EVOLUTION OF MAMMALIAN MOLAR TEETH

OSBORN

EVOLUTION OF
MAMMALIAN MOLAR TEETH

BIOLOGICAL
STUDIES AND ADDRESSES.

READY.

I. EVOLUTION OF MAMMALIAN MOLAR TEETH.

IN PREPARATION.

II. ADAPTIVE RADIATION OF MAMMALS.

III. EVOLUTION OF THE VERTEBRATES.

IV. RECTIGRADATIONS IN EVOLUTION.

V. SOME GREAT NATURALISTS.

VI. SEVEN FACTORS OF EDUCATION.

12

BIOLOGICAL STUDIES AND ADDRESSES. VOL. I

EVOLUTION OF MAMMALIAN MOLAR TEETH

TO AND FROM THE TRIANGULAR TYPE

INCLUDING COLLECTED AND REVISED RESEARCHES ON
TRITUBERCULY AND NEW SECTIONS ON THE FORMS
AND HOMOLOGIES OF THE MOLAR TEETH IN
THE DIFFERENT ORDERS OF MAMMALS

BY

HENRY FAIRFIELD OSBORN
Sc.D., LL.D., D.Sc.
DACOSTA PROFESSOR OF ZOÖLOGY IN COLUMBIA UNIVERSITY
CURATOR OF VERTEBRATE PALAEONTOLOGY IN THE AMERICAN MUSEUM
OF NATURAL HISTORY

EDITED BY

W. K. GREGORY, M.A.
LECTURER IN ZOÖLOGY IN COLUMBIA UNIVERSITY

New York
THE MACMILLAN COMPANY
LONDON: MACMILLAN AND CO. LTD.
1907

106

GLASGOW: PRINTED AT THE UNIVERSITY PRESS
BY ROBERT MACLEHOSE AND CO. LTD.

PREFACE

THE older odontography or description of teeth treated each type as a distinct and perfect form in itself. Cuvier's *Odontographie des Mammifères*, Giebel's *Odontographie*, Owen's *Odontography* are examples of more or less comprehensive treatises in the pre-evolutionary spirit. They antedate the discovery of what may be called the 'new odontography,' which is based upon the unity of dental type, upon the evolution of the teeth of mammals from a common reptilian prototype, and which treats of each form in relation to its origin, its descent, its gradual complication, and the laws of analogous evolution or independent production of similar forms.

The new odontography centres around the 'tritubercular theory' of Cope. This theory had wider acceptance ten years ago than it has to-day: there has been a strong reaction against certain features of it on the part of many of the most able anatomists. This is partly due to misunderstanding, partly to the fact that all the evidence has never been fully marshalled, partly to the discovery of new embryological and palæontological evidence which may disprove certain features of the theory: but chiefly to the fact that some of the most decisive and convincing palæontological evidence in support of the theory has not been clearly advanced. It is hoped that this collection of the contributions of the writer, with additional observations, illustrations, and data, and with a discussion of various other theories and criticisms will serve to convince the reader and student that the new odontography in its general principles rests upon an adequate basis of evidence and, while subject to modification in many details, marks a turning point in the science of the teeth.

The present volume treats only the primary evolution of the molar and premolar teeth of mammals, and is thus more restricted in scope than the admirable 'Dental Anatomy' of Tomes which covers the teeth of the vertebrates generally.

The writer is especially indebted to his assistant Mr. W. K. Gregory for invaluable assistance not only in bringing together and rearranging the essays and figures, but for many original suggestions, and for the critical *resumé* of the opposing views which is set forth in the last chapter.

HENRY FAIRFIELD OSBORN.

Columbia University and
American Museum of Natural History,
September, 1907.

CONTENTS

CHAPTER I.

THE TRANSITION FROM THE REPTILIAN TO THE MOST PRIMITIVE MAMMALIAN TEETH.

CHAPTER II.

CHAPTER III.

TRITUBERCULY IN RELATION TO THE HUMAN MOLAR TEETH AND THE PRIMATES.

CHAPTER IV.

CHAPTER V.

CHAPTER VI.

CHAPTER VII.

CHAPTER VIII.

CHAPTER IX.

OBJECTIONS AND DIFFICULTIES, AND OTHER THEORIES.

I. That the tritubercular type is not primitive :

CHAPTER X.

INTRODUCTION.

The teeth are the hardest of the tissues, and, unlike other tissues, are not improved, but on the contrary constantly worn away and finally destroyed, by prolonged use. Yet they are also the most progressive of the tissues. For example, in the evolution of the horse, no other system of organs undergoes so profound a change as that of the teeth.

The fitness which they present for every possible mode of capturing and eating fills volumes of the older works on descriptive anatomy and teleology, and is even now constantly disclosing new and fascinating subjects for the study of adaptations.

Because of their hardness the teeth are the most generally and perfectly preserved of all fossilized organs: hence they are the especial guides and friends of the palæontologist in his peculiar field of work from imperfect evidence. Thus it happens also that the palæontologist has been obliged to study the teeth in more detail even than has been done by the comparative anatomist or zoologist.

All this use of the teeth for teleological, descriptive, and taxonomic purposes is, however, entirely aside from the main purpose of the present volume, which is, to set forth the mode of evolution chiefly of the complex crowns of the molar teeth of mammals, how the main types originated, and how they can be compared with each other and with those of reptiles. The evolution is not, however, traced to its final modifications in the elaborate hypsodont and tubercular types, but only so far as the formation of the fundamental patterns.

That comparison can be made on a grand scale most attractive to the student, both of homologies and analogies, is a recent discovery. It dates back only to the year 1883, when what may be called the law of trituberculy was discovered by Cope.[1] No harmony existed in our ideas and descriptions of the grinding teeth of mammals previous to that time, although Huxley in his discussion of the teeth of the Insectivora had anticipated the discovery of such a harmony. Many of the details and of the broader outlines of the law were either touched

---

[1] *American Naturalist*, April 1883, pp. 407-408.

upon or fully discussed by the great comparative anatomist Cope, who dwelt, however, chiefly upon the basal Eocene stage. In 1887 the present writer took up the subject in the earlier Mesozoic stages of the evolution of the mammals, and in later years pursued it into the later Eocene and all subsequent Tertiary stages.

The theory was everywhere welcomed as a decided advance on the old odontology and odontography, in which there was no unifying principle either of homologies or of nomenclature. It has been applied more or less throughout the whole class of mammalia, first in palæontological, then in embryological and anatomical lines; but thus far only to a rather limited extent by zoologists, or students of living mammals, and, so far as the writer knows, still less by anthropologists. It has been critically examined, discussed, and either partly or wholly adopted, or entirely rejected as unproven, by various authors.

The chief contributors to the development and critical examination of the theory are the following:

From the palæontological standpoint, Cope, Osborn, Schlosser, Scott, Earle, Rütimeyer, Lydekker, v. Zittel, Ameghino, Goodrich, Wortman, Smith Woodward, Gidley.

Among the zoologists who have either advocated or opposed the theory are Lankester, Newton Parker, Fleischmann, H. Allen, Forsyth Major, Dybowski, Winge, Sims, Beddard.[1]

Among anatomists, Schwalbe and Dwight have accepted the theory, while Howes failed to find sufficient evidence for it.

The most influential opponents of certain features of the theory are those who have examined it embryologically, namely, Kükenthal, Röse, Taeker, Leche, M. F. Woodward.[1]

Four distinct principles have been developed in connection with the general theory, as follows:

I. First Principle. The Primitive Tritubercular Type.

The discovery of the oldest fauna of the age of mammals, or Tertiary period, near the Puerco Cañon in Northwestern New Mexico, was announced by Professor Edward D. Cope in 1879. These small and strange fossil mammals exhibited a general similarity in all the molar or grinding teeth, even among animals which evidently had great diversity of feeding habits. This similarity consisted in the possession of *three main tubercles on the crowns of both upper and lower molars, disposed in triangles.** This was evidently a primitive type of molar tooth, and in 1883

---

[1] These names are placed in the general order in which the criticisms appeared. (See pp. 200-227.)

*[In addition to the main tubercles there were often smaller cuspules, "styles" and "talons," but the upper molars of the Carnivores and Ungulates were all roughly speaking "tritubercular," the lower molars all "tuberculo-sectorial" or of plainly derived types.]

Professor Cope[1] appropriately named it the *tritubercular type.*[2] By comparison with the teeth of more recent animals, the further conclusion was reached that the *tritubercular type was ancestral to many if not to all of the higher types of molar teeth.* This is one of the most important generalizations ever made in mammalian comparative anatomy; it outranks in importance the proof of the primitive pentadactyl nature of the feet of hoofed animals. In the writer's opinion, the evidence in favour of it is so overwhelming that primitive trituberculy is no longer an hypothesis or a theory, but an established fact. In the accompanying table it will be seen that those orders in which generalized ancestral forms are positively known to possess tritubercular molar teeth (I) and those orders in which primitive tritubercular teeth or some of the immediately derivable types are occasionally observed, although the line of descent has not actually been traced (II), far outnumber those (III) in which we must reason by analogy, because we have as yet no positive light on the descent of the teeth.

I. Mammalian orders in which ancestral forms are positively known, which exhibit tritubercular or plainly derived types of molars.	II. Orders in which tritubercular or *plainly derived* types of molars are occasionally observed although the line of descent has not actually been traced.	III Orders in which we have as yet no positive light on the descent of the molars.
Edentata Tæniodonta (Ganodonta) (p. 151).		All other Edentates (p. 152).
Insectivora primitiva (Mesozoic) (pp. 26-30).		Monotremata (p. 107).
Insectivora (p. 117).		Multituberculata (p. 101). Cetacea[3] (p. 190).
Marsupialia Polyprotodontia (cf. Oligocene *Peratherium*, p. 109).	Marsupialia Diprotodontia (p. 109).	Carnivora Pinnipedia (p. 143).
Carnivora Creodonta (p. 131).	Rodentia Duplicidentata (p. 148).	
Carnivora Fissipedia (p. 135).	Rodentia Simplicidentata (p. 146).	
Tillodontia (p. 151).		
Primates (p. 157).	Ancylopoda (cf. *Schizotherium*, *Chalicotherium*, (p. 184).	
Amblypoda (*e.g.* *Pantolambda* p. 165).		
Condylarthra (*e.g.* *Protogonodon*, p. 169).	Zeuglodontia (p. 191). Hyracoidea (p. 185).	
Artiodactyla (*e.g.* *Trigonolestes*, *Homacodon*, p. 171).	Proboscidea (*e.g.* *Mœritherium*, p. 186). Sirenia (cf. *Halitherium veronense*, p. 189).	
Perissodactyla (*e.g.* *Hyracotherium*, *Systemodon*, p. 174).	Toxodontia and other South American Ungulata (p. 189).	

---

[1] *American Naturalist*, April, 1883, pp. 407-408.

[2] *N.B.* The lower molars generally show also a talonid or heel.

[3] *Zeuglodon* not included.

This main principle of the tritubercular theory has been widely but by no means universally accepted. Able comparative anatomists, chiefly Ameghino, Röse, Forsyth-Major, have urged against it that a molar tooth with a number of tubercles is still more primitive. According to this rival view, commonly known as the *polybuny theory* (πολύς, many, βουνός, a hillock), the tritubercular type, even in the Cretaceous period, was the result of a secondary suppression of some of the numerous original tubercles. This opposing view deserves fair consideration and a clear statement (see p. 205).

This first generalization as to primitive trituberculy in the later Mesozoic and Tertiary periods must be clearly distinguished from the following second generalization as to the earlier Mesozoic origin of trituberculy.

II. SECOND PRINCIPLE. THE ORIGIN OF THE TRITUBERCULAR TYPE FROM THE SINGLE REPTILIAN CONE.

Professor Cope's active and inquiring mind did not, however, stop at this point. He asked himself, "If the oldest Tertiary mammals exhibited a common tritubercular type, what do the mammals which lived during the Mesozoic period, or age of reptiles, show as to the *origin* of the tritubercular type?" He had neither the time nor the material to enter thoroughly into this inquiry; but he looked into Owen's memoir on Mesozoic mammals far enough to clearly perceive that the tritubercular type developed during the long Mesozoic period, from an ancestral reptilian type of tooth consisting only of a single cone or cusp. Therefore he made a second generalization: *that the tritubercular type sprang from a single conical type by the addition of lateral denticles.* "I have already shown," he says,[1] "that the greater number of the types of this series have derived the characters of their molar teeth from the stages of the following succession. First, a simple cone or reptilian crown, alternating with that of the other jaw. Second, a cone with lateral denticles. Third, the denticles to the inner side of the crown forming a three-sided prism, with tritubercular apex, which alternates with that of the opposite jaw."

III. THIRD PRINCIPLE. CUSP ADDITION OR DIFFERENTIATION.

In the second generalization is, however, involved a third, which has also been the subject of wide difference of opinion, namely, the successive addition of new denticles, cuspules or smaller cones on the sides of the original reptilian cone; this may be simply known as the *cusp addition*

---

[1] *Origin of the Fittest*, p. 347.

principle; it is a process analogous to budding or outgrowth in other tissues.

An opposed theory, advanced by Ameghino, Röse, and Kükenthal is that of *concrescence*, namely, that from an original large supply of conical reptilian teeth in the primitive longer jaws, and from the multiple succession or replacement of such teeth, the cones were clustered or grouped, by fours or more, and thus arose respectively the quadritubercular, and multitubercular or polybunic types, the tritubercular and triconodont stages being secondary (Ameghino).

IV. Fourth Principle. Reversed Upper and Lower Triangles.

Still another or fourth principle, entirely distinct from the foregoing, is involved in the sentence quoted above, "Third, the denticles to the *inner* side of the crown [in the *lower* jaw] forming a three-sided prism, with tritubercular apex, which alternates with that of the opposite [or *upper*] jaw." This principle involves the theory which rests upon strong but perhaps not altogether conclusive palæontological evidence (pp. 32, 43, 217) that in the *lower molars the reptilian cone is external and the two denticles internal, while in the upper molars the reverse is the case*, namely, *the reptilian cone is internal and the denticles are external.* This principle, if a true one, enables us to establish a kind of serial homology between the main primary cones and secondary denticles or cusps of the upper and lower teeth respectively. Osborn expressed such an homology in a system of nomenclature (protocone, paracone, metacone, etc.), which Professor Cope welcomed and accepted.

According to this principle, the evolution and relation of both the upper and lower molars are those of a pair of reversed triangles in every stage above the protodont and triconodont; thus, it might be simply known as the *trigonal theory*; but since it was based by Cope and the writer entirely upon the evidence afforded by the Mesozoic molar teeth, it may be more strictly termed the 'PALÆONTOLOGICAL THEORY.'

As applied to the upper molars, this theory and the homologies it involves with the lower molars have been far more vigorously and generally opposed than either of the other principles; in fact, the chief weight of opinion has now gathered against it from three different classes of positive evidence, namely, embryological, anatomical, and palæontological by comparison with premolar evolution, also from the negative argument that the evidence at hand among the Mesozoic mammals does not demonstrate the principle in the upper teeth.

The theory opposing the palæontological theory in morphological contrast first sprang from embryological evidence, and may, therefore, be known as the 'EMBRYOLOGICAL THEORY.' It is another instance of the apparent conflict between palæontological and embryological evidence as witnesses of the ancient order of development. The final verdict, therefore, will be most interesting. Briefly, the embryologists, especially Röse, Taeker, Kükenthal, M. F. Woodward, Marett Tims, have shown that in the upper molars the cusp which Cope and Osborn assert to be the *oldest*, is, on the contrary, later in development than the paracone, and *therefore* (?) not the oldest palæontologically. The oldest upper cusp, according to the 'embryological theory,' is the *antero-external cusp* (paracone), and this is homologous with the reptilian cone; from this there is a slowly evolving triangle in the upper molars, according to the same authorities the reptilian cone is, however, central or apical in the lower teeth, embryology quite agreeing with palæontology. From this it would follow that the only serial homologies which can properly be established are those between the lower and upper reptilian cones.

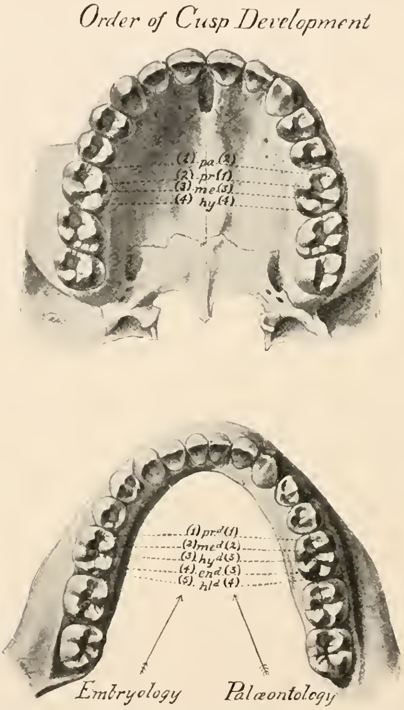


FIG. 1. Order of cusp development as attested by Embryology (fide Röse) (left-hand numerals) and by Palæontology (fide Osborn) (right-hand numerals). Typical (synthetic) dentition of Man, from Selenka. (The paraconid is not represented in human molars. See p. 59 and Fig. 38.)

The embryological theory, in brief, is to the effect that *while in the lower molars the central reptilian cone remained external and the two* *denticles arose internally, forming a triangle, in the upper molars the reptilian cone remained at the antero-external angle and the two denticles arose on the inner and posterior sides.*

It will thus be seen that the difference between the palæontological and embryological theories is radical. The latter finds not only strong support but a beautiful illustration by analogy in the normal modes of evolution of the simple premolar teeth into the complex molar type (see pages 194-200). It is developed in what may be termed the 'PREMOLAR-ANALOGY' theory.

The accompanying figure clearly demonstrates the fundamental difference between these theories. There is no middle ground between them. If the premolar analogy be correct, the Osbornian cusp homologies of the upper teeth are of less value, *but the homological nomenclature should be retained for convenience because it has found its way so largely into literature.*

Although the writer has devoted a vast amount of time and study to the development of the 'palæontological theory,' and is personally inclined to believe in its tenability, there is no denying the great force of the objections which have been urged against it and the need of substantial proof from the early Mesozoic mammals, even in addition to that which is freshly adduced in the present work. The arguments *pro* and *con* are, therefore, partly stated in course of these collected essays. and especially brought together in the new chapter IX. at the close.

ORIGIN OF THE TRIANGLE.

An important feature of the fourth principle is the *position and mode of origin of the cusps of the triangle.*

Four different modes of origin have been suggested:

The *first* suggestion is that the triangle originated as such, the denticles appearing from the outset on the inner and outer sides respectively of the lower and upper cones.

The *second* suggestion is that the denticles first arose on the anterior and posterior sides of the reptilian cone, and were secondarily rotated inwards and outwards respectively: the latter is known as the '*cusp rotation*' theory, or rather hypothesis.

Osborn[1] set forth *both* the above modes guardedly in the following language:

"There can be no doubt that the cusps seen upon the inner face of the inferior molars of this genus [*Spalacotherium*] are homologous with the para- and meta-cones, and there are several facts which

---

[1] "The Structure and Classification of the Mesozoic Mammalia," *Jour. Acad. Nat. Sci., Phila.*, Vol. IX., No. 2, July, 1888, p. 243.

support Cope's hypothesis[1] that they represent a stage of inward rotation of cusps which were at an earlier stage in the same fore and aft line with the main cusp. These are, that in *Phascolotherium* the lateral cones are seen to be slightly internal to the main cone, so that their median slopes descend upon the inner face; in *Tinodon,* of a later geological period, this disposition is slightly more pronounced: in *Menaeodon* it is still more marked, but less so than in *Spalacotherium.* These genera, although evidently in two different lines of descent, afford the desired transition stages. The *Spalacotherium* [*Peralestes*] molar as seen from above[2] has a striking resemblance to the anterior sectorial triangle of the *Stypolophus* or *Didymictis* molar of the Puerco. It is, in fact, sub-triangular, the superior molars probably having the lateral cones rotated outwards, so that the upper molars form an alternating series, the ridges connecting the main and later cones acting as sectorial blades." Again, in the "Evolution of Mammalian Molars to and from the Tritubercular" type, Osborn pointed out (*Amer. Naturalist,* Dec., 1888, p. 1075) that "it has been assumed by Cope and the writer (*op. cit.*, p. 243) that the para- and meta-conids were first formed upon the anterior and posterior slopes of the protoconid and then rotated inwards, but it is also possible that they were originally formed upon the inner slopes." There is thus evidence for cusp rotation, but it is not an essential part of the tritubercular theory, because, as above stated, the denticles may have *arisen* on the inner and outer sides of the cone from the outset (see p. 33).

The *third* suggestion is that after the main cone had been established the lateral cusps or denticles arose as *cingules* on the broad external cingulum of the upper molars and from the broad internal cingulum of the lower molars. This hypothesis, suggested by Osborn (*Mesozoic Mamm.*, p. 245) from a study of the molar teeth of the Jurassic Amblotheriidæ, has been supported by the observations of Gregory. The comparison of the molar teeth of such forms as *Amblotherium, Phascolestes, Dryolestes* (see pp. 29, 30), lends support to this view, which is more fully discussed on page 33 (footnote).

The *fourth* suggestion or hypothesis is the newest: it springs from embryological evidence (Woodward, Tims) and from another interpretation of the palæontological evidence (Gidley). It ends with the idea that the oldest cone in the *upper molars* is the paracone (of Osborn) on the *outer* side of the crown, from it extends *inward* a broad ledge like a heel which finally rises up and secondarily forms the prominent protocone (of Osborn). According to this hypothesis the paracone is the primary (or reptilian cone), the protocone is secondary or a deriva-

---

[1] "The Creodonta," *American Naturalist,* 1884, p. 259.

[2] Owen, *The Mesozoic Mammalia,* Plate I., Fig. 32c.

tive cone. This hypothesis accords with the embryological theory and the premolar analogy theory.

It is quite possible that the tritubercular or triangular stage arose independently in different groups of animals, by two or possibly three different modes of origin, as outlined in the four suggestions above advanced, on the principle of convergence of similar forms from dissimilar beginnings. This, however, does not invalidate the theory of the passage of the majority if not of all the higher mammalia through the tritubercular stage, however arrived at.

SUMMARY.

To sum up, it must be clearly re-stated that the four great principles of molar evolution *do not stand or fall together.* The first or *primitive trituberculy* principle is now almost undeniable for the majority of mammals; entirely apart from the disputed question of the original homology of the cusps of the upper and lower teeth, there is no question whatever as to the beautiful and almost incredible homologies between the cusps of the molar teeth in the most diverse orders of mammals. The upper carnassial of the Carnivora and the upper molars of the Equidæ, for example, are types adaptively so far apart, it is small wonder the older odontologists did not even suspect the existence of homogeny or common derivation, through which we can now compare cusp for cusp. The *reptilian cone origin* theory is next in order of demonstration and acceptance: it has recently gained strength by the very general admission that the Theriodont reptiles are at least nearly ancestral to the mammals. The *cusp addition* theory also finds more advocates at present than the concrescence theory, and rests upon indisputable evidence. Finally, the greatest conflict of evidence exists between the Cope-Osborn palæontological and the embryological plus premolar-analogy theories of the homologies of the upper and lower cusps (see pp. 208-227).

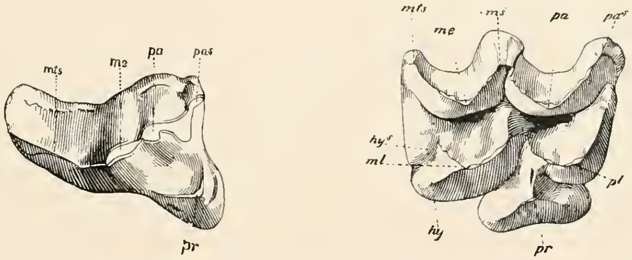


FIG. 2. Two divergent derivatives of the tritubercular molar pattern. Right-hand figure, a grinding molar of the modern horse; left-hand figure, a sectorial molar of a Flesh-eating mammal (*Oxyæna*) of the Eocene Period.

Arrangement of this Volume.

The writer became interested in trituberculy while attempting to monograph the Mesozoic mammals; in course of this work many new ideas came out, and many other ideas arose, apparently new, which the writer subsequently found by more extensive reading had already occurred to Professor Cope, and had been expressed in out-of-the-way and unlooked-for places.

The writer thus had the opportunity of fully developing the *Mesozoic origin of trituberculy*, a part which Professor Cope had been obliged to leave in the stage of suggestion. Subsequently the writer took up the molar teeth of the monkeys and lemurs, and then of the hoofed animals, which strangely enough form a perfect morphological succession of types, and thus enjoyed the opportunity of working out what might be called the secondary and tertiary addition, suppression, or modification of cusps as illustrated in the modern Carnivores and Ungulates. These papers are republished here in chronological order with editorial notes. All corrections and insertions by the Editor are indicated in [ ] brackets. All *figure* references are to figures as arranged and numbered in this volume. The original pagination of the reprinted essays is not given.

Certain of the more purely philosophical and biological questions, as distinguished from the anatomical, that is, matters of causation and of evolution theory, are touched upon at one or two points in these pages, but are more fully treated in another volume of these collected papers, entitled *Rectigradations in Evolution* (cf. pp. 228-239).

CLASSIFICATION OF THE MAMMALIA ADOPTED IN THIS BOOK

(See especially pages 91-192).

Class **MAMMALIA** Linnæus

- Sub-class 1. **PROTOTHERIA** Gill (egg laying mammals)
  - Infra-class. Ornithodelphia De Blainville
    - ? Order: ***Protodonta** Osborn (Of uncertain systematic position) (p. 18.)
      - *Dromatherium* } (Triassic)
      - *Microconodon* }
    - Order: **Monotremata** Geoffroy Saint Hilaire (p. 105.)
      - *Ornithorhynchus*
      - *Echidna*
    - ? Order: ***Allotheria** Marsh (Multituberculata Cope), of uncertain systematic position (p. 101.)
      - Examples
      - *Plagiaulax*
      - *Polymastodon*
      - *Tritylodon*
      - *Microlestes*
- Sub-class 2. **EUTHERIA** Gill (Viviparous mammals)
  - Infra-class 1. Didelphia De Blainville (Metatheria Huxley)
    - ? Order: ***Triconodonta** Osborn (Of uncertain systematic position, usually regarded as carnivorous Marsupials) (p. 21.)
      - Examples
      - *Amphilestes*
      - *Triconodon*
    - Order: **Marsupialia** Illiger (Pouched mammals) (p. 108.)
      - Sub-order: Polyprotodontia Owen
        - Examples
        - Opossums (*Didelphys*)
        - Dasyures
        - Thylacynes, etc.

The asterisk (*) denotes an entirely extinct order.

Sub-order: Diprotodontia Owen (p. 109.)
Examples
Kangaroos
Phalangers, etc.

Infra-class 2. MONODELPHIA De Blainville (Placentalia of authors, Eutheria Huxley)

Cohort Unguiculata (clawed mammals)

Order: ***Pantotheria** Marsh (Trituberculata Osborn, Insectivora Primitiva Os.) (p. 22.)
Examples
Amphitherium
Dryolestes
Amblotherium

Order: **Insectivora** Cuvier (p. 117.)
Examples
Moles
Shrews
True Hedgehogs (*Erinaceus*)
Tenrecs (*Centetes*), etc.

Order: **Dermoptera** Illiger
"Flying-lemur" (*Galeopithecus*)

Order: **Cheiroptera** Blumenbach (p. 129.)
Sub-order: Megacheiroptera Dobson
Pteropodidæ (fruit bats)
Sub-order: Microcheiroptera Dobson
Examples
Vespertilios
Vampires
Nose-leafs, etc.

Order: **Feræ** Linnæus (Carnivora of authors) (p. 131.)
*Sub-order: Creodonta Cope (p. 132.)
Examples
Patriofelis
Hyænodon
Mesonyx
Sub-order: Fissipedia Flower (Carnivora Vera Flower) (p. 135.)
Examples
Cats (Felidæ)
Civets (Viverridæ)
Hyænas (Hyænidæ)

* Extinct.

Cohort Unguiculata (clawed mammals)

Dogs (Canidæ)
Raccoons (Procyonidæ)
Bears (Ursidæ)
Mustelines (Mustelidæ)

Sub-order: Pinnipedia (p. 143.)

Eared or Fur seals (Otariidæ)
Walruses (Odobænidæ)
Earless seals (Phocidæ)

Order: ***Proglires** Osborn (of uncertain relationships) (p. 145.)

Example
Mixodectes

Order: **Rodentia** Vicq d'Azyr (p. 144.)

Examples
Squirrels (Sciuridæ)
Beavers (Castoridæ)
Rats (Muridæ)
Porcupines, Cavies, etc. (Hystricomorpha)

Order: ***Tillodontia** Marsh (p. 151.)

Examples
Tillotherium
Esthonyx

Order: ***Tæniodonta** Cope (Ganodonta Wortman, possibly related to the Edentates) (p. 151.)

Examples
Hemiganus
Psittacotherium
Calamodon

Order: **Edentata** (Vicq d'Azyr) (Xenarthra Gill) American Edentates (p. 151.)

Examples
Ant bears (Myrmecophagidæ)
Ground Sloths (Megatheriidæ)
Sloths (Bradypodidæ)
Armadillos (Dasypodidæ)
Glyptodonts (Glyptodontidæ)

Order: **Pholidota** Weber

Manis (Scaly Anteater)

Order: **Tubulidentata** Flower (p. 152.)

Orycteropus Aard-Vaark

* Extinct.

Cohort Primates (nailed mammals)

Order: **Primates** Linnæus (p. 157.)
  Sub-order: *Mesodonta Cope (American lemuroids)
    Examples
    Notharctus
    Anaptomorphus
  Sub-order: Lemuroidea Mivart
    Examples
    Lemurs
    Galagos
    Aye-Aye (Cheiromys)
    Tarsier, etc.
  Sub-order: Anthropoidea Mivart
    I. South American or Platyrrhine monkeys
      Marmosets (Hapalidæ)
      Capuchins, etc. (Cebidæ)
    II. Old World or Catarrhine monkeys
      Baboons, Apes (Cercopithecidæ)
      True Monkeys (Semnopithecidæ)
      Anthropoid apes (Simiidæ, Gibbon, Gorilla, Chimpanzee)
      Man (Hominidæ)

Cohort Ungulata (hoofed mammals)

Order: ***Condylarthra** Cope (p. 168.)
  Examples
  Protogonodon
  Euprotogonia
  Phenacodus

Order: ***Amblypoda** Cope (p. 164.)
  Examples
  Periptychus
  Pantolambda
  Coryphodon
  Uintatherium

Order: **Artiodactyla** Owen ("even-toed" hoofed mammals) (p. 171.)
  Examples
  Pigs (Suidæ)
  Hippopotami (Hippopotamidæ)
  Deer (Cervidæ)
  Giraffes (Giraffidæ)

* Extinct.

Cohort Ungulata (hoofed mammals)

Pronghorn Antelope (Antilocapridæ)
Sheep
Goats
Antelopes
Oxen
Bovidæ
Camels (Camelidæ)
Oreodonts (Oreodontidæ)
Tragulines or Chevrotains (Tragulidæ)

Order: **Perissodactyla** Owen ("odd-toed" hoofed mammals) (p. 174.)

Examples

Tapirs (Tapiridæ)
Horses (Equidæ)
Palæotheres (Palæotheriidæ)
Titanotheres (Titanotheriidæ)
Lophiodonts (Lophiodontidæ)
Rhinoceroses (Rhinocerotidæ)

? Order: ***Ancylopoda** Cope (probably an early Eocene offshoot of the Perissodactyla) (p. 184.)

Examples

Macrotherium
Chalicotherium

Order: **Proboscidea** Illiger (p. 186.)

Examples

Mœritherium
Dinotherium
Mastodon
Elephas (Asiatic and African Elephants, Mammoths)

Order: **Sirenia** Illiger (p. 188.)

Examples

Manatees (Trichechidæ)
Dugongs (Halichoridæ)
Rhytina (Rhytinidæ)

Order: ***Embrithopoda** Andrews (Barypoda Andrews)

Arsinoïtherium

Order: **Hyracoidea** Huxley (p. 185.)

Dassies (*Hyrax*, the Coney of the scriptures)
Megalohyrax, etc.

* Extinct.

Cohort Ungulata (hoofed mammals)

Super-order: **NOTUNGULATA** (Roth) Scott (South American Ungulates) (p. 189.)

Order I. ***Toxodontia** (Owen) Scott
  Sub-order 1. *Toxodontia Scott
    Examples
    Toxodon
    Nesodon
  Sub-order 2. *Typotheria Zittel
    Examples
    Pachyrucos
    Icochilus
    Typotherium
  Sub-order 3. *Homalodotheria Scott
    Homalodontotherium

Order II. ***Astrapotheria** (Ameghino)
  Astrapotherium

Order III. ***Litopterna** Ameghino (p. 189.)
  Proterotherium
  Macrauchenia

Order: **Pyrotheria** Ameghino (short-footed South American Ungulates)
  Pyrotherium

Cohort Cetacea (whales)

Order: ***Zeuglodontia** Van Beneden (p. 191.)
  Examples
  Protocetus
  Zeuglodon

Order: **Odontoceti** Gray (toothed whales) (p. 190.)
  Squalodonts (Squalodontidæ)
  Fluviatile dolphins (Platanistidæ)
  Dolphins (Delphinidæ)
  Belugas } (Delphinapteridæ)
  Narwhals }
  Beaked whales (Ziphiidæ)
  Sperm whales (Physeteridæ)

Order: **Mystacoceti** Gray
  Whalebone whales (Balænidæ)
  Right whales (*Balæna*)
  Humpbacked whales (*Megaptera*)
  Finbacked whales (*Balænoptera*)

*Extinct.

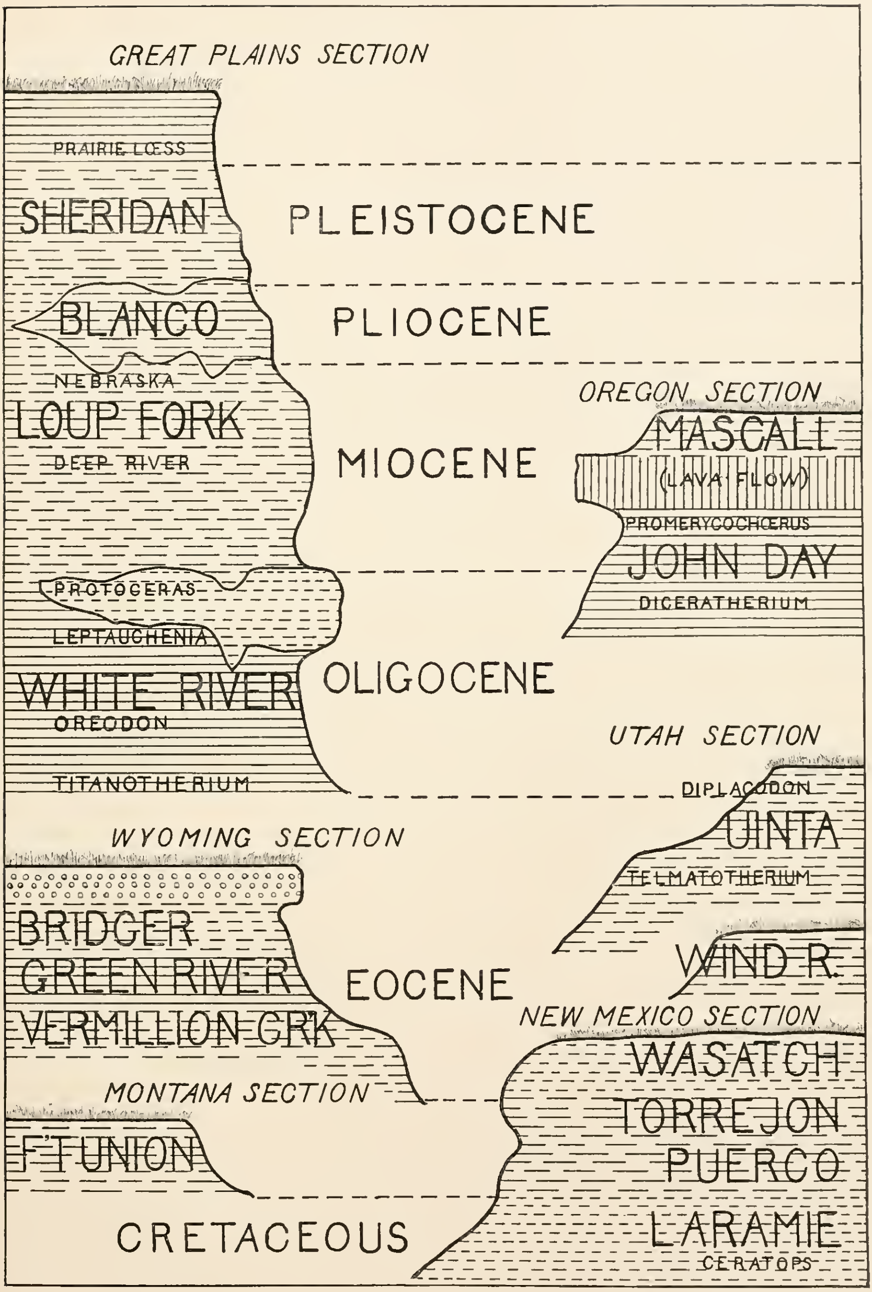


FIG. 2*a*.—Diagram showing the chronological and stratigraphic succession of the Cretaceous, Tertiary and Pleistocene formations of the western states, in which fossil mammals are found.

CHAPTER I.

THE TRANSITION FROM THE REPTILIAN TO THE MOST PRIMITIVE MAMMALIAN TEETH. BEGINNINGS OF THE NOMENCLATURE.

1.

THE UPPER TRIASSIC MAMMALS, DROMATHERIUM AND MICROCONODON.

[*Reprinted.*]

(Read before the *American Philosophical Society*, April 15th, 1887. Published in the *Proceedings*, 1887, p. 109.)

THE mammalian jaws[1] discovered by Professor Emmons in the Upper Triassic beds of North Carolina, and ascribed to a single genus, *Dromatherium*, were recently examined by the writer and found to belong to separate genera. The type mandible of *Dromatherium* is preserved in the Williams College Museum, and differs widely from the mandible preserved in the Museum of the Philadelphia Academy. These differences have already been pointed out,[2] but require to be more fully stated, as both Professors Marsh and Cope have expressed doubts as to the distinct separation of these genera. The accompanying lithographic figures bring out the characteristic features of these mandibles much more fully than in the pen drawings which accompanied my earlier description.

In many respects these genera agree with each other, and stand separate from the Jurassic mammals of both England and America. There is, first, a considerable diastema behind the canine, a very rare feature in the division of Mesozoic mammals to which these genera belong, although always present in the division to which *Plagiaulax* and its allies belong, viz., the sub-order *Multituberculata* Cope.

---

[1] [The chief reason for considering these jaws mammalian is that they are composed of a single bone, there being no evidence of the separation into dentary, articular, and angular elements, as in the jaws of reptiles. H.F.O. *November*, 1904.]

[2] *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1886, p. 359. I find upon a second examination of Prof. Emmons' original figure, that I unintentionally criticised it too severely in the former article, p. 359. While far from accurate, the figure is not so misleading as I at first supposed.

Dromatherium has three premolars and seven molars, but the number in *Microconodon* is quite uncertain, as only four of the series are preserved. The molars agree in one particular, which separates them widely from other Mesozoic genera, viz., in the imperfect division of the fangs. This division is indicated merely by a depression at the base of the crown, as in the genus *Dimetrodon*, among the Theromorph * reptiles.

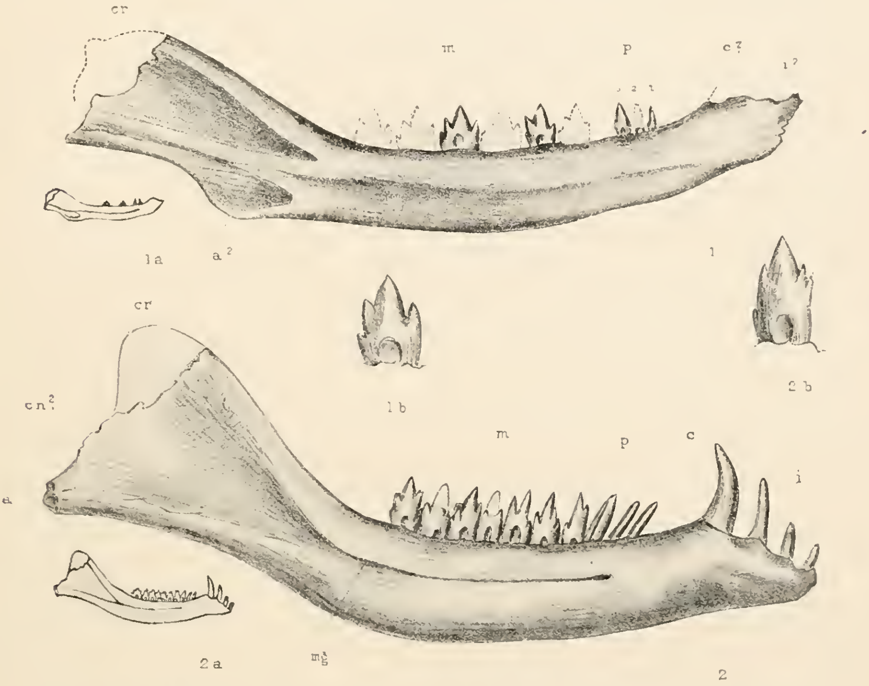


FIG. 3. No. 1. *Microconodon tenuirostris.* The outer surface of the right mandibular ramus, enlarged. The two premolars preserved are the first and third, with the fang of the second between. The space behind the third was occupied either by a fourth premolar and the first molar, or by the first and second molars. The molars preserved are, therefore, either the second and fourth, or the third and fifth. The dotted outlines are purely conjectural.

1*a*. The same, natural size. 1*b*. The fourth or fifth molar, much enlarged.

No. 2. *Dromatherium sylvestre.* The inner surface of the left mandibular ramus, enlarged.

2*a*. The same, natural size. 2*b*. The second molar, much enlarged.

ABBREVIATIONS.—*a*. Angle; *c*. canine; *cn*. condyle; *cr*. coronoid; *i*. incisors; *mg*. mylohyoid groove †; *m*. molars; *p*. premolars.

In all other respects these mandibular rami differ widely. The *Microconodon* ramus is two-thirds the length of that of *Dromatherium*; it is flattened and slender, with a nearly straight lower border beneath the molar alveoli, and a characteristic depression of the border which possibly represents the angle of the jaw, as in Prof. Owen's genus *Peramus* (Fig. 16.) The coronoid process is low and the vertical diameter of the jaw at this point is very narrow. This ramus offers a great contrast to that of

---

* [*Dimetrodon* is now classified with the *Sphenodon*-like reptiles.—ED.]

† [Now believed to be the groove for Meckel's cartilage.—ED.]

Dromatherium, which is very stout and convex with a thick lower border, projecting widely from the matrix, an elevated coronoid process, while the curvature of the lower border is unbroken by any downward projection. If these differences may be given merely a specific value, and attributed in part to the fact that the *Microconodon* jaw is seen upon the outer surface, and that of *Dromatherium* upon the inner surface, let us compare closely the teeth in the two genera. Unfortunately the canine and incisors of the *Microconodon* ramus are wanting. We first observe that the premolars of *Dromatherium* are styloid and procumbent; if erect they would rise above the level of the molars; they have no trace of a cingulum. In the other genus the premolars are subconical, and, although erect, they do not reach the level of the molar tips; they show a faint posterior cingulum, and the third premolar has the same evidence of a division of the fang which is seen in the molars, while in *Dromatherium* there is no trace of such a depression, but a distinct groove on the postero-internal face of the tooth reaching nearly to the summit. The molars of *Dromatherium* are narrow and lofty; the general pattern of the crown consists of a single main cone with a high anterior and lower posterior accessory cusp upon its slopes; but these cusps are very irregular in disposition. For example, in the second molar there are two anterior cusps; in the third molar the posterior cusp is nearly as large as the main cusp; in the fifth molar there is a trace of a postero-external cusp; in the last molar both the anterior and posterior cusps are distinctly bifid at the tip. In *Microconodon*, on the other hand, the molars are comparatively low and broad, with a low anterior and higher posterior accessory cusp; these cusps are regular and very prominent; there is also a well-marked posterior cingulum, which cannot be distinguished in the corresponding molars of the other genus.

Although the two posterior molars are wanting in *Microconodon*, the rise of the coronoid probably marks the position of the last molar; taking this estimate of the posterior point of the molar-premolar series and comparing it with the length of the series in *Dromatherium*, we find that while the ramus of one genus is only two-thirds the length of the other, the total space occupied by the molar-premolar series is very nearly the same. Estimated in another way, the molar-premolar series of *Microconodon* is a little less than one-half the entire length of the jaw ($\frac{6}{13}$), while that of the other genus is exactly one-third the length of the jaw. This discrepancy is due to the difference in the proportions of the molars; in one genus they are low and broad at the base, in the other they are unusually high and compressed.

It is difficult at present to assign any systematic position to either of these genera. *Dromatherium* is entirely unlike any known mammal, fossil or recent. The form of the molars is extremely primitive both in respect to the incomplete separation of the fangs and the remarkable variations in the number and size of the accessory molar cusps. In fact the molars appear to be in what may be called an experimental stage of structure. The accessory cusps are sometimes large and distinct, as in the third true molar; sometimes minute as needle points, as in the second molar. The incomplete separation of the fangs is a reptilian character, which when correlated with the styloid premolars and recurved canine-incisor series, places *Dromatherium* very remote from any of the known Mesozoic mammals. *Microconodon*, on the other hand, is of a somewhat more recent type, the premolars have the trace of a low posterior heel, and the molars have that regular tricuspid division of the crown which is first observed in the genus *Amphilestes* (Fig. 5) of the English Lower Jurassic and characterizes a large number of the Jurassic mammals.

2.

A NEW CLASSIFICATION OF THE MESOZOIC MAMMALS.

[In order to make the following section clearer we insert here a brief classification of the Mesozoic (Lower and Upper Jurassic) mammals of the orders Triconodonta and Pantotheria (Trituberculata).—ED.]

A. Infra-class Marsupialia.

1. ORDER: TRICONODONTA OSBORN.

1. FAMILY: TRICONODONTIDÆ MARSH.

Probably carnivorous pro-Marsupials. Molars with three stout crest cusps, the anterior and posterior cusps derived from the crown, and a strong internal cingulum, rising into anterior, median and posterior prominences. Opposition of upper and lower molars subtrenchant. Postcanine teeth 7 to 11, usually 7. Angle of jaw inflected. Coronoid broad, recurved.

a. Subfamily Amphilestinæ Osborn.

Lower Jurassic. Anterior and posterior cusps of molars much lower than middle cusps, all three cusps being in the same fore-and-aft line. Postcanine teeth 9-11. Angle distinct in outside view. Mandible rather slender.

Genus *Amphilestes.* Lower Jurassic (Stonesfield Slate), England. Figs. 4 (No. 1), 5.

b. Subfamily Triconodontinæ Osborn.

Upper Jurassic.* Anterior and posterior cusps of molars progressively increasing in size, finally equalling the middle cusps. All three cusps in line. Postcanine teeth 7. Angle not seen in outer, side view. Canines erect and piercing. Mandible stout.

1. *Triconodon* Upper Jurassic,* England (Middle Purbeck Beds). Figs. 11, 11*a*.

2. *Priacodon* (probably a synonym of *Triconodon*), Upper Jurassic (Como Beds), Wyoming. Fig. 8.

3. *Triacanthodon*, Upper Jurassic * (Middle Purbeck Beds), England. Fig. 7.

c. Subfamily Phascolotheriinæ Osborn.

Lower and Upper Jurassic. Anterior and posterior cusps of lower molars progressively shifting to inner slopes of central cusps. Postcanine teeth 7. Premolars and molars alike (or premolars greatly reduced in number). Angle not seen in outer side view.

1. *Phascolotherium*, Lower Jurassic (Stonesfield Slate), England. Figs. 4 (No. 3), 6.

2. *Tinodon*, Upper Jurassic * (Como Beds), Wyoming. Fig. 10.

INCERTÆ SEDIS.

d. Subfamily Spalacotheriinæ Osborn.

Upper Jurassic. Molars with large central cusp and two smaller cusps somewhat internal to it. Premolars and molars unlike (or premolars not greatly reduced in number). Angle not seen in outer side view. Postcanine teeth 7-10. Mandible slender.

Spalacotherium, Upper Jurassic * (Middle Purbeck Beds), England. Fig. 11.

Menacodon, Upper Jurassic (Como Beds), Wyoming. Fig. 9.

Peralestes, Upper Jurassic * (Middle Purbeck Beds), England.

B. Infra-class Placentalia.

ORDER: PANTOTHERIA MARSH (TRITUBERCULATA OSBORN).

Probably insectivorous pro-placentals, angle of mandible not inflected, lower molars primitively of the tuberculo-sectorial type, with a central external and three internal cusps, pa^d, me^d, hy^d, the latter probably derived from the internal cingulum. Upper molars subtriangular, the

---

*[Throughout this book the Purbeck Beds of England and the Como or Atlantosaurus Beds of Wyoming are called Upper Jurassic, but English and Continental geologists now regard them as Lower Cretaceous in age.—ED.]

trigon reversing the pattern of lower molars, the accessory cusps being on the outer side of the main or internal cusp, probably also derived from the cingulum. Molars progressively styloid and piercing, often with recurved tips. Lower incisors typically procumbent, spatulate, p_3 and especially p_4 typically larger than m_1, erect and piercing. Postcanine teeth usually 11 (p 4, m 7).

1. *Family Amphitheriidæ Owen.*

Lower and Upper Jurassic. Lower molars tuberculosectorial bifanged, incisors more erect. Condyle low, coronoid broad, angle well rounded below, sharply depressed. Postcanine teeth 9-12. Incisors more erect.

Amphitherium, Lower Jurassic (Stonesfield Slate), England. Figs. 15, 17.

Amphitylus, Lower Jurassic (Stonesfield Slate), England. Fig. 4 (No. 2).

Peramus, *Leptocladus*, Upper Jurassic (Purbeck Beds), England. Figs. 18, 26.

2. *Family Amblotheriidæ Osborn or Stylacodontidæ Marsh.*

Upper Jurassic. Molars progressively styloid and piercing, finally with single fang, canine with single fang. Coronoid more slender. Angle small, continuous with lower contour of mandible. Mandible graceful and slender. Incisors procumbent, spatulate. P_3, p_4 larger than m_1. Postcanine teeth 11-12.

1. *Amblotherium* (Upper molars = ? *Peralestes*) Upper Jurassic (Purbeck Beds), England. Figs. 11, 23.
2. *Peraspalax*, Upper Jurassic * (Purbeck Beds), England. Figs. 4 (No. 9), 22.
3. *Achyrodon*, Upper Jurassic * (Purbeck Beds), England. Fig. 24.
4. *Phascolestes*, Upper Jurassic * (Como), Wyoming. Figs. 31-34.
   Dryolestes (probably a synonym of *Phascolestes*).
5. *Laodon*, Upper Jurassic * (Como Beds), Wyoming. Fig. 30.
6. *Stylodon* (Upper molars = ? *Kurtodon*). Fig. 29.
   Stylacodon, Upper Jurassic * (Como), Wyoming (a synonym of *Stylodon*?)
7. *Asthenodon*, Upper Jurassic * (Como), Wyoming. Fig. 35.

3. *Family Paurodontidæ Marsh.*

Upper Jurassic. Molars feebly tuberculo-sectorial, that is, with accessory cusps poorly developed. Molars bifanged. Postcanine teeth 6. Mandible very short and stout.

---

* See note on page 22.

Paurodon Marsh. Upper Jurassic* (Como), Wyoming. Some approach toward these distinctive characters is made by *Achyrodon* of the Amblotheriidæ (Stylacodontidæ), from early members of which family *Paurodon* may have descended. Fig. 26.

4. *Family Diplocynodontidæ Marsh.*

Upper Jurassic. Upper molars with large crushing protocones; lower molars with very broad basin-shaped talonids.

Diplocynodon, Upper Jurassic * (Como Beds), Wyoming. Fig. 20.
Docodon, Upper Jurassic * (Como Beds), Wyoming. Fig. 21.
Enneodon, Upper Jurassic * (Como Beds) Wyoming.

3.

ILLUSTRATIONS OF THE CHIEF TRICONODONTA AND TRITUBERCULATA.

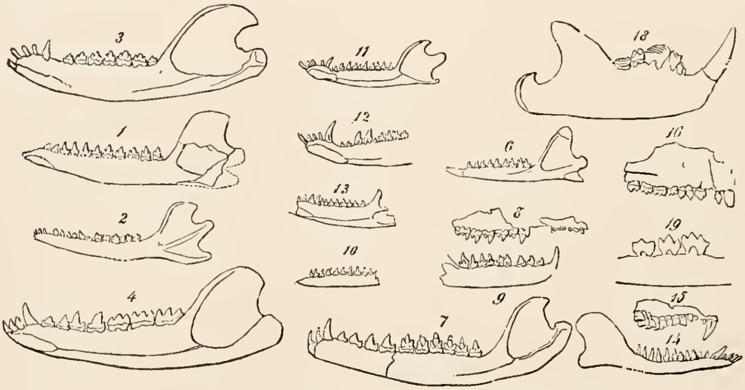


FIG. 4. The types of the British mesozoic mammals, representing the natural size. 1. *Amphilestes.* 2. *Amphitherium.* 3. *Phascolotherium.* 4. *Triconodon mordax.* 6. *Peramus.* 7. *Spalacotherium.* 8. *Peralestes.* 9. *Peraspalax.* 10. *Leptocladus.* 11. *Amblotherium.* 12. *Phascolestes.* 13. *Achyrodon.* 14. *Stylodon.* 15. *Athrodon.* 16. *Bolodon.* 18. *Plagiaulax minor.* 19. *Stereognathus.*

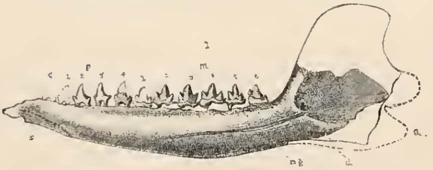


FIG. 5. *Amphilestes.* Lower Jurassic, England. Internal view, enlarged.

FIG. 6. *Phascolotherium.* Lower Jurassic. England. Internal view, enlarged.

FIG. 7. *Triconodon* (*Triacanthodon*). Upper Jurassic, England. External view, enlarged.

*See note on page 22.

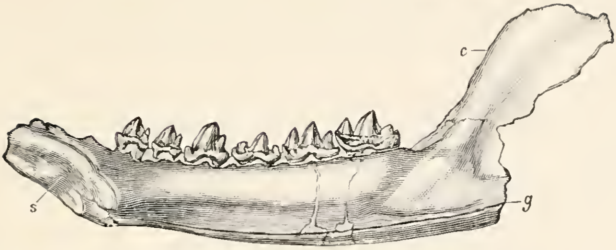


Fig. 8. *Triconodon* (*Priacodon*). Upper Jurassic, America. Internal view. $\times \frac{3}{1}$. After Marsh.

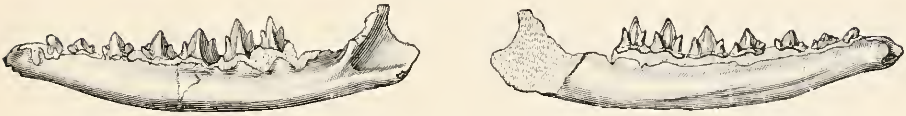


Fig. 9. *Menacodon*. External and internal views. $\times \frac{3}{1}$. Upper Jurassic, America. After Marsh.

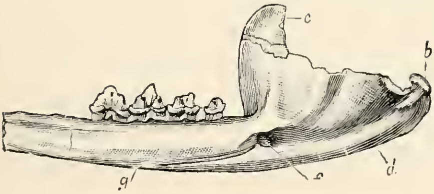


Fig. 10. *Tinodon*. Upper Jurassic, America. Internal view. $\times \frac{3}{1}$. After Marsh.

Fig. 11. *Spalacotherium*. Upper Jurassic, England. Internal view, enlarged.

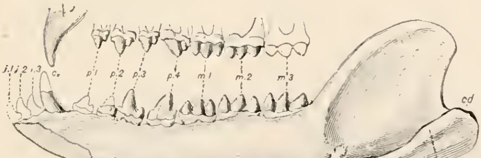


Fig. 11*a*. Upper and lower teeth and lower jaw of *Triconodon ferox* from the Purbeck Beds, Upper Jurassic (Lower Cretaceous), England. $\times \frac{3}{2}$.

Figs. 7-11*a*. Jurassic Triconodonta. Lower Teeth and Jaws. (All enlarged.) For the natural size of Figs. 5, 6, 7, 11 see Figure 4.

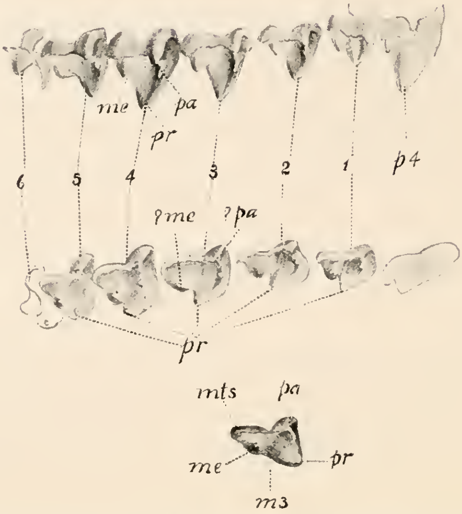


Fig. 12. Superior molars of *Peralestes* Owen. Upper Jurassic, England. Right side. External, oblique and crown views. These upper molars were probably associated with lower molars of the type seen in *Spalacotherium* (Fig. 11). *mts*, metastyle; *pr*, *pr*, *pr*, main internal cusps believed to be protocones; *?pa*, *?me*, smaller external cusps believed to be para- and metacones.

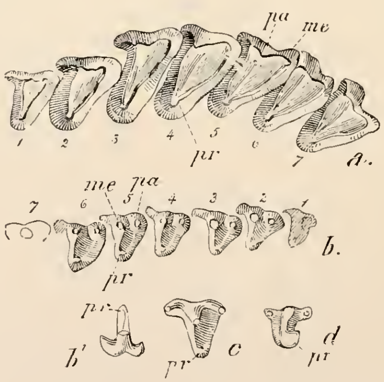


Fig. 13. *a*, *Kurtodon*. Superior molar series of the left maxilla, viewed upon the wearing surface. *b*, *Amblotherium soricinum*, inferior molar series, viewed from above. b^1 *A*. (*Peraspalax*) *talpoides*. A lower molar viewed upon the internal face. *c*. The same. A lower molar viewed from above. *d*, *Achyrodon nanus*. A lower molar viewed from above. Much enlarged.

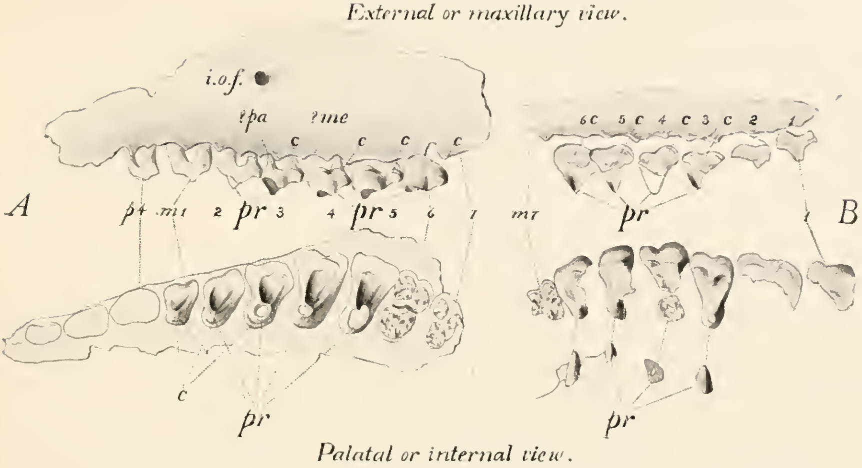


FIG. 14. Superior molars of *Dryolestes* Marsh. Upper Jurassic, Wyoming. *A*. Series of the left side, external and crown views. *B*. Series of the right side, external, crown and internal views. Yale Museum. *c, c, c*, external and internal cingula. *i. o. f.* infraorbital foramen. Other abbreviations as in Fig. 12. (Cf. Fig. 207_2 and p. 220.)

Jurassic Triconodonta? (Fig. 12) and Pantotheria (Trituberculata). Upper Teeth. and Jaws. For scale see Fig. 4.

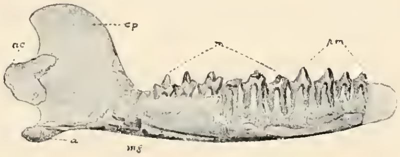


FIG. 15. *Amphitherium prevostii.* Lower Jurassic, England. Internal view, enlarged. After Goodrich.

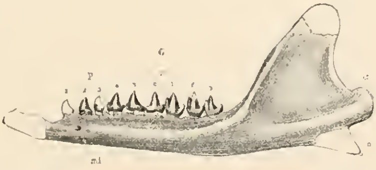


FIG. 16. *Peramus.* Upper Jurassic, England. External view, enlarged.

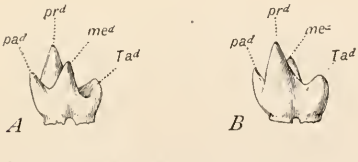


FIG. 17. Inferior molars of *Amphitherium prevostii.* *A*, inner view of a molar of the right side; *B*, outer view of a molar of the left side (restored), enlarged. After Goodrich.

Figs. 15-17. Jurassic Pantotheria (Trituberculata). Lower Teeth and Jaws. For scale see Fig. 4.

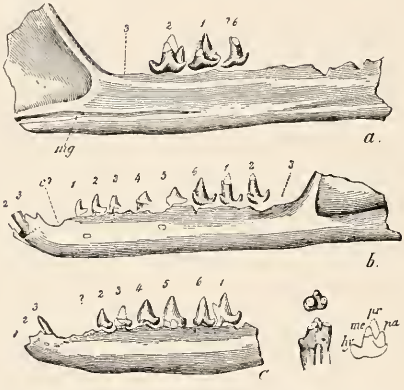


Fig. 18. *a. Peramus* (*Spalacotherium*) *minus* Owen. Internal view of left mandibular ramus. *b. P.* (*Leptocladus*) *dubius* Owen. External view of left mandibular ramus. *c. P. tenuirostris* Owen. Outer face of anterior portion of left ramus. Also, second molar of *Amphitherium Prevostii* Owen, internal view, and second molar of *P. minus*, enlarged from fig. 1 *a* above; internal view. *pr*, protoconid; *pa*, paraconid; *me*, metaconid; *hy*, hypoconid; *mg*, Meckelian groove. Much enlarged.

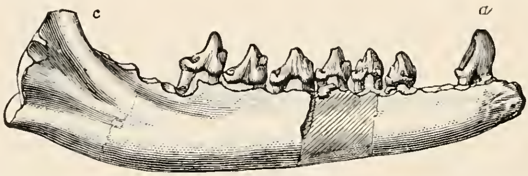


Fig. 19. *Enneodon*, Family Diplocynodontidæ. Upper Jurassic, America. External view. × $\frac{3}{1}$. After Marsh.

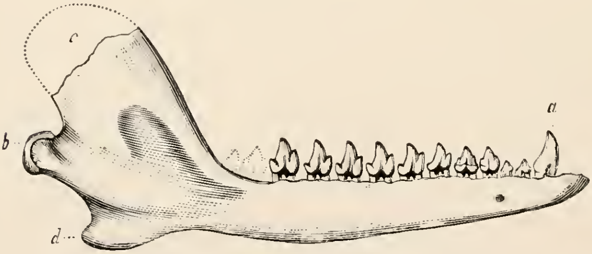


Fig. 20. *Diplocynodon*, Family Diplocynodontidæ. Upper Jurassic, America. External view. × $\frac{2}{1}$. After Marsh.

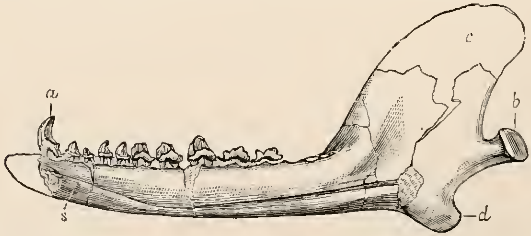


Fig. 21.—*Docodon*, Family Diplocynodontidæ. Upper Jurassic, America. Internal view. × $\frac{2}{1}$. After Marsh.

Jurassic Pantotheria or Trituberculata. Lower Jaws. Amphitheriidæ (Fig. 18) and Diplocynodontidæ (Figs. 19-21). For scale see Fig. 4.

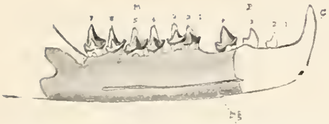


FIG. 22. *Peraspalax.* Upper Jurassic, England. Internal view, enlarged.

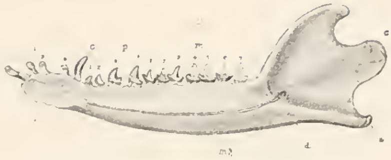


FIG. 23. *Amblotherium.* Upper Jurassic, England. Internal view, enlarged.

FIG. 24. *Achyrodon.* Upper Jurassic, England. Internal view, enlarged.

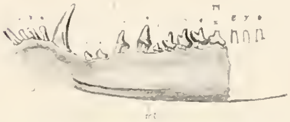


FIG. 25. *Phascolestes.* Upper Jurassic, England. Internal view, enlarged.

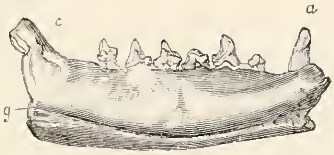


FIG. 26. *Paurodon.* Upper Jurassic, America. Internal view. ×$\frac{3}{1}$. After Marsh.

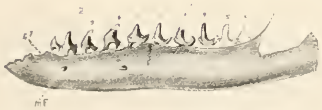


FIG. 27. *Peramus* (*Leptocladus*). Upper Jurassic, England. Internal view, enlarged.

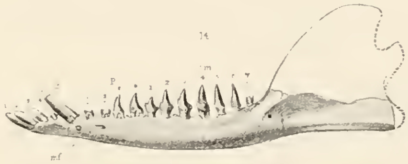


FIG. 28. *Stylodon.* Upper Jurassic, England. External view, enlarged.

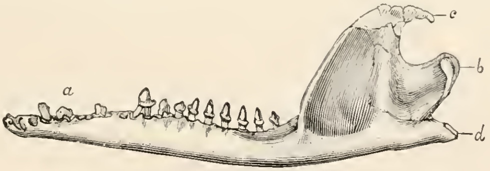


FIG. 29. *Stylodon* (*Stylacodon*). Upper Jurassic, America. External view. ×$\frac{3}{1}$. After Marsh.

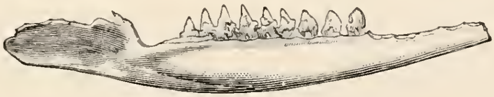


FIG. 30. *Laodon.* Upper Jurassic, America. Internal view. ×$\frac{4}{1}$. After Marsh.

Jurassic Pantotheria or Trituberculata. Lower Jaws. Amblotheriidæ or Stylacodontidæ and Paurodontidæ. For scale of Figs. 22, 25, 27, 28, see Fig. 4. Figs. 26, 29 are three times natural size.

FIG. 31. *Phascolestes vorax.* Upper Jurassic, N. America. Oblique crown view. $\times \frac{3}{1}$.

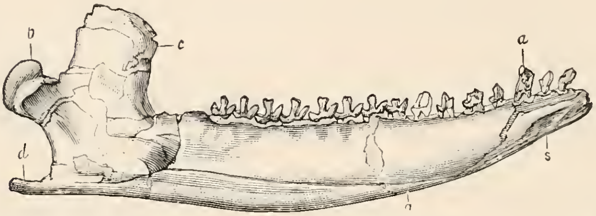


FIG. 32. *Phascolestes* (*Dryolestes*) *priscus.* Upper Jurassic, America. Internal view. $\times \frac{3}{1}$.
After Marsh.

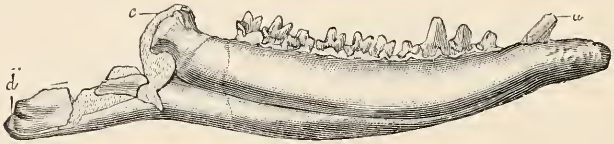


FIG. 33. *Phascolestes* (*Dryolestes*) *vorax.* Upper Jurassic, America. Internal view. $\times \frac{3}{1}$.
After Marsh.

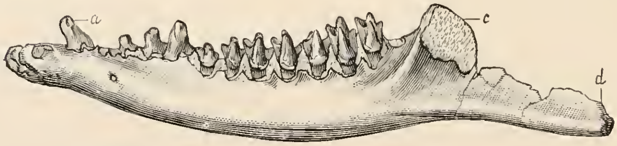


FIG. 34. *Phascolestes* (*Dryolestes*) *vorax.* Upper Jurassic, America. External view. $\times \frac{3}{1}$.
After Marsh.

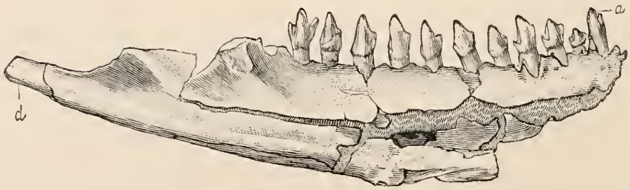


FIG. 35. *Asthenodon.* Upper Jurassic, America. External view. $\times \frac{3}{1}$. After Marsh.

Figs. 31-35. Jurassic Pantotheria or Trituberculata. Lower Jaws. Amblotheriidæ.

4.

THE ORIGIN OF THE TRITUBERCULAR TYPE SOUGHT (1888) AMONG THE MESOZOIC MAMMALIA.

[Extract from Memoir entitled "The Structure and Classification of the Mesozoic Mammalia." *Journ. Acad. Nat. Sci. Phila.*, Vol. IX., No. 2, July, 1888.]

(*a*) If, as now seems probable, the derivation of the mammalian molar from the single reptilian cone can be demonstrated by the comparison of a series of transitional stages between the single cone and the three-cone type, and from the latter to the central tritubercular type, the separate history of each cone can certainly be traced throughout the series in its various degrees of modification, development, and degeneration. The remarkable part played by the tritubercular molar has been unfolded by the discoveries and writings of Cope. It is undoubtedly the ancestral molar type of the Primates, the Carnivora, the Ungulata, the Cheiroptera, the Insectivora, and of several, if not all, of the Marsupialia. For example, we can trace back the quadritubercular bunodont, or parent ungulate type, to the *tritubercular*; this to the type with three cones in line, which we may call the *triconodont* type, and this in turn to the *haplodont*[1] reptilian crown. A nomenclature may be suggested for these cones, with reference to their order of development and primitive position, to keep clearly before the mind their homologies during secondary changes of form and position. The primitive cone may be called the *protocone*; upon the anterior and posterior slopes of which appear, respectively, the *paracone* and *metacone*. After the tritubercular crown is produced, by the rotation of the lateral cones, inwards in the lower jaw and outwards in the upper jaw, the *hypocone*, or heel, is developed, giving us the tubercular-sectorial molar. Exclusive of the *Multituberculata* and of *Stereognathus* (Fig. 51, No. 5) this is the most advanced stage of molar development thus far found in the mesozoic period.

The protocone of *Dromatherium* (Fig. 3, No. 2) is prominent and constant through the molar series while the para- and meta-cones are irregular in size and position, always close to the main cone and in several teeth either splitting into two needle-like cusplets or bifid at the tip. Altogether, they are in what appears to be an experimental stage of development. *Microconodon* (Fig. 3, No. 1), however, from the same strata, has well defined para- and meta-cones which are widely separated from the main cone, the crown presenting the pure triconodont type. This reoccurs in *Amphilestes* (Figs. 4, 5), of the lower Jurassic, and *Triconodon* (Figs. 4, 7) of the upper Jurassic. In this series we are struck by the

---

[1] See Cope: "The homologies and origin of the types of molar teeth of the Mammalia Educabilia," *Jour. Phila. Acad.*, 1874.

gradual increase of size and prominence of the lateral cones until they are upon the level of the main cone and sub-equal to it, this increase being accompanied by a marked elongation of the crown so that the three molars of *Triconodon* occupy a greater proportion of the jaw than is taken by the seven molars of *Dromatherium*. This unmodified triconodont type is very rare in the more recent mammalia. It persists in the lower jaw, at least, of *Dissacus* from the Puerco, and in the lower molars of *Thylacinus*, the upper molars presenting an internal heel.*

(*b*) In his paper upon the Creodonta,[1] Cope observed that the *Spalacotherium* molars (Figs. 4, 11) represents a stage of transition between the triconodont and tritubercular molars. There can be no doubt that the cusps seen upon the inner face of the inferior molars of this genus are homologous with the para- and meta-cones,† and there are several facts which support Cope's hypothesis that they represent a stage of inward rotation of cusps which were at an earlier stage in the same fore and aft line with the main cusp. These are, that in *Phascolotherium* (Figs. 4, 6) the lateral cones are seen to be slightly internal to the main cone so that their median slopes descend upon the inner face: in *Tinodon* (Fig. 10), of a later geological period, this position is slightly more pronounced; in *Menacodon* (Fig. 9) it is still more marked, but less so than in *Spalacotherium* (Fig. 11). These genera, although evidently in two different lines of descent, afford the desired transition stages. The *Spalacotherium* molar as seen from above[2] has a striking resemblance to the anterior sectorial triangle of the *Stypolophus* or *Didymictis* molar of the Puerco. It is in fact sub-triangular, the superior molars probably having the lateral cones rotated outwards, so that the upper and lower molars form an alternating series, the ridges connecting the main and lateral cones acting as sectorial blades.

The question now arises whether the *Stylacodon* (Fig. 29) molar represents the next higher stage of development, viz., the tubercular-sectorial molar in which the anterior triangle is followed by a low heel. And if so has the *Stylacodon* type passed through the stages of inward rotation of the lateral cusps? The superior aspect of the *Stylacodon* molar presents an anterior triangle with the long styloid cone forming the apex and connected by divergent ridges with the anterior pair of cusps; behind these is a third cusp not connected by a ridge with the styloid cone. In the upper jaw the three cusps are external and the single cone internal, these relations are reversed in the lower jaw. We cannot well

---

* [This condition is now believed to be not primitive but secondary in both the genera mentioned.—Ed.]

[1] "The Creodonta," *American Naturalist*, 1884, p. 259.

† [But see page 33* where the homologies of these cusps with the paraconid and metaconid of Trituberculates are doubted.—Ed.]

[2] Owen, *The Mesozoic Mammalia*, Plate I., Fig. 32c.

avoid the inference that the *Stylacodon* lower molar is a specialized tubercular-sectorial, that the styloid external cusp, which until Marsh's discovery of *Dryolestes* (Figs. 31-34) was regarded as the single summit of the crown, is the protocone while the anterior pair of internal cusps represent the paracone and metacone, followed by a third element, the hypocone or heel. This is further confirmed by the transition to the simpler *Spalacotherium* type seen in the molars of *Asthenodon* (Fig. 35) in which the hypocone is entirely wanting while the remainder of the crown is closely similar to that of *Stylacodon.* The internal cusps present many degrees of development in different members of the Stylacodontidæ; in *Laodon* (Fig. 30) they are much less prominent than in *Dryolestes,* the heel being also inconspicuous. While the relations of the four cones composing the Stylacodont crown strongly suggest the tubercular-sectorial molar there is one matter of doubt in the way of the derivation of this tooth from the *Spalacotherium* type (Fig. 11): that is, the position of the fangs. In *Spalacotherium* and *Menacodon* (Fig. 9) the fangs are paired and placed beneath the para- and metacones. In the Stylacodonts the external fang is directly beneath the protocone: the question is, does this represent the anterior or posterior, or an additional fang?

4. The molars which have been considered thus far show directly or indirectly the triconodont type, *i.e.*, the presence at some stage of their evolution of the central and two lateral cones. In the Amphitheriidæ (Figs. 15-21) it is clear that the main cone and the lesser one, upon its anterior slope, represent the protocone and paracone but it is uncertain whether the basal cusp, seen for example upon the external face of the *Diplocynodon* molar (Fig. 20) is homologous with the metacone or hypocone. The latter alternative excludes the development of the metacone or the passage of these genera through a triconodont stage, and implies a considerable separation of the Amphitheriidæ from the stem of the two families already considered. The former involves the supposition that the metacone has metamorphosed into a heel.* The most primitive molar in this family is seen in *Ennacodon*[1] (Fig. 19). The crown has an obtuse recurved protocone, more like that of a premolar; upon the anterior slope is a rudimentary paracone which affords the only means of distinguishing the molars from the premolars. The posterior slope terminates in a low extended heel. This molar pattern largely

---

* [The questions and difficulties here stated are largely resolved by the hypothesis that in the Triconodontidæ the so called para- and metaconids are direct outgrowths from the molar crown, while in the Amphitheriidæ and Amblotheriidæ the para-, meta- and hypoconids have been derived from the internal cingulum. See page 8.—Ed.]

[1] Marsh, "American Jurassic Mammals," *Am. Jour. Sc.*, April, 1887, Pl. X., Fig. 4.

confirms the second of the above alternatives, viz., that this heel is to be compared to the hypocone of the tubercular-sectorial crown. Further confirmation is seen in the fact that this heel is not above the level of the internal cingulum, as in the metacone of all the triconodonts, but is continuous with the broad shelf-like projection of the internal cingulum, which is well represented in the internal aspect of the *Diplocynodon* (Fig. 20) molars. The concave internal slope of the protocone descends into this shelf and the cingulum rises at the margin into numerous crenations, which cannot properly be called cusps. The *Diplocynodon* (Fig. 20) molar presents a decided advance upon that of *Enneodon* in the development of the paracone, which is much more prominent. In *Amphitherium* (Figs. 4, 15, 17), the paracone is subequal to the protocone in several of the molars, and the heel is on the level of the internal cingulum, from which, according to Owen, there arise one or two small cusps.[1] Internal cusps which develop in this manner are from the first separated from the external cusps by a longitudinal valley instead of being united with it by divergent ridges, and cannot therefore at any stage possess a sectorial blade, such as is more or less distinctly developed in the *Spalacotherium* and *Stylacodon* molar.

5. It follows also that the triangle of cusps presented by the *Peraspalax* molar (Fig. 22) cannot, with probability, be considered as representing a tritubercular stage, and that the Amphitheriidæ furnish the key to the mode of derivation of the internal cusps of the molars of the Peralestidæ (Fig. 12). The inferior molars of *Peraspalax* and *Paurodon* (Fig. 26) are apparently very similar, consisting of a prominent external cone, and two internal cusps followed by a third cusp at the end of the crown. As pointed out in the synopsis of molar types, this internal surface strongly suggests the *Dryolestes* pattern (Figs. 31-34), but may be clearly distinguished by the absence of transverse ridges and the presence of a longitudinal valley between the cusps instead of a transverse valley opening inwards. The internal cusps have probably, therefore, arisen from the internal cingulum,[2] but these molars do not seem to be a later development of the *Amphitherium* type (Fig. 15), because both the paracone and metacone are wanting, the main cone showing no trace of the lateral cusps

---

[1] As previously stated the writer has not personally examined the internal surfaces of the molars of this genus.

[2] Numerous instances of the origin of molar cusps from the cingulum might be cited. One of the most important is seen in the transition from a tritubercular to a quadritubercular superior molar by the addition of the postero-internal cusp which is primitively a cingule; this was first demonstrated by Dr. Harrison Allen, *op. cit.* Mivart (*Jour. of Anat. and Phys.*, Vol. II., p. 138) shows how the four cusps of the Insectivore molars are frequently fortified by additional cusps from the cingulum.

upon its slopes.* The superior molars of *Peralestes*,† however, when viewed from above, present one large internal and two smaller external cusps disposed in a triangle opening outwards, and as this is the general disposition of superior cusps of the tritubercular type, we must admit the possibility that the smaller cusps do represent the para- and meta-cones in a stage of inward rotation not accompanied by the production of the sectorial blades, for this is by no means an essential feature of the tritubercular molar. The history of the derivation of the molars of the Peralestidæ must, therefore, be left in some doubt; while the balance of evidence points to a line of development similar to that in progress in the Amphitheriidæ, although the line of descent appears to be different.

Reviewing this study of the molars the following are the principal deductions: (*a*) The molars of all the mesozoic mammals of this group present one main cusp which is either so central or so prominent that it may be considered homologous with the single reptilian cone or protocone. (*b*) In one line of genera two lateral cusps, the para- and meta-cones, appear upon the anterior and posterior slopes of the protocone. This is a central and frequently repeated stage of evolution. It gives rise to two lines of molar development; in the first, the para- and meta-cones are retained in the same fore and aft line, as the persistent triconodont type, but increase greatly in size; in the second, they are rotated inwards as the tritubercular type, which finally acquires a heel. (*c*) In a second line of genera the paracone appears upon the anterior slope of the protocone, but the metacone is not developed, being replaced by a basal talon or hypocone which extends inwards to form the internal cusp. (*d*) In a fourth line of genera neither the para- nor meta-cones are developed upon the sides of the protocone, but they are replaced by basal cusps derived from the cingulum.

---

* [*Per contra* the conditions seen in *Amphitherium* may have been derived from those seen in *Peraspalax*.—Ed.]

† [Supposed to correspond with the lower molars of the *Spalacotherium* type, Fig. 11.—Ed.]

CHAPTER II.

FIRST OUTLINE (1888) OF TRITUBERCULAR EVOLUTION IN MAMMALS.

[Reprinted directly from the paper entitled "The Evolution of Mammalian Molars to and from the Tritubercular Type,"[1] *The American Naturalist*, December, 1888.]

THE dentition in the recent Mammalia is so diverse that the most sanguine evolutionist of fifteen years ago could not have anticipated the discovery of a common type of molar, in both jaws, as universal among the Mammalia of an early period as the pentadactyle foot, and as central in its capacity for development into the widely specialized recent types.

The tritubercular molar, discovered by Professor Cope in the Puerco, is exactly such a type, and may be considered with the pentadactyle foot as playing a somewhat analogous rôle in mammalian history, with this important difference—the unmodified pentadactyle foot was probably inherited direct from the reptiles, and its subsequent evolution, with a few exceptions, has been in the direction of the greater or less *reduction* of primitive elements towards special adaptation, as, to borrow an extreme illustration, in the transition from *Phenacodus* with 26 elements in the manus to *Equus* with only 12 such elements. On the other hand, the tritubercular tooth was not inherited, but in all probability developed within the mammalian stock, from a hypothetical form with almost, if not quite simple conical molars, implanted by single fangs, in a nearly homodont series.[2] No such primitive type of mammalian dentition is actually known, although *Dromatherium* approximates it; but the apparent reversion to this type among the *Cetacea*, and apparent

---

[1] Read in the geological section of the British Association at Bath, September, 1888. Read in abstract by Professor Cope, National Academy of Sciences, at New Haven, Nov., 1888.

[2] See Author, "Structure and Classification of the Mesozoic Mammalia," *Jour. Phila. Academy*, 1888, p. 240.

retention of it in the *Edentata*,[1] [*] support all the independent evidence upon this point derived from the Mesozoic Mammals.

The principle of growth was the regular addition of new parts to the simple cone, not at random, but according to a certain definite order which apparently progressed independently in different phyla, through a series of subtritubercular stages until trituberculy[2] was attained.

The tritubercular molar consists essentially of three cusps, forming what may be called the primitive triangle, so disposed that the upper and lower molars alternate. This, when attained, formed a central stage from which the great majority of recent molar types have diverged by the addition, modification, and reduction of cusps; we must except the Monotremes, the Edentates, and possibly the Cetaceans, although there is considerable evidence that the cetacean molars were once of the triconodont type.[3] [†] Among extinct orders, the Multituberculata (*Plagiaulax*, *Tritylodon*, etc.) must also be excepted from this series and discussion.

The almost universal predominance of trituberculy in the early geological periods, is very significant of the uniformity of molar origin. Of twenty known Mesozoic genera,[4] all except three[5] [‡] show trituberculy in some of its stages. In the Lower Eocene, eighty-two Puerco species, representing twenty-six genera and five orders (Creodonta, Tillodontia, Lemuroidea, Condylarthra, Amblypoda), only four species have quadritubercular teeth, all the remainder are tritubercular.[6] Prof. Rütimeyer has recently pointed out the predominance of this type in the nearly parallel Egerkingen beds. The contemporary Cernaysien fauna in the collection of Dr. Lemoine at Rheims, recently examined by the writer, shows exclusively tritubercular molars or their derivatives. By the Middle Eocene, the lines of divergence towards the

---

[1] See Oldfield Thomas, "The Homologies and Succession of the Teeth in the Dasyuridæ," *Phil. Trans.*, 1887, p. 458.

[*] [Evidence is presented on pp. 151, 190, that the haplodonty of certain Edentata and of the Cetacea is secondary.—Ed.]

[2] A term first employed by Rütimeyer, "Ueber Einige Beziehungen zwischen den Säugethierstämmen Alter und Neuer Welt," *Abh. d. schweiz. pal. Gesellsch.*, Vol. XV., 1888, p. 54.

[3] See Brandt, *Die Fossilen u. Subfoss. Cetaceen Europas*, Taf. XXXII., Figs. 4-9.

[†] [But this in *Zeuglodon* was probably a secondary derivation from the tritubercular type. See p. 191.—Ed.]

[4] The list given by the writer (*op. cit.*, p. 247) is found to contain several synonyms. See "Additional observations upon the Structure and Classification of the Mesozoic Mammalia," *Proc. Phila. Acad.*, Nov., 1888, p. 292.

[5] Dicrocynodon (Diplocynodon), Docodon, Enneodon, Marsh.

[‡] [The author refers only to the orders Protodonta, Triconodonta, Pantotheria.—Ed.]

[6] Cope, "Synopsis of the Vertebrate Fauna of the Puerco Series," *Am. Phil. Soc.*, 1888, p. 298.

existing types of molars were well advanced, but trituberculy persisted in the dentition of several orders, in which it is found to-day (Lemuroidea, Insectivora, Carnivora, and many Marsupialia).

It follows that it is quite as essential for the comparative anatomist to thoroughly grasp the meaning and history of each of the component cusps of the tritubercular molar and of their derivatives, as it is to perfectly understand the elements of the manus and pes. For, the homologies of the cusps can now be determined almost as certainly as those of the digits. Take a human molar, for example, every component tubercle has its pedigree, and it can be demonstrated, almost beyond a doubt, which of these tubercles is homologous with the single reptilian cone. The writer recently (*op. cit.*, p. 242) proposed the adoption of a distinct nomenclature for the different cusps of the tritubercular molar, and offered a series of terms for the primary cusps based as far as possible upon the primitive position and order of development, and in most instances in accord with their secondary position. This nomenclature can be extended to the secondary cusps in the sexitubercular superior and quinquetubercular inferior molars. The terms now in general use are based, for the most part, upon the secondary or acquired position, and in no instance upon the homologies of the cusps in the upper and lower molars, or even in corresponding molars of different genera, thus involving much confusion. For example, the antero-internal cusp of the lower molar of *Mioclænus* is not homologous with the antero-internal cusp of *Hyopsodus*, nor with the antero-internal cusps of the upper molar of either genus.

The present contribution is based principally upon the writer's studies among the Mesozoic Mammalia, and, with some additions, upon Professor Cope's numerous essays upon the tritubercular type in the Tertiary Mammalia.[1]

Four propositions may be laid down for discussion:

(1) That trituberculy was acquired during the Mesozoic period, in a series of stages beginning with the single cone and attaining to the primitive sectorial type in the Jurassic period.

(2) The majority of Mesozoic mammals showed trituberculy in some of its stages. Present evidence goes to show that the remaining, or aberrant types, if such existed, did not persist. The majority of the persisting forms of later periods were derived from the forms with

---

[1] Professor Cope's essays abound with discussions and notes upon the origin and succession of the tritubercular type. (See collection in *Origin of the Fittest.*) He has outlined the transition from the single cone to the tritubercular crown (p. 347); tubercular sectorial (p. 246); the quadritubercular type (p. 245 and p. 359); the *Spalacotherium* molars as a transition to the *tritubercular* (p. 259). The acquisition of the superior and inferior quadritubercular molar (p. 361). The prediction of the discovery of Carnivora with triconodont molars (p. 365), and of the simple tritubercular type in both jaws (p. 362).

simple tritubercular molars, of earlier periods. It follows that trituberculy was an important factor in survival.

(3) The definite homologies of the primary and to some degree of the secondary cusps in the upper and lower molars can be established.

(4) The mode of succession of tooth forms favours the kinetogenesis theory advanced by Ryder and Cope.

There are three general observations to be made:

First. In attempting to complete the history of each of the cusps we naturally find that the palæontological record is not sufficiently perfect to admit of our following a certain type along a single phylum back to the primitive type. We must at the outset proceed upon the principle of similar effects, similar causes. For example, since the history of the development of the intermediate tubercles in the superior molars of the Lemuroidea (Pseudolemuroidea, Schlosser) is perfectly clear during the Wasatch and Bridger epochs—it is safe to infer that the intermediate tubercles of the Ungulate molars, which are fully developed in the underlying Puerco, had the same history. *Second.* There are in each period *aberrant types* which embrace either incomplete or degenerate tritubercular stages, *i.e.* a high specialization in which the past record is obliterated, or, finally, stages in non-tritubercular lines of development. *Third.* In the parallel evolution of trituberculy in different phyla we find that the progression is by no means uniform. In every geological period in which the fauna is well known we observe *progressive* genera which outstrip the others in reaching a certain stage of molar development, contrasted with *persistent* types which represent arrested lower stages of development, while between them are the *central* types which represent the degree of evolution attained by the majority of genera. The latter may be said to constitute the stage which is characteristic of the period.

The stages of trituberculy may now be defined as seen in different types in their order of succession:

I. *Haplodont* Type (Cope).[1] A simple conical crown. The fang usually single and not distinguished from the crown. This type has not as yet been discovered among the primitive Mammalia.

A. *Protodont* Sub-Type.[2] The crown with one main cone, and lateral accessory cuspules; the fang grooved. There is some question as to the advantage of distinguishing this as a type, for it stands

---

[1] "The Homologies and Origin of the types of Molar Teeth in the Mammalia Educabilia," *Journ. Phila. Acad.*, 1874. The term *Homodont* was previously applied to this type by Rütimeyer, "Odontographie der Hufthiere, etc," *Verhr. d. Naturforsch, Gesellsch. in Basel*, Band III., 1863, p. 563. In the writer's opinion this term has acquired a special significance as applied to a whole series of teeth, viz., the reverse of "heterodont," and may well be retained in this sense.

[2] Osborn, *op. cit.*, p. 222.

intermediate between types I. and III. Example, *Dromatherium* of the American Triassic (Fig. 3).

II. *Triconodont* Type (Osborn, *op. cit.*, p. 242). The crown elongate, trifid, with one central cone and two distinct lateral cones. The fang double. Example, *Triconodon* (Fig. 8).

III. *Tritubercular* Type (Cope). The crown triangular, surmounted by three main cusps, the central cone placed internally in the upper molars and externally in the lower molars. Example, the lower molars of *Spalacotherium* (Fig. 11) and *Asthenodon* (Fig. 35). This type is rare in its primitive condition as above defined.

The upper and lower molars are alike in types I. and II.: in type III. they have a similar pattern, but with the arrangement of the homologous cups reversed. These types are all primitive. In the following sub-types, the primitive triangle forms the main portion of the crown, to which other "secondary" cusps are added, the homologies of which in the upper and lower molars are somewhat doubtful. Parallel and with an intimate relation to the addition of the secondary cusps, is the division of the tritubercular into a secodont and bunodont series, according to the assumption of a purely cutting or crushing function. In departing from the primitive type, the upper and lower molars diverge in structure, and the homologies of the secondary cusps in each are somewhat doubtful.

Lower Molars.

A. *Tubercular Sectorial*, Sub-type (Cope). (*a*) The primitive triangle elevated and its cusps connected by cutting crests; a low posterior heel. (*b*) This type embraces a *quinquetubercular* form in which the heel consists of two cusps, an internal and external.[1] (*c*.) In the Bunodont series it develops into the *quadritubercular* form, by the loss of one of the primitive cusps.

Upper Molars.

B. *Tritubercular.* (*a*). The primitive triangle in the secodont series purely tricuspid. (*b*) This embraces a *quinquetubercular* form in which "intermediate" tubercles are developed, both in the Secodont and Bunodont series. (*c*) In the Bunodont series a postero-internal cusp is added, forming the *sexitubercular* molar.

NOMENCLATURE OF THE CUSPS. As above stated, there is no doubt about the homologies of the three "primary" cusps (protocone, paracone, metacone) in the upper and lower molars. They may be given the same terms, with the arbitrary suffix *id*, to distinguish the

---

[1] *American Naturalist*, April, 1883, p. 407.

lower cusps. The first "secondary" cusps (hypocone, hypoconid), which are added to the upper and lower molars of the primitive triangle, modify the crown from a triangular to a quadrangular shape, and hence may be considered homologous. The three additional secondary cusps (protoconule, metaconule, entoconid) evidently have no homology with each other.

TERMS NOW IN USE.	PROPOSED TERMS.[1]	ABBREV.
Upper Molars.		
Antero-internal-cusp,	Protocone.	pr.
Postero- ,, ,, or 6th cusp,	Hypocone.	hy.
Antero-external ,,	Paracone.	pa.
Postero- ,, ,,	Metacone.	me.
Anterior Intermediate cusp,	Protoconule.	pl.
Posterior ,, ,,	Metaconule.	ml.
Lower Molars.		
Antero-external cusp,	Protoconid.	pr^d.
Postero- ,, ,,	Hypoconid.	hy^d.
Antero-internal cusp, or 5th cusp,	Paraconid.	pa^d.
Intermediate or antero-internal cusp (in quadritubercular molars),	Metaconid.	me^d.
Postero-internal cusp,	Entoconid.	en^d.

Evolution of the Cusps. The cusp evolution in the Mesozoic period has been fully discussed by the writer (*op. cit.*, pp. 240-4) and in the Tertiary period, by Professor Cope, so that only a brief résumé is necessary here. In *Dromatherium* (Fig. 3), from the upper Triassic, the oldest mammalian type known, with the exception of *Microlestes*, the molars have a main protoconid with several minute lateral cuspules, differing in size in the different teeth, but in general giving a trifid appearance to the crown. The molars of the contemporary *Microconodon* (Fig. 3) also have unpaired fangs, but distinctly trifid crowns, with the anterior and the posterior cusps, or para- and meta-conids, upon the slopes of the protoconid. This Triconodont type reappears, with the addition of a cingulum and paired fangs, in *Amphilestes* (Fig. 5) and *Phascolotherium* (Fig. 6) of the lower Jurassic and persists in *Triconodon* (Figs. 7, 8) of the upper Jurassic. In this succession we observe especially the relative subsidence of the protoconid and upgrowth of the para- and meta-conids. Contemporary with *Amphilestes* is the classical genus *Amphitherium* (Fig. 15). A recent examination of the type specimen by the writer revealed the very interesting fact that the molars of this genus are probably of the primitive tubercular-sectorial type—the oldest known example. Only the paraconid, metaconid and hypoconid have been observed heretofore, but one can see the tip of the main external cusp between the internal pair.

---

[1] I am much indebted to my colleagues Professors Macloskie and Winans for assistance in the selection of these terms.

This pattern is repeated, with a considerable elevation of the heel, in *Peramus* (Fig. 18) of the upper Jurassic.[1] Neither of the two foregoing are of the primitive heelless tritubercular type which is apparently found in *Spalacotherium* (Figs. 11), also upper Jurassic, and in the nearly related if not synonymous *Peralestes* (Fig. 12). Contemporary with the above, are numerous genera of the *Stylodon* order; among these, *Asthenodon* (Fig. 35) is of the primitive tritubercular type without the hypoconid, all the remainder present various modifications of the tubercular-sectorial.

This covers our knowledge of trituberculy in the Mesozoic period. No bunodont forms are known—they were probably developed during the Cretaceous, for a few are found well developed in the Puerco. In the Secodont series many of the types do not widely depart from those seen in the Jurassic, but the Bunodont series are universally characterized by the initial or advanced development of the proto- and meta-conules in the upper molars and the appearance of the *entoconid* upon the inner side of the hypoconid below.

The Principles governing Cusp Development. It is remarkable to note in how many particulars the actual succession of molar development in the Mesozoic period coincides with the theoretical scheme of origin of trituberculy proposed by Cope[2] and supported by Wortman[3] several years ago. At that time *Spalacotherium* and the genera now embraced under the Triconodontidæ were the only Mesozoic mammals whose molar structure was fully known, and the views of these authors were partly speculative and partly deductive from recent dental anatomy.

Two hypotheses may be advanced to explain the evolution of the tritubercular type. The first is that the type has been acquired by the selection of accidental variations in the production of new cusps and modelling of old ones. The second is, that the interaction of the upper and lower molars in the movements of the jaws has resulted in local increase of growth at certain points, resulting first in new cusps, then in a change of position and of form in the cusps. Both hypotheses are open to numerous objections and are by no means mutually exclusive, but the whole subject is so complicated as to require a separate treatment. The balance of evidence in tritubercular evolution seems to favor the second or kinetogenesis theory—as apparently witnessed in two laws of cusp development:

I. The primary cusps first appear as cuspules, or minute cones, at the

---

[1] This genus includes also *Leptocladus dubius* Owen, and *Spalacotherium minus* Owen (Fig. 18). See *Proc. Phila. Acad.*, Nov., 1888, p. 292.

[2] "The Evolution of the Vertebrata Progressive and Retrogressive," *American Naturalist*, April, 1885, p. 350.

[3] "The Comparative Anatomy of the Teeth of the Vertebrata," 1886, p. 418.

first points of contact between the upper and lower molars in the vertical motions of the jaws.

II. The modelling of the cusps into new forms, and the acquisition of secondary position, is a concomitant of interference in the horizontal motions of the jaws.

The second law applies especially to the evolution of the molars after the acquisition of the tritubercular stage, and has been ably proposed and supported by Ryder,[1] principally in its application to recent types of teeth. The first, although not heretofore distinctly formulated, is partly founded upon facts and principles advanced by Cope, and applies chiefly to the stages which have been discussed in this essay.

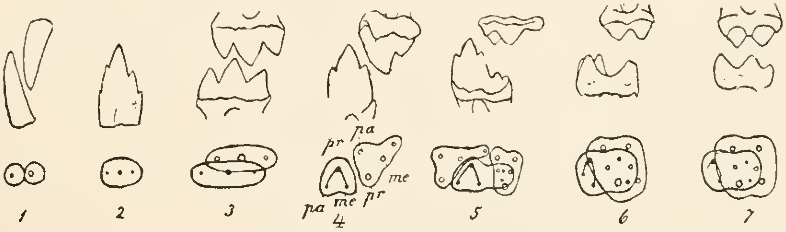


Fig. 36. Molars of opposite jaws in normal mutual relation. 1. *Delphinus*. 2. *Dromatherium*. 3. *Triconodon*. 4. *Spalacotherium* (lower), *Peralestes* (upper). 5. *Viverravus*. 6. *Mioclaenus*. 7. *Hyopsodus*.

During the homodont mammalian or sub-mammalian molar stage, the jaws were probably isognathous* and the simple cones alternated as in the Delphinidæ (Fig. 36, No. 1). The first additions to the protocone appeared upon its anterior and posterior surfaces. The growth of the para- and meta-conids involved anisognathism,[2] for we find in the later triconodonts that the lower molars closed inside of the upper (*Triconodon*, Fig. 36, No. 3). There are several transition forms, such as *Tinodon* (Fig. 10) and *Menacodon* (Fig. 9) between the primitive triconodont type and *Spalacotherium* (Fig. 11), and it has been assumed by Cope and the writer (*op. cit.*, p. 243) that the para- and meta-conids were first formed upon the anterior and posterior slopes of the protoconid and then rotated inwards, but it is also possible that they were originally formed upon the inner slopes. In the complemental formation of the upper and lower

---

[1] "On the Mechanical Genesis of Tooth Forms," *Proc. Phila. Acad.*, 1878, p. 45.

*[From recent discoveries among the South African Theriodonts it seems more probable that even in the ancestral reptile-mammals the upper jaws bit outside of the lower jaws and teeth, *i.e.* the jaws were anisognathous. The isognathism of the Dolphins is probably secondary.—Ed.]

[2] As employed by Ryder (*op. cit.*, p. 45): "So as not only to indicate respectively parity and disparity in transverse diameter of the crowns of the upper and lower molars, but also the parity or disparity in width transversely, from outside to outside," etc.

It is clear that in the homodont condition, with the teeth simply piercing the food, the greatest comminution (of the food) is effected by isognathism; in the triconodont stage, the jaws must be anisognathous to close upon each other, but the tritubercular stage admits a return to isognathism by the alternation of the triangles.

triangles the jaws remained nearly isognathous (Fig. 36, No. 4). There is no evidence as to the origin of the hypoconid, which as a rule preceded the hypocone, as it was developed very early. In the Stylacodontidæ (Figs, 22-35), *Phascolestes*, *Amblotherium*, etc., the crowns rapidly increased in transverse diameter, and, in some genera (*Kurtodon*, Fig. 13) they so far lost the tritubercular aspect that, but for the connecting form *Asthenodon* (Fig. 35), we might hesitate to place them in this series. The key to the further evolution of the crown is seen in the bunodont series during the lower Eocene period.

The superposition of the lower and upper molar patterns brings out many interesting facts. First, even in the complex crowns of the bunodont molars the primitive triangles retain their primitive alternating arrangement. Second, the jaws are somewhat anisognathous. Third, in support of the first law of cusp development, we observe that the protoconule and metaconule are developed at the points of contact with the ridges which extend from the hypoconid, and, secondly, that the hypocone appears at the point where the paraconid abuts against the hypocone. It follows from a comparison of numerous species of *Pelycodus* and *Mioclænus* that as the hypocone develops the paraconid recedes, as first observed by Cope; a fact difficult to reconcile with the kinetogenesis theory. In this manner the inferior primitive triangle is broken, the upper molars develop into the sexitubercular, the lower into the quadritubercular type.

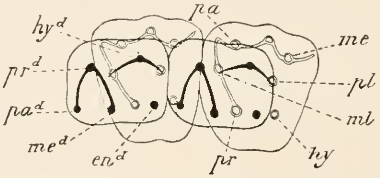


FIG. 37. Diagram of quadritubercular molars of both jaws in normal mutual relation; the superior molars in double lines; the inferior in black.

The complemental development of the upper and lower molars in the known genera of successive horizons is approximately displayed in the subjoined table. The Eocene list of genera will be greatly reduced, especially in the tritubercular-sectorial type, when the upper and lower jaws are found associated, and it must be clearly understood that the subtypes *a*, *b*, *c*, in this table, are closely related by transition forms. In fact, in carnivorous forms, the extreme secodont and bunodont types are frequently seen side by side, as in the first and second inferior molars of *Didymictis*. The chief distinction between these two series is the greater development of the secondary cusps and the almost invariable loss of the paraconid in the latter; this is effected by the broader surfaces of contact in the bunodont crowns. In the secodont series, on the other hand, the

		Secodont Series.			Bunodont Series.				
	I. A.	II.	III.	a.	a. c.	b.	c.		
Molars, - Upper, -	—	Triconodont.	Tritubercular.	Tritubercular.	Tritubercular.	Quinquetuberc.	Sexitubercular.	Aberrant.	Lophodont.
Molars, - Lower, -	Protodont.	Triconodont.	Tritubercular.	Tuberc. Sectorial.	Quadritubercular.	Quinquetuberc.	Quadritubercular.		Symborodont.
Middle Eocene,[1] Bridger, - -	—	—	—	22	4	7	9	1	11
Lower Eocene,[2] Puerco, - -	—		—	6	2	2	1	—	—
Upper Jurassic,[3] -	—	3	2	5	—	—		4	—
Lower Jurassic, -	—	3		1	—	—	—		—
Triassic, - - -	1	1	—	—	—	—	—	—	—

---

[1] From Prof. Marsh's list of Bridger genera, excluding the Rodentia (see various papers). The Insectivora and Creodonta belong to sub-type a; the Lemuroidea, to sub-types b and c.

[2] From Prof. Cope's list of Puerco genera (see "Synopsis, etc.")

[3] From Author's list of Mesozoic genera (see *op. cit.*, p. 247).

development of the secondary cusps is subordinated, and the metaconid is almost invariably suppressed.[1]

Adapis and *Anaptomorphus* are examples of sub-types *a*, *c*, associated; for it frequently happens that the paraconid atrophies without a complete enlargement of the hypocone. A study of the diagram demonstrates, however, that the association of sub-types *b* and *c* is impossible. The recent monkeys [Primates] *Tarsius* and *Loris* afford a good illustration of the association of tritubercular, quinquetubercular, sexitubercular, and quadritubercular molars.

The subsequent evolution of the molars in different orders was variously characterized, first, by loss of the primary cusps, *e.g.* the metaconid in the Carnivora, the paraconid in the Ungulata. Second, by the loss of some of the secondary cusps, *e.g.* the proto- and meta-conules in the Artiodactyla.[2]* Third, by the metamorphosis in the form of the cusps. This subject has been fully treated by Rütimeyer, Kowalevsky, Cope, Schlosser, and others.

The Relation of Trituberculy to the Persistence of Mammalian Phyla.—The above table shows somewhat indefinitely, but none the less positively, the general progression of the Mammalia to and from the primitive tritubercular type. As already stated, even with our present very limited knowledge, certain stages appear to have been characteristic of certain periods, as follows: the triconodont in the lower Jurassic; the primitive tritubercular and tubercular sectorial in the upper Jurassic: the secodont and bunodont sub-types of trituberculy, predominated in the Puerco; in the Bridger, the Perissodactyl ungulates had mostly passed beyond into the lophodont and symborodont types, and the Artiodactyls were approximately in the stage of sub-type *c*; but the Lemuroidea, Creodonta, Insectivora, etc., were, almost without exception, tritubercular.

There can be little doubt that, parallel with the tritubercular forms, in each period, there were aberrant or degenerate types, but it is difficult to determine which these are. Many Mesozoic types which the writer formerly considered aberrant, have now proven to be tritubercular.[3] The upper Jurassic genera included under the Diplocynodontidæ (see Marsh, *Amer. Journ. Sc.*, April, 1887, p. 338) are apparently aberrant. There

---

[1] See Cope, "Origin of the specialized Teeth of the Carnivora," *Am. Naturalist*, March, 1879.

[2] Schlosser, "Beitrage zur Kenntniss der Stammgeschichte der Hufthiere," *Morph. Jahrb.*, 1886, p. 123, has especially drawn attention to the probability that the Artiodactyla were derived from sexitubercular forms.

*[Many Artiodactyl families, *e.g.* Trigonolestidæ, Leptochœridæ, Dichobunidæ, Anthracotheriidæ, Elotheriidæ, retain the protoconule. The loss of the metaconule is only apparent, for it is represented in the enlarged postero-internal cusp, analogous in position to a cingulum-hypocone, in the molars of most Artiodactyla.—Ed.]

[3] See "Additional Observations upon the Structure and Classification of the Mesozoic Mammalia," *Proc. Phila. Acad.*, Nov., 1888.

are several degenerate types among the Puerco and Wasatch Creodonts, such as *Dissacus* and *Mesonyx*. But there is a striking proof of the superiority of the tritubercular molar in the fact that, according to our present knowledge at least, the Jurassic mammals possessing aberrant or degenerate molar types did not persist into the Puerco, nor did such types in the Puerco persist into the Bridger. There is some doubt as to the persistence of the sub-tritubercular stages; the writer formerly considered the *Thylacynus* molars as triconodont: but Mr. Lydekker has called attention to the probability that the metaconid has disappeared and been replaced by a heel as in the sectorial teeth of the Carnivora. The disappearance of the degenerate types may be attributed to the general principle that rapid specialization and loss of parts leads ultimately to extinction, by depriving the animal of the means of adaptation to new conditions or surroundings. The mechanical superiority of the tritubercular type over every other has been repeatedly demonstrated in its plastic capacity of adaptation to the most extreme trenchant and crushing functions.

CHAPTER III.

TRITUBERCULY IN RELATION TO THE HUMAN MOLAR TEETH AND THE PRIMATES.

1.

ONTOGENETIC DEVELOPMENT OF THE TEETH.

[Reprinted from a paper in the *Anatomisches Anzeiger*, Jahrg. VII. (1892), 8vo, Jena, pp. 740-747, entitled "The History and Homologies of the Human Molar Cusps (a review of the contributions of Dr. A. Fleischmann, Dr. Julius Taeker, and Dr. Carl Röse) ".]

THE embryonic development of the cusps of the molar teeth in the Mammalia has lately been discussed in two very interesting papers by Taeker[1] and Röse,[2] and the homologies of the upper and lower cusps have been investigated by Fleischmann.[3] The work of the latter is based upon the comparative study of recent types of molars, and the author reaches the conclusion that the system of homologies proposed by Cope[4] and expanded by Osborn[5] between the upper and lower molars is erroneous.

Taeker's paper is chiefly devoted to the study of the succession and embryonic form of the molar cusps in different Ungulates: he supports by ontogeny the view based upon palæontology that the ancestral cusps were conical; he shows that in the *lower molars* the ontogenetic order of development corresponds with the phylogenetic order as traced by Cope among the fossil forms, but that in the *upper molars* the ontogenetic order does not correspond with the primitive phylogenetic succession as traced

---

[1] "Zur Kenntnis der Odontogenese bei Ungulaten," Dorpat, 1892.

[2] "Über die Entstehung und Formabänderungen der menschlichen Molaren," *Anat. Anz.*, 1892, Nr. 13 u. 14.

[3] "Die Grundform der Backzähne bei Säugetieren und die Homologie der einzelnen Höcker," Berlin, 1891.

[4] "The mechanical Causes of the Development of the Hard Parts of the Mammalia," *Journ. of Morphology*, 1889. Also earlier papers.

[5] "The Structure and Classification of the Mesozoic Mammalia," *Journ. Acad. Nat. Sc. Phila.*, 1888, p. 240; also: "The Evolution of Mammalian Molars to and from the Tritubercular Type," *American Naturalist*, 1888.

by Cope. Upon the whole, however, he finds a very striking parallelism[1] between embryogeny and phylogeny both as to the form and succession of the cusps (see Table on p. 51).

Röse's paper is also of great value in proving that in *Homo* and *Didelphys*, representing two widely separate classes, the embryonic history of the lower molars approximately repeats the ancestral history; he independently supports Taeker in the conclusion that the upper molar cusps do not repeat the ancestral order assigned by the Cope-Osborn theory, he therefore agrees with Fleischmann that we have mistaken the history and homologies of the upper molar cusps, and suggests very courteously that the Osborn nomenclature should be transposed to correspond with the embryological order; he further advances the original theory that the mammalian cusps have arisen not by addition to the single reptilian cone, but by the fusion of a number of cones together. I will first consider the main principles involved in these papers, and then mention some of the less important special points. The following table exhibits the correspondence and contrast between the phyletic and embryonic succession, as well as the homologies and order of appearance, according to the Cope-Osborn theory.

From this table the striking parallelism between ontogeny and phylogeny in the lower molars is brought out. Also the contrast between the early appearance of the *hypoconid* both in phylogeny and ontogeny and the late appearance of the *hypocone* phylogenetically and ontogenetically.

1. *That the primitive form of mammalian molar was a single cone to which all the other cusps have been successively added.* I may first take up the different theory of cusp origin proposed by Röse, and observe that whatever support it may receive from embryology is offset by the overwhelming evidence of palaeontology. In figure 38, I have epitomized the slow transformation of the single-fanged conical reptilian tooth (1), such as we see persisting in the Cetacea,* into the low-crowned human lower molar (8). The first departure towards the development of lateral cusps is seen in the triassic *Dromatherium* (2); the second is in the contemporary *Microconodon* (3); the third is in the jurassic *Spalacotherium* (4); in the fourth (*Amphitherium*, Jurassic) (5), we see the three cusps of the primitive triangle and the first cusp of the talon, hy^d. In *Miacis* of the lower Eocene (6) the figures of the internal and crown views of the three molars show how the primitive anterior portion (trigonid) of the crown was reduced to the level of the posterior portion (talonid) while retaining all of its cusps. In the next figure (7) we see the lower molars of the

---

[1] See Osborn, "Odontogenesis in the Ungulates," *Amer. Nat.*, 1892, p. 621. A fuller review of Dr. Taeker's paper.

*[More probably secondary in Cetacea. See pp. 79, 190.—Ed.]

oldest monkey or lemur known, *Anaptomorphus*, which illustrate the loss of the antero-internal cusp or paraconid, pa^d,—this is present as a rudiment in m^1 and m^2, but has disappeared in m^3. This accounts for the history of all the cusps in the human lower molar. Thus in the rich series of Mesozoic[1] and lower Eocene Mammals we can observe the actual rise, succession, and decline of all the six cusps, and do not require any new hypothesis to explain their appearance.

Dr. Röse supports his fusion hypothesis by a reference to the Multituberculates (p. 101); he could hardly have made a more unfortunate choice, because between the little pauci-tubercular *Microlestes* of the upper Triassic and the multi-tubercular *Neoplagiaulax* of the lower Eocene we can follow the successive addition of tubercles with ease. I expect soon to demonstrate that the molars of this aberrant group were also of tritubercular, *i.e.* haplodont origin.[*]

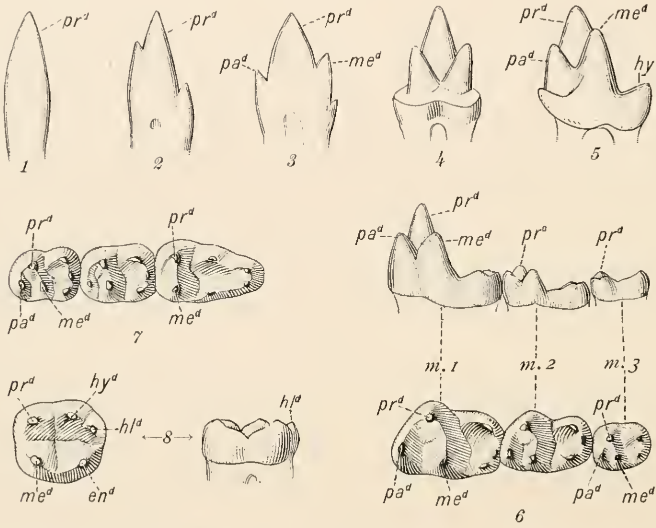


FIG. 38. Evolution of the cusps of the Human Lower Molar. [1. Simple conical, reptilian tooth. 2. *Dromatherium.* 3. *Microconodon.* 4. *Spalacotherium.* 5. *Amphitherium.* 6. *Miacis.* 7. *Anaptomorphus.* 8. *Homo.*]

It is a striking fact that all[†] the molars of the Triassic and Jurassic periods are distinguished by one conic cusp much larger and more prominent than the others which are smaller and upon a lower level. What are the positions and homologies of this cusp in the upper and lower teeth?

---

[1] See the Memoirs of Owen and Osborn upon the Mesozoic Mammalia.

[*] [See, however, the later views expressed on page 105, foot note.—ED.]

[†] [Even in *Microlestes* one cusp is higher than the others. (See Fig. 48, p. 102.) But too much importance should not be attached to this fact.—ED.]

TABLE SHOWING THE PHYLOGENETIC ORDER AS OBSERVED BY COPE AND OSBORN, AND THE ONTOGENETIC ORDER AS OBSERVED BY RÖSE AND TAEKER. (Cf. Fig. 1, p. 6.)

A. Phylogenetic Order.				B. Ontogenetic Order.				
Geological Periods.	Order.	Comparative.	Human.	Order.	Primates[2].	Marsupials[2].	Ungulates[3].	Order.
		UPPER MOLARS.						
Permian	1	Protocone	Ant. lingual.	1	Paracone	Paracone	Paracone	1
Triassic & Jurassic	2 & 3	Paracone	,, lateral.	2	Protocone	Proto- ,,	Meta- ,,	2
		Metacone	Post. ,,	3	Metacone	Meta ,,	Proto- ,,	3
Cretaceous	—							
Eocene & Miocene	4	Hypocone	Post. lingual.	4	Hypocone	Hypo- ,,	Hypo- ,,	4
		LOWER MOLARS.						
Permian	1	Protoconid	Ant. lateral.	1	Protoconid	Protoconid	Protoconid	1
Triassic & Jurassic	2 & 3	Paraconid	(degenerated[1]).	2	Metaconid	Para- ,,	Meta- ,,	2
		Metaconid	Ant. lingual.	3	Hypoconid	Hypo- ,,	Hypo- ,,	3
Jurassic	4	Hypoconid	Post. lateral.	4	Entoconid	Ento- ,,	Ento- ,,	4
Cretaceous	5	Entoconid	,, lingual.	5	Hypoconulid	Meta- ,,		5
Lower Eocene	6	Hypoconulid	,, mesial.					

[1] This cusp degenerates both in the early Primates and Ungulates.

[2] As I understand Dr. RÖSE.

[3] ,, ,, Dr. TAEKER.

2. *That the protocone is invariably the anterior lateral (antero-external) cusp in the lower molars and the anterior lingual (antero-internal) cusp in the upper molars.* The former part of this proposition is now almost self-evident. It is absolutely proven in such a series as we see in Figure 38, and is now corroborated by the embryological researches of Taeker and Röse.

As to the present position or homologue of the reptilian protocone in the upper mammalian molar there is relatively, I admit, more room for doubt, mainly for the reason that fossil upper jaws are very scarce. If, as held by Fleischmann and Röse, the *antero-external* cusp is the protocone, then the whole system of homologies held by Cope and myself falls to the ground. Let us look at the evidence:

First: In the numerous upper jaws of *Triconodon* (Figs. 7, 8) of the upper Jurassic, the main cusp is always the middle one of the three, corresponding with the large middle cusp of the lower molars which we know to be the protocone. Second: In the upper molars of *Spalacotherium** (Jurassic), in which the lower molars are of the simplest tritubercular type (Fig. 36, No. 4), the most prominent cusp by far is the *antero-internal*, supporting my view. Third: In all the Amblotheriidae † of the upper Jurassic there is a triangle of cusps in both upper and lower molars, in each the apex is formed by the most prominent styliform cusp, *this is antero-external in the lower molars and antero-internal in the upper molars.* Is it at all probable, at this early period, when the protoconid is still the most conspicuous cusp in the lower molars that a corresponding cusp of the same form, but reversed position, invariably found in the upper molars is *not* homologous? According to the Fleischmann-Röse view it is not, but the main lower cusp is homologous with one of the spurs of the main upper cusp. Fourth: There are other important grounds of a mechanical nature. Starting with the study of modern, instead of the oldest fossil forms, Fleischmann has, I believe, reached not only an erroneous conception of the homologies of the separate cusps, but of the equally important homologies in the functional regions of the upper and lower crowns. In each we may distinguish two regions:

The elevated primitive triangle (trigon) with a primitive cutting, piercing or sectorial function.

The depressed heel (talon), with a primitive crushing or grinding function.

In the earliest stages the upper and lower molars were simple triangles of cusps, as in the modern Cape Mole, *Chrysochloris.* ‡ The lower molar had the apex (protoconid) turned outwards and the base (para-

---

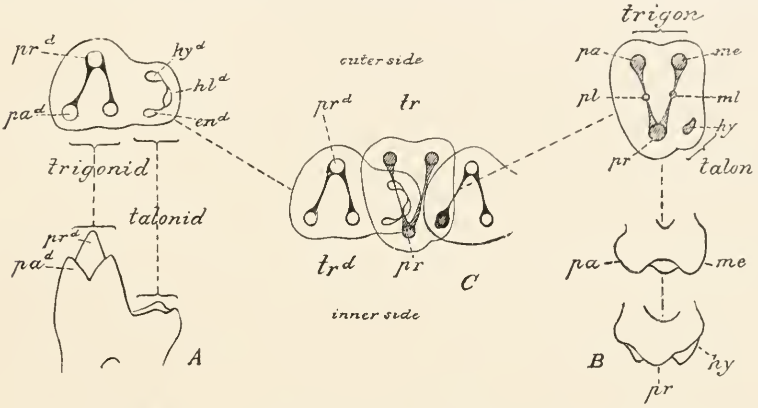
*[Regarded as a synonym of *Peralestes.* (See p. 35 and Fig. 12.)—Ed.]

†[Represented by *Kurtodon* (Fig. 13, p. 26), *Dryolestes* (Fig. 14, p. 26).—Ed.]

‡[According to the views expressed on pages 124, 126, 227, the form of the molars in *Chrysochloris* is entirely secondary.—Ed.]

and meta-conids) turned inwards, while the upper molar had these relations reversed. As shown in the accompanying diagram (Figure 39), the opposition of these triangles makes a perfect cutting mechanism, and as Cope has shown this is effective at every stage of development. If the protocone were at the outer angle of the upper molars, it is impossible to conceive of an effective series of intermediate stages.[*]

The first step[†] towards the crushing function is the development of the hypoconid upon the incipient talonid which is later reinforced by two more cusps, the entoconid and hypoconulid. *Thus the entire heel or talonid is complete upon the lower molars before it commences to develop upon the upper molars,* as shown in *Anaptomorphus* (Fig. 36, No. 7, and Fig. 40, No. 9, Fig. 130) as well as in the ontogeny.



Lower Molar. Upper and Lower Molars opposed. Upper Molar.

FIG. 39. Key to Plan of Upper and Lower Molars in trituberculate mammals. Each tooth consists of a triangle (*trigon*) with the protocone (*pr*) at the apex. The apex is on the inner side of the upper molars and on the outer side of the lower molars. [In *C* the upper molar is too far internal and posterior. The protocone of the upper molar should fit into the basin of the talonid of the lower molar. See Figs. 60, 208, 209.—ED.]

Upon the upper molars the talon is only developed in bunodont types, such as the Primates and Ungulates, to still further increase the crushing area of the crowns; it always arises as seen in the Primates (Fig. 40), by a slow upward growth from the cingulum, opposite the protocone. In its early stages the hypocone, *hy*, always resembles the early stages of the hypoconid and conclusive proof of its talon-like character is seen among the Condylarthra (*Haploconus*), in which it appears as a wide separate heel. So far, therefore, from the truth of Fleischmann's supposition that the upper molars have one more element (the "entomere") than the lower, exactly the reverse is the case, for the lower molars early acquire much the greatest extension of the talon, while retaining all the elements of the trigon.

---

[*] [In opposition to this, however, see the views of Gidley in Fig. 208.—ED.]

[†] [This paragraph appears misleading. See pp. 61*, 68*, 82*.—ED.]

A beautiful illustration of the fundamental pattern of trigon and talon in the upper human molars is shown in Röse's figure 4 of the molar of a six months' child (Fig. 42). The protocone makes the apex, and is connected by two spurs with the two external cusps, the space between which is comparatively open as in the primitive forms.

Thus the homology of the antero-internal cusp of the upper molar with the protocone is well supported by palæontology and by dental mechanics, but how shall we meet the embryological counter-evidence established by the agreement between the independent investigations of Röse and Taeker?

This is also, I believe, explained by a study of the fossil forms. As we have seen in the most primitive types the protocone was the most prominent cusp in both jaws, but in course of later development of the upper molars, during the Cretaceous and Eocene periods, the protocone was depressed to the level of the paracone and metacone (see the primitive Carnivora, Creodonta, and Insectivora). On the other hand, in the lower molars the protoconid retained its relatively prominent position and size. If the ontogenetic development of the lower molars corresponds with the ancestral order, it is probably because the relative primitive position of the cusps was conserved: whereas in the upper molars, in which there is less correspondence, it was lost. I find in the lower Eocene Ungulates that the paracone and metacone are more important cusps than the protocone. So far as the fossil Primates of the lower Eocene are known, we find the protoconid is the most prominent cusp in the lower molars, while in the upper molars the protocone is less prominent than the external cusps. Röse's argument really turns therefore upon the expectation that fœtal development should repeat ancestral history of the Cretaceous period! As the flattened form of the crown is from the start a Cænozoic type, we should hardly expect the order of cusp succession to invariably revert to a Mesozoic type. While not thoroughly convincing, there is a great deal of force in this way of meeting the embryological data.

Nomenclature. Röse (p. 400) apparently mistakes the homologies of the lower molar cusps of man, for he has overlooked the fact that the primitive anterior lingual cusp, or paraconid, has degenerated in the Primates (excepting in a few Lemurs) while it persists in *Didelphys.* It is not seen in the human lower molar at all. Its declining stages mark the loss of sectorial function and can be readily followed in the lemurs, and fossil monkeys; as shown by Cope and myself it degenerates while the hypocone in the upper molars develops. It follows that the anterior lingual in man is the metaconid, while in *Didelphys* it is the paraconid and the mid-lingual is the metaconid. The posterior lateral cusp is undoubtedly the hypoconid. Röse proposes the term "pentaconid" for the distal or posterior intermediate cusp (*hl^d*, Fig. 38, No. 8). The term is inappropriate, because this is not the fifth but the sixth cusp when we reckon the paraconid. It is analogous to the intermediate tubercles of the upper molars—I have therefore suggested the term "hypoconulid" for it; this cusp is almost universal among lower Eocene Mammalia; in the last lower molar it forms the additional lobe; it is found strongly developed in many of the higher Primates.

Röse (p. 406) expresses the belief that the typical form of primate molar was quadritubercular as opposed to Cope's view that trituberculy in human dentition is a reversion to the Lemurine type. The study of the fossil forms as well as of any complete zoölogical series can leave no doubt that the quadritubercular form is a comparatively recent acquisition.

In conclusion, I would refer both these authors to the types of molar teeth found among the Mesozoic Mammalia. It was while studying the rich collection in the British Museum that I became convinced of the force and universal application of the tritubercular theory proposed by Cope.

American Museum of Natural History,
New York, *July* 18*th*, 1892.

2.

The History of the Cusps of the Human Molar Teeth.

Address before the New York Institute of Stomatology, April 19th, 1895.

[Reprinted, under the title given above, from the *International Dental Journal*, July, 1895.]

I wish to congratulate the members present upon the formation of this *Institute of Stomatology*. It seems to me to mark one of the stages in the remarkable specialization of human knowledge when, at the present time, it is proposed to devote the work of an entire society to the scientific study of the mouth parts, as I understand your object to be; and I also gather from the fact that you have asked me, as a comparative anatomist, to deliver an address this evening, that you look at the subject in two ways,—from the stand-point of applied or practical science and from the stand-point of theory. It is on the theoretical side that I should like to bring before you this evening the *history or origin of the cusps of the human molar teeth*.

We take up this skull of an Eskimo, and you will observe that the teeth (Fig. 40, No. 11) are slightly worn, and that the molars have four cusps.[1] Half a century ago this would have been considered as something ultimate, simply as an adaptation to human diet; but now that we have come to understand the doctrine of evolution, we ask ourselves, What is the meaning of these cusps? what is their history? what is their origin? Now, these four cusps which are present on the four corners of the teeth might be explained by evolution in three ways. We might imagine that the crown of the tooth was originally a low rounded summit, and that on the summit these four cusps appeared at each angle: no one has advocated this. Or we might imagine that they represent the coming together of a number of tips of pointed teeth, such as we see in the jaw of this member of the dolphin family; this is the theory which has been recently advanced in Germany, and it has been called the "*cusp concrescence*" theory. Or, again, we might imagine that these cusps have originated by a gradual addition to the sides of a primitive single cone: this we call the "*cusp differentiation*" theory, or the theory of cusp addition, in distinction from concrescence. The differentiation theory is supported by Cope, by myself, and others in this country.

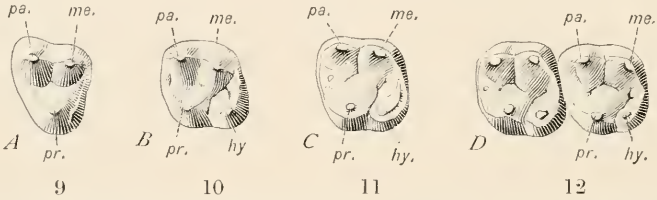


Fig. 40. Evolution of the Human Upper Molars. 9. *Anaptomorphus*, a lower Eocene monkey. 10. An upper Eocene monkey. 11 and 12. Human: 11, Esquimaux; 12, Negro. See addition of "talon," *hy*, to "trigon" composed of *pa*, *pr*, *me*.

Now, suppose an evolutionist were to trace back the history of the monkeys and of other animals among their fossil ancestors, he would find that the further back his researches extended the more simple the types of the teeth would be; he would find that the teeth of the oldest types of ancestral mammals have a simple conical form, the form that is preserved in the teeth of the whales and the dolphins of the present day (Fig. 42**A*, p. 64), or in the Edentates as represented in the group to which the sloth and the armadillo of South America belong.*

We have the same type of conical tooth preserved in the human canines, and if we turn from the teeth of man, in which the canine has almost entirely lost its original laniariform or flesh-tearing shape, to that of the lower monkeys, we see that the canine is really a

---

[1] E. D. Cope, "On the Tritubercular Molar in Human Dentition," *Jour. of Morphology*, July, 1888, p. 7.

*[In both groups the simple conical form is now believed to be secondary (pp. 79, 151, 191).—Ed.]

pointed tooth; so that we may draw a suggestion from this fact that all the teeth of the series at one time were pointed.

It is moreover true that wherever we find these pointed teeth they are present in the jaw in large numbers, sometimes sixty or seventy on one side and usually running far back into the mouth, and it is this fact which led to the suggestion of the theory of "concrescence" in the formation of molar teeth.

The Concrescence Theory.

You might at this stage be not inclined to take this "concrescence theory" seriously, but my address has been suggested largely by the fact that it has been taken very seriously by some well-known anatomists in Germany: as seen in the position of Professor Schwalbe,[1] in a recent article, in which he reviews the entire literature in regard to the formation of teeth published during the past fourteen or fifteen years, and concludes that in the concrescence theory and the differentiation or cusp addition theory the evidence is so evenly balanced that he cannot decide between them. It is, therefore, a question *sub judice*, and worthy of the attention of odontologists. As to the source of this theory, it was proposed simultaneously by two Germans, both of whom claim the credit of originating it. One is Dr. Carl Röse, a physician of Freiburg, a man of fine powers of research and great energy, since he has, during the past few years, issued in rapid succession a series of valuable papers on the embryological development of the teeth, which place him in the front rank of students of this subject in this decade. The other is Professor W. Kükenthal, of Jena, whose views sprang principally from the study of the teeth of whales. While these two writers are in doubt as to which should enjoy the precedence, I find, in correspondence with my friend Dr. Ameghino, of the Argentine Republic, also originally a physician and now a distinguished palæontologist, that he promulgated this theory as far back as 1884. In a work which he published at that time, entitled *Filogenia* he says: "For the reasons we are about to give it is evident that all mammals which possess compound teeth have in past periods possessed a very much larger number of teeth, but of quite simple conical form, like those of the modern dolphin. The most primitive mammals must also have had a number of very elevated teeth, but it is difficult at the present time to determine how large this number was. Nevertheless, if we take as an example a mammal in which the dentition is complete, as in the *Macrauchenia*[2] or in the horse, and

---

[1] "Ueber Theorien der Dentition," *Anatomischer Anzeiger Centralblatt*, 1894.

[2] This is one of the peculiar extinct South American hoofed animals.

if we reduce the number of its compound teeth, we find that the most remote ancestors of these forms must have possessed more than one hundred and fifty teeth. This number is certainly not exaggerated, because *Priodon*, the giant tatusia (armadillo), a mammal in an already quite advanced stage of evolution, possesses nearly one hundred simple teeth, and in the dolphin this number rises from one hundred and fifty to one hundred and seventy." I read this to show that if there is any truth in the concrescence theory, Dr. Ameghino partly deserves the credit for it. Moreover, we learn from Schwalbe that the same theory was advanced by Professor Gaudry in 1878, and still earlier by Professor Magitot in 1877.

Now let me illustrate, in a very simple manner, what is meant by the theory of concrescence and how we can imagine that the human molars have been built up by bringing together a number of isolated teeth. Placing a number of conical teeth in line, as they lie in the jaw of the whale, they would represent the primitive dentition. In the course of time a number of these teeth would become clustered together in such a manner as to form the four cusps of a human molar, each one of the whale-tooth points taking the place of one of the cusps of the mammalian tooth,—in other words, by a concrescence, four teeth would be brought into one so as to constitute the four cusps of the molar crown. Vertically succeeding teeth might also be grouped.

Now, what evidence is there in favour of this theory, and what is there against it? First, there is this, that all primitive types of reptiles from which the mammalians have descended and many existing mammals, as we have noted, have a large number of isolated teeth of a conical form; secondly, we find that by a shortening of the jaw, the dental fold or embryonic fold, from which each of the numerous tooth-caps is budded off in the course of development, may be supposed to have been brought together in such a manner that cusps which were originally stretched out in a line would be brought together so as to form groups of a variable number of cusps according to the more or less complex pattern of the crown.

What may be advanced against this theory? This, and it is conclusive to my mind: we find at the present time that cusps, quite similar in all respects to each of the cusps which form the angles of the human molar, are even now being added to the teeth in certain types of animals, such as the elephant, whose molar teeth cusps are being complicated now or until very recent times. Then we find in the Mesozoic period certain animals with tricuspid teeth. Now, according to the theory of concrescence these teeth ought not to show any increase of cusps in later geological periods; but as we come through the ages nearer to the present time we find that the successors of those animals show a very much larger number of cusps. How is this increase of cusps to be accounted for? Has there been a reserve store of conical teeth to increase the cluster? No. Most obviously, to every student of the fossil history of cusps there is no reserve store, but new cusps are constantly rising up on the original crown itself by cusp addition.

However, do not let me give you the impression that these researches of Röse and Kükenthal are not of the greatest value and interest: we shall see later on how the very facts of embryology which are advanced by Dr. Carl Röse in support of his hypothesis can be turned against him and used to support the differentiation theory.

. . . .

I have no doubt many of you have observed, in the examination of human lower molars, that occasionally instead of having four cusps they have five. The fifth cusp always appears in the middle of the heel, does it not, or between the posterior lingual and the posterior buccal? You find this in the monkeys and in many other mammals, but I know of no record of the ancient anterior lingual reappearing.

So we see that the human lower molar tooth with its low, quadritubercular crown has evolved by addition of cusps and by gradual modelling from a high-crowned, simple-pointed tooth. Now this, and I say it with great confidence, is what has actually taken place. It has not come about by bringing together single reptilian cones: it has been simply by the addition of one cusp after another to an original single reptilian cone until there were six cusps, and then, in the adaptation and fitting of the lower teeth to the upper, one of the cusps has disappeared. This cusp was the primitive anterior lingual, or, in comparative anatomy, the *paraconid* (Fig. 38, No. 8).

Now let us follow the history of the upper teeth and see why the "primitive anterior lingual," or paraconid, in the lower jaw has disappeared.

You are constantly in your practice, observing that one tooth in the lower jaw gets into the way of another tooth and has to be pushed out of place in order to place its opponent in the upper jaw into its proper position. This is exactly what Nature has done; Nature has abandoned that lower cusp simply because, in the simultaneous transformation of the upper teeth from a three-cusp to a four-cusp type, there was no room for it.

Mechanical Relations of the Upper and Lower Teeth.[*]

Let us examine the upper teeth. We must say, in the first place, that our evidence here is not nearly so complete, because a lower jaw, from its thin nature, is more apt to be preserved fossil than an upper jaw: so that in the older rocks we meet with ten lower jaws to one upper jaw, and we cannot get the same evidence as to the history of the upper jaw that we have of the lower: but although we are not able to trace the history of the upper teeth with the same accuracy or degree of certainty, we have every reason to think it was the same. We find the upper teeth shaped like a *triangle*, as in Figs. 12, 13, 14, so we may imagine that the same triangle which was formed in the lower jaw was formed in the upper jaw, with this important difference, that in the upper jaw the base of the triangle was turned outward, whereas in the lower jaw the base of the triangle was turned inward (Fig. 36, No. 4).

What I mean by this is illustrated in the accompanying figure (Fig. 41, *A*—*J*), which is an epitome of the whole history. The upper teeth are represented solid, the lower teeth as hollow circles. In *A* we see a row of single cusps, the lower somewhat inside of the upper. In *B* the lateral cusps are added. In *C* they are enlarged. In *D* the cusps are pushed outward and inward into triangles. In *E* a spur is added on the lower molar triangle, which in *F* and *G* grows out into a broad heel. In *H* and *I* a spur appears upon the upper molar triangle, and in *J* this causes the lower molar triangle to lose its anterior cusp. Nature has corrected any possible interference between these triangles in a simple manner by turning the base of the triangle of the upper molars outward towards what you call the buccal side. In the lower jaw, on the other hand, the base of the triangle is turned inward to the lingual side, so that finally we have the two triangles alternating, coming together as in *D* and making a beautiful cutting mechanism; because if any food gets in between these triangular shears the food tends to press these teeth forward and backward, therefore crowding the teeth more closely together and tending to tighten and improve the shear, whereas if the teeth were placed in line, as in *C*, and food were to get in between, the effect would be to crowd the two jaws apart and lessen the exact cutting power of the shear.

Now we see that we can compare the lower and upper triangles to each other. How about the heels or spurs, and why were they developed? They were developed because these animals required

---

[*] [Other and more recent views as to the mechanical relations of the evolving tooth parts are presented on pp. 61*, 68*, 82*, Figs. 208, 209.—Ed.]

crushers as well as cutters*: they required to break up their food, and consequently a crushing surface was developed in each heel. In the course of time the animal gave up its cutting and tearing function, and in all the group of animals to which man belongs it acquired a purely crushing function, as seen in the teeth of the baboon. As that became necessary, the next step was to transform the entire upper tooth into a crusher as well as the lower, and to

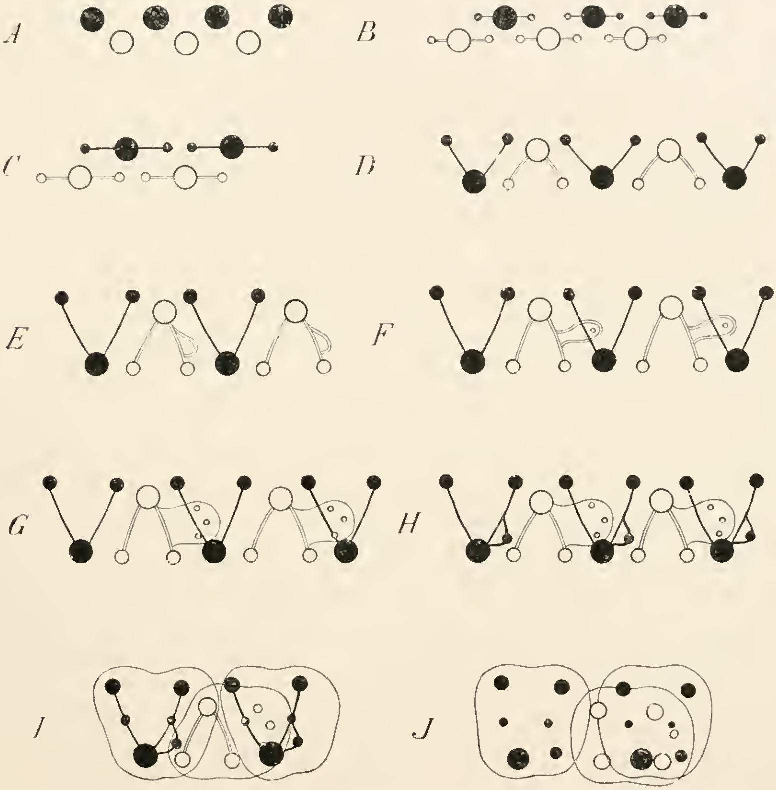


FIG. 41. Mechanics of Cusp Addition (diagrammatic). Compare with shaded drawings in Figure 38. *A*, the conical stage* (No. 1); *B*, *C*, the triconodont stages* (Nos. 2, 3); *D*, the first triangular stage† (No. 4); *E*, *F*, *G*, the triangular upper molar, the lower molars, with triangle and heel (Nos. 5, 6, 7, 9); *H*, *I*, upper and lower molars, with triangle and heel; *J*, human type, upper molars, with four cusps, triangle, and heel (Nos. 10, 11, 12); lower molars, with five cusps, antero-internal cusp having disappeared (No. 8). [Compare this diagram with that of Mr. Gidley on p. 208. It is now regarded by Professor Osborn as erroneous in several particulars.—ED.]

* Note that the upper teeth (black) bite outside the lower teeth (see Fig. 221).

† Note that the protocones bite inside of and between the lower teeth (see Fig. 221).

---

*[While the anterior and posterior *sides* of the upper and lower triangles no doubt formed the principal cutting surfaces, yet the principal piercer and crusher in the upper molars is the internal tip of the triangle, namely, the protocone, which opposes the talonid below. The hypocone is an accessory crusher developed to oppose the trigonid and the space back of the preceding lower molar.—ED.]

fill out all the spaces between them, so that a square lower tooth would abut against a square upper tooth, as in *J*, and this was done by simply adding a heel to this tooth. Now, what would that heel come against in *I*? It would come against the anterior cusp of the lower triangle; therefore that cusp had to be removed, so when the upper heel was developed this lower cusp was removed and the lower molar, which had six cusps, presented only five; then the second lingual cusp was pushed forward as in *J*, and the tooth was transformed into a quadritubercular molar.

Evidence that the Upper Human Molars were Triangular.

How do we know that is so? We have some conclusive evidence of it in other animals of the group to which man belongs. Beginning with the lemurs, the lowest type of monkeys, and entirely separate in many respects from the higher types, we find almost without exception that the upper teeth are triangular, there being no posterior cusp, so that Fig. 40, No. 9, accurately represents a tooth of the lemurs, and it also represents the tooth of the true monkeys which we find in the Eocene period; in other words, all monkeys or all primates (the group to which man belongs) had at the outset this triangular upper molar. Then earlier or later in the Eocene or Miocene the spur began to be developed which transformed a three-cusp tooth or a triangular tooth into a quadritubercular tooth. That spur became enlarged and finally, in civilized races of men, we have a tooth of this form as the prevailing type of tooth. These stages are shown in Fig. 40.

Now, we might say that the evidence is not perfectly satisfactory, because we have no positive reason for believing that the human teeth were derived from such a type as this; they may have come along another line of descent, and for that reason we have to show here, through the kindness of one of the members of the dental profession in this city, the teeth of an Eskimo (Fig. 40, No. 11), which, as Professor Cope has pointed out, differ from the teeth of all negroes, all Indians, and all the lower races of men, in presenting in a much clearer manner the primitive triangular arrangement of the cusps that characterize the lemurs. A friend has just been telling us what very few of us knew,—that the Eskimos do not chew their food: they simply swallow it whole or gulp it down: and their food consists largely of blubber. Blubber does not form much resistance to the teeth, and, whether as a mechanical or an inherited effect of the lack of resistance of soft food through many generations of blubber-eating Eskimos or not, the teeth of these Eskimos are exceptionally *tritubercular*. This fact was pointed out by Professor Cope in his article entitled, "Lemurine Reversion in Human Dentition."[1]

Up to a certain point in their evolution the molar teeth of all mammals followed exactly the same route.* It follows that if we once grasp the principles of cusp addition upon this triangular ground plan we can compare the cusps of the molars of man with those of any other mammal. In the teeth of the bear, for example, the homology is very obvious indeed. But in the teeth of the cat the homologies can only be determined when we procure the ancestral forms of cats, for in the evolution of the large sectorials many cusps have degenerated. Some years ago, when I had fully demonstrated the truth of Cope's theory by my own studies, I saw the importance of using a set of standard terms for the cusps. These have since been almost universally adopted by comparative anatomists, but have not, as yet, I believe, made much headway among human odontologists. They are, as follows, as applied to the human teeth :

UPPER MOLARS.

Anterior palatal	Protocone	Primitive triangle, or "trigon."
Anterior buccal	Paracone	
Posterior buccal	Metacone	
Posterior palatal	Hypocone	Primitive heel, or "talon."

LOWER MOLARS.

Anterior buccal	Protoconid	Primitive triangle, or "trigonid."
Anterior lingual	Metaconid	
Posterior buccal	Hypoconid	Primitive heel, or "talonid."
Posterior lingual	Entoconid	
Posterior mesial	Hypoconulid	

When we understand that all the teeth of all mammals have this key, this tritubercular key, we can unlock the comparisons through the series and point out the homologies.

There is further evidence in support of the theory of cusp addition which I will now briefly mention. It is that brought forth by the very investigations of Dr. Carl Röse, which he has used to support the concrescence theory. We should expect, in the embryonic jaw that the calcification of the tooth-germ would be very significant, because we know that the embryonic structures in their development follow the order of addition or evolution. The order of evolution is, to a certain extent, repeated in embryonic development. How is it with the teeth? Dr. Röse has given a most exact account of the mode of calcification of the tooth-germ within the jaw; this is also now to be had in the form of wax models, prepared by Professor Zeigler, of Freiburg.

---

[1] *Journal of Morphology*, Vol. II., 1888, pp. 1-24.

* [At the present time this statement seems very doubtful.—ED.]

To begin with the lower molars, the dental cap in the jaw forms a broad, saucer-like surface, and then at the corners of that cap calcified points appear (Fig. 42*). In what order (Fig. 1) do they appear? The order is shown in the following table:

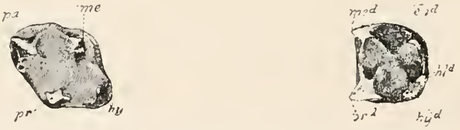


Fig. 42. Developing Upper and Lower Molars of a four weeks old child. Note the resemblance in the upper molar to the molar of the Eocene Primate in Fig. 40 No. 10. After Röse.

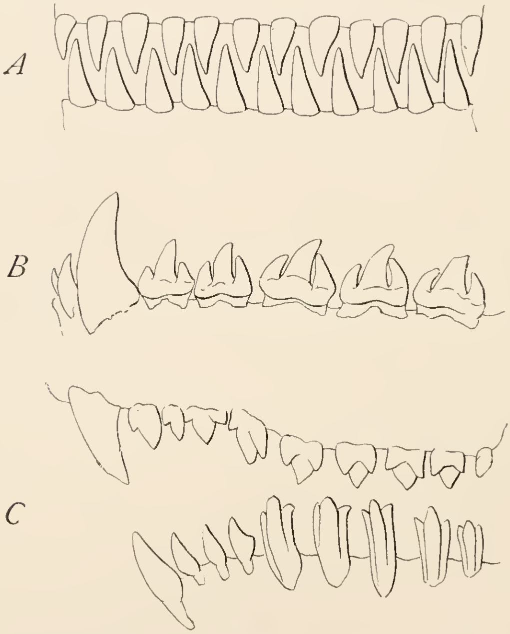


Fig. 42*. The three Primary Forms of Molar Teeth, secondarily attained in three modern forms. *A*, Haplodont, of the Dolphin. *B*, Triconodont, of the Leopard Seal, *Ogmorhinus leptonyx*. *C*, Tritubercular, of the Cape Mole, *Chrysochloris* (see p. 125).

Comparison of Evolution and Embryonic Development.

	Order by "Cusp Addition Theory."	Order of Embryonic Development.
Upper Molars	1. Anterior palatal.	1. Anterior buccal.
	2. { Anterior buccal.	2. Anterior palatal.
	Posterior buccal.	3. Posterior buccal.
	4. Posterior palatal.	4. Posterior palatal.
Lower Molars	1. Anterior buccal.	1. Anterior buccal.
	2. Anterior lingual.	2. Anterior lingual.
	3. Posterior buccal.	3. Posterior buccal.
	4. Posterior lingual.	4. Posterior lingual.
	5. Posterior mesial.	5. Posterior mesial.

In the lower molar teeth the order of calcification is precisely the order of evolution,—in other words, the anterior buccal was the first to evolve, representing the reptilian cone; it is also the first to calcify. The anterior lingual is the second in age, and also the second to calcify. The third and the fourth cusps calcify almost simultaneously. So we find that the order of embryonic development exactly repeats the order of historical development, and in every way presents the strongest kind of confirmation of the theory of cusp formation which we have been discussing. But this you see is not exactly the case in the upper molars. Nevertheless, out of eight cusps in the upper and lower molars considered together, *six* cusps calcify in the order in which they were successively added to the single reptilian cone.

Gentlemen, I trust that I have not in this address taken you too far afield. I have reached a conclusion on this subject which could be elaborated in much greater detail. In closing, I would like to refer to the work of Dr. J. L. Wortman, who is here this evening, and who was for some years a collaborator with Professor Cope in Philadelphia, and who in association with Professor Cope had quite a share in the establishment of the "tritubercular or cusp addition" theory. This theory is now a rival to the "concrescence" theory: and, while it may not seem a matter of great importance, if the concrescence theory may not seem one we ought to take seriously, still, in view of the attention which it has gained in Germany, it is time that we produce and bring forward the unimpeachable evidence which we get of the history of these teeth from the rocks, the solid evidence from the geological formations, the evidence of comparative anatomy, which, as we have just seen, is so far supported by the evidence of embryonic development.

BIBLIOGRAPHY.

Works of reference in addition to those cited above:

Röse, "Ueber die Entwickelung und Formabänderung der menschlichen Molaren," *Anatomischer Anzeiger*, Band VII., 1892.

Kükenthal, "Ueber den Ursprung und die Entwickelung der Säugethierzähne," *Jenaische Zeitschrift für Naturwissenschaft*, Band 28, 1893.

Osborn, "The Evolution of Mammalian Molars to and from the Tritubercular Type," *American Naturalist*, 1888, p. 1067.

"The History and Homologies of the Human Molar Cusps," *Anatomischer Anzeiger*, VII., 1892, pp. 740-747.

Cope, "The Mechanical Causes of the Development of the Hard Parts of the Mammalia," *Journal of Morphology*, III., 1889.

CHAPTER IV.

TRITUBERCULY IN ITS APPLICATION TO THE MOLAR TEETH OF THE UNGULATES OR HOOFED MAMMALS. COMPLETION OF THE NOMENCLATURE.

1.

Disadvantages of Previous Systems of Nomenclature of the Molar Cusps.

[Extract from article entitled "The Nomenclature of the Mammalian Molar Cusps," *The American Naturalist*, October 1888.]

In view of the evidence for the almost universal presence of the tritubercular stage in the present or past history of the upper and lower molars, I have already advocated a distinct nomenclature for the different cusps which compose this molar and its derivatives, up to the stage of the acquisition of six tubercles in the upper molars and five in the lower. This is the final stage in which the tubercles remain distinct. The nomenclature now in general use is based, for the most part, upon the secondary or acquired position, and in no instance, so far as I know, upon the demonstrable homologies of the cusps in the upper and lower jaws. Compare, for example, the molars of *Mioclænus* and *Hyopsodus*. By those familiar with Cope's writings upon this subject, it will be recognized at once that the antero-internal cusp of the lower molar of *Mioclænus* is not homologous with the antero-internal cusp of the upper molar of the same genus, nor is it homologous with the antero-internal cusp of the lower molar of *Hyopsodus*.

2.

Methods of Analysis of Molar Elements, Nomenclature of the Molars of Ungulates.

[Extract from Osborn and Wortman, "Fossil Mammals of the Wahsatch and Wind River Beds Collection of 1891," *Bull. Amer. Mus., Nat. Hist.*, Vol. IV., No. 1, Oct. 20th, 1892, pp. 84-93.]

In October, 1888, a table of nomenclature for the cusps of the molar teeth of mammalia was published in the *American Naturalist*.[1] The

---

[1] Osborn, "The Nomenclature of the Mammalian Molar Cusps," *op. cit.*, p. 927.

terms were carefully chosen with reference to the gradual rise of these cusps from the single cone of the reptilian type, through the tritubercular to the sexitubercular stages.[1] They have since been wholly or in part adopted by Cope, Scott, Lydekker, Schlosser,[2] Flower, and lately by Rütimeyer.[3] The tritubercular stem form has been recognized by Döderlein and Fleischmann, but these authors have employed various Greek symbols for the cusps. The latter has opposed the adoption of similar terms for the main cusps of the upper and lower molars, upon the ground that Cope and myself have mistaken the homologies: this objection would be fatal to a uniform system of nomenclature for the upper and lower cusps if it could be sustained, but a comprehensive survey of the Mesozoic trituberculates, especially of the Amblotheriidæ and Spalacotheriidæ, leaves no doubt that *the antero-external cusp in the lower molars and the antero-internal cusp in the upper molars of the mammalia are homologous with the reptilian cone and with each other;* these cusps are invariably the most prominent, and are always styliform in primitive types; they always form the apices of the primitive crown; they persist in almost all mammals, while one or all of the later cusps may disappear.

This cardinal point established, it will be a great gain for palæontology and comparative odontology when the further truth is recognized that *the possibilities of modification of type in the molars are limited*, that essentially similar types of teeth are evolved independently over and over again, and that in course of what Schlosser has well termed ‘modernization’ we find such diverse orders as Primates, Ungulates, Insectivores, Marsupials, Rodents, all exhibiting the same laws of dental modification, and the same or similar ‘secondary’ cusps, crests and peripheral styles.

Except in the Cetacea and Edentata, these modifications centre around the simple tritubercular crown, which seems to possess unlimited capacity of adaptation by the development of some parts and degeneration of others, by changes of form and position, and by the addition of secondary cusps.

The first step is to distinguish and separate clearly the primary and secondary regions of the primitive crown, for originally they have absolutely different functions; the part first developed in both upper and lower molars is the anterior primitive triangle or *trigon*, which has a cutting or piercing function; out of its three cones all ‘secodont’ types of molars are evolved. The part next developed is the *talon*, or heel, which has

---

[1] See also “Evolution of Mammalian Molars to and from the Tritubercular Type,” *Am. Nat.*, December, 1888.

[2] Schlosser, “Die Differenzierung des Säugethiergebisses.” *Biologisches Centralblatt*, Juni. 1890.

[3] *Die Eocäne Säugethier-Welt von Egerkingen*, Zurich, 1891.

a crushing or grinding function, and therefore plays a chief rôle in all 'bunodont' types. The first diagram exhibits the relations of these two portions of the crown in the upper and lower molars, and the six primary and secondary cusps which typically develop upon each (Fig. 41).*

We will not enter here into the well-understood transformation of this tuberculo-sectorial type into the sexitubercular bunodont type, seen typically in the upper and lower molars of the Puerco *Protogonia* [*Euprotogonia*, Fig. 149, p. 169], which is the least specialized ancestral bunodont form that has been discovered. We may lay emphasis upon the fact that the *parent form of ungulate molar has six tubercles* both above and below instead of six above and four below as formerly supposed.

It is important to remember, as an exception to the law of sexitubercular origin, that all the Amblypoda and all the Periptychidæ†[1] (among the Condylarthra) developed their upper molars upon the trigonal basis, out of the three tubercles of the tritubercular crown, and without becoming sexitubercular, that is, without the addition of the hypocone or talon.

Now how shall we study the molar teeth of the early Ungulates, especially of the apparently similar primitive forms of Perissodactyls, which are so difficult to distinguish? The following steps must be taken:

First. Locate each of the six primary and secondary cusps, as far as they are present.

Second. Note the *form* of each, whether rounded (bunoid), crested (lophoid), or crescentic (selenoid).

Third. Note the *position* of each upon the crown with relation to the other cusps.

Fourth. Note the *relative size* or development of each.

Fifth. Note the relative development of the *cingulum*, in different parts of the contour.

Sixth. Note the presence of one or more *peripheral secondary cusps*, which develop from the cingulum, or external borders of the crown.

Finally. If *crests* are formed or forming, note the points at which the transverse crests unite with the external cusps (paracone and metacone, parastyle and mesostyle).

---

*[From the evidence furnished by the molars of the Jurassic and Cretaceous mammals, of the Eocene trituberculate Creodonts, Insectivores, and Primates (*e.g. Anaptomorphus*), it seems probable that the talonid or heel in the lower molars appeared much earlier than the so-called "talon" or hypocone in the upper molars. See Gidley's views on page 221, Fig. 208. The hypocone of the upper molars (p. 59; Figs. 144, 147, 252), was developed *pari passu* with the degeneration of the paraconid, and fits in between the entoconid of one lower molar and the metaconid of the next lower molar. It is really a secondary crusher, analogous with the protocone.—Ed.]

[1] There are considerable grounds for removing the Periptychidæ from the Condylarthra to Amblypoda.—O.

†[See p. 164.]

These differential features, it will be observed, follow the progressive order of evolution in the molar crowns, for in ‘modernization’ we see, first, a *degeneration* of one or more of the primary cusps, then a *remodelling* of the form of each cusp which may affect the twelve upper and lower cusps very differently: for example, in such an ancient type as *Meniscotherium* we find one bunoid, two lophoid, and three selenoid cusps in each of the upper molars. Third, the cusps begin to shift their positions upon the crown. Fourth, they begin to develop unequally. Fifth, the cingulum, which is primitively a complete peripheral band, begins to disappear at certain points. Sixth, one or more peripheral cusps grow up from the cingulum or upon the sides of the main cusps. Finally, as the crests develop, the unequal development of the cusps causes the transverse crests to unite at different points with the external crest.

We find that if such analysis be applied to the elements of the molar teeth we derive an absolutely infallible means of distinguishing different lines of descent, for the above are the main features of divergent evolution.

The primitive horse, tapir, rhinoceros and titanothere all stand apart and cannot be confused: each have their clear differentia. To check the possibility of being misled by *parallelism* in molar form, we should next observe the dental series as a whole, the proportionate development of different members of the series—the *metatrophism;* this often furnishes the final proof or disproof of relationship, so far at least as can be derived from the dentition alone.

The above method of analysis is the outgrowth of an extremely careful study and comparison of all the early Condylarthra and Perissodactyla, and it has been found necessary to exercise the closest scrutiny to distinguish these early stages of divergence.*

Now to turn to the subject of nomenclature, the system of terms was originally based upon the actual homologies of the primary elements of the trigon and trigonid, but in extending it to the other parts of the crown and to the secondary cusps it was found that we must apply similar terms to some of the later elements in the upper and lower teeth, which are merely analogous to each other (performing a similar function) occupying a similar position, and developing at about the same period, otherwise the terms soon multiply so as to become a burden rather than a convenience. [See Figs. 43, 135.]

As far as possible, therefore, the same prefixes are retained for the secondary parts of the molars as for the primary; thus the anterior transverse crest of the upper molars is called the *protoloph,* as it is invariably developed by the union of the protocone, protoconule and paracone or parastyle, never from the metacone. The anterior transverse

---

[*It should be noted that the molars of the Lower Eocene ancestors of the horse (*Eohippus*) and of the tapir (*Systemodon*) are closely similar.—Ed.]

crest of the lower molars is termed the *metalophid* because it is always developed from the metaconid or metastyle, and protoconid, never from the paraconid; the posterior transverse crest of the lower molars is termed the *hypolophid*, because it is mainly formed by the hypoconid and entoconid, never from the metaconid or paraconid. The external crest of the upper molars is composed of so many cusps that it requires a distinct prefix, but is readily remembered as the *ectoloph*. So with the peripheral cusps, one or more of which are developed in all Ungulates, and are especially numerous in molars of the Equidæ; to these the terminal *-style* is applied in lieu of the English term 'pillar' proposed by Huxley—we can readily locate the *parastyle* as the antero-external buttress which is developed near the paracone, the *mesostyle* as developed on the outer wall between the paracone and metacone. Similarly, in the lower molars, we find in several lines of Ungulates, but again most conspicuously in the Equidæ, that the metaconid and entoconid are reinforced by little cusps which grow up behind them (*a*, *a* and *b*, *b*, Rütimeyer): these may be termed respectively the *metastylid* and *entostylid*, while the pillar arising secondarily in the primitive position of the paraconid may be termed the *parastylid*.

The principles upon which this terminology is based are therefore very simple.

1. The termination *-cone* is given to the main primary or central cusps, and *-conule* to all intermediate cusps.

2. The termination *-style* is proposed for the peripheral cusps arising mainly from the cingulum.

3. The termination *-loph* is applied to the crests.

4. The seven prefixes are based upon the succession and position of the elements in the primitive evolution of the crown, viz.: *proto-*, *para-*, *meta-*, *hypo-*, *ento-*, *ecto-*, *meso-*. The prefixes are first applied to the cones; then to the styles, according to their proximity to the cones; then to the crests, according to the cones which mainly compose them.

5. Homologous and analogous elements in the upper and lower jaws are given similar terms, but distinguished arbitrarily by the terminal *-id*.

Upon the opposite page are given the terms formerly employed by French, German, and English authors for the teeth of the Ungulates before their common tritubercular origin had been discovered by Cope. In his 'Enchaînements du Monde Animal' Professor Gaudry, as far back as 1878, worked out most clearly the homologies of the molar elements in the Ungulates from the sexitubercular-quadritubercular stage onwards; the valuable earlier studies of Rütimeyer[1] are well known. But now that the ungulate molar has been found to converge to the unguiculate molar type, and both are found to contain the same elements, and to spring from

---

[1] *Beiträge zur Kenntniss der fossilen Pferde, Berlin, 1863.*

TERMINOLOGY OF THE PRIMARY AND SECONDARY ELEMENTS OF MAMMALIAN MOLAR TEETH.

	GAUDRY, FILHOL, French authors.	RÜTIMEYER, KOWALEVSKY, German authors.	HUXLEY, FLOWER, LYDEKKER, English and American authors.	Terms based upon primitive homologies	Abbr.
PRIMARY CUSPS.					
Upper Molars,	denticule interne du premier lobe	Innenpfeiler des Vorjochs (innern Hauptgipfeln.)	antero-internal, anterior pillar	protocone	pr
	,, externe ,, ,,	-	antero-external, anterior crescent	paracone	pa
	,, ,, second ,,	-	postero- ,, posterior ,,	metacone	me
	,, médian premier ,,	Zwischengipfel, Tuberkel	antero-intermediate tubercle	protoconule	pl
	,, ,, second ,,	,, ,, ,,	postero- ,, ,,	metaconule	ml
	,, interne ,, ,,	Innenpfeiler das Nachjochs (innern Hauptgipfeln.)	postero-internal, posterior pillar	hypocone	hy
Lower Molars,	,, externe du premier ,,	-	antero-external cusp	protoconid	pr^d
	,, (interne antérieure) ,,	-	,, internal, fifth cusp	paraconid	pa^d
	,, ,, du premier ,,	-	,, internal cusp	metaconid	me^d
	,, externe du second ,,	-	postero-external ,,	hypoconid	hy^d
	,, interne ,, ,,	-	,, internal ,,	entoconid	en^d
	,, médian ,, ,,	-	postero-median, third lobe	hypoconulid	hl^d
CRESTS.					
Upper Molars,	crête externe	Aussenwand	external crest, dorsum	ectoloph	
	premier lobe, crête antérieure	Vorjoch	anterior crest, or collis	protoloph	
	second lobe, crête postérieure	Nachjoch	posterior ,, ,,	metaloph	
Lower Molars,	premier lobe, crête antérieure	Vorjoch	anterior crest	metalophid	
	second lobe, crête postérieure	Nachjoch	posterior ,,	hypolophid	
	-	Schlussjoch	third lobe	hypoconulid	
PERIPHERAL CUSPS.					
Upper Molars,	-	Pericones, Randgipfeln	anterior buttress, ridge, costa	parastyle	ps
	-	,, ,,	median ,, ,,	mesostyle	ms
	-	,, ,,	posterior ,, ,,	metastyle	mts
	-	-	,, prominence, pillar	hypostyle	hs
Lower Molars,	-	-	reduplication of metaconid	metastylid	mts^d
	-	-	,, entoconid	entostylid	es^d

PRIMARY AND SECONDARY DIVISION OF CROWN.

Primitive triangle, anterior portion of crown.	*Upper Molars.*	Trigon (protocone, paracone, metacone).	Secondary talon, heel, Post. portion of crown.	*Upper Molars.*	Talon (hypocone).
	Lower ,,	Trigonid ,, ,, ,,		*Lower* ,,	Talonid (hypoconid, entoconid, hypoconulid).

the same Mesozoic source, it is important to unify our methods of description by adopting a set of terms which refer back to the primitive form and position in place of those which were based upon the comparatively modern form and position.

3.

The above discussion of the homologies of the molar elements of ungulates was followed in 1890 by a contribution which may be entitled:

APPLICATION OF THE THEORY OF TRITUBERCULY TO THE PERISSODACTYLA.

(Scott, W. B., and H. F. Osborn, "Preliminary Account of the Fossil Mammals from the White River and Loup Fork Formations contained in the Museum of Comparative Zoology. . . . The Perissodactyla," by Henry Fairfield Osborn.—*Bull. Mus. Comp. Zool.* XX., No. 3, 1890, pp. 88-91.)

The Horse Molars.

The upper molars of *Mesohippus* [Fig. 161*d*] clearly show the first step in the formation of the *posterior pillar*, *pp.*, which is so conspicuous a feature in *Anchitherium*, in the posterior valley. This can also be observed in a still simpler stage in a specimen of *Anchilophus*, from the French Phosphorites. Step by step with the development of this cusp appears the *posterior pillar*, *p*, in the lower molars, behind the entoconid; this accessory cusp can be traced back to the teeth of *Epihippus*. When it finally unites with the entoconid, in *Hipparion*, it forms the posterior twin cusp (*b*, *b*, Rütimeyer), which is analogous to the anterior pair formed by the union of the metaconid and *anterior pillar a* (*a*, *a*, Rütimeyer).

Thus the transition from the *Mesohippus* to the *Anchitherium* molars is very gradual, as shown in the accompanying figures. By tracing back the rise of the eleven elements which compose the upper *Equus* molar, we find that six belong to the primitive sexitubercular bunodont crown. Two elements of the ectoloph, the *anterior pillar* and *median pillar*, rise from the simple primitive basal cingulum of the *Hyracotherium* molar; the same mode of development, we have just seen, is true of the *posterior pillar*. The eleventh element, the fold of the postero-external angle of the crown, *p*, is not prominent until we reach *Equus*. The term "posterior pillar" is taken from Lydekker; the other terms, "median" and "anterior," are applied to parts which have an analogous origin from the basal cingulum. The remaining coronal cusps are readily identified with their homologues in the primitive tritubercular molar.

The Rhinoceros Molar.

The peculiarities of the molars of *Aphelops* [cf. Fig. 175, p. 181] will be made more clear by a few observations upon the molars of the rhinoceroses in general. The three main crests of the lophodont crown may now be distinguished in part by terms which express their homologies with the elements of the sexitubercular superior and quadritubercular inferior molars of the primitive ungulate, *Phenacodus*. In the upper molars, the outer crest is formed by the union of the primitive paracone and metacone, to which is joined the anterior pillar (see *Mesohippus*, p. 175): it may be called the *ectoloph*. As the anterior crest is formed by the union of the protocone, protoconule, and paracone, it may be termed the *protoloph*. The posterior crest, which unites the primitive metacone, the metaconule, and the hypocone, may be termed the *metaloph*. The outer surface of the ectoloph in the primitive molar of the rhinoceros is marked by three vertical ridges corresponding to its three primitive component elements, *me, pa, ap* [pas]; one or all of these disappear in the flattening of the surface. It will be observed that nothing corresponding to the 'median pillar' of the superior molar of the horse is developed. In the lower molars (the paraconid disappearing), the union of the metaconid and protoconid forms the anterior crest or *metalophid*, while the hypoconid and entoconid unite to form the *hypolophid*.

The secondary enamel folds, which are developed from the three crests, bear a most interesting analogy to those observed in the horse series, beginning with *Protohippus* [*Eohippus*, Fig. 166]; they are outgrowths of the same regions of the crown and subserve the same purpose. They are, moreover, of like value in phylogeny. The useful descriptive terms introduced by Busk, Flower, and Lydekker, should be adopted in part.[1] These secondary elements consist, first, of three folds projecting into the median valley, one from the ectoloph the *crista*; one from the protoloph, the *crochet*;* one from the metaloph, the *antecrochet*.† Secondly, the ectoloph unites with the posterior cingulum and metaloph. Thus the anterior and posterior valleys may be cut off by the union of these folds into from one to three 'fossettes,' precisely analogous to the 'lakes' in the horse molar, except that they are not filled with cement.

---

[1] The terms 'protoloph' and 'metaloph' are, however, substituted for 'anterior collis' and 'posterior collis' of Lydekker. The term 'anterior pillar' = 'first costa,' and 'paracone' = 'second costa.' The mode of evolution of the 'pillar' must have been similar to that in the horses, where Lydekker has proposed this term for the 'posterior pillar.' It is very appropriate, because the pillars in their earliest development can be shown to rise independently from the cingulum (see *Mesohippus*, p. 175), and not as folds of the main elements of the crown, as we should infer from their fully developed stage.

*[Should have read *antecrochet*.—Ed.]

†[Should have read *crochet*.—Ed.]

CHAPTER V.

SECOND OUTLINE (1897) OF TRITUBERCULAR EVOLUTION IN MAMMALIA. WITH DISCUSSION OF CRITICISMS.

[Reprinted from an article entitled "Trituberculy: A Review dedicated to the late Professor Cope," *The American Naturalist*, December 1897, pp. 993-1016.]

THE morphology of the crowns of the mammalian teeth has sprung up practically as a new branch of study since Edward D. Cope and other palæontologists have demonstrated the unity of derivation of all the complex forms from the tritubercular type. The older works and ideas of Cuvier, Owen, Huxley and others are of comparatively little service now, for they treat the teeth of each order of mammals as of so many distinct types, whereas they must now be treated as modifications of one type. This new odontography of the mammalia may be dated from the time when it was recognized that the crowns of the teeth of the Unguiculata and Ungulata, in the comprehensive Linnæan sense, are based upon a common type and are composed of homologous elements of similar origin, as developed by Cope, Osborn, Scott, Schlosser and others. It dates also from the new embryology of the teeth as studied by Leche, Kükenthal, Taeker, Röse, Woodward [M. F.] and others, with the revelations as to primitive form, number, and milk succession.

But to fully establish the morphological branch in its new era we must first demonstrate the theory of a tritubercular archetype. This has been opposed in one form or other by nearly all English morphologists, namely: Lankester, Forsyth-Major, Newton-Parker, M. F. Woodward, E. S. Goodrich, Marion Tims. It has been accepted only by Flower and Lydekker. In Germany it has been accepted by v. Zittel, Schlosser and Rütimeyer; Schlosser, especially, has made important contributions to the evidence. The theory is accepted somewhat reservedly by the embryologists Röse, Leche, Taeker and others, who have attacked rather the homologies of the upper and lower cusps than the theory itself. In France it appears to have made little headway. In America, Scott, Allen, Wortman, Earle and many others are working upon the tritubercular theory and have made important additions to it. It is difficult for the writer to take the "primitive polybuny" hypothesis seriously, although it is advocated more or less positively by such able morphologists* as Forsyth-Major,† Lankester, Goodrich‡ and Parker. The fact that the Multituberculates and Monotremes and certain Rodents exhibiting this type are primitive is no evidence that the polybunic type itself is primitive. We know nothing of the history of the degenerate Monotreme teeth, but we know that the further we go back among the ancestors of the Multituberculates and Rodents the less "polybunic" and more tritubercular they appear.

This demonstration once made, as a matter of convenience in thought and description, we must revise the old systems of nomenclature which were based upon secondary forms rather than upon primary homologies, and which, as a rule, differ in every type of mammals and among odontologists of every land and establish a new odontography or descriptive method. Finally, we must trace out all the lines of divergence in both forms and determine the principles which guide them. The importance of a uniform nomenclature is seen at once in the accompanying table of terms used among the rhinoceroses and horses alone. It could not have been anticipated that the diverse molars of the horse and of the rhinoceros, for example, would be limited in their variations, in a late geological period, by their unity of origin in an extremely early§ geological period. Yet such is undoubtedly the case. Compare the accompanying figures of *Merychippus* (Fig. 162) and of *Aceratherium* (Figs. 175, 176). Imagine that you see the simple bunodont molar of such a form as Owen's *Hyracotherium vulpiceps* [*leporinum*] (Fig. 159), underlying these diverse crests and crescents. Consult Taeker's *Zur Kenntniss der Odontogenese bei Ungulaten* and you will find that this sexitubercular archetype is not imaginary, but is a constantly recurring fact of embryonic development—all the crests and crescents being preceded in the embryo by simple cones. Then compare carefully the variations in the two teeth as follows: The two "cement lakes" of *Merychippus* with the two "fossettes" of *Aceratherium*, enclosed in the former by crescentic spurs, and in the latter by the "antecrochet" and "crochet"; the posterior "lake" and "fossette" similarly enclosed by an upgrowth of the posterior basal cingulum. Can any one question the homologies between these secondary adaptations to a diet of grasses when it is seen that they spring from the same primary cusp centres? In the lower Eocene the sexitubercular prototype passes directly back into the tritubercular archetype. So throughout the whole mammalian scale not only ungulates, but primates, carnivores, insectivores, rodents are

---

*[This list should have included especially Dr. Florentino Ameghino (see pp. 201-204 of this work).—H. F. O.]

†[See p. 205.]

‡[See p. 206.]

§[That is, *relatively* early, *i.e.* the Cretaceous period.—Ed.]

	MOLAR TEETH OF ALL THE MAMMALIA.	FOR RHINOCEROS MOLARS.	FOR RHINOCEROS MOLARS.	FOR UNGULATE MOLARS.	FOR HORSE MOLARS.
	Terminology based upon evolution from a tritubercular, ancestral molar type.	Terminolgy used by English authors, Boyd-Dawkins (1867), Busk (1870), Lydekker (1882), and Foote (1882).	Terminology used by Cuvier (1836) and De Blainville (1846), Gaudry (1878), Pavlow (1892).	German and Russian authors, Rütimeyer and Kowalevsky (1893).	Huxley and Lydekker (1886)
Primary Molar Cones	Protocone		Denticule interne du pr. lobe	Innenpfeiler des Vorjochs	Anterior pillar
	Paracone	Second Costa	Denticule externe, pr. lobe		Anterior crescent
	Metacone	Costae (in part)	Denticule externe, sec. lobe		Posterior crescent
	Hypocone		Denticule interne, sec. lobe	Innenpfeiler des Nachjochs	Posterior pillar
Premolar Cones	Deuterocone Tritocone Tetartocone				
Secondary Pillars or Styles	Parastyle	First Costa = Buttress		Pericones, Randgipfeln	Anterior ridge
	Mesostyle				Middle ridge
	Metastyle				Posterior ridge
	Hypostyle	Posterior collis (in part)			Posterior prominence
Secondary Crests	Ectoloph	Exterior lamina = Dorsum	=crête externe	Aussenwand	
	Protoloph	Anterior collis	Colline seconde, crête ou lobe antérieure	Vorjoch	
	Metaloph	Median collis	La troisième colline crête ou lobe postérieure	Nachjoch	
Valleys	Praesinus	Anterior Valley	Vallon oblique		
	Postsinus	Posterior Valley	Fossette postérieure		
Secondary Folds	Crochet	Posterior combing plate { Uncus Crochet	Crochet		
	Antecrochet	Anterior combing plate { Antecrochet	Crochet antérieur		
	Crista	Crista	Ante-(crochet)		
Secondary Cavities	Prae, Medi, and Postfossettes		Fossettes Fossette postérieure		Cement Lakes
Cingulum	Cingulum	Posterior collis (in part) = cingulum, guard	Bourrelet	Wulst	

found playing similar variations upon the primitive tritubercular type. There are surprisingly few distinct types, but an almost unlimited number of sub-types, or variations of form. As we descend among the older rocks and the various series begin to converge, it becomes increasingly difficult to distinguish the different orders by their teeth alone. Thus it came about that all the Eocene monkeys were at first referred to the ungulates, or to transition groups, as expressed in M. Filhol's composite term *Pachylémuriens.*

Tritubercular Homologies.

Embryological Evidence.—The progress which has been made in the embryology of the teeth is largely in the matter of the succession of double series, as indicated by vestiges of earlier and later sets of teeth, the so-called milk and permanent sets. Embryogenesis, however, has also led to a very minute study of the order of succession of the cones of the molar teeth, and without entering into the matter in detail, it may be briefly stated that all authors are unanimous in describing the cones of the lower molar teeth in different groups as developing in the same order in which they are supposed to have arisen in the past, according to the tritubercular theory, namely: Protoconid, Paraconid, Metaconid, Hypoconid. In the upper teeth, on the other hand, embryogenesis has been found to contradict the conclusions reached by the tritubercular theory of palingenesis, for all authors have agreed that the order is Paracone, Metacone, Protocone, instead of Protocone, Paracone, Metacone. When these facts were first brought out by Taeker, Röse and others, the writer, with undiminished confidence in the force of palæontological evidence, advanced as an explanation the fact that the protocone had become secondarily reduced in the upper molars, and that the embryogeny no longer recapitulated the order of evolution. This explanation has received a measure of support in the latest researches by Woodward [M. F.], in which it is shown that in those Insectivora in *which the protocone is still the most prominent cusp of the superior molars, this cusp also appears first in embryogeny*, the paracone and metacone following. Woodward points out that this is not the case in other Insectivora, for they agree with the Primates, Ungulates and other types which have been carefully investigated, in the late appearance of the protocone. Woodward infers from these conflicting facts that there were two modes of cusp evolution within the order Insectivora, one in which the protocone appeared first, and another in which the protocone appeared third or last. Such a double genesis seems to the writer highly improbable.*

It is, however, certainly important, as Woodward and many others have observed, to strengthen the palæontological evidence for the tritubercular

---

*[See, however, the opposing views on pages 123-126, 227.]

cular theory. The writer has recently made strenuous efforts to secure additional evidence, which have not thus far been successful. In the meantime too great emphasis cannot be laid upon the fact that *all the existing palæontological evidence points in the same direction*, namely, to the presence of the chief cone upon the inner side of the upper molars, and upon the outer side of the lower molars. An important oversight on the part of those who are still unconvinced of the tritubercular theory, is the necessity of a mechanical adaptation of the upper to the lower teeth in every stage of development, which is perfectly met by the tritubercular theory.* Given the universally acknowledged *trigonid* or triangular arrangement of cusps in the lower teeth, no mechanical relations can be imagined in an upper molar crown which originated with the external cusps, paracone and metacone.

If the main object of palæontological research is to trace back various lines of descent as far as possible, the very unity of primitive type makes this apparently more difficult than before, but not really so. We were working before upon a false basis, or no basis at all; we can now advance upon the certain basis of primitive form and the one requisite of progress is to employ much more exact methods of description and analysis.

The Three Primary Forms.

So far as the molar teeth were concerned, there were, to our present knowledge, but three great primary forms, which succeeded each other as stages and also persisted. From one or other of these all the known recent or fossil mammalian teeth have diverged, including probably the Multituberculates. These types are illustrated in the accompanying cut. First, the *haplodont* crown, which links the mammals with the reptiles; second, the *triconodont* crown which was predominant in the Lower Jurassic period; third, the *tritubercular* crown which appeared in the [Upper Jurassic or] Lower Cretaceous[1] and has been by far the most productive. The transitions between these great types are found among the Mesozoic mammalia and have already been worked out with considerable care.†

From each of these great primary stages it would at first appear that some of the mammalia directly derived their dental type, for both the "haplodont" and "triconodont" crowns are seen to-day among the Cetacea. Yet there is ground for uncertainty here, for as the progressive

---

* [See especially Cope, "On the Mechanical Causes of the Development of the Hard Parts of the Mammalia," *Jour. Morph.*, Vol. III., Sept. 1889, pp. 226-274. In opposition see pp. 61*, 68*, 82*, Figs. 208, 209, of this volume.—Ed.]

[1] It now appears advisable that the so-called Como (Atlantosaurus) Beds of North America and the Purbeck Beds of England should be placed in the base of the Cretaceous instead of in the Upper Jurassic as formerly. [See p. 22*.]

† [See, however, p. 222.]

stages are "haplodont," "triconodont," "tritubercular," so the retrogressive stages reverse this order, passing from "tritubercular" back to "triconodont" then into "haplodont." Another view therefore is that such primary forms have been secondarily acquired. The apparently "triconodont" lower molar of *Thylacynus* is, for example, an indirect retrogression from a tritubercular ancestral form. Again among the aquatic carnivora, in the series of molars of the Seals, the eared Seals and the Walruses, we see the backward stages from the "triconodont" to the "haplodont"; and it is therefore probable that the "tritubercular" was the form of molar possessed by the Pinnipedia when they diverged from the Fissipedia. There is considerable evidence that a similar retrogression has simplified the molar crowns of modern Edentates, for it is now certain that at least the Gravigrada were descended from tritubercular ancestors, the Ganodonta [Tæniodonta]. Again, among the Cetacea, all their oldest allies, such as *Zeuglodon*, are triconodont, not haplodont. With both these groups, therefore, there are the possibilities of direct or of retrogressive origin of the "triconodont" molar.

This uncertainty hardly extends to the "triconodont" stage, which is typically shown in the Lower Jurassic *Amphilestes*, *Phascolotherium* and the later *Triconodon*. It is a very significant fact that this type dies out in the Upper Jurassic. It is true we find many more recent "triconodont" teeth, the lower molar of *Mesonyx* for example, which are positively known to be of tritubercular origin. Richard Owen compared the lower molars of *Thylacinus* with those of *Triconodon*, but we have found that what appeared to him to be similar cusps are not really homologous. Thus while it is possible that the ancestors of some of the modern haplodent and triconodont mammals never reached the tritubercular stage, it is by no means a settled fact. On the other hand, excepting the isolated group of Multituberculates and the single genus *Dicrocynodon* Marsh, *the molars of every known fossil mammal* from the close of the Lower Cretaceous until the close of the Eocene period bear the tritubercular stamp.*

This would appear to support the generalization that all mammals passed through the third primary or tritubercular stage, yet it must be borne in mind that all our evidence is derived from inhabitants of fresh water basins,† and that the persistent haplodont and triconodont types may have been living contemporaneously in the seas.

But the Multituberculates and Monotremes, were they tritubercular in origin? The teeth of *Ornithorhynchus* are so degenerate and irregular

---

*[This statement applies chiefly to the orders Insectivora, Carnivora, Primates, Ungulata, since the trituberculate derivation of the Monotremata, Multituberculata, Edentata, Rodentia, Cetacea, remains to be proven.—Ed.]

†[Or at least from epicontinental as opposed to marine deposits.—Ed.]

that many features of primitive form may be lost; they may quite as readily be interpreted as tritubercular as multitubercular, especially in the embryonic stage as described by Poulton.

It is not difficult however to establish the principle that a true multitubercular tooth may spring from a tritubercular tooth. As pointed out elsewhere, my friend, Prof. J. A. Allen, directed my attention to the "multituberculate" rodents. A comparison of *Mus*, *Dipodomys* and *Perognathus* beautifully illustrates the stages between "trituberculy" and "multituberculy" in living types. The three rows containing twelve tubercles in the latter genus are derived respectively from the "external," "intermediate" and "internal" cusps of a sexitubercular bunodont type similar to the *Hyracotherium* molar on a small scale. The additional cusps are successively added to each row. Thus the upper molar of *Perognathus* is closely analogous to that of the Mesozoic Multituberculata, especially to such a type as *Tritylodon*. Passing also from the higher Multituberculata to the lower and more ancient, we find fewer and fewer cusps until we reach a "paucitubercular" parent form in the Upper Triassic *Microlestes*. *Microlestes* itself was not tritubercular; it had a basin-shaped crown surrounded by irregular tubercles; this basin, however, was not dissimilar to that in molars of the Eocene rodent *Plesiarctomys* which is obviously of tritubercular origin.*

This evidence has been recently reinforced in a most striking manner by the discoveries of Professor Seeley in the Karoo Beds of South Africa, from which two principal conclusions may be derived: First, that *Tritylodon*, formerly placed with the mammalia, contains a large number of reptilian characters. Since the fossil is closely related on the other hand to the remaining Multituberculata, it appears possible that we have in the *Gomphodontia* the group from which the Multituberculates sprang. A study of the dentition of other Theriodonts in the Karoo Beds shows that while *Tritylodon* and *Trirachodon* are typically Multituberculates, others, such as *Diademodon* † have a trituberculate pattern, exactly such a pattern as we find in certain Lower Eocene mammals. Altogether there is certainly increasing support for the writer's hypothesis, that the multituberculate tooth is of tritubercular origin.

The Early Stages of Sexituberculy.

The Trigon. Respect for Cope's priority should not prevent our ultimately adopting the late Professor Rütimeyer's term *trigonodont* for

---

* [The derivation of some multituberculate types from trituberculate types does not prove that *all* multituberculate types have been derived from trituberculate types, and reasons are presented on p. 105* for thinking that the ancestral multituberculate molar as represented in *Microlestes* was not derived from a typical tuberculo-sectorial lower molar.—Ed.]

† [See p. 92.]

the third stage, retaining the term "tritubercular" as descriptive of the whole transformation, and as peculiarly appropriate to certain types of teeth, such as the superior molars of the lemurs. "Trigonodont" is most appropriate because the first step in molar morphology is to identify the "primitive triangle," and the term "tubercular" hardly applies to a lofty pointed cutting crown. Our studies among the Mesozoic mammals have left no doubt that the upper and lower triangles, or "trigon" and "trigonid," were derived from the reptilian protocone by the addition of lateral cusps. The mechanical perfection of this type consisted in the fact that the lateral cusps were developed upon or shifted to the outer side in the upper molars, and to the inner side in the lower molars, thus producing an interlocking "shear." The "trigon" was essentially a cutting apparatus, so perfect that many mammals retained it without further evolution. Thus *Chrysochloris*, the little Insectivore of the Cape, presents a fine example of this type, persistent in its molars* (Fig 42*).

The Talon. But in a great majority of trituberculates the "talon" was added as a crushing apparatus. It invariably appeared first in the lower molars (where we may distinguish it as the "talonid") and pressed into the basin of the superior "trigon." At first it was a mere spur (hypocone) as in *Amphitherium* or in the existing *Calcochloris* (allied to *Chrysochloris*), but between the Jurassic and Upper Cretaceous periods the talonid widened into a basin-like shelf supporting an outer cusp, the "hypoconid"; an intermediate cusp, the "hypoconulid," and an inner cusp, the "entoconid." Thus we find in the majority of the Upper Cretaceous (Laramie) and Puerco or lowest Eocene mammals that the lower molars bear six cusps; the above-mentioned three on the talonid and three on the trigonid (protoconid, paraconid, metaconid). With these six cusps the equipment of the lower molar was complete, and it was ready for transformation into the molar of a primate, ungulate or carnivore, as the case might be.

But why notice such a detail as the posterior intermediate cusp or hypoconulid? Because, to give only two reasons, this cusp plays an important rôle in the ungulates: it is invariably present,† except perhaps in the Coryphodons, and forms the third lobe of the last lower molar, which is thus proved to be a primitive character; again, it is found throughout all the Primates, and although seldom availed of, this cusp constitutes an important and distinctive character as between the different races of man. Its extreme antiquity is appreciated by few anthropologists, and at the present time it is degenerating. (See Fig. 40, Nos. 11, 12.)

---

*[It should be borne in mind, however, that some authors (*e.g.* Forsyth Major) hold that the heelless condition of the *Chrysochloris* molars is secondary. See also pp. 124, 225 below.—Ed.]

†[That is, in the more generalized forms.—Ed.]

While these changes were taking place, the upper molars remained comparatively stationary in the persistence of the simple trigon, up to the close of the Cretaceous period, the main change being a depression of the level of the trigon. All three cusps in some groups were depressed from the high secodont to the low bunodont level. In the majority of the carnivorous types we find that only the protocone was depressed and that the pair of outer cusps, paracone and metacone, persisted in their high primitive level; the crown being thus prepared for the transformation into the true "sectorial." But in the omnivorous and herbivorous types, all three cusps are depressed and the upper molars always increased their crushing area by the addition of a heel or "talon," exactly analogous to that previously developed upon the lower molars.* As is well known, this "hypocone" is an upgrowth from the cingulum and its typical mode of development is well shown in the Primates (Figs. 128-132). While this was going on the trigon was also supplementing its bunodont equipment by the addition of the little intermediate cusps "protoconule" and "metaconule."† These always appeared where the "talonid" abuts against the "trigon." Thus, finally, the upper molar, like the lower, was provided with six cusps and both were ready to diverge into any ungulate form.

All these foregoing stages persist and may be readily studied and verified among some of the living marsupials, insectivores, lemurs and monkeys, and can be seen in any well-equipped osteological museum almost as well as among the fossil series.

The Nomenclature of the Molar Cusps and Crests.

The system proposed by the writer some years ago has now been adopted by many of the American, English and German writers who are studying the fossil series. It is based upon simple principles:

1. The termination "*-cone*" is employed for all the primary central cusps derived from the crown of the tooth, while the diminutive *-conule* is employed for the smaller "intermediates" or cuspules.

2. All peripheral cusps or elements developed mainly from the cingulum or external borders of the crown are distinguished as *-styles* ("pillar" or "buttress"). The only exception is the "hypocone," which, while arising from the cingulum, soon takes its place upon the crown.

---

*[The hypocone of the upper molars is analogous *in position* to the hypoconid of the lower molars, but in function it is more analogous to the paraconid which it replaces, since it fits into the space between the entoconid of one and the metaconid of the following lower molar. A closer functional analogy is with the protocone of the upper molars, since the protocone and hypocone of one upper molar fit into the talonid (hypoconid) and trigonid of two successive lower molars.—Ed.]

†[In many, if not all, cases the protoconule and metaconule were developed long before the hypocone. Compare the Jurassic and Cretaceous Trituberculates (pp. 96, 218, 220), *Pantolambda* (Fig. 140), and certain insectivores (p. 128).—Ed.]

3. The crests, transverse and longitudinal, are always composed of two or more cusps and styles, and are distinguished by the termination *-loph*.

4. The prefixes "*proto-*," "*para-*," "*meta-*," "*hypo-*," "*ento-*," etc., refer back to the primitive position or order of development in the triconodont and tritubercular stages.

5. The suffix *-id* is employed arbitrarily to distinguish the elements of the lower molars from those of the upper.

The use of the terms "trigon" and "talon" for the cutting and crushing regions of the crown, respectively, is especially advantageous among the upper Mesozoic and lower Cainozoic mammals, where it is necessary to refer constantly to the relations of the upper and lower crowns in apposition, as in the evolution of the sectorial and lophodont types. As to the form of the cusps, we pass from simple pointed cusps to three well-known modes of modification to which the adjective "bunoid," "lophoid," and "selenoid" may be applied. A combination of these terms gives us a permanent system of distinguishing the complex forms of ungulate molars from each other, by referring first to the form of the protocone; second, to that of the outer paracone and metacone. Thus in *Palæosyops,* as the protocone is bunoid and the outer cusps are selenoid, the crown may be distinguished as "buno-selenodont." In *Palæotherium* the protocone is "lophoid," and it may be described as "lopho-selenodont." *Rhinoceros* is truly "lophodont," since all its six cusps are "lophoid." These are preferable to the terms "tapirodont," "symborodont," "bathmodont," "loxolophodont," etc., proposed by Cope, because the latter are associated with generic types.

The Evolution of the Ungulate Molar.

The fact of derivation of all ungulate molars (excepting in the Amblypoda) from sexitubercular upper and lower crowns, leads us to look sharply for traces of these six tubercles [as modified] from the primitive plan of *Euprotogonia.* These six cusps are almost invariably found in the upper molars of both perissodactyls and artiodactyls up to the middle of the Eocene period, as typified in *Hyracotherium* and *Homacodon* or *Dichobune.* In the lower molar the trigon loses the "paraconid" and the talon loses the "hypoconulid," the latter persisting only in the last molar as the "third lobe." This loss was accompanied by the complete transformation of the lower molars from the "secodont" to the comparative "bunodont" type, as effected in the lowering of the "trigonid" to the level of the "talonid." This is exemplified in the steps between the first and third molars of the creodont genus *Miacis* (Fig. 38, No. 6). In a side view of all early ungulate molars, such as *Hyracotherium,* we see that the "trigonid" is still the highest portion of the crown. In the ungulates, unlike the carnivores, all three molars were affected simultaneously. An exactly similar levelling process can now be observed in a comparative series of recent Lemurs and Monkeys. To summarize the five steps toward the establishment of the ungulate primitive type: the addition of the lower talonid, the lowering of the cusps of the upper trigon, the addition of the upper talon and simultaneous lowering of the lower trigonid, the loss of the paraconid and hypoconulid. By these changes the cutting was transformed into the crushing type. The development of the talon necessitated the loss of the "paraconid," for they both occupy the same space when the jaws are closed; the stages of this gain to the upper molar and loss to the lower are well shown in the species of *Euprotogonia.*

All these changes belonged to the constructive period and took place presumably before the great divergence of the ungulate orders began; or it may have been partly due to parallelism or homoplasy, because we find that the molars of *Trigonolestes,* the earliest known artiodactyl, are tritubercular.* Some groups, such as those to which *Coryphodon, Uintatherium* and *Periptychus* belong, built up their whole molar structure upon the tritubercular or trigonal basis.

From this point onward dated the period of "modernization." An important legacy of the old triangular form was the *oblique arrangement of the outer and inner cusps* parallel with the sides of the primitive triangles. Thus all the primitive crests developed upon these cusps were oblique and not directly transverse. The main features of modernization upon which we must now closely direct attention are:

1. The addition of one or more peripheral cusps or "styles" as upgrowths from the cingulum. These reached their most extreme development in the Equidæ. (See Fig. 49.)

2. The persistence or degeneration of the cingulum at certain points, for all primitive molars are completely invested by a broad cingulum.†

3. The modelling of the cusps into the "bunoid," "lophoid" or "selenoid" form.

4. The metatrophic or unequal growth of the cusps, especially as affecting the external pair, protocone and metacone, in the upper molars.

5. The shifting of the cusps from their primitive position upon the crowns.

6. The shifting point of union of these transverse crests with the external crest.

The differential features of the development of ungulate molars all group around these six heads. If we were examining an isolated molar tooth from the lower Eocene, the first step would be to locate its primary cusps and then note its divergence as tested by the above differentia. We would then be in a position to make a conjecture as to the series in

---

* [See pages 171, 172.—Ed.]

† [More or less.—Ed.]

which this molar belonged—as no two series are modified similarly in all these respects. Yet the prevailing method among many palæontologists is to pass lightly over most of the differentia and, for example, group widely divergent forms under the Lophiodontidæ as if in the constitution of these dense enamelled tissues nature could lightly pass from one to another.

A few words now upon the secondary "styles."* Their function is evidently to increase and elaborate the crushing surface of the crown. In *Phenacodus* the first to appear is the "mesostyle" between the paracone and metacone, but this genus was on a side line of the Condylarthra. In all true perissodactyls and artiodactyls, the first peripheral cusp to appear is the antero-external buttress of the upper molars, which we call the "parastyle," since it adjoins the paracone. The "mesostyle" appears later, and only in those ungulates in which the paracone and metacone are moulded into crescents. Thus the lower Eocene *Hyracotherium* does not exhibit this cusp, but it appears as a distinctive feature of the middle and upper Eocene *Pachynolophus* (*Orohippus*). The mesostyle was strongly developed in all the selenodont, buno-selenodont and lopho-selenodont types, such as the Artiodactyla and *Meniscotherium*, *Chalicotherium*, *Palæosyops*, the palæotheres and horses. Look at an upper molar of *Merychippus* and see what an important rôle these styles play (Fig. 162). First, we observe the "parastyle" and "mesostyle," next most important is the "hypostyle," which develops near the hypocone upon the posterior cingulum of *Mesohippus* and *Anchitherium* and finally completes the border of the "anterior fossette" or cement lake. The horse molar, by the way, furnishes the best illustration of the value of tracing back the various portions of the crown to their birth-place in the primitive crown of *Hyracotherium*. Every turn in this labyrinth of folds is thus made perfectly clear.[1]

A corresponding set of styles grows up on the lower molars, and it is very easy to locate them with reference to the reciprocal upper set if we simply keep in mind the fact that throughout the whole course of development the elements of each trigonid are placed just in front of those of the corresponding trigon, that is, the protoconid and metaconid fit just in front of the paracone and protocone, as shown in the diagram (Figs. 37, 39*c*). Thus the inferior entostylid is developed near the entoconid, while the superior hypostyle develops near the hypocone. The first of the inferior

---

*[The para- and metastyles as well as the proto- and metaconules are very ancient elements of the molar crowns, since they appear in the Upper Jurassic and Upper Cretaceous trituberculates. The termination "style" as used in this book is applied (1) to all cusps originally external to the para- and metacones; (2) to the "protostyle," "hypostyle," "entostylid," etc.—Ed.]

[1] Mr. Lydekker has courteously called attention to the fact that in the earlier study of this subject the writer misinterpreted the descriptive terms employed by Huxley.

styles to develop is the "metastyle," a reduplication of the metacone, the well known "a-a" of Rütimeyer.

In all ungulates in which the "mesostyle" is developed the external cusps remain of the same size. In the tapirs no "mesostyle" appears, yet these cusps are symmetrical; but in the rhinoceroses, which also lack the mesostyle, the first fact to note is the asymmetrical growth of these cusps; the metacone is elongated while the paracone is reduced and crowded up against the parastyle. This point was observed by Cope in seeking for a definition of the Rhinocerotidæ in 1875. The rhinocerotine molar, whether of *Hyrachyus*, *Amynodon* or *Aceratherium*, has the further distinction that it is the only type in which a complete ectoloph is formed, and second, as Cope has already observed, the asymmetry of the external cusps is emphasized by the flattened metacone and conic paracone. Figure 175 illustrates also the three projections from the ectoloph, protoloph and metaloph, namely, the "crista," "antecrochet" and "crochet." These, with the three "fossettes" formed by them, were noted and named by Cuvier, and, as shown by Falconer, Flower, Lydekker and others, are of great specific value.[1] We have already seen that Cuvier's term "fossette" may be substituted for the "cement lakes" in the horse's molar. The terms formerly adopted, or proposed, by Lydekker,[2] after English usage, and those in German and French usage, have already been given in the Table.

There is another line of perissodactyls in which the metacone is flattened but not elongated, and no complete ectoloph is formed. I refer to the little Wasatch genus *Heptodon* (which Cope has erroneously placed in the ancestry of *Hyrachyus*), also *Helaletes* of the Bridger, an undoubted successor of *Heptodon*, which Marsh was wrongly led to consider an ancestor of the Tapirs. The molars, studied by our six differentia, are found to differ from those of the rhinocerotine *Hyrachyus* by the incomplete ectoloph, also by the shifting inwards of the metacone and consequent shortening of the metaloph. In looking about for molars with similar differentia, we find those of the true *Lophiodon* of Europe, *L. isselense*, for example, stand nearest.

Now, how shall we distinguish the early Tapirs? First, there is no mesostyle; second, the paracone and metacone (as observed by Cope) are both conic and symmetrical; third, a feature of great importance, apparently unnoticed hitherto, is that the protoloph and metaloph spring from the anterior bases of the paracone and metacone, and not from near the apices of these external cusps as in all molars of rhinocerotine affinity. We find, as a general law, that where the external cusps are symmetrical

---

[1] As pointed out by Lydekker, the writer mistakenly transposed these terms "crochet" and "antecrochet" in a former paper, *Bull. Mus. Comp. Zool.*, 1890, p. 81.

[2] "Siwalik Rhinocerotidæ," *Pal. Indica.*

as in Palæotheres, Horses and Tapirs, the transverse crests always arise in front; where they tend to asymmetry as in Helaletes, Lophiodon and Rhinoceros, the crests tend to rise from or near the apices.

Enough has been said to make clear the new method of procedure in the analysis and discrimination of early ungulate molars. Let us apply this form of statement and description to the aberrant lower Wasatch genus *Meniscotherium* as a resumé:

Upper Molars, buno-selenodont; paracone, metacone and protoconule selenoid; metaconule reduced, lophoid, united with hypocone; a large parastyle and mesostyle. *Lower Molars*, seleno-lophodont; metaconid reduplicated by metastylid. We find that a similar analysis may be given of *Chalicotherium*, excepting only "protoconule reduced." It is thus suggested that *Meniscotherium* may be related to *Chalicotherium*.*

This method may be summarized as follows: Look for traces of *primitive* ancestral structure in the form and position of the cusps. Second, determine the divergent form, position, proportions and relations of the cusps. Third, determine the secondary cusps, crests and foldings, their form and relations. Finally, let us turn to a wholly different molar type and examine the complex and aberrant molars of *Coryphodon*. Can we establish any homologies between its elements and those of any of the ungulates we have been considering? Fortunately we are partly guided by the molar of the Puerco genus *Pantolambda* Cope, which is even older than the Coryphodons. This is our key to the ancestral or primitive form, and by its aid Cope has, we think, rightly interpreted the homologies of the Coryphodon molar elements. We first note that nature has here evolved a lophodont crown from the tritubercular or trigonal basis, for there is no distinct talon or hypocone except in the unique form *Manteodon*. *Pantolambda* has no parastyle,† but a prominent mesostyle and a pair of selenoid external cusps, also a selenoid protocone with a spur leading toward a protoconule and suggesting an incipient protoloph. The selenoid external cusps of this type suggest a comparison with the lopho-selenodont perissodactyls, and we are able to reach the following result.

In a large series of *Coryphodon* molars we see first that the protoloph is formed of the protocone, protoconule and parastyle, exactly as in the horses. Unlike the horse (*Anchitherium*), the ectoloph is more or less detached from the protoloph, but the examination of a large series of specimens in the American Museum and Cope's collection convince us that it is composed of the same elements as in *Anchitherium*, namely, the paracone, which has almost lost its crescentic form, the mesostyle, which is much less prominent, and the metacone, which is still crescentic. This

---

* [See however p. 184, where *Chalicotherium* is held to be more probably an aberrant Perissodactyl.—Ed.]

† [This is obviously a *lapsus calami*, the parastyle being especially prominent. See Fig. 140.—Ed.]

Fig. 43. Epitome of the stages leading up to the typical Eutherian Molars, according to the theory of trituberculy, chiefly illustrating the nomenclature.

enables us to describe this molar as follows: It is of buno-selenodont origin and has a complete protoloph and ectoloph, *but no metaloph.* Its homologies with the elements of the Anchitherium molar are clearly shown by a comparison of Fig. 144 and Fig. 160. This illustrates again the necessity of starting upon the trigonal basis instead of upon the basis of two lobes, as in the work of French palæontologists. In his *Enchaînements du Monde Animal,* Prof. Gaudry has admirably worked out the upper molars of the perissodactyla and artiodactyla from the sexitubercular stage onwards. He divides the tooth into two lobes, a "premier lobe," including our protocone, protoconule and paracone and a "second

FIGURE 43.

No. 1. "Haplodont" or simple conical molars, the hypothetical starting point.

2. Relations of haplodont upper and lower molars in the Dolphin. (The haplodonty of Dolphins may be secondary, see p. 190.)

3. "Protodont" lower molar of *Dromatherium* (p. 19), showing main cone and accessory cuspules.

4. Protodont lower molar of *Microconodon* (p. 19), accessory cuspules better developed and incipient heel or talonid.

5. Progressive stages of "triconodont" inferior molars. Three cusps in line with "cingulum" out-growths from the base (*a*) *Amphilestes* (inner face), (*b*) *Phascolotherium* (inner face), (*c*) *Triconodon* (inner face), (*d*) *Amphilestes* (outer face) (p. 24).

6. Triconodont inferior molars of a seal (*Ogmorhinus*). (Secondary, p. 143.)

7. "Tritubercular" inferior molars of *Menacodon*; (*a*) external, (*b*) internal view. The small cusps are internal to the protoconid (p. 32).

8. Tritubercular inferior and superior molars of *Chrysochloris.* In the upper jaw the apex of the triangle is *internal*, in the lower *external* (see also No. 10).

9. "Tuberculo-sectorial" inferior molar of *Amphitherium* showing pointed-cusped "trigonid," and a low posterior, obtuse "talonid" or heel, an out-growth chiefly from the base of the crown. The heel is "tubercular," functioning as a pestle or crusher, the trigonid "sectorial," with cutting ridges and piercing cusps (p. 27).

10. (*a-e*) Typical tuberculo-sectorial inferior and superior molars. The talonid bears three cusps "hypoconid" (hy^d postero-external), "entoconid" (en^d postero-internal), "hypoconulid" (hl^d posterior). Somewhat incorrect (see Fig. 39).

11. Inferior molars of *Miacis* (a primitive Carnivore) showing in m_2, m_3 depression of trigonid to level of talonid; all cusps now "bunoid" or low and conical (p. 84).

12. Inferior molars of *Anaptomorphus* (primitive Primate) showing (in m_3) degeneration of paraconid, elongation of hypoconulid (pp. 50, 158).

13. A "quadritubercular" superior molar (*Olbodotes*, an Eocene Insectivore, or Rodent) showing three main cusps (pr, pa, me) with a fourth ("hypocone," postero-internal) growing up from the cingulum, changing the crown contour from a triangular to a quadrate outline; rudimentary "para," "meso," and "metastyles" are present on the external edge of the crown (Fig. 104).

14. Quadritubercular superior molar of an Eocene Primate *Adapis* (Fig. 132).

15. "Sexitubercular" superior molar of *Notharctus* (an Eocene Primate) showing the four main cusps (pr, pa, me, hy) with the addition of two small intermediate conules "pl," "ml," also the well developed external parastyle, mesostyle, and metastyle (Fig. 77).

lobe" including our hypocone, metaconule and metacone. All subsequent authors in France follow this system, which indeed works well for one group. But what we need now is a system which will apply not only to all groups of ungulates, but to unguiculates as well, so that when we reach the upper Cretaceous borderland between unguiculates and ungulates we can employ the same set of terms and the same basis of description.

I can only conclude by expressing the conviction that the tritubercular theory of Cope rests upon such conclusive evidence* that its universal adoption as the key to the interpretation of all molar teeth cannot be long deferred. It is one of the chief anatomical generalizations of the present century.

[The Bibliography given in the foregoing article is here omitted. See Bibliography at end of volume.—Ed.]

---

* See pp. 226, 227.

CHAPTER VI.

CHRONOLOGICAL OR GEOLOGICAL SUCCESSION OF MOLAR TYPES.

A review of the dental types as observed in the successive geological periods presents us with the ideas of successive stages belonging to these periods, of the enormously long era of time required for the transformation of the teeth, and of the very significant fact that only two fundamentally distinct dental types have thus far been discovered; first, the (I) *tubercular*, and its derivative, the multitubercular, the origin of which is still a matter of hypothesis, and second the great (II) *haplodont*, *protodont*, *triconodont*, *tritubercular* sequence, among the manifold offsprings of which we find again arising secondarily the haplodont, triconodont, tubercular and multitubercular.

1. Reptilian Ancestors of Mammals in the Trias.

It is now generally believed that the Theriodontia, an order of reptiles found chiefly in South Africa, are, as the name indicates, not far from the actual ancestors of the mammalia. It is true they exhibit a very large number of reptilian characters: but mingled with these are features of the

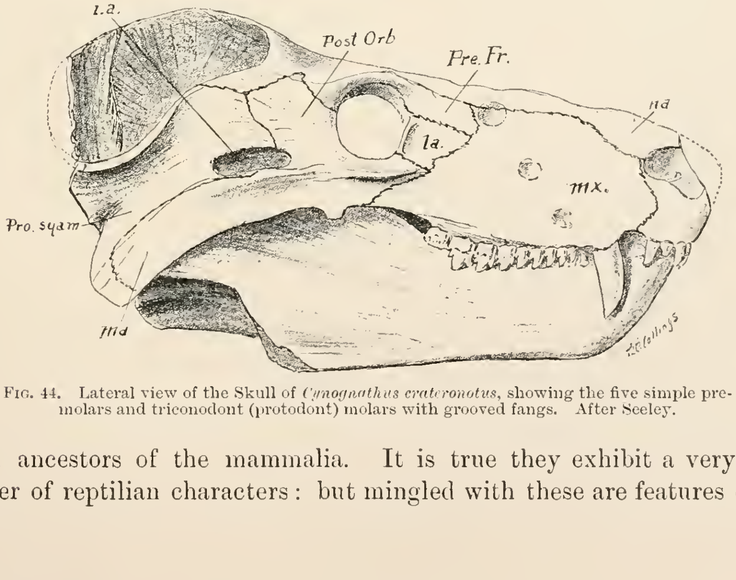


Fig. 44. Lateral view of the Skull of *Cynognathus crateronotus*, showing the five simple premolars and triconodont (protodont) molars with grooved fangs. After Seeley.

skeleton and characters of the teeth in which they closely resemble primitive mammals. There is moreover the negative evidence that they constitute the only known group from which the mammals could have descended.

The teeth of Theriodonts exhibit four types as follows: The first or *haplodont* type consists of simple, recurved reptilian-like crowns, implanted with single fangs, as in the genus *Ælurosaurus*.

Second, of the *protodont* type, with crowns implanted by partially divided or very slightly grooved fangs, consisting of a single main cone, with lateral denticles somewhat irregular in character. The best example of this type is *Cynognathus* (Fig. 44).

The third, or *tuberculate*, type is entirely different, and probably belongs to omnivorous or herbivorous animals;* it is typified by the genus *Gomphognathus* (Fig. 45); the molar teeth are covered with irregular tubercles (*Diademodon mastacus*), in which the writer has observed some disposition towards a tritubercular arrangement, or triangle of three larger

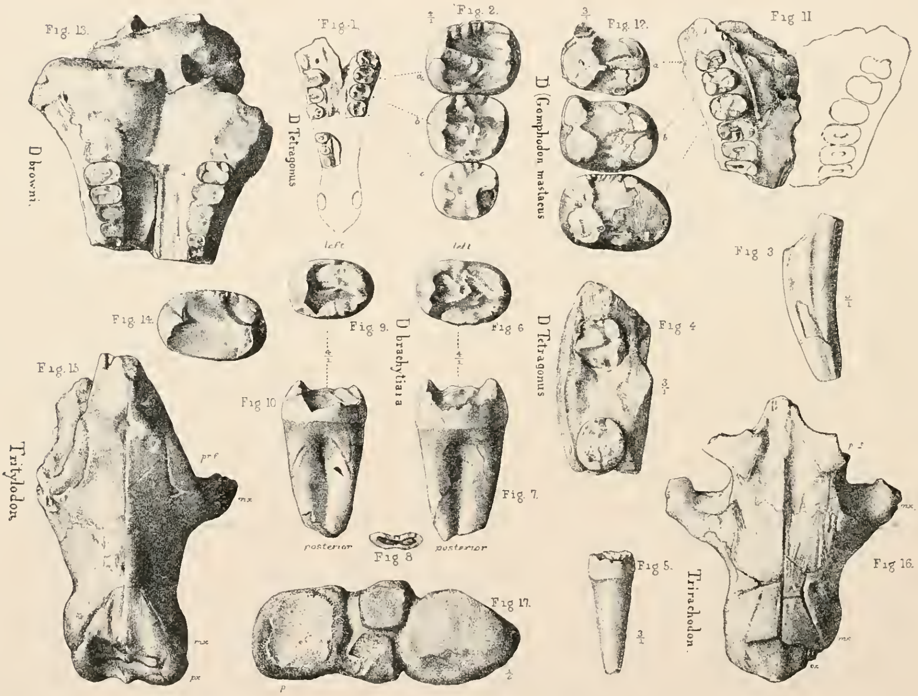


FIG. 45. Dental and Cranial structures of the Theriodonts. *Diademodon mastacus*, analogous to a low-crowned trituberculate, like *Arctocyon*. *D. tetragonus*, trituberculate structure more obscure; note the general resemblance to the molar crown of certain squirrels. *D. brachytiara*, showing the incipient division of the fang. The skull of *Tritylodon* is greatly reduced. All upper teeth except Figs. 4, 5. After Seeley.

---

*[Or more probably to carrion feeders (Broom). — ED.]

cusps, or the crown is more or less basin-shaped, with an irregular, raised border (*D. brachytiara*); the latter teeth are analogous to those of *Microlestes*, of the Upper Triassic or Rhætic of Germany (Fig. 48).* It will be observed that the opposite series of grinders converge towards each other anteriorly; these teeth are therefore multicuspidate but not strictly "multituberculate," because in the true Multituberculates the opposite tooth rows are parallel and the jaw motion palinal or from in front backward. These teeth, with irregularly disposed tubercles or basin-shaped crowns, are most closely analogous to those of certain squirrels.

The fourth type is the *multituberculate*, seen in the genus *Tritylodon* † (Figs. 46, 48), in which the opposite series of teeth are parallel; the grinding teeth are covered with tubercles arranged in regular, parallel rows, with grooves between, adapted to a fore-and-aft motion of the jaw.

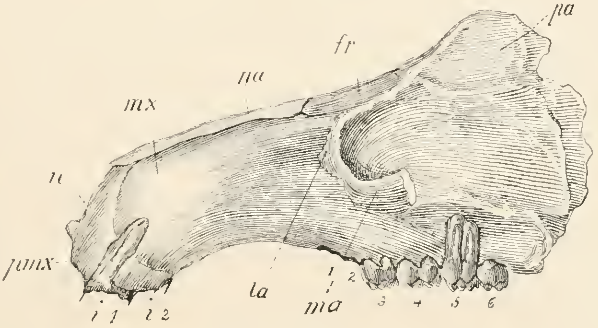


Fig. 46. *Tritylodon longævus*, anterior portion of the skull upon the left face, two thirds natural size. After Owen.

Certain of these Theriodonts‡ present the same dental formula as in the generalized dentition of the most primitive mammals. Their resemblances to the Protodonta and Multituberculata in tooth structure are so striking that since they belong practically to the same geological period the probability of actual affinity is to be considered.

---

* [But these are *upper* not lower teeth; they are elongate transversely (as in upper molars generally) not antero-posteriorly as in the lower molars of *Microlestes*. The lower molars (Fig. 45, Nos. 4, 5) were single-rooted, round teeth, with a depressed crown bearing a low transverse median ridge (Broom).—Ed.]

† [Broom has recently shown that *Tritylodon* is more probably a mammal. Ed.]

‡ [Certain Theriodonts (e.g. *Trirachodon*) had more or less lophodont molars with a low, irregular medium cross crest. Traces of such a crest are seen also in *Ornithorynchus* (?) *Kurtodon*, *Diplocynodon*, *Dryolestes*, *Sciurus*, *Lepus*. Similarly in the lower molars a transverse crest connecting the protoconid and metaconid is seen in *Diademodon*, *Trirachodon*, *Paurodon*, *Amblotherium*, *Centetes*, etc. This cross crest may possibly have some bearing on the origin of the tritubercular type.—Ed.]

2. The Triassic Mammals.

The supposed Triassic mammals again include the two grand divisions of tuberculate or grinding teeth, and of pointed or piercing teeth. They are distinguished as mammalian by the more or less complete division of the root into two fangs.

Among the former is the genus *Microlestes* of the Upper Triassic or Rhætic of Germany, known from a single molar (Fig. 48, No. 1). The so-called *Microlestes* teeth in the Rhætic of England (Fig. 48, Nos. 2, 3) are rounded or basin-shaped, with irregular tubercules on the sides; they undoubtedly belong to a different species or even genus, as they are broader and more basin-shaped, resembling in fact the hinder molars of *Plagiaulax*.

The other division is believed to be represented by the Protodonta, which we have already described in detail (pp. 18-21), with large single cones, more or less regularly developed lateral denticles, and partially divided fangs. Numerically, these molars have one fang and three cusps, namely, protocone, paracone, metacone.

3. Mammals of the Jurassic.

We now meet with the multituberculates, considerably specialized into different types.

The other mammals present two great types of teeth: first, the *triconodont* with large main cones and lateral denticles both in the upper and lower molars, as exhibited in *Amphilestes* (Fig. 5) and *Phascolotherium* (Fig. 6); these animals are believed to be Marsupials. The second type is the *tritubercular*, or more strictly, tuberculosectorial, that is, with tubercular or crushing heel and sectorial trigon, as exhibited in *Amphitherium* (Figs. 15, 17). (See pp. 21-30.)

The Upper Jurassic* exhibits the surviving triconodont types, among which are such teeth as those of *Spalacotherium* (Fig. 11), which appear to exhibit a transition between the triconodont and tritubercular. In the same geological period the tritubercular types are diversified into two distinct kinds, both of which have their parallels among later Insectivora.† Numerically, these upper molars have three fangs and three main cusps, namely, protocone, paracone, metacone, also a parastyle, metaconule; the lower molars have two fangs and from three to four cusps, namely, protoconid, paraconid, metaconid and hypoconid.

---

* [As stated on p. 22, the Purbeck and Atlantosaurus Beds are by some regarded as of Lower Cretaceous age.—Ed.]

† [*I.e.* one type, represented by *Peramus*, *Amphitherium*, resembles the teeth of *Micropternodus* (Fig. 71): a second type represented by *Stylodon* parallels the high piercing type of *Chrysochloris*.—Ed.]

Mr. Gidley's observations upon American Jurassic mammals are given on pages 219-223.

4. Upper Cretaceous Mammals.

(See also pp. 105, 115, 116.)

A very long geological interval, representing an enormous period of time, separates these mammals from those of the Upper Jurassic. With few exceptions our entire knowledge of the upper Cretaceous mammals is derived from collections made in the Laramie formation of the Rocky Mountain region. These collections again embrace the two great dental types of multituberculates (Fig. 55) and trituberculates. All the multituberculate types of teeth and jaws are too far specialized to give origin to any of the modern divisions of mammalia, either placental or marsupial.

The *trituberculates* (Fig. 47; see also pp. 115, 116) are represented in the American Museum collection by a series of isolated upper and lower molars, also by a number of fragmentary jaws; and among the latter are some in which the angle is apparently inflected, indicating Marsupial relationship. It is possible that, besides Marsupials, we find here Insectivores, primitive Carnivores, and the ancestors of ancient types of Ungulates; but it is obvious that the determination of relationships from such isolated material is a very difficult and hazardous matter.

Nevertheless, the teeth of trituberculate type are of extraordinary interest, since they lend strong support to the theory of the unity of origin of the molar types of the higher mammals from a tritubercular stem, instead of from a multitubercular, as has been suggested.

The *upper molars* so far as known, are of the simple, generally low-crowned tritubercular type as distinguished from the high sharp cusped crowns of the Jurassic molars. The main triangle of cones, or trigon, is of symmetrical form. In the majority of specimens, the largest cone is the main internal one, or protocone (Fig. 47, *A*, *D*), while the external cones, paracone and metacone, are symmetrical, invariably of smaller diameter, and as a rule less elevated. These proportions sustain the 'palæontological' theory that the reptilian cone is internal* rather than the embryological and premolar analogy theories, that the reptilian cone is antero-external in the true molars as in the premolars. The outer wall of the crown is reinforced by a cingulum, on which secondary spurs or cuspules are developed, sometimes of very large size, more or less homologous with the 'styles' of the tertiary types of molars (*e.g.* Fig. 68).

Another feature recently discovered among Jurassic mammal teeth is the presence of intermediate tubercles or conules on the trigon. A very

---

* [This may be a *non sequitur*, because the great elevation and size of the paraconid in Hl, Al, Fig. 47, need not be interpreted as indicating its relative antiquity.—Ed.]

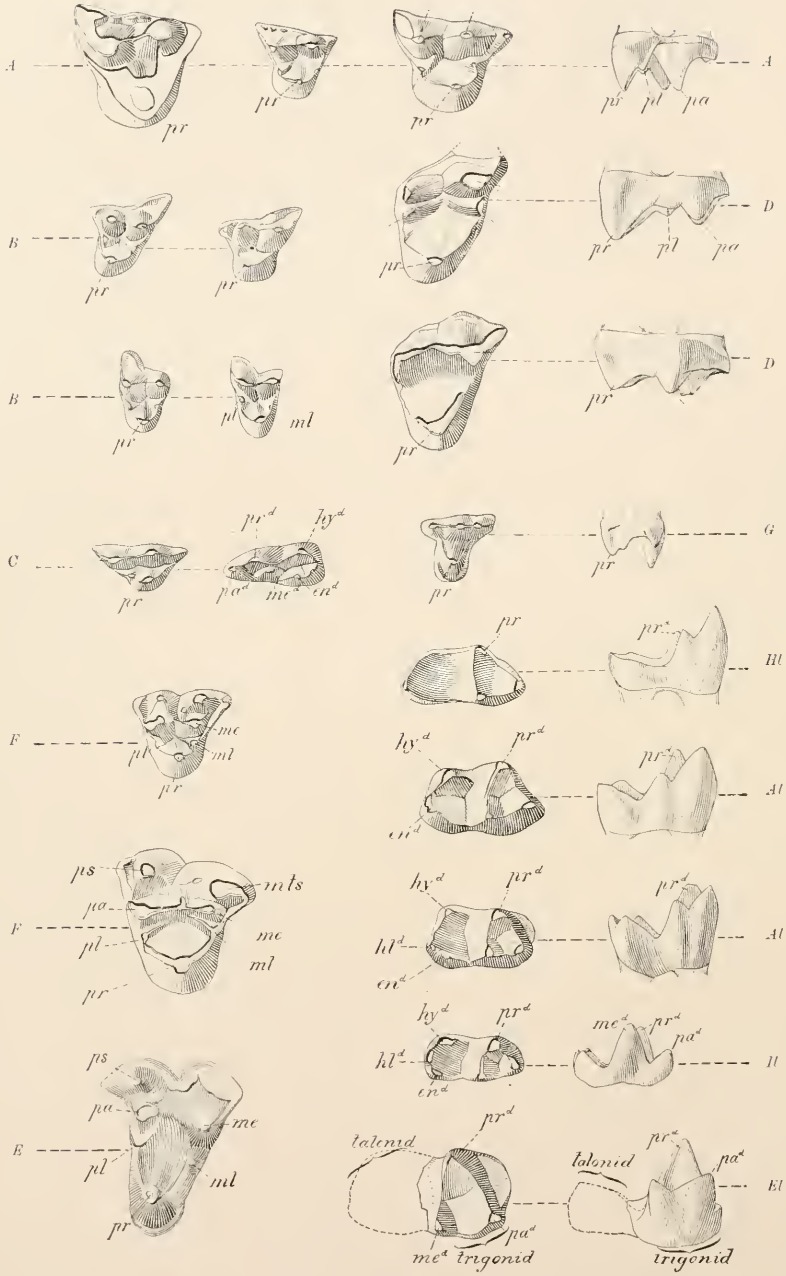


Fig. 47. Upper Cretaceous (*Laramie*) Trituberculates. [All figures three times natural size.]

Abbreviations.—*pr.* protocone; *pa.* paracone; *me.* metacone; *pl.* protoconule; *ml.* metaconule; *ps.* parastyle; *mts.* metastyle; *end.* entoconid; *hl.* hypoconulid.

primitive feature is the entire absence of an internal cingulum and consequent absence of any cusp corresponding with the hypocone; in fact, all these teeth are still strictly triangular in form, although the outer wall may be somewhat irregular. A prominent cutting metastyle, analogous to that seen in primitive Creodonts, is developed.

In the *lower molars* we observe an elevated anterior triangle or trigonid. As a rule the protoconid or reptilian cone is the most prominent cusp, but in certain specimens (Fig. 47 *Hl*) this cusp is somewhat depressed. A progressive character is the reduction of the antero-internal cusp, or paraconid. But the most strikingly progressive feature, as compared with Jurassic molars, is the broadening out of the heel of the crown or talonid to support three cusps, the hypoconid, hypoconulid, and entoconid respectively.*

Thus there are three main features, as compared with the Jurassic molars: (1) general depression of the crown of the upper molars, accompanied by a strong development of the *external cingular cusps* and of *conules*, but not by an *internal* cingular development; therefore there is (2) an entire absence of the postero-internal cusp or hypocone; (3) there is a striking development of the heel or talonid of the lower molars with two or three cusps, and more or less depression of the trigonid. In general, these progressive features relate these teeth very much more closely to those of the Basal Eocene than to those of the Upper Jurassic.

Numerically, the most progressive of these upper molars have from two to three fangs; from three to five cusps, namely protocone, paracone, metacone, protoconule and metaconule; and two to three cingules, parastyle, mesostyle, and metastyle; the lower molars have two or more fangs and from five to six cusps, protoconid, paraconid, metaconid, hypoconid, hypoconulid and entoconid.

---

* [This broadening of the talonid was probably correlated with the depression and transverse broadening of the protocone.—Ed.]

In Figs. *A*, *B*, *D*, the long sectorial spur from the outer wall is more probably the metastyle than the parastyle, consequently this is probably the posterior side of the tooth; although if the tooth happened to be m^3, the elongate spur would be anterior, *i.e.* parastyle.

A.—Crown and side views of three superior molars, probably of the right side. Types of *Protolambda hatcheri* Osborn.

B.—Crown views of four superior molars of the left and right sides. Genus *Pediomys* Marsh.

C.—A superior molar, and an inferior molar of the right side. Type of *Synconodon sexicuspis* Osborn.

D.—Crown and anterior views of two superior molars of the left side. Genus not determined.

E.—Crown view of a right superior molar. *Didelphops vorax* Marsh, after Marsh.

F.—Crown views of two superior molars, probably of the left side. Type of *Ectoconodon petersoni* Osborn.

G.—Crown and side views of a superior premolar or molar (cf. *Dryolestes*, *Ictops*). Genus not determined.

El.—An inferior molar of the left side. *? Didelphodon.* Crown and inside views.

Al.—Two inferior molars of the left side. Genus undetermined. Crown and inside views.

Hl.—Crown and inside views of a lower molar of the left side. Genus not determined.

Il.—Crown and inside views of a lower molar of the left side. Genus not determined.

5. Basal Eocene Mammals.

In the basal Eocene, Puerco, Torrejon, and Fort Union formations of North America, we again find the mammals divided into multituberculates and trituberculates.

Among the latter the law of trituberculy was first perceived by Cope; they include animals possibly related to the Primates and Rodentia, also ancestral Edentata(?), Creodonta ancestral to the Carnivora, Condylarthra collateral ancestors of the Perissodactyla and Artiodactyla, and Amblypoda, a very primitive order of Ungulates totally distinguished from all others by the fact that the teeth evolve throughout on the triangular or tritubercular basis.

The American Museum collection as revised by Dr. W. D. Matthew, omitting the Multituberculates, contains 1200 identified specimens, referred to 62 species, 33 genera, 6 orders. *All the upper molars of these animals without exception are either:* (1) *purely tritubercular or triangular,* or (2) *transitional to the quadritubercular and quadrate form by the addition of a hypocone.* This more extended knowledge of the basal Eocene not only reinforces the evidence originally advanced by Cope, but affords an almost overwhelming body of proof as to the fundamentally trigonal tritubercular character of the upper molars of these orders.

The molar teeth exhibit a marked progression upon those of the Upper Cretaceous, in three very important characters: (1) there is an internal cingulum in a very large percentage of the upper molar teeth, (2) a hypocone or postero-internal cusp is developing from this cingulum in a somewhat smaller percentage of upper molars: (3) the paraconid or antero-internal cusp of the lower molars is disappearing in some of the lower molars.

Numerically, the most progressive upper molars present three fangs, six cusps: namely, protocone, paracone, metacone, hypocone, protoconule, metaconule, and two styles, parastyle, mesostyle, and metastyle. The lower molars present also six cusps, protoconid, paraconid, metaconid, hypoconid, hypoconulid and entoconid, the latter three arising from the talonid or heel.

6. Lower Eocene Mammals.

In the lower Eocene, Suessonien of Europe, Wasatch of North America, the majority of modern groups of mammals are represented, including the following orders: Primates, Rodentia, Insectivora, Creodonta, Carnivora, Tillodontia, Edentata, Condylarthra, Amblypoda, Perissodactyla, Artiodactyla.

All of these animals are either tritubercular or in stages evolving from trituberculy into higher forms of molar teeth as described in other chapters (see pp. 37, 45, 132, 151, 158, 170, 171, 175, 178).

Résumé of Geological Succession of Types.

It does not appear necessary to present any further proofs of the fact that apart from the Multituberculates the geological succession of types of molar teeth presents so few exceptions to the main law of trituberculy and the principle of cusp addition that these exceptions may be designated as aberrant. The advance of the teeth from type to type corresponds with the advance of geological time as follows:

	Upper Molar Type.	Maximum Total of Cusps in one pair of Upper and Lower Molars.
Triassic,	Haplodont, Protodont, Triconodont, with single or grooved fangs, - -	6
Jurassic,	Triconodont, Tritubercular, with 2 or 3 fangs, -	8 cusps, 1-2 styles.
Cretaceous,	Tritubercular, - - -	11 cusps, 2 styles.
Basal Eocene,	Tritubercular, Quadritubercular, and higher stages, -	12 cusps, 3-4 styles.
Upper Eocene,	Tritubercular and all the derived types, - -	12 cusps, 6 styles.

CHAPTER VII.

THE ORIGINAL OR PRIMITIVE STRUCTURE OF THE MOLAR TEETH IN THE DIFFERENT ORDERS OF MAMMALS.

MAJOR CLASSIFICATION OF THE MAMMALIA.

THE Table of Classification on pages 11-16 naturally introduces the brief review of the various orders of mammals with reference to the structure of their grinding teeth which forms the subject of this chapter.

The reptilian superorder Therapsida, including the order Cynodontia, is the only one of the numerous orders of reptiles in which striking resemblances to the mammals are observed in the skeleton as well as in the teeth (see p. 91). These animals appear to stand nearest the reptilian stock from which the mammals sprang, and to most nearly fulfil the hypothetical groups, *Hypotheria*, *Promammalia*, *Sauromammalia* proposed respectively by Huxley, Haeckel, and Baur.

The two grand divisions of the Mammalia proper, the (1) **Prototheria** or egg-laying mammals, and (2) **Eutheria** or viviparous mammals, include fourteen extinct and eighteen living orders, or thirty-two orders altogether. It will be shown that in *thirty* of these orders tritubercular evolution can either be directly demonstrated or is rendered in a high degree probable by analogy. In *three orders only* the Monotremata, Allotheria (Multituberculata), and Cetacea, does there remain considerable doubt as to the mode of dental evolution.

In the two great divisions of the Eutheria, namely, the **Didelphia** (Marsupialia) and **Monodelphia** (Placentalia), tritubercular evolution, although proceeding independently, has arrived at closely similar adaptive types, thus affording remarkable instances of parallel evolution.

The Placentalia are conveniently divided into four great groups, which it is true have a descriptive rather than strictly taxonomic value, namely :

1. The **Unguiculata**, including all the clawed animals of primarily insectivorous (Insectivora, Cheiroptera), or carnivorous habits (Carnivora), and secondarily of prevailing herbivorous habits (Rodentia, Edentata).

In a general way these animals are conservative and exhibit some of the earlier stages of tritubercuty as well as the extreme specializations for exclusively carnivorous and herbivorous diet.

2. The second group includes the **Primates**, which are primarily frugivorous and omnivorous. In a general way also, these monkeys and lemurs are transitional between an earlier insectivorous and a frugivorous and herbivorous diet; thus the study of their teeth forms an admirable introduction to the study of the teeth of the Ungulata.

3. The third great group includes all the hoofed animals or **Ungulata**, of which the food is primarily herbivorous and secondarily omnivorous in certain cases. In a general way again, the Ungulata exhibit the extremes of complication of the crowns by cusp addition and cusp modelling.

4. The fourth great group includes the **Cetacea**, in which the teeth are specialized for various kinds of sea food, or entirely wanting. They exhibit what is probably a retrogressive dentition from an earlier type, such as that presented by certain of the Unguiculata.

PROTODONTA.

The molar teeth of the Protodonta have been described on page 18 as transitional from the haplodont to the triconodont condition. Similar changes are observed among the Theriodontia, as described on page 91; and analogous changes, that is, the addition of lateral cusps to a central cusp, have occurred frequently among the Vertebrata.

It is possible that the Protodonta are not mammals; but the incipient division of the fang and the apparent absence of angular and articular bones of the jaw render it probable that they are at least very early types of mammals, probably of egg-laying habits, like the Monotremes. A jaw somewhat resembling those of *Dromatherium* and *Microconodon* has recently been described by Broom* in South Africa from the Upper Beaufort Series (Karoo system), which are considered of Upper Permian or Triassic age.

SPECIAL REFERENCES.

Osborn, H. F., "On the Structure and Classification of the Mesozoic Mammalia," *Journ. Acad. Nat. Sci. Phila.* (2) IX., 1888, p. 222, *antea*, pp. 31-35.

Osborn, H. F., "The Triassic Mammals, *Dromatherium* and *Microconodon*; *Proc. Amer. Philos. Soc.*, Apr. 1887, *antea*, pp. 18-21.

ALLOTHERIA OR MULTITUBERCULATA.

Because the Multituberculata are among the oldest known mammals, first occurring in the Rhætic or Upper Triassic, it has been urged that the

---

* *Geol. Mag.* Dec., IV., Vol. X., 1903, p. 345.

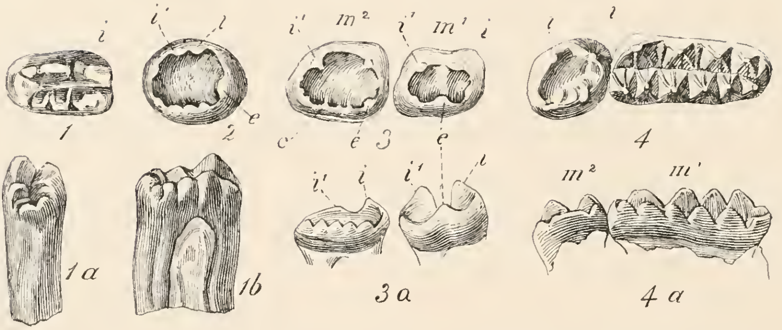


Fig. 48. 1. *Microlestes antiquus* (Stuttgart Collection), a lower molar viewed from above; 1*a*, posterior face; 1*b*, external face, greatly enlarged. 2. *Microlestes* (*Plagiaulax?*) *moorei*, from above. 3. *Plagiaulax minor*, the lower molars viewed from above; 3*a*, external face of same enlarged 6½ diameters. 4. *Ptilodus trovessartianus*, lower molars viewed from above; 4*a*, external face of same; *i i*¹, internal tubercles; *e e*¹, external tubercles. Original.

Fig. 49. *Meniscoëssus*, Laramie or Upper Cretaceous of North America. Probably an upper molar viewed upon the wearing surface, enlarged two diameters.

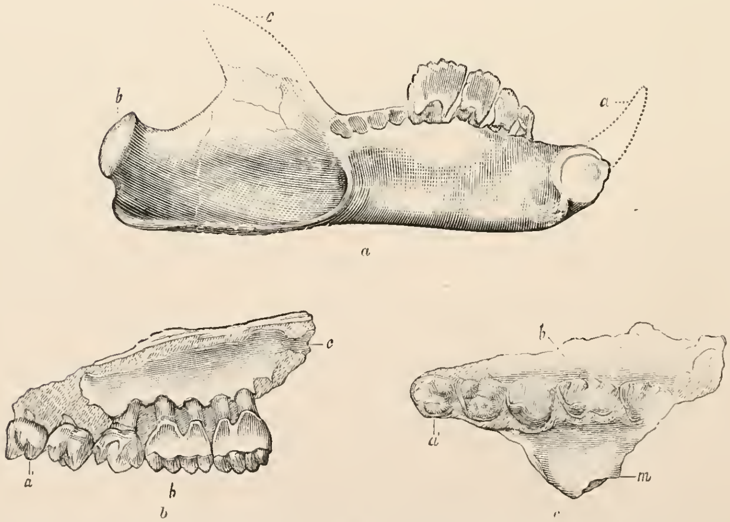


Fig. 50. *a*, Left lower jaw of *Ctenacodon serratus*, Marsh, from the Upper Jurassic or Basal Cretaceous of North America, inner view, three times natural size; *b*, Right upper jaw of *C. potens*, inner view x 4. *c*, The same seen from below. *a*, First premolar, *b*, fourth premolar as interpreted by Professor Marsh. After Marsh.

Figs. 48-50. The molar tooth forms of the Multituberculate family Plagiaulacidæ.

Multitubercular pattern is a primitive one. Forsyth Major's argument on this subject is discussed on pages 205-208, and the conclusion is reached that there is quite as much evidence for considering the multituberculate molar as secondary or evolved from a still earlier tritubercular type. There are several grounds for considering that such an evolution may have taken place.

1. The earliest multitubercular molars known, those of *Microlestes*[1] (Fig. 48, Nos. 1, 2) are comparatively simple, consisting of a central depression or basin indented on the edges by larger and smaller tubercles. Thus the earliest multituberculate molars known have comparatively few cusps, in other words, are *paucitubercular*, whereas the latest multituberculate molars known have a very large number of tubercles, or are *multitubercular*.

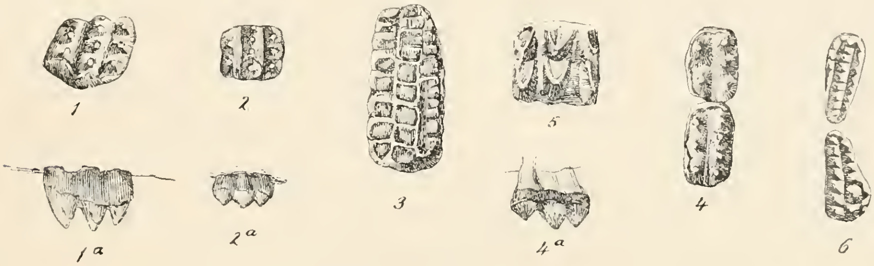


Fig. 51. The molar tooth forms of typical Multituberculates.

1. *Triglyphus*, from the Rhætic (Triassic) of Germany, an upper molar; 1*a*, ditto, in side view, natural size. 2, 2*a*, *Tritylodon*, from the Triassic of South Africa, an upper molar, m^2, wearing surface and outside view, natural size. 3. *Polymastodon*, from the Basal Eocene of North America; the second upper molar, natural size. 4. *Bolodon*, from the Upper Jurassic of England, the third and fourth upper molars, enlarged about 6 diameters. 5. *Stereognathus*, from the Upper Jurassic of England, a lower molar enlarged about 2½ diameters. 6. *Chirox*, from the Basal Eocene of North America, the upper molars enlarged 1¾ diameters.

2. Basin-shaped crowns more or less similar to those of *Microlestes moorei* are known to be secondary or of tritubercular origin in several distinct families of mammals. Thus certain Rodents (p. 205), Fruit-bats (p. 129), the Kinkajou (*Cercoleptes*, p. 142), *Myrmecobius*, (p. 112), exhibit more or less distinctly basin-shaped crowns of which the edges are elevated, and yet retain more or less clearly the primitive tritubercular pattern.

3. The depression of the centre of the crown to form a basin out of what was primitively a projecting point or cone finds its analogies in the invagination of the incisor teeth of the horse, and in the basin-shaped

---

[[1] The evidence tending to connect *Microlestes* with the Multituberculates is briefly that: (1) the *M. moorei* molar closely resembles that of *Plagiaulax minor* (Fig. 48, Nos. 3, 3*a*); (2) *Plagiaulax minor* presents many resemblances to *Ctenacodon* and *Ptilodus*, typical Multituberculates; (3) an enlarged grooved premolar, probably representing a less specialized condition than that seen in the later Multituberculates has been recorded by Dawkins from the Rhætic beds in which the *Microlestes moorei* molar was found; (4) Dr. Ameghino brings evidence to connect the Multituberculates (including *Microlestes*) with the Diprotodont Marsupials, especially the South American forms described by him.—Ed.]

third incisors of the Rat Kangaroo (*Bettongia*). In *Arctocyon* (p. 133) the crown is depressed but not at all basin-shaped. The molars which gave origin to the Rhætic *Microlestes* basin-shaped type may, therefore, have been either simply conic or haplodont, or even possibly tritubercular.

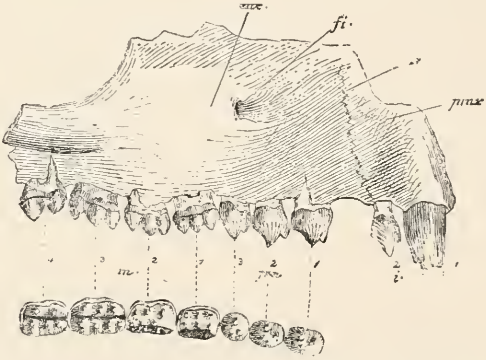


FIG. 52. The outer surface of the right maxilla of *Bolodon*, from the Middle Purbeck Beds (Upper Jurassic, England). ×$\frac{4}{1}$.

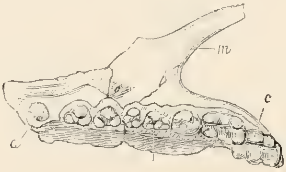


FIG. 53. Views of the maxilla of *Allodon laticeps*, Marsh, seen from below, from the Atlantosaurus, Beds (Upper Jurassic, North America). × 4.

FIG. 54. *Chirox plicatus*, Cope. ×$\frac{3}{2}$. *a*, viewed from below, palate with dentition, three promolars and two molars *in situ*; *b*, viewed from the outer side. From the Torrejon Formation, Basal Eocene, Stage II. New Mexico. After Cope.

Figs. 52-54. The molar tooth forms of the Multituberculate families Bolodontidæ, Chirogidæ.

It must be clearly stated, however, that the *Microlestes antiquus* molar bears no close resemblance to any of these types and there is no clear evidence in the *Microlestes* molar itself of derivation from the tritubercular type.

4. Some additional evidence on this point is derived from the study of the dentition of the molar teeth of the Monotremes (p. 107).

5. Still another possibility is that the molar form of *Microlestes antiquus* may be derived from that seen in *Phascolotherium* by the upgrowth of heavy cusps from the internal cingulum (compare Fig. 48, No. 1, and Fig. 6).

6. Again, this molar might represent a pattern allied to that of the *Amphitherium* molar (Figs. 15, 17), that is the highest anterior (?) cusp above the anterior (?) root (Fig. 48, Nos. 1*a*, 1*b*) may be a protoconid, the first cusp on the opposite side of the tooth a metaconid, and all that portion of the tooth above the second root may be the talonid. Or again, the *Microlestes* molar might have been derived from that of the Amblotheriidæ by the upgrowth of the cingulum cusps on the inner sides of the crown and the loss of the transverse connecting ridge.*

SPECIAL REFERENCES.

Ameghino, F., "Los Diprodontes del Orden de los Plagiaulacideos y el Origen de los Roedores y de los Polimastodontes," *Anales del Mus. Nac. de Buenos Aires*, Tom. IX., 1903, pp. 81 à 192.

Osborn, H. F., "The Structure and Classification of the Mesozoic Mammalia," *Jour. Acad. Nat. Sci. Phila.*, Vol. IX., No. 2, July, 1888.

Owen, Richard, "Monograph of the Fossil Mammalia of the Mesozoic Formations," *Palæontogr. Soc. Lond.*, 1871.

Owen, Richard, "On the Skull and Dentition of a Triassic Mammal (*Tritylodon longævus*)," from South Africa; *Quar. Jour. Geol. Soc.*, 1884.

Lemoine, Victor, "Étude sur le Neoplagiaulax de la Faune Éocène inférieur des Environs de Reims," Extr. *Bull. Soc. Géol. de France*, Feb. 1883.

Cope, E. D., "The Tertiary Marsupialia," *Amer. Naturalist*, 1884, p. 687.

Marsh, O. C., "The American Jurassic Mammals," *Amer. Jour. Sci. and Arts.*, April, 1887.

Marsh, O. C., "Review of Osborn's Memoir on the Structure and Classification of the Mesozoic Mammalia," *Proc. Acad. Nat. Sci. Phila.*, June, 1887.

Falconer, H., "On the disputed Affinity of the Mammalian Genus Plagiaulax from the Purbeck Beds," *Collected Memoirs*, Vol. II., pp. 430-451.

MONOTREMATA.

The true molars of *Ornithorhynchus* when first described (Poulton,[1] 1888) were adduced by Cope as multituberculate and as tending to demonstrate the affinity of the Multituberculata to the Monotremata. When critically examined, however, the molars of *Ornithorhynchus* are found to be very degenerate both in structure and in pattern, and it

---

*[Against all these speculations one might advance another speculation, that *Microlestes*, *Tritylodon* and the Multituberculates, appearing in the Triassic, were not closely related to trituberculate mammals (which are first known in the Upper Jurassic or Basal Cretaceous) but were independent offshoots from the Theriodontia.—ED.]

[1] Poulton, E. B., "The True Teeth and the Horny Plates of *Ornithorhynchus*," *Quar. Jour. Microsc. Sci.*, Vol. XXIX., Aug. 1888.

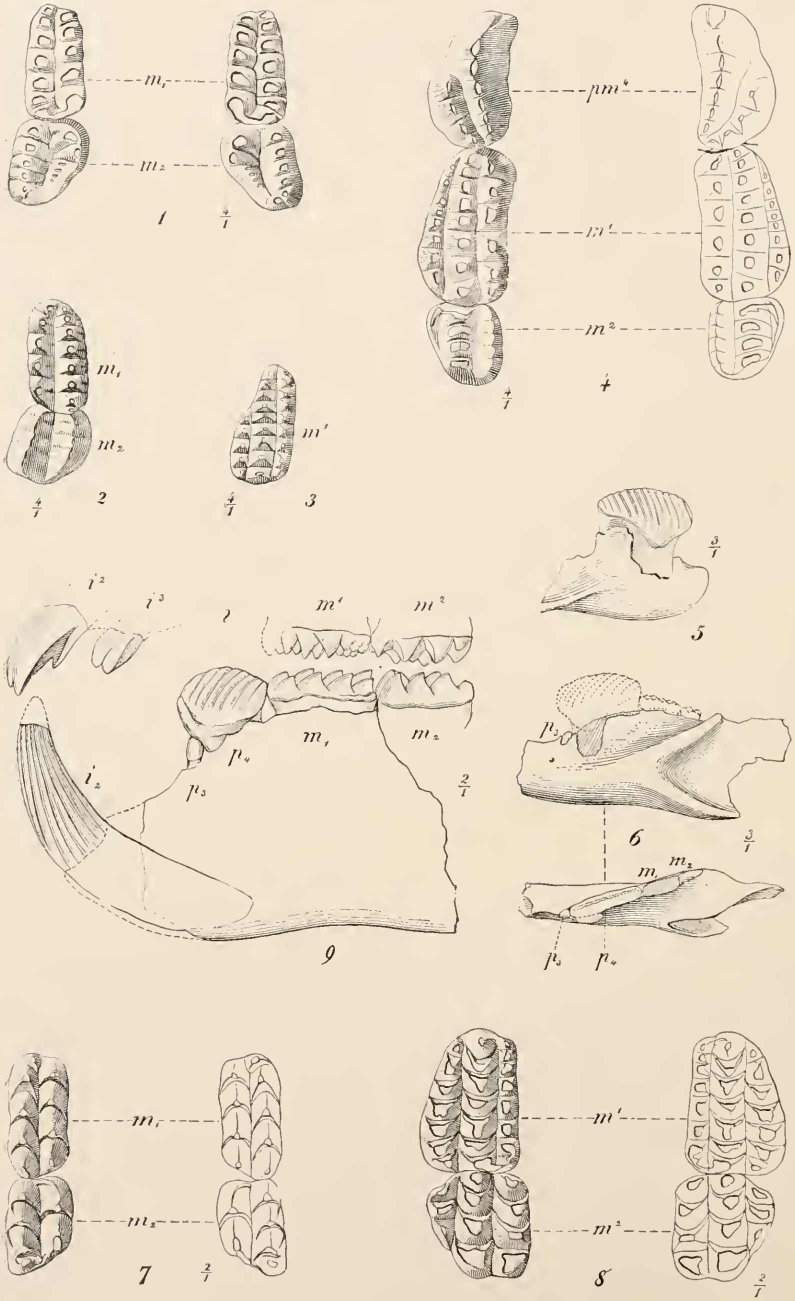


Fig. 55. Dentition of North American Upper Cretaceous Plagiaulacidæ (*Ptilodus*) and Polymastodontidæ (*Meniscoëssus*).

1. *Ptilodus.*—First and second inferior molars; on left side *in situ*, on right side reversed. These teeth belong to two individuals.

cannot truly be said that they actually resemble those of any Multituberculate in the strict sense, because all the higher Multituberculates exhibit an extremely regular mechanical disposition of the cusps, whereas in this living Monotreme the cusps are extremely irregular. Secondly, it does not appear that the *Ornithorhynchus* molars can be cited as evidence either for or against the tritubercular theory because of the evidently secondary and largely degenerative changes which they have undergone; they bear evidence (Fig. 56) of descent from a more primitive regularly

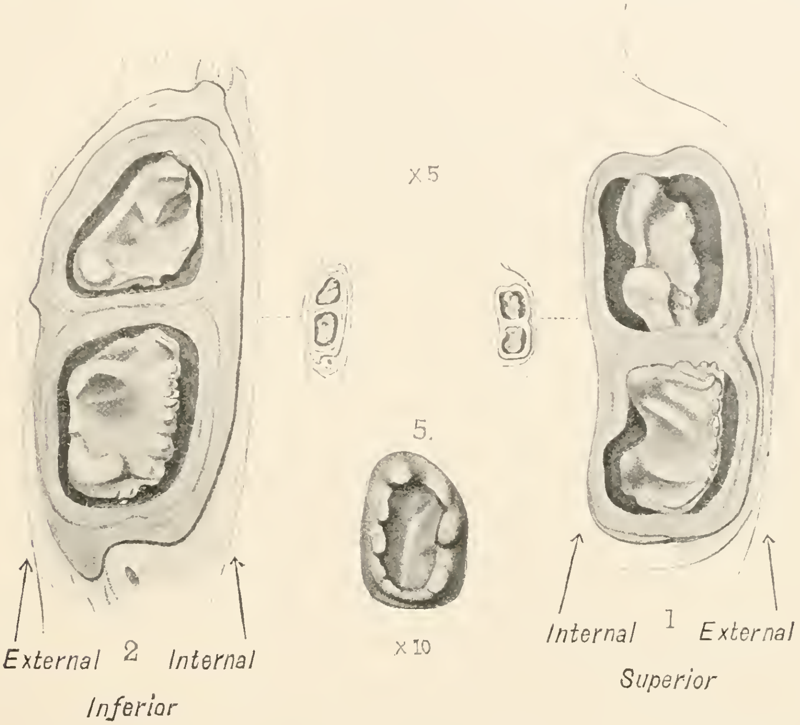


Fig. 56. Molar teeth of *Ornithorhynchus paradoxus*, before being shed and functionally replaced by the horny epithelial plates. After Oldfield Thomas. Nos. 1, 2. Superior and inferior teeth and horny dental pads. No. 5. Crown view of a molar of "*Microlestes*" *moorei*.

---

2. *Ptilodus.*—First and second inferior molars, worn considerably. These teeth belong to two individuals.

3. *Ptilodus.*—First superior molar of the left side.

4. *Ptilodus.*—Fourth superior premolar, first and second molars placed together and reversed in outline to show probable relations. The three shaded teeth on the left side of drawing belong to three individuals.

5, 6. *Ptilodus.*—External and superior views of two lower jaws, showing proportions of the teeth.

7. *Meniscoëssus.*—First and second inferior molars of two individuals placed together and reversed to exhibit the natural position.

8. *Meniscoëssus? conquistus.*—First and second superior molars of two individuals placed together and reversed to show the natural position.

9. *Meniscoëssus.*—Composition side view of upper and lower dentition as far as known. Teeth and jaws combined from eight individuals. The superior premolars are not yet known with certainty.

cuspidate condition. As described and figured by Thomas,[1] the *posterior superior* molars exhibit two high conical *internal* cusps, from which minute ridges run downward to the external borders of the crowns, the edges of which are peculiarly crenulate rather than cuspidate, in the ordinary sense of the word. In the posterior *inferior* molar there are two high cusps on the external side connected by transverse ridges, with a series of crenulations on the internal side.

It is especially noteworthy (1) that unlike the Multituberculates the lower molars reverse the pattern of the upper molars (as in tritubercular teeth generally) and (2) that the highest cusps are on the inner side of the upper molars and on the outer side of the lower molars. *So far as these facts are of value they would support the hypothesis that these are degenerate tritubercular teeth.*

MARSUPIALIA.

It was early perceived by Cope that the molars of *Didelphys* (Figs. 57, 58 *e*) are of the tritubercular type, very similar, in fact, to those of the early Eocene Creodonts. We are indebted to Dr. B. Arthur Bensley[2] for a careful study of the molar teeth of Marsupials in general and an exposition of the very striking parallels which they present to the evolution of the molar teeth in Placentals. In fact, on the supposition that the Marsupials separated at a very early period from the Placentals and that subsequently the dental as well as the general evolution of the two groups was entirely separate and independent, the teeth exhibit some of the most convincing proofs of parallel or homoplastic evolution of which we know.

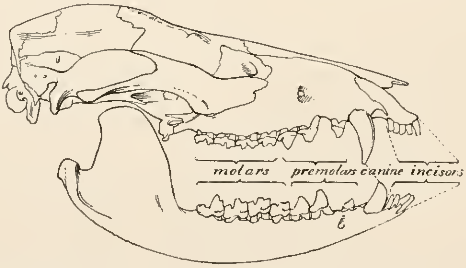


FIG. 57. Skull and dentition of the common Opossum (*Didelphys virginiana*); a typical Polyprotodont Marsupial, with the dental formula *Inc.* $\frac{5}{4}$, *Can.* $\frac{1}{1}$, *Pms.* $\frac{3}{3}$, *Ms.* $\frac{4}{4}$ or 50 teeth in all. × $\frac{1}{2}$. After Matthew.

---

[1] Thomas, O., "On the Dentition of *Ornithorhynchus*," *Proc. Roy. Soc.*, Vol. XLVI., 1889, pp. 126-131, Pl. 2.

[2] *Amer. Naturalist*, Vol. XXXV., 1901, p. 251; also *Trans. Linn. Soc.*, *London*, 2nd Ser., "Zool.," Vol. IX., Pt. 3, Dec. 1903.

Primitive Tuberculo-sectorial Types.

Bensley shows that the Oligocene opossum (*Peratherium*) molar may be taken as the theoretical starting point from which development took place along two main lines, namely (1) the carnivorous and (2) the omnivorous and herbivorous.

If we arrange the teeth of the Australian Marsupials according to the analogy with the Placentals, we obtain such a result as is shown diagrammatically in Figure 58, Nos. 1, 2. The primitive tritubercular, tuberculo-sectorial type is here represented by the teeth of *Dasyurus viverrinus* (58 *d*), but would be still more strikingly illustrated by the teeth of one of the purely insectivorous forms of the Dasyuridæ (*Sminthopsis, Antechinomys, Phascologale*). All these Marsupials exhibit molar teeth which may be readily compared in pattern cusp for cusp with those of *Didelphys.*

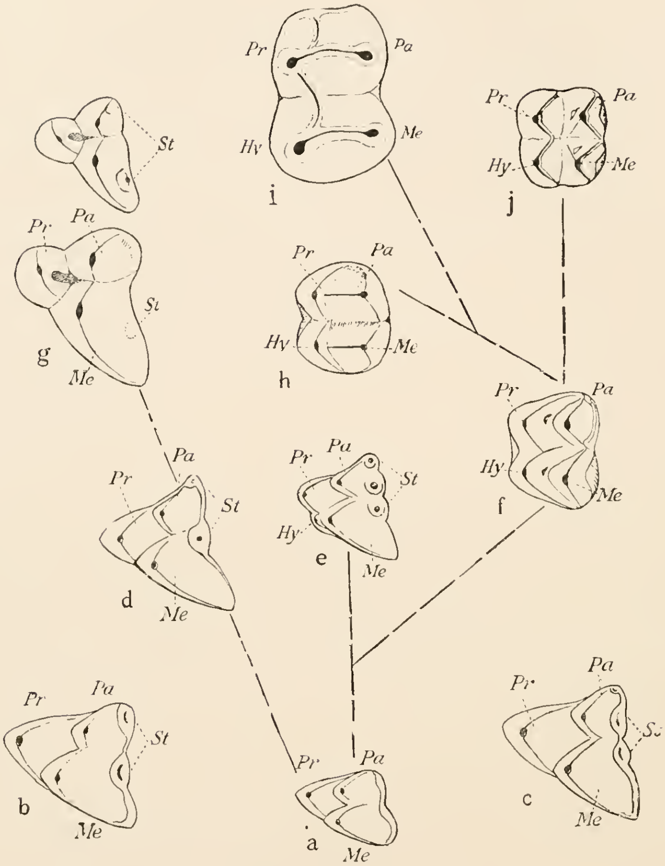
Carnivorous Marsupials.

From this archetype, so to speak, the first line is the carnivorous line to be compared among the Placentals with the specialized Creodonta (*Oxyæna*, etc.). Among Marsupials the carnivorous evolution is entirely confined to the single family Dasyuridæ, and it culminates in the teeth of the Tasmanian wolf (*Thylacynus cynocephalus*). The teeth of this animal are represented in Figure 58, *g*; they show all the essential characters of the teeth of *Dasyurus* except that in the lower teeth the metaconid is absent (this cusp also disappears in the lower cutting teeth of the Felidæ among Placentals). The progressive carnivorous adaptation is effected in the upper molars by a conversion of the paracone and metacone and metastyle into cutting blades and by a degeneration of the other styles, which become reduced to very inconspicuous tubercles. In the lower molars the corresponding cutting blades are formed by the elevation and lateral compression of the paraconid, protoconid and hypoconid, while at the same time the cusps on the other side of the crown, the metaconid, hypoconulid and entoconid are either reduced or disappear (metaconid).

Omnivorous and Herbivorous Marsupials.

Turning to the second group, which leads to the omnivorous and herbivorous adaptations of the teeth, we find that the first stage is represented in the molars of the Bandicoots (Peramelidæ) Fig. 58 *c*, 59. Analogy with the evolution of these teeth is to be sought among the primitive insectivorous-omnivorous Placentals, *e.g.* among the modern Insectivora, in *Tupaia* and *Myogale.*

The main trend is toward cusp addition; thus the upper molars



Upper Molars of the Left Side.

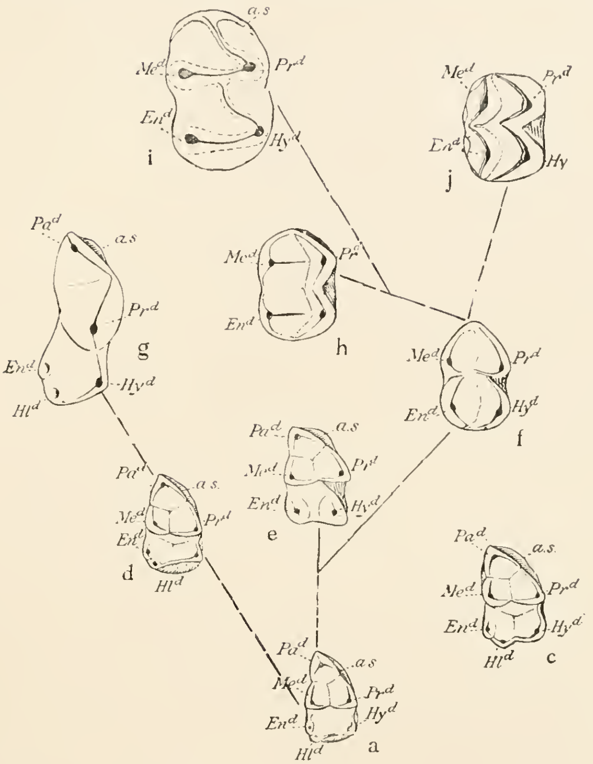
Fig. 58, No. 1. Adaptive Radiation of the Tritubercular Molar Type in the Marsupialia. From Bensley. (Cf. Fig. 58, No. 2.)

a, b, c, Insectivorous type. *a,* Oligocene Opossum (*Peratherium fugax*); *b,* Recent Opossum (*Didelphys azaræ*); *c, Didelphys virginiana. a, d, g,* Progressive carnivorous specialization. *d, Dasyurus viverrinus*; *g, Thylacynus cynocephalus. e,* Progressive insectivorous-omnivorous type (*Perameles nasuta*); *f,* Omnivorous to herbivorous type (*Petauroides volans*). *h,* Incipient lophodont, herbivorous type (*Trichosurus vulpecula*). *i,* Perfected lophodont, herbivorous type (*Macropus sp.*). *j,* Selenodont herbivorous type (*Phascolarctos cinereus*).

of *Perameles nasuta*[1] (Fig. 58, *e*) show all the essential characters of those of *Dasyurus,* and they show the addition of an incipient hypocone; in the third molar the hypocone is not very pronounced and the tooth is still triangular; but in the second molar the hypocone is well developed and the tooth is now quadrate. Thomas (1888, p. 220) describes the triangular and quadrate modifications as characteristic of this family (the Bandicoots). The lower molars of *Perameles*

---

[1] The upper molars of *Perameles macrura* (Figs. 59, 60) closely resemble those of the Insectivore *Myogale,* as shown in unworn teeth; thus they exhibit the many sharp cusps and the double mesostyle characteristic of several insectivorous forms.



Lower Molars of the Left Side.

Fig. 58, No. 2. Adaptive Radiation of the Tritubercular Molar Type in the Marsupialia (continued). From Bensley. (Cf. Fig. 58, No. 1.)

a, b, c, Insectivorous type. *a*, Oligocene Opossum (*Peratherium fugax*); *b*, Recent Opossum (*Didelphys azaræ*); *c*, *Didelphys virginiana*. *a, d, g*, Progressive carnivorous specialization. *d*, *Dasyurus viverrinus*; *g*, *Thylacynus cynocephalus*. *e*, Progressive insectivorous-omnivorous type (*Perameles nasuta*); *f*, Omnivorous to herbivorous type (*Petauroides volans*). *h*, Incipient lophodont, herbivorous type (*Trichosurus vulpecula*). *i*, Perfected lophodont, herbivorous type (*Macropus sp.*). *j*, Selenodont herbivorous type (*Phascolarctos cinereus*).

nasuta (Fig. 58, No. 2, *e*) persistently resemble still more closely those of *Dasyurus*, the omnivorous modification being only developed in the posterior heel where the hypoconulid is reduced.

Perfected Omnivorous Marsupials.

The perfected omnivorous modification among Marsupials is met with in the Phalangeridæ. The two examples of the Phalangers examined by Bensley were *Trichosurus vulpecula*, in which the molars are highly specialized, and *Petauroides volans*, the teeth of the latter being represented in Fig. 58, *f*. Although these teeth illustrate the completed quadritubercular condition, they are only approximately transitional; as among the Placentals, the hypocone is completely formed in the upper molars and the paraconid is correspondingly reduced in the lower molars. The anterior shelf in the lower molars (*a.s.*) which is prominent in the Peramelidæ and Dasyuridæ and very conspicuous in the molars of the Macropodidæ (Fig. 58, *i.*), is here absent. There are also no vestiges of the external styles in the upper teeth.

Crescentic and Crested Herbivorous Marsupials.

The crescentic or selenoid modification of the cusps, which is so characteristic of the Artiodactyl Ungulates among Placentals, appears to be developed only in *Phascolarctos* (Fig. 58 *j.*) among the Marsupials.

The crested or lophoid modification of the cusps so common among the perissodactyl ungulate Placentals is widely represented in the Macropodidæ (Fig. 58 *i.*). The incipient stages leading up to this crested condition are seen in the teeth of the specialized Phalanger *Trichosurus vulpecula* (Fig. 58 *h*) and also in those of *Hypsiprymnodon moschatus* among the Macropodidæ, or Kangaroos. A further parallel to the perissodactyl Ungulate placentals is witnessed in the development of a hypselodont modification of the crested crowns among certain Macropodidæ.

The derivation of all the molar types in the Marsupials from a tritubercular pattern is rendered still further probable by the existence of annectant forms which tend to unite the specialized, quadri-to sexitubercular Diprotodonts (Kangaroos, Phalangers, Wombats), with the generalized tritubercular Polyprotodonts (Dasyures and Opossums). Thus *Cœnolestes,* the only living American Diprotodont lacks the characteristic Diprotodont reduction and syndactyly of the second and third digits of the hind foot and is further allied to the Polyprotodonts by its close external resemblance to the Dasyurid genus *Phascologale.* On the other hand, the Polyprotodont Bandicoots (Peramelidæ) exhibit the syndactyly of the Diprotodonts. Among fossil forms the gap between the two sub-orders is largely bridged over by the extraordinary genus *Wynyardia* of Baldwin Spencer,* which presents a perfect mélange of characters seen elsewhere only in the Opossums and Daysures (Polyprotodonts), and in the Phalangers and Kangaroos (Diprotodonts).

Aberrant and Specialized Types.

The apparently triconodont lower molars of *Thylacynus* are thus shown to be secondary.

The multicuspidate true molars of *Myrmecobius* further support the view that an elongate or basin-shaped and polybunous crown may have arisen from a more tritubercular crown, because they still retain traces

---

* [" A Description of Wynyardia bassiana, a Fossil Marsupial from the Tertiary Beds of Table Cape, Tasmania," *Proc. Zool. Soc. Lond.*, Nov. 20, 1900, pp. 776-795, Pl. XLIX.]

of the tritubercular crown. The secondary development of a number of sharp piercing cuspules seems here as in the Insectivora (p. 117) to be correlated with insectivorous diet. *Notoryctes*, the Marsupial Mole (Figs. 61, 62) has tritubercular upper and lower molars; in the upper molars the high pointed protocone is at the apex of a V, formed by two ridges diverging downward and outward to the basal external portion of the crown, ending in the para- and metacone respectively; on the internal or lingual side, at the base of the crown, the V is surrounded by a deep U-like internal cingulum The lower molars reverse this pattern except that they lack the U-like cingulum.* According to Gidley the principal cusp (marked *pr*) is really the paracone + metacone, the protocone appears as an internal ledge (marked *cing*), but there is no evidence for this except analogy with the supposed case in Insectivora (see pp. 124, 227).

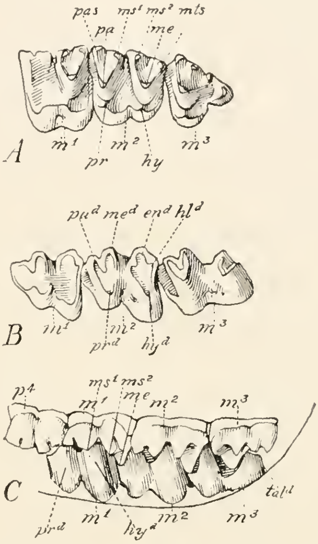


Fig. 59. Molars of *Perameles macrura* from a specimen in the Yale Museum. × $\frac{2}{1}$. *A*, Crown view left upper molars. *B*, Crown view left lower molars. *C*, Upper and lower molars in opposition, as seen obliquely from the outer side and below.

The molars of the Bandicoot (*Perameles*, Figs. 59, 60) show a general parallelism with those of *Didelphys*, *Galeopithecus*, certain Moles and Shrews, and certain Eocene Artiodactyls (*Cænotherium*, *Tapirulus*) in several respects. First the mesostyle is doubled (ms^1, ms^2) permitting the formation of two complete triangles from the paracone, metacone, and styles of the upper molars. Second, the lower molar pattern consists

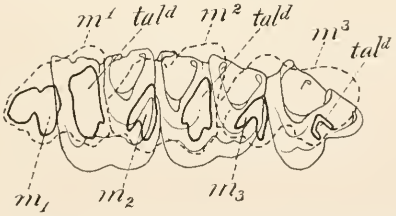


Fig. 60. Diagram showing spatial relations of the patterns of the upper and lower molars when in contact of *Perameles macrura* (Cf. Fig. 69). Compare the somewhat similar pattern of the molars in the Mole, and in *Myogale*.

---

* [As in other mammals without a talonid in the lower molars, the protocone is much elevated. The internal ledge (*cing.*) appears to correspond with that in *Chrysochloris* (Fig. 68).—Ed.]

of two triangles, the hinder one being formed from the enlarged talonid, the apices of these triangles being external and fitting in the spaces between successive outer triangles of the upper molars.*

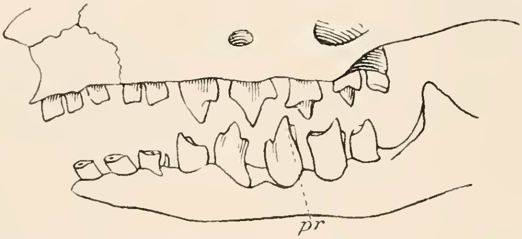


FIG. 61. Dentition of the Marsupial Mole, *Notoryctes typhlops*. $\times\frac{4}{1}$. After E. C. Stirling.

Thus, in conclusion, the various Marsupials afford the most convincing evidence of tritubercular origin. It is only necessary to understand the intermediate stages and to compare even the most highly specialized teeth with analogous types among the Placentals, to be convinced of the universal tritubercular derivation. Howes (*Rept. Brit. Assoc.*, Belfast, 1902) declared he could not conceive the derivation of the *Diprotodon* molar from the tritubercular type, but comparison of these teeth with those of *Macropus* and the stages leading to the *Macropus* type, together with the still stronger but more indirect evidence afforded by the Placentals[1] indicates that the *Diprotodon* molar will ultimately be found to be of tritubercular origin.

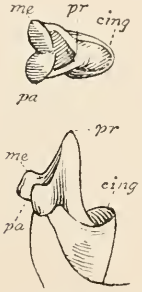


FIG. 62. First upper molar of *Notoryctes typhlops*, upper figure, crown view; lower figure, anterior view. $\times\frac{6}{1}$. After E. C. Stirling.

SPECIAL REFERENCES.

Dentition of Marsupials (figures and descriptions).

Owen, Richard, *Odontography*, 1840-1845.

Tomes, C. S., *A Manual of Dental Anatomy*, 1898.

Bronn, H. G., *Klassen und Ordnungen des Thier-reichs*, Bd. I., pp. 169-177.

Schlosser, M., *Die Affen . . . Marsupialier . . . des Europäischen Tertiärs*, etc., Wien, 1887-90.

De Blainville, H. M. D., *Ostéographie des Mammifères*, Tome III., Paris, 1839-1864.

Bensley, B. A., "On the Evolution of the Australian Marsupialia; with Remarks on the Relationships of the Marsupials in general." *Trans. Linn. Soc.*, 28 Ser., Vol. IX., Pt. 3, Dec. 1903, pp. 83-217.

---

*[As in other mammals the protocone opposes the talonid of the preceding lower molar, the hypocone opposes the trigonid of the corresponding lower molar. —ED.]

[1] Compare the similar lophodont molars of the Tapir with the lophodont to quadritubercular molars of *Systemodon* (Fig. 172).

Molar Teeth of Multituberculates, Marsupials (?), and Placentals in the Upper Cretaceous.

Some years ago the interesting discovery was made of a great number and variety of teeth in fragmentary jaws of mammals in beds of Upper Cretaceous age in North America. The specimens are so fragmentary and isolated that it is difficult to classify them; some probably represent Placentals, others probably represent Marsupials, whilst still others are possibly Prototheria (Multituberculata).

As shown in Figs. 47 and 55, from Osborn, among these forms are two prevailing types of teeth, namely, the highly specialized *multituberculate* teeth, which had reached almost their final extreme of evolution, and the less specialized *trituberculate* teeth which are in a comparatively early stage of evolution.

The **Multituberculates** (see p. 95 and Fig. 55) prove that regularly *successive cusp addition* had taken place since the earlier Jurassic stage, as a result of which the first upper and lower molars exhibit as many as 23 and 12 tubercles respectively in *Ptilodus*, or 21 cusps and 9 cusps respectively in *Meniscoëssus*. This law of successive cusp addition from the posterior basal cingulum is entirely analogous to that which occurs in the complicated molars of the Proboscidea. It demonstrates that cusp origin in the Multituberculata at least is not by concrescence but by cusp addition.

Trituberculates.—In this group (see also pp. 95-97, Fig. 47), all the upper molars known are of the simple, generally low-crowned, tritubercular type, that is, they consist of the trigon to which no trace of the hypocone or postero-internal tubercle has been added. About ten distinct kinds of upper molars have been found altogether. They are all much more recent in type than the few upper molars known of Jurassic mammals, which are invariably high-crowned or piercing; on the other hand, they are somewhat older in type than the prevailing molar teeth of the basal Eocene or Puerco, because they lack all traces of the hypocone, which is very common in Puerco teeth. These Cretaceous *upper molars* exhibit, however, two other characters found also in the Jurassic, namely, (1) small *conules* or intermediate tubercles; (2) external *styles*, or extensions of the cingulum on the outer wall; in some cases these styles are very prominent, forming distinct cusps (Fig. 47).

The primitive features of the upper molars all point toward a tritubercular ancestry. We observe first the large size of the internal cusp or protocone, which certainly supports the theory that this cusp was earlier in evolution than either of the outer cusps.* Second, we observe the striking symmetry of the external cusps or paracone and metacone, giving a symmetrical form to the trigon or main triangle

---

* [See criticism of the similar view expressed on p. 95.—Ed.]

of cusps,* which also lends strong support to the theory that the large protocone was the original cusp of a trigon and that the para- and metacones were added as lateral or external cusps of equal size. The "premolar analogy" or "paracone theory," on the other hand, receives no support whatever from the study of these superior molar teeth.

In general it may be said that the upper molars are intermediate between the Jurassic and the basal Eocene stages of evolution. They thus lend overwhelming proof, if any more were needed, of (1) the progressive evolution of trituberculy among the mammals, (2) of the law of adaptation of the crown by cusp addition. These principles are equally well illustrated in the lower molars.

The lower molars (Fig. 47, Al, Hl, etc.) are relatively more progressive, because (1) not only is the broad heel or talonid well developed, but on this heel the three typical cusps, hypoconid, hypoconulid, and entoconid, are in some cases present. (2) Another progressive character is that the usually elevated trigonid has already been modified in one type (Fig. 47, Il) by the degeneration of the antero-internal cusp or paraconid, although possibly the small size of the paraconid may be a primitive character. (3) These lower teeth are of two types; first, the secodont or tuberculo-sectorial with elevated triangle or trigonid and a lower heel or talonid, as illustrated in Fig. 47, Hl, Al, El; second, a slightly more bunodont type, in which the trigonid has become secondarily depressed although still above the talonid. This secondary depression is carried much further in certain Primates and Ungulates of the basal Eocene. All the other lower molars present unusual features. The one marked Hl has an extremely high paraconid, a feature noticeable, though in a less degree, in the two marked Al. On the other hand in No. Il. the paraconid is small and the metaconid is higher than the protoconid.† In the upper molars, No. 7 may be regarded either as a fourth premolar of the type seen in the Creodont, *Pseudopterodon minutus*, or as a molar of the type seen in the Oligocene insectivore *Ictops thomsoni* (Fig. 66). A noticeable feature of all the upper molars is the indentation in the middle of the outer border of the crown, as in *Peralestes* (Fig. 12), *Kurtodon* (Fig. 13), *Dryolestes* (Fig. 14), and many modern trituberculate insectivores (Figs. 65-80).

SPECIAL REFERENCES.

Osborn, H. F., "Fossil Mammals of the Upper Cretaceous Beds," *Bull. Amer. Mus. Nat. Hist.*, Vol. V., 1893, pp. 311-330.

---

*[A marked advance upon the condition seen in the Upper Jurassic *Dryolestes*, where the paracone was large and medio-external instead of at the anterior tip of the triangle.—Ed.]

†[The metaconid is almost directly internal to the protoconid and connected with it by a transverse cutting crest, as in *Amblotherium* and other Upper Jurassic genera.—Ed.]

INSECTIVORA.

The first statements to be made are: (1) while Insectivora show a *persistent and prevailing trituberculy or triangular arrangement of the* upper and lower cusps, it is also true that (2) the *mode or sequence* of origin of these *upper cusps,* and the *homologies* of different cusps and of different portions of the upper molar crowns are uncertain. According to the evidence presented by Mivart (*Proc. Zool. Soc.,* 1868) and Gidley (quoted below pp. 123-126) in the trigonal molars of *Centetes, Chrysochloris* and other Zalambdodonta, the main cusp is homologous with the paracone or paracone + metacone of other animals, the protocone being represented by the internal ledge marked *hy* in our Figs. 68, 69, B, C.

Among extinct and modern Insectivora, owing apparently to the persistence of very primitive feeding habits, we observe also the persistence of very primitive stages of tritubercular evolution in the molar teeth. The lower molars of certain Eocene and Oligocene Insectivores, such as *Apternodus* and *Micropternodus,* are practically identical in pattern with those of the Jurassic *Amphitherium, Amblotherium,* and *Dryolestes,* presenting an extraordinary instance of persistence of type.

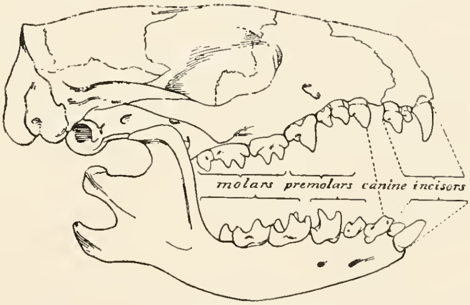


FIG. 63. Skull and dentition of the Hedgehog (*Erinaceus europæus*), a typical dilambdodont insectivore.

Insectivores retaining these primitive tritubercular molars have been distinguished by Gill as Zalambdodonta (with a single external lambda or crescent), whereas the more specialized Insectivores with quadrate or subquadrate molars, such as *Erinaceus,* have been termed Dilambdodonta (with two external lambdas or crescents). There is no doubt that the quadrate or dilambdodont condition is secondary because we have, first, analogy with other groups in which the quadrate is always found to succeed the tritubercular form: second, there is the direct evidence in the unworn molars of *Erinaceus,* and especially of *Gymnura,* and some of their fossil predecessors, as shown

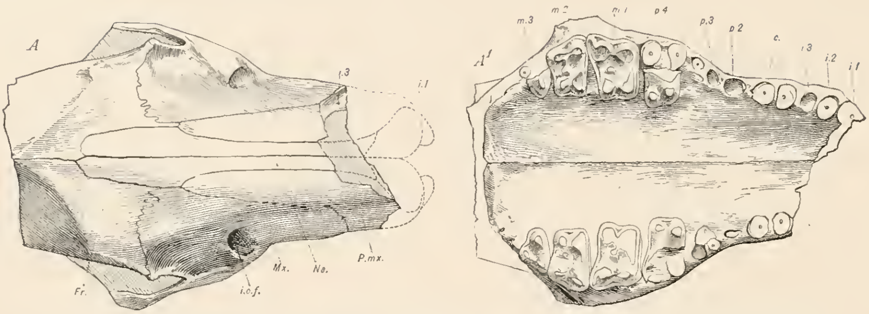


FIG. 64. *A*, top view of facial portion of skull and *A'* upper teeth and palate of *Proterix loomisi*, a primitive Erinaceid from the Upper Oreodon Beds, Lower Oligocene, showing molars of tritubercular origin. $\times \frac{2}{1}$. After Matthew.

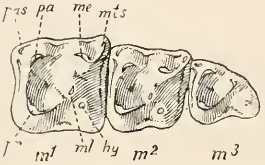


FIG. 65. Upper molars of a primitive recent member of the Erinaceidæ (*Gymnura* sp), showing clear traces of the tritubercular pattern. Note the upgrowth of the hypocone. From a specimen at Yale University. $\times \frac{2}{1}$.

FIG 66. Upper p^4-m^3 of *Ictops thomsoni* from the Titanotherium Beds, Lower Oligocene. These teeth somewhat resemble those of the Mesozoic genus *Dryolestes* (Figs. 14, 207, No. 2). $\times \frac{2}{1}$. After Matthew.

FIG. 67. Upper and lower teeth of *Ictops acutidens*, from the Titanotherium Beds, Lower Oligocene. A member of the family Leptictidæ, which family, according to Matthew, might "without serious straining of relationships be included as a primitive sub-family of Erinaceidæ, with which they agree well enough in skeleton and in most skull characters." In accordance with their primitive condition they have tritubercular molars, with a rapidly developing hypocone. The molars of the modern *Gymnura* are of the same general type (cf. Fig. 65). $\times \frac{2}{1}$. After Matthew.

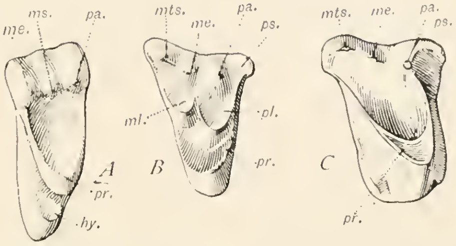


Fig. 68. Molars of tritubercular Insectivores: *A.* "*Chrysochloris,*" m^2 right; *B. Potamogale,* m^2 right (after Allman, *Trans. Zool. Soc.*, 1866, pp. 1 *et seq.*); *Centetes* sp. (All enlarged.) According to Gidley the outer cusps marked *ps*, *pa*, *me*, *mts*, are stylar cusps, the cusp marked *pr* is really the paracone or paracone+metacone while the ledge-like internal projection marked *hy* in *A* and indicated by the anterior basal upgrowth in *C* is the so-called protocone, the posterior basal upgrowth being the hypocone; in *B* the cusps marked *pl*, *ml* are almost certainly the para- and metacones respectively. See Addendum, p. 225.

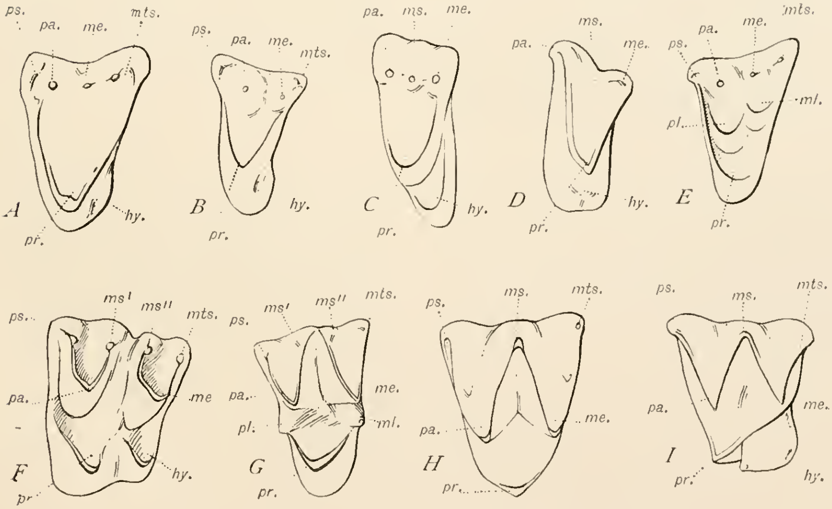


Fig. 69. Possible but uncertain homologies (according to the tritubercular theory) of the true molar cusps in Zalambdodont (*A*-*E*) and Dilambdodont (*F*-*H*) Insectivora, and Cheiroptera (*I*). *A. Centetes*; *B. Ictops thomsoni* (after Matthew). *C.* "*Chrysochloris*"; *D. Solenodon* (after Dobson), 1882. *E. Potamogale* (after Allman). *F. Myogale*; *G. Galeopithecus*; *H. Proscalops* (after Matthew). *I. Nyctinomus brasiliensis*, a bat (after H. Allen, 1893). For another interpretation of the cusps in *A* see the text. In *E* especially the homologies of the cusps are very uncertain.

Postscript.—December, 1906. An apparent solution of this puzzling problem is given on page 225.

The abbreviations in Figs. 68, 69 are incorrect and should be disregarded. The true interpretations are given in the text.

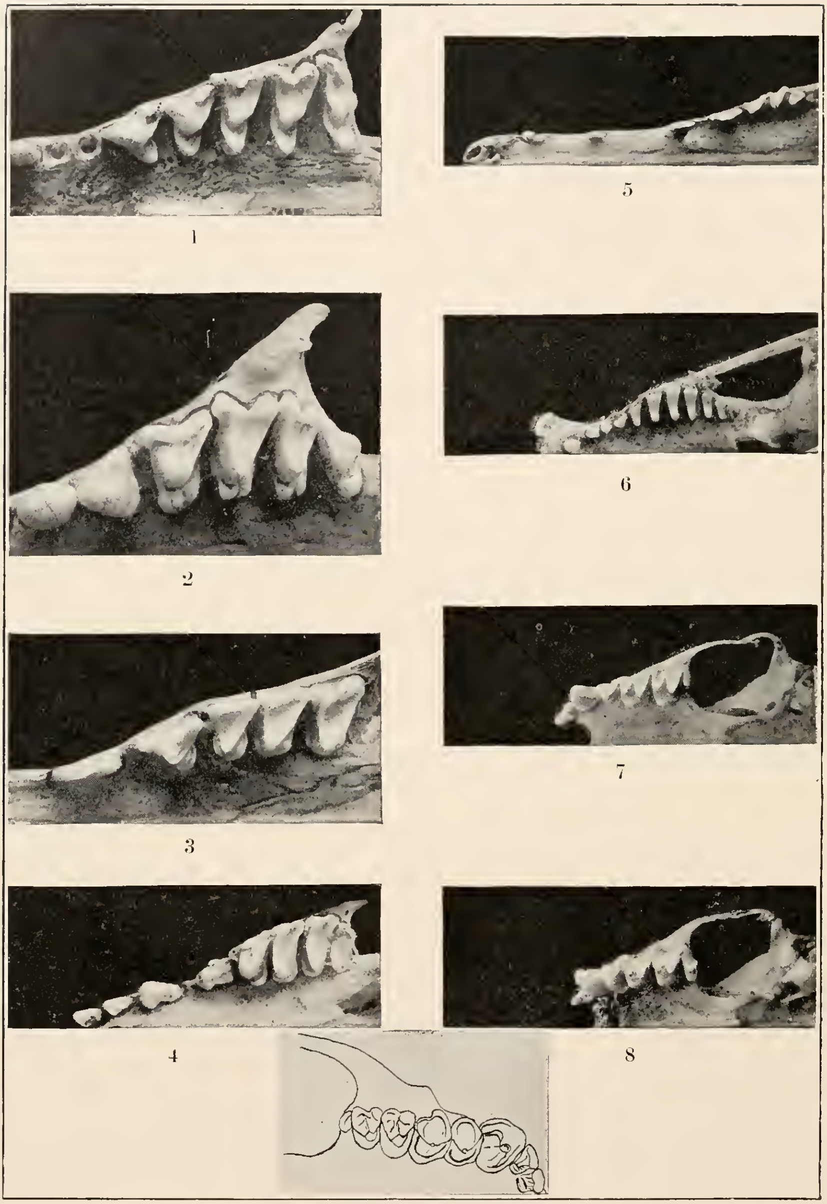


Fig. 69*a*. Cheek teeth of Zalambdodont Insectivores and certain bats. From Gidley.
(*All figures except No.* 9 *three times natural size.*)

No. 1. *Potamogale*—Left upper jaw (No. 124327, U.S.N.M.); habitat, Africa.
2. *Solenodon*—Left upper jaw (No. 2230, U.S.N.M.); habitat, Cuba.
3. *Centetes*—Left upper jaw (No. 63316, U.S.N.M.); habitat, Madagascar.
4. *Ericulus*—Left upper jaw (No. 122488, U.S.N.M.); habitat, Madagascar.
5. *Hemicentetes*—Left upper jaw (No. 63319, U.S.N.M.); habitat, Africa.
6. *Chrysochloris*—Left upper jaw (No. 61686, U.S.N.M.); habitat, Africa.
7. *Vespertilio fuscus*—Left upper jaw (No. 62736, U.S.N.M.); habitat, Washington, D.C.
8. *Scotophilus kuhli*—Left upper jaw (No. 113463, U.S.N.M.); habitat, Philippines.
9. *Harpiocephalus*—Right upper jaw. (Outline drawing taken from a plate prepared in 1880 by Wilhelm Peters for a monograph of the bats. This monograph was never published.)

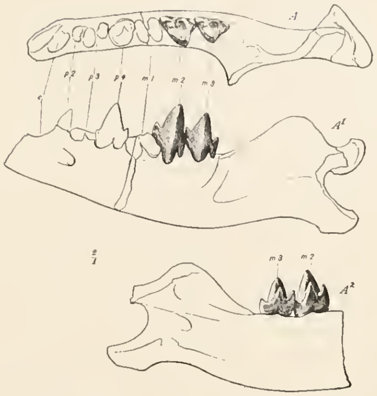


FIG. 70. Lower jaw and teeth of *Apternodus mediævus.* From the Oligocene of Montana. Provisionally assigned to the Insectivora, but possibly allied to the Cheiroptera (Matthew). The talonid is represented by the minute posterior basal spur. *A*, upper, A^1, external and A^2 internal views. $\times \frac{2}{1}$. After Matthew. The molars somewhat resemble those of certain Mesozoic trituberculates (e.g. *Peramus*, Fig. 18, *Peraspalax*, Fig. 22).

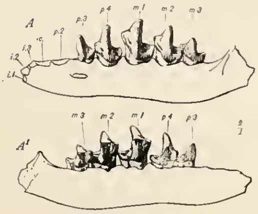
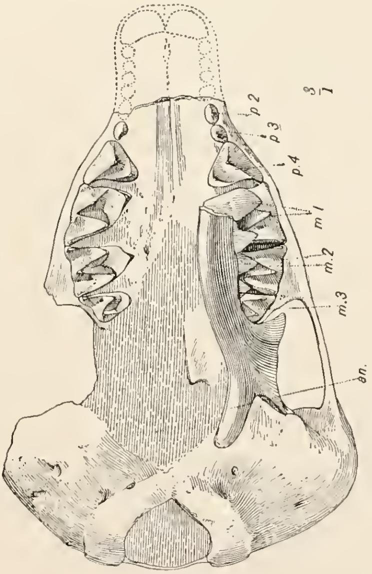


FIG. 71.



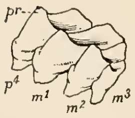


FIG. 72.

FIG. 73.

FIG. 71. Lower jaw and teeth of *Micropternodus borealis.* From the Middle Oligocene of Montana. Probably allied to the Zalambdodont Insectivores. $\times \frac{2}{1}$. After Matthew.

FIG. 72. Upper molars of one of the Centetidæ (*Ericulus setosus*) viewed obliquely from the rear, showing resemblances to the teeth of the Upper Jurassic genus *Kurtodon* (Fig. 13). Compare also Fig. 207, No. 2. $\times \frac{2}{1}$. From a specimen at Yale University (Peabody Museum).

FIG. 73. Inferior view of skull and teeth of *Proscalops miocœnus,* a primitive Mole from the Upper Oligocene of Colorado. $\times \frac{3}{1}$. After Matthew.

in Figs. 64-67, that the hypocone is secondarily developed. Moreover, even in the quadritubercular *Hylomys*, *Necrogymnurus*, and *Galerix*, the third upper molar is tritubercular.[1]

The remote ancestors of the Zalambdodonta or more primitive division, with trigonal or triangular molars, have already been described under the "Insectivora Primitiva" (pp. 22-30). Under the modern representatives of this primitive type have usually been included such forms as *Centetes*, *Solenodon*, and *Chrysochloris* (Figs. 68, 69). More recently, on embryological grounds (pp. 209-213), this comparison has been seriously questioned, and there are a number of authorities who believe that the homologies proposed between the cusps in the recent Insectivores and in the Jurassic Insectivores are unfounded. Our most recent discoveries, however, seem to lend fresh support to the older view; these discoveries include a lower Oligocene Insectivore fauna from Montana, fully described and figured by Matthew.[2] Among these animals we especially note *Apternodus* (Fig. 70), in which the lower teeth strikingly resemble those of *Amphitherium*: and *Micropternodus*, in which the lower molars resemble those of *Solenodon*. Again the teeth of *Ictops thomsoni* (Fig. 66) remind us of the upper teeth of *Phascolestes* (*Dryolestes*, Fig. 14). A higher stage of evolution is represented by the lower and upper teeth of *Ictops acutidens* (Fig. 67). Moreover, the teeth of *Ericulus setosus* (Fig. 72) suggest those of the Upper Jurassic (or Basal Cretaceous) genus *Kurtodon* (Fig. 13).

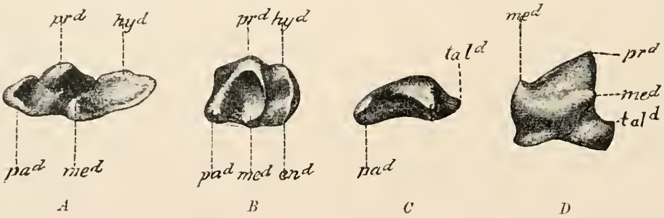


FIG. 74. Tuberculosectorial and carnassial lower molars in a Viverrid and Insectivores. *A. Eupleres goudoti*, a very primitive Viverrid, resembling an Insectivore (crown view of m_1). $\times \frac{4}{1}$. *B. Centetes ecaudatus* (crown view of m_1), representing the ancestral form of *C.* $\times \frac{4}{1}$. *C*, *D*. Carnassial modification of m_2 in an Insectivore, *Hemicentetes madagascariensis*. *C*. Crown view. $\times \frac{7}{1}$. *D*. Inner side view. $\times \frac{7}{1}$. Note the lateral compression of the tooth, enlargement of pr^d, pa^d, reduction of me^d, tal^d, as in the carnassial of Carnivora (Fig. 94, D). All from Forsyth Major, *Philos. Trans.*, Vol. 185 (1894), *B*. p. 24.

From another locality and from a more recent horizon in the American Oligocene is the form *Proscalops miocænus*[3] (Fig. 73), a primitive mole with rather simple trigonal molars, in which, however,

---

[1] Matthew, W. D., *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX., 1903, p. 228.

[2] "The Fauna of the Titanotherium Beds at Pipestone Springs, Montana," *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX., 1903.

[3] Matthew, W. D., *Mem. Amer. Mus. Nat. Hist.*, Vol. I., Pt. VII., 1901.

the three external styles, parastyle, mesostyle, and metastyle, are strongly developed, as in the molars of *Pantolambda* (Fig. 140).

A very interesting fact is that the molar dentition of the Centetidæ has in one case followed the same line of carnassial specialization as in *Oxyæna* (Fig. 92), and *Patriofelis* among the Creodonta, the upper and lower sectorials becoming highly shear-like (Figs. 74, 75).*

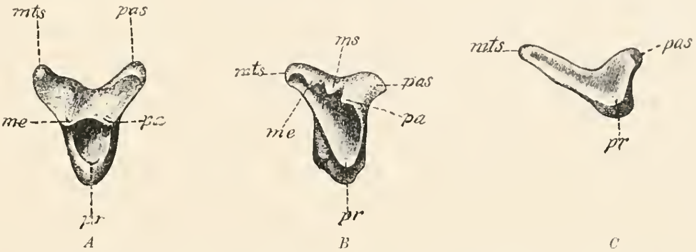


Fig. 75. Tritubercular and carnassial upper molars in a Viverrid and two Insectivores. *A. Eupleres goudoti.* Crown view, m^1. $\times \frac{4}{1}$. *B. Centetes ecaudatus.* Crown view, m^1. $\times \frac{4}{1}$. *C. Hemicentetes madagascariensis*, m^2. $\times \frac{7}{1}$. Note the long sectorial modification of the metastyle, correlated with the blade-like character of the lower molars. In *A* and *B*, *pr* probably represents the fused para + metacone, the proto and hypocones being represented by the small basal cingular outgrowths in *B*. All from Forsyth Major (*op. cit.* p. 23), but relettered. (Cf. Figs. 68, 69, 69 *a*.)

Discussion of the Gidley-Woodward Interpretation.

The following interpretation of Gidley supports that of Woodward, which is presented on pp. 208-213 (see also pp. 226, 227):

"Woodward[1] found that in *Centetes* and *Ericulus* the main internal cusp, usually termed the protocone, was first to develop, but he believed this cusp to be the paracone, the whole tooth representing only the antero-external triangle of such a form as *Talpa*, the protocone and metacone not having been developed. This, as stated by Woodward, is a modification of Mivart's view published in 1868,[2] in which he states his belief that in *Centetes*, *Chrysochloris*[3] and like forms, the main portion of the crown represents the union of the two external prisms of *Talpa* and like forms. According to Mivart, the main internal cusp of *Centetes*, *Ericulus*, *Chrysochloris*, etc. [Fig. 62 *a*, Nos. 3, 4, 6], was derived by the fusion of the paracone and metacone, while the protocone and hypocone are wanting or rapidly diminishing in size and importance. According to both Woodward and Mivart,

---

*[In *Erinaceus* also, p^4 is a generalized sectorial with depressed antero-internal cusp and oblique shear, and m_1 similarly has an enlarged oblique protoconid-paraconid shear and reduced heel.—Ed.]

[1] *Proc. Zool. Soc. London*, 1896, 588-589.

[2] *Journ. Anatomy and Physiol.*, Vol. II., 139, 1868.

[3] "The form figured by Mivart has since been removed to a distinct genus, *Bematiscus*, Cope, *Am. Nat.*, XXVI., 1892, 127. The typical *Chrysochloris* upper molar has no trace of a protocone."

therefore, in these forms, which have been considered typical trituberculates, the outer cusps are developments of the cingulum, while the main internal cusp has been wrongly termed the protocone and is in reality the paracone, according to Woodward, or combined paracone and metacone, according to Mivart, while the inner cusp (protocone) is greatly diminished in size or has entirely disappeared. These two authorities, therefore, are agreed on the two points of principal importance regarding *Centetes* and *Ericulus*, viz.: (1) the location of the paracone in the main internal cusp and (2) the ultimate loss of the protocone. I strongly concur in these views, for in a series of upper molars, including *Potamogale*, *Solenodon*, *Centetes*, *Ericulus*, *Hemicentetes* and *Chrysochloris* (see Figs. 1-6, Pl. IV. [our Fig. 69 *a*]), the stages suggesting the gradual diminishing and final disappearance of the protocone are very complete, amounting almost to demonstration, and there can be little doubt that the molars of the *Centetes* and *Chrysochloris* type have been derived from forms similar to that of *Potamogale*, involving the loss of the protocone. In consequence of this the paracone, or combined paracone and metacone, comes to be the principal inner cusp. In *Potamogale* [Fig. 69 *a*, No. 1] the protocone is quite prominent and still typical in form, while in *Solenodon* [No. 2] it is much reduced and is beginning to divide transversely, or more probably is beginning to separate from a likewise reducing hypocone. This is in favour of the view held by Mivart that the simple inner cusp in *Potamogale* and like forms is in reality the fused protocone and hypocone. The reduction is carried still further in *Centetes* [No. 3], in which two inner cingulum-like cusps appear, one on each side of the enlarged paracone. In *Chrysochloris* [No. 6] and *Hemicentetes* the inner cusp (protocone and hypocone) has entirely disappeared.

"Regarding Mivart's 'fusion theory,' I am inclined to believe that Woodward has not given due weight to the evidence cited by Mivart and that there is considerable support for this theory to be found in the modern bats and insectivores. Mivart considered the *Potamogale* molar as an intermediate form between molars of the *Talpa* type, having two external triangular prisms, and those of *Centetes* and *Ericulus* [No. 4], having only one such prism. He pointed out that in *Potamogale* there is 'a very interesting approximation of the triangular prisms,' in which the paracone and metacone, although still remaining distinct, are in very close juxtaposition. This view is strongly supported by a series of bat molars to which Mr. G. S. Miller has kindly called my attention. In this series, which includes *Vespertilio* [No. 7], *Scotophilus* [No. 8] and *Harpiocephalus* [No. 9], are suggested the successive steps from *Talpa* to *Potamogale* in the insectivore group. *Vespertilio* represents the normal or more generalized form, in which the protocone is large, the paracone and metacone are widely separated, and the external styles are nearly equal in size. The mesostyle is much reduced in *Scotophilus* and is drawn inward, the paracone and metacone are more closely oppressed and the protocone is somewhat shortened. In *Harpiocephalus*[1] the mesostyle has disappeared, the parastyle and metastyle have drawn closer together and compose the entire outer portion of the crown, while the paracone and metacone are closely approximated, forming the greater part of the inner portion of the crown, the protocone being very much reduced. Thus in *Harpiocephalus* a stage is reached nearly analogous to that of *Potamogale*, the principal difference being that the metacone is the dominant cusp instead of the paracone, as in the latter genus.

"From these comparisons it seems reasonably clear that such forms as *Centetes*, *Ericulus* and *Chrysochloris* have attained a secondary or pseudo-tritubercular form by passing through some such stages of evolution as are suggested by the two series here selected. Other examples of a fusing paracone and metacone and reducing protocone may be found in the molars of some of the creodonts and carnivorous marsupials and in the sectorials of many of the carnivores.

"From the foregoing it now seems to be demonstrated beyond question that the main inner cone of *Centetes* and *Ericulus* is not the protocone as observed in normal groups, but, if not entirely made up of the primary cusp (paracone), it at least involves that element, and Woodward's contention that the evidence of embryology is in entire harmony for the molars and premolars is not controverted by these seeming exceptions as supposed by Osborn."*

Homologies. The reasons the cusps of the superior molar teeth of Insectivora are difficult to homologize are: (1) that in certain types the strong development of the styles on the external cingulum tends to confusion with the paracone and metacone, as also in the case of certain Cretaceous mammals (*e.g. Didelphops*, Figs. 47, *F*, *E*), of certain Amblypoda (*e.g. Coryphodon*, Fig. 141), and in Marsupials (Figs. 58, 59); (2) the strong development of the paracone in certain types tends to confusion with the protocone; (3) in order to secure a greater number of sharp piercing cusps the mesostyle divides† into two

---

[1] "The skull of *Harpiocephalus* from which this description was taken was obtained by Mr. G. S. Miller through the kindness of Oldfield Thomas, of the British Museum. Unfortunately it came too late to be photographed and figured uniformly with the series. Its place is taken on Plate III., by an outline drawing from a figure for Wilhelm Peters' *Fledermäuse des Berlines Museums für Naturkunde* (a projected monograph of the bats)."

* [Gidley, J. W., "Evidence bearing on Tooth Cusp Development," *Proc. Washington Acad. Sci.*, Vol. VIII., 1906, pp. 93-95.]

† [In certain Marsupials and Insectivores the presence of two distinct mesostyles may be a primitive character.—Ed.]

distinct cusps in *Myogale* (Fig. 69 *F*), and the intermediate conules (*pl*, *ml*) are very prominent in *Galeopithecus* (Fig. 69 *G*). It is these confusing elements which have led to the proposal of such diverse homologies by different authors. Mr. Gidley interprets the cusp homologies as follows: In Fig. 69 *A-I* the cusps marked *ps*, *pa*, *ms′*, *ms″*, *me*, *mts* are all peripheral or stylar cusps, none of them homologous with the paracone and metacone of other mammals. In *A*, *C*, *D* the cusps marked *pr* are really paracone or paracone + metacone, the protocone being represented by the internal ledge marked *hy*. In *E-I* the ledge-protocone is fully established. In *E* the cusps marked *pl*, *ml* are really the paracone and reduced metacone. On this interpretation *A*, *C*, *D*, instead of being primitive, represent a secondary simplification by fusion of the paracone and metacone. This interpretation also harmonizes with the probability of an inward displacement of the para- and metacones in *F-I*, as in many genera. (Cf. Figs. 67, 75, 83, 85 (m^3, m^2), 90, 94, 116, etc.) Again, the molar pattern of *Ictops acutidens* tends to connect the tritubercular pattern of *Ictops thomsoni*, with the quadritubercular pattern of *Erinaceus* and higher types, but it does not justify the identification of the main internal cusp as homologous in modern Zalambdodont and Dilambdodont Insectivores.

The teeth of Insectivora, therefore, require thorough re-examination on the basis of the tritubercular theory to test these disputed points. (See Addendum, page 225.)

For those to whom the original materials are not accessible, the following references to works which contain numerous figures will be especially valuable:

SPECIAL REFERENCES.

FIGURES OF TEETH OF INSECTIVORA.

Bronn, H. G., *Klass. u. Ord. d. Thierreich's*, Bd. I., pp. 202-211, 233 (*Galeopithecus*).

Dobson, G. E., *Monograph of the Insectivora*, Pt. I. 4to. 1882.

Owen, R., *Odontography*, 1840-45.

Tomes, C. S., *A Manual of Dental Anatomy*, 1898.

De Blainville, *Ostéographie des Mammifères*. (See esp. "Cladobates," *Tupaia*.) Paris, 1839-64.

Schlosser, M., *Die Affen. . . . Insectivoren . . . des Europäischen Tertiärs*, etc. Wien, 1887-90.

Leche, W., *Zur Morphologie des Zahnsystems der Insectivoren. Anat. Anz.*, Bd. XII., 1897, p. 513.

Leche, W., *Zur Entwickelungsgeschichte des Zahnsystems der Säugetiere.* Stuttgart, 1895.

Matthew, W. D., "The Fauna of the Titanotherium Beds at Pipestone Springs, Montana," *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX., 1903, pp. 197-226; "A Fossil Hedgehog from the American Oligocene," *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX., 1903, p. 228; "Fossil Mammals from the Tertiary of North-eastern Colorado," *Mem. Amer. Mus. Nat. Hist.*, Vol. I., Pt. VII., pp. 375-376.

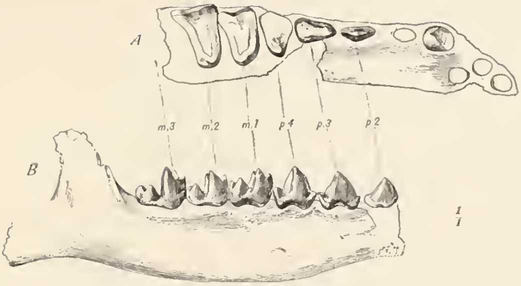


Fig. 76. Upper and lower teeth of *Palæosinopa veterrima*, an Insectivore from the Wasatch Formation, Lower Eocene, Wyoming, the teeth showing resemblances to the teeth of the most primitive Creodonts. $\times \frac{1}{1}$. The upper molars have the internal cusp somewhat depressed, a feature emphasized in the Creodonts (Figs. 84-90).

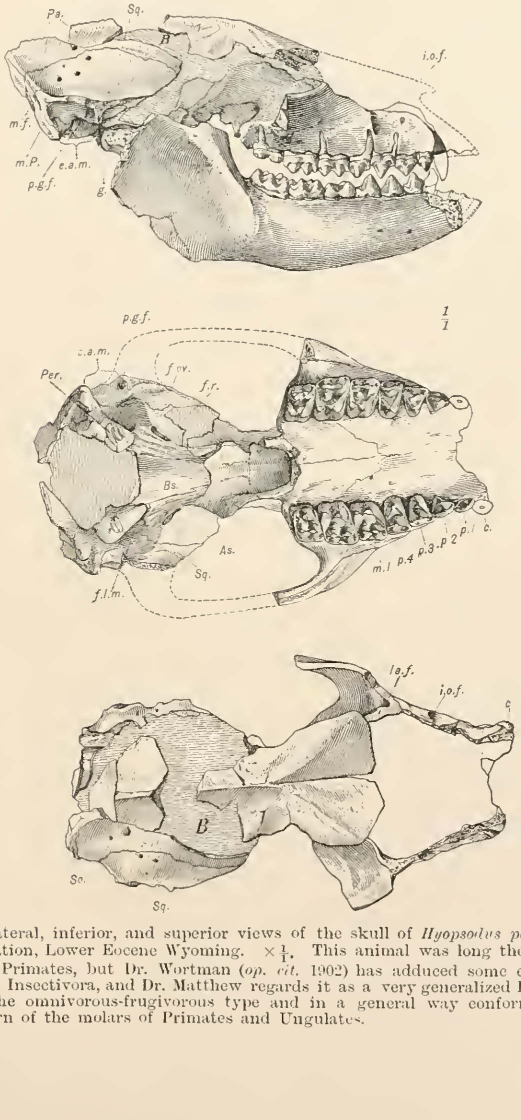


Fig. 77. Lateral, inferior, and superior views of the skull of *Hyopsodus paulus*, from the Wasatch Formation, Lower Eocene Wyoming. $\times \frac{1}{1}$. This animal was long thought to belong to the Eocene Primates, but Dr. Wortman (*op. cit.* 1902) has adduced some evidence for its removal to the Insectivora, and Dr. Matthew regards it as a very generalized Eutherian. The teeth are of the omnivorous-frugivorous type and in a general way conform to the ideal ancestral pattern of the molars of Primates and Ungulates.

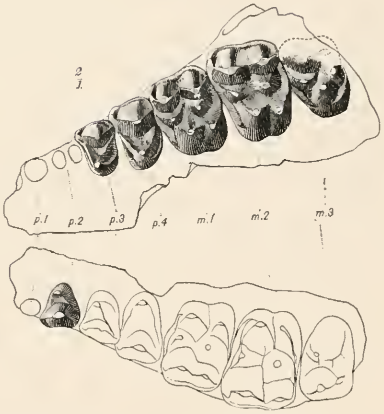


Fig. 78. Upper teeth of *Hyopsodus marshi* from the Bridger Formation, Middle Eocene. Note the quadrate contour of the molars, the well-developed intermediate conules and hypocone. $\times\frac{2}{1}$. (The opposite dental series converge too much in the figure.) (Cf. Figs. 77, 79.)

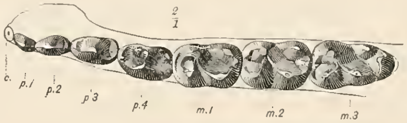


Fig. 79. Lower teeth (crown view) of *Hyopsodus lemoinianus*, from the Wasatch Formation, Lower Eocene. Note the absence of the paraconid, the presence of a well-developed posteromedian cusp, the hypoconulid on m_1, m_3. (Cf. Figs. 77, 78.) $\times\frac{2}{1}$.

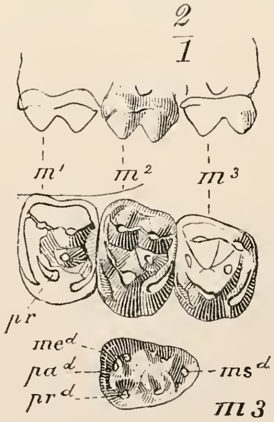


Fig. 80. Teeth of *Diacodexis* (*Hyopsodus*) *laticuneus*, a genus now referred to *Hyopsodus*. From the Wasatch Formation, Lower Eocene. $\times\frac{2}{1}$.

CHEIROPTERA.

The following quotation may be made from the writings of an author (Oldfield Thomas) who is in no way committed to the tritubercular theory: it becomes especially clear by reference to the preceding section on the Insectivora:

> "The earliest Bats, or Palaeochiroptera would have been cuspidate-toothed and insectivorous like their ancestors the terrestrial Insectivora. Among them there would presently have arisen a form like *Harpyia*, fruit-eating but still with cuspidate teeth and no doubt markedly 'tuberculo-sectorial' premolars and molars. Then, while the modern *Harpyia* would have arisen in one direction by the reduction of the incisors, in another there would have followed some form like *Pteralopex*, still retaining to a certain extent cuspidate teeth. Then the cusps would have more and more tended to disappear, the result being *Pteropus* and its allied

FIG. 81. Skull, crown view of upper teeth and internal view of right upper canine of *Pteralopex atrata* Thomas, a Fruit-Bat, which, instead of having cusp-less cheek teeth as in other Megacheiroptera, has retained cuspidate teeth more or less suggestive of the tuberculo-sectorial type. × $\frac{1}{1}$. After Oldfield Thomas.

genus, of which some few species (*e.g. Pteropus anciteanus* and *leucopterus*, and *Cynopterus*) retain remnants of the ancient cuspidate structure, while others (*e.g. Pteropus coronatus*, . . .) have lost all trace of molar cusps." Oldfield Thomas, *Proc. Zool. Soc.*, 1888, pp. 474-475.

In the treatises especially of Harrison Allen[1] and of Matschie[1] we have examples of the teeth of Cheiroptera studied respectively from the tritubercular standpoint and from the older standpoint in which there was no especial attempt to establish tritubercular homologies. The very interesting and important work of Matschie on the Fruit Bats develops particularly the secondary formation from a tritubercular crown of a basin-shaped crown with a depressed centre and a rim surmounted with irregular cusps, analogous to that which we find among the most primitive Multituberculates. If all the

Fig. 82. Superior view of the right half of the lower jaw of a Microcheiropter, *Artibeus perspicillatus*, showing the progressive change in m_1, m_2 of a cuspidate into a "basin-shaped" molar. $\times \frac{4}{1}$. After H. Allen.

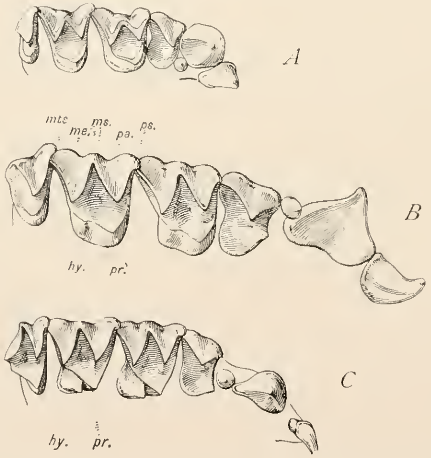


Fig. 83. Progressive stages in the development of the hypocone in Microcheiroptera. *A.* Tritubercular stage (*Atalapha cinerea*). $\times \frac{4}{1}$. *B.* Transitional stage (*Promops perotis californicus*). $\times \frac{4}{1}$. *C.* Quadritubercular stage with strongly-developed hypocone (*Nyctinomus brasiliensis*). $\times \frac{6}{1}$. After H. Allen. Possibly the series may be reversed, and we may be witnessing in the stages *C, B, A,* the secondary loss of the hypocone, caused by the shortening of the skull and tooth row.

---

[1] See titles under "Special References."

stages leading to this secondary basin-shaped formation are carefully examined it will be found that they invariably point back to a more symmetrical tritubercular arrangement. A similar case occurs in the Microcheiroptera in the genus *Artibeus* (Fig. 82), where the first and second inferior molars[1] have become basin-shaped and irregularly cuspidate remotely resembling the *Microlestes* molars (p. 102). The nearest relatives of this genus are plainly tritubercular.

According to Mivart and Gidley certain bats show a secondary simplification of the molar pattern by fusion of the para- and metacones as in the supposed case of the Zalambdodont Insectivores.

In general, therefore, the Cheiroptera definitely support the tritubercular theory, since the molar teeth are clearly derivable from simple tritubercular types such as we find among the Insectivora.

SPECIAL REFERENCES.

Bronn, *Klassen u. Ord. d. Thierreichs*, Bd. I., pp. 211-223.

Owen, R., *Odontography*, 1840-45.

Giebel, C. G., *Odontographie*, 1855.

Schlosser, M., *Die Affen . . . Chiropteren . . . des Europäischen Tertiärs*, etc. Wien, 1887-90.

Allen, H., "A Monograph of the bats of North America," *Bull. U.S. Nat. Mus.*, No. 43. Washington, 1893, p. 198, 38 pll.

Matschie, P., *Die Megacheiroptera des Berliner Museums für Naturkunde*. Berlin, 1899. (This monograph contains 14 fine lithographic plates on the skull and body-form of the Fruit-Bats, Pteropodidæ.)

CARNIVORA.

The carnivorous quadrupedal placental mammals may be divided into three grand divisions, namely:

The **Creodonta**, which were primitive Carnivores of Cretaceous and Lower Eocene age, the special peculiarity of which is that the carnassial or specialized cutting teeth in the upper and lower jaws are not the same as those in the true Carnivora. In the true Carnivora invariably the fourth upper premolar and first lower molar are transformed into carnassials: whereas in the Creodonta one or more of their first, second, and third upper and lower true molars may transform into carnassials. The second great division is the **Fissipedia**, including the modern terrestrial Carnivora, which have been termed Carnassidentia by Wortman, in reference to the distinctive possession of sectorials formed out of the fourth upper premolar and first lower molar. The third great group is the **Pinnipedia**, the water living forms, in which the teeth have been

---

[1] H. Allen, "A Monograph of the Bats of North America," *Bull. U.S. Nat. Mus.*, No. 43, 1893, Pl. V.

secondarily modified for effective prehension rather than for the fine cutting or mastication of the food, which consists principally of fishes. Here we find the haplodont and triconodont forms secondarily attained.

Creodonta. In general the earliest or basal Eocene Creodont molars are very important because they present types of upper and lower teeth which are transitional between those of the Insectivora Primitiva, the trigonodont Insectivora, the upper Cretaceous mammals, and those of the higher or more specialized Creodonta and Fissipedia. Many early types of molars referred to the Creodonta closely resemble certain molars in the Upper Cretaceous, but the two distinctive features are that they almost invariably present (1) an internal cingulum (wanting in the Upper Cretaceous mammals) and (2) a more or less well developed hypocone rising from this cingulum.

Fig. 84. Typical trituberculate molars in very primitive Creodonts. Left upper figure, *Tricentes subtrigonus*; right upper figure, *Chriacus baldwini*; central figure, *Chriacus truncatus*; all Oxyclænids from the Torrejon Formation, Basal Eocene, Stage II, New Mexico. Lower figure, *Triisodon heilprinianus*, family Triisodontidæ (? Mesonychidæ), Puerco Formation, Basal Eocene, Stage I, New Mexico. All × $\frac{1}{1}$.

It was among these Lower Eocene Creodonts that Professor Cope discovered his great generalization as to primitive trituberculy, the upper molars being universally tritubercular, while the lower molars are universally tuberculo-sectorial.

Molar evolution in the Creodonts follows three general lines: first, development of carnassial teeth as an adaptation in the purely carnivorous forms (Figs. 90, 91); second, the persistence of more blunt tritubercular teeth in the omnivorous forms (Figs. 84, 85); third, development of irregularly low-crowned teeth in certain very specialized omnivorous forms, as in *Arctocyon* and *Anacodon* (Fig. 86). The low, irregular molars of the third type are so specialized in *Anacodon* that the primitive tritubercular pattern is vanishing; but in the less specialized *Arctocyon* and the still less specialized *Clænodon*, the tritubercular origin of these teeth is perfectly apparent.

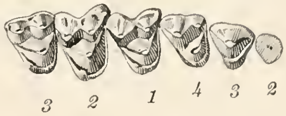


FIG. 85. Upper teeth of *Deltatherium fundaminis*, an Oxyclænid Creodont from the Torrejon Formation, Basal Eocene, Stage III. ×$\frac{1}{1}$. The hypocone is developing as a small cusp from the basal cingulum.

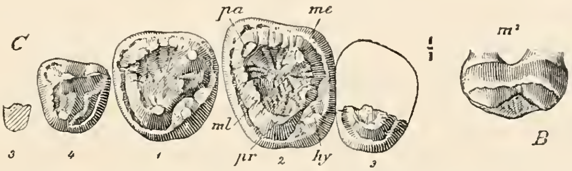


FIG. 86. *C*, Crown view, p^4-m^3 of *Anacodon ursidens*, family Arctocyonidæ, of the Creodonta, from the Wasatch Formation, Lower Eocene. ×$\frac{1}{1}$. Note the secondary obscurement of the tritubercular pattern by the upgrowth of the basal cingulum, especially in the region of the hypocone, the flattening of the crown (compare the side view *B*), the wrinkling of the surface. Analogous conditions are seen in the Gorilla and the Bears.

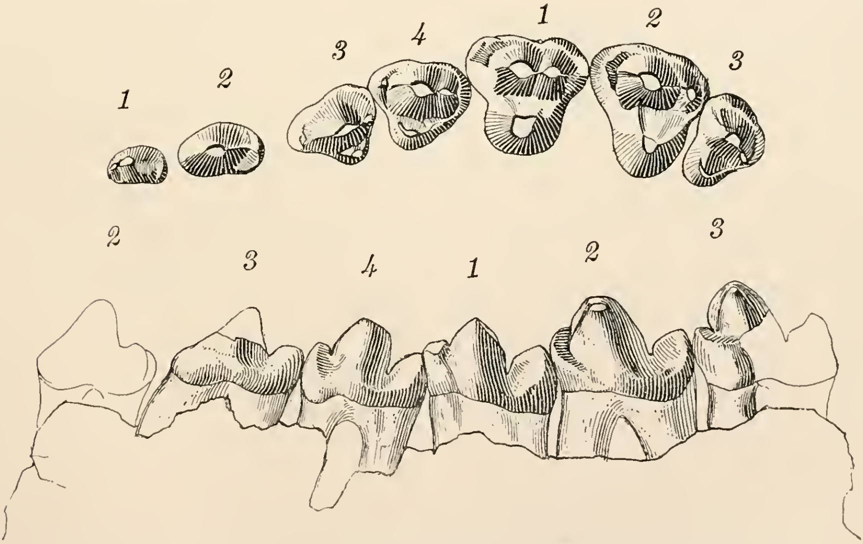


FIG. 87. Upper and lower teeth of *Dissacus saurognathus*, a Mesonychid Creodont, from the Basal Eocene (Torrejon). The upper molars differ from those of the majority of the contemporary Creodonts in the small size of the metacone, the ledge-like character of the protocone; the lower molars are laterally compressed, subtrenchant, with greatly reduced metaconid. They have been cited by Dr. Wortman as favouring the premolar analogy theory. (See page 216.)

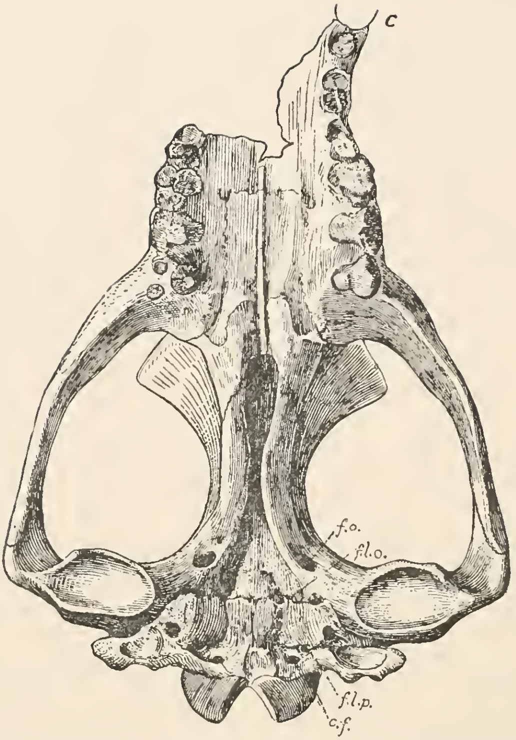


FIG. 88. Inferior surface of the skull of *Mesonyx uintensis*, family Mesonychidæ, of the Creodonta, from the Uinta Formation, Upper Eocene. $\times \frac{1}{4}$. Note the bluntly tritubercular molars.

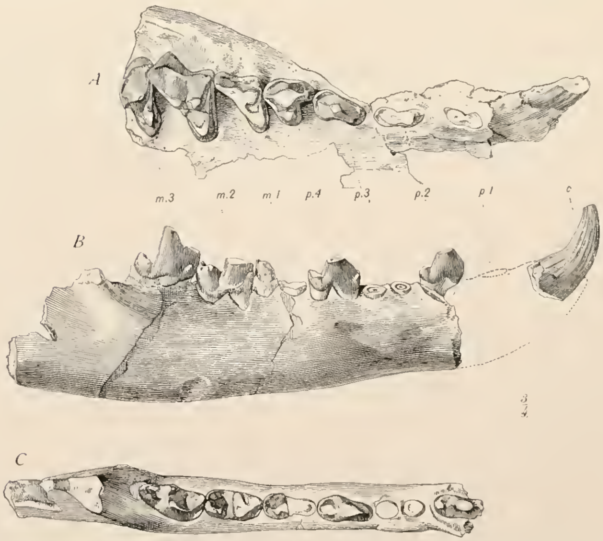


FIG. 89. Upper and lower teeth of *Sinopa opisthotoma*, family Hyænodontidæ, sub-order Creodonta, from the Wasatch Formation, Lower Eocene, Wyoming, showing the sectorial modification of m^1, m^2 and m_2, m_3. *A*, Superior view, upper teeth; *B*, Outer side view, lower teeth; *C*, Superior view, lower teeth. $\times \frac{3}{4}$. After Matthew.

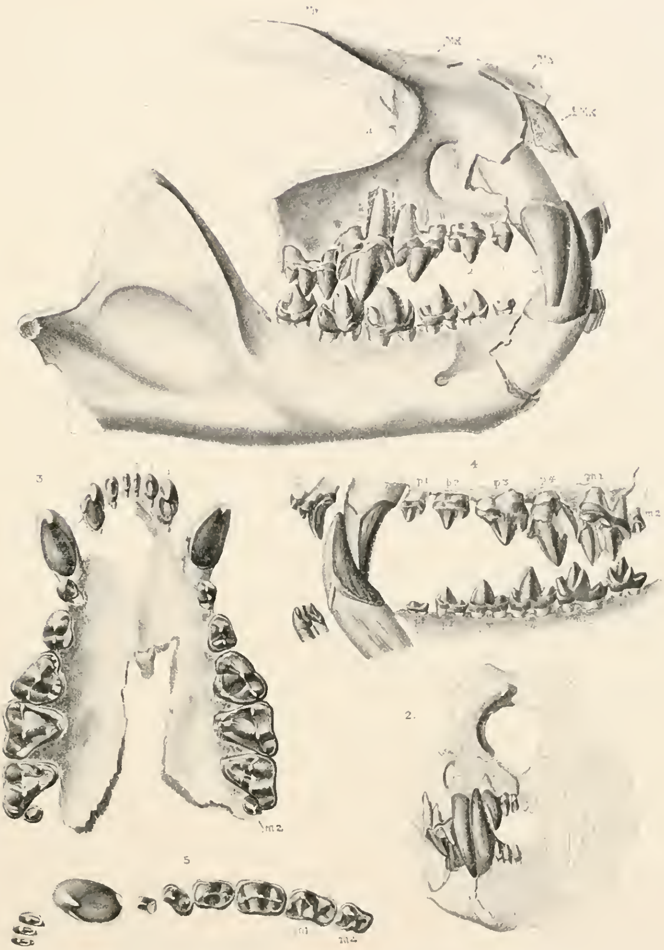


Fig. 90. Skull (partial) and dentition of *Palæonictis occidentalis*, a short-faced Creodont from the Wasatch Formation, Lower Eocene. 1. Side view ($\times\frac{1}{3}$), showing enlargement and sectorial modification of p^4, m^1 ($\times\frac{1}{2}$). 2. Front view ($\times\frac{1}{3}$). 3. Palatal view, upper jaw ($\times\frac{1}{2}$), showing tritubercular molars, sectorial modification of the posterior side of p^4, m^1, reduction of m^2. 4. Internal view, upper and lower teeth, showing sectorial modification of p^4, m^1, and m_1, m_2. 5. Superior view of lower teeth, showing tuberculosectorial character of m_1, m_2.

Evolution of Carnassial Teeth in Creodonta and Fissipedia.

1. *Lower Carnassials in Fissipedia.*

In order to thoroughly grasp the principles of transformation of a tritubercular into a sectorial type, let us first examine such a series of the lower teeth as are represented in Fig. 95.[1] In *A* and *B* we see the external and internal aspects of the tuberculo-sectorial

---

[1] From Osborn and Wortman, "Foss. Mamm. Wasatch and Wind River Beds," *Bull. Amer. Mus. Nat. Hist.*, 1892, p. 99.

crown, in which the trigonid or triangular arrangement is still perfectly apparent and the broad heel or talonid is still persistent in these three characteristic cusps. In the types represented in *C* and *D* the heel has begun to degenerate. In *E* the talonid has become very simple, the metaconid is degenerating, the trigonal arrangement has been lost because the paraconid is rotating

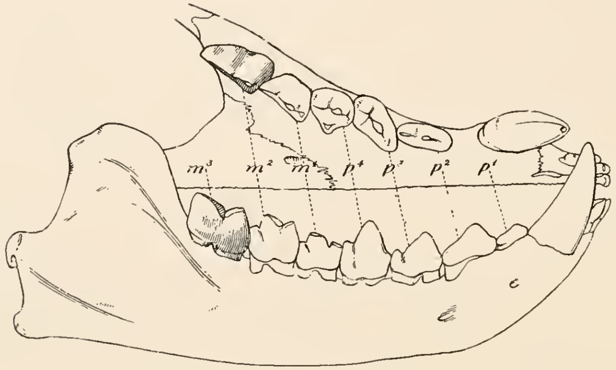


Fig. 91. Upper and lower teeth of a Creodont, *Hyænodon*. Carnassial teeth, $\frac{m^1, m^2}{m_2, m_3}$ (first and second upper, and second and third lower molars). The perfected carnassials $\frac{m^2}{m_3}$ are shaded. After Matthew.

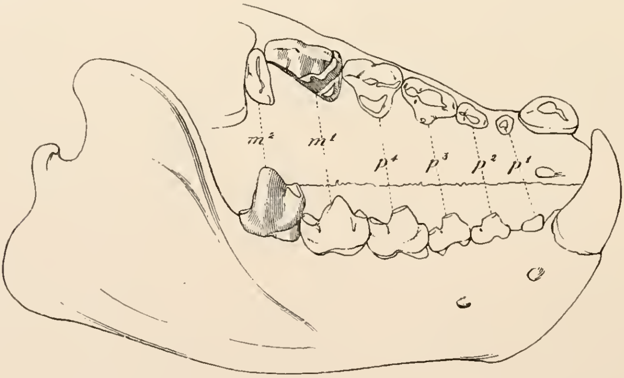


Fig. 92. Upper and lower teeth of a Creodont, *Oxyæna*. Carnassial teeth $\frac{m^1}{m_2}$. (First upper and second lower molar). After Matthew.

outward and forward,—lending support, by the way, to the cusp rotation theory (p. 32 (*b*)). In *F* (*Dinictis*) the paraconid is nearly subequal with the protoconid, and the metaconid is vestigial, while the talonid is still further reduced. In *G* (*Felis*) the metaconid is altogether wanting, the talonid is vestigial, the paraconid and protoconid are in the same fore-and-aft line, of nearly equal size, and sharply lophoid or sectorial. The *carnassial specialization* in this case involved the development or transformation of two cusps (paraconid and protoconid) at the expense or degeneration of four cusps (metaconid, hypoconid, hypoconulid, entoconid).

Carnassial specialization in general involves the great *reduction* of a number of elements. It is thus diametrically the reverse of certain types of herbivorous specialization, in which there is a constant increase of the number of elements.

FIG 93. Upper and lower teeth of a Fissipede or true Carnivore, the Lion. Carnassial teeth $\frac{p^4}{m_1}$, (fourth upper premolar and first lower molar). After Matthew.

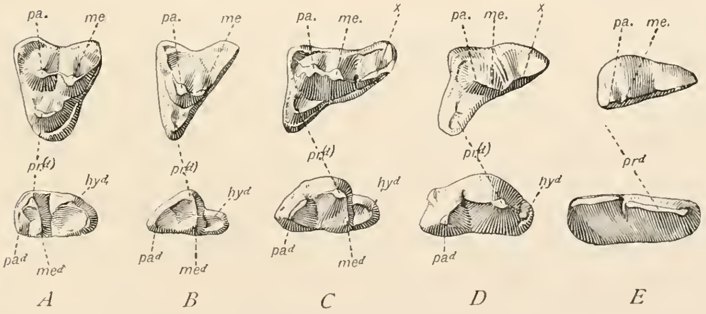


FIG. 94. Evolution of the sectorial upper and lower molars in the Creodonts. *A.* Typical tritubercular upper and tuberculosectorial lower molars in *Triisodon heilprinianus*, family Mesonychidæ, Puerco Formation. Stage I., Basal Eocene. *B. Sinopa opisthotoma*, family Hyænodontidæ, Wasatch Formation Lower Eocene. Note: the shearing modification of the posterior side of the upper molar and of the anterointernal side of the lower molar, the small size of the talonid, the reduction of the metaconid. *C. Oxyæna forcipata*, family Oxyænidæ, Wasatch Formation. Note the further accentuation of the characters mentioned under *B.* *D. Pterodon dasyuroides*, family Hyænodontidæ, Upper Eocene and Oligocene, France. Note: the concrescence of the metacone with the paracone, the loss of the metaconid, and (almost) of the talonid (hy^d), the anterior shifting of the protocone, the lateral compression of the lower tooth. *E. Hyænodon horridus*, family Hyænodontidæ, White River Formation, Oligocene. Completed carnassial modification, resulting in long shearing blades, in the upper sectorial composed of the paracone, vestigial metacone and enlarged metastyle; in the lower sectorial of the enlarged paraconid and protoconid. All the figures represent the first upper molar (m^1) and the second lower molar (m_2). From Scott and Osborn.

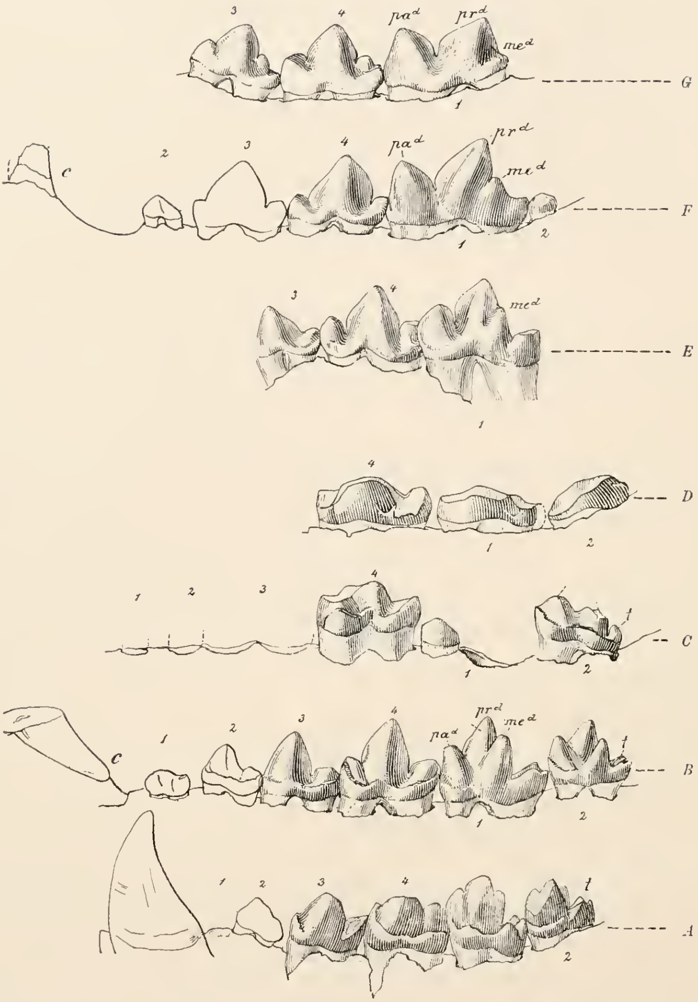


FIG. 95. Inferior teeth of various Creodonts (*A*-*E*) and true Carnivores (*F*, *G*), showing the homologies of the cusps of the specialized lower carnassial tooth. *A. Palæonictis gigantea*, Lower Eocene, France, outer view, showing tuberculo-sectorial molars, with a small low talonid. *B. Palæonictis occidentalis*, Wasatch Formation. Lower Eocene, Wyoming, inner view. *C. Ambloctonus sinosus*, Wasatch Formation. Worn teeth, inner view, showing reduced talonid (*t*). *D.* The same, outer view. *E.* Milk teeth of *Patriofelis*, family Oxyænidæ, sub-order Creodonta, (inner view). Bridger Formation, Middle Eocene, Wyoming. Note the lateral compression of the teeth, the enlargement of the protoconid and paraconid, the reduction of the metaconid. *F. Dinictis felina*, one of the Machærodont Felidæ, sub-order Carnivora Vera (Fissipedia), White River Formation, Oligocene. Inner view showing blade-like character of the tooth, enlargement and separation of the paraconid, reduction of the metaconid and talonid. *G. Felis concolor* (Puma). Inner view. Note vestigial character of the talonid (me^{d}), disappearance of the metaconid.

2. Convergence of Upper Carnassials in Creodonta and Fissipedia.

The independent evolution of the carnassial teeth among Creodonta and Fissipedia affords the most distinctive and interesting example of *convergent evolution, whereby similar adaptations are reached from dissimilar* *beginnings,* so that if we did not know the intermediate history we would be entirely misled. This results from the fact as noted above, that, in the Creodonta, teeth becoming upper sectorials are chiefly the molars, whereas in the Fissipedia they are invariably the fourth upper premolars: although the initial pattern of the upper molars and of the upper premolars is different, the crown being composed of cusps some of which at least are not homologous with each other, the result of adaptation is to make these two teeth appear to be entirely similar. (Series I., II., Fig. 96.)

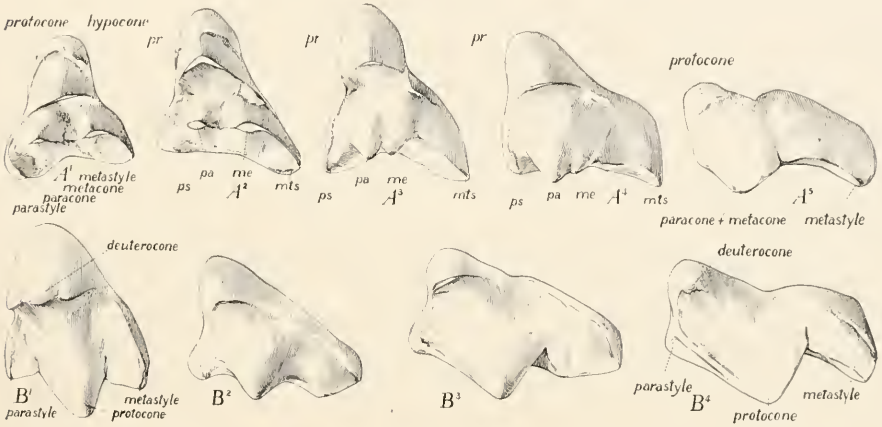


FIG. 96. Convergent Evolution of Carnassials in Creodonta and Fissipedia. Arranged by Dr. W. D. Matthew from specimens in the American Museum of Natural History. These series represent morphological but not direct evolutionary sequences.

I. (Upper row). **Creodonta**. *First upper true molar* of the right side evolving from the trituberculer into the carnassial type in the Hyænodontidæ.

A^1. *Deltatherium* of the Basal Eocene. Generalized tritubercular molar with three primary cusps (*pr., pa., me.*), a rudimentary hypocone, and two external styles (*pas., mts.*).

A^2. *Sinopa opisthotoma* of the Lower Eocene. Forward shifting of the protocone (*pr.*), backward prolongation and cutting shape of the metastyle (*mts.*), reduction of the parastyle (*pas.*).

A^3. *Sinopa whitiæ* of the Middle Eocene. The progressive changes described under A^2 more strongly accentuated; also incipient reduction of the protocone (*pr.*), and its approach toward the paracone (*pa.*), but especially the approximation of the paracone to the metacone.

A^4. *Pterodon* of the Lower Oligocene. Still further accentuation of the above tendencies, namely, approximation of the metacone to the paracone (*me., pa.*), reduction of metacone (*me.*), enlargement of metastyle (*mts.*), reduction of parastyle (*pas.*), anteroversion of protocone (*pr.*) and its approximation to the paracone.

A^5. *Hyænodon* of the Middle Oligocene, representing the final stage. Protocone (*pr.*) reduced to a mere cingulum, paracone and metacone (*pa., me.*) completely confluent, metastyle (*mts.*) greatly elevated, laterally compressed, giving us a cutting blade laterally compressed, composed mainly of two elements, namely, *paracone+metacone*, and metastyle.

II. (Lower row). **Fissipedia**. Superior *fourth premolar* evolving from tritubercular into carnassial form in Palæonictidæ, Miacidæ, Canidæ.

B^1. *Palæonictis*. A Creodont of the Lower Eocene. Generalized fourth premolar type, with protocone, deuterocone, and cusps corresponding to parastyle and metastyle.

B^2. *Didymictis* of the Basal Eocene. We note the forward shifting of the deuterocone, the reduction of the parastyle, the enlargement of the metastyle.

B^3. *Daphænus*, a dog of the Lower Oligocene. Forward shifting of the deuterocone, still further reduction of the parastyle, elevation of the protocone and of the metastyle.

B^4. *Canis*, a recent dog, showing the vestigial deuterocone and parastyle, and the subequal metastyle and protocone.

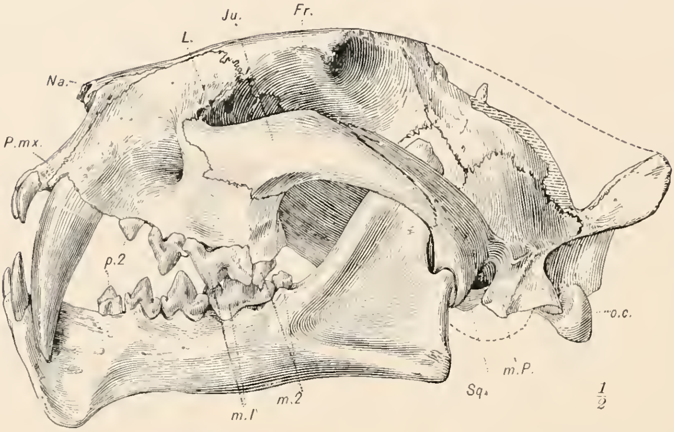


Fig. 97. Skull and jaw of *Dinictis squalidens*, a primitive Machærodont Felid from the Oligocene of Colorado. Note the position of the carnassials (p^4, m_1) in relation to the areas of insertion of the muscles of mastication. The action of the lower teeth on the upper teeth is from behind forward and upward. $\times \frac{1}{2}$. After Matthew.

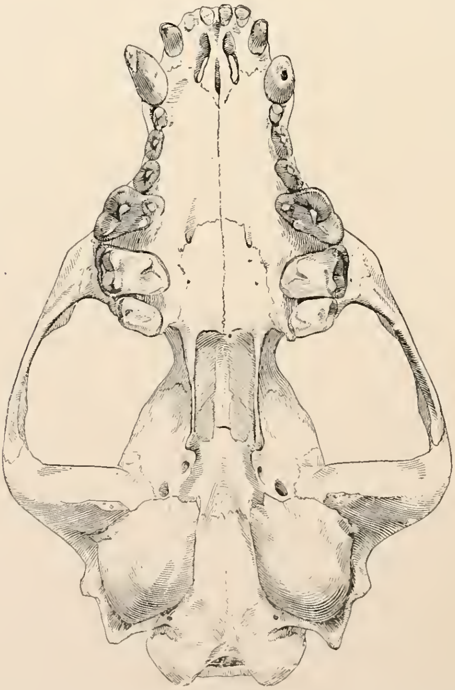


Fig. 98. Inferior view of the skull of *Phlaocyon leucosteus*, an ancestral Raccoon (Procyonid) from the (Upper) White River Formation, Oligocene Colorado, showing the subsectorial modification of p^4, the crushing character of m^1, m^2, the absence of m^3. $\times \frac{1}{1}$. After Matthew.

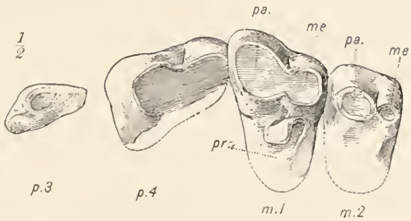


FIG. 99. Crown view of the worn upper cheek teeth of a gigantic Amphicyonine Canid *Borophagus gidleyi*, from the Upper Miocene of Texas, showing tritubercular molars (m^1, m^2), and carnassial p^4. The enlargement of the paracone (*pa.*) is apparently secondary. ×½. After Matthew.

FIG. 100. Skull and jaw of *Mustela ogygia*, an extinct species of marten (family Mustelidæ), from the Upper Miocene of Colorado. Note especially the carnassial teeth, which as in the Felidæ have been developed in the fourth upper premolar, and first lower molar. Note also the reduction of the first upper molar and the absence of the other post-carnassial teeth, another analogy with the Felidæ. $\times\frac{1}{1}$. After Matthew.

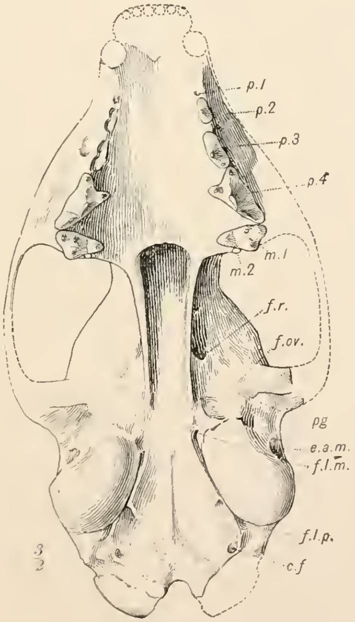


FIG. 101. Inferior view of the skull of *Bunælurus lagophagus*, a primitive Musteline, from the Oligocene of Colorado. Note especially the carnassial modification of p^4, the reduction of m^1, the practical disappearance of m^2. $\times\frac{3}{2}$. After Matthew (1902).

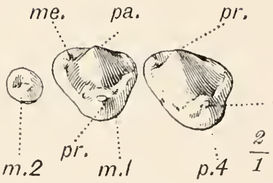


Fig. 102. Crown view of the right upper cheek teeth of the Binturong (*Arctictis binturong*), showing the loss of the third molar, the great reduction of the second (m^2), the simplification of the first (m^1) by the loss of the metacone (me), and the reduction of the protocone (pr), the convergence in form between m^1 and p^4, the greater or less flattening down of the crowns of p^4-m^2; all this apparently in adaptation to frugivorous diet. The nearest allies of the Binturong, the Paradoxures, have more normal teeth, while the most primitive, more carnivorous members of the family Viverridæ (*e.g. Genetta*) have tritubercular upper and tuberculosectorial lower molars. $\times\frac{2}{1}$.

Fissipedia.

The tritubercular and tuberculo-sectorial teeth of primitive Procyonidæ, Mustelidæ, Viverridæ, Ursidæ, Canidæ, Felidæ, and Hyænidæ are too well known to require special emphasis. In general the Procyonidæ exhibit the bunodont, tritubercular type. The Ursidæ exhibit a depressed and secondarily bunodont, quadritubercular and tuberculo-sectorial dentition; as seen by comparison of the more sectorial molars of the Polar Bear, *Thalassarctos*, with the more depressed molars of the relatively omnivorous Black Bear. The teeth of the bear were originally more elevated like those of the dog, then secondarily elongated, and finally depressed and irregularly tubercular.

Degenerate Types.

Adaptation to different habits has given rise to a great variety of secondary modifications. For example, (1) to the flat or even basin-shaped crown of *Cercoleptes*, (2) to the degenerate tuberculate teeth of *Arctictis* (Fig. 102); the extreme similarity between p^4 and m^1 in this animal, the enlargement of the paracone and the reduction of the metacone, the ledge-like appearance of the protocone, make the resemblance which has arisen between these teeth analogous to that which has arisen in *Mesonyx*,—namely it is a case of convergence.[1]

In general answer to the analogy argument (p. 215) it has been shown in the case of the sectorials of Creodonta and Fissipedia above, that (*a*) final similarity of form is no indication of derivation from homologous parts; (*b*) the exact similarity of p^4 and m^1 in *Arctictis* (Fig. 102) is another case of independent or convergent evolution, or the production of analogous crowns from non-homologous cusps (see pp. 138, 139): (*c*) fruit-eating habits (*Arctictis* is said to be frugivorous) frequently lead to the degeneration or aberrancy of the molar crowns

---

[1] [But see also the indications in Figs. 14, 66, 67, 69*a*, 76, 84, 85, 105, 116, 117, 118, 131, 139, etc., that the similarity between p^4 and m^1 is *not* wholly due to convergent evolution.—Ed.]

(p. 103); (*d*) the enlargement of the paracone and reduction of the metacone occurs also in *Dinocyon* (Fig. 99), in the Mesonychid Creodonts (Figs. 87, 88, and p. 216), and is probably secondary; (*e*) no fossil ancestral viverrines are known with such aberrant molars.

SPECIAL REFERENCES.

Figures of Molars of Carnivora.

Bronn, H. G., *Klass. u. Ord. d. Thierreich's*, Bd. I., pp. 179-202.

Owen, R., *Odontography*, 1840-1845. See especially for histology of the teeth.

Giebel, C. G., *Odontographie*, 1855.

Schlosser, M., *Die Affen . . . Carnivoren des Europäischen Tertiärs*, etc. Wien, 1887-90.

PINNIPEDIA.

The teeth of the aquatic Carnivora, or Pinnipedia, are so much modified secondarily that until we trace their ancestral history we cannot feel any confidence in attempts either to homologize the cusps or to trace these teeth back to a tritubercular or triconodont stage. Weber[1] adduces much evidence in favour of their derivation from the Bears. In that case the ultimate derivation of their molars from the tritubercular type would be obvious.

As figured above, *Phoca gichigensis* (Fig. 103 *A*) exhibits a tooth analogous to that of the Triconodonta among the primitive Marsupials (Fig. 6), that is, with a main central and two lateral cusps. We have seen that somewhat similar molars with several cusps in a fore-and-aft line have evolved secondarily out of tuberculo-sectorial molars in the case of the Marsupial *Thylacynus* (Fig. 58, II. g) and of the Creodonts *Mesonyx* (Fig. 87, lower teeth) and *Hyænodon* (Fig. 91).

Phoca vitulina exhibits a type more suggestive of *Zeuglodon* (Fig. 194, p. 191), the central cusp is less prominent, and the lateral and posterior cusps more elevated and connate. According to Dr. J. A. Allen,[2] within this single species, *Phoca vitulina*, there is a wide range of individual and sexual variation in the cheek teeth, as regards the number and position of the cusps, the size of the crown, its position in the tooth row, etc., so that we may infer that at least in this species a high rate of evolution or variation is even now in progress, while in the past the evolution has obliterated the primitive pattern of the teeth. In *Phoca grœnlandica* the lower molars are suggestive of the tuberculo-sectorial type.

The third type, *Zalophus californianus*, the Sea-lion (Fig. 103 *C*), presents in the upper molars at least an example of the *secondarily haplodont crown*, in which the main outer cusp is probably the paracone,

---

[1] *Die Säugetiere*, 8vo, 1904, p. 551.

[2] *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI., 1900, pp. 468-470.

which has been developed at the expense of the degenerating inner cusps, which included originally an elevated protocone.

The secondarily triconodont cheek teeth of the Leopard Seal (*Ogmorhinus leptonyx*) are shown in Fig. 42*.

SPECIAL REFERENCES.

Bronn, H. G., *Klassen und Ordnungen des Thierreich's*, Bd. I., pp. 105-108.
Owen, R., *Odontography.*
Tomes, C. S., *A Manual of Dental Anatomy*, 1898.
De Blainville, H. D., *Ostéographie des Mammifères.*

FIG. 103. Secondary evolution of triconodont and haplodont types in Pinnipedia. Internal view. *A. Phoca gichigensis* (family Phocidæ or Earless Seals). *B. Phoca vitulina* (Harbor Seal). *C. Zalophus californicus* (California Sea Lion, family Otariidæ or Eared Seals). All × $\frac{1}{1}$.

RODENTIA.

We naturally look among the brachyodont, short-crowned types of Rodents, such as the squirrels and mice, for the ancestral form of Rodent teeth. Matthew[1] and Osborn[2] have hypothetically traced the Rodents back to a lower Eocene ancestor in the family Mixodectidæ; Osborn has gone so far as to call these animals **Proglires**,[3] whereas Wortman[4] has revived the view expressed by Cope that

---

[1] "A Revision of the Puerco Fauna," *Bull. Amer. Mus. Nat. Hist.*, Vol. IX., 1897, pp. 259-323.

[2] "American Eocene Primates and the Supposed Rodent Family Mixodectidæ," *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI., 1902, pp. 203-213.

[3] Recent studies by Matthew indicate the nearer affinity of these animals to the Insectivora, with possible relations to the Lemuroids.

[4] "Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum," *Amer. Journ. Sci.*, Vol. XVI., Nov. 1903, pp. 345-352.

these animals are not Rodents but Lemurs related to the aberrant order represented by the living *Cheiromys* or Aye-Aye. The evidence for either of these antagonistic hypotheses is by no means final. If these animals are truly primitive Rodents or Proglires, they settle the tritubercular question so far as Rodents are concerned, because the teeth are typically tritubercular above and tuberculo-sectorial below (Fig. 104). Pending the positive discovery of the remote ancestors of the Rodents, it may be said that the most primitive existing and fossil forms of brachyodont rodents, as the Eocene and Oligocene Ischyromyidæ, Sciuridæ, exhibit apparent traces of the tritubercular pattern in the molar teeth.

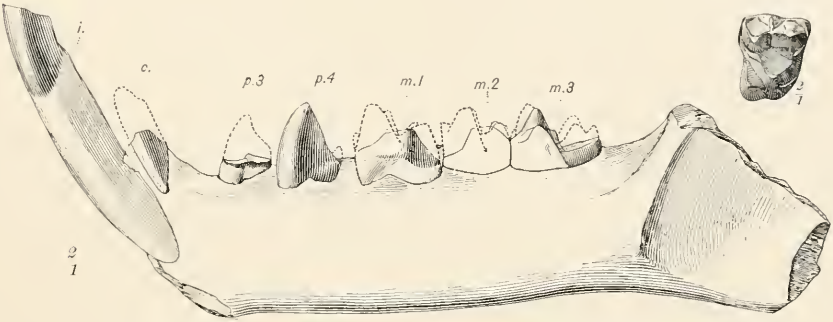


Fig. 104. Tritubercular molars in the "Proglires," possibly related to the Rodents. Upper figure, an upper molar of *Olbodotes copei* from the Torrejon Formation, Stage II. Basal Eocene, showing a primitive tritubercular crown, with a hypocone growing up from the basal congulum. Lower figure, lower jaw and teeth of *Mixodectus pungens* also from the Torrejon Formation, showing enlarged incisor and tuberculo-sectorial molars. See note 3, page 144. $\times \frac{2}{1}$.

SIMPLICIDENTATA.

The animals included within the sub-order Simplicidentata (*i.e.* with a single pair of incisors, as contrasted with the Duplicidentata, or Rabbits and Hares) are traced back by Tullberg in his great monograph,[1] to an ancestral type in which the molars exhibit four cusps. Schlosser[2] also has figured a morphological series of upper and lower molars, showing the probable stages of evolution from the bunodont tritubercular (?) molars of *Arctomys* to the hypsodont complex molars of *Hystrix*. Forsyth Major, on the contrary, who has made an exhaustive study of the teeth of Rodents, regards the teeth of primitive squirrels, which are apparently tritubercular, as secondarily derived from a polybunous form by the loss of certain cusps. It is more consistent

---

[1] *Ueber das System der Nagethiere.* Upsala, 1899.

[2] "Die Differenzierung des Säugetiergebisses," *Biol. Centralbl.*, Bd. X., Nr. 8, 1890, S. 251.

with the evolution of the mammalian molar teeth in general to suppose that the primitive Oligocene Sciurid of Fig. 105 actually exhibits a tritubercular crown above without the hypocone, and a quadritubercular crown below, in which the paraconid is vestigial. (Compare Fig. 106.)

Among the rats and mice we observe a secondary cusp addition and evolution, which has obscured the primitive tritubercular pattern if such existed, closely parallel or analogous to that of the multituberculates in the development of three parallel rows of tubercles above and two parallel rows of tubercles below. (See pp. 102-104.)

FIG. 105. Left upper cheek teeth of a primitive Squirrel, *Sciurus* (*Prosciurus*) *vetustus* from the Titanotherium Beds (Lower Oligocene) of Montana, the molars showing apparent derivation from the tritubercular pattern. ×$\frac{4}{1}$. After Matthew.

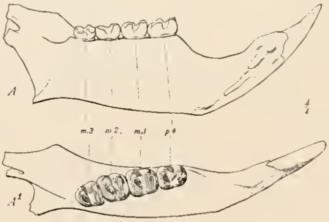


FIG. 106. Lower jaw and teeth of *Gymnoptychus minimus*, a primitive Sciuromorph (?) from the Titanotherium Beds of Montana; the molars apparently indicate derivation from the tuberculo-sectorial type. M_1 seems to show a vestige of the paraconid. ×$\frac{4}{1}$. After Matthew.

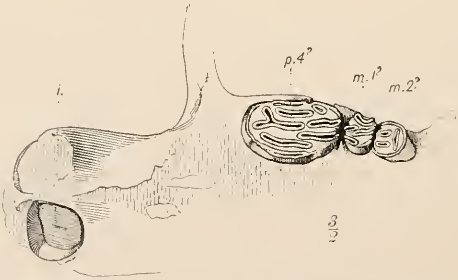


FIG. 107. Upper teeth (crown view) of *Mylagaulus monodon* (Cf. Fig. 108), showing the small size of m^1, m^2, the great development of p^4. In the rootless hypsodont teeth the enamel is folded into longitudinal "lakes." All traces of a simpler crown pattern have been lost, as in many other Hystricomorphs, Castoridæ, etc. ×$\frac{3}{2}$. After Matthew.

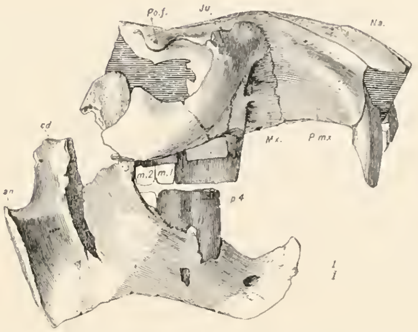
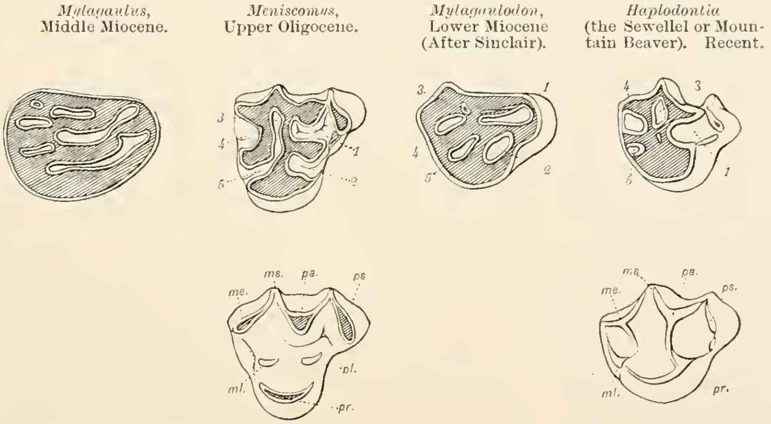


FIG. 108. Facial portion of skull, and lower jaw of *Mylagaulus monodon*, from the Upper Miocene of Colorado, a Sciuromorph Rodent (family Mylagaulidæ), in which the true molars are reduced and the fourth premolar greatly enlarged (Cf. Fig. 107). ×$\frac{1}{1}$. From Matthew.


Mylagaulus, Middle Miocene.

Meniscomys, Upper Oligocene.

Mylagaulodon, Lower Miocene (After Sinclair).

Haplodontia (the Sewellel or Mountain Beaver). Recent.

FIG. 109. Traces of trituberculy in the fourth upper premolars of the Rodent families Mylagaulidæ and Haplodontiidæ. "Osborn's molar cusp nomenclature is used as a matter of convenience, not necessarily implying homology with the cusps of the true molars." (Matthew.) If the fourth upper premolar in these families has been derived from a tooth with the tritubercular *form*, the first molar was probably tritubercular in *form* and in *origin*. After Matthew.

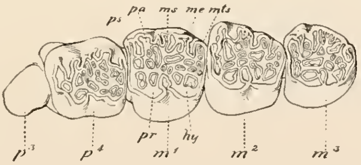


FIG. 110. Upper cheek teeth of *Eutypomys thomsoni*, an Oligocene Castorid Rodent from the Oreodon Beds, allied to the Beavers, but with less hypselodont and more primitive teeth, which apparently retain traces of the protocone, hypocone, paracone, metacone, and of the external styles (*pas*, *ms*, *mts*). ×$\frac{3}{1}$. After Matthew.

FIG. 111. Side view of the skull and jaws of *Eutypomys thomsoni* (cf. Fig. 110) showing subhypsodont cheek teeth.

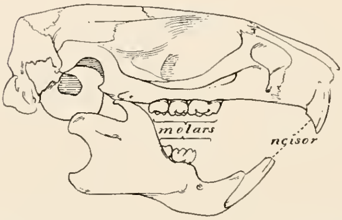


FIG. 112. Skull of the Rat (*Mus rattus*), illustrating the type of dentition characteristic of the Myomorph Rodents. The motion of the jaw is proal, *i.e.* from in front upward and backward. × $\frac{1}{1}$. After Matthew.

DUPLICIDENTATA.

In the Duplicidentate Rodents (or Rabbits, Hares, and Pikas), otherwise known as Lagomorpha, the crown has undergone a complete metamorphosis into hypselodont, columnar and rectangular form. These specialized adult crowns show no trace of separate tubercules or of anything but a strictly transverse pattern, yet where the permanent teeth are unworn, especially among certain fossil species, we find

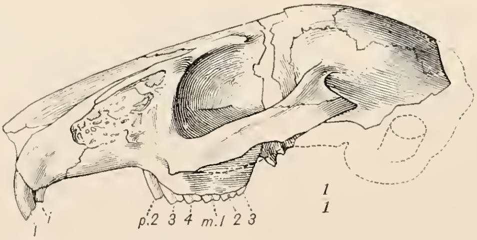


FIG. 113. Skull of *Palæolagus intermedius*, an ancestral Hare from the Oligocene of Colorado, illustrating the upper dentition of the Duplicidentate Rodents. × $\frac{1}{1}$. After Matthew.

more or less evident traces of the primitive pattern. The milk teeth also still retain vestiges of a triangular pattern with three main tubercles, internal to which is a deep notch or internal folding. This notch in the adult teeth extends entirely across the crown, forming the double transverse ridge which so deeply divides the crown that the anterior and posterior moieties have been supposed by Marett Tims[1] to represent the fusion of two originally separate elements. This notch, however, is entirely secondary.

The ancient pattern of the molars is homologized by Forsyth Major[2] himself with that of the molars of *Pelycodus*, a primitive and strictly tritubercular primate; it certainly suggests as the ancestral condition a triangular to quadrate, low-cusped, brachyodont, three-rooted tooth, with the protocone centrally placed. This type of tooth is associated with omnivorous or insectivorous habits and a chiefly vertical motion of the mandible, as compared with the oblique to fore-and-aft grinding motion and herbivorous diet to which the adult teeth of the Duplicidentata are adapted. Thus the milk teeth of even this highly specialized group of Rodents revert to a tritubercular pattern.

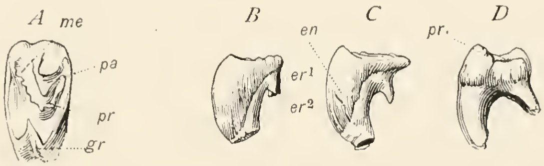


FIG. 114.—Apparent traces of tritubercuIy in Lagomorpha (Duplicidentata). After Forsyth Major.

A. Upper molar of a primitive Ochotonid (Lagomyid) *Titanomys fontannesi* from the Middle Miocene of Europe. Note: (1) the beginning of the groove on the internal side, which in the later Hares, etc., sinks inwards and divides the crown into two portions; (2) apparent vestiges of the tritubercular pattern.

B. Anterior view of the same tooth. Note the reduction of the external roots, the hypertrophy of the internal root, the spreading of the enamel upon the anterior and inferior portions of the crown.

C. *Lepus cuniculus*, milk molar 1, showing retention of much less specialized condition than in the adult.

D. Second upper molar of a Flying Squirrel (*Pteromys melanotis*) to illustrate the ancestral type of molars from which the specialized type in the Duplicidentata molars proabably arose. (Cf. Fig. 115.) All figures $\frac{3}{1}$.

Palæontological evidence leads to the same conclusion. If the known fossil American ancestors of the Hare be arranged in chronological order (Fig. 115), it is seen that as we go back in time the molars are less hypselodont, the broad band of enamel which is confined to the inner side of the teeth in *Lepus* spreads out over the whole tooth, and in the earliest stage the vestiges of two roots are

---

[1] *Journ. Anat. a. Physiol.*, Vol. XXXVII., 1903, p. 144.

[2] "On Fossil and Recent Lagomorpha," *Trans. Linn. Soc. Lond.* (2), VII., 1899, pp. 433-520.

clearly seen on the buccal or external side of the tooth, which in some specimens have large and well defined alveoli. Two morphologically older but geologically more recent stages are figured by Forsyth Major (Fig. 114). Taken in connection with the fact that the crowns of these teeth show a vestigial triangular pattern and in comparison with the molar of *Sciuropterus xanthipes* (*op. cit.*, Pl. 39, Fig. 15), and with the fact that the hypertrophy of the lingual portion of the tooth is secondary, little doubt remains that we have here a tooth with three originally subequal roots disposed in a triangle, and a trigonal and probably tritubercular crown.

Thus both divisions of the Rodentia, when studied from the anatomical or comparative zoölogical standpoint, or from the standpoint of the milk teeth, or from the standpoint of palæontology, apparently lead back to a tritubercular, trigonal pattern of the crown. As among all the other divisions of the mammalia we confidently predict the absolute demonstration by palæontology of the derivation of the Rodentia from trituberculate ancestors. On the other hand, Dr. Wortman[1] has shown that in certain ancestral Eocene Sciuromorphs (*Paramys*) in the course of molarization of the inferior premolars, the apex of the original single-pointed premolar remains in the antero-internal cusp and not the antero-external cusp of p_1—p_4, whereas in the Ungulata, Carnivora, Insectivora, Primates, and probably other orders, the primitive tip or true protoconid is in the antero-external cusp. Hence, if the true molar cusps are homologous with similarly placed cusps in the premolars (see pp. 195-200) the so-called protoconid or antero-external cusp in the molars of brachyodont Rodents is not homologous with the similarly placed cusp of other orders. Dr. Wortman also

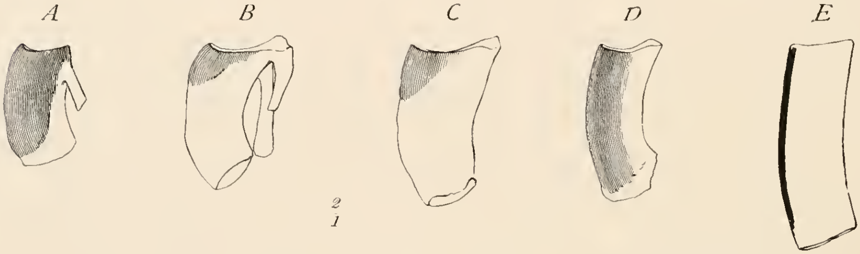


Fig. 115.—Evolution of hypselodont rootless crowns in the upper molars of American ancestors of the Hares (Leporidæ), showing (1) the disappearance of the external roots of the tooth, (2) the limiting of the enamel to a broad band on the inner side. From Matthew.

A. Palæolagus brachyodon. Titanotherium Beds, Lower Oligocene.
B. Palæolagus turgidus (less worn). Oreodon Beds, Middle Oligocene.
C. Palæolagus turgidus (more worn). Oreodon Beds.
D. Palæolagus intermedius. Leptauchenia Beds, Upper Oligocene, the crown is now rootless, the enamel is becoming confined to the anterior face.
E. Lepus americanus. Recent. The enamel is now confined to the anterior face. $\times \frac{2}{1}$.

---

[1] *Amer. Jour. Sci.*, Vol. XV., June, 1903, pp. 216-218.

points out that the hypsodont and folded molars of *Steneofiber*, *Palæocastor* and *Castor*, may have been derived from the more brachyodont teeth of *Sciurarus*, which in many respects is closely related to *Paramys*. "In like manner *Mysops* and *Sciurarus* afford the stem types from which both the Hystricomorphs and Myomorphs were in all probability derived." All of this, if proved, would show (1) the derivation of all Rodent molars from the brachyodont Sciuromorph type, and (2) that the nomenclature of Trituberculy could only be applied to the molar cusps of Rodentia as a matter of convenience not as indicating homologies with similarly placed cusps in other orders.

SPECIAL REFERENCES.

Owen, R., *Odontography*, 1840-45.

Giebel, C. G., *Odontographie*, 1855.

Bronn, H. G., *Klass. u. Ord. des Thierreich's*, Bd. I., pp. 150-169.

Tullberg, T., *System der Nagethiere*. Upsala, 1899.

Schlosser, M., "Die Differenzierung des Säugetiergebisses," *Biol. Centralbl.*, Bd. X., Nr. 8 u. 9, 1890 (especially pp. 250-251).

TILLODONTIA.

Esthonyx from the Wasatch or Lower Eocene almost certainly represents an early stage of the Tillodontia.[1] The pure trituberculy of its molars brings this group also in line with the great majority of early mammals. (Fig. 116.)

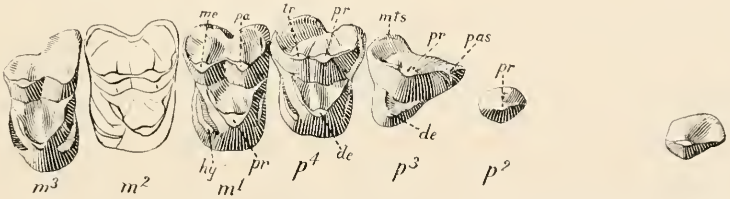


FIG. 116. Upper cheek teeth of *Esthonyx acutidens*, a Tillodont from the Wind River Formation, Lower Eocene, representing the ancestral pattern from which the *Tillotherium* teeth must have been derived. × $\frac{4}{3}$.

EDENTATA AND TÆNIODONTA.

The teeth of all the known specialized Edentates are so highly modified not only by the loss of enamel, but by the simplification of the pattern of the crown to a conical or haplodont condition, to a tubular condition, or to the compressed columns of the Gravigrade Sloths, that until recently no light whatever was thrown by comparative zoölogy on the ancestral forms of the molar teeth. The first discovery

---

[1] See Wortman, J. L., in *Bull. Amer. Mus. Nat. Hist.*, Vol. IX., 1897.

pointing toward such ancestry was recorded by Thomas[1] in the vestigial milk teeth of *Orycteropus*, the posterior milk molar retaining a simple crown with two roots.

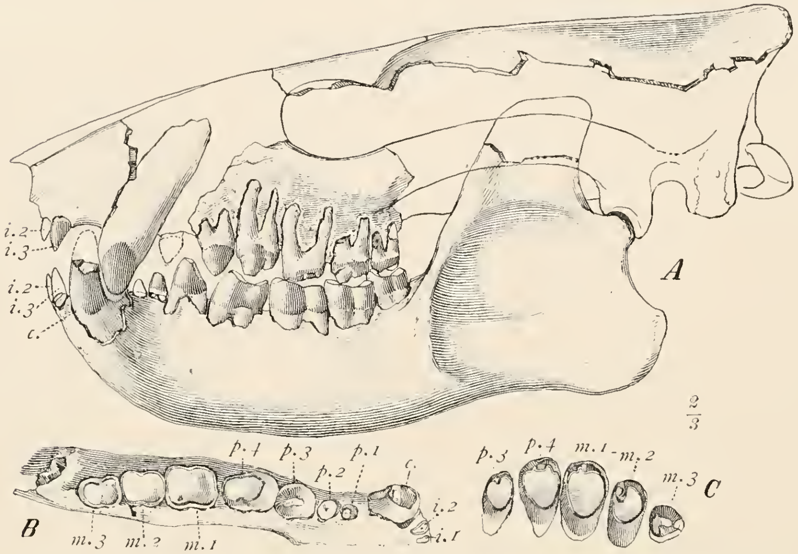


FIG. 117. *A*. Skull of *Conoryctes comma*, family Conoryctidæ, order Tæniodonta, from the Torrejon Formation, Stage II. Basal Eocene, New Mexico.
B. Superior view, lower teeth.
C. Superior view, upper teeth. The upper teeth show apparent traces of tritubercular derivation, the lower of tuberculo-sectorial derivation. ×⅔. (From Wortman, after Scott and Osborn.)

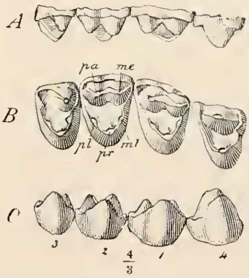


FIG. 118. Upper cheek teeth of *Onychodectes tissonensis*, family Conoryctidæ, order Tæniodonta, from the Puerco Formation, Stage I. Basal Eocene, New Mexico.
A. Outer side view. *B*. Crown view. *C*. Inner or lingual side view. The molar teeth are obviously tritubercular, suggesting those of the Oxyclænid Creodonts (Fig. 84). ×4/3. (From Wortman, after Scott and Osborn.)

It has, of course, been generally assumed that in the ancestors of the Edentates, the molar teeth were not only rooted and covered with enamel, but that they possessed a more complicated pattern of the crown.

---

[1] "A Milk Dentition in Orycteropus," *Proc. Roy. Soc.*, Vol. XLVII., 1890, pp. 246-248, Pl. 8.

In 1896 Dr. J. L. Wortman[1] of the American Museum expedition discovered that the animals long described by Cope partly as Tæniodonta and partly as Creodonta exhibited strong resemblances in the skeleton to the Gravigrade Sloths, there being an especial similarity of structure between *Psittacotherium* and *Megalonyx*. This discovery was a direct confirmation of the prophetic remark of Dr. Max Schlosser,[2] that certain forms (*Esthonyx*, *Calamodon*, *Psittacotherium*), which, on the one hand, are evidently (*Onychodectes* and *Hemiganus*), related to the

FIG. 119. Lower jaw and teeth of *Onychodectes tissonensis*, family Conoryctidæ, order Tæniodonta, from the Puerco Formation, the most Creodont-like member of the order Ganodonta; showing lower molars of tuberculo-sectorial derivation. $\times\frac{1}{1}$. (From Wortman, after Scott and Osborn.)

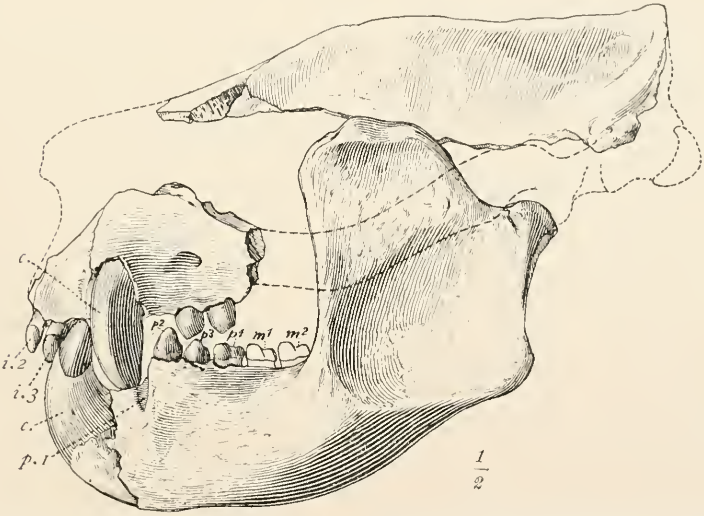


FIG. 120. Skull and dentition of *Hemiganus otariidens*, family Stylinodontidæ, order Tæniodonta, from the Puerco Formation, Stage I, Basal Eocene, showing the enlarged gnawing canines and other characters pointing toward *Psittacotherium* and *Calamodon*. $\times\frac{1}{2}$. (From Wortman, after Scott and Osborn.)

---

[1] "Psittacotherium, a member of a new and primitive sub-order of the Edentata." *Bull. Amer. Mus. Nat. Hist.*, Vol. VIII., 1896, pp. 259-262.

[2] Quoted by Wortman from Schlosser's "Die Differenzierung des Säugetier Gebisses," *Biolog. Centralblatt*, June, 1890, p. 252.

Creodonts, can, on the other hand, be regarded as the ancestors of a part, at least, of the Edentates; to the extent that in such a line the formation of *prismatic* teeth out of the tritubercular and tuberculo-sectorial type can be traced.[1]

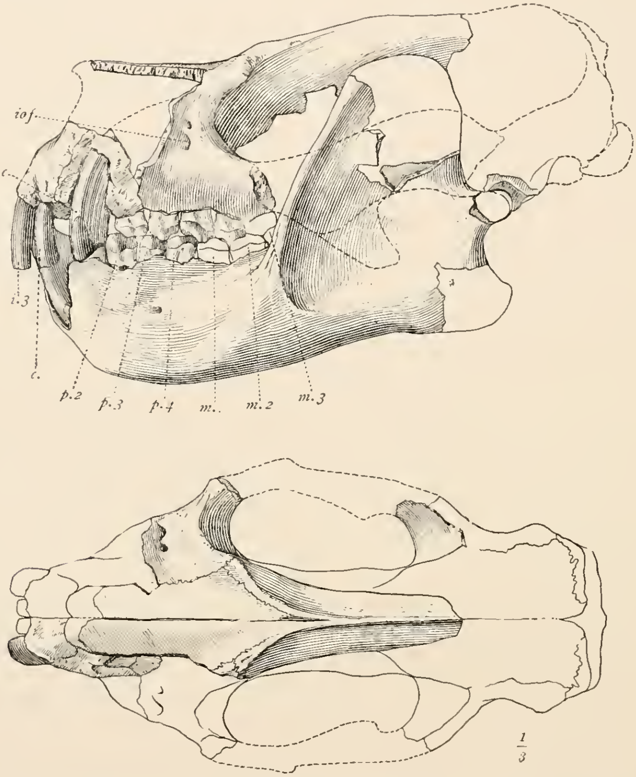


Fig. 121. Side and top views of the skill of *Psittacotherium multifragum*, family Stylinodontidæ, order Tæniodonta, from the Torrejon Formation, Stage II., Basal Eocene, showing the enlarged gnawing canines. ×$\frac{1}{3}$. (From Wortman, after Scott and Osborn.)

To this group Wortman[1] gave the name Ganodonta (equivalent to Tæniodonta Cope) in reference to their enamelled teeth.

All the early members of this group of Tæniodonta have tuberculate teeth, in which, however, the enamel is so delicate that it rapidly wears off. In *Psittacotherium*, for example, the lower teeth are quadritubercular (Fig. 123), in *Calamodon* (Fig. 124) the unworn lower teeth are crested and exhibit all the five cusps (proto-, meta-, hypo-, entoconids, and hypoconulid) of the primitive crown, having completely lost, however, the paraconid. In the remotely related *Onychodectes* (Figs. 118, 119) the upper molars are again strictly tritubercular, while

---

[1] Wortman, J. L., "The Ganodonta and their Relationship to the Edentata," *Bull. Amer. Mus. Nat. Hist.*, Vol. IX., 1897, pp. 59-110.

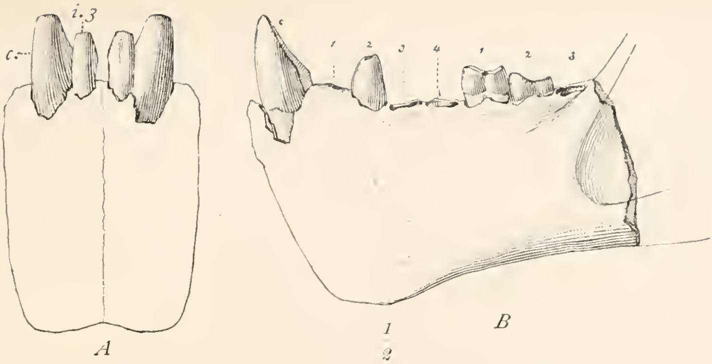


Fig. 122. Front and side views of the jaw of *Psittacotherium multifragum*, showing enlarged gnawing canines, and molars of tuberculo-sectorial derivation. ×½. (From Wortman, after Scott and Osborn.)

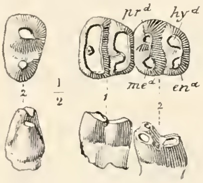


Fig. 123. Superior and side view of the second upper premolar and the first and second lower molars of *Psittacotherium multifragum*, family Stylinodontidæ, order Tæniodonta, from the Torrejon Formation, Stage II., Basal Eocene, New Mexico. The lower molars may have been derived from the tuberculo-sectorial type by the loss of the paraconid. ×½. (From Wortman, after Scott and Osborn.)

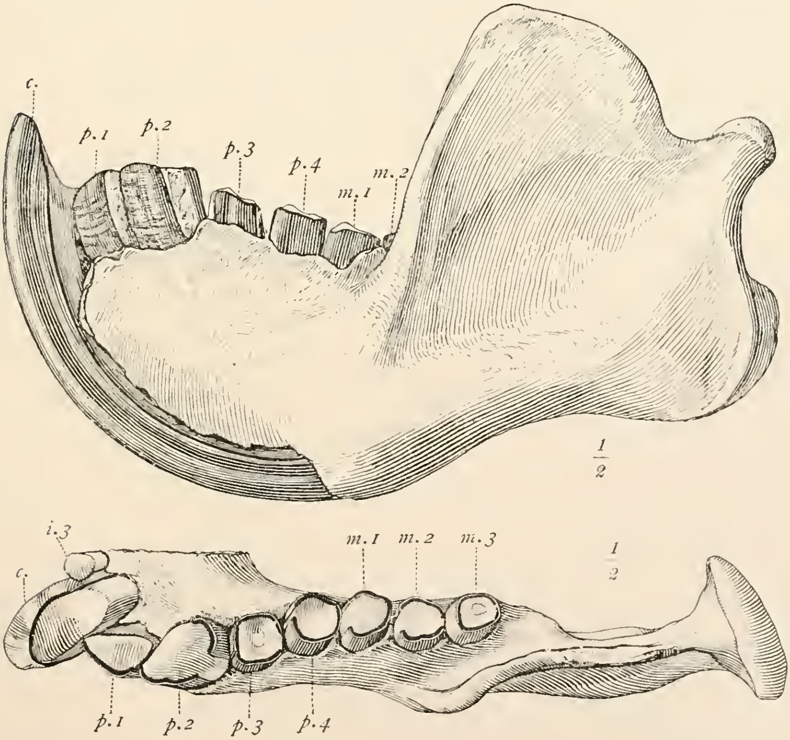


Fig. 124. Side and superior view of the lower jaw and teeth of *Calamodon simplex*, family Stylinodontidæ, order Tæniodonta, from the Wasatch Formation, Lower Eocene. Note the greatly enlarged rootless canine, the cylindrical molars with imperfect enamel. ×½. (From Wortman, after Scott and Osborn.)

the lower molars are also obviously derived by depression of the trituberculo-sectorial pattern.

Opinions differ as to the value of the evidence that these forms are true ancestors of the American Edentates, but the balance of structural characters is certainly very strongly in favor of this theory. If it shall be finally positively confirmed by future discovery, the American Edentata will also be definitely ranged in the tritubercular ranks. It should be stated, however, that Professor Scott seriously questions the supposed ancestral relationship of the Tæniodonta to the American Edentates, because he says the Tæniodonts are much less like the Santa Cruz Miocene Ground Sloths than like the descendants of the latter, the Pleistocene Ground Sloths; and hence he interprets the resemblances between Ganodonts and Edentates as an instance of convergent evolution.

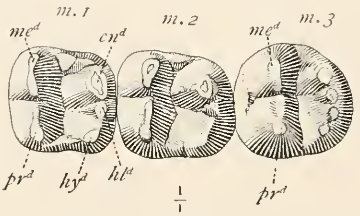


Fig. 125. Crown view of unworn lower molars of *Calamodon simplex*, family Stylinodontidæ, order Tæniodonta, from the Wasatch Formation, Lower Eocene. × $\frac{1}{1}$. Molars apparently derived from the tuberculo-sectorial type by the loss of the paraconid (compare analogous conditions among Primates and Ungulates). (From Wortman, after Scott and Osborn.)

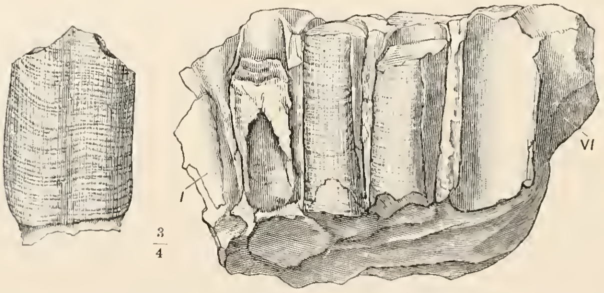


Fig. 126. Single tooth and fragment of the lower jaw with teeth of *Stylinodon mirus*, family Stylinodontidæ, order Tæniodonta, from the Wind River Formation, Stage II., Lower Eocene, representing a highly specialized Tæniodont with hypsodont rootless cheek teeth, which have lost the enamel on the inner and outer sides, and all traces of tuberculo-sectorial derivation. × $\frac{3}{4}$. (From Wortman, after Marsh.)

SPECIAL REFERENCES.

Owen, R., *Odontography*, 1840-45.
Giebel, C. G., *Odontographie*, 1855.
Bronn, H. G., *Klassen u. Ordnungen des Thierreich's*, Bd. I., pp. 147-150.

PRIMATES.

Cope's contention as to the tritubercular origin of the teeth of Primates rested upon the strongest possible proofs both from comparative zoölogy and from palæontology. The tritubercular pattern is still the prevailing one among the Lemuroidea, while the Anthropoidea radiate from tritubercul y into quadritubercul y, and into crested forms. Osborn's recent revision[1] of the American Eocene Primates proves that the molars exhibit a fundamentally triangular pattern in every one of the twenty-two or more known species. The various types exhibit a familiar succession of stages from a more triangular condition with an extremely rudimentary hypocone, to a quadrate, sexitubercular

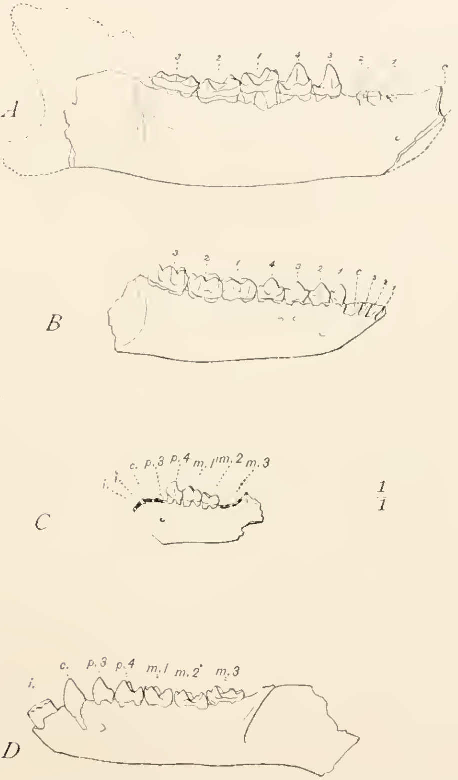


FIG. 127. Jaws of American Eocene Primates, etc., natural size.

A. Pelycodus tutus, family Notharctidæ, order Primates.

B. Hyopsodus paulus, probably an Insectivore.

C. Anaptomorphus æmulus, analogous to *Tarsius*.

D. Microsyops sp., family Mixodectidæ, one of the so-called "Proglires." × 1/1.

---

[1] *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI., 1902, pp. 169-214.

condition, stages which have already been treated in the evolution of the human molar teeth (pp. 50, 55).

The special characters of this evolution were brought out in the same paper. An interesting feature of some of these American Eocene monkeys is that some of them pass from a tritubercular into a quadri- and finally into a sexitubercular condition, with a prominent hypocone and large intermediate tubercles, closely homoplastic with the grinding teeth of primitive Ungulates (Figs. 132, 149). Similarly the premolars progress by the addition of internal cusps.

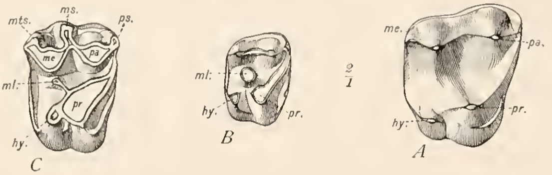


FIG. 128. Superior molars of (*A*) *Adapis magnus*, a lemuroid from the Eocene of France; (*B*) *Hyopsodus vintensis*, an Insectivore (?) from the Eocene of North America; and (*C*) *Notharctus* sp., a Primate, from the Eocene of North America; all three apparently derived from the same tritubercular ground plan, by the upgrowth of the hypocone. *A* and *B*, × $\frac{2}{1}$.

The normal dentition of man is beautifully illustrated in Figs. 1 and 134, p. 161, taken from Selenka's admirable monograph.[1] In modifying his figure (Fig. 1) we have expressed the tritubercular homologies on one side of the jaw and the embryonic order of evolution of the cusps in numerals on the opposite side. In this connection reference may be made to the discussions of the relative value of embryological and palæontological evidence on pp. 49, 214.

FIG. 129. Skull and dentition of a Lower Eocene (Wasatch) Primate *Anaptomorphus homunculus*, with tritubercular upper molars. Partially reconstructed. The premaxillary portion of the skull is wanting. × $\frac{1}{1}$.

Certain peculiar variations of the human molar teeth may be referred to here which are often described by anthropologists as anomalies, but which really are either homogenetic or homoplastic with cusps well known in the lower mammalia.

Protostyle or tuberculus anomalus. On the anterior side of the protocone in the upper molars we have observed in many of the lower mammals, especially in the Periptychidæ (*Periptychus*, *Ectoconus*,

---

[1] *Menschenaffen*, Wiesbaden, 1900.

Fig. 137), that a special cusp is developed, to which we have given the name *protostyle,* from its proximity to the protocone.

From a recent paper by P. Adloff[1] we learn that this was originally designated by Carabelli as occasionally occurring in the human molars, and hence named by him *tuberculus anomalus.* Batujeff regarded this as a progressive structure, pointing out (1) that the tuberculus anomalus, while most frequently found on the first upper molar, is also occasionally found on the second and third molars; (2) that it is more frequently observed in higher races than in lower races, to which Adloff adds, (3) that among recent and extinct anthropoid apes the tuberculus anomalus is certainly not present.

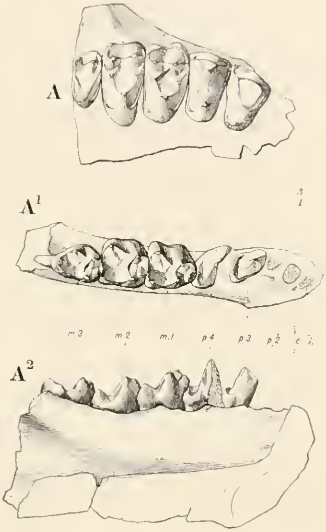


Fig. 130. Upper (A) and lower (A^1, A^2) teeth of *Anaptomorphus homunculus.* (Cf. Fig. 129.) The upper teeth are tritubercular, in the lower teeth the paraconid is seen to be much reduced. $\times\frac{3}{1}$.

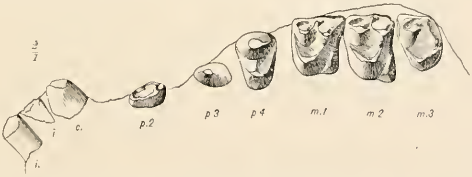


Fig. 131. Origin of the hypocone from the basal cingulum, as shown in *Indrodon malaris*, a Basal Eocene (Torrejon) Primate (?) of uncertain relationship. $\times\frac{2}{1}$.

Adloff in this connection calls attention to the anomalous detachment of cusp components of the human molar crown as evidence of

---

[1] "Zur Frage nach der Entstehung der heutigen Säugethierzsahnformen," *Zeitschrift f: Morphologie u. Anthropologie*, Bd. V., pp. 357-384.

a process the reverse of concrescence. He concludes (p. 379), that as each tooth has primitively sprung by concrescence of cusps derived from successive dentitions, so in incipient retrogression these cusps break apart again into their original components.

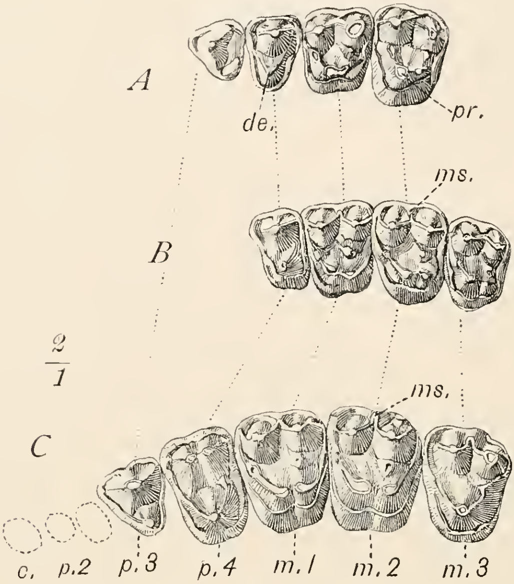


FIG. 132. Evolution of the upper molars in the Notharctidæ, a family of American Eocene Primates. *A*, *Pelycodus frugivorus*, Wasatch Formation (Lower Eocene), the teeth showing clear traces of tritubercuIy. *B*, *Notharctus nunienus*, Wasatch Formation, p^4 and m^1-m^3 more quadrate. *C*, *Notharctus* sp., Bridger Formation (Middle Eocene), p^4 quadrate, with two external cusps; m^1-m^3 large, with well-developed mesostyle (*ms*). $\times \frac{2}{1}$.

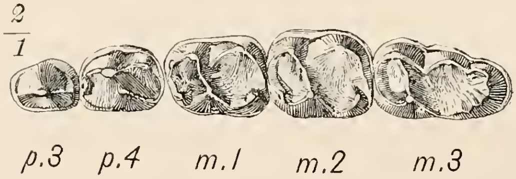


FIG. 133. *Notharctus* sp., Bridger Formation, Middle Eocene. Crown view, lower teeth, showing the loss of the paraconid in m_1-m_3, enlargement of the postero-internal cusp or entoconid. $\times \frac{2}{1}$.

Apart from this new evidence for the concrescence theory, to which we do not feel able to attach much weight, the question of the existence of the progressive evolution of the 'tuberculus anomalus' or protostyle in the human teeth is especially interesting, as another instance of *homoplasy*, or the independent evolution of an apparently homologous cusp in different orders (see p. 236).

SPECIAL REFERENCES.

Owen, R., *Odontography*, 1840-45.

Giebel, C. G., *Odontographie*, 1855.

Bronn, H. G., *Klass. u. Ord. des Thierreich's*, Bd. I., pp. 223-236.

Schlosser, M., *Die Affen Lemuren . . . des Europäischen Tertiärs*, etc. Wien, 1887-90.

Selenka, E., *Menschenaffen*, Wiesbaden, 1900.

Topinard, P., "De l'Évolution des Molaires et Prémolaires chez les Primates et en particulier chez l'Homme," *L'Anthropologie*, No. 6, Nov.-Dec., 1892.

Gaudry, A., "Sur la Similitude des Dents de l'Homme et de quelques Animaux," *L'Anthropologie*, T. XII., 1901.

Osborn, H. F., "Revision of the American Eocene Primates," *Bull. Amer. Mus. Nat. Hist.*, Vol. XVII., 1902, pp. 159-184.

Wortman, J. L. "Studies of Eocene Mammals, . . ." Part II. Primates, *Amer. Jour. Sc.* [4], Vol. XV., Mar. 1903, May 1903, June 1903.

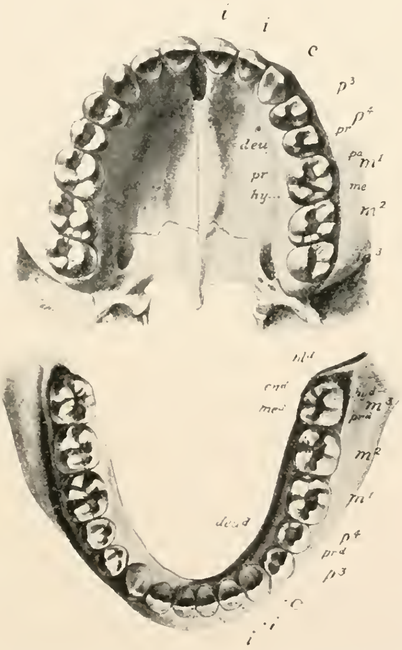


Fig. 134. Normal, ideal, human (Caucasian) dentition, based upon a photograph of a specimen, modified after several other specimens. From Selenka, after Röse. Traces of tritubercuIy are evident in the upper molars; the lower molars have lost the paraconid. The crowns of the teeth are bluntly tuberculate, in adaptation to omnivorous diet. × $\frac{5}{6}$.

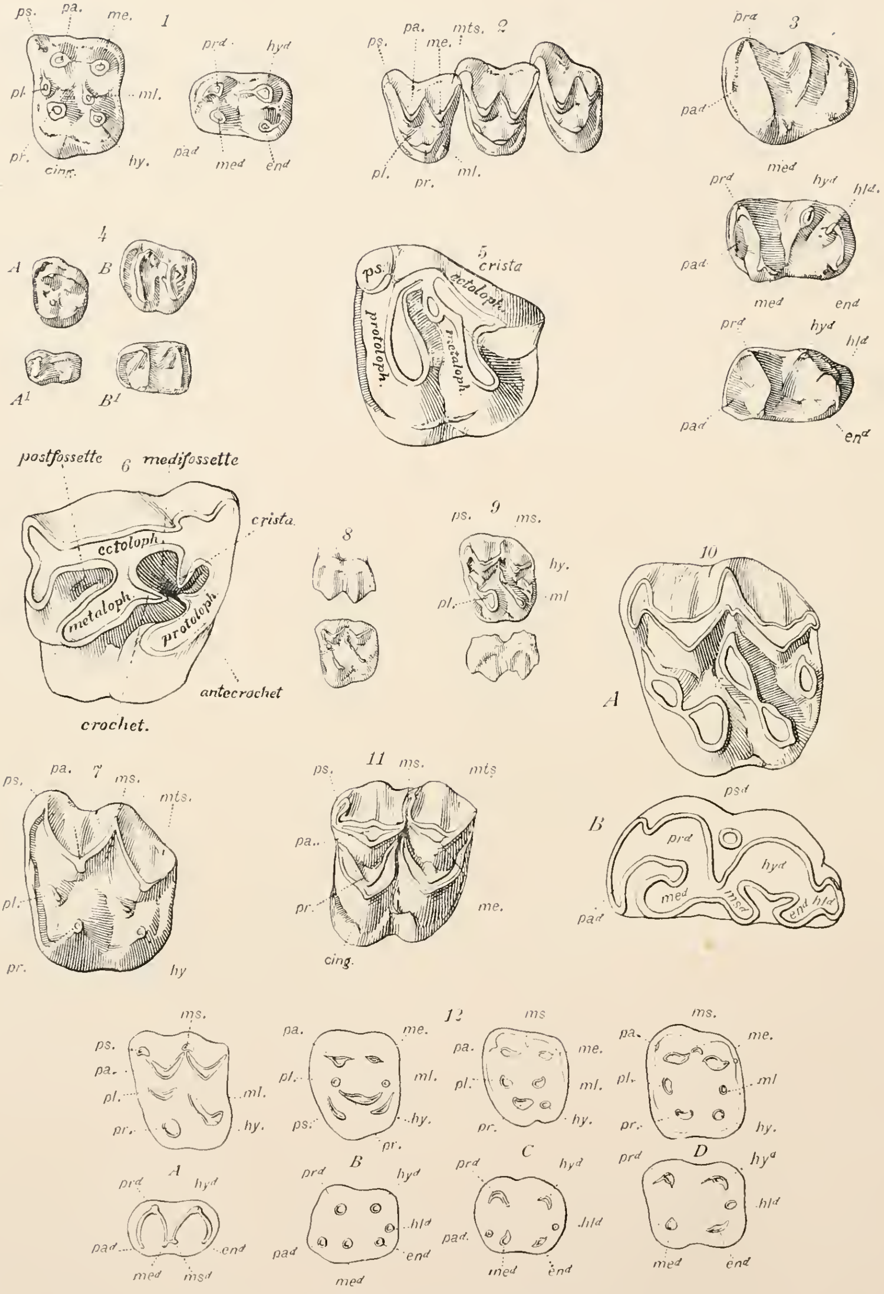


FIG. 135. Diagram showing typical modifications of the tritubercular pattern in Ungulates (cf. Fig. 43).

SUPER-ORDER **Ungulata**.

SPECIAL REFERENCES.

Dealing with the teeth of Ungulates from the tritubercular standpoint.

Schlosser, M., "Beitrage zur Kenntniss der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer," *Morphol. Jahrb.*, 12, Taf. V., VI. (see especially the "Allegemeiner Theil. Das Gebiss der Perissodactylen und Artiodactylen und seine Beziehungen zu dem der Condylarthra." pp. 97-112).

"Die Differenzierung des Säugetiergebisses," *Biol. Centralbl.*, Bd. X., Nr. 8, 1890 (especially pp. 247-250).

Osborn, H. F., *Antea*, pp.

FIGURE 135.

No. 1. "Sexitubercular" superior and "quinquetubercular" inferior molar of *Hyracotherium* (Eocene ancestor of the Horse), showing in the upper molar six main cusps, a parastyle developing from the cingulum, and an encircling cingulum, continuous in the lower molar with the hypoconulid. The paraconid of the lower molar is vestigial or wanting. The crown is low ("brachyodont") with low, conic cusps ("bunodont").

2. Superior molars of *Pantolambda* (Eocene Amblypod). The triangular pattern of the crown has been retained, the protocone remaining central in position; the outer cusps have become crescentic ("selenoid"), the parastyle (ps) is extremely large (Fig. 140).

3. Three stages in the degeneration of the paraconid seen in the lower molars of Amblypoda (Fig. 144).

4. Superior and inferior molars of *A*. *Systemodon* (Eocene tapiroid) and *B*. *Tapirus*. The parastyle is seen developing from the cingulum, the intermediates (pl., ml.) are conspiring with the outer and inner cusps to form the "ectoloph," "protoloph," and "metaloph" (cf. 8) of the modern Tapir (*B*). In the lower molars the paraconid is vestigial or absent.

5. "Lophodont" type. Primitive Rhocerotoid molar (*Hyrachyus*) showing completed "protoloph," "metaloph," "ectoloph."

6. "Lophodont" type. Modern Rhinoceros molar showing accessory folds, "antecrochet," "crista," "crochet."

7. "Bunoselenodont" type. Primitive Titanothere (*Palaeosyops*). Internal cusps "bunoid," external "selenoid."

8. "Lophoselenodont" type. Primitive (Eocene) Horse, *Eohippus*. Traces of the original triangular pattern of the crown are still discernible.

9. "Lophoselenodont type." Primitive Horse (*Pachynolophus*). The "intermediate conules" (pl., ml.) will become crenulate and with the ectoloph, and the hypostyle, will produce the complex crown pattern of the modern Horse.

10. *A*. Upper molar of *Anchitherium*, *B*. Lower molar of *Merychippus*, Miocene horses (cf. Fig. 160).

11. "Selenodont" Artiodactyl type (*Protoceras*). All cusps crescentic.

12. Ground plan of molars in various Ungulate sub-orders. *A*. Condylarthra (?) (*Meniscotherium*), *B*. Amblypoda (*Periptychus*), *C*. Perissodactyla (*Hyracotherium*), *D*. Condylarthra (*Phenacodus*).

AMBLYPODA.

The indisputably triangular and tritubercular nature of the molars of the primitve Amblypoda is demonstrated in the accompanying figures (Figs 137-146) of several of the lower Eocene types.[1] All of these teeth bear a close general resemblance to the tritubercular molars of Creodonts. The peculiar and distinctive feature of the evolution of the upper molar teeth in the Amblypoda is that they do not pass into a quadritubercular or quadrangular stage by the forward shifting of the protocone and upgrowth of the hypocone, like all the other Ungulates, but develop special types of bunodont, selenodont, and lophodont molars out of the primitive triangle.

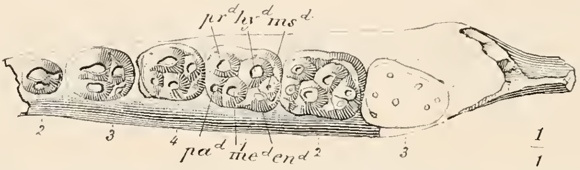


FIG. 136. Lower teeth of *Ectoconus ditrigonus*, a Basal Eocene (Puerco), relative of *Periptychus*. Compare the lower molars of *Euprotogonia* (Fig. 149) and *Protogonodon* (Fig. 148) among the Condylarthra. × 1/1.

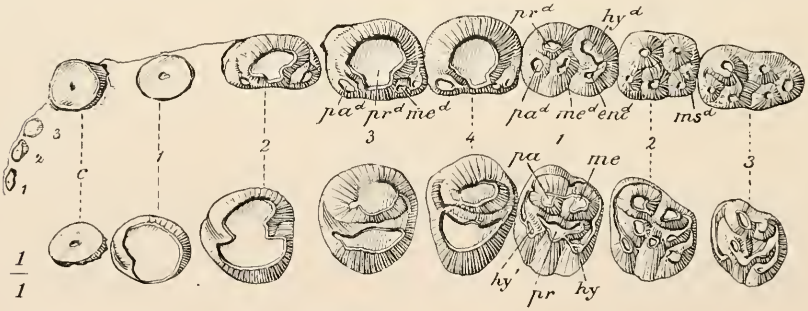


FIG. 137. Upper and lower teeth of a primitive Amblypod, *Periptychus rhabdodon*, from the Puerco Formation. Stage 1. Basal Eocene, × 1/1. The upper molars are clearly derived from the tritubercular type, the lower from the tuberculo-sectorial type. The upper molars develop a protostyle (*hy'*), the protocone remaining central in position. (Contrast *Phenacodus*, Fig. 150). The bluntly cuspidate crowns apparently indicate an omnivorous-herbivorous habit.

In some forms (*e.g. Periptychus*, Fig. 137, *Ectoconus*, Fig. 136, *Conacodon*, Fig. 139) the cusps remain bunoid.

In other basal Eocene forms (*Pantolambda*, Fig. 140) the cusps become crescentic or selenoid, reminding us strongly of the teeth of some Insectivora (for example, *Proscalops*, Fig. 73) on a large scale.

---

[1] [According to Matthew these primitive types belong to the group which gave rise to the typical Condylarths and Amblypods, but are much more primitive than the typical Amblypods, and cannot be ordinally separated from the Condylarthra.—ED.]

Fig. 138. Upper and lower teeth of *Hemithlæus kowalevskianus*, from the Basal Eocene (Puerco). Compare Figs. 137, 139. × 1/1. After Matthew.

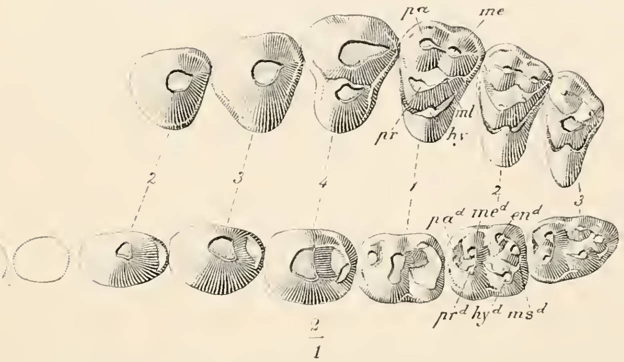


Fig. 139. Upper and lower teeth of *Conacodon entoconus*, a Basal Eocene (Puerco) relative of *Periptychus*. × 2/1. Observe the reduction of the paraconid in the lower molars correlated with the development of the hypocone from the basal cingulum of the upper molars. The upper molars remain tritubercular, although the protocone is somewhat pushed forward. (Cf. *Phenacodus*). The cusp marked *ms^d* is the hypoconulid.

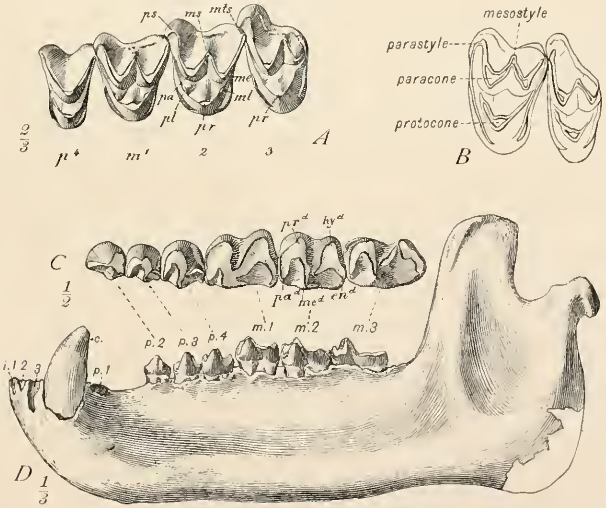


Fig. 140. Primitive Amblypod, *Pantolambda cavirictus*, from the Torrejon Formation. Stage II. Basal Eocene. *A.* Superior molars; *B.* Diagram of same; *C.* Inferior grinders; *D.* Mandible. Observe the central position of the protocone as in all the Amblypoda, the crescentic cutting modification of the para- and metacones, the strong development of the para-, meso-, and metastyles. In the lower molars, the paraconid is reduced and there is a tendency to form two sharp ridges, the first from the protoconid and metaconid, the second from the hypoconid and entoconid. (Cf. *Coryphodon*, Fig. 141.)

Out of this three-crescent type the crested or lophoid type of *Coryphodon* (Figs. 141, 143) and *Uintatherium* (Fig. 142) have evolved, as partially discussed on page 87. As shown in Figs. 140, 141, 144, 145, 146 the *lower* molars of *Uintatherium* are closely linked to those of *Coryphodon* and *Pantolambda* through the genus *Bathyopsis* (Fig. 144-146), which is strictly intermediate in its mandible and inferior molars, and thus supports the view that the *upper* molars also of *Uintatherium* have passed through stages represented in a general way by *Pantolambda* and *Coryphodon*. The steps in this evolution are the most complicated and difficult to understand, especially the rotation of the ectoloph, a feature which is less positively demonstrated than the other features of this exceptional evolution.

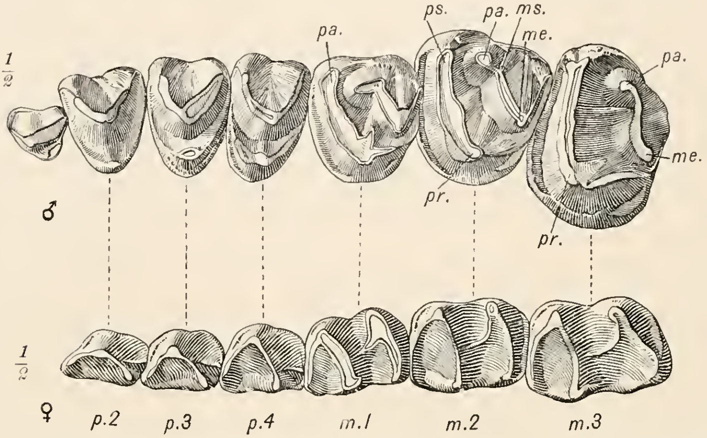


FIG. 141. Left upper and right lower teeth of *Coryphodon testis*, a hornless Amblypod from the Wasatch Formation, Lower Eocene. As compared with the molars especially m^3, of *Pantolambda* (Fig. 140), observe the great development of the ridge from the protocone to the parastyle (protoloph), the posterior displacement of the paracone, the reduction of the mesostyle, the reduction of the posterior limb of the V formed by the metacone. In the lower molars observe the heightening of the anterior and posterior ridges. ×½.

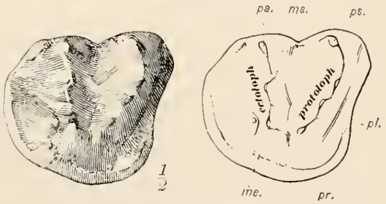


FIG. 142. *A.* Second upper molar of *Uintatherium* from the Bridger Formation, Middle Eocene. *B.* Diagram of same. As compared with the molars of *Coryphodon* (Fig. 141) observe that the ectoloph has apparently been rotated posteriorly around the metacone as an axis, while the metacone itself has approached the protocone, with the final result that the protoloph and ectoloph diverge toward the external side of the tooth. ×½.

SPECIAL REFERENCES.

Osborn, H. F., "Evolution of the Amblypoda, Pt. I., Taligrada and Pantodonta." *Bull. Amer. Mus. Nat. Hist.*, Vol. X., 1898, pp. 169-218.

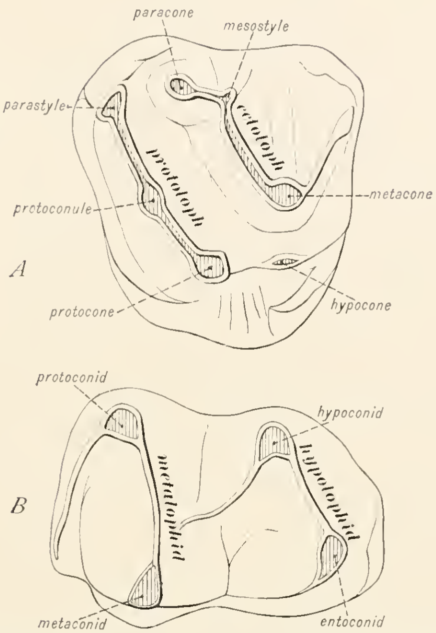
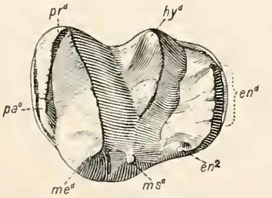
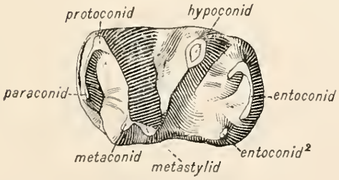


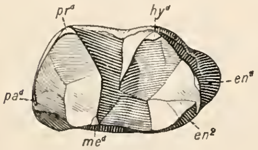
Fig. 143. Scheme of upper and lower molars in *Coryphodon*. (Compare Fig. 141.)



Uintatherium.

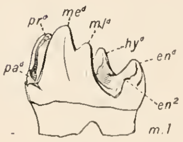


Bathyopsis.

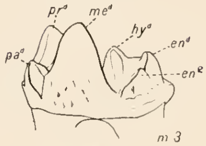


Pantolambda.

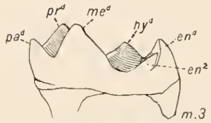
Fig. 144. Evolution of the lower molars in the Amblypoda. Crown view.



Bathyopsis.



Coryphodon.



Pantolambda.

Fig. 145. Evolution of the lower molars of Amblypoda. Internal view.

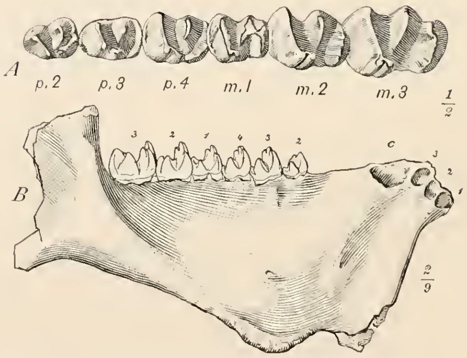


Fig. 146. Lower teeth ($\times \frac{1}{2}$) and mandible ($\times \frac{2}{9}$) of *Bathyopsis fissidens*, an Amblypod from the Wind River Formation, Stage II., Lower Eocene. In the structure of its lower molars this animal is more like *Uintatherium* than *Coryphodon*. (Cf. Fig. 144.)

Condylarthra.

These Ungulates are contemporary with the Amblypoda, but unlike them their molar teeth evolve from trituberculy into quadrituberculy.

The proof of the tritubercular ancestry of these oldest and most generalized hoofed animals is furnished by the oldest form *Protogonodon* (Fig. 148) and by the diminutive predecessor of *Phenacodus*, the species *Euprotogonia minor* (Fig. 151); in this species the crown is still triangular, but the hypocone is seen developing on the second

FIG. 147. Upper and lower teeth of *Mioclænus turgidus*, a primitive Condylarth (?) (family Mioclænidæ), from the Torrejon Formation, Stage II., Basal Eocene. Note the loss of the paraconid in the lower molars, the bluntly rounded character of the cusps of the upper molars. $\times \frac{1}{1}$. Possibly an Insectivore. (Cf. *Hyopsodus*, Fig. 78.) From Osborn and Earle.

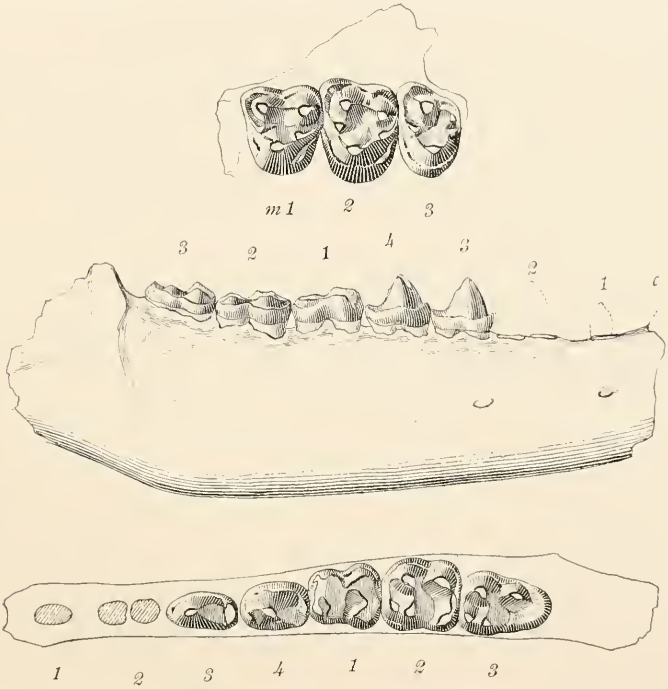


FIG. 148. Upper molars, lower jaw and superior view of lower teeth of *Protogonodon pentacus*, a very primitive Condylarth possibly ancestral to the Phenacodontidæ, from the Puerco Formation, Stage I., Basal Eocene. (Cf. Figs. 147-151). This animal was apparently intermediate between the Creodonta and the Condylarthra. (Cf. Figs. 84, 149.) $\times \frac{1}{1}$. After Osborn and Earle.

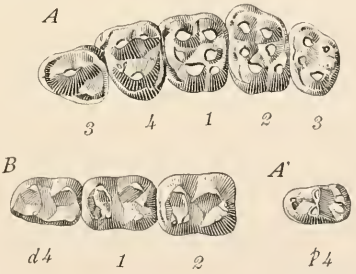


FIG. 149. Upper and lower teeth of *Euprotogonia puercensis*, from the Torrejon Formation, Stage II., Basal Eocene, a Condylarth more primitive than *Phenacodus* (Fig. 150). $\times \frac{1}{1}$. After Osborn and Earle.

superior molar (A, m^2), and in the lower molars (C, m_1, m_2) the paraconid still persists. The intermediate cusps or conules in the upper molars are well developed.

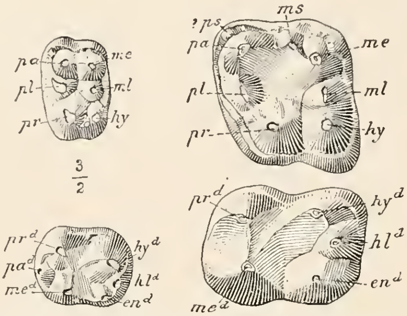


FIG. 150. (Left hand figure). Upper and lower molars of *Euprotogonia puercensis*, from the Basal Eocene (Torrejon) representing the ancestral molar patterns of *Phenacodus primævus* (right hand figures) from the Lower Eocene (Wasatch).

Various species of *Protogonodon*, *Euprotogonia* and *Phenacodus* thus exhibit beautifully the evolution into the sexitubercular, bunodont superior molar crown, out of which the upper molars of all the higher hoofed animals have evolved, the crown passing from the more triangular into the more quadrate form. Similarly, the lower molars lose the paraconid but retain the hypoconulid.

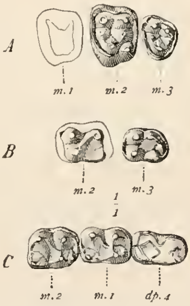


FIG. 151. Upper and lower molars of *Euprotogonia minor*, a small Phenacodont Condylarth from the Torrejon Formation, Stage II., Basal Eocene, showing traces of trituberculy combined with progressive upgrowth of the basal cingulum, intermediate cuspules and hypocone in the upper molars, and with the reduction of the paraconid in the lower molars. $\times \frac{1}{1}$.

SPECIAL REFERENCES.

Schlosser, M., "Beiträge zur Kenntniss der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer," *Morphol. Jahrb.* 12, Taf. V., VI. See especially pp. 97-112.

Matthew, W. D., "A Revision of the Puerco Fauna," *Bull. Amer. Mus. Nat. Hist.*, Vol. IX., 1897. Especially pp. 293-320

ARTIODACTYLA.

Of this even-toed group of hoofed mammals the most ancient representative is found in the lower Eocene or Wasatch beds. It is the little species *Trigonolestes chacensis* (Fig. 152) of the Wasatch, which is undoubtedly an Artiodactyl, as shown by the associated astragalus.

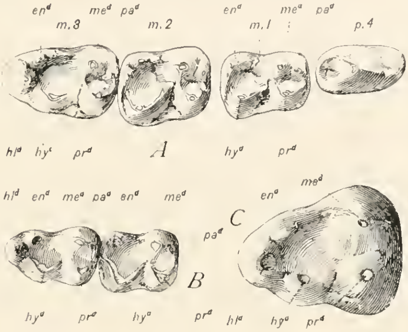


FIG. 152. Lower teeth of *Trigonolestes* a very primitive Artiodactyl from the Wasatch Formation, Lower Eocene.

A. Trigonolestes chacensis, paraconid small but distinct. ×$\frac{3}{1}$. *B. Trigonolestes metsiacus*, paraconid reduced. ×$\frac{3}{1}$. *C. Trigonolestes etsagicus*, paraconid vestigial or absent, all cusps low and rounded. ×$\frac{5}{1}$.

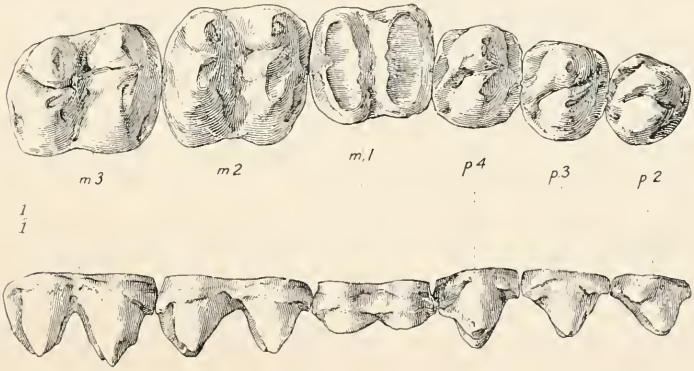


FIG. 153. A quadritubercular to bilophodont Peccary, *Platygonus bicalcaratus*, family Dicotylidæ, from the Blanco Beds, Pliocene, of Texas. ×$\frac{1}{1}$. After Gidley. The incipient bilophodont condition* is seen in *Dicotyles* and even among Baboons (*Cynocephalus*).

---

*[The more or less completely bilophodont type has been secondarily developed independently in many other families. Among Artiodactyla we also have *Listriodon* (Suidæ), *Tapirulus* (Anoplotheriidæ); among Perissodactyls, the Tapiridæ, not to mention the early Equidæ and the Rhinocerotidæ, Lophiodontidæ in which the anterior and posterior crests are connected by the high external cusps or crest. Among the Proboscidea we have especially Dinotheriidæ and *Palæomastodon*: among Pyrotheria, *Pyrotherium*; in certain other Ungulates, *e.g. Uintatherium, Arsinöitherium*, the bilophodonty is not strictly typical. Among Sirenia we have *Manatus*; among Marsupials, the Kangaroo and *Diprotodon*. Even certain Theriodont reptiles (*Trirachodon*) developed a transverse crest in each molar and the whole series of cheek teeth was thus functionally analogous to a bilophodont dentition.—ED.]

As the name indicates, the upper molars are triangular; the inferior molars exhibit a well defined trigonid, with the paraconid reduced but still distinct, in fact the teeth are almost tuberculo-sectorial. Comparison of a series of lower molar teeth of species belonging to this genus (*T. metsiacus, T. etsagicus*) show a progressive degeneration of the paraconid, depression of the trigonid, and elevation of the talonid; in other words, the development of a bunodont crown (Fig. 152).

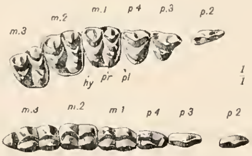


Fig. 154. Upper and lower cheek teeth of *Bunomeryx elegans*, from the Uinta Formation (Upper Eocene), a small bunoselenodont Artiodactyl. Note the crescentic outer cusps, the large crescentic intermediates (*pl. ml.*), especially the very large metaconule which is preoccupying the position usually assumed by the hypocone, which here remains minute (*hy*). $\times \frac{1}{1}$. After Wortman.

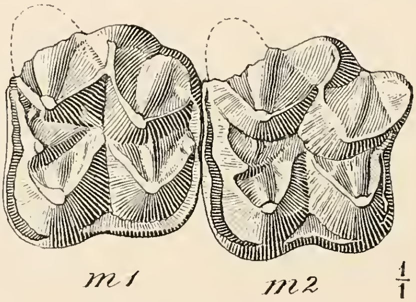


Fig. 155. Upper molars of *Anthracotherium karense*, a bunoselenodont Artiodactyl from the Protoceras Beds, Upper Oligocene, showing the greatly enlarged metaconule, which takes the place of a hypocone. (Cf. *Bunomeryx*, Fig. 154.) $\times \frac{1}{1}$.

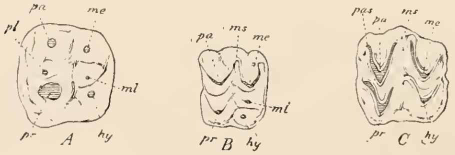


Fig. 156. Principal types of molars among Artiodactyls.

A. Bunodont. All cusps conic. Examples Primitive Suillines (Elotherium, Peccaries, etc.).
B. Bunoselenodont. Outer cusps only crescentic, inner cusps conic, or subcrescentic. Example, Anthracotheres (*Ancodus*).
C. Selenodont. All cusps crescentic. Examples, *Merycopotamus*, Deer, Antelopes, Camels. In *C* the cusp marked *hy* appears to be the enlarged metaconule. (Cf. Figs. 154, 155.)

In the Eocene *Helohyus* the molars are fully bunodont, that is, with low, rounded cusps: the paraconid is extremely minute. The series also shows the progressive molarization of the premolars and lends support to the theory that the molar pattern was originally triangular, and sharply differentiated from the premolar pattern, and that the premolars are becoming molariform by adding the cusps in a different order from that of the molars (see pp. 194, 195).

Among the Oligocene Suilline or Pig-like Artiodactyls we find in *Leptochœrus* (Fig. 157) persistent tritubercular molars which were mistakenly referred to the Primates.

Thus we have the most direct evidence of tritubercular ancestry among the Artiodactyls, in which the bunoselenodont, and finally the purely selenodont types were evolved.*

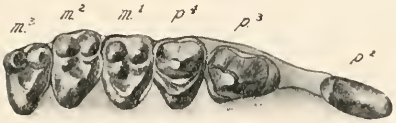


Fig. 157. Upper cheek teeth of *Leptochœrus gracilis*, a very primitive Artiodactyl retaining tritubercular molars, from the Oreodon Beds, Middle Oligocene, × 2/1. After Marsh.

Another line of evolution is by the formation of transverse crests sometimes forming a bilophodont crown as in *Platygonus*, a Pliocene Peccary (Fig. 153).

In the bunodont type of *Elotherium* (Fig. 156 *A*) the upper molars show the protocone, paracone, metacone and hypocone, and the intermediate conules (*pl*, *ml*). The lower molars, however, have already lost the paraconid. In all Artiodactyls the metaconule is very large, often replacing completely the cingulum-hypocone (Figs. 154, 155).

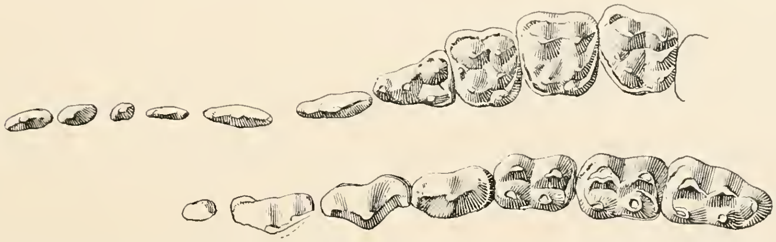


Fig. 158. Upper and lower cheek teeth of *Dichobune leporinum*, a primitive Anoplotheriid from the Upper Eocene of France, retaining conic cusps in the molars. (Cf. Figs. 147, 157). About twice natural size. The premolars are laterally compressed as in Eocene Camelidæ, Oreodontidæ Protoceratidæ, etc. The enlarged metaconule and the small hypocone (cf. Fig. 154) is well shown. The upper teeth belong to the milk set, the lower to the permanent set.

SPECIAL REFERENCES.

Schlosser, M., "Beiträge zur Kenntniss der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer," *Morphol. Jahrb.* 12. See especially pp. 97-112.

---

* [It is an interesting fact that the main internal cusps (pr) of the upper molars and the external cusps of the lower molars of the most ancient Artiodactyla were not perfectly round or bunoid as commonly supposed, but subcrescentic, as in the most ancient Perissodactyla (e.g. *Lambdotherium*, *Eohippus*), Condylarthra (*Protogonodon*), Amblypoda (*Hemithlæus*, *Conacodon*, *Pantolambda*), Primates (*Indrodon*), Creodonts (*Oxyclænids*), Insectivores (*Ictops*, *Dryolestes*). The purely bunoid or round cusped condition is probably secondary, like the perfected crescentic condition.—Ed.]

PERISSODACTYLA.

The probably tritubercular origin of the molar teeth of the odd-toed Ungulates or Perissodactyla has been discussed in the case of horses, rhinoceroses, and tapirs on pp. 72, 75, 85-87. The key to the origin of the primitive sexitubercular superior molars, from which the elaborate pattern of all these teeth were evolved, is to be found not only among the Condylarthra (pp. 168-170), but also in the study of the various types of teeth in the horses themselves. From this sexitubercular type the crown evolves by a bunoid, lophoid, or selenoid

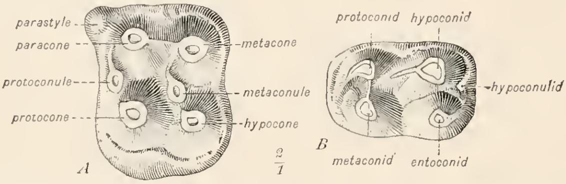


FIG. 159. Upper and lower molar of *Hyracotherium leporinum* from the London Clay (Sparnacien) Lower Eocene, showing the fundamental ancestral pattern of the Perissodactyl molars, *i.e.* Upper molars with four well rounded cusps and two small conules, the rudiments of the proto- and metaloph, lower molars with four main cusps, lacking the paraconid, and with an incipient hypoconulid. The hypocone and metaconule are apparently twin cusps, the hypocone not being derived from the cingulum. ×$\frac{2}{1}$. After Owen.

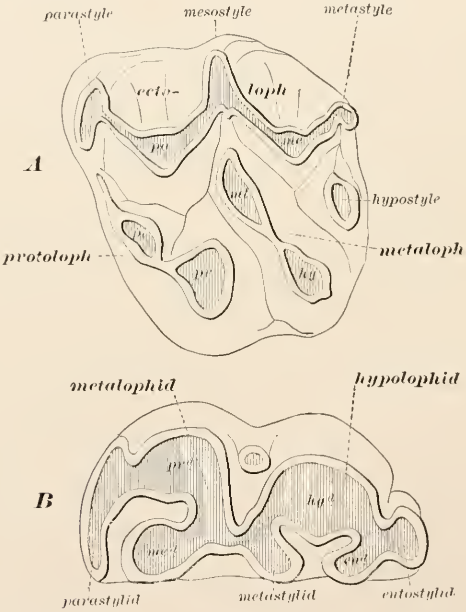


FIG 160. The Secondary cusps of an Ungulate Molar. *A. Anchitherium*, upper. *B. Merychippus*, lower. The Primary cusps are indicated by abbreviations.

modelling of the cusps. In the Titanotheres, for example (Figs. 167-171), the protocone and hypocone remain bunoid, the paracone and metacone have become selenoid, and the small ridges formed by the proto- and metaconules have become vestigial, the crown thus consisting of two outer crescents and two inner cones; but even in this specialized crown traces of the primitive triangular arrangement of three primary cusps remain. In the little *Lambdotherium* (Fig. 167) we have a perissodactyl (probably an ancestral Titanothere), in which the tritubercular derivation of the molars is indisputable. In these teeth among the horses, the styles and intermediate conules (*pl*, *ml*) play an important rôle (p. 85). The key to the evolution of the teeth of the horses as compared with that of the Titanotheres is given in Figs. 135, 159, 160. The type attained is lopho-selenodont.

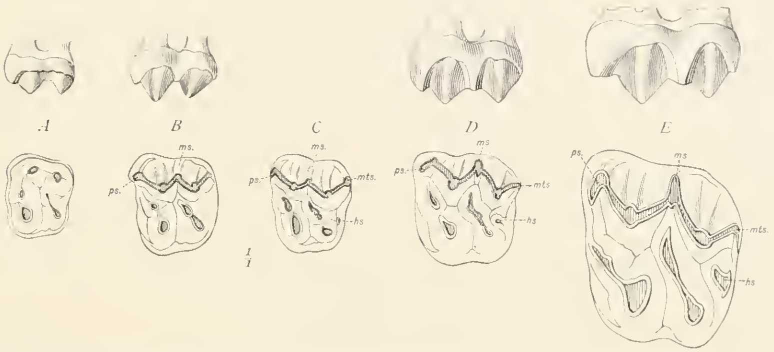


Fig. 161. Evolution of the upper molars in the Equidæ. *E.* after Kowalevsky. The series figured is not a phylogenetic one, since animals belonging to several different lines of descent are represented; but it is a morphological series and (with Figs. 162-164) shows the principal successive stages of molar evolution in the Equidæ. All figures natural size.

A. *Hyracotherium*, Lower Eocene.

B. *Pachynolophus*, Middle Eocene. Note *ps*, *ms*, and crescentic *pa*, *me*.

C. *Anchilophus*, Lower Oligocene. Note *mts* and hypostyle *hs*.

D. *Mesohippus*, Middle Oligocene.

E. *Anchitherium*, Lower Miocene.

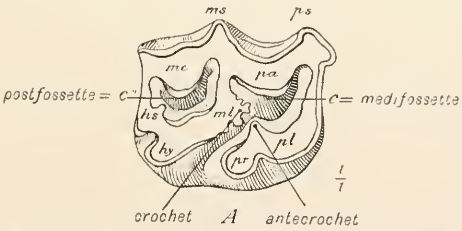


Fig. 162. Upper milk molar of *Merychippus* sp. from the Upper Miocene, showing the completed ground plan of the molar pattern of the modern Horse. (Cf. Figs. 160, 161.) × 1/1.

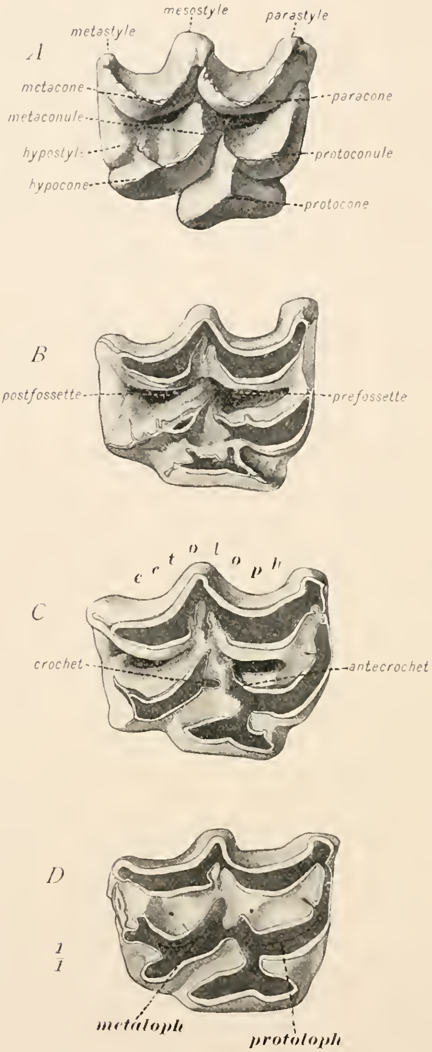


Fig. 163. Cusps, Crests, Styles, Crochets, and Fossettes in the molar teeth of the Horse. The specimens figured belong to a North American Pleistocene species, *Equus complicatus*.

A. Unworn crown.

B-D. Successive stages of wear. All figures natural size.

The Tapiridæ, as shown in Figs. 172-174, develop a sub-lophodont dentition, the protoloph and metaloph being well developed, while the ectoloph does not form a completely united crest.

In the Rhinocerotidæ we have the extreme lophoid evolution, in which the crown consists of the completed proto-, meta-, and ectolophs (Figs. 175-182).

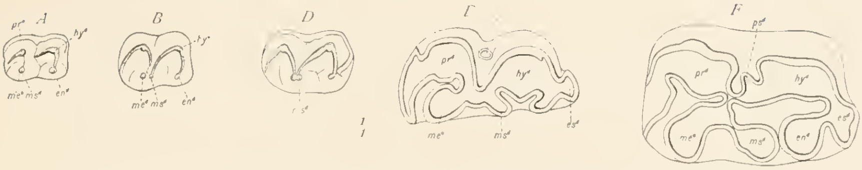


FIG. 164. Evolution of the lower molars in the Equidæ. *Morphological* not *phylogenetic*. (Cf. Fig. 161.)

A. Hyracotherium, Lower Eocene.

B. Pachynolophus, Middle Eocene. Note appearance of metastylid (ms^d) by fissure of the metaconid.

D. Mesohippus, Middle Oligocene. Note appearance of entostylid. (Marked ms^d).

E. Hipparion, Pliocene. Note great expansion and posterior fold of the metaconid (me^d, ms^d), protostylid (ps^d), endostylid (es^d). Worn tooth.

F. Equus. All figures natural size. Worn.

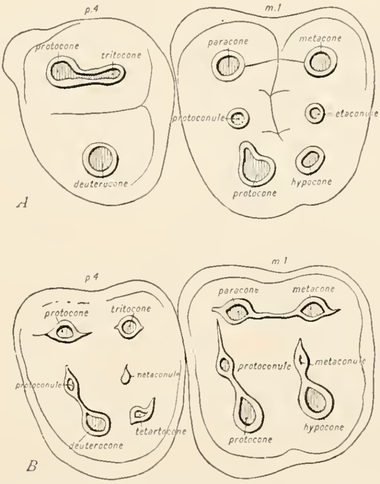


FIG. 165. Premolar Terminology, proposed by Scott and adopted in this volume. Primitive Ungulate Types. Fourth upper premolar and first molar of *A. Euprotogonia*, and *B. Hyracotherium.*

Through all these higher stages the homologies with the primitive tritubercular crowns can readily be traced.

SPECIAL REFERENCES.

Hatcher, J. B., "Recent and Fossil Tapirs," *Amer. Jour. Sci.* (4), Vol. I., 1896, pp. 161-180.

Wortman, J. L., and Earle, Charles, "Ancestors of the Tapir from the Lower Miocene of Dakota," *Bull. Amer. Mus. Nat. Hist.*, Vol. V., 1893, pp. 159-180.

"Species of Hyracotherium and allied Perissodactyls from the Wahsatch and Wind River Beds of North America," *Bull. Amer. Mus. Nat. Hist.*, Vol. VIII., 1896, pp. 82-110, pl. II.

Osborn, H. F., "The Extinct Rhinoceroses," *Mem. Amer. Mus. Nat. Hist.*, Vol. I., 1898, pp. 75-164.

Schlosser, M., "Beiträge zur Kenntniss der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer," *Morphol. Jahrb.* 12. Especially pp. 97-112.

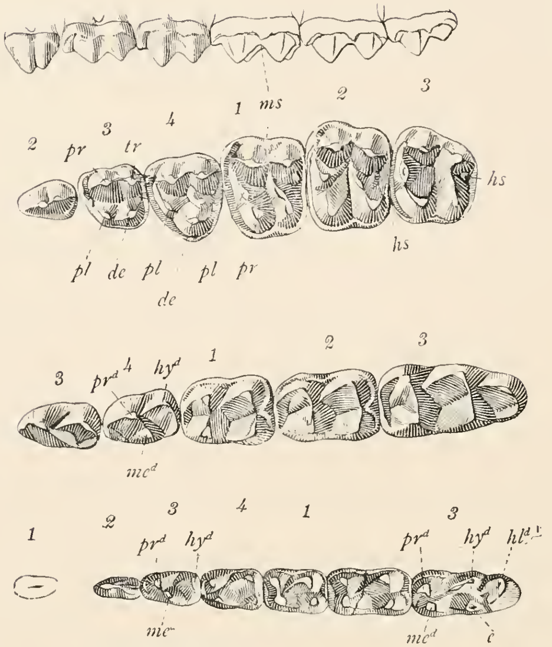


FIG. 166. Upper and lower cheek teeth of several Lower Eocene Equidæ. All $\times\frac{1}{1}$.

First or upper figure. Upper cheek teeth of *Eohippus* (*Protorohippus*) *venticolus*, Wind River Formation, Lower Eocene, Stage II. Side view.

Second figure. Crown view of the same.

Third figure. Lower cheek teeth of *Eohippus cristatus*, Wasatch Formation, Lower Eocene, Stage I.

Fourth (*lower figure*). Lower teeth of *Eohippus index*, Wasatch Formation, Lower Eocene. All figures natural size. After Wortman.

Observe: (1) The general similarity in the molar pattern to that of the Eocene Tapiridæ, as shown in the development of two transverse ridges in the upper and lower teeth, a feature destined to be emphasized in the Tapiridæ but highly modified in the Equidæ. (Cf. Figs. 160-164, 172-174.) (2) The incipient character of the mesostyle (*ms.*), and the appearance of the hypostyle (*hs.*) in m^1-m^3. (3) The complication of the fourth premolar p^4, by the development of a protoloph from the protoconule and deuterocone, and of a small metaloph from the metaconule, whereas in p^3, the protoloph is developed from the protoconule only, the metaloph from the deuterocone. (4) In the lower molars note (1) the molarization of p_4, (2) the development of an oblique crest running from the hypoconid (*hyd.*) to the metaconid, (3) the faintly incipient twinning of the metaconid; all three features being progressively developed in the later Horses.

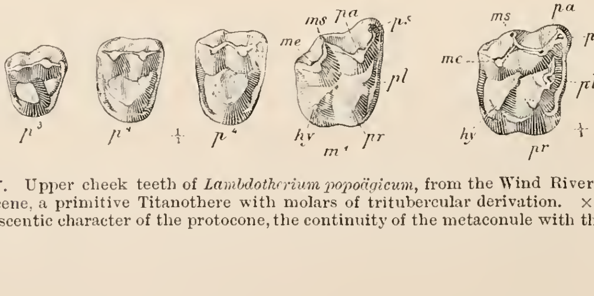


FIG. 167. Upper cheek teeth of *Lambdotherium popoägicum*, from the Wind River Formation. Lower Eocene, a primitive Titanothere with molars of tritubercular derivation. $\times\frac{1}{1}$. Observe the subcrescentic character of the protocone, the continuity of the metaconule with the hypocone.

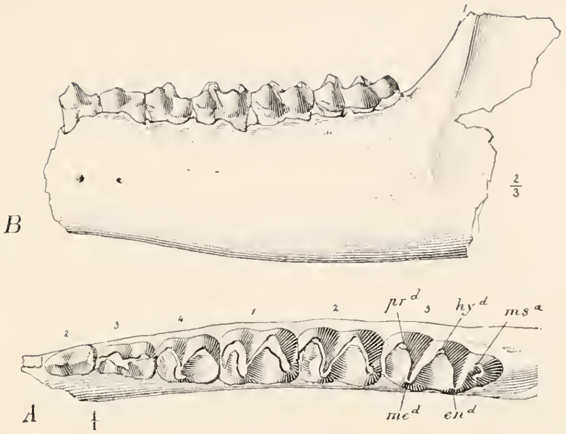


FIG. 168. Lower jaw and teeth of *Lambdotherium popoägicum* (cf. Fig. 167). The inferior molars retain a vestige of the paraconid, the fourth premolar is becoming molariform. $\times \frac{2}{3}$.

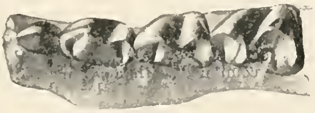


FIG. 169. Lower premolars of an undescribed species of the family Titanotheriidæ, Uinta Formation, Upper Eocene, showing progressive molarization of p_1-p_4. $\times \frac{2}{3}$.

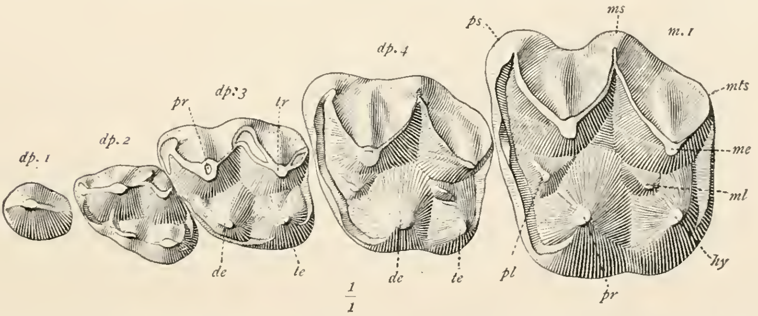


FIG. 170. Upper milk molars dp^1-dp^4, and first permanent molar of a primitive Middle Eocene Titanothere (*Palæosyops major*). The external cusps are becoming crescentic, producing a bunoselenodont type; the primitively triangular arrangement of the three main cusps is still evident. The fourth milk molar is seen to be closely similar to the first permanent molar. The cusps of the milk molar are lettered in accordance with Scott's premolar nomenclature (see pages 195-200), but it is probable that the cusp marked *te* in dp^3 corresponds to the postero-internal cusp of dp^2 and the antero-internal cusp (*de*) of dp^4, as in the Equidæ (cf. Fig. 166). Unlike the Equidæ the Titanotheres have greatly reduced the proto- and metaconules of the molars. $\times \frac{1}{1}$.

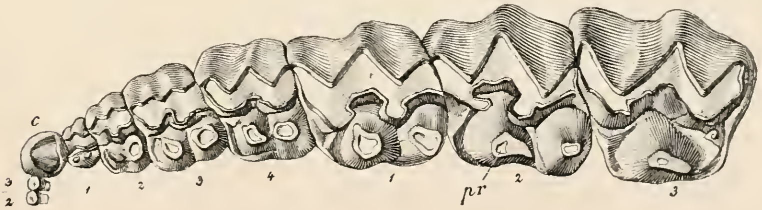


FIG. 171. Upper dentition of a specialized Oligocene Titanothere (*Brontotherium tichoceras*). The molars are now quadrate, the outer cusps sharply V-shaped. $\times \frac{1}{3}$.

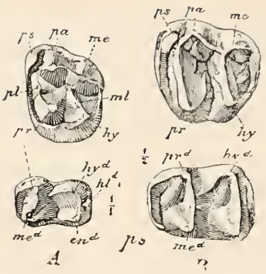


FIG. 172. *A*. Upper and lower molar of a Lower Eocene (Wasatch) Tapiroid *Systemodon semihians* (?)

B. Upper molar of a recent Tapir *Tapirus americanus*, showing the completed bilophodont pattern. $\times \frac{1}{1}$.

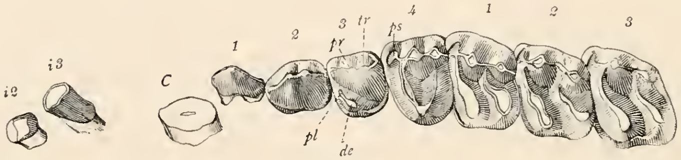


FIG. 173. Bunolophodont teeth of a primitive Tapiroid (*Systemodon primævus*), from the Wasatch Formation, Lower Eocene. Observe the general similarity in pattern to the teeth of contemporary Equidæ (Fig. 166) combined with a stronger development of the protoloph and metaloph, a greater obliquity of the tooth as a whole, and a somewhat more central position and larger size of the paracone. $\times \frac{1}{1}$. After Wortman.

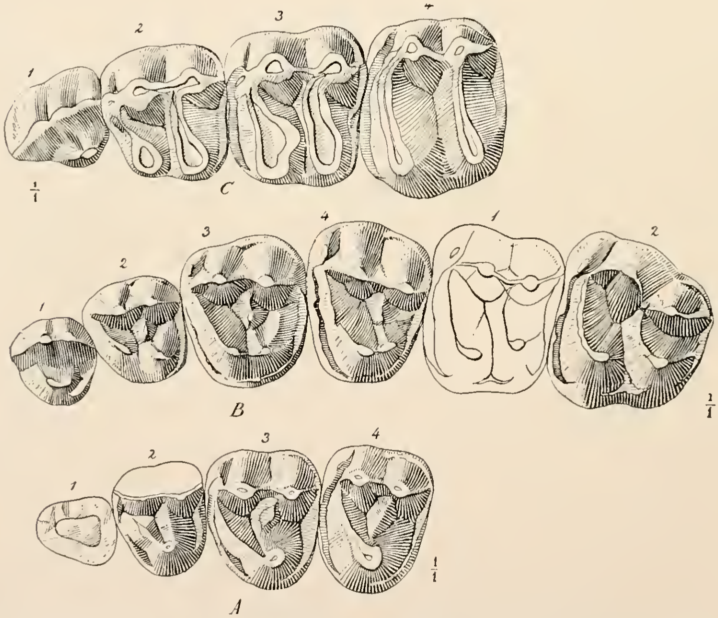


FIG. 174. Evolution of the premolars in *Protapirus* and *Tapirus*. After Wortman and Earle.

A. *Protapirus simplex*. Oreodon Beds, Middle Oligocene.

B. *Protapirus obliquidens*. Protoceras Beds, Upper Oligocene.

C. *Tapirus americanus*.

In *A*, premolars 1-4 are all comparatively simple and there is no metaloph.

In *B*, the internal cusp (deuterocone) of p^3, p^4 has split into two and there is an imperfect metaloph.

In *C*, $p^2 - p^4$ are fully molariform. $\times \frac{1}{1}$. After Wortman and Earle.

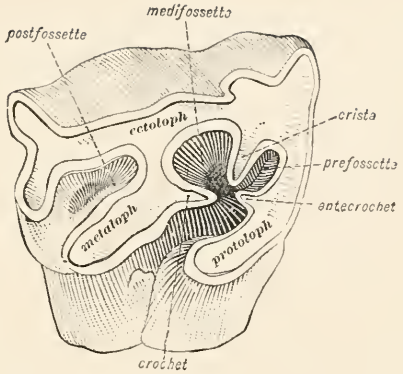


Fig. 175. Typical Rhinoceros molar, showing terminology of the crests and folds.

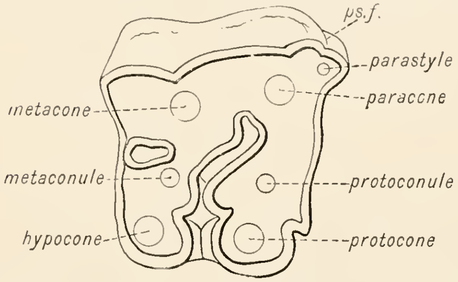
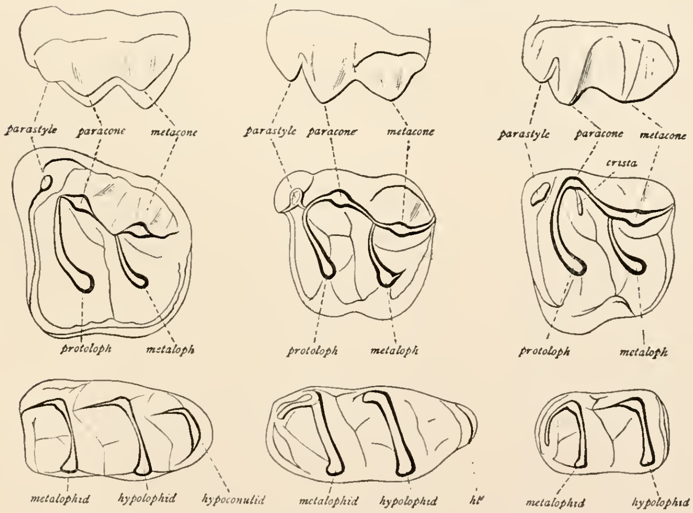


Fig. 176. Topographic relations of the parts of the typical Rhinoceros molar pattern to the sexitubercular ancestral ground plan.



Tapiroid. (*Protapirus*). Lophiodont. (*Lophiodon*). Rhinocerotoid. (*Hyrachyus*).

Fig. 177. Typical lophodont molars of Perissodactyls.

In the Tapiroid type the paracone and metacone are subequal or symmetrical, strongly convex externally. In the Rhinocerotoid type, the paracone is more or less convex, the metacone elongate, externally flattened to concave. The Lophiodont type is intermediate. It is noteworthy that in the Middle Eocene or Bridger Stage, the molars of the various Perissodactyls are rather similar. Thus some molars of the Tapirid *Systemodon* approach the *Protorohippus* type among Equidæ, some molars of the Lophiodont *Helaletes* approach the *Hyrachyus* type; while the latest representatives of *Hyrachyus* show some approach toward the *Hyracodon* type among Rhinoceroses.

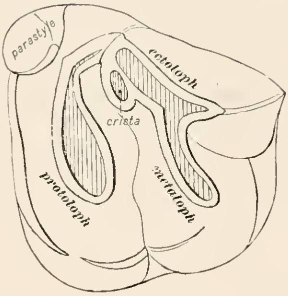


FIG. 178. Superior molar pattern of a primitive Hyracodont Rhinoceros *Hyrachyus agrarius* from the Bridger Formation, Middle Eocene, showing a general resemblance to the Lophiodont type, from which this differs in the smaller paracone and flatter metacone. The crista as in Rhinoceroses generally is merely a portion of the internal face of the paracone (cf. Fig. 175).

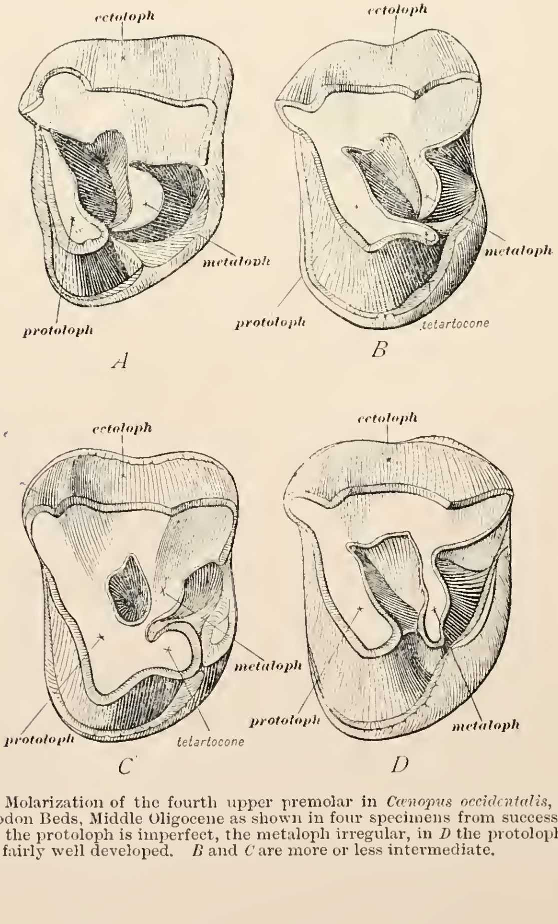


FIG. 179. Molarization of the fourth upper premolar in *Cænopus occidentalis*, a Rhinoceros from the Oreodon Beds, Middle Oligocene as shown in four specimens from successive geological levels. In *A*, the protoloph is imperfect, the metaloph irregular, in *D* the protoloph is complete, the metaloph fairly well developed. *B* and *C* are more or less intermediate.

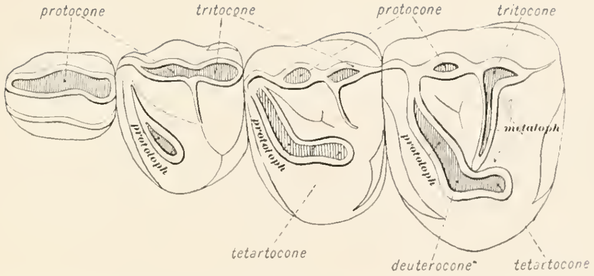


FIG. 180. Progressive molarization of the premolars from $p^1 - p^4$ in *Hyrachyus agrarius*, family Hyracodontidæ, a Rhinocerotoid from the Bridger Formation, Middle Eocene

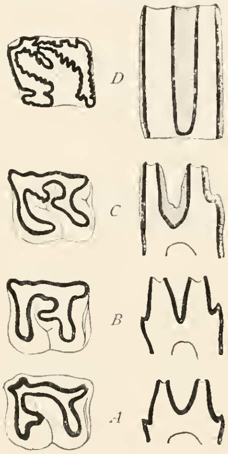


FIG. 181. Four stages in the evolution of the molars in the Rhinoceroses. After Gaudry.

A. Aceratherium lemanense, Upper Oligocene, Europe.

B. Rhinoceros pachygnathus, Lower Pliocene, Europe.

C. Rhinoceros antiquitatis, Pleistocene, Europe.

D. Elasmotherium sibericum, Pleistocene, Europe. After Gaudry and Boule.

We note (1) the progression from brachyodonty to hypselodonty, (2) from roots to open-pulps, (3) the increasing verticality of the slopes of the crests, (4) the development of the cement, (5) the increasing plication of the enamel. Stage *A* parallels the Stegodonts among Proboscidea (pp. 186-188). Stage *D* parallels the elephants, and also many of the South American Ungulates, and even the rootless grinders of many Rodents.

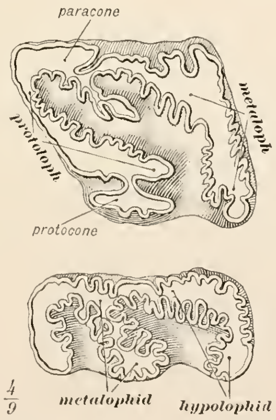


FIG. 182. Extreme specialization of the Rhinoceros molar type, in *Elasmotherium sibericum*, from the Pleistocene of Siberia. The plication of the enamel has increased the cutting surface, and the efficiency of the tooth for grinding hard dry grasses or shrubs. (Compare the enamel lakes in the Horse molar, Fig. 163). × $\frac{4}{9}$. After Gaudry and Boule.

CHALICOTHEROIDEA OR ANCYLOPODA.

The Ancylopoda are apparently a group of aberrant Perissodactyla in which the nails or generalized hoofs have become secondarily modified into large claws. The types of this order are the genera *Macrotherium*, *Chalicotherium*, and *Ancylotherium*, in which the superior molar teeth exhibit a strong general resemblance to those of Titanotheres among Perissodactyla: that is, they are buno-selenodont (Fig. 184), or, strictly speaking, buno-lopho-selenodont, because they combine bunoid, lophoid, and selenoid modelling of the cusps. These molars have evidently evolved from a sexitubercular ancestral type, and we reason by analogy that they were of tritubercular origin.

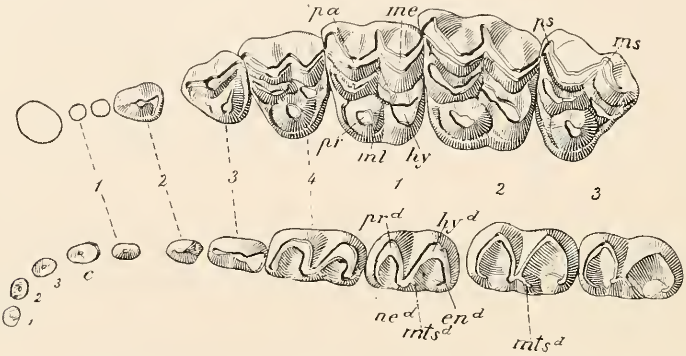


FIG. 183. Bunoselenodont upper cheek teeth of *Meniscotherium terrærubræ*, a Condylarth (?), from the Wasatch Formation, Lower Eocene. Note the large selenodont protoconule, the oblique metaconule-hypocone; in the lower molars, the twinning of the metaconid (me^d), a feature also independently developed in the Equidæ, Fig. 166. × $\frac{2}{1}$.

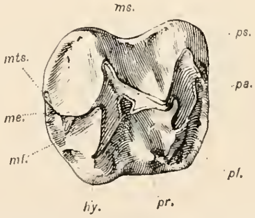


FIG. 184. Buno-lopho-selenodont molar (m^3) of *Schizotherium modicum*, an Ancylopod from the Eocene of France. In the drawing the height and size of the protocone and hypocone is considerably foreshortened.

In *Meniscotherium* we have a genus of much greater geological age, which exhibits a somewhat similar type of grinding tooth (Fig. 183). It has been considered by Osborn for this and other reasons as a possible ancestor of the Ancylopoda, though still a member of the order Condylarthra. However recent observations tend to show that these resemblances are not indicative of genetic relationship but that the

Chalicotheres have more probably been derived from Lower Eocene Titanotheres.

SPECIAL REFERENCE.

Osborn, H. F., "The Ancylopoda, Chalicotherium, and Artionyx," *Amer. Naturalist*, Feb., 1898, pp. 118-133. [The discussion about *Artionyx* is based upon a foot now known to appertain to the Oreodont Artiodactyl *Agriochœrus*.]

HYRACOIDEA.

The Hyraces, including many existing African and West Asiatic species, also the fossil forms *Pliohyrax* Osborn, *Saghatherium* Andrews, *Megalohyrax* Andrews, exhibit strong evidences of derivation from a buno-lopho-selenodont ancestral type. The superior molar teeth (Figs. 185, 186), consist of two short, transverse crests, the proto- and metalophs, and an elongate external crest, the ectoloph. The latter has been compared with that of the rhinoceros, but actually resembles that of the Eocene

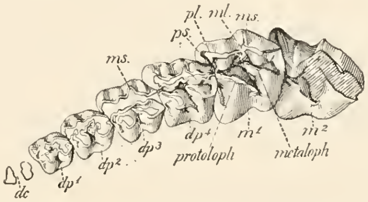


Fig. 185. Milk dentition of a Hyraeoid (*Saghatherium antiquum?*), from the Upper Eocene of Egypt, with buno-lopho-selenodont cheek teeth. × $\frac{1}{1}$.

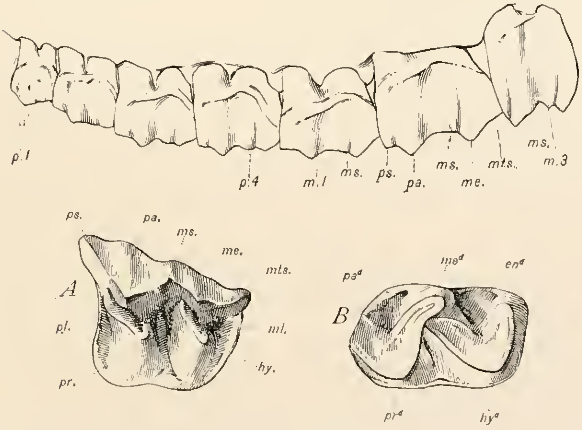


Fig. 186. *Upper figure*, *Hyrax syriacus*, upper cheek teeth, external view. × $\frac{3}{2}$. *Lower figures*, *A*, *Hyrax capensis*, third upper molar, unworn. × $\frac{3}{1}$. *B*, *H. syriacus*, third lower molar, worn. × $\frac{3}{1}$.

horses more closely, because it consists of two halves, a paracone and a metacone, divided by a faint vertical ridge, the mesostyle; this ridge is much more strongly marked in the extinct genera, mentioned above. It proves that the ancestral types of teeth among the Hyracoidea were lopho-selenodont, like those of *Palæotherium* perhaps, the more remote ancestors being sexitubercular and tritubercular. The lower molars exhibit the double crested pattern, similar to that seen in so many Perissodactyla.

It is an interesting fact that the fossil Hyracoids retain the primitive double rooted canine, a tooth which undoubtedly (see p. 194) once belonged to the premolar series.

SPECIAL REFERENCES.

Osborn, H. F., "On Pliohyrax Krupii Osborn, A Fossil Hyracoid from Samos, Lower Pliocene, in the Stuttgart Collection," *Proc. Fourth International Congress of Zoology*, Cambridge, 1898, pp. 173-174, Pl. 2.

Forsyth Major, C. J., "Pliohyrax græcus from Samos," *Geol. Mag.*, N.S., Dec., IV., Vol. XI., pp. 547-553, Dec. 1899.

Andrews, C. W., "Notes on an Expedition to the Fayûm, Egypt, with Descriptions of some New Mammals," *Geol. Mag.*, Dec., IV., Vol. X., No. 470, Aug. 1903, pp. 339.

PROBOSCIDEA.

The highly complex, plated tooth of *Elephas* is so far remote from the molar crown of the general type seen in *Protogonodon* (Fig. 148) or even in *Hemithlæus* (Fig. 138) that it might seem hopeless to attempt to show derivation of the former from the latter; but the palæontology of the Proboscidea renders such a connection absolutely certain.

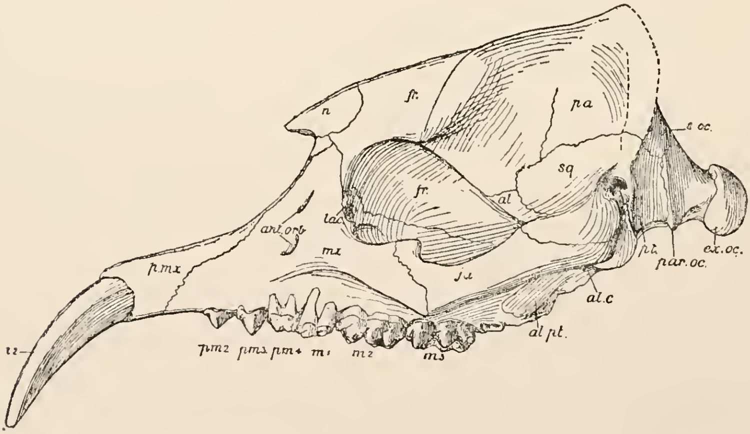


FIG. 187. Side view of the skull of *Palæomastodon beadnelli*, from the Upper Eocene of Egypt. After Andrews. About $\frac{1}{10}$ natural size.

The gradations leading back from the plated teeth of *Elephas* through *Stegodon*, with its numerous crests and short crowns, to *Mastodon*, were long ago followed in Falconer and Cautley's *Fauna Antiqua Sivalensis* and in Gaudry's *Enchaînements du Monde Animale*: but the recent researches of Andrews have carried the evolution back through *Palæomastodon* (Figs. 187, 188) to the quadritubercular molars of *Mœritherium*, a middle Eocene stage representing the African atavus of the Proboscidea. By analogy with all the other groups we have been considering, there is no question that the quadritubercular molars of *Mœritherium* (Figs. 189, 190) sprang from an ultimately tritubercular type.

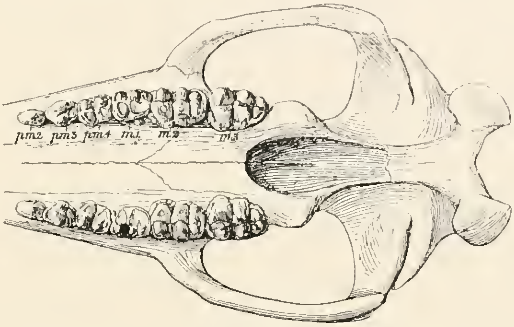


FIG. 188. Upper cheek teeth and basal view of skull of *Palæomastodon beadnelli*, (cf. Fig. 187). After Andrews. Scale, about $\frac{1}{10}$.

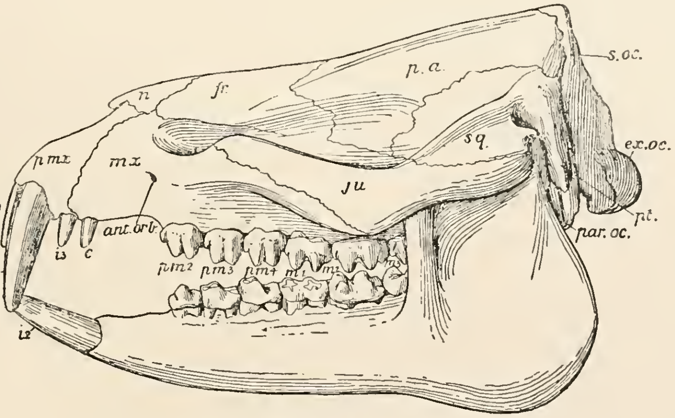


FIG. 189. Side view of the skull of *Mœritherium lyonsi*. (Cf. Fig. 190.) After Andrews. Scale, about $\frac{1}{5}$.

The quadritubercular molar of the *Mœritherium* type by (1) transverse connection of its pairs of cones, produced a bilophodont crown similar to the lower molars of the Tapirs; (2) by continuous upgrowth of successive cingula (talons and talonids) it transformed a bilophodont into a trilophodont crown, a trilophodont into a tetralophodont, etc. Thus, the plates of the teeth of *Elephas* owe their origin to upgrowths of the posterior basal cingulum.

We have many analogies among other hoofed animals with Proboscidean molar evolution. Among Suina, *Perchœrus* has plainly quadritubercular upper molars, and shows the origin of a double trefoil analogous to that seen in *Mastodon.* The Hippopotamus also shows a double trefoil. *Listriodon* of the Middle Eocene of Europe exhibits lophodont teeth remarkably similar to those of *Dinotherium.* The hindermost molar of the wart-hog (*Phacochœrus*) parallels the molars of the Proboscidea in the development of complex many-columned teeth from the constant upgrowth of the talon posteriorly.

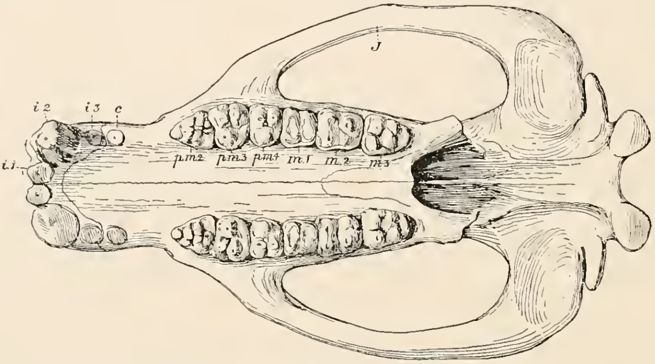


Fig. 190. Inferior view of the skull and teeth of *Mœritherium lyonsi*, from the Middle Eocene of Egypt. After Andrews. Scale, about $\frac{1}{5}$.

SPECIAL REFERENCES.

Falconer, H., and Cautley, P. T., *Fauna Antiqua Sivalensis*, Part I., pp. 1-64, 4to, 1846.

Andrews, C. H., "On the Evolution of the Proboscidea," *Philos. Trans. Roy. Soc.* Ser. B, Vol. 196, pp. 99-118. London, 1903.

Gaudry, A., *Les Enchaînements du monde animal dans les temps géologiques Mammifères tertiaires*, 8vo, 1878, pp. 172-191.

SIRENIA.

The bilophodont molars of the Sirenia (Fig. 191) do not offer any difficulty to the theory of trituberculy, because of the many other cases in which bilophodonty has evolved from sexi-, quadri-, and trituberculy.

Considerable evidence has been adduced for the belief that the

Sirenia are an aquatic offshoot from the Ungulata. De Blainville first made the bold suggestion that they were related to the Proboscidea, and in 1902 Andrews again directed attention to the numerous anatomical similarities of these two groups, reinforcing them by the new evidence offered by the ancestral *Mœritherium*, which closely resembles *Prorastoma* not only in the teeth but in the humerus. Lydekker, on the other hand, in 1892, pointed out the likenesses between the third and fourth upper milk molars of *Prorastoma veronense* and those of the selenodont Artiodactyl *Merycopotamus dissimilis*.

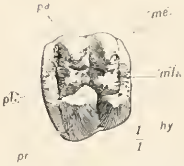


FIG. 191. Unworn molar of American Manatee (*Trichechus manatus*), showing "masked selenodonty." $\times \frac{1}{1}$.

Of the affinities of the Sirenia and Ungulata in general, as expressed in the table on p. 75, there can be little doubt, but for their more specific relationships we must wait for additional evidence.

SPECIAL REFERENCES.

Andrews, C. W., "On the Evolution of the Proboscidea," *Phil. Trans. Roy. Soc. Lond.*, Ser. B, Vol. 196, 1903, pp. 99-118.

Lydekker, R., "On a remarkable Sirenian Jaw from the Oligocene of Italy and its bearings on the Evolution of the Sirenia," *Proc. Zool. Soc. Lond.*, Febr. 2, 1892, pp. 77-83.

SOUTH AMERICAN UNGULATES.

The Ungulates of South America include the highly specialized Typotheria, Homalodotheria, Toxodontia, and Astrapotheria, in all of which the teeth present the extreme of lophodont modification and of elongation or hypselodontism. Close analogies are found among the teeth of the Equidæ and Rhinocerotidæ, and especially of the Amynodontidæ. Naturally there is little trace left of the archaic and simpler constitution of the teeth in these highly specialized crowns.

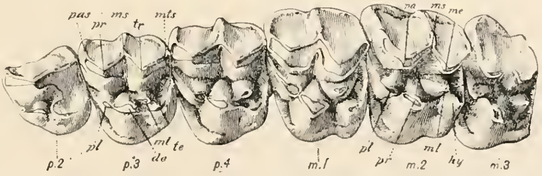


FIG. 192. Upper cheek teeth of *Proterotherium* sp., a primitive Litoptern from the Santa Cruz Formation, Middle (?) Miocene, Patagonia. Compare the somewhat similar buno-lopho-selenodont molars of *Palæotherium*, *Protorohippus* (Fig. 166), *Saghatherium* (Fig. 185), *Meniscotherium* (Fig. 183), *Schizotherium* (Fig. 184) and *Cænotherium*, family Anplotheriidæ, order Artiodactyla.

It is very suggestive, however, that the most primitive of the Litopterna, the fifth of these South American orders, retain unmistakable indications of a primarily triangular crown pattern. In

Proterotherium (Fig. 192), for example, we see the trigonal disposition of three main cusps. The still more ancient Ungulates from the *Notostylops* beds of Patagonia, exhibit molar teeth of the type seen among the Amblypoda and Condylarthra, namely the tritubercular, bunodont type, and lend the strongest of all the recent evidence which has come forward in support of the tritubercular theory.

Pyrotherium, believed by Ameghino to be ancestral to the Proboscidea, has simple, bilophodont molars.

Doctor Ameghino, although rejecting Osborn's homologies of the molar cusps, and holding widely divergent views as to the ultimate origin of the molars, yet brings forward a great deal of evidence[1] to show the derivation of all the inferior molar types of South American orders from a *Proteodidelphys* (Fig. 202) type which has a typically tuberculosectorial lower dentition more primitive even than that of *Didelphys* (see pp. 202, 204).

SPECIAL REFERENCES.

Ameghino, F., *Contribucion al Conocimiento de los Mammíferos Fósiles de la Republica Argentina.* Buenos Aires, 1889. Numerous contributions to *Anales del Museo Nacional de Buenos Aires*, *Boletin del Instituto Geografico Argentino*, *Boletin Acad. Nac. Ciencias Cordoba*, *Anales Soc. Cientifica Argentina*, etc.; especially "Recherches de Morphologie Phylogénétique sur les Molaires Supérieures des Ongulés," *An. d. Mus. Nac. des Buenos Aires*, *Tom. IX.*, 1904.

Lydekker, R., *Palaeontologia Argentina II.* La Plata, 1893.

Owen, R., *The Zoology of H.M.S. Beagle*, Pt. I., "Fossil Mammalia," London, 1840.

CETACEA.

Aquatic adaptation has gone to such an extreme in the teeth of the Cetacea that all traces of tritubercular ancestry, if such ever existed, have been entirely obliterated. It has been suggested that the Cetacea are so ancient that they branched off before the haplodont reptilian crown had begun the series of modifications leading to trituberculy (Fig. 43), but the presence of accessory cuspules in the posterior molars of certain recent and Miocene Platanistidæ and of vestigial low cusped, two rooted teeth in embryos of Whalebone Whales, the analogy with the secondary haplodont molar teeth of certain Pinnipedia (Fig. 103), and the fact that the placentation and reproductive organs of the Cetacea are of a very high Eutherian type, are all more in accordance with the hypothesis that the ancestors of the Cetacea possessed more complicated tooth crowns, and that the existing haplodont types are all secondary.

---

[1] "On the Primitive Type of the Plexodont Molars of Mammals," *Proc. Zool. Soc. Lond.*, May 2, 1899, pp. 555-571.

ZEUGLODONTIA.

The derivation of the serrated cutting molars of *Zeuglodon* from a more normal type retaining vestiges of the ancient inner portion of the crown, is demonstrated by recent discoveries in Egypt (Figs. 193, 194)

FIG. 193. Inferior surface of the skull of *Protocetus atavus*, from the Lower Middle Eocene of Mokattam, near Cairo, Egypt; a very primitive Zeuglodont, thought by Prof. Fraas to represent an aquatic offshoot of the Creodonta. The cheek teeth while elongate anteroposteriorly retain vestiges of the internal protocone and of its root. Aquatic adaptation is also indicated in the elongation of the snout, the prehensile modification of the anterior teeth, the secondary bridging over of the posterior nares, the enlargement of the auditory bullæ. About $\frac{1}{5}$. After Fraas.

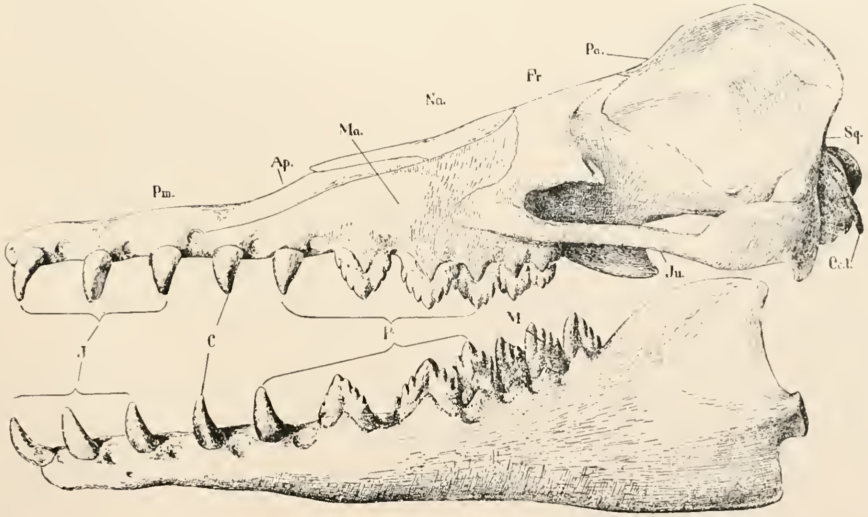


FIG. 194. Restoration of the skull of *Zeuglodon osiris*, from the Middle Eocene of Egypt, showing a further advance of the specialization noted under Fig. 193. Much reduced. After Stromer von Reichenbach.

by which the Zeuglodontia are thought by Professor Fraas to have been connected with the Creodonta and especially the Hyænodontidæ. If in turn the Zeuglodonts should be shown to be related to the Odontocete Whales, through *Squalodon* and the Miocene Platanistidæ, the ultimate derivation of the Cetacean cheek teeth from the tritubercular type would no longer be in doubt.

CHAPTER VIII.

EVOLUTION OF THE PREMOLARS.

In the early geological periods the premolar teeth of mammals were very simple in structure, as shown in the following description and figures by Osborn[1] of the premolars of the Triassic and Jurassic mammalia:

1. Premolars in Primitive Mammals.

"The *premolars* of *Dromatherium* [Fig. 195 *A*] are very unique. They are tall and styloid and single fanged: the last premolar has a vertical groove upon the posterior face. In *Microconodon* [Fig. 195 *B*], which belongs to a somewhat more recent type, the premolars have a faint posterior heel, and the last shows the trace of a double fang. In all the Jurassic genera the premolars, where fully functional, are bifanged, and possess a convex anterior face and concave posterior slope terminating frequently in a heel. As in the molars, the cingulum plays an important part in connection with the basal cusps. It is present upon the internal face of the premolars of all the Jurassic genera except *Kurtodon* [Fig. 195 *15*], and is observed upon the outer surface in *Diplocynodon* [Fig. 20]. It thus in many cases enables us to draw the line between premolars and molars, as in both the Peralestidæ *Peralestes*, *Peraspalax* [Figs. 12, 22, 195 *9*], and in the genera of the Insectivorous Sub-group the inner faces of the molars are smooth.

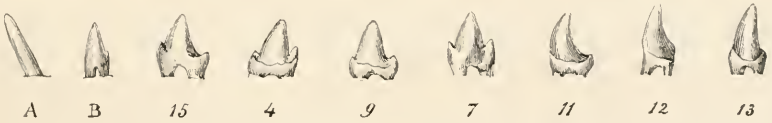


Fig. 195. The premolar tooth forms of the mammals of the Mesozoic order Pantotheria or Trituberculata. The premolar represented is invariably the most posterior of the series; the anterior face is to the left. *A*. *Dromatherium*. *B*. *Microconodon*. 15. *Kurtodon*. 4. *Triconodon*. 9. *Peraspalax*. 7. *Spalacotherium*. 11. *Phascolestes*. 12. *Dryolestes*. 13. *Achyrodon*. Nos. *A*, 4, 9, 11, 12 are seen upon the inner surface, the remainder upon the outer surface.

---

[1] Osborn, H. F., "The Structure and Classification of the Mesozoic Mammalia," *Jour. Acad. Nat. Sci.*, Philadelphia, Vol. IX., No. 2, July, 1888, pp. 225-226 and pp. 239-240.

The cingulum generally embraces the entire inner face of the crown, forming anterior and posterior cingulum cusps or *cingules,* which are characteristic of the insectivorous forms, while in the supposed carnivorous and omnivorous forms, distinct basal cusps rise posteriorly and sometimes anteriorly [*Triconodon*, Figs. 8, 195 *4*] above the cingulum. As in the latter genera the cingulum is present with the basal cusps, it probably precedes them in evolution, but there is no direct evidence (in the Triconodonta) of the conversion of *cingules* into true basal cusps, such as we find in the molars.

A review of the premolars of all the genera shows that they are sharply distinguished from the incisors and from the molars, and less distinctly from the canines in many instances.[1] In several genera they have undergone considerable specialization, as in the production into lofty cones of pm_{3-4} of *Achyrodon* [Fig. 195 *13*], or the apparently incipient assumption of the molar pattern in *Kurtodon* [Figs. 195 *15*]."

2. Adaptation of Premolars.

The premolar teeth in general are quite as *adaptive and independent* in evolution as the molars. While in many families of mammals the first, second, and third, and more rarely the fourth promolars retain more or less of this simple ancestral structure: in other families the premolars become greatly complicated. They either (*a*) enter upon an especial adaptive evolution of their own, as for example in the upper sectorials of the Cats (Felidæ), or the elaborate fourth premolars of the Plagiaulacidæ (pp. 102, 106), or (*b*) by a serial analogous development they more or less closely mimic the structure and supplement the exact functions and uses of the molar teeth: this mimicry reaches its highest extreme among the Perissodactyl or odd-toed Ungulates, such as the horses, where the premolars gradually *metamorphose into the molar pattern* and even become superior to the molars in size and complication.

3. Various Upper Premolar Types.

1. Persistence of a simple conical form throughout. Realized in the inferior premolars of *Dromatherium* (Fig. 3).

2. The posterior or 4th superior premolar becomes sectorial, the anterior premolars remaining more or less simple and conical, *e.g.* most Carnivora.

3. The 4th, 3rd, and 2nd superior premolars become more or less uniformly bicuspid, *e.g.* most Primates.

---

[1] There is strong support among the Jurassic mammals and the recent Insectivora for the opinion first expressed by E. Ray Lankester, that the *canine* is originally a bifanged tooth and represents a modified *anterior premolar*.

4. The 4th superior premolar more or less completely transforms into the molar pattern, the third, second, and first remaining simpler (*e.g.* some Artiodactyla, as *Agriochœrus*).

5. The 4th and 3rd superior premolars transform into the molar pattern, the first and second adopting an entirely different order of evolution (*e.g. Galeopithecus*).

6. The 4th, 3rd, and 2nd premolars successively partially transform in the molar pattern. Example, many Perissodactyla, such as the Titanotheres and Rhinocerotidæ.

7. The 4th, 3rd, and 2nd premolars completely transform into the molar pattern. Example, some Perissodactyla (Equidæ).

This *premolar metamorphosis* into the molar pattern observed in types 4, 5, 6, 7, above is a very gradual process, requiring hundreds of thousands if not millions of years, and from the biological standpoint most interesting as illustration of convergence, because *form exactly similar to that of the molars* is finally attained from somewhat dissimilar beginnings.

4. Cusp Addition in the Premolars.

The first broad and systematic treatment of the subject of premolar evolution was that by Professor W. B. Scott.[1] It is somewhat too special to be cited in full here. We accept Scott's interpretation in full as regards the upper premolars, but have adopted a different interpretation of the evolution of the lower premolars.

Superior Premolars.

It is important to note here that *all of the following description* is based on the older Cope-Osborn theory that the superior premolars have followed a different order of cusp addition from the molars; this is now met by the newer theory (see Chapter IX.) that the premolars follow practically the *same* order of cusp addition as that originally followed by the molars. Pending the solution of this question the comparisons which follow are made on the basis of the older theory.

We may take the progressive complication of the fourth superior premolar as a standard; the order of succession of the cusps in this tooth is rather constant, while in the more anterior premolars there are more various modes of complication.

First stage. As early as the Basal Eocene period the fourth upper premolar, in every known genus in which the premolars tend to imitate

---

[1] "The Evolution of the Premolar Teeth in Mammals," *Proc. Acad. Nat. Sci. Phila.*, 1892, pp. 405-444.

the molars, is complicated by the addition on the inner or lingual side of the protocone of a second cusp, which has appropriately been called the *deuterocone* [δέυτερος, second; κῶνος, cone] by Scott. This *bicuspid stage*, which is retained in the 'bicuspids' of man and other primates, is the starting point, and brings out clearly the important initial fact *that in the premolars the protocone remains upon the outer or buccal side* of the crown, while in the molars (as we have tried to show above, pp. 35, 217) it shifts to the inner or lingual side. From this it follows that the deuterocone of the premolars has no exact serial homologue in any of the cusps of the molars, although it becomes functionally analogous to the protocone; it follows, moreover, that all the cusps which are subsequently added to the premolars are analogous, but not serially homologous, to those in the molars (Fig. 196).

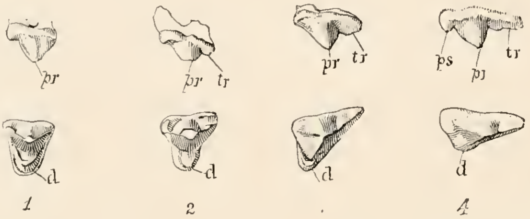


FIG. 196. Fourth upper premolar of Creodonts and Carnivores in various stages of evolution. (Cf. Figs. 84-92.) After Scott.

1. *Deltatherium fundaminis*, family Oxyclænidæ.
2. *Sinopa whitiæ*, family Hyænodontidæ. (Cf. Fig. 89.)
3. *Cynodictis gracilis*, family Canidæ.
4. *Felis concolor*, family Felidæ.

The *Second stage* of premolar complication usually consists in the addition of a second outer cusp, posterior to the protocone, which, as the third in the series, Scott has called the *tritocone* [τρίτος, third]; this in turn is analogous in position and function with the metacone of the molars. This tritubercular *tricuspid* or trigonodont premolar stage imitates very closely the tritubercular or trigonodont molar tooth, and frequently the tritubercular types of premolars display intermediate conules corresponding in position with the proto- and meta-conules of the molars, but obviously not homologous with them. The gradual development of this tritubercular premolar stage is beautifully shown in series of teeth of *Euprotogonia* and *Phenacodus*, in which the tritocone may be seen in all stages of development from its incipiency, and in which the more anterior premolars are seen taking up the stages which have already been

FIG. 197. Second upper premolar of *Protorohippus venticolus*, a lower Eocene Equid (cf. Fig. 166), showing the division of the crown into two cusps "protocone," "tritocone." After Scott.

passed through by the fourth premolar, until it reaches the size of a protocone (Figs. 197, 198).

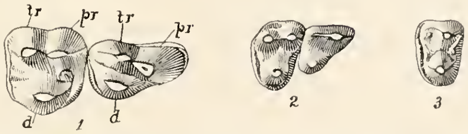


FIG. 198. Complication of the superior premolars in Condylarthra. 1. P^3, p^4 of *Phenacodus primævus*, showing a complicated p^4. 2. P^3, p^4 of *Phenacodus wortmani* with simpler p^4. 3. P^4 of *Euprotogonia subquadrata*. After Scott.

This stage is very widely exhibited in the Middle and Upper Eocene Ungulates and Creodonts and persists till the present time, with some modifications in the sectorial or carnassial fourth premolar of the Carnivora, in many Insectivora, and in some forms of the Artiodactyla.

The *third and final stage* in the metamorphosis of the premolar into the molar pattern is reached by the addition of a fourth main element, which Scott has called the tetartocone [τέταρτος, fourth]: it corresponds in position and is analogous with the hypocone of the molars. As observed by Scott, the tetartocone usually arises in the same manner as the hypocone of the molars, namely, by the addition of a cusp at the postero-internal angle of the crown immediately behind the deuterocone (Fig. 199, No. 1).

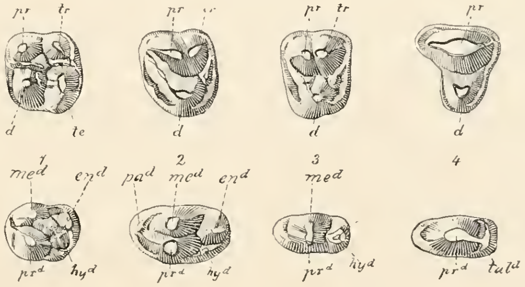


FIG. 199. Fourth upper and lower premolars of various Artiodactyla. After Scott.

1. *Dicotyles torquatus*, family Dicotylidæ. Molarization nearly complete.
2. *Thinohyus lentus*, family Dicotylidæ. Molarization much less complete.
3. *Perchærus probus*, family Dicotylidæ.
4. *Trigonolestes brachystomus*, family Trigonolestidæ, showing simple upper and lower premolar.

In the normal or usual evolution of the tetartocone behind the deuterocone variations occur characteristic of different families of mammals. Sometimes (in some Perissodactyla, *e.g.* Titanotheres) a ridge extends back from the deuterocone, which splits in two, forming the deuterocone anteriorly, the tetartocone posteriorly.

This brief survey of the steps of premolar evolution proves that these teeth follow an order of differentiation quite at variance with that attributed to the molars, even when the final results are the same. It is another remarkable instance of convergence in evolution, and proves that similarity in form and in position affords an unsafe guide to serial homology (see, however, Chapter XI.).

Inferior Premolars.

As shown in the foregoing comparison of the Jurassic mammals, and in other primitive mammals, the primitive form of the lower premolar is a simple, more or less recurved cone, obviously corresponding to the protocone of the molars, and implanted by a single fang.

The metamorphosis of the inferior premolars also begins with the fourth premolar, and extends anteriorly. While the order of cusp development is less regular and constant than in the upper teeth, we find that the lower premolars may be more closely compared with the lower molars, that is, *there is more evidence of serial homology between the cusps of the lower premolars and lower molars.* This fact fortunately enables us to use the same terminology for the premolars as for the molars. Professor Scott was led to take a different view, and proposed several new homologues in the lower premolars, such as the paraconid, deuteroconid, metaconid, tetartoconid, which may be eliminated by a somewhat different interpretation of the development.

Comparison of the lower premolars should be made, not with the molars of the Triconodonta, but with the molars of Trituberculates. Such comparison shows that the premolar evolution may be interpreted as substantially similar to the molar evolution.

The *initial stage* is the simple, single-fanged, conical cusp, the protoconid of *Dromatherium* (Figs. 3, 195 *A*).

Even in the Jurassic mammals the *second stage* appears in the two-fanged crown with more or less developed posterior basal cusp, which corresponds in position and function with the *talonid or hypoconid* of the tritubercular molars of such a type as *Amphitherium* (Fig. 15). In the subsequent evolution of the crown this hypoconid remains on the outer or buccal side of the crown as in the molars; it is therefore practically homologous serially with the hypoconid of the tritubercular molars rather than with the metaconid of the triconodont molars. Most of the existing Unguiculates as well as some recent, and many extinct Ungulates, retain more or fewer premolar teeth which depart but little from this type.

As a *third stage* an anterior basal cusp comparable to the paraconid both of the tritubercular and triconodont molars is added. This cusp, in fact, corresponds in the subsequent evolution of the teeth with the paraconid of the true molars; and may, therefore, be considered as more or less serially homologous with that molar element.

As a *fourth stage* (or in some cases as the third stage of development the order of succession not being constant) there appears a cuspule on the inner side of the crown of the protoconid which corresponds in position with the metaconid of the true molars of the tritubercular *Amphitherium* type, and subsequently develops into an exactly analogous form. (This is the deuteroconid of Scott's terminology.)

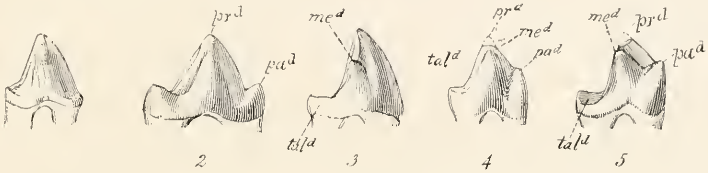


FIG. 200. Fourth lower premolars of Creodonts in various stages of complication. After Scott.

1. *Tricentes subtrigonus.* family Oxyclænidæ.
2. *Clænodon protogonoides*, family Arctocyonidæ.
3. *Chriacus stenops*, family Oxyclænidæ.
4. *Chriacus schlosserianus.*
5. *Deltatherium fundaminis*, family Hyænodontidæ, tuberculo-sectorial pattern nearly completed, with a high trigonid and low talonid.

As a *fifth stage* a cusp is sometimes added to the premolar crown on the internal or lingual side of the hypoconid, occupying the position held by the entoconid in the true molars. (To this Scott gave the name of 'tetartoconid,' regarding it as serially comparable with the tetartocone of the upper premolars.)

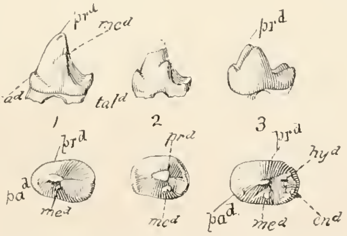


FIG. 201. Premolar complication in Condylarthra (Phenacodontidæ). Fourth lower premolar of right side, internal aspect. 1 and 2. *Protogonodon pentacus*, showing incipient metaconid and talonid. 3. *Euprotogonia plicifera*, showing better developed metaconid and talonid, incipient paraconid. The tuberculo-sectorial pattern is thus nearly attained. After Scott.

On the completion of these four stages, the premolar reaches a condition analogous to the 'tuberculo-sectorial' stage of the molars, namely, with an elevated *trigonid* composed of the protoconid, paraconid and metaconid, and with a depressed *talonid* composed of the hypoconid and entoconid.

The subsequent transformation of the fourth inferior premolar in various type is shown in the preceding and accompanying figures (Figs. 200, 201).

In comparatively few mammals, however, are these four stages completed. With many exceptions (such as the sectorial p^4 opposed by the sectorial m_1 in the Carnivora), the evolution of the lower *premolars* is normally correlated with that of the upper *premolars*, which agree roughly with the seven upper premolar types enumerated on pages 194, 195. For example, in the Equidæ, three of the corresponding upper and lower premolars assume the molar form, but in *Galeopithecus*, $p^{3 \cdot 4}_{3 \cdot 4}$ become molariform, while the independently adaptive $p\frac{1 \cdot 2}{1 \cdot 2}$ become elongate and denticulate.

CHAPTER IX.

OBJECTIONS AND DIFFICULTIES AND OTHER THEORIES.

Two classes of criticism have developed:

I. That the tritubercular type is not primitive.

II. That the Cope-Osborn theory of the origin of the superior molars is incorrect.

Let us consider these in order.

I. That the Tritubercular Type is not Primitive.

1. The 'Plexodont' or Progressive Simplification Theory of Ameghino.

In 1884,[1] 1896,[2] and 1899[3] Dr. Florentino Ameghino fully stated an original theory of the origin of the grinding teeth, in which there are four main propositions:

First (*op. cit.*, 1889, p. 556), that aside from the haplodont reptilian type, the most primitive type of inferior molar is not the protodont, triconodont, or tritubercular, but the *plexodont*. The original plexodont upper or lower molar is supposed to have been quadrangular, quadritubereulate, quadriradiculate (*op. cit.*, 1896, pp. 18, 19, 25, 61, 64). The oldest known form of complete plexodont molar, that of *Proteodidelphys* (Fig. 202 and *op. cit.*, 90, p. 556) has an anterior and a posterior lobe, each of them carrying three cusps, which are designated in the following terms, the names in parenthesis being those of Osborn's nomenclature (*op. cit.*, p. 557).

ma, median-anterior (paraconid).
ae, antero-external (protoconid).
ai, antero-internal (metaconid).
pe, postero-external (hypoconid).
pi, postero-internal (entoconid).
mp, median-posterior (hypoconulid).

---

[1] *Filogenia*, 8vo, 1884.

[2] "Sur l'Évolution des Dents des Mammifères," *Bol. Acad. Nac. de Cienc.*, T. XIV., 1896, pp. 381-517.

[3] "On the Primitive Type of the Plexodont Molars of Mammals," *Proc. Zool. Soc. Lond.*, May 2, 1899.

Second, that the plexodont molar made its appearance suddenly (p. 571, bottom), the only theory which can explain it in a satisfactory manner being that it arose by the fusion or the concrescence of "the dental germs or embryos of several simple teeth" (*op. cit.*, '99, p. 555).

Third (p. 556, § 1), that the tritubercular, triconodont and protodont stages are secondary simplifications of the plexodont stage.

Fourth, that the plexodont type is the starting point of *all the post canine cheek teeth* including the premolars. (The teeth of Monotremes, Edentates, Cetaceans are supposed to have been independently derived from the haplodont type.)

The 'plexodont' type of Ameghino as illustrated in *Proteodidelphys* (Fig. 202) is identical with the six-cusped 'tuberculo-sectorial' type of Cope: briefly stated, therefore, the plexodont theory is that this type, instead of being an intermediate stage, as in the Cope-Osborn theory, is a primordial stage from which, on the one hand, the tritubercular, triconodont and protodont types have been derived by *retrogressive* simplification or loss of cusps, and, on the other hand, the higher omnivorous (bunodont) and herbivorous (hypselodont) stages have been derived by progressive modification of the relative size of the different parts without the addition of new cusps (p. 565, *op. cit.*). In the 1899 paper Dr. Ameghino demonstrates this unity of type in all the South American mammals, namely the Marsupialia, Toxodontia, Litopterna, Primates, etc.

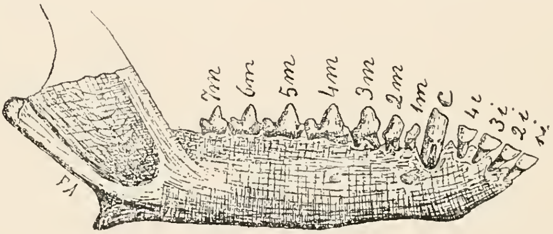


FIG. 202. Lower jaw and teeth of *Proteodidelphys præcursor*, a small Polyprotodont Marsupial from the Chubut Formation. (?Upper Cretaceous) of Patagonia. × $\frac{4}{1}$. The true molars ("5m," "6m," "7m") are in a very primitive stage of the tuberculo-sectorial modification. After Ameghino.

We give below several of this author's ingenious arguments (*op. cit.* 1896).

P. 19. Teeth with a single root (*e.g.* incisors) and simple crown are primitive. Molars with two, three or four roots *generally* represent the fusion of two, three or four teeth. But roots may coalesce as well as crowns, so that the number of original teeth may be greater in many cases than that of the roots. Coalesced roots often retain an external groove at the line of juncture, and distinct nutrient canals, one for each component (*e.g.* ox teeth). Superior molars of man, ruminants, horses and other Ungulates, represent the fusion of four simple primitive teeth.

Thus Ameghino seems to exclude as improbable any secondary division of roots. He also regards such specialized forms as Cetaceans and Edentates as primitive in their teeth.

P. 20. Probably in all superior molars which are quadrangular, but with three roots, the internal root represents a fusion of two roots. Continuation of this process may result in a single root. Two rooted canines = 2 fused teeth, in normal canines the coalescence has extended to the roots. [Dr. Ameghino does not bring forward any direct evidence to *prove* the alleged coalescence.]

P. 29. "We have shown (*Filogenia*, pp. 88 to 112) that after the fusion which produced the plexodont teeth [quadrangular, quadri-tubercular, quadriradiculate] they soon became either still further complicated by the formation of new tubercles, or more simply by the gradual atrophy of the cuspids, tubercles, etc. We have always particularly emphasized these changes, for . . . having examined an enormous number of teeth in almost all groups of mammals, we are convinced of the great facility with which these organs change in form, by the addition or suppression of cuspids, tubercles, enamel folds, creux rentrants valleys, etc., of the crown.

"We do not share in the opinion that multituberculate molars must be the result of the fusion of as many simple teeth as there are cuspids on their crowns; the number of fused teeth could only be four or five at most for each tooth. The presence of this kind of molars in the Trias supports the theory of fusion, because if these teeth were the result of gradual complication not only would it be necessary to push back the origin of the mammals to an excessively distant epoch, but also we ought to find in pre-Triassic beds numerous forms intermediate between the conic and the multicuspidate. However, as we do not find any such forms, we are brought to the belief that plexodont teeth are established by a rapid process such as fusion would be." (Translation.) [Another equally rapid process would be the direct modelling up of a cylindrical or conic crown into a basin-shaped crown with cuspidate edges.]

P. 25. "It is incontestable that the triangular type dominates in the ancient epochs, but this is quite natural since being a modification of the quadrangular type it should of necessity be more abundant: in consequence of the principle formulated elsewhere 'that modified or collateral forms should always be infinitely more numerous than the main stem from which lateral branches spring.'" (Translation.)

In support of the simplification hypothesis as applied to the premolars, the author endeavours to show (*op. cit.*, 1899):

(1) The *true molars* of all these orders can be reduced to this type (pp. 558-565).

(2) The so-called premolars of *Proteodidelphys* (pp. 556, 557) are more complex than those of its descendants, *Eodidelphys, Microbiotherium, Didelphys.* [To the present author the premolars of *Proteodidelphys* seem *less* complex and *more* primitive than those of *Didelphys.*] When complex lower premolars do occur in different orders they are to be interpreted as reversions to the ancestral plexodont type (p. 566, § 2).

(3) The less complex condition of lower premolars generally is secondary (p. 568), due to the want of space for the complete development of these teeth, which resulted from a fore-and-aft shortening of the whole tooth row: for (*a*) modern placental cheek teeth represent two series (p. 569), that is, the first series = true molars + milk molars, the second series = replacing teeth or premolars; (*b*) formerly (p. 569) (in South American forms) the first series was all in use at one time and *exhibited the same form from one end of the series to the other;* (*c*) on account of the gradual intercalation of the two series the space left free for the incoming premolars was shortened and that for the milk molars was increased so that the premolars progressively simplified and the milk molars became more complicated. Similar reasoning applies to the upper premolars (p. 569, footnote).

He concludes (p. 571): "The clear result of all these facts is that the famous theory of the gradual complication, of triconodonty and trituberculy, is an untenable hypothesis. Nowhere do we meet with the stages leading from haplodonty to plexodonty; all those which have been mentioned are, on the contrary, as I believe I have demonstrated, but the result of simplification of molars which were formerly more complicated."

In answer to these ingenious arguments for the simplification theory may be adduced the facts newly stated in Chapter VII., pp. 100-192.

2. Objections by Fleischmann and Mahn answered by Scott.

In 1891 A. Fleischmann[1] and R. Mahn[2] rejected both the nomenclature and the homologies of Trituberculy for reasons which were discussed in great detail and apparently shown to be insufficient, by Prof. W. B. Scott in 1892.[3]

---

[1] "Die Grundform der Backzähne bei Säugethieren," *Sitzungsberichte d. kön. preuss. Akad. d. Wiss. zu Berlin*, 1891, p. 891.

[2] "Bau und Entwicklung d. Molaren bei Mus und Arvicola," *Morphol. Jahrb.*, Bd. XVI., p. 652.

[3] "The Evolution of the Premolar Teeth in the Mammals," *Proc. Acad. Nat. Sci. Phila.*, 1892, pp. 409-412.

3. The Primitive Polybuny Theory.

In a very interesting and exhaustive paper, *On Some Miocene Squirrels, with Remarks on the Dentition and Classification of the Sciurinæ* (p. 179), Dr. C. J. Forsyth Major, after a very careful consideration of the simpler dental types in Rodents, concludes (pp. 196-215) with a full discussion entitled "On the Primitive Type of Sciurine Molar and of the Eutherian Molar in General."

"Trituberculism," he observes, "or, as we rather ought to call it, the reptilian-cone theory, is no more a theory, but has become a dogma. I am a heretic, and may say that I opposed the theory already in 1873, viz. before it was invented;[1] since that time I have kept silent for various reasons. . . . It would appear that the Allotheria, the Multituberculata (p. 202), ought to have been a stumbling-block for the theory. But this is not the case; they have been simply pushed aside on account of being an aberrant order. Nevertheless, I shall refer to them later on. . . . The adherents of trituberculism assert that they have proved the Mammalian molar to be traced back to a more and more simple form. I have tried to show that they have failed to do so, and in my turn assert that the molar of Placentalia can be traced to a polybunous form, and that the real tritubercular pattern is a more specialized secondary stage. So that, as a matter of course, the cardinal point to be established is to show, that the more complex forms, which in the Lower Eocene as well as in the recent period are found side by side with the simpler forms, trituberculate or otherwise, are indeed the primitive, the more generalized type."

This point is supported by a detailed argument, of which we can present merely a brief summary. The starting point is that (1) brachyodont teeth are more primitive than rootless or hypselodont teeth; (2) that the more brachyodont a molar is the more polybunous it is. The latter statement is illustrated by comparison of Eocene and recent squirrels, in which the author observes that the most brachyodont molars exhibit flat, elongate crowns covered with small cusps which tend toward a longitudinal arrangement. An example of this (Type 1) is *Sciurus indicus*. Type 2, *Sciurus vulgaris*, which he believes represents a less brachyodont successive stage, shows four more or less transverse ridges with three intervening valleys. Type 3, *Xerus getulus*, a sub-hypsodont squirrel, exhibits a more distinctly lophodont or crested crown, approaching that of the more specialized Rodents. Again (p. 213), among the New Guinea mice (*Chiruromys*), we find multicuspidate teeth "of a

---

[1] Forsyth Major, "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz. Nebst Beiträgen zu einer vergleichenden Odontographie von Ungulaten und Unguiculaten," 1873, *Palæontographica*, XXII.

very generalized type, precisely such as we anticipate to meet with in a refuge for old and little modified forms."

The first conclusion drawn is that in the most brachyodont Sciurine molars the crowns are quadrate, and the cusps tend toward longitudinal arrangement with two entire outer and inner 'marginal series' of cusps in the lower molars, and with two 'marginal' and a more or less complete 'intermediate series' in the upper molars. From this it is inferred (p. 205) that the multicuspidate or polybunous condition is the most primitive, and that the triangular or tritubercular condition represents an extreme of specialization.

Analogous arguments are applied by this author to other mammals. The polybunous molar of *Ælurus* is regarded as one of the most primitive among the Carnivora, the polybunous *Arctocyon* is regarded as the most primitive among the Creodonts. By similar reasoning we should consider the polybunous tuberculate molars of the bear and of the orang as respectively more primitive than the high pointedly cusped molars of the typical Viverrines (cf. Fig. 102), or of the lower Primates (see pp. 158-160). The author concedes (p. 185), that in certain bats (see p. 129), and in *Cheiromys* the basin-shaped molar is retrogressive on account of the secondary assumption of fruit-eating habits; but regards (p. 213) the basin-shaped polybunous molar of *Microlestes* as primitive and ancestral both to the multituberculate and trituberculate types.

By similar reasoning he finally reaches the conclusion that in the primitive molars of placentals the cusps were arranged in longitudinal rows, three rows with two intermediate grooves in the upper teeth, and two rows with one intermediate groove in the lower teeth; in other words, that the ancestral type of Eutherian molar was multituberculate.

Dr. A. Smith Woodward (*Vert. Pal.*, p. 269) feels the force of this argument as well as that of the embryologists, and concludes. "Hence this—at first sight—brilliant generalization [of primitive trituberculy] can only be accepted at present as a convenient working hypothesis which remains on its trial."

Mr. E. S. Goodrich[1] in his discussion of the Lower Jurassic mammalia, after enumerating several gaps in the argument for the tritubercular theory, concludes: "The common ancestor of the tritubercular sectorial mammals and of the Multituberculates probably had teeth of an indefinite multituberculate pattern, which gave rise, on the one hand, to elaborate multituberculate teeth, and on the other to the tritubercular sectorial. Thus the development of two longitudinal rows of three cusps would give rise to the type of lower molar common amongst the Multituberculata; the fusion of the two anterior of these cusps or the loss of one would

---

[1] "On the Fossil Mammalia of the Stonesfield Slate," *Quar. Jour. Micr. Sci.*, Vol. XXXV., 1894, pp. 407-432.

yield the tritubercular sectorial tooth common among the Marsupials and Placentals; while the loss of the inner cusps would result in the formation of a triconodont molar. The conclusion reached is, therefore, that the primitive mammalian molar bore a crown with several cusps."

This seems to be a clear statement of the polybuny theory, although the reader must consult the authors themselves for the detailed arguments by which it is supported. According to the author last quoted, not only the tritubercular but the triconodont molar is of multitubercular origin.

4. Summary of Objections to the Polybuny Theory.

Our own contrary view may be advanced with equal show of evidence that even the most primitive Multituberculates known had already passed through previous fewer-cusped or even tritubercular stages (see p. 80). A third and perhaps preferable alternative is that the simple "multituberculate" lower molar of the Triassic *Microlestes* was derived from the triconodont type by the transverse broadening of the base of the tooth and the upgrowth of the internal basal border. Other possible modes of derivation are discussed in pages 103-105.

The general answer to this line of reasoning is that which applies equally to many other generalizations which are founded chiefly upon anatomical and zoölogical comparison, namely: that there is a danger of inverting a series, of placing the most specialized teeth at the bottom of a theoretical scale of evolution, while the most primitive are placed at the top. This criticism certainly can be demonstrated as correct so far as the argument applies to *Arctocyon* (see p. 133) and *Ælurus* (see p. 142), as we feel reasonably certain that the presumed ancestors or oldest representatives of each of these types have elevated and distinct cusps, and in each case the low-crowned, tuberculate condition is secondary. Among the Rodents we have, it is true, not yet traced the phyletic succession as fully as in other series, but we have strong grounds for considering trituberculate upper molars such as those of *Plesiarctomys* as the most primitive (see pp. 145-151).

The chief difficulties in the 'polybuny theory' may be summarized as follows: (1) The examples cited as primitive are tubercular low-cusped crushing teeth; all zoölogical and palæontological evidence goes to show that such crowns are secondary as compared with more pointedly cusped, piercing-cutting-crushing teeth such as those seen in Polyprotodont Marsupials (p. 109), Insectivores (p. 117), Creodonts (p. 132). (2) Palæontology offers strong negative evidence against it, for *Microlestes* very probably[1] leads up through *Plagiaulax* and *Ctenacodon* into the

---

[1] Osborn, H. F., "Structure and Classification of the Mesozoic Mammals," *Jour. Acad. Nat. Sci.*, Phila., 1888, pp. 214-216.

later Multituberculates which are the only known group of polybunous mammals in the Mesozoic period, and all of these have sharply defined and modeled cusps, elongate crowns, parallel grinding series, enlarged chisel like incisors, correlated with chiefly horizontal jaw motions and gnawing habits—conditions far too specialized to have given rise to any of the later fewer-cusped or trituberculate types. (3) Embryological evidence is against the polybuny theory, there being no trace of previous polybuny, but on the contrary quite generally in the true molars a triangular disposition of the cusps first developed. (4) According to the polybuny theory one cusp is as old as another, but if either the 'tritubercular' or the 'embryological' or the 'premolar-analogy' theories be correct one of the cusps is older than the others.

II. That the Cope-Osborn Theory of the Origin of the Superior Molars is Incorrect.

This concerns the *superior molars* only. Strong evidence is brought forward from embryogeny, from the analogy of premolars, from palæontology, that in the superior molars the *protocone* (of Osborn) is not homologous with the primitive or original reptilian cusp of the crown.

In previous pages of this volume we have stated and discussed the evidence against the Cope-Osborn theory of the origin of the upper molars.

Let us now review this evidence.

1. Cusp Homologies founded on Embryogeny.

The most thorough presentation of the development of tooth cusps in its bearings upon the homologies of the upper cusps is that by M. F. Woodward,[1] published in 1896.

In course of this important article he refers to the deficiency of the palæontological evidence among trituberculates, so far as the upper teeth are concerned, to establish the homology of the upper and lower protocones beyond question, concluding: "We consequently have no palæontological evidence to support the assumption that a tritubercular stage is passed through by the mammalian *upper* molar in its evolution from a protodont or possibly a triconodont tooth. . . . If the triconodont tooth be a stage in the evolution of the mammalian molar, then I should believe that the anterior cone disappeared, the main cone becoming enlarged as the paracone and the posterior as the metacone. . . . At this stage the upper teeth overhang and bite out-

---

[1] "Contributions to the Study of Mammalian Dentition, Pt. II., On the Teeth of certain Insectivora," *Proc. Zool. Soc. Lond.*, 1896, pp. 557-594.

side the lower molars, and the future antero-internal cone (protocone) was developed as an internal shelf acting as a mortar for the cusps of the lower teeth and at a much later period developed a cusp. The hypocone arose in a similar way with the elongation of the teeth. . . . In the *Centetidæ* and *Peralestes*, the upper molars could not have overhung the lower ones to the same extent, consequently no internal lobe bearing the protocone was developed and the external cingulum was very largely developed." Thus Woodward's position agrees in the main with the views recently put forward by Gidley on palæontological grounds (p. 219).

The author therefore accepts the tritubercular theory from the Eocene period onwards, but endeavours to establish another theory as to the origin of the superior tritubercular type: he excludes the triconodont and protodont stages, unless we suppose that the anterior cusp disappeared.

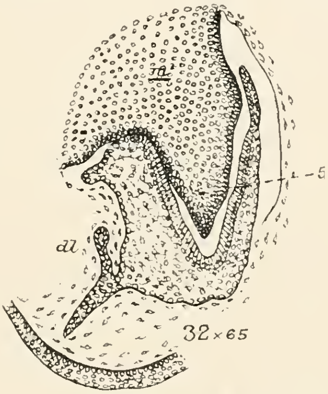


FIG. 203. Transverse section of the germ of the first upper molar of a young Mole (*Talpa*) "showing the primitive dentine germ giving rise to the paracone (5)," the protocone appearing as an internal extension or talon from the base of the paracone, which is hence supposed by Woodward to be the most ancient portion of the crown. The dental lamina *dl* on the lingual side of the developing true molar may represent the vestiges of a post-permanent m^1. $\times \frac{65}{1}$. After M. F. Woodward.

As regards embryological testimony, he first refers to the papers of Röse on the human teeth, Taeker on the teeth of Ungulates, and Leche on the teeth of Marsupials, as concurring in the demonstration that *the paracone* (of Osborn) *is the first cusp to develop in the upper molar teeth.* He continues (*op cit.*, p. 585) from his own researches upon the relatively primitive Insectivora, "If the protocone represents the summit of the original protodont tooth of the ancestor of the Mammalia it must be the direct continuation of the primitive dentinal germ, and as such should be found to develop in a line with the axis of that structure. That this is not the case is well seen in Fig. 32, Pl. XXVI. [Fig. 203], where the paracone is found to be identical with the primitive dentinal germ, and the protocone appears as a mere internal ledge growing out from the base of this structure, the metacone and subsequently the hypocone being similarly derived from a backward extension of the base of the primitive dentinal germ." Incidentally he adds, "I have failed to find any support for the concrescence theory, neither do I consider that any of the evidence put forward by Röse and Kükenthal is at all conclusive in its favor."

Order of Embryonic Cusp-Development, according to Woodward.

GROUP I.	GROUP II.
(4 genera: *Erinaceus*, *Gymnura*, *Sorex*, *Talpa*). With quadri- or quinquetubercular upper molars.	(2 genera: *Centetes*, *Ericulus*). With tritubercular upper molars.
1. Paracone.	1. 'Protocone' (=pa+me. See p. 245).
2. Metacone.	2. 'Paracone' } ? together.
3. Protocone.	3. 'Metacone' }
4. Hypocone.	
(5. Metaconule.)	
1. Protoconid.	1. Protoconid.
2. Metaconid.	2 or 3. Paraconid } ? together.
3. Heel { Entoconid. Hypoconid.	3 or 2. Metaconid }
4. Paraconid.	4. Hypoconid.

As regards the adult structure of the teeth and the embryonic order of development of the molar cusps, Woodward divides the Insectivora into two groups, as above.

GROUP I. *Quadritubercular Molars.* The first of the quadritubercular types investigated is the Malayan *Gymnura*, the adult molar teeth of which, according to Woodward, "resemble those of the hedgehog (*Erinaceus*) in pattern:[1] like that genus, they exhibit five cusps which are strongly developed, and in the upper jaw there is a well-marked cingulum, with a small anterior and posterior cusp present in addition: in the lower jaw the paraconid is less developed than in *Erinaceus*." In the developing fœtus (p. 567) the second superior molar "was less developed, and here the para- and metacones were the most strongly developed, while the protocone was present in the form of a large *antero-internal shelf* [italics ours], but hardly as yet developed into a distinct cusp, though the hypocone and metaconule had done so." In the Shrews of the genus *Sorex* (*op. cit.*, p. 570) the author also finds in a young stage that the plan of the dental germ is "roughly triangular, the main and only cone being situated at the anterior extremity and slightly nearer the external border." From the position of this cone, and from a comparison of the

---

[1] [With the important exception at least in some specimens (Fig. 65, p. 118) that the hypocone is less developed, and the whole tooth strongly suggests that of the tritubercular to quadritubercular Eocene genus *Leptictis* (Figs. 66, 67).—ED.]

cusp ontogeny as seen in the molar of the *Talpa*, with which it is identical in pattern, I think one may conclude that *this single cusp is the paracone* [italics ours], the posterior extension representing the metacone, while the internal shelf indicates the position of the future proto- and hypocone." In the moles (genus *Talpa*, p. 579) the adult upper molars are "mainly tritubercular, but a very small hypocone is present: the protocone is small, whereas the paracone and metacone, especially the latter, are very large, and show a tendency to become crescentic or V-shaped, . . ." Even in the earliest fœtal stages examined two slight prominences were already visible, corresponding to the para- and metacones: these cusps were alone conspicuous in the younger stages, the antero-external or paracone being the largest, though in the adult Mole this is a smaller cusp than the metacone.

This, the author thinks, shows that the paracone is the first to develop; "*the internal protocone appears late, as a low and inward extension of the base of the paracone* [Fig. 203], *and cannot possibly be regarded as the original axis of the tooth.*"

The embryogenic succession of the upper and lower cusps is as follows:

Upper Molars.	Lower Molars.
1. Paracone.	1. Protoconid.
2. Metacone.	2. Metaconid.
3. Protocone.	3. Hypoconid.
4. Parastyle.	4. Entoconid.
5. Hypocone.	5. Paraconid.

In all these three genera the order of cusp development in the *lower molars* corresponds substantially with that given by the palæontological theory.

Thus Woodward confirms Röse and Taeker's results, and says (p. 584) that "the order of cusp ontogeny is in entire accord with the supposed order of cusp phylogeny as advanced by the supporters of the Cope-Osborn tritubercular theory."

Group II. *Tritubercular Molars.* The most important form examined by Woodward is the Tenrec of Madagascar, the genus *Centetes.* In the adult the molars have usually been regarded as of columnar and typical tritubereulate type, consisting of an elevated internal cusp (protocone) and more depressed external cusps (para- and meta-cone): as we shall see, Woodward interprets the homologies of these cusps in an entirely different manner. He observes (p. 573), in fœtal development, that the first superior molar is composed of a prominent main cone slightly inclined inwards, this is undoubtedly the cusp determined as protocone of the adult tooth, according to the Cope-Osborn theory, while growing outwards low down from this main dental germ are two smaller ones, a slightly more pronounced anterior cone and a less developed postero-external cone, corresponding respectively to the para- and meta-cone as homologized by Cope and Osborn. The embryogenic sequence is as follows:

1. Protocone.	1. Protoconid.
2. Paracone.	2. Metaconid.
3. Metacone.	3. Paraconid.
	4. Hypoconid.

Similarly in the young jaws of *Ericulus* (*op. cit.*, p. 574) Woodward finds that in the fœtal first superior molar the protocone (as homologized by Cope and Osborn) "forms the main mass of the tooth, while the para- and meta-cones (as homologized by Cope and Osborn) form two rounded external shelves, not at present conical"; in the second superior molar "the protocone and the small antero-external paracone are alone visible."

Summary of Woodward's Conclusions.

Woodward (1) entirely confirms the conclusions of previous authors that in the lower teeth the evidence of embryology and palæontology is identical. (2) In (I.) the quadrituberculate Insectivora he strongly reinforces the previous testimony of Röse, Kükenthal, Leche and Taeker, namely, that the paracone develops first and the protocone is a secondary shelf. (3) In (II.) the trituberculate Insectivora, on the contrary, he brings forward facts which seem to support the palæontological theory and homologies; it is in these animals, according to the Cope-Osborn theory, that the protocone is still the highest and chief cusp of the crown and thus should appear first in ontogeny, while in the quadritubercular types the protocone being more depressed and the para- and meta-cone being more elevated, the earlier appearance of the latter might be interpreted as due to adaptive acceleration or cœnogenesis. In his discussion of these facts, however, Woodward does not admit this interpretation of adaptive acceleration or cœnogenesis, but maintains that the Cope-Osborn homologies are incorrect, and that the main internal cusp in the *trituberculate group* is homologous with the antero-external cusp in the quadrituberculate group, as shown in the accompanying diagram (Fig. 204). More in detail, he observes: "With regard to the tritubercular upper molars of the *Centetidæ*, I should conclude that the main cone of this type of tooth, usually termed the protocone, was really the paracone: the whole tooth representing only the antero-external triangle of such a form as *Talpa*, *i.e.* the crescentic paracone with its two external cingulum cusps, the last named being commonly but incorrectly described as para- and meta-cone in *Centetes*: that in the *Centetidæ* no marked indications of the protocone or metacone are as yet visible, while in *Chrysochloris* (Fig. 36-7) the first indication of the protocone has appeared, viz., the internal shelf."

Thus he concludes as to homologies that the reptilian cone of the upper cheek teeth of the ancestral mammal is homologous with the protocone of the premolars, with the paracone of most molars, and with the falsely called protocone of the molars of trituberculate Insectivores and of the Jurassic genus *Peralestes* (Fig. 204). Stated in another way his conclusions are that, (1) *the antero-external cone, or paracone above and protoconid below, is the reptilian cone both in the molars and premolars,* a conclusion supported by the Danish observer Winge:[1] (2) the falsely called protocone of the upper molars is borne on an internal ledge or extension of the base of the crown of secondary origin: (3) the metacone is a similar backward development of the paracone which rises very early in ontogeny long before the protocone: (4) the evidence advanced in support of the tritubercular theory is insufficient to prove that the upper molars primarily evolved on the lines of that theory; (5) owing to want of material trituberculists have been led to assume that the upper molars of the early mammalia passed through similar stages to those which they have determined for the lower teeth, and consequently they have in most cases incorrectly identified the primary cone; (6) that as regards the actual primary cone (paracone above, protoconid below), its ontogeny recapitulates its phylogeny.

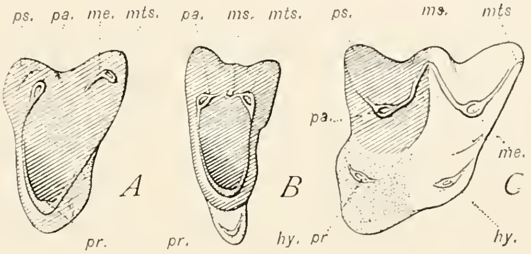


FIG. 204. Shading illustrates Woodward's hypothesis of the homological relations of the tritubercular, zalambdodont molar types of *Centetes* (*A*) and *Chrysochloris* (*B*) to the sexitubercular dilambdodont molars of *Talpa* (*C*). The whole of the *Centetes* molar is supposed to correspond to the anterior outer portion of the *Talpa* molar, while the "hypocone" of the *Chrysochloris* molar is homologized with the antero-internal portion of the crown of *Talpa*. The posterior half of the *Talpa* molar is supposed to be a neomorph or secondary upgrowth of the posterior side of the tooth. But according to Gidley's interpretation the single V in *Centetes* and *Chrysochloris* is secondary and represents the fusion of the two V's (*pa*, *me*) seen in *Talpa*.

The abbreviations are incorrect. For true interpretation see p. 225, Addendum.

Ontogenetic Order according to Marett Tims.

Dr. F. W. Marett Tims[2] has reached partly identical conclusions chiefly from the embryology of the teeth of the dog, namely, that the cheek teeth of the dog are composed of

(1) A Primary Cone = paracone of *ms*, protocone of *pms* = protoconid of lower *ms* and *pms*.

---

[1] "Om Pattedyrenes Tandskifte isaer med Hensyn til Taendernes Former." *Vidensk. Meddel. fra den Naturh. Foren. i. Kjobenhavn*, 1882, p. 15.

[2] "On the Tooth-genesis of the Canidæ," *Jour. Linn. Soc.*, Vol. XXV., *Zool.*, No. 164, 1896, pp. 445-480.

(2) A Secondary Cone = metacone of *ms*, tritocone of *pms* = hypoconid of lower *ms* and *pms*.

(3) Three cingulum cusps

(*a*) anterior = deuterocone, minute in all except lower sectorial where it = the paraconid.

(*b*) posterior = shear (metastyle) of sectorial.

(*c*) centro-internal = protocone of dpm^4 = heel (internal cingulum of m^1) = metaconid of lower teeth.

This theory agrees with the "premolar analogy" theory and with the theory of Gidley in identifying the paracone of the molars, the protocone of the premolars, and the protoconid of the lower premolars and molars as the primary cusp.

Summary of Objections to the Embryological Theory.

In reply to this strong presentation of the facts of embryogeny the following points may be made: 1. It is possible that the superior tritubercular molar arises independently of previous protodont and triconodont stages; but the evidence afforded by the lower molar teeth of *Spalacotherium*, which are incipiently tritubercular, tends to connect these stages (Figs. 11, 12, and p. 32 *b*). 2. We do not positively know the structure of the upper molars in *Spalacotherium*; but the presumption that they were somewhat similar to the lower molars is strongly supported by the fact that in the closely related genus *Triconodon* the upper molars are exactly similar.* 3. The *supposed* upper molars of *Spalacotherium*, named *Peralestes* by Owen, although of somewhat irregular form, present a pattern reversing that in the lower molars of *Spalacotherium*, namely, with a large internal cusp, with a closely connected antero-external crest surmounted by a cuspule, and with a freer and more detached postero-external cone. Figure 12 in Chapter I., not heretofore published, was directly taken from camera-lucida outlines of the upper molars of *Peralestes* shaded with pencil. It shows that the earlier figures of Osborn and Woodward were only partially correct, and it tends to demonstrate, apparently beyond a doubt, the existence of a large, prominent *internal* protocone, and of an antero-external paracone shelf as originally homologized by Osborn, a postero-external conical metacone, and an external cingulum embracing the outer side of the crown at the base corresponding with the internal cingulum of the lower molars of *Spalacotherium*.† 4. The comparison of a series of zalambdodont (tritubercular) and dilambdodont (quadri-

---

* [The presumed relationship between *Triconodon* and *Spalacotherium* is denied by some authors.—Ed.]

† [The supposed "protocone" of *Peralestes* might possibly be homologous with the paracone of later mammals.—Ed.]

to sexti-tubercular) Insectivora favors the view that the high internal cusp (protocone) in the former is homologous with the low antero-internal cusp of the latter (Figs. 64-80).* 5. Since all the orders in which the paracone appears first (Dilambdodont Insectivores, Carnivores, Primates, Perissodactyls and other Ungulates) are derived from Eocene forms in which the inner side of the crown is depressed, there has been *plenty of time* for embryogeny to have become adapted to this condition and for the main axis of the developing tooth germ to have become shifted to the outer side (p. 54). 6. The high protocone of trituberculate Insectivores and the depressed ledge-like protocone of quadrituberculate Insectivores alike fit into the talonid of the lower molars, and thus both function like the protocone of mammals in general (Gregory).†

The Cope-Osborn theory, however, has to meet three further sets of objections:

First, those derived from the *comparison of the premolars and molars* clearly set forth by Wortman (see pp. 195, 142, 216).

Second, those derived from a restudy of the teeth of Jurassic mammals themselves, developed by J. W. Gidley (p. 219).

Third, further comparison of the teeth of Insectivores, Chiroptera, and other orders, developed by Gidley (see p. 124).

2. The Premolar Analogy Theory.

The theory that *the superior molars originally acquired trituberculy in a manner similar to that which can be traced in the premolar metamorphosis* has been designated in the introduction as the 'premolar analogy theory' (pp. 6, 7).

Premolar evolution, as the key to molar evolution, was suggested in 1880 by Huxley, in the following passage:[1] "The exact correspondence in plan of these teeth [of *Otocyon*] is the more interesting, since, in *Centetes*, it is easy to trace the successive changes by which the simple and primitive character of the Mammalian cheek-tooth exhibited by the most anterior præmolar passes into the complex structure of the crowns of the posterior teeth" (Huxley, *Collected Papers*, Vol. IV., p. 450).

It was also advocated by Schlosser,[2] but upon different grounds, namely: that in primitive jaws the upper overhangs the lower, and the upper teeth fit not simply between but also slightly outside of the lower ones; accordingly it is more probable that the true protocone must be

---

[1] "Review of the Cranial and Dental Characters of the Canidæ," *Collected Memoirs*, Vol. IV., p. 450.

[2] "Die Entwickelung der verschiedenen Säugethierzahnformen im Laufe der geologischen Perioden," *Sonder-Abdr. aus den Verh. d. odontolog. Gesellsch.*, Bd. 3, Heft 2 u. 3, 1891. p. 9.

*[But see pp. 126, 225 Addendum.—Ed.]

†[Erroneous. See p. 225.—Ed.]

sought in one of the outer cusps, as it is in the premolars, which, indeed, begin their complication on the inner side. In so far as this observation applies to the Creodonta, Condylarthra, Ungulata, there is indeed much force in it.

Scott has also expressed the belief that premolar and molar cusps are in the main serially homologous; in other words, that the molars originally evolved as the premolars did subsequently.

More recently Wortman[1] supports the premolar analogy theory on palæontological grounds, and advises the total abandonment of the theory of trituberculy, asserting emphatically that the cusps in the molars were added in exactly the same manner and in precisely the same order as in the premolars (Fig. 205).

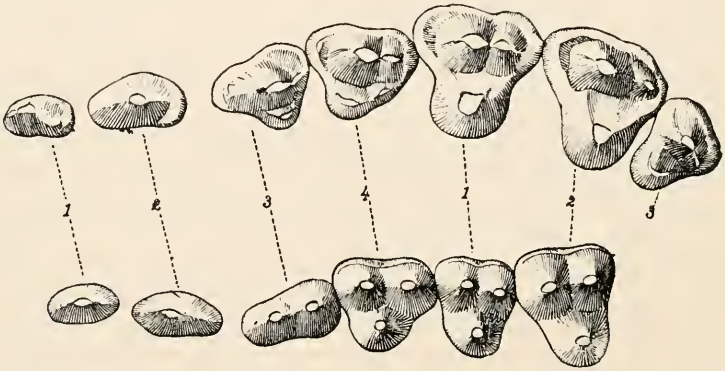


FIG. 205. *Upper figure*, Upper cheek teeth of *Dissacus saurognathus* from the Torrejon Formation, Stage II, Basal Eocene. *Lower figure*, Upper cheek teeth of *Mesonyx obtusidens* from the Bridger Formation, Middle Eocene. Dr. Wortman regards the *Dissacus* teeth as representing the ancestral pattern of the *Mesonyx* teeth and believes the internal cusp or "protocone" of the molars to be a secondary upgrowth of the basal cingulum like the corresponding cusps of the premolars.[2] After Wortman.

The two great facts which apparently support this theory are: first, that we can actually follow the premolars passing by cusp addition from the haplodont into the sexitubercular condition exactly like the molars; second, that according to the Cope-Osborn theory the protocones or reptilian cones are on the *outer* side of the upper premolars and on the *inner* side of the upper molars, certainly an anatomical paradox which has never yet been explained away; third, when it is further considered that embryogeny or ontogeny supports this inference, that in the embryos of the majority of mammals the antero-external cusp (Osborn's paracone) of the true upper molars is the first to develop, do we not secure a concurrence of testimony which seems irresistible?

---

[1] ["Origin of the Tritubercular Molar,"] *Amer. Jour. Sci.*, Vol. XIII., Jan. 1902, pp. 94-95; Vol. XVI., Nov 1903, pp. 365-368.

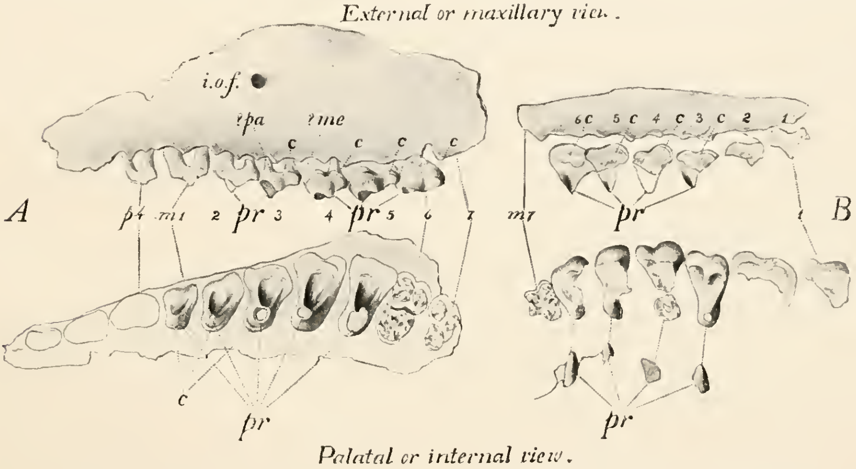
[2] [Dr. Matthew's recent investigations on the Mesonychidæ do not substantiate the supposed facts on which this argument is based.—ED.]

Osborn (1904) *presents New Palæontological Difficulties in the Premolar Analogy Theory.*

The crucial test of the premolar analogy theory is the homology of the protocone of the superior molar.

If the protocone is the antero-external cusp in the upper premolars and the antero-internal cusp in the upper molars, the premolar analogy theory falls to the ground, and the Cope-Osborn theory remains thoroughly substantiated. From Osborn's latest contribution (1904) to the tritubercular theory[1] we make the following abstract:

In addition to the evidence afforded by the upper teeth of *Triconodon*, in which the main cone is central, and that seen in the upper teeth of *Peralestes* (in the British Museum), in which the main cone is internal (Fig. 12), and the upper teeth of *Kurtodon* (British Museum), in which the main cone is internal (Fig. 13), the original theory was supported by Professor Marsh's statement that in the upper molars of *Dryolestes* (Yale Museum) the main cone was internal; in each case the main cone is believed to be the protocone or reptilian cone.


External or maxillary view.

Palatal or internal view.

FIG. 206. Superior molars of *Dryolestes* Marsh. Upper Jurassic, Wyoming. *A*. Series of the left side, external and crown views. *B*. Series of the right side, external, crown and internal views. Yale Museum. *c*, *c*, *c*, external and internal cingula. *i. o. f.* infraorbital foramen. Other abbreviations as in Fig. 12. (Cf. Fig. 207 (2) and p. 220.)

The two specimens here referred to in the Yale Museum exhibit perfectly the structure of both crowns and fangs, of seven superior molar teeth, bringing out the following important points (Fig. 206):

(1) The molars are sharply distinguished from the premolars, which are bifanged teeth with simple, laterally compressed crowns.

---

[1] Osborn, H. F., "Palæontological Evidence for the Original Tritubercular Theory," *Amer. Jour. Sci.*, Vol. XVII., Apr. 1904. pp. 321-323.

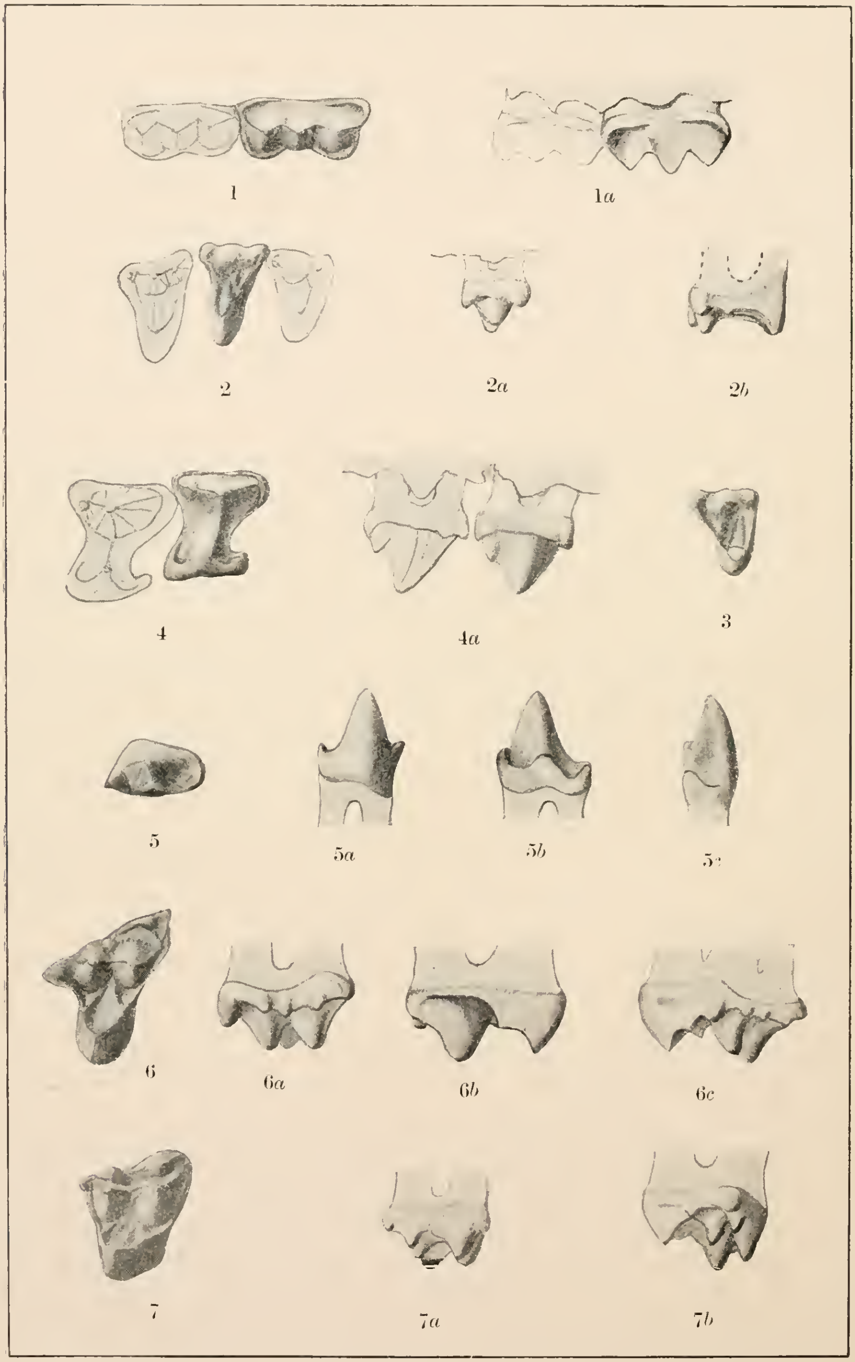


Figure 207.

(2) The molar crowns are broadly transverse or triangular, and upon the *internal* side of each is a large, conical, pointed cusp, *pr*, supported by a large stout fang, Fig. 206 A, *m6*, *m7*; around the inner side of each of these cusps is a delicate cingulum, Fig. 206 A, *c*.

(3) The *external* portion of the broadly triangular crown is supported on two smaller fangs, Fig. 206 A, *m6*, *m7*.

(4) The external portion of the crown is depressed, and bears one large antero-external cusp *? pa* and one smaller postero-external cusp *? me* which is either partly worn away or less pronounced in development.

(5) Outside of this external wall there is also a faint basal cingulum, *c*, *c*, *c*.

(6) Connecting these low external cusps with the elevated internal cusp are two transverse ridges; the anterior transverse ridge is higher and stronger than the posterior.

This palæontological evidence appears to lend no support to the evidence of embryogeny that the paracone (*pa*) or antero-external cusp is the oldest cusp. On the contrary, it appears to prove that the pointed, conical, internally placed cusp supported upon a single stout fang is the main cusp or protocone, serially homologous with the main cusp of the simple preceding premolar teeth.

Gidley's Restudy (1906) *of Jurassic Mammals Supports Embryogeny and the Premolar Analogy Theory.*

It will be seen that *embryogeny* and *premolar analogy* concur in evidence that the reptilian cone is represented in the *antero-external* cusps of the superior molars. Mr. J. W. Gidley[1] now brings *palæontology* to the support of this position.

His conclusions are based on a fresh study of *unworn* superior molars of Jurassic mammals in the U.S. National Museum, which were not accessible to Osborn. These teeth are represented in Fig. 207, which may be compared with the worn teeth of Fig. 206.

FIGURE 207. FROM GIDLEY.

Nos. 1 and 1*a*. *Triconodon? bisulcus* Marsh (Atlantosaurus beds), left upper molars, m^2 and m^3; crown and external views. Six times natural size (No. 2698, U.S.N.M.).

2, 2*a*, and 2*b*. *Dryolestes* sp. (Atlantosaurus beds), left upper molars; crown, external, and posterior views. Seven times natural size (No. 2845, U.S.N.M.).

3. *Dryolestes*, first right upper molar, m^1; crown view. Eight times natural size (No. 2839, U.S.N.M.).

4 and 4*a*. *Dicrocynodon* sp. (Atlantosaurus beds), left upper molars; crown and external views. Six times natural size (No. 2715, U.S.N.M.).

5, 5*a*, 5*b*, and 5*c*. *Paurodon* sp. (Atlantosaurus beds), right lower molar, m_2; crown, external, internal, and posterior views. Eight times natural size (No. 2733, U.S.N.M.).

6, 6*a*, 6*b*, and 6*c*. *? Pediomys* sp. (Laramie beds), left upper molar; crown, external, posterior, and anterior views. Eight times natural size (No. 5062, U.S.N.M.).

7, 7*a*, and 7*b*. Gen. et. sp. indt. (Laramie beds), left upper molar; crown, external, and anterior views. Eight times natural size (No. 5076, U.S.N.M.).

---

[1] Gidley, J. W., "Evidence bearing on Tooth-Cusp Development," *Proc. Washington Acad. Sci.*, Vol. VIII., 1906, p. 106.

Referring to Osborn's figures of *Dryolestes* (Fig. 206), Gidley * says: "But there are two important cusps not noted by Osborn, one an external cusp placed anterior to the main external cusp, the other a small but well-defined intermediate cusp appearing on the posterior transverse ridge. Thus there are five distinct cusps instead of three, as stated by Osborn, and these do not form a trigon in the sense that this term has been used, for the main external cusp is in the middle of the base of the triangle instead of forming one of its angles.

"Considering the outer portion of the *Dryolestes* molar as homologous to the three cones and two fangs of *Triconodon*, the derivation of this type of tooth is much simplified, it being not so far removed from the primitive reptilian condition, and though diverging on different lines, is no more specialized, as a whole, than the *Triconodon* type of tooth, the differentiation being carried on more rapidly in the latter in the special development of the anterior and posterior lateral cones and their accessory cusps, while in *Dryolestes* the specialization has apparently been centralized in the development of the high, narrow, heel-like cusp and its supporting fang on the inner side of the molar.

"This view is strongly supported by the evidence obtained from still another characteristic Atlantosaurus-beds type of molar represented by *Dicrocynodon*. In this form, Pl. V,† fig. 4, the same primitive arrangement of three cusps and two fangs is preserved in the outer portion of the tooth, while on the internal side a large secondary cusp has been developed differing widely in character from that of *Dryolestes*. This cusp is a laterally compressed cone supported by *two* rudimentary fangs and is joined to the outer portion of the tooth by a high, wedge-shaped ridge. The base of the inner cone is greatly expanded antero-posteriorly, curving gently outward toward the external portion of the tooth. Thus the crown, as a whole, is greatly constricted medially with the inner and outer portions superficially resembling each other.

"From these observations two important conclusions may be drawn: First, that, leaving out of consideration the multituberculates, there are among the mammals of the Atlantosaurus beds at least three distinct forms of upper molars representing three primitive types of about equal specialization apparently leading off in entirely independent lines. Probably only one of these, *Dryolestes*, represents an ancestral type from which the Upper Cretaceous and later forms possessing trigonodont molars may have been derived. Second, that the evidence

---

* "Evidence bearing on Tooth-Cusp Development," *Proc. Washington Acad. Sci.*, Vol. VIII., 1906, p. 96.

† [Fig. 207.]

derived from the Atlantosaurus-beds mammals entirely supports the evidence of embryology and agrees in general with the 'pre-molar analogy' theory. Thus, the evidence from all sources points overwhelmingly to the conclusion that the primary cone is to be found on the *outer* side in the upper molars of primitive trituberculate forms

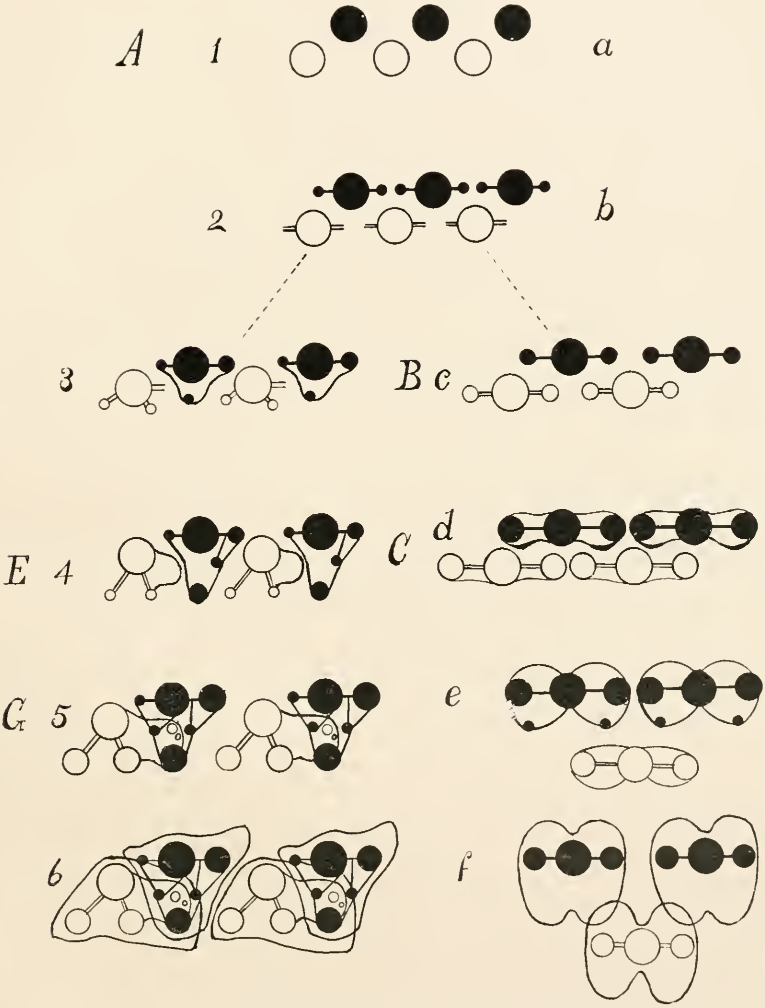


Fig. 208. [Gidley's] *Suggested Phyletic History of Two Types of Complex Molars.* [As in Osborn's diagram [see Fig. 41, p. 61], the solid black dots represent the cusps of the upper molars, the circles, those of the lower molars.] 1 to 6, Phyletic history of the "Tritubercular" type; *a* to *d*, Phyletic history of the "Triconodont" type; *e*, *f*, From the brachyodont Triconodont stage to the bilobed hypsodont type of molar.

A, *B*, *C*, *E*, and *G* compare with *A*, *B*, *C*, *E*, and *G* in Osborn's diagram [see Fig. 41, p. 61]; 4, *Dryolestes* type, Atlantosaurus beds (? Upper Jurassic); 5 and 6, *Protolambda* or *Pediomys* type, Laramie beds (Upper Cretaceous); *d*, *Triconodon* type, Atlantosaurus beds (? Upper Jurassic); *f*, *Palæolagus* type, White River beds (Oligocene). From Gidley.

and in all forms derived from a tritubercular type of tooth as well, except where the main inner cone (protocone) has been reduced secondarily. The opposite view held by the tritubercular theory now apparently stands on very insufficient evidence, and the proposition that the protocone, of Osborn, represents the primary cusp is entirely without support.

"The lower molars of the Atlantosaurus beds mammals furnish abundant additional evidence along the line of conclusions regarding the shifting of three cusps from a straight line to form the primitive triangle. In such forms as *Dryolestes* and *Paurodon* we have tritubercculate molars in the primitive or forming stage, and, what is most significant, the cusps resemble very closely, both in position and relative proportions, those of the premolars of later types in their early stages of transition to the molariform pattern. In the lower molars of *Paurodon* the crown consists of a high, pointed cusp (protoconid), centrally placed, a low posterior heel, a small antero-internal cusp (paraconid), and a very small median internal cusp (metaconid). The last two form the base of the trigonid. In *Dryolestes* both the trigonid and the pimitive heel are somewhat more advanced in development. In still other forms, such as *Menacodon* and *Tinodon,* the two internal cusps are relatively large and the trigonid is fully developed, while the heel, or talonid, is very small or entirely wanting. In all the paraconid and metaconid are entirely on the internal side of the crown, and in these and all the material examined there is not the slightest evidence of any shifting of the cusps, but they seem to have arisen in the positions they now occupy.[1] In *Paurodon* the heel is apparently as much or more developed than either of the internal cusps and seems to have made its appearance even in advance of the metaconid. Also the metaconid is still very rudimentary and is just budding off near the base of the protoconid, but little posterior to its apex and midway of the entire length of the crown, while the place of origin assigned to it by the tritubercular hypothesis is already occupied by the comparatively large heel.

"From these observations it seems apparent that the trigonid of the lower molars is not the reverse of the trigon of the upper molars, as held by advocates of the tritubercular theory, and the homologues of the elements of the upper and lower -molars, as proposed by this theory, are far from being apparent. (This also accords with the conclusions of Winge.)

"The lower molars of *Triconodon* differ from any of the forms just

---

[1] This is in accord with the general conclusions on tooth cusp development reached by Herluf Winge as early as 1882. Vidensk Meddelelser fra den naturhist. Forening i Kjöbenhavn, 1882, p. 18.

described. They are composed of three nearly equal cone-like cusps arranged like those in the upper molars of this genus in an antero-posterior line. There is no cusp corresponding with the metaconid in *Dryolestes.* There is a continuous basal cingulum on the inner face of the crown, and the posterior cusp is in no way homologous, except in position, to the heel in the lower molars of *Paurodon* and *Dryolestes.*

"The mammals from the upper Cretaceous Laramie beds show a great advance in development. The molars of the tritubereulate forms of this horizon have passed into a second well-defined stage of specialization which, though varying greatly in detail in the various types, conforms in general to a distinctive pattern which may readily have been derived from some Atlantosaurus-beds form, such as *Dryolestes.* An upper molar of *Pediomys* Marsh, a typical example of the Laramie tritubercular molar, compared with the corresponding tooth of *Dryolestes,* presents the following differences and indicates the principal lines of progression:

"(1) The main internal cusp (*protocone*) is much broadened antero-posteriorly; (2) a second small V-shaped intermediate cusp (*protoconule*) has been added; (3) the postero-external cusp (*metacone*) has greatly increased, nearly equaling, both in size and importance, the median external, or primary, cone (*paracone*), while the antero-external cusp (*parastyle*) has remained small and undeveloped. A correspondingly progressive development marks the trigonid and heel of the lower molars."

Summary and Conclusions [*Gidley*].

"Summing up the evidence derived from this preliminary study, the following conclusions are suggested:

"1. That the evidence obtained from the Mesozoic mammal teeth furnishes no support to the tritubercular theory in so far as it involves the position of the protocone and the derivation of the trigonodont tooth from the triconodont stage through the shifting of the lateral cones outward in the upper molars and inward in the lower molars.

"2. That it supports entirely the embryological evidence that the primary cone is the main antero-external cusp, or *paracone,* having retained its position on the *outside* in most upper molars (see exceptions above, p. 124).

"3. That it agrees in the main with Huxley's 'premolar analogy' theory, as supported by Scott.

"4. That the molars of the Multituberculates, *Triconodon, Dryolestes,* and *Dicrocynodon,* were apparently derived independently from the simple reptilian cone: hence the supposition follows that the trituberculate type represents but one of several ways in which the complex molars of different groups may have been derived.[1]

"5. That in the forms derived from the tritubereulate type of molar the order of succession of the cusps is not the same in all groups, and apparently homologous elements are sometimes developed from different sources. Hence it follows that *no theory involving an absolute uniformity of succession in the development of complex molars will hold true for all groups of mammals.*

"In the foregoing pages I have restricted the use of Osborn's tooth-cusp nomenclature for the reason that, in this particular discussion, there are some cases in which it is not strictly applicable and might lead to confusion.

"On similar grounds Dr. Wortman[2] has expressed the opinion that all attempts to establish a tooth-cusp nomenclature founded on supposed homologies are 'foredoomed to failure' and should be entirely abandoned as 'useless and confusing.' I agree with the general sentiment expressed (*op. cit.*, p. 366) that, owing to the adoption of different plans in different groups of mammals for increasing the complexity of their molars, no terminology founded on the basis of cusp homologies can be made strictly applicable to all the mammalia. I do not, however, consider this sufficient ground for abandoning absolutely so convenient a system of nomenclature as that proposed by Osborn. Granting that many of the terms proposed are founded on mistaken homologies, it does not necessarily follow that they need be in the least confusing, as suggested by Wortman. For in any system used, in order to make that system of greatest convenience and highest utility, the names once adopted should be permanent and not subject to transfer or substitution on any ground of changed conceptions of homologies or history, for the same reason that generic and specific names are retained regardless of the fact that they may have been given to denote some supposed affinity or characteristic which may later have proved entirely erroneous.

"Viewed from the nomenclature standpoint, therefore, the convenient names proposed by Osborn have come to assume an individuality which conveys a far more definite meaning than any purely descriptive terms, be they of relative position or supposed homologies. Moreover, they have the valuable advantages of clearness and brevity in description. On these grounds, in the opinion of the present writer, and for the added reason that great confusion would inevitably result from any change in a terminology that has found its way into so many publications, Osborn's nomenclature should be retained as originally proposed. Thus the term

---

[1] Somewhat similar conclusions have been reached from different reasoning by E. S. Goodrich, M. Tims and others.

[2] *Amer. Journ. Science* (4), Vol. 16, 1903, 265-368.

'protocone' always means the main anterointernal cusp of a normal upper molariform tooth, whether that element is regarded as the original primary cusp or otherwise.

"The objection that the terms are not universally applicable is scarcely worthy of consideration since they are widely applicable to the great majority of mammalian molar types, without in the least interfering with the use of terms descriptive of 'relative position only,' which may be used in any cases where Osborn's terms do not apply."

Addendum, December, 1906 (Gregory).

A careful study of the excellent series of Insectivore skulls in the National Museum, while fully confirming Gidley's interpretation of the homologies of the molar cusps (p. 124), yet does not sustain his broader conclusion that the paracone in normal tritubercular molars is older than the protocone.

(1) The upper molar pattern of *Potamogale* (Figs. 69, 69 *a*), is fundamentally similar to that of *Myogale* (Fig. 69 F). Its high central cusp is evidently composed of an enlarged anterior and much reduced posterior cusp, and these cusps have the same spatial and functional relations with the cusps of the lower teeth as the para- and metacones of *Myogale*, while the low internal cusp functions like the protocone. *Solenodon* also has a low internal platform like that in *Myogale*, but much reduced, bearing two small cusps which function like the proto- and hypocones of *Myogale*. The main high pointed cusp in *Solenodon* is surely equivalent to the large para- and closely appressed reduced meta-cone of *Potamogale*. This high main cusp (pa + me) is evidently less specialized in *Potamogale* than in *Solenodon*, *Centetes*, etc., and further, the small basal, proto- and hypocones are in a *more primitive* condition in *Solenodon* than in *Centetes*, where they are vestigial and now functionally replaced by the enlarged high para- + metacone. In *Hemicentetes* the true protocone has vanished and the teeth parallel the carnassials of Carnivora (p. 137), where the protocone is likewise secondarily reduced.

(2) Thus, contrary to the more usual view, the "trituberculy" of *Centetes* and *Chrysochloris* is a secondary acquirement or *pseudotrituberculy*, and the fact that the high main cusp (pa + me) in *Centetes* develops in ontogeny more rapidly than the vestigial internal ledge, or protocone, does not prove that in *Potamogale*, *Myogale*, and in normal tritubercular molars the outer cusp (paracone) appeared phylogenetically earlier than the internal cusp (protocone).

Fig. 209. Internal view of the right upper and lower cheek teeth of the Zalambdodont Insectivore *Centetes* (No. 1), the Marsupial *Didelphys* (No. 2), the Dilambdodont Insectivore *Erinaceus* (No. 3) and the Titanotheroid Ungulate *Telmatherium* (No. 4). The main internal cusp (pr) is apparently homologous in Nos. 2, 3, 4, since it fits behind the metaconid into the basin of the talonid, while the hypocone (when developed) fits into the basin of the trigonid (Nos. 3, 4); but in No. 1, when the mandible is correctly articulated, the main upper cusp *does not* fit into the small talonid (*t*) like a normal protocone, but is somewhat external to it, and occupies the position of an inwardly grown paracone. (See Addendum, p. 225).—Ed.]

p = protocone.
h = hypocone.
m = metaconid.
t = talonid.

Conclusion (Osborn).

It must not be understood by the reader that the author of this volume is doggedly maintaining a theory of the origin of the upper molars, in which he has had a part, simply from personal reasons. On the contrary he believes the question to be still *sub judice* and will be the first to acknowledge his error—if error it prove to be.

The author moreover feels the full force of the very strong evidence arrayed against the Cope-Osborn view. The evolution of the upper molars is certainly not so simple as it at first appeared. It was never maintained by Osborn, as is proven in his full series of papers here reproduced,[1] that the molar of *Triconodon* (Fig. 11a), gave rise to that of *Dryolestes* (Figs. 206, 207, Nos. 2, 3), or even that all mammals passed fully into a triconodont stage, such as that of *Amphilestes* (Fig. 5). The starting point of the superior molars was supposed to be an extremely primitive triconodont type either with the cusps in line or with the pattern of molars of the *Spalacotherium* (Fig. 11) type inverted as shown in *Peralestes* (Fig. 12).

---

[1] See pp. 8, 33.

CHAPTER X.

RECTIGRADATIONS AS A RESULT OF LATENT OR POTENTIAL HOMOLOGIES IN THE TEETH.

By *rectigradations* I refer to the origin of new cusps or cuspules which appear determinately, definitely, orthogenetically in both the upper and lower teeth—quite *independently* in different orders of mammals, and separated perhaps by vast intervals of time.

There is some *law of predisposition* operating here. If it were not for this law the cusps of the teeth of mammals would present an infinite variety of origin, whereas they actually present a singular uniformity of origin except in the multituberculates and other possible exceptions noted in the preceding chapters. It is the *modelling* of the cusps after they appear which gives the infinite variety.

We do not know what conditions this "law of predisposition": we only see evidence of the influence of *community of origin* or hereditary kinship.

In 1902 I supposed this law was what E. Ray Lankester meant by *Homoplasy*, as shown below, but it appears from his letter cited below (p. 239) that I was mistaken—Lankester's *homoplasy is equivalent to analogous evolution, to parallelism, or convergence.*

1. Homoplasy as a Law of Latent or Potential Homology.

(Reprinted under the title given above from *The American Naturalist*, Vol. XXXVI., April, 1902, No. 424, pp. 259-271.)

> My study of teeth in a great many phyla of Mammalia in past times has convinced me that there are fundamental predispositions to vary in certain directions; that the evolution of the teeth is marked out beforehand by hereditary influences which extend back hundreds of thousands of years. These predispositions are aroused under certain exciting causes and the progress of tooth development takes a certain form converting into actuality what has hitherto been potentiality.
>
> *Science*, N.S., Vol. VI., No. 146 (Oct. 15, 1897), pp. 583-587.

In previous communications, as shown in the above quotation, I have spoken of the "potential of similar variation," as covering cases of the independent evolution of identical structures in the teeth of different families of mammals, especially in relation to the homologous "antecrochet" and "crochet" folds in the teeth of horses, rhinoceroses, and we may now add, of titanotheres (Osborn, '94, p. 208). In the present communication I propose to treat somewhat more fully of the same phenomenon, as a special form of homology which has been clearly defined by Lankester in 1874 as *homoplasy*, but into which paleontology has brought the idea of "potential."

The Broad Significance of Analogy.

We are familiar with the classic distinction of analogous organs as having a similarity of function: *analogy* (Owen, '43, p. 374), "a part or organ in one animal which has the same function as another part or organ in a different animal"; Lankester ('70): "Any two organs having the same function are analogous, whether closely resembling each other in their structure and relation to other parts or not; and it is well to retain the word in that wide sense." Analogous organs may or may not be homologous. "Analogy" is therefore an extremely broad and comprehensive term, and it appears that we must include under it all cases of the similar evolution of organs either of common or of different origin due to similarity of function. For example, the "analogous variation" of Darwin, the "homoplasy" of Lankester in part at least, the "convergenz" of German writers, the "homomorphy" of Fürbringer, the "heterology," "parallels," and "parallelism" of Hyatt, of Cope ('68, also *Origin of the Fittest*, p. 96), of Scott, and of most American writers, are all illustrations of analogy and may be very misleading as to homology.

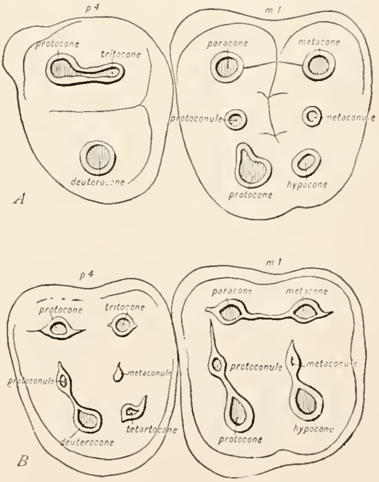


Fig. 210. Fourth upper premolar and first molar of primitive ungulates. *A*, *Euprotogonia*; *B*, *Hyracotherium*. Not believed to be genetically related, yet exhibiting independent or homoplastic evolution of homologous cusps.

As Scott observed in 1896, "Parallelism[1] and convergence of

---

[1] The term "parallelism" was employed by Cope in his essay of 1868 on the "Origin of Genera" (reprinted in the *Origin of the Fittest*) in two quite different senses: first, in relation to recapitulation in ontogeny,—"Those which accomplish less [stages] are *parallel* with the young of those which accomplish more [stages]"; second, quite in the modern sense (*op. cit.*, pp. 96-104) of independently acquired resemblances in different

development are much more general and important modes of evolution than is commonly supposed. By parallelism is meant the independent acquisition of similar structure in forms [*i.e.*, animals] which are themselves nearly related, and by convergence such acquisition in forms [*i.e.*, animals] which are not closely related, and thus in one or more respects come to be more nearly alike than were their ancestors."

The term "homoplasy" (Lankester) has been long used by the writer and others in a somewhat similar sense, but it is not equivalent either to "parallelism" or "convergence." As will be seen below, the fundamental idea is different, because homoplasy always involves homology, while parallelism and convergence may or may not involve homology.

ANALOGY IN EVOLUTION.

ANALOGY.

- *Analogous Variation* (Darwin). Similar congenital variation in more or less distantly related animals and plants.
- *Parallelism.* Independent similar development of related animals, plants, and organs.
- *Convergence.* Independent similar development of unrelated animals, bringing them apparently closer together.
- *Homoplasy* (Lankester) (?*Homomorphy*, Fürbringer). Independent similar development of homologous organs or regions giving rise to similar new parts.

In brief, analogy embraces similar changes due to similar adaptation in function both in homologous and in non-homologous organs, both in related and in unrelated animals.

THE LIMITED SIGNIFICANCE OF HOMOLOGY.

Owen ('43, p. 379), Lankester ('70), and Fürbringer have especially defined and elaborated the very ancient conception of homology, as employed by Oken, Geoffroy St. Hilaire, and Vicq d'Azyr: *homology* (Owen, '43), "the same organ in different animals under every variety of form and function"; *homogeny* (Lankester, '70): "Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*." E. B. Wilson ('95, pp. 101-124) has shown that the comparative anatomical test of homology is more reliable than the embryological. Gegenbaur ('98, pp. 23-25) has given a full presentation of the distinctions as the basis of comparative anatomy: in his recent great work ('98, p. 23)

---

groups. As employed by Scott in his essay "On the Mode of Evolution in the Mammalia" ('91, pp. 363-367), "parallelism" is used in a very broad sense as affecting the skeleton and teeth, on the principle "that identical modifications of structure, constituting evolution of types, have supervened on distinct lines of descent," as embracing not only single characters but whole series of them.

he presents the matter in terms which may be briefly analyzed with the usages of other authors, as follows:

I. Homology, General: as of vertebræ and limbs.
  1. homotypy: as of opposite limbs, eyes, kidneys, etc.
  2. homodynamy: (in part the "general," in part the "serial," homology of Owen; the "meristic" homology of Bateson). Corresponding limbs, parts, segments (*e.g.*, the humerus and femur) on the same side of the body.
  3. homonomy: parts which are in the same transverse axis of the body, or on only one section of the longitudinal axis; *e.g.*, the rays of the fins of fishes, the single fingers and toes of the higher vertebrates are homonomous organs.

II. Homology, Special: (the "homogeny" of Lankester).
  1. complete homology of elements which have retained their relations unchanged, as of single bones from the Amphibia to the Mammalia.
  2. incomplete homology, as of organs which have either gained new parts or lost certain of their parts.
    a. *defective*, as in comparison of fins of teleosts and of selachians.
    b. *augmentative*, as in the heart of cyclostomes and of the higher vertebrates.
    c. *imitative*, as where different vertebræ connect with the ilium and become sacral.

III. Homomorphy (Fürbringer): from these homologies certain structures are to be distinguished as *homomorphic* which are more or less similar to each other but stand in no phylogenetic connection.[1]

Homomorphy comes nearest, as we understand it, to the "homoplasy" of Lankester, but the latter term has the priority of definition.

Distinction between Homogenous and Homoplastic Organs.

In the strictest sense, special or genetic homology, the "homogeny" of Lankester, is the only absolute homology. For example, in all four-limbed vertebrates, or Tetrapoda (Credner), the first and second phalanges of the tibial digit or hallux are homogenous; the earliest tetrapods had such phalanges, so far as we can judge from both paleontology and embryology, and all others are derivatives.

But suppose we should discover that these two phalanges had originated independently in several different classes of vertebrates, and were not derivatives; should they then be considered analogous or homologous? "Again," says Lankester ('70), "it may perhaps be

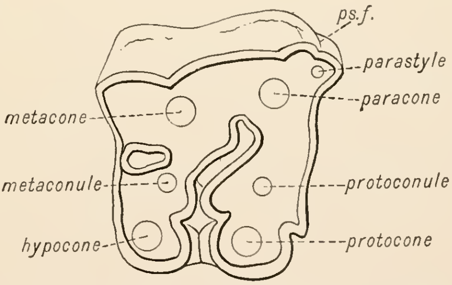


Fig. 211. Ideal embryonic ground plan of rhinoceros molar, showing relation of primitive cusps to the folds and crests.

---

[1] Literally translated from Gegenbaur.

admitted that the common ancestors of the Osseous Fishes and Mammalia had a skull of decidedly undifferentiated character, with a much less amount of differentiation than is observed in the skulls of either of these groups. It is only in so far as they have parts represented in the common ancestor that we can trace *homogeny* in these groups; and yet the *homology* of a vast number of bones in the skull of the two is discussed and pointed out." Suppose, accordingly, that in the formation of dermal roofing bones in different orders of fishes a pair of bones corresponding in position to the parietals should arise independently, or that in the evolution of the teeth cusps should arise independently having the same form and position,—what criterion should be applied? All such structures are habitually regarded as homologous, yet it is apparent that they are not derivatives of each other and therefore not homogenous or homologous in the strictest sense.

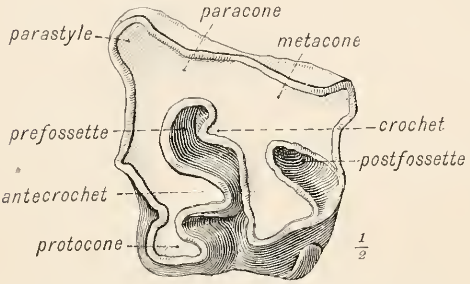


Fig. 212. Molar tooth of an Upper Miocene rhinoceros (*Teleoceras*), showing origin of secondary folds.

Such cases of independent evolution of apparently homologous organs I recently proposed[1] to signify as *potential*, or *latent homology*, borrowing the term "latent" from Galton as indicative of a germinal rather than of a patent or adult character, and the physical term "potential" as expressing the innate power or capacity to develop a certain organ. But my colleague, Prof. Edmund B. Wilson, pointed out to me that such cases were almost exactly covered by the *original definition* of the word "homoplasy" by Lankester ('70, p. 42), as shown in the subjoined quotations from his essay:

> When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting *modifications*[2] of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. I propose to call this kind of agreement *homoplastic* or *homoplasy*.[3] . . . What is put forward here is this: that under the term "homology," belonging to another philosophy, evolutionists have

---

[1] In a communication before the National Academy of Science, Nov. 13, 1901.

[2] Italics are mine.

[3] At this time Lankester accepted Herbert Spencer's Lamarckian views. Subsequently he abandoned the mechanical inheritance theory for the pure natural selection theory.

described and do describe two kinds of agreement,—the one, now proposed to be called "homogeny," depending simply on the inheritance of a common part; the other, proposed to be called "homoplasy," depending on a common action of evoking causes or moulding environment on such homogenous parts, or on parts which for other reasons offer a likeness of material to begin with.

$$\text{Homology thus includes} \begin{cases} \text{Homoplasy.} \\ \text{Homogeny.} \end{cases}$$

It follows that subsequent writers, including myself, have misused the term "homoplasy," confusing it with "parallelism" and "convergence," which, as we have seen, may affect absolutely non-homologous structures. *Homoplasy should be confined to structures in which there is an element of homology.*

Independently of Lankester (that is, not familiar with his paper) I had therefore reached a similar conclusion through years of observation in paleontology. I would now like to expand an idea which he also lightly suggested in 1870 in the words, "*or on parts which for other reasons show a likeness of material to begin with.*"

The Law of Homoplasy as in Part Identical with Definite or Determinate Variation.

As observed in the evolution of the teeth especially, homoplasy appears to be of very great importance, not on the technical grounds of uniformity in nomenclature, but because it seems to coincide with the principle of definite or determinate evolution, a principle which may be of wider application.[1] From the time of the "Origin of Species" it has been admitted that evolution, so far as it depends upon variation, is not in every possible direction, but is limited to certain changes, the expression of certain hereditary or constitutional causes which we do not in the least understand. The evolution of the teeth of mammals enabled me in 1889 to give many concrete

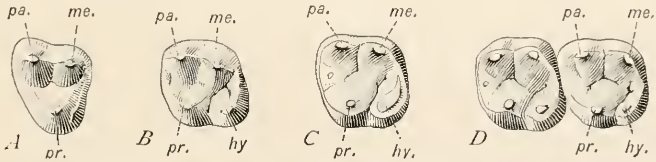


FIG. 213. Superior molars of primates, Anaptomorphus to Homo, showing independent or homoplastic origin of the hypocone, *hy*, from the cingulum.

---

[1] See especially the correspondence of Darwin and Asa Gray; also Osborn, The Palæontological Evidence for the Transmission of Acquired Characters, *Nature*, Jan. 9, 1890; the Orthogenesis and Orthoplasy of Eimer, Lloyd Morgan and Baldwin; Baldwin's *Dictionary of Philosophy and Psychology*, Vol. I., p. 243.

illustrations of this principle and to show that variation is hardly the proper term to apply to rudiments which do not arise in a variable but in a fixed manner.

It appears that von Waagen suggested the term "mutation" for immeasurable variations somewhat similar to these. Scott in 1891 ('91, p. 388) pursued the idea further in the following striking passage: "These facts at least suggest the possibility that individual variations are not incipient species, but that the causes of transformation lie deeper, and act with more or less uniformity upon large numbers of individuals. It may, perhaps, be the outcome of future investigations, that while variations are generally due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies operating long in a uniform way, and the results controlled by natural selection. While this *may* be true, a great many facts must be gathered in its support, before it can be regarded as more than a suggestion." Scott subsequently, in his article "Variations and Mutations," expanded this idea: "Bateson's results, as compared with those of paleontology, confirm this distinction in many significant ways and emphasize strongly the difference between variation and that steady advance along definite lines which Waagen called mutation." This paper in turn is said to have influenced de Vries's recent work, *Die Mutationstheorie*.

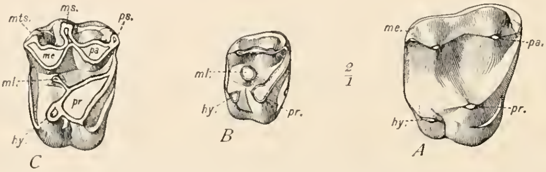


FIG. 214. Superior molars of primates. *A*, *Adapis*; *B*, *Hyopsodus*; *C*, *Notharctus*. Showing homoplastic cusps, *hy*, *ml*, *ps*, *ms*, *mts*.

It is a singular coincidence that the human teeth were selected by both Empedocles and Aristotle to test the "survival of the fittest" *versus* the purposive or teleological theory of evolution. I pointed out in the papers above referred to (Osborn, '89, pp. 561-566; '90) the significant fact that new cusps of the molar teeth do not appear at random, but at certain definite points; that they are at first so minute that they can barely be perceived, so that it is difficult to theoretically assign them a survival value in the struggle for existence; that the mechanical or Lamarckian explanation is the only one which can be offered;[1] I laid the chief stress, however, not upon the mechanical explanation, but upon definite or determinate origin, and this has been confirmed by the subsequent study of thousands of

---

[1] Ryder and Cope confidently advanced the mechanical explanation; it is not without grave difficulties, owing to the lack of an heredity theory.

teeth in different families of mammals. The still more significant fact that this definite and determinate evolution was proceeding independently in a great many different families of mammals did not at the time impress itself so strongly upon my mind.

If molar teeth are found independently evolving in exactly similar ways in such remote parts of the world as Switzerland, Wyoming, and Patagonia, it is obvious that the process is not governed by chance but represents the operation of some similar or uniform law deduced from the four following considerations:

Firstly, the teeth differ from all the other tissues and organs of the body in being preformed, beneath the gum.[1] Unlike all other organs they are not modified, improved, or rendered more adaptive by use; on the contrary, after the first stage of wear, the longer they are used the more useless and less adaptive they become.

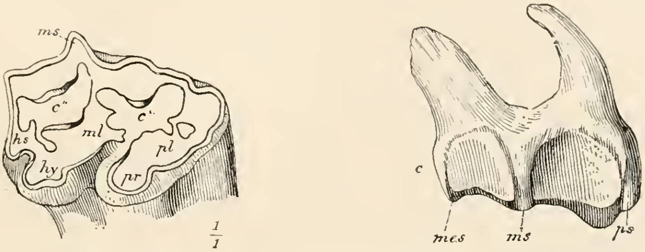


FIG. 215. Superior molar of *Merychippus*, showing styles *ps*, *ms*, *mts*, and conules *pl*, *ml*, homoplastic with those of the wholly unrelated primate molar, Fig. 5, *C*.

Thus, new structures in the teeth do not first appear as *modifications* (as distinguished from congenital variations) in course of life, as is so often if not invariably the case with new structures in the skeleton. New cusps, folds, crests, and styles are invariably congenital. Thus, of all organs of the body the teeth most exclusively and purely represent the current of stirp, germinal, or constitutional evolution.

Secondly, the teeth are, nevertheless, among the most progressive organs in the body. Whereas the adaptation of the skeleton, among the mammals at least, is by a constant loss or numerical reduction of parts, the adaptation of the teeth is by a constant addition and modelling of parts (Osborn, '88, pp. 1067-1079).

Thirdly, according to the present paleontological evidence many of the different families and orders of mammals diverged from each other at a time when they possessed three cusps on the upper molar teeth and from three to five cusps on the lower molar teeth. This being the case, only the cusps comparable in different orders of

---

[1] The importance of this fact was first pointed out to me by Prof. E. B. Poulton of Oxford.

mammals with these original three upper and five lower cusps are derivatives or homogenous.

Fourthly, it follows that the new cusps of the teeth furnish an example of homoplasy independent of the individual modification.

Thus, we may say that in the teeth at least *homoplasy involves a law of latent or potential homology*, without professing to understand what is its significance.

We should, *a priori*, expect that if additional cusps were added independently in different families and orders of mammals in different parts of the world, under highly different conditions, the teeth of the higher Mammalia would present very great diversity. As a matter of fact, the new cusps in different families are absolutely uniform up to a certain limit.[1] In the twenty-three orders of placentals and in the seven marsupial families, many of which are adaptively equivalent to orders, the independently developed fourth to eleventh cusps of the upper molars, if so many are developed, are uniform and may be termed homologous; the eight cusps and folds succeeding the original homogenous three arising, if at all, at similar points and presenting a latent homology or homoplasy. The record in the upper molar teeth stands thus:

HOMOLOGY.

HOMOGENY	HOMOPLASY
Primitive three cusps common to all mammals.	Cusps or folds which are or may be independently developed in different orders.
Protocone	Hypocone
Paracone	Metaconule
Metacone	Protoconule
—	Parastyle
—	Mesostyle
—	Metastyle
—	Protostyle
—	Hypostyle

This expresses the comparison of mammals as a whole. Within many of the orders, such as the Perissodactyla, which arise from six cusped ancestors, the homology is different.

HOMOLOGY.

HOMOGENY	HOMOPLASY
Protocone	Parastyle
Paracone	Mesostyle
Metacone	Crista
Hypocone	Crochet
Protoconule	Antecrochet, etc.
Metaconule	—

---

[1] The excess of this limit is in multituberculism, or polybunodonty, where cuspules are indefinitely multiplied.

The elements to which these terms are applied are best exemplified in the molar teeth of some of the primitive horses (Fig. 215).

The teeth are by no means the only structures which evolve under this principle, the skull, vertebral column, and limbs also evolving under it more or less completely: but the teeth afford a singularly beautiful illustration of it because they exclude individual modification.

The chief object of this communication is to enforce the recognition of homoplasy as something which must be accounted for. These homoplastic cusps do not arise from selection out of fortuitous variations, because they develop directly and are not picked from a number of alternates. Neither does it appear that the mechanical-inheritance theory, if granted, would produce such a remarkable uniformity of result. We are forced to the conclusion that in the original tritubercular constitution of the teeth there is some principle which unifies the subsequent variation and evolution up to a certain point. Herein lies the appropriateness of Lankester's phrase, "a likeness of material to begin with."

Philosophically, predeterminate variation and evolution brings us upon dangerous ground. If all that is evolved in the Tertiary molar tooth is included in a latent or potential form, in the Cretaceous molar tooth we are nearing the *emboîtement* hypothesis of Bonnet or the archetype of Oken and Owen. Embryologists have recently gotten into the same dilemma, and my colleague, Wilson, has proposed to drop the idea "homology" altogether and substitute the idea "equivalent." In the present case, however, I think we have to deal with homology, or, more strictly, with a *principle intermediate between homology and analogy.*

In a paper recently read before the American Morphological Society (December, 1901), this author has urged the necessity of adhering as closely as possible to the historical standard in the embryological study of homology, and of avoiding the use of the term "homology" when this standard is not available. He therefore suggests for descriptive purposes the use of the non-committal terms "equivalent" and "homoblastic," the former being applied to embryonic structures of like fate (*i.e.*, giving rise to homologous parts), the latter to those of like embryonic origin. The only decisive test of the homology is historic community of derivation (*i.e.*, homogeny).

BIBLIOGRAPHY.

'68 Cope, E. D., "On the Origin of Genera," *Proc. Acad. Nat. Sci. Phila.*, October, 1868.

'87 Cope, E. D., *The Origin of the Fittest*, 8vo, New York.

'98 Gegenbaur, Carl, *Vergleichende Anatomie der Wirbelthiere*, 8vo, Leipzig, 1898.

'70 Lankester, E. R., "On the Use of the Term 'Homology' in Modern Zoölogy and the Distinction between Homogenetic and Homoplastic Agreements," *Ann. Mag. Nat. Hist.*, Ser. 4, Vol. IV., pp. 34-43.

'89 Neumayr, M., *Die Stämme des Thierreiches*, 4to, pp. 60-61, Vienna, 1889.

'88 Osborn, Henry F., "The Evolution of Mammalian Molars to and from the Tritubercular Type," *Amer. Nat.*, Vol. XXII. (December, 1888), pp. 1067-1079.

'89 Osborn, Henry F., "The Palæontological Evidence for the Transmission of Acquired Characters," *Amer. Nat.*, Vol. XXIII. (1889), pp. 561-566.

'90 Osborn, Henry F., "Evolution and Heredity," *Biological Lectures, 1890, Marine Biological Laboratory, Woods Hole.*

'94 Osborn, Henry F., "The Rise of the Mammalia in North America," *Proc. Amer. Assoc. Adv. Sci.*, Vol. XLII. (1893), pp. 187-227.

'43 Owen, Richard, *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals, delivered at the Royal College of Surgeons in* 1843, 8vo, London, 1843.

'91 Scott, W. B., "On Some of the Factors in the Evolution of the Mammalia. On the Osteology of Mesohippus and Leptomeryx, with Observations on the Modes and Factors of Evolution in the Mammalia," *Journ. of Morph.*, Vol. V., No. 3 (1891), pp. 379-402.

'94 Scott, W. B., "On Variations and Mutations," *Amer. Journ. Sci.*, Vol. XLVIII. (November, 1894), pp. 355-374.

'96 Scott, W. B., "Palæontology as a Morphological Discipline," *Biological Lectures, 1895, Marine Biological Laboratory, Woods Hole*, pp. 43-61, Boston, 1896.

'01 de Vries, Hugo, *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*, 8vo, Leipzig, 1902.

'95 Wilson, E. B., "The Embryological Criterion of Homology," *Biological Lectures, 1895, Marine Biological Laboratory, Woods Hole*, pp. 101-124, Boston, 1895.

2. LANKESTER'S REPLY TO THE PRECEDING ARTICLE.

Dr. E. Ray Lankester demurred from Osborn's interpretation of his definition of "homoplasy" as shown in abstract in the following letter:

". . . . Homoplasy does *not* demand an element of homology. I expressly say 'homogenous parts or parts which *for other reasons* offer a likeness of material to begin with.' That alternative entirely destroys your contention. I recognized (as hitherto combined under one term 'homology') *only* homogeny—or hereditary quality—and homoplasy or moulded non-heredity quality. The 'likeness' due 'to other reasons' than homogeny—above spoken of—cannot be homogeny. The 'likeness' which clearly enough is included and pointed to in the whole paragraph—as favouring the action of homoplasy—is *either* a likeness of true homogeny (that is of form and relation inherited), *or* a likeness of similarity in material, in position, or in initial form—not due to close homogeny—but possibly a likeness of such a general character as the 'likeness of material' (not of elaborated form and parts) in two epidermal surfaces. Thus the beak of the bird and of the turtle might be developed homoplastically from a common ancestor's snout which had no beak—but in both the bird-line and the turtle-line horn-producing epidermis is the chief material brought into greater development.

"So in the bi-chambered hearts of bird and mammal the *material* is muscular tissue and the peculiar muscular tissue of the heart.

"I should like to know what cases of 'convergence' you can cite in which there is not some remote homogeny as to the tissues at work, which is a totally different thing from inherited community of the *special form* considered. You would not call a four-chambered seed-vessel and a four-chambered heart cases of convergence nor of homoplasy! (except in the very remotest degree which if entertained makes all shape and structure in a minimal degree homoplastic with all other). Can you name cases of convergence or parallelism which are not covered by the definition I gave of homoplasy? What organs are parallel in any two animals and yet have no likeness at all—even the most general—in their *material*.

"Yours sincerely,

"E. RAY LANKESTER.

"*P.S.*—Every living thing owes its properties to homogeny, that is to say, its fundamental properties to a homogeny common to it with all other living things, and as you run down group within group there must be a more and more specialized homogeny affecting members of smaller and smaller groups.

"But this factor can be detached in our consideration of structure from the homogeny of actual completed *form* and *mechanism*. The one is much more remote and less specific than the other; and they need to be given each its due rank and place; not to be confused."

3. CONCLUSION (OSBORN), 1906.

The newly and independently arising cusps, described above as 'homoplastic,' should be described as *rectigradations*.*

---

*The term 'rectigradation' was defined in *Science*, N.S., Vol. XXI., June 23, 1905, p. 961, as follows: "Fourth, *rectigradation*, a new term with which I propose to characterize what in the year 1889 I described as 'definite variations'; it embraces changes which many writers have described as 'orthogenetic,' under the supposed law of direct change, usually in an adaptive direction, which is described as Orthogenesis; these probably are the 'mutations' of Waagen."

BIBLIOGRAPHY.

ADLOFF, P. "Zur Kenntniss des Zahnsystems von Hyrax," *Zeitsch. f. Morph. u. Anthrop.*, Bd. V., Heft I., S. 181-200, Stuttgart, 1902.

"Zur Frage nach der Entstehung der heutigen Säugethierzahnformen," *Zeitschr. f. Morph. u. Anthrop.*, Bd. V., Heft II., S. 357-382, Stuttgart. 1902.

AMEGHINO, FL. *Filogenia*, 8vo. 1884.

"Sur l'Évolution des Dents des Mammifères," *Boll. Acad. Nac. Ciencias en Cordoba*, T. XIV., 1896, pp. 381-517.

"Recherches de Morphologie phylogénétique sur les molaires supérieures des Ongulés," *An. d. Mus. Nac. de Buenos Aires*, T. IX. (Ser. 3*a*, T. III.), pp. 1-541, 631, fig. 9.

"On the Primitive Type of the Plexodont Molars of Mammals," *Proc. Zool. Soc. London*, May 2, 1899.

BATESON, W. "On Numerical Variation in Teeth with a Discussion of the Conception of Homology," *Proc. Zool. Soc. Lond.*, 1892, pp. 102-115.

Material for the Study of Variation, 8vo. London, 1894.
(Great Variability of Mammalian Teeth.)

BAUME. *Odontologische Forschungen. Versuch einer Entwicklungsgeschichte des Gebisses.* 1882.

BEAUREGARD. "Sur les Deux Dentitions des Mammifères," *Bull. Soc. de Biologie*, 1888, Nos. 9, 10.

COPE, E. D. "On the Homologies and Origin of the Types of Molar Teeth of Mammalia Educabilia," *Jour. Acad. Nat. Sci. Phila.*, n.s., VIII., Pt. I., pp. 71-89. 1874.

[On the Origin of the Sectorial Tooth of the Carnivora.]

"Systematic Catalogue of the Vertebrata of the Eocene of New Mexico. . . ." *Rept. Geogr. Expl. and Surveys W. of the 100th Meridian* (Wheeler), 1875, pp. 5-7.

"On the Mechanical Genesis of Tooth Forms," *Proc. Acad. Nat. Sci. Phila.*, 1878, p. 45.

"The Origin of the Specialized Teeth of the Carnivora," *Amer. Naturalist*, XIII., March, 1879, pp. 171-173.

"Note on the Trituberculate Type of Superior Molar and the Origin of the Quadrituberculate," *Amer. Naturalist*, XVII., 1883, pp. 407-408.

"On the Trituberculate Type of Molar Tooth in the Mammalia," *Pal. Bull.*, No. 37, *Proc. Amer. Phil. Soc.*, XXI., Dec. 7, 1883, pp. 324-326.

"On the Evolution of the Vertebrata, Progressive and Retrogressive," *Amer. Naturalist*, XIX., Mar., April, 1885, pp. 347, 350.

"On Lemurine Reversion in Human Dentition," *Amer. Naturalist*, XX., 1886, pp. 941-947.

Cope, E. D.
The Origin of the Fittest, 8vo, 1887. (See especially pp. 245, 246, 259, 347, 359, 361, 362, 365.)

"On the Tritubercular Molar in Human Dentition," *Jour. Morphol.*, July, 1888, p. 7.

"Synopsis of the Vertebrate Fauna of the Puerco Series," *Trans. Amer. Philos. Soc.*, XVI., Aug. 1888, p. 299.

"The Mechanical Causes of the Development of the Hard Parts of the Mammalia," *Jour. Morphol.*, Vol. III., 1889, pp. 137-271.

Dewoletsky, R. "Neuere Forschungen über das Gebiss der Säuger," *Sep. aus dem Jahresberichte des k.k. Staats-Obergymnasiums in Czernowitz*, 1894-95, Czernowitz.

Dybowski. "Studien über Säugetierzähne," *Verh. d. k.k. Zool., Botan. Ges. in Wien*, 8vo, 1889.

Fleischmann, A. "Die Grundform der Backzähne bei Säugethieren und die Homologie der enzelnen Höcker," *Sitzungsber. d. k. Preuss. Akad. d. Wiss.*, Berlin, 1891.

"Mittheilung über die Zahnentwicklung von Hyrax," *Abhl. Natur. hist. Gesellsch.* Nuremburg, 1894.

Flower, W. H. "Remarks on the Homologies and Notation of the Teeth of the Mammalia," *Jour. Anat. Physiol.*, III., pp. 262-278, 1869.

Gaudry, A. *Enchaînements du Monde Animal dans les Temps géologiques; Mammifères Tertiares*, Paris, 1878. (Supports concrescence theory.)

"Sur la Similitude des Dents de l'homme et de quelques Animaux," *L'Anthropologie*, Janv.-Avr., 1901.

Gervais, P. *Histoire naturelle des Mammifères*, Paris, 1854. (Suggests concrescence idea.)

Gidley, J. W. "Evidence bearing on Tooth-Cusp Development," *Proc. Washington Acad. Sci.*, Vol. VIII., 1906, pp. 91-110, pll. iv.-v.

Goodrich, E. S. "On the Fossil Mammalia of the Stonesfield Slate," *Quar. Jour. Micr. Sci.*, XXXV., 1894, pp. 407-432. (Supports "polybuny" theory.)

Hoffmann. "Ueber die Entwicklung des Kronencementes an den Backenzähnen der Wiederkäner mit Berücksichtigung der Zahnentwicklung in Allgemeinen," *Zeitschr. für wiss. Zool.*, Bd. LVIII., 1894, pp. 566-617.

Huxley, T. H. "On the Cranial and Dental Characters of the Canidae," *Proc. Zool. Soc. Lond.*, 1880, pp. 283-284.
(Regards molar of Centetes as primitive for Carnivora. Interprets molar cusps by the "premolar analogy" theory.)

Klever, E. "Zur Kenntniss der Morphogenese des Equidengebisses," *Morphol. Jahrb.*, Bd. XV., 1889, Leipzig.

Mahn, R. "Bau und Entwicklung. d. Molaren, bei Mus und Arvicola," *Morphol. Jahrb.*, Bd. XVI., p. 652. (Criticises Trituberculy.)

Major, C. J. Forsyth. "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz. Nebst Beiträgen zu einer vergleichenden Odontographie von Ungulaten und Unguiculaten," *Palaeontographica*, 1873, XXII.
(Opposes three-cusped origin of mammalian molars.)

Major, C. J. Forsyth.

"On some Miocene Squirrels, with Remarks on the Dentition and Classification of the Sciurinæ," *Proc. Zool. Soc.*, Feb. 28, 1893, pp. 179-215. (See pp 196-214 for polybuny theory.)

"On *Megaladapis madagascariensis*, an extinct gigantic Lemuroid from Madagascar. . . ." *Philos. Trans. Roy. Soc.*, Vol. 185 (1894) B, pp. 15-38, especially pp. 22-24. (Discusses the so-called tritubercular type of molar in Viverridæ, Centetidæ, Lemuridæ.)

"On the Malagasy Rodent Genus *Brachyuromys*; and on the Mutual Relations of some Groups of the Muridæ (*Hesperomyinæ*, *Microtinæ*, *Murinæ*, and *Spalacidæ*) with each other and with the Malagasy Nesomyinæ," *Proc. Zool. Soc.*, June 1, 1897, pp. 713 *et seq.* ("Polybuny" theory.)

"On Fossil and Recent Lagomorpha," *Trans. Linn. Soc. Lond.* (2), VII., pp. 433-520.

"On the Change and Form of the Teeth in the Centetidæ a Malagasy Family of Insectivora," *Ann. Mag. Nat. Hist.*, ser. 6, Vol. XX., Dec. 1897, pp. 525-544.

Mivart, St. G. "On the Osteology of the Insectivora," *Jour. Anat. and Physiol.*, Vol. I. and II., 1863, p. 117 *et seq.* (Adopts idea of "concrescence of cusps" in *Chrysochloris.*)

Kükenthal, W. "Das Gebiss von *Didelphys*," *Ant. Anz.*, Bd. VI., 1891, pp. 658-666.

"Einige Bemerkungen über die Säugethierbezahnung," *Anat. Anz.*, 1891, Nr. 13.

"Ueber den Ursprung und die Entwickelung der Saugethierzähne," *Jenaische Zeitschrift für Naturwissenschaft*, Bd. XXVIII., 1893.

"Entwickelungsgeschtliche Untersuchungen am Pinnipediergebisse," *Jenaische Zeitschr. f. naturw.*, Bd. XXVIII., 1893, pp. 76-118.

"Die Bezahnung der Zahnwale," *Denkschr. d. med.-naturw. Gesellsch.*, Bd. III., 1893, pp. 387-448.

Kowalevsky. "Monographie der Gattung *Anthracotherium*, Cuv.," *Palæontographica*, N.F. II., 3 (XXII.), 1873, 1874, pp. 210, 263, 264.

Lataste, F. "Sur le Système dentaire du Genre Daman et l'Étude de la Dent canine," *Zool. Anz.*, 1887, p. 268.

"Considerations sur les Deux Dentitions des Mammifères," *Jour. de l'Anat. et de la Physiol.*, 1888, p. 200.

Leche, W. "Studien über die Entwicklung des Zahnsystems bei den Säugethieren," *Morphol. Jahrb.*, Bd. XIX., 1892, p. 502, XX., p. 113.

Osborn, H. F. "The Upper Triassic Mammals *Dromatherium* and *Microconodon*," extracted from *Proc. Acad. Nat. Sci. Phila.*, Dec., 1886, and *Proc. Amer. Phil. Soc.*, April, 1887, *antea*, pp. 18-21.

"The Structure and Classification of the Mesozoic Mammalia," *Jour. Acad. Nat. Sci. Phila.*, IX., No. 2, July, 1888, *antea*, pp. 31-35.

"The Nomenclature of the Mammalian Molar Cusps," *Amer. Naturalist*, XXVI., Oct. 1888, pp. 436, 437, *antea*, p. 66.

"Additional Observations upon the Structure and Classification of the Mesozoic Mammalia," *Proc. Acad. Nat. Sci. Phila.*, Nov., 1888, pp. 292-301.

"The Evolution of Mammalian Molars to and from the Tritubercular Type," *Amer. Naturalist*, XXII., Dec., 1888, pp. 1067-1079, *antea*, pp. 36-47.

Osborn, H. F., and Wortman, J. L. "Fossil Mammals of the Wasatch and Wind River Beds," Collection of, 1891, *Bull. Amer. Mus. Nat. Hist.*, Vol. IV., No. 1, Oct., 1892, pp. 84-90, *antea*, pp. 66-72.

Osborn, H. F. "Odontogenesis in the Ungulates," *Amer. Naturalist*, XXVI., 1892, pp. 621-623.

"The History and Homologies of the Human Molar Cusps," *Anat. Anz.*. VII., Jena, 1892, Nr. 23, 24, *antea*, pp. 48-55.

"The Rise of the Mammalia in North America," *Proc. Amer. Assoc. Adv. Sci.* XLII., Aug., 1893, pp. 189-227, *Amer. Jour. Sci.* (3), XLVI., pp. 379-392, 448-466.

"The History of the Cusps of the Human Molar Teeth," *International Dental Journal*, July, 1895, *antea*, pp. 55-65.

"Trituberculy: A Review Dedicated to the late Professor Cope," *Amer. Naturalist*, XXXI., Dec., 1897, pp. 993-1016, *antea*, pp. 74-90.

Nawroth. "Zur Ontogenese bei Schweinemolaren," *Inaugural Dissertation*, Berlin, 1898.

Owen, R. "Monograph of the Fossil Mammalia of the Mesozoic Formations," *Monograph Palæontograph. Soc.*, XXIV. (for 1870), 4to, 1871.

Pouchet et Chabry. "Contribution à l'Odontologie des Mammifères," *Jour. de l'Anat. et de la Physiol.*, 1884.

Poulton, E. "The True Teeth and the Horny Plates of *Ornithorhynchus*," *Quar. Jour. Micr. Sci.* XXIX., 1889, pp. 9-48.

Röse, C. "Ueber die Entwickelung des Menschlichen Gebisses," *Verh. d. Deutsch. Odont. Ges.*, Bd. 3, 1891.

"Ueber die Zahnentwickelung des Menschen," *Schweiz. Viertel-jahrsschrift für Zahnheilkunde*, Bd. II., 1892.

"Ueber die Zahnentwickelung der Beuteltiere," *Anat. Anz.*, Bd. VII., 1892, pp. 639-650, 693-707.

"Ueber die Entstehung und Formabänderungen der Menschlichen Molaren," *Anat. Anz.*, Bd. VII., 1892, Nr. 13, 14, pp. 392-421.

"Zur Phylogenie des Säugetiergebisses," *Biolog. Centralbl.*, Bd. XII.. Nr. 20, 21, pp. 624-638, 1892.

"Ueber die Zahnentwickelung der Beutelthiere," *Anat. Anz.*, Bd. VIII., 1893, pp. 566-577.

"Ueber die erste Anlage der Zahnleiste beim Menschen," *Anat. Anz.*, Bd. VII., 1893, Nr. 1, pp. 29-32.

"Das Zahnsystem der Wirbelthiere," *Ergebn d. Anat. u. Entw. Merkel u. Bonnet*, IV., 1894, pp. 542-591.

Rost. *Versuch einer Phylogenie des Säugethiergebisses*, Jena, 1884.

Rütimeyer, W. "Beiträge zur Kenntniss der fossilen Pferde und zur vergleichenden Odontographie der Hufthiere überhaupt," *Verh. d. naturf. Ges. in Basel*, III., 1863, pp. 558.

Ryder, J. A. "On the Mechanical Genesis of Tooth Forms," *Proc. Nat. Sci. Phila. Acad.*, 1878, pp. 45-80.

Schlosser, M. "Beiträge zur Kenntniss der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer," *Morpholog. Jahrbuch*, XII., 1887, pp. 1-136.

Schlosser, M.

"Ueber Beziehungen der Ausgestorbenen Säugethierfaunen und ihr Verhältniss zur Saugethierfauna der Gegenwart," *Biol. Centralbl.* Bd., VIII., No. 19, Dec., 1888, pp. 582-631.

"Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiars und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten, I-VIII., Wien, 1887-1890 (*Beitrage Palæontologie Oesterreich-Ungarns*).

"Die Differenzierung des Säugetiergebisses," *Biol. Centralbl.* Bd. X., 1890.

"Die Entwickelung der verschiedenen Säugethierzahnformen im Laufe der geologischen Perioden," *Verh. deutsch. odontol. Ges.*, Bd. 3, Heft 2, 3, 1891.

"Ueber die systematische Stellung der Gattungen, *Plesiadapis*, *Protoadapis* *Pleuraspidotherium* und *Orthaspidotherium*," *Neues Jahrb. f. Mineralogie, Geologie, und Paläontologie*, Jahrgang, 1892, Bd. II., pp. 239, 240.

Schwalbe, G. "Ueber Theorien der Dentition," *Verh. d. Anat. Gesell. Strassburg*, 13-16, Mai, 1894.

Scott, W. B. "The Evolution of the Premolar Teeth in the Mammals," *Proc. Acad. Nat. Sci. Phila.*, 1892, pp. 405-444.

Seeley, H. G. "On the Nature and Limits of Reptilian Characters in Mammalian Teeth," *Proc. Roy. Soc.*, Vol. 44, 1888, pp. 129-141.

Stehlin, H. G. "Ueber die Geschichte des Suidengebisses," *Abh. d. schweiz. paläontolog. Ges.*, Vol. XXVI., 1899, Vol. XXVII., 1900, Zürich, 1899-1900.

Taeker, J. "Zur Kenntniss der Odontogenese bei Ungulaten," *Inaugural Dissertation*, Dorpat, 1892.

Thomas, O. "On the Homologies and Succession of the Teeth in the Dasyuridæ, with an Attempt to trace the History of the Evolution of Mammalian Teeth in General," *Philos. Trans.*, Vol. 1887, B., pp. 443-462.

"A Milk Dentition in *Orycteropus*," *Proc. Roy. Soc.*, Vol. 47, 1890, pp. 246-248.

"On the Dentition of *Ornithorhynchus*," *Proc. Roy. Soc.*, Vol. 46, 1889, pp. 126-131.

Tims, H. W. Marett. "Notes on the Dentition of the Dog," *Anat. Anz.*, Bd. XI., 1896, pp. 537-546.

"On the Tooth-genesis in the Canidæ," *Jour. (Zool.) Linn. Soc. Lond.* XXV., 1896, pp. 445-480, XXVIII., 1901, pp. 261-290.

"On the Succession and Homologies of the Molar and Premolar Teeth in the Mammalia," *Jour. Anat. Phys.*, XXXVI., 1902, pp. 321-343.

"The Evolution of the Teeth in the Mammalia," *Jour. Anat. and Physiol.*, Vol. XXXVII., 1903, pp. 131-149.

Tomes, C. S. *A Manual of Dental Anatomy, Human and Comparative*, 8vo, Philadelphia, 1898.

Topinard, P. "De l'Évolution des Molaires et Prémolaires chez les Primates et en particulier chez l'Homme," *L'Anthropologie*, No. 6, Nov., Dec., 1892.

Weber, M. *Die Säugetiere*, Jena, 1904.

Winge, H. "Om Pattedyrenes Tandskifte, især med Hensyn til Tændernes Former." *Vidensk. Meddel. Naturh. Foren i Kjöbenhavn*, 1882.

"Jordfundne og nulevende Pungdyr (Marsupialia) fra Lagoa Santa, Minas Geraes, Brasilien," *Med. Udsigt over Pungdyrenes Slægtskab. E Museo Lundii*, Kjöbenhavn, 1893.

WOODWARD, A. SMITH. "Outlines of Vertebrate Palæontology for Students of Zoology," University Press, Cambridge, 1898.

WOODWARD, M. F. "Contributions to the Study of Mammalian Dentition, Part I., On the Development of the Teeth of the Macropodidæ," *Proc. Zool. Soc. Lond.*, May 2, 1893, p. 449-473.

"On the Succession and Genesis of the Mammalian Teeth," *Science Progress*, I., 1894, pp. 438-453.

"On the Milk Dentition of the Rodentia, with a Description of a vestigial Milk Incisor in the Mouse (*Mus musculus*)," *Anat. Anz.*, Bd. LX., Nr. 19, 20, 1894.

"Contributions to the Study of Mammalian Dentition, Pt. II., On the Teeth of certain Insectivora," *Proc. Zool. Soc. Lond.*, 1896, pp. 557-594.

"On the Teeth of the Marsupialia, with especial Reference to the Premilk Dentition," *Anat. Anz.* XII., Bd. XII., Nr. 12, 13, 1896.

WORTMAN, J. L. *The Comparative Anatomy of the Teeth of the Vertebrata*, 8vo, 1886.

[Origin of the Tritubercular Molar] "Studies of Eocene Mammalia in the Marsh Collection. . . ." Part I., "Carnivora," *Amer. Jour. Sci.*, Vol. XIV., Jan. 1902, pp. 93-98 ; Part II., *Amer. Jour. Sci.*, Vol. XVI., Nov. 1903, pp. 365-368.

ZUCKERKANDL. *Die Backenzähne des Menschen.*

Congress der deutschen und österrischen anthropologischen Gesellschaft, Wien, 1889.

INDEX.

GLASGOW: PRINTED AT THE UNIVERSITY PRESS BY ROBERT MACLEHOSE AND CO. LTD.