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TRITUBERCULY:

A Review Dedicated to the Late Professor Cope

BY

HENRY F. OSBORN

TRITUBERCULY: A REVIEW DEDICATED TO THE LATE PROFESSOR COPE.[1]

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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 paleontologists 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 développed 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 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

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[1] Reprinted from THE AMERICAN NATURALIST, December, 1897.

archetype. This has been opposed in one form or other by nearly all English morphologists, namely: Lankester, Forsyth-Major, Newton Parker, M. A. 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.

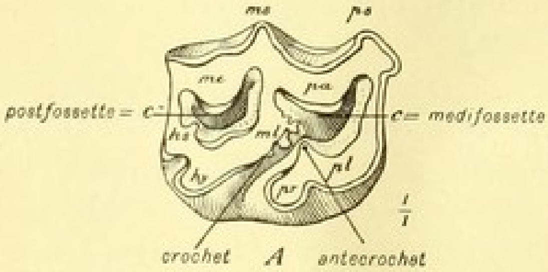

Fig. 1.—Horse Molar, *Merychippus*, Showing secondary folds.

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

		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.	Terminology used by English authors, Boyd-Dawkins ('67) 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 troisiéme 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	

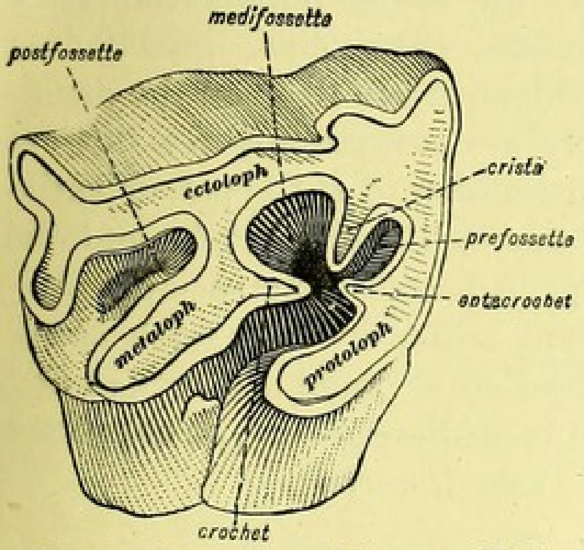

Fig. 2.—Rhinoceros Molar. Undetermined species, showing secondary folds.

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* and of *Aceratherium.* Imagine that you see the simple bunodont molar of such a form as Owen's *Hyracotherium vulpiceps*, 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

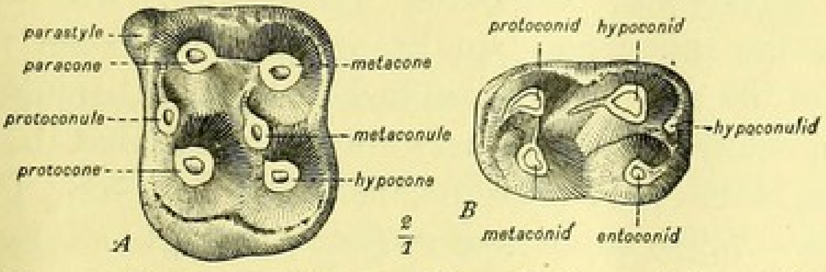

Fig. 3.—Simple Bunodont Molar.—*Hyracotherium vulpiceps*, after Owen.

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 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 *Pachy-lémuriens.*

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 in 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 or 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, 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.

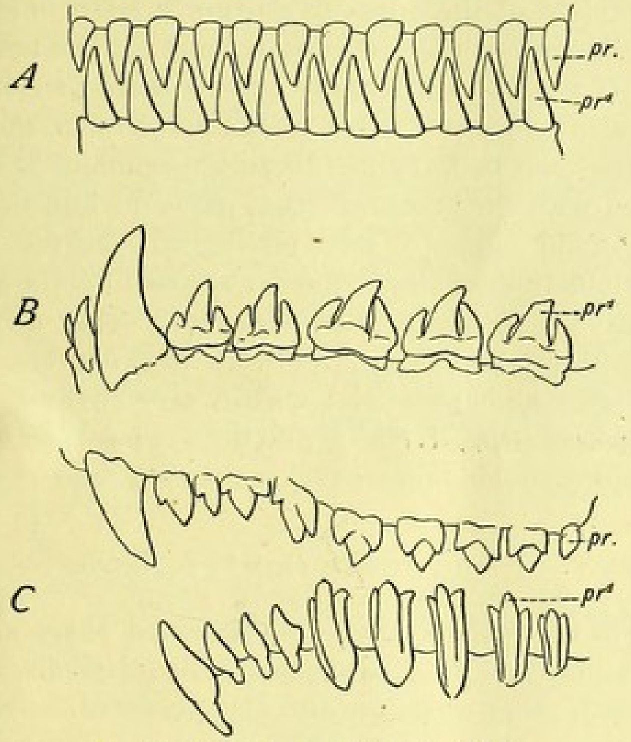

Fig. 4.—The Three Primary Forms.

A. Haplodont, of the Dolphin.
B. Triconodont (? Secondary) of the Seal, *Leptonyx.*
C. Tritubercular of the Cape Mole, *Chrysochloris.*

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

1. 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 Lower Cretaceous[1] and has been by far the most productive. The transitions between these great types

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[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.

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 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 *Thylacinus* 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. Again, among the Cetacea, all their oldest allies, such as *Zeuglodon*, are triconodont, not haplodont. With both these groups, therefore, there are therefore the possibilities of direct or of retrogressive origin of the "triconodont" molar.

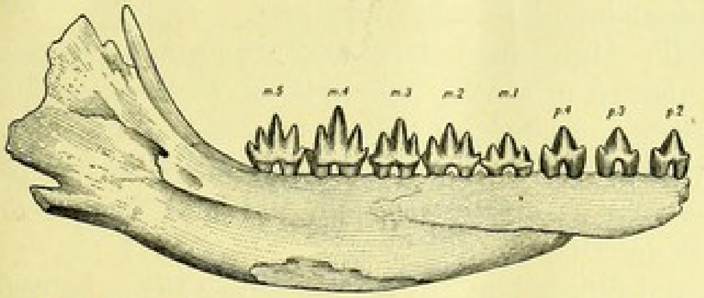


Fig. 5.—Amphilestes, a Jurassic triconodont, primary.

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 haplodont 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 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 later 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

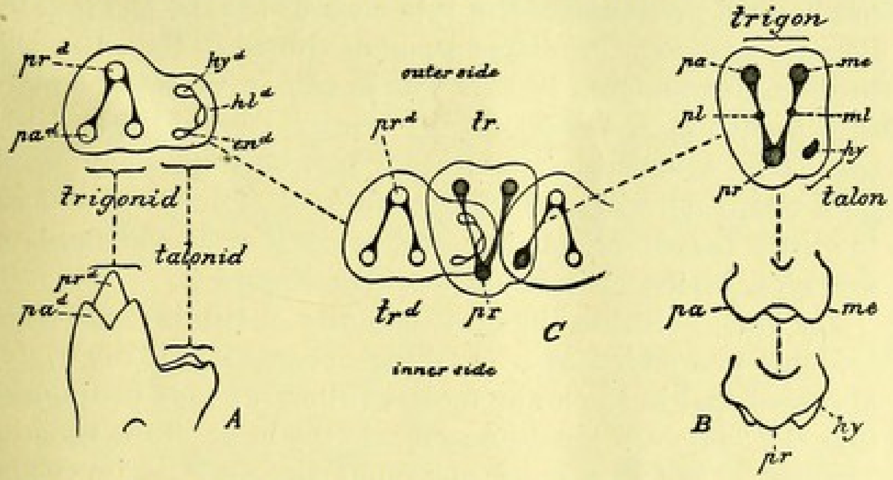


Fig. 6.—TRIGON AND TALON. Mechanical relations of tritubercular molars; also homologous and functionally analogous parts.

increasing support for the writer's hypothesis, that the multituberculate tooth is of tritubercular origin.

2. 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 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 evoluiton. Thus *Chrysochloris*, the little Insectivore of the Cape, presents a fine example of this type, persistent in its molars. (See Figure 4).

The Talon.—But in the 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 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

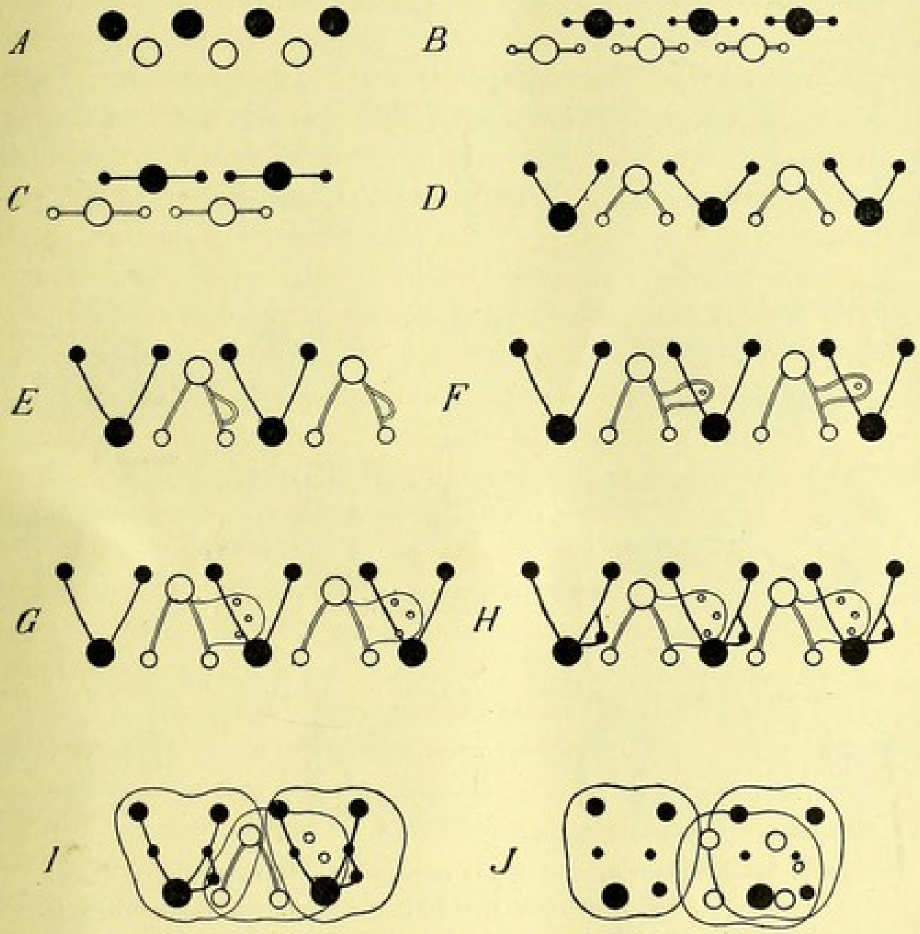


Fig. 7.—Phyletic and Mechanical History of the Molar Cusps.

A. Reptilian stage, Haplodont, Permian. *B.* Protodont stage (*Dromatherium*) Triassic. *C.* Triconodont stage (*Amphilestes*). *D.* Trituberculer stage (*Spalacotherium*). *E.* Tritubercular-tuberculo sectorial, Lower Jurassic. *F.* The same, in Upper Jurassic. *G.* The same, in Upper Cretaceous. *H.* The same, Puerco, Lower Eocene. *I.* Sexitubercular-sexitubercular, Puerco. *J.* Sexitubercular-quadritubercular, Wahsatch.

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 Figure 8).

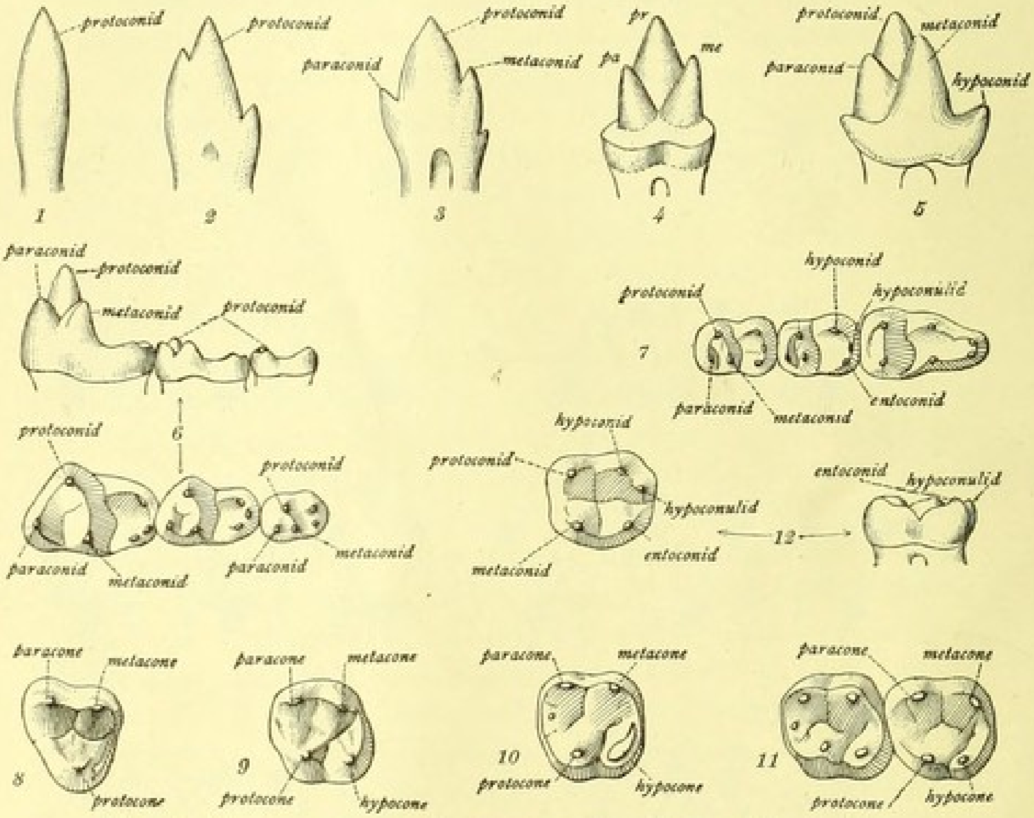


Fig. 8.—Epitome of the Evolution of the Human Molar Teeth.
1. Reptile. 2. Dromatherium. 3. Microconodon. 4. Spalacotherium. 5. Amphitherium. 6. Miacis. 7–8. Anaptomorphus. 9–12. Various Primates 11–12. Homo. A succession of molar *types*, not of ancestral types.

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 de-

This is the width of the letter press on the page as this figure will not look well, when the letters are crowded together, it would be best to leave out the right hand tooth D, & to put in the lettering to the third [illegible] tooth in the figure

pressed and that the pair of outer cusps, paracone and metacone, persisted on 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 (Fig. 9). 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.

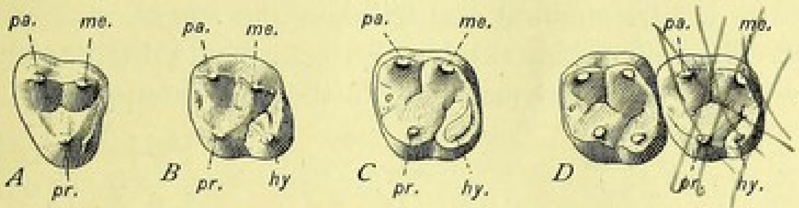


Fig. 9.—Superior molars of Primates, Anaptomorphus to Homo, showing evolution of *hypocone*, *hy*, from the cingulum.

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:

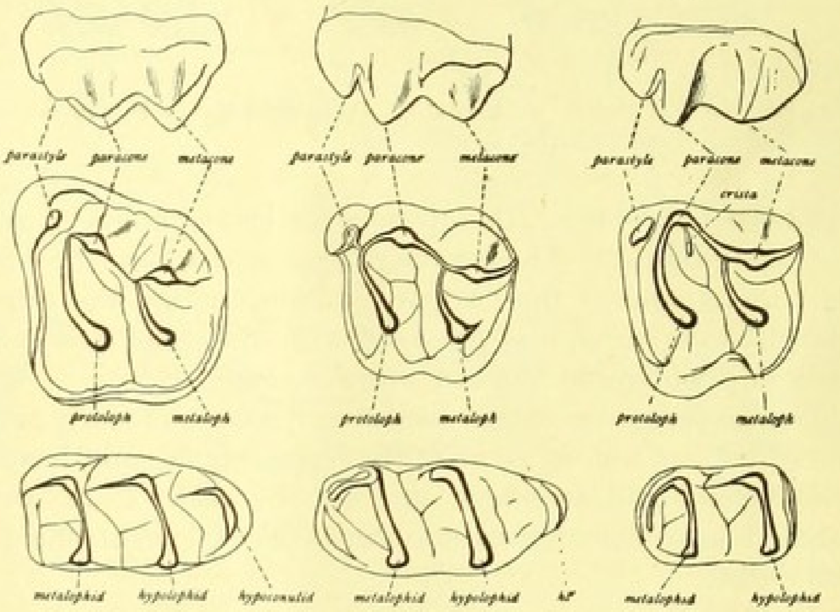
1°. The termination "*-cone*" is employed for all the primary central cusps derived from the crown of the tooth, while the diminutive *-conule* is employed for the smaller " intermediates " or cuspules.

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.

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.



Tapir Type. Lophiodon Type. Rhinoceros Type.

Fig. 10.—Modelling of the Cusps.

The use of the terms " trigon " and " talon " for the cutting and crushing regions of the crown, respectively, is especially advantageous among the 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 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. 8). 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.*

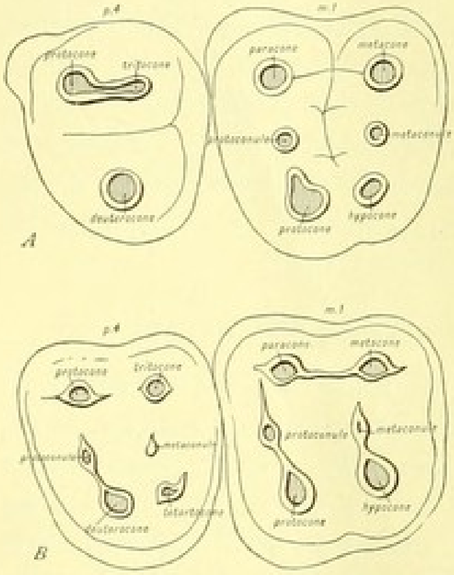


Fig. 11.—Premolar Terminology, proposed by Scott. Primitive Ungulate Types. Fourth upper premolar and first molar of *A. Euprotogonia*, and *B. Hyracotherium.*

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 paralellism 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. 10.)

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 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. 1). 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]

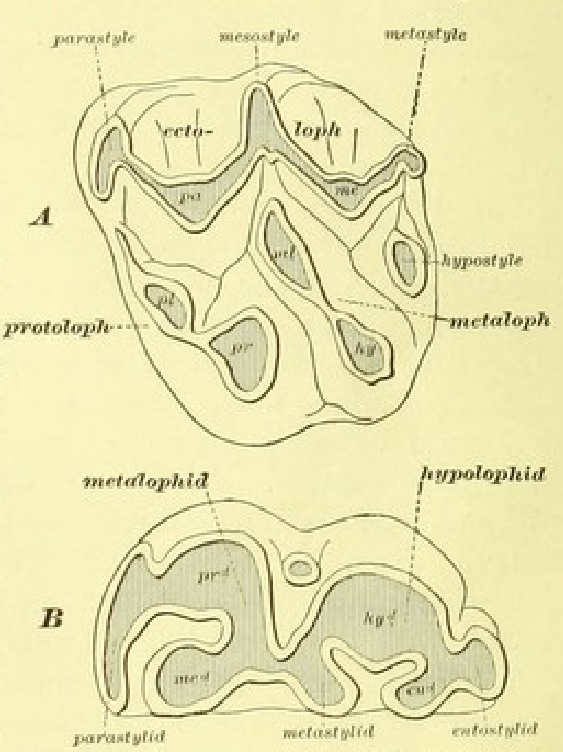


Fig. 12.—The Highest Development of the Styles. *A*. Upper molar of Horses, *Anchitherium* and *B*. *Merychippus*.

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

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[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.

in front of the paracone and protocone, as shown in the diagram (Fig. 6). Thus the inferior entostylid is developed near the entoconid, while the superior hypostyle develops near the hypocone. The first of the inferior 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, Amonodon* 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 2 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.[2] 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[3], after English usage, and those in German and French usage, have already been given in the Table

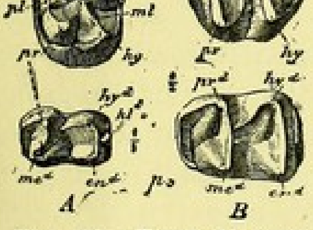

Fig. 13.—Tapir Molars. Primitive *Systemodon,* and modern *Tapirus.*

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[2] 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.

[3] "Siwalik Rhinocerotidæ," Pal. Indica.

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 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 proto-

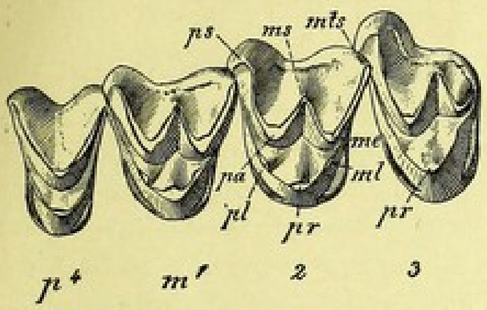

Fig. 14.—Molars of *Pantolambda*, the ancestor of *Coryphodon.*

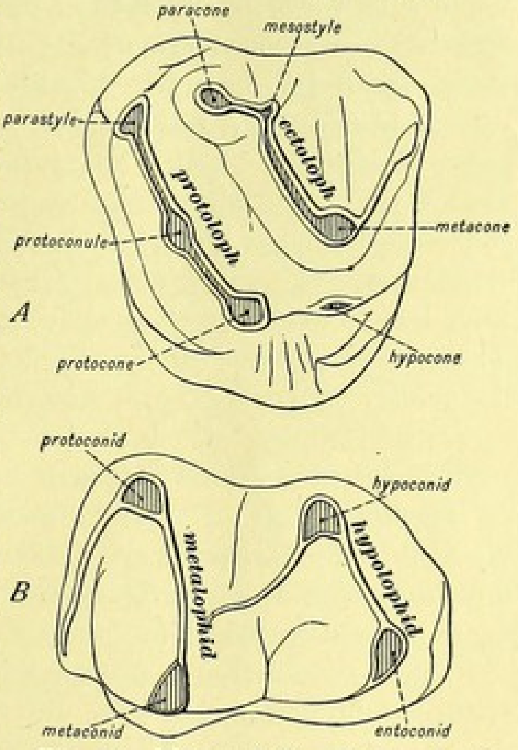

Fig. 15.—Molars of *Coryphodon*, showing shifting of the Crests.

conule 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 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. 12 and Fig. 15. 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 " Enchainements 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 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.

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