

ART. LXI.—*The Rise of the Mammalia in North America*;
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York.

[Continued from page 392.]

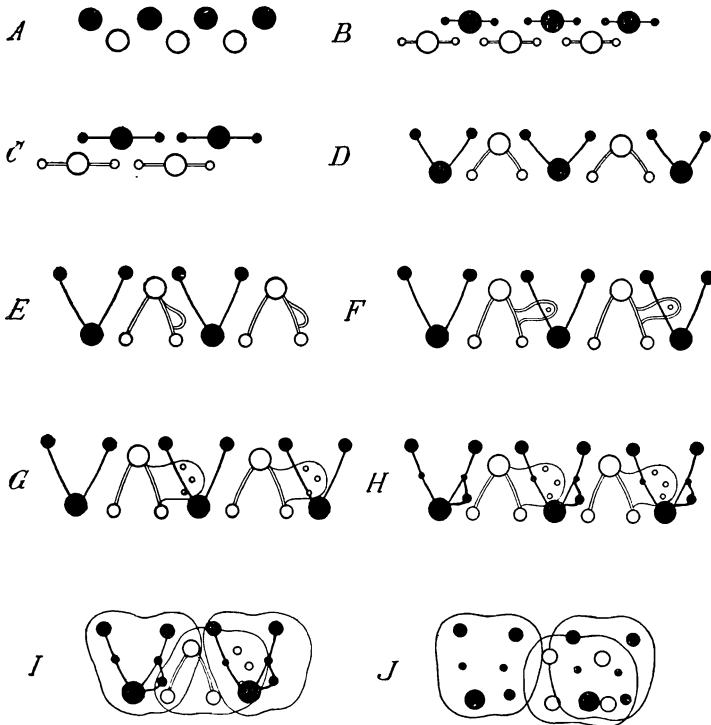
PART II.

Origin and Evolution of Trituberculism.

“CONCRESCENCE” is the newest theory of cusp evolution—an expansion by Kükenthal and Röse of views earlier expressed by Gaudry, Magitot and Dybowski. As Kükenthal derives three conical Cetacean teeth by splitting apart a triconodont molar, he conversely derives a triconodont molar by bringing together three reptile cones. Smith Woodward has called attention to the support the epidermal structures of the fishes give to this hypothesis, yet as applied to mammalian teeth, it comes from a one-sided Morphology which regards only the wonderful though mutilated chapters of Embryology when the untorn pages of Paleontology are at hand. Between the Trias and the Puerco, we are, so to speak, in at the birth of every successive cusp, and can observe positively that the law of cusp evolution is direct upgrowth from the smooth slopes of the crown or from the cingulum, that fertile parent of new cusps. Each new cusp is usually preceded by an abraded surface, and prophesied by an excessively minute hillock. It follows from this that cusps range in size and height directly according to their age—a principle beautifully demonstrated in some of the Mesozoic teeth. If the Kükenthal-Röse theory were correct, the oldest triconodonts should be iso-conid, whereas we know that the three equal cones of Triconodon are all a very late development; the earlier forms show the lateral cones receding to the needle-points of *Dromatherium*.

The tritubercular molar owes its survival to the original advantage of its triangular form, and to the possibilities of free cusp addition—as worked out by Cope, Wortman, Schlosser, Scott, and myself. Rüttimeyer’s term, “trigonodont,” best expresses the primitive structure of the upper and lower teeth, as of two interlocking triangles with their open bases turned outward in the upper and inward in the lower jaw. These “trigons” cutting past each other, made a shear so perfect that many Insectivora retained it without further evolution. But in most Trituberculates a talon was next added to the lower molar (Jurassic stage) as a pestle crushing into the upper valley; this talon gradually widened into a broad heel sup-

porting three cusps, as found in the Cretaceous. Consider the extreme antiquity of the three homologous cusps borne upon the back part of the human molar. This addition gave the opposed molars two shears and one crusher, and was so perfectly adapted to the needs of Lemurs and many Insectivores and Carnivores, in short, of most clawed animals, that they stopped at this point. Not so with the Herbivora, which required more extensive crushing surfaces. The upper molars, which had remained triangular through the Cretaceous and into the basal Eocene, began to develop a little talon, like that



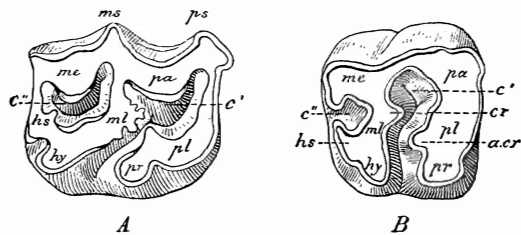
Phyletic History of the Cusps of the Ungulate Molars.
Upper molars in heavy lines, lower in light lines.

A. Reptilian Stage. Haplodont, Permian. B. Protodont Stage (*Dromotherium*), Triassic. C. Triconodont Stage (*Amphilestes*). D. Tritubercular Stage (*Spalacotherium*). E. Tritubercular-tuberculo Sectorial (*Amphitherium*).^{*} F, The same, in Upper Jurassic. G, The same, in Upper Cretaceous. H, The same, Puerco, Lower Eocene. I. Sexitubercular-sexitubercular. Puerco. J, Sexitubercular-quadrutubercular. Wahsatch.

^{*} Since this drawing was published I have learned that the talon of the lower molar of *Amphitherium* is considerably larger than here represented.

early seen in the lower molars, and at the same time both upper and lower molars entirely sacrificed their primitive cutting powers, and were converted from secodont into bunodont types by bringing the primitive trigons down to the level of the talons. At the same time, the upper molars acquired intermediate tubercles, and the triangular or oblique arrangement of the tubercles was shifted into the quadrangular or transverse arrangement. This outline is the result of fifteen years' observation.

With square crowns (*vs.* triangular) and six conic cusps above and below the molars of the Artiodactyl and Perissodactyl Herbivora ended their first constructive period and started upon their modernization. From this point we direct our attention upon the numerous combinations of three or four forms assumed by these single cones. The important thing now is to determine at what period these combinations were established, for there is wide difference of opinion as to when ungulate divergence began. To this I refer later. Taeker has recently shown how every modern embryonic lophodont or selenodont molar first exhibits the archetypal cones of the primitive bunodont. This law, together with my own parallel studies of the evolution of the horse and rhinoceros molars, led me to the discovery that these *embryonic primi-*



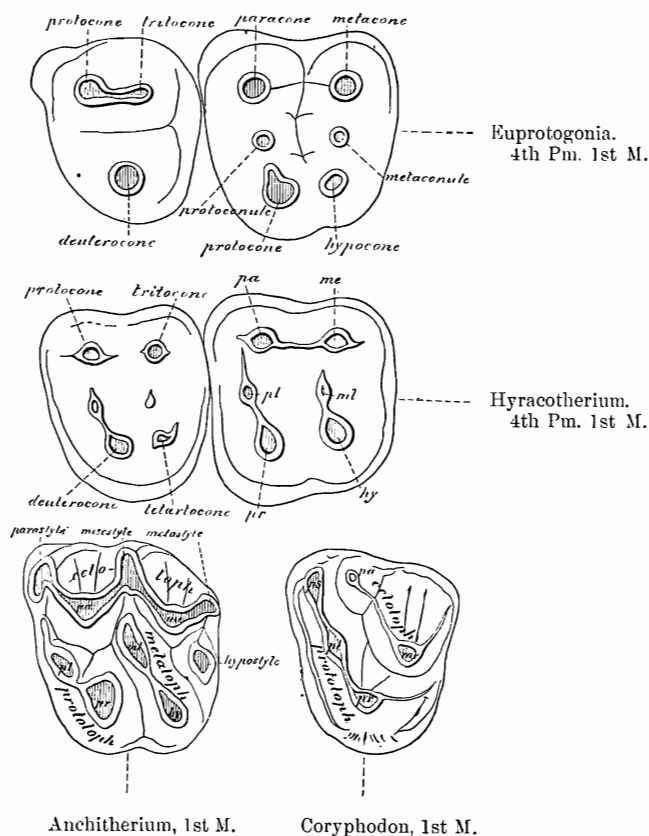
The Limits of Variation.

A, Merychippus. B, Aceratherium. Showing the secondary enamel foldings of the crests arising from the centers of the ancestral cones.

tive cones are also the main growth centers, for, in the upper Miocene, long after the Perissodactyla have separated from each other, we see the influence of the archetypal form in the generic and specific variations of the molars. Compare the teeth of *Merychippus* and of *Aceratherium*, and imagine that you see underlying the diverse crests and crescents the simple bunodont molar of such a form as *Hyracotherium leporinum* of the London Clay. You will then notice that the characteristic secondary folds and spurs of the Miocene teeth spring from the old bunodont cones, that the two "cement lakes" of *Merychippus* are equivalent to the two "fossettes" of *Acera-*

therium, because the "crescentic spurs" of the horse and the "crochet" and "antecrochet" of the rhinoceros spring alike from the primitive "intermediate tubercles."

In view of these discoveries of the uniformity of mammalian molar type, a uniform terminology has become as necessary for the dental cusps as for the carpal and tarsal elements of the feet. Professor Gaudry's once admirable system, elaborated in his "*Enchaînements*," was based upon the supposed



Homologies in the Horse and Coryphodon Molars and Premolars.

division of the ungulate molar into a "first lobe" and "second lobe," and is still followed in France. Yet it has two drawbacks: it precludes the comparison of the ungulate with the unguiculate molar, for neither lobe includes the complete triangle; still more inconvenient is the fact that we cannot compare the higher ungulates with the older Coryphodons and Peripptychidæ in which the molars were developed upon the

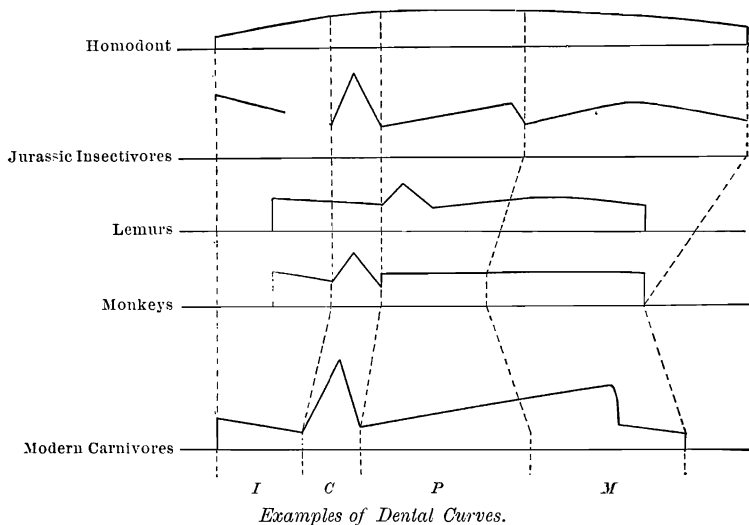
triangular plan; these teeth have only the first lobe and half the second. The upper molars of *Hipparion* and *Coryphodon* illustrate the advantages of this new system of comparison and of terminology.

Scott has made a further advance in Odontology by working out the laws of premolar evolution or cusp addition. In many groups we know that from one to four of the premolars gradually acquire the exact form of the molars in order to further increase the grinding surface, and we should *a priori* expect that the cusps would be added in the same order, and therefore be homologous with the molar cusps. This, as Schlosser and myself had observed, is not the case. Scott shows the order of cusp development in the premolars is very nearly the same in all the mammals, and yet is entirely different from the order followed in the molars. This law again, unexpectedly ties the clawed and hoofed mammals together; the sequence of cusps in palingenesis is similar to that observed by Tacker in embryogenesis, and Scott is justified in proposing a new terminology (protocone, deuterocone, tritocone, etc.) for the premolar cusps, which will in the end prove to be a great convenience.

I alluded above to the well-known extreme and very confusing similarity of the tritubercular molars in the early stages of divergence. Trituberculism is at once the cause of clearness and of doubt when we get back to the stem mammals of widely different phyla. This has led to strange misconceptions of phyletic affinities as exemplified in Filhol's division "*Pachylémuriens*," a supposed mixture of lemur and ungulate stock. There was never any such mixture, and the question comes up how to distinguish unlike forms with like teeth? I have proposed to make use of a *dental curve* which will express the incipient atrophy of some parts, and hypertrophy of other parts of the series, a metatrophism which will naturally terminate in the reduction of some teeth, and excessive development of others. This has not been by any means fully worked out, but I believe it will prove to be of great service in directing attention to some of the initial tendencies of divergence, which are not expressed either in the dental formula or in the patterns of the teeth. Below are some of these curves. When worked out by the composite method, we will find certain primary curves characteristic of the ordinal divisions, and minor curves distinguishing the lesser divisions. Of course the laws of parallelism will also be found in force here; flesh-eating, insect-eating, and grass-eating animals will be apt to have similar curves even when evolved in different groups, but here the dental formula and succession will come to our aid.

Breaks and Links in the Mesozoic Fauna.

By our hypothesis all three sub-classes flourished together during the American Mesozoic; the Marsupials disappeared, then the Monotremes, and by the end of the basal Eocene the Placentals were in exclusive possession of the northern continent.



Although we have great reason to congratulate ourselves upon the rapid progress of discovery, there still remain great gaps in Mesozoic time between certain horizons and in the lineal phyletic series of both the Mesozoic and Cenozoic. For a time standard we may take advantage of the remarkably constant evolution of the Plagiaulacidae in the Mesozoic, and of the Equidae in the Cenozoic—as certain invertebrates are made use of in older rocks. The grooves and tubercles of Plagianlax and the cusps and styles of the horses are added with the precision of clockwork, and supposing that the rate of evolution has been about the same, we can approximately estimate both the periods of deposition and the intervals as below.

	PLAGIAULACIDAE.				
	Stonesfield.	Purbeck.	Laramie.	Puerco.	Cernaysian.
Number of Premolars,	?	4-3	2	2-1	1
Grooves on Premolars,	?	7-9	11-14	12-15	14
Molar Tubercles: outer; inner;	?	4:2	6:4	6:4	9:6

Estimating the geological intervals by dental evolution and faunal succession, there is first the great gap between the Trias of Microlestes and Dromatherium and the Jurassic of the

Stonesfield slate; there is a relatively shorter interval, but still a considerable one between this and the Purbeck or *Atlantosaurus* beds. Then follows another long and very important interval between the *Atlantosaurus* beds and the Laramie (Upper Cretaceous). The gap between the Laramie and Puerco was relatively short as indicated by the comparatively limited evolution both of the *Plagianlacids* and *Trituberculates*. The Puerco itself was a long period in which the *Plagianlacids* underwent considerable changes. Then follows an interval which it is most important to fill by future exploration, for between the Puerco and the Wahsatch the differentiation of the even and the odd-toed ungulates must have occurred. The Wahsatch proper does not mark a very extensive evolution of the forms it contains. It passes after a slight break into the base of the Bridger (Wind River) and then begins that splendid and almost uninterrupted succession of lake basins, terminating in the Pliocene. I append a table, to be compared with that published by Marsh in his admirable address of 1877, and exhibit the great progress of the last sixteen years.

The general faunal succession is marked by the sudden appearance and disappearance of certain series and rise and fall of great groups. In the Trias appears the remarkable protodont or primitive-toothed *Dromatherium*; we cannot determine its Order at present. We still have no American fauna corresponding to the intermediate Stonesfield of England. In the Jurassic *Atlantosaurus* beds the three supposed representatives of the *Monotremes* (*multituberculates*), *Marsupials* (*triconodonts*) and *Placentals* (*trituberculates*), appear in equal numbers; the latter are generally characterized by the primitive dental formula. In the Laramie the *Multituberculates* continue in great profusion, and the *Marsupials* and *Placentals* are also numerous.

The serial succession of the *Trituberculates* from the Mesozoic is still an unknown chapter; we are utterly unable to connect the *Dromatheriidae* of the Trias, the *Triconodontidae*, *Amphitheriidae* and *Amblotheriidae* of the Jura with each other, or with any Cretaceous or lower tertiary mammals. The serial relations of the *Multituberculates*, on the other hand, have been made much clearer by the discovery of the Laramie fauna. Cope and Marsh in this country, and Smith Woodward in England, have at last broken into the long barren Cretaceous. In studying the accurate figures published by Marsh and a large collection of teeth recently made for the American Museum by Wortman and Peterson, I find that this Laramie fauna is widely separated from the Jurassic in its general evolution, and as Gaudry, Lemoine and Cope have observed, it approaches more nearly the basal Eocene of the Puerco and

THE SUCCESSION OF THE NORTH AMERICAN MAMMALIA.

PERIODS.	HORIZONS.	CHARACTERISTIC GENERA. NEW TYPES APPEARING.	TYPES BECOMING EXTINCT.
Pleistocene. TRUE PLEISTOCENE.	EQUUS.	<i>Equus</i> , 5 species. Elephant, <i>E. primigenius</i> . Mastodon. Llamas. Camels, <i>Eschaltius</i> , <i>Holomastoides</i> . Elk, <i>Alces</i> . <i>Ptilodonta</i> . Sloths, <i>Myodon</i> , <i>Glyptodon</i> . <i>Ursus</i> .	
	BLANCO.	<i>Equus</i> , 3 species. Mastodon, 3 sp. Llamas, <i>Pitacucha</i> . <i>Platygonus</i> . Sloth, <i>Megalonyx</i> . <i>Felidae</i> (?) <i>Hyaenidae</i> . <i>Mustelidae</i> .	
MIOCENE.	LOUP FORT.	<i>Prochippus</i> . <i>Hipparion</i> . Mastodon. Rhinoceroses, <i>Aphelops</i> , 5 species. <i>Cynidea</i> . <i>Felidae</i> . Rodents. <i>Elanoides</i> . Camels and Llamas, <i>Procamela</i> , <i>Protolabis</i> . <i>Oreodonts</i> , 3 genera. Deer, <i>Gastromeryx</i> , <i>Cosmoryx</i> .	Extinction of <i>Oreodonts</i> and hornless rhinoceroses.
	DEEP RIVER.	<i>Prochippus</i> . <i>Anchitherium</i> . First Mastodonts. <i>Oreodonts</i> , <i>Cyclopidius</i> . <i>Chalicotherium</i> . <i>Tylopoda</i> . <i>Miohippus</i> . Two-horned Rhinoceros, <i>Diceratherium</i> . Pecaries. <i>Oreodonts</i> . Rodents. <i>Cynidea</i> , <i>Felidae</i> . <i>Tylopoda</i> .	Disappearance of <i>Chalicotherium</i> . Ext. of <i>Oreodonts</i> , <i>Hyaenodonts</i> . Extinction of <i>Elotheres</i> and <i>Hypomys</i> .
	JOHN DAY.	(?) <i>Miohippus</i> . Artionyx. Appearance of triangulines, <i>Kithures</i> , <i>Hypomys</i> , pigs and peccaries, true dogs, cats, monkeys, <i>Leptacanthus</i> , <i>Colodon</i> . <i>Chalicotherium</i> . <i>Aceratherium</i> . <i>Protopithecus</i> . <i>Artiotherium</i> . <i>Asiaticus</i> . <i>Tylopoda</i> , <i>Pachrotherium</i> . <i>Oreodonts</i> , <i>Hyaenodont</i> . Rodents. Insectivores.	Extinction of <i>Hyaenodonts</i> . Extinction of <i>Amynodonts</i> .
	WHITE RIVER. PROTEROGENES. (Upper.) ORKODON. (Middle.) TITANOTHERIUM. (Lower.) UINTA.	<i>Ephippus</i> . <i>Amynodon</i> . Titanotheres, <i>Diplotodon</i> . First <i>Oreodonts</i> , <i>Protoreodon</i> . First <i>Tylopoda</i> , <i>Leptacanthus</i> . Tapirs. <i>Hyaenodonts</i> . Rodents. <i>Oreodonts</i> , <i>Mesonyx</i> . <i>Pachynolophus</i> . Appearance of <i>Amynodonts</i> and horned Titanotheres. <i>Palaosyops</i> . <i>Hyaenodonts</i> . <i>Triplous</i> . <i>Achenodon</i> .	Extinction of <i>Diplotodon</i> , of some <i>Oreodonts</i> . Extinction of <i>Tylopoda</i> .
EOCENE.	BRIDGER. WASAKIE. (Upper.)	<i>Pachynolophus</i> . Appearance of Insectivora, Cheloptera, <i>Hyaenodonts</i> , <i>Umbelliferum</i> . <i>Palaosyops</i> . <i>Oreodonts</i> . <i>Coryphodon</i> . <i>Phenacodus</i> .	Extinction of <i>Diplotodon</i> , of some <i>Oreodonts</i> . Extinction of <i>Tylopoda</i> .
	FRINGER. (Middle.) WIND RIVER. (Lower.) WALSATCH.	<i>Hyaenodonts</i> . Appearance of <i>Artiodactyls</i> , <i>Perissodactyls</i> : tapirs, horses, <i>Umbelliferum</i> . <i>Oreodonts</i> . First <i>Oreodonts</i> . <i>Leontis</i> and <i>Monkys</i> . <i>Oreodonts</i> , 6 families, <i>Palaosyops</i> .	Extinction of <i>Coryphodon</i> and <i>Cynodactylus</i> . Extinction of <i>Artiodactyls</i> .
	Interval.	(Differentiation of modern clumped and hoofed placentalis.)	
	PUEBLO.	<i>Ptilodus</i> . <i>Neoplagiatus</i> . <i>Polypastodon</i> . Ancient types of Ungulates, Carnivores and Insectivores. <i>Ambylopoda</i> , <i>Cynodactylus</i> . <i>Tamodon</i> . <i>Tamodon</i> . <i>Leontis</i> .	Extinction of <i>Multituberculatus</i> , (? <i>Monotremes</i>). Disappearance of <i>Marsupials</i> .
UPPER CRETACEOUS.	Interval.	(Differentiation of ancient clumped and hoofed placentalis.)	
	LARAMIE.	<i>Ptilodus</i> . <i>Bolodontidae</i> (<i>Multituberculatus</i>). <i>Trituberculatus</i> . <i>Trituberculatus</i> and <i>Marsupials</i> , typical dentition.	
MIDDLE JURASSIC.	Interval.	(Differentiation of ancient clumped and hoofed placentalis.)	
	ATLANOSURUS.	<i>Cladodon</i> . <i>Plagiatus</i> , <i>Bolodon</i> . <i>Multituberculatus</i> (? <i>Monotremes</i>). <i>Trituberculatus</i> (? <i>Marsupials</i>). <i>Trituberculatus</i> , primitive dentition.	
UPPER TRIASSIC.	Chatham Coal Beds.	<i>Protodonta</i> , <i>Dromotherium</i> , <i>Microcanodon</i> , primitive <i>Trituberculatus</i> (? <i>Monotremes</i>).	

the Cernaysian of France. The Multituberculates of the Laramie include the Plagiaulacidæ, represented by *Ptilodus*, the form with two premolars, and *Meniscoëssus*, with two premolars and crescentic tubercles. *Meniscoëssus* has a smaller fourth premolar, and is found to lead off to the huge plagiaulacid *Polymastodon* of the Puerco. The only other Multituberculates found are those related to *Bolodon* of the Jurassic and *Chirox* of the Puerco. The other mammals of the Laramie range from the mouse to the opossum in size; they have superior molars of the simple tritubercular type—the low cusped or bunodont molar predominating in the upper jaw, and the tuberculo-sectorial in the lower. The dental formula is mostly the typical p. 4, m. 3. Yet, judging by the angular region of the jaws, we have here both Placentals and Marsupials. Some of the teeth remind us strongly of those in the Puerco; their determination, however, is very difficult, for the jaws and teeth are almost entirely isolated. From another exposure of the Laramie, Cope has recently found the remarkable type *Thlæodon*—remarkable because it is a highly specialized trituberculate of typical dentition with a jaw which bears resemblance to that of the Multituberculates and of *Ornithorhynchus*. There is no placental angle nor strong marsupial inflection. This raises the supposition that *Thlæodon* may be one of the persistent trituberculate Monotremes which we are now looking for.

In the Puerco or basal Eocene, a very marked change occurs, for the American fauna loses some of its cosmopolitan character, the Multituberculates or monotremes die out and the marsupials are not found at all; in fact they do not reappear in North America until the Miocene.

Ancient and Modern Placental Differentiation.

The Puerco is essentially an archaic fauna and is to be regarded as the climax of the first period of placental differentiation, a culmination of the first attempts of nature to establish insectivorous, carnivorous and herbivorous groups. These attempts began in the Cretaceous, and some of the types thus produced died out in the Puerco, some in the Wahsatch and Bridger; only a few flesh-eaters survived to the Miocene. It is most important to grasp clearly the idea of this functional radiation in all directions of this old Puerco fauna, resulting in forms like the modern insectivores, rodents, bears, dogs and cats, monkeys, sloths, bunodont and selenodont ungulates, and lophodont ungulates. This was an independent radiation of placentals, like the Australian radiation of marsupials. What

was the cause of the wide-spread extinction of these types? So far as the ancient clawed types are concerned, their teeth and feet seem to be as fully adaptive in many cases as those of the later ungulates; the hoofed types were certainly inferior in tooth evolution, for all their molars evolved on the triangular basis instead of the sextitubercular; the most sweeping defect of both the clawed and hoofed types, was the apparent incapacity for brain growth, their bodies went on developing while their brains stood still. Thus the stupid giant fauna, the Dinocerata, which rose out of this period, gave way to the small but large-brained modern types. It is noteworthy that the latest survivors of this wreck of ancient life were the large-brained Hyænodons.

Some of the least specialized spurs of this radiation appear to have survived and become the centers of the second or mid-Tertiary radiation from which our modern fauna has evolved. Yet we have not in a single case succeeded in tracing the direct connection. To sum up, we find on the North American continent evidence of the rise and decline and disappearance of monotremes and marsupials, and two great periods of placental radiation, the *ancient radiation* beginning in the Mesozoic, reaching a climax in the Puerco and unknown post-Puerco, and sending its spurs into the higher Tertiary, and the *modern radiation* reaching its climax in the Miocene, and sending down to us our existing types.

Another Eocene center was lower South America, which has of late dimmed the prestige of North America in yielding strange forms of life. One theory of this Patagonian fauna is that it was an independent center of functional radiation like the Puerco and Australian, full of adaptive parallels, but not yielding to Europe or America any of their older types. But Ameghino, to whose energetic researches we are chiefly indebted, believes that he finds a lower Eocene life zone—a sort of *south polar* center—which supplied both America and Europe. The Puerco he believes is no older than the Santa-cruzian which in turn is very much older than the Parana and Pampean formations, which Burmeister has made so well known. This yields the Homunculus patagonicus which parallels Cope's Anaptomorphus in presenting a dentition as advanced in reduction as that of man. Ameghino finds here the ancestors of the Macrauchenidæ; he believes the Homodontotheridæ are the ancestors of the Chalicotheriidæ—thus mistakenly deriving a buno-selenodont from a lophodont type; the Proterotheriidæ, he believes, replace the Condylarthra and

Hyracotherium in the ancestry of the horses. Similarly the Microbiotheriidae are the stem of the creodonts and carnivores. I cannot coincide with any of these views. The Multituberculates are far older and widely different from the Abderites to which Ameghino traces their ancestry. I fully concur with the opinion of Cope, Zittel, Scott and others that this fauna is of somewhat later age, that it was directly connected with Australia and somewhat later with North America, supplying us, as has always been supposed, with our sloths. I quote from a recent address by Scott:

“The oldest mammals from South America are those from Patagonia, which Ameghino has referred to the Eocene, but which are more probably Oligocene or Miocene. This fauna is of extreme peculiarity and isolation; it is made up chiefly of edentates, rodents and ungulates of those very aberrant types known as Litopterna and Toxodontia, which are so widely different from the hoofed mammals of the northern hemisphere: together with some primitive forms of primates, creodonts and marsupials. The marsupials are of extraordinary interest, for they comprise not only forms allied to the opossums, but also to recent Australian forms such as *Thylacinus*, *Dasyurus* and *Hypsiprymnus*. This is a most unexpected fact and seems to point unmistakably to a great southern circumpolar continent.”

The North American Puerco thus remains the most extensively known and productive lower Eocene center yet we have very slender threads of positive evidence to connect its fauna with the later placental radiation.

The Creodonts of Cope occupy the same relation to the modern insectivores and carnivores that the Condylarthra do to the ungulates. The American group has been recently enriched by the discoveries of Wortman, and the literature by the careful revision of Scott. This author has divided them into eight families, placing the forms which most resemble the Insectivora in the new family, *Oxyclenidae*. These families illustrate superbly the same law of functional radiation later repeated in the placental and marsupial carnivores. The *Mesonyx* family presents some analogies to the *Thylacines*. The modern bears are paralleled in the *Arctocyons*, with their low tubercular molars; Wortman and myself, with fresh materials, have recently added *Anacodon* to this family, a genus which was doubtfully regarded by Cope as an ancient ungulate. The Cats and *Hyænas* are imitated in the *Oxyænas* and *Hyænodons*, some of the Miocene forms of which Scott suggests developed aquatic habits; as above noted, some of this family acquired large brains and persisted well into the Miocene. A

still more remarkable likeness to the Cats is exhibited in the *Palæonictis* family, which, unlike the *Hyænodonts*, forms its sectorials out of exactly the same teeth as the true cats. The first American *Palæonictis* was found two years ago by Wortman, and this author and myself have suggested that this may be the long-sought ancestor of the *Felidæ*. The *Civets* are anticipated in the *Proviverridæ*; yet both Cope and Scott, the highest authorities on this subject, believe that the dog-like *Miacidæ* alone formed the connecting link between the *Creodonta* and the true *Carnivora*.

The foot structure of the ancient *Puerco* ungulates is still only partly known. Cope has divided these animals into the *Amblypoda* and *Condylarthra*. The *Amblypoda* are represented in the *Puerco* by a large form called *Pantolambda*, with selenodont triangular upper molars, and possibly by *Peripitychus*, with bunodont triangular molars. The *Pantolambda* molars were, as Cope has shown, converted into those of *Coryphodon*, the great lophodont *Amblypod* of the *Wahsatch*, by a process exactly analogous to that in which the *anterior* half of a *Palæotherium* molar was formed, that is, they acquired outer and anterior crests but no posterior crests. This *Coryphodon* molar type was still later converted into the *Uintatherium* type by swinging around the outer crest into a transverse crest. I have recently made a careful study of the fore and hind feet of *Coryphodon*, and have found that while the fore foot was subdigitigrade like that of the elephant, the hind foot was fully plantigrade, the entire sole resting upon the ground. The relation or connection between the *Bridger Dinocerata* and these earlier *Amblypoda* is still unknown. The *Puerco Peripitychus* left no descendants. The other ungulates of the *Puerco* were the *Condylarthra*, including the primitive *Phenacodontidæ*, the supposed ancestors of the *Artiodactyls* and *Perissodactyls*. Much remains to be done to clear up their relationships.

Succession of the Perissodactyls.

In the *Wahsatch* and *Wind River* we find not only the last of the *Phenacodonts* and *Coryphodonts* and the first of the *Dinocerata*, but the first of the true *Artiodactyls* and *Perissodactyls*. Recent studies of Cope, Schlosser, Pavlow, Filhol have been directed to the phylogeny of the *Perissodactyls* with very different conclusions. I agree most closely with Schlosser, and have endeavored to show that the molar teeth give us a key to their natural arrangement as shown in this column.

...	{	Titanotheres.	Upon one side the Titanotheres present
	{	Horses.	the bunio-selenodont extreme with most
...	{	Palæotheres.	analogies to the Artiodactyla in tooth struc-
	{	Tapirs.	ture and in their truly Artiodactyl fore
...	{	Lophiodonts.	feet and bony horns. (If, as Cope sup-
	{	(Helaletes).	poses, the Diplarthra form a natural group,
	{	Hyracodonts.	some Perissodactyls should certainly be
....	{	Amynodonts.	more Artiodactyl than others.) The
	{	Rhinoceroses.	

Horses and Palæotheres diverge from the bunio-selenodont type towards the Lophodont; they were early separated in foot structure. The Tapirs, Lophiodonts, and Helaletes show well-marked transverse crests and incipient external crests. This brings us to the other Lophodont extreme, the Rhinoceros-like forms, with complete transverse and external crests. There are many other minor characters which support this as the natural arrangement of the Perissodactyls. I think it can be shown conclusively that these eight or nine series diverged from each other before the Wahsatch, and that all attempts to derive them from each other in later periods will break down. They will be found to converge into the unknown Sub-Wahsatch period, to stem forms as indicated by the brackets.

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The Titanotheres have been traced by Cope back to Lambdotherium in the Wahsatch; in the Wind River the true Palæosyops is found, and in the Bridger this becomes the predominant perissodactyl family, and spreads out into a great variety of forms, which have recently been carefully described by Earle. In the Washakie there are some still larger forms, and Marsh has traced the line through the teeth of Diplacodon of the Uinta to the true Titanotheres. Still the origin of the flattened skull and remarkable anterior pair of horns has never been known; Hatcher reports species with very small horns in the base of the Titanotherium beds (Lower Miocene). Wortman has just reported to me the brilliant discovery of an upper Eocene (Bridger and Washakie) Palæosyops with a flattened skull and rudimentary horns just appearing upon the nasals! This forms the desired connecting link.

The early history of the horses, probably starting with the Puerco Condylarth Euprotogonia, and passing through Hyracotherium, Pachynolophus, Epilippus, Meshippus, is now familiar enough. It is the later history which requires elucidation, and is producing the most unexpected number of parallel lines of horses, out of one of which only our modern horse sprang. Here we are especially indebted to Cope, Pavlow, and Scott. By general consent Hipparion comes out of its old position in the true line as displaying the most extreme

variations in the crowns of the molar teeth in compensation for the backward evolution of its feet. Scott has been especially investigating the upper Miocene horses; I quote from the MSS. he has kindly lent me, in which he proposes to remove also the classical *Anchitherium* of Cuvier. He says: "These American genera, *Meshippus* and *Miohippus* may confidently be regarded as important members of the equine stem, while *Anchitherium* (of Europe) from present information would appear to belong to an abortive side branch leading to no permanent results." Scott has also discovered an important intermediate form linking *Miohippus* with *Protohippus*.

The *Palæotheres* have not been found in America.

The Tapir line has been traced by Cope and myself back to *Systemodon* of the Wahsatch, and *Isectolophus* of the Bridger and Uinta. These forms have simple premolars, but bear the most striking resemblance to the Tapirs in the molars both above and below. All previous attempts to determine the Miocene representatives of the Tapirs have been erroneous. Wortman and Earle have just published an account of two lower Miocene species of true Tapirs, which, both in foot and tooth structure, definitely carry the American Tapir line up to the middle Miocene, where it is again lost sight of. These species belong to the genus *Protapirus*, which Filhol has found in the Oligocene of France, thus adding an important geological parallel. The Wahsatch Tapirs were a little larger than the Horses or *Hyracotheres* which were about the size of a fox, and much smaller than the ancestral *Titanotheres*.

Another family of small, slender perissodactyls more nearly allied to the *Lophiodons* of Europe than any other American forms are the *Heleatidæ*, distinguished by feet tending to monodactylism, and narrow hoofs like those of the deer; even in the Wahsatch *Heptodon* the lateral toes are quite short and raised off the ground. The molars, like those of the *lophiodons* of Europe, are intermediate between those of the Tapir and the *Rhinoceros*, but both teeth and feet preclude our uniting these forms either with the Tapirs or with the *Hyrachyus* family, as Cope has done. The Bridger successor is *Heleletes*, which Marsh mistakenly supposed was an ancestral Tapir, and the integrity of this line is now firmly established by the discovery of the Miocene *Colodon*. This is described by Marsh as a successor of *Heleletes*, and Wortman and Earle have just published an account of the teeth and feet, showing that *Colodon* is widely separated from the contemporary true Tapirs, and is the last member of the *Heptodon-Heleletes* line.

The *Rhinoceroses* of America comprised the true *Aceraitheriinae* and *Diceratheriinae*, and what may be called the

pseudo-rhinoceroses, the Hyracodons and Amynodons; all these forms present the true Rhinoceros molar pattern, but they diverge most widely in the structure of the anterior teeth and of the feet. The Hyracodons first appear in the numerous and diversified Hyrachyus of the Bridger, some of which exhibited rudimentary horns upon the back part of the nasals (Colonoceras); they retained a full set of equal-sized incisors and canines, and acquired a horse type of skull, skeleton, and locomotion. Scott has well named them the "cursorial rhinoceroses." Colonoceras probably did not, as Marsh has suggested, branch off into Diceratherium, for the horns of this true rhinoceros are developed at the ends of the nasals; the Hyrachyinae sent off as a side branch the deer-like Triplopus of the Washakie, and terminated in the Hyracodons of the lower Miocene.

The Amynodons, at the time of their discovery by Marsh, were naturally supposed to be the long-sought Eocene rhinoceroses, but I have shown that no Amynodon can fill this rôle. Garman's discovery of the skull of the remarkable Miocene Metamynodon tended to confirm my views, and I have now to report the discovery of many skulls and a nearly complete skeleton by the American Museum Expedition. This proves that the Amynodontidæ were remarkable side forms. In wide contrast with the true rhinoceroses, the upper and lower canines develop into huge, partly recurved tusks, like those of the boar. As in Elasmotherium, the premolars become greatly reduced, and the molars tend to hypsodontism. The lower molars are long and narrow, like those of the anomalous Cadurcotherium of the Oligocene of Europe—it is thus rendered probable that Cadurcotherium is not a sloth, as Filhol has suggested, but is an aberrant rhinoceros, related to, if not identical with, the Amynodons. The hypsodontism in some Metamynodon teeth is accompanied by a partial loss of enamel. To complete the aberrant character of this family, we find that it has four equal-sized and completely functional toes in the fore-foot, like those of the Titanotheres, not with the fifth toe reduced as in the contemporary Aceratheria.

The true Rhinoceroses, we remember, are distinguished by the entire loss of upper canines. Wortman has just reported finding rudimentary upper canines in both the milk and permanent dentitions of the older Miocene species. The true rhinoceroses suddenly appear in the lower Miocene of America and Oligocene of Europe; we have not yet traced them back. In a collection of lower Miocene skulls recently obtained for the American Museum we find that the premolars are still very simple. In the higher Oreodon beds all traces of the superior canine are lost, and the premolars have become more like the

molars. As the origin of the rhinoceroses still remains a mystery, so their later evolution needs clearing up. The American series suddenly terminate in the huge, hornless forms of the upper Miocene. I find there is still no unanimity of opinion as to the phyletic relationships of the Miocene, Pliocene and existing species of Europe.

Succession of the Artiodactyls.

The Eocene Artiodactyl phylogeny is still far behind that of the perissodactyls, but the Miocene and Pliocene succession has been worked up with great success and clearness by Cope and Scott. The latter says in a recent paper: "All the great groups of Artiodactyla are seen to arise independently from the Buno-Selenodonta which forms as it were a lake, from which several streams, flowing partly in parallel partly in divergent directions, are derived."

The Elotheriidae appear in Parahyus of the Bridger and Achænodon of the Washakie, and terminate in the middle Miocene in the gigantic *Elotherium ramosum*, an animal with a skull three feet long, both the jaws and skull being armed with long branching processes. The true bunodont pigs and peccaries have not yet been found lower than the White River.

Scott has traced the Oreodons back to Protoreodon of the top of the Eocene. The aberrant Agriochæridæ, he believes, were doubtfully connected with the true Oreodons by a lower Eocene stem form. The true Oreodons, which existed in great herds in the lower Miocene, have been divided by Cope and Scott into three parallel lines extending into the Loup Fork, namely, the large Merycochærus, the medium-sized Merychys and the small, highly-specialized Pitheciestes.

The Tragulines are represented by Leptomeryx, Hyppoboschus and Hypisodus. Leptomeryx is believed to be a side member of the main family.

Here I may speak of the recent discovery of the characters of the Protoceratidae, a new family with a remarkable ensemble of characters. In 1891 Marsh described the female skull of Protoceras with a small pair of parietal protuberances. The male skull was found by the American Museum party of 1892. It is armed not only by upper canine tusks, but by four pairs of cranial protuberances, two of which might be dignified by the name of osseous horns; it thus presents the armature of an Uintatherium upon a small scale. Besides parietal and two pairs of frontal protuberances, there are a pair of most exceptional maxillary plates. The fore foot is like that of Tragulus, while the hind foot is didactyl like the deer. We can at present form no idea of its affinities.

The oldest American Artiodactyl certainly known is the tritubercular *Pantolestes* of the Wahsatch. Cope believes the line of American Llamas may have sprung from this, and have been continued through *Homacodon* of the Bridger. The first undoubted cameloid is *Leptotragulus* of the Uinta, a comparatively recent discovery. It has strikingly reduced feet for such an early form. *Pæbrotherium* of the White River and John Day has quite the proportions of the living llama; thence the line passes into *Protolabis* of the Deep River and John Day. Scott believes that these forms are undoubtedly related to both the camels and llamas, and that in the Loup Fork, perhaps in the two species of *Procamelus*, the division occurs, *P. angustidens* passing into the camels, and *P. occidentalis* into the llamas. The Pliocene *Homocamelus*, *Holomeniscus* and *Eschatius*, Scott believes may represent a highly specialized side line of camels; while *Pliauchenia*, still imperfectly known, may belong on the llama side.

The deer represented by *Cosoryx* and *Blastomeryx* are, so far as we know, not of American origin, for they first appear in the Upper Miocene at Loup Fork.

The Ancylopoda.

The order Ancylopoda Cope presents the most signal exception to the law of correlation. It is only quite recently that Filhol, Forsyth Major and Depéret have brought together the sloth-like phalanges with the ungulate type of teeth of the Chalicotheriidæ. Since 1825, when Cuvier described the phalanges from Eppelsheim as those of a "*pangolin gigantesque*," referring to their deep clefts, and 1833, when Kaup named the teeth, these structures were always considered distinct. It is probable that *Moropus* and other supposed Sloths described by Marsh from our Miocene also belong in this exceptional order. As now restored by Filhol and myself, this remarkable Chalicotherium had a gait less clumsy than the Sloth, and something between a huge cat and a hoofed animal; it combined the skull of a primitive ungulate with the molars of an eocene titanother, for the premolars are simple. The limbs, wrist and ankle bones are chiefly ungulate and perissodactyl. In viewing this combination of characters, the first question to settle is which set of characters is secondary and adaptive. I agree with Depéret, as against Filhol who regards this as an aberrant edentate, that the unguiculate characters are secondary; but I do not believe it is very near the Perissodactyla. It seems to have sprung rather from the primitive ungulate stem before it had parted with its unguiculate characters. Perhaps it came off from the Wahsatch

Meniscotherium, a member of the Condylarthra, which it very closely resembles in its skull and molar structure and in its dental curve. Marsh, by the way, has just added to our knowledge of this little Walsatch genus by describing its fore and hind feet, which are more primitive than those of Phenacodus or Hyrax. While the Creodonta were imitating all modern carnivores, is it not possible that the Condylarthra gave off a sloth-like form for fossorial and semi-arboreal habits?

Last summer while this problem was being discussed, we were brought face to face with the exact counterpart of Chalicotherium which may be called a *clawed odd-toed* form, by the surprising discovery of a hind foot, which represents a *clawed even-toed* animal. This was found by the American Museum party in the Protoceras beds of South Dakota, and has been named Artionyx. This foot has a truly Artiodactyl tarsus and metatarsus like that of the pigs or oreodons. Yet it possesses five toes terminating in large unclawed claws. It has been suggested by Wortman and myself that it represents an Artionychine (even-clawed) division and that Chalicotherium represents a Perissonychine (odd-clawed) division of the Ancylopoda; in other words, that a double parallelism exists with the Ungulata. Another explanation may be that these genera are highly specialized Artiodactyla and Perissodactyla respectively; Scott has made the ingenious suggestion, tending to support this theory, that the Artionyx foot is the long unknown foot of the aberrant oreodont Agriochœrus of Leidy. This summer will probably determine the truth of this suggestion, for two parties are hunting in the beds in which Agriochœrus and Artionyx occur.

Thus an immense number of problems still await solution, and demand the generous coöperation of European and American specialists in the use of similar methods of research, in the prompt publication of descriptions and figures, and in the free use of museum collections. I may be pardoned for calling general attention to the service which the palæontological department of the American Museum is trying to render in the immediate publication of stratigraphical and descriptive tables of western horizons and localities.

The Factors of Evolution.

A few words in conclusion upon the impressions which a study of the rise of the mammalia gives as to the factors of organic evolution. I refer also to recent papers by Cope, Scott and myself.

The evolution of a family like the Titanotheres presents an uninterrupted march in one direction. While apparently

prosperous and attaining a great size, it was really passing into a great corral of inadaptation to the grasses which were introduced in the middle Miocene. So with other families and lesser lines, extinction came in at the end of a term of development and high specialization. With other families no causes for extinction can be assigned, as in the lopping off of the smaller Miocene perissodactyls. The point is that a certain trend of development is taken leading to an adaptive or inadaptive final issue—but extinction or survival of the fittest seems to exert little influence *en route*.

The changes *en route* lead us to believe either in predestination—a kind of internal perfecting tendency, or in kinetogenesis. For the trend of evolution is not the happy resultant of many trials, but is heralded in structures of the same form all the world over and in age after age, by similar minute changes advancing irresistibly from inutility to utility. It is an absolutely definite and lawful progression. The infinite number of contemporary developing degenerating and stationary characters preclude the possibility of fortuity. There is some law introducing and regulating each of these variations, as in the variations of individual growth.

The limits of variation seem to lie partly in what I have called the “potential of evolution.” As the oöperm or fertilized ovum is the potential adult, so the Eocene molar is the potential Miocene molar. We have seen that the variations of the horse and rhinoceros molars, apparently so diverse, are really uniform,—is not this evidence that the stem perissodactyl had these variations *in potential*, waiting to be called forth by certain stimuli? This capacity of similar development under similar stimuli is part of the law of mammalian evolution, but this does not decide the crucial point whether the stimulus is spontaneous in the germ or inherited from the parent. I incline to the latter opinion.

Columbia College, August 3, 1893.

