evolution and early therian relationships.

Several Jurassic mammalian orders appear to go back independently to the Triassic. Several therapsid lines became progressively more mammal-like during the Triassic. There is an obvious inference to be drawn from what Olson (1944, p. 123) calls this "provocative" situation, but at present we are unfortunately unable to draw it in any convincing detail. As noted above, teeth of triconodont type occur in cynodonts and molars similar to those of *Morganucodon* occur in a bauriamorph,[2] but as far as I am aware, no molars that could surely be regarded as similar in structure to those of multituberculates or of symmetrodonts are yet known in therapsids. Splendid studies of the cranial and post-cranial morphology of mammal-like reptiles are available, and these are of the greatest general interest, but it must be observed that they are not directly helpful to students of Mesozoic mammals, who would like to link up their orders with the therapsid groups. The knowledge available to these unfortunates is largely limited to the dentition, a state of affairs only too likely to continue, and the dentition is the least known part of therapsid hard anatomy. This situation is uncom-

[1] I am accordingly unable to follow those, e.g., Kretzoi, who would grant mammalian status to some but not to all of the non-therian groups. Either all are mammals (sens. lat.) or this term should be restricted to the Theria alone.

[2] These resemblances are interesting and perhaps suggestive, but it would be premature to conclude that they necessarily indicate phyletic relationships.

fortably reminiscent of the story of the blind men and the elephant, and until it is remedied the phyletic relations between the earliest mammals and the mammal-like reptiles will remain obscure. An adequate odontography of the Therapsida is one of the major desiderata in vertebrate paleontology.

The taxonomic arrangement of the Mesozoic orders and the Monotremata remains for consideration. Inclusion of symmetrodonts and pantotheres in one grand division with the marsupials and placentals—the subclass Theria—does not now seem open to serious question. Subdivision into three infraclasses, Pantotheria, Metatheria, and Eutheria, likewise appears to be both valid and necessary, as already stated. It is in the treatment of the non-therian orders that problems arise. Simpson considered the Multituberculata to represent one subclass, for which he employed Marsh's term, Allotheria, and he followed the consensus in placing the Monotremata in another, Prototheria, leaving the Triconodonta incertae sedis. With the recognition of the Docodonta, we are now faced with two orders that do not fit into the subclass arrangement. One possible course of action would be to leave the Docodonta as incertae sedis with respect to subclass affinities, together with the Triconodonta. This would make the "waste basket" larger than either of the two formal, non-therian divisions: in essence a frank confession of our large measure of ignorance concerning these orders.

Another course would be to refer all of the non-therian orders to a single subclass. This would have the merit of combining in one division, co-ordinate in rank with the Theria, all groups that were, in comparison, of relatively minor importance in the history of the class as a whole. The result, however, would be more convenient than natural. It would brigade orders that are widely diverse in structure, of which the two better known —Monotremata and Multituberculata—are as distinct from each other as either is from the Theria. A third course would be to refer each of the non-therian orders to a distinct subclass,[1] but to take so definite a step would imply a knowledge we do not possess. It cannot now be stated with certainty whether or not triconodonts and docodonts had some degree of relationship to or common origin with multituberculates or monotremes. Pending additional data, therefore, caution is the part of wisdom and the first possibility, namely, to list the Triconodonta and Docodonta as incertae sedis in regard to subclass affinities, is adopted.

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[1] This course was strongly favored over the second during a lively discussion of the problem that took place during the meetings of the Society of Vertebrate Paleontology in 1953.

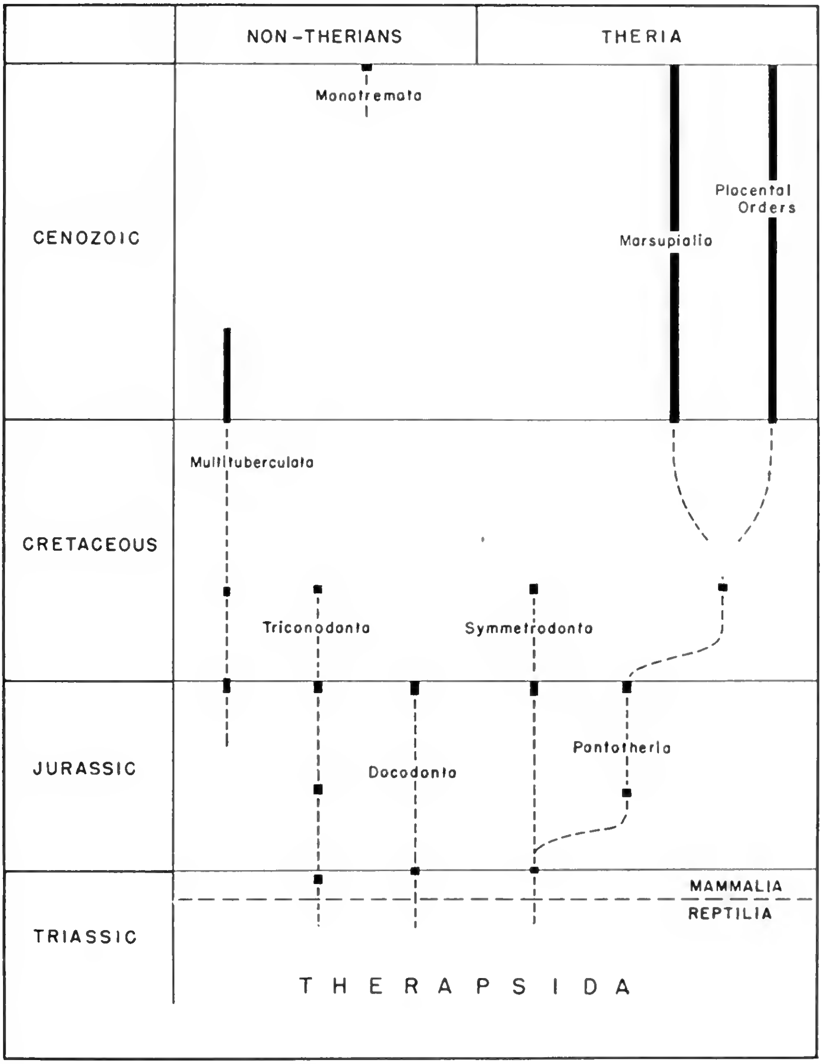

FIG. 17. Known geologic ranges (solid black) and suggested relationships of the major groups of mammals.

These views are summed up in the following classification and in the accompanying diagram (fig. 17).

- Class MAMMALIA
  - Subclass PROTOTHERIA
    - Order MONOTREMATA
  - Subclass ALLOTHERIA
    - Order MULTITUBERCULATA
  - Mammalia of uncertain subclass
    - Order TRICONODONTA
    - Order DOCODONTA
  - Subclass THERIA
    - Infraclass PANTOTHERIA
      - Order SYMMETRODONTA
      - Order PANTOTHERIA
      - [The earliest tribosphenic forms may prove referable to a third order directly ancestral to the other two infraclasses]
    - Infraclass METATHERIA
      - Order MARSUPIALIA
    - Infraclass EUTHERIA
      - Order INSECTIVORA, etc., etc.

SUMMARY

The fragmentary remains of Albian mammals and other vertebrates found together in the upper part of the Trinity Sand in Montague County, Texas, occur in bone beds, and not in isolated pockets as previously supposed. The beds, not all at exactly the same stratigraphic level, are within the upper 150 feet of the formation.

Mammals discovered to date include numerous incomplete specimens of triconodonts and multituberculates, a few symmetrodonts, and some fragments of therian mammals of uncertain infraclass affinities but of eutherian–metatherian grade. Nearly all the triconodont remains appear referable to *Astroconodon denisoni*, but there is some suggestion that a smaller species is also present; the fragmentary humerus described previously may well belong to *A. denisoni*. The multituberculates, the first discovered in the American Early Cretaceous, are represented by more than one form; all are plagiaulacids. The symmetrodonts are members of the Spalacotheriidae, the first of this family to be found in the Cretaceous.

The Theria of uncertain infraclass affinities are of great interest. Upper molars of these forms have a wide external shelf with one very large stylar cusp and variable minor ones. Paracone and metacone are well separated and nearly central in position. A low protocone was present. The large stylar cusp is homologous with the large centro-external cusp in pantotheres, for which the name stylocone is proposed. The lower molars have a high trigonid and a much lower, although well-developed, talonid. The entoconid is small, the hypoconulid and hypoconid larger but not always completely separated. Jaw fragments, tentatively placed here, suggest the antemolar formula I_4, C, P_4. It is conceivable that some of these forms may represent the group from which the Eutheria and Metatheria arose.

The Husin Series, in Manchuria, which has yielded mammalian remains, is suspected to be of Early Cretaceous rather than of Late Jurassic age.

The evolution of therian molar teeth is reviewed in the light of the new evidence provided by the Early Cretaceous material. The molars of the Forestburg therians of uncertain subclass affinities are of tribosphenic type. They indicate that dentitions of this sort, from which arose all the highly varied kinds evolved among marsupials and placentals, probably came into existence during the Early Cretaceous and that the great eutherian–metatherian radiation went on slowly for some 50 to 60 million years prior to the Cenozoic. The structure of the Forestburg molars supports the view that in the upper molars of Jurassic pantotheres the primary cusp is internal and is the paracone, the large centro-external cusp—the stylocone—is a stylar element, the metacone is postero-external to the paracone, and no protocone exists. Stylocone and paracone are usually joined by a crest, and the homologue of the cusp on the anterior crest of symmetrodont molars is only occasionally represented by a small vestige. The pantothere trigonid is fully comparable with the tribosphenic one; the rudimentary nature of the talonid is correlated with the absence of a protocone. Symmetrodont molars bear cusps homologous with those present in pantotheres. Symmetrodonts, pantotheres, and tribosphenic forms constitute a structural and broadly ancestral series.

The earliest therian molars were reversed triangles, the primary cusps internal above and external below. The primitive triangle in the upper molars—the primary trigon—was transformed by the addition of the protocone internally, and was replaced by a secondary trigon, composed of paracone, metacone, and protocone. Osborn's cusp terminology, as originally applied, referred to the primary trigon, and this raises a nomenclatural problem. The terminology universally in use for tribosphenic dentitions and their derivatives must be extended to the primary trigon without regard for priority.

"Duchy 33," a molar of symmetrodont type found in the Rhaeto-Lias, indicates that molars of reversed triangle type arose within a group of therapsids and were inherited by the symmetrodonts. Divergent specialization within the Symmetrodonta led to the evolution of "acute-angled" and "wide-angled" forms, the former the source of the pantotheres. There is no evidence that rotation of cusps ever occurred, but the hypothetical possibility cannot be entirely excluded; the data necessary for a solution of this long-standing controversy must be sought within the Therapsida. If rotation did occur, it may have involved only the crests from paracone and protoconid on which the main subsidiary cusps arose. Some, but by no means all, of the various cusps of therian molars appear to be equivalent in the upper and lower series. A few trends in molar evolution give the impression of a controlling axis, but molar evolution as a whole is random with regard to any postulated axis. It is the functional relationships between upper and lower teeth that are all-important in evolution. Complementary parts of the molars come under the control of common genetic factors. The developmental paths followed by mutations newly affecting such parts may be independent of the paths followed by mutations that earlier affected them. Maintenance and improvement or changes in the direction of functional trends may thus involve the addition or reduction of the same or of different elements in the two series, the establishment of gradients that occasionally do, but usually do not, give the appearance of axial controls, and the replacement of these gradients by others. The trend culminating in the reversed symmetry of the symmetrodont molars was one of the rare type in which uppers and lowers became alike in structure and function. All elements in the two series may well be equivalent in this group, but knowledge as to which is equivalent to which (other than the two primary cusps) must await further discovery. The symmetry of these earliest therian molars profoundly influenced, but did not "control," later evolutionary stages. Subsequent modifications, e.g., enlargement of the stylocone in the pantothere stage and addition of a protocone and a basined talonid in the tribosphenic, occurred without regard to maintenance of this symmetry and in the end obliterated it.

Symmetrodont molars were primarily alternating, shearing teeth, the edges engaging within the embrasures between the uppers, a type of action termed embrasure-shearing. Prior to completion of the shear, there appears to have been some crest on crest action. The cusp on the anterior crest, the metacone, the paraconid, and the metaconid probably arose on the crests running from the paracone and the protoconid as parts of the embrasure-shearing functional complex.

Pantothere molars are very similar to those of the most specialized living zalambdodont insectivores; the latter have in fact reinstated the primary trigon. Not only are the cusps comparable and evidently homologous in both, but all wear surfaces seen in pantotheres are duplicated in zalambdodonts. A potent tool for the interpretation of pantothere occlusion is thus available. In centric occlusion, the pantothere paracone and protoconid lay along a zigzag line, as in therian mammals generally. The whole stylar area, comprising the greater part of the upper molars, was thus external to the trigonid of the lowers. In active occlusion, the trigonid, in addition to the embrasure-shearing action, also worked across the wide primary trigon, the crests of the two series engaging each other, and the teeth of one side only being in use at a time. Grinding of this peculiar crest on crest type preceded crushing in therian molar evolution, and was a keynote in the adaptive shift from the symmetrodont to the pantothere dentition. An initial increase of ectental motion and of crest on crest action would have conferred a selective advantage on the characters in which pantothere molars differ from symmetrodont. It is suggested that the angle of the therian mandible arose during this adaptive shift.

The acquisition of true opposition and of crushing was the keynote of the adaptive shift that transformed the pantothere dentition into the tribosphenic. In pantotheres the talonid was enlarged in comparison with that of symmetrodonts, serving as a stopping device and as an additional shearing surface. The inner side of the upper molar and the heel of the lower thus came to act as a functional unit, and the way was open for incorporation of mutations affecting this unit as a whole. Addition of a rudimentary protocone and a basined talonid followed, and the evolution of the secondary trigon began.

The triangular trigonid persisted without major modification from the symmetrodont to the tribosphenic stage. It is an example—a very long-drawn-out one—of the evolutionary principle that no change is so sudden that old structures and functions are at a stroke supplanted by new; there is always a period of transfer during which the one replaces the other.

Therian premolars remained simple until after the tribosphenic stage had been reached. Premolars of metatherians and eutherians convey no hint of the symmetrodont and pantothere stages of molar history and cannot do so for evident reasons. The view that the molarization of the premolars recapitulates molar history is misleading, and the same is true of the molarization of milk molars.

The molars of non-therian mammals—triconodonts, multituberculates, monotremes—differ fundamentally from those of therians in never having passed through a reversed triangle stage. The two main subsidiary cusps arose in the same antero-posterior line with the primary ones. Further additions on the external or internal sides of this original row arose from cingula. Application of the therian nomenclature to cusps other than the primary ones is not justified. A true angle, in the therian sense, did not evolve in any of these forms.

The Docodontidae agree with the non-therian orders in possessing molars of cusp-in-line type and in lacking a true angle. The family is not referable to the Pantotheria, and the order Docodonta is recognized for its reception.

Opinions on the relationships of the Mesozoic Mammalia and of the Monotremata are briefly reviewed. The available evidence supports the view that, the therian groups excepted, none of the known Mesozoic orders is very closely related to any of the others. The Symmetrodonta and at least some non-therian orders appear to have arisen independently from therapsid reptiles. Ignorance of the therapsid dentition prevents accurate tracing of phyletic lines across the arbitrary reptilian–mammalian dividing line. Inclusion of the Symmetrodonta within the infraclass Pantotheria is fully justified. The order Pantotheria is believed to have arisen from "acute-angled" symmetrodonts toward the end of Early or the beginning of Mid-Jurassic time, and to have given rise in Early Cretaceous (Neocomian) time to a group with tribosphenic molars, the direct ancestors of the metatherians and eutherians. Of known pantotheres, the dryolestids are the most likely ancestors of the earliest tribosphenic forms. Recognition of a subclass Theria, including the infraclasses Pantotheria, Metatheria, and Eutheria, hardly seems open to question. Subclass treatment of the non-therian groups is a more difficult problem, one complicated by recognition of the order Docodonta, which, like the Triconodonta, does not fit the current subclass arrangement. For the present it is preferable to list both orders as Mammalia of uncertain subclass affinities. Since the Monotremata and Multituberculata are as distinct from each other as either is from the Theria, the subclasses Prototheria and Allotheria are fully justified.

ADDENDUM

The manuscript of this paper was essentially completed late in 1952. It has been possible since then to incorporate some new information provided by specimens subsequently found and to bring the Introduction down to date. During the intervening years very little has been published on Mesozoic Mammalia. Two contributions that have appeared may be briefly noted.

Friant (Proc. Zool. Soc. London, **124:** 561–567, 1954) has presented a note asserting that the Jurassic multituberculate *Plagiaulax* is a diprotodont marsupial, a view first advanced almost a century ago. Her opinion is based on the superficial resemblance of the lower dentition to that of such marsupials as *Bettongia* and on a belief that the jaw was fundamentally similar in the two groups, a supposition which involves the mistaken identification of the plagiaulacid pterygoid crest as the therian angle. Simpson (Amer. Jour. Sci., (5), **11:** 228–250, 1926) had long before discussed such similarity as exists, and had correctly ascribed it to convergence. Friant does not allude to his several detailed refutations of the evidence that had been adduced in favor of multituberculate-marsupial relationships—analyses that convincingly demonstrate the untenability of such views.

Very recently, a brief preliminary notice of one of the most exciting events in the long history of the search for Mesozoic mammals has appeared. Dr. K. A. Kermack and his co-workers have continued the exploration of fissure fillings so ably carried on earlier by Dr. Kühne. Three new fissures containing mammalian remains have been discovered, one of which, Pant, is extraordinarily rich. From the matrix obtained, more than a thousand teeth and hundreds of bones have so far been recovered, jaws, cranial elements, vertebrae and leg bones being represented. Kermack, Kermack and Musset (Proc. Geol. Soc. London, no. 1533, pp. 31–32, 1956) state that the horizon is Triassic rather than Liassic in age, perhaps as early as Keuper. Two mammals occur, a symmetrodont and a non-therian identified as a triconodont, the latter accounting for nearly all the material found. Only three items of morphological information are given: the non-therian has the mammalian jaw articulation, the jaw has a small angle, and the periotic apparently bears a thin anterior extension that formed part of the lateral wall of the brain case. This last feature is characteristic of the Monotremata, and the authors conclude that ". . . the Pant triconodont . . . should probably be classified as a monotreme." The presence of an angle, they believe, indicates that this process has been secondarily lost in later triconodonts and also in other groups that lack it.

The questions that immediately arise are these: Is the non-therian from Pant really a triconodont? May it not be a docodont? The evidence thus far available is scanty but I nevertheless suspect the latter to be the case. A primitive docodont, *Morganucodon*, is known to occur in these fissures, later docodonts have a well-developed pseudo-angle, and the Pant mammal has an "angle," the position of which, although not stated, may be comparable to that of *Docodon*. Photographs of an upper and a lower molar and a ramus fragment with three molars of the Pant mammal have appeared in a recent issue of *The Illustrated London News* (**227,** no. 6087, p. 1065, December 17, 1955). So far as can be seen from these illustrations, there is a resemblance between the lower molars and those of *Morganucodon*. The presence of an "angle" is a decided argument against reference to the Triconodonta. Had such a process ever come into existence in that order parts of the very powerful muscles of mastication would certainly have inserted on it, and such an arrangement would not have been liable to secondary loss in the absence of any degeneration of the dentition.

If, as seems conceivable, the non-therian from Pant is a docodont, then the possibility of relationship between this group and the monotremes emerges from the realm of the non-testable (p. 86). One of the oldest problems in the higher taxonomy of the Mammalia may, in fact, be on the way to solution.

REFERENCES

Adams, L. A.

1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. Ann. N.Y. Acad. Sci., **28:**51–166, figs. 1–5, pls. 1–13.

Allen, G. M.

1910. *Solenodon paradoxus.* Mem. Mus. Comp. Zool., **40:**1–53, pls. 1–9.

Bohlin, B.

1945. The Jurassic mammals and the origin of the mammalian molar teeth. Bull. Geol. Inst. Univ. Upsala, **31:**363–388, figs. 1–10.

Butler, P. M.

1937. Studies of the mammalian dentition. I—The teeth of *Centetes ecaudatus* and its allies. Proc. Zool. Soc. London, (B), **107:**103–132, figs. 1–28, pls. 1–3.

1939a. Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc. Zool. Soc. London, **109:**1–36, figs. 1–28.

1939b. The teeth of the Jurassic mammals. Proc. Zool. Soc. London, **109:**329–356, figs. 1–12.

1941. A theory of the evolution of mammalian molar teeth. Amer. Jour. Sci., **239:**421–450, figs. 1–10.

1952a. The milk molars of Perissodactyla, with remarks on molar occlusion. Proc. Zool. Soc. London, **121:**777–817, figs. 1–16.

1952b. Molarization of the premolars in the Perissodactyla. Proc. Zool. Soc. London, **121:**819–843, figs. 1–93.

Dobson, G. E.

1882–90. A monograph of the Insectivora, systematic and anatomical, pp. i–iv, 1–172, pls. 1–28. London: J. van Voorst.

Fiedler, W.

1953. Die Kaumuskulatur der Insectivora. Acta Anat., **18:**101–175, figs. 1–23.

Frechkop, S.

1933a. Notes sur les mammifères. XIII—Note préliminaire sur la similitude des molaires supérieures et inférieures. Bull. Mus. Roy. Hist. Nat. Belg., **9,** (7), pp. 1–11, figs. 1–6.

1933b. Notes sur les mammifères. XV—Les relations entre les molaires antagonistes chez les mammifères végétariens. Bull. Mus. Roy. Hist. Nat. Belg., **9,** (41), pp. 1–35, figs. 1–18.

1935. Notes sur les mammifères. XVIII—Trituberculie, polyisomerisme et symétrie des dents des mammifères. Bull. Mus. Roy. Hist. Nat. Belg., **11,** (25), pp. 1–24, figs. 1–9.

Gidley, J. W.

1906. Evidence bearing on tooth-cusp development. Proc. Washington Acad. Sci., **8:**91–106, figs. 11–12, pls. 4–5.

Granger, W.

1908. A revision of the American Eocene horses. Bull. Amer. Mus. Nat. Hist., **24:**221–264, figs. 1–5, pls. 15–18.

GREEN, H. L. H. H.

1937. The development and morphology of the teeth of *Ornithorhynchus*. Phil. Trans. Roy. Soc. London, (B), **228:**367–420, figs. 1–14, pls. 32–49.

GREGORY, W. K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., **27:**1–524, figs. 1–32.

1916. Studies on the evolution of the Primates. I. The Cope–Osborn "Theory of Trituberculy" and the ancestral molar patterns of the Primates. Bull. Amer. Mus. Nat. Hist., **35:**239–257, figs. 1–18, pl. I.

1922. The origin and evolution of the human dentition, pp. i–xviii, 1–548, figs. 1–353, pls. 1–15. Baltimore: Williams and Wilkins Co.

1926. Paleontology of the human dentition. Ten structural stages in the evolution of the cheek teeth. Amer. Jour. Phys. Anthrop., **9:**401–426, figs. 1–8.

1927. Mongolian mammals of the "Age of Reptiles." Sci. Month., **24:**225–235, figs. 1–10, pls. 1–2.

1934. A half century of trituberculy. The Cope–Osborn theory of dental evolution, with a revised summary of molar evolution from fish to man. Proc. Amer. Phil. Soc., **73:**169–317, figs. 1–71, pl. I.

1947. The monotremes and the palimpsest theory. Bull. Amer. Mus. Nat. Hist., **88:**1–52, figs. 1–17, pls. 1–2.

GREGORY, W. K., and SIMPSON, G. G.

1926. Cretaceous mammal skulls from Mongolia. Amer. Mus. Nov., no. 225, pp. 1–20, figs. 1–19.

IMLAY, R. W.

1952. Correlation of the Jurassic formations of North America, exclusive of Canada. Bull. Geol. Soc. Amer., **63:**953–992, 1 chart.

JEPSEN, G. L.

1940. Paleocene faunas of the Polecat Bench formation, Park County, Wyoming. Part I. Proc. Amer. Phil. Soc., **83:**217–345, figs. 1–22, pls. 1–5.

KOBAYASHI, T.

1939. The geological age of the Mesozoic land floras in western Japan discussed from the stratigraphic standpoint. Jap. Jour. Geol. Geog., **16:**75–103.

KRETZOI, M.

1946. On Docodonta, a new order of Jurassic mammals. Ann. Hist.-Nat. Mus. Nat. Hungarici, **39:**108–111, figs. 1–2.

KÜHNE, W. G.

1949. On a triconodont tooth of a new pattern from a fissure-filling in South Glamorgan. Proc. Zool. Soc. London, **119:**345–350, figs. 1–2.

1950. A symmetrodont tooth from the Rhaeto-Lias. Nature, **166:**696–697, 1 fig.

MARSH, O. C.

1880. Notice of Jurassic mammals representing two new orders. Amer. Jour. Sci., (3), **20:**235–239, figs. 1–2.

MATTHEW, W. D.

1913. A zalambdodont insectivore from the Basal Eocene. Bull. Amer. Mus. Nat. Hist., **32:**307–314, figs. 1–6, pls. 60–61.

1922. *In* GREGORY, W. K., 1922, The origin and evolution of the human dentition, pp. xiii–xiv.

MIVART, ST. G.

1868. Notes on the osteology of the Insectivora. Jour. Anat. Phys. London, **2:**117–154, 6 figs.

OISHI, S.

1940. The Mesozoic floras of Japan. Jour. Fac. Sci. Hokkaido Imp. Univ., (4), **5:**123–489, 1 fig., 1 table, pls. 1–48.

OLSON, E. C.

1944. The origin of mammals based upon cranial morphology of the therapsid suborders. Sp. Pap. Geol. Soc. Amer., no. 55, pp. i–xv, 1–136, figs. 1–27, tables 1–35.

OSBORN, H. F.

1888a. On the structure and classification of the Mesozoic Mammalia. Jour. Acad. Nat. Sci. Philadelphia, (2), **9:**186–265, figs. 1–17, pls. 8–9.

1888b. The evolution of mammalian molars to and from the triangular type. Amer. Nat., **22:**1067–1079, 1 fig.

1897. Trituberculy, a review dedicated to the late Professor Cope. Amer. Nat., **31:**993–1016, figs. 1–13.

1904. Paleontological evidence for the original tritubercular theory. Amer. Jour. Sci., **17:**321–323, pl. 21.

1907. Evolution of mammalian teeth, to and from the triangular type, pp. i–ix, 1–250, figs. 1–215. Edited, with an introduction and numerous annotations, by W. K. GREGORY. New York: The Macmillan Co.

OWEN, R.

1871. Monograph of the fossil Mammalia of the Mesozoic formations. Palaeontogr. Soc., **24:** i–vi, 1–115, figs. 1–26, pls. 1–4.

PARRINGTON, F. R.

1941. On two mammalian teeth from the Lower Rhaetic of Somerset. Ann. Mag. Nat. Hist., (11), **8:** 140–144, figs. 1–3, pl. 2.

1947. On a collection of Rhaetic mammalian teeth. Proc. Zool. Soc. London., **116:** 707–728, figs. 1–8, pl. I.

PARRINGTON, F. R., and WESTOLL, T. S.

1940. On the evolution of the mammalian palate. Phil. Trans. Roy. Soc. London., (B), **230:** 305–355, figs. 1–16.

PATTERSON, B.

1934. Upper premolar-molar structure in the Notoungulata, with notes on taxonomy. Field Mus. Nat. Hist., Geol. Ser., **6:** 91–111, figs. 10–22.

1949. Rates of evolution in taeniodonts, pp. 243–278, figs. 1–7, table, *in* Genetics, Paleontology and Evolution, edited by G. L. JEPSEN, G. G. SIMPSON and E. MAYR. Princeton: Princeton University Press.

1951. Early Cretaceous mammals from northern Texas. Amer. Jour. Sci., **249:**31–46, figs. 1–3.

1955. A symmetrodont from the Early Cretaceous of northern Texas. Fieldiana, Zool., **37:**689–693, fig. 145.

RIGGS, E. S., and PATTERSON, B.

1935. Description of some notoungulates from the Casamayor (*Notostylops*) beds of Patagonia. Proc. Amer. Phil. Soc., **75:**163–215, figs. 1–4, pls. 1–5.

ROMER, A. S.

1945. Vertebrate paleontology. 2nd ed., pp. i–viii, 1–687, figs. 1–377, tables 1–4. Chicago: The University of Chicago Press.

ROTH, S.

1927. La diferenciación del sistema dentario en los ungulados, notoungulados y primates. Rev. Mus. La Plata, **30:**171–255, pls. 1–13.

Schlaikjer, E. M.

1933. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. I—A detailed study of the structure and relationships of a new zalambdodont insectivore from the middle Oligocene. Bull. Mus. Comp. Zool., **76**:1–27, figs. 1–8, 1 pl.

Schulman, H.

1906. Vergleichende Untersuchungen über die Trigeminus-Musculatur der Monotremen, sowie die dabei in Betracht kommenden Nerven und Knochen. Denkschr. Med.-Nat. Ges. Jena, **6**, 2 Th. (Semon's Zoologische Forschungsreise in Australien, **3**, II, 2 Th.), pp. 297–400, figs. 1–11, pls. 49–58.

Scott, W. B.

1892. The evolution of the premolar teeth in the mammals. Proc. Acad. Nat. Sci. Philadelphia, pp. 405–444, figs. 1–8.

Shikama, T.

1947. *Teilhardosaurus* and *Endotherium*, new Jurassic Reptilia and Mammalia from the Husin coal-field, south Manchuria. Proc. Japan Acad., **23**:76–84, figs. 1–5.

Simpson, G. G.

1925a. Mesozoic Mammalia I. American triconodonts. Amer. Jour. Sci., (5), **10**, part 1, pp. 145–165, figs. 1–7; part 2, pp. 334–358, figs. 8–21.

1925b. Mesozoic Mammalia II. Tinodon and its allies. Amer. Jour. Sci., (5), **10**: 451–470.

1925c. Mesozoic Mammalia III. Preliminary comparison of Jurassic mammals except multituberculates. Amer. Jour. Sci., (5), **10**: 559–569, figs. 1–3.

1926. The fauna of Quarry 9. Amer. Jour. Sci., (5), **12**:1–11, figs. 1–2.

1927. Mesozoic Mammalia VI. Genera of Morrison pantotheres. Amer. Jour. Sci., (5), **13**:409–416.

1928a. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum (Natural History), pp. i–x, 1–215, figs. 1–56, pls. 1–12. London: published by order of the Trustees of the British Museum.

1928b. Affinities of the Mongolian Cretaceous insectivores. Amer. Mus. Nov., no. 330, pp. 1–11, fig. 1.

1928c. Mesozoic Mammalia XII. The internal mandibular groove of Jurassic mammals. Amer. Jour. Sci., (5), **15**:461–470, figs. 1–7.

1929a. American Mesozoic Mammalia. Mem. Peabody Mus. Nat. Hist. Yale Univ., **3**:i–xv, 1–235, figs. 1–62, pls. 1–32.

1929b. The dentition of *Ornithorhynchus* as evidence of its affinities. Amer. Mus. Nov., no. 390, pp. 1–15, figs. 1–2.

1933. Paleobiology of Jurassic mammals. Palaeobiologica, **5**:127–158, figs. 1–6.

1935. The first mammals. Quart. Rev. Biol., **10**:154–180, figs. 1–19.

1936. Studies of the earliest mammalian dentitions. Dental Cosmos, **78**:791–800, 940–953, figs. 1–10.

1937. Skull structure of the Multituberculata. Bull. Amer. Mus. Nat. Hist., **73**:727–763, figs. 1–9.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**:i–xvi, 1–350.

1949. The meaning of evolution. A study of the history of life and of its significance for man, pp. i–xvi, 1–364, figs. 1–38. New Haven: Yale University Press.

1951. American Cretaceous insectivores. Amer. Mus. Nov., no. 1541, 1–18, figs. 1–7.

Suzuki, K.

1949. Development of the fossil non-marine molluscan faunas in eastern Asia. Jap. Jour. Geol. Geog., **21**:91–133, tables 1–23.

TAKAI, F.

1940. A monograph on the lycopterid fishes from the Mesozoic of eastern Asia. Jour. Fac. Sci. Imp. Univ. Tokyo, (2), **6**:207–270, figs. 1–12, pls. 1–9.

TOLDT, C.

1904–1905. Der Winkelfortsatz des Unterkiefers beim Menschen und bei den Säugetieren und die Beziehungen der Kaumuskeln zu demselben. Sitz. kaiserl. Akad. Wiss. Wien, math.-nat. Kl., **113**:1–66, pls. 1–3 (1904); **114**:1–162, fig. 1, pls. 1–3 (1905).

WATSON, D. M. S.

1942. On Permian and Triassic tetrapods. Geol. Mag., **79**:81–116, figs. 1–5.

WOOD, H. E.

1927. *Hoplophoneus mentalis* and cusp homologies in cats. Jour. Mamm., **8**:296–302, figs. 1–6.

WOODWARD, M. F.

1896. Contributions to the study of mammalian dentition. II. On the teeth of certain Insectivora. Proc. Zool. Soc. London, **1896**:557–594, figs. 1–2, pls. 23–26.

WORTMAN, J. L.

1901–1902. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. I. Carnivora. Amer. Jour. Sci., (4), **11**:333–348, figs. 1–6, pl. 1; 437–450, figs. 7–17, pl. 2, (1901); **12**:143–154, figs. 18–30; 193–206, figs. 31–43; 281–296, fig. 44, pls. 3–6; 377–382, figs. 45–48; 421–432, figs. 49–60, pls. 7–8 (1901); **13**:39–46, figs. 61–64; 115–128, figs. 65–70; 197–206, figs. 71–82, pl. 8, a; 433–448, figs. 83–95, pls. 9–10 (1902); **14**:17–23, figs. 96–99 (1902).

YABE, H., and SHIKAMA, T.

1938. A new Jurassic mammalia from south Manchuria. Proc. Imp. Acad. Tokyo, **14**:353–357, figs. 1–3.

YOUNG, C. C.

1940. Preliminary notes on the Mesozoic mammals from Lufeng, Yunnan, China. Bull. Geol. Soc. China, **20**:93–111, figs. 1–11.

1945. A review of the fossil fishes of China, their stratigraphy and geographic distribution. Amer. Jour. Sci., **243**:127–137, 1 table, 1 map.

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