PALEOBIOLOGY OF JURASSIC MAMMALS.

By

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With 6 figures.

Introduction.

Of the numerous problems relating to the rise of the *Mammalia*, some of the most important are paleobiological in nature. True understanding of the early history of mammals involves not only knowledge of their morphology, but also some conception of the conditions under which they lived, of their habits, and of their place in the Mesozoic faunas.

Such a study involves three related lines of inquiry: first, the habits of the mammals themselves, so far as these can be inferred from their imperfect remains; second, the nature of the environment in which they lived; and third, their ecological relationships to the accompanying biota. This is almost a virgin field for research. The habits of a single group, the Multituberculata, have been discussed at some length by various students, and will be only briefly mentioned here, but the three other orders have not been studied from a paleobiological point of view. The four Jurassic orders, Multituberculata, Triconodonta, Symmetrodonta, and Pantotheria,

will be discussed individually and as members of the fauna of three geologic formations, Stonefield, Purbeck, and Morrison.

The morphologic data on which this study rests have been published elsewhere (SIMPSON, 1928, 1929) as well as two shorter papers chiefly paleobiological or paleoecological in subject and hence related to the present study (SIMPSON, 1926 A, 1926 B).

Occlusion, food habits, and dental evolution.

The most important contribution which the paleobiological study of Jurassic mammals has to make to an understanding of mammalian evolution as a whole lies in their actual exhibition of early dental structures as correlated with function — a useful check to speculation as to the origin of later structures and functions. From a paleobiological point of view it is the occlusion of teeth that is the reflection of function, rather than primarily the structure on which this occlusion depends.

COPE (1896) divided all occlusal types into three main categories:

I. Psalidodect mastication. "Inferior molars work within superior molars but not between them." This includes only the triconodonts.

II. Amoebodect mastication. "Part or all of inferior molars work alternately to and between superior molars." This includes most carnivorous and some herbivorous mammals.

III. "Molar teeth of both jaws oppose each other." This includes most herbivores.

This classification of molar dentitions which overlap each other, those which alternate with each other, and those which oppose each other is clear and useful, but it does not reduce occlusal relationships to the elements of definitely biological significance.

The primary factor in occlusion is the direction of motion of the teeth, and here there is a very important dual division: (1) Motion chiefly vertical, orthal, i. e., the jaw moving in an arc with the glenoid articulation as its center, and (2) motion chiefly horizontal (propalinal, ectal, ental), i. e., the teeth brought into contact by orthal motion, but actual mastication accomplished by grinding forward, backward, laterally, or in a combination of these directions. From the point of view of motion, only, the following are the chief categories:

I. Motion chiefly in an arc with the glenoid articulation as its center.

    A. Simple opposition — the teeth coming to rest on contact. Including restricted orthal of COPE.

    B. With slight horizontal component, anteroposterior as in coryphodonts or lateral as in triconodonts. Chiefly shearing types. Psalidodect and amoebodect of COPE.

II. Motion chiefly horizontal after the teeth are in contact.

    A. Lateral — chiefly transverse.

        1. From without inwards, ectal of COPE.

        2. From within outwards, ental of COPE.

    B. Propalinal — chiefly anteroposterior.

        1. From before backwards, proal of COPE.

        2. From behind forwards, palinal of COPE.

There are in occlusion four general principles: alternation, opposition, shearing, and grinding. These may be more specifically classified as follows:

    I. Alternating.

    II. Opposing —

        a. Positive elements (cusps, crests) into negative elements (basins, valleys).

        b. Positive elements against other positive elements.

    III. Shearing —

        a. Parallel passage of crests sharing equally in shear.

        b. Oblique passage of a crest along a surface.

    IV Grinding —

        a. Cusps or cusp rows grinding in valleys.

        b. Opposed crested surfaces.

Examples will make the meaning of these divisions clear. Dolphins have almost purely alternating teeth. Human molars are mainly opposing teeth, positive against negative. Human incisors may be used optionally as opposing teeth, positive against positive, or as shearing teeth. Felid carnassials are shearing teeth, with parallel relative motion of two opposing crests. Triconodont molars are shearing teeth with oblique motion of a crest along a wearing surface. Multituberculate molars are grinding teeth, cusp rows against valleys, and elephant molars are grinding teeth with opposing crested surfaces.

Opposing teeth are primarily and usually omnivorous, shearing teeth carnivorous, and grinding teeth herbivorous.

The heterodont mammalian dentition normally exhibits different occlusal types in different parts of the dentition. In man the incisors are shearing or opposing positive to positive, the canines are alternating, and the cheek teeth are opposing mainly positive against negative.

Still more important is the fact that single teeth, particularly molars, may be of complex occlusal type. Many carnivore carnassials are at the same time alternating, opposing, and shearing. In cats shearing has developed to the reduction of alternation and complete loss of opposition. Tapir molars are opposing, shearing, and grinding.

Alternation in occlusion, as the term is used here, demands orthal movement of the jaws. Once the teeth have come into occlusion, they are locked by their alternation and little horizontal motion is possible. The function is primarily that of grasping or piercing, secondarily that of breaking. Opposition is not incompatible with horizontal motion, and in fact is essential in the development of grinding, but in its pure form it also is accompanied by orthal motion only. Its primary function is crushing. Shearing depends on motion sometimes not purely orthal but never quite horizontal. Its function is cutting. Grinding, finally, which names its own function, must be accompanied by horizontal motion.

Historically, alternation is the oldest occlusal principle and it is almost inseparable from the existence of a dentition at all. Complete loss of alternation is correlated with specific adaptation and, in harmony with DOLLO's law, such specific adaptation is usually irreversible. Loss of alternation may follow emphasis on shearing only, as in triconodonts, or on grinding only, as in elephants. These animals did not, and we might say could not, ever return to any other occlusal type or correlated food habit demanding alternation.

In the lower vertebrates, and particularly the reptiles, the nature of jaw suspension makes orthal motion obligatory and horizontal motion very limited or absent. Thus in evolving from the primitive occlusion with alternation only, they may develop shearing teeth or opposing teeth, but cannot develop true grinding teeth. Among cynodonts, such forms as *Cynognathus* developed shearing teeth, and this is true in greater degree of the ornithopod dinosaurs.

Diademodon among cynodonts, and various members of other reptilian groups, such as the crocodilian *Allognathosuchus*, developed opposing teeth.

Each of the four Jurassic orders of mammals shows in its molars a characteristic advance over the primitive condition of alter nation only:

Multituberculata: alternation lost, replaced by grinding.

Tricondonta: alternation lost, replaced by shearing.

Symmetrodonta: alternation retained, supplemented by shearing.

Pantotheria: alternation retained, supplemented by shearing and opposition.

The first two are essentially inadaptable, that is, they are so highly adapted to one type of occlusion, one direction; of jaw motion, and one sort of food that any considerable new and different adaptation is almost impossible.   Alternation is lost beyond recall, and irrevocable specialization strictly limits their destinies and circumscribes their further development.   The symmetrodont molar is more adaptable in retaining alternation, yet, without obviously losing the potentiality of doing so, it has not in fact developed the additional principle of opposition.   This would seem to place it at a great disadvantage in adaptability in comparison with the pantotheres. Furthermore, like the triconodonts but to a less degree, it is strongly specialized for one type of occlusion, motion, and food.

The pantothere type of molar, on the contrary, is essentially adaptable and this fact is of extraordinary importance in the evolution of the Mammalia.   It contains within itself the capacity to develop into any other occlusal type, adapted to any kind of food.   By more extensive development of opposition and loss of the primitive sort of alternation, changes mechanically simple and demonstrated in numerous phylogenetic sequences, it could give r'se to a purely opposing occlusion and from this to a grinding dentition. Change to an opposing occlusion has in fact occured within the Pantotheria *(Docodon)*.   By such changes or by varying emphasis of the three principles already present, alternation, shearing, and opposition, it could give rise to any known mammalian occlusal type. This it apparently did, in fact, for the primitive so-called tuberculosectorial molars, which are adaptable in the same way and in even greater degree, seem to be merely a perfecting of the pantothere type from which they may be derived by the growth of one or two new cusps

and the greater development of opposition (broadening and basining of the talonid).

This view of molar evolution and its basis in occlusal types and their adaptability, is much more fully documented than can be explicitly pointed out in this paper. Two of the many points in which it differs from other current theories may be mentioned. It sees in the pantothere alternating-shearing-opposing molar a type equally primitive and much more adaptable than the alternating-shearing symmetrodont molar which plays a more important role in the old tritubercular theory. It also opposes the widespread, but, it seems to me, baseless view that bunodonty is a primitive or an adaptable character. In reality complete bunodonty is almost invariably a specialized and very inadaptable condition, involving loss of alternation and of shearing, a loss which appears to be irrevocable and which very strictly limits the further potentialities of the dentition.

Multituberculate molars have little or nothing in common with those of the other Jurassic orders, either in heritage or in habitus. Triconodonts and symmetrodonts share emphasis on shearing, yet the way in which they accomplish this is very different, as shown below. Symmetrodonts and pantotheres share the retention of alternation, the basic pattern of triangular, interlocking teeth, yet the functional emphasis is quite different. These facts are most clearly interpreted as examples of the nature and limits of convergence and divergence, of habitus and heritage:

			Habitus	Heritage
		Tricono-donta		Elongate teeth, not interlocking.
	Same habitus; Different heritage.		Carnivorous. Shearing teeth.	
Same heritage; Different habitus.		Symmetro-donta		Triangular teeth, interlocking.
		Pantotheria	Insectivorous-Omnivorous. Tuberculosectorial teeth.	

Multituberculata.

The habits of multituberculates have long been a subject of speculation and study. The various earlier opinions and all the evidence bearing on the matter have already been presented and thoroughly discussed (SIMPSON 1926 A, SIMPSON and ELFTMAN 1929). The details need not be repeated here. Further discoveries and subsequent study have not been very extensive, and do not yet affect the general conclusions already reached, which are, in brief, as follows:

1. The usual multituberculate dentition is tripartite: incisors adapted for grasping, piercing, and in some cases gnawing, premolars adapted for holding and cutting, and molars adapted for grinding.

2. Together with the jaw and skull structure, this dentition is clearly specialized for a regimen mainly or entirely herbivorous. The incisors served for piercing husks, opening cones, extracting seeds, and the like; the premolars for cutting integuments and chopping food into smaller pieces; and the molars for grinding and crushing it. In the Jurassic, the principal food was probably *Gristhorpia*-like fruits, conifer seeds, cycadeoid roots and seeds, etc.

3. By analogy with later allies and other evidence indirect but suggestive, the Jurassic multituberculates were probably quadrupedal, saltatory, and arboreal.

4. They were ecologically analogous to the smaller rodents of Tertiary faunas.

Triconodonta.

Knowledge of triconodonts is almost confined to teeth and jaws, so that it is largely on the food habits of the groups that paleobiological discussion must center.

This question has not hitherto been very seriously considered. OWEN (1871) pointed out the analogy between *Triconodon* and *Thylacinus*, and OSBORN (1888) reëmphasized this analogy and placed the triconodonts in a „Carnivorous Series" in his suborder Prodidelphia. This view has not been challenged or further discussed except for doubts as to the physical prowess of these beasts and a suggestion that they were rather insectivorous-carnivorous than predaceous-carnivorous.

The following facts bear on the triconodont jaw musculature (Fig. 1):

1. The zygomatic arch is stout, arises posterior to the molar series, is not expanded, and continues the curve of the maxilla.

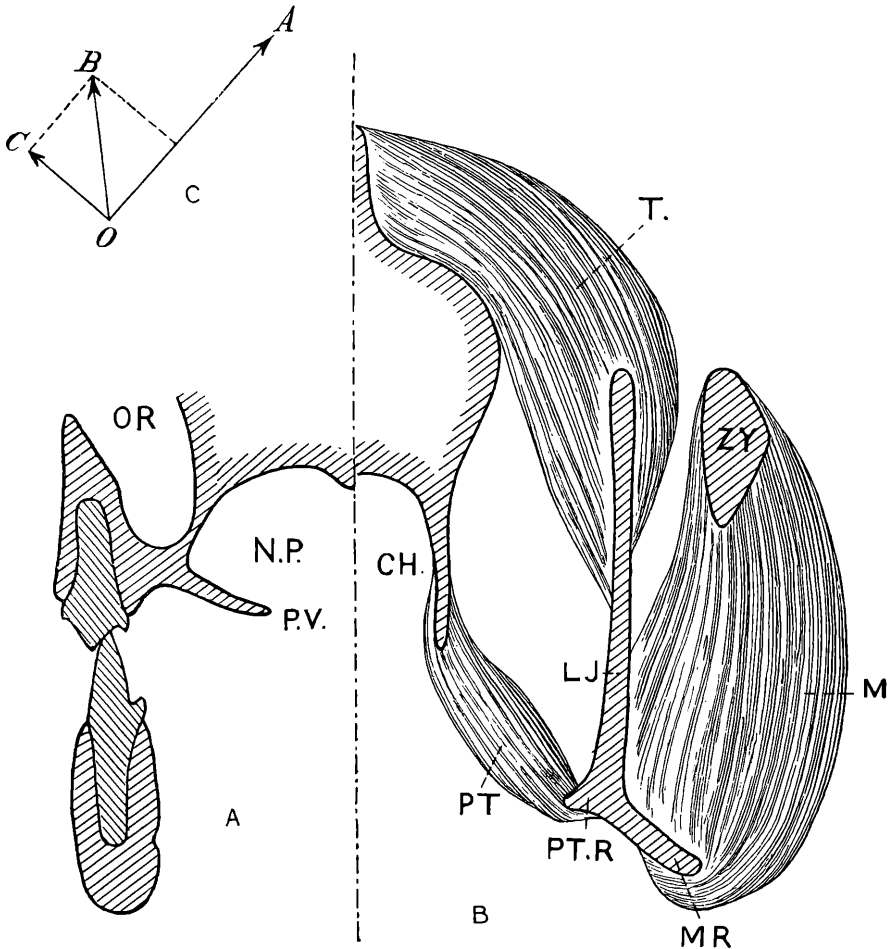2. The masseteric origin is large, well marked, and posterior to the molars.

Fig. 1: Musculature and mechanics of mastication in a triconodont: *Priacodon*.
A. Section through skull, in cheek region. N. P. Narial passage. P. V. Palatal cavity. OR Orbit. — B. Same, other side, more posterior, in temporal region CH. Choanae. LJ Lower jaw. M Masseter muscle. MR Masseteric flange of mandible. PT Pterygoid muscle. PT. R Pterygoid ridge of mandible. T. Temporal muscle. ZY Zygoma. — C. Parallelogram of forces, to demonstrate the great strength with which the teeth shear together in occlusion. O—B direction of pull of jaw muscles. O—A direktion in which lower molar must move while in contact with the upper. O—C resultant force pressing the lower molar against the surface of the upper.

3. The masseteric insertion is in a deep fossa and along a wide flange-like crest, almost directly below the origin.

4. The coronoid process is unusually high, broad, and strong. It rises directly behind the last molar.

5. The pterygoid fossa and crest are well marked, but the latter, especially, is weaker than in the Multituberculata, for example, and there is no true angular process.

The inferences based on these facts are as follows:

1. The masseter was large, its pull almost vertical, imparting a purely orthal motion to the jaw. Its lateral pull was significant, but slight relative to the vertical component.

2. The temporal muscle was also very powerful, with a strong leverage, especially with the jaws widely open. Its pull would furthermore tend to neutralize that of the masseter laterally and to supplement it vertically.

3. The pterygoid muscles were weaker than in most herbivores, but stronger than in some carnivores. Their pull was about equally upward and inward. They probably served chiefly to balance and steady the jaws against the outward pull of the masseter, the symphysial union being much weaker than in most later carnivores.

The musculature was of definitely carnivorous type, with some special adaptation to the unusual mechanics of the jaws and dentition.

The articular condyle is at or below the molar level, is strongly expanded transversely, points backward and little upward, and is convex in anteroposterior section. These are all characters commonly found in predaceous carnivores, and seldom in other animals.

The triconodont dentition was one of the most ideally carnivorous ever evolved. All of the more highly predaceous Tertiary and Recent mammals converge towards it more or less, although with some fundamental distinctions. The canines were large, that of the lower jaw fitting into a diastema immediately anterior to the upper canine. The premolars exhibit two types in the Order. In the earlier and generally more primitive genera they are somewhat similar to the molars, with symmetrical tricuspid shearing crowns. In the more advanced genera they are higher, more or less recurved and asymmetrical, adapted to grasping and piercing.

The molar cusps are arranged in a longitudinal series and the teeth are so crowded anteroposteriorly that there is no interruption in the cutting edge. Their action is unique, not a simple vertical shear of two serrate edges as in the Felidae, for example. Each projection of the lower series engages in an oblique valley on the inside of the upper teeth. During the latter part of a bite the cusps of the lower molars rake obliquely upward, inward, and backward on the upper teeth. Since the combined pull of the masticatory muscles is upward and slightly outward, the lower molars are pressed with great force against the uppers, so that the toughest food must inevitably be cut (see Fig. 1). This mode of wear seems to have been very severe on the upper teeth, which are reduced to mere stumps in some of the specimens.

The shearing power of the edge is considerably uncreased by the fact that it is nowhere horizontal, but formed by the steeply inclined slopes of sharp cusps. The serrate edge would also pierce and hold the food as it is cut. In very young animals the accommodation of lower and upper teeth was not perfect, but they very soon became worn so that every part of the crest, from the anterior end of the first molar to the posterior end of the last was in active contact with the opposing teeth.

The lower teeth were checked and prevented from piercing the palate by contact of the first and third cusps with the upper internal cingulum. The higher middle cusps of the lower molars were received in pits or in a continuous groove in the palate internal to the upper molars.

It has been supposed that the small size of the triconodonts must have limited their diet and necessitated habits in large part insectivorous. The smallest triconodonts, however, were not less powerful than the smaller mustelines, and the largest was about as large as a gray fox. The dentition is even more strictly predaceous in adaptation than in these living carnivores. The triconodonts were certainly sufficiently powerful to kill animals up to their own size or even larger. Their teeth were quite incapable of crushing food, almost excluding omnivorous or insectivorous habits.

Prey available to the triconodonts was abundant. They were associated not only with numerous herbivorous and insectivorous mammals, none of which were too large for them to overcome, but also with many small reptiles. So far as size is concerned they

could even have coped with the young of many of the dinosaurs. There were also amphibians and possibly even fish available to them.

In keeping with this strong evidence of actively predaceous habits, the triconodont brain was remarkably macrosmatic.

In short, all that is known of triconodont structure is wholly and unmistakably of carnivorous type, and in spite of their great antiquity they are among the mammals most highly adapted to this type of food and mode of life.

Symmetrodonta.

The jaws and muscular attachments of the symmetrodonts were rather like those of the triconodonts. Both temporal and masseter muscles were powerful and the latter had a nearly vertical course, while the pterygoids were less developed than in the multituberculates. The musculature seems to have been of definitely carnivorous type.

In the dentition, also, there is considerable functional resemblance to the triconodonts, apparently due, however, to some community of habit rather than of ancestry. In *Spalacotherium* the canine is fairly large, in *Tinodon*, unexpectedly, rather small. The premolars are of simple cutting or piercing type suggestive in a general way of those of the earlier triconodonts. The molars are convergent to the triconodont pattern in having a long serrate shearing edge, each molar with a high central cusp and two symmetrically placed lateral cusps. The resemblance, however, is not closer than to some recent carnivores and insectivores and does not extend to the details of mechanical adaptation or occlusal relationships.

In the triconodonts the cusps of each row of teeth are in a straight line, those of the lower series all internal to those of the upper series in full occlusion (Fig. 2 A'). In the symmetrodonts, on the contrary, the cusps are arranged in triangles and the lower teeth alternate with the uppers in occlusion, fitting into the triangular interdental embrasures (Fig. 2 B· and 3). A further and biologically more significant difference lies in the action of the cutting mechanism in the two groups (Fig. 2 A and B). As already detailed, that of the triconodonts involves an oblique grinding of the lower edge on the inner slope of the upper teeth. In the symmetrodonts, as in recent carnivores, there is no lateral compo-

nent, the teeth alternate and interlock, and the cutting is done by
both upper and lower crests equally as in a pair of shears. The
triconodonts cut their food by a sort of chopping, while the
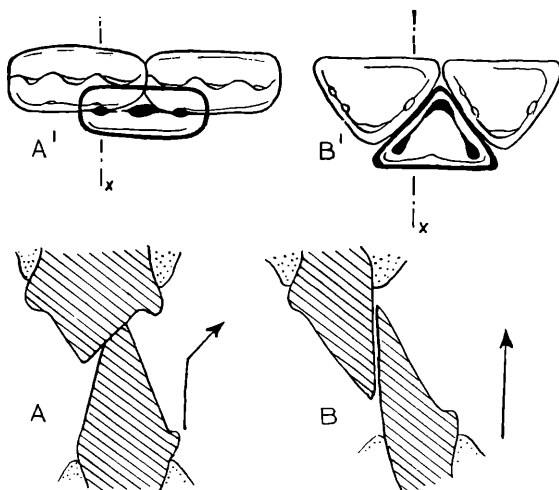symmetrodonts literally sheared it.

Fig. 2: Occlusion in triconodonts and symmetrodonts. A' Triconodont occlusion, lower teeth
darker. A Section of same along line X. B' Symmetrodont occlusion, lower tooth darker.
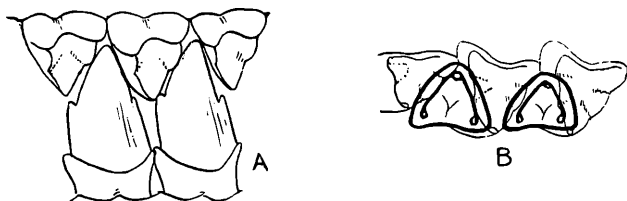B Section of same along line X. The arrows indicate direction of motion.

Fig. 3: Occlusion in symmetrodonts. A External view of left molars coming into occlusion.
B Occlusion diagram, lower molars darker.

The symmetrodonts seem to have been carnivorous, like the
triconodonts and like the later mammals with analogous molar
patterns and occlusion. They were perhaps less powerful than the
triconodonts, less able to cut very tough tissues, and their prey may
have been more feeble, a suggestion borne out by the reduction of
the canine in *Tinodon*. They appear to have been a much less
abundant faunal element than the triconodonts.

Pantotheria.

As already suggested above, the pantotheres are the most important and interesting of Jurassic mammals, not because they have such strange or unique characters as the other three orders, but for the very fact that they are not so aberrant and show early stages in the development of the marsupial and placental dentitions as a whole.

There are four fairly distinct groups of pantotheres in the Jurassic which I have redefined as families: Amphitheriidae, Dryolestidae, Paurodontidae, and Docodontidae. The Amphitheriidae, with the single genus *Amphitherium*, are apparently the most primitive and, in keeping with this, are older. The Dryolestidae and Paurodontidae are two divergent and not very advanced specializations from an amphitheriid ancestry, while the Docodontidae are very peculiar and more strongly divergent.

The jaw musculature did not differ very markedly in these various groups. The actual muscular origins are not known in any case, but it is known that in many of the later Jurassic forms the zygoma was rather slender, expanded, and arose outside the last two or three molars rather than posterior to them (as in triconodonts). The coronoid process is always well developed, but varies in detail. In *Amphitherium* (Fig. 4 A) it is recurved and pointed, and this is accentuated in *Amblotherium* where it becomes strongly hooked (Fig. 4 C). In *Phascolestes* it es broad and rounded, and somewhat similar but more slender and sloping in *Peramus* (Fig. 4 D). A definite and non-inflected angular process is always present, but it is quite varied in structure (see Fig. 4). In *Amphitherium* it is a sharply distinguished triangular process directed backward and downward, and it is almost the same in the paurodontid *Peramus*. In the dryolestids generally, it is smaller, thik and styliform, and points straight backward. The angular process of *Docodon* (Fig. 4 B) is similar in relative size and shape to that of *Amphitherium*, but is distinctive in being thicker and being separated on the internal side from the ascending ramus above it by a deep, broad groove running forward to the dental foramen.

The condyle is not strongly transverse, but generally with a rather flattened and oval articular surface. In *Amphitherium* and the dryolestids it is moderately elevated above the dental level and directed upward and backward, and it is similar but lower in

the paurodontids. In *Docodon* it is lower, near the dental level, and is also directly more nearly straight posteriorly (see Fig. 4).

Paurodon has a relatively shorter and deeper jaw, but the other known pantotheres all have long, slender mandibles. As in all Jurassic mammals, the symphysis is unfused and the two rami were capable of some degree of independent motion.
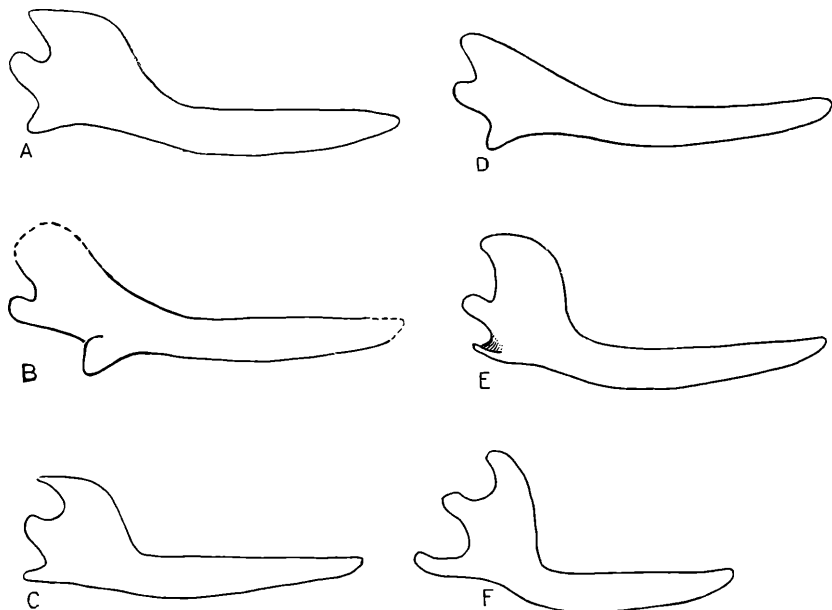

Fig. 4: Outlines of lower jaws of pantotheres and other mammals. A *Amphitherium*, B *Docodon*, C *Amblotherium*, D *Peramus*, E *Didelphis*, F *Erinaceus*. Not to scale.

The types of mandibles are all adapted principally to orthal motion but they are not definitely specialized in this direction, as are the triconodonts, and retain considerable freedom of motion. Among later mammals, they resemble the most primitive forms of placentals (Fig. 4 E and F) ; particularly the early or less specialized insectivores, but also the ancestral types in a number of other groups, Carnivora, Edentata, etc., in which no strong specialization in dentition or food habits has yet occurred and which are known or inferred to be insectivorous[1]) to omnivorous.

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[1]) "Insectivorous" is used for convenience to mean a diet like that of the so-called insectivores. This diet is by no means literally confined to insects, but usually includes small invertebrates generally, or even some vertebrates on occasion, although the animals are not strictly predaceous, or it grades into an omnivorous regimen.

The dentition is, of course, the most important evidence regarding food habits. The three families Amphitheriidae, Dryolestidae, and Paurodontidae may be considered together. In the Amphitheriidae, earliest and most primitive, the molars are elongate anteroposteriorly and are numerous. In the Dryolestidae they are equally or more numerous, but are compressed anteroposteriorly, as if crowded for space, an adaptation somewhat analogous to that of zalambdodonts among the Insectivora. In the paurodontids, on the contrary, they are reduced in number and retain the anteroposterior elongation. I see no direct connection between these divergent advances and food habits, and the general mechanics of occlusion, etc., remain about the same.

The incisors are always small and unspecialized. The canine varies in relative size, sometimes large and laniary, sometimes hardly larger than the premolars, but always differentiated to some degree and caniniform. These anterior teeth thus have not acquired the specializations so characteristic of the insectivores, almost the only features positively characterizing that otherwise rather generalized and vaguely defined group: tendency to enlarge and in various ways to specialize some of the incisors and to reduce the canines which become incisiform, premolariform, or even disappear.

Contrary to frequent statements, the premolars in these three families are never molariform and show no definite tendency to become so. They are rather simple, with one high, piercing or to a very minor degree shearing cusp, generally followed by a very minor heel and somewhat recurved. The last premolar usually overtops the succeeding molar. The premolars are in greater part purely prehensile organs.

The Amphitheriidae and Dryolestidae are strikingly characterized by the large number of true molars, usually seven or eight. The Paurodontidae, however, have at most four molars. Primarily, the molars in occlusion are a sequence of interlocking triangles, the apex external on the lower teeth and internal on the upper (Fig. 5 D). In both cases the anterior and posterior sides of the triangle form sharp blades which shear tightly past each other in occlusion and serve to cut food (Fig. 5 A). Efficiency is increased by the fact that the edge of each blade is in no case horizontal, but is divided into two strongly inclined parts by a median notch. 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 and holds the food with no chance to slip out on either side. The cusps proper, as opposed to these crests, and the alternating trigons which they form, serve to grasp the food strongly and to lock it in position while it is cut and ground, and also to break and crunch it.
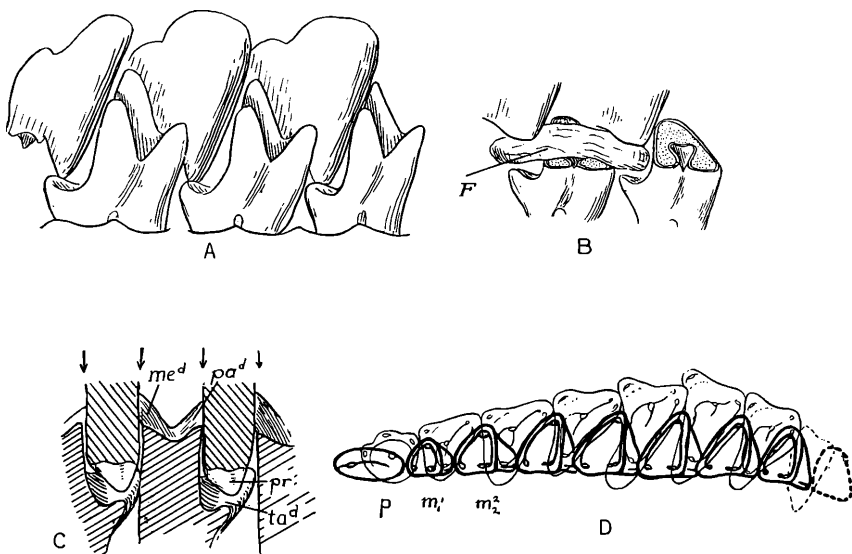

Fig. 5: Occlusion in a dryolestid pantothere. A Internal view of left molars coming into occlusion. B Wear of trigonids in an old pantothere, and crushing action of the trigonids on a food fragment, F. C View from the outside of the internal portion of a molar series in occlusion which has been sectioned longitudinally, arrows showing planes of shear, and the protocone, pr, shown in contact with the talonid, ta^d. D Occlusion diagram, lower molars darker.

In addition to this interlocking grasping and shearing apparatus, there is a mortar and pestle formed by the talonid of the lower molars, the mortar, and the large inner cusp of the upper molars, the pestle (Fig. 5 C). This serves a purely mechanical purpose in limiting the motion of the jaw, stopping it before the cusps can pierce the gum[2]), and it also serves the adaptive purpose of supplementing the grasping and shearing functions with pounding and, to a limited degree,

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[2]) There apparently was no such limitation in the symmetrodonts. This seems a remarkable omission, but it must have been replaced by the wedging together of the anterior alternating teeth.

grinding. This part of the dental apparatus is not well developed in the pantotheres, the talonid being relatively small, without a closed basin, and with a single cusp. As is well known, in the more primitive later marsupials and placentals it is relatively much larger, basined, and with three cusps[3]). Still it clearly is a useful part of the teeth in pantotheres and represents the fundamental functional basis for the principle of opposition so important in most later mammals.

Although pantothere molars of the families now under discussion are correctly referred to as essentially triangular, they are not tritubercular. The tritubercular dentition, as defined by OSBORN, has "three main tubercles on the crowns of both upper and lower molars disposed in triangles" (1907, p. 2), further "the crown triangular, surmounted by three main cusps, the central cone placed internally in the upper molars and externally in the lower molars" (ibid., p. 40). It is implied that these teeth have only the primary relationship of interlocking or alternating, and only the primary function of grasping. Such a tooth is stated by OSBORN to be "rare in its primitive condition as above defined" (1907, p. 40). In fact it is an abstraction, non-existent in nature with very rare exceptions all of which appear to be purely *secondary;* of the two examples given, *Spalacotherium* and *Asthenodon,* the first did not have three tubercles on the upper teeth, while the latter (a synonym of *Dryolestes)* did not have literally tritubercular teeth in either upper or lower jaw. The most primitive dentitions of most Tertiary orders were not tritubercular but tuberculosectorial, as is specifically stated in OSBORN's expression of the so-called tritubercular theory, this later part of which now seems so fully in accord with all the facts as hardly to be open to any very serious question.

These pantothere teeth are likewise almost tuberculosectorial, as that word was defined and used by OSBORN, or better, pre-tuberculosectorial. The upper molars have one inner cusp and generally one outer with smaller antero- and posteroexternal accessory cusps. The lower molars have a tricuspid trigonid and a unicuspid talonid. In summary these structures, occlusion, and function, may be tabulated as follows:

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[3]) It seems fairly certain that the small talonids of most pantotheres are primitive and not degenerate, but the evidence for this statement involves a longer discussion of molar evolution than can be given here.

Structure	Occlusion	Function
1. Cuspidate triangles, the upper with apex internal, the lower with apex external.	Alternating, inter-locking.	Grasping, piercing, and to a limited extent, secondarily crushing (see below).
2. Crested, notched anterior and posterior borders.	Shearing.	Cutting.
3. Internal cusp of upper molars and talonid of lower molars.	Opposing.	Crushing, and to a limited extent, secondarily grinding.

One action of the pantothere molars is not at once obvious from their structure and perhaps would not be noticed or emphasized were it not for the wear that results from it. In old individuals, in addition to the wear of protocone, talonid, and shearing crests clearly to be expected, the trigonid is sometimes also deeply and somewhat obliquely truncated (see Fig. 5 B). This rather clearly is a result of crushing and breaking resistant matter (such as the chitinous integument of insects), by a process resembling that of supporting a stick of wood at the two ends and breaking it by striking the unsupported middle part. Although not opposed to any other surface, the trigonid does in this way secondarily serve for crushing.

The whole dental apparatus seems to be adapted for a diet consisting chiefly of invertebrates but in part omnivorous and more or less analogous to that of the smaller opossums, perhaps some small dasyurids, and many insectivores. The dentition is, of course, unlike any of these late groups in exact structure, but seems closely analogous to them in function. It lacks, however, any of the more striking and definite specializations of most insectivores, for instance, and probably was less specifically adapted to one particular type of food. Comparison with *Myrmecobius*, dating from Owen and often repeated, is not a good one, for in *Myrmecobius* the molars are degenerate and have lost the complex and exact occlusal relationships so striking in the pantotheres. Some of the allies of *Myrmecobius* with the dentition more truly primitive, are more nearly analogous although of distinctly more predaceous-carnivorous type than in the pantotheres.

There remains to be discussed the family Docodontidae, represented by *Peraiocynodon* in the Purbeck and by the much better known *Docodon* in the Morrison. In these the teeth have become quadrate, rather than triangular, the cusps are in general somewhat blunter and heavier, the shearing crests have disappeared as such, supplementary cusps have arisen, and the talonids have become relatively much larger and are well basined. There is conclusive structural evidence that these are related to the other pantotheres and merely represent a rather superficial specialization, but functionally
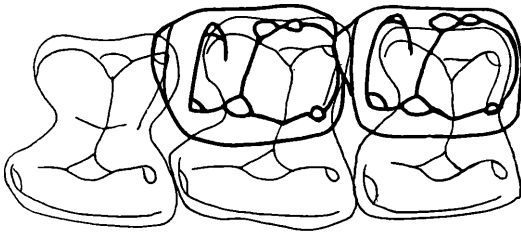

Fig. 6: Occlusion in *Docodon,* lower molars darker.

they are very different. In the docodonts occlusion involves almost exclusively opposition (Fig. 6). They may be considered as somewhat more durophagous than other pantotheres, but a more probable analogy seems to be with later forms, e. g. many bunodont primates, which are frugivorous-omnivorous. This end has been obtained in a way differing structurally from any later development. It is a premature specialization in a lateral and sterile offshoot of the pantotheres.

Environments and ecology.

The Rhaetic or Rhaeto-Liassic mammals, are more conveniently considered as of Triassic type whatever their exact horizons and have at present little real significance in the study of mammalian history. The single known Jurassic mammal from Africa *(Brancatherulum)* and the very dubious or erroneous South American records may also be ignored for present purposes. There are, then, three Jurassic mammalian faunas of which the general environments and their relations to those environments are to be studied: Stonesfield, Purbeck, and Morrison.

Stonesfield.

The Stonesfield mammals are derived from the so-called Stonesfield Slate of the Oxford district in England. It is called „slate" only because of the use made of it, and is really composed mostly of limy sandstone and gritty oölite. Its age is Middle Jurassic, Bathonian. (For references to stratigraphy, etc. see SIMPSON, 1928).

The biota may be briefly tabulated as follows:

Invertebrates: Marine or brackish: a few brachiopods, ammonites and belemites. Numerous pelecypods and gastropods. The assemblage suggests a near shore and shallow water facies. Terrestrial: Insects of several sorts, chiefly beetles, but some dragon flies and others.

Vertebrates: Fishes — over forty species are known, some, such as *Ceratodus* and the many ganoids, suggesting nearby fresh-water, but the majority marine, including many sharks. Reptiles — the marine element is seen in a plesiosaur and three marine crocodiles. The pterosaurs, omnipresent in the Jurassic, are represented by two species of *Rhamphocephalus*. The truly terrestrial reptiles have but a single representative, *Megalosaurus bucklandi*. Mammals — known from lower and upper jaws often in very fair preservation and showing little sign of wear.

Plants: There is a large land flora, including many ferns (over ten species of *Sphenopteris, Taeniopteris, Cladophlebis*, etc.), cycads *(Williamsonia)* and conifers *(Brachyphyllum)*.

Although plainly deposited in the sea, this biota includes no forms indicative of deep water. The marine forms are those of shallow seas and the admixture of fern fronds, driftwood, insects, and mammals assures us that land was not far away. It is highly probable that all these land forms came from the same region, which may be pictured as a humid temperate coastal area overgrown with rich vegetation and peopled by numerous insects and small mammals as well as by large dinosaurs. The insects suggest an abundant food supply for the pantothere, *Amphitherium*, and the sorts of vegetation present are ideal for the little herbivores, represented by the aberrant multituberculate *Stereognathus*, while these two sorts of mammals themselves as well as the smaller reptiles, no doubt fell before the prowess of the triconodonts *Amphilestes* and *Phascolotherium*. Thus even in this little known fauna the chief

stations of mammalian existence are filled. The foliage and drift-wood driven from the land suggest offshore tempests or stream freshets, and it seems not unlikely that the mammals were carried away in the rafts of vegetation or in roots and branches and that their jaws were thus deposited with little injury after the dissolution of their dead bodies some distance from their original home. The occurrence of well preserved limb bones as well as numerous uncharacteristic fragments lends some further evidence for this view. The occurrence emphasizes the distinction between living place, dying place and burial place of fossils. The place of burial of the Stonesfield mammals is certainly very different, although probably not very far, from the living place.

Purbeck.

The Purbeck mammals are derived from the Purbeckian, uppermost Jurassic, of Durdlestone Bay in England. With two exceptions the mammals occur in a single bed, about one foot in thickness, of fresh-water origin but intercalated with some marine and brackish beds. (For references to stratigraphy see SIMPSON, 1928.)

In this limited stratum and single locality mammals were fairly abundant, and so well preserved that they cannot have been carried far. In a few cases upper and lower teeth are associated, in others both rami of the mandible occur (never true in the Morrison), and there are even some very crushed skulls and associated parts of skeletons. Probably burial was in or near the living place, and followed very quickly after death.

The more peculiar physical features of the Purbeck are: (a) the absence of coarse sediments, (b) the abundance of calcium carbonate, (c) the alternation of old soils and subaqueous deposits, and (d) the fluctuation between fresh-water, brackish, and marine conditions (as many as nine or ten alternations having been observed).

At the close of Portlandian time uplift occurred. It was sufficiently rapid that no transitional beds were laid down, but so gentle that no considerable erosion took place and no angular disconformity was caused. The upper beds of the Portlandian are all limestones and the resulting land surface was broad, absolutely level,

but little above the sea, and very limy. Standing fresh-water natur-
ally accumulates on such an undrained, recently emergent surface,
and this water must have been saturated with calcium carbonate.
In such waters the calcareous algae, the ubiquitous ostracods, and
other lime-secreting organisms flourished, and limestones and marls
were deposited. Some limestone was also deposited inorganically.
From time to time in various rather limited areas the low land was
drained sufficiently to permit the formation of a soil and the growth
of large forests of cycads and conifers. At other times the waters
of the sea commingled with those of the still incompletely emergent
land, and brackish waters covered a certain area. In middle Pur-
beckian time the sea temporarily covered the entire region once
more, but only to a shallow depth, and then withdrew again.
Sluggishly flowing bayous and rivers may have opened into or
crossed the shallow lakes, lagoons, and swamps, but stream action
as a dynamic force was practically absent. The series is essentially
a still-water one. The transition to Wealden conditions is a transi-
tion from lagoon and swamp conditions to a delta. The Wealden
deposits are the sands and clays of a great river system.

Of the many Purbeckian animals a large percentage certainly
never saw a mammal, indeed only a few small reptiles are definitely
associated with the mammals. It is justified, however, to assume
that any forms occurring in the formation may conceivably have
influenced mammalian life.

Invertebrates: The molluscs are largely littoral marine species,
chiefly gastropods and cephalopods. Some fresh-water forms occur,
Lymnaea, Planorbis, Paludina, Physa, Unio, etc., and a good many
brackish water ones, *Rissoa, Cardium, Cyrena, Corbula*, and many
others. Ostracods are very abundant in both fresh and salt water
facies, over fifteen species and a number of varieties being known.
A characteristic echinid, a sponge, and some poorly known marine
foraminifera are also known. It is very doubtful whether any of
these aquatic invertebrates influenced the mammals in any signifi-
cant way. The insects of the Purbeck are abundant. None occur
at the mammal locality, but the conditions for their preserval are
peculiar and they must also have lived here although not preserved.
At least one hundred and seventy-eight species are known, represen-
ting the Coleoptera, Hymenoptera, Neuroptera, Lepidoptera, Diptera,

Hemiptera, and Orthoptera. This providentially revealed richness of insect life is significant, for they must have furnished a large part of the diet of the majority of Purbeck mammals, the insectivorous pantotheres.

Vertebrates: Fishes were abundant. Besides a doubtful teleost there are thirty-three ganoids, chiefly fresh-water forms, and three sharks. None of these forms can have furnished food for the mammals, nor can they have been habitual enemies of the latter. Among reptiles, the single plesiosaur and pterosaur can hardly have influenced the mammals directly. Scanty remains indicate a megalosaur, an iguanodont, and an armored dinosaur, but these animals probably came from some distance and certainly were not abundant nor significant to the mammals. There were reptiles comparable in size to the latter, however. These, described by OWEN, are so fragmentary that their ordinal relationships are in doubt, but not their existence. *Nuthetes* was a carnivore of a size ideal for preying on such mammals as were not nimble. *Macellodus* and *Saurillus* were smaller and less voracious, more liable themselves to the attack of mammalian carnivores. A rhynchocephalian, *Homaeosaurus*, is also present and may also have fallen before the triconodonts, while all these insectivorous small reptiles would provide active competition for the pantotheres. The waters swarmed with forms so menacing that death instant and certain must have been the lot of any mammal unhappy enough to enter them. Of chelonians there were at least nine species, all of them of a size to enjoy mammalian food, but most significant of all were the swarms of crocodiles of not fewer than eleven species. It is exceedingly interesting to note here the occurrence of blunt-nosed dwarf crocodiles analogous in every respect to the mammal-eating forms of today and seeming to show in their small size an adaptation to their diminutive prey. There can be little doubt that these were the chief foes of the mammals outside their own ranks.

Plants: The Purbeck region was heavily forested. The known forms, comprising an indeterminate ?angiosperm, five conifers, six cycadeoids, three ferns, a rush, and two algae, give a hint of the composition of the flora, but naturally represent only a small portion of the rich plant life certainly present. The first three groups, and perhaps also the fourth probably figured in the multituberculate diet.

This more complete picture of a Jurassic mammalian environment seems to be an elaboration and definition of what was dimly seen at Stonesfield. The mammalian facies was probably about the same, but at Stonesfield the observer is distant from the actual scene of life and only a few unfortunates are floated out to tell their story, whereas in the Purbeck he is actually present in the mammalian haunts. These are in a great swamp, with only here and there a low island. Sometimes the sea encroaches, but more often it is a short distance away and the sparklingly clear but heavily mineralized waters sluggishly drain, rather than flow, towards it. Mammals and small reptiles are fairly abundant in the trees and in the ferny underbrush of this swamp, while the water below and around them teems with turtles and crocodiles.

Morrison.

With only a few exceptions the Morrison mammals are from single Quarry, Marsh's Quarry 9, near Como (or Aurora), Wyoming. The age is believed to be Upper Jurassic (SIMPSON, 1926 C), although some students still place it in the lowest Cretaceous.

The character of the Morrison environment, especially as regards the physical conditions, has been considered in some detail by MOOK (1916, 1918) whose work has been drawn on to a considerable extent in preparing the following briefer account.

From an environmental point of view, the most important characteristics of the Morrison are:

1. Wide distribution — with its direct equivalents it must formerly have covered over a million square miles.

2. Uniform character, although heterogeneous in detail. Chiefly variegated clays or fine quartz grits with interstitial clay. Quartz and arkosic sandstones not rare. A little volcanic ash and some limestone in the lower part. Little gravel or conglomerate except in the western portion.

3. All beds lenticular, varying from a few feet to many miles in extent. Stream channels with scour and fill. Sandstone cross-bedded in aeolian and stream types.

4. Thickness small and relatively constant for such a widely distributed continental formation.

The conditions are obviously very different from those of the Purbeck. The Purbeck was laid down along a low coast in a region flooded by the sea at times; the Morrison occupied a great inland plain with the nearest arm of the sea hundreds of miles distant. The Purbeck sediments were in general laid down in quiet and usually very clear waters; the Morrison ones are the deposits of dynamic agencies, running streams and the wind, or of muddy temporary pools and lakes. The Morrison habitat was a broad and very level plain, bounded on the west by highlands whence flowed many strong permanent rivers and streams. The latter. spread out and anasto mosed as they crossed the great plain and a very intricate network of waterways was formed. The main channels accommodated a great amount of water, flowing on a low gradient but far from stagnant and they retained their muddy and even sandy load for great distances. Numerous ox-bow lakes, deep lagoon-like abandoned or nearly isolated channels and backwaters, probably marked the plain besides the wandering streams. Between the verdure-flanked watercourses and lakes were drier and more barren expanses where the wind piled up low hills of sand and where the xerophytic cycads and sparse herbs grew.

The abundant cycads and the varied reptilian fauna would seem to indicate a moderately to very warm climate. Recently (WIELAND, 1925) the suggestion has been made that a temperate to cool climate is not barred. It is true that the sauropods lived in the water and that this may have tended to equalize climatic excesses, and it is also true that modern reptiles can survive quite heavy winters if a large portion of the year be warm. Nevertheless these waters were those of highland-born streams, which would certainly never be warmer than the general environment. Furthermore, large reptiles were numerous on land also and their very bulk would seem to require activity during nearly or quite the whole year. Truly large modern reptiles do not inhabit regions where frost is frequent. Even aside from the question of necessarily continuous growth in attaining their vast size, there are grave difficulties in imagining a brontosaur or brachiosaur as hibernating. There is no feature of the lithology nor of the fauna or flora which yields positive evidence for a cool or even temperate climate. The conclusion seems necessary that the climate was warm to tropical with frost or long cold spells rare or absent.

The question of humidity and precipitation has also been placed in some doubt. It has been generally assumed that the climate was moist, but WIELAND finds evidence that the cycads were singularly adapted to withstand drought. This is difficult but not impossible to reconcile with all the other evidence. Lithologically, we find that there are no evaporation deposits, there is much ferrous iron, the stream deposition is not torrential, there is evidence of numerous semipermanent lakes, wind-blown sand is not rare, but never forms thick beds, kaolin and quartz are the common constituents and only the most resistant felspars have not been entirely decomposed. As for the fauna, there are numerous animals requiring permanent and large bodies of fresh-water: fish, crocodiles, turtles, and especially the great sauropods. The conclusion that at least a large part of the year was very moist is irresistible. On the other side must be weighed the presence of lung fishes and the evidence of the sun-loving cycadeoids. The area in which the living *Neoceratodus* lives is not truly arid and the animal never leaves the water. In the summer, however, there is relatively little precipitation so that the smaller streams become stagnant and restricted. Some such condition as this may well be indicated for the Morrison, a sub-tropical climate, humid on the average, but with a relatively wet and a shorter relatively dry season. The cycads probably grew in exposed situations such as the low porous sand hills between the numerous water courses and lakes.

The biotic environment as a whole was as follows:

Invertebrates: Fresh-water molluscs were numerous. There are known ten species of fresh-water clams *(Unio)* and the same number of gastropods of several genera. Five species of ostracods also occur. It is very doubtful whether any of these were available to the mammals as a staple of diet.

It must be accounted the greatest single gap in our knowledge of the Morrison that no insects are known from it. They were certainly present, and in very great numbers, but conditions seem to have been unfavorable for their preservation, save perhaps in some favored spot still undiscovered. They probably resembled those of the Purbeck, and we should except to find many species of Coleoptera, Neuroptera, Diptera, Hemiptera, and Orthoptera. These still unknown insects were of importance, for they probably formed the greater part of the diet of the Pantotheria.

Vertebrates: The fishes of the Morrison are poorly preserved and hence little known. *Ceratodus* was not rare, and although they have still to be studied it is clear from the collections that small ganoids were likewise common. Small or stranded fish were probably eaten by the mammals on occasion, but were certainly not essential to the latter. On the other hand, no remains of fish sufficiently large to eat mammals have been found.

Amphibia: This class is represented by a single frog. In common with all small animals of the time, these frogs may occasionally have fallen prey to triconodonts, but certainly only very rarely.

Reptiles: These are the dominant creatures of the Morrison. There were several sorts of small lizard-like animals (Rhynchocephalia and possibly true lizards) which were probably terrestrial and which undoubtedly were of great importance for the mammals not only as prey for the carnivores but also as competitors of the insectivores — eating insects, grubs, worms, etc.

As in the Purbeck, the waterways swarmed with moderate sized carnivorous reptiles. Crocodiles were quite common and, on an average, of a size to prey on the mammals. Turtles of more than one sort were also common and some of them probably also ate mammals when possible.

The importance for the mammals of the dinosaurs for which the Morrison is famous would depend largely on the size of the latter. Most of the dinosaurs were certainly too large to help or harm the mammals in any way. This is especially true of the sauropods which, great masters as they seemed of the whole region, probably had not the slightest effect or influence on the mammals, just as the tiny creatures of Africa take no cognizance of the elephant. The land-living stegosaurs must be placed in the same category. The ornithopods present a much greater range in size. They were adapted for food rather unlike that of any mammal, but some of them *(Laosaurus)* were so small that their young could well have been slain by the predatory triconodonts. The carnivorous dinosaurs, again, were mostly so large as seldom to come in contact with a mammal. Some of more limited size and some of the young individuals may have preyed on mammals.

Little significance attaches to the presence of a pterodactyl, and the reported bird must be considered in the same light.

Plants: The known plants of the Morrison include several valid species of *Cycadella* or *Cycadeoidea* and two of conifer wood, along with many very doubtful traces of reeds and other small and tender plants. It cannot be supposed that more than a very insignificant fraction of the flora is known. The rich flora of the succeeding Kootenai with ferns, gingkos, cycads, and numerous gymnosperms may give some hint of the floral richness of Morrison time. It is necessary to picture the quiet waters of the lakes and lagoons as overgrown with luscious and succulent water plants, while along the shores were reedy marshes or a tangled growth of ferns and shrubs. Here and there were groves or forests of conifers with many cycadeoids scattered over the more exposed and barren stretches.

It has been suggested that the Morrison is of different age in different parts, and it is certain that it was laid down under slightly but definitely different conditions in different regions. A study of the definitely mammalian facies of Quarry 9 has already been published (SIMPSON, 1926 B). There it is pointed out that there are two significant cenobiotas, one terrestrial and one aquatic. The mammals are doubtless all terrestrial, the multituberculates eating parts of land plants, competing with the smallest herbivorous dinosaurs, and the pantotheres eating land invertebrates, competing with the rhynchocephalians and lizards. Triconodonts and symmetrodonts preyed on all these forms and competed with small predaceous dinosaurs. The aquatic cenobiota was probably important to the mammals only as these fell victims to the crocodile and turtles. The Quarry 9 fauna is chiefly a microfauna and the facies suggested is that of an overgrown swamp. In other quarries of the same region small forms are rare or absent and the great dinosaurs, here almost absent, are abundant.

The last available source of evidence as to the mammalian environment is furnished by the way in which their remains occur. All the material in Quarry 9 is scattered and dissociated, except for one or two turtle carapaces there being hardly two bones found in association. None of them show signs of wear, and although isolated the most delicate structures are often preserved. One or two mammal jaws had been weathered before burial, but most of them

are extremely fresh in aspect. Limb bones and vertebrate, while they do occur, are rare, the remains consisting mainly of upper and lower jaws. Although it is very commonly stated that the number of lower jaws greatly exceeds that of the uppers, that is not the case, the numbers being nearly equal. There are numerous fragments and slivers of bone scattered through the matrix but broken too much to be identified. They are not rounded and show no signs of weathering or of stream-wear. All these facts seem very difficult to explain if one supposes the remains to have been carried any distance by the stream. The fragmentary and isolated character of the material is not hard to explain. The waters teemed with carnivorous reptiles, as has been shown. Obviously no mammal which had the misfortune to enter these waters, either before or after death, had any chance of being buried whole[4]). He would immediately be dismembered by carnivores, the more resistant and less tempting parts, such as the jaws, much more frequently escaping destruction than the flesh-enclosed and brittle limb-bones, vertebrae, and ribs or than the thin, brain-enclosing cranium.

Conclusions.

Dental evolution is one of the most essential factors in the evolution of mammals. For the paleontologist, it is incomparably the most important factor, since far the greater part of his work must of necessity be based on teeth alone. Change of dental form, in itself, is not the important point in considering mammalian evolution. The mammals were living creatures, and the teeth are not inorganic objects but a means for obtaining and utilizing nourishment. This paleobiological approach to the subject infuses it with life and gives real meaning to the study of teeth.

In the occlusion of teeth, which considers them as dynamic things in active use, there are four main principles: alternation, opposition, shearing, and grinding. Dentitions as a whole, and more complex single teeth show combinations of these principles and the corresponding functions. The Jurassic mammals show on the one hand (especially multituberculates and triconodonts) early emphasis

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[4]) The occurrence of a mammal jaw actually inside the ribs of a turtle carapace is interesting, but perhaps accidental.

of one or another of these functions achieved in a wholly different way from the later mammals, and on the other hand (most panto-theres) the achievement of a less specifically adapted and much more adaptable type with three of these functions combined, mechanically capable of developing any one or any useful combination of the four, and prototypal to later mammalian dentitions.

The multituberculates were herbivorous, not, of course, grazing or browsing, but plant feeders analogous to small rodents. The tri-conodonts were carnivorous, and apparently very active predaceous forms, rather analogous to the small mustelids. Symmetrodonts were likewise carnivorous, but less predaceous in type than the tricono-donts. The pantotheres were less specifically adapted to one particular sort of diet. Some appear to have been insectivorous-omnivorous, others possibly omnivorous-frugivorous.

These Jurassic mammalian faunas thus form a society in which most of the modes of life, or at least of food habits, open to creatures of their size were followed. The most important ecological positions filled by mammals in the Tertiary but not adumbrated in the Meso-zoic mammals were those of grazing and browsing animals. These now very important modes of life were occupied not at all by mammals and chiefly by dinosaurs in the Mesozoic, insofar as they were then available. But almost without exception, grazing and browsing animals are and always have been much larger than the Mesozoic animals. The small size of the latter is thus another essential factor in their development. That they never achieved any great size, so far as known, during those millions of years, was doubtless due in large measure to the insupportable competition and enmity of the abundant large reptiles.

The known Jurassic mammals are very limited in facies. They seem all to have occupied temperate to subtropical, well watered, wooded lowlands, coastal as in the Stonesfield and Purbeck, or inland in great drainage basins, as in the Morrison. No direct evidence is available, but this unites with other still more theoretical considerations in suggesting that many of these early mammals, perhaps all of them, were aboreal. That there were not also highland forms, or forms adapted to a more arid climate is not a justifiable conclusion. The deposits of such environments are hardly known to us in the Jurassic.

The Jurassic mammals had faunal and floral associations amply providing them with possible food. Competitors were present, but apparently were not very abundant or important. Enemies were numerous even outside their own ranks, chiefly among the small dinosaurs, turtles, and crocodiles. But they successfully occupied their own isolated niches in the Mesozoic world, far removed from the cognizance of the true lords of the era, the great reptiles.

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