PART II.

GENETIC RELATIONS OF THE MAMMALIAN ORDERS.

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INTRODUCTION.

REMARKS ON THE PRINCIPLES OF RESEARCH IN MAMMALIAN PHYLOGENY.

Difficulty of reaching correct phylogenetic results.— The greatest stumbling blocks of the phylogenist lie: first in the difficulty of distinguishing between primitive and specialized characters, secondly in the tendency to assume relationship between two given forms on the basis of resemblances that may have been brought about by either parallel or convergent evolution. From the earliest times comparative anatomists and palæontologists have repeatedly misread the record, mistaken analogy for homology, and interchanged descendants and ancestors.

The general aspects of this problem have been very fully dealt with by Cope (1896), Scott (1891), and Osborn (1902, 1904, 1905, 1910) and need not be discussed here; but the universality of parallel evolution and the confusing intermixture, in every form, of hereditary characters and homoplastic resemblances to distantly related forms, are conditions which seem to call for some formulation and brief discussion of the principles which have been applied in the following studies on mammalian phylogeny.

Necessity for conducting phylogenetic research in accordance with the strict rules of the inductive process.— In the study of the genetic relations of mammals there are very few maxims which are of universally deductive application. Phylogeny is essentially an inductive subject, a reasoning by analogy, which is the shifting sand whereon hypotheses and theories are built. In general, the student must (1) concede nothing more than he is forced to, (2) strive to separate probability from plausibility, (3) test his hypotheses by the principle of negation, and (4) avoid explaining the little known through the less known. Above all (5) he must strive to keep in touch with all data bearing on the subject, (6) make constant reviews to see that no pertinent fact has been omitted and (7) test again and again his basal assumptions.

These principles may indeed seem to be obvious councils of perfection; but so much zoölogical study has been vitiated by the neglect of them that it has come to be scarcely respectable to draw up a phylogenetic tree.

Among the phylogenetic principles which have become fairly well established the following seem to require notice in the present study.

Bearing of the imperfection of the record upon the interpretation of mammalian phylogeny.— One of the cardinal postulates of the phylogenist should be the well known imperfection of the geological record. There is much evidence to show that many existing orders of mammals were already represented in the Cretaceous or even earlier epochs, that is, that certain of the more fundamental ordinal characters are older than the Tertiary; and that therefore the points of separation of these orders occur where the discovered record is extremely meagre. Many families also may have acquired their family characters in some area as yet unopened by palæontological exploration, such as northern Asia.

Palæontology may be said to be little more than comparative anatomy applied to faunas of different periods, *i. e.*, to sections of the phylogenetic tree taken at various planes. The true chronological succession of forms is obscured by many factors, notably: (1) the imperfect knowledge of the time equivalence of Tertiary mammal horizons in different continents (*cf.* Osborn, 1900), (2) the intermingling of immigrant and autochthonous elements in a fauna through migration (*cf.* Depéret, 1908), (3) the intermingling of persistent primitive and highly specialized forms in the same fauna.

Reconstruction of synthetic types.— For these reasons the phylogenist must attempt a sort of survey by triangulation: the characters of known forms merely affording variously situated points for the backward projection of assumed lines of development to their intersection in undiscovered synthetic types.

Persistent primitive forms.— The very factors which complicate the problem, however, serve also to elucidate it, because the immigrant elements in one fauna furnish examples of a fauna originally bred elsewhere; while in each age the persistent primitive forms and structures carry us back to the stem forms of antecedent ages.

Relative phylogenetic value of characters of the dentition and of the feet.— As shown above (pp. 42[1], 80) this question is an historic one: Which set of characters is more often adaptive and more likely to exhibit misleading homoplastic resemblances between ordinally separated forms, the characters of the dentition or the characters of the feet?

Before attempting to answer this question we note the predominant place of the dentition in mammalian palæontology. The majority of fossil mammalian species, especially in Europe, are known chiefly through the dentition, and dental characters enter very prominently into the classification of the species, genera and families. Even many orders take their names from characters relating either to the teeth or to the food and manner of using the teeth; as "Protodonta," "Triconodonta," "Trituberculata," "Insectivora," "Creodonta," "Carnivora," "Rodentia," "Tillodontia," "Simplicidentata," "Duplicidentata," "Tubulidentata," and "Toxodontia." Generally in cases where the ordinal position of an animal is known on other grounds, the teeth offer a safe criterion of its specific, generic, family and subordinal affinities.

Characters of the dentition often inferior in value to characters of the feet.— Where the ordinal or superordinal affinity is in doubt the teeth are often, but not always, inferior in value to the feet.

(1) Great *differences* in the dentition may occur even among members of the same family, in cases where the mutual affinity is clearly indicated in the feet.

(*a*) Contrast, for example, the cat-like cheek teeth of *Cryptoprocta* with the bunoid cheek teeth of *Arctictis*; yet both genera belong in the Viverridæ. Still greater differences may occur within the limits of the same suborder or order.

(*b*) How great is the difference between the many-columned last molar of *Phacochœrus* and the two-ridged molar of *Dicotyles*; yet the resemblances in the feet clearly indicate the superfamily alliance between the genera in question.

(*c*) What a wide difference between the many-plated molars of *Hydrochœrus* and the simple molars of *Sciurus*; and yet there can be no doubt that both are correctly referred to the same order; again the feet are more alike than the cheek teeth.

(*d*) The Australian Diprotodont Marsupials show a great adaptive radiation in the dentition, which includes such very diverse types as the specialized sectorial dentition of *Thylacoleo* and the prismatic rodent-like dentition of *Phascolomys*; and yet all these Marsupials are closely related in numerous weighty characters; and here again the foot-structures, while differing greatly in adaptive features, retain clear evidence of derivation from a single type.

(*e*) Between the two living genera of Monotremes most striking differences obtain in the dentition: the transitory teeth of *Ornithorhynchus* are of the many-cusped type and all the adaptations of the adult are for a shell-crushing diet; but in *Echidna*, in adaptation to ant-eating habits, the teeth are lacking entirely. The feet of these animals, on the contrary, while differing in external adaptations to aquatic and dry land habits respectively, are full of the most significant, detailed evidences of close relationship (p. 154).

Examples of this kind might be multiplied almost indefinitely, showing that great differences in the dentition are quite compatible with near (subordinal or ordinal) relationship of the forms in question.

(2) On the other hand very many striking *resemblances* between the dentition of different forms have frequently been brought about either by parallel or by convergent evolution, in cases where the ordinal separation is clearly indicated in the feet.

(*a*) The cheek teeth of *Hyrax*, for example, superficially resemble those of Rhinoceroses, but it is practically certain (pp. 360) that these resemblances are secondary; and here again the detailed structure of the feet (apart from resemblances in the mere number of digits) correctly indicates the wide gap between the two groups.

(*b*) The cheek teeth of *Meniscotherium* (p. 355), an Eocene Condylarth, furnish in most respects an ideal prototype for the cheek teeth of *Chalicotherium* (as first pointed out by Osborn, 1893, pp. 127–130); but evidence (p. 399) that the ancestors of *Chalicotherium* were only very indirectly related to *Meniscotherium* is again revealed in the feet.

(*b*) The molar teeth of *Macrotherium*, another member of the Perissodactyl-Chalicotheriidæ are so much like those of *Anoplotherium* that de Blainville (1839–1864) and Depéret (1892), apparently regarded the two forms as being ordinally related and standing near the border line between the Perissodactyls and Artiodactyls. But *Macrotherium* and its allies are shown by the structure of the feet and skull to be related to the Perissodactyls

(p. 400), while the feet of *Anoplotherium* show that it is an aberrant Artiodactyl.

Foot-structure also subject to the deceptive effects of parallel evolution.— Reduction in the number of digits, pursued independently in different genetic lines, brings about some curiously close parallelisms.

(*a*) The hind feet of *Theosodon*, a Patagonian Litoptern, are tridactyl, and analogous in certain respects to those of the Perissodactyl genus *Colodon* of the North American Oligocene; while the monodactyl feet of *Thoatherium*, another Litoptern, are remarkably horse-like. These resemblances have caused Ameghino (*e. g.*, 1904, pp. 518–521) to place the Litopterns in the order Perissodactyla. But the detailed relations of the carpals and of the tarsals in the Litopterns suggest that they have no close relationship with the Perissodactyls; and this conclusion is supported by much other evidence (p. 379).

(*b*) Both the manus and pes of *Nesodon*, a Santa Cruz Toxodont, are similar to those of a Rhinoceros (Gaudry, 1908, p. 9, fig. 34) and this general similarity extends also to the hind feet (Gaudry, *l. c.*, p. 11, figs. 39–41); while the general characters of the skull and cheek teeth also recall those of the Rhinocerotoid *Metamynodon*. These resemblances seem to have been regarded by Lydekker (1896, pp. 83, 84) as indicating a genetic relationship between Rhinoceroses and Toxodonts. But notwithstanding these resemblances the two groups differ in so many seemingly "non-adaptive," or palæotelic, characters that the relationship between them is probably similar to that obtaining between Litopterns and Hippoids; namely, in both cases we seem to be dealing merely with the terminal members of adaptively parallel and partly convergent series, which are probably related only very indirectly through descent from different families of the Condylarthra.

(*c*) The manus of the Perissodactyl genus *Titanotherium*, with its four somewhat spreading digits and broad carpus is superficially similar to that of the Artiodactyl *Hippopotamus*; but here again the wide ordinal separation of the two forms is faithfully revealed in the detailed characters of the carpus, which in *Titanotherium* conforms to the Perissodactyl, in *Hippopotamus* to the Artiodactyl, type.

Effect of close kinship upon parallel evolution.— Where there is a close relationship between ancestors the results of parallel evolution in descendants become still more striking.

(*a*) The similarity between the manus of *Titanotherium* and that of *Metamynodon*, an Oligocene Rhinocerotoid, is even greater than the similarity between the manus of *Titanotherium* and that of *Palæosyops*, its own collateral ancestor. In this case even the detailed relations of the carpals (which served to separate *Titanotherium* from the Artiodactyl *Hippopotamus*)

fail except in regard to minor details, but the cheek teeth correctly indicate that *Titanotherium* and *Metamynodon* belong to very distinct families of Perissodactyls,— a conclusion which is supported by much additional evidence.

(*b*) The fore arm and feet of *Arsinoïtherium* (Andrews, 1906) from the lower Oligocene of Egypt are remarkably similar to those of Proboscideans, the hind limb and foot are full of resemblances to the heavy bodied Amblypoda; but the cheek teeth may be a development of the Hyracoid type. In this instance it is probable that we have a mingling of hereditary and homoplastic resemblances, and that *Arsinoïtherium* is actually related, more or less distantly, to all three orders, Amblypoda, Proboscidea and Hyracoidea.

Both teeth and feet often inferior in interordinal value to the carpals, and especially to the tarsals.— In brief it has been shown that in certain cases the cheek teeth are misleading guides to the relationships between orders, and in other cases the number of digits and the *general* characters of the manus and pes are equally misleading guides. But in perhaps the majority of instances, and with the exceptions noted above (p. 109) *the detailed characters of the carpals, and still more of the tarsals, especially the astragalus, yield more reliable indications of ordinal relationships than the characters of the cheek teeth.* The fuller evidence for this view is given below, especially in Chapter XI under the headings "Marsupialia," "Insectivora," "Rodentia" and "Ungulates."

Each case to be judged on its own merits.— While the carpals and tarsals are in the majority of instances reliable guides to ordinal affinities, it must be understood that no single characters or set of characters are always reliable; that, as Linnaeus discovered (p. 34), a character may be of great value to the systematist in one order and of very little value in another; that in short every case must be judged on its own merits.

Why primitive characters survive in the carpals and tarsals.— Why is it that the carpals and tarsals, in their detailed characters, correctly indicate remote relationship (ordinal or interordinal) more often than do the cheek teeth? Does this fact indicate: (*a*) that *food-habits and tooth-structure have in the cases cited changed more rapidly than locomotive habits and foot-structure*?

Does it indicate: (*b*) that *changes in food-habits and tooth-structure have a wider range of possibilities* than changes in locomotive habits and foot-structure?

Does it indicate: (*c*) that the *teeth are more subject to orthogenetically divergent tendencies than are the carpals and tarsals*?

Whatever may be the true explanation of these facts the following considerations should not be lost sight of.

The shape of the teeth in a given race is of course determined primarily by germinal, hereditary, perhaps "orthogenetic," factors. But even if it is true that changes in the soma are in general not transmitted to the germ, yet the form and conditions of one part of the soma must in some way, in the long run, act and react on the evolution of other parts of the soma; because the correlation (mutual adaptation) of organs is a universally observed fact. The shape of any given tooth must then be determined to some degree by *somatic conditions*: such as the interaction between upper and lower teeth (p. 190), the indirect influence of each tooth upon adjacent teeth (p. 194), the size and arrangement of the muscles of mastication, and the like.

The shape of the teeth is also profoundly influenced, in the long run, by a wholly external, "environmental," factor, namely the nature of the food, and this is true even although it is not known how the result is effected.

In the case of the carpals and tarsals there is also a set of somatic factors: such as the weight of the animal, the pull of the muscles, the interaction between adjoining facets, etc. Each of these somatic factors must be in part hereditary, in part adaptive *i. e.*, depending on the nature of the environment. But assuming that in some way environmental conditions do affect evolution, then the environment can not operate on the evolution of the carpals and tarsals directly, but only through the intervention of the parts that are in contact with them.

Primitive characters often retained in sheltered parts of the organism.— In general, primitive or largely hereditary (palæotelic) characters seem to be retained longer in parts which come less directly into relation with the environment. This law is well illustrated in the mammalian reproductive system. Amid the innumerable modifications of the external form, teeth, limbs, skeleton and digestive apparatus in the Placental orders, the uterus varies only from the "duplex" to the immediately derived bicornuate and "simplex" types. In many instances (*e. g., Ornithorhynchus, Orycteropus, Castor*) a very primitive type of uterus may coëxist with a very highly specialized skull and dentition.

Great phylogenetic value of so called "non-adaptive" "morphological" or palæotelic[1] *characters.*— We are thus brought to one of the guiding principles of the following investigation, a principle which also seems to have led de Blainville, Gill (*cf.* p. 91) and others to the best features of their classifications: namely, that the parts which come more directly and simply into relation with special food-habits and special environments (such as the teeth, claws or hoofs, digestive system, etc.) are more plastic, and frequently

[1] The words *palæotelic* and *cænotelic* may be invented, as being more expressive than "morphological" *vs.* "adaptive," to contrast ancient, with newer, characters. A palæotelic character becomes cænotelic by a change of function.

of less value as criteria of remote interordinal relationships, than those parts, (such as the brain, reproductive organs, foramina of the skull, auditory ossicles etc.), the relation of which to the environment is more indirect and complex. If, however, any of these sheltered, persistently-surviving palæotelic organs or characters are brought into more direct relations with new conditions, either environmental or somatic, they become just as "adaptive," or cænotelic as the rest. For example: (*a*) the auditory ossicles of the Fissipede Carnivora, as figured by Doran (1879), are in general of a recognizable ordinal type, but those of the Pinnipedia, in response to the new aquatic conditions, rapidly lose this type, and finally, in the most highly specialized forms (the Sea-elephants), take on several superficial points of resemblance to the Cetacean type. (*b*) Again, in the brain of the Pinnipedia (Weber 1904, p. 545) the cerebrum retains very strong evidence of relationship with the Fissipedia, but the olfactory parts are reduced — an aquatic adaptation which is accentuated in the Sirenia and Cetacea.

The phylogenetic value of palæotelic characters is occasionally lessened (p. 423) by sudden departures from type, which may be made possible by the lower value of these characters in terms of natural selection.

Importance of determining the order of appearance of diagnostic characters. — The relative age of different characters should in all cases be a prime object of research. This historical method (although open to many pitfalls) when judiciously applied seems more likely to lead to lasting phylogenetic results than the time-honored method of setting down all the resemblances and differences between two animals, without further analysis, and then striking a balance at the end.

Osteology the core of phylogenetic research.— The last principle requiring notice here is one well recognized by many palæontologists. It is that osteology must after all constitute the core of the true theory of mammalian history. It is only by means of the skeleton that we are able to correlate the knowledge of living with that of fossil mammals and thus to synthesize the results of palæontology, systematic mammalogy and comparative anatomy.

Summary.— Some obvious corollaries of the foregoing principles are: (1) that the phylogenetic and broader systematic value of a character can rarely be appraised with confidence until its general adaptive purpose is understood; (2) that the trend of adaptation of the whole organism and of its race should be sought for; (3) that far reaching homologies and conclusions should never be based upon isolated or sporadic resemblances, in possibly cænotelic characters, between widely removed forms. The phylogenetic relations of orders requires in brief: (1) a consideration of a very wide range of characters drawn from all parts of the organism, (2) a careful analysis of the intricate complex of homology and analogy, of adaptation

and change of function, and (3) a constant search for the little-noticed, palæotelic characters which are likely to prove the most significant of remote relationship.

CHAPTER I. THE ORIGIN OF MAMMALS AND THE PROBLEM OF THE OSSICULA AUDITUS.

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The living and fossil Amphibia are admitted by most contemporary authorities to be very far removed in the sum of their characters from the direct ancestors of the mammals. After a very careful review of the subject Professor Kingsley (1900, pp. 250–255) concludes "that it is impossible that the mammals have descended from any form distinctly urodelan nor is there any known stegocephalan which will meet the requirements of the

case." And yet Kingsley is so impressed with certain comparisons between the Mammalia and the Amphibia in respect to the relations of the quadrate and its supposed homologue the mammalian incus, of the anterior abdominal vein, of the mesenterial structures, of the amnion and trophoblast and of the hair, that he concludes that all the osteological resemblances between the mammals and the mammal-like reptiles of the Permian and Trias are the results of parallel development; and that the mammals have descended from forms "with amphibian affinities but more primitive in structure than any known stegocephalan." He therefore implies (p. 255) that the common ancestors of the Amphibia, Reptilia and Mammalia must be sought in the Devonian. The purpose of the present article is to show that so far as the osteological evidence indicates it is not necessary to have recourse to unknown Devonian amphibians for the ancestry of the Mammalia; but that all recent evidence tends to support the view developed by Owen (1876), Seeley (1888–1895), Osborn (1898–1903) and Broom (1901–1908), namely, that the ancestry of the mammals is to be sought within, or very near to, the Triassic reptilian order of Cynodontia ("Theriodontia" in part).

I. The Synapsid Reptiles.

The subject may conveniently be approached by a cursory review of the reptilian orders constituting the subclass *Synapsida* of Osborn (1903). These are typically distinguished by their prevailing resemblances to the Mammalia, especially in the possession of a single temporal arch in the skull, and they contrast with the Diapsida, or primitively two-arched reptiles which center around the Rhynchocephalian type. The composition of the Synapsida, as defined by Osborn (1903, pp. 455, 456) is as follows:

The Diadectids, Chelonia, etc.

First we may set aside certain highly specialized groups which are more or less widely removed from the ancestors of the mammals. Among these are: (1) The Permian Diadectidæ, the original type of the order Cotylosauria Cope (see Williston, 1908). These distinctly foreshadow the Chelonia in many significant characters, as observed by Cope, Case (1905) and Hay (1908, p. 29). (2) The Chelonia themselves. (3) The Placodontia, which Jaekel (1907) has recently shown to include forms resembling the Chelonia in the general configuration of the body, but allied in other directions to the Nothosaurs and Plesiosaurs. (4) The Nothosaur-Plesiosaur group, which is considered by some authorities (Williston, 1907) to be derived from very

primitive Therocephalians (see below), by others (*e. g.*, Broom, 1904.3, Andrews, 1896) to be an early off-shoot of the Rhynchocephaloid group.

Procolophon and the Pelycosauria not Synapsida.

Two other single-arched Permian orders, the Procolophonia and the Pelycosauria, by many authors have been superordinally associated with one or more of the above mentioned groups under the well known term Theromorpha. In regard to *Procolophon* however Broom (1905.5) has shown that while it is related on the one hand to the earliest Synapsida, its tarsus and other characters place it rather on the side of the Diapsida. The Pelycosauria, as revised by Case (1907) approach the Synapsida in some characters, but the tarsus figured by Osborn (1907, p. 270) differs considerably from the typical Synapsid type, and this, joined with other characters, indicates that the group, as held by Osborn (1903) and Case (1907, p. 158), is an offshoot from the base of the Diapsidan series.

Turning now to the more generalized Synapsida we note the following groups:

Pareiasauria.

(1) In the Pareiasauria of South Africa, as described by Seeley (1888.1), the top of the skull approximates to the Stegocephalian type, especially in the relations of the bones and in the absence of any fenestration. The pectoral and pelvic girdles and limb bones are also of a very lowly, almost Stegocephalian type. The Pareiasauria retain a cleithrum (epiclavicle) and a plate-like pelvis without any thyroid ("obturator") fenestra. The phalangeal formula according to Broom (1908, pp. 1050–1051) has probably not yet been reduced to the typical Synapsid form of 2, 3, 3, 3, 3; but approaches the higher formula 2. 3. 4. 5. 3, which is characteristic of even the most primitive Diapsida and which may have been inherited from Microsaurian ancestors. The Pareiasauria are shown to be Reptiles and not Amphibians by the reduction of the parasphenoid and the presence of a single median occipital condyle.

(2) More or less nearly related to the Pareiasauria are the American Permian family Pariotichidæ of Cope, which are often referred to the Cotylosauria. These forms have recently been redescribed by Case (1899), Broili (1904) and Williston (1908). Like the Pareiasauria they resemble the Stegocephalia in the arrangement of the bones of the roof of the skull and in many characters of the shoulder girdle and limbs; while the base of the skull is reptilian in type. A cleithrum has not yet been observed (Williston,

1908, p. 143) but in most other characters they stand near to the common stem of the Diapsida and Synapsida (Osborn, 1903; Broom, 1908).

The next group, the superorder or order Therapsida of Broom (1905.2) includes a series of four orders or suborders, the lowest of which approaches the Pareiasauria and the Pariotichidæ, while the highest approaches the Mammalia.

Dromasauria.

This very generalized order recently defined by Broom (1907.1), is so far known only from a single type, *Galechirus scholtzi*, found in the Middle Permian of South Africa (Broom, 1909). The genus retains the abdominal riblets which are characteristic of the Microsauria and of the more primitive Diapsida, but which are lost in the typical Therapsida, while the facial region is "not unlike that of *Palæohatteria*, there being no specialized canine." But in the structure of the lower jaw, shoulder girdle, pelvis, limb bones, phalangeal formula etc. the genus approximates the order described below (Broom, 1908, p. 1051).

Therocephalia.

As defined by Broom (1903.5, p. 7) this Permian suborder, represented by *Ælurosaurus*, *Ictidosuchus* and other genera, stands on a lower plane than the "typical Theriodonts," *Cynognathus* and *Galesaurus*, as shown by the retention of the following generalized characters:

The palate is of the general type retained in the Rhynchocephalia, (Broom, 1903.2, 1903.6), while the occipital condyle is single as in the typical reptiles. A pineal foramen is retained (Broom, 1903.4). The lower jaw (Fig. 2, No. 1) has large angular, surangular and articular elements, as in the Dromasauria. Among their progressive characters, the Therocephalia had already developed the single temporal arch, containing the same elements as in the mammals, but distinguished by being continuous with the frontals back of the orbit. The manus is known in *Theriodesmus* (Seeley, 1888.2), a genus which Broom (1907.3, p. 3) refers to this order. It had all the characters which might be expected in the manus of the remote ancestors of the mammals (see below, p. 439). The pes is not known.

The Therocephalia enjoyed a great adaptive radiation, the larger forms, forming the sub-order Dinocephalia of Seeley (1895.1, p. 1014) being as big as a rhinoceros, while the smallest, *Scaloposaurus*, (Owen, 1876, pl. XVI, Figs. 10–15) had a mole-like skull. The teeth are recurved and caniniform.

Anomodontia Proper.

The Anomodontia, as limited by Broom (1905. 1) are also Permian forms. They are contemporaneous with the known Therocephalia but are believed by Broom to have been derived from earlier members of that order. The typical genus *Dicynodon* and its allies are very aberrant in skull structure. The edentulous muzzle was encased in a horny beak and there are either two great walrus-like tusks or none at all. The related Endothiodonts (Seeley, 1895.1, p. 1015; Broom, 1905.1) retain small round teeth on the maxillaries, palatines and pterygoids, thus recalling the Cotylosaurs. All are distinguished by the peculiar ⅂ -shaped squamoso-quadrate region. The well-developed secondary palate is about the only striking analogy to mammalian conditions among the cranial characters. The manus and pes, which are known especially in *Oudenodon* (Broom, 1901), are probably a development of the Cotylosaurian type. They show strong resemblances in the phalangeal formula and in the ungual phalanges to the Monotreme type (*cf.* Fig. 28, p. 440). The carpals and tarsals, while very generalized, also show strong evidence of affinity with the stem of the mammals (see p. 439). The Endothiodonts retain small teeth in the roof of the mouth but are otherwise like the typical Anomodonts (Broom, 1905.1).

Cynodontia (*Theriodontia* in part).

These are the forms that Owen, Seeley, Osborn and Broom have recognized as standing close to the stem of the mammals. They are found in the Upper Triassic of South Africa and are separated by a wide stratigraphic interval from the Permian Therocephalians (Broom, 1907.4). They have advanced much beyond the Therocephalians: notably, in regard to the dentition, in the loss of the pineal foramen, and in all those characters which tend to ally them with the mammals,— especially in the reduction of the quadrate, articular, angulare and in the enlargement of the dentary (*cf.* Figs. 1*B*, 2*B*).

II. Relations of the Mammalia to the Triassic Cynodontia.

The structural relations of the Cynodonts to the Mammalia may be considered under two general headings: first, their primitive reptilian characters, secondly, the characters in which they foreshadow the mammals. This leads to a discussion of the fate of the quadrate and the origin of the mammalian auditory ossicles.

Primitive, reptilian characters of the Cynodontia.

The Cynodont skull (Figs. 1*B*, 2*B*) is distinguished from the generalized mammalian skull by characters which appear for the most part to be of a primitive rather than divergent nature. Separate pre- and post-frontals and (except in *Bauria*) a post-orbito-malar bar are retained, the opposite occipital condyles are continuous across the mid-line, the basioccipital is extremely short, the palatine plate of the maxillary is short, the secondary palate is limited to the anterior part of the skull; the pterygoids are large anteriorly but are smaller than those in *Sphenodon* and the Therocephalia; ending anteriorly in large flanges,[1] running inward toward the middle line and overlapping the basisphenoid; alisphenoids diverging posteriorly; the reduced quadrate and articular apparently had not yet begun to function as accessory auditory ossicles (see below). The skeleton of Cynodonts differs from that of mammals in many important particulars. A well developed proatlas is present. The cervical vertebræ of *Cynognathus* (Seeley, 1895.4, p. 98) bear large separate intercentra, structures which are not found in the cervical vertebræ of mammals, but which may be represented by the chevrons in the tail and *possibly* by minute intercentra in the lumbar region of certain Insectivores, especially in the embryo (see however p. 265 below). The dorso-lumbar vertebræ of *Cynognathus* (Seeley, *loc. cit.*, p. 105) bear peculiar broad, flattened ribs which curve backward, and distally overlap each other.

The femur of *Cynognathus* (Seeley, *loc. cit.*, p. 120) is very primitive and seems to indicate that the limb was held well out from the body. The greater and lesser trochanters together form a great broad curved crest upon which rests the small sessile head; the femur thus contrasts sharply in form with all known mammalian types.

In *Diademodon* the lesser trochanteric ridge is not so big and offers a better, but still distant, comparison with the Monotreme type (Broom, 1905.4, p. 100). The pelvis in *Cynognathus* is typically reptilian in its broadly triangular ilium (Seeley, 1895.4, p. 113). That of *Diademodon* is noticed below (p. 119).

Characters in which the Cynodontia foreshadow the Mammalia.

Skeleton.— The atlas of *Cynognathus* (Seeley, 1895.4, pp. 100–102) resembles that of *Ornithorhynchus* in the median ventral extension of the anterior facet. The cervical vertebræ also bore ribs.

[1] These flanges were called "transverse palatines" by Seeley but Broom (1909.2) has recently proved that they are entirely comparable with the mammalian pterygoids.

The shoulder girdle of *Cynognathus* (Seeley, *loc. cit.*, p. 93) realizes all the ancestral mammalian conditions which are indicated in the Monotremata and embryonic Diprotodont Marsupialia. The broadly curved anterior border, derived, Broom suggests (1899, p. 768) from the cleithrum of the Pareiasauria, is clearly homologous with the acromion of marsupials and placentals, and with the anterior border of the scapula in the Monotremes (pp. 152, 157). The rudimentary prespinous fossa is confined to the upper anterior part of the scapula. The glenoid cavity is extended transversely as in Monotremes, and is partly formed by the large coracoid. The procoracoid is pierced by the procoracoid foramen (lost in mammals). The humerus (represented in several of the Gomphodontia) was exceedingly mammalian in type (Seeley, 1895.3, p. 29). It is strictly comparable in all its parts with the typical mammalian humerus. The manus is only partly known: *i. e.*, in *Microgomphodon* (Seeley, 1895.3, pl. i, fig. 7) and *Ælurosuchus* (Broom, 1906.2, pl. x, fig. 7). It apparently resembled the Therocephalian type, and therefore probably contained all the ancestral mammalian conditions (see p. 442 below). The pes is also only partly known (in *Microgomphodon*, Seeley, 1895.3, pl. i, fig. 6) but seems to conform to the type more fully displayed in *Oudenodon*, and probably therefore contained the same elements as did the pes of the ancestral mammals (see p. 453 and Fig. 28, p. 440).

The pelvis of *Diademodon* (Broom, 1905.4, pl. x, fig. 3) shows a decided approach toward the mammalian condition in the following characters: (1) The antero-superior part of the ilium is produced upward and forward, while the posterior angle is slightly reduced, thus foreshadowing the much more advanced conditions in the mammalian ilium. (2) A considerable thyroid ("obturator") fenestra, lying between the pubis and ischium, appears for the first time. (3) The pubis is "very mammal-like in structure." Broom (1907.3, p. 6) infers that it may possibly have borne epipubic cartilages.

Skull.— The resemblances in the dentition of the Cynodonts to the mammalian type were noted by Owen and all succeeding writers. The dentition of *Cynognathus* is heterodont, with incisors, canines, premolars and molars, and the cheek teeth are of the incipiently triconodont mammalian type. The dentition of *Sesamodon* (Broom, 1905.3), apparently an ally of the Gomphognathidæ is very mammalian, the dental formula being I. $\frac{3}{4}$, C. $\frac{1}{1}$, Pm + M. $\frac{7}{7}$. The cheek teeth had small, transversely expanded well-enameled crowns which were ground down after the fashion of mammalian teeth. This seems to indicate that the motion of the jaw was not strictly vertical as in *Cynognathus*, but that as in the carnivorus Marsupials the posterior end of the jaw moved slightly from side to side (see p. 220).

In mammals this lateral vibration of the posterior end of the jaw, when the dentary came into contact with the squamosal (see below) may have conditioned the development of a transversely oval condyle.

The skull of *Galesaurus*, a small ally of *Cynognathus*, is in top and side view much like that of *Didelphis*, the resemblance extending even to the nasals, which broaden posteriorly in a characteristically Marsupial fashion (Owen, 1876, pl. xviii, fig. 8). The jugal has a strong postorbital process, which is continuous with the postorbital process of the postorbital above. In the Carnivorous Marsupials the malar also extends forward and sends up a postorbital apophysis (Fig. 1*A*, *p.o.Ma.*).

The characters of the mammalian zygomatic arch are completely realized in *Bauria* (Broom, 1909.1, p. 272), since in this Cynodont the jugal (malar) is not connected with the post-orbital, so that the orbit remains open posteriorly.

The practical identity in the characters of the base of the skull[1] in *Galesaurus*, *Cynognathus* and *Gomphognathus* indicates the close ordinal alliance of these genera to each other (*cf.* Seeley, 1895.4, p. 139 and 1895.3, p. 24). This region (Fig. 1, *B*) seems to show certain underlying resemblances to the generalized mammalian condition in so far as they are preserved in the skulls of *Didelphis* and *Thylacynus* (Fig. 1, *A*). The hard palate, though as yet confined to the anterior part of the skull, is composed of the same elements as in the mammals. The apparent large size and relations of the pterygoids at first sight appear as a very fundamental difference from the mammalian skull; but Broom has very recently determined (1909.3) that the pterygoids, unlike those of typical reptiles, did not extend back to the quadrate, but were comparable, in their relations with the surrounding bones, to the pterygoids of mammals. The remaining differences between the pterygoids of Cynodonts and those of mammals may be explained as a result of three simultaneous processes: (1) the backward prolongation of the palatines caused the posterior border of the latter bones gradually to usurp the position of the anterior flanges of the pterygoids; (2) the reduction of the articular (p. 140) of the lower jaw caused the reduction of the powerful pterygoid muscles which were inserted on the articular and attached to the pterygoid flanges. (3) Perhaps in order to support the pterygoid muscles the alisphenoids sent down a flange on either side, external to the pterygoids, which were finally reduced to mere scales of bone. But in spite of all these reductions the pterygoids in primitive mammals still retain their ancient contact with the palatines and still extend inward below the floor of the sphenoids (*cf.* Fig. 1*A*, *pt*).

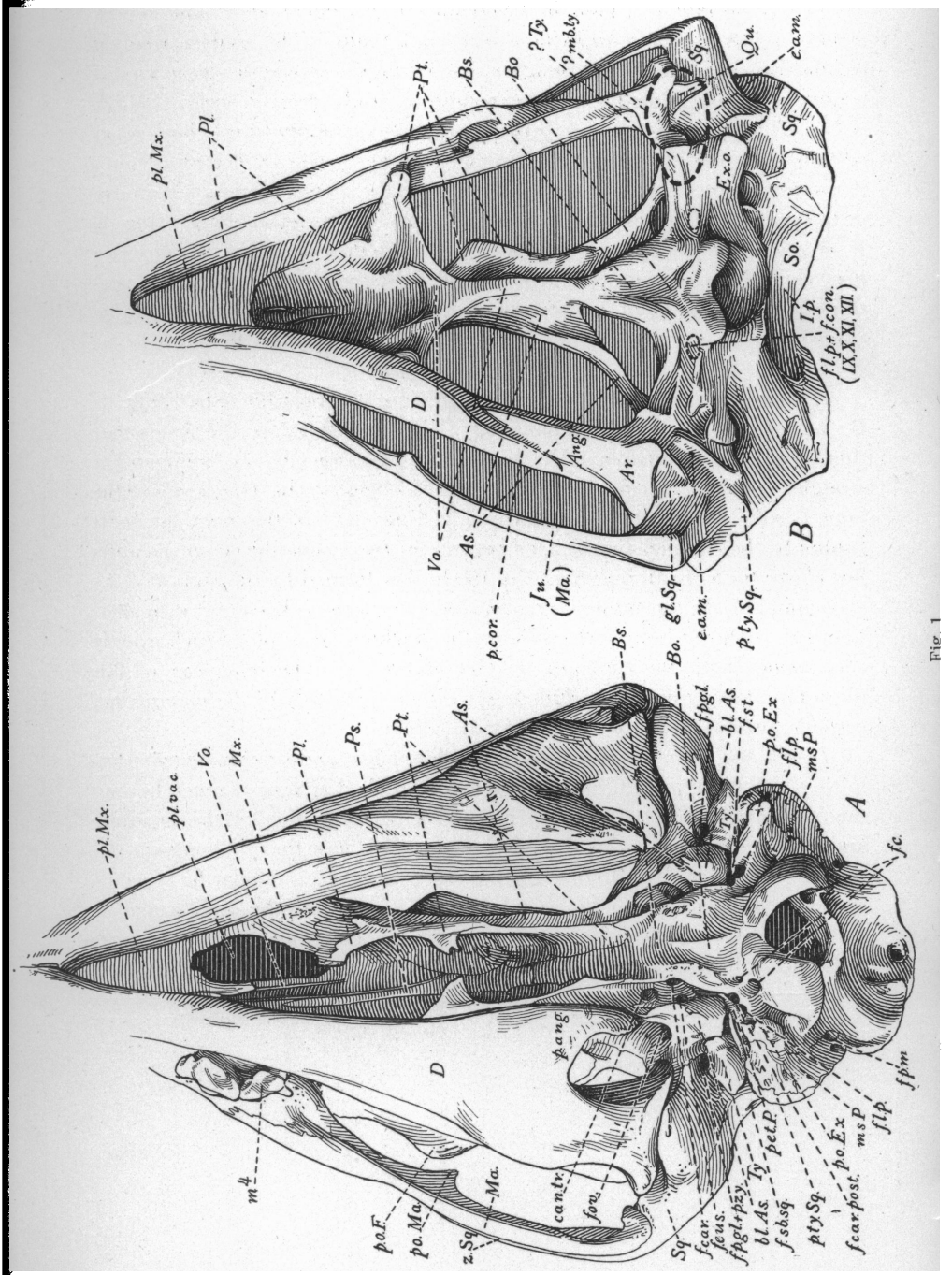
[1] As may be observed upon casts of the original skulls.

The basioccipital region in Cynodonts is extremely short antero-posteriorly, a fact probably implying a very small brain. The occipital condyle is bilaterally paired and although still continuous across the basioccipital is quite prophetic of the mammalian condition, as observed by Seeley (1895.3, p. 1). The exoccipitals are broad laterally-expanding wings, but, as in certain Insectivores and other mammals, are not produced downward into paroccipital processes. Immediately back of the glenoid region is a groove in the position of the osseous external auditory meatus of mammals (Fig. 1, B, *m. a. e.*) which is apparently homologous with that structure. At any rate it is, as in the mammals, bounded anteriorly by the postglenoid region, posteriorly by an apparent post-tympanic process, and superiorly by a ridge connecting the superior border of the zygomatic arch with the lambdoidal crest.

Running inward from the articular region is a horizontal bar (Fig. 1, B, *?ty.*) of somewhat doubtful homology. Broom (1904.2, p. 491) holds that this bone is the tympanic. He thinks that it cannot be a "rudimentary straight cochlea" (Seeley, 1895.4, p. 138), because in *Oudenodon* "the bone is solid, so that it cannot have lodged any part of the inner ear." It cannot be the columella auris itself because in *Dicynodon* the columella auris lies above the bone in question, "in the hollow formed by the bone and the exoccipital." In the skull of *Trirachodon kannemeyeri,* Broom (*l. c.*, p. 493) found a "delicate bony rod of about the thickness of a pin, which exactly corresponds with the tympanic in *Cynognathus.*" The homology of this important bone must be definitely settled if the history of the mammalian ossicula auditus is ever to be elucidated.

Lower jaw.— In the relations of the lower jaw and its component parts to the skull the typical Cynodonts [1] (Fig. 2, *B*) had advanced much beyond the Therocephalians (Fig. 2, *A*) in the further reduction of the quadrate and in the development of the dentary, which is now the predominant element of the lower jaw (Broom, 1908, p. 1053). The surangular has become reduced; the rather slender angular is conjoined with the small articular. All these characters foreshadow the mammalian conditions, as will be more fully shown below.

[1] *Bauria* is much more primitive, since it retains a large angular and surangular (Broom, 1909.1, p. 272).


pl.Mx.
Pl.vac
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msP
fc.
A
D
Ang
Ty
pet.P
Sq
fcar
fous
fpgl+pzy
bl.As
fsb.sq
ptySq
fcar.post.
m4
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gl.Sq.
e.a.m.
p.ty.Sq.

Fig. 1

Fig. 1. Basicranial region of (A) *Thylacynus cynocephalus* and (B) *Cynognathus platyceps*, viewed obliquely from below. *A* from a specimen in the American Museum; *B* from a cast of the skull of *Cynognathus platyceps* Seeley. The identification of the elements in the latter skull is partly on the authority of Dr. R. Broom. $\times \frac{56}{100}$ nat. size.

pl. Mx., palatal shelf of maxillary.
pl. vac., palatal vacuity.
Vo., vomer.
Pl., palatine.
Ps, presphenoid.
Pt., pterygoid.
As., alisphenoid.
B.s, basisphenoid.
B. o., basioccipital.
m^4., fourth upper molar.
p.o.F., postorbital process of frontal.
p.o.Ma. " " " malar.
Ma., malar (= *Ju.* jugal).
Sq., squamosal.
z. Sq., zygomatic process of squamosal.
gl. Sq., glenoid portion " "
Qu, quadrate.
Ar., articular.
Ang., angular.
D., dentary (mandible).
p. cor., coronoid process of dentary.
p. ang., angle (processus angularis).
can. tr., transverse (venous) canal of basisphenoid.
f. ov., foramen ovale.
f. car., entocarotid canal of basisphenoid.
f. eus., Eustachian opening.
bl. As., bullate expansion, or "tympanic process," of alisphenoid.
f. p. gl., postglenoid foramen.
f. p. zy., postzygomatic foramen.
f.sb.Sq., subsquamosal foramen.
Ty., tympanic.
?mb. ty., hypothetical position of tympanic membrane.
pet.P., petrous portion of periotic.
p. ty. Sq., post-tympanic process of squamosal.
e.a.m., osseous external auditory meatus.
f. car. post., posterior carotid foramen.
p. o. Ex., paroccipital process of exoccipital.
ms. P., mastoid process of periotic.
f. st. m., stylomastoid foramen.
f. p. m., postmastoid foramen.
f.c., condylar foramina, external and interna openings.

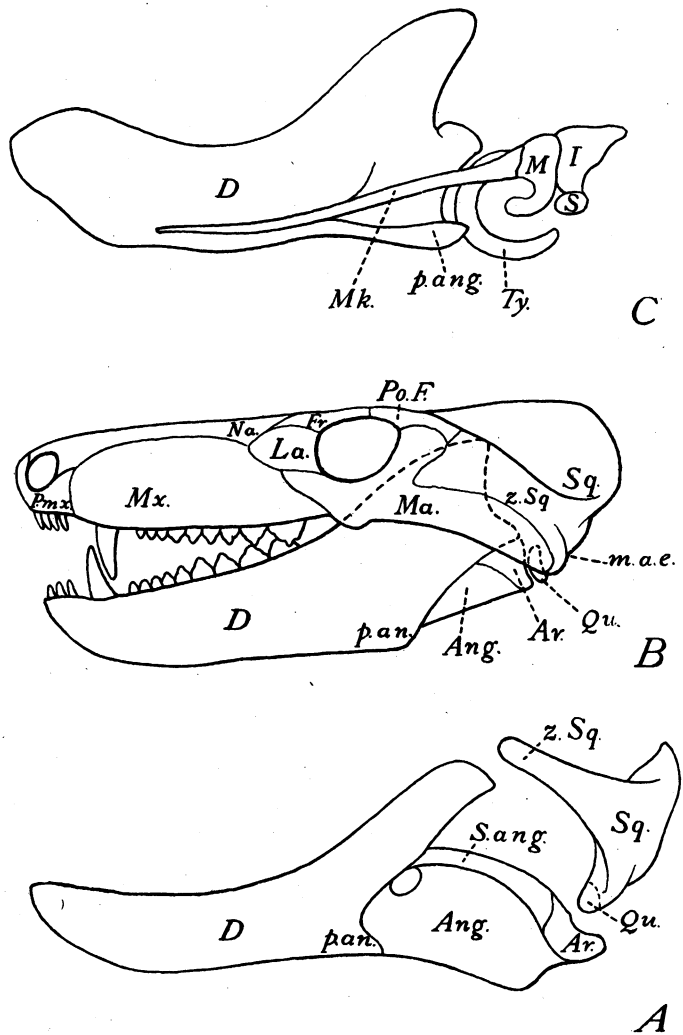

Fig. 2. Morphology of the lower jaw and ossicula auditus.

A. Lower jaw of a Permian Therocephalian, *Lycosuchus vanderrieti*, diagrammatic. After Broom.

D, dentary; *p. an.*, processus angularis; *Ang*, angulare; *S. ang.*, surangulare; *Ar.*, articulare; *Qu*, quadrate; *Sq.*, squamosal; *z. Sq.*, zygomatic process of squamosal.

B. Skull and lower jaw of *Cynognathus platyceps*. Diagrammatic composition from figures by Broom.

Abbreviations as in *A* above and in Fig. 1, p. 122. *m. a. e.* osseous auditory meatus.

C. Developing lower jaw and ossicula auditûs of a fœtal *Macropus*. After Bensley.

D, dentary; *Mk*, Meckelian cartilage, continuous with *M*, malleus; *I*, incus; *S*, stapes; *Ty.*, annulus tympanicus; *p. ang.*, processus angularis.

III. Evidence from Comparative Anatomy and Ontogeny on the origin of the Middle and Outer Ear.

The Cartilages of the External Ear.

Numerous attempts have been made, so Kingsley informs us (1900, p. 253), to derive the cartilages of the external ear of mammals from "opercular structures like those of the teleostomes," and more especially from branchiostegal rays. But the gap between mammals and fishes is so extremely wide that it is no wonder these attempted homologies have never proved convincing. Ruge however (1898) showed that in the Monotremes the cartilaginous passage of the external ear is continuous with the dorsal portion of the hyoid arch, from which, he inferred, the ear-cartilages must have been derived. The figures given by Versluys (1899) show that in many lizards the proximal portion of the hyoid arch is attached to the skull and to the extracolumella, or tympanic portion of the columella auris, just above the external auditory passage, where it would be in a position to support an ear conch if such were developed. In *Sphenodon* (Howes and Swinnerton, 1901, pl. IV, figs. 4–9) the hyoid is attached to the extra-columella on the outer border of the skull. It may be remarked however that Ruge did not *demonstrate* that the cartilage of the ear conch in Monotremes was a derivative of the hyoid cornu, since he dealt only with structures already formed. Parker (1886, p. 270) found that in developing Marsupials "a folded cartilage protects the Eustachian tube [*cf.* Weber, 1904, p. 145], and outside the former the *meatus externus* is protected by a more or less segmented tube of cartilage, which ends outside in the continuous *concha auris*." The possibility is thus suggested that the ear conch is serially homologous with these rings, which in turn appear to be neomorphs, perhaps analogous to the rings of the trachea. The development of a cartilaginous ear conch, through the hypertrophy either of the proximal end of the hyoid arch or of the rings of the meatus, was at any rate only one incident in a remarkable series of improvements and changes of function in the accessory auditory apparatus, whereby the relatively simple mechanism of reptiles gave rise to the intricate and delicately adjusted mechanism of mammals.

The tympanic cavity.

The external auditory meatus and the Eustachian tube, which together form the tubo-tympanal canal, are generally considered to be the homologue of the first gill cleft. When the tubo-tympanal canal first appears in the

embryo the meatus is filled with cuticle of ectodermal origin and corresponds to the outer portion of the gill tube; the Eustacian canal opens into the pharynx and like it is lined with endoderm. The external meatus and the Eustachian canal are separated by a membrane, the supposed homologue of the septum between the inner and outer gill cavities in fishes; this according to Minot (1892, p. 738) is the "Anlage" of the tympanic membrane (*cf.* Fig. 3, *A*). The tympanic cavity in man (Minot, *l. c.*, p. 739) arises as a

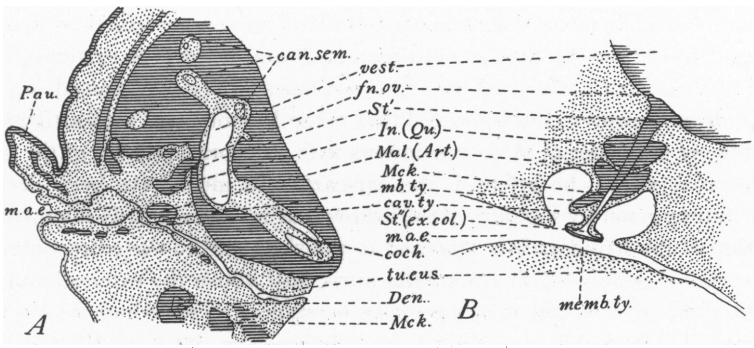

Fig. 3. Morphology of the ossicula auditus and adjacent parts; illustrating the quadrate = incus, malleus = articular theory.

A. Cross section of the auditory region in a human embryo of three months. After Minot.

B. Hypothetical cross section of the auditory region in an adult pro-mammal.

A shows the developing ossicula (*St'.*, *Mal.*, *In.*) wholly outside of the incipient tympanic cavity (*cav. ty*).

B shows the reduced quadrate (*Qu* = *Inc.*) and articulare (*Art.* = *Mal*) abutting against the columelliform stapes (*St'*). The tympanic cavity (*cav. ty.*) is growing up around the ossicula. The distal portion of the stapes (*St'.* = extra-columella) is supposed on this theory to have given rise to the manubrium mallei.

P. au., pinna auris.
m.a.e., external auditory meatus, continuous with *tu. eus*, Eustachian tube.
can. sem., semicircular canals.
vest., vestibule.
fn. ov., fenestra ovalis.
St'., proximal portion of stapes (columella).
In (*Qu.*), incus (= quadrate).
Mal. (*Art.*), malleus (= articulare).
mb. ty., tympanic membrane.
cav. ty., tympanic cavity.
St"., distal portion of stapes (= extra-columella).
coch., cochlea auris.
Mck., Meckelian cartilage.
Den., dentary.

dilatation from the tubo-tympanal canal, which grows up from below and surrounds the auditory ossicles. Accordingly these finally appear to be within the tympanic cavity "but," says Minot (*l. c.*, p. 240), "they are, of course covered by the tympanal epithelium or entoderm, and are, therefore morphologically outside the cavity just as the intestine is outside the peritoneal cavity." A similar process takes place in other mammals (*cf.*, Parker, 1886, plates showing cross-sections, van Kampen, 1905, pp. 324–329). In the developing *Sphenodon* (Howes and Swinnerton, 1901, pl. v) and lizard

(Kingsley, 1900, fig. 3), the tympanic cavity is seen to agree with that of the mammals in arising immediately externally to the cochlea and above and inside the cornu of the hyoid (*cf.*, Kingsley, *l. c.*, fig. 1, and Mead, 1909, fig. 4). In the lizard (*cf.*, Versluys, 1899, fig. 1) and in *Ornithorhynchus* (Weber, 1904, p. 145) the Eustachian tube is replaced by a wide communication between the tympanic and the pharyngeal cavities. It therefore seems reasonable to regard the tympanic cavity of the lizard as in the main homologous with that of the mammal.

The tympanic membrane.

From the considerations which follow it appears likely that the tympanic membrane of mammals may be considered as homologous, at least in part, with the tympanum of reptiles. The tympanic membrane in man (Cunningham, 1902, pp. 706–707) consists of three layers: (1) the stratum cutaneum, continuous with the external meatus; (2) the membrana propria, consisting of two sets of fibres, radial and circular, which center around the handle of the malleus; (3) the stratum mucosum, continuous with the general mucous lining of the tympanic cavity. In the tympanum of reptiles the stratum cutaneum and the stratum mucosum are present but the membrana propria is said to be lacking (Denker, 1901, p. 658). Versluys, however (1899, p. 359), in describing the tympanum of lizards speaks of a middle layer of connective tissue provided with elastic fibres (and apparently homologous with the membrana propria) as sometimes occurring. It is however generally vestigial, he says, and in this case the lizard tympanum would be structurally comparable only with the dorsal segment of the mammalian tympanum the "pars flaccida," where also the membrana propria is lacking.

A further correspondence between the tympanum of reptiles and that of mammals lies in the fact that the reptilian extracolumella and its supposed homologue the mammalian manubrium mallei are in both cases inserted between the inner and outer layers of the tympanum (*cf.* Versluys, 1899, p. 360, Kingsley, 1900, p. 232 and Cunningham, 1902, p. 707). The reptilian differs from the mammalian tympanum in its location, since it is attached to the posterior border of the quadrate and to the articular region of the mandible and therefore lies much above the three-layered portion of the membrane in mammals. But in the Cynodont reptiles (Fig. 1, *B*, *mb. ty.*) the quadrate is so much reduced that the location of the tympanic membrane must have corresponded more nearly with that of mammals. Here, as in so many other characters, the Cynodonts may have bridged over the morphological gap between reptiles and mammals.

The tympanic annulus.

The foregoing considerations in regard to the membrana propria may have some bearing on the origin of the tympanic annulus, which generally first ossifies in the periphery of the membrana propria. The suggestion is, that this is a secondary ossification and that the whole bone is a neomorph, just as is the inner part of the tympanic or ento-tympanic (van Kampen, 1905, p. 705). It might be questioned whether the supposed cartilaginous "Anlage" of the tympanic ring which Parker (1886, pl. v) figures in the embryonic *Tatusia* may not be homologous with the "annulus fibro-cartilaginous" of human anatomy, which is merely the thickened periphery of the tympanic membrane (Cunningham, 1902, p. 706). Van Kampen however (1905, p. 708), regards the tympanic bone as a transformed dermal jaw element, the surangulare, while Broom homologizes the mammalian tympanic with an element of the same name in the mammal-like reptiles (p. 121).

In adult Monotremes and Marsupials (*cf.* Doran's figures, 1879) the tympanic ring is closely connected with the large anterior process of the malleus, which process also is of dermal origin (see p. 132). The position of the tympanic ring in Monotremes and primitive Marsupials and Placentals is oblique rather than vertical, possibly because the tympanic cavity arises below and internally to the ossicular chain; and in Cynodonts (p. 127 and Fig. 1, *B*) the tympanic membrane probably lay on a plane below the quadrate and articular.

All the above mentioned facts must be taken into account in the final solution of the question whether it is a transformed jaw element, or whether the tympanic bone is a neomorph in mammals, analogous in that respect to the cartilaginous ear conch and to the entotympanic, and developed in connection with the membrana propria or, finally, whether it is homologous with the "tympanic" of Therapsids.

Gadow's theory (1901) that the tympanic bone is derived from the quadrate rests chiefly upon the following considerations: (1) In reptiles the posterior border of the quadrate serves for the attachment of the tympanic membrane, and in the Crocodile the quadrate and the whole auditory chain suggests the mammalian conditions (*cf.* Figs. 5, *A*, p. 134). (2) In the fœtal *Orycteropus* the tympanic is a semi-ring with three arms, in a measure recalling the quadrate of lizards and likewise articulating by its upper (proximal) end with the squamosal. (3) The knob of this tympanic "almost touches" a certain process on the mandible, which process is supposed to be the homologue of the secondarily inverted angle of the marsupials. (4) This "vanishing mandibulo-tympanic joint" lies immediately

behind the cartilaginous prolongation of the Meckelian cartilage *i. e.*, in the approximate position of the quadrate-articular joint of reptiles. From these parallel relations of quadrate and tympanic to the mandible, and relying on the other considerations already enumerated, Dr. Gadow concludes that the tympanic is homologous with a part at least of the quadrate, and he holds that the inner or posterior angle of mammalian jaws is also a reminiscence of this former mandibulo-tympanic connection. This argument appears to be open to several objections as follows:

(1) It seems strange that the Crocodile, a highly specialized predatory reptile of aquatic habits and belonging to an order which is very remote from the ancestry of the mammals, should be supposed to have retained in far greater degree than does *Sphenoden* and other reptiles the primitive conditions which furnish the key to the homologies of the mammalian ossicula.

(2) In the other direction *Orycteropus*, it is true, is in many respects a primitive Placental Mammal, but the structural gap between all Placentals and all modern reptiles is so almost immeasurably great that a sporadic resemblance between the relations of the tympanic in the fœtal *Orycteropus* and of the quadrate in the Crocodile seems to be a highly unreliable item of evidence in support of so far reaching a theory. Of very different character is the evidence (reviewed below) for the homology of the quadrate and articular with the incus and malleus respectively, since this is founded on several independent lines of comparison between all reptiles on the one hand and all embryonic mammals on the other. And if to this it be replied that the force of the comparison between the Crocodile and the fœtal *Orycteropus* rests not in the separate items themselves but in the totality of the resemblance, the rejoinder is that the validity of the homology between the quadrate and the tympanic rests upon the validity of the homology between the extracolumella and the malleo-incudal mass, a homology which is shown below to encounter serious objections.

(3) While the posterior border of the quadrate serves to support the tympanic membrane in the Crocodile and other recent reptiles this could not have been the case (at least to the same extent) in the Cynodonts, whose claims to relationship with the mammals are certainly at least worth considering. In the Cynodonts the reduced condition of the quadrate and the position of the supposed osseous auricular meatus indicate that the tympanic membrane was possibly stretched in part upon the descending flange of the squamosal (Fig. 1, *B*, *ty. m.*). We conclude therefore that Dr. Gadow's case for the derivation of the tympanic from the quadrate has not been made out.

The Stapes.

Whereas comparative anatomists differ as to the homology and origin of the more distal elements of the ossicular chain of mammals, practically all agree that the stapes of mammals is homologous with the stapes, or proximal portion of the columella auris, of reptiles and amphibians. In all these forms the stapes, both in ontogeny and in the adult has essentially similar relations to the internal ear: namely, it is a primitively cylindrical plug, fitting into the fenestra ovalis (*cf.* Figs. 3*A*, *St*, 7*C*).

The mammalian incus and body of the malleus.

Perhaps the majority of present day comparative anatomists and embryologists, after the most elaborate and thorough researches (*cf.* Kingsley, 1900; Weber, 1904, pp. 74–76; Gaupp, 1898, 1908) accept Reichert's view of 1837 that the quadrate of reptiles became free from the squamosal, and, by reduction in size and change of function was transformed into the incus of mammals.

The embryology of Monotremes (*cf.* Gaupp, 1908) Marsupials (*cf.* Parker, 1886, p. 272) and Placentals (*cf.* Parker, 1886; Kingsley, 1900) reveals a remarkable uniformity of conditions, and strong evidence in favor of the view that the mammalian incus and malleus represent transformed jaw elements (*cf.* Figs. 1, 3, 4, 7). The embryonic incus and malleus in all mammals are relatively very large, and this is in harmony with the view that in their ancestral history they were still larger, and discharged some function other than that of a sound conducting apparatus (Gegenbaur, Kingsley). However the fact that the stapes and the whole auditory capsule are also very large in embryonic mammals deprives the foregoing argument of much weight, and indeed suggests cænogenesis (Broom). The malleus and incus form the suspensorium for the Meckelian cartilage (Fig. 2*C*, 4*B*, 7) and are held to be derivatives of the pterygo-quadrate-Meckelian, or first, gill arch.

Perhaps the most weighty item of evidence for regarding the malleus as a transformed articular is that in the embryos of all mammals the malleus is entirely continuous with the Meckelian cartilage and seems to form its posterior portion, just as does the cartilaginous "Anlage" of the articular of reptiles. If the malleus is not homologous with the reptilian articular then this malleo-meckelian connection of all mammals must be entirely secondary, as maintained by Broom (1907.3, pp. 8–10).

The incudo-malleolar joint suggests the joint between the quadrate and articulare; while the body of the malleus forms the posterior expansion of

the Meckelian cartilage, just as does the articular in embryonic reptiles and amphibians (Fig. 7*C*).

It is scarcely necessary to refer to the objection (Weil, 1899) that because the incus is at first undifferentiated from the malleo-Meckelian bar, therefore it is morphologically a part of the lower jaw. Kingsley (1900, p. 239) and Broom (1907.3, pp. 9–10) have very fully met this objection by citing the well-known fact that in many cases structures which are known to be morphologically distinct are differentiated from a continuous stroma of procartilage.

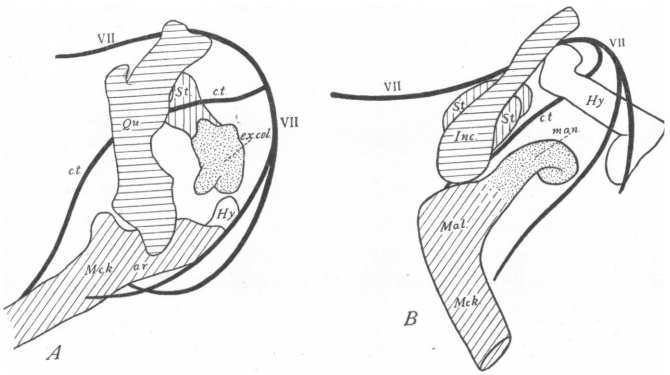

Fig. 4. Morphology of the auditory ossicles and adjacent parts in the embryo Lizard (*A*) and Pig (*B*). Modified from Kingsley.

The homologies between the several elements in the Lizard and the Pig (according to the quadrate = incus theory) are indicated by similar shading.

Lizard.	*Pig.*
Qu., quadrate	= *Inc.*, incus.
St., stapes	= *St.*, stapes.
Hy., hyoid cornu	= *Hy.*, hyoid cornu.
ex. col. extracolumella	= manubrium mallei.
ar., articular region of Meckelian cartilage	= *Mal.*, corpus mallei.
Mck., Meckelian cartilage	= *Mck.*, Meckelian cartilage.
VII, facial nerve	= VII, facial nerve.
c. t., chorda tympani	= *c. t.*, chorda tympani.

A well known reason for homologizing the incus and body of the malleus with the quadrate and articulare respectively, lies in the identical relations of these bones in the two classes, not only to the internal ear and the tympanic cavity but also to the chorda tympani nerve, which is a major branch of the seventh or facial nerve. A comparison of the embryonic conditions in the mammal (Fig. 4, *B*) and in *Sphenodon* (Howes and Swinnerton, 1901, pl. v, fig. 12) shows that the incus on the one hand and the quadrate on the other arise *externally* to the cochlea, *dorsally* to the stapes and to the "Anlage" of the tympanic cavity, and *internally* to the outer border of the

squamosal. Moreover, as shown by Kingsley (*cf.* 1900, figs. 10, 14) the incus of mammals and the quadrate of reptiles both lie *above and in front* of the chorda tympani, while the malleus of mammals and the articulare of reptiles lie *below and behind* the chorda tympani (Fig. 4). Broom, however (1907.3), does not think that these comparisons prove that the incus is homologous with the malleus, and he believes that the position of the chorda tympani in mammals is secondary (*cf.* p. 143).

The tensor tympani muscle, which is inserted into the manubrium mallei is thought to be a derivative of the pterygoid muscle because it is innervated by the third or mandibular branch of the fifth nerve (Weber, 1904, pp. 144–145, 160). This favors the view that the malleus represents a lower jaw element, the articular.

The anterior process of the malleus.

Below and around the cartilaginous bar (Figs. 2*C*, 4*B*) which connects the developing malleus with the Meckelian cartilage a dermal splint is formed (*cf.* Parker's figures of embryonic mammals, 1886), which seems to occupy the position of the angulare in *Cynognathus* (Fig. 2, No. 2) and which Parker and other authors have homologized with the angulare of modern reptiles. This derm bone is variously named the processus "longus," "gracilis," "Folianus," "anterior."

The manubrium of the malleus.

The manubrium mallei (Fig. 2*B*, 7*C*), being fastened in the middle layer or membrana propria of the tympanic membrane (p. 127) corresponds with the extracolumella of reptiles, which is also fastened between the inner and the outer membrane (*cf.* p. 127). Kingsley (1900, p. 232) states that in the pig the manubrium "arises distinct from the body of the malleus" and is at first, like the extracolumella, "a separate element developing in the tympanic membrane and only later uniting with the rest of the structure." Mead however (1909, p. 188, and pl. iii) found that the manubrium in the pig was continuous with the malleus, Fischer (1901, p. 501, and Taf. xxx, Fig. 4) found the same condition in the mole and Dr. Broom informs the writer that the same is true in the Marsupials, and that in his opinion the manubrium has not been derived independently of the maleus. Kingsley's figures show that the extracolumella, like the manubrium, arises below and *externally* to the tympanic cavity and much below the level of the stapes and quadrate or incus; and that the extracolumella further agrees with the manubrium in its position with reference to the chorda tympani and "hyomandibular" nerves: namely below the former and above the latter (Fig. 4, *A*).

If the manubrium has not had a phylogenetic history distinct from that of the body of the malleus this would constitute an objection to homologizing the malleus with the articular (see below).

Rival hypotheses of the origin of the incus and malleus and of the fate of the quadrate and articular.

Gadow (1901, pp. 396–398) believes that both the incus and the malleus have been derived from the reptilian columella and its appendages, the suprastapedial, etc. This opinion is also held by Broom (1907.3, pp. 10–11), while similar views were held by Peters, Dollo, Baur and Cope (1883). These all base their argument chiefly on the similarity in function and relations between the extracolumella and the incus and malleus; because, as stated above, the extracolumella, like the manubrium of the malleus is fastened externally in the tympanic membrane, while internally, like the incus, it articulates with the stapes. Kingsley held that the malleus is really a compound bone and that the assumed homology with the extracolumella applies only to the manubrium, but as stated above Kingsley's view that the manubrium is a separate element has not been confirmed. The extracolumella of the Crocodile has a dorsal process called the suprastapedial, which Broom (1907.3, p. 10) homologizes with the incus. On the other hand the variability of the extracolumellar processes of the Reptilia and the difficulty of homologizing them within the class (Gadow, 1901, p. 399) rather warns against attempting to seek the homology of one of them in the mammals, which lie so far outside the limits of the modern Diapsida. If Broom and Gadow are right then the Crocodile is more primitive than *Sphenodon* with respect to its auditory ossicles. Broom's hypothetical diagram (1907.3, p. 10, *cf.* Fig. 5 above) of the ossicula in an embryo Cynodont is in fact a graphic average between the embryonic conditions in the Crocodile and in the mammal.

Another comparison in favor of homologizing the incus and malleus with the extracolumella and its appendage the suprastapedial respectively, has been adduced by Gadow (1901, p. 398). In the embryo crocodile (*cf.* Fig. 5, *A*, *col. art*) the *extracolumella* is joined with the posterior or articular expansion of Meckel's cartilage by a bar of cartilage or connective tissue, which may be designated as the "columella-articular" bar. In the embryo mammal (Fig. 7, *C*) the *malleus* is prolonged anteriorly into the Meckelian cartilage, and the part in front of the malleus may be designated as the "malleo-meckelian" bar. Since the extracolumella has the same relations to the "columella-articular" that the malleus has to the "Malleo-meckelian" Gadow homologizes the extracolumella with the malleus (the incus is assumed to be a part of the same mass). But this argument simply begs the

question, by assuming the homology of the "columella-articular" with the "malleo-meckelian." For if on the other hand the malleus be assumed to represent the articular (a view which is supported by many authors) then

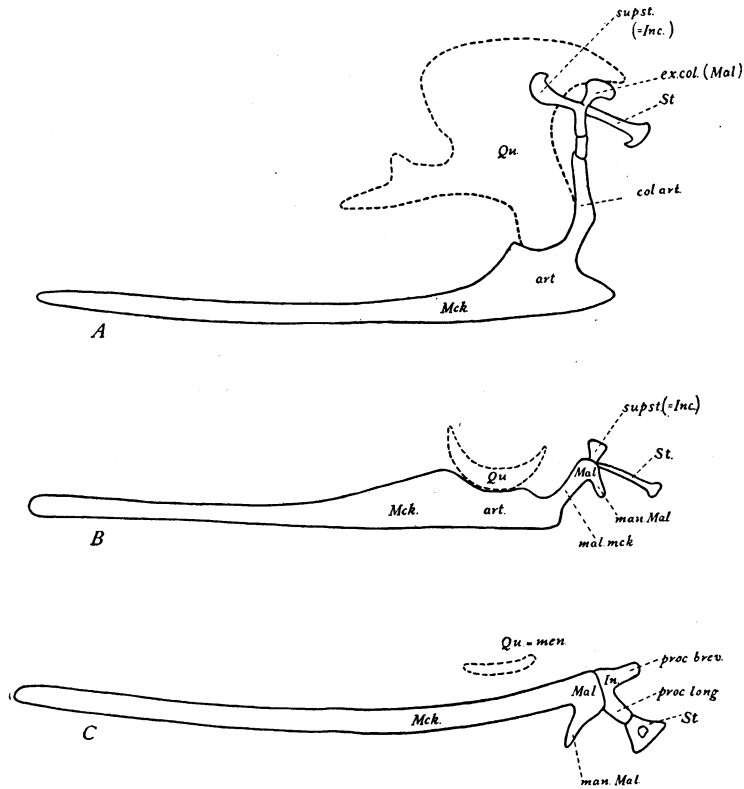

Fig. 5. Broom's theory of the evolution of the mammalian ossicula auditus. After Broom (lettering modified).

A. Embryo crocodile; *B*, hypothetical restoration of the conditions in an embryo Cynodont; *C*, embryo mammal.

sup. st., suprastapedial.
ex. col., extracolumella (= Malleus).
St., stapes.
col. art., columella-articular bar.
mal. mck., malleo-meckelian bar.
man. Mal., manubrium mallei.
Other abbreviations as in Figs. 3, 4.

the "columella-articular" bar of the Crocodile lies *behind* the articular and, as in *Sphenodon*, it may be homologous with some part of the hyoid cornu, *i. e.*, of the second gill arch; while the "malleo-meckelian" bar of the mam-

mal lies *in front* of the articular and is a part of Meckel's cartilage, and therefore belongs to the first gill arch. The cogency of Gadow's argument on this point seems therefore to be open to doubt.

The Fate of the Quadrate.— Various other theories have been proposed to account for the fate of the quadrate in the mammalia.

Albrecht (1884) held that the quadrate became reduced and was absorbed in the squamosal; but the principal evidence he adduced in support of this view was a malformed idiot's skull which showed *on one side* a separate bone in the assumed position of the quadrate. This is a fair example of the kind of "evidence" which formerly was often accepted in the domain of comparative anatomy and even of palæontology. Isolated points of resemblance between the most widely removed forms were used to support far reaching homologies, with little regard to the totality of evidence drawn from all parts of the organism.

Osborn also (1898, p. 331), in view of the great reduction of the quadrate in the Cynodonts, not unnaturally favored the theory that the quadrate had been absorbed into the squamosal, but this view (which was also held by Baur) lacks direct confirmatory evidence.

Broom (1890, 1906, 1907.3) sees in the reduced quadrate of the Cynodonts the homologue of the interarticular disc, or meniscus, which lies between the mandibular condyle and the glenoid fossa of mammals (*cf.* Fig. 5, *C*). The presence of an ossified meniscus in the rodent *Pedetes* proves only that this element may occasionally become ossified. Further considerations on the origin of the meniscus are given below (p. 138).

Supposed mechanical objection to the theory that the incus and malleus represent transformed jaw elements.

From the foregoing it appears possible but not by any means proven that the middle elements of the mammalian ossicular chain have attained their present relations through a change of function, whereby they gradually become relieved of the jaw-supporting function and, being pushed against the stapes-extracolumella, came thus to participate in its function of transmitting vibrations to the inner ear. Gaupp (1905, p. 136) has undertaken to conceive the conditions during the time when the new and old joints both functioned together; but in his diagram, which is based on the conditions in the Lacertilia, the anterior joint, between the new mandibular condyle and the squamosal, is separated by a considerable interval from the old joint, between the articular and the quadrate.

Apart altogether, however, from the fact that all known streptostylic reptiles belong to the Diapsida, which appear to be widely removed in many

characters from the ancestral mammals, there are several weighty objections to Gaupp's diagram. First it assumes that the coronoid process of the mammalian mandible is a neomorph, developed later than the mandibular condyle; but there is strong palæontological evidence (Fig. 6, Nos. 1–7) that the coronoid was originally very large and broad, and in reality older than the condyle (see below p. 137). Secondly the diagram in question assumes that the quadrate could bend backward and forward like that of a Lizard, but if the Cynodonts represent the prototypal conditions of the Mammalia, then the motion of the quadrate must at first have been very limited. Thirdly this process, as conceived by Gaupp on the basis of the conditions in the recent Lacertilia, has been objected to by Gadow (1901, p. 410) on the ground that while it was in progress the Promammal "could not use its jaw and could not hear."

IV. Application to the conditions in the Cynodontia of the Theory that the Incus is derived from the Quadrate, the Malleus from the Articular.

While it might or might not have been a mechanical impossibility for the mammalian relations of the lower jaw and ossicula auditus to have evolved out of the conditions represented in the Lacertilia, it is at any rate almost certain that in the Cynodonts a double articulation between the skull and mandible is foreshadowed, if not actually realized; and yet it is evident that in spite of this both the jaw and the stapes-extracolumella must have been mechanically workable and useful. Broom (1904.2, pp. 495, 496) has suggested that the mammalian conditions must have been initiated by the backward prolongation of the condylar process of the dentary till it came in contact with the glenoid region of the squamosal(Fig. 2, *B*). This hypothesis is strengthened by the fact that the condylar process of the dentary shows an increasing backward prolongation in the following series of Triassic Cynodonts and so called mammals: *Bauria, Cynognathus, Trirachodon, Dromatherium.*

The double articulation between jaw and skull which would thus result would be homologous, so far as concerns its separate elements, with the double articulation conceived by Gaupp, *i. e.*, the new joint would be by way of the condylar process and the glenoid portion of the squamosal, while the older one would be by way of the small articulare and quadrate. But if the conditions thus foreshadowed in the Cynodonts were actually realized, these two articulations would be so close together that they would function

practically as a single fulcrum for the lower jaw (*cf.* Fig. 7, *B*), especially if there was a light movement between the angulare and the dentary; and

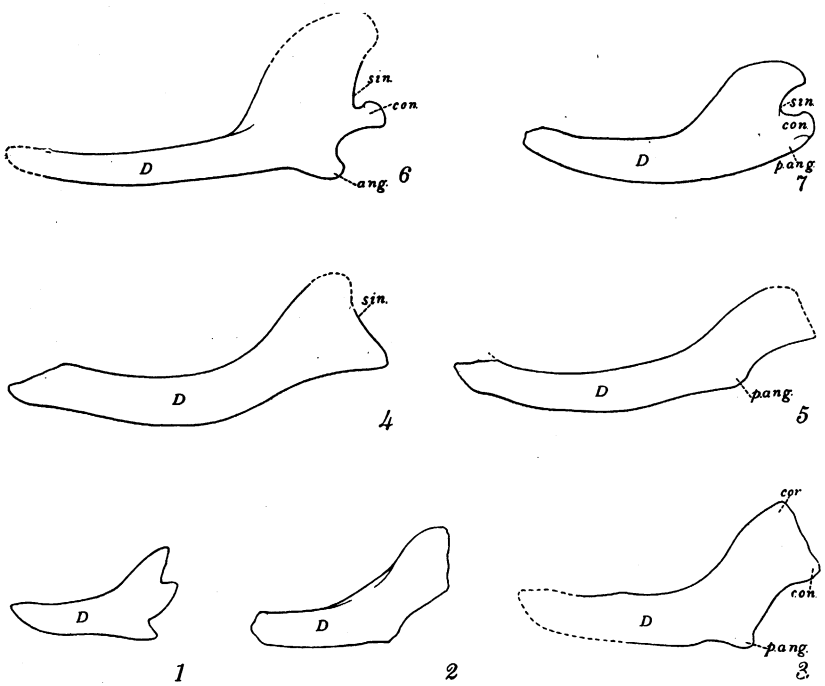

Fig. 6. Morphology of the mandibular condyle, coronoid and angle in Mesozoic Therapsids and Mammals. Scale various.

D., dentary.

p. ang., processus angularis.

sin. corono-condylar sinus.

con. condyle.

cor. coronoid.

No. 3. Lower jaw of a Triassic Cynodont reptile, *Diademodon mastacus*, after Broom. Incipient condyle and corono-condylar sinus, angular process well developed.

No. 2. Lower jaw of a Triassic Cynodont, *Tribolodon freresi*, after Seeley. Large coronoid with sloping anterior border.

No. 4. Lower jaw of a Triassic Promammal (?) *Dromatherium sylvestre*, after Osborn. Condyle prominent, coronoid very broad and sloping anteriorly, corono-condylar sinus (*sin.*) incipient.

No. 5. Lower jaw of a Triassic Promammal (?) *Microconodon tenuirostris*, after Osborn. Angular process incipient.

No. 1. Lower jaw of a Triassic Promammal (?) *Karoomys browni*, after Broom. Angle and condyle well developed.

No. 7. Lower jaw of a Middle Jurassic mammal *Phascolotherium bucklandi*, after Osborn. Angle inflected, condyle sessile, corono-condylar sinus well marked; coronoid very broad, sloping anteriorly.

No. 6. Lower jaw of an Upper Jurassic mammal *Docodon striatus*, after Marsh. Condyle pedunculate but not raised very much above the level of the teeth, angle well developed, coronoid very broad and sloping anteriorly.

this would entirely meet Gadow's objection (cited above) to Gaupp's "double articulation" theory.

The slender character of the angular and articular bones, and the instability of their connection with the dentary, combined with the backward and upward pull of the powerful temporal muscles upon the large dentary, may have conditioned the backward growth of that element until its posterior (condylar) extension found secure lodgment against the squamosal. The new joint would then be more in line with the pull of the temporal muscle and would be mechanically better and more stable than the old joint.

These considerations are in harmony with the arguments against the view (p. 135), that the quadrate was transformed into the meniscus. That the new condylar process of the dentary did not impinge altogether against the quadrate, but partly above it, is indicated by Broom's detailed side view of this region in *Cynognathus* (*op. cit.*, pl. xxxv, figs. 5, 6). In the front view of this region in *Gomphognathus* (*op. cit.*, pl. xxxv, figs. 2, 3) the condylar process is represented as *below* the level of the quadrate, but this is because the jaw is depressed at an angle of 90° to the palate.

When the condylar process of the dentary grew backward we may imagine that it did not abut directly against the squamosal bone itself but merely pressed against the muscles which occupy this region in reptiles. This would agree with the conclusion reached by Kjellberg (1904) who sees in the meniscus merely the tendinous origin of some of the fibres of the external pterygoid muscles, which fibres are attached to the meniscus in man (Cunningham, 1902, p. 260) *Echidna* (Lubosch, 1906) and other mammals. Lubosch (1906, pp. 591–594) regards the meniscus as representing a separated portion of the periosteum of the lower jaw.

In order to substantiate the conclusion that the mandibulo-squamosal joint in mammals is a wholly new structure, into which the quadrate and articular did not enter, we recall the facts: (1) that embryological research gives no warrant for the belief that the mammalian jaw is composed of more than one element (except for the occasional vestiges of a splenial); (2) that the oldest known mammalian jaws, from the Triassic, Jurassic and Basal Eocene never show any trace of sutures; (3) that in the Cynodonts the broad ascending ramus, or corono-condylar region appears from Broom's researches (1904.2) to be a part of the dentary.

In proportion as the new squamoso-mandibular joint became established the old quadrato-articular joint would probably dwindle in size and become available for the change of function which is the chief condition for the transformation of the quadrate and articular into the incus and malleus. But there are two important difficulties which must be met before the view that the quadrate became the incus, the articular the malleus may be con-

sidered as even probable: (1) How did the reduced quadrate, which is generally spoken of as being "fixed" in the Cynodontia, become sufficiently free from the squamosal to enable it to assume the functions of the incus? and (2) how did the reduced articular gain contact with the stapes without interfering with the hearing function?

(1) The quadrate in *Galesaurus* and *Cynognathus* (*cf.* Gadow, 1901, fig. 4; Broom, 1904, 2, pl. xxxv) appears to be fixed in the squamosal by its dorsal portion (*cf.* Fig. 1, *B*, *Qu.*), but even here it seems possible that the lower end may have been capable of a slight antero-posterior motion. A little atrophy of the posterior wall of the descending flange of the squamosal, which is certainly very thin at this point, would greatly increase the mobility of the lower end of the quadrate. In *Gomphognathus kannemeyeri* (Broom, *op. cit.*, pl. xxxv, figs. 2, 3) the quadrate is a small bone flattened antero-posteriorly; in the front view it appears to be held in place against the squamosal only by the articular, and that too only on its inferior surface, and there is nothing in Broom's figures to show why these two bones together may not have moved more or less against the squamosal. This quadrate of *Gomphognathus* parallels the incus of primitive mammals in the following particulars: (*a*) it is a very small flattened bone attached to the squamosal and located at the postero-external corner of the skull, just internally to the backward prolongation of the zygomatic arch (*cf. Echidna* and Parker's section of the skull in the embryo *Tatusia*: 1886, pl. iv, fig. 11); (*b*) it articulates by a convex surface with the articular (the supposed homologue of the malleus) and this circumstance suggests the large convexo-concave articulation between the incus and the malleus in embryo mammals. If the quadrate and articular were further reduced in size it seems possible that they might acquire enough mobility to function as the incus and malleus, which indeed move through very small arcs.

(2) The problem of the manner in which the reduced quadrate and articular could gain contact with the middle of the primitive stapes-extracolumella without interfering with the hearing function is very obscure, and until all the mechanical stages are clearly conceived the whole hypothesis must remain on trial; but whatever the final answer may be it must take into account the following among other considerations:

(*a*) The fact that the tympanic cavity arises as a diverticulum from the Eustachian tube, and enfolds the ossicula from below and internally (p. 126).

(*b*) The oblique position of the tympanic membrane in primitive mammals, and the fact that the membrana propria appears to be an adjustment for regulating the tympanum (p. 127).

(*c*) The supposed homology of the extracolumella with the manubrium mallei (p. 132).

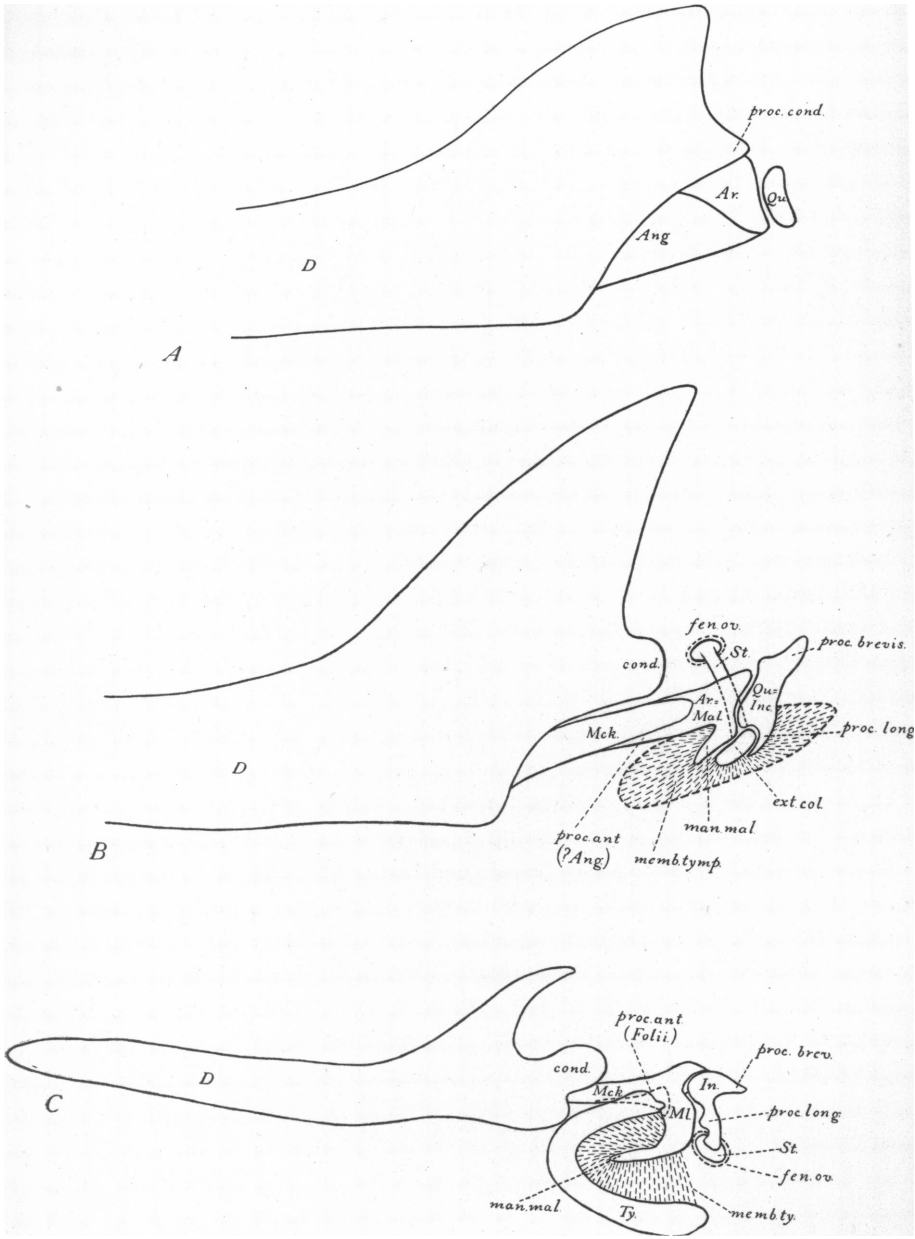

Fig. 7. Diagram illustrating the application to the conditions in the Cynodontia of the quadrate = incus, articular = malleus theory. *A. Cynognathus*, after Broom; *B*, hypothetical intermediate stage; *C*. embryo mammal (*Tatusia*) after Parker.

Abbreviations as in previous figures.

(*d*) The probable position of the tympanic cavity in Cynodonts (Fig. 1, *B*), immediately below and internal to the posterior end of the jaw (p. 127).

(*e*) The position and relations of the supposed tympanic bone of Therapsids (p. 121).

Summary.

The foregoing review of the mammal-like reptiles of the Permian and Triassic appears to show that it is quite unnecessary to have recourse to unknown Amphibian-like creatures of the Devonian in the search for the immediate ancestors of the Mammalia. Nor does it favor the view that the mammals are descended from streptostylic reptiles or from any reptiles of the subclass Diapsida. There seems, in fact to be a large body of evidence in favor of the view advocated by Osborn and Broom that the mammals have been derived from the Triassic reptilian order Cynodontia, although not from any known member of it. As is well known the Cynodontia foreshadow the mammalia: especially in the constitution of the temporal arch, in the development of the secondary palate and of paired occipital condyles, in the possession of incisors, canines premolars and molars, and in the enlargement and functional importance of the dentary. Perhaps even more suggestive of mammalian affinities are the resemblances in the pterygoids, in the phalangeal formula (so far as known) in the humerus, carpus, tarsus, shoulder girdle and pelvis. Structurally if not genetically the Cynodontia certainly bridge over the gap between mammals and reptiles; because in combination with the above mentioned mammalian features they possess many reptilian characters, inherited from the orders below them. For example they retain a bar connecting the jugal with the postorbito-frontal (absent in *Bauria*), and the pterygoids have anterior flanges (although lacking the pterygoquadrate portion); a quadrate, articular, angular, surangular and splenial are present, and the vertebræ have intercentra. All these are characters which may reasonably be sought in the remote ancestors of the mammalia.

As regards the mammalian auditory ossicles, the theory which homologizes the mammalian incus with the reptilian quadrate, the body of the malleus with the articular, rests upon considerable evidence, which has been developed, especially by Reichert, Kingsley and Gaupp. The strength of this theory proceeds from the fact that it is founded upon morphological relations common to all embryonic mammals on the one hand and all modern reptiles on the other. Gaupp's corollary that the Promammals once had two joints between the jaw and the skull was shown to be open to serious objections, but only in so far as it assumed the mammals to have been

derived from streptostylic reptiles of the type represented in the Lacertilia; and strong anatomical and palæontological evidence reviewed above shows that the squamoso-mandibular joint in mammals is, in fact, a neomorph.

An attempt was made to demonstrate (pp. 136, 140) that the application of the above mentioned "quadrate-incus" doctrine to the conditions in the Cynodontia might explain to a certain degree the supposed transformation of reduced jaw elements into *accessory* auditory ossicles. Upon this assumption these structures only very gradually gave up the suspensorial function, dwindled greatly in size and began to come into functional relations with the stapes-extracolumella, possibly serving at first merely as a point of support for the middle part of this jointed column (Fig. 7, *B*). But until every mechanical and morphological stage in the progressively intimate relations of the primary and secondary ossicles to each other and to the muscles be clearly conceived and supported by well founded analogies, the quadrate-incus, articular-malleus theory must remain somewhat doubtful. In its defense it might be said that the functional integration of the stapes-extracolumella with the vestigial quadrate and incus was but one incident in the wonderful metamorphosis of saurians into mammals, a process which involved the transformation of scales of some sort into hairs, of skin glands into milk-secreting organs. But it must be admitted that in these cases the change of function was less radical and the intermediate steps more easily conceived than in the supposed case now under consideration.

The quadrate-incus theory may not be seriously hampered by the partial fixity of the quadrate in Cynodonts because a secondary increase in the mobility of the quadrate is quite conceivable under the conditions assumed (p. 139); but a more serious objection is the fact that Kingsley's view of the separate origin of the manubrium of the malleus has not been confirmed by subsequent research, and therefore the opposing arguments for homologizing the malleus with the extracolumella rather than with the articular have not been fully met.

Turning now to the opposing theory, held notably by Gadow and Broom, we note that it makes no demand for a very hardly conceived and elaborate change of function, since it regards the tympanic membrane and the auditory ossicles of the lizard and crocodile as strictly homologous with those of mammals; and it assumes only that:

extracolumella = malleus,
suprastapedial = incus,
stapes = stapes.

On the other hand the weak points of this theory appear to be as follows:

(1) The connection between the malleus and Meckel's cartilage, which is universal in mammalian embryos of all orders, must be assumed to be

secondary and to have resulted from the proximity of these elements during the course of development. Broom, however, has cited supposedly analogous cases where structures which are known to be distinct morphologically become connected in ontogeny and arise from a continuous cartilage.

(2) The fate of the quadrate is still unsettled. According to Gadow a part of it at least has become transformed into the mammalian tympanic bone, but this view appears to have extremely little evidence in its favor. According to Broom the quadrate has been reduced into the interarticular disc or meniscus. Broom interprets the conditions in the Cynodontia as pointing in this direction, but the ontogeny of the mammals has so far not lent any direct support to this view, but has been interpreted by Kjellberg as indicating that the meniscus is a neomorph, derived from the fibres of the pterygoid muscles.

(3) The general theory in question assumes that the crocodile is more primitive than *Sphenodon* in the condition of its auditory ossicles, a fact which appears contrary to what might have been expected.

(4) The suprastapedial, which Broom homologizes with the incus, is an inconstant element in the Reptiles, which show a wide range of variability in the appendages of the columella (Versluys) and therefore the suprastapedial is hardly free from the suspicion of being a neomorph.

(5) The theory under consideration must assume that the chorda tympani, which lies above the ossicular chain in the reptiles has passed through it and come out on the under side (Broom), since it appears below the chain in mammals. Such migrations of nerves through bones are of course not rare (Broom) and the variable position of the carotid foramen in a single family, the Viverridæ, appears to be a case in point.

Whichever of these two theories shall finally be adopted will apparently be entirely reconcilable with the view that the mammals have been derived, not from unknown Devonian amphibia, not from streptostylic reptiles allied to the lizards, but from as yet undiscovered Synapsid reptiles of the order Cynodontia.

CHAPTER II. GENETIC RELATIONS OF THE MONOTREMATA.

Analysis.

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I. Outline History of the Classification.[1]

1791 (?). Shaw describes the spiny anteater of New South Wales under the name "*Myrmecophaga aculeata.*"

1795. Geoffroy refers to Shaw's species as representing a new genus, "Aculeata," of Edentates.

1798. G. Cuvier gives the generic name *Echidna* to "Les Fourmiliers épineux." (Name preoccupied by *Echidna* Forster 1788, a genus of Morays).

1799. Shaw describes the Duck-billed Platypus under the name "*Platypus anatinus.*" The name "Platypus" being preoccupied *Ornithorhynchus* Blumenbach replaced it.

1800. "Les Monotrèmes" made a family of "les Édentés" by Cuvier.

1800. "*Ornithorhynchus paradoxus*" described by Blumenbach. According to Gervais (1836), Geoffroy and Lamarck both considered the group as forming a class by itself intermediate between Mammals, Birds and Reptiles.

1803. The name "Les Monotrèmes" applied by Geoffroy to include *Echidna* and *Ornithorhynchus* as an "ordre" with the following characters: "Doigts onguiculés; point de veritable dents; un cloaque commun, versant a l'exterieure par une seule issue." (Quoted by Gill, 1903, pp. 433–434).

[1] Compiled chiefly from Palmer, 1904.

1816. De Blainville removes them from the Edentates, at first classifying them along with the Marsupials provisionally in a grand division (p. 76), but later (1834) formally assigning them to a distinct subclass "Ornithodelphia" (p. 82).

1838. Bonaparte applies the name "Monotremata" in Latin form, in a systematic sense.

1877. *Echidna bruynii* Peters and Doria, made the type of a new genus "*Acanthoglossus*" by Gervais. *Acanthoglossus* being preoccupied Gill substituted *Zaglossus* and Gervais (later) substituted *Proëchidna* (Palmer).

Reptilian Characters in the Integument. The Origin of Hairs.

From a study of the development of the hairs in *Echidna*, Römer (1898) establishes the probability that *the ancestors of the mammals were scaly creatures.* The following observations are especially important in this connection:

(1) In certain regions of the body in the young *Echidna* (Römer, Taf. 1, fig. 11) each spiny hair protrudes from the apex of a broadly-triangular scale-like structure. These structures are arranged in transverse rows, which alternate and overlap in a very scale-like manner. They are not, however, regarded by Römer as true scales.

(2) On either side of the backwardly-pointed tip of the hair-spine two or more small papillæ occasionally appear. These Römer interprets as the last vestiges of true scales, which were probably also arranged in transverse imbricating rows and determined the scale-like arrangement of the intervening rows of hair-spines. These papillæ are composed of the same histological elements as both hairs and scales, but they protude from, and are not sunken into, the surrounding integument.

(3) The internal basal papilla of the hair-spine itself, instead of being a small bulb in the root of the hair as in higher mammals, extends over half way up the shaft and this fact greatly increases the similarity between such a hair-spine and an insunken reptilian scale.

(4) Römer believes with de Meijere (1894) and Weber (1904) that hairs have gradually replaced scales.

The preceding observation of Römer naturally lead to the question *whether the hairs in the ancestral mammals may not have arisen much as in Echidna, i. e., as flattened spiny hairs between the scales?*

This hypothesis is consistent with many facts, of which the following may be cited:

(1) The observations of Poulton (1894) on *Ornithorhynchus* and of

Spencer and Sweet (1899) on certain Marsupials show that some hairs are from the first not radially symmetrical, as usually in mammals, but flattened dorso-ventrally, with the cortical layer thicker on the dorsal surface.

(2) *Pari passu* with the reduction of the scales, the heavy spines may have been replaced by finer and finer spines, just as the strong-spined *Echidna aculeata typica* grades into the hairy *Echidna aculeata setosa* (Thomas, 1885).

(3) If spiny hairs are a primitive mammalian character this may possibly explain their frequent retention and progressive specialization in the very lowly orders Insectivora and Rodentia.

The former *coëxistence and intermingling of hairs and scales* in ancestral mammals is also supported by numerous facts:

(1) The coëxistence of hairs and true "reptilian" scales in *Manis* (Weber, 1894). The primitive nature of these scales has been questioned by Beddard (1902, p. 189), but defended by Weber (1904, pp. 420–421) [1].

(2) The mingling of hairs and minute scales in the fœtal *Dasypus* and in the tail of *Didelphis, Petrogale* and many Insectivores and Rodents. The tail, being of little adaptive importance in the economy of many animals might be expected to retain in some instances very ancient hereditary characters (p. 334).

(3) The mingling of hairs and a scale-like pattern of the epidermis in the manus and pes of many Insectivores and Rodents.

(4) The fact that when hairs and scales are intermingled the hairs are usually grouped together in threes. Hence in other cases de Meijere (1894) regards the occurrence of "Dreihaargruppen" alone as a vestige of the former coëxistence of hairs and scales (Weber, 1904, pp. 11, 12).

Reptilian Characters in the Reproductive Organs. The Origin of Lactation.

The completely Sauropsidan character of the female genitalia and the retention of oviparity in the Monotremes are too well known to require special comment, but there is one character in the male organ that may be cited here which shows how far below the remaining mammals the Monotremes stand: namely the fact that the penis has not yet acquired its double function of ejecting both the urinary and reproductive products, but transmits the latter alone (Weber, 1904, p. 326). In the Monotremata also the ureters open into the urinogenital canal, while in the Theria they open into

[1] In view of the completely mammalian nature of *Manis* in respect to other characters, and of its numerous highly aberrant specializations, it would seem more likely that the scales are entirely secondary.

the bladder (Weber, 1904, pp. 244, 246). However, in respect to the bending of the vas deferens around the ureters the Monotremes agree rather with the Placentals than with the Marsupials (Weber, 1904, p. 244).

When we turn to the accessory reproductive characters of Monotremes especially the organs and process of lactation, we find very illuminative conditions which suggest what may have been *the history of lactation in the mammals.*

Semon (1895) gave an excellent account of the brooding habits, nature of the milk, etc., of the Monotremes in his 'Zoologisches Forschungsreisen,' and more briefly (1899) in his 'In the Australian Bush' (pp. 160–164). Eggeling (pp. 332–340) showed that the sweat glands and the mammary glands of Monotremes were both derived from the same undifferentiated type. Bresslau in his 'Entwickelung des Mammarapparates der Monotremen....' (1907) gave an extended description of the developmental stages of the marsupium. His principal conclusions (*l. c.*, p. 512) are: that the primary "Anlagen" of the marsupium indicate that it arose in the ancestral mammals in much the same way as did the brooding ridges in birds, namely, as a result of incubating the egg; and that this habit caused an increase in the blood vessels and glands in the mammary fields, which served at first to aid in keeping the egg warm. Afterward these glands gave rise by a change of function to the milk glands.

Mivart (quoted by Darwin, 1872, p. 322), in attacking the theory of natural selection, raised the following objection: "Is it conceivable that the young of any animal was ever saved from destruction by accidentally sucking a drop of scarcely nutritious fluid from an accidentally hypertrophied cutaneous gland of its mother?" Darwin (1872, *l. c.*), in endeavoring to meet this objection suggested that the mammary glands were at first developed within the marsupial sack, cited the rise of the marsupium in the fish *Hippocampus,* and emphasised the idea that the sucking habit was "at first acquired by practice at a more advanced age, and afterward transmitted to the offspring at an earlier age."

Upon these and similar observations may be based the following general hypothesis of the origin of lactation.

(1) From the intimate developmental connection between hairs, sebaceous and suboriparous glands and milk glands it may be inferred that the milking habit was at first a by-product of the general process whereby reptiles with variable body temperature (pœcilothermous) were transformed into mammals with a constant body temperature (homœothermous). The Monotremes, with an imperfectly developed homœothermy, are equally primitive in the organs and processes of lactation.

(2) The secretion of the proto-lacteal glands at first may have served to raise the temperature of the egg during incubation (Bresslau, 1907).

(3) Localization and hypertrophy of the protolacteal glands in the brooding area thereupon followed (Darwin).

(4) The eggs at first would not be carried along when the mother left the nest; but they might gradually come to adhere to the brooding surface by means : (*a*) of its depressed character (*b*) possibly in part by the adhesive quality of the proto-lacteal fluid (*cf.*, the large albuminous element in the milk of *Echidna*); (*c*) eventually by means of the raised borders of the brooding area which finally became the marsupium (*cf.*, marsupium in *Hippocampus*, Darwin).

(5) The intimate association between the maternal brooding area and the *egg* would be a necessary antecedent of the intimate association between the maternal brooding area and the *young*.

(6) The mother at first merely settled down over the egg but afterward came to transfer the egg (*cf. Echidna*) and later the young (*cf.* Marsupials) to the pouch.

(7) In the pro-mammals the eggs were large-yolked (*cf. Echidna*) and the young were hatched in an advanced condition, as in many reptiles (Darwin).

(8) These advanced young may have hatched out in the pouch, or after leaving it, may often have been driven back to it to seek for warmth. When the mother moved about they may have clung to the long hairs in the mammary field or buried their heads in this warm bosom.

(9) At the base of these hairs the protolacteal glands were pouring out their albuminous, oily fluid. This may have served at first to keep the young warm, just as it formerly served to keep the egg warm.

(10) The milking habit was initiated when the young ones discovered that the material milk secretion tasted good. They would then at first lick it from the base of the hairs (*cf. Echidna*).

(11) Licking would gradually give place to sucking and all its complex reflexes, while the nutritive quality of the milk improved.

(12) The newly born (or hatched) young gradually become virtual *external parasites* upon the mother. They retain and greatly develop the habit and organs of sucking, which they acquire at a constantly earlier period of development (Darwin).

(13) The keratin in the egg shell becomes eliminated.

(14) The maternal teats and marsupium meanwhile are being perfected. In the Marsupials, by means of the compressor mammæ muscles and other maternal adaptations, the milking efforts of the young are at first assisted and then largely supplanted, so that the young finally become mere larvæ, with special larval organs, such as the intranarial prolongation of the epiglottis.

(15) In the pro-placentals the parasitic adaptations become more largely intra-uterine as the egg-laying period is delayed. The nutritive contents of the yolk sack are reduced, and the vascular uterine walls finally come in contact with both allantois and yolk sack (*cf. Manis*). Nutritive material in the maternal blood passes at first by osmosis to the embryo. In the Marsupials it is the yolk sack placenta, in the Placentals, the allantoic placenta which finally predominates.

(17) *Pari passu* with the prolongation of intra-uterine development the Placentals give up the imperfect marsupium, vestiges of which seem to be represented in the protractor muscle of the prepuce in Carnivora and Artiodactyla (Weber, 1904, p. 35).

IV. Reptilian, Archaic and Aberrant Characters in the Skeleton of Monotremes, tending to separate them widely from the Higher Mammals and collectively indicating that they are an extremely Early Offshoot of the Mammalian Stock.

Skull.[1]— **A. Top and side views.**— *Chondrocranium* unusually massive and well developed (Parker, 1885–86, p. 80). Contrast the fenestrated chondrocranium of most Placentals.

Frontals facing forward and upward, rather small between orbits (*e. g.*, like *Tritylodon*). Brain confined to the occipital and parietal segments. (Primitive mammalian character).

Separate postfrontals. Of these structures Van Bemmelen (1901.2, p. 794 says: "....ein Postfrontale ist zwar nach meinem Befunden vorhanden, aber nicht in dem character eines Deckknochens, sondern als selbständiger Knochenkern in vorderen Theil der sogenannten Parietalplatte des Primordialcranium." Hence homology with reptilian postfrontal is doubted.[2] At any rate unique in mammals. "Prefrontal" in *Ornithorhynchus* (described by Seeley) due to overlap of nasals by frontals. Interpreted as orbital portion of frontal by van Bemmelen.

Broad *median parietal* homologous (?) with the interparietal of Marsupials and Placentals.

Broad *squamosal,* leaving open canal posteriorly, analogous to posttemporal arcade in *Sphenodon* and possibly homologous with a similarly placed canal in Anomodonts. Unique in mammals.

No separate *lachrymal* (van Bemmelen). (Aberrant character.)

Jugal absent in *Echidna,* represented by a vestigial postorbital apophysis

[1] *Cf.* van Bemmelen 1901.2, Taf. xxx–xxxii; Lubosch, 1906, Taf. 26, and text fig. 1, 2.

[2] Homologized by Lubosch (1906, text fig. 1, 5) with the orbitosphenoid (*Ornith.*) or orbitosphenoid + postfrontal (*Echid.*)

of the zygomatic process of the maxillary in *Ornithorhynchus*. (Van Bemmelen, *l. c.*, Taf. xxx.) (Aberrant.)

Zygomatic process of squamosal extending back of glenoid (Primitive). Glenoid fossa in *Ornithorhynchus* external to auditory region (*cf.* Cynodontia.)

Septo-maxillary separate in embryo (Gaupp, 1905). A reptilian character retained also in *Dasypus* (Broom, 1906. 1, p. 370.)

Very large *mastoid portion of periotic*, analogous in position to opisthotic and epiotic of reptiles, extending dorsally as a broad plate postero-lateral to the parietal and in *Ornithorhynchus* extending beneath glenoid fossa of squamosal. (Primitive.) The periotic complex consists of three parts: (1) mastoid, exposed on postero-lateral part of brain case external to parietal; (2) mastoid process, seen in palatal view posterior to the tympanic fossa; (3) petrosal, lodging the semicircular canals, etc.

B. Palatal view.— The *dumb-bell bone* or prevomer of *Ornithorhynchus* is equivalent to the palatine process of the premaxilla in other mammals (Broom, 1903.1), to the anterior paired vomer of fœtal Insectivores, etc. (W. K. Parker, 1886) and to the vomer of Lacertilia and Ophidia (van Bemmelen, 1901, p. 753). (Primitive.)

Posterior nares in both genera extended backward further than in any other mammal except *Myrmecophaga*. (Partly secondary (?).)

Pterygoids. According to Gaupp (1905) the flattened pterygoids of Monotremes are homologous with the elements of the same name in Sauropsida, but not with the so called pterygoids of other mammals which he calls the "parabasale" and homologizes with the lateral wings of the parasphenoid (presphenoid rostrum) of reptiles. A comparison of the pterygoids of fœtal Monotremes (van Bemmelen, 1901, pl. xxxi, xxxii) and of fœtal Edentates and Insectivores (Parker, 1886) fails however to convince the writer that the pterygoids of Monotremes have any different homology and derivation from those of Placentals (*cf.* also *Cynognathus* p. 120).

The *palatine and pterygoid* enter into the floor of the brain-case (Aberrant).

Occipital condyles with a median basioccipital portion (*i. e.*, tripartite, *cf.* Cynodontia). Possibly a fossorial adaptation.

Carotid foramen.— The entocarotid (*cf.* van Bemmelen, 1900.2, plate; 1901.2, pl. xxx, xxxi) pierces the floor of the cranium at the posterior end of the basisphenoid, an arrangement which approximates more closely to the Marsupial than to the Placental condition.

Occipital fenestra. In *Ornithorhynchus* in front of the occipital condyle on each side is a large fenestra which corresponds with the combined foramen condylare (nerve XII) and foramen jugulare (for. lac. post., nerves, IX,

X, XI) (*cf.* van Bemmelen, pl. xxx). In *Echidna* these nerves pass out through an oblique fissure above the mastoid process.

In both genera the *optic foramen* is united with the foramen lacerum anterius (sphenorbitale) as in Marsupials. The *foramen rotundum* (V_2) is distinct in *Ornithorhynchus* but united with the sphenorbital fissure in *Echidna.*

As stated below (p. 427) in *Ornithorhynchus* there is only a single *olfactory foramen* instead of a cribriform plate (unique; aberrant) while in Echidna the plate is present and is *horizontal.* (Aberrant ?.)

There is no *osseous arch above the external auditory meatus* (*i. e.*, no post-tympanic process of the squamosal. (Aberrant.) In *Ornithorhynchus* the small round tympanic opening, at the bottom of which lies the fenestra vestibuli seu ovalis, is antero-internal to the prominent mastoid process of the periotic. In *Echidna* the *tympanic fossa* (the roof of the tympanic cavity) is a large triangular depression bounded posteriorly by the prominent transverse mastoid process and antero-internally by the flattened pterygoid.

The *tympanic opening* is approximately horizontal. Weber (1904, p. 320) suggests that this may not be interpreted as a primitive character without some uncertainty, on account of the degenerate nature of the lower jaw in both genera; but the horizontality of the tympanic ring in many embryo mammals (*cf.* Parker, 1886) and in certain adult Marsupials and Insectivores, together with the fact that the tympanic cavity arises below and internal to the tympanic ring, establishes the presumption that the horizontal position is a primitive one.

Auditory bones.— Tympanic ring more or less semicircular, not expanded (primitive); in *Echidna* touching the temporal process of the pterygoid. The latter character, if the tympanic represented the transformed quadrate (Gadow, see p. 128 above) would no doubt be regarded as primitive, but it seems more likely to be the result of the extreme backward prolongation of the palate, with the consequent posterolateral displacement of the pterygoids (*cf.*, van Bemmelen's Taf. xxxi). Tympanic ring connected with very large anterior or Folian process of the malleus (Primitive, *cf.* the figures of Marsupials and embryonic Edentates and Insectivores given by Doran, 1879, and Parker, 1886). Ossicula auditus relatively large (primitive); malleus firmly connected with incus (aberrant); stapes columelliform, imperforate (primitive). Cochlea, very primitive, not spirally wound but turning only through 180° (Denker, 1901).

For further notes on the Monotreme skull see pp. 155, 156.

Vertebral column, limbs.

Axis. Anterior facet of odontoid with a ventral extension very similar to that in *Cynognathus* (Primitive).

Cervical vertebræ without autogenous transverse processes but with true cervical ribs (primitive), as in Reptilia, which remain suturally separate from the centrum till late in life. (Unique among mammals, save that in *Perameles* the transverse process of the axis is also rib-like.) These cervical ribs have a capitular and a tubercular portion between which runs the vertebral artery, which perforates the seventh cervical (as well as C 2–6), as it does in Marsupials.

Dorso-lumbar vertebræ. The number of these vertebræ to be assigned to Monotremes depends upon the interpretation of the sacrals. Howes (1885, p. 89) gives 4 sacrals to *Echidna* and 3 to *Ornithorhynchus.* In that case both genera would have 19 dorso lumbar vertebræ (*Proëchidna* 20) a number characteristic of primitive Marsupials. But in the view of the writer the anterior "sacral" is only a slightly modified lumbar and the posterior sacral only a slightly modified caudal. In that case the vertebral formulæ would be as follows: *Ornithorhynchus* C. 7, D. 17, L. 2, S. 1, CS. 1, Cd 19;

Echidna C. 7, D. 16, L. 5, S. 2,—, C 10.

In the *dorsal vertebræ* "the canals for the exit of the spinal nerves perforate the neural arch" instead of issuing between the vertebræ (Flower, 1885, p. 65) (Unique ?).

Epiphyses. There are *no epiphyses* on the presacral vertebræ. (Secondary, *cf.*, Sirenia, but of uncertain adaptive significance.)

Ribs with reduced tubercula, not articulating with transverse processes but attached to centra only, "the greater part of the articular surface being below the neuro-central suture, the reverse of what occurs in the higher Mammals" (Flower, *l. c.* p. 65). (Possibly reptilian in part.)

Sternal ribs. Becoming fully osseous as in Armadillos, but very peculiar inasmuch as they ossify by ectososis, as in Birds (Parker, quoted by Flower, *l. c.*, p. 119).

Fore limb. The position of the fore and hind limbs is unique among mammals. The scapula is inclined forward, overlapping the neck vertebræ. The extreme forward inclination is probably secondary (pp. 119, 433). The humerus, instead of facing forward and downward as in other mammals, faces inward and downward (partly primitive, partly aberrant). The elbow is turned sharply outward. The glenoid fossa of the scapula is close to the mid-line of the sternum instead of being widely removed from it as it is in other mammals. This condition is correlated with the large size of the coracoid and procoracoid (Primitive).

Scapula. The anterior border of the scapula, as shown by its connection with the clavicle, and by the relations of the muscles, is homologous with the spina scapulæ and acromion of the other mammals (Wilson and McKay, 1893, Broom, 1899). The prespinous fossa is absent (*Echidna.* ? Secondary), or rudimentary (*Ornithorhynchus.* Primitive). The glenoid fossa is transversely elongate and is borne by the coracoid (primitive) and scapula, whereas in most mammals it is antero-posteriorly elongate and the coracoid portion is generally reduced (compare, however, certain Edentates, Weber, 1904, p. 97, in which the true-coracoid takes a considerable part in the glenoid). The procoracoids ("epicoracoids" Weber) overlap in the median line above the T-shaped interclavicle ("episternum") exactly as in Cotylosaurs and other Permian reptiles. (Primitive.) The T-shaped interclavicle is unique in mammals but somewhat doubtfully identified vestiges of it, called "præclavia" occur in higher Mammals (p. 237).

Humerus. The humerus resembles that of the mammal-like reptiles (p. 119) in the following points: (1) Proximal and distal ends greatly expanded. (Secondary emphasis of a primitive character.) (2) Proximal end with very large tuberosities (*cf.* Fig. 27, no. 2, p. 437), the head being markedly elongate in the direction of the tuberosities. (Partly primitive.) (3) Smaller ectocondylar or "supinator" crest and enormous entocondylar crest with large entepicondylar foramen. (Partly primitive.) (4) Capitellum for radius subglobular. (Primitive, *cf.* p. 436.) (5) Ulnar trochlea on posterior face of humerus, the proximal portion of the ulna being hidden by the radius in front view. On the front face of the humerus, there is no ulnar trochlea, the articular surface being occupied exclusively by the radius. (Largely primitive.)

Since all of these characters are true of both *Ornithorhynchus* and *Echidna* (notwithstanding the marked divergence in life habits) and are also found in *Sphenodon, Pareiasaurus,* and *Naosaurus,* it seems very probable that they are at least in some measure primitive reptilian characters.

The *ulna* is remarkable for the expansion and bifurcation of the distal end of the olecranon (possibly a fossorial character, *cf. Chrysochloris*).

The manus and pes are full of marked peculiarities.

Manus. The scaphoid and lunar are fused at least in adults. (Secondary.) The magnum of *Ornithorhynchus* (Cuvier, 1825, pl. xiv, fig. 13) is fused at its supero-external angle with the cuneiform. (Aberrant.) The unciform is very shallow. In both genera the trapezium is small and does not suggest serial homology with the metacarpals (*cf.* p. 442).

The digits are somewhat more subequal than in most mammals. In *Ornithorhynchus* there is the usual mammalian overlap at the proximal ends of the metacarpals, metacarpal IV overlapping III, III overlapping

II and II overlapping I. (Primitive.) The manus bears no marked suggestion of former opposibility in digit I. In *Echidna* the proximal ends of the metacarpals are more in line. The manus of *Echidna* as a whole rather resembles that of *Oudenodon* (*cf.* Broom, 1901, pl. xvi).

Hind limb.— Pelvis. The most noteworthy feature (aside from the epipubic bones) is the small round thyroid or "obturator" fenestra; the ventral aspect of the pelvis is rather "plate-like" *i. e.*, as in Permian Reptiles (p. 115). (Primitive.) The pectineal tubercle as in Marsupials and certain Placentals is well developed. The ilium in *Echidna* is fully mammalian in character, *i. e.*, it is a trihedral bar, rather short, and with a reduced postero-dorsal projection (contrast Therapsid reptiles, p. 118, 119). In *Ornithorhynchus* the dorsal border of the ilium is everted. In *Echidna* the acetabulum is perforate, as in Sauropsida (not so in *Ornithorhynchus*). The acetabular notch, for the ligamentum teres is lacking.

Femur. In *Ornithorhynchus* the inclination of the neck and head of the femur to the shaft is much less than in ordinary mammals. The greater and lesser trochanters are on directly opposite sides of the shaft. In *Echidna* the first and third trochanters are continuous and are represented by a single plate-like extension. Comparison with other archaic mammals indicates that this may be a primitive character. The patellar surface in both genera is flat and not grooved as it is in typical mammals (Primitive). The femur in *Ornithorhynchus* is turned outward much more than in other terrestrial mammals. (Partly primitive.)

Fibula. The fibula is remarkable for the dorsal extension above the level of the distal end of the femur. In Marsupials and certain Insectivores (*Microgale*, p. 251) the fibula also has a proximal expansion, which however never attains the development that it does in Monotremes.

Pes. The pes of Monotremes comprises the same elements as that of other mammals but the tarsal bones are modified in a very extraordinary manner. The tarsal spur (vestigial or reduced in females) is borne on the postero-inferior border of the large quadrangular tibial sesamoid, which in turn articulates with the internal end of the tibia and with the internal inferior side of the tarsus. The astragalus is flattened inferiorly; its upper surface bears a high postero-external convexity for the support of the fibula, and a lower, antero-internal concavity for the tibia. The calcaneum is a squarish depressed bone, and points backward and downward, parallel to the long axis of the body and at right angles to the pes, which is turned outward. In *Echidna* the tuber calcis forms a downwardly pointed hook and the whole calcaneum is much smaller than the astragalus. The latter has a very large convex postero-external condyle bearing the fibula and most of

the tibia, and a shallow antero-internal depression for the internal malleolus of the tibia. These characters are unique among mammals.

Analysis of skeletal characters. The characters reviewed above may be classified under the following headings: (1) reptilian characters not preserved in higher mammals; (2) reptilian characters preserved also in higher mammals; (3) characters of doubtful origin; (4) primitive mammalian characters not definitely known to be of reptilian heritage; (5) specialized or aberrant characters.

1. *Reptilian characters not preserved in higher mammals*: Squamoso-parietal canal; cochlea auris not spirally wound; cervical vertebræ with true ribs; scapula, with acromial border anterior, prespinous fossa rudimentary; large coracoids and procoracoids, the latter overlapping in the middle line; T-shaped interclavicle; glenoid fossa of shoulder girdle very near mid line; long axis of humerus held in a nearly horizontal plane, elbows held well out from the body; humerus with head elongate anteroposteriorly; femur (*Ornithorhynchus*) flattened, head not sharply inclined to shaft, greater and lesser trochanters very large, subequal; pelvis with small obturator foramen.

2. *Reptilian characters, preserved also in varying degree in higher mammals.* Septomaxillary retained in embryo *Echidna* (p. 150); dumb-bell bone (prevomers) of *Ornithorhynchus* (*cf.* fœtal Insectivora); mastoid large, possibly homologous with opisthotic of reptiles; frontals not covering cerebrum; very large pterygoids (*cf.* Edentata); occipital condyles with considerable basi-occipital portion; stapes columelliform (*cf. Manis*); malleus in ontogeny connected with Meckel's cartilage; 26–27 presacral vertebræ (*cf.* 27 in *Oudenodon*, Broom, 1901, p. 27); humerus with stout ento- and ectocondyles, entepicondylar foramen and globular capitellum for radius; phalangeal formula, 2. 3. 3. 3. 3; elements of carpus and tarsus derived from the plan preserved in mammal-like reptiles (pp. 440, 442); manus and pes fully plantigrade.

3. *Characters possibly reptilian but doubtful.* Separate "post frontals," developing in the chondrocranium; entocarotid piercing floor of cranium; optic foramen united with for. lac. anterius; zygomatic portion of squamosal extending very far back, the glenoid fossa in *Ornithorhynchus* even overlapping the mastoid and lying external to the mastoid process. Ribs articulating only with centra; ungual phalanges resembling those in *Oudenodon*.

4. *Primitive mammalian characters, not definitely known to be of reptilian heritage.* Chondrocranium unusually solid and massive; frontals facing forward and upward; median parietal probably homologous with paired interparietals, mastoid exposed on postero lateral part of brain case and extending inferiorly into prominent mastoid process; tympanic ring

semicircular, oblique rather than vertical in position, connected with large anterior process of malleus; ossicula auditus relatively large; stylomastoid foramen present; 7 cervical and 19–20 dorso lumbar vertebræ; epipubic bones (*cf.* Marsupialia); ilium trihedral, large pectineal tubercle on pelvis; fibula expanding proximally; heel pointing downward.

5. *Specialized or aberrant characters.* Among the very numerous features belonging under this category are the following: the divergent modifications of the snout in *Ornithorhynchus* and *Echidna*; lachrymal absent; jugal absent (*E*) or vestigial; hard palate prolonged very far backward, causing the pterygoids to approach the auditory region; palatine and pterygoid entering the floor of the brain case; olfactory opening single (*O*), ethmo-turbinals enlarged and extending backward below the olfactory peduncle (*E*); malleus and incus firmly connected; no osseous arch above the external auditory meatus; condylar foramen (in *O*) fused with for. lac. post; single olfactory foramen (*O*); canals for spinal nerves perforating neural arch; no epiphyses on presacral vertebræ; ribs with reduced tubercula; sternal ribs fully osseous (by ectostosis); scapula inclined sharply forward; humerus with extreme development of crests; olecranon bifid; femur (*O*) pointing almost directly outward; pes (*O*) pointing outward, digits II–V curved backward; tarsal spur bone an enlarged tibial sesamoid; astragalus bearing both tibia and fibula; tuber calcis at right angles with cuboid.

Many of the peculiar skull characters: such as the very broad condyles nearly continuous across the basioccipital, the powerful mastoid processes (which served for the attachment of heavy muscles) may possibly be a result of primarily fossorial adaptations (p. 161).

Characters which demonstrate that the Monotremes are true Mammals.

The numerous characters cited below (p. 157) which tend to connect the Monotremes with the Marsupials, reinforce other mammalian characters, as follows:

(1) Four optic lobes as in Mammals, contrasted with two in lower vertebrates (Flower, quoted by Beddard, 1907, p. 110).

(2) Jacobson's organ agreeing in its principal features with the mammalian type (Seydel, quoted by Weber, 1904, p. 323).

(3) Alimentary canal showing "no great divergencies from the normal structure" (Beddard, *l. c.*, p. 109).

(4) Liver with the usual mammalian subdivisions (Beddard, *l. c.*, p. 110).

(5) Diaphragm perfectly normal (Beddard, *l. c.*, p. 109).

(6) Stylomastoid foramen for exit of facial nerve piercing the mastoid process inferiorly at its external angle. This foramen is constant in mammals (Weber, 1904, p. 53).

(7) Seven cervical vertebræ, as in mammals.

(8) 19 or 20 dorso-lumbar vertebræ (*O.*), as in primitive mammals.

(9) Large pectineal tubercle on pubis, as in many primitive mammals.

(10) Auditory ossicles of adult not differing in essentials from those of other mammals (Doran, 1879).

(11) Ontogeny of the auditory ossicles also of mammalian type: *e. g.*, cartilaginous "Anlage" of malleus continuous with Meckel's cartilage (Gaupp, 1908).

(12) Tympanic membrane with middle layer, or membrana propria as in typical mammals (*cf.* p. 127 above, Denker, 1901).

Characters suggesting Affinity with the Marsupials.

Both groups possess the following characters in common:

(1) Typical mammalian hairs, formed in identically the same manner (Spencer and Sweet, 1899) the differences being in detail only (see p. 146).

(2) Acinose and tubular glands.

(3) Milk glands which, while differing from those of Marsupials in mode of development, are regarded as derivatives of a single type (Weber, 1904, p. 31).

(4) The glandular mammary area in Monotremes is homologized by Gegenbaur, Ruge and Weber (1904, pp. 31, 34) with the teats of Marsupials, while the pouch is probably homologous in the two groups.

(5) The cartilages of the larynx are homologous and strikingly similar in the two groups; the cricoid cartilages in *Echidna* realize the ancestral condition of the Marsupials since they remain unconnected dorsally (Weber, 1904, p. 218).

(6) Epipubic bones, preformed in cartilage.

(7) Three auditory ossicles of similar embryonic history. Although in the Monotremes there are some secondary fusions and modifications, yet there is a general resemblance between the ossicula in the Monotremes and Diprotodonts, which is especially noticeable in the similar elongation of the anterior process of the malleus (*cf.* Doran, 1879).

(8) Optic foramen not separated from foramen lacerum anterius (sphenorbital), a reptilian inheritance (*cf.* Parker, 1886, p. 271).

(9) In the fœtal Marsupials (at least in the Diprotodont genera *Tricho-*

surus, Phascolomys and *Petrogale* and in the Polyprotodonts, *Perameles* and *Dasyurus*) the shoulder girdle passes through a characteristically Monotreme stage (Broom, 1899). The scapula is inclined somewhat forward, the large coracoid reaches the sternum, the precoracoid is large and is pierced by a precoracoid foramen, and the glenoid cavity is elongate transversely and shared by the acromion. In both groups the acromion and border of the spina scapulæ are homologous with the curved anterior border of the scapula in *Cynognathus* (Broom).

(10) While the Marsupials are no longer oviparous, evidence of former oviparity is seen in the large yolk sack and especially in the retention of a vestigial shell membrane in the egg of *Dasyurus* (J. P. Hill, 1908, p. 649).

(11) Both azygos veins persist in many Marsupials and in *Echidna* (Beddard, 1907, p. 219).

These and other resemblances outweigh all the differences in skull, skeleton and soft anatomy and demonstrate that *the ancestral lines of the Marsupials and Monotremes converge into a common source which had already acquired many essentially mammalian characters.*

Naturalness of the Order Monotremata.

The families Ornithorhynchidæ and Echidnidæ, notwithstanding wide adaptive divergence form a perfectly natural group. Among the many *divergent adaptations* between *Echidna* and *Proëchidna* on the one hand and *Ornithorhynchus* on the other are the following:

(1) Cerebrum well furrowed in *Echidna* but quite smooth in *Ornithorhynchus* (Weber, 1904).

(2) Tympanic fossa (roof of tympanic cavity very small in *Ornithorhynchus,* very large in *Echidna.*

(3) The differences in the shape and structure of the snout both externally and internally, and in the fenestræ cribrosæ, or olfactory openings (see p. 151).

(4) The transitory cheek teeth of *Ornithorhynchus* are multi-cuspidate, while *Echidna* has no teeth at all.

(5) Lower jaw extremely reduced in *Echidna,* but large enough to crush small mollusc shells in *Ornithorhynchus.*

(6) Integument more or less spiny in *Echidna* and *Proëchidna,* but extremely fine and fur-like in *Ornithorhynchus.*

(7) Fore feet webbed in *Ornithorhynchus,* Armadillo-like in *Echidna.*

(8) The difference in the astragalus (p. 154).

(9) Dorso-lumbar vertebræ: large and powerful in *Echidna,* but very weak in *Ornithorhynchus.*

If the two genera were extinct and known only from imperfect skulls their close relationship might be doubted or unsuspected.

The more significant *points of agreement* between the two families include the following:

(1) The fundamental similarities (combined with differences in proportion) in the scapula, coracoid and procoracoid, humerus, radius and ulna, carpals, pelvis, femur, tibia and fibula, tarsals, and tarsal spur. The astragalus and calcaneum also present a unique ordinal type (p. 154).

(2) The underlying similarity in the cranium (*e. g.*, chondrocranium massive, rounded, large median parietals, very small frontals, backward prolongation of palate, pterygoids and palatines entering into floor of brain case, jugal vestigial or absent, arrangement of foramina, etc.).

(3) The close similarity in the reproductive system. In this instance, as in many others, the characters of the girdles, limb-bones, carpals and tarsals, and reproductive system are more significant of affinity (pp. 110, 111) between adaptively divergent animals than the characters directly relating to food habits, such as the dentition, jaws, digestive tract, etc.

Summary of the Genetic Relations of the Monotremes.

The Monotremes resemble the Anomodonts (proper) in the phalangeal formula and in many characters of the tarsus, humerus and shoulder girdle; they retain structures in the embryo which have been interpreted as the last vestiges of scales (p. 145) and the reproductive organs of both sexes exhibit numerous reptilian characters; so that one is at first tempted to adopt the hypothesis that they have been derived from some family of Permian or Triassic reptiles other than that (or those) which gave rise to the higher mammals. Upon this hypothesis the numerous characters, which give the Monotremes their systematic rank as mammals would have to be explained as parallel developments; and if this were so it would seem reasonable to assume that the mammal-like reptiles which gave rise to the Monotremes had already begun to acquire the first rudiments of hair, of the diaphragm of lacteal glands etc. But as to this, there is some indirect evidence that not even *Cynognathus*, which was surely more advanced toward the mammals than were the Anomodonts, had proceeded very far toward acquiring the distinctly mammalian characters above mentioned. The hard palate of *Cynognathus* was limited to the anterior end of the pharynx. Here then is evidence of a reptilian mode of respiration and consequently of a relatively unstable body-temperature. But it has already been shown (p. 147) that the development of both a hairy covering and of

lacteal glands was probably a by-product of the process which transformed pœcilothermal reptiles into homœothermal mammals. The inference is that *Cynognathus* possessed neither rudimentary hairs nor milk glands. The large size of the pterygoids and the retention of a functional articular bone indicates a corresponding development of the pterygoid muscles, and this in conjunction with numerous other reptilian features in the skeleton (*e. g.*, in the femur, cervicals, pelvis) raises the presumption that reptilian characters likewise predominated in the rest of the economy. Again it seems likely that in *Cynognathus* the auditory ossicles were of the reptilian type, since the quadrate and articular were still functional as such (p. 118). Consequently there is little ground for inferring that the Cynodonts had acquired external ear cartilages like those of mammals (*cf.* p. 125).

While not in the least incompatible with the hypothesis that the mammal-like reptiles were remotely ancestral to the Mammalia as a class, these considerations seem unfavorable to the suggestion that they had progressed very far in the direction of the Monotremes and give added weight to the long list of characters (p. 156) in which the Monotremes were found to be typically Mammalian. The adult skull of the Monotreme is very far advanced beyond any reptilian type in the side, top and palatal aspects. The development of the skull is thoroughly mammalian (Gaupp) and the supposed reptilian features are of somewhat doubtful significance (p. 155). The ossicula auditus in the adult state are likewise mammalian, while in their development they go as far as, but no further than, those of other mammals in suggesting that the incus and malleus are transformed jaw-elements. The inference is that the Mammalia are monophyletic rather than diphyletic in origin; *i. e.*, that the common ancestors of Monotremes, Marsupials and Placentals were already mammals.

The Monotremata share with the Marsupials many important characters listed above (p. 157) especially the resemblances in the auditory ossicles, the possession of epipubic bones, the lack of a separate optic foramen, the perforation of the sphenoid by the entocarotid artery, the characters of the larynx, the fundamental characters of the brain (Elliot Smith, 1894), the tendency for both azygous veins to persist, etc.

Their association with the Marsupials in the Australian fauna is also an indication of common origin; and at the time when the ancestors of the Marsupials had a shoulder girdle of the Monotreme type (p. 157) and were also oviparous (p. 148), the gap between the two groups was evidently far less than at present.

The Monotreme stock must have begun to diverge from the Marsupio-Placental remnant at an exceedingly remote epoch. Not only do they retain many reptilian characters not found in higher types, notably in the

reproductive system, shoulder girdle and pelvis, but also they have had time to acquire so many deep seated peculiarities in the skull that the Monotreme skull may be set in a class by itself, in contrast to the primitive Marsupio-Placental type.

The immediate common ancestor of *Ornithorhynchus* and *Echidna* may provisionally be conceived as follows:

In the present cycle of life habits both existing types of Monotremes are animalivorous, and hence it may be inferred that the common ancestor was probably insectivorous. The true teeth of *Ornithorhynchus* indicate that in the stem form the cheek teeth were short crowned and irregularly cuspidate, perhaps analogous to those of *Myrmecobius*, but few in number. Front teeth were lacking. The snout was rather short, tapering and somewhat depressed at the end (*cf.* embryonic Monotremes); the orbito-temporal fossa was short, the maxillary and squamosal portions of the zygoma were stout, the jugal (as in Placental Insectivores) was already reduced. The glenoid fossa of the squamosal was located well back, but not so far as in the existing genera, the angle of the jaw was inflected (*cf. Ornithorhynchus*) and the pterygoid muscles well developed. The hard palate, as in Phlangers, Edentates and Insectivores, was carried well backward, probably not fenestrated (*cf.* p. 220), and the pterygoids were large and flattened; the ethmoturbinal complex was well developed, the frontals were small, sloped downward and forward and did not cover the cerebrum; the median parietal was large, the occiput rounded, the occipital plane slightly inclined forward, the mastoid exposure large; the broad condyles as in Armadillos may have been correlated with the habit of digging with the snout; the foramen magnum was surmounted by a median vertical opening.

The large odontoid was suturally separate from the axis and ended in a cylindrical peg which articulated with the basioccipital. The six cervical ribs were well separated from the centra and the vertebral artery passed between the head and the tubercle of each; in the dorso-lumbar vertebræ the spinal nerves notched the base of the neural arches and the epiphyses were reduced. The dorsolumbars were of nearly uniform size and character with low neural spines, the neural arches being broad and flat in top view, with prominent prezygapophyses, which permitted but little lateral movement. The lumbar parapophyses were reduced or absent. There were about 17 dorsals and perhaps three or four lumbars (p. 152). The primary sacrum consisted of only one vertebra; the caudal parapophyses were broad and flat.

The majority of the foregoing characters indicate semi-fossorial and perhaps partly amphibious habits; and it is also a fair inference from the existing genera that in the ancestral form the body was stocky, the ribs,

sternum, and reptilian shoulder girdle heavy, the limbs stout and provided with powerful muscles, the feet fully plantigrade, armed with heavy claws and well adapted for both digging and swimming. No trace whatever of the primary syndactyly which is retained to some extent even in highly specialized Marsupials (p. 215) is observed in the pes of Monotremes, nor are there any evidences of former marked divergence of the pollex and hallex. The general conclusion is that the Monotremes began to separate from the mammalian stock before the Marsupials acquired arboreal habits (p. 226).

CHAPTER III. GENETIC RELATIONS OF THE MESOZOIC ORDERS: PROTODONTA, MULTITUBERCULATA, TRICONODONTA AND TRITUBERCULATA.

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The Protodonta.

In his description of the lower jaws of the American Triassic genera *Dromatherium* and *Microconodon*, Professor Osborn (1907, p. 19) says, "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."

This reason would doubtless be conclusive if the jaws of Cynodont reptiles were not known; but comparison (Fig. 6) of the jaws of *Dromatherium* (No. 4) and *Microconodon* (No. 5) with those of *Tribolodon* (No. 2) and *Diademodon* (No. 3) reveals the possibility that small angular and articular bones may in fact have been present in life but not preserved in the fossil remains of *Dromatherium* and *Microconodon* already discovered. The condylar process of the dentary in *Dromatherium*, so far as the cast of the fossil shows, is prolonged backward more than in *Diademodon*, and may well have touched the glenoid region of the squamosal; but its apparently slender character may indicate that *the reduced quadrate-articular-angular chain still retained part of its old supporting function* (*cf.* pp. 137, 124). The broad corono condylar portion is similar in type to that of the Cynodont genera *Cynognathus* (Fig. 2, *B*), *Trirachodon*, *Tribolodon* and *Diademodon*. It has also the same gentle forward and downward sweep.

In *Microconodon* the incipient development of the angular process of the dentary is similar in position to, but broader than, that in the reptile *Diademodon*, while the molars are more advanced in form than, but of the same general type, as those in the reptiles *Tribolodon* and *Cynognathus*. Again, the styliform premolars of *Microconodon* are rather suggestive of those in *Diademodon* (Broom, 1905.4).

So far as the evidence shows, the Protodonta differ from and are more primitive than all known mammals, first in the low development of the corono-condylar notch, or sinus, separating the coronoid process from the condyle posteriorly, secondly in the arrangement of the incisors (in *Dromatherium*), which extend down on the front of the symphysis. On the other hand, the Protodonta are more progressive than the reptiles in the division of the fangs of the molars and in the slightly greater backward prolongation of the condylar process of the dentary. They seem to foreshadow in several features the coronoid, mandible and cheek teeth of the genus *Priacodon* Marsh from the Como Beds (Upper Jurassic) of Wyoming.

There seems accordingly to be considerable reason for accepting Seeley's view (1895.4, p. 90) that the Protodonta may be related to the Cynodontia; but in view of their more progressive characters as compared to the Reptiles,

and of the lack of evidence for placing them in either of the mammalian subclasses it seems advisable to treat them provisionally as representing a transitional group to which the name "Promammalia" of Haeckel may conveniently be applied.

Definitions.

Class MAMMALIA. Condylar process of dentary articulating with the squamosal. Quadrato-articular joint with squamosal much reduced or (usually) absent. Lower molars with at least two incipient fangs.

Sub-class Promammalia Haeckel. (Hypothetical definition). Quadrato-articular joint much reduced but still retaining its primary function in part. Oviparous; integument retaining some scales mingled with the hairs. (Compare the definition of Prototheria, p. 230.)

Order Protodonta Osborn. Dentary the main functional element of the lower jaw. Corono-condylar region very broad. Corono-condylar sinus shallow. Lower molars with two incompletely separated fangs, a single pointed main cusp and small anterior and posterior cusps. Talonid spur incipient. Premolars styliform.

Family Dromatheriidæ.

Genus *Tribolodon* Seely. No angular process, molars with larger anterior and posterior cusps, but division of fangs only beginning. (Possibly a Cynodont).

Genus *Dromatherium* Osborn. Lower incisors three, styliform, erect, arranged in a decreasing series which descends anteriorly upon the symphysis, the upper incisors probably overhanging the lower in a similar descending series. Canine piercing, recurved. P 4, M 6. No angular process. Opposite rami weakly conjoined at symphysis ? P_1–p_3 procumbent.

Genus *Microconodon* Osborn. A small angular process, excavated on the internal face as if embracing a separate angular bone. Molar crowns lower, with anterior and posterior cusps better developed than in *Dromatherium*. A well marked depression between the anterior and posterior fangs. Symphyseal region stout. Third lower premolar with incipient fangs, premolars erect.

THE ALLOTHERIA, OR MULTITUBERCULATA.

Historical development of the ordinal classification.[1]

1847. Plieninger describes the single lower molar of *Microlestes antiquus* from the Keuper (Upper Trias near Württemburg).

[1] Compiled chiefly from Palmer's "Index Generum Mammalium.'

1855. Charlesworth describes a fragmentary lower jaw, *Stereognathus, oölithicus* from the Stonesfield Slate (Middle Jurassic).

1857. Falconer describes the mandible and teeth of *Plagiaulax* from the Purbeck (Upper Jurassic).

1864. Dawkins describes the grooved premolar of a relative of *Plagiaulax* (*Hypsiprymnopsis*) from the Rhætic of Somersetshire, England.

1866. Murray erects for *Stereognathus* the family Stereognathidæ.

1866. Fraas describes a tooth with three rows of cusps from the Rhætic and proposes the name *Triglyphus*.

1871. Owen monographs the Mesozoic Mammalia and treats the genera *Microlestes, Plagiaulax,* and *Stereognathus* as a division of the Diprotodont Marsupials.

1871. Owen proposes the name *Bolodon* for some upper jaw fragments.

1872. Gill proposes the family name Plagiaulacidæ.

1879. Marsh describes some small jaws and teeth (*Ctenacodon*) from the Upper Jurassic ("Atlantosaurus Beds") of Wyoming.

1880. Marsh erects the order Allotheria to include "*Plagiaulax,* the allied genus *Ctenacodon,* and possibly one or two other genera."

1881, 1882. Cope describes *Ptilodus* (1881) and *Polymastodon* (1882) from the Basal Eocene of New Mexico.

1882. Cope describes *Meniscoëssus* from the Laramie (Upper Cretaceous) of Wyoming.

1882. Lemoine describes *Neoplagiaulax* from the Basal Eocene near Rheims, France.

1884. Owen describes the front part of a skull with teeth, named *Tritylodon* from the Upper Triassic of South Africa.

1884. Cope uses the name "Multituberculata" as a suborder of the Marsupialia, to include the Tritylodontidæ, Polymastodontidæ and Plagiaulacidæ.
"Multituberculata" is thus virtually a synonym of Allotheria Marsh.

1884. Cope in his 'Tertiary Vertebrata' gives evidence of the Marsupial nature of *Polymastodon* (*Catopsalis*).

1887. Cope erects the family Chirogidæ.

1888. Osborn revises the group, dividing it into the families Plagiaulacidæ, Bolodontidæ, Tritylodontidæ and Polymastodontidæ.

1903. Ameghino includes in the group the Patagonian families Polydolopidæ Ameghino (1897) and Promysopidæ Ameghino. These however may prove to be highly modified Cænolestoids (p. 211).

1909. Gidley describes a skull and lower jaws of *Ptilodus* (all previously known skull material had been very imperfect), shows that this genus possesses many characteristically Marsupial features, and

that the upper dentition of *Plagiaulax* must have conformed to the *Bolodon* type.

Affinities of Tritylodon and Microlestes.

Aside from the American Triassic genera *Dromatherium* and *Microconodon* (p. 163), which can scarcely be considered full-fledged mammals (p. 164), the oldest known mammals are *Tritylodon longævus* Owen, founded on the front part of a skull probably from the Lower Jurassic (Broom, 1909.3, p. 289) of South Africa, and the genus *Microlestes* from the Rhætic of Germany and England. Broom (1903) has recently described the jaw of a small animal (*Karoomys*), from the Upper Triassic of South Africa, which may possibly have belonged to a mammal.

Tritylodon was regarded as a mammal by Owen, Osborn and Lydekker and more recently by Broom, but Seeley (1895.2, pp. 1025–1028) treated it as a relative of the Gomphodont reptiles. There does not appear to be very convincing evidence for this allocation. *Tritylodon* does indeed somewhat resemble *Trirachodon* in the top view of the snout but Owen's figures reveal no evidence of a postorbito-frontal bar on either side, a character which might be expected to be present in a supposed relative of *Gomphagnathus*. On the other hand the wide post-incisive diastema of *Tritylodon* appears to be lacking in the Gomphognaths in which also the opposite molar rows curve inward and converge anteriorly. In *Tritylodon* they are straight and parallel. In the known Gomphognaths the upper cheek teeth consist of transverse ovals, often with an irregular transverse ridge. In *Tritylodon* the molars bear three longitudinal rows of small tubercles, an arrangement known elsewhere only in Multituberculates.

Tritylodon is either a Multituberculate or offers a very close convergent resemblance to that general type. Its resemblances to Multituberculates are very many in proportion to the total number of known characters. The upper incisors, judging from their relative position (which recalls the conditions in Duplicidentate Rodents) and in connection with the Multituberculate pattern of the molars, may well have been of the peculiar prehensile-incisive type seen in the Upper Jurassic *Allodon* Marsh. The molars are somewhat like those of *Meniscoëssus* of the American Upper Cretaceous, but the small cusps, arranged in three longitudinal rows, are rounded and not sub-crescentic. The hard palate apparently extends well backward. The excursion of the mandible was probably from in front upward and somewhat backward but the backward motion could hardly have been as extreme as in *Castor*, otherwise the small tubercles would have been worn down level with the crown. But even a slight backward movement of the mandible

would have been impossible if the articulation had been by way of the quadrate and articular. Accordingly Broom concludes (1907, p. 7) that the jaw worked by means of a mandibulo-squamosal articulation and that therefore *Tritylodon* was a mammal.

If *Tritylodon* is a Multituberculate (and no contradictory evidence appears at present) then it must go with the Multituberculata into the Marsupialia. The existence of a highly specialized Marsupial in the Lower Jurassic (Broom) would indicate a still earlier origin of the Marsupial stem. At the same time the profile of the *Tritylodon* skull is rather suggestive of what may be conceived to have been the ancestral Monotreme type, *i. e.*, a long snout, long diastema, small anteriorly placed orbit, narrow frontals, multicuspid molars. It is also significant that in *Ornithorhynchus* the glenoid fossa is extended antero-posteriorly and that the jaw can move backward and forward to some extent.

Another early Multituberculate is *Microlestes* (figured by Osborn, 1888, p. 214), and known from three species founded upon isolated lower teeth from the Upper Triassic, or Rhætic, of Germany and England. The evidence tending to connect *Microlestes* with the Multituberculates is briefly as follows:

(1) The *Microlestes antiquus* molar while more elongate and compressed, resembles the second lower molar of *Plagiaulax minor*, a Multituberculate of the Upper Jurassic, in possessing a high antero-internal cusp on the raised internal border and a row of small external cusps. In both genera the molars have a median longitudinal basin and two roots.

(2) The lower molar called "*Microlestes*" *moorei*, comes from a formation from which only one other mammalian fossil is known: *viz.*, the type of *Hypsiprymnopsis rhæticus* Dawkins. This is a grooved lower premolar of Multituberculate type.

The order Multituberculata, being thus already well differentiated in the Upper Triassic, is known also in the Jurassic of England and the continent and persisted into the Upper Cretaceous and Basal Eocene of Europe and North America. Its reported presence in the Eocene of South America appears somewhat doubtful (p. 211).

Origin of the Multituberculate Molar.

The order Multituberculata had a very long history stretching from the Upper Triassic into the Basal Eocene, during which it presents several modifications of a very well defined molar type.

It has been suggested that the Multituberculate molar may have been derived from the tritubercular type, and certain supposedly analogous cases

of the evolution of a "basin-shaped" molar out of a degenerate tritubercular type have been cited (Osborn, 1897, and 1907, pp. 103–105).

The writer at one time accepted this view but further study has not tended to support the argument. First, the supposedly analogous cases (*loc. cit.*, p. 80) are shown by examination of photomicrographs [1] to resemble the Multituberculate type chiefly in the possession of a more or less depressed crown with cusps arranged in two anteroposterior rows. But little resemblance exists between the molars of any Multituberculate and the molars of the Rodent *Perognathus* (*l. c.*, p. 356), of *Cercoleptes*, of *Myrmecobius*, or of certain fruit bats. However the resemblances to Ameghino's Patagonian Eocene genera *Propolymastodon* and *Pliodolops*, which may possibly have been derived from trituberculate forms, are much more striking.

Secondly the Multituberculate molars and premolars retain no direct evidence of derivation from a tritubercular type, but on the contrary suggest a totally independent mode of origin, as shown by comparison of the dentition of the Multituberculates *Ptilodus* and *Ctenacodon* with the primitive tritubercular dentition of the Basal Eocene Oxyclænidæ. There is no similarity whatever in the molars; the upper premolars of *Ctenacodon* have it is true three cusps, but the main single cusp is on the external side of the tooth *i. e.* the reverse of the condition in Trituberculates.

Thirdly, the Multituberculate molar, appearing in the Upper Triassic and following its own lines of evolution until the close of the Basal Eocene, so far as known is a far older type than the tritubercular molar, which is first known in an undeveloped condition in the Middle and Upper Jurassic (*e. g.*, *Amphitherium*) and which ran through its principle evolution in the Tertiary.

The conclusion indicated is that the theory of trituberculy (which is most successful in explaining the dental evolution of the more typical mammals) is unnecessarily impaired by endeavoring to make it apply to the Multituberculata.

There is somewhat better, but still very insufficient evidence for deriving the Multituberculate type of molar from a generalized triconodont type. In both these supposedly Marsupial orders, the molar cusps are at least arranged in an antero-posterior line and the jaw motion was originally chiefly vertical (see below). In the relatively primitive Multituberculate *Ctenacodon* the second molar has four cusps in a fore and aft line and an external cingulum that might be a development of the one in *Triconodon*. In both groups the wearing surface is chiefly on the inner sides of the upper and on the outer sides of the lower molars. However these resemblances may not imply close relationship.

[1] See Elliot, D. G., Land and Sea Mamm. N. and Mid. Amer. etc., Field Columbian Museum, Chicago, 1904, pp. 163, 171.

In regard to the Multituberculate dentition it seems to be sometimes taken for granted that in the Plagiaulacidæ the motion of the jaw was much as in the more highly specialized types of Rodents, namely decidedly antero-posterior. But the mandibular condyle of *Plagiaulax* and *Ctenacodon* is an elongate oval the long axis of which is strongly inclined to the plane of the grinding teeth; hence the motion of the mandible must have been forward and upward and then slightly backward. The large piercing lower incisors, which probably fitted into prehensile-incisive upper incisors of the *Bolodon* type, must have moved principally upward and only slightly backward. The same conclusion is indicated by the enlarged obliquely-grooved premolar. Finally even in the more highly specialized *Meniscoëssus* (Osborn, 1907, fig. 55, p. 106) the well formed small crescents would require and permit only a small upward and backward pull of the jaw. Apparently it is chiefly in *Polymastodon* that the molar cusps become much worn down at the tips (Fig. 8).

Marsupial affinities of the Multituberculata.

The most important discovery bearing on the genetic relations of the Multituberculates is that recently made by Gidley (1909) who has described the skull of *Ptilodus* (*Chirox*) as being typically Marsupial in type. Thus it has the inflected angle of the jaw, the fenestrated palate, the backward extension of the malar into the glenoid fossa, etc. Gidley also finds that the upper dentition of *Plagiaulax* must have been of the type represented by *Bolodon* Owen. He concludes that the Multituberculates are Diprotodont Marsupials.

This conclusion had been reached by Falconer, Owen, Marsh, Cope, Osborn and Ameghino but the evidence had always remained very incomplete. Cope (1882. 2, p. 259), upon the discovery of the multicusped teeth of *Ornithorhynchus* suggested that the Multituberculates were related to the Monotremes. Confirmatory evidence that the Multituberculates are Marsupials is offered by remains of *Polymastodon taöensis* in the American Museum of Natural History (Fig. 8). In this Basal Eocene genus as noted by Cope in his 'Tertiary Vertebrata,' the angle of the jaw is inflected and the dental foramen is at the apex of a deep fossa for the external pterygoid muscle like that occurring in the Diprotodonts. The posterior portion of the zygomatic arch is deep and extends to the occiput, the malar running well back to the glenoid region, features seen in both Cynodonts and primitive Marsupials.

Cope also referred to *Polymastodon* certain skeletal remains, but according to Dr. Matthew this association is probably incorrect.

The Marsupial affinities of the Multituberculates thus seem to be fairly well settled, but as to their being true Diprotodonts the writer cannot yet feel certain for the following reasons: (1) because so far as indicated by Marsh's *Allodon fortis* the enlarged incisor in Multituberculates is i^2, whereas

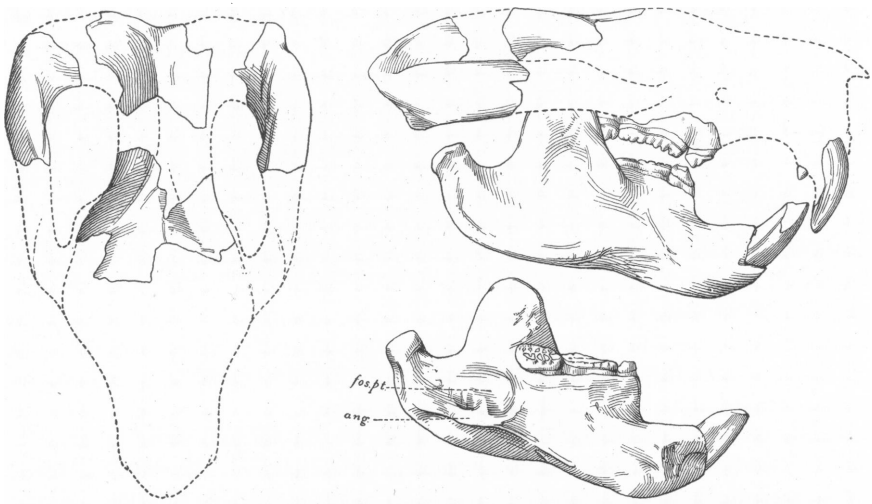


Fig. 8. Skull and lower jaw of *Polymastodon taëensis* Cope. Skull, Amer. Mus. No. 3075, reconstructed by Dr. W. D. Matthew; lower jaw composition from Amer. Mus. Nos. 968 and 748. $\times \frac{2}{5}$.

in Diprotodonts it seems to be i^1 (*cf.* Weber, 1904, p. 339, fig. 263); (2) because the Multituberculates differ greatly from the true Diprotodonts in the characters of the cheek teeth; (3) because homoplastic resemblances, especially among related groups, is so frequently shown in the dentition.

The Orders Triconodonta and Trituberculata.

Historical Development of the Classification.[1]

1814? Two small fragmentary fossil jaws (later made the types of *Amphitherium prevostii* and *Phascolotherium bucklandii*) are brought to Mr. W. J. Broderip from Stonesfield Slate (Middle Jurassic) near Oxford.

1824. Dr. Buckland announces the discovery of the remains of Mesozoic mammalia in his paper 'On Megalosaurus.'

[1] The early history of the discovery of Mesozoic mammal remains is sketched by Goodrich (1894, pp. 409–412).

——. Cuvier examines the jaw later named *Amphitherium prevostii*, notes its resemblances to *Didelphis* and also its greater number of teeth.

1818–1842. Controversy in regard to Mesozoic mammals. Buckland, Prévost, Cuvier contend that the fossils in question are mammalian and truly Mesozoic. De Blainville takes the opposing view that they are reptilian.

1838. De Blainville publishes his 'Doutes sur le prétendu Didelphe de Stonesfield,' urging that it showed evidence of a suture on the inner side of the jaw and inferring that the jaw was composed of more than one bone as in the Reptilia. This supposed suture was later taken to be a mylohyoid groove and recently has been shown by Bensley (1902) to have lodged the Meckelian cartilage.

1838. De Blainville proposes the name *Amphitherium prevostii* (*Didelphis prevostii* Cuvier MS.) in allusion to the supposedly ambiguous nature of the remains.

1842. Owen finally demonstrates the mammalian nature of the remains and discovers that the molar teeth in *Amphitherium prevostii* are of the type now known as tuberculo-sectorial.

1871. Owen monographs the Mesozoic Mammals and assigns the trituberculate insectivore-like genera *Amblotherium, Peralestes, Achyrodon, Peraspalax, Peramus* and *Stylodon* to a division of the Marsupialia (p. 111).

1879–1880. Marsh discovers Upper Jurassic triconodonts and tritubercules in North America and erects for them the order "Pantotheria" (1880), holding that they cannot be placed satisfactorily in any of the present orders, although recognizing the resemblances of certain families to the Insectivores.

1888. Osborn reviews and refigures all these animals and under the Triconodontidæ of Marsh he groups the subfamilies Amphilestinæ Osborn, Phascolotheriinæ Osborn, and Spalacotheriinæ, which he regards as primitive Marsupials. He includes the Stylacodontidæ and Amblotheriidæ in a distinct suborder of the Placentals, the "Insectivora Primitiva." He also attempts to trace in the orders Protodonta, Triconodonta and Insectivora Primitiva the early stages of the tritubercular type of molars.

1893. Osborn groups together the Amphitheriidæ and Amblotheriidæ [Stylacodontidæ] under the name "Trituberculates" and suggests that they are the Jurassic representatives of the Eutheria (Placentals). He compares their tuberculosectorial molars with those of modern Insectivores and says "they alone [of the Jurassic mammals] exhibit the typical angular placental jaw" (1893, p. 204).

1893. Osborn (in Zittel's Palæontologie) substitutes the monomial term Trituberculata for Insectivora Primitiva and now includes in the group the families Amphitheriidæ, Amblotheriidæ and Stylacodontidæ. He assigns the Triconodontidæ to a new order, the Triconodonta.

1894. Goodrich contributes a valuable article, "On the Fossil Mammals from the Stonesfield Slate" in which he redescribes and gives careful figures of the types of the species of *Amphitherium, Amphitylus, Amphilestes Phascolotherium.*

1907. Osborn (1907, pp. 18–23) further revises the classification and brings together many new and old figures of specimens.

Special interest of these Mesozoic Orders.

Nearly a century has elapsed since the geologist Broderip received from the hands of "an ancient stonemason" two small fragmentary jaws from the Stonesfield Slate which were the means of overthrowing the dogma that "no mammals occur in the Mesozoic." Notwithstanding the later array of generic and specific names of Mesozoic mammals, these minute jaws and teeth still retain some of the ambiguous meaning which was signalized in the name *Amphitherium,* inasmuch as they offer suggestions, rather than proof, of relationship to different groups of mammals.

Yet the few positive facts which they have yielded, when viewed against the general background of palæontological knowledge, appear as important landmarks in mammalian history. Standing in geological time between the partly-known reptilian ancestors of the mammals and the better known fauna of the Tertiary, these Mesozoic orders include certain members which so far as the scanty evidence indicates were also more or less intermediate in structure. In certain features they retain reminiscences of more ancient types, in others they foreshadow the Polyprotodont Marsupials and Insectivores of a later period.

The Triconodonta.

The Triconodonts as described by Owen, Osborn and Marsh are known from the Stonefield Slate and Middle Purbeck (Middle and Upper Jurassic respectively) of England and from Marsh's "Atlantosaurus Beds" (Morrison formation) of Wyoming. The order as defined by Osborn (1907, pp. 21–22) includes the genera *Amphilestes, Phascolotherium, Triconodon, Priacodon, Tinodon, Spalacotherium, Menacodon* and *Peralestes,* all known chiefly

from mandibular rami with teeth. Upper teeth are known only in *Triconodon* and *Peralestes*.

Naturalness of the Group.

The question whether the order as thus defined includes any extraneous elements or is a truly natural assemblage seems to be answered as follows: The oldest genera *Amphilestes* and *Phascolotherium* from the Stonesfield Slate present the triconodont type of molar in a low stage, reminiscent in some features of the Upper Triassic *Microconodon* (p. 164). There is a strong internal cingulum which rises opposite the main middle cusp. In *Triconodon* and *Priacodon* of the Upper Jurassic the anterior and posterior cusps have become subequal with the main middle cusp. The coronoid, known in *Triconodon* and *Phascolotherium*, is very broad, the condyle sessile and confluent with the inflected angular border. Aside from the progressive development of the anterior and posterior cusps in the molars the chief differences between the genera lie in the dental formulas:

Amphilestes: I.$\frac{4}{4}$, C.$\frac{1}{1}$, P.$\frac{4}{4}$, M.$\frac{5}{5}$ (Goodrich).
Triconodon: I?$\frac{3}{3}$, C.$\frac{1}{1}$, P.$\frac{4}{4}$, M.$\frac{4 \text{ or } 3}{4 \text{ or } 3}$ (Osborn).
Phascolotherium: I.$\frac{4}{4}$, C.$\frac{1}{1}$, P.$\frac{3}{3}$, M.$\frac{5}{5}$ (Osborn, Goodrich).

So far as the published evidence goes the ordinal association at least of *Amphilestes, Phascolotherium, Triconodon* and *Priacodon* seems to be warranted.

To judge from figures and descriptions *Menacodon* Marsh is also a related genus. Its dental formula is I.$\frac{?}{?}$, C.$\frac{1}{1}$, P.$\frac{3}{3}$, M.$\frac{4}{4}$ (Osborn). Its premolars resemble those of *Priacodon* (?*Triconodon*) in certain significant details; the internal basal cingulum is present and the central cusp of the molars is larger and higher than the anterior cusps. But these are now somewhat internal to the main central cusps so that in the last molar the three cusps are arranged in a triangle with sharp pricking points, the whole resembling the molar type seen in *Spalacotherium tricuspidens* Owen. The ramus in *Menacodon* is slender (more so than in *Amphilestes*) and the angle seems to have been inflected. *Spalacotherium* as described by Owen and by Osborn, resembles *Triconodon* in the canines and incisors and *Amphilestes* in the premolars. In the lower molars the paraconid and metaconid are internal to the protoconid and spring outward much as in *Menacodon*. The basal cingulum is very broad and shelf-like. The angle was inflected, the condyle confluent with the angle, and the coronoid rose very abruptly but was not so broad as in *Tinodon*. The lower molars of *Spalacotherium* agree with those of other Triconodonts and contrast with those of Tritubercula in many points as shown below:

Molar characters seen in Spalacotherium and the remaining Triconodonta.

Metaconid *postero-internal* springing obliquely inward and backward from internal base of the protocone.

Paraconid and metaconid sub-equal; tips on same level.

A strong internal cingulum rising into a centro-internal prominence.

No talonid on the cheek teeth.

Characters believed to be universal in the Trituberculata.

Metaconid *centro-internal* directly internal to protoconid and usually connected with it by a prominent transverse ridge.

Paraconid smaller than metaconid; tip on level lower than that of metaconid.

Internal cingulum absent (or possibly grown up into paraconid and metaconid).

Talonid on molars seemingly always present, at least on inner side.

Accordingly there seems to be considerable evidence in favor of Osborn's view (1888, p. 230) that *Spalacotherium* belongs with the Triconodonta and not with the Trituberculata.

Peralestes probably not a member of the Triconodonta.

The next important question is: *What are the affinities of the upper teeth called Peralestes?* Were they "probably associated with lower molars of the type seen in *Spalacotherium*" (Osborn, 1907, p. 25, fig. 11), or was *Peralestes* "obviously related to *Peraspalax*" (Osborn, 1888, p. 206)?

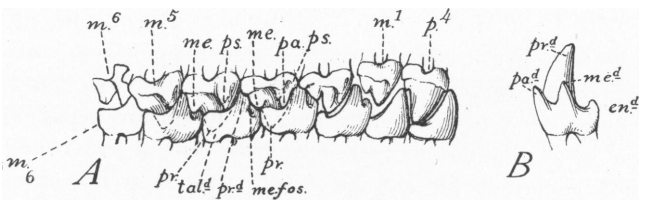


Fig. 9. Cheek teeth of *Peralestes longirostris.*

A. Upper teeth after Osborn; lower teeth hypothetically reconstructed, showing talonid for the reception of the high protocone and anterior fossa for the reception of the metacone (compare *Didelphis*). The tip of the protoconid is hidden. External view, much enlarged.

B. Internal view of a lower molar hypothetically reconstructed, showing high protoconid, asymmetrical arrangement of trigonid, low talonid. The protoconid as represented may be too high. In *A* the talonid may be too large.

A careful study of the descriptions and figures of the *Peralestes* teeth seems to enable one to interpret and harmonize the apparent differences in the drawings given by Owen (1871, pl. i) and Osborn (1888, pl. viii, fig. 8; 1907, p. 26, fig. 12 [1]).

[1] The diagram of the *Peralestes* molar on page 43 of the work cited does not agree with Osborn's detailed drawings and descriptions and represents the *Peralestes* tooth as almost typically tritubercular.

As shown in oblique upper side view (Osborn, 1907, p. 26; *this work*, Fig. 9, *A*) the molar of *Peralestes* may conveniently be conceived as a modification of the *Didelphis* molar type. It is much narrower transversely, the protocone is very high and curved externally, and the large metacone occupies the postero-external slope of the protocone. The metastyle shear is not so sharp as in *Didelphis* and there are no small external cingular cusps. The anterior edge of the protocone in the type has been worn by a lower tooth (Osborn).

The resemblance to a reversed *Spalacotherium* type (Osborn) consists chiefly in the fact that the protocone is flanked by two smaller cusps which are in turn guarded by a heavy basal cingulum. But these resemblances are not sufficient to indicate that the *Spalacotherium* molars fitted into the *Peralestes* molars. The distorted triangular contour of the *Peralestes* upper teeth and the asymmetrical interspaces would seem ill adapted to receive the symmetrical triangular contours of the *Spalacotherium* lower teeth. From a study of the relations of the known upper teeth of *Peralestes* and a comparison with those of its nearest analogue *Didelphis*, we should be led to expect the following characters in the *Peralestes* lower molars, which are represented in the accompanying hypothetical reconstruction (Fig. 9*A*):

(1) An asymmetrical arrangement of the cusps of the trigonid.

(2) Protoconid very high, recurved posteriorly.

(3) Protoconid in horizontal section wedge-shaped, the protoconid-paraconid shear running obliquely forward and downward, the protoconid-metaconid shear directly inward.

(4) The very large metacone in *Peralestes* is even further internal than in *Didelphis* and must therefore have fitted into the space immediately in front of the trigonid and behind the talonid of the preceding molar. The metacone may have been received into a distinct fossa on the antero-external base of the protoconid, as in *Didelphis* and *Didelphops*.

(5) Talonid very low, for reception of high protocone above, concave superiorly.

If this interpretation be at all correct then the lower molars of *Peralestes* were obviously very different from those of *Spalacotherium* and the removal of *Peralestes* from the order Triconodonta seems advisable.

Where then are the allies of *Peralestes* to be sought?

Some of the characters predicated above of the lower teeth of *Peralestes* are realized in *Peramus tenuirostris* (Osborn, 1907, p. 27, fig. 16), *e. g.*, the oblique protoconid-paraconid shear, and low upwardly-curved talonid. But *Peralestes* cannot belong directly with *Peramus* on account of the different number of molars. *Leptocladus dubius* (Osborn, 1907, pp. 28–29) agrees with our hypothetical lower dentition in its recurved protocones and six

molars but the protoconid-paraconid shear is not oblique. *Peraspalax*, which Osborn originally suggested might go with *Peralestes* (1888, p. 206) has the desired oblique protoconid-paraconid shear but the molar heels appear to be too small.

The foregoing considerations seem to indicate that *Peralestes* is related to *Peramus*, *Leptocladus* and *Peraspalax* and is not a member of the Triconodonta but of the Tritubercülata as defined by Osborn (1907, pp. 22–23).

To return to the question as to the probable characters of the upper teeth of *Spalacotherium*, in view of the symmetrical relations of the upper and lower cusps in *Triconodon*, and of the mechanical conditions implied in *Spalacotherium*, it seems quite probable that the upper teeth of the latter genus (and of *Menacodon* as well) consisted of a symmetrical triad of sharp cusps and that the upper and lower teeth in opposition nearly fulfilled the characters of "reversed cutting triangles" (Osborn).

Relations of the Tritubercülata to the Triconodonta.

After the exclusion of *Peralestes* we have to enquire *in what manner are the Triconodonts related to the Tritubercülates?*

The dental formula of *Amphilestes*, $I.\frac{4}{4}$, $C.\frac{1}{1}$, $P.\frac{4}{4}$, $M.\frac{7}{7}$ (Osborn), is like that of typical Tritubercülates. As far back as the Upper Triassic this formula was closely approximated by that of the Cynodont *Diademodon mastacus* ($P.\frac{4}{4}$, $M.\frac{8}{8}$, Broom, 1905.4) so that it may well be a primitive character inherited by Triconodonts and Tritubercülates. Another character foreshadowed in *Diademodon* and seen in both Triconodonts and Tritubercülates is the sharp differentiation of the premolars from the molars. In both orders also p_1 to p_4 increase rapidly in size, p_4 being a high-pointed tooth much higher than m_1.

These characters scarcely seem sufficient to point to anything more than the remote common origin of the orders as here accepted.

The Triconodonta retain some very ancient characters besides those mentioned above under the dentition. The angle of the lower border of the jaw is inflected as in recent Marsupials. In *Triconodon* also the fourth deciduous premolars alone was replaced by a successor (Osborn). The coronoid is very broad, the condyle sessile (Fig. 6, no. 7). The latter looks backward rather than upward and implies a glenoid-squamosal region extending down below the level of the teeth as in Cynodonts. The groove on the inner side of the jaw for the Meckelian cartilage (Bensley) is pronounced.

Conclusions. The Triconodonta and their bearing on the origin of the mammalian molar.

(1) The order Triconodonta, after the exclusion of *Peralestes*, is probably a natural group, allied to the Marsupials and ordinally distinct from the Trituberculata (as here understood), but inheriting in common with that group several characters (*e. g.*, dental formula, distinction between premolars and molars, p_4 higher than m_1) that may run back even to the Cynodont reptiles.

(2) Nothing is known unfavorable to Osborn's hypothesis that the triconodont molar type was derived from the Protodont type.

(3) The hypothesis of the origin of the triangular pattern of the molars by rotation of the cusps is supported by such evidence as there is only *when strictly limited to the Triconodonta.*

(4) The upper teeth of *Peralestes* (p. 174) belong more probably to the Trituberculata, and their presumed connection with the lower molar teeth of *Spalacotherium* is discredited (p. 175); hence the only cited evidence of morphological and genetic transition from the triconodont to the tritubercular type seems to fail at the critical point.

The Trituberculata (Pantotheria in part).

The order Trituberculata as defined by Osborn (1907, pp. 22–24) includes the families Amphitheriidæ, and Amblotheriidæ (Stylacodontidæ), Paurodontidæ and doubtfully the Dicrocynodontidæ. To this assemblage *Peralestes* should probably be added (p. 174). *Amphitherium* and *Amphitylus* both come from the Stonesfield Slate (Middle Jurassic), the other genera date from the Upper Jurassic (or possibly Lower Cretaceous) *i. e.*, from the Purbeck of England and Morrison of Wyoming. Most of the genera are founded on lower jaws with teeth; upper teeth are known only in *Dicrocynodon, Kurtodon, Dryolestes* and *Peralestes.*

Generalized characters retained among Trituberculates.

The order is of especial interest because it appears to be remotely related on the one hand to the Metatherian order Triconodonta and on the other hand to the common stem of the more generalized Placental orders Insectivora and Creodonta. The Trituberculata present so many analogies in the dentition to the Insectivora that certain families were at first named Insectivora Primitiva by Osborn (1888, p. 247); but without further evi-

dence from other parts of the skeleton such resemblances in dentition can not be trusted as sufficient evidence of close affinity (p. 108).

Different members of the order inherit certain characters from very remote possibly unknown prototherian or even Cynodont ancestors, as follows:

(1) The sharp differentiation of premolars from molars (compare the Cynodont *Diademodon mastacus* Broom, 1905.4, pl. x). Marsh gave the character "premolars and molars imperfectly differentiated" as diagnostic of the order Pantotheria but Osborn found (1888, p. 257, footnote) that the premolars and molars were well differentiated in all the specimens examined by him.

(2) Pm_4, a large pointed tooth projecting much above the level of m_1. This character seems to be quite typical.

(3) Dental formula typically $I.\frac{4}{4}$, $C.\frac{1}{1}$, $P.\frac{4}{4}$, $M.\frac{6-6}{}$. This formula may have given rise by reduction to those of both Marsupials and Placentals. It was already approximated in Cynodont reptiles (*cf.* $I.\frac{5}{4}$, $C.\frac{1}{1}$, P + M? in *Ælurosuchus* (Broom, 1906.2, pl. x) and I.–, C.–, $P.\frac{4}{4}$, $M.\frac{7}{7}$ in *Diademodon* (Broom, 1905.4, pl. x).

(4) Canine often bifanged, more or less premolariform.

(5) Incisors chiefly lateral in position, chin very long and slender, opposite rami weakly attached at the symphysis.

(6) Coronoid sometimes very broad, *e. g.*, *Amphitherium*, but occasionally narrower, *e. g.*, *Amblotherium*.

(7) Condyle, although often higher than in Triconodonts, still near the level of the cheek teeth and looking more backward than upward. This implies a descending glenoid region and together with the long mandible also implies that the basifacial axis was not bent downward.

(8) Corono condylar sinus not deep.

(9) Angle often a small apophysis but more advanced than in *Diademodon*. Angle sometimes partly inflected (*Amphitherium prevostii*).

(10) "Cerebral hemispheres smooth" Marsh.[1] Cerebrum probably confined chiefly to the parietal segment; basioccipital segment probably very short; rhinencephalon probably large.

(11) The foregoing characters taken in connection with the tuberculosectorial lower molars, indicate a type of skull in the more generalized forms (*Amphitherium*) which would resemble that of the smallest Didelphids (*Marmosa pusilla, Peramys*) in many characters.

To these characters, inherited from very remote ancestors, it is probable that we should add two others hitherto taken to be a sign of specialization, namely:

[1] This character is said to be indicated in one of Marsh's specimens (Osborn, 1888, p. 257).

(1) Upper molars (in *Dryolestes*) very wide transversely, short antero-posteriorly and not really triangular.

(2) Lower molars (except in *Dicrocynodon*) short antero-posteriorly as compared with those of higher mammals, with an asymmetrical trigonid and an incipient protolophid.

Importance of Amphitherium.

Its primitive characters. The most generalized member of the order and one which probably possessed all the characters listed above is the famous genus *Amphitherium*, which so far as its mandibular and dental characters indicate might represent the common stock of the later Polyprotodont Marsupials, and Placental Insectivores and Creodonts.

Two great facts about *Amphitherium* are first, that it is a very primitive Middle Jurassic mammal in which the tuberculo-sectorial type of lower molar is seen in a generalized condition and secondly that from the general similarity of its lower molars to those of *Didelphis* and many other mammals with tuberculosectorial lower molars we can infer with great probability that the upper molars will also be found to be of a generalized "tritubercular" type. *Amphitherium*, then, occupies a most important place in mammalian phylogeny in general, and in the Theory of Tuberculy in particular.

Lower teeth of Amphitherium not derived from the Triconodont type. The cheek teeth of *Amphitherium prevostii* Blainville as described very carefully by Goodrich (1894, pp. 414–415), offer so good a comparison with those of *Didelphis* that Cuvier described the jaw of *Amphitherium* as "celle d'un petit carnassier dont les machelières resemblent beaucoup à celles des Sarigues, mais il y a dix dents en série, nombre que ne montre aucun carnassier connu" (quoted by Goodrich, *l. c.*, p. 410). They are more primitive than those of *Didelphis* in several respects:

(1) The number of true molars is greater (as six is to four) and the individual teeth are relatively smaller; there appear also to be five premolars (Goodrich, Osborn).

(2) The protoconids are higher, and the para-, meta- and entoconids lower, the talonids much smaller; the latter fact implies a high protocone (pp. 175, 180).

Amphitherium agrees with *Didelphis*, with the other Trituberculates and with primitive mammals generally in the fact that the trigonid is not symmetrical, the metaconid being almost directly internal to the protoconid. This important fact seems to have been neglected hitherto in the development of the theory of Tuberculy (p. 187). The paraconid, metaconid and entoconid are also in the same antero-posterior line and when compared

with the conditions in *Paraspalax* and *Paurodon* (Osborn, 1907, p. 29) give the appearance of having been an upgrowth of an internal basal cingulum, which is otherwise not patently represented. None of these peculiar features are foreshadowed in any degree in *Spalacotherium* (p. 174) in which the cutting trigon is symmetrical, the thorn-like paraconid and metaconid diverge outward and upward and are not continuous with the strong internal basal cingulum, and in which there is no suggestion of a heel. Consequently there seems little evidence for the view (see also *Peralestes*, p. 174) that the tuberculo-sectorial molar type (as represented in *Amphitherium*) has been derived from the generalized triconodont type by way of the *Spalacotherium* type. On the contrary some evidence will be presented (p. 185) that the tuberculo-sectorial type has been evolved in an entirely different manner.

Probable characters of the upper molars. The next inquiry is *to what extent the characters of the unknown upper molars of Amphitherium may be inferred from the characters of the known lower molars.* The views developed below are illustrated by the accompanying hypothetical reconstruction of an upper molar of *Amphitherium* (Fig. 10).

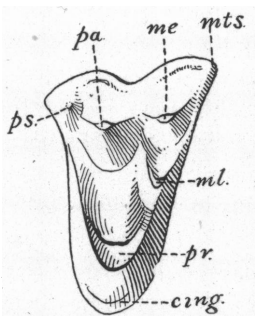


Fig. 10. Hypothetical reconstruction of an upper molar of *Amphitherium prevostii*. Greatly enlarged.

From the greater number of lower teeth and their relatively short anteroposterior diameters it is practically certain that the upper teeth, as compared with those of *Didelphis*, were relatively shorter antero-posteriorly and broader transversely, and in so far approached the *Dryolestes* type (Fig. 12, *B*). The talonid as in *Dryolestes* is much lower than in *Didelphis* and this very likely implies that its complement, the protocone, was relatively high. It might be thought that a low talonid would rather imply a small shelf-like internal cusp, or "protocone," as it does in the premolars of Tertiary mammals but this was not the case in *Dryolestes* and other Jurassic genera (*cf.* Fig. 12, *B*). The protocone of *Didelphis* acts not only as a pestle to the mortar-like talonid but also as a check which (together with the metacone) prevents the protoconid from piercing the roof of the mouth. If, in *Amphitherium* the low talonid had been opposed by a very low protocone in the upper molar the two molars could not have come in contact, because the protoconid was high. In *Amphitherium* the protocone must have been higher than in *Didelphis* and about as high as in *Dryolestes*.

The interspaces between successive protocones in *Amphitherium* were doubtless occupied when the jaws were closed by the paraconid and metaconid of the lower molars. These cusps did not oppose anything in the

upper teeth but as in all primitive tuberculosectorial dentitions served chiefly to pierce and hold the small living prey.

The posterior borders of the upper molars were probably more directly transverse and less oblique than in *Didelphis*; because the short talonid would not leave room for an oblique posterior shear; consequently the metastyle shear in the upper molars must have been less prominent than in *Didelphis*. Unfortunately it is not certain that the antero-external face of the trigonid lacked the deep fossa for the metacone (Bensley's "anterior cingulum") which is so characteristic of *Didelphis* and its allies; but at any rate it seems reasonable to infer that the metacone in *Amphitherium* was not set so far internally as it is in *Didelphis* and was not greatly enlarged and sharply V-shaped on its internal surface. From the inferred anteroposterior shortness of the upper molar, and from the general resemblance of the lower molar of *Amphitherium* to the lower molar of *Dryolestes* it also seems reasonable to infer that, as in the upper molar of *Dryolestes*, the metacone was smaller than the paracone and like it rounded rather than V-shaped. As to the character of the outer or overhanging part of the upper molars, the lower molars afford no direct inference; but the conditions in *Peralestes*, *Dryolestes* and *Didelphops* indicate the presence of a parastyle, a metastyle and perhaps of an external cingulum indented at its mid-point.

Summing up these inferential characters of the upper molars of *Amphitherium* we get a very primitive tritubercular molar of the same general type as that in *Dryolestes*, as figured by Osborn (1907, p. 27, fig. 14) and by Gidley (1906, pl. v, fig. 2 [1]): namely a slightly asymmetrical triangle, shorter on its anterior leg and very broad transversely; antero-posterior diameter perhaps somewhat greater than in *Dryolestes*, a high protocone, a large paracone directly external to the protocone, a smaller metacone, a parastyle, an external cingulum indented at its middle point, and perhaps a small metastyle (Fig. 10). Whether the paracone and metacone were crescentic externally we have no means of knowing, but the rounded character of these cusps in related genera does not favor the assumption.

Origin of the Tritubercular Molar Type.

The existence of Jurassic Therians with very generalized tuberculosectorial lower, and tritubercular upper, molars raises the problem of the mode or modes in which this highly effective molar type has been derived.

It has been argued above that the "Cusp-rotation" theory, while possibly valid for the Triconodonta (p. 177), remains entirely unproven for the Tri-

[1] Gidley's figure is also given in Osborn, 1907, p. 218, No. 2.

tuberculata. It is not necessary to rehearse any of the opposing arguments which have been discussed in Osborn's 'Evolution of the Mammalian Molar Teeth' (pp. 7, 8, 33, 227); but it nevertheless seems advisable to develop here some new criticisms against various old views, to endeavor to reconcile conflicting evidence and to strive for a new synthetic view of the evolution of the molar teeth in the Theria.

The "Premolar" Analogy Theory.

One great line of argument against the theory of Trituberculy is known as the "Premolar Analogy Theory" (Osborn, 1907, pp. 215–219).

The transformation of the premolars into molariform types among the Tertiary mammals has been described by Scott (1892, pp. 405–444). Huxley, and later Wortman (1902, pp. 93–98, 1903, pp. 365–368), concluded that the premolars indicate in their transformation the precise steps by which the molars had attained the tritubercular type.

Wortman (1902, p. 94) figures two genera of Eocene Creodonts, *Dissacus* and *Mesonyx*, the first being perhaps a collateral ancestor of the other, in which there is every appearance of a progressive transformation of the molars after the same manner as the premolars. He concludes (*l. c.*, p. 97) that it is "so inherently improbable that in the matter of cusp development the premolars have had one history and the molars another, that the evidence would require to be of the most direct and positive kind even to place such a proposition on the ground of reasonable probability."

Several considerations however appear to indicate that this argument should not be accepted without reservation. First, "inherent improbabilities" have at times become demonstrated facts in science. The principle of convergent and parallel evolution between entire organisms is now so well known that the "inherent improbability" of convergence or parallelism between closely related structures, such as premolars and molars may not be taken for granted.

Secondly, the sharp differentiation of premolars from molars is usual if not universal not only in Basal Eocene and Jurassic Therians (Osborn, 1904, p. 322) but was present in some forms as far back as the Upper Triassic (*Diademodon, Dromatherium, Microconodon*). In the most primitive Polyprotodont Marsupials and in the Jurassic Trituberculata p.$\frac{4}{4}$, being simple conical teeth, are wholly unlike m. $\frac{1}{1}$. In the Basal and Lower Eocene Creodonts, Insectivores, "Primates" (*Indrodon*), Ganodonts, Condylarths, Amblypods, etc., p^4 is at first a bicuspid tooth and later becomes more molariform.

Thirdly while the molarization of the premolars is well established, the

presumed evolution of the true molars from a premolariform type must have taken place during the Mesozoic, since the early stages of the process are never observed in the Tertiary. But no Cretaceous or Jurassic forms have been discovered in which the upper molars show the one essential feature of the presumed premolariform mode of complication, namely: "protocone" represented by a small basal ledge springing from the internal side of the tooth. Owing to the scarcity of the upper teeth of Mesozoic mammals this of course is not conclusive; but certainly in the only Jurassic Trituberculates in which the upper teeth are known, namely *Peralestes*, *Kurtodon* and *Dryolestes*, the supposed protocone is the largest cusp on the crown. This argument has already been advanced in outline by Osborn (1904, pp. 321–323) but he omitted a very important link, namely a demonstration that the high internal cusp in those genera was truly homologous with the protocone of "normal" tritubercular types.

This link has been partly supplied in the preceding discussion (pp. 174, 180) of the teeth of *Peralestes* and *Amphitherium*, in which it is shown that the internal cusp probably fitted into the talonid and therefore functioned like the protocone of Creodonts and all other typically tritubercular mammals Gidley (1906, p. 96, quoted in Osborn, 1907, p. 220) has supplied evidence for the same view in the case of *Dryolestes*. Being, however, an adherent of the "premolar analogy theory" Mr. Gidley sees in the protocone merely a greatly hypertrophied "heel." In *Dryolestes* he says "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." He applies also the same idea to *Dicrocynodon*. The outer parts of the crown of both *Dryolestes* and *Dicrocynodon* he regards as homologous with the three cones and two fangs of *Triconodon*; but of the inner portion of the crown of *Dicrocynodon* (*l. c.* fig. 207) he says "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."

Now this large internal cusp in *Dicrocynodon* presumably fitted into the basin-like talonid of the lower molar and therefore functioned like a normal protocone and like the protocone of *Dryolestes*. Why, therefore, should the great difference in the *shape* of the protocone in the two genera and the division of the supporting fang in *Dicrocynodon* imply that the protocone itself is a neomorph?

A most valuable part of Mr. Gidley's paper is that he has emphasized the fact that *the protocone of the upper tooth always fits into the talonid of the lower* (*cf.* Fig. 13). Because the talonid of the *premolars* of many

Tertiary families is at first small, like the internal shelf-like "deuterocone" of the upper premolars, and because the two develop together *pari passu* so that the deuterocone finally develops into a cusp resembling the protocone of the molars, Gidley seems to conclude that the same is true of the *molars* of Jurassic mammals.

According to this a very low and small talonid ought to imply a small protocone; but as shown below in the Jurassic Trituberculates a high pointed protocone of the type seen in *Dryolestes* was probably received into a low small talonid; and instead of the protocone being a "heel" evoked as in the premolars by the preëxistence of the talonid, the reverse has probably been the case. The peculiar recurved protoconid and small concave talonid of *Peramus* and *Leptocladus* (Osborn, 1907, p. 28, fig. 18), on this hypothesis imply the existence of a high protocone. The high large protocone of *Peralestes* was (it has been argued above, p. 174) received into a low talonid, while the small talonid of *Amphitherium* (p. 180) seems to require a large protocone. In short, the theory that the protocone is of more recent origin than the paracone and has been called into existence as a "heel," *pari passu* with the development of the talonid below is not favored by the present interpretation of the evidence furnished by the Jurassic Tuberculata.

The Theory of Tritubercuły correct in its basal postulate, the originally reversed relations of trigon and trigonid.

The well known plasticity of the dentition in mammals and the frequency of convergent evolution raises an *a priori* presumption that the tritubercular type has arisen more than once in mammalian history; and it is indeed possible that the so called protocone is not always strictly homologous throughout the mammalia; while even among Jurassic mammals the more or less triangular upper molars of *Peralestes* and *Dryolestes* may have attained their observed features by two different roads of development. But this does not imply that the celebrated theory of tritubercuły has been entirely disproven by its numerous critics. *Stripped of all non-essentials and interpreted in a new manner the fundamental thesis of the Theory of Tritubercuły may still be correct: namely, that the trigon above and the trigonid below are morphologically reversed structures, and that all the accessory parts are the offspring of a main "protocone," the tip of which lies on the inner side of the upper, and on the outer side of the lower, molars.* The writer therefore ventures to put forth into the already crowded field still another hypothesis, which may at least help to make clear some mechanical principles that will be of some assistance later on in this work.

Mechanics of molar evolution in the Jurassic.

The molars of *Peralestes* (Fig. 9, p. 174) seem not to have been derived from the *Spalacotherium* or Triconodont type with symmetrical trigon. The upper molars of the remote ancestors of the Tituberculata as represented by both *Dryolestes* and *Peralestes* may on the contrary be conceived as follows (Fig. 11): The molars were small and many in number (more than six). The transverse diameter of each crown was relatively great, the crown was much narrower on the inner side, and hence roughly cuneiform in cross section; the narrower internal side culminated in a high rounded tip, the protocone. Each tooth was supported on two large roots, an internal and an external one. The teeth were well spaced.

The lower molars alternated with the upper but were much smaller, they were also slightly compressed in cross section at the base and were supported on a compressed root which had already become constricted in the middle. Each roughly pyramidal protoconid was sub-triangular in cross section, the rounded apex of the triangle being external. When the jaws engaged with each other the protoconid of each lower molar fitted into the space immediately in front of the protocone of the corresponding upper molar. The tip of the protoconid was slightly external (buccal) to the tip of the protocone (Fig. 11) but internal (lingual) to the broad external base of the protocone, the site of the future parastyle and external cingulum.

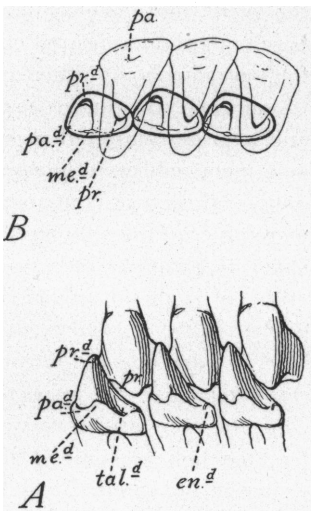


Fig. 11. Hypothetical reconstruction of the upper and lower molars in the ancestors of the Tituberculata.

A. Internal view showing paraconid (*pa.d*) metaconid, (*me.d*) entoconid (*en.d*) growing up from the internal cingulum; protoconid (*pr.d*) pyramidal, talonid (*tal.d*) receiving tip of large protocone (*pr.*) of upper molars. Right side.

B. Projection of upper on lower molars. Protoconids and metalophids fitting between protocones; paracone (*pa*) centro-external, incipient.

Here are all the essential conditions for a future tritubercular dentition, without any migration of cusps, and with the upper and lower main cusps located in exactly the same positions with respect to the inner and outer sides of the tooth and to each other which they occupy in typical tritubercular types.

The talonid on the lower molar was initiated through the circumstance that each lower molar, being pulled from behind, upward and forward,

was struck on the posterior basal side by the protocone of the corresponding upper molar (Fig. 11).[1] The anterior external face of the protoconid sheared past the posterior side of the upper tooth, and since both protocone and protoconid were wedge-shaped, the relation of reversed cutting triangles, which is so indirectly effected under the Tritubercular theory, may have been established at a very early period in the evolution of the tritubercular dentition.

How on this hypothesis did the trigonid arise? Possibly in response to the *lateral* movement of the posterior part of the lower jaw (p. 119) a heavy basal cingulum appeared on the outer side of the upper, on the inner side of the lower, molars. This cingulum in the lower molars rose into an anterior prominence, the future paraconid, a median prominence, the metaconid, and a postero-internal prominence, the entoconid.[2] The small paraconid and metaconid were lingual to the line of the upper protocones and did not oppose any cusps, but merely aided in holding the food in place for the piercing-crushing action of the protocone and protoconid. We now have a lower molar only a little simpler than that of *Paurodon*, as figured by Gidley (1906, pl. v, fig. 5), or of *Peraspalax* as figured by Osborn (1888, fig. 10, No. 9).

The paracone and metacone sprang up *in situ* on the anterior and posterior external slopes, respectively, of the protocone. In *Peralestes* the metacone, being relatively very far internal, may have assisted in holding the food for the protoconid of the succeeding lower molar which was immediately posterior and internal to it.

Thus the trigon above and the trigonid below, although having the reversed relations postulated in the Theory of Tuberculy, have probably not arisen in accordance with that theory: the paraconid and metaconid below may be upgrowths of the *internal cingulum*, the paracone and metacone, above may have grown up from the slopes of the protocone, *in situ*, and well within the line of the parastyle and external cingulum.

The conditions in *Dryolestes* are foreshadowed to some extent in the Upper Triassic *Diademodon* (Fig. 12, *A*) in the following respects:

(1) In *Diademodon* the small lower molars fit *between* the upper molars, the anterior half of the lower molar engaging the posterior half of the preceding upper molar, the posterior half of the lower molar engaging the anterior half of the corresponding upper molar, after the manner of a talonid (Broom, 1905.4).

[1] This hypothesis does not assume that "acquired" characters are transmissible but simply that changes have often originated *as if* in response to mechanical stimuli and requirements.

[2] The latter cusp in the writer's opinion is older than the hypoconid, which later grew up externally to the tip of the protocone (in the closed position of the jaws) and fitted into *the central basin of the trigon of the upper molar* (*cf.* Fig. 12, *D*).

(2) The upper molars in *Diademodon* present an internal border rising to a middle point, suggestive of the protocone.

(3) The lower molars of *Diademodon* have a transverse ridge analogous to a protolophid, and if the external tip of this ridge were produced dorsally it would, in mastication, occupy precisely the relations of a protoconid in a tritubercular molar.

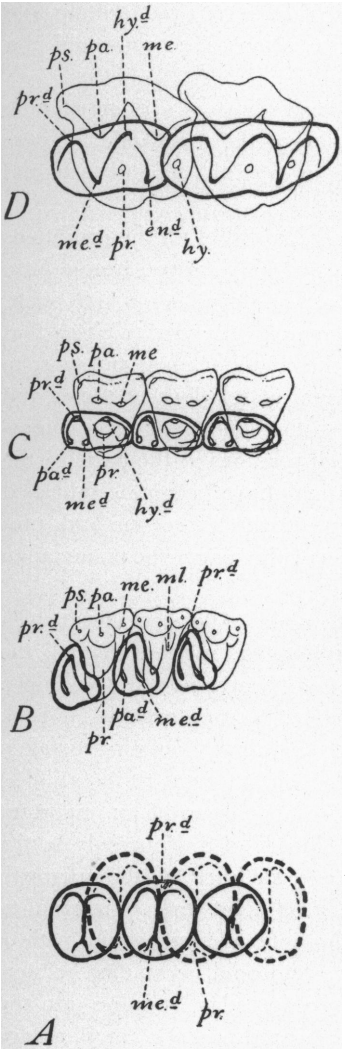
(4) The well defined protolophid mentioned above is a ridge running directly inward from the protoconid to the site of the metaconid. These cusps are connected by an incomplete ridge in typical tuberculo-sectorial molars (Fig. 12, *B*, *C*.).

It is not suggested that the *Diademodon* molars fulfill all the conditions of the ancestral tritubercular type, which was probably derived from a form in which the protocone and protoconid were both produced into a high point. The comparison with *Diademodon* is made merely in order to show that when attention is directed less exclusively to the *origin of cusps* and more to *contours of molar crowns* and to actual mechanical relations of upper and lower teeth, it becomes unnecessary to resort to the hypothesis of the migration of cusps, in order to account for the spatial relations of the parts of the tritubercular molar; because these relations may have become established long before the appearance of any cusps except the protocone and protoconid, and may even antedate the acquisition of the diagnostic mammalian characters.

The molar pattern of Protodonts and Triconodonts does not constitute a valid objection to this view, *i. e.*, it is not necessary to suppose that all the pre-tritubercular molar types that ever existed are represented in the known Protodonts, Triconodonts and Multituberculates; because even as far back as the Cynodonts a wide adaptive radiation of molar types had already taken place.

The *protolophid* of *Dryolestes* (Fig. 12, *B*) appears to be an important structure which has been neglected by the Theory of Tuberculy in the earlier stages of molar evolution. This was formed first by the upgrowth of the metaconid from the basal cingulum, at a point directly internal to the protoconid and secondly by the junction of this metaconid with a descending ridge of the protoconid. As the protoconid became more perfectly wedge-shaped in cross section, its posterior edge, running into the small metaconid below, became sharper and sheared past the anterior edge of the upper molar. As the paracone grew up, the front view of the upper tooth would present a concavity, facing downward, between the paracone and the protocone. Similarly the back view of the lower trigonid would present a concavity, facing upward, between the protoconid and the metaconid. The anterior part of the paracone and the metacone, together with

the basal edge of the tooth would thus form an imperfect protoloph, across which sheared the incipient protolophid of the lower molar. This proto-



D. Telmatherium, Middle Eocene Ungulate. Upper molars very wide anteroposteriorly, lower molars long anteroposteriorly. Protocone fitting into basin of talonid, hypocone into basin of trigonid, paraconid vestigial; space between upper molars limited to inner side.

C. Triisodon, Basal Eocene Carnivore. Upper molars widening anteroposteriorly, metacone equal to paracone; lower molars lengthening anteroposteriorly by development of the talonid, which receives the broad protocone.

B. Dryolestes, Upper Jurassaic (upper molars after Gidley, lower molars after Osborn). Upper molars wide transversely; lower molars small, short anteroposteriorly, fitting between upper molars. (The latter as drawn may be spread apart too much on the inner side). Talonid incipient, paracone centro-external, metacone small.

A. Diademodon, Triassic Cynodont (upper molars after Seeley, lower molars after Broom). Upper molars wide transversely, lower molars small, short anteroposteriorly, fitting between upper molars. pr^d, protoconid.

Fig. 12. Projection of upper on lower molars, illustrating the "Wedge Theory."

lophid was not yet established in *Amphitherium* but was well developed in *Dryolestes*, and became very important in many later types.

The protoloph above was further improved by the posterior limb of the

V-shaped *metaconule*. This cusp was at first developed to fit into the space between the antero-external border of the *talonid* of the corresponding lower molar and the anterior proto-paraconid edge of the *trigonid* of the following lower molar (Fig. 12, *C*). It would also help to press the food against the hypoconid when that cusp appeared.

Mechanics of tritubercular evolution in the Cretaceous and Basal Eocene.

The Jurassic *Dryolestes* represented a stage in which the upper molars were more than twice as many (8) as in the higher mammals (3) but correspondingly narrow, especially on the inner side. *Amphitherium* was somewhat more progressive both in the reduction of the number to six and *probably* in the somewhat greater antero-posterior diameter of the individual teeth (Fig. 12). *The chief advance in the dentition of Cretaceous and Basal Eocene mammals was the reduction in number and concomitant increase in antero-posterior diameter of the upper teeth and the consequent development of a more open triangle and of the cusps on the posterior half of the tooth.* This also required a lengthening in the lower molars, especially of the talonid (Fig. 12).

With increasing size and power of the individual teeth the jaw and muscular attachments became larger and the opposite rami became more strongly connected at the symphysis. We may assume that the outer side of the upper molars widened faster, especially the metastyle, the external cingular cusps greatly developed, while the para- and metacones in some phyla became crescentic. The protocone is also crescentic in all the earliest tritubercular types, so that the bunodont, or purely circular cusps, formerly assumed to be the starting point in many orders, may be secondary (Gregory, in Osborn, 1907, p. 173, foot-note).

This stage of evolution is represented in *Pediomys* Marsh (figured by Gidley, 1906, pl. v, fig. 6), by *Didelphops* Marsh and by other Upper Cretaceous mammals figured by Osborn (1907, p. 96, fig. 47).

Origin of the hypocone.—The upper molar in widening (phylogenetically), widened faster at the base than at the summit of the crown, consequently a line of fracture took place near the base of the crown, and an internal basal cingulum, resulted, which was analogous to the older external basal cingulum. The development of the hypocone from this structure has been shown in many families by Osborn. The antero-external edge of the trigonid, namely the protoconid-paraconid ridge, sheared past the posterior edge of the preceding upper molar. Consequently upon the appearance of the posterior internal basal cingulum of the upper molar the anterior edge of the trigonid now began to overlap this posterior cingulum, a stage illustrated in the Basal

Eocene Oxyclænidæ. The trigonid itself had formerly merely filled the interspace between successive protocones but its basin now began to be occupied by the postero-internal cingulum, or hypocone. The subsequent disappearance of the always low paraconid, which interfered with the development of the hypocone has also been noted by Osborn. But a cardinal fact which has not hitherto been sufficiently emphasized is that *the hypocone is an accessory crusher, fitting into the basin of the trigonid of the succeeding lower molar, just as the protocone fits into the talonid of the corresponding lower molar* (*cf.* Gregory, in Osborn, 1907, p. 61, foot-note; *cf.* Figs. 12, 13 below). Inasmuch as the protocone and hypocone had a very different origin, the subsequent similarity of the two cusps furnishes an excellent case of convergent evolution among cusps, and this case helps us to understand how premolars and molars may sometimes attain a perfect similarity of pattern and yet consist partly of non-homologous components.

In the later mammals the protocone became depressed as the talonid grew up, while the trigonid became depressed as its pestle, the hypocone, developed; so that finally the anterior and posterior moieties of the lower tooth attained practically the same level.

Broadening of the talonid and origin of the hypoconid. The talonid was at first merely a narrow posterior spur, rising internally into the entoconid. This condition is retained in the Jurassic Trituberculates and in the Eocene and modern Zalambdodont Insectivores. The protocone at first fitted into the space external to the talonid. As the talonid widened transversely a small cusp, the hypoconid, grew up, fitting behind and external to the protocone, further widening of the talonid caused the protocone to be received into the basin of the talonid internal to the hypoconid, and at the same time the hypoconid was received into the central valley of the trigon above (Fig. 12, 13).

In order to summarize the foregoing observations on the spatial relations of the parts of the upper and lower molars in a generalized tritubercular stage, the following table is inserted:

Functions and spatial relations of the parts of the upper and lower molars in a generalized tritubercular dentition (*cf.* Figs. 11, 12, 13).

I. *Overhanging cusps* (serving either as points of insertion or as fulcra).
   Upper molars: Parastyle, external cingulum, metastyle, external face of paracone and metacone.
   Lower molars: Paraconid, metaconid (at first filling space between successive protocones).
   Entoconid, internal to protocone of corresponding upper molar.

Hypoconulid, posterior to hypocone of corresponding upper molar.

II. *Interlocking cusps.*

Upper molars: Protocone, fitting into talonid basin of corresponding lower molar.

Hypocone, fitting into trigonid basin of following lower molar.

Paracone (inner side), fitting into mid-valley of corresponding lower molar.

Metacone (inner side), fitting into anterior valley of following lower molar (= interspace between talonid of corresponding and trigonid of following molar).

Protoconule, fitting into inner valley between protoconid and hypoconid of corresponding lower molar.

Metaconule (inner face) fitting into valley between talonid of corresponding and trigonid of succeeding lower molars.

Lower molars: Protoconid, fitting into valley, or space between metacone of preceding and paracone of corresponding upper molars.

Hypoconid, fitting into mid-valley of trigon of corresponding upper molar.

Conclusions in regard to Tritubercuły.

From the imperfect evidence at hand the following conclusions appear to be indicated:

(1) The multituberculate molar type is much older than the tritubercular type (p. 167). The supposed analogies with basin-shaped molars of tritubercular derivation are not at all convincing, partly because none of the alleged instances show much more than a verbal resemblance to the true multituberculate type (p. 168). The multituberculate molar may conceivably be derived from a type more or less analogous with the Triconodont type.

(2) While the Triconodonta may be related to the Trituberculata, the assumed evidence of derivation of the tritubercular from a generalized Triconodont molar seems invalid (p. 174), partly because *Peralestes* probably has no near relationship with *Spalacotherium* (p. 176).

(3) The lower molars of *Amphitherium* are among the most generalized tuberculo-sectorial types known (p. 179) and a detailed study of them affords grounds for inferring certain very primitive characters in the upper molars (p. 180).

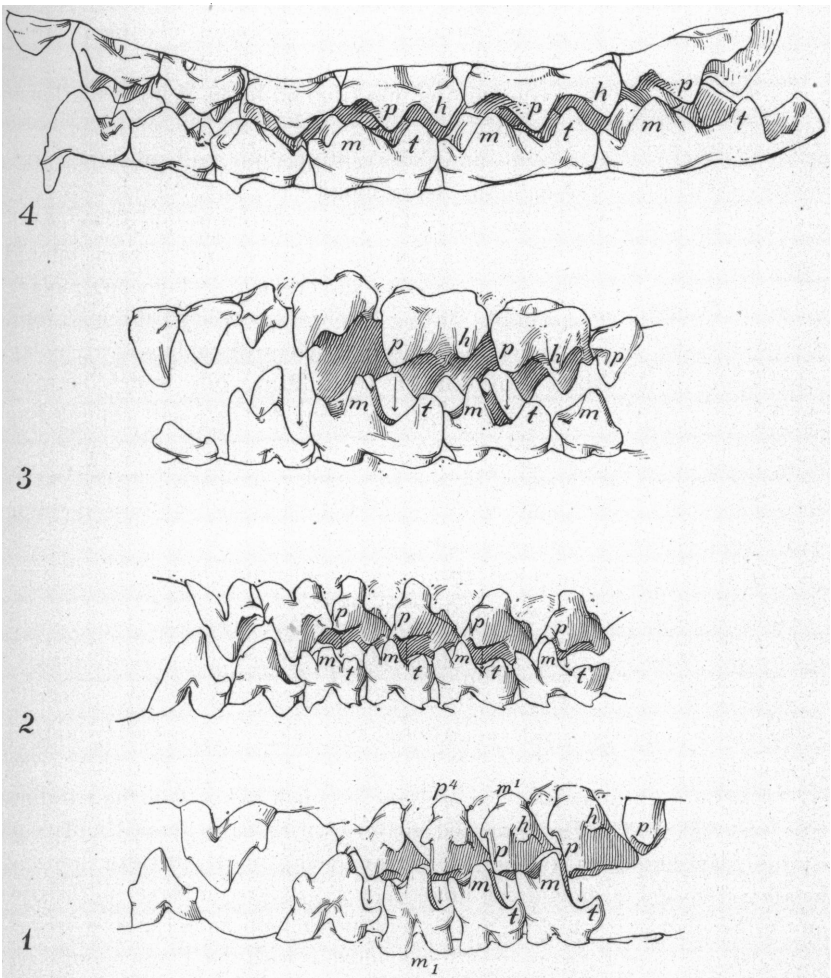


Fig. 13. Internal view of the cheek teeth (right side) in various mammals, showing that the protocone fits into the valley of the talonid of the corresponding lower molar, while the hypocone fits into the valley of the trigonid of the next succeeding lower molar. The para- and metaconid fit into the space between the upper teeth. No. 1. *Centetes*, No. 2, *Didelphis*, No. 3, *Erinaceus*, No. 4, *Telmatherium cultrideus*, an Eocene Titanothere. Prepared under the writer's direction for Professor Osborn's 'Evolution of the Mammalian Molar Teeth.'

p. = protocone, *h.* = hypocone, *m.* = metaconid, *t.* = talonid.

(4) The evolution of the premolars in Tertiary mammals may offer an unsafe guide to the history of the molars in the early Jurassic, (p. 182), and the theory (Wortman, Gidley) that the protocone is a "heel" developing *pari passu* with the talonid fails to explain the conditions in several Jurassic Trituberculates with a high protocone and very small talonid (p. 184).

(5) The foregoing considerations lead to a new theory of the origin of the tritubercular molar which may be designated as the "*Wedge Theory.*" Its basal inferences are as follows: (*a*) The protocone in Jurassic Trituberculates is not a neomorph, developed as in the premolars of Tertiary mammals (contrast Gidley, Wortman) but represents the "summit of the reptilian crown" (Osborn); but this crown was not the "simple cone" conceived by Cope and Osborn: (*b*) In the stage preceding the tritubercular stage, before the acquisition of any secondary cusps the upper and lower molars were not similar (contrast the Theory of Trituberculy) but quite dissimilar in form, the upper molars being very wide transversely and somewhat larger than the lower molars, which were short antero-posteriorly (Fig. 11). (*c*) The relation of reversed wedges obtaining between the upper and lower molars is not a secondary but a primary condition antedating the appearance of the para- and metacones (contrast Trituberculy). (*d*) As regards the Jurassic Trituberculates the secondary cusps arose approximately in the locations in which they are observed without any marked rotation, or migration of cusps (contrast Trituberculy). (*e*) The paraconid metaconid and talonid arose from the basal cingulum; the paracone arose from the outer part of the crown, the metacone budded off from the paracone; the parastyle, metastyle and metaconule arose very early.

(6) The Wedge Theory further differs from the Theory of Trituberculy in the following particulars:

(*a*) It looks backward to unknown Cynodontia with transversely widened upper molars, rather than to the Protodonta and Triconodonta, for an explanation of the peculiar spatial relations of the parts of the upper and lower molars.

(*b*) It centers attention as much upon the changes in the contour of the crown as upon the development of cusps.

(*c*) It devotes almost as much attention to interspaces, depressions and valleys as it does to cusps.

(*d*) It regards the principles of "change of function" and of "morphological correlation of parts" as of prime importance.

(*e*) While recognizing what may be called the individuality and self-initiative character of cusps, the present hypothesis nevertheless subordinates the parts to the whole much more fully than does the Theory of Trituberculy.

It regards a cusp primarily as an organic member of a whole crown, and secondarily as an independent unit of structure.

(*f*) Each cusp develops, it is true, its own individual *shape*, but this does not disprove its correlation, in the strictest Cuvierian sense, with other cusps or parts of the same organism. Cusps often serve in pairs or in series, as fulcra, across which resistent material is broken (*e. g.*, *Palæosyops*), and in this instance a cusp may be correlated in form and position with a cusp or with a depression on an adjacent molar as well as on an opposing molar. In many dentitions, breaking, triturating and cutting are accomplished through so complex a system of levers that sometimes hardly any two cusps on a crown may have the same work to do, and the cusps assume different shapes, as in upper molars of *Meniscotherium*.

There may well be a principle of orthogenesis and of independent evolution operating "in every part of every organ" (Osborn), but it is obvious that this tendency can be expressed only in so far as the very complex mechanically adaptive conditions will permit; since in any organism every part is more or less intimately environmental to every other part.

Additional Notes on the Trituberculata.

Peralestes. Evidence is given below (p. 174) to show that *Peralestes* does not belong with *Spalacotherium* and is a member not of the Triconodonta but probably of the Trituberculata (p. 176). However, the upper molars designated under the term *Peralestes* differ considerably from any of the upper molars known in the Trituberculata, namely those of *Dicrocynodon*, *Kurtodon* and *Dryolestes*. They also differ in several characters from the hypothetical upper molars which have been inferred (p. 180), from a study of the lower teeth, to have pertained to *Amphitherium*. *Peralestes* may however be allied to *Peramus*, *Leptocladus* and *Peraspalax*. These are known from lower teeth, which agree in several characters with the hypothetical type inferred (p. 174) for the lower teeth of *Peralestes*.

In brief it seems probable that the family Peralestidæ Osborn (1888, p. 247) is a member of the Trituberculata, and is a valid family, although later merged by Osborn (1888.2., p. 301) in the Triconodontidæ.

Kurtodon. In this genus, the type of the Kurtodontidæ of Osborn (1888, p. 234), the upper molars (see Osborn, 1907, p. 26, Fig. 13) are extremely wide and in the single known specimen well worn; but they seem to represent an exaggerated form of the *Dryolestes* type with which they agree in the possession of a parastyle, a centro-external paracone, a high pointed protocone and a slight internal cingulum. The worn molars as figured show a transverse ridge running out from the protocone analogous to the similarly placed ridge in *Diademodon brachytiara* and their excessive

width also recalls the conditions in that reptile, and strengthens the inference (p. 193) that in the ancestors of the Trituberculata the upper molars were very wide transversely. The molars also are analogous to those of *Microgale* among Insectivores. From the characters of the molars and of the high piercing canines it seems likely that there may have been a transverse grinding action of the *posterior* part of the mandible as in *Sesamodon* (p. 119) the Marsupials and the Zalambdodont Insectivores.

Dicrocynodon. Mr. Gidley has drawn attention to the fact (1906, p. 100) that the outer cusps and cingulum of the *Dicrocynodon* molar are comparable with those of *Dryolestes* and indirectly with those of *Triconodon*, but he regards the large internal cusp as a secondary heel, "differing widely in character from that of *Dryolestes*."

The fact that it is supported by *two* rudimentary fangs would not disprove its homology with the single cusp in *Dryolestes*. The transverse ridge seen in *Diademodon brachytiara*, which is present in *Kurtodon* (p. 194) and reduced in *Dryolestes*, is highly developed in *Dicrocynodon*. The interspace back of this ridge shows that the protoconid was large while the talonid was also very large. In short, so far as the evidence goes, the *Dicrocynodon* molar might be derived as readily from the hypothetical type figured on page 185 as from the Triconodont type.

Paurodon. The type specimen (see Osborn, 1907, p. 29, Fig. 26) should be reëxamined in order to make sure that the tooth interpreted by Marsh as a canine is not a broken p_4. If it is a canine the reduction in the number of post-canine teeth to 7, taken in connection with the number of incisors, canines and premolars in related genera, would show that the typical dental formula of the Placentals, $\frac{3.1.4.3.}{3.1.4.3.}$ appeared in some instances as far back at least as the Upper Jurassic or Lower Cretaceous.

Summary of the possible relations of the Trituberculata to the Higher Mammalia.

Amphitherium so far as indicated by the lower jaw and teeth seems to have been the most generalized member of the order. Its dental formula (p. 179) might give rise by reduction to that of either the Polyprotodont Marsupials or the Placentals. The lower incisors and canines (if resembling those of related genera), the simple premolars and the lower molars realize the required ancestral conditions for the Polyprotodonts, Creodonts and Insectivores. The probable characters of the upper molars, in so far as they can be inferred from a careful study of the lower molars and from the upper molars of related genera, point in the same direction. The angle of the lower jaw was partly inflected in *Amphitherium prevostii* but not in

A. (*Amphitylus*) *oweni.* The coronoid was broad as in the Polyprotodont Marsupials.

The Amblotheriidæ, Stylacodontidæ, Kurtodontidæ and Dicrocynodontidæ, formerly brought together by Osborn as the suborder Insectivora Primitiva (1888, p. 247) but later grouped by him (in Zittel's Palæontologie) with the Amphitheriidæ as the order Trituberculata, present so many analogies in the dentition and mandible to the Insectivora that if experience had not taught us to distrust the dentition as a guide to interordinal affinities, no hesitation would be felt in placing all these families except the Dicrocynodontidæ in the Placental order Insectivora. Some of the features occurring among both the Trituberculata and the Insectivora include the following:

(1) Incisor series prolonged backward on the side of the mandible.

(2) Canine either erect, recurved, or more or less premolariform, with two roots.

(3) Cheek teeth with prong-like, more or less recurved cusps.

(4) Lower molars short antero-posteriorly, with very small low talonid and high trigonid.

(5) Upper molars very broad transversely, narrow antero-posteriorly (*Kurtodon, Dryolestes.* Compare *Microgale, Ericulus*).

(6) Condyle sometimes set low, near level of cheek teeth.

(7) Coronoid varying from broadly triangular (*cf. Centetes*) to delicate, recurved (*cf. Tupaia*).

(8) Two mental foramina (*Leptocladus*), beneath p_2 and m_1, respectively.

In case the affinity of the Trituberculata to the Insectivora should ever be proven certain characters may be discovered that would warrant placing the Trituberculata in the Monodelphia (Placentalia). But in view of the characters shared by *Amphitherium* with certain Triconodonts and Polyprotodonts on the one hand and with the "Insectivora Primitiva" on the other it does not seem advisable at present to separate the Triconodonta and Trituberculata by placing the former in the Marsupialia, the latter in the Monodelphia; accordingly, in the classification adopted below (p. 464) the Trituberculata are placed in the infraclass Metatheria, the earliest representatives of which are usually regarded as ancestral to both Marsupials and Placentals.

On account of the very limited material it is difficult to find any characters for diagnostic purposes that apply to all members of the Trituberculata.

The group is separated from the Polyprotodont Marsupials by the retention of four premolars (five ? in *Amphitherium*) and usually by the higher number of molars and incompletely inflected angle. From the Placentals the group is separated frequently by the higher number of incisors ($\frac{4}{4}$) and molars (usually 6–8, but in *Paurodon* 3 ?).

CHAPTER IV. GENETIC RELATIONS OF THE MARSUPIALIA.

Analysis.

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I. Outline Taxonomic History of the Marsupialia.

South American and Mexican opossums were described by early Spanish travelers (Seba, Hernandez and others) under a number of names recorded by Gesner ("Semivulpa"), Ray (1693) and Linnæus (1758). "The Possum," "Opasum," "Possowne" (said to be an Indian word) were names used by the early Virginians. In 1640 the Dutch traveller Marggrav, as quoted by Ray (1693), gave a detailed description of the "Carigueija brasiliensibus" (whence the French "Sarigue), especially dwelling upon the extrauterine mode of development in the pouch, or "marsupium" (Ray), which was mistaken for the uterus. Later it was recognized that the opossum had also a true uterus, whence Linné's name "Didelphis," or double-wombed.

1762. Brisson refers the animals later called phalangers to *Didelphis*, under the name *D. orientalis.*

1765. Buffon calls attention to the syndactylous condition of the second and third digits of the hind foot, and calls the animal Phalanger "parce qu'il a les phalanges singulièrement conformées...." (Palmer 1904, p. 528). Buffon being a monomial writer, the generic name technically dates from Storr, 1780 (p. 49).

1771. Captain Cook's voyage results in the discovery of Australian Marsupials (p. 38).

1777. Erxleben regards the Kangaroo as a gigantic relative of the Jerboa and names it *Jaculus giganteus* (Palmer, 1904, p. 355).

1780. Storr separates *Phalanger* from *Didelphis* and frees the group, which he names "Plantares," from its former association with *Sorex, Talpa,* etc. (p. 49).

The progress in recognizing the different genera is indicated in the following five dates (from Palmer, 1904):

1790. *Macropus* Shaw.

1791. *Petaurus* Shaw.

1794. *Gigantomys* Link = *Macropus.*

1795. *Kangurus* Cuvier and Geoffroy = *Macropus.*

1795. *Phalangista* Cuvier and Geoffroy.

The next important systematic event was:

1795. *Dasyurus* added to the *Didelphis* group by Geoffroy and Cuvier, who adopt Vicq d'Azyr's term "Pédimanes" for the group and place it between "les Carnivores" and "les Rongeurs." These authors recognized the essential characters of the group, but the deceptive analogies of the teeth (one of the leading criteria) led Cuvier in his classification of 1800 to place "*Kangurus*" at the head of the Rodentia, but next to *Phalangista* the last of the "Pédimanes," which, in turn were placed next to the "Carnivores" in the superordinal assemblage "Les Carnassiers." The supposed intermediate position of the Marsupials between plantigrade "Carnivores" and "Rongeurs" was accepted also by Duméril and others (see p. 68).

New genera continued to be added as follows (Palmer):

1796. *Dasyurus* Geoffroy.

1799. *Coescoes* Lacépède.

1803. *Phascolomis* Geoffroy.

1804. *Potorous* Desmarest.

1804. *Perameles* É. Geoffroy.

1811. *Halmaturus* Illiger.

1811. *Hypsiprymnus* Illiger.

1816. *Phascolarctos* de Blainville.

1816. De Blainville joins the Marsupials and Monotremes in the subclass "Didelphes" [1] divided into two grand divisions "Normaux" (Marsupials) and "Anomaux" (Monotremes). The resemblances in the teeth and body-form to various Monodelphians are accordingly recognized as being secondary (see pp. 76, 82). The "Didelphes Normaux" are subdivided into two divisions, "Carnassiers" and "Rongeurs," corresponding in a general way to the Polyprotodontia and Diprotodontia. In his classification of 1834 de Blainville clearly anticipates the generalizations implied in the terms "Diadactyla" and "Syndactyla."

1817. Cuvier (p. 79) abandons the term "Pédimanes" for "Marsupiaux," and removes *Kangurus* to that group (see p. 79); in so doing he implicitly confesses that foot structure in this case is of less taxonomic importance than reproductive characters.

1836. Gervais in modifying de Blainville's classification (above), divides the Marsupials ("Didelphes") into two groups: (1) "les Eleutherodactyles," including "les Pédimanes" ("Sarigue, Chironecte"), and "les Phascologales" ("Dasyure, Phascologale, Thylacine"); (2) "les Syndactyles," including the syndactylous forms (*i. e.*, Bandicoots, Phalangers, Kangaroos, etc.).

1863. The first known South American Diprotodont (later called *Cœnolestes obscurus*) is described by Tomes from imperfect material under the name *Hyracodon fuliginosus*; its Marsupial affinities, however, are not recognized (*vide infra*, "1895, Thomas").

1866. Owen, as a result of his important studies of *Diprotodon*, *Thylacoleo*, and *Nototherium*, proposes the terms 'diprotodont' and 'polyprotodont,' as characteristic of the two sections; but this grouping had been anticipated by de Blainville.

1880. Huxley suggests the derivation of all the Marsupials from forms with a prehensile pes (p. 200).

1882. Moreno applies the name *Palæothentes aratæ* to certain fragmentary remains which were afterward (1887) referred by Ameghino to his genus *Epanorthus* (Palmer, 1904, p. 505).

1889. Ameghino describes a number of fossil South American Diprotodonts and proposes the family "Epanorthidæ," (= Palæothentidæ).

1896–1899. Hatcher collects in Patagonia numerous specimens of fossil Polyprotodonts and Diprotodonts (see 1905, Sinclair, below).

1896–1900. Hill's studies of the relations of the embryonic membranes

[1] Linné's term "Didelphis" referred (as stated above) to the possession of an external "womb" (*i. e.*, pouch), in addition to the true uterus; but de Blainville's term ("les Didelphes"), while etymologically the same, referred to the possession of two distinct true uteri.

of Marsupials show that certain Marsupials possess a true allantoic placenta in addition to the larger yolk sack placenta, a fact tending to bring the Marsupials much nearer to the Placentals.

1895. Oldfield Thomas describes *Cœnolestes obscurus* as a "still existing survivor of the Epanorthidæ of Ameghino, and the representative of a new family of recent Marsupials," and recognizes the identity of the new material with the "*Hyracodon*" of Tomes (preoccupied by *Hyracodon* Leidy).

1899. Dollo demonstrates the adaptive radiation in the feet and argues that the ancestors of the Marsupials were arboreal animals.

1903. Bensley reviews the Australian Marsupials with reference to the adaptive radiation of both feet and teeth, fully supporting Dollo's hypothesis and showing further that the Didelphidæ are structurally prototypal to all the remaining families.

1903. Ameghino figures the lower jaws and dentition of a number of fossil Patagonian Diprotodonts. Of these several genera (*Propolymastodon Polydolops*, etc.), resemble the Multituberculate family Polymastodontidæ in certain characters (p. 212).

1905. Sinclair (Mem. Princeton Univ. Exped. to Patagonia), monographs the Marsupialia of the Santa Cruz Beds, using the material collected by Hatcher. He demonstrates that the carnivorous forms were related to the Tasmanian Wolf and fall within the family Thylacynidæ, that the Diprotodont families Epanorthidæ, Garzonidæ, etc. of Ameghino were all closely related to the existing *Cœnolestes* and that *Microbiotherium* was closely allied to the smaller species of South American opossums.

1909. Gidley describes the skull of the Multituberculate genus *Ptilodus*, demonstrates the characters of the upper dentition in the Plagiaulacidæ, and shows that the Multituberculates are structurally Diprotodont Marsupials.

II. The Polyprotodontia.

The Theories of Dollo and Bensley.

That the ancestors of the Marsupials possessed a grasping type of pes and were therefore fitted for arboreal habits was the conclusion of Huxley (1880) and Dollo (1899). Bensley (1901, 1903) developed this idea by applying to the problem of the Marsupials those principles of dental evolution which had already been worked out in the study of Tertiary Placentals. Among Bensley's chief conclusions were the following:

(1) The modern Polyprotodonts and Diprotodonts are closely related in structure and were probably derived from a single type.

(2) The foot-structure and many other characters of this prototype are realized in the existing Didelphidæ, especially the smaller species of *Marmosa*. The prototypal dentition is represented in the Oligocene Didelphid *Peratherium fugax*.

(3) Starting from this type the divergent lines of adaptation were traced: as regards diet from insectivorous to carnivorous, omnivorous and herbivorous types, and as regards modes of locomotion from arboreal to terrestrial, fossorial, saltatorial and cursorial types. Bensley's conclusions rest partly on the assumption that the tritubercular molar was prototypal in the Marsupialia as well as in the Placentalia. His studies of the evolution of the feet tended to confirm this assumption.

A tabular summary of the morphogenetic and functional relations of the Polyprotodont families (Fig. 14), based largely upon Bensley's observations is given below:

Adaptive Radiation of the Polyprotodontia.

DIDELPHOIDEA Opossums, Dasyures, Thylacynes, etc.

DIDELPHIIDÆ.

Marmosa group.

Arboreal.[1]

Size small, primitively mouse-like.

Tail primitively prehensile, scaly (non-prehensile, hairy in *Peramys*). Pes 5-toed, digit I opposable, digits radiating.

Pes eleutherodactylous[2] (*Peramys*, secondarily terrestrial) to incipiently syndactylous[3] (occasionally in *Marmosa*).

Plantar pads separate, transversely striate.

Gait plantigrade, primitively scansorial.

Insectivorous.

Polyprotodont (I $\frac{5}{4}$).

Molars simple, tritubercular; metacone enlarged, cusps pointed.

? *Peratherium, Marmosa, Peramys, Microbiotherium, Dromiciops, Caluromys* (*Philander*).

Didelphis group.

Arboreal to terrestrial,

Size larger.

Pes eleutherodactylous (digits separate, II = III). Other limb-characters much as in preceding group.

Insectivorous-omnivorous-carnivorous.

Polyprotodont.

Molars tritubercular but stouter, somewhat less piercing, with long posterior blade.

[1] The words in italics refer to special habitat and diet. Under these headings are listed the principal characters relating to locomotion and dentition.

[2] *I. e.*, with all the digits remaining separate.

[3] *I. e.*, with digits II and III conjoined.

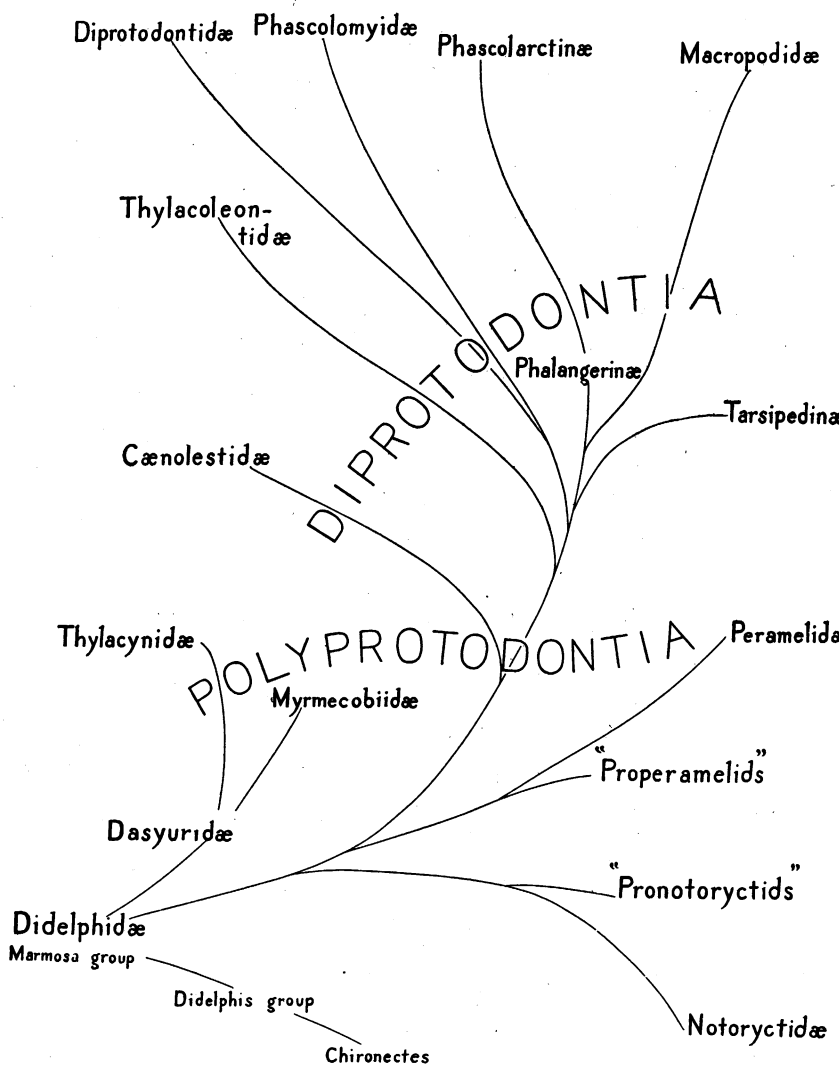


Fig. 14. Morphogenetic relations of the families of the Polyprotodontia and Diprotodontia.

Metachirus, Didelphis.

Chironectes (Water Opossum).

Terrestrial-aquatic.

Pes with webbed digits, manus with external tubercle on carpus. Tail flattened.

Piscivorous.

Teeth as in *Didelphis.*

DASYURIDÆ (derived from primitive Didelphiidæ).

Chiefly terrestrial (primitively arboreal).

Size increasing, from mouse-like (*Phascologale*) to badger-like (*Sarcophilus*).

Tail non-prehensile, hairy.

Pes: hallux progressively reduced to zero.

Pes eleutherodactylous: digits parallel, II = III = IV.

Tarsus progressively elongating (*Phascologale* to *Antechinomys*); or first elongating (*Dasyurus*), then broadening (*Sarcophilus*).

Tarsus with plantar pads fusing or modified.

Gait plantigrade-cursorial (*Phascologale*), to digitigrade-saltatorial (*Antechinomys*).

Insectivorous to carnivorous.

Polyprotodont: I $\frac{5-4}{3}$, median incisors becoming enlarged in insectivorous forms; posterior premolar variable.

Molars varying from tritubercular with sharp piercing cusps in insectivorous forms (*Phascologale*), to sectorial in the carnivorous *Sarcophilus.*

MYRMECOBIIDÆ (Derived from primitive Dasyuridæ).

Terrestrial.

Hallux reduced, slight traces of former syndactyly.

Insectivorous (*ant-eating*).

Polyprotodont. Dentition degenerating in adaptation to ant-eating habits.

Molars irregularly cuspidate, of tritubercular derivation, number secondarily rising to $\frac{5}{5-6}$ (Bensley).

Tongue elongate protrusile (*Myrmecobius*).

THYLACYNIDÆ. Tasmanian Wolf and Tertiary "Sparassodonts" of Patagonia. (Derived from very primitive unknown Dasyuridæ).

Terrestrial.

Size increasing, from opossum-like (*Amphiproviverra*) to coyote-like (*Borhyæna*).

Hallux reduced or wanting.

Eleutherodactylous.

Semiplantigrade, cursorial.

Carnivorous, predaceous.

Polyprotodont (I $\frac{4-3}{3}$).

Molars varying from tritubercular-sectorial to advanced sectorial type.

Amphiproviverra, Cladosictis, Prothylacinus, Thylacynus, Borhyæna.

PERAMELOIDEA.

"PROPERAMELIDÆ" Bensley (hypothetical).

(Derived from primitive Didelphiidæ).

Arboreal to terrestrial.

Pes narrow, with beginnings of syndactyly; hallux, opposable but small, digit IV bigger than II, II = III.

Insectivorous.

Polyprotodont.

Molars tritubercular, bunodont.

PERAMELIDÆ.

(Derived from Properamelidæ).

Terrestrial, semifossorial, cursorial.

Size and form rabbit-like.

Tail non-prehensile, hairy.

Pes narrow, elongating, finally macropodiform, hallux reduced, finally to zero.

Pes syndactylous, digits II and III becoming vestigial, IV increasing.

Plantar pads in pes becoming reduced.

Digits in manus becoming reduced, either after the mesaxonic (*Perameles*) or paraxonic fashion (*Chœropus*).

Fossorial, ungues deeply cleft.

Gait cursorial, subplantigrade to extreme digitigrade.

Insectivorous-omnivorous (vegetarian).

Polyprotodont, I $\frac{4-5}{3}$.

Molars tri- to quadritubercular, bunodont to hypsodont, metacone (as in Artiodactyls) finally replacing hypocone (*Thylacomys*).

Peragale, Perameles, Chœropus.

NOTORYCTOIDEA.

"PRONOTORYCTIDS" hypothetical).

(Derived from Properamelidæ: Bensley, Dollo).

Terrestrial, fossorial.

Pes broad, with incipient syndactyly, hallux opposable.

Insectivorous.

Polyprotodont.

Molars tritubercular, paracone and metacone appressed.

Talonid of lower molars reduced (correlated with shortened skull).

NOTORYCTIDÆ.

(Derived from "Pronotoryctids").

Terrestrial, fossorial.

Pes very broad, with vestigial syndactyly.

Form *Chrysochloris*-like.

Insectivorous-vermivorous.

Polyprotodont I $\frac{4-3}{3}$, P $\frac{2}{3-2}$.

Upper molars somewhat resembling those of *Chrysochloris*: paracone and metacone fused into a single high piercing cusp, protocone (plus hypocone ?) low. Talonid of lower molars absent.

Notoryctes.

The question as to the *phylogenetic* validity of this series is raised by the scarcity of palæontological evidence and by the general fact that supposedly evolutionary series drawn from existing faunas have often proved erroneous. The following brief review of the more important fossil Polyprotodonts seems to lend further support to Dr. Bensley's conclusions.

Fossil Polyprotodontia.

In the Santa Cruz (Miocene) deposits of Patagonia are found certain minute Polyprotodonts (*Microbiotherium* Ameghino) which are comparable in size to some of the smaller South American opossums. In Sinclair's description (1901, pp. 408–415) of *Microbiotherium* he shows that although "placed by Ameghino in a separate family, the Microbiotheridæ, this genus possesses so many important characters in common with the Didelphidæ that the propriety of its reference to the latter family seems beyond question." The chief peculiarity of *Microbiotherium* is the elongation of the premaxillaries and the extreme posterior position of the canine. These features may indicate partly insectivorous habits. The dental formula is the same as in *Didelphis*. The upper molars are tritubercular, with rounded paracone and metacone and Sinclair observers that they resemble closely the molars of some of the subspecies of *Caluromys* (the "Philander" opossum). The external cingulum and metastyle spur is more reduced than in the living opossums and the molars may thus represent an early stage in the development of the bunodont omnivorous molar. The lower molars of one species retain the antero-external cingulum seen in *Didelphis*. The palatal vacuities are very large. The skeleton is of Didelphid type with certain Dasyurine peculiarities (Sinclair).

In the Oligocene of North America and Europe occurs another minute Polyprotodont genus *Peratherium* Aymard described by Cope (1884, p. 789). This also has the dental formula of *Didelphis* (at least in *D. fugax, fide* Cope). The upper molars are tritubercular with V-shaped para- and metacones, the metacone slightly enlarged, and there is a pronounced external cingulum. The protocone is well developed and pointed. The nasals spread widely posteriorly. *Peratherium* is also reported from the Upper Eocene of England and France. In *Peratherium* ("*Didelphys*") *aymardi* Filhol,[1] a small species in which the lower jaw is less than half as large as in *D. virginiana*, the lower premolars are less elongate and the space between the canine and m_1 is shorter than in *Didelphis* (*i. e.*, primitive characters). The coronoid is broadly triangular, the broad angle is very prominent in external view. The mental foramina are below p_1 and m_1, about as in *Didelphis*.

[1] Ann. Sc. Géol., tome 8, 1877, p. 251, fig. 387.

In the Upper Cretaceous of North America occur isolated molars and jaw fragments, apparently representing small species of Didelphoids, which have received the names *Didelphops* and *Pediomys* Marsh (figured in Osborn, 1907, p. 96). *Didelphops* is distinguished by the hypertrophy of the external elements of the crown, especially the parastyle (?) and metastyle (?). Certain specimens of the *Didelphops* molars are narrow transversely with a deep median indentation of the external cingulum and high crescentic protocone — all very primitive features. The palate is fenestrated (Wortman, 1901, p. 337). The angle of the jaw is sharply inflected.

The most primitive true Polyprotodont known is the genus *Proteodidelphys* Ameghino (*cf.* 1906, p. 288), known from a minute lower jaw from the "*Proteodidelphys* Beds" (upper part of the Chubut formation). This fossil is stated by Ameghino (1906, p. 508) to come from below the Notostylops beds, and from below the level on which carnivorous Dinosaurs were found. It may therefore be of Upper Cretaceous or of Basal Eocene age. It agrees with *Didelphis* in its dental formula but is distinguished by many very primitive characters and may represent a distinct family. As figured by Ameghino, the condyle is very low, near the level of the cheek teeth; the angle is incompletely inflected, apparently not much more than in *Amphitherium*. The two dental foramina are located as in *Didelphis*. The antemolar portion of the jaw is short, the chin heavy. The broad-topped incisors are of the cutting and "cupped," or posteriorly cingulate, type. The canine is straight and erect, with two fangs; the anterior premolars are short antero-posteriorly, but are bifanged; the ultimate premolar is more molariform than in *Didelphis*, having a prominent internal cingulum and a small paraconid and talonid. The molars have a short talonid with two cusps, a hypo- and an entoconid. Ameghino (1903, p. 161) notes certain resemblances to the Upper Jurassic *Paurodon*. While *Proteodidelphys* is much more advanced than *Paurodon*, yet in the totality of its characters it seems to carry the Polyprotodont type a step backward toward the generalized Jurassic Trituberculate type. The cupped incisors may be either primitive or secondary, but it is interesting to note that incisors, canines, premolars and molars are somewhat less sharply differentiated in *Proteodidelphys* than in later forms.

Thus the palæontological record indicates a considerable antiquity for the Didelphid type, but so far does not reveal any of the annectant forms leading to the higher families (except possibly the Cænolestidæ, p. 209).

No Tertiary Dasyuridæ are known but the smaller insectivorous forms make a rather close approach to the Didelphid type and the family is distinguished chiefly by the loss of certain primitive characters retained in the Didelphiidæ (*cf.* Bensley, 1903, pp. 90–99, 163–169).

The Tasmanian Wolf (*Thylacynus*) is represented in the Santa Cruz formation of Patagonia by a series of genera which were set apart as an order, the "Sparassodonta" by Ameghino but which have been proven by Sinclair (1904, pp. 333–408) to belong to the family Thylacinidæ. The family shows a remarkable series of resemblances in general proportions and dental characters to some of the Creodonts among Placentals.

In *Borhyæna*, the largest and most specialized genus, the incisors are reduced to $\frac{3}{3}$, the upper molars have long metastyle blades and reduced protocones. In the lower molars the metaconid is absent, the talonid is very small, and the large compressed proto- and paraconids form a compressed blade. The enamel departs from the normal Marsupial type with enamel tubules entering the dentine and resembles the Carnivore type (Tomes, 1906).

The zygomata arch widely and there is a high sagittal crest; the brain case is narrow, especially back of the orbits, and the face is very broad and heavy in top view. All these features are paralleled in the Mesonychid and Oxyclænid Creodonts (pp. 300–302). According to Ameghino and Lydekker (1900) *Borhyæna* differs conspicuously from other Marsupials in the replacement of the canine as well as of the ultimate premolar, while in the related genera *Prothylacynus* and *Amphiproviverra* the canine, the ultimate and the penultimate premolars are all replaced. According to Sinclair this may mean merely that these Miocene Polyprotodonts had not advanced so far as the modern forms in the suppression of the permanent, and retention of the milk, dentition.

Among the true Marsupial characters retained by *Borhyæna* are the following, recorded by Sinclair: the nasals spread posteriorly excluding the maxillaries from contact with the frontals, the angle of the jaw is sharply inflected, the atlantal intercentrum is not fused with the base of the neural arch, the transverse processes of the seventh as well as of the second to sixth cervicals are perforated by the vertebral artery, the ectocuneiform is displaced beneath the cuboid as in *Thylacynus*.

Amphiproviverra, the smallest and least specialized member of the family retains a large opposable hallux. The cranial foramina and skull structure are much as in *Dasyurus*. The peculiar family characters in the dentition, namely the absence of the metaconid, the reduced metacone and the vestigial external styloid cusps, are already established. The family Thylacinidæ is thus seen to be a specialized cursorial offshoot either of very primitive Dasyuridæ or more directly from the Didelphiidæ.

The Patagonian Thylacynes are further discussed below (pp. 302, 303).

Myrmecobius, the Peramelidæ, Notoryctes.

After a very careful examination of a large series of specimens Bensley concluded (1903, pp. 99–107) that *Myrmecobius* is more probably an aberrant Dasyurid rather than a direct descendant of the Jurassic Trituberculata, and that the high number of molars and their irregularly cuspidate character were a result of degenerative processes accompanying the adoption of ant-eating habits.

The systematic position of the Polyprotodont Peramelidæ has been a matter of some doubt. The pes being strongly syndactylous and like that of the Macropodidæ, the Peramelidæ have sometimes been placed with the Diprotodonts under the term "Syndactyla," in contrast with the remaining Polyprotodonts which are called "Diadactyla" and (earlier) "les Éleutherodactyles" (*cf.* Gervais, 1836). But Thomas (1895) observed that although *Cœnolestes* is evidently a Diprotodont, yet it is non-syndactylous; and on the other hand, among the Polyprotodonts the pes of the Didelphid *Marmosa pusilla* is incipiently syndactylous, while that of the allied *Peramys brevicaudata* is quite eleutherodactylous (Bensley, 1903). Hence, in the case of the Peramelidæ, Thomas concluded that the syndactyly was of less taxonomic and phylogenetic value than the polyprotodonty. On the other hand, in its mode of placentation *Perameles* is nearer to the Diprotodont *Phascolarctos* than to the typical Polyprotodonts (*cf.* Hill, 1898). With regard to these and several other characters the Peramelidæ are thus more or less intermediate between the two suborders and tend to support the theory that the Diprotodonts have been derived from very early Polyprotodonts.

The cheek teeth of the Peramelidæ are derivable much more readily from the Didelphid than from the Diprotodont type. The high crowned molars present a peculiar modification of the tritubercular type. In *Perameles obesula* the molars parallel those of the Insectivore *Myogale* (Gregory, in Osborn, 1907, p. 113). In *Thylacomys* the main cusps are rounded and the enlarged metacone is displaced inwards and occupies the position of a hypocone (Bensley, 1903). In their placental arrangements the Peramelidæ seem to have departed from the common type less than have any other Marsupials, since the allantoic placenta, though reduced in size, is still functional, whereas in *Dasyurus, Macropus,* etc., it is vestigial and replaced by the yolk-sack placenta (Hill). Quite possibly however the allantoic placenta of *Perameles* may be merely a progressive character in which the Peramelidæ parallel the Placentals (Bensley, 1903, p. 85). The pouch opens backward as in Polyprotodonts.

The Notoryctidæ or Marsupial Moles are another Polyprotodont family

about whose affinities some doubt has been expressed. Being very highly specialized for a mode of life like that of the Cape Golden Moles (Chrysochloridæ), *Notoryctes* parallels that family in so many ways that Cope (1892) was inclined to believe that real genetic affinity between the two groups was indicated. Even the peculiar narrow triangular form of the molars in *Chrysochloris* has its parallel in *Notoryctes* (Bensley, 1903, pp. 117–123). But it is shown below (p. 255) that *Chrysochloris* is a true Insectivore while *Notoryctes* is a true Marsupial in the proximal expansion of the nasals, in the possession of vestigial epipubic bones, of a pouch opening backward, and in many other characters (Stirling, 1891).

The pes of *Notoryctes* has the appearance of retaining the last vestiges of former syndactyly (Dollo, 1899; Bensley, 1903, p. 172, fig. 6 C.). It seems likely that the nearer affinity of *Notoryctes* is with the Australian Polyprotodonts, especially the Peramelidæ, (Dollo, Bensley) rather than with the Didelphiidæ.

III. The Cænolestoidea, or Paucituberculata. (Epanorthidæ, Abderitidæ, Garzoniidæ, Cænolestidæ, etc.)

Santa Cruz and recent Cœnolestoids.

From the Santa Cruz Formation (? Miocene) of Patagonia Ameghino has described, under many generic names, a group of small Diprotodont marsupials that is represented in the existing fauna of Bolivia and Ecuador by the very rare and important form, *Cœnolestes obscurus* Thomas (1895). This rat-like animal exhibits the Diprotodont dentition in an interesting and rather primitive stage (Fig. 15). The hypertrophy of the median pair of lower incisors, the reduction of the remaining incisors and canines, and the lateral and extended position of the upper and lower incisor series are all conditions which are closely paralleled in different lines of marsupial and placental insectivores; as remarked by Bensley, these characters indicate that the Cænolestidæ and all the higher Diprotodonts have been derived from small insectivorous forms. The first and second upper molars of *Cœnolestes* are subquadrate with four low rounded cusps, but the third molar is triangular and has the appearance of being tritubercular. In *Palæothentes* (*Epanorthus*) *intermedius* of the Santa Cruz Beds (Sinclair, 1901, pl. lxiii, Fig. 7) the first upper true molar is usually quadrate, while the second to fourth are triangular; in *P. minutus* even m^1 is roughly triangular and the remaining molars are clearly a bunodont, omnivorous modification of the tritubercular type; this in turn may have been derived

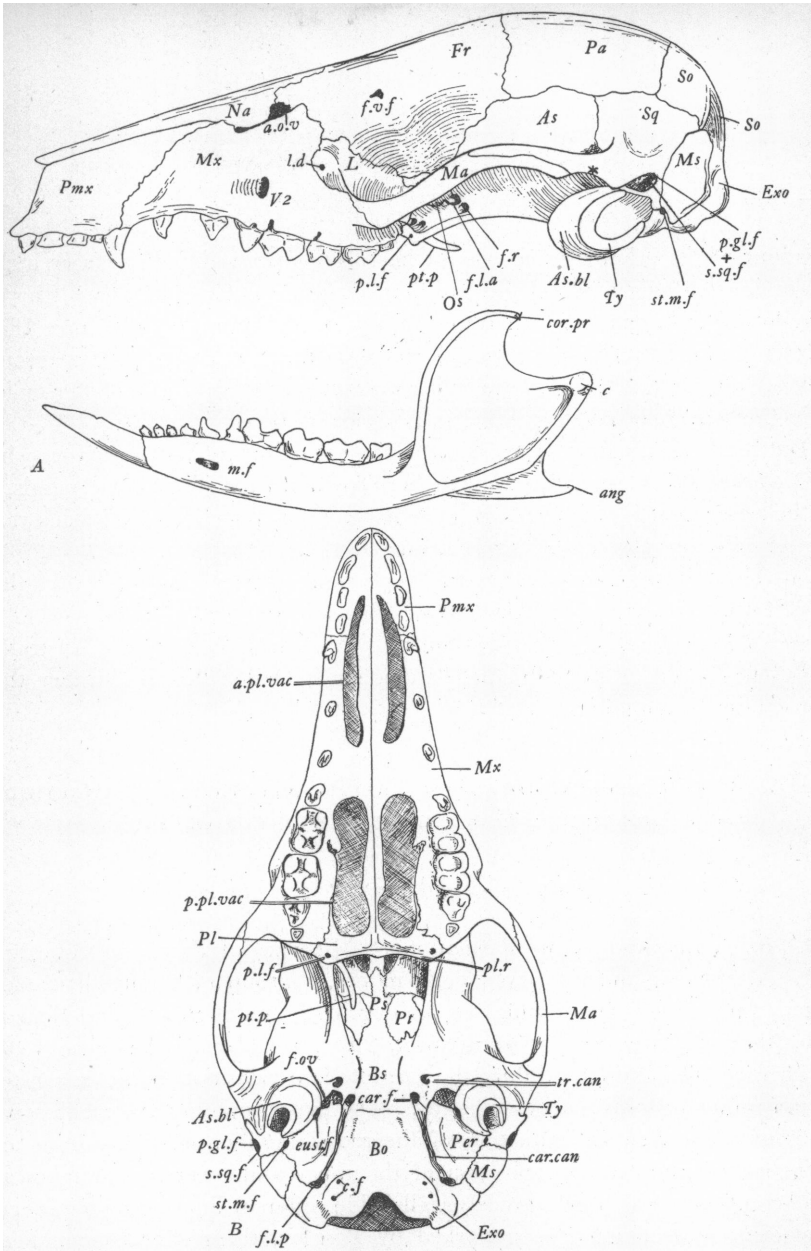


Fig. 15. Skull and lower jaw of *Cænolestes obscurus* Thomas. Am. Mus. Nat. Hist. No. 10,559. Enlarged slightly more than three diameters. After Miss Dederer.

A. Side view. *a. o. v*, Antorbital vacuity; *ang*, angle; *As*, alisphenoid; *As.bl*, alisphenoid bulla; *c*, condyle; *cor.pr*, coronoid process; *Exo*, exoccipital; *f.l.a*, sphenorbital foramen; *f. r*, foramen rotundum; *f.v.f*, venous foramen in frontal; *Fr*, frontal; *L*, lachrymal; *l.d*, lachrymal duct; *m.f*, mental foramen; *Ma*, malar; *Ms*, mastoid; *Mx*, maxilla; *Na*, nasal; *Os*, orbitosphenoid; *p.gl.f*, post-glenoid foramen; *p.l.f*, postero-lateral palatal foramen; *Pa*, parietal; *Pmx*, premaxilla; *pt. p*, pterygoid process of palatine; *s.sq.f*, subsquamosal foramen; *So*, supra-occipital; *Sq*, squamosal; *st.m.f*, stylomastoid foramen; *Ty*, tympanic; *V²*, infra-orbital foramen. The * indicates the glenoid facet.

B. Basal view. *As.bl*, alisphenoid bulla; *a.pl.vac*, anterior palatine vacuity; *Bo*, basi-occipital; *Bs*, basisphenoid; *c.f*, condylar foramina; *car.can*, carotid canal; *car.f*, carotid foramen; *eust.f*, Eustachian opening; *Exo*, exoccipital; *f. ov*, foramen ovale; *f.l.p*, foramen lacerum posterius; *Ma*, malar; *Ms*, mastoid; *Mx*, maxilla; *Per*, periotic (pars petrosa); *p.gl.f*, post-glenoid foramen; *Pl*, palatine; *p.l.f*, postero-lateral palatal foramen; *pl.r*, palatal ridge; *p.pl. vac*, posterior palatine vacuity; *Ps*, presphenoid; *Pt*, pterygoid; *pt.p*, pterygoid process of palatine; *Pmx*, premaxilla; *s.sq.f*, subsquamosal foramen; *st.m.f*, stylomastoid foramen; *tr.can*, transverse canal; *Ty*, tympanic.

from the type represented in *Microbiotherium tortor* (Sinclair, 1901, pl. lxii), which, as in the Cœnolestoids, has a large rounded metaconule in the position of a hypocone. The lower molars of the Cœnolestoids are a modification of the tuberculo-sectorial type, the trigonid and talonid being very clearly defined. In the presumably most primitive genus *Halmarhiphus* the normal cusps of the tuberculo-sectorial crown are very clearly defined (Sinclair, *l. c.*, p. 420). All the molars in *Cœnolestes* and *Halmarhiphus* have a prominent antero-external cingulum as in *Didelphis*. *Halmarhiphus* and *Cœnolestes* occasionally retain the antemolar dental formula of *Didelphis* (Sinclair).

The fourth upper premolar and first lower molar among the Cœnolestoids vary greatly in character. In the less specialized genera *Cœnolestes*, *Halmarhiphus*, and *Garzonia* they are simple in form; in the larger form *Abderites* the first lower molar has a high piercing sectorial blade, fluted anteriorly and analogous to that in the Plagiaulacidæ. Sinclair has adduced evidence (*l. c.*, pp. 417–418) to show that this sectorial molar has been derived from the tuberculo-sectorial type of *Halmarhiphus*.

Accordingly there is seen to be considerable though not positive evidence that the Cœnolestoids have been derived from the Didelphoid type, and this is strengthened by the similarities pointed out by Miss Dederer (1909) between the skull of Cœnolestes and those of the smaller Dasyuridæ. On the other hand, in certain characters of the dentition they are prototypal to the Diprotodont type and especially the smaller phalangers.

The pes, however, as stated above, is entirely eleutherodactylous and shows no trace of the syndactyly so characteristic of the Diprotodontia. This may be an adaptation to terrestrial and cursorial habits as in the smaller Dasyures; but the detailed characters of the skull show no striking Diprotodont characters and the writer is inclined to regard *Cœnolestes* and its allies as an independent suborder, an offshoot of primitive Polyprotodonts, which has paralleled the Diprotodonts in certain characters of the dentition.

The so called "Multituberculates" of Patagonia. Are they not highly modified Cœnolestoids?

The most serious theoretical difficulty in the derivation of the Cœnolestoid dentition from the tritubercular and tuberculo-sectorial type lies in the fact that, according to Ameghino's figures (1903, pp. 31–192), the forerunners of the Cœnolestoidea in the far older Notostylops Beds (? Basal Eocene), have molar teeth which are of the multituberculate rather than of the tuberculo-sectorial type. It may be well then to inquire whether the genera *Polydolops, Pliodolops,* etc., are related to the Cœnolestoids, or, as Ameghino believes, to the Multituberculates.

There can scarcely be much doubt that the lower jaw designated as *Parabderites bicrispatus* by Ameghino (*l. c.*, Fig. 74), from the Colpodon Beds, pertains to a Cænolestoid. Now the jaw and teeth of *Parabderites* are extremely like those of *Archæodolops* from the Notostylops Beds (Ameghino, *l. c.*, Fig. 75) and these offer a close comparison with the *Polydolops* teeth, which in turn lead readily and unmistakably into all the other "*-dolops*" genera of the Notostylops Beds. None of these genera show any clear evidence of derivation from tritubercular and tuberculo-sectorial types, but on the contrary certain of them (*Propolymastodon*, *Pliodolops*) approximate the Multituberculate type, as represented in *Ptilodus* and *Polymastodon*, in the following characters:

(1) The angle in *Propolymastodon* is strongly inflected. This, however, would be true of almost any Marsupial. (2) The second incisors (Ameghino) are much enlarged and subscalpriform, with the enamel confined to the anterior edge; they are followed by a diastema; the remaining incisors and canines having apparently disappeared. (3) The last premolar is a high pointed tooth, grooved anteriorly, larger than in *Polymastodon*, but smaller than in *Meniscoëssus*. (4) The molars are elongate-oval in crown view, presenting two rows of tubercles on the inner and outer edges respectively, and separated by a deep median longitudinal valley. (5) $P_{\overline{3}}$ in *Polydolops* is reduced to a small peg at the base of the enlarged $p_{\overline{4}}$, very much as in *Meniscoëssus*.

To offset these resemblances we have chiefly the following *differences*, which are all such as might separate more advanced from more primitive forms.

The North American Polymastodonts have advanced beyond *Propolymastodon*: (*a*) in the loss of m_3; (*b*) in the strictly rectangular outline of the base of the cusps in *Polymastodon* and in the crescentic shape of the cusps in *Meniscoëssus* (*c*) in the presence of a third external row of cusps in the upper molars, whereas in *Polydolops* there are only two rows. In *Pliodolops*, it is true, there are three rows but the cusps are very irregularly arranged and of polygonal outline at the base, whereas in the Multituberculates they are arranged in very straight antero-posterior rows and are sharply rectangular at the base.

There are, however, certain objections against taking these resemblances and differences at their face value, as Dr. Ameghino does, and concluding from them that the Polymastodontidæ are derived from the Promysopidæ (*Promysops* and *Propolymastodon*):

(1) Conclusions as to the genetic relations of orders, when based on dental remains alone, should always be accepted with caution (pp. 107, 108).

(2) Marsupials in general and especially South American families of

many orders seem to abound in examples of homoplastic and convergent resemblances to animals of other orders. The resemblances between *Propolymastodon* and *Polymastodon* are perhaps not much closer than the resemblances of *Borhyæna* to *Oxyæna*, of *Nesodon* and *Astrapotherium* to *Metamynodon* and *Cadurcotherium*, of *Thoatherium* to *Mesohippus*, of *Protypotherium* and *Archæohyrax* to *Hyrax*, etc.; and yet in each of the cases named the resemblances are very probably due either to convergence or to homoplasy. Among the Cænolestoid relatives of *Propolymastodon* one genus, *Orthodolops* (Ameghino, *l. c.*, p. 131) somewhat resembles *Sciurus* in both upper and lower teeth, while *Cephalomys*, a Patagonian rodent, has a deciduous p_4 suggesting that of the Multituberculate *Ptilodus* (Ameghino *l. c.*, p. 98); and yet *Orthodolops* can hardly be regarded as a relative of *Sciurus*, nor *Cephalomys* of *Ptilodus*.

(3) The extreme plasticity of the cheek teeth in the Multituberculata, Cænolestoidea and Diprotodontia is well illustrated in the great range in form of the ultimate upper premolars and first lower molar. In *Garzonia* and *Cœnolestes* m_1 is simple, in *Abderites* it is highly grooved, while in *Propolymastodon* it is intermediate. In *Bettongia* it is the posterior premolar which is highly grooved, while in the more advanced *Macropus* the same tooth is simple. In *Ptilodus* the anterior cheek tooth is highly grooved, in the related *Polymastodon* it is reduced and simple.

(4) Assuming that the early Tertiary *Propolymastodon* is related to the Cænolestoids and also structurally ancestral to the Upper Cretaceous and Basal Eocene Polymastodontidæ, how are we to account for the ancestry of the Upper Triassic Multituberculates *Tritylodon*, *Triglyphus* and *Microlestes*? Is the order Multituberculata diphyletic? If so, where is the break in the fairly close morphological sequence represented in the genera *Microlestes*, *Plagiaulax*, *Ptilodus*, *Meniscoëssus* and *Polymastodon*?

(5) The reduction of the lower lateral incisors, canines and anterior premolars in Cænolestoids does not favor the hypothesis that the tuberculosectorial dentition of the Polyprotodont *Microbiotherium* might be derived ultimately from the "multituberculate" type of *Propolymastodon*; because the Cænolestoid antemolar dentition, even if it had appeared early enough to give rise to that of the Triassic Multituberculates, could hardly have given rise to the antemolar dentition of *Amphitherium* and the Polyprotodonts.

In brief, the evidence for inferring that *Propolymastodon* and its allies are not Multituberculates but highly modified Cænolestoids is: (1) that they seem to be connected with the Cænolestoids by a series of structurally intermediate forms; (2) that *Propolymastodon* and its allies differ from the true Multituberculates in certain important particulars; (3) that in view of the great plasticity of the cheek teeth in the Multituberculates and Diproto-

donts the general resemblances between *Propolymastodon* and *Polymastodon* are possibly convergent; (4) that in fact the resemblances between South American and other groups are in many cases the result of convergence, and not indicative of close affinity; (5) that if *Polymastodon* is assumed to be a Multituberculate we are led into seemingly contradictory hypotheses of the derivation and relationships of Multituberculates, Cænolestoids and true Diprotodonts.

The most reasonable provisional conclusions from these very puzzling facts seem to be the following:

(1) *Propolymastodon* is a "pseudo-Multituberculate" offshoot of the Cænolestoids. The latter (p. 211), seem to be derived from the Polyprotodonts, or at least from Mesozoic forerunners of the same.

(2) *Propolymastodon* and the series of Cænolestoids serves to illustrate in what manner the true Multituberculate lower molar *might have been* derived from a tuberculo-sectorial lower molar and *vice versa*: but they do not by any means prove that either type *was* derived from the other (see p. 168).

(3) The known forerunners of the Cænolestoidea in the Notostylops Beds represented an early specialized offshoot and are not structurally ancestral to the later Cænolestoids.

At the same time the contrary hypothesis should not be forgotten, namely:

(1) That the Notostylops Beds genera *Polydolops, Propolymastodon,* etc., are survivors of a group of Triassic Diprotodonts which gave rise to the Multituberculates on the one hand and to the Cænolestoids and Australian Diprotodonts on the other.

(2) That the resemblances of both the Diprotodonts and Cænolestoids to the Polyprotodonts are due partly to convergence and partly to inheritance of primitive characters from a remote Triassic Marsupial stock.

A clearer knowledge of the genetic relations of these Patagonian forms is of the utmost importance in the study of Marsupial phylogeny. The wide difference between the theoretical relations of the Cænolestoids to other Marsupials and the imperfect indications of the geological record are revealed in the tables on pages 228, 229.

Wynyardia bassiana Spencer.

This species (Spencer, 1900), which is from the Eocene (or Oligocene) of Table Cape Tasmania, is another form that helps to bridge over the structural gap between the Polyprotodontia and the Diprotodontia. The skull (which unfortunately lacks the dentition) approaches that of the Dasyuridæ in many features of the cranium proper and zygoma, but the premaxillaries are stated to approximate in form to those of *Trichosurus*

and to indicate a fair-sized incisor dentition. The lower jaw shows a deep transverse groove on the alveolar border which may indicate the presence of an enlarged grooved premolar or molar (Spencer, *l. c.*, p. 784). A somewhat similar deep alveolar groove occurs below the enlarged grooved p_4 in the Patagonian Cænolestoid *Garzonia minima* (*cf.* Ameghino, 1903, p. 157, fig. 81). The glenoid region of the squamosal suggests the Diprotodont type and the same is true of certain features of the femur, tibia and pelvis. A closer comparison of *Wynyardia* with the Cænolestoids seems desirable.

IV. The Australian Diprotodonts.

The probable course of adaptive and morphological divergence in the dentition and foot-structure of the Diprotodontia have been very fully worked out by Bensley (1903); his chief results may be summarized and combined with the observations of others in the following table and in Fig. 14 (p. 202):

Adaptive Radiation of the Diprotodontia.

HYPSIPRYMNOIDEA (Phalangeroidea).
- Phalangeridæ.
  - Phalangerinæ Bensley. (True Phalangers.)
    - *Arboreal.*
      - Size, from mouse-like (*Dromicia*) to opossum-like (*Trichosurus*).
      - Tail prehensile, partly scaly (*Dromicia*), to bushy (*Trichosurus*).
      - Pes: hallux fully opposable.
      - Syndactyly in pes marked, digit IV large to very large (*Dactylopsila*).
      - Tarsus with plantar pads primitively separate and transversely striate (*Acrobates*).
      - Gait plantigrade, climbing; *Acrobates* and *Petaurus* with flying membranes.
    - *Insectivorous to omnivorous, to vegetarian.*
      - Diprotodont, I. $\frac{3}{1}$, C. $\frac{1}{0}$.
      - Molars quadrituberculate, cusps bunoid, no external styles or intermediate conules.
      - *Acrobates, Distæchurus, Dromicia, Gymnobelideus, Petaurus, Dactylopsila, Phalanger, Trichosurus.*
  - Tarsipedinæ Bensley.
    - *Arboreal.*
      - Size small.
      - Tail prehensile.
      - Pes rather long, with opposable hallux, hallux nailless.
      - Syndactyly in pes extreme, D. IV greatly enlarged.
    - *Mellivorous-insectivorous.*
      - Diprotodont.

Molars degenerate, greatly reduced, haplodont, variable in number.
Tongue elongate, protrusile.
Tarsipes.

PHASCOLARCTINÆ (Crescent-toothed Phalangers and Koala).
Arboreal.
Size and habits variable. *Pseudochirus* phalanger-like, *Petauroides*, large Flying Phalanger, *Phascolarctos* (Koala) Sloth-like.
Tip of tail naked (*Pseudochirus*, *Petauroides*) or tail absent (*Phascolarctos*).
Pes with fully opposable hallux.
Pes strongly syndactylous.
Herbivorous.
Diprotodont.
Molars with strongly crescentic cusps.

MACROPODIDÆ.
Terrestrial.
Size variable. The Rat Kangaroos are rabbit-like, the Giant Kangaroos (*Palorchestes*) of the Pleistocene, had a skull as big as that of a horse.
Tail non-prehensile, used as a secondary support.
Pes becoming elongate, hallux reduced (*Hypsiprymnodon*), usually wanting.
Pes strongly syndactylous, digits II and III becoming vestigial, digit IV greatly enlarged.
Plantar pads reduced (*Hypsiprymnodon*) to wanting (*Macropus*).
Gait hopping; smallest forms partly fossorial.
Herbivorous (food: roots, grass), grazing.
Diprotodont. Incisors sharp and cutting, lower incisors with scissors-like effect (*i. e.*, with slight transverse motion).
Molars bilophodont; brachyodont to hypsodont; posterior upper and lower premolars enlarged, grooved (Potoroinæ, Bettongiinæ) or reduced (Macropodinæ).

PHASCOLOMYIDÆ.
Terrestrial-fossorial.
Size beaver-like.
Tail reduced.
Pes broad, with large claws, hallux reduced.
Of syndactylous derivation but digits II and III secondarily enlarged.
Plantar pads degenerate.
Gait plantigrade, shuffling.
Herbivorous.
Diprotodont. I$\frac{1}{1}$, Incisors much enlarged, rodent-like, but motion of jaw vertical.
Molars strongly bilobate, hypsodont, curved.
Phascolomys, †*Phascolonus.*

DIPROTODONTIDÆ.
Terrestrial.
Size very large, about that of a small *Megatherium*, but with enormous head.
Pes with very large tarsus and reduced digits, turning inward, the outer elements much enlarged (Stirling and Zietz).
Digits II and III subequal and showing traces of syndactyly.
Herbivorous.
Diprotodont, with enlarged procumbent I $\frac{1}{1}$; i^2, i^3 small.
Molars completely bilophodont.
†*Nototherium*, †*Diprotodon.*

THYLACOLEONTIDÆ.
Terrestrial ?
Size that of a small lion.
Carnivorous ? (Broom, 1898).
Diprotodont, with enlarged compressed, piercing-cutting median incisors.
$P\frac{3}{3}$, greatly enlarged, shearing; molars much reduced, tubercular.
† *Thylacoleo.*

V. Summary of the Arguments in Favor of Retaining the Divisions "Polyprotodontia" and "Diprotodontia" rather than "Diadactyla" and "Syndactyla."

(1) The nearer affinities of the syndactylous Peramelidæ are apparently with the Polyprotodontia rather than with the Diprotodontia.

(2) The Cænolestidæ, perhaps more nearly allied to the Diprotodontia, are non-syndactylous (p. 211).

(3) One species of the Polyprotodont *Marmosa*, the most primitive living genus of Marsupials, shows a marked tendency toward syndactyly (Bensley, 1903, pl. vii, Fig. 7).

(4) "*Polyprotodontia*" and "*Diprotodontia*" may be defined from several characters but "Diadactyla" and "Syndactyla" from but one character.

VI. Primitive Mammalian Characters of the Marsupial Skull.

Comparison of the skulls of Marmosa *and* Didelphis.

Additional reasons for believing that the smaller Didelphidæ are structurally prototypal to the remaining Marsupials are found in the general

† Extinct.

characters of the skull. The following comparison of a smaller insectivorous Didelphid (*Marmosa simonsi*) with a larger more specialized, more carnivorous form (*Didelphis virginianus*) will serve to illustrate how many differences may result merely from an increase in size and a change from insectivorous to semi-carnivorous habits.

The skull of *Marmosa* (Fig. 16) agrees with those of the more primitive Placental Insectivora (*e. g., Microgale, Ictops*) in its minute size, broadly triangular contour as seen in top view, rather short face, pointed muzzle, relatively large rounded brain case without sagittal or occipital crests, incisors row anteroposterior rather than transverse, canines small, premolars pointed, upper molars sharp-cusped, triangular, and lower molars tuberculosectorial.

It is reasonably certain that these characters, especially the relatively large rounded brain case, are directly dependent upon minute size and insectivorous habits. In these features *Marmosa* contrasts strongly with *Didelphis*, the skull of which in its carnivorous adaptations, resembles that of the Creodonts. In *Marmosa* both the face and mid-cranial region are short, in *Didelphis* they are both elongate. In *Marmosa* the glenoid facets of the squamosals on either side appear relatively further forward; in *Didelphis*, by the elongation of the parts anterior to them, they are left near the back of the skull, while the basisphenoid for similar reasons appears very short. In *Marmosa* the lachrymal is proportionately short, the internal proximal processes of the nasals are more pronounced and the visible portion of the proximal end of the nasals is not so wide. In correlation with the shorter mid-cranial region the constriction back of the orbits is much less pronounced (than in *Didelphis*), and the orbits also are less removed from the temporal fossæ. In the occiput, in consequence of the feeble development of the crests the mastoid exposure is relatively broader than in *Didelphis* and appears more in the side view. The paroccipital processes, as in the skulls of small Insectivores, are barely indicated.

These adaptive divergences do not conceal an agreement in all the fundamental marsupial and primitive mammalian characters of the external aspect of the skull, as follows: The basisphenoid in both genera is grooved and pierced by the *entocarotid artery* (see below, p. 223), while immediately in front of this lies the "*transverse canal*" (p. 223). The basioccipital is grooved or pierced on its external border, next to the petrosal, by the *posterior carotid foramen* (p. 223). The optic foramen is not separated from the *sphenorbital* (for. lac. ant.) *i. e.*, the nerve does not pierce the orbitosphenoid; the *foramen rotundum* forms a tubular opening immediately behind the sphenorbital. The *sphenopalatine* (internal orbital) foramen, the *stylomastoid, postmastoid* and other foramina described below (p. 224) all exhibit

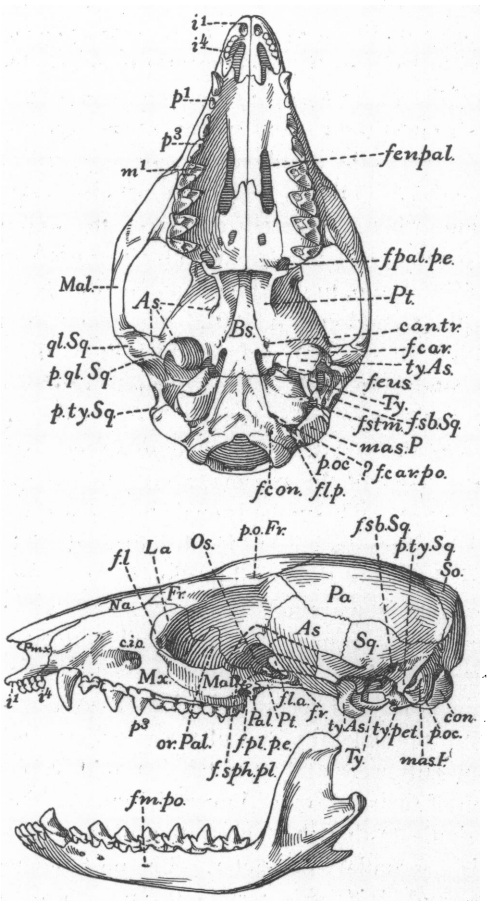


Fig. 16. Skull of *Marmosa simonsi*. *A*, side view, with lower jaw. B, palatal view. U. S. Nat. Mus. No. 121155. × $\frac{2}{1}$.

f.pl.a, anterior palatine foramina.
fen. pal, palatal vacuities.
f.pal.p.e., postero-external palatine foramen.
f.l.a., foramen lacerum anterius (sphenorbital fissure).
f.r., foramen rotundum.
can.tr., transverse canal.
f.car., entocarotid foramen.
f.eus., Eustachian opening.
ty. As., bullate portion (tympanic process) of alisphenoid.
gl. As., glenoid portion of alisphenoid.
f. m. po., posterior mental foramen.
f.p.z. post zygomatic foramen.
?f. car. post., ?posterior carotid foramen.
f. st. m., stylomastoid foramen.
f. p. m., postmastoid foramen.
f.c., condylar foramina.

Other abbreviations as in preceding figures.

fundamental similarities in *Marmosa* and *Didelphis*. These two types further agree in the dental formula, general form and arrangement of the teeth and in the inflected angle of the mandible. The *orbitosphenoid* is very small and lies above and in front of the sphenorbital fissures which are confluent in the middle line; the *vertical plate of the palatine* is large, the *alisphenoid* is large and extends on to the glenoid surface of the squamosal. Internally to the post-glenoid process the alisphenoid sends back an inflated expansion the "*alisphenoid bulla.*" This is seen in a primitive stage in the genera under consideration, where it merely embraces the anterior part of the membranous tympanum. The *malar* in both genera is very large and has a prominent postorbital apophysis which may possibly be a remnant of the postorbital bar in the Cynodonts (p. 120). The malar extends back to the glenoid fossa and has an articular surface which limits the lateral vibration of the mandibular condyle (p. 119). The zygomatic process of the *squamosal* is relatively short and is received anteriorly between the long inferior, and short superior, fork of the malar. The squamosal sends back a ridge which runs from the dorsal edge of the zygoma, above the external auditory arch to the lambdoidal crest. This ridge is analogous to a similar one in *Cynognathus* (p. 121). In *Marmosa* it is but feebly indicated. The orbital portion of the *lachrymals* is large but the facial portion in *Marmosa* is very limited; the lachrymal foramen is marginal. The *pterygoids* are reduced to thin scales of bone and in this respect *Marmosa* and *Didelphis* both appear to have become more specialized than *Thylacynus* (Fig. 1, A). The *palatal fenestræ* are prominent in both genera. Parker (1886, p. 270) found that in the developing skull the palatal plates of the maxillary and palatine bones in Marsupials generally were at first not fenestrated but became so by the gradual absorption of their substance in certain areas. This conspires with other evidence to indicate that the fenestration of the palate in Marsupials and Insectivores is a secondary character. The posterior part of the palate in both *Marmosa* and *Didelphis* terminates in a prominent *transverse palatal ridge*, which is pierced at its opposite external corners by a prominent foramen, which is possibly for the posterior palatine nerve (a branch of V_2).

The internal view of the skull of *Didelphis* also reveals many primitive mammalian characters. The *cerebral chamber* is longer than high, the *olfactory fossa* is large and long; the long axis of the brain case makes only a very gentle angle with the nasal cavity. Beginning at the posterior end of the skull we observe the following structures: The paired *condylar foramen*, piercing the exoccipital; the *foramen lacerum posterius* (f. jugulare), lying between the basioccipital and the periotic; the *internal auditory meatus* (for the facial and auditory nerves) piercing the petrous; and above it the circular *floccular fossa*. Running through the occipital wall of the supra-

occipital and basioccipital are sections of the *transverse venous sinus*. In front of the periotic lies the internal opening of the *foramen ovale* (V_3). In the floor of the basisphenoid we see the *pituitary fossa*, without anterior or posterior clinoid processes, and immediately external to it is the *carotid foramen*. External to this, in turn, lies a longitudinal groove for the Gasserian ganglion (of the trigeminus) terminating anteriorly in the *foramen rotundum* (V_2), which tunnels through the alisphenoid. Anteriorly to the foramen rotundum and pituitary fossa is the *sphenorbital fissure* (for. lac. ant., for nerves II, III, IV, V_1, VI); above and in front of this is the small mesially placed *orbitosphenoid*, which in *Didelphis* is hollow and invaded anteriorly by the posterior ethmoturbinals. Between the antero-lateral border of the orbitosphenoid, the frontal, and the cribriform plate is the *ethmoid foramen* (for the internal nasal nerve, a branch of V_1).

A noteworthy feature of the internal view of the skull of *Didelphis* is that on account of the imbricating relations of the edges of several bones the external boundaries are widely removed from the internal boundaries. Thus the parietals broadly overlap the frontals exteriorly so as to confine the latter to the olfactory region; but interiorly the *frontals* extend well backward so as to cover the anterior and antero-superior portions of the cerebrum. The *alisphenoid* which has a very extensive external distribution is limited internally to a moderate anteroposterior wing. The *squamosals*, which are so large in the external view of the Marsupial skull, in *Didelphis* are almost excluded from the brain cavity, and represented only by a narrow strip in front of the petrosal. The *alisphenoids* are fused with the basisphenoids even in young skulls.

As regards the ethmoturbinal complex *Didelphis* is seen to have a large well-ossified *mesethmoid*, which is continuous posteriorly with the median wall of the orbitosphenoid and ends anteriorly in a subvertical edge. The mesethmoid is supported inferiorly in the dorsal channel of the slender quill-like *vomer*. The ethmoturbinal scrolls are limited to the middle and posterior portions of the nasal cavity, the anterior part of which is occupied by the well developed *maxilloturbinals*.

Primitive Mammalian Characters of the Marsupial chondrocranium.

An analysis of Parker's researches (1886) on the development of the skull in Marsupials, Edentates and Insectivores, yields the following list of characters, which indicates that the Marsupial chondrocranium, in its underlying features, represents a lower plane of mammalian evolution than does that of primitive Placentals.

(1) Boat-shaped chondrocranium with orbitosphenoid wing flush with

the alisphenoid (Parker, *l. c.*, p. 271). In the Placentals, in consequence of the early development of the large lateral masses of the cerebrum, the wall of the chondrocranium is "ruptured" (*l. c.*, p. 8) and the ala temporalis (alisphenoid) appears as a projecting wing of cartilage.

(2) Cartilaginous nostrils subterminal and giving off tongue-shaped cartilages which coöperate with the "antero-lateral vomers" (prevomers) to protect Jacobson's organs.

(3) Whole nasal labyrinth small especially in the young, "not more than half as large as in an average Placental Mammal" (*l. c.*, p. 271); but nasal labyrinth much more complex than in any reptile (*l. c.*, p. 8). Cribriform plates suberect, flattish (*l. c.*, p. 272).

(4) Meatus externus protected by a more or less segmented tube of cartilage, which is continuous with the concha auris (*l. c.*, p. 270). (Indicates that the cartilages of the ear conch are neomorphs in the mammals, and not necessarily derived from the hyoid arch (*cf.* p. 125)).

(5) Presphenoid (*l. c.*, p. 271) developing as an independent cartilage. (In Placentals it generally appears as a ventral union of the orbitosphenoids.)

(6) Optic nerve (*l. c.*) not piercing the cartilaginous orbitosphenoid, but, from its first appearance, issuing through the sphenoidal fissure, as in reptiles. (Contrast most Placentals.)

(7) Internal carotid piercing basisphenoid (*cf.* Monotremata; p. 150). (In Placentals it generally enters through the foramen lacerum medium, pp. 430, 431).

(8) Clinoid processes and concavity for the pituitary body but little developed (*cf. Solenodon*, p. 253).

The arrangement of the cranial foramina in Marsupials.

Strong evidence for the common origin of the Polyprotodont and Diprotodont divisions of the Marsupialia lies not only in the structure of the feet (pp. 201, 217) but more especially in the common plan of arrangement of the cranial foramina and of the parts relating to audition, in such adaptively diverse forms as *Marmosa, Didelphis, Phascologale, Dasyurus, Thylacynus, Perameles,* of the Polyprotodontia; *Cœnolestes, Phalangista, Phascolarctos, Hypsiprymnus, Macropus* and *Phascolomys* of the Diprotodontia. Representatives of all these genera have been examined by the writer, with the coöperation of several fellow students especially Dr. C. S. Mead.

The majority of the foramina mentioned above as occurring in the Didelphids are equally characteristic of other Marsupials. The *optic foramen* (as is well known) is not independent but is confluent with the *foramen lacerum anterius* (sphenorbitale), which also transmits nerves

III, IV, VI and the frontal branch of the trigeminus (V_1). The opposite anterior lacerate foramina are confluent so that a bristle may be passed through the skull at this point.

The *foramen rotundum* (for the maxillary branch of the trigeminus, V_2) is generally a very prominent tubular opening directed forward at some little distance behind the foramen lacerum anterius. In the interior of the skull it is continuous with a longitudinal groove or fossa for the Gasserian ganglion (V_{1-3}), on either side of the sella turcica and external to the carotid foramen.

Transverse canal.— There is frequently a prominent foramen or canal which tunnels the floor of the basisphenoid transversely, and may be designated as the "*transverse canal.*" In the opossum, according to Wortman, (1902, p. 440) its office is the "transmission of a vein, a branch of which gains access to the cranial cavity through a small foramen in the floor of the pituitary fossa." This canal strongly suggests the "canalis transversus" of Simplicidentate rodents, which likewise, according to Tullberg, transmits a vein (Weber, 1904, p. 474). To judge from Sinclair's description (1901) of the skull of *Borhyæna,* the transverse canal appears to be absent in some at least of the fossil carnivorous Marsupials of Patagonia, but it is present in the Diprotodonts examined as well as in *Didelphis.*

No true alisphenoid canal perforates the alisphenoid bone, but in the opossum a slight groove just in front of the transverse canal may mark the forward course of the ectocaroted, or maxillary branch of the carotid artery.

Posterior to the transverse canal and occupying approximately the position of the foramen ovale in the dog lies the *entocarotid canal* which perforates the basisphenoid, entering forwards. This has long been known as a constant feature of the Marsupial skull; but Wíncza (1898, quoted by van Kampen, 1905, p. 383) reports that in *Acrobates pygmæus* the carotid enters the skull in the same manner as in most Placentals, *i. e.*, through the foramen lacerum medium.

Lying between the petrosal and the basioccipital is a foramen which may provisionally be termed the *posterior carotid foramen,* which probably transmits a posterior branch of the entocarotid. It is present in all the Polyprotodonts examined, but was not recognized in the Diprotodonts.

Perforating the posterior part of the alisphenoid near the alisphenoid bulla and looking either forward or outward and downward toward the inner side of the mandible is the *foramen ovale,* for the mandibular branch of the trigeminus (V_3).

The *Eustachian canal* lies between the tympanic expansion of the alisphenoid and the petrosal. It is frequently lodged in a groove on the internal side of the tympanic portion of the alisphenoid, issuing from the tympanic cavity, and running forward and inward.

Postglenoid. This venous foramen, which is only exceptionally absent in mammals occurs also in the Marsupials.

Postzygomatic. This small venous foramen, first described by Cope (1880), is associated with the postglenoid, and like it contributes to the system which comprises the transverse occipital sinus, the mastoid, postparietal, the jugular (for. lac. post.) and other foramina. It opens below or within the lip of the postglenoid foramen and runs forward. As observed by Cope (1880, p. 454) it is characteristic of the Marsupialia and distinguishes the carnivorous Marsupials from their Placental analogues.

Subsquamosal (Cope). This is another tributary to the transverse canal. In the Polyprotodonts it is located in the external portion of the roof of the auricular meatus, behind and above the postglenoid + post zygomatic opening, and below the squamosal ridge which connects the zygoma with the lambdoidal crest. In the Diprotodonts through the failure of the postzygomatic ridge the subsquamosal sometimes becomes identical with the post squamosal (Cope).

Postsquamosal (Cope). This is another part of the venous system of the transverse sinus. It is a lateral foramen in the postero-superior part of the squamosal in front of the lambdoidal crest and above and behind the subsquamosal foramen. It is often reduced or absent.

Mastoid foramen. On the occipital surface of the mastoid bone at or near its supero-external corner. A part of the same venous system. Frequently, but not always present in Marsupials and primitive Placentals.

Jugular foramen ("For. lac. post.," "for. vagi"). The final member of the venous system under consideration. Also transmits nerves IX, X, XI. In *Didelphis* and *Thylacynus* it lies immediately postero-externally to the posterior carotid foramen, posterior to the petrosal and internal to the base of the paroccipital process (Fig. 1, A, *f. l. p.*).

Stylomastoid foramen and canal. At the postero-external angle of the petrosal is the stylomastoid foramen, which transmits the facial or seventh nerve, after its passage through the petrosal (p. 430). The stylomastoid foramen is constant in mammals, but by the growth of the surrounding parts it is often covered up or difficult to locate. In *Didelphis* it is exposed in front of the internal base of the mastoid. In *Thylacynus* it lies at the bottom of a canal formed by the tympanic, the mastoid and the paroccipital. In *Diprotodonts* the canal appears to issue on the postero-external border of the skull between the tympanic and the mastoid. The stylohyoid bone is attached to the petrosal in or near the stylomastoid canal, often posterointernally to it.

Condylar foramen. Located immediately in front of the occipital condyle and transmitting the twelfth or hypoglossal nerve.

Accessory condylar foramen. An accessory or second condylar foramen, in front of the main one, seems to be characteristic of both Polyprotodonts and Diprotodonts. Its supposed presence in Creodonts is mentioned below (p. 302).

VII. Taxonomic History of the Divisions Prototheria, Metatheria and Eutheria.[1]

1816. De Blainville groups the Monotremes and Marsupials as "Didelphes" in contrast with the "Monodelphes" or Placentals (p. 77).

1834. De Blainville takes the step he had suggested in 1816 and raises the "Ornithodelphia" (Monotremes) to a rank coördinate with that of "Didelphia" and "Monodelphia." (p. 82).

1837. Bonaparte uses these two main divisions (see p. 84) under the terms "Ovovivipara" (Marsupials and Monotremes) and "Placentalia."

1866. Hæckel, recognizing that the Marsupials and Placentals have been derived from a common stem (later called "Prodidelphia") in his phylogenetic diagrams correctly represents the relations of the three groups.

1872. Gill uses the term "Eutheria" to include both the Marsupials and Placentals (pp. 92, 230).

1880. Huxley restricts the term "Eutheria" to the ancestors of the Placentals and invents the term Metatheria for the remote ancestors of Marsupials plus Placentals. The terms "Prototheria," "Metatheria" and "Eutheria" were used by Huxley chiefly as denoting successive stages of development.

VIII. Summary of the Genetic Relations of the Marsupials.

It is generally believed that the earliest mammals had a shoulder girdle of the Monotreme type and were probably oviparous, and reasons have been adduced above (p. 161) for inferring that they were also semifossorial in habits. From this early Prototherian type the Monotremes have departed very widely in many of their skull-characters (p. 156). The primitive Marsupial skull on the whole approaches the Cynodont skull much more nearly than does that of the Monotremes, especially in the general conformation of the lateral aspect, in certain characters of the malar and squamosal (p. 207), in the proximal spreading of the nasals (p. 120), in the long sagittal crest, narrow brain case and relations of the pterygoids (p. 120). But in

[1] The references to this historical summary appear under Part I (see list of references).

the early mammals the skull had already advanced far beyond that of the Cynodonts in the backward prolongation of the hard palate, in the reduction of the quadrate and articulare and *possibly* in the transformation of these bones into the incus and malleus respectively (p. 140).

After the branching off of the Monotremes the Marsupio-Placental remnant still retained certain reptilian features in the skull, but owing to the assumption of semi-arboreal habits it lost the Monotreme characters of the shoulder girdle, clear traces of which (Broom) are still retained in embryo Diprotodonts (p. 157). Improved climbing powers resulted from the atrophy of the episternum and procoracoid, the reduction of the coracoid, the pulling outward of the glenoid away from the middle line and the development of the prespinous fossæ and its muscles.

At this point the divergence into Marsupials and Placentals may have begun. The forerunners of the Marsupials, we may imagine, went on improving the arboreal characters, finally acquiring the rudiments of syndactyly in the pes, which, from its occurrence (Bensley) in *Marmosa pusilla* (p. 217), may be suspected to be a primary character in the Polyprotodontia as well as in the Diprotodontia (p. 215). The Pro-Placentals however avoided this particular feature of arboreal specialization, as well as the lengthening of the fourth digit of the pes, merely retaining a partly divergent pollex and hallux. The change from oviparity to viviparity was meanwhile proceeding in the manner outlined above (p. 148). The pro-Marsupials laid stress on the extra-uterine, or marsupial adaptations, so that the young, through the retention and emphasis of certain embryonic features, such as the intranarial epiglottis, acquired larval characters. Peculiar relations between the maternal teat and the mouth of the offspring, joined to the desirability of precocious independence in gaining food, may have conditioned the early specialization of the last upper and lower milk molar and the suppression (except in certain Sparassodonts, p. 207) of the anterior milk molars (Leche, quoted by Weber, 1904, p. 341). The Pro Placentals on the contrary, laying stress on the intra-uterine adaptations, as well as on the improvement of lactation, lengthened the period during which the young are dependent on the mother, with the result that a more leisurely and full development of both milk and permanent dentitions followed.

The Marsupials also acquired certain peculiar specializations which were avoided both by Monotremes and by Placentals. The allantois, which, as in *Perameles*, may have begun to unite with the uterine wall was crowded out by the yolk sack, which also assumed this function.

The hard palate, which possibly was prolonged backward at a very early period began secondarily to acquire fenestræ, or to enlarge its fenestræ, through the absorption of tissue (p. 220). The pterygoid fossa of the mandible

became greatly pronounced: possibly in proportion as the ancient pterygoid muscles shifted their attachment from the dwindling pterygoids to the uprising pterygoid wings of the alisphenoid. The "alisphenoid bulla," at first a mere depression in the hinder border of the glenoid region, for the reception of the anterior wall of the membranous tympanic cavity, grew backward, finally embracing the tympanic annulus and bridging over the petrosal to unite with the paroccipital process and mastoid.

Within the order Marsupialia the genetic relations of the suborders Multituberculata, Diprotodontia, Cænolestoidea Polyprotodontia appear to be somewhat as follows: The Prototherian ancestors of the Monotreme-Marsupial-Placental stem (p. 229) probably had incisors canines, premolars and molars. Perhaps as far back as the Upper Triassic this type, by dental reduction gave rise to the Multituberculata which paralleled the true Diprotodonts and retained certain primitive features in common with them but were nevertheless not ancestral to them (p. 170).

The remaining stock, preserving their heritage of four kinds of teeth, gave rise at different times to the Diprotodonts, Cænolestoids and existing Polyprotodonts.

There can be little doubt that these three suborders are intimately related to each other, as shown by the fundamental agreement in the foramina (p. 222), in the general architecture of the skull (p. 221) and in the foot-structure (p. 201). This inference is supported by the existence of several groups (Peramelidæ (p. 208), Cænolestoids (p. 209), *Wynyardia* (p. 214)) which combine structural features otherwise peculiar either to the Polyprotodontia or to the Diprotodontia. Moreover, with regard to every detail of the dentition, cranial foramina, alisphenoid bulla, lower jaw, etc. all well-founded analogies sustain the inference that, morphologically, the Kangaroos have been derived from primitive Didelphids and not *vice-versa*.

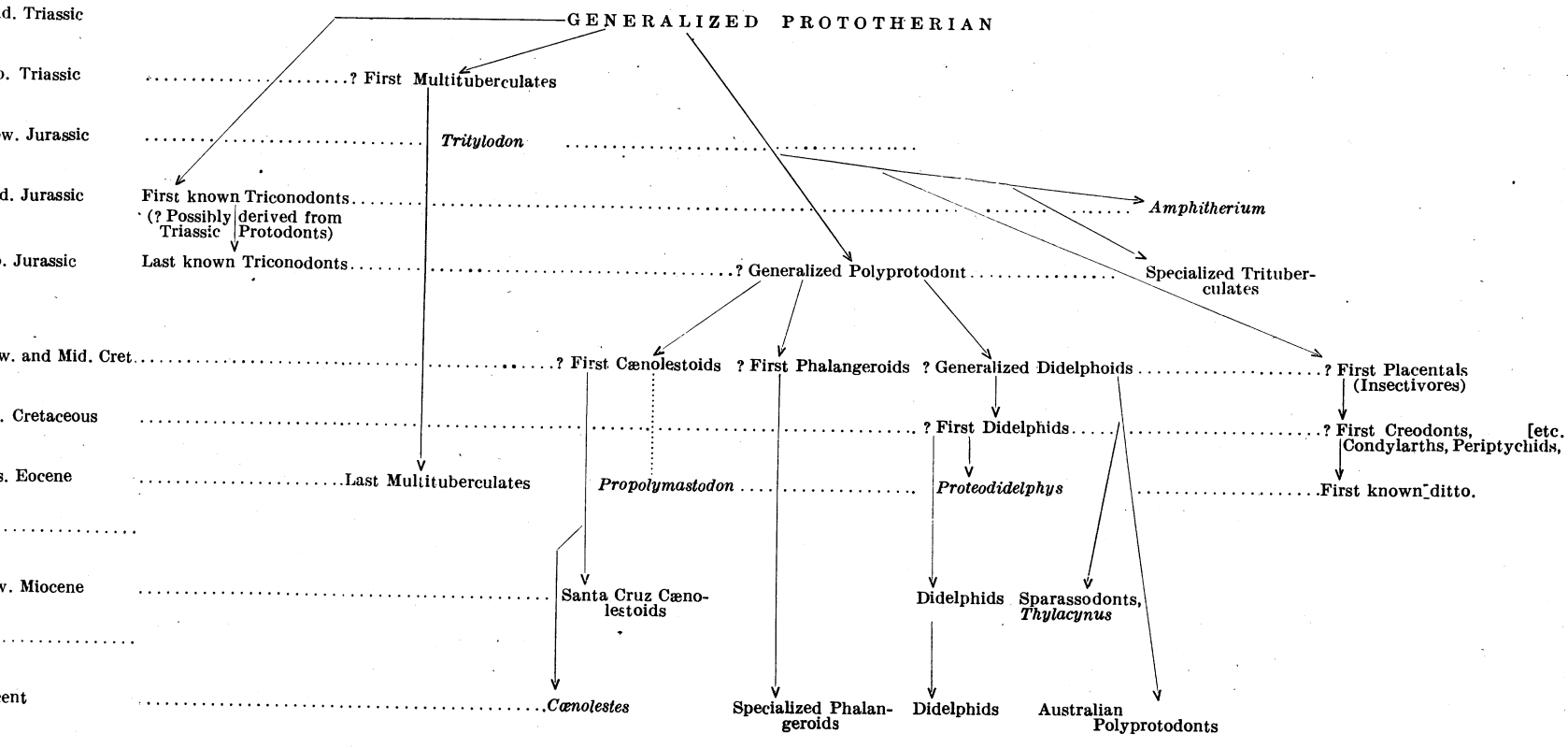
On the other hand in several features the Diprotodonts appear to be more primitive than the Didelphids. It is only among the Diprotodontia, for example, that we find a structure which appears to be homologous, and is certainly structurally identical with, the pecten of the eye in *Apteryx* (Johnson, 1901).

Again the malleus of Diprotodonts approaches the Monotreme type, in the length and breadth of the anterior (Folian) process and in the union of the latter with the tympanic (Dobson, 1879); while the stapes is often columelliform; and there is some evidence to show that these are very primitive mammalian characters (p. 151); whereas in the Polyprotodont *Didelphis* the stapes and malleus approximate to the Placental type (Doran, 1879, pl. lxiv, fig. 15). The Diprotodonts, moreover, exhibit the tendency for the persistence of both azygous veins to a greater degree than do the Polyprotodonts (Beddard, 1907, p. 219).

IX. Known Geological Succession of the Marsupials and Placentals.

	Triconodonts	Multituberculates	Cœnolestoids	Phalangeroids	Polyprotodonts	Trituberculates	Placentals
Mid. Triassic							
Up. Triassic		*Triglyphus* *Microlestes*					
Low. Jurassic	.....	*Tritylodon*					
Mid. Jurassic (Stonesfield Slate)	*Amphilestes* *Phascolotherium*	*Stereognathus*	.....	.....	.....	*Amphitherium* *Amphitylus*	
Up. Jurassic (Purbeck, Morrison)	*Triconodon* *Priacodon* *Spalacotherium*	*Bolodon*, *Plagiaulax* *Ctenacodon*	.....	.....	.....	*Peralestes, Kurtodon* *Dryolestes, Amblotherium* *Dicrocynodon*	
Low. & Mid. Cret.	.....	.....	.....	.....	.....	.....	.....
Up. Cretaceous	.....	*Meniscoëssus* *Polymastodon*	.....	.....	*Didelphops, Pediomys*	.....	Laramie Insectivores (?)
Bas. Eocene	.....	*Neoplagiaulax* *Ptilodus* (*Chirox*)	*Propolymastodon* *Polydolops*	.....	*Proteodidelphys*	.....	Insectivores, Creodonts, Peripty-chids, Condylarths, etc.
.....							
Low. Miocene (Santa Cruz)	.....	.....	*Abderites* *Epanorthus* *Garzonia*	.....	*Microbiotherium*, "Sparassodonts"		
.....							
Recent	.....	.....	*Cœnolestes*	Australian Diprotodonts	Didelphids and Australian Polyprotodonts		

X. Hypothetical Succession of the Marsupials and Placentals.



From the foregoing it appears probable that the Diprotodontia have retained certain primitive mammalian characters, which have been lost in the Polyprotodontia, while on the other hand the Didelphids have remained primitive in the dentition, skull, and foot-structure. The problem of the genetic relations of the Diprotodontia and the Polyprotodontia is complicated to a certain extent by the existence of the Cænolestoids; but the opinion may be expressed that probably the resemblances of certain Cænolestoids to the Multituberculates (p. 214) is an instance of convergence between related suborders, and that the same is true, but to a less extent, of the resemblances of other Cænolestoids to the Diprotodont phalangers.

The foregoing views of the relations of the suborders of Marsupials to each other and to the stem of the Placentals are expressed in the accompanying tables (p. 229).

The consideration of the more detailed evidence of the common origin of the Marsupials and Placentals may be deferred until after the review of the Insectivores and Creodonts (p. 307).

XI. Diagnoses of the divisions Prototheria, Didelphia, Monodelphia.

SUBCLASS PROTOTHERIA. Reptilian angular bone absent (at least *in propria forma*). Oviparous; no secondary teats. Shoulder girdle and humerus much as in the mammal-like reptiles: prespinous fossa of the scapula absent or rudimentary, lower part of the anterior border of the scapula corresponding to the spina scapulæ and acromion of higher mammals; large coracoids and procoracoids overlapping in the mid-ventral line; large T-shaped interclavicle; glenoid facet for humerus very near the sternum. Habits primarily semifossorial. Epipubic bones present. No corpus callosum.

SUBCLASS THERIA [1] Parker and Haswell.

(= Eutheria Gill, 1872, non Huxley.)

Viviparous, with teats; coracoid and procoracoid reduced, not touching sternum; interclavicle absent or vestigial; glenoid facet for humerus widely separated from sternum; prespinous fossa present (much reduced in Cetacea). Habits primarily semi-arboreal.

1. Infraclass Didelphia de Blainville.

Epipubic bones; no corpus callosum (Elliot Smith, 1894); angle inflected (save in *Tarsipes*); typically with only the posterior milk molar replaced by a successor; $p\frac{2}{2}$ absent; molars typically $\frac{4}{4}$.

[1] It is unfortunate that the term "Eutheria" has come to stand for two very distinct concepts: first, for Marsupialia + Placentalia (Gill, Osborn, Beddard); secondly, for the Placentalia alone (Huxley). Although Gill's usage of the term has the priority (p. 92), it will probably be impossible at this late date to eradicate Huxley's usage of the term, which is very widely disseminated through the literature. Rather than contribute to this regrettable confusion, and recognizing that the law of priority has not generally been applied rigidly in the case of larger taxonomic groups, the writer has employed the term "Theria," as used by Parker and Haswell, as the equivalent of "Eutheria" Gill.

2. Infraclass Monodelphia de Blainville (Placentalia Bonaparte, Eutheria Huxley).
   No epipubic bones; a corpus callosum; angle typically not inflected; all the antemolar teeth typically represented by both milk and permanent teeth; $p\frac{2}{2}$ typically present; molars typically $\frac{3}{3}$.

CHAPTER V. GENETIC RELATIONS OF THE INSECTIVORA AND TILLODONTIA.

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Outline History of the Classification.

1693. Ray groups the hedgehog, armadillo, mole, shrew, tamandua, bat and sloth in the "quadrupeda pede multifido vivipara, rostro productiore anomala: ac primo dentata."

1758. Linnæus places *Erinaceus, Talpa* and *Sorex,* together with *Sus, Dasypus* and *Didelphis* in the Order "Bestiæ."

1779. Blumenbach puts the genera *Sorex, Talpa, Didephis* among the "Glires Murina."

1780. Storr puts *Vespertilio, Sorex, Talpa* and *Erinaceus* with certain arctoid plantigrade carnivores in a "sectio" of the comprehensive order "Primates."

1792. Vicq d'Azyr distributes the Insectivores in the orders "Taupens ou Taupes," "Soriciens" and "Carnivores."

1795. Geoffroy and Cuvier put the Insectivores and Arctoid Carnivores in the "*ordre Plantigrades.*"

1800. Cuvier joins the Insectivores with *Ursus, Taxus, Nasua, Procyon, Potos* [*Cercoleptes*], *Ichneumon* in the group "*Plantigrades,*" between the "Cheiroptères" and the "Carnivores" in the comprehensive order Carnassiers."

1817. Cuvier excludes the plantigrade Carnivora and renames the groups "les Insectivores," including as major divisions "les Herissons" (*Erinaceus*), "les Musaraignes" (*Myogale,* Soricidæ, *Scalops* and *Chrysochloris*), "les Tenrecs" (*Centetes*) and "les Taupes" (*Talpa*).

1834. De Blainville unites the Insectivora more intimately with the Chiroptera as a division "claviculés," of the "Carnassiers" contrasted with the Carnivora as "non-claviculés"; this makes easier the total separation from the Carnivora.

1839. De Blainville, in his 'Ostéographie' restricts the term "Carnassiers" to the Carnivora, but retains a nominal connection between the two groups as "Secundatès."

1837, 1840. Bonaparte totally divorces the Insectivores from the Carnivora, placing the former in the "Ineducabilia" in company with Bruta, Chiroptera and Glires.

1855. Wagner, in his supplementary volume (1855) to Schreber's 'Säugethiere,' reviews the order and adds to it the genus *Galeopithecus* "previously associated with the lemurs or bats or isolated as the type of a distinct order" (Gill). His classification was based on adaptive resemblances.

1864.[1] Wilhelm Peters (quoted by Gill) in the last of a series of four contributions, extending from 1846 to 1864, divides the Insectivores into two great groups, which after the exclusion of *Galeopithecus* were afterward named "Menotyphla" and "Lipotyphla" by Haeckel.

A. Intestine with a large cœcum:

"Galeopitheci," "Tupayæ," "Macroscelides."

[1] The classifications of Peters, Haeckel and Gill are taken from Gill's excellent 'Synopsis of Insectivorous Mammals' (1874).

B. Intestine simple, without cœcum:

"Centetinæ" (*Centetes, Solenodon, Ericulus, Echinogale*).

"Erinacei" (*Erinaceus, Gymnura*).

"Talpina" (*Myogale, Urotrichus,* and other Talpids, *Chrysochloris*).

"Sorices" (*Sorex*).

1866. Haeckel places the Insectivora as the third order of the Discoplacentalia, dividing the group as follows: "Subordo I. Menotyphla"... Insectenfresser mit Blinddarm" including "1. Familia Cladobatida s. *Scandentia,*" *Cladobates, Tupaja*; "2. Familia Macroscelidia, s. *Salientia,*" *Macroscelides, Rhynchocyon.* "Subordo II. Lipotyphla....Insectenfresser ohne Blinddarm"..." 1. Familia Soricida," *Sorex, Crossopus, Crocidura*; "2. Familia Talpida," *Talpa, Condylura, Chrysochloris*; "3. Familia Erinaceidea," *Erinaceus, Gymnura*; "4. Familia Centetida," *Centetes, Solenodon.*

1867–1871. Mivart contributes to the 'Journal of Anatomy and Physiology' for 1867 and 1868 a series of important "Notes on the osteology of the Insectivora." This was supplemented in an article on *Hemicentetes* in the 'Proceedings of the Zoological Society,' 1871. His revised classification (1871) was as follows:

Galeopithecidæ: *Galeopithecus.*

Macroscelididæ: *Macroscelides, Petrodromus, Rhynchocyon.*

Tupaiidæ; *Tupaia, Ptilocercus, Hylomys* [now included under Erinaceidæ].

Erinaceidæ; *Gymnura, Erinaceus.*

Centetidæ: *Centetes, Hemicentetes, Ericulus, Echinops, Solenodon.*

Potamogalidæ; *Potamogale.*

Chrysochloridæ; *Chrysochloris, Chalcochloris.*

Talpidæ.

Subfamily 1. Talpina: *Scalops, Scapanus, Condylura, Talpa.*

Subfamily 2. Myogalina: *Urotrichus, Myogale.*

Soricidæ: *Sorex.*

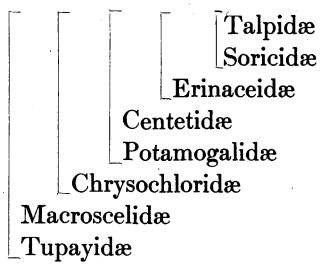
Mivart calls attention (1868, pp. 138–140) to the confusing homologies of the different cusps of the molars in the Centetidæ and other families, and suggests that the main internal cusp in the upper molar of the Centetidæ represents the "two external principal cusps of a quadricuspid molar" (1871, p. 72).

1872. Gill, in his 'Arrangement of the Families of Mammals' (1872) adopts the following classification:

Suborder Dermoptera.
Galeopithecidæ.
Suborder Insectivora Vera.
Superfamily Soricoidea.
Fam. Talpidæ.
Subfam. Talpinæ.
Subfam. Myogalinæ.
Fam. Soricidæ.
Superfam. Erinaceoidea.
Fam. Erinaceidæ.
Subfam. Erinaceinæ.
Subfam. Gymnurinæ.
Superfam. Centetoidea.
Fam. Centetidæ.
Subfam. Centetinæ.
Subfam. Solenodontinæ.
Fam. Potamogalidæ.
Superfam. Chrysochloridoidea.
Fam. Chrysochlorididæ.
Superfam. Macroscelidoidea.
Fam. Macroscelididæ.
Subfam. Rhynchocyoninæ.
Subfam. Macroscelidinæ.
Fam. Tupayidæ.
Insectivora incertæ sedis.
Leptictidæ < *Leptictis* Leidy.

This classification was not only the best up to that time but in the opinion of the writer was better than almost any that came after it. Nor has it been rendered obsolete by later discoveries or changes in method.

Gill's ideas as to the degrees of kinship between the various groups were expressed diagrammatically thus:



This expresses very nearly the conception of relationships held by the writer.

1874–75. Gill, in his 'Synopsis of Insectivorous Mammals' gives a full review of the literature, taxonomy and osteology of the group. In the classification adopted the suborders "Dermoptera seu Pterophora" (Gray) and "Bestiæ seu Insectivora Vera" are recognized. In the diagram representing the supposed degrees of relationships the Bestiæ are divided into two sections, corresponding to the later terms Zalambdodonta and Dilambdodonta Gill, the first subdividing into the Centetoid and Chrysochloroid families, the second into the Tupaioid, Erinaceoid, and Soricoid families.

1876–1884. Cope associates the Insectivora with various groups, especially the Creodonta, Mesodonta and Tillodonta, as suborders of the order Bunotheria, a generalized Placental group.

1880. Huxley emphasizes the "central position" of the Insectivora, among the higher Mammalia, regarding them as giving the ancestral characters of practically all the other orders.

1882 (1883). Dobson, in his monograph on the Insectivora, Part I, adopts Gill's classification with the addition of a new family (Solenodontidæ) and two subfamilies (Oryzorictinæ and Geogalinæ). He gives a very thorough and fully illustrated account of the osteology, myology, visceral anatomy, urinary and generative organs of the principal families, except the Tupaioidea and Dermoptera.

1885. Gill, in the Standard Natural History, Vol. V, p. 136, adopts the terms "Zalambdodonta" and "Dilambdodonta," constituted as above.

1888. Osborn, "while admitting the risk of systematic determination upon the basis of such analogies" (*i. e.*, of the dentition), holds that "we cannot deny there is far more ground at present for placing the Stylacodontidæ [a Jurassic family] in or near the line of the Insectivora than in any other order." He accordingly names this group the "Insectivora primitiva," *i. e.*, as a suborder of the Insectivora (1888, p. 261).

1903. Wortman removes the Eocene Hyopsodontidæ from the Primates and places it in the Insectivora.

1905. Matthew describes the important Eocene genus *Pantolestes* Cope (p. 305).

1907. Leche contributes to his work 'Zur Entwickelungsgeschichte des Zahnsystems der Säugetiere,' an important monograph on the phylogeny of the Centetidæ, Solenodontidæ and Chrysochloridæ.

1909. Matthew, in his monograph on the Bridger Eocene Carnivora and Insectivora, favors Huxley's view that "the Insectivora represent more nearly than any other order the central stock from which the various groups of placental mammals have descended". He shows that the Hyopsodontidæ

are structurally allied to the Insectivora on the one hand and to the Mioclænidæ and other primitive Placentals on the other.

The Zalambdodonta.

(Centetoidea Gill + Chrysochloroidea Gill.)

The various families of Zalambdodonts, which are now so diverse in structure, have been dispersed from their primal mode of life (which may have been arboreal), into the same terrestrial, fossorial and semiaquatic habits which have offered a secure refuge to many other lowly vertebrate groups. According to Matthew, who has discovered Chrysochloroids and Centetoids in the Oligocene of North America (*cf.* pp. 258, 259) the members of these groups have been driven southward from an original Holarctic center of distribution into such outlying faunal areas as Madagascar, West Africa, South Africa, the West Indies and Miocene Patagonia.

THE CENTETIDÆ.

The Centetidæ, once established in the great island of Madagascar, deployed into a number of well marked lines of adaptation, which have been described by Peters, Mivart (1867–68, 1871), Dobson (1883), Forsyth Major (1897), Leche (1907) and others. *Centetes* parallels *Didelphis* and the Creodonts in its enlarged canines, long skull, broad scapula, etc.; *Ericulus* parallels *Erinaceus* in several features of the dentition as well as in its spiny covering; *Hemicentetes* has evolved sectorial molars with long metastyle blades; *Oryzoryctes* has acquired marked fossorial characters; *Limnogale* resembles the aquatic shrews; finally, *Potamogale* represents an otter-like adaptation to rapid swimming. Fortunately, as in the case of the Marsupials, some of the more primitive members of this radiation have survived to the present time, and from the various species of *Microgale* Leche has been able to learn much of the morphological history of the group.

Are the molars of the Centetidæ "pseudotritubercular"?

The molars of *Centetes* were formerly supposed to represent the tritubercular dentition in a very simple form, but the researches of Mivart (1867–68), Forsyth Major (1897), and M. F. Woodward (1896) have been interpreted by Gidley (1906, p. 93) as indicating that the molars of *Centetes* are, in fact, "pseudotritubercular," that their high pointed V represents the

paracone of normal tritubercular molars, that their true protocone is the vestigial internal basal ledge, and that they have been derived from a type of molar represented in *Potamogale*.

The important monograph of Leche (1907) brings much new evidence from an entirely different source to bear upon this still very difficult problem and seems to favor the contrary view that the *Potamogale* molar is, after all, the derived or pseudotritubercular type, and that the main internal cusp in the *Centetes* molar is homologous with the protocone rather than with the paracone or para + metacone of normal tritubercular teeth (Fig. 17). Leche's work (1907) shows that the problem of the origin and cusp-homologies of the Centetoid molars cannot be solved through the consideration of dental characters alone, but only by careful study of various parts of the organism throughout the series, with the view of discovering the general trend of evolution of the forms in question.

According to Leche's view, the most primitive member of the Centetidæ is the minute shrew-like form *Microgale pusilla*. The genus *Microgale* includes some ten species, all of small size, of which some are more adapted for digging, others, with elongate hind limbs and tail, for hopping. In *M. longicaudata* the tail is very primitive in that it is covered with slightly imbricating scales arranged in whorls between which short hairs project (Dobson). In *Centetes* the tail is lost. In *Microgale* and its allies the hairy covering retains its primitive undifferentiated form, whereas in *Ericulus* and *Centetes* it develops defensive spines. Through the larger intermediate forms *M. cowani* and *M. dobsoni*, *Microgale* foreshadows the obviously more specialized *Oryzoryctes*, *Limnogale*, etc. The adult *Microgale* retains a form of skull displayed by the embryo *Centetes*, and the nasals remain separate even in old animals, whereas they very early coalesce in *Centetes*. The fourth digit in the pes is the longest (*cf.* Marsupials). The so called episternum, the monotreme-like nature of which was noted above, is preserved, whereas it is much reduced in *Centetes*. The number of dorso-lumbar vertebræ (usually 21–22) is nearer the primitive number, 19 or 20, than it is in *Centetes* (23–24). The milk dentition persists into the fully adult state as in the Oligocene Leptictidæ (p. 260) and certain other Insectivores.

The female generative organs are as in *Centetes*, but in the male the testes have begun their descent and lie in the pelvis (Dobson, 1883, p. 86). This is one of the few characters in which *Microgale* has progressed further than *Centetes*. *Microgale longicaudata* and *dobsoni* retain a free os centrale carpi, but in *M. cowani* the scaphoid, lunar and centrale coälesce. The tibia and fibula have also fused distally, whereas they remain free in *Centetes*.

Leche (1907, p. 41) holds that *Microgale* is equally primitive in its dentition (*cf.* our Fig. 18, *B*). In the smaller species the upper incisors, canines

and premolars are less differentiated from each other than in the higher types, even the incisors showing an incipient division of the root and a pronounced posterior cingulum cusp. It may however be remarked that these characters of the incisors and canines might perhaps better be regarded

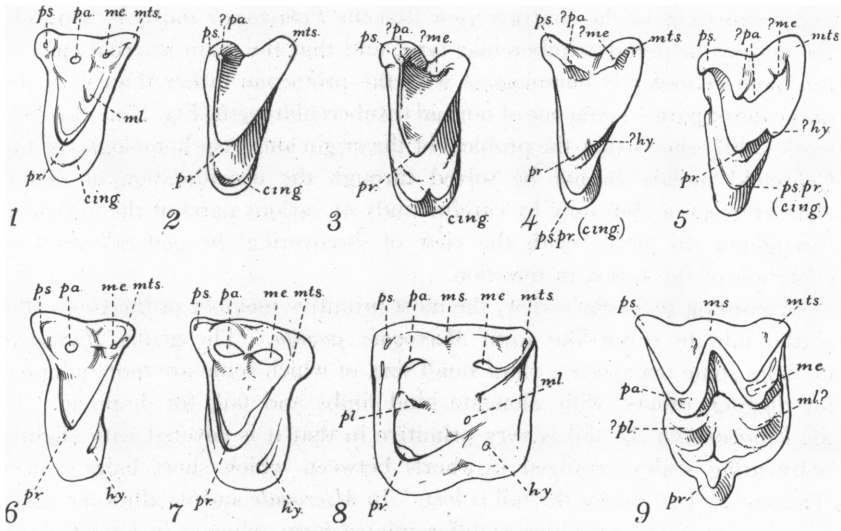


Fig. 17. Homology of the molar cusps in the Lipotyphlous Insectivora.

No. 1, *Dryolestes* sp. after Gidley; cingulum after Osborn. No. 2, *Microgale dobsoni*, original. No. 3, *Solenodon paradoxus*, original. No. 4, *Potamogale velox*, original. No. 5, *Potamogale velox*, posterior milk molar, after Leche. No. 6, *Ictops thomsoni*, after Matthew. No. 7, *Ictops acutidens*, after Matthew. No. 8, *Gymnura* sp., after Osborn. No. 9, *Proscalops miocœnus* from photomicrograph (Matthew).

In the Zalambdodonts (nos. 2–5) the para- and metacones appear to be reduced, the external cingulum gives rise to irregular cusps (*ps. mts*); the high internal cusp according to this view is homologous with the protocone of *Dryolestes* (no. 1). The basal cingulum in *Microgale* (No. 2) and *Potamogale* (nos. 4, 5) grows out into a "pseudoprotocone."

In the Erinaceoids (nos. 6–8) the simplest molar type (*Ictops thomsoni*, no. 6) agrees in essentials with *Dryolestes*. The tooth is narrow anteroposteriorly, the paracone centro-external, the metacone small. The basal cingulum however (*hy*) is better developed and confined to the postero-internal border. In *Ictops acutidens* (no. 7) the tooth is broader anteroposteriorly, the metacone and hypocone better developed. In *Gymnura* (no. 8) and *Erinaceus* the antero-posterior broadening becomes very pronounced and the prominent hypocone completes the quadrate contour of the crown.

In the Soricoids (*e. g.*, *Proscalops*, no. 9) the homologies are less clear but the low internal cusp appears to be a pseudoprotocone + protocone.

as secondary. In *Centetes* the canines are sharply differentiated from the incisors, the incisors are small and the skeleton presents many analogies to the flesh-eating Creodonts. The upper molars in *Microgale* differ from those in *Centetes* chiefly in the somewhat better development of the internal basal ridge and in the antero-posterior narrowness of the whole tooth, which

is suggestive of the Jurassic *Dryolestes*. In the lower molars (m_1, m_2) the talonid is very small, placed on a very low level and lacks a hypoconid. In m_3 the talonid is better developed. The lower jaw and lower molars show significant resemblances to those of *Apternodus mediævus* Matthew (*cf.* p. 259).

In *Solenodon*, which in most other characters also is more specialized than *Microgale*, the internal basal ledge in the molars is more pronounced (Fig. 17, no. 3). In *Potamogale* the internal basal ledge assumes the form of a low V-shaped cusp, while, in correlation with the antero-posterior broadening of the crown (see p. 189 above), the main or outer V is more open and tends to bud off an incipient posterior V (Fig. 17, no. 4). These features are more strongly expressed in the milk dentition (Fig. 17, no. 5), a fact of doubtful significance.

The low internal cusp in the *Potamogale* molar (Fig. 12, *B*) corresponds in function and position to the protocone of normal tritubercular teeth because as shown by examination of a specimen in the National Museum (No. 124327) it clearly fits into the basin of the talonid, which in the *Potamogale* molars is much more developed than in any Centetid.

And yet in spite of this correspondence in function with a protocone it seems probable that this internal basal cusp in *Potamogale* is not homologous with the protocone of *Ictops* and of normal tritubercular teeth, but with the basal internal cingulum, which is seen in various stages of development in *Tupaia*, *Ptilocercus*, all the Zalambdodonts, Leptictids, Erinaceids, *Myogale*, *Proscalops* (Fig. 17, no. 9) and the modernized shrews and moles. And although the high internal V in *Microgale* did not fit directly into the basin of the talonid like a normal protocone, this appears to be because there is properly speaking no basin of the talonid for it to fit into; this is owing to the lack of a hypoconid, which in fully developed tritubercular teeth fits outside the protocone, which, in turn, is thus received into the valley between the entoconid and the hypoconid.

If then the basal internal cusp of the *Potamogale* molar be homologous with an upgrowth of the basal internal cingulum, while the main V-shaped cusp be homologous with the protocone of *Ictops* we have a general analogy with the fourth premolar of such a Creodont as *Chriacus*. According to this view the para- and metacones of *Potamogale* are represented not by the main V and its incipient posterior offshoot but by the reduced external cusps which may have been derived by reduction from the paracone and metacone of such a form as *Ictops thomsoni* (Fig. 17, no. 6).

Potamogale a specialized Centetid. The validity of the conclusion that the basal internal cusp of the *Potamogale* molar is a cingulum upgrowth, not homologous with the true protocone of other mammals, depends largely

upon the proof that this West African genus is truly an aquatic offshoot of a *Microgale*-like form and thus not the type of a very distinct family but merely an outlying member of the Madagascan Centetidæ.

In support of this view Leche (1907, pp. 127–129) has adduced considerable evidence. In the first place the diet of *Potamogale* is, for an Insectivore, aberrant and peculiar, since it subsists upon fish, for the capture of which its whole organization is aberrantly modified. In its antemolar dentition *Potamogale* parallel *Cynogale benneti*, a Viverrid of similar aquatic piscivorous habits (Leche). But this peculiar antemolar dentition of *Potamogale* is linked morphologically to that of the very primitive *Microgale* by way of the intermediate conditions in *Limnogale*. Secondly, *Potamogale* is connected with *Microgale* by the profile and ventral contour of the skull, by the arrangement of the pterygoids, by the form of the glenoid fossa, by the fused nasals, etc. (Leche, 1907, p. 128), and to this list may be added the resemblances in the auditory region and the close agreement in the position of the principal foramina.

The peculiar syndactyly of the second and third digits in the pes of *Potamogale* (suggestive of the Marsupial syndactyly) is shown by its late appearance in the embryo to be a relatively recent acquirement (Leche). *Potamogale* is likewise more highly specialized than the remaining Centetidæ in the following characters: (1) large size, as compared with *Microgale*; (2) peculiar newt-like swimming habits; (3) total loss of clavicles and highly modified manubrium sterni: (4) loss of entepicondylar foramen (very unusual in lipotyphlous Insectivora); (5) loss of gall bladder; (6) descent of the testes into a true "cremaster sack"; (6) change from insectivorous to piscivorous habits. In view of these marks of high specialization and at the same time of derivation from a *Microgale*-like form it now seems contrary to the balance of evidence to accept the view, as the writer formerly did (in Osborn, 1907, p. 225) that the tritubercular molar type of *Potamogale* was prototypal to the molar types of the remaining Zalambdodonts.

THE SOLENODONTIDÆ.

Solenodon was considered by Dobson (1882, p. 87) to be the type of a family "distinct from Centetidæ but, nevertheless, associated with it and Potamogalidæ in the same group or superfamily Centetoidea" (see also *l. c.*, p. 96). Dobson laid stress (p. 87) on the analogies in the skull between *Solenodon* and the Talpoid genus *Myogale*, but Leche (1907, p. 145) thinks that "Dobson hat den Unterschied zwischen *Solenodon* und Centetidæ

bedeutend überschatzt," and "Dass keine näheren geneologischen Beziehungen zu den Talpidæ bestehen....darf wohl als ausgemacht gelten." Leche shows (pp. 144–145) that *Solenodon* is allied to the Centetidæ by the possession of a number of characters, including the following: (1) fibula articulating solely with the astragalus; (2) fibula free from tibia; (3) several peculiarities in the musculature; (4) the characters of the dentition — which may readily be derived from those in *Microgale* of the Centetidæ. The molars have the internal basal ledge produced into two small cusps.

As will be shown below the specializations of *Solenodon* include no feature that is inconsistent with derivation from a Zalambdodont ancestor. Thus the peculiar groove on I_2 is feebly represented in *Microgale, Potamogale, Chrysochloris* and *Scalops* (Leche). The analogies with *Myogale* in the skull are of very superficial character (see below, page 242) and relate chiefly to the interorbital constriction, the transversely expanded mandibular condyle, the enlargement of the anterior upper incisors and the round topped premolars.

Notes on the Comparative Osteology of Solenodon paradoxus.

The osteology of *Solenodon cubanus* and of the rarer *S. paradoxus* has been described by various authors, including Brandt, Peters, Mivart (1878, p. 123), Dobson (1883), Leche (1907), and Allen (1908). Through the courtesy of Dr. J. A. Allen the writer is enabled to supplement these descriptions and to review the evidence bearing on the relationship of the Solenodontidæ to the Centetidæ, and, more remotely, to the early Tertiary Leptictidæ. The observations on these problems may, it is hoped, contribute to the general question of the relationship of the Insectivora to the Marsupials and Placentals (p. 299). The officials of the United States National Museum have courteously loaned a skeleton of *Microgale dobsoni* and a skull of *Potamogale velox* which are also referred to in the following notes.

The material at hand includes three skeletons, one of a young individual (Amer. Mus. No. 28272) which shows well the sutures and limits of the bones. The skull of an adult female (No. 28271) has been sectioned in the median line and affords valuable morphological details.

The *dentition* and mode of dental replacement, having been so fully described by Leche (1907) and Allen (1909), call only for the remark that they reveal no special Marsupial resemblances but are, on the contrary, very typically Placental, and, more particularly, Zalambdodont, in character. The question of the homology of the molar cusps is referred to below (p. 290).

Skull.— The *general proportions* of the young skull are much less dolichocephalic than in the adult and in so far approach the mesaticephalic proportions of the embryonic *Centetes* (Parker,[1] 1886, pl. 32). The basifacial and basicranial axes make only a very slight angle with each other.

The *nasals* in the young skull (Amer. Mus. No. 28272) are still suturally distinct in the mid line, as in the embryo *Centetes*, but in the adults the opposite nasals have completely coalesced, although the position of the suture is indicated by a groove. The *frontals* in the young skull send forward two large V-shaped extensions which are broader than those in the young *Centetes*. In the adult Solenodons these Vs are completely coalesced with the nasals, but the anterior limits of the temporal muscles make it appear falsely as if the naso-frontal sutures were above the orbits and as if the nasals broadened proximally after the Marsupial fashion.

In the top view the skull, even of the old individuals, differs from that of *Solenodon cubanus* in the feebleness of the *interorbital constriction*, the middle portion of the skull being almost cylindrical as in the other Zalambodonts. The interorbital constriction in *S. cubanus* is one of the features emphasized by Dobson (1883, p. 87) as serving to separate the Solenodontidæ from the other Zalambdodonts, but it is seen to be due on the one hand to the broadening of the brain case and on the other to the primitive breadth of the frontal region above the large olfactory scrolls of the ethmoids; and is accordingly merely a primitive mammalian character and a very insufficient indication of near affinities with *Myogale*.

The young *Solenodon* skull possesses a pair of good sized *interparietal bones* (Fig. 18, A^2, *Ip.*) separated by a median but slightly asymmetrical suture, and partly overlaid by the parietals.

The interparietal appears in Marsupials, Rodents, *Orycteropus* and many other orders (Weber, 1904, p. 50) and usually fuses with one or another of the adjacent bones. In many forms it arises from paired ossific centres so that the young *Solenodon* is very primitive in this respect. A large, apparently unpaired, interparietal appears in the fœtal and young *Erinaceus*, *Centetes*, *Hemicentetes* and *Microgale* (*cf.* Parker, 1886, pll. 33–35).

The *lachrymal* in *Solenodon*, as in *Erinaceus*, is a small narrow bone placed well up on the side of the face and pointing obliquely upward and backward as in *Centetes*, but it is smaller than in that genus (contrast the large lachrymal of Marsupials). As in *Centetes* and *Hemicentetes* the lachrymal foramen is marginal and is bounded antero-inferiorly by the malar ridge of the maxillary. The *maxillary* extends well up on the inner side

[1] Statements in regard to the young and embryonic *Erinaceus*, *Talpa*, *Sorex*, *Centetes*, *Hemicentetes*, *Microgale*, *Rhynchocyon*, in the following description are based on Parker's figures (1886, pll. 20–36).

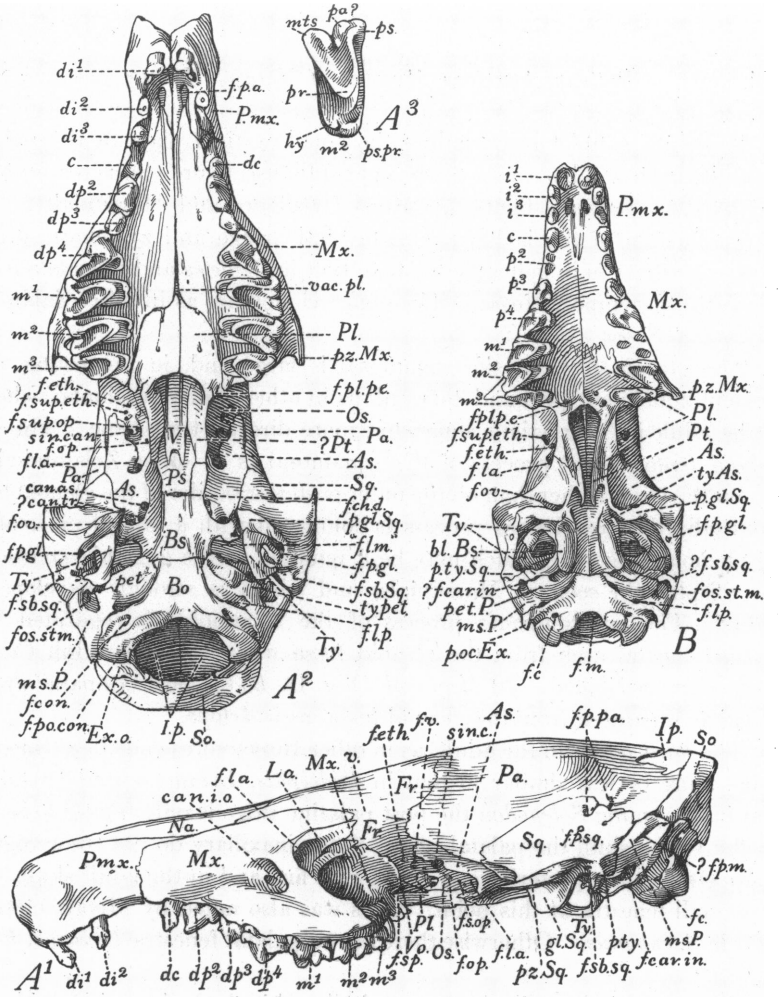


Fig. 18. Cranial morphology of *Solenodon paradoxus* and *Microgale dobsoni*; A^1 Skull of *Solenodon paradoxus*, juv. Am. Mus. No. 28272, side view. × $\frac{4}{3}$. A^2. Ditto, inferior view, same scale. A^3. Second right upper molar of same. × $\frac{2}{1}$. *B*. Skull of *Microgale dobsoni*. U. S. Nat. Mus. No. 49673, inferior view. × $\frac{2}{1}$.

di^1, *di*^{2}, *di*^{3}, *dc*, *dp*^{2}, *dp*^{3}, *dp*^{4}, deciduous teeth,
i^1, *i*^{2}, etc. permanent teeth.
Pmx., premaxillary.
Mx., maxillary.
p.z. Mx., zygomatic process of maxillary.
Pl., palatine.
Pt., pterygoid.
Vo., vomer.
Ps., presphenoid.
Os., orbitosphenoid.
As., alisphenoid.
Bs., basisphenoid.
Sq., squamosal.
p.gl.Sq., post-glenoid process of squamosal.
p.ty. Sq., post-tympanic " " "
Bo., basioccipital.
P., petrosal.
Ty., tympanic.
ms.P., mastoid portion of periotic.
Na., nasal.
Fr., frontal.
Pa., parietal.
Ip., interparietal.
So., supraoccipital.
f.p.a., anterior palatine foramen.
f.pl.p.e., postero-external palatine foramen.
f.s.p., spheno-palatine foramen.
f.eth., ethmoid foramen.
f.sup.eth., supra-ethmoid foramen.
f.op., optic foramen. (The optic nerve in Microgale is stated to pass out through the f.l.a.)
f.s.op., suboptic foramina.
f.l.a. + *f.r.*, foramen lacerum anterius plus foramen rotundum.
can.as., alisphenoid canal.
f.eus., Eustachian opening.
f. ov., foramen ovale.
f.p.gl., post-glenoid foramen.
f.p.z., post-zygomatic foramen.
f. st. m., stylomastoid foramen.
f. p.m., postmastoid foramen.
f.c., condylar foramen.
f. sq. pa., squamoso-parietal foramina.

of the orbit, completely excluding the small vertical plate of the palatine from the orbit. This seems to be a general Insectivore character, so far as indicated by Parker's figures (contrast Carnivora and Marsupials).

The region of the lachrymal, antorbital bridge and zygomatic process of the maxillary is in general similar to that in *Centetes* and the same is true of the orbito-temporal fossa. The *malar* is lacking, as in other Zalambdodonts and *Sorex*.

The *glenoid fossa* of the squamosal is large and, in the young skull, looks obliquely outward and forward, as in other Zalambdodonts; whereas in the adult its long axis is somewhat more directly transverse. The *postglenoid* (*entoglenoid*) process of the squamosal as in other Zalambdodonts lies on the inner rather than on the outer posterior border of the glenoid fossa. Internally the postglenoid process is connected with a lateral crest of the alisphenoid (Fig. 18), which may be a remnant of the glenoid extension of the alisphenoid seen in Marsupials, and which is strongly developed in *Ictops*. The *post-tympanic* process of the squamosal is separated by a distinct meatal arch from the glenoid fossa whereas in the adult *Centetes* the two are conjoined. In *Microgale* (Fig. 18, *B*) the post-tympanic process is widely separated from the glenoid fossa, as in *Ictops*.

The *hard palate* in the adult, as in other Insectivores ends in a transverse ridge more or less similar to that in *Didelphis*, *Erinaceus* and Creodonts. But in the young *Solenodon* the post palatine ridge is only faintly indicated. In the young skull the palatal plates of the maxillary do not come together completely at the posterior end in the mid line and in the adult skulls there is a small fenestra at this point. This was also noted by Mivart (1868, p. 124) in *S. cubanus*. Otherwise there are no palatal fenestræ (contrast *Erinaceus*).

The *vomer* is large in the young skull and is flanked on either side by a large subhorizontal wing, which, as in *Thylacynus* appears to be continuous anteriorly with a lateral scroll of the ethmoid. In the young *Solenodon*, through the shallowness of the orbital plate of the palatine, a portion of this vomerine wing is left exposed on the side wall of the skull (Fig. 18, A^2, ?*Vo*). In *Centetes* the orbital plate of the palatine appears to be represented by a small wing, which is pierced by the sphenopalatine foramen, and which covers this vomerine exposure.

The existence of true *pterygoids* (Fig. 18 *pt.*) in *Solenodon* can scarcely be affirmed from the material at hand, but in the fœtal *Centetes* Parker so names the vertical pterygoidal flanges, which, as in other Insectivores are said by him to have a cartilaginous core. The pterygoids and pterygoid flanges of the palatines in *Solenodon* form on each side a single long ridge, as in other Zalambdodonts, and also as in *Ictops*, the pterygoid fossæ not being developed (contrast *Erinaceus*).

The *orbitosphenoid* is of the Placental type, that is it is pierced by the optic foramen and is not depressed dorsoventrally in such a manner that the opposite sphenorbital fissures are confluent below it (contrast Marsupials). In the sagittal section of the skull the anterior portion of the orbitosphenoid is seen to be invaded, as it is in *Didelphis* (p. 221), by the backward prolongation of the ethmoidal chamber.

The *alisphenoids* form the lateral wings of the basisphenoid and in the young skull, as also in the embryonic *Centetes*, are not suturally separate from that bone. The temporal wing of the alisphenoid is relatively much smaller than in *Didelphis*, and, as in typical Placentals, it is pierced by the alisphenoid canal and is excluded from the glenoid fossa. A descending flange forms the backward continuation of the pterygoidal ridge and an external inferior branch runs outward to meet the postglenoid crest of the squamosal. This branch is not curved posteriorly for the tympanic chamber (contrast *Centetes*).

The *basisphenoid* contrasts with that of *Erinaceus*, *Centetes* and *Microgale* in lacking the descending lateral wing, which in those genera embraces the tympanic cavity. On the dorsal or cerebral surface of the basisphenoid (as shown in a sagittal section) the pituitary depression is absent and, as in Marsupials and *Erinaceus*, there are no anterior and posterior clinoid processes. In *Centetes* however a small posterior clinoid process is present.

Between the basi- and pre-sphenoids in the median line, in the young *Solenodon* (Fig. 18, *A*), is a small hole which appears to be homologous with a similarly placed foramen in *Centetes*; in the latter genus this foramen lodges a ventral apophysis of the vestigial chorda dorsalis (Leche, 1907, p. 68). Parker (1886, pl. 19, figs. 1–4) figures a similar foramen in *Erinaceus* but called it a "pituitary hole," although one of his specimens (fig. 3) seems to have retained a considerable piece of the notochord. Mead (1909, figs. 2, 5) shows that in the Pig also the vestigial notochord communicates with the pharynx. The ventral surface of the pre- and basisphenoids is flat as in *Microgale*, whereas in *Centetes*, *Ericulus* and *Erinaceus* there is a large round pit in the median line surrounding the foramen for the chorda.

The *basioccipital*, as in *Centetes*, *Microgale*, certain Creodonts and Marsupials is very short. This bone bears a pair of accessory occipital condyles and the latter together with the exoccipital condyles are much like those in *Centetes*. *Paroccipital processes* of the exoccipital are lacking in the young skull (contrast other Zalambdodonts) but are indicated as a pair of small knobs in the old female. They are also lacking in the skull of *Solenodon cubanus* figured by Leche (1907, p. 72).

The auditory prominence of the petrosal is larger than in *Centetes*. It is ovoid, with the inner side closely appressed to the basioccipital whereas in

Centetes it is separated from the basioccipital by the backward extension of the tympanic flange of the basisphenoid. On its inferior surface it also bears a depression which is apparently caused in ontogeny by the pressure of the tympanic chamber, as shown by comparison with *Microgale* (Fig. 18, *B*). In all these details the petrosal of *Solenodon* resembles that of *Ictops*. The petrosal of *Solenodon paradoxus* sends out a small postero-external wing (Fig. 18, A^2, *pr. ty. pet.*), which in the adult articulates with the postero-internal border of the tympanic. A similar process was observed by Brandt in *S. cubanus* (van Kampen, 1905, p. 425) and is also represented in *Microgale* (Fig. 13, *B*). There seems strong evidence for homologizing this tympanic wing of the petrosal in Centetoids with the entotympanic of Marsupials and Menotyphla (van Kampen, 1905, p. 452).

The *mastoid portion* of the periotic is relatively large in the young *Solenodon*, and is broadly continuous with the petrous. It faces obliquely outward and backward and is well seen in the side view as in *Microgale* (Fig. 18), and *Potamogale*, whereas in *Ictops* and *Centetes* it faces backward rather than outward, and is seen best in the occipital view. On its inferior surface the mastoid has a deep circular pit or notch (Fig. 18, A^2, *f. st. m.*), which may have served for the attachment of the stylomastoid bone. A similar pit occurs in *Centetes* and *Erinaceus*. The ring shaped *tympanic* is relatively large and broad. Anteriorly it rests against the postglenoid process of the squamosal (contrast *Centetes*). It is oblique rather than horizontal or vertical in position.

Nerve foramina. The foramina are best demonstrated from an internal view of the skull in sagittal section. In the *olfactory foramina*, piercing the cribriform plate nothing remarkable was noted. The *ethmoid foramen*, for the recurrent, ethmoid branch of the ophthalmic division (V_1) of the trigeminus, as in *Didelphis* and Placentals, is located just behind and externally to the inferior part of the cribriform plate. This foramen issues externally as in Fig. 18, A^2 (*f. eth.*). Behind and much below and internal to the ethmoid foramen and also internal to the large sphenorbital fissure is the minute optic foramen, piercing the orbitosphenoid as in typical Placentals and agreeing in its small size with that of *Centetes*, and *Potamogale*. The *foramen lacerum auterius* (f. sphenorbitale, nerves III, IV, V_1, VI) is very large and circular. Some distance behind it, and perforating the base of the alisphenoid, is a small foramen which at first sight looks like the foramen rotundum. But this foramen faces backward, and therefore cannot transmit the superior maxillary branch (V_2) of the trigeminus. Moreover it issues externally in the posterior opening of the alisphenoid canal and must therefore have transmitted a branch of the external carotid artery. The inference is that the *foramen rotundum* in *Solenodon*, as in *Centetes* and other

Insectivores, is not distinct but is confluent with the foramen lacerum anterius. The *foramen ovale* (V_3) is large and circular as in *Centetes*. It perforates the alisphenoid at a point just internal to the glenoid fossa of the squamosal. The *internal auditory meatus* (VIII), facial canal (VII), *foramen lacerum posterius* (IX, X, XI) and the *condylar foramen* (XII), as well as the *sphenopalatine* (V_2) *post palatine canal* (V_2) and the stylomastoid (VII) foramina are all located about as in *Centetes*. The *condylar foramen* (XII) in one of the adults is double, as is not seldom the case in Marsupials, Insectivores and Rodents (*cf.* p. 329).

Foramina for the carotids. The alisphenoid canal (Fig. 18, A^2, *can, as.*) for the *ectocarotid* artery is located as in *Centetes* and *Ictops*. As remarked above (p. 246) an internal branch of this artery may have pierced the base of the cranium internally to the foramen ovale. The *entocarotid* probably entered the tympanic cavity in or near the deep circular notch between the petrosal and the mastoid (Fig. 18, A^2, *for. st. m.*). In *Erinaceus* according to Winge and other authorities (quoted by van Kampen, 1905, pp. 383, 429–430), the entocarotid after entering the tympanic chamber from the rear divides into two main branches: (1) an internal branch, the true entocarotid, which perforates the basisphenoid at the anterointernal corner of the tympanic chamber, immediately back of the alisphenoid; (2) an external branch, the stapedial artery, which pierces the stapes. This again subdivides into two branches: (a) ramus inferior (arteria maxillaris interna), running forward in a groove in the roof of the tympanic chamber, leaving the latter through a notch in the tympanic wing of the alisphenoid; (b) ramus superior (arteria meningea media), entering the cranial cavity through the foramen spinosum, "gelegen vorn im Tegmen tympani in der lateral Wand der Facialisrinne" (van Kampen, 1905, p. 430). In the sectioned skull of *Solenodon* the difference from *Erinaceus* in this region is so considerable that I cannot positively identify the course of any branch of the entocarotid. An oblique canal which tunnels the basisphenoid, entering near the anterointernal angle of the petrosal and in the mid line joining its fellow of the opposite side, at first sight suggests the true entocarotid canal of *Erinaceus* and *Centetes*; but the fact that it does not open into the cranial cavity but continues across the basisphenoid, suggests rather the venous transverse canal, which is similarly located in Marsupials and Rodents. In the young skull the large open *foramen lacerum medium* recalls the somewhat similar aperture in *Ictops*, and suggests that the true entocarotid may have entered through this aperture, as it does in typical Placentals. But in one of the adult skulls the roof of the tympanum is preserved and seems to cover this aperture completely. In *Centetes* the foramen lacerum medium is obliterated by the hypertrophy of the tympanic wings of the ali- and basisphenoids.

Venous foramina. The skull of even the adult *Solenodon paradoxus* is remarkable for the great number of small venous foramina which pierce it in many regions and which make the task of identifying the normal Insectivore foramina very difficult. Immediately above the small ethmoid foramen (Fig. 18, A^2, *f. eth.*) is a foramen (double in the young skull) which may be termed the *supra-ethmoid* and which leads dorsad, between the inner and outer tables of the frontal. This foramen was not recognized in *Centetes* or *Erinaceus.* Back of it and just in front of the anterodorsal process of the alisphenoid, is a pit into which open two canals: the lower one, which may be designated as the *supra-optic* (*f. sup. op.*) runs downward and backward and joins the suboptic described below; the dorsal foramen (*"sin. can."*) is the anterior opening of what Parker calls the "sinus canal" of *Microgale,* this runs backward along the side of the skull, and sends off branches to the post-parietal and post-glenoid foramina and to the transverse occipital sinus. It is present in *Microgale* and *Erinaceus.* The *suboptic foramen* is located just below the optic foramen; its canal runs downward and backward to the transverse sinus in the presphenoid. It has a similar position and course in *Erinaceus* (Mivart, 1867, p. 283), but appears to be absent in *Centetes* (Mivart, 1868, p, 299).

The *post-parietal* (*f. p. pa.*), *post-squamosal* foramina (Fig. 18, A^1) as well as the *post-glenoid,* the *sub-squamosal* (*f. sb. sq.*) and *post-mastoid* all form part of the same system, which is more or less completely developed in Marsupials (*cf.* p. 224), and to a varying degree in the lower Placentals. Postero-externally to the condylar foramen is another member of the series, the *venous condylar foramen,* which appears to be homologous with that in Marsupials. As in *Thylacynus* this venous foramen in *Solenodon* leads into a canal which issues in the occipital aspect immediately above the condyle. In *Solenodon* another branch runs upward and issues on the inside of the skull above and behind the petrosal.

The *cervical vertebræ* agree in general characters with those of *Erinaceus* and *Centetes.* As in many primitive forms, the centra are broad and depressed. The transverse processes of C. 1–6 are pierced by the vertebral artery but not that of C. 7 (a typical Placental character). The parapophysis of C. 6 is larger than that of the others, as in so many other mammals. There are twenty *dorso-lumbar vertebræ* (16+4) and two true sacrals, followed by two caudo-sacrals. In the adult these four vertebræ, with their neural spines, coälesce. Dobson gives the vertebral formula for *Solenodon cubanus* as C. 7, D. 15, L. 4, S. 5, "coccygeal" 2, caudals 21. The more proximal *caudal vertebræ* are very large and the tail itself, as in *Orycteropus* and many other archaic mammals, is very stout near the root. The caudal chevrons are paired. Below and between the six caudals, the sacrals and

five presacral vertebræ appear disc-like, apparently osseous "intercentra." In the other vertebræ these appear to be represented by the interarticular discs. The *lumbars*, as in other fossorial mammals, lack forwardly directed parapophyses.

The *scapula* in the young specimen is relatively much narrower than in the adult, a primitive Insectivore character. In the adult it is much broader than in *Erinaceus*, with the postero-superior angle produced. The coracoid is a good sized, inwardly curved process apparently continuous with the glenoid epiphysis. The acromion, as in so many primitive types, is bifid, the anterior fork being tipped by a separate epiphysis. The spine of the scapula is quite deep, another primitive character. The posterior border of the scapula in the adult is reflected outward and this makes it easy to understand how, by a further development of this tendency, the subscapularis muscle might gain partial attachment on the external side of the scapula (*cf.* Edentata).

The *humerus* is of primitive fossorial type (Fig. 27, no. 15, p. 437), broad distally, with very stout entocondyle and an entepicondylar foramen; the supinator crest extends half way up on the back of the shaft, the capitellum is globular, and the internal trochlea is occupied in the front portion by the radius (p. 433). There is no supratrochlear foramen (contrast *Erinaceus*). The large deltoid crest is of the flattened type, forming a long narrow triangle, as in Edentates and *Sorex*. The bicipital groove is pronounced; the head is a narrow oval, with the long axis at right angles to the plane of the distal end of the humerus.

The heavy *radius* and *ulna* are strongly curved longitudinally, as in *Ictops* and *Erinaceus*, but the shafts (in the adult) are much compressed, as in Edentates. The radius is very broad distally. The long curved olecranon is transversely expanded at the proximal end, as in many other semi-fossorial animals.

Manus. The proximal row of *carpals* (Fig. 19, A^1) are flattened. The radial sesamoid ("prepollex") is present, as in other Zalambdodonts and Rodents. The *scaphoid* is prolonged posteriorly, broadly overlaps the large *trapezoid*, and touches the proximal end of metacarpal I. The *centrale* is large and flattened and lies wholly between the flattened trapezium and the scaphoid. The *lunar* is much wider than high and rests upon both magnum and unciform; in the back view the lunar-unciform connection is broader (Fig. 19, A^2). This lunar-unciform contact, which is very probably a primitive character for many higher orders (p. 452), may in some cases have been broadened by the increase in size of the distal end of the radius and the reduction of the ulna; for in *Microgale* where the ulna is relatively larger, the lunar barely touches the unciform. The *cuneiform* is narrow (contrast

Creodonts) and nearly flat superiorly. The *pisiform* is small. The *magnum* is high and narrow, with parallel sides. The *unciform* is likewise high

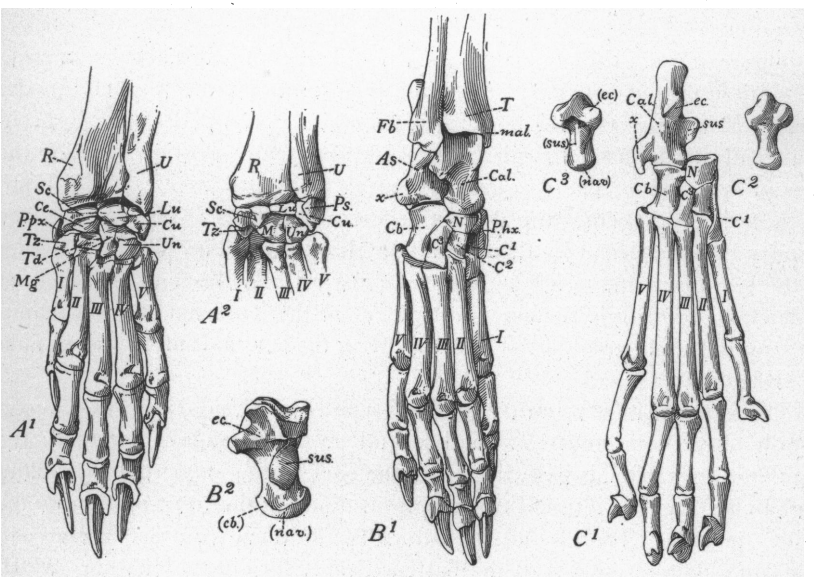


Fig. 19. Morphology of the manus and pes in *Solenodon* and *Microgale*.

*A*1. *Solenodon paradoxus*, Am. Mus. No. 28271. Left manus anterior view. Slightly enlarged. *A*2. Ditto posterior view of carpus. Natural size. Shows lunar resting on both magnum and unciform as in many other primitive mammals (p. 446).

*B*1. Right pes of same. × $\frac{1}{1}$.

*B*2. Back view of left astragalus of same. × $\frac{3}{2}$.

*C*1. *Microgale dobsoni* U. S. Nat. Mus. No. 49673. Right pes. × $\frac{3}{1}$.

*C*2. Front view of right astragalus of same. × $\frac{3}{1}$.

*C*3. Ditto, back view.

R., radius.
U., ulna.
Sc., scaphoid.
Ce., centrale.
Lu., lunar.
Cu., cuneiform.
P.px., "prepollex."
Tz., trapezium.
Td., trapezoid.
Mg., magnum.
Un., unciform.
I, II, III, IV, V, metacarpals.
x, process for attachment of tarso-metatarsal ligament.
T., tibia.
Fb., fibula.
Cal., calcaneum.
As., astragalus.
P.hx., "prehallux."
N., navicular.
*C*1., *C*2., *C*3., ento-, meso- and ectocuneiform.
Cb., cuboid.
I, II, III, IV, V, metatarsals.
(*ec.*), ectal facet.
(*sus.*), sustentacular facet.
(*nav.*), navicular facet.
(*cb.*), cuboid facet.

and unusually narrow. The *digits* are stout, moderately long and not spreading. The thumb is not divergent. The *metacarpals* overlap each other on the external side from digit II to digit IV (a primitive mam-

malian character). Metacarpal III is slightly longer than metacarpal IV. The distal ends of the metacarpals and phalanges are transversely cylindrical. On the inferior surface there are very slight if any keels. The paired metacarpal sesamoids are large, the ungues are large and compressed, not fissured at the tips.

The foregoing characters of the manus of *Solenodon* suggest that the very large claws are used for scraping and tearing and not for grasping, and this is confirmed by Mr. Verrill's notes (1907) on the living animal. The manus of *Solenodon* accordingly appears to be modified away from what the writer conceives as the primitive Placental type (p. 446) in a number of characters: especially in the flattening of all the carpal facets, in the relatively small size of the trapezoid, width and flattening of the magnum superiorly, width of the lunar, relatively small size of the trapezoid, slight reduction and non-divergence of digit I. Much more primitive characters are retained in the manus of *Ericulus nigrescens* as figured by Mivart (1871, pl. v., fig. 4). In this Zalambdodont the digits are short and divergent, the thumb and trapezoid are large, all the carpal facets are more oblique, the magnum is smaller and narrows superiorly, the lunar is deeper and much narrower.

The *pelvis* of the young *Solenodon paradoxus* is much like that of *Microgale*, as figured by Leche (1907, p. 81). The ilium is a rounded bar, faintly trihedral. The pelvis of an adult female (Amer. Mus. No. 28271) differs markedly from one of the same species figured by Leche (1907, p. 82) in the ventral view: instead of the long symphysis pubis being present, the opposite ossa innominata are widely separated in the dried skeleton and the symphyseal region of the pubis ends in a point, as in *Erinaceus*. The pelvis, in its broader features, compares well with that of *Erinaceus*. The os cotylare, if present, is indistinguishable from the acetabular epiphysis.

The *femur* is short and somewhat flattened; the head and broad lesser trochanter are bent upon, and the great trochanter is continuous with, the shaft, as in *Erinaceus*, but the third trochanter is more distinct. The condyles are broad and the patellar trochlea gently concave.

The *tibia* and *fibula*, though still unfused, are closely conjoined in the distal third, and the upper end of the tibia curves outward from the fibula, the whole arrangement suggesting an incipient fusion of the two bones (this fusion is realized in *Microgale*). The proximal end of the tibia is broad and flat, the intercondylar or median ridge being low, as in certain other plantigrade types (*e. g.*, *Mephitis*). The fibula expands proximally and in *Microgale* this expansion is large and suggests the Marsupial type.

The *pes* (Fig. 19, B^1, B^2) is longer and narrower than the manus. The astragalus is wholly different from the Didelphid type in its long slender

neck, very broad, anteroposteriorly shallow, convex head and sharply grooved trochlea, which has sharp high keels and vertical internal and external malleolar faces. The inner and outer keels are subequal. On the back surface the ectal facet is sharply triangular. Superiorly it is well separated from the dorsal continuation of the trochlea. The sustentacular facet is a large oval, located nearer to the internal than to the external border of the neck. Below the decurved ectal facet is a pit which occurs in *Erinaceus* and may possibly represent the vestiges of an astragalar foramen. This foramen is also represented in certain plantigrade Mustelidæ such as *Mephitis*, in which the astragalus is somewhat similar to the *Solenodon* type. In general, however, the astragalus in *Solenodon* contrasts with the *Mephitis* type in that both the trochlea and the head are shallower than in the latter, and the ectal facet is triangular instead of quadrangular. The astragalus of *Microgale* (Fig. 19, C^2, C^3) like that of *Solenodon* has a broad trochlea, slender neck, transversely convex head, triangular ectal facet and oval sustentacular; but the trochlear keels are much less sharp and the inner keel is small and low, so that the trochlea as a whole appears to make a sharper angle with the neck. In *Ericulus* to judge from Mivart's figure (1871, pl. v, fig. 5) the disparity between the inner and outer crests of the trochlea is even more pronounced, the inner one being very small. In *Centetes* also the inner crest is much smaller than the outer and the whole trochlea is large, and gently concave. The neck is very oblique. In *Erinaceus* the relative size of the trochlea becomes greater, but the inner and outer crests are parallel. In this form as in *Solenodon* the ectal facet is well separated from the dorsal prolongation of the trochlea.

The *cuboid* touches the astragalus. In *Microgale* it is separated from the astragalus, possibly because the navicular in this form is deeper. The *calcaneum*, as in other plantigrade types, has a short tuber and a flat spreading antero-inferior end. A large process (Fig. 19, *x*), on the inferior outer angle of the astragalus, perhaps serving for the attachment of the tarso metatarsal ligament, occurs in *Solenodon, Centetes, Ericulus, Microgale,* and is indicated in *Erinaceus*. The calcaneum bears no facet for the fibula, which as in Centetidæ articulates solely with the external malleolar surface of the astragalus.

Internal to the elongate *entocuneiform* (a primitive mammalian character) is a long *pre-hallucal sesamoid* which articulates proximally with the internal angle of the head of the astragalus. The mesocuneiform is short and quadrate, the ectocuneiform longer, the cuboid large and over twice as long as it is broad. The cuboid overlaps the ectocuneiform. The evenly developed digits call for no special note save that distally digits II, III and IV appear subequal, III being slightly the longest, a frequent Insectivore character.

In the proportions of the digits and of the cuneiforms the pes of *Solenodon* is suggestive of that of the common rat.

Phyletic Interpretation of the Osteological Characters of Solenodon paradoxus.

Primitive Marsupio-Placental Characters. General architecture of skull and skeleton. Basifacial and basicranial axis nearly continuous; olfactory chamber relatively large, cerebral chamber relatively small. Interparietal paired; orbitosphenoid invaded anteriorly by ethmoid chamber; pituitary depression slight, without posterior clinoid process; basioccipital very short. Alisphenoids with prominent palatine flanges. Posterior border of palate ridged. General arrangement of ethmoids and maxillo-turbinals. Tympanic ring-shaped, oblique rather than vertical. Arrangement of following nerve foramina: olfactory, internal auditory meatus, facial canal, fenestra ovalis, foramen lacerum anterius and posterius, sphenopalatine, post-palatine stylomastoid, and condylar foramina (the last occasionally double). Venous foramina: transverse canal in basisphenoid (*cf. Didelphis*), ? sinus canal in temporal region, post-parietal, post-squamosal, post-glenoid, post-mastoid foramina. Upper molars derived from the tritubercular type, lower molars with trigonid and small talonid.

Tail stout at proximal end, with large chevrons. Scapula with bifid acromion, high spine and large coracoid; a stout clavicle; Humerus with stout crests, entepicondylar foramen and globular capitellum. Manus with five clawed digits, separate centrale, large trapezoid and a "præpollex." Ilium rod-shaped. Femur with third trochanter. Pes with five well clawed digits, entocuneiform very long, mesocuneiform short, a "præhallux"; manus and pes fully plantigrade.

Points of special resemblance to Marsupials: Vomer with large lateral posterior wings, joining ethmoid scroll. Large venous condylar foramina. A remnant of the tympanic wing of the alisphenoid. Posterior mental foramen beneath m_1.

Primitive Placental Characters. Dental formula derived by slight reduction from $\frac{3.1.4.3.}{3.1.4.3.}$; deciduous dentition well developed. Orbitosphenoid pierced by optic foramen and *not* depressed dorsoventrally in such a way that the opposite sphenorbital fissures are confluent beneath it (contrast Marsupials); alisphenoid relatively small and not entering the glenoid fossa. Optic foramen separate from foramen lacerum anterius.

Seventh cervical vertebra not pierced by vertebral artery; dorso-lumbars 20.

Many other characters listed under the next heading may perhaps belong also under the present heading.

Primitive Insectivore characters. General configuration of young skull, especially the long tubular snout; opposite alveolar borders of premaxillaries parallel. I $\frac{1}{2}$ enlarged (the extreme enlargement is secondary). Canine bifanged (possibly independently acquired). Premolars conical, $p\frac{1}{1}$ absent; fourth upper and lower premolar submolariform. Molars with high pointed cusps; enlarged internal cusp of upper molars homologous with protocone of *Ictops* and *Dryolestes*, (*cf.* Fig. 17, no. 3), basal internal cusps derived from the cingulum; lower molars with very small talonid, lacking hypoconid; protocone of upper molars received into cingulum fossa or space back of protoconid (all as in Jurassic Trituberculates and presumably primitive). No post orbital process, orbit broadly continuous with temporal fossa. Palate well ossified, fenestræ slight or absent (*cf. Ictops*, vacuities in *Erinaceus* secondary). No ectopterygoid fossæ, the pterygoid wings of the palatines and alisphenoids forming a single straight ridge on either side; true pterygoids probably represented by cartilages. Tympanic branch of alisphenoid joining post-glenoid crest of squamosal; post-tympanic process separated from glenoid fossa.

Auditory prominence of petrosal ovoid, closely appressed to basioccipital, with depression on inferior surface (all as in *Ictops*). Basioccipital contributing largely to the occipital condyles. Mastoid exposure large. Hole between basi- and pre- sphenoids in the mid line probably an apophysis of the vestigial "hypobasal notochord." Foramen rotundum confluent with sphenorbital fissure. Prominent "sinus canal"; suboptic foramen leading to presphenoid sinus.

Osseous intercentra below posterior dorsals and lumbars. Humerus of young with slight vestige of supratrochlear foramen (entirely lost in adult). Radius and ulna curved longitudinally. Ilium rod shaped. Pelvis with general resemblances to that of *Erinaceus* (however, Leche's specimens of *S. paradoxus* has a long symphysis pubis).

Tibia and fibula with tendency to fuse distally. Digits II, III, IV, of both manus and pes, subequal, digit III being slightly longer especially in the pes; distal metapodial joints transversely cylindrical, keels slight or absent; ungues compressed not fissured at the tips (secondarily fissured in Talpidæ). Astragalus with tibial notch near to internal trochlear crest, the latter prominent; external and internal malleolar facets subvertical, neck somewhat oblique, head transversely flattened, ectal facet triangular, sustentacular facet an elongate oval set near the internal posterior border. Calcaneum with short tuber, large sustentaculum, spreading antero-inferior base; a prominent antero-external process.

Primitive Zalambdodont characters. Upper molars remaining V-shaped, with basal pseudoprotocone and hypocone; para- and metacones reduced,

situated on external border, parastyla prominent, a median external notch. Lower molars retaining high trigonid, low talonid and postero-external cingulum-fossa for the reception of the protocone; no hypoconid. Dental formula: $\frac{3.1.3.3.}{3.1.3.3.}$ Posterior mental foramina below m_1 (below the last premolar in Hyopsodontidæ, Leptictidæ Erinaceidæ, Tupaiidæ; *cf.* Matthew, 1909, p. 126).

Skull subcylindrical. Nasals fused proximally (in adult); malar absent, long low sagittal crest, broad occiput. Mastoid facing obliquely outward rather than backward (*cf. Microgale, Potamogale*; contrast however Leptictidæ, Erinaceidæ). Infraorbital canal short and wide; lachrymal foramen external, optic foramen very small, foramen lacerum anterius large, foramen rotundum united with for. lac. anterius. Lower border of mastoid with a circular pit near which opens the stylomastoid foramen, and probably entocarotid foramen. Glenoid fossa of squamosal facing obliquely outward and partly backward; postglenoid process located internally and well separated from post-tympanic process. Fibula not touching calcaneum.

Solenodont characters. $I\frac{1}{2}$ much enlarged, i_2 with deep internal groove. Pseudoprotocone and hypocone forming small distinct cusps. A prenasal ossicle. Skull retaining a slight interorbital constriction. No tympanic wings on basisphenoid (possibly secondary). Petrosal with a small tympanic process. A "supra-ethmoid" and a "supra-optic" venous foramen. Carpus specialized in enlarged magnum, and flattened lunar. Astragalus with sharp internal trochlear keel and long neck.

The general bearing of the preceding analyses is discussed below (p. 267).

THE CHRYSOCHLORIDÆ.

The very thorough researches of Mivart (1867, 1868), Dobson (1887) Leche (1907) and others have demonstrated that the Cape Golden Moles are a very highly specialized but early offshoot of the Zalambdodont stem.

Far less indubitable however appears Leche's conclusion (1907, pp. 141–142) that certain characters (*e. g.*, structure of the zygomatic arch, dental replacement in old animals, relations of the rectus abdominis muscle, etc.) indicate that the Chrysochloridæ are the lowest type among all existing Eutheria, and that, although highly aberrant and degenerate in many characters they occupy a more primitive, lower position than does any other group of Insectivores and actually approach the Monotremes and reptiles!

Chrysochloris resembles the Marsupial Mole *Notoryctes* in so many characters that Cope (1892) inferred an immediate genetic connection between the two genera and regarded *Notoryctes* as a transitional form connecting the Insectivores with the Marsupials. Leche shows that the

resemblance extends in far more diverse directions than might have been expected, including such characters common to both groups as the following: (1) Iridescence of the hair; (2) presence of a nasal shield; (3) general configuration of the skull; (4) presence of a "third lower arm bone" (an ossification in the tendon of the flexor digitorum profundus muscle — only the distal end ossified in *Notoryctes*); (5) peculiar specialization of the claws (different digits, however, are concerned in the two cases); (6) great reduction of the thyroid ("obturator") foramen; (7) insertion of the latissimus dorsi muscle; (8) form of the brain (extraordinarily similar).

To this list of convergent characters may be added, somewhat doubtfully: (9) similarity in the dentition, especially in the molars. This character Leche omits because "ein gemeinsamer Charakter sehr alten Datums sein kann, und nicht der Konvergenz seine Entstehung zu verdanken braucht." While very true as a general proposition, this dictum is very possibly not applicable here. Bensley (1903, p. 120), accepting the view that in *Chrysochloris* the main internal cusp is equivalent to the combined para- and metacone of *Talpa*, suggests that in *Notoryctes* also the main internal cusp is homologous with the combined para- and metacone of Didelphids. There are however reasons for doubting (pp. 238, 290) this assumed cusp homology even in *Chrysochloris*. But at any rate, in view of the probability that *Notoryctes* is a highly specialized offshoot of the Polyprotodont stock, it seems likely that the total lack of a talonid in the lower molars of *Notoryctes* is a secondary condition and that the spacing of both upper and lower molars is an indication that formerly the anteroposterior diameters of both upper and lower molars were greater than at present, and that therefore the resemblances between the molars of *Chrysochloris* and those of *Notoryctes* are in part due to convergent or parallel modifications from somewhat similar beginnings.

(10) A further resemblance lies in the fact that in *Notoryctes* the number of incisors are reduced to $\frac{3}{3}$ while the total number of teeth is the same as in *Chrysochloris* (Leche, 1907, p. 58).

Several additional resemblances between *Notoryctes* and *Chrysochloris* appear in the skeleton, *e. g.*, humerus with entocondyle greatly produced; olecranon very long and hook-like. Leche regards this as the most complete case of convergence known among the higher animals.

The following observations may now be added in order to reinforce Leche's conclusion that there is at most only a very remote (subclass) genetic connection between *Notoryctes* and *Chrysochloris*:

(1) The skull of *Chrysochloris* presents only a superficial analogy with that of *Notoryctes*: In *Notoryctes* the malar is rather stout and appears to be of the normal Polyprotodont type; in *Chrysochloris* the malar is lacking and the zygomatic arch is composed chiefly of the zygomatic process of

the maxillary (Leche). Instead of the condition of the zygomatic arch being an indication of affinity to the Monotremes, as held by Leche (p. 141) it may rather be due to the derivation of *Chrysochloris* from some Zalambdodont which had already lost the malar, but which later evolved a new zygomatic arch out of the zygomatic process of the maxillary, which grew backward until it touched the zygomatic process of the squamosal. Here then would lie a deep seated difference from the *Notoryctes* skull.

In *Notoryctes* the cranial sutures tend to remain open (Stirling, 1891) as in Marsupials, but in *Chrysochloris* as in Insectivora they are obliterated even in the very young skull.

The conditions in the auditory region in *Notoryctes* and *Chrysochloris* are radically different. A comparison of specimens of *Chrysochloris aurea* and *Notoryctes typhlops* in the American Museum shows that in *Notoryctes* the conditions are directly comparable with those in the smaller Dasyurids such as *Antechinomys* and *Phascocologale, i. e.*, there is a very large "alisphenoid bulla," which conjoins posteriorly with an expansion of the petrosal, the entotympanic (p. 246), while the true tympanic takes no part in bounding the tympanic cavity, but lies in the postero-external border of the alisphenoid bulla (*cf.* also van Kampen, 1905, p. 404). In *Chrysochloris* on the contrary the conditions in this region are rightly described by Leche (1907, p. 73) as "ein Differenzierungsprodukt des Verhaltens bei Centetidæ und zwar zunächst der ursprünglichsten Formen dieser Familie, der Oryzoictinæ." As in *Microgale* (Fig. 13, B), the tympanic processes of the ali- and basisphenoid form a rim which in *Chrysochloris* is semicircular and embraces the periphery of the expanded hemispherical tympanic. No better example could be cited, of the importance of the auditory region in the study of ordinal relationships, and of "palæotelic" characters of this kind as compared with "cænotelic" or adaptive resemblances.

The proximal ends of the nasals of *Notoryctes* spread widely, as in Marsupials. In *Chrysochloris*, owing to the absence of sutures it cannot be affirmed positively that the nasals do not spread proximally, but in the top view of the skull the nasal region compares so closely with that in the Centetoidea that there seems little reason to doubt that the nasals ended proximally in a median V and likewise very early coalesced. The *Chrysochloris* skull also shows the tubular form of the fronto-parietal region which is so characteristic of the Centetoids.

The jaw of *Notoryctes* has a typically inflected angle, a sharp external masseteric ridge, and a pterygoid fossa, as in Marsupials, whereas the characters of the *Chrysochloris* jaw may readily be derived from those of the *Microgale* type.

(2) Many of the similarities in the skeleton are associated with differ-

ences which are equally striking and more significant of the wide genetic separation in the two forms. For example, in the humerus of both forms the entocondylar process is greatly produced. But this is only an exaggeration of a feature that is common among fossorial mammals, (*e. g., Orycteropus, Dasypus, Spalax*) and is associated with very striking differences in the other parts of the bone (*e. g.*, in the deltoid and supinator crests, greater and lesser tuberosities). The long, hook-like olecranon of the ulna is equally a fossorial character which is realized to a less extent in *Spalax* and *Dasypus*. The scapula of *Notoryctes* is of the broad fossorial type, with a second or posterior spine analogous to that in Edentates, while the scapula in *Chrysochloris* is of the *Sorex* type with high spine, narrow blade and broad bifid acromion. The pelvis of *Notoryctes* approaches that of *Chrysochloris* in the great reduction of the thyroid fenestra, yet it retains strong evidence of derivation from the Marsupial type, especially in its vestigial marsupial bones (Stirling, 1891, p. 178), while the pelvis of *Chrysochloris*, presents no feature inconsistent with derivation from the *Microgale* type. The pes of *Notoryctes* and *Chrysochloris* are very unlike, the pes of the former showing some traces of the Marsupial syndactyly (Winge, Dollo; Bensley, 1903 p. 172) while the pes of *Chrysochloris* conforms to the Insectivore type.

These resemblances and differences have been cited at some length, partly in illustration of the principles discussed on pages 107, 111, 463.

The occurrence of Chrysochlorids in the Oligocene of North America has been recorded by Matthew (1906) who referred to that family the following forms: *Xenotherium unicum* Douglass (1906), based on a skull without teeth; *Apternodus mediævus* Matthew (1903.1) based on a fragment of a lower jaw with several molar teeth, *Micropternodus borealis* Matthew (1903.1) an imperfect lower jaw; *Arctoryctes terrenus* Matthew (Lower Miocene) based on a humerus with marked Chrysochlorid characteristics. The skull of *Xenotherium* (*cf.* Douglass, 1906, pl. xxi) resembles that of *Chrysochloris aurea* (*cf.*, Dobson, 1883, pl. xi) not only in general appearance but especially in many significant details: such as the hemispherical form of the bullæ, the form of the snout, zygomatic arch, peculiar lateral occipital crest on the squamosal, etc. The only important difference is in the character of the cheek-teeth alveoli, which in *Xenotherium* are circular, in *Chrysochloris* triangular. On the other hand *Xenotherium* parallels the Miocene Talpid *Proscalops* (*cf.* p. 265) in its brachycephalic proportions and in several of the characters noted above, but the molars must have been very different.

In regard to *Apternodus*, Matthew now (1909) describes it as having "Molars as in *Centetes*, premolars reduced to three." The possibility that the genus may be a member of the Centetoidea is also indicated by the following observations:

The type lower jaw of *Apternodus mediævus*, so far as known, presents many resemblances to the jaw of *Microgale dobsoni*: *e. g.*, peculiar shape of angle, ridge on inner side of angle, sharp ridge above and in front of dental foramen, position of condyle, molars with high pointed protoconid, very small talonid, no hypoconid. The differences are mostly such as separate more primitive from more advanced forms. In *Apternodus* the protoconids are not so tall and not directed backward, the protoconid-paraconid shear is less pronounced, not so sharply turned forward, the metaconid is less reduced, the external cingulum is prominent, while in *Microgale* it is much reduced.

Micropternodus (*cf.* Matthew, 1909, pl. li) is also very likely a primitive member of the Centetidæ. The talonid is less reduced than in *Apternodus* These two genera seem to throw but little light on the question whether the small size of the talonid in Zalambdodonts is a primary or a secondary character.

THE NECROLESTIDÆ.

The genus *Necrolestes* Ameghino from the Santa Cruz Beds (Lower Miocene) is the Patagonian analogue of the Cape Golden Moles. After a very thorough examination of the dentition skull, vertebræ and limbs Professor Scott (1903–5) showed that the resemblances between the two genera are very numerous and close and that "the differences are, for the most part, such as usually occur between the earlier and later members of a phylum or of two allied phyla. ....It is not suggested that *Necrolestes* is to be regarded as the ancestor of any of the existing *Chrysochloridæ*, for it is itself specialized in a different, though moderate way. What does seem probable is that *Necrolestes* is an offshoot from some early members of the family which was at the same time the ancestor of *Chrysochloris*" (*op. cit.*, pp. 379–380). Professor Scott also compared *Necrolestes* with *Notoryctes* and showed that in every detail the former approximated to the Placental Insectivore type, the latter to the Marsupial type, and that the resemblances between the two genera were entirely convergent.

Necrolestes is less differentiated than *Chrysochloris* in the dentition, in the retention of a faint postorbital constriction, stouter zygomata, more moderate squamosal swelling on side of head, more normal carpals, etc. It has a long bony rostrum which suggests the cartilaginous rostrum of the Shrew (*cf.* Parker, 1885–6, pl. 31) and of the Centetidæ. This bony rostrum may also be represented among living forms by the prenasal ossicle of *Solenodon*. *Necrolestes* is more specialized than *Chrysochloris* chiefly in the characters of the femur. The series of seven cheek teeth (including the canine) de-

creases from the front backward and converges slightly toward the mesial line, features which are emphasized in *Xenotherium*.

The Erinaceoidea.

THE LEPTICTIDÆ, ERINACEIDÆ, DIMYLIDÆ.

The most primitive representatives of this group are the Eocene and Oligocene Leptictidæ. They have already lost one upper and one lower incisor, except *Ictops acutidens*, which retains three small lower incisors (Matthew, 1903, p. 207, fig. 5); but in the form of the cheek teeth they are much more primitive than the Erinaceidæ and some of them retain the minute $pm\frac{1}{1}$, which are lost in most Insectivores. The *molars* in *Palæictops* and *Ictops* suggest those of the Jurassic *Dryolestes* in their antero-posterior narrowness, and sometimes (*e. g.*, in the very small *Ictops thomsoni* Matthew, 1903.1) also in the large size and centro-external position of the paracone. But in the larger species *Ictops major* (Douglass, 1906, pl. xxii) the molars are much broader antero-posteriorly and the para- and metacones are subequal. In all Leptictids $p\frac{4}{4}$ are molariform. The lower molars are tuberculosectorial with reduced paraconids and large hypoconids. In crown view the inner and outer cusps are rather widely separated. The replacement of the teeth takes place only after the animal has attained full adult dimensions (Matthew, 1909, p. 534). This delayed replacement is also characteristic of certain Zalambdodonts and may be a primitive Insectivore character.

In *Proterix* Matthew (1903.2), a primitive member of the Erinaceidæ which shows clear evidence of derivation from the Leptictidæ, the molars are broader antero-posteriorly and the hypocone is well developed. The molars are in fact described as definitely Erinaceid, only the last molar remaining tritubercular, as it does in *Hylomys*, *Neurogymnurus*, and *Galerix*.

In the living Erinaceidæ the antero-posterior broadening of the molars is still more emphasized and they are more bunodont and omnivorous in type than in the earlier forms. At the same time the fourth upper premolar has acquired a sectorial postero-internal blade, paralleling that in the modern Carnivora.

The **skull** of *Ictops* (figured by Douglass, 1906, pl. xxii) offers some interesting points both of resemblance and contrast to that of its modern relatives *Gymnura* and *Erinaceus* and shows how much change may have taken place since the Oligocene, even in very primitive forms. In *profile* the skull slopes anteriorly into a long slender muzzle, much as in the primitive Centetoid *Microgale*, and contrasts with the relatively straight profile and heavy muzzle of *Gymnura* and *Erinaceus*. The *mid-cranial region* is not elongate

as it is in the Centetoids, and the skull is gently constricted back of the orbits. The smooth cerebral hemispheres (as shown by the natural cast of the brain) were confined almost wholly to the parietal segment, only the large olfactory lobes occupying the frontal segment (as in primitive mammals generally). The opposite *temporal crests* were considerably separated and not pronounced. The *zygomata* were slender, but heavier than in the Erinaceidæ, not inclined sharply downward and forward as they are in *Erinaceus*. There was a depression in the maxillary at the anterior root of the zygoma. This is not represented in *Erinaceus*. The *orbito-temporal fossa* was ovoid as in Menotyphla, less extended antero-posteriorly than in the Centetidæ.

In palatal aspect the skull rather suggests that of *Microgale* but is relatively broader. The *palate*, as in *Gymnura*, was not fenestrated and the posterior border did not, as it does in *Erinaceus*, terminate in a prominent transverse ridge but was rounded (*cf. Solenodon*). Hence two of the so-called Marsupial characters of *Erinaceus* were absent in its Oligocene forerunner. There is, however, a postero-external palatal foramen as in Marsupials, Creodonts and Menotyphla. The *basicranial region* differs considerably in details but not in fundamental characters from the same region in *Erinaceus* and *Gymnura*. The *pterygoidal ridges* of the palatine and alisphenoid are single on each side, as in Centetidæ so that there are no ectopterygoid fossæ. The *tympanic flange of the basisphenoid* appears to be lacking and the large ovoid petrosal is closely appressed to the side of the basioccipital (*cf. Solenodon*). This (if the drawing of *Ictops montanus* be correctly interpreted) is perhaps surprising, because the Miocene *Caylux-otherium* (*Neurogymnurus*) (*cf.* Filhol, 1884, pl. i), which is generally regarded as an Erinaceid and therefore as a relative of the Leptictidæ, already had the tympanic wing of the basisphenoid highly developed. The *"tympanic" process of the alisphenoid* in *Ictops*, as in the Zalambdodonts, is continuous with the postglenoid ridge of the squamosal. In *Erinaceus* the alisphenoid portion of this ridge is present and is notched inferiorly for a branch of the entocarotid (p. 247), but the squamosal portion of the post-glenoid ridge is atrophied. *Ictops* further agrees with the Zalambdodonts or rather with *Solenodon* in the fact that the *post-glenoid and post-tympanic processes* are well separate (widely so in *Ictops*), whereas in *Erinaceus* these two are represented by the single "post-glenoid" process, which is located behind the post-glenoid foramen; the post-glenoid process in Zalambdodonts lies nearer the inner border, in *Ictops* on the outer border, of the glenoid fossa. The large *tympanic fossa* of *Ictops* is accordingly bounded anteriorly by the combined alisphenoid-post-glenoid ridge. Externally it is bounded by a long ridge of the squamosal corresponding to the external auditory

meatus and connecting the post-glenoid and post-tympanic processes. Thus as seen from above the tympanic fossa of *Ictops montanus* is very broad and square externally, whereas in *Erinaceus*, through the coalescence of the post-glenoid and post-tympanic process, the tympanic fossa is triangular. The *mastoid exposure* in *Ictops* faces backward, in *Erinaceus* backward and outward. In this one point *Erinaceus* agrees better with the Zalambdodonts than does *Ictops*. The large round pit in the under surface of the basisphenoid of *Erinaceus* is not represented in *Ictops*. *Occipital condyles* are represented in one specimen (Douglass, *l. c.*, pl. xxii, fig. 1) as extending entirely across the basioccipital. The *paroccipital* processes appear to have been absent (*cf. Microgale*). The *occiput* was broad and nearly flat. The *angle of the mandible* was gently inturned, as in certain species of *Erinaceus*.

In the *skeleton* Douglass's figures show that the curved shaft of the ulna was stout, the olecranon short, the femur had a well developed third trochanter, the fibula was already fused with the tibia; the astragalus had a well-grooved narrow trochlea and the anterointernal end of the astragalus was produced into a broad prominence, which is not however prolonged into a distinct process (contrast *Mircogale*); the tuber of the calcaneum was stout and not long, betokening a plantigrade foot. All these are characters which might be expected in an ancestor of *Erinaceus*.

In conclusion, *Ictops* was apparently much more primitive than *Erinaceus:* in the very small size of some of its species, in the long slender muzzle, small subcaniniform upper canines, procumbent lower incisors, very primitive narrow tritubercular upper molars, slender mandible, horizontal well developed malar, unfenestrated palate, unexcavated basisphenoid, large post-glenoid ridge, separate post-glenoid and post-tympanic processes. In practically all these characters *Ictops* makes some approach backward toward the stem of the Zalambdodonta.

The foregoing review of the chief characters of *Ictops*, the most primitive of the Leptictidæ, confirms the lowly position of that family and its ancestral relation to the Erinaceidæ. *Ictops* also possessed a number of the characters assumed below (p. 272) for the ancestors of the Tupaiidæ and other Menotyphlous Insectivora, but how far these indications are valid is at present impossible to say.

The Leptictid skeleton and skull, so far as known, do not show any fossorial adaptations (unless the fusion of the tibia and fibula be so interpreted) and some of the smaller species may have been arboreal.

Of the recent Erinaceidæ *Gymnura* and the nearly allied *Hylomys* [1] are more primitive than *Erinaceus* in the following characters:

[1] Excellent figures of the skeleton of *Hylomys peguensis* are given by Anderson (1874, pl. lxiv).

(1) Smaller size. (2) Longer muzzle, which makes some approach to that of *Ictops* in form. (3) $I\frac{3}{3}$, $p\frac{4}{4}$ (reduced to $i\frac{2}{2}$, $p\frac{3}{2}$ in *Erinaceus*). (4) Molars retaining clearer traces of trituberculy than in *Erinaceus*. (5) Tail present (reduced in *Erinaceus*). (6) Partly climbing habits and arboreal adaptations. Under side of tail rough (Blanford), stiff spines on feet to aid in climbing (Dobson, 1883). (7) Humerus retaining entepicondylar foramen. (8) Scaphoid and lunar separate in young, united in old individuals (Dobson, 1883, p. 21). (9) Pollex constant (tending to reduction in some species of *Erinaceus*). (10) Third trochanter in femur retained in reduced condition. (Still more reduced in *Erinaceus*).

The genetic relations of the Erinacoidea are discussed below (p. 266).

"*Cayluxotherium*," (*Neurogymnurus*), an Erinaceid from the Upper Eocene or Oligocene (Phosphorites) in France has palatal vacuities and very large stout tympanic wings of the basisphenoid (*cf.* p. 261).

The Dimylidæ are noticed below (p. 267).

The Soricoidea.

THE SORICIDÆ AND TALPIDÆ.

The Talpidæ and Soricidæ have very probably diverged from a common stem, the typical Talpidæ having acquired high fossorial specializations in the limbs while the Soricidæ have developed a very peculiar and highly modified antemolar dentition. The Talpidæ alone have preserved the malar bones, although in a greatly reduced condition, while the Soricidæ have retained very primitive limbs, and frequently a cloaca (Dobson). The tympanic in the Soricidæ remains horizontal and ring shaped and the arrangement of the three branches of the entocarotid approximates that in *Erinaceus* (van Kampen, 1905, pp. 434–435).

The connection of the Talpidæ and Soricidæ is indicated by the survival in the ancient fauna of Thibet and China of certain primitive Talpids, notably *Uropsilus soricipes* (figured by Milne Edwards, 1868–74, pl. xl, xla; described also by Dobson, 1883, p. 145). This interesting genus in the general characters of the skull and body resembles *Urotrichus* of the Myogalinæ (*vide infra*) but in its fore feet and tail it resembles the Shrews (Dobson). The humerus, while foreshadowing that of the Moles in its strong muscular attachments, is still of the normal Soricoid type (Dobson, p. 164). The manus, pes and shrew-like tail are scaly (Dobson).

The semiaquatic Desmans (*Myogale moschata* and *M. pyrenaica*) together with the fossorial genera *Urotrichus* and *Neürotrichus* form a very primitive subfamily of Talpoids, of which *Myogale* parallels the Zalambdodont genus

Solenodon in the chisel-like enlargement of the anterior incisors and in certain features of the skull (p. 242). But a comparison of the base, and top views of the cranium of *Myogale* with that of the Talpidæ (Dobson, 1883, pl. xx) leaves little doubt as to the Talpoid affinities of this group. This impression is confirmed by the characters of the scapula (Dobson, *l. c.*, pl. xv) and humerus, in which, however, the Talpoid peculiarities are still in an unemphasized condition.

The dental characters of the Myogalinæ are clearly represented in the Miocene Talpoid *Proscalops* Matthew (1905.2, 1909, pl. li; *cf.* Fig. 17, no. 9, above).

The tympanic region in *Myogale* is of especial interest because it elucidates the structure of this region in the Talpoidea and furnishes a strong bond of affinity between the Soricoid, the Erinaceoid and the Centetoid superfamilies (*vide infra*). The tympanic wing of the basisphenoid is greatly expanded and forms with the broad ring-shaped tympanic a large composite bulla which on the anterointernal end extends to the mesopterygoid fossa and almost meets its fellow of the opposite side. Anteriorly the tympanic ring is partly embraced by the well developed tympanic branch of the alisphenoid; posteriorly the petrosal also contributes a tympanic branch to the bulla (*cf. Solenodon*, p. 246) and van Kampen suggests (1905, p. 452) that this branch is homologous with the entotympanic of Menotyphla and Marsupials. The large entocarotid foramen deeply notches this branch of the petrosal. The Eustachian foramen is seen near the anterior end of the bulla, at the junction of the tympanic wings of the ali- and basisphenoids with the true tympanic annulus. Immediately external to the foramen ovale is a foramen, which seems comparable with the foramen for the inferior branch of the stapedial artery in *Erinaceus* (p. 247).

The affinities of the Soricoidea are discussed below (p. 265).

Genetic Interrelations of the Lipotyphlous Insectivores (Summary).

The preceding observations afford strong evidence for the inference that the Lipotyphlous Insectivores form a natural group divisible into the four well separated superfamilies which were recognized by Gill in 1872, *viz*: the Centetoidea (including the Centetidæ Potamogalidæ and Solenodontidæ), the Chrysochloroidea (including the Necrolestidæ and Chrysochloridæ), the Erinaceoidea (including the Leptictidæ Erinaceidæ, Dimylidæ) and the Soricoidea (including the Soricidæ, Myogalidæ and Talpidæ). The Chrysochloroidea are probably a specialized offshoot of the Centetoidea and the two superfamilies form a natural group, the Zalambdodonta of Gill (1885), which, however, scarcely ranks as a suborder, unless the Lipotyphla as a

whole are to be regarded as an order. Whether the Lipotyphla should be so regarded depends upon the question (p. 285) whether the Tupaioidea and Macroscelidoidea have been derived from forms which might come within the definition of the Lipotyphla.

Soricoidea. The Talpidæ seem to be linked ancestrally with the Soricidæ through the primitive genera *Myogale*, *Urotrichus* and *Uropsilus* the first of which approaches the typical Talpidæ, while the last is Shrew-like in almost everything except its dentition.

Remote affinity of the Soricoidea with the Erinaceoidea is revealed in the characters of the larynx, lungs, vascular system, liver and especially in the urinary and generative organs (Dobson, pp. 157–159). The condition of the tympanic region in the Soricidæ is more primitive than in the Erinaceidæ, since the tympanic bone remains ring-shaped and neither the basi- nor the alisphenoid send down tympanic processes. The arrangement of the three branches of the entocarotid conforms in general to the primitive Lipotyphlous plan (van Kampen, 1905, p. 435). The so called intercentra, which are doubtfully to be homologized with the intercentra of reptiles, (Weber, 1904, p. 86) are found below the lumbar vertebræ in *Talpa* and in a reduced condition in *Erinaceus*, and are also well marked in *Myogale* (Dobson, p. 147).

Affinities between the Soricoidea and the Centetoidea are suggested by Leche (1907, p. 121), who cites in this connection: the general form of the skull (*cf. Sorex* and *Microgale*), the strong postglenoid process, the loss of the malar in the Soricidæ, the form of the hinder part of the palate, the presence of a cloaca (in many Soricidæ), and the occurrence of an accessory erectile gland in the penis. According to Leche's suggestion the molars in Talpidæ and Soricidæ may be similar in their mode of formation to those in the Centetidæ, that is, the internal depressed ledge is possibly a "pseudoprotocone" (p. 238). In *Proscalops* Matthew (1909, pl. li) the basal cingulum pseudoprotocone is doubtfully distinct from the true protocone (Fig. 17, no. 9). In *Myogale* the pseudoprotocone has increased in size and is barely distinct from the protocone. In typical Soricidæ and Talpidæ the two cusps are no longer distinguishable. Leche says also that *Microgale* with respect to its antemolar dentition furnishes a morphological stage in the evolution of the peculiar antemolar dentition of the Soricidæ.

Additional evidence of affinities with both the Erinaceoidea and the Centetoidea is furnished by the numerous resemblances in the arrangement of the foramina: *e. g.*, in *Sorex* the "sinus canal" on the side of the skull is very prominent (Parker, 1885–6, pl. 31), the foramen rotundum is confluent with the foramen lacerum anterius; the entocarotid foramina are described above, one branch perforating the basisphenoid as in Marsupials,

Erinaceus and *Centetes*. In the Soricoidea also the cartilaginous snout in the embryo is prolonged far beyond the premaxillaries (*cf.* the cartilaginous snout of the embryo *Centetes*, the prenasal ossicle of *Solenodon* and the bony rostrum of *Necrolestes*). Finally the Soricoidea resemble the Erinaceidæ and the Centitidæ in the possession of a common type of malleus: one with "a wide lamina and a processus gracilis [Folii] united to the tympanic ring after the fashion of the Marsupials" (Doran, 1879, p. 444).

Winge has suggested (*cf.* van Kampen, 1905, p. 452) "dass die Übereinstimmung zwischen *Talpidæ* und *Chrysochloridæ* nicht bloss durch Anpassung zu erklären ist.... sondern wohl wirklich auf Verwandtschaft beruht" (van Kampen). But the numerous resemblances cited above, as well as certain generalized Centetoid features of *Necrolestes*, seem only to warrant the inference that the stem form of the Soricoidea (which was doubtless not yet Mole-like in its limbs) is related to the stem of the Centetoidea on the one hand and to the stem of the Erinaceoidea on the other.

Erinaceoidea. The Erinaceidæ, through the more primitive genera *Gymnura, Hylomys* and the Oligocene *Proterix*, seem to be linked securely to the very primitive Eocene and Oligocene Leptictidæ. Of these the less specialized forms of the genus *Ictops* are more primitive than the typical Erinaceidæ in many characters especially the following: the skull as a whole is mesaticephalic whereas in *Erinaceus* it is brachycephalic with the muzzle broad and short; the zygomatic arches are well developed, the post-glenoid and post-tympanic processes are separate, the palate is not fenestrated; the pterygoidal ridges are single (*i. e.*, there are no ectopterygoid fossæ), the tympanic wings of the basisphenoid if present are but moderately developed; and the "tympanic" or postglenoid ridge of the alisphenoid is well developed (*cf. Microgale*).

The dentition also is very primitive: the canines remain subcaniniform, $p\frac{1}{1}$ are retained, the upper molars (in *Ictops*) are of a simple tritubercular type with a low hypocone and narrow anteroposteriorly; the milk dentition persists until the animal has attained adult stature.

The common origin of the Erinaceoidea and the Centetoidea is indicated especially by the following characters: In both families the malleus is of the same type, namely with the processus gracilis very broad and perforated by the chorda tympani nerve (Doran, 1879, p. 444), while the incus and stapes in the two families are also closely similar (Doran, *l. c.*, p. 440, pl. 62, figs. 11–14). The base of the cranium in *Centetes* and *Erinaceus* presents very numerous resemblances recorded above (pp. 244, 245), especially the median pit, the median foramen for the chorda, the strong development of the tympanic wing of the basisphenoid, the course of the three branches of the entocarotid artery and the arrangement of most of the foramina. Leche lays

stress upon the similarity in brain structure (1907, p. 121), while Dobson (1883) calls attention to important agreements in the musculature. Certain of these similarities may well have been developed independently in the two groups, but taken collectively they leave no doubt of a community of origin. The Miocene Dimylidæ of Schlosser, known chiefly from the dentition, appear to be a specialized offshoot of the Erinaceid stem (*cf.* Zittel 1891–93, p. 568).

Chrysochloroidea. This superfamily (pp. 255, 259) is shown to be an offshoot of the stem of the Centetoidea by the peculiar characters of the dentition, the general architecture of the skull, shape of the pelvis, etc. This inference is reinforced by the evidence furnished by the tympanic region, the peculiarities of which are readily derived from the conditions preserved in *Microgale* (Leche). These further tend to disprove the suggestion of any near affinity with the Talpidæ: for, in the Chrysochloridæ the true tympanic bone becomes hemispherical and is encircled at its base by a continuous horizontal ring, formed from tympanic branches of the petrosal, basi- and alisphenoids; and, although in the Talpidæ the same elements contribute to the complex bulla, and thereby reveal the subordinal relationship of the two families, yet here the proportions of the several elements are very different, the basisphenoid wing being very large, while the true tympanic remains as a broad subvertical zone with a large meatus. The malleus and incus of *Chrysochloris* are extremely specialized and peculiar and throw no light upon its relationships (Doran, 1879, p. 438, pl. 62, figs. 9–10). The stapes however is of the widely open stirrup type which is common among Insectivora.

The Patagonian Miocene genus *Necrolestes* (p. 259) suggests as the common stem form of the Chrysochloridæ and Necrolestidæ a brachycephalic but long snouted Zalambdodont. As all known Zalambdodonts except these two families are markedly dolichocephalic it is evident that the gap between the Chrysochloroidea and the Centetoidea has not yet been bridged over by palæontological discovery.

Centetoidea. Perhaps the dominant feature of the Centetidæ is the progressive lengthening of the skull especially of the middle and facial parts. Correlated with this and perhaps also with the large size of the olfactory lobes of the brain, is the loss of the postorbital constriction and the resulting cylindrical shape of the anterior part of the brain case. The malars are absent, the nasals coalesce very early, the sagittal crest is very long and low, the posterior mental foramen lies beneath m_1. $P\frac{1}{1}$ are lost; the upper molars consist of a high internal V-shaped cusp, reduced external cusps and a small "pseudoprotocone" and hypocone. The lower molars have a very small talonid without a distinct hypoconid. The dorsolumbar vertebræ (21–24) are more numerous than in the Erinaceoidea (20).

Since the common origin of the Centetoidea and Erinaceoidea seems well assured from the evidence cited on page 266, we must believe that most of the special Centetid characters above enumerated, except possibly the V-shaped protocone of the upper molars, the lack of a hypoconid, and the position of the posterior mental foramen, have been acquired by the Centetidæ after they became separated from the forerunners of the Erinaceoidea.

The date of this separation can at present only be determined within very wide limits. It was certainly not later than the Lower Eocene, for in the Eocene and Oligocene the family Leptictidæ had already become Erinaceoid in many characters, while by the time of the Lower Oligocene the Zalambdodonts had differentiated into Chrysochlorids (p. 258) and Centetids (*Apternodus*, p. 259), the Solenodontidæ also possibly being represented by *Micropternodus* (p. 259).

As to the lower limit for the date of separation there is still less to guide us. If the *Potamogale* upper molar be more primitive than the *Microgale* molar then the morphological gap between the *Microgale* and presumably the *Apternodus* molar on the one hand and the *Ictops* molar on the other is very profound and the separate phylogenetic lines representing the Leptictidæ and the Centetidæ would have to be prolonged back very far before they would run together. If on the contrary (as seems on the whole more probable) the *Microgale* molar is the primitive Centetid type, then the principal difference between it and the more primitive *Ictops* molar lies in the reduction of the paracone and sometimes its fusion with the parastyle. In that case the lower limit for the separation of the Erinaceoids and Centetoids might perhaps be the Basal Eocene or Upper Cretaceous.

Solenodontidæ. The analysis of the characters of *Solenodon paradoxus* given on pages 253–255 fully supports the view that this family belongs in the Zalambdodonta and has only a subordinal relationship with *Myogale*, which resembles it in several homoplastic characters in the skull and incisors.

In several characters (*e. g.*, retention of postorbital constriction, a suboptic canal communicating with the presphenoid sinus, absence of tympanic wing on basisphenoid, form and relations of petrosal) *Solenodon* resembles either *Ictops* or the Erinaceidæ rather than the Centetidæ, and the resulting suggestion is that the Solenodontidæ have been derived, not from any early Madagascan Centetids but from some more generalized Holarctic Zalambdodonts, such as *Micropternodus* of the American Oligocene (p. 259).

The Menotyphla.

The group including the families Tupaiidæ and Macroscelididæ appear to be very widely removed from the other Insectivora, so far, in fact, that it

is probable they should be set apart as an entirely distinct order, Menotyphla Haeckel, as indicated in 1884 by Leche (1884–1885).

No monograph of the same scope as those of Dobson and Leche on the lipotyphlous Insectivores has been devoted to the Menotyphla. Preserved specimens and skeletons are rare, at least in American museums, and no figures of the skull and skeleton appear in the leading modern text-books on mammals. Excellent figures of the skeletons and skulls of different members of the group are, however, given in de Blainville's 'Ostéographie,' and by Peters (1852) and Mivart (1868).

Parker (1885–86, p. 247), Elliot Smith (1902) and Broom (1902) have recognized Marsupial affinities in the Macroscelididæ but writers in general seem to ignore the importance of the Menotyphla as a group in the study of the genetic relations of the mammalian orders. No other living Placental suborder shows resemblances and possibly affinities to so many widely different orders as do the Tupaiidæ. In the skull and dentition, as will be shown, the different forms present certain resemblances to the Leptictidæ, to *Galeopithecus*, to the Chiroptera and to the Lemurs; while in the brain of *Macroscelides* and in the tympanic region of *Tupaia* and *Ptilocercus* we find a remarkable combination of Marsupial and Placental features (*vide infra*).

The following review of the genetically more significant characters of the Menotyphla is based partly on the skeletal material in the National Museum (which the writer has had the privilege of examining through the courtesy of Drs. True and Lyon), partly on the figures of the skeleton given by de Blainville and Peters (1852), and partly on the writings of Mivart (1868), Weber (1904), van Kampen (1905) and others.

THE TUPAIIDÆ.

Habits. The very squirrel-like appearance and habits of the Oriental Tree Shrew (*Tupaia*) are described by Gill (1885, p. 14). The Tupaias contrast sharply with the lipotyphlous Insectivores in their thoroughly arboreal and diurnal habits, lively disposition and great agility, as well as in their mixed diet of fruit and insects. They occasionally sit up on their haunches and hold their food between the fore legs. They sleep in rudely constructed lairs in the highest branches of the trees. In adaptation to arboreal habits the manus and pes are provided with strong claws, slightly divergent pollex and hallux and well developed palmar and plantar pads (Fig. 20).

Ptilocercus lowii Gray (1848, pl. ii), the Pen-tailed Tree Shrew of Sarawak and Borneo, is likewise arboreal and is very phalanger-like, especially in its tail, which as in *Distœchurus*, ends in a vane of stiff hairs on either side.

Hairs. In *Ptilocercus* as in *Macroscelides* the hairs on the tail are grouped in threes behind the scales (Weber, 1904, p. 363) a very primitive mammalian character (see p. 146), while in *Ptilocercus* the proximal part of the tail is scaly (Beddard, 1902).

Cæcum. Peters observed that *Macroscelides* and its allies, unlike other Insectivores have a cæcum and Hæckel therefore applied the name " Meno-

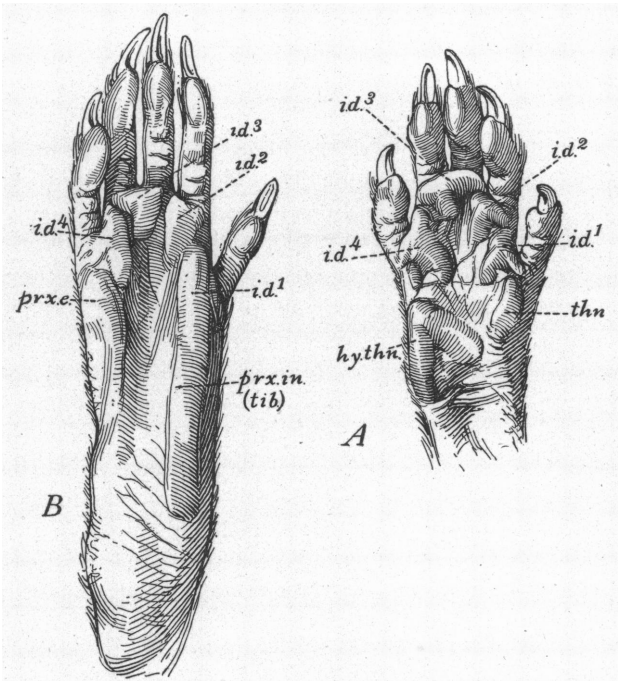


Fig. 20. *A.*, Palmar surface of the manus, *B.*, plantar surface of the pes of *Tupaia* sp. Arboreal adaptations shown in the divergent pollex and hallux, strong claws and arrangement of palmar and plantar pads. × ⅔.

i.d^1., *i.d*^{2}., *id*^{3}, *i.d*^{4}., interdigital pads.
then., thenar pad.
hy.thn., hypothenar pad.
prx.in., internal proximal pad.
prx.e., external proximal pad.

typhla" to the group including the Tupaiidæ and Macroscelididæ. But Flower, Beddard and Chapman, (1904) state that at least in *Tupaia tana* the cæcum is wanting, although a minute cæcum is retained in *T. belangeri* (Beddard, 1902, p. 511).

Sublingua. The sublingua of *Tupaia* is stated to be like that of the Lemuroid *Chiromys* (Garrod, quoted by Beddard, 1902).

Testes. The Tupaiidæ stand higher than any other Insectivores in the permanent descent of the testes into a hairy scrotum, as opposed to a temporary descent into a "cremaster sack." But the conditions are more primitive than in typical Placentals: first, because the opposite testes are not appressed to each other but each remains enclosed in its own cremaster sack in the scrotum; secondly, because the testes do not continue their descent beyond the penis but remain anterior to it and thus parallel the conditions in *Macropus* (*cf.* Weber, 1904, p. 271, fig. 226).

Uterus. In *Tupaia*, as in *Gymnura*, the median corpus uteri may become so short that the right and left uteri are almost entirely separate (Weber), but they never open separately into the vagina and the conditions are thus much less primitive than in *Orycteropus* and many Rodents.

Dentition. Tupaia (Fig. 22, *B*) and *Ptilocercus* (Fig. 21) lack only i^3 and $p\frac{1}{1}$ of the complete Placental formula. I^1 is subvertical (in *Ptilocercus* it is also enlarged) and pointed and its posterior side coöperates with the procumbent i_1 i_2 in seizing the food. This condition could apparently give rise to the diprotodont modification observed in the Mixodectidæ and certain lemuroids. I^2 (?) in *Tupaia* is simple, in *Ptilocercus* it is a relatively large premolariform tooth with a small posterior basal cusp. It opposes the minute i_3 and the compressed sub-premolariform lower canine. I^3 appears to be represented in *Ptilocercus* by a minute alveolus. The *upper canine* in *Tupaia* is small conic, not recurved. In *Ptilocercus* it is like the adjacent premolar (p^2) and has two roots. The *lower canine* in both genera is quite small, and works in front of p^2, $p\frac{1}{1}$ apparently being absent.

Thus with regard to the front teeth *Ptilocercus* and *Tupaia* agree in family characters. The former however approaches the conditions seen in the primitive Zalambdodont *Microgale* much more closely than does *Tupaia*; but it seems quite possible that these resemblances are homoplastic.

$P\frac{2}{2}$, $p\frac{3}{3}$ are much more reduced in *Ptilocercus* than in *Tupaia* and in this reduction the former genus parallels the Shrews, *Myogale* and other Insectivores with enlarged anterior incisors. $P\frac{4}{4}$ and $m\frac{1-3}{1-3}$ in *Tupaia* have higher more pointed cusps than in *Ptilocercus*, in which omnivorous adaptations are indicated in the more bunodont crown and stouter hypocone; and this fact, taken in connection with the enlarged anterior incisors and stouter malars of *Ptilocercus* suggest greater powers of mastication and perhaps a larger proportion of fruits and seeds in the diet. The *upper molars* of *Ptilocercus* (Fig. 21) have in certain respects departed less from the primitive type exhibited in *Ictops* than have those of *Tupaia*: for in *Tupaia* the para- and metastyles are very prominent and the mesostyle (in correlation with the enlargement of the hypoconid) is very large and exhibits a tendency to divide in two (*cf. Galeopithecus*) whereas in *Ptilocercus* the mesostyle is

absent. In the latter genus the metastyle is enlarged, oblique; the hypocone oblique, broadly ledge-like and continuous with an internal cingulum (absent in *Tupaia*); reduced metaconules are present and the molars as a whole are of the general type seen in the Middle Eocene (Bridger) *Nyctitherium nitidum* (*cf.* Matthew, 1909, pl. l, fig. 6). Resemblances to certain of the Bridger Insectivores is especially clear also in the lower dentition, which compares well with that of *Entomolestes grangeri* (*cf.* Matthew, 1909, pl. l, fig. 2) in many significant details.

In brief the dentition of *Ptilocercus* has departed from the primitive Insectivore type represented in *Ictops* in so far as it reveals a slight emphasis of the tendencies toward diprotodonty, toward reduction of the premolars and toward the omnivorous modification of the molars; but on the whole it is a rather primitive Placental dentition. The dentition of *Tupaia* has avoided these tendencies and has retained more completely the triangular form of the upper molars; but on the other hand it has emphasized the insectivorous features, such as enlarged styles, sharply pointed cusps, etc., and has acquired a large and more or less divided mesostyle.

Skull (Figs. 21, 22). In many characters the *skull of the Tupaiidæ differs widely from that of any Lipotyphlous Insectivore* and approaches the lemuroid type. The braincase is large and rounded, the skull-top broadly convex between the orbits, the large orbits enclosed posteriorly by processes from the frontal and malar; the skull as a whole is mesati- to brachycephalic, contrasting strongly with the Zalambdodont type, and further lemuroid resemblances are shown in the tympanic region (see below), in the partial bending down of the face upon the basicranial axis, in the presence of a malar foramen etc.

So far as concerns only general characters and proportions, there seems little to refute the suggestion that the *ancestral Tupaiid had a skull resembling that of Ictops* in respect to the following characters: muzzle moderately elongate, postorbital constriction gentle, breadth between orbits considerable, brain case rounded, temporal crests well separated, anterior part of zygoma stout, posterior part slender; small postglenoid well separated from post-tympanic process, ectopterygoid fossæ absent or incipient.

As compared with this hypothetical norm or ancestral type *Ptilocercus seems more primitive than Tupaia* in the following characters: smaller braincase and orbits, narrower interorbital region, somewhat stouter zygomata, less reduced postglenoid process, greater space between the postglenoid and posttympanic, no secondary septa in the bulla, smaller bulla, partly exposed petrosal, better defined tympanic wing of alisphenoid, optic foramen well separated from foramen lacerum anterius; no supraorbital foramen. In the skull figured by Mivart (1867, p. 303) the postorbital

processes of the frontal and malar have not yet met and this region also is accordingly less specialized than in *Tupaia*.

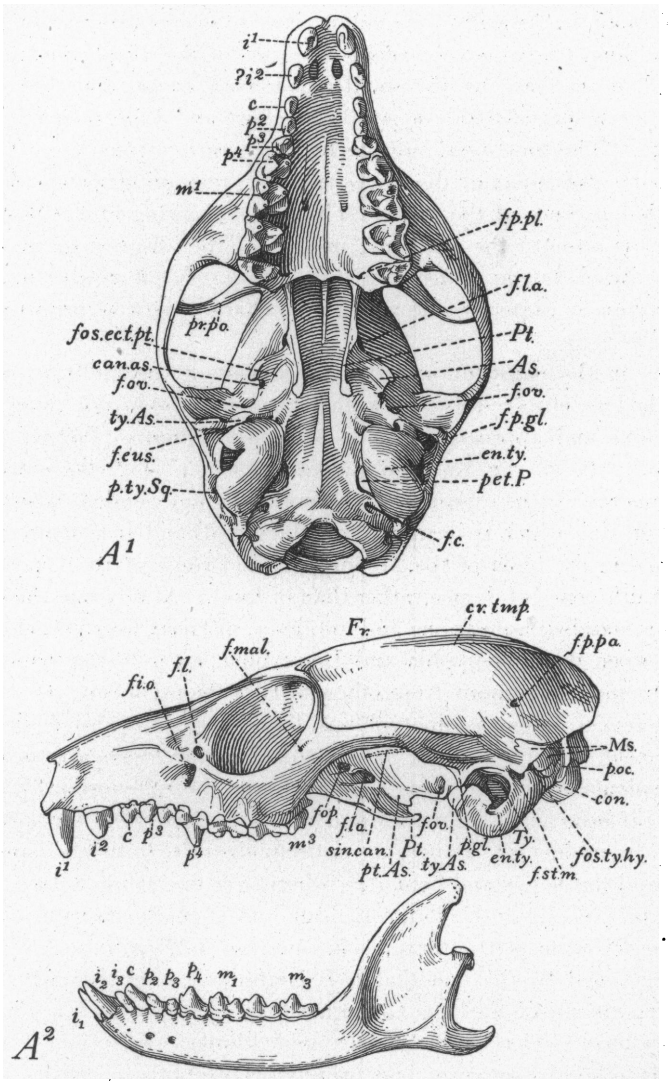


Fig. 21. Skull and lower jaw of *Ptilocercus lowii* Gray. U. S. Nat. Mus. No. 112611. × $\frac{3}{4}$. *A*1, palatal view, *A*2, side view. Abbreviations as in Fig. 18, p. 243.
en.ty., entotympanic; *Ty.*, ectotympanic.

Amid all these differences the *skulls of Tupaia and Ptilocercus reveal their family relationship* not only in the details cited above (p. 272) but espe-

cially in their close agreement in the characters of the base of the skull. In both genera the *palate* is thinly ossified and in *Tupaia* this thinness causes small irregular vacuities in the hinder part. The true *pterygoids* end in small backwardly directed processes, which are widely separated from the low, triangular pterygoid processes of the alisphenoid; these are tunneled at the base by the small alisphenoid canal, and the two wings together form on each side a peculiarly short and wide *ectopterygoid fossa* (Fig. 21). The functional *bulla* in both genera is formed from the greatly expanded entotympanic, the true tympanic remaining as a delicate ring inside the entrance of the bulla. The tympanic wing of the basisphenoid is slight or absent; the tympanic process of the alisphenoid in *Tupaia* is much reduced, but in *Ptilocercus* (Fig. 21, *ty. As.*) it retains more of the concavity on its posterior side which is so characteristic of primitive marsupials.

Thus in the constitution and arrangement of the auditory region the Tupaiidæ, as observed by all authorities, *differ radically from the other Insectivores* and approach the non-Malagasy Lemurs (Weber, 1904, pp. 366, 745). If, as van Kampen suggests (1905, p. 452) the entotympanic represents merely the expanded and secondarily independent tympanic wing of the petrosal, which is seen in many Marsupials and Insectivores, then the difference in the bulla of the Menotyphla and those of the Lipotyphla becomes a difference of degree rather than of kind. At any rate the difference as it now stands is a great one and implies a relatively long period of separation between the Menotyphla and Lipotyphla, an inference which is reinforced by much testimony from other parts of the organism.

Differences from the lipotyphlous Insectivores are also evident in the *arrangement of the foramina.* In *Tupaia* the *optic foramen* is so large that only a spicule of bone remains between it and the sphenorbital fissure. In *Ptilocercus* however it is smaller and well separated from the latter. The *foramen rotundum* in *Tupaia* is entirely distinct from the sphenorbital fissure and lies below and behind it, whereas in lipotyphlous Insectivores as well as in *Ptilocercus* the foramen rotundum is confluent with that fissure. The identification of the foramen in question in *Tupaia* as the rotundum is strengthened by the fact that it is continuous internally with a groove which has the position of the Gasserian fossa (for nerve V_2). The *foramen ovale* is almost hidden beneath the expanded bulla.

As in other Insectivores and primitive Placentals an *alisphenoid canal* pierces the base of the pterygoid flange of the alisphenoid (*cf. Ptilocercus,* Fig. 21, *c. al.*) and there is a prominent *sinus canal* on the side of the brain case, opening anteriorly in a *supraorbital foramen.*

Lower jaw. The slender lower jaw of *Tupaia* is not distinguished by

any marked specializations, and parallels that of *Myrmecobius*. The coronoid is delicate, the angle hook-like and slightly inturned, and the condyle transverse but not much extended. The jaws figured by Anderson (Yunnan Expedition, pl. vii) vary considerably in the different species, and this variability is likewise shown in the position of the mental foramina which are usually below p_3 and p_4, but sometimes below c and p_2.

In *Ptilocerus*, in correlation with greater powers of mastication and the diprotodont modification of the incisors the lower jaw is shorter and stouter especially anteriorly, and the coronoid process and the fossa for the temporal muscles are larger and better developed (Fig. 21).

Ossicula auditus. According to Doran (1879, p. 442) the malleus of *Tupaia*, "in being neckless and devoid of lamina....much resembles that of some of the lower Primates, especially *Midas* or *Hapale*, or certain Lemurs, the shallow articular facets being a Ceboid feature. The incus has a high and narrow body and in general characters is "very like the same in many Monkeys and Lemurs." The stapedial crura are straight (they are curved in Lipotyphla). The stapes is pierced by a bony canal (as in Lipotyphla).

The *vertebral formula*, as determined from a skeleton of *Tupaia* sp. in the National Museum is C. 7, D. 13, L. 6, S. 3, Cd. 26; as determined from de Blainville's figures of *Glisorex* (*Tupaia*) *ferrugineus* it is C. 7, D 13, L 7, S 2, Cd. 23. Mivart, however (1867, p. 294), states that there are only 5 or 6 lumbars, so that the dorsolumbars appear to vary (DL 18–20). This formula compares with that of primitive forms in other groups as follows[1]:

	Dorso-lumbars (average)	Sacrals (average)
Monotremata	19—20 (*cf.* p. 153)	3—4
Marsupialia	19 (13 + 6)	2—3
Creodonta	20 (13 + 7)	3
Carnivora	20 (13 + 7)	3
Lemuroidea	19—20 (12—13 + 6—7)	3
Tupaia	19—20 (13 + 6—7)	3
Gymnura	20 (15 + 5)	3
Microgale	22 (16 + 6)	2
Solenodon	19—20 (15—16 + 4)	2
Sorex	20 (14 + 6)	4
Galeopithecus	18—19 (13—14 + 7—5)	4—5
Rodentia	19 (12—13 + 7—6)	3—4
Ardiodactyla	19—20 (13 + 6 frequent)	4—5

In its vertebral formula *Tupaia* is thus evidently very primitive, more so than most other Insectivores.

In correlation with the non-fossorial, climbing habits, the *sacrum* is

[1] The table is based upon data given in Bronn's ' Thierreich ' (pp. 240–252) and by Leche (1907, p. 77.)

Fig. 22. *A.* Skeleton of *Tupaia ferruginea.* After de Blainville. × $\frac{7}{10}$. *B.* Left upper cheek teeth of *Tupaia modesta.* Amer. Mus. No. 26658. × $\frac{3}{1}$.

attached to the ilium by means of only one much enlarged transverse process. The lumbar vertebræ have forwardly directed parapophyses, this indicating fairly well developed leaping muscles which are lacking in the fossorial Insectivores.

As the majority of the remaining characters of the skeleton are given below (p. 279) under the heading "primitive mammalian characters," only a few additional points need be noted here.

The *ilium* has lost the primitive rod-like shape, which is preserved in *Microgale*, and has a narrow spatulate concave surface for the gluteal muscles. There is a prominent pectineal process on the neck of the ilium, as in Monotremes, Marsupials, *Orycteropus*, etc.

The *pubo-ischiadic symphysis* in all the Menotyphla is relatively long, much longer than is usually the case in the Lipotyphla.

The *limbs* are much longer and the elbows and knees better exserted from the body than in the Lipotyphla; the humerus and femur are of approximately equal length with the forearm and lower leg respectively, whereas in the Lipotyphla they are shorter.

The slender *humerus* has an entepicondylar foramen, a long low deltoid crest and a small supinator crest, all as in many other primitive mammals.

The *femur* retains a well developed third trochanter. The patella trochlea is not deeply grooved (*cf.* the flat trochlea of Marsupials and *Solenodon*).

The *fibula* is complete and separate. Proximally it expands considerably (*cf. Microgale*) but not as much as in Marsupials.

The *hand and foot* are rather long and slender. The palmar and plantar surfaces (Fig. 20) exhibit generalized arboreal characters. The ungues are compressed. The pollex and hallux of *Tupaia* diverge slightly, but *Ptilocercus* is represented by Gray (1848) with a spreading hand and a divergent pollex and hallux.

The *carpus* resembles that of *Ericulus* in the following details: the scapholunar is broad and shallow (in *Ericulus*, however, the scaphoid and lunar are merely appressed to each other), the relatively large flattened centrale rests upon the trapezoid and articulates with the side of the magnum; the lunar rests chiefly on the centrale and partly on the unciform, but in front view appears as in *Lemur*, to be excluded from contact with the magnum by the centrale. Resemblances to the carpus of *Sorex* are seen in the flattening and horizontality of the transverse facets. Resemblances to *Galeopithecus* and certain lemuroid types are the compression of the small sized magnum and its close appression to the unciform. In brief the carpus, like the rest of the anatomy serves to emphasize the position of *Tupaia* as a morphologically annectant form between the true Insectivores and the lemuroids.

The *astragalus* of *Tupaia* is of especial interest because on the whole, it resembles the Primate types and contrasts with those of all the Lipotyphla in important details. As in the lemurs the trochlea is narrow above (proximally) and broader below, the inner or tibial crest less prominent than the outer or fibular crest and the trochlear concavity very slight; the trochlea also extends postero-dorsally above the ectal or calcaneal facet. The malleolar facets are subvertical and that on the tibial side extends antero-inferiorly below the trochlea. The head (navicular facet) is very ovoid and extends well up on the antero-external corner. In the back view also the resemblances to the lemuroids are numerous. The ectal facet is obliquely extended and the rather long sustentacular facet is broadly continuous below with the navicular facet; whereas in the Lipotyphla the ectal facet is usually subtriangular and the oval sustentacular is separated from the navicular facet. The *calcaneum* as in other plantigrade and arboreal mammals has a very short tuber.

Dissection of an alcoholic specimen of *Tupaia* sp. shows that the lemuroid characters of the tarsus may be related to arboreal habits, *e. g.* the strong internal and external malleoli, with their vertical facets on the astragalus, evidently serve to prevent lateral dislocation and to limit the motion of the astragalus upon the tibia to the fore and aft plane; the dorsal continuation of the trochlea permits extreme extension of the foot upon the tibia, the long oblique neck and oval head may permit the sole to be turned inward as in climbing, the short tuber calcis enables the foot to be extended very suddenly and is thus of advantage in leaping.

Adaptive Contrasts between Tupaia and Solenodon.

The foregoing descriptions of *Solenodon* (pp. 253–255) and *Tupaia* (pp. 272–278) offer some instructive contrasts when considered in connection with the diverse habits of the two forms. In *Solenodon* all the skeletal adaptations, such as the very powerful limbs, plantigrade feet, heavy claws, arched back and very stout tail, indicate a slow-moving type analogous to *Orycteropus*. In *Tupaia* the skull and skeleton express with equal clearness the animal's arboreal habits, quick senses and great agility. It is very probable that the arboreal type of skeleton represented in *Tupaia* is on the whole more primitive (except as to the large brain case, and other features) than the terrestrial, semifossorial type represented by *Solenodon*; partly because the latter is distinguished by certain specializations, such as the loss of divergence of the pollex and hallux, the development of very strong trochlear ridges on the astragalus, the incipient coälescence of the tibia and fibula, the loss of lumbar parapophyses etc.

Phyletic Interpretation of the more Important Characters of the Tupaiidæ.

Primitive Marsupio-Placental Characters. ? Arboreal habits and adaptations (p. 226); ? diet including insects and fruits; hairs on tail in groups of three (*Ptilocercus*); $p\frac{4}{4}$ not molariform; upper molars tritubercular, lower molars tuberculo-sectorial; arrangement of the majority of the cranial foramina except the optic and carotid foramina and the alisphenoid canal; lachrymal foramen marginal or external; tympanic ring-shaped; seven cervical vertebræ, parapophyses on lumbars; sacrum attached to pelvis by one enlarged transverse process; vertebræ, ribs, sternum, scapula, clavicle, pelvis and limb bones all normal; tail long, back arched; an entipicondylar foramen; a third trochanter; pelvis with normal pubic symphysis; tibia or fibula not united, borne on astragalus alone; manus and pes plantigrade, digits V–V, claws compressed, pollex and hallux divergent; carpus normal, with free centrale; tarsus normal.

Special resemblances to Marsupials. Phalanger-like appearance of *Ptilocercus*; scrotum in *Tupaia* remaining prepenial; slight palatal vacuities (*Tupaia*); alisphenoid forming a small tympanic process; an entotympanic, possibly derived from the tympanic process of the petrosal of Marsupials (van Kampen); a venous posterior condylar foramen (*Ptilocercus*).

Primitive Placental Characters (*cf.* also, "Marsupio-Placental" characters above). Dental formula derived by reduction from $\frac{3.1.4.3.}{3.1.4.3.}$; $m\frac{3}{3}$; milk dentition well developed (Weber, 1904, p. 370); $p\frac{4}{4}$ not molariform; an alisphenoid canal; optic well separated from foramen lacerum anterius (*Ptilocercus* only).

Insectivore characters. Insectivorous habits; elongate snout, elongate premaxillaries; reduced canines; incipient diprotodonty; $p\frac{1}{1}$ absent (a frequent, but not invariable, Insectivore specialization); $p\frac{2-3}{2-3}$ more or less reduced; molars in *Tupaia* with sharp pointed cusps and enlarged styles; resemblances to *Ictops* in the skull of the ancestral Tupaiid; foramen rotundum confluent with for. lac. anterius (*Ptilocercus*); "sinus canal" and supraorbital foramen prominent; stapes pierced by a bony stapedial canal; digits II, III, IV subequal in both manus and pes, digit III being slightly the longest; centrale carpi large; scaphoid uniting with lunar; uterus bicornis.

Lemuroid characters. Arboreal habits, ability to sit up and hold the food between the hands; omnivorous modification of the molars (*Ptilocercus*) brain and brain case large, cerebrum invading the frontal segment, face bending down upon cranium; skull wide between orbits, a postorbital bar, large orbits; supraorbital (*Tupaia*) and malar foramina; ectopterygoid

fossæ suggesting lemuroid condition; bulla chiefly from entotympanic; malleus and incus approximating to the lemuroid and ceboid types (Doran), stapes with straight crura; lemuroid resemblances in the lower jaw, especially of *Ptilocercus*; hands and feet rather long, provided with lemuroid palmar pads; certain features of the carpus (p. 277); characters of the astragalus; a lemuroid sublingua; testes descending into a hairy scrotum; placenta discoidal, deciduate.

Menotyphlous characters: Cæcum present, at least in some species (often reduced or absent); bulla formed chiefly from the enlarged entotympanic; parapophyses on lumbar vertebræ well developed; puboischiadic symphysis long; limbs longer than in Lipotyphla and well exserted from the body; astragalar trochlear extending dorsad above ectal facet; sustentacular facet of astragalus elongate and broadly continuous with navicular facet (may not hold in Macroscelididæ).

Tupaiid characters (contrast Macroscelididæ): Arboreal habits and adaptations; skull broad between orbits; orbits large, limited posteriorly by a postorbital bar formed from the frontals and malars; peculiar ectopterygoid fossæ; dental formula $\frac{2.1.3.3.}{3.1.3.3.}$; $I\frac{2}{2}$ enlarged, $c\frac{1}{1}$ small; $p\frac{2-3}{2-3}$ reduced; upper molars triangular, tritubercular; diet including fruits and insects; ilium spatulate; testes descending into a hairy prepenial scrotum.

THE MACROSCELIDIDÆ.

The leading authorities on the general anatomy of this group are Peters (1852, Taf. xix–xxiv) and Mivart (1867, pp. 295–298). Parker (1885–86, pl. 36), figures the fœtal skull of *Rhynchocyon*. De Blainville (1838–1864, Insectivores, pll. iii, v) figures the skull and skeleton of Macroscelides.

Brain. The brain of *Macroscelides* is of extraordinary interest. The base of the brain, according to Elliot Smith (1902) presents an assemblage of characters found equally in Insectivora, Polyprotodont Marsupials and Dasypodidæ. In the cerebrum the anterior commissure is smaller than in Marsupials; "above it is a typically metatheroid commissure of crescentic shape such as occurs in *Perameles, Notoryctes, Didelphys* and *Myrmecobius*." The hippocampal formation extends forward on to the upper surface of this (anterior) commissure just as happens also in the Metatheria. But a typical Eutherian character is the "undoubted corpus callosum' which is "exceedingly large and thin, and exhibits a state of affairs which is almost unknown beyond the limits of the Primates." "Both in shape, size and position [high up near the dorsal margin of the hemisphere] this .... is as unlike the primitive generalized condition of the corpus callosum, such as is found in *Erinaceus*, as it is possible to imagine."

Jacobson's organ. In all the peculiarities of its Jacobson's organ, *Macroscelides*, according to Broom (1902, p. 227), resembles the Marsupials rather than the Placentals, and Broom believes that it is "a very near relative of the Marsupials, with probably very little affinity with the more typical Insectivores."

Testes. In the Macroscelididæ (as in *Centetes*) the testes retain permanently their primitive position near the kidneys. There is no trace of an inguinal ligament nor any other structural feature which might indicate a former descent of the testes and a secondary return (as in Cetacea) to the earlier condition (Weber, 1904, p. 270).

Dentition. The *incisors* show the insectivorous modification, i^1 and i_2 being slightly enlarged. The tips of the crowns of the lower incisors are more or less trilobed, a peculiarity which is emphasized in the three-pronged incisor tips in *Rhynchocyon*, which are thus structurally prototypal to the comb-like incisors of *Galeopithecus*. The *canine* is two-rooted and premolariform, *i. e.*, with two roots and two cusps.

Dental formula. Mivart (1867, p. 296) gave the dental formula of *Macroscelides* as $\frac{3.1.3.3.}{3.1.3.3-(4).}$, but Thomas (1890, p. 445) showed, from the relations of the milk and permanent dentitions that the first pair of molariform teeth in both jaws are really $p\frac{4}{4}$, and that the revised formula is $\frac{3.1.4.2.}{3.1.4.2 \text{ or } 3.}$. Accordingly *Macroscelides* is one of the few Insectivores that retain $p\frac{1}{1}$, and the supposed occasional m_4 (Mivart, 1867, p. 298) is really m_3.

The *cheek teeth* are quadritubercular, subhypsodont and without cingula, and are thus analogous to those of *Perameles*. This type of hypsodont molar is rather frequent in fossorial and semifossorial animals and may be adapted to withstand the detrital action of the earth which is mixed with the food (Bensley). The molar cusps are rounded, and the upper molar crowns are practically bilophodont.

Skull.[1] The skull is entirely unlike that of any lipotyphlous Insectivore but is allied to that of *Tupaia* by the structure of the bulla. The tympanic forms a tubular auditory meatus which fits internally into the inflated entotympanic. The basisphenoid and the petrosal also take some part in limiting the tympanic cavity but not to the same degree as in lipotyphlous Insectivores (van Kampen, 1905, p. 444). The alisphenoid is inflated, immediately in front of the bulla, and Parker (1885–86, p. 275 and pl. 36) found that in *Rhynchocyon* the alisphenoid developed large tympanic wings, which in the embryo were "well marked hollow shells" (*cf.* Marsupials). The region of

[1] The following description of the skull applies chiefly to the highly specialized *Macroscelides*. The skull of *Rhynchocyon* (Peters, 1852, taf. xxii) approaches that of *Tupaia* in its broad convex forehead, distinct postorbital processes on malar and frontal, broad palate, hamular process on pterygoid, etc. A general resemblance to the skull of *Galeopithecus* is also evident

the mastoid, squamosal and exoccipital is also swollen and cancellous, recalling similar conditions in the Rodent family Heteromyidæ and in *Phascologale* among Marsupials. The *brain case* is large and rounded but narrow between the orbits (contrast *Tupaia*). The *orbital fossa* is very large but the postorbital processes are absent (*Macroscelides*) or small (*Petrodromus*). The malar extends back to the glenoid, as in *Tupaia* certain Rodents and Marsupials. The malar has a large anterior surface for the insertion of the anterior part of the masseter (*cf. Tupaia*). The *glenoid fossa* is extended anteroposteriorly more than in *Tupaia* and much as in primitive Rodents. The *palatal vacuities* are very extensive antero-posteriorly. This "Marsupial" feature is reinforced by the prominent raised posterior rim of the palate and by the palatal foramen at the postero-external angle of the palate. (A similar foramen appears in *Ictops* and other Lipotyphla and in certain Creodonts.) A large *interparietal* is figured by Parker in *Rhynchocyon* (*op. cit.*, pl. 36), and this genus appears to agree further with lipotyphlous Insectivores in having a median perforation in the basisphenoid (probably for the vestigial notochord) and cartilaginous pterygoids. The vomer is stated by Parker (*op. cit.*, p. 275) to have the postero-lateral wings "as large as in average Marsupials" (*cf., Solenodon,* p. 253).

Ossicula auditus. According to Doran (1879, pp. 440–442, 444, pl. 62, figs. 15, 16) the malleus in the Macroscelididæ is of very peculiar type. In the Lipotyphla the processus gracilis (Folii) is curved so as to fit accurately to the tympanic ring, as in Marsupials, but in *Macroscelides* and *Rhynchocyon* the processus gracilis forms a thin straight bar which fits into the Glaserian fissure; the extremely constricted neck and the narrow lamina are also characteristic. The malleus of *Petrodromus* departs less widely from the *Sorex* type. The incus of *Petrodromus* tends toward that of *Tupaia*. The stapes in the Macroscelididæ has straight crura as in *Tupaia* (contrast the curved crura of Lipotyphla); the stapes is perforated by a bony canal for the stapedial artery, as in Lipotyphla.

Cranial foramina, etc. As described by Mivart (1867, p. 296) the optic foramen is large and very slightly separated from the sphenoidal fissure. In *Rhynchocyon* Parker (1885–86, p. 275) found that the optic was entirely confluent with the foramen lacerum anterius. A *suboptic* foramen, analogous to that in the Erinaceoidea and Centetidea is also present. The *foramen rotundum,* as in most Insectivores, is confluent with the foramen lacerum anterius. The alisphenoid canal is absent (contrast Tupaiidæ) and there is also no supraorbital foramen. The lachrymal foramen "opens well within the orbit" (contrast Tupaiidæ). Mivart also states that there is a "small carotid foramen near the margin of the auditory bulla (immediately opposite the middle of the occipital condyle)." The mental foramen "opens beneath the antepenultimate molar" (*cf.* Tupaiidæ).

Skeleton.— The Macroscelididæ are terrestrial, saltatorial and more or less fossorial in habit and structure, paralleling the Peramelidæ. These habits are reflected in the following modifications in the skeleton of *Macroscelides*: (1) forearm long and slender, with fused radius and ulna; (2) pes elongate; (3) femur short; (4) fibula reduced and fused with the tibia; (5) ilium erect; (6) pubic symphysis short; (7) lumbar and sacral spines large; (8) back arched; (9) neck short; (10) head held sharply inclined to the neck. In the pes the astragalus has a deep trochlea with a prominent projecting internal rim. The digits are very elongate but compare in essentials with those of *Tupaia*. In *Rhynchocyon* and *Petrodromus* the hallux is wanting. In *Rhyncocyon* (*cf.* Peters 1852, Taf. xxiii) the skeleton is in many features intermediate between those of *Tupaia* and *Macroscelides*.

The *vertebral formula*, as determined from de Blainville's figure of *Macroscelides rozetii* is C 7, D. 13, L 7, S. 3, Cd. 26. Mivart states (1867, p. 298) that both Peters and de Blainville assigned 7 lumbar vertebræ to this genus, but also that in a certain specimen of *M. intufi* there are but 19 dorsolumbars. Accordingly *Macroscelides* may be regarded as having 19 to 20 dorsolumbars, whereas *Tupaia* has 18 to 20 (Mivart, *op. cit.*, p. 294). In *Rhynchocyon cirnei* the formula is: C.7, D.13, L.8, S.3, Cd. 28 (*cf.* Peters *l. c.*, Taf. xxiii) *i. e.*, DL. 21.

The *carpus* of *Rhynchocyon* is noticed below (p. 445).

Phyletic interpretation of the more important characters of the Macroscelididæ.

Primitive Marsupio-Placental Characters. Testes remaining abdominal; brain and Jacobson's organ very primitive in certain features.

Special resemblances to the Marsupials: brain with a "typically metatheroid commissure" etc.; Jacobson's organ of Marsupial type; malar extending back to glenoid fossa; large palatal vacuities; alisphenoid scarcely overlapping the orbitosphenoid (Parker); optic foramen more or less confluent with for. lac. anterius; a concave tympanic process of the alisphenoid (*Rhynchocyon*); vomer with large postero-lateral wings.

Primitive Placental characters: a corpus callosum; placenta discoidal deciduate (Broom, 1902, p. 227); dentition derived from $\frac{3.1.4.3.}{3.1.4.3.}$ by the loss of one or more molars; manus pentadactyl (*Petrodromus* only); carpus with free centrale.

Primitive Insectivore characters. A long cartilaginous snout; premaxillaries elongate, canines more or less premolariform; $p\frac{4}{4}$ molariform; a large interparietal; a median (chordal) perforation in the basisphenoid (*Rhynchocyon*); pterygoids terminating in small cartilages; stapes perforated

by a bony stapedial canal; foramen rotundum confluent with foramen lacerum anterius, a suboptic foramen (*Rhynchocyon*); mental foramen opening beneath p_3.

Primitive Menotyphlous characters. Bulla formed chiefly from the entotympanic, tympanic ring-shaped (here tubular); postorbital processes (*Rhyncocyon*); malar with enlarged area for the insertion of an anterior slip of the masseter; malar extending back to glenoid (*cf. Tupaia*); brain case large and rounded, broad between orbits (*Rhyncocyon*); astragalus a modified form of the *Tupaia* type; vertebral formula differing from that of *Tupaia* only in the presence of one or two additional lumbar vertebræ; parapophyses well developed on lumbars.

Macroscelid characters. Corpus callosum approximating the Primate type; lower incisors with denticulate tips (*Rhyncocyon*); dental formula $\frac{3.1.4.2.}{3.1.4.2. \text{ or } 3.}$; cheek teeth quadritubercular, bilophodont, hypsodont; malleus with constricted neck and narrow lamina, processus gracilis a straight bar fitting into Glaserian fissure; lachrymal foramen internal; no alisphenoid canal; saltatorial and fossorial modifications of skeleton.

Genetic relations of the Menotyphla.

The Tupaiidæ and Macroscelididæ have been shown to resemble each other in many significant details, especially in the mode of formation of the bulla, in the general characters of the auditory ossicles, in the vertebral formula, etc. and the conclusion indicated is that the two families are more nearly related to each other than either is to any other known family of mammals. The structural gap between *Tupaia* and *Macroscelides* is, in fact, largely bridged over by *Rhynchocyon cirnei.*

These agreements are accompanied by a very wide divergence in habits between *Tupaia* and *Macroscelides,* which has gone far to obscure the underlying resemblances beneath a great number of adaptive differences in the skull, dentition and skeleton. The pronounced Marsupial characters in the brain and Jacobson's organ in *Macroscelides* may not however be considered as widening the gap between the two families until it is shown that neither *Tupaia* nor *Ptilocercus* retain any trace of those characters.

Not improbably the *stem form of the Menotyphla* may be conceived as a Cretaceous Insectivore of arboreal habits, with the general appearance of *Ptilocercus* but with the Marsupial characters in the brain and Jacobson's organ which have been recorded in *Macroscelides.* Of the front teeth $i\frac{1}{2}$ were probably slightly enlarged, the tritubercular molars may perhaps have been intermediate in character between those of *Ictops* and of *Ptilocercus,* and thus they would also approximate to those of such basal Eocene forms

as *Indrodon* and *Olbodotes*. This ancestral Menotyphlan family also very probably resembled the ancestral Lipotyphlan in the dental formula $(\frac{3.1.4.3}{3.1.4.3})$, well developed milk dentition and general characters of the skull and skeleton. The postorbital processes were slight, the brain case smaller, the tympanic process of the petrosal (destined to expand into the entotympanic) might have been scarcely larger than it is in *Solenodon*. The arrangement of the foramina also may have approximated to the primitive Lipotyphlous condition, *i. e.*, with separate optic foramen, rotundum confluent with for. lac. anterius, entocarotid entering tympanic chamber from the rear and giving rise to three branches, "sinus canal" prominent; stapes widely open. In the skeleton digits II, III, IV were subequal, digit III being slightly the longest; a large centrale carpi, entepicondylar foramen, third trochanter, and many other primitive mammalian characters which are ascribed below to the more remote common ancestors of both Menotyphla and Lipotyphla.

The Tertiary History of the Menotyphla.

The Tertiary history of the Menotyphla is unknown, unless, indeed the Middle Eocene (Bridger) Insectivore *Entomolestes grangeri* (Matthew, 1909) shall prove to be a member of the Tupaiidæ. It was formerly thought that *Galerix* Pomel, from the Miocene of Europe, was related to *Macroscelides* but Leche has shown that it is a typical Gymnurine and therefore an Erinaceid (Weber, 1904, p. 382). A comparison of the skull of the Oligocene Leptictid *Ictops* with those of *Tupaia* and the Macroscelididæ does not lead to any decisive results. *Ictops* seems much more primitive than the modern forms in the basicranial region and in the dentition; but, as the fibula had already become fused with the tibia and the astragalus seems to have had a well grooved trochlea,[1] this genus cannot be directly ancestral to the Tupaiidæ, and it seems probable, from the greatness of the morphological gap between the Tupaiidæ and the Lipotyphla, that the two suborders must have diverged at a very early date, possibly much before the Lower Eocene.

The relations of the Menotyphala with the Primates are discussed below (pp. 321–322).

[1] (*cf.* Douglass, 1906, pl. xxii.).

"Marsupial" Characters in the Insectivora.

In the preceding pages we have noted a great many important characters (especially in the general architecture of the skull and in the arrangement of many of the cranial foramina) which are common on the one hand to all Marsupials and on the other to primitive Placentals of widely different orders (pp. 218, 253, 279), so that there is very strong evidence of the former existence of an ancestral Marsupio-Placental stock. The so-called Marsupial characters of Insectivores have been regarded as a direct heritage from this Marsupio-Placental stock, but in view of the widespread tendency for derivatives of a common stock to acquire similar characters after they have become separated from it and from each other, it seems not impossible that certain "Marsupial" characters of various Insectivores may have been acquired independently within the limits of the several modern families.

Such so called "Marsupial" characters are often variable in the different species and sometimes appear to be related to particular adaptive or cænotelic requirements. Under this category may be mentioned the following:

(1) *Palatal vacuities*: apparently secondary in the Erinaceoidea (p. 261) and Zalambdodonta (p. 254). Absent in *Ptilocercus*, barely indicated in *Tupaia*, very large in *Macroscelides*.

(2) *Pronounced post palatal transverse crest*: apparently secondary in Erinaceoidea (p. 261) and possibly also in Zalambdodonta; absent in *Tupaia*, moderate in *Ptilocercus* and *Macroscelides*.

(3) *Tympanic wing of alisphenoid.*[1] Only in *Ptilocercus* and the embryo *Rhynchocyon* does it at all approach the characteristic Marsupial condition and form a concave shell; in the Lipotypla it primitively forms merely a straight ridge separating the tympanic fossa from the glenoid region.

(4) *Optic foramen not separated from the sphenorbital fissure.* Confluent with it in *Microgale, Sorex*, certain Talpidæ, *Macroscelides, Rhynchocyon*. Intermediate conditions in certain Talpidæ (Dobson), *Tupaia*. Well separated in Erinaceoidea, most Zalambdodonts, *Ptilocercus*.

(5) *Branch of entocarotid perforating basisphenoid:* in *Erinaceus* (at least occasionally), *Centetes* (but *cf.* also Vespertilionidæ, *Orycteropus*, Herpestinæ; van Kampen, 1905, p. 383). Enters through foramen lacerum medium in *Sorex* (van Kampen, 1905, p. 435).

(6) *A fourth upper molar:* occurring exceptionally in *Centetes* (*cf. Otocyon*).

(7) *Vomer with large postero-lateral wings: Solenodon, Rhynchocyon.*

(8) *Malar extending back to glenoid fossa: Macroscelides* (probably secondary).

[1] See also p. 329.

(9) *Angle of lower jaw inturned:* moderate in *Ictops*, slight in most species of *Erinaceus*, pronounced in *E. deserti, E. algirus* (Dobson, 1882–83, p. 37). Never approaching the characteristic Marsupial shape.

(10) *Posterior mental foramen beneath* m_1: Zalambdodonts, *Pantolestes, Myogale.*

(11) *Nineteen dorso-lumbar vertebræ: Tupaia* varies however from 18 to 20; *Macroscelides*, 19–20; *Rhynchocyon*, 21.

Some of the foregoing characters may well have been acquired independently in the different phyla and all of them indeed never occur in the same form, but as a whole they are reinforced by the remarkably detailed "Marsupial" features in the brain and Jacobson's organ of *Macroscelides.* The conclusion is: that in addition to the large number of primitive Marsupio-Placental characters which Insectivores share with other lowly Placentals there is also a considerable number of special "Marsupial" resemblances, some of which may also be of primary and not secondary derivation, and which, taken as a whole, indicate that the order Insectivora is structurally nearer to the Marsupio-Placental stem than is any other existing Placental order.

Speculations on the Origin of the Order Insectivora.

So little is known about early Tertiary Insectivores (except the Leptictidæ and certain other groups) that speculations on the origin and history of the group must be based largely upon existing structures and conditions, and consequently the difficulty of distinguishing palæotelic from cænotelic or adaptive conditions confronts us at every turn. But after considering numerous contrary hypotheses the writer tentatively adopts the following as being on the whole the most likely phylogenetic interpretation of the facts and analyses which have been assembled in the preceding pages.

According to this hypothesis the characters of the family of mammals which gave rise to the modern order Insectivora may be conceived as follows:

(1) *Time of appearance pre-Tertiary.* The occurrence of well differentiated Zalambdodonts and Erinaceoids in the Lower Oligocene, and of Leptictids, Soricoids, Mixodectids, Pantolestids and possibly Tupaiids (p. 285) in the Eocene, joined to the frequency of "Marsupial" characters in modern Insectivores, the wide interval between the Lipotyphla and Menotyphla, and the generalized Placental characters of the order as a whole, all indicate a relatively great antiquity for the stem form, as compared with other Placental orders, some of which probably ran back into the Upper Cretaceous.

(2) *Habits semi-arboreal, insectivorous-omnivorous.* Of the existing Lipotyphla none are arboreal and the majority are terrestrial, partly or wholly fossorial, and often partly aquatic, and only one genus *Gymnura* retains any distinct arboreal adaptations (p. 263), although the spreading hand and foot of *Ericulus* may also be an arboreal heritage. Nevertheless the least specialized genera of the existing Lipotyphla, namely *Microgale* and *Gymnura* (*Hylomys*) are also those whose skeleton presents the fewest differences from that of the arboreal Tupaiidæ; and in the Oligocene *Ictops* (p. 262) the skeleton, so far as known, appears less specialized in a terrestrial, semi-fossorial direction than does that of its modern descendants the Erinaceidæ. Of the existing Menotyphla the skeleton of the arboreal Tupaiidæ also appears far more generalized, especially in the limbs and backbone, than does that of the terrestrial, saltatorial Macroscelididæ.

There is also considerable indirect evidence for ascribing to the stem Insectivores semi-arboreal insectivorous-omnivorous habits. Such habits seem the best fitted to give rise by adaptive radiation to all others.[1] The habit of running along the branches, of jumping from branch to branch, favors an even development of all the muscles of the limbs, hands and feet and puts a premium on a high average development of mental faculties; whereas aquatic, fossorial, cursorial, saltatorial and volant habits all imply limitation of movement of the limbs in particular directions, and the hypertrophy of certain parts at the expense of others, with resultant one-sided specialization of the nervous system. This is fully illustrated in the various types of terrestrial, fossorial and aquatic Insectivores, which are all highly specialized in these particular directions; whereas the trunk and limbs of the arboreal Tupaiidæ are distinguished not only by the almost entire lack of hypertrophy of one part over another but also by the retention of very numerous characters (such as a free centrale carpi, a third trochanter, entepicondylar foramen, pentadactyly, etc., etc.), which, on any theory, are admitted to be primitive mammalian characters.

The semi-arboreal habit also favors the retention of small size and it is obvious that the opposite condition, increasing size and weight, means larger muscles and greater need for the development of special processes on the bones; this tends, as it were, to upset the balance of form-determining forces and to start new or peculiar lines of specialization.

The chief articles of food available to small semi-arboreal animals are nestlings, eggs, insects and fruits, and this mixed fare would prevent any one

[1] Palæontological evidence for the arboreal habit of the stem Placentals has been adduced by Matthew (1904).

part of the digestive tract from becoming overspecialized.[1] Nor does the mixed fare require very powerful masticatory muscles, the development of which frequently occasions profound changes in the skull and dentition of carnivorous and herbivorous mammals.

(3) *Size small,* perhaps no bigger than that of *Hylomys* or *Microgale.* The larger Centetidæ (p. 236) are probably less primitive than the minute *Microgale,* while one of the larger of the living Insectivores *Potamogale* is also highly specialized (p. 240). The larger Erinaceinæ may also lead back through the small *Gymnura* and *Hylomys* to a very small Leptictid such as *Ictops thomsoni.*

There is also considerable indirect evidence that very small size is an ancestral character in many groups of mammals: *e. g.,* (*a*) The most ancient forms reputed to be mammals (*Dromatherium,* etc.) are of extremely small size; (*b*) The Jurassic Trituberculates (p. 177) are all of very small size and certainly primitive in other respects also. (*c*) Among Marsupials the smallest forms, *Proteodidelphys* (p. 206), *Peratherium* (p. 205), *Marmosa, Phascologale* (p. 203), etc. are also believed to be the most primitive in other respects. (*d*) Among Tertiary Ungulates and Carnivores the various lines have been demonstrated, in every case known, to lead back to relatively small forms.

(4) *Snout tubular more or less elongate, probably with a stout cartilaginous skeleton.* This character is shown in nearly all existing Insectivores in various degrees of development. It seems to be correlated with the insectivorous diet and to be a development of the less emphasized projecting type of muzzle which is preserved in *Didelphis.* In the Insectivores it is also accompanied by the following character.

(5) *Premaxillaries more or less elongate, upper incisors arranged in an anteroposterior series.* This very early became a distinctive character of the Insectivores and in its fully developed stage serves to distinguish them from the ancestral Primates and still more from the ancestral Creodonts. This condition was very likely derived from the intermediate condition preserved in *Didelphis,* Eocene Lemuroids and Pantolestids, in which the opposite incisor series are neither transverse (as in Carnivores) nor anteroposterior in position, but converge more or less obliquely toward the middle line. $I\frac{1}{2}$ may have been slightly enlarged and i_2 procumbent.

(6) *Canines small, single rooted.* It might at first be thought that the more or less double rooted, premolariform canine which is realized in *Microgale* and which recalls the double rooted canine of certain Jurassic

[1] Chalmers Mitchell (1905) regards the extreme simplicity of the digestive tract in the exclusively insect and worm eating forms as a secondary specialization. Only the Menotyphla retain a more normal mammalian development of the different parts, including the cæcum.

Trituberculates is the primitive type. But even in the latter group single rooted caniniform canines also occurred (*cf. Amblotherium*) and the small double rooted canine in modern Insectivores may be associated with an exclusively insectivorous diet. In *Hyopsodus, Ictops, Ericulus, Centetes* and *Tupaia* the canine is simple. If however the double rooted canine shall prove to be an ancestral Insectivore character, then it will serve to distinguish that order from the ancestral Polyprotodonts, Creodonts, Primates and Basal Eocene Prot-ungulates, which probably had normal, small caniniform canines.

(7) *Premolars* $\frac{4}{4}$, *simple,* $p\frac{4}{4}$ *not molariform.* $P\frac{4}{4}$ are molariform in *Ictops,* the Zalambdodonta and *Macroscelides.* In the Erinaceidæ and Tupaiidæ p^4 is subsectorial.

(8) *Upper molars simple, tritubercular,* much as in *Ictops, i. e.,* narrow anteroposteriorly with high V-shaped protocone, small para- and metacones, small para- and metastyles and metaconule, slight external and internal cingulum, the latter possibly with an incipient hypocone. This type appears to be the most primitive in the order; for, on the one hand it points back to the type represented by the Jurassic Trituberculate *Dryolestes,* on the other hand it approaches the general type seen in the Eocene Pantolestids, Oxyclænids, Mixodectids, and "prot-ungulates." This primitive molar pattern may have given rise to the modern types in the following ways (*cf.* Fig. 17, p. 238):

(*a*) The Zalambdodont molar (Fig. 17, *2–5*) may have been derived by the fusion of the paracone and parastyle, reduction of metacone, emphasis of para- and metastyle, and of the internal cingulum, including the pseudoprotocone and the hypocone (p. 238).

(*b*) The Erinaceid type (Fig. 17, *6–8*) has been derived by the anteroposterior broadening of the molar and emphasis of the hypocone (p. 260).

(*c*) The Soricoid type (Fig. 17, *9*) as represented by *Proscalops* may have been derived by the development of the pseudoprotocone and its fusion with the protocone and by the great emphasis of the para-, meso-, and metastyles, which connect with the para- and metacones so as to form the two external Vs.

(*d*) The *Ptilocercus* type (Fig. 21, p. 273) may have been derived by the slight emphasis of the metastyle, anteroposterior broadening of the crown and oblique development of the hypocone.

(*e*) The *Tupaia* type (Fig. 22*B*) was formed by the great development of the para-, meso- and metastyles so as to produce two external Vs, and the division of the mesostyle in correlation with the enlargement of the hypoconid. The hypocone remained very small.

(*f*) The *Macroscelides* type may have been formed after the manner of the bilophodont m^2 of *Erinaceus.* Here the protocone unites with the

protoconule, the two together forming the protoloph, which connects externally with the paracone. Similarly the enlarged hypocone unites with the metaconule, which joins the metacone, all forming the metaloph.

(9) *Lower molars tuberculosectorial,* with high trigonid and low talonid. From the widespread occurrence of a well developed talonid in Eocene mammals of many orders, and in all Insectivores except the Zalambdodonts, it seems likely that the extremely reduced condition of the talonid and absence of a distinct hypoconid in that group is partly secondary, and perhaps correlated with the development of a sectorial rather than crushing function. If this be true the general resemblance of the lower molars of Zalambdodonts to those of certain Jurassic Trituberculates is secondary.

(10) *Dental formula* $\frac{3.1.4.3}{3.1.4.3}$. This primitive Placental formula is realized among the existing families only in the Gymnurinæ, Myogalinæ, Talpinæ.

(11) *Milk dentition well developed,* not replaced until the animal attains adult size. This is regarded by Leche as a very primitive mammalian character and possibly may have characterized the ancestral Insectivore (p. 260).

(12) *Cerebrum small, smooth; cerebellum not covered.*

(13) *Olfactory parts large or moderately developed.* Possibly the extreme macrosmatism of the Zalambdodonts may be a secondary Insectivorous adaptation. The large size of the olfactory bulbs in those forms probably conditions in part the peculiar cylindrical development of the skull (p. 267).

(14) *Brain case small, rounded,* temporal crests more or less parallel (*cf. Ictops, Microgale, Ptilocercus*); later uniting into a long low sagittal crest (Zalambdodonts, *Pantolestes*).

(15) *General architecture of skull much as in Ictops* (p. 261). There is considerable evidence (p. 262) that *Ictops* has retained many primitive conditions especially in the base of the cranium and that the ancestral Insectivore was not distinguished either by ectopterygoid fossæ, large tympanic flanges on the basisphenoid or united post-glenoid and post-tympanic processes. The malars were probably rather slender.

(16) *"Marsupial" characters in the skull probably fewer than in later Insectivores.* Very possibly the palate was not fenestrated, the optic nerve may have pierced the orbitosphenoid (p. 246), one branch of the entocarotid may have entered through the foramen lacerum medium (p. 247), instead of piercing the basisphenoid.

(17) *Venous foramina much as in Solenodon* (p. 248). Possibly including a prominent "sinus canal" on the side of the head, a "transverse canal" tunneling the basisphenoid, and a suboptic foramen *e. g., Solenodon, Erinaceus, Macroscelides.*

(18) *Alisphenoid canal* present or in course of development.

(19) *Entocarotid entering tympanic chamber* from the rear and giving rise to three branches (p. 247).

(20) *Auditory ossicles in process of acquiring the Insectivore characteristics.* Stapes becoming widely open, pierced by the large stapedial branch of the entocarotid; malleus with a distinct head, wide lamina, long processus gracilis, the latter fitted to the ring shaped tympanic.

(21) *Skull retaining a large number of primitive Marsupio-Placental characters* in addition to numbers 6–19 mentioned above. The preceding studies of the skull of the Marsupials (p. 217), of *Solenodon* (pp. 242, 253) and of *Tupaia* (p. 279) reveals a very large number of underlying characters in common, especially in the arrangement of the majority of the cranial foramina, structure of the ethmoid, vomer, relations of the pterygoid, alisphenoid, short basioccipital, etc.

(22) *General characters of the skeleton much as in Tupaia,* especially the vertebral formula and characters of the shoulder girdle, humerus, femur, pelvis. In the ancestral Lipotyphla the carpus and tarsus probably foreshadowed those of *Ericulus* (p. 251) and thus approximated the primitive Creodont type; but in the ancestral Menotyphla the carpus and tarsus suggested those of *Tupaia* and thus remotely foreshadowed the Primate type. In both manus and pes digits II, III, IV were subequal, digit III being slightly the longest; the pollex and hallux were slightly divergent; the claws were compressed and well developed.

(23) *Testes remaining abdominal (cf. Centetes, Macroscelides).*

(24) *Uterus bicornis or duplex.*

As thus conceived the family of ancestral Insectivores would be ordinally related to the contemporary ancestors of the Creodonts. It would be distinguished from them chiefly by smaller size and less robust structure, more elongate snout and premaxillaries, smaller canines, smaller and more sharply cusped molars, and perhaps by habits which were more arboreal, less predatory and more insectivorous frugivorous.

The Tillodontia.

It is customary to place the Tillodontia in the neighborhood of the Rodentia and to regard the order as ancestral to the latter; but an examination of the skull and skeletal remains of *Tillotherium* Marsh (1875) and of its ally *Esthonyx* as described by Wortman (1896), shows that apart from the pair of enlarged rootless incisors and the concomitant reduction of the other incisors and canines, there is not a single decisively Rodent character in the whole skull and skeleton. As scalpriform incisors have been evolved quite

independently in several different orders, Weber (1904, p. 514) seems quite justified in concluding that the supposed connection with the Rodentia is very problematical.

The evidence for the view that the Tillodontia are *not related to the Rodentia* is as follows:

(1) The dentition, except the incisors, is wholly unlike that of any known Rodent. The most primitive dentition in the group is that of *Esthonyx*, in which the tritubercular molars (figured by Osborn, 1907, p. 151) are of a peculiar type, which is entirely unlike that of the oldest Eocene Rodents of the family Ischyromyidæ (*cf.* p. 327.)

(2) The skull as figured by Marsh (1875) shows many significant differences from the Rodent type. In *Tillotherium* the mandibular condyle and its glenoid facet are transversely instead of antero-posteriorly elongate, the post-glenoid process of the squamosal is well developed, so that the motion of the jaw in gnawing must have been largely vertical. The basicranial region is very unlike that of the oldest known Rodents, the Eocene Ischyromyidæ and is rather of the Creodont type. The bulla instead of being large and inflated as in all Rodents appears to have been uninflated. There is no suggestion of the peculiar Rodent foramina (p. 329), nor does the angle of the jaw foreshadow any of the various Rodent peculiarities. The large facial exposure of the lachrymal is another Creodont character which tends to separate *Tillotherium* from the Rodents.

On the other hand the Tillodontia retain many primitive features besides those mentioned above, pointing to derivation from the Insectivore-Creodont stock, as follows:

(1) The most primitive member of the group is *Esthonyx burmeisteri* from the Lower Eocene (Wasatch), as shown by Wortman (1896). This species retains a dental formula of I.$\frac{2}{3}$, C.$\frac{1}{1}$, P.–, M.$\frac{3}{3}$, which is an immediate derivative of the primitive Insectivore-Creodont formula; and the material proves that the pair of incisors which is destined to become scalpriform and rootless is i$\frac{2}{2}$. A progressive hypertrophy of the anterior lower incisors seems frequently to be a result of insectivorous diet (Bensley, 1903, p. 124; *cf. Cœnolestes, Distœchurus, Erinaceus, Solenodon, Chiromys*, etc.) and the molars of *Esthonyx* might also readily have been derived from the supposedly insectivorous-carnivorous type of the Oxyclænidæ.

(2) *Tillotherium*, even though highly modified in certain respects, also resembles the Insectivore-Creodont type in the following characters of the skull: muzzle very heavy, long narrow mid-cranium, low sagittal crest, small brain case, rather slender zygomata, large orbit broadly continuous with temporal fossa, lachrymal foramen marginal, facial exposure of lachrymal considerable, two anterior dental foramina; characters of the base of the cranium of Creodont type.

(3) In the skeleton the manus and pes are pentadactyl, unguiculate, probably plantigrade (Marsh), there is a free centrale carpi (*Esthonyx*), the humerus has an entepicondylar foramen, the femur a third trochanter, the tibia and fibula are distinct, and the astragalus is slightly grooved above.

CHAPTER VI. GENETIC RELATIONS OF THE CARNIVORA (CREODONTA, FISSIPEDIA, PINNIPEDIA).

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I. The Creodonta and Fissipedia.

Outline history of the ordinal classification.

1. *THE CREODONTA.*

Incomplete remains of representatives of this order were referred by Cuvier and de Blainville to "les Carnivores," and de Blainville regarded his *Arctocyon primævus* (1841) as a member of his 'Subursi,' a group including not only the forms now called Procyonidæ but also *Arctictis*, *Mydaus* and *Meles*. Zittel (1892, p. 580) states that the discovery of good material of

Hyænodon (1838) and *Pterodon* (1839) inaugurated a controversy which has continued to the present time. Laizer and Parieu, Laurillard, Pomel, Aymard and Gaudry regarded *Hyænodon* and its allies as related to the carnivorous Marsupials; de Blainville, Gervais, Pictet, Owen, Lydekker and Filhol emphasized their resemblances to the Placentals. Finally Filhol proved that *Hyænodon* had three deciduous molars and lacked epipubic bones.

Cope in 1876 proposed the order "Bunotheria" to embrace various suborders of Eocene and later Unguiculates, including the "Creodonta." Into the latter suborder he put the "Insectivora with tritubercular superior molars" ("Talpidæ, Chrysochloridæ, Esthonychidæ, Centetidæ (= Leptictidæ olim")) and the extinct carnivorous families "Oxyænidæ, Miacidæ, Amblyctonidæ, Mesonychidæ." The term "Creodonta" was restricted to its generally accepted meaning by Schlosser (1886). Huxley (1880) suggested that *Hyænodon* and *Pterodon* might be an "extreme development of that type of the Insectivora which is at present represented by *Centetes*." He also believed that the ancestors of the modern carnivores were "pentadactyle, plantigrade, claviculate and had brains with relatively small cerebral hemispheres and large, completely exposed, cerebella," that they had the dentition and jaw angle of *Otocyon* and were provided with epipubes. "According to our present system of classification, such a mammal would be grouped among the Insectivora, or as a transitional form between them and the *Didelphia*."

The discovery by Ameghino (1887) of *Borhyæna* and other fossil Patagonian "Sparassodonts," which resembled the carnivorous Marsupials on the one hand and the Creodonts on the other, caused the revival of the old view that after all the Creodonta had been derived directly from Mesozoic carnivorous Marsupials (Ameghino, Lydekker). The affinities of the "Sparassodonts" are discussed below (p. 303).

Wortman (1901) after transferring the Viverravidæ from the Creodonta to the "Carnassidentia" (true Fissipede Carnivores) took the view that "the Creodonta and Carnassidentia probably arose side by side from the Mesozoic Marsupials...." and he referred the origin of the Creodonta to some such type as the Upper Cretaceous genus *Didelphops* Marsh.

Matthew (1906) replied to this that "if we set aside superficial and adaptive characters, and rest principally upon deep-seated resemblances such as are found in the characters of the base of the skull, the dental and dorsolumbar formulæ, etc., we find every known creodont very much nearer to the modern Carnivora than to the modern marsupials." This problem is discussed below (p. 298).

The family and superfamily classification of the Creodonts has been

developed especially by Cope (1876), Scott (1892), Schlosser (1886), Zittel (1893), Osborn (Columbia Univ. lectures), Wortman (1901–2) and Matthew (1901, 1906, 1909).

The progress of discovery is indicated by the following brief list (compiled chiefly from Palmer's 'Index Generum Mammalium') of the more important and best known genera of Creodonts.

1838. *Hyænodon* Laizer & Parieu. Hyænodontidæ. Oligocene France.
1839. *Pterodon* Blainville. Hyænodontidæ. Oligocene France.
1841. *Arctocyon* Blainville. Arctocyonidæ. Basal Eocene France.
1842. *Palæonictis* Blainville. Palæonictidæ. Lower Eocene France.
1862. *Proviverra* Rütimeyer. Hyænodontidæ. Lower Eocene France.
1870. *Patriofelis* Leidy. Oxyænidæ. Middle Eocene, Wyoming.
1871. *Sinopa* Leidy. Hyænodontidæ. Middle Eocene, Wyoming.
1872. *Stypolophus* Cope (= *Sinopa*). Hyænodontidæ. Middle Eocene, Wyoming.
1872. *Mesonyx* Cope. Mesonychidæ. Middle Eocene, Wyoming.
1872. *Viverravus* Marsh. Miacidæ. Middle Eocene, Wyoming.
1872. *Uintacyon* Leidy. Miacidæ. Middle Eocene, Wyoming.
1872. *Limnocyon* Marsh. Oxyænidæ. Middle Eocene, Wyoming.
1872. *Miacis* Cope. Miacidæ. Middle Eocene, Wyoming.
1874. *Oxyæna* Cope. Oxyænidæ. Lower Eocene, New Mexico.
1874. *Pachyæna* Cope. Mesonychidæ. Lower Eocene, New Mexico.
1875. *Didymictis* Cope. Miacidæ. Middle Eocene, Wyoming.
1876. *Dromocyon* Marsh. Mesonychidæ. Middle Eocene, Wyoming.
1881. *Deltatherium* Cope. Oxyclænidæ. Basal Eocene, New Mexico.
1881. *Dissacus* Cope. Mesonychidæ. Basal Eocene, New Mexico.
1883. *Chriacus* Cope. Oxyclænidæ. Basal Eocene, Wyoming.
1884. *Oxyclænus* Cope. Oxyclænidæ. Basal Eocene, New Mexico.

Other American genera were later described by Scott, Osborn and Earl, Wortman, Matthew. European representatives, chiefly of the Oxyclænidæ and Hyænodontidæ, have been described by Filhol, Schlosser, Depéret and others. Representatives of the Hyænodontidæ from the Fayûm of Egypt have been described recently by Andrews (1903–6) and Osborn (1909).

2. *THE FISSIPEDIA.*

1693. Ray divides the narrow clawed unguiculates into two groups: (1) those with several incisors in each jaw [*i. e.*, the Carnivores], (2) those "with one pair larger, of which kind all are plant eaters" [Rodentia]. Ray's list of the former throws light on the origin of numerous technical and

popular names. With some omissions and abbreviations it is given below, with the native and English names used by Ray. The first group [carnivores] he subdivided as follows:

Majora, rostro

Brevi, capite rotundiore, Felinum genus ["Leo," "Tigris," "Pardalis," "Lynx," "Catus Pardus," "Felis domestica seu Catus," "Ursus"].

Productiore, Caninum Genus. Under this heading are included among others: LUPUS, Wolf and Jackal; CANIS [10 species listed]; VULPES, Ἀλώπηξ; Animal ZIBETHICUM....the Civet Cat; COATI....Rattoon s. Rackoon; COATI MONDI....; YZQUIEPATL seu Vulpecula [Skunk], Carigueya, the Possum; .... TAXUS sive Meles, the Badger, Brock or Gray; LUTRA, the Otter; PHOCA seu *Vitulus marinus*....the Sea-Calf or Soile; EQUUS MARINUS Hippopotamus falso dictus, Anglis *Mors* à Russis mutato nomine, Belgis *Walrus*, Danis *Rosmarus*, the Morse or Sea-Horse; MANATI, seu Vacca marina, the Sea Cow.

Under the same heading but set apart as belonging to "Genus Mustelinum vermineúmve" were listed many of the Mustelidæ and Viverridæ as follows: *Mustela vulgaris*, the Weasell or Weesel; VIVERRA Indica; MUNGO [?Mungoose]; Mustela candida s. Animal ERMINEUM, the Ermine or Stoat; *Mustela silvestris*....The Ferret, nonnullis Furo....; *Putorius*, the Polecat or Fitchet, MARTES alliis Foyna, A Martin or Martlet; Mustela ZIBELLINA the Sable; GENETTA; ICHNEUMON.

This is a tolerably good classification of the Carnivora and left comparatively little for Linnæus to do except in the matter of applying binomial names.

1748. Linnæus (2d ed. Syst. Nat.) includes under "Feræ" the genera *Ursus, Felis, Mustela, Lutra, Canis, Phoca,* [*Phoca*], *Meles, Erinaceus, Dasypus, Talpa,* and *Vespertilio.*

1758. Linnæus (10th ed.) excludes from Feræ all but *Phoca, Canis, Felis, Viverra, Mustela, Ursus.*

1766. Linnæus (12th ed.) includes under Feræ the genera *Phoca, Canis, Felis, Viverra, Mustela, Ursus, Didelphis, Talpa, Sorex, Erinaceus.*

1797. Blumenbach's classification in 1797 was as follows: Ordo Digitata. (*a*) Digitata Glires. (*b*) Digitata Feræ. (*c*) Digitata Bruta. Under the "Digitata Feræ" were included certain Insectivores, *Didelphis,* the Kangaroo, and *Viverra, Mustela, Ursus, Canis, Felis.*

1795. Geoffroy and Cuvier break up the Linnæan orders, distributing the true Carnivores in the orders "Vermiformes" (*Mephitis, Mustela,*

Lutra), "Carnivores" (*Civetta, Hyæna, Canis, Felis*), and "Amphibies" (*Phoca, Rosmarus, Manatus, Trichechus*).

1800. Cuvier apparently follows Blumenbach, placing *Ursus, Taxus, Nasua, Procyon, Potos* [*Cercoleptes*], and *Ichneumon* [*Herpestes*] under "les Ours" next to various Insectivora as a division of "Les Plantigrades" in the order "Carnassiers." *Phoca* and *Trichechus* (Walrus) alone constitute "les Amphibies" among the "mammifères à pieds en nageoire."

1817. Cuvier includes under "les Carnivores," the four divisions: "les Plantigrades" [Arctoids], "les Digitigrades" [typical carnivores], "les Amphibies" ("Phoques," "Morses"), "les Marsupiaux."

1834. De Blainville segregates all the Carnivora in a grand division "non-claviculés" of the "ordre Carnassiers," the other grand division "claviculés" including the "Cheiropteri," "Orycteri" (Taupes, etc.), "Insectivori."

1837. In Bonaparte's classification the Carnivora are widely separated from the Insectivora. The former are placed in the great group "Educabilia," the latter in the "Ineducabilia." He revives the Linnæan term Feræ for the Fissipedes, setting the Pinnipedes apart in the next order, for which he uses Illiger's term Pinnipedia.

1839. De Blainville restricts the term "Carnassiers" to include the Carnivora, the association with the Insectivora (now called "Insectivores") being rather of a superordinal nature (Secundatès).

1866. Haeckel puts the order "Carnaria", including the Carnivora and Pinnipedia, in the legion "Deciduata".

1872. Huxley also includes both Insectivora and Carnivora in the "Deciduata" and especially in 1880 adduces evidence to show that the Carnivores, in common with several other higher orders, may have been derived from early representatives of the Insectivora.

The family and superfamily classification of the Fissipedia were developed especially by Flower, Mivart, Cope, Winge, and more recently by Weber.

Among the best known of the earlier described genera of fossil Fissipedes are the following: *Potamotherium* Geoffroy, 1833, an ancestral otter; *Machairodus* Kaup, 1833; *Amphicyon* Lartet, 1836; *Pseudælurus* Gervais, 1848–52; *Cynodictis* Bravard & Pomel, 1850; *Daphænus* Leidy, 1853; *Dinictis* Leidy, 1854.

ARE THE CREODONTS DERIVED DIRECTLY FROM CARNIVOROUS MARSUPIALS?

The old theory of the derivation of the Placental Carnivora from the Carnivorous Marsupials has recently been discussed by Dr. J. L. Wortman (1901–1902) whose views may be gathered from the following passages:

"It would appear from the present trend of evidence that we shall be compelled eventually to return to the old idea of a direct Marsupial ancestry of all the Monodelphian orders" (p. 335). This does not mean that "the living Marsupials are those ancestors" since they have a number of "modernized features" among which are cited the mode of replacement of the teeth, the increased number of incisors in Polyprotodonts, and the inflected mandibular angle.

Dr. Wortman holds that the "Mesozoic representatives of the carnivorous Marsupials are not far removed from the hypothetical forms, to which it seems to me, the present evidence points with no doubtful signs, as the ancestors of the Carnivora" (*l. c.*, p. 335). By "Mesozoic representatives of the carnivorous Marsupials" he seems to refer to Cretaceous Didelphoid forms, since he states (pp. 336–337) that "just what the Cretaceous Marsupials, when more fully known, will show with respect to these characters [namely, the relations of the milk and permanent dentitions, the inflected angle of the jaw, etc.] cannot now be predicted; but we do know that such a type as *Didelphops* Marsh, in its dentition and palate, resembles the living carnivorous Marsupials, and it is to some such type in particular that I would refer the origin of the Creodonta." In another passage (1901, p. 282) he states: "Present evidence points to the fact that the two groups [Creodonta and Carnassidentia] probably arose side by side from the Mesozoic Marsupials ...." And again (1902, p. 143) he says: "That they [the Creodonta] were derivatives or offshoots of any preëxisting groups of Placentals or Eutherians is exceedingly unlikely...." "On the contrary, all the facts point very strongly to their origin, along with Carnassidentia, from Implacental or Marsupial Metatherians. It is likewise conceivable that from this same general substratum the other Eutherian orders arose" (p. 144).

In brief, Dr. Wortman seems to hold that the Creodonta, Carnassidentia [Carnivora Fissipedia + Palæonictidæ + Viverravidæ], Insectivora and perhaps other orders have been derived independently from carnivorous implacental Metatheria of the Mesozoic era, typified in palate and dentition by the Cretaceous *Didelphops*. The opposite conclusion, which is defended in the present chapter, embodies the following propositions:

(1) That Lower Eocene Creodonts, and Carnassidents were closely related to each other by virtue of derivation from Mesozoic Insectivorous Placentals.

(2) That the immediately ancestral family of these primitive placentals was not fully carnivorous but insectivorous-carnivorous; not implacental but more probably with both allantoic and yolk-sack placentæ; not Cretaceous Marsupials with four molars and three premolars on each side and with large palatal vacuities, but possibly Cretaceous Insectivores, allied on

the one hand to *Pantolestes* (p. 305) and on the other to the ancestral Lipotyphla, with a dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$ simple premolars, simple tritubercular upper and tuberculosectorial lower molars and rather small canines; skeleton retaining generalized arboreal characters; tympanic region with little or no "alisphenoid bulla."

(3) That the resemblances between Creodonts and carnivorous Marsupials are due: first, to the inheritance of primitive characters from a very remote, perhaps Jurassic, Marsupio-Placental stock; secondly, and perhaps chiefly, to the independent development in the two groups of similar adaptations to predatory carnivorous habits.

Dr. Wortman cites some nineteen characters (1902, p. 336) which he regards as "primitive features of the Marsupial Carnivores." These he thinks strengthens the hypothesis of the derivation of the Creodonts from Mesozoic Implacental Metatheria.

Many of these characters are directly correlated with flesh-eating, predaceous habits: for example, the carnivorous dentition, the high sagittal and lambdoidal crests, the stout zygomata, the large downwardly-projecting paroccipitals, and the hatchet-shaped spine of the axis. These characters as a class do not necessarily indicate *close* kinship between flesh-eating Marsupials and flesh-eating placentals any more than the resemblances between the Wombat and the Beaver indicate close kinship between Diprotodonts and Rodents. Nor would the lack of such adaptive characters in common in two given groups indicate a wide genetic separation, as is shown by comparison of the smaller insectivorous Dasyures with the Creodont-like *Sarcophilus* of the same family. Another character in the list, namely the fusion of the scaphoid and centrale, seems an unsafe criterion of close genetic kinship, since the same coalescence has probably occurred also in the Edentates (Fig. 23, p. 393), Perissodactyls (p. 394), Artiodactyls (Fig. 26, p. 405) and other groups.

The remaining points of resemblance listed by Dr. Wortman appear to the writer to be for the most part primitive Marsupio-Placental characters, which are preserved to a greater or less extent in the Insectivora and other orders beside the carnivorous Marsupials and Creodonts. Under this category may be included the following:

No. 3. "The large lachrymal spreading out upon the face." In the more primitive members of the Dasyuridæ and Didelphiidæ this feature is much less emphasized.

Matthew (1906, p. 210) has shown that the facial expansion of the lachrymal appears to be correlated with the position of the orbits with respect to the cheek teeth. In the modern Carnivores the orbits are further forward and the facial expansion of the lachrymal is reduced.

No. 9. The "large size of the lumbar vertebræ as compared with the dorsals, and their tendency in some forms (Opossums) to develop the double tongue and groove articulations." Possibly correlated originally with arboreal habits. Large lumbars preserved in many primitive Unguiculates.

No. 10. The "large deltoid crest and characteristically broad distal end of the humerus." This character was probably established in the very remote ancestors of the mammals (see p. 119). It is preserved to a greater or less extent in several orders (p. 437).

No. 12. The "subequal size of ulna and radius" (*i. e.*, of shaft). Undoubtedly another very ancient character, preserved in several orders.

No. 13. The "large size of the lesser trochanter of the femur." A primitive mammalian character. Very pronounced in Cynodonts (p. 118), Monotremes (p. 154), Triconodonts (?)[1]; progressively reduced in Marsupials, Creodonts, Fissipeds. Lower trochanter relatively large in *Viverravus protenus* (Matthew, 1901, p. 11) *i. e.*, in a representative of the Carnassidentia.

No. 14. The "large size of the fibula and its extensive articulation with the proximal surface of the astragalus instead of upon its outside." Another primitive mammalian character, antedating the development of a vertical external malleolar facet on the astragalus.

No. 15. The "very primitive form of the astragalus." The astragali of all Creodonts appear to be much more advanced than those of the primitive Didelphiidæ; and the more generalized Creodont types represented in *Arctocyon, Oxyæna, Sinopa,* approach the most primitive Fissiped types in many respects (p. 456).

No. 16. The "small size of the brain." A primitive mammalian character which is not confined to Marsupials and Creodonts but is also retained in the primitive "Carnassident" *Viverravus protenus* (p. 310).

No. 17. The "dorso-lumbar vertebral formula of 19." No doubt this number of dorso-lumbar vertebræ is a very primitive one (p. 275), since it occurs more or less frequently among Monotremes, Marsupials, Rodents, Edentates, Insectivores and Artiodactyls. But it is not especially characteristic of Creodonts, since it is 20 (according to Matthew, 1906, p. 231) in *Sinopa, Oxyæna, Hyænodon* and probably in *Patriofelis, i. e.*, exactly as in the Fissipedia. The Mesonychidæ (represented by *Dromocyon*) are therefore the only Creodonts retaining the Marsupial number (19) of dorso-lumbars.

No. 18. The "posterior spreading of the nasals so as to exclude contact between frontals and maxillary in front." A very ancient character

[1] This character is well shown in a cast of a small femur from the Stonesfield Slate which is doubtfully referred to *Triconodon.*

already well established in the Triassic Cynodont *Galesaurus,* and preserved not only in Marsupials and certain Creodonts but also in the early Artiodactyls (*Achænodon*) and in the Edentates.

In brief, the preceding list of resemblances between Marsupials, Creodonts and Carnassidents seems to fall roughly into two classes: (1) homoplastic resemblances and (2) primitive characters inherited by the groups in question from very remote, perhaps Upper Jurassic or earlier, ancestors. To this list of primitive characters might be added two others recorded elsewhere by Dr. Wortman namely the small pelvic opening (p. 307) and the Didelphid-like sternum of *Dromocyon.* (For the latter point see Matthew, 1906, p. 221.)

On the other hand, deep seated differences between Marsupial and Placental Carnivores are not lacking. In cases like the one under consideration no character or single set of characters can be relied upon invariably as infallible guides to remote genetic connections. But in general the arrangement of the cranial foramina (which Dr. Wortman especially has elucidated in the Creodonta) and the underlying architecture of the skull seem more likely to retain very ancient features than characters which are more directly related to a particular life habit.

From Wortman's very careful and full description of the skull of *Dromocyon* (1901, pp. 292–295) it is seen that even in the Mesonychidæ, the Creodont family which shows the most numerous resemblances to the carnivorous Marsupials, the arrangement of the cranial foramina is distinctly of the Placental Carnivore rather than of the Marsupial type. That is, they possess an alisphenoid canal for the ectocarotid, the basisphenoid is not perforated for the entocarotid artery as it is in the Marsupials, and the "optic foramina are distinct from each other and occupy the usual position in the carnivorous skull, just in advance of the sphenoidal fissure" (*l. c.,* p. 294), whereas in Marsupials there are no true optic foramina and the optic nerves issue through the opposite sphenoidal fissures (f. l. a) which coalesce mesially.

In regard to the accessory "condyloid" canal in Marsupials Matthew (1906, p. 214) has cited evidence unfavorable to its supposed homology with the similarly named but somewhat differently placed foramen, in the Creodonta and Carnassidentia.

The glenoid region of the squamosal of *Dromocyon* strongly suggests that of *Thylacynus,* but the malar in Creodonts never enters the glenoid fossa, as it does invariably in Marsupials. Nor is there any indication that the alisphenoid participated in the articular surface of the glenoid, a very prominent feature in all Polyprotodont Marsupials, and one showing clearly in the Santa Cruz "Sparassodonts." There is never an "alisphenoid bulla"

(tympanic process of the alisphenoid) in Creodonts, but on the contrary only a true tympanic bulla, which in *Dromocyon* is inflated and has a tubular meatus. The basi-occipital in the carnivorous Marsupials is short and wide, whereas in placental carnivores it is progressively long. (It is, however, relatively short in certain specimens of *Mesonyx*.) As to the inflected angle of the jaw, Wortman admits (1901, p. 336) that this is probably secondary in the Mesonychidæ, since according to Matthew (1901, p. 34) the angle is less inflected in the Basal Eocene *Dissacus* and becomes progressively more inflected as we pass from this to the Upper Eocene *Mesonyx uintensis* "where it is almost like that of a Marsupial." The accessory posterior palatine foramina have the appearance of nutritive foramina, such as occur in *Hyæna*, and do not appear to be homologous with the posterior palatal vacuities of Marsupials. The thickened round posterior border of the palate differs from the high transverse ridge with projecting angles which is so characteristic of carnivorous Marsupials and many Insectivores. However, *Thylacynus* approximates in this respect the Creodont type. In the Insectivores this character seems to be secondary (p. 286). The Creodonts appear to lack the foramen on the postero-external angles of the palatal ridge which is very characteristic in Marsupials and many Insectivores, but which again is reduced or wanting in *Thylacynus*.

The remaining Creodonts and Carnassidents, according to Wortman's descriptions, are much more advanced toward the normal Placental Carnivore type and do not show so many resemblances to the Marsupials.

Supposed relations of the Creodonts to the "Sparassodonta" (Borhyæninæ).

If the Creodonts and especially the Mesonychidæ were derived from Cretaceous carnivorous Marsupials they might be expected to show some special palæotelic resemblances, to the carnivorous Marsupials (Borhyæninæ) of the Patagonian Miocene, described above (p. 207). But a careful comparison of the two groups, as figured by Wortman (*op. cit.*) and Sinclair (1901) respectively, fails to reveal any resemblances which may not be interpreted either as due to similar life-habits or to the retention of very ancient Marsupio-Placental characters.

On the contrary, there are many differences which may not lightly be set aside as due to differences in life-habits and which appear to point to very ancient separation between the "Sparassodonts" and the Creodonts. A number of these characters have been recorded above (p. 207) but two more may now be added: first, in the manus of Creodonts and other primitive Placental orders the lunar is large and the magnum is typically small, whereas in all the carnivorous Marsupials, including even *Thylacynus* and the cursorial Santa Cruz forms the reverse is the case. Secondly, leaving out of

account the peculiar displacement of the ectocuneiform beneath the cuboid in the pes of the Thylacinidæ, the astragalus of these and of all known Marsupials is much lower in development (p. 454) than it is in the Basal Eocene Creodonts, and quite unlike that of the very family, the Mesonychidæ, which is supposed by Dr. Wortman to lie nearest to the Marsupials.

Dr. Wortman's view that in the structure of the feet the Arctocyonidæ stand "much nearer to the carnivorous Marsupials.... than to any Carnassident" (*op. cit.*) evidently refers to general resemblances only, because the carpus and tarsus are radically different in the two groups (*cf.* p. 310). The tendency to opposibility of both pollex and hallux, which is responsible for much of the resemblance between *Clænodon* and the carnivorous Marsupials, is probably merely one of the indications of arboreal ancestry in the central Placentals as well as in Marsupials (pp. 200, 288).

In fine, the case for a direct independent derivation of the Creodonts and higher carnivores from Mesozoic carnivorous Marsupials of the type of *Didelphops* seems hardly to have been substantiated.

GENETIC RELATIONS OF THE CREODONTA TO THE INSECTIVORA.

As shown above Huxley, Cope and many others believed that the Creodonta were derived from or were closely related to, the Insectivora; but Dr. Wortman has recently challenged this view (1901, p. 335) in the following words: "There appears to be a sort of vague belief that the Carnivora have arisen from the Insectivora, and one frequently hears the expression 'Insectivore-creodont ancestors.' Now, as a matter of fact, the Insectivora, as we at present know them, are not more primitive than a large majority of the Creodonts; but on the contrary, with very few exceptions, all the living Insectivores are considerably specialized, and even those that do exhibit a more or less generalized structure are far removed from the typical ideal ancestor of the Carnivores. Nor do the few known fossil Insectivores help us much towards such a belief, for in all of them, so far as we know, the peculiar conformation of the anterior part of the skull is almost as strongly marked as it is in their living representatives. The very general enlargement of the premaxillæ and modification of the incisors, with the reduction or disappearance of the canine, constitute one of the striking osteological peculiarities by means of which they may nearly always be distinguished from any known Creodont or Carnassident."

The ancestral Insectivores were more primitive than the ancestral Creodonts.

That the Insectivora as an order are more primitive than any other *recent* Placental order is a conclusion for which strong evidence has been cited above (pp. 287–292). On the other hand the majority of the living In-

sectivores may be conceded to be, on the whole, more aberrantly specialized than the majority of Eocene Creodonts. Admitting the partly secondary character of the elongation of the premaxillaries in typical Insectivores, we still have left the more important question: which is more primitive, the prototypal Insectivore family as reconstructed above (p. 287) or the relatively primitive Creodont type, such as *Sinopa*? To put the question in another way, were the Insectivores derived from terrestrial forms with short premaxillaries, transversely arranged incisors and large canines, or were the Creodonts derived from small semiarboreal insectivorous forms analogous to *Marmosa, i. e.*, with slightly elongate premaxillaries, opposite incisors arranged in converging series, rather small canines.

The Insectivora as an order possess two characters which have been shown by cumulative evidence to distinguish the ancestors of many other groups such as the Marsupials (p. 289), Rodents (p. 331), Ungulates, Primates (p. 321) and others, namely small size and insectivorous-omnivorous habits.

The Creodonta themselves seem to run back into *small, probably insectivorous-carnivorous forms.* Certainly the very large forms *Harpagolestes, Pterodon* and *Patriofelis,* representing three of the leading families, are far more specialized in their dentition (figured *e. g.*, by Osborn, 1907, pp. 131–135) than their small relatives *Dissacus, Sinopa* and *Oxyæna* in which the traces of former tritubercuły are much clearer. These in turn are all more highly specialized than the small Basal Eocene members of the Oxyclænidæ. The latter family includes forms (*Tricentes, Chriacus*) the molars of which approach the Insectivore type illustrated in *Leptictis* and *Pantolestes* so that their position in the Creodonts is somewhat doubtful (Matthew). The very small Lower Eocene *Palæosinopa,* which strongly resembles *Didelphodus,* a primitive member of the Hyænodontidæ, is related to *Pantolestes,* a true Insectivore (Matthew). The latter, although an undoubted Insectivore, approaches the Creodonts in its large size, heavy muzzle, long constricted postorbital region, *Dissacus*-like molars, etc. (Matthew, 1909). In *Palæosinopa* and *Pantolestes* the canines are larger than in most Insectivores but the incisors are arranged more antero-posteriorly than transversely and the premaxillary is slightly elongate.

The earlier Creodonts also retain a more or less divergent pollex and hallux which, as remarked by Matthew (1904, p. 813–814), is strong evidence of arboreal origin. The oldest Creodont skull known, that of *Triisodon heilprinianus* Cope (figured by Matthew, 1901, pp. 30–31) resembles that of the lowest Insectivora in the possession of a long cylindrical midcranial region and very small brain case.

On their part the Insectivora are allied to the Carnivora by many prim-

itive characters, such as the dental formula, pentadactyly, the general characters of the carpus and tarsus. Some other Placental orders retain more or less of these primitive characters, but they are separated from the Creodonts and Insectivores by well marked specializations, such as the reduction of the dental formula or the hypertrophy of particular parts.

The Lipotyphlous Insectivora also occasionally foreshadow the Carnivora in their more or less imperfect adaptations to carnivorous habits. Under this head may be mentioned first the development of a semi-carnassial fourth upper premolar in *Erinaceus* and secondly the many carnivorous features of *Centetes*, such as the long canines, the broad mandibular coronoid, the broad blade of the scapula, the long skull resembling that of *Hyænodon*.

Additional resemblances between Insectivores and Carnivores. In his description of the skull of *Limnocyon*, a Middle Eocene member of the Oxyænidæ, Dr. Wortman (1902, pp. 202–203) says: "....the position of the posterior lacerated foramen is posterior and external to the periotic, as in the Insectivora, and not postero-lateral, as in the Carnassidentia; the entocarotid enters the tympanic chamber and divides in a manner similar to that of the modern Insectivora, the main branch grooving the outer lateral aspect of the periotic, in front of, and below the *fenestra ovalis*, the other passing between the crura of the stapes and thence into the brain case...."

The Creodonta seem to be characterized usually by the presence of an alisphenoid canal, which occurs frequently in the Insectivora but never in the Carnivorous Marsupials and where this is absent (as in *Sinopa agilis*) the forward course of the ectocarotid is marked by a slight groove in the alisphenoid (Wortman, 1902, p. 440). A similar variability of the alisphenoid canal is observed in *Erinaceus*. In this form there is also a transverse venous canal leading into the antrum of the basisphenoid (Wortman, *l. c.*) and this is a point of similarity not only to the opossum but also to *Solenodon* (*antea*, p. 243). The optic foramen is always separate from the foramen lacerum anterius, as it is in the most primitive Lipotyphlous Insectivores.

Characters separating the Creodonta from the Insectivora. The known Creodonta differ from the known Lipotyphlous Insectivora in the following characters:

(1) Apart from the Oxyclænidæ, which may possibly be Insectivores (Matthew), the Creodonts all exhibit advanced carnivorous adaptations in the dentition and skull. The gap between the two orders is partly bridged over by *Pantolestes* and *Palæosinopa*, Eocene Insectivores with many Creodont features in the skull (Matthew, 1909).

(2) The Creodonts are more progressive than the Lipotyphlous Insectivores in several features of the skeleton: (*a*) The scapula so far as known has a very broad prespinous fossa and relatively shallower blade — a car-

nivorous adaptation. (*b*) The pelvis always has a stout puboischiadic symphysis. In *Dromocyon* however the pelvic outlet as figured by Wortman (*l. c.*, 1901, p. 425) is very small, but not as small as it is in Lipotyphlous Insectivores. (*c*) The limbs are longer or at least not so much bent and generally better fitted for cursorial habits; the feet are digitigrade rather than plantigrade. (*d*) In the manus and pes of Creodonts the subequality and symmetrical arrangement of digits II, III and IV, which is characteristic of the Insectivora (p. 254), is less marked. In *Dromocyon*, as figured by Wortman (Nov. 1901, p. 382 and Dec. 1901, pl. vii), digits III and IV of both manus and pes are very distinctively paired and so also are digits II and V. In *Sinopa*, as figured by Matthew, 1906, pp. 224, 228), this condition is much less pronounced and some slight approach is made to the Insectivore condition; the Insectivore resemblance is more marked in *Patriofelis*, as figured by Osborn (1900, p. 269). In the Creodonta Inadaptiva the ungual phalanges are cleft, whereas in most Insectivora (except Talpidæ, Chrysochloridæ) they are uncleft, as in the Creodonta Adaptiva (p. 308).

Conclusions. All such differences however seem to be due to the divergent habits of the Insectivora and Creodonta and to the necessity of comparing Eocene Creodonts with recent Insectivores, and do not in themselves imply a very ancient separation between them. But in view of the presence of fairly large Creodonts in the Basal Eocene it is probable that the separation of the Creodonts and Insectivores must long antedate the beginning of the Tertiary.

In fine the Mesozoic ancestors of the Carnivora were probably small, semiarboreal, insectivorous and partly carnivorous Placentals, with a dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$, a well developed milk dentition, small tritubercular upper molars, simple premolars, small simple canines, incisors of opposite sides arranged in a convergent rather than transverse series. The muzzle was broad and heavy, the skull constricted back of the orbits, the brain case very small, probably surmounted by a long low sagittal crest, the zygomata not large, the optic foramen independent, and an alisphenoid canal present. The skeleton retained many primarily arboreal adaptations. These hypothetical forms thus approached the ancestral Insectivores (p. 254) but very early began to emphasize the flesh-eating, raptorial habits and structures, to increase in size and to spend more time on the ground. As thus conceived they would resemble the contemporaneous Polyprotodont Marsupials in many characters but they may have been distinguished from them by the following characters among others:

(1) Entocarotid entering through foramen lacerum medium, an alisphenoid canal, a distinct optic foramen.

(2) Orbitosphenoid not compressed dorsoventrally in the Marsupial fashion (p. 245).

(3) Palate not strongly fenestrated.

(4) Tympanic process of alisphenoid, if present, not forming a hollow shell for the tympanic cavity.

(5) Angle of lower jaw not sharply inflected.

(6) Epipubic bones reduced or absent.

(7) Astragalus with neck well developed.

(8) Dental formula $\frac{3.1.4.3.}{3.1.4.3.}$; milk dentition not reduced.

GENETIC RELATIONS BETWEEN CREODONTA AND FISSIPEDIA.

Constitution of the Creodonta. The suborder Creodonta includes several diverse groups of chiefly Eocene Carnivora which have been divided by Schlosser and by Matthew (1901, pp. 1–38) into three groups. The first of these, the CREODONTA PRIMITIVA, including only the Basal Eocene Oxyclænidæ with more or less simple tritubercular molars, may possibly be Insectivores (Matthew). The second group, the CREODONTA ADAPTIVA, included the Arctocyonidæ, Miacidæ ("Viverravidæ") and Palæonictidæ. In the first two families the ungues were compressed and the fourth upper premolar and first lower molar were not modified into carnassials. The third family, the Palæonictidæ, was removed from this group to the Fissipedia by Wortman because p^4 and m_1 show an early stage in the carnassial modification.[1] The third group was called CARNIVORA INADAPTIVA[2] in reference to the fact that they were definitely excluded from ancestry of the Fissipedia because the specialized carnassial, when present, was developed behind p^4. The ungual phalanges are flattened and fissured. The first family is the Mesonychidæ, an early Eocene cursorial side branch which parallels the Artiodactyls in its foot structure. In this family p^4 remained simple, the upper molars were bluntly cusped, tritubercular, the lower molars compressed and trenchant. The second and third families (Oxyænidæ and Hyænodontidæ) seem to be more nearly related to each other than either are to the Mesonychidæ. These parallel the Felidæ and Canidæ or the Hyænidæ respectively in general proportions, and develop their carnassials from the teeth behind $\frac{p.^4}{m.1}$, namely, from the true molars.

The Miacidæ as connecting the two suborders. The question of the

[1] Matthew also has recently (1909) removed *Palæonictis* from the "Adaptiva," which as thus restricted he calls the "Eucreodi."

[2] Matthew now distributes the Creodonta Inadaptiva under two sections: the "Acreodi," including only the Mesonychidæ, and the "Pseudocreodi" (forms with false carnassials), including the Oxyænidæ (*Oxyæna Patriofelis Palæonictis* etc.) and the Hyænodontidæ.

derivation of the Carnivora Fissipedia largely depends upon one's conception of the nature and limits of that group, which, as shown by the labors of Cope, Marsh, Scott, Osborn, Wortman, Matthew, and several European palæontologists, is certainly an offshoot of the stock that gave rise to the higher Creodonts.

The dentition of the typical Fissipeds such as the civet, the dog, the cat, and the marten, represents a high stage of evolution of the tritubercular type. In the Jurassic Trituberculates the small antero-posteriorly narrow upper molars were as many as six or eight in number on each side, and the premolars were compressed and conical. In the most primitive carnivorous Marsupials, which probably represent the Cretaceous stage, the molars are reduced to four but the premolars are still simple; in the Basal Eocene Oxyclænidæ, which are very primitive Placentals, perhaps Insectivores or ancestral Creodonts, the tritubercular molars are reduced to three in number and the fourth premolar has become bicuspid. In the Eocene Creodont families Arctocyonidæ and Mesonychidæ, the center of gravity, so to speak, of the dentition still lies in the large crushing upper molars; in the Hyænodontidæ the molars become compressed and shear-like. But in the Oxyænidæ the center of the dentition is shifted forward by the loss of the posterior upper molar, and the shearing function in the upper jaw is predominant on the postero-internal extension of the first molar.

In the Basal Eocene *Didymictis* (*Viverravus*) *haydenianus* Cope (1884, pl. xxiiie, figs. 12, 13) a specialized forerunner of the Miacidæ (Viverravidæ), the center of the dentition is shifted still further forward, since the shearing function is concentrated on the postero-internal blade of p^4 and on the antero-internal blade of m_1, while the post-carnassial teeth are much reduced, only the small m^2 remaining. Finally, in the Felidæ, the center of dentition reaches its anterior limit, since p^4 alone is carnassial and of large size, m^3 and m^2 are absent and m^1 is reduced to a vestige.

In Cope's original definition (Palæontological Bulletin, No. 20, 1876, pp. 1–4; Tertiary Vertebrata, p. 251) *Didymictis*, and consequently by implication the family it represents, were included in the Creodonta. The characters used to define the group also clearly include *Didymictis*.

However, the character of the carnassials in *Didymictis* and the Miacidæ so sharply separates them from the Arctocyonidæ, Mesonychidæ, Oxyænidæ and Hyænodontidæ and allies them with the Fissipedia that Wortman (1901, pp. 337–338) has grouped the Miacidæ ("Viverravidæ") with the Fissipede Carnivora under the subordinal term "Carnassidentia." It is also shown by Matthew in his recent memoir on the Bridger Carnivora (1909, p. 353) that the Miacidæ include several divergent lines of specialization some of which seem to be directly ancestral to the modern Carnivore families.

But the transference of the Miacidæ to the Fissipedia is demurred to by Matthew upon three grounds. First because the Miacidæ, as stated above were included by implication in the original definition of the Creodonts; secondly, because they are separated from their descendants among the Fissipedia and allied to the Creodonta by the possession of many primitive characters (*e. g.*, the scaphoid, lunar and centrale, although closely appressed, have not yet fused into a single bone); thirdly, because of the existence of certain forms recently described by Matthew which tend to ally the Miacidæ with the Arctocyonidæ.

Apart from this new evidence, there seems to be other reasons also (Matthew, 1901, p. 7) for placing the Arctocyonidæ in the Creodonta Adaptiva (Eucreodi) in company with the Miacidæ: (*a*) The manus of *Clænodon*, a Basal Eocene Arctocyonid (Matthew, 1901, fig. 6, p. 7) foreshadows the Fissipede type in the fusion of the centrale with the scaphoid and the close appression of the scaphoid and lunar, the three bones, conjointly having the appearance of a scapho-lunar-centrale, rather resembling those of the Miacid *Oödectes*, as figured by Wortman (1901, p. 154); and contrasting with the same bones in the other Creodonts. (*b*) The divergent hallux and pollex is a primitive character retained partly in the Fissipede *Cercoleptes* (Matthew). (*c*) The claws also are narrow and compressed, as in Miacidæ, and contrast with the fissured claws of the Mesonychidæ, Oxyænidæ, and Hyænodontidæ (Matthew).

The Basal Eocene *Arctocyon* certainly differs from the typical Miacidæ in its extremely small brain case, a feature which also distinguishes the Fissipedia from the earlier Creodonta. But this hardly disproves a close alliance between the Arctocyonidæ and Miacidæ. There is cumulative evidence that the progressive improvement in the brain of Tertiary phyla, if it could be followed backward into the Basal Eocene and Cretaceous, would lead in every instance into a very lowly type of brain, encased in a narrow brain case. The evidence given in the preceding chapter tends to show that certain lowly brained Mesozoic Insectivora gave rise to the large brained Menotyphla (p. 272) and to many other Placental orders. The brain case of *Arctocyon* is of course very small, but it is hardly if at all smaller in the Lower Eocene Miacid *Viverravus protenus* (*cf.* Matthew, 1901, p. 9, fig. 1).

It seems in short to be largely a matter of definitions whether the Miacidæ shall be included in the Creodonta or in the Fissipedia.

Additional evidence of close relationship between the two suborders.

Additional evidence that the Creodonta and Fissipedia are closely related is furnished by the agreement in the general arrangement of the cranial

foramina and architecture of the skull in the two groups. The entocarotid artery in *Sinopa agilis*, a primitive member of the Hyænodontidæ, must have entered the brain case through the foramen lacerum medius (Wortman, 1901, p. 440) as in the Fissipedia. In his description of *Sinopa grangeri*, Matthew (1906, pp. 208, 213) has noted several features which suggest the Oligocene Canids *Cynodictis* and *Daphænus*: especially in the tympanic region (*l. c.*, p. 214), in the post glenoid region (p. 215), in the long basicranial region and in the occiput. Apart from the aberrant Hyænodont features, the differences which separate the skull of *Sinopa* from that of Fissipedia are primitive features, such as the slight posterior spreading of the nasals, the interorbital constriction, small brain case, small backwardly directed paroccipital processes (an Insectivore character), and an accessory condylar foramen (see p. 218), the remains of which seem to persist in *Daphænus* (*l. c.*, p. 214).

The derivation of the Miacidæ and, through them, of the Fissipedia from unknown Insectivore-Creodont ancestors is also indicated in the following characters of the Lower Eocene *Viverravus protenus* (figured by Matthew, 1901, p. 9): persistence of the astragalar foramen, heavy muzzle, marked interorbital constriction, weak zygomata, long low sagittal crest (*cf. Pantolestes*). The skull also is very large in proportion to the skeleton; the tail large (presumably long); neck longer than in most modern Carnivora; limbs rather short with large joints and heavy muscular attachments; feet small, spreading; scaphoid and lunar separate; fibula large; humerus with prominent long deltoid crest, broad distal extremity and entepicondylar foramen (Matthew).

Conclusion. The derivation of the Fissipedia from the Creodonta by way of the Miacidæ has been well established by Wortman and Matthew and new evidence has been adduced by the latter author for the relationship of the Miacidæ and Arctocyonidæ. The phalanges in the Arctocyonid-Miacid-Fissipede group are always primitively compressed while in the Mesonychid-Oxyænid-Hyænodont group, so far as known, they are always depressed and distally fissured (Matthew). It remains to show that in spite of this difference both groups may have been derived from the Oxyclænidæ.

(1) The two types of ungual phalanges may sometimes occur in the same suborder, for *Erinaceus* has compressed, *Talpa* has deeply fissured ungues.

(2) The two groups are not very widely separated in the Basal Eocene so far as the skull and dental structures are known. For example, the skull of *Triisodon heilprinianus* (Matthew, 1901, pp. 30–31, figs. 10–12), an early Mesonychid, retains many primitive characters in common with *Arctocyon*; nor has it assumed any very marked Mesonychid features in the dentition.

(3) The dentition of the Oxyclænidæ (represented by *Tricentes, Chriacus*, etc.) is structurally more or less prototypal to that of both groups. The Mesonychid type may be derived from it by way of *Triisodon*. The Oxyænid and Hyænodont dentitions, however, even in their most primitive known stages have already advanced far beyond it. The Arctocyonid and Miacid dentitions, while divergently specialized, present no features incapable of derivation from the Oxyclænid type.

The derivation of these various lines of Creodonts and ancestral Fissipedes will not be settled until more intermediate stages, as well as the skull structure of the Oxyclænids, shall be discovered; however the Oxyclænid dentition is intermediate in character between the various Carnivorous dentitions on the one hand and the simple Insectivore type represented in *Ictops* and *Pantolestes* on the other. If the Oxyclænidæ should be proved to be allied to the ancestral Lipotyphla and thus to fall within the definition of the order Insectivora, it will follow that the various lines of Creodonts and the ancestral stem of the Fissipedia have been derived independently from an "Insectivore-Creodont" stock of possibly Upper Cretaceous age.

II. The Pinnipedia.

Outline history of the ordinal classification.

1693. Ray includes "Phoca" and the walrus ("Morse") with the other Carnivora in the "Quadrupeda vivipara unguiculata, multifida, carnivora majora capite longiore."

1735–1766. Linnæus includes *Phoca* in the order Feræ.

1780. Storr assigns the seals to the Phalanx Pinnipedia, one of his three primary divisions of the Mammalia.

1779–1797. Blumenbach proposes the order Palmata to include (*A*) Palmata Glires, (*B*) Palmata Feræ (*Phoca, Lutra*), (*C*) Palmata Bruta.

1795. Geoffroy and Cuvier apparently follow Blumenbach in placing *Phoca* and *Rosmarus* with *Manatus, Trichechus* (the Dugong) in "les Amphibies," an old group which had been very properly broken up by Linnæus.

1800. Cuvier restricts "les Amphibies" to include only "les Phoques" and "les Morses," and places the order next to "les Cétacés" in a grand division "à pieds en nagoire" of the Mammalia.

1811. Illiger uses Storr's term Pinnipedia both as an order and as a "familia."

1816. De Blainville groups "Les Phoques," "les Taupes," and "les Cheiroptères" as a grand division "anomaux" of the ordre "Carnassiers."

1817. Cuvier removes "les Amphibies" from the vicinity of the Cetacea,

reducing them to the rank of a division of "les Carnivores" which constituted in turn one of the divisions of "les Carnassiers."

1834. De Blainville breaks up this unnatural assemblage and joins the seals with the other Carnivora, placing the "*Pinnigradi ou Phoques*" ("auxquels on est conduit par les Chiens et les Protèles") as a division "anomaux" coördinate with the division "normaux" ("Plantigradi" and "Digitigradi"), both divisions being embraced in "les non-claviculés" [= Fissipedia and Pinnipedia] of the group "Carnassiers."

1840. Bonaparte separates entirely the Feræ from the Insectivora and gives the "Pinnipedia" equal rank with Feræ.

1872. Gill, following other authors (*e. g.*, Haeckel 1866), divides Feræ into two suborders, Fissipedia and Pinnipedia.

1897. Wortman tries to derive the Pinnipeds from the Creodont genus *Patriofelis.*

1905. Weber supports the view that seals are related to the arctoid Carnivores, adducing many resemblances in the soft parts (*cf.* p. 314, below).

1909. Matthew shows that the Eocene Insectivore *Pantolestes* foreshadows the Walruses in many characters, some of which may imply a certain degree of affinity.

Supposed Derivation of the Pinnipedia from the Creodonta.

The Middle Eocene Creodont *Patriofelis* shows certain characters in the feet and limbs which Dr. Wortman (1894, pp. 129–164) interpreted as aquatic adaptations. In addition to this the Pinnipedia (or at least the more primitive ones) retain many other characters; such as an alisphenoid canal, a vestigial astragalar foramen (in *Zalophus*) a large astragalo-cuboid contact, etc., which are also seen in *Patriofelis.* Dr. Wortman therefore conjectured (*l. c.*, p. 162) that the supposedly amphibious *Patriofelis* "took to the open sea and finally came to feed upon fish exclusively." This caused the degeneration of the powerful dentition into the simple teeth of the Pinnipedia. In 1900 Professor Osborn (*l. c.*, pp. 269–270), after restudying the material, concluded that *Oxyæna* and *Patriofelis* were powerful terrestrial or partly arboreal animals analogous to the cats in habits of feeding, and that their many resemblances to the Pinnipedia were due to derivation from common Insectivore-Creodont ancestors. In 1902, Dr. Wortman (*l. c.*) replied at some length to this conclusion and adhered to his original opinion. Matthew (1909, pp. 429–432) now adduces strong evidence to show that the limbs of *Patriofelis* were adapted neither for aquatic nor for arboreal life, and that the animal was a large, heavy-bodied, slow moving type, with rectigrade limbs.

But whether *Patriofelis* was partly aquatic or not may after all throw but little light on the origin of the Seals, because *Patriofelis* and *Oxyæna* possess several characters which seem to debar them from near relationship with that group.

The Pinnipedia possess a large, wholly consolidated scapho-lunar-centrale like that in the Fissipedia, whereas in the Oxyænidæ these bones are entirely separate. If the amphibious ancestors of the Pinnipeds had had these elements separate it seems that aquatic adaptation would have increased the separation and flexibility of the carpals as it has in the Cetacea. It must be confessed, however, that the consolidation of the scaphoid, lunar and centrale in the Sirenia weakens the force of this argument. The Oxyænidæ and the Pinnipedia differ radically in the dentition; in the former the molars are larger than the premolars, whereas in the Pinnipedia the premolars are relatively large and the molars are reduced or absent. In the Oxyænidæ the molars were of a peculiarly specialized sectorial character and if the Pinnipedia had been derived from that family it is likely that somewhere in the group some traces of these characters would be found. In no Pinniped do the cheek teeth retain the slightest resemblance to those of the Oxyænidæ but the pattern of the postcanine lower teeth of *Phoca gichigensis* Allen (1902) might readily be derived from those of the curious Amphicyonine Canid *Cynarctus saxatilis* Matthew (1902, p. 281, fig. 1). The degenerate and varied molars of the Pinnipedia range from a secondarily triconodont to a secondarily haplodont condition (*cf.* Osborn, 1907, p. 144, fig. 103). That a haplodont crown can be very quickly evolved out of a tritubercular crown is indicated by the peg-like teeth of *Proteles,* whose nearest relatives are the tritubercular Viverridæ.

Genetic Relations with the Fissipedia.

The derivation of the Pinnipedia from arctoid Fissiped Carnivora has been supported by Weber, (1907, p. 551), who has shown that in spite of markedly divergent habits, the Seals retain a number of very significant characters in common with the Bears. The maxilloturbinals are greatly enlarged and scroll-like and exclude the ethmoturbinals from the anterior nares as in the "Hypomycteri" (Bears, Dogs, Mustelines); the long intestine lacks a duodeno-jejunal flexure and lies in a simple mesentery, the kidneys and liver are divided into a number of separate lobules; in the male Cowper's glands are wanting and there is a large os penis. As in other Fissipedes, the placenta is deciduous and zonary, the uterus bicornuate, the brain has fou -centic gyri which bend around the Sylvian fissure. The bulla in neral appearance resembles the Arctoid rather than the Æluroid type,

although van Kampen has shown (1905, pp. 537, 542, 545) that in both the Phocidæ and the Otariidæ the bulla is a composite one, formed from the entotympanic and the true tympanic (annulus tympanicus) as in the Æluroidea.

This evidence tends to separate the Pinnipedia from genetic relations with the Creodonta and to ally them with the Arctoid Fissipeds, possibly as Weber suggests, with the Amphicyonine Canids. At the same time it must be admitted that this hypothesis has not yet satisfactorily accounted for several peculiar features cited by Wortman as common to the Pinnipedia and the Oxyænid Creodonta, especially the presence of a subungual foramen, the exceptionally large size of the trapezium, the large astragalo-cuboid contact, the oblique cubo-calcaneal facet, etc. If the Pinnipedia are to be derived from Arctoid Fissipeds it must be from genera retaining or foreshadowing all the characters listed by Wortman on pages 159–160 of the article cited.

CHAPTER VII. GENETIC RELATIONS OF THE DERMOPTERA, CHIROPTERA AND PRIMATES.

Analysis.

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I. The Dermoptera.

Historical Notes.

According to Gervais (1836) Bontius, a naturalist-voyager of the sixteenth century, observed the animal now generally called *Galeopithecus volans* at Batavia and elsewhere and described it as "Vespertilio admirabilis." Seba called it *Felis volans ternatea* (in allusion to the locality, Ternate, one of the Moluccas).

1758. Linnæus includes it with the lemurs under the name "Lemur volans."

1780. Pallas translates Petiver's "Chats-Singes" into "Galeopithecus" and regards it as intermediate between Lemurs and Bats.

1800. Cuvier removes the "Galéopithèques" to the group "Cheiroptères" of the "ordre Carnassiers," placing them at the end of the Cheiroptères and next to "les Plantigrades" (Insectivores, etc.).

1811. Illiger applies the term "Dermoptera" as a "familia," coördinate with "Cheiroptera" in the "ordo" "Volitantia."

1816. De Blainville associates "les Galéopithèques" with "les Tardigrades" (*Bradypus*) in a grand division ("anomaux") of the "ordre Quadrumanes."

1864. Peters, following Wagner, unites *Galeopithecus* with the Insectivora, a view accepted by Huxley (1872) and most English authors.

1872. Gill adopts Illiger's term "Dermoptera," regarding the group as a suborder of the Insectivora.

1885. Leche monographs the genus and argues for its removal to a separate order, "Galeopithecidæ."

1902. H. C. Chapman regards *Galeopithecus* as a modified descendant of the ancestors of the Chiroptera, remotely related to the Lemuroidea and Insectivora. This view was also adopted by Weber (1904).

1906. Miller (op. cit., p. 41) regards the group as constituting a family of the Chiroptera.

Genetic Relations of Galeopithecus.

The derivation of *Galeopithecus* from Insectivores resembling the Tupaiidæ (a view supported by Leche in his monograph of 1885) is rendered probable by many facts cited by Leche, including the following: the brain case in *Galeopithecus* is larger than in any Insectivores except the Menotyphla (p. 272). The orbits are large, the well defined supra orbital border is pierced by a foramen; the olfactory fossæ are large, the occipital plane is vertical; the lachrymal has both a facial and an orbital portion and the lachrymal canal is within the orbit. The resemblances in the skull to *Rhynchocyon* have already been noted (p. 281).

The stapes and incus of *Galeopithecus*, according to Doran (1879), more resemble those of the Macroscelididæ and Tupaiidæ than of the shrews, moles and hedgehogs and in one or two characters are strikingly like the Primate type. The malleus is very generalized and shows diverse resemblances to the Primates and the Macroscelididæ (1879, p. 443). The comblike incisors of *Galeopithecus* are foreshadowed by the denticulate incisors

in *Rhynchocyon*. The peculiar cuspidate upper molars bear traces of derivation from the triangular types seen in *Tupaia* and *Ptilocercus*. The pelvis is intermediate in character between that of Insectivora and that of Bats. A rudimentary sublingua (fully developed in *Tupaia* and Lemurs) is present and the digestive tract resembles that of the typical Menotyphla in the possession of a cæcum.

Notwithstanding these and similar resemblances the numerous differences from the Menotyphla in the male and female reproductive organs and throughout the organism (*cf.* Weber, 1904, p. 410) show that the Dermoptera must have separated from that group at a very early date.

Leche (1886) expressed the opinion that in the young *Galeopithecus* the auditory bulla corresponds in structure with that in the Menotyphla, Chiroptera and Prosimiæ; but van Kampen (1905, p. 446) showed that the swollen bulla and tubular meatus are both formed from the annulus tympanicus; whereas in the Menotyphla the bulla is composite, the inner part being formed from the enlarged entotympanic. As in the Insectivora the alisphenoid takes part in the limitation of the tympanic cavity anteriorly, but there is no stapedial artery and the entocarotid canal terminates anteriorly in the foramen lacerum medium ("anterius," van Kampen, *op. cit.*, p. 464).

Galeopithecus may also be related remotely to the Lemurs (Chapman) with which it agrees in superficial skull characters, in the possession of a sublingua and of a cæcum divided into pockets, in the structure of all the female genitalia except the uterus, which has retained the primitive double condition. The external generative organs closely resemble those of Lemurs, the clitoris being concealed by a circular fold of integument as in *Chiromys* (Chapman). There are also several important points of agreement in the musculature. The skeleton presents some analogies to that of *Indris* (*cf.* de Blainville, 'Ostéographie').

The relationship of the Dermoptera with the Fruit Bats is indicated by many characters noted by Leche. Among the most noteworthy of these is the fact that the patagium of *Galeopithecus* (which extends between the long fingers as well as completely surrounding the body) is supplied by the same muscles and nerves as in the Chiroptera. While asleep *Galeopithecus* hangs head downward, suspended by its hind claws like a Bat. It also resembles the Fruit Bats in the low position of the mandibular condyle, and in many characters of the shoulder girdle, episternum, musculature, stomach, uterus, placenta, and mammæ.

II. The Chiroptera.

Historical Notes.

Early naturalists generally regarded bats as birds with "ailes-de-peau" which brought forth living young (Gervais, 1835). During the renaissance the ancient view was still held, even by Aldrovandus, who minutely described them (Gervais).

1693. Ray places the bats in the "anomalous" division of the unguiculates, along with the sloth. He says that except with regard to their wings and mode of flight they do not agree with birds any more than does the winged lizard, but are essentially viviparous quadrupeds. The bats are treated under the heading "Quadrupeda multifida rostro breviore anomala, & primò volatica seu Vespertiliones." The Sloths are described under the next section, "Secundo gressile, tardipes. Ai sive Ignavus" [*Bradypus tridactylus*].

1735. Linnæus in the first edition of the 'Systema' places the Bats after the carnivores. Later he placed them with the "Anthropomorpha" (later = Primates). He regarded them as intermediate between the Lemurs and *Bradypus* and named them "Vespertilio."

1779. Blumenbach proposes the name "Chiroptera" for the group.

1792. Vicq d'Azyr groups the Bats in the ordre "ailepieds" (*cf.* the classic Latin epithet "ali-pes," wing-footed, applied to Mercury).

Through the labors of Daubenton and Geoffroy, Fréd. Cuvier, Leach, and others, many new kinds and divisions were recognized, so that by 1820 Desmarest enumerated ninety-five species.

1800. Cuvier groups "les Cheiroptères" with *Galeopithecus* and places them next to "les Plantigrades" in the order "Carnassiers."

1816. De Blainville intimately unites them with "les Taupes" (Talpidæ) and "les Phoques" (Pinnipeds) as a main division "anomaux" of the order Carnassiers. *Galeopithecus* he places with the Primates.

1834. De Blainville removes the Pinnipedia from this group.

1839. De Blainville places the "Cheiropteri" with the "Orycteri" and the "Insectivori" in a grand division "Claviculés" of the Carnassiers.

By all subsequent authors the bats were restored to their ordinal independence.

1872. Gill divides the order into the "Animalivora" and "Frugivora."

1880. Huxley emphasizes their relationship to the Insectivora.

1875. Dobson divides the order into the suborders "Megacheiroptera" and "Microcheiroptera."

1904. Weber gives an excellent review of the morphology and classification; in the latter he combines Winge's results with those of earlier authors.

1907. Gerrit S. Miller in his 'The Families and Genera of Bats' reviews the history of the classification and the morphology of the order, defines the families and genera and gives extensive keys and synonymy. He recognizes "at least 173 genera and 36 families."

Genetic Relations.

The group was very highly specialized as far back as the Eocene and the palæontological evidence as to its origin is therefore of a negative character, as in the case of the Rodents, Edentates and all other groups which probably acquired many of their ordinal characters before the known Tertiary record began. Nevertheless there can be little doubt that the Chiroptera are an offshoot of late Mesozoic or early Tertiary arboreal Insectivores, which must have resembled *Galeopithecus* in many characters. This is indicated in the assemblage of characters given by Weber (1904, pp. 382–396), especially the following: Brain macrosmatic, smooth or sparsely furrowed, cerebellum uncovered; testes descending periodically into a subcutaneous cremaster sack; penis pendulus (*cf.* Primates) often with an os penis (*cf.* Insectivores); uterus duplex, bicornis or simplex: placenta discoidal, deciduate, with large allantoic chorion and vestigial yolk sack; dentition diphyodont, dental formula a derivative by reduction of $\frac{3.1.4.3.}{3.1.4.3.}$; teeth primitively tritubercular-tuberculo-sectorial [1]; digits primitively pentadactyl, carpus with embryonic centrale, tympanic ring-shaped, often connected with the osseus bulla. The ossicula auditus according to Doran (1879) much resemble those of the Soricidæ and allied Insectivora, particularly in the malleus, which approaches also the Marsupial type.

The Microchiroptera are more specialized than the Megachiroptera and the latter in turn are remotely allied to *Galeopithecus* (see p. 317) which thus serves to connect the Chiroptera with the Lemuroidea and Menotyphlous Insectivora.

III. The Primates.

Outline History of the Classification.

1693. Ray divides the "Unguiculata pede multifido, digitis aliquodque separatis" into: (1) those with flat nails, "Πλατυώνυχα & Ανθρωπόμορφα,

[1] Oldfield Thomas has adduced evidence that even the peculiar molars of the Fruit Bats have been derived from a cuspidate tritubercular-tuberculo-sectorial type (1888, pp. 474–475). This conclusion is supported by Miller (*op. cit.*, 1907, pp. 44–45), who states that in the Phyllostomidæ there is "a complete series of stages connecting the normal form of the teeth with one nearly resembling that of the Megachiroptera."

Simiæ," and (2) those with narrower claws (*i. e.*, the remaining unguiculate forms).

1735. Linnæus in the first edition of the 'Systema Naturæ' includes under the order "Anthropomorpha" the genera *Homo, Simia, Bradypus.*

1758. Linnæus includes in the order "Primates" the genera *Homo, Simia, Lemur* (including the Lemuroids and *Galeopithecus*), *Vespertilio.*

1780. Storr includes in his comprehensive group "Primates" the following sections.

"Sectio I, Palmares." *Homo.*

"Sectio II, Palmoplantares." *Simia, Prosimia, Procebus, Tarsius, Lemur.*

"Sectio III, Plantares." *Didelphis, Phalanger.*

1779–1797. Blumenbach, "the father of anthropology," assigns man to a separate order "Bimanus," applying Boddaërt's term "Quadrumana" to the remaining Primates.

1792. Vicq d'Azyr classifies the apes, monkeys and lemurs under "les Pédimanes."

1800. Cuvier separates "les Quadrumanes" from "les Bimanes" and divides "les Quadrumanes" into "Singes" [Anthropoids] and "Makis" [Lemuroids].

1811. Illiger substitutes the names "Erecta" for "les Bimanes" and "Pollicata" for "les Quadrumanes."

1816. De Blainville classifies "les Quadrumanes" as follows:

"Normaux: (1) Singes: du continent ancien, les Singes;
du continent nouveau, les Sapajous.
(2) Makis: les Makis, les Loris, l'Aye-Aye."

De Blainville thus correctly allocated the Aye-Aye and justly separated Old World from New World anthropoids. A second grand division "*anomaux*" includes *Galeopithecus* and the Sloths.

1834. De Blainville clearly anticipates Owen's division "Catarrhinæ" and "Platyrrhinæ," in the division of the Anthropoids into those with "narines rapprochées" ("Pitheci") and those with "narines éloignées" ("Neopitheci"); the Lemurs are now called "Pseudopitheci."

1842. Geoffroy rejects the views of Cuvier and Blumenbach as to the ordinal distinctions of the Bimana (*Homo*) and supports the Linnæan view that mankind belongs zoölogically with the Primates.

1858. Darwin's 'Origin of Species,' and later the 'Descent of Man' initiates a vast literature dealing with the relations and classification of the family Homnidæ.

1866. Owen, developing Bonaparte's cerebral system of classification, separates the "Bimana" as a subclass of mammals under the term "Archencephala."

The subsequent history of the classification of the Primates is too extensive to be followed here. Notwithstanding the labors of Mivart, Forsyth Major, Gaudry, Filhol, Grandidier, Schlosser, Branco, Selenka, Hubrecht, Cope, Osborn, Wortman, and others, the exact relations of the Tertiary and Recent families is still more or less unsettled and calls for a general review of the main lines of evidence.

At least one great result, the derivation of Man from some as yet undiscovered Tertiary Primate may be considered to be as well established as any of the great postulates of geology. It rests upon evidence which has been gathered from every possible source and tested by a long line of defenders and critics. To the palæontologist who has acquired by experience some ability to distinguish between the effects of convergent evolution and the marks of ancestral kinship there can be no doubt whatever about the meaning of the resemblances obtaining throughout the entire organism between Man and the Catarhine Primates. The resemblances are such as generally denote ancestral kinship, the differences are such as denote adaptive divergence from a common type.

Genetic relations of the Primates.

The separation of the Prosimiæ and Simiæ may well date back to the Lower Eocene, but that the two groups were at that time closely related seems to be well established: first, by the very numerous and deep seated characters still retained in common by the two orders (see Weber, 1904, p. 741); secondly, by the existence of such generalized forms as the Middle Eocene Notharctidæ; thirdly, by the annectant character of *Tarsius*, which, while still a "Lemur of lemurs" is related in the other direction to the Anthropoidea (Elliot Smith, 1903); fourthly by the agreement in fundamental brain characters between the Lemurs and Anthropoids (Elliot Smith, *op. cit.*).

The derivation of the order from large-brained arboreal Insectivores resembling in many ways *Tupaia* and *Ptilocercus* is indicated by the following considerations:

(1) The dental formulæ of the Primates are all derivatives of $\frac{3.1.4.3.}{3.1.4.3.}$.

(2) The molars were primitively tritubercular above and tuberculosectorial below, perhaps resembling those of the modern *Ptilocercus* in many characters.

(3) The upper fourth premolars were bicuspid, the lower premolars high and pointed. The diet was probably insectivorous-frugivorous.

(4) The course of the entocarotid in Lemuridæ and Chiromyidæ corresponds with that in the Tupaiidæ (van Kampen, 1905, p. 680).

(5) Many Primate characters of the skull are foreshadowed in *Tupaia* and *Ptilocercus* (pp. 273, 274).

(6) The bulla tympani in the Lemuridæ is formed from the inflation of the entotympanic, exactly as in *Tupaia* and *Ptilocercus*, the tympanic remaining as a bony ring (van Kampen, 1905, p. 677).

(7) The ethmoturbinal complex, according to Paulli, is closely connected with the Insectivore type (Weber, 1904, p. 745). As in that group, there are four endoturbinals and five olfactory scrolls.

(8) The malleus of *Tupaia*, according to Doran (1879, pp. 441–442), "differs from that of any other insectivorous mammal.... and much resembles that of some of the lower Primates, especially *Midas* or *Hapale* and certain Lemurs...."

(9) The shortening of the face in some of the earliest Primates is foreshadowed in *Ptilocercus* (Fig. 21, p. 273), while the more elongate face in *Notharctus* and *Adapis* is foreshadowed in *Tupaia*.

(10) The manus and pes of the lemuroids represent a development of characters suggested in the Menotyphlous Insectivores. The opposibility of the pollex and hallux is foreshadowed in *Ptilocercus*, the carpal callosities in *Tupaia* (p. 270); the subequality and symmetrical arrangement of digits II, III, and IV (digit III being the longest) are foreshadowed in all Insectivores, and the same is true of the free centrale carpi, and the lunar-unciform contact. The peculiar Primate astragalus is distinctly suggested in *Tupaia*, while the very small size of the mesocuneiform is also an Insectivore heritage. The bicornuate uterus, entepicondylar foramen, and third trochanter are primitive Placental characters.

In order to emphasize the hypothesis that the orders Menotyphla, Dermoptera, Chiroptera and Primates have had a common origin, possibly from some Upper Cretaceous family resembling in many characters the Tupaiidæ, these four orders may be embraced in a single superorder, which may be named **Archonta**[1] in allusion to the fact that Linnæus included in the Primates the genera *Homo, Simia, Lemur* (including the Lemuroids and the "Flying Lemur"), *Vespertilio.*

[1] Ἄρχων chief, *cf.* German *Herrenthiere.*

CHAPTER VIII. GENETIC RELATIONS OF THE RODENTS AND EDENTATES.

Analysis.

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I. The Rodentia.

Outline History of the Ordinal Classification.

The characters of the dentition of the group are so striking and the representatives of the order form so many passages from one type to another that the modern conception of the group was reached much more rapidly than was the case in other orders.

1693. Ray describes under the "Quadrupeda vivipara pede multifido herbivora binis prælongis dentibus anterioribus in utraque maxilla, seu Leporinum Genus" the following animals (*l. c.*, p. 204):

"Lepus, Λαγὼς....The Hare"; "Cuniculus, Δασύπους, A Rabbit or Cony"; "Cuniculus Brasiliensis Tapeti dictus" [= *Lepus brasiliensis*]; "Cuniculus Brasiliensis Aperea dictus" [= *Cavia aperea*]; "Hystrix, the Porcupine"; "Cuanda Brasiliensibus Marcgr Tlaquatzin spinosum Hernand." [? *Cœndou* (= *Synetheres*) *prehensilis*]; "Castor sive Fiber, The Beaver"; "Sciurus vulgaris," "Sciurus virginianus cinereus major, the great grey Virginia Squirrel"; "Sciurus Zeylanicus pilis in dorso nigricantibus Rukkaia dictus" [*Sciurus macrourus*]; "Sciurus Americanus volans, the flying squirrel" [*Sciuropterus volucella*]; "Sciurus Getulus Caii apud Gesnerum The Barbary Squirrel" [*Xerus getulus*]; then follows some fifteen species under the term "Mus," including, beside the true rats and mice, the "mus aquaticus sive Rattus aquaticus" [*Fiber zibethicus*], "Mus aquaticus exoticus. The Muscovy or Musk Rat," [? *Crocidura myosura*]; "Mus Avellan-

arum major, Sorex Plinii, Gesn. The Greater Dormouse or Sleeper" [*Myoxus glis*]; "Mus Avellanarum minor, Angl. The Dormouse or Sleeper" [*Muscardinus avellanarius*]; "Mus Noricus vel Citillus Gesn." [*Spermophilus citillus*]; "Cricetus Gesn." [*Cricetus cicetus*]; "Mus alpinus Plin. Marmosa Italis [*Arctomys monax*]"; "Mus seu Cuniculus Americanus & Guineensis Porcelli pilis & Voce, Cavia cobaya Brasiliensibus dictus, Marcgr. The Guiny Pig [*Cavia cobaya*]"; "Mus Sylvestris Americanus Cuniculi magnitudine Porcelli pilis & voce. Aguti vel Acuti Brasiliensibus dictus. Marcgr." [*Dasyprocta aguti*]; "Mus Brasiliensi magnus, Porcelli pilis and voce, Paca dictus. Marcgr." [*Cœlogenys paca*]; "Mus Norwagicus vulgo Leming Wormii" [*Lemmus lemmus*]; "Glis Gesneri & aliorum, Rell vel Rellmus. Helvetiis"; Mus indicus arboreus Striatus [?].

1735. Linnæus in the first edition of the 'Systema Naturæ' establishes the order "Glires" to include the genera *Hystrix, Sciurus, Castor, Mus, Lepus, Sorex.*

1748. Linnæus, 6th edition, also includes *Didelphis.*

1758. Linnæus mistakenly adds *Rhinoceros,* removes *Sorex, Didelphis.*

1766. Linnæus removes *Rhinoceros,* adds, "Noctilio americanus."

1778. Pallas divides the Linnæan genera of rodents and carefully describes the anatomy.

1779. Blumenbach puts the Rodents into the Order "Digitata" as a division (A) coördinate with (B) the Carnivorous and (C) the edentate "Fissipeda."

1780. Storr uses the term "Rosores" for the group.

1792. Vicq d'Azyr uses the term "Rodentia."

1795. Geoffroy and Cuvier include the Kangaroo in the group.

1800. Cuvier also includes the Aye-Aye, which was thought to connect the order with the Primates.

1811. Illiger calls the order "Prensiculantia" and divides it into eight "familiæ," removing the extraneous genera *Daubentonia* [*Chiromys*], *Halmaturus.*

1817. Cuvier excludes the Kangaroo but retains the Aye-Aye, divides the order into "claviculés" and "non-claviculés."

1816. De Blainville removes the Aye-Aye to the Primates (following Illiger); he divides the order into "Grimpeurs" [Sciuromorphs], "Fouissiers" [Myomorphs], "Coureurs" [Lagomorphs], "Marcheurs" [Hystricomorphs].

1834. De Blainville more clearly anticipates the divisions of Brandt.

1842. Waterhouse divides the order Rodentia into three suborders, based on characters of the jugal, of the infraorbital foramen and of the lower jaw, namely "Murina," "Hystricina," "Leporina."

1849. Gervais sets apart the Lagomorphs as a suborder, under Illiger's term "Duplicidentata."

1851–1855. Brandt proposes his four subordinal divisions "Lagomorpha," "Sciuromorpha," "Myomorpha," "Hystricomorpha."

1899. Tullberg monographs the entire group. He divides the Simplicidentata into two great series "Sciurognathi" and "Hystricognathi." The former divides into the "Myomorphi" and "Sciuromorphi" the latter into the "Bathyergomorphi" and "Hystricomorphi." The Myomorphi again include the "Ctenodactyloidei," "Anomaluroidei" (Pedetidæ + Anomaluridæ), "Myoidei." The Sciuromorphi include the "Geomyoidei," "Castoroidei," "Sciuroidei."

Naturalness of the Order.

Before taking up the problem of the general relations of this order it is necessary to inquire whether the two suborders, Duplicidentata and Simplicidentata, which are separated by many important characters and between which no fossil linking forms have been discovered, are in truth related or whether the numerous resemblances that tend to connect them may not be due largely to convergent evolution.

Mr. Gidley has suggested (1906, p. 99) that the oldest known type of Duplicidentate molars, that of the Oligocene *Palæolagus*, might have been derived from the Mesozoic triconodont type by the intervention of a hypothetical intermediate stage. This hypothesis seems, however, to rest on very scanty evidence. The Triconodonts, if their inflected angle proves anything, are Marsupials (Metatherians) allied remotely to the Polyprotodonts; but it would be difficult to point to any definitely Marsupial characters in the Duplicidentates except perhaps the perforation of the transverse process of the seventh cervical vertebra by the vertebral artery; while very typical Placental characters abound. Dr. Forsyth Major, although an opponent of the theory of tuberculy, shows (1899, pp. 433–520) that the upper molars of certain Miocene Duplicidentates retain clear evidence of derivation from a sharply triangular type which is wholly unlike the Triconodont type; and that the deep groove which finally sinks in and divides the Leporid molars into distinct anterior and posterior halves is a secondary character, initiated perhaps by the hypertrophy of the postero-internal ridge or hypocone (see also Osborn, 1907, p. 149).

The Duplicidentata (Weber, 1904, p. 493) possess many deep seated characters in common with the Simplicidentata, such as: a typically complete uterus duplex, a discoidal deciduate placenta, a small allanto-chorion, a large cup-shaped invaginate yolk sack in which the embryo lies, nineteen

dorso-lumbars (D 12, L 7), and four endoturbinals with five scrolls. These are, it is true, mostly primitive mammalian characters but they are not found in this combination elsewhere and taken in connection with other characters, are very significant. A comparison of the crania of *Lepus* and *Ochotona*, representing the Duplicentata, with those of *Capromys*, and *Pedetes*, representing the Simplicidentata, reveals an ordinal agreement in the arrangement of the cranial foramina, and in the characters of the petrosal, bulla, mastoid, interparietal, condyles, palate, jugal, orbital and temporal fossæ (see below p. 329).

Origin of the Rodentia.

Assuming then that the Duplicidentata and Simplicidentata are correctly associated in the same order, *which of the superfamily or subordinal groups may be regarded as the most primitive, and in what respects does it approach toward other orders?*

The known Lagomorpha (Duplicidentata), as stated above, have retained very primitive characters in the reproductive system (Weber, 1904, pp. 485–486) but the skull and skeleton have become highly specialized.

The Hystricomorph series seems to be the least promising group in which to look for primitive mammalian characters, in view of the presence of such highly specialized characters as the greatly expanded antorbital fenestra, the narrow palate, complexly folded hypsodont cheek teeth, and perfected rasp-like action of the jaw in mastication. The known Tertiary Hystricomorphs exhibit the same characters.

The Anomaluroidea (Pedetidæ, Anomaluridæ) mingle certain characters of the Sciuromorphs, Myomorphs and Hystricomorphs with others of their own but they do not appear to assist in the problem in hand. The Myomorpha are all obviously more specialized than the more primitive Sciuromorpha in the characters of the skull.

Primitive characters of the Eocene genus Paramys.— The Sciuromorpha (including in this group both the typical forms and the Aplodontiidæ, Geomyidæ, Heteromyidæ, etc.) embrace many forms with hypsodont complex cheek teeth and highly specialized skulls; but among the Sciuridæ occur also some relatively primitive forms with bunodont cheek teeth; and among the presumable ancestors of this division we find in the Lower to Upper Eocene genus *Paramys*, of the family Ischyromyidæ, the most primitive of all known Rodents. As figured by Cope (1884, pl. xxiv a, figs. 1–14, *"Plesiarctomys" delicatissimus*) and by Scott and Osborn (1889, pl. xi, *Paramys sciuroides*), this genus differs from later Sciuromorphs notably in the following primitive characters: the postorbital processes are slight or

absent and the skull is markedly constricted back of the orbits; the antero-external slip of the masseter muscle evidently had not yet excavated an oblique antorbital depression for its reception, and Dr. Matthew informs the writer that apparently the external slip of the masseter was limited anteriorly, as it is in *Aplodontia* and the Hystricomorpha (primitive characters), and on account of the downward direction of the small infraorbital foramen it appears unlikely that the internal slip of the masseter had invaded that foramen.

The rest of the skeleton of *Paramys* differs in no important respect (so far as figured by Cope) from the generalized Sciuromorph type. It has the characteristic ilium and limb bones. Its astragalus is also of the Rodent type: with wide trochlea, sharp keels, no astragalar foramen, a short broad neck, and a wide convex head, which is flattened antero-posteriorly and twisted on the neck so that its long axis points obliquely backward and inward. Other generalized characters, observed in American Museum material of *Paramys* by Dr. Matthew, include the very long and large tail, entepicondylar foramen in humerus, third trochanter on femur, toes 5–5, separate scaphoid, lunar and centrale, separate radius and ulna, tibia and fibula.

Cheek teeth of Paramys.— The molars are roundly triangular in form, consisting of a blunt inner cusp from which two diverging ridges pass to the para- and metacones; the anterior cingulum is either not prominent (*P. delicatissimus*, Cope, 1884, pl. xxiv a, fig. 1a), or more prominent and connected with the parastyle; but this anterior crest, which became pronounced even in the Oligocene *Prosciurus vetustus* Matthew (1903, p. 213) was not so high and prominent in *Paramys* as it is in *Arctomys*. The crown of the lower molars is divided into two parts, the anterior corresponding to the trigonid, the posterior to the talonid. The antero-internal cusp is elevated; it is possibly the metaconid; the talonid is broadly basined, with well developed hypo- and entoconids.

"Trituberculy" vs. the "Premolar Analogy" Theory in the Rodentia.— The dentition of *Paramys* thus seems to approach the tritubercular-tuberculosectorial type; but Dr. Wortman (1903, pp. 217–218), in criticising the theory of trituberculy, takes the view that the principal cusp in the lower molar of *Paramys* is not antero-external like the "protoconid" of normal molars, but antero-internal, as it is in the premolar (p_4), which is assuming the molar form. As Dr. Wortman believes that molars have generally passed through the stages later revealed in the premolars, he infers that since the true "protoconid" in the lower premolars of *Paramys* is evidently on the inner side, it is so also in the molars.

This conclusion, if true, tends to remove the Rodentia very far from the

typical Placental orders. But Dr. Wortman's argument seems to be weakened to some extent by the following considerations:

(1) While the premolars in certain groups (*e. g.*, Zalambdodonts) appear to furnish reliable indications of the early history of the molar cusps, in other groups (*e. g.*, Ungulates) they appear not to do so.

(2) *Paramys* has already departed from the typical Placentals rather widely in the skull structure; and in its lower teeth the primitive trigonid may have been modified in the manner described below.

(3) Dr. Wortman takes the view that the true protoconid in the lower molar of *Paramys* is on the internal side. A frequently reliable criterion of the homology of cusps is not position but function with reference to the parts of the opposing teeth. The main internal cusp of the upper molars of *Paramys* is certainly analogous with the protocone of most mammals because in life (as shown by comparison with *Arctomys* and *Didelphis*) it fitted into the basin of the talonid of the lower molars. In the lower molars the functional protoconid is the reduced antero-external cusp of the lower molars; because, like normal protoconids, it fitted into the space behind the metacone of an upper molar and in front of the paracone of the next upper molar. This space in the more advanced forms was gradually filled by the rising parastyle-cingulum ridge, while the tip of the protoconid was lowered. The high antero-internal cusp of the lower molars, which Dr. Wortman regards as the original tip of the crown, is probably not the true protoconid but either the paraconid, the metaconid or the paraconid + metaconid; because, like these cusps in normal trituberculate mammals, it fitted into the internal space between two upper molars. The raising of the parastyle, lowering of the protoconid and decided elevation of the antero-internal lower cusp in the modern Sciurid are seen to be mechanically correlated phenomena (see below).

(4) The mechanical reason for the peculiar obliquity and atypical development of the Sciurid lower molar is the obliquely lateral vibration of the mandible in mastication. True propalinal (antero-posterior) motion is only possible in gnawing with the incisors, when the molar crowns are not in contact. Anteroposterior motion during mastication would be precluded by the irregular wearing surface of the crown. Even in Rodents (except Caviidæ) in which the wearing surface of the complexly folded crown is perfectly plane, the movement of the mandible in mastication (so far as can be judged from the skull and jaw alone), seems to be obliquely lateral rather than strictly antero-posterior.

The molar pattern of *Paramys*, which all authorities regard as the most primitive pattern among Rodents, accordingly seems to offer no insuperable obstacle to the view that the Rodents have been derived from mammals

with a normal tritubercular dentition; but nevertheless it may indicate a very ancient separation from the Insectivores; and even although Dr. Wortman's evidence be wholly insufficient, his conclusion that the trituberculy of Rodents is partly secondary must be admitted as a possibility not yet disproven.

General morphology of the Rodent skull.— The evolution of the scalpriform incisors and of the jaw action described above (p. 328) has doubtless conditioned: first, the development of the elongate mandibular condyles and glenoid sockets, and secondly, the readjustment and modification of nearly all the bones of the skull; so that among known Rodents relatively few points of resemblance to the typical Placentals are left.

The *cranial foramina* (examined by the writer in *Lepus, Ochotona, Sciurus, Arctomys, Mus, Hystrix, Cavia*) conform in general to the normal Placental type. The orbito-sphenoid is pierced by a large optic foramen; the lachrymal, infraorbital, sphenopalatine, ethmoid, anterior and posterior palatine foramina, the foramen lacerum anterius, foramen rotundum, foramen ovale, eustachian opening, foramen lacerum posterius, condylar, post-glenoid, stylomastoid, and mastoid foramina are all present. The alisphenoid canal (occasionally absent) is apparently not the large tunnel leading forward to the foramen lacerum anterius but a small canal external to it. The foramen ovale is also prominent, except in Lagomorphs and Hystricomorphs, where it appears to be confluent with the foramen lacerum medius. The basisphenoid is perforated by a transverse canal, which, as in *Didelphis* and certain Insectivores (p. 291) is stated by Tullberg (Weber, 1904, p. 474) to transmit a vein. The entocarotid and its stapedial branch are variously developed (van Kampen, 1905, p. 566). When the former is well developed it often runs through a canal or groove lying between the bulla and the petrosal and enters the cranium through the foramen lacerum posterius. In *Lepus* it pierces the bulla. The condylar foramen, as in certain Insectivores, is double or even triple (some specimens of *Arctomys*), perhaps in correlation with the primitively composite nature of the hypoglossus nerve (C. S. Mead). The presphenoid is sometimes bounded on either side by longitudinal vacuities. The elongate anterior palatine foramina are often confluent inferiorly. *Tympanic region.* The lateral margins of the basisphenoid are often raised and more or less excavated on each side for the very large inflated tympanic bulla; this fact tends to indicate that in the case of *Microgale* and other Insectivores the functional participation of the ali- and basisphenoid in the bulla is no indication of relationship to the Marsupials but a result of the pressure exerted by the expanding bulla upon the borders of the adjacent bones. The *infraorbital foramen* is invaded in the higher Rodents by an internal anterior slip of the masseter muscle and

expanded into a finally enormous fenestra. The apparent *ectopterygoid fossæ*, according to Weber (1904, p. 474), in most instances are formed by the spreading of the pterygoids, which often end in backwardly projecting hamular processes. But in the young *Lepus* these fossæ seem to be normal and comparable with those in *Erinaceus, Hyrax,* etc., *i. e.,* bounded internally by the pterygoids and externally by the pterygoid wings of the alisphenoid. They lodge the large ectopterygoid muscles, which sometimes (*e. g., Hystrix*), as in *Erinaceus algirus,* etc. (p. 287) cause the angle to be sharply inflected.

Relationship of Rodents to Insectivores.— The Rodents appear to approach somewhat more closely toward the Insectivores than toward any other of the typical Placental orders. They are *more primitive than the Insectivora* in the possession of a completely double uterus, of a uniformly large yolk sack, and sometimes of an accessory yolk sack placenta (Lee, 1908, p. 918), and of the dorso-lumbar vertebral formula of D 13 + L 6 = 19, which only rises to 23 and 25 in very specialized types; whereas in Insectivora only *Tupaia, Solenodon* and the Talpidæ retain the lower number, while in all the others it varies from 20 to 24. On the other hand, in the conditions of the testes the Rodents are somewhat *more advanced than the most primitive Insectivores*; because the testes do not retain their primitive position but descend at least partially and to a varying extent, in some cases even into a scrotum.

The *ethmoid complex,* according to Paulli (quoted by Weber, 1904, p. 474) closely resembles the Insectivore type, *i. e.,* there are four endoturbinals with five scrolls, and a very large naso-turbinal. The *ossicula auditus* are extremely variable in form in different families. The malleus in the Myomorpha has a broad lamina and an orbicular apophysis as in Shrews and Bats (Doran, 1879, pp. 410, 418). The Jacobson's organ of Rodents is of a very peculiar type (Broom, 1898). In the more primitive forms the *manus and pes,* as in Insectivora is characterised by the subequality and symmetrical arrangement of digits II, III and IV, digit III being somewhat the longest. The carpus frequently retains a free centrale and primitively a well defined lunar-unciform contact. Fusions of the scaphoid and lunar, of the tibia and fibula, occur in both Rodents and Insectivores. The radial, ulnar and tibial sesamoids, which occur also among the Insectivora, are developed to a high degree in various Rodents, sometimes simulating the digits in becoming jointed and provided with a claw-like structure. The names "præpollex," "postminimus," and "præhallux" have been applied to these structures, but Weber (1904, p. 476) regards them not as true digits but as pure sesamoids. At any rate they seem to be very ancient structures since they are foreshadowed in the manus of the Permian *Theriodesmus* (p. 440). The

Rodent *astragalus*, as represented by that of *Paramys* (described above, p. 327), differs in details from the Insectivore types seen in *Solenodon, Centetes, Erinaceus, Talpa,* and *Tupaia,* especially in its very broad trochlea; but on the whole it agrees much better with the Insectivore than with the Creodont types. The Rodent astragalus (Fig. 30, p. 454) also resembles the Tubulidentate and Xenarthrous types (especially those of the Santa Cruz Edentates) in many respects. The average *humerus and femur* of Rodents appear to be less primitive in details than those of the lowest Insectivora, especially with regard to the frequent reduction of the entepicondylar foramen and third trochanter. Perhaps the most noteworthy feature of the *vertebræ* is that in *Lepus, Cavia* and others the transverse process of the seventh cervical is pierced as it is in Marsupials. The pseudo-sacral vertebræ in Rodents often have large transverse processes which tend to unite with the ischium.

There are pretty clear indications (especially in the Duplicidentata) that the *dental formula* of Rodents has been derived by reduction from $\frac{3.1.4?3.}{3.1.4?3.}$, and that the dental replacement was formerly normal (Weber, 1904, p. 480). The evidence for the derivation of the Rodent cheek teeth from the tritubercular-tuberculosectorial type has been cited above (p. 327).

Hypothetical Reconstruction of the ancestral Rodents.— The ancestral Rodents probably exhibited the following characters: mandibular condyle narrow; post-glenoid process very small (as in *Tupaia*), or even absent (as in *Macroscelides*); premaxillaries elongate, anterior upper incisors (I^1_1) somewhat enlarged (*cf. Solenodon*), lower incisors ($I_{\frac{?}{?}}$) procumbent (*cf. Tupaia*); canines and anterior premolars reduced; cheek teeth adapted for frugivorous-omnivorous diet. These conditions are all realized in the Basal Eocene Mixodectidæ, which Osborn and Matthew were formerly inclined to regard as ancestral Rodents ("Proglires" Osborn, 1902, pp. 203–213); but the upper molars in this family contain no suggestion whatever of the peculiar features seen in the Lower Eocene *Paramys*; the lower molars likewise were normally tuberculo-sectorial, without the hypertrophy and internal displacement of the antero-internal cusp, or the reduction of the protoconid and asymmetry of the talonid, which are characteristic of the most primitive Rodents; so that in spite of the resemblances in the astragalus it seems more likely that the Mixodectidæ are not ancestral Rodents but aberrant Insectivores (Matthew, 1909).

The ancestral Rodents may also have been adapted for semi-arboreal life, since, so far as the evidence goes, they were not distinguished by strongly marked fossorial, aquatic, or cursorial adaptations; they were probably claviculate, well clawed, pentadactyl, with well developed pollex and hallux, with small body and long tail, free tibia and fibula, unreduced lumbar parapophyses; the foregoing characters together with the assumed frugivorous-

omnivorous modification of the cheek teeth are consistent with arboreal habits, which are retained in some of the less specialized representatives of the modern groups, *e. g., Sciurus, Myoxus, Anomalurus, Octodon, Hystrix.*

As regards the soft anatomy the stem Rodents may be conceived to have retained many primitive Mammalian characters in common with the Marsupials, Edentates and Insectivores, and some of these characters were transmitted to various modern genera. The right and left uteri were entirely distinct and a reduced cloaca may have been present (*cf. Castor*); the yolk sack was large (in certain modern forms it even forms a small true placenta; (*vide supra*); the brain was of low type, macrosmatic and with small, smooth cerebra; traces of scales may have persisted, especially on the tail; the eye also was probably of low type, for according to Lindsay Johnson ophthalmoscopic examination of many modern Rodents reveals the following among other primitive mammalian characters: crystalline lens appearing as if formed of concentric circles; fundus usually of reddish-gray type; an aster of radiating fibres present; choroid vessels often visible; small but distinct pecten retained in *Dasyprocta* and others (*cf.* Marsupials).

Conclusion. The known Lower Eocene Rodents had already acquired the ordinal characters in the skull and dentition, and the Lower Oligocene Lagomorphs were almost as well differentiated from the contemporary Sciuromorphs as are the modern Hares from the Squirrels; so that the two suborders could hardly have run together before the Basal Eocene; while the point of union of the Rodent stem with any other mammalian order may lie well back in the Cretaceous.

The early hypertrophy of the incisors and the consequent modifications of the skull and jaws marked but did not obliterate many primitive Placental characters, and it seems not improbable that the stem forms of the Rodentia were Mesozoic Placentals, allied to the ancestors of the modern Insectivora and possibly to the contemporary ancestors of one or more of the Paratherian or Edentate orders.

II. The Edentate Orders.

Outline History of the ordinal Classification.

1693. Ray groups "Echinus terrestris Tatou sive Armadillo, Talpa, Musaraneus, Tamandua, Vespertilio, & Ai sive Ignavus" [Bradypus] in a division "Anomala" of the "Unguiculata."

1758. Linnæus includes in the order "Bruta" the genera *Elephas, Trichechus* [*Manatus*], *Bradypus, Myrmecophaga, Manis.*

1771. Thos. Pennant includes the following forms under "Digitated

Quadrupeds": "4. Without cutting teeth, Sloth and armadillo." "5. Without teeth; Manis, Ant Eater."

1778. Pallas describes the "Aard Vark" under the name *Myrmecophaga africanum.*

1779–1797. Blumenbach puts the edentates ("Bruta") in the order "Digitata" as a group (C) coördinate with (B) the "Digitata Feræ" and (A) the "Digitata Glires."

1792. Vicq d'Azyr applies the term "Edentati" to the "Paresseux," "Tatous," "Fourmiliers," "Pangolins."

1795. Geoffroy and Cuvier remove *Bradypus* to the order "Tardigrades."

1800. Cuvier includes *Echidna* in "les Édentés," brackets *Megatherium* and *Bradypus* ("les Paresseux") as the sole occupants of "les Tardigrades."

1817. Cuvier divides "les Édentés" into "les Tardigrades (Paresseux, Megatherium)"; "Édentés ordinaires (Tatous, Oryctéropes, Fourmiliers, Pangolins)"; "Monotrèmes (Echidnés, Ornithorinques)."

1811. Illiger adds *Prochilus* (*Melursus*) to the Tardigrada, groups *Dasypus, Orycteropus* and *Manis* as "Effodientia," and removes *Echidna* and *Ornithorhynchus* to a separate order "Reptantia."

1816. De Blainville associates *Bradypus* with *Galeopithecus* and removes the Tardigrades to a subordinal group "anomaux" of "les Quadrumanes" at the same time associating "les Édentés" (as a suborder "normaux") with "les Cétacés" (as a suborder "anomaux") under the "ordre Édentés."

1839. De Blainville, after long discussion, provisionally leaves *Bradypus* in "les Primatés," but treats the other Edentates as a grand division "Maldentés" of "les Monodelphes," contrasting with all the other Monodelphians ("Bien dentés"); this foreshadows Thomas's "Paratheria."

1842. Owen reunites *Bradypus* with Edentates, dividing the order Bruta thus:

Tribus Phyllophaga: "Familia" Tardigrada, *Bradypus, Cholœpus*; Familia Gravigrada, *Megalonyx, Megatherium, Mylodon, Scelidotherium, Cœlodon, Sphenodon.*

Tribus Loricata: Armadillos [and Glyptodonts ?].

Tribus Edentata: Anteaters (*Myrmecophaga, Orycteropus,* Pangolins).

1855. P. Gervais proposes to elevate the Edentates to the rank of a subclass (Weber, 1904, p. 412).

1872. Huxley divides the Edentata or Bruta into the Phytophaga or vegetable feeders, and the Entomophaga or insect feeders as follows:

Phytophaga[1]: Tardigrada, Gravigrada;

Entomophaga[1]: Mutica (*Myrmecophagus* and *Cyclothurus*), Squamata

[1] "Phytophaga" used by Wagner, "Entomophaga" used by Tschudi, both in Wiegmann's Archiv. Naturgesch. Bd. II, 1844 (communicated by Dr. T. S. Palmer).

(Manis), Tubulidenta (*Orycteropus*), Loricata (Dasypodidæ, Glyptodontidæ).

1883. Flower shows that the Megatheriidæ are intermediate between the Bradypodidæ and the Myrmecophagidæ and proposes the following classification:

Order Edentata:

Suborder Pilosa (Bradypodidæ, Megatheriidæ, Myrmecophagidæ).

Suborder Loricata (Dasypodidæ).

Suborder Squamata (Manidæ).

Suborder Tubulidentata (Orycteropodidæ).

1884. Gill characterises the American Edentates as having Xenarthral vertebræ in contrast with the Orycteropods and *Manis* which are Nomarthral.

1887. Oldfield Thomas shows that in regard to the relations of the milk and permanent dentitions the Edentata are different from all other Placentals, and hence he proposes to set them apart as a group "Paratheria," coördinate with the Eutheria of Huxley.

1891. Weber monographs the genus *Manis* and proposes to give ordinal rank to the groups Squamata (Manidæ), Tubulidentata (Orycteropodidæ) and Xenarthra [American Edentates].

1903–1905. Scott monographs the Edentata of the Santa Cruz formation (Miocene) of Patagonia.

1904. Weber substitutes the term "Pholidota" for Squamata (preoccupied) and gives ordinal rank to each of the great groups.

The Tubulidentata.

Primitive characters.— As described by Weber (1904, pp. 414–419), the South African Aard Vark (*Orycteropus capensis*) is in many respects a primitive Placental. The *uterus* is completely double (as in Rodents); the *testes* lie in a cremaster sack which is still in open communication with the body cavity; the *brain* is of a very low type with large olfactory parts and small nearly smooth cerebra which leave the cerebellum quite uncovered; the *tail* is very large at the base, *i. e.*, imperfectly differentiated from the body. The arrangement of the *muscles*, according to Windle and Parsons (1899), is very generalized. The skull and skeleton [1] likewise retain many primitive characters. The *dentition* [2] retains some evidence that the formula was formerly $p\frac{6}{6}$, $m\frac{3}{3}$; a milk dentition also was once functional and the

[1] Notes based chiefly on a skeleton in the U. S. National Museum and partly on Cuvier's excellent figures in the *Ossemens fossiles* (tome 5, partie premiêre, pl. xii).

[2] *Fide* Broom.

milk teeth were brachyodont with two roots (*cf.* Thomas, 1890).[1] The *premaxillaries* are widely separated from the frontals; the *nasals* spread proximally; the *lachrymal* is large, spreading on the face; the lachrymal foramen is external; the *orbital* and *temporal fossæ* are very near together and broadly continuous (*cf. Manis, Tupaia,* Rodents); the *orbito-sphenoid* is pierced by the optic foramen and the stapes by the stapedial artery (Weber, 1904, p. 416); an *alisphenoid canal* is present; the *tympanic* is ring-shaped, but there is no bony entotympanic (contrast Xenarthra, Van Kampen, 1905, p. 467); a *tympanohyal* is present (absent in other Edentates — Parker, quoted by Weber, 1904, p. 415); the *malleus* has a broad lamina and a stout processus gracilis (folianus) as in *Sorex* and Marsupials; in other features it approaches that of *Priodon* (Doran, 1879, pl. 64, fig. 14); the bicrural *stapes,* as in many primitive mammals, is pierced by the stapedial branch of the ento-carotid (Hyrtl, quoted by van Kampen, 1905, p. 467); the *interparietal* is prominent; the *mastoid* is well exposed posteriorly; the *occipital condyles* are confluent across the basioccipital. The *vertebral zygapophyses* are normal, the transverse process of the seventh cervical vertebra is pierced by the vertebral artery (*cf.* Marsupials and certain Rodents); the *dorso-lumbars* number 21 (D 13, L 8); only the *first sacral vertebra* has the transverse process broadly expanded for the support of the *ilium*; the latter has a big pectineal process and a prominent postero-superior extension (which Broom, 1905.4, homologises with the posterior angle of the ilium in Theriodonts). The *scapula* has a large coracoid process and bifid acromion, the *clavicle* is well developed. The *humerus* retains an entepicondylar foramen and prominent crests; the *radius and ulna* are capable of more or less pronation and supination; the ulna has a stout shaft; the *femur* retains a stout third trochanter. The *feet* are semiplantigrade, the pes is pentadactyl. The *astragalus* diverges distally from the calcaneum; it is pierced by a large foramen and has a well grooved trochlea; the relations of its ectal, sustentacular and navicular facets are much as in *Phenacodus,* but the head is globular instead of flattened. The *entocuneiform* is long as it is in many Insectivores and Rodents.

Specialized characters. These underlying primitive characters are combined with specializations characteristic of the order. The *milk dentition* is vestigial (*cf.* Broom, 1909, and Thomas, 1890). No trace of *incisors* remain in the adult. The antemolar teeth drop out in old animals; they are much less specialized than the three *molars,* which are hypsodont and

[1] Broom in a recent paper (1909) gives the dental formula for the milk and permanent dentitions as follows: I. $\frac{1.2.3}{1.2.3}$; C. $\frac{1}{1}$; P. $\frac{?\,3.4.5.6.}{2.3.4.5.6.}$ $\frac{1.2.3.}{1.2.3.4\,5.6.}$; M. $\frac{1.2.3.}{1.2.3}$

covered with cement but are without enamel, and composed of irregular usually hexagonal prisms of dentine; each prism in cross section shows a central pulp cavity and radiating dentinal canals. In correlation with the excessively large rhinencephalon, the number of *ethmoid scrolls* rises to eleven (the highest among mammals), of which the posterior five extend beneath the olfactory bulbs, much as in *Echidna* and are thus vertical in position (Weber, 1904, p. 416, fig. 313). This condition is probably secondary, however, in both forms, because the primitive position of the cribriform plate (as shown in *Ornithorhynchus*, Marsupials, Rodents, Insectivores, etc.) is anterior and not partly inferior to the rhinencephalon. The nasoturbinal and first four endoturbinals in *Orycteropus* are normal and resemble those in Insectivora. The *carpus* is very abnormal in the wide separation of the lunar from the unciform leaving a lacuna between them. There is no free centrale; in the U. S. National Museum specimen and in the individual figured by Cuvier the scaphoid appears to be fused with the lunar, but Weber states (p. 415) that the scaphoid and lunar are separated; the unciform is very small. The pollex is lacking; there is a tendency toward didactyly in both manus and pes. In the *manus* the phalanges of digits II and III are symmetrically modified with reference to the median line and superficially suggest those of camels; the unguals too are more or less cameloid in type, being high and compressed. In the *pes* the unguals are more depressed; the distal keels of the metacarpals extend on to the front face.

Comparison with other groups.

Orycteropus contrasts with the Xenarthra and Pholidota in many characters, *i. e.*, in the possession of a distinct interparietal, in the characters of the brain, the uterus, placenta, testes and teats. The astragalus, however, agrees better with the Xenarthrous type than with any other (*cf.* Ameghino, 1906, p. 18), and the skull and skeleton, especially the scapula and limb bones, show some marked adaptive resemblances to those of *Priodon*. The musculature, according to Windle and Parsons (1899), presents "two features not found elsewhere than in the Edentata." Dr. Matthew has suggested to the writer that the Tubulidentata may possibly have been derived from the Ganodonta, because the Stylinodontidæ show some interesting analogies to *Orycteropus* in the general appearance of the cheek teeth, and phalanges.

No striking resemblances to the Rodents are evident, except the great length of the entocuneiform, which is merely a primitive mammalian character.

The hypothesis that the Tubulidentata are remotely related to the

lower Ungulata has been supported by Elliot Smith, Lönnberg and Weber. Elliot Smith (1898, p. 277) concludes that in its brain characters *Orycteropus* "is distinctly comparable with a primitive Ungulate type" from which it differs only in the high development of the olfactory parts. The astragalus also, both with regard to its facets and to its general conformation, rather resembles the astragalus of the more primitive Notoungulata. (*Cf.* Ameghino, 1906.)

Lönnberg (1906) controverts Owen's opinion that each cheek tooth is a complex of separate denticles analogous to that in certain Selachians, and also dissents from Weber's opinion (1904, p. 417) that it formerly had elaborate enamel folds. He believes that the ancestral Tubulidentate had low-crowned, simple-rooted cheek teeth, with reduced enamel. The pulp originally had short, irregularly branched canals, which entered the dentine, a condition preserved in part in the small, less specialized anterior teeth; the crown of the tooth soon wore off but the roots lengthened and gave rise to the bicolumnar molars of *Orycteropus;* while, with increasing hypsodonty, the branching pulp-tubules became parallel. If this theory be true the cheek teeth offer no obstacle to the hypothesis that the Tubulidentata are derived from the Condylarthra (Lönnberg). However, about the only direct points of resemblances to that group are the dorso-lumbar number of 21 and the characters of the astragalus. At any rate, the prevailing resemblances of *Orycteropus* as regards the brain, dentition and astragalus seem to be with the Protungulates rather than with the Insectivores and Creodonts; although distant relationship both with the Ganodonta and Xenarthra is also possible.

The Pholidota (Manidæ).

The anatomy and development of *Manis*, as well as its systematic and phyletic isolation have been thoroughly discussed by Weber (1894) in his monograph on that animal and in his 'Die Säugetiere' (pp. 420–429).

Manis differs from Orycteropus in the development of true scales,[1] in the convoluted brain, in the peculiar characters of the digestive tract, in the bicornuate uterus, in the relations of the testicle, which lies outside of the inguinal canal, and in the very large yolk sack and diffuse placenta; while the skull and skeleton offer equally distinctive details.

The Pholidota are *distinguished from the Xenarthra* by many characters of the reproductive organs and placentation. In the skull the strong general resemblances to *Myrmecophaga* are interpreted by Weber (1904, p. 422) as convergent adaptations to ant-eating habits and are accompanied by deep seated differences: *e. g.*, the lachrymal is reduced and not pierced by the

[1] See footnote 1, page 146.

lachrymal foramen, the pterygoid does not share in the backward prolongation of the palate; while the vertebral column differs from that of most Xenarthra (except the Middle Eocene *Metacheiromys*, Osborn, 1904) in the lack of accessory zygapophyses in the dorso-lumbar region. The entotympanic when present is greatly reduced, whereas in Xenarthra it is well developed (van Kampen, 1905, p. 470).

On the other hand the Pholidota *resemble the Xenarthra* in the lack of an interparietal, in the high number (7) of ethmoidal scrolls, in the columnar stapes (Doran, 1879) (*cf.* the barely separated stapedial crura in Bradypodidæ and *Tolypeutes*) in the lack of a sinus hypotympanicus and in the large size of the sinus epitympanicus (van Kampen, 1905, p. 473), while the musculature of *Manis*, according to Windle and Parsons (1899), shows many peculiarities not seen elsewhere except in the Xenarthra. The scales seem to involve the same histological elements as do the vestigial scales on the tail of the Myrmecophagidæ (*cf.* Weber, 1904, p. 433, fig. 330, and p. 420, fig. 316). The third digit of the manus, especially the claw, is much enlarged, as it is in the Myrmecophagidæ and likewise forces the animal in walking to rest on the outer border of the foot and on the dorsal surface of the flexed outer fingers.

Points of resemblance with several other groups are shown by the embryonic manus and pes figured by Weber (1904, p. 424). The marked functional tridactyly in the manus, digit III being the largest, suggests Insectivores or *Hyrax*; the strictly serial carpus with its rectangular elements is also a point of resemblance to *Hyrax*. The union of the scaphoid and lunar suggests the Monotremes, certain Rodents and Insectivores; the prominence of the "præpollex" suggests Monotremes, embryonic *Didelphis*, Insectivores and Rodents. The centrale is not present, at least as a separate element. The proximal end of the fifth digit is spreading and nearly in contact with the ulna. In the embryonic pes, the lower end of the astragalus has an extensive contact with the cuboid (*cf.* Amblypoda); the three cuneiforms are subequal instead of the middle one being the smallest as in normal mammals. The "præhallux" is present; functional tridactyly is evident but not so pronounced as in the manus. In both manus and pes the digits are spreading, the pollex and hallux rather divergent; the ungual phalanges of digits II–V in the adult are deeply cleft, as they are in *Perameles*, *Talpa*, and *Chrysochloris* (Weber); in the embryo they are split half way down to the base and the opposite halves spread outward at right angles to each other.

To these various and ambiguous points of resemblance to other groups *Manis* adds many peculiarities of its own: first, in regard to the loss of parts (*e. g.*, total loss of teeth, jugal, interparietal, clavicle, centrale carpi, third

trochanter); second, in regard to the unique modification of parts (*e. g.*, xiphisternum, stomach, extreme development of scales, extreme length of tail). Finally there are primitive Placental characters: *e. g.*, large olfactory organs, large cerebellum, moderately small cerebrum, very large yolk sack, primitive conditions of the testes and accessory glands and of the female reproductive organs and independent optic foramen (*cf.* Weber, 1904, pp. 425–429). The dorso-lumbars either retain the primitive number of 19 (D 14, L 5) or rise to as many as 22.

The possibility of relationship with the Xenarthra is indicated by the characters cited above, especially by the presence of a reduced entotympanic; but *Manis* may equally well, so far as other evidence goes, be a highly modified survivor of unknown Mesozoic Placentals. A South American origin for the group has been suggested by Ameghino (1906, p. 377), who figures an astragalus described under the name "*Argyromanis patagonica*," which shows a resemblance to the astragalus of *Manis*; but such evidence is often insufficient to establish relationship.

The Xenarthra.

In 1696 John Ray, finding that certain mammals would not fit into his dichotomous scheme, collectively characterized the Armadillo, Tamandua Sloth and others as "Quadrupeda vivipara unguiculata anomala"; and it must be confessed that after more than two centuries of research the Edentates are still "anomala" both to the systematist and phylogenist. It has indeed been shown that the Aard-Varks and Pangolins are ordinally separate from each other and from the American Edentates, and as regards the latter it has further been shown that the Sloths, Ground Sloths and Antbears are relatively nearly related and form a natural suborder, the Pilosa of Flower or Anicanodonta of Ameghino, coördinate with the suborder Loricata of Flower or Hicanodonta of Ameghino, including the Armadillos and Glyptodonts; but no structurally intermediate forms between these two suborders have been discovered even in the lowest Tertiary deposits of Patagonia, and in spite of an extensive knowledge of the numerous recent and fossil forms, the relationship of the whole order, both to the other "Edentates" and to the typical Placentals, remains very largely a matter of speculation.

Cuvier and many later writers, perhaps on account of the fossorial adaptations common to Monotremes and Edentates, treated the two groups as if they were more or less closely related. W. K. Parker (1885–86) compared the columnar, imperforate stapes of the Sloths with that of the Monotremes, and both Parker and Ameghino, noting especially the relatively large size of the coracoid in the Ground Sloths, attempted to derive the shoulder-girdle of Edentates directly from the Monotreme type. Gervais proposed to

assign to the Edentate series the rank of a subclass; Thomas (1887), impressed by the anomalous modifications of the dentition, suggested that the Edentate orders might be collectively designated as "Paratheria," in contrast with the Metatheria and Eutheria. Elliot Smith (1898), from his comprehensive studies on the brain of Edentates concludes that they are remotely related to the Carnivores, perhaps by descent from early Creodonts.

The general drift of these opinions is that the Edentates are the highly aberrant descendants of some very lowly and ancient mammalian stock. And certainly the modern Edentates retain many characters of low aspect. In addition to the columella-like stapes of the Sloths and *Tolypeutes* and the relatively large coracoid of the Ground Sloths may be mentioned the following, gleaned from Weber (1904) and other authorities. A septomaxillary presumably homologous with the element of the same name in certain reptiles, has been recorded (Broom, 1906.1) in *Dasypus*. The brain is macrosmatic and frequently of low type (Elliot Smith); the cochlea auris makes only two to two and a half turns; the testes usually remain abdominal; the penis is often on a low stage and in Sloths is even of an embryonic type; the vagina sometimes shows traces of former longitudinal division, although the opposite uteri are completely united; the yolk sack is large; two venæ cavæ persist; indications of the former presence of scales are not lacking (Weber, 1904, pp. 432–433); the tail is sometimes very thick at the base, as is often the case in archaic mammals. Under ophthalmoscopic examination, the eye, according to Lindsay Johnson (1901), reveals certain features in common with Monotremes, Marsupials and Rodents: *e. g.*, the fundus is of uniform color with hardly perceptible stippling, the lens appears as if composed of concentric circles.

Comparison of the Xenarthra with other Orders.

The Xenarthra agree with typical Placentals in the general features of their development (Parker, 1885–'86). The structural resemblances of the Xenarthra to the Tubulidentata and the Pholidota have already been discussed. The question of their relationship with the Ganodonta (= Tæniodonta) is still open. According to Wortman (1897), these Basal to Upper Eocene forms tend to connect the Xenarthra with the Creodonta, but Professor Scott (1903–05) is inclined to regard the resemblances between the Ganodonta and Xenarthra as due to convergence; because the Patagonian Miocene forms, which might be expected to approach the Ganodonta, in reality show less resemblance to them than do the modern Edentates. Dr. Ameghino also, whose knowledge of the fossil Xenarthra is very extensive,

does not accept the Ganodonta as ancestral Xenarthra (1905.2, pp. 230–235).

In case the Xenarthra have been derived from Placentals having a dental formula of $\frac{3.1.4.3}{3.1.4.3}$ (and the retention of a milk dentition in *Tatusia* and of front teeth in the Santa Cruz armadillo *Peltephilus* rather strengthen this supposition), the most primitive Ganodont genera *Onychodectes* and *Conoryctes* would serve to illustrate the probable characters of the ancestral Xenarthra. These genera resemble the Creodonts and primitive Insectivores in having a long low sagittal crest, a small brain case, a narrow postorbital region and heavy face, and teeth of four kinds. The upper molars are ovate-triangular, the lower molars of tuberculo-sectorial derivation. In case the Ganodonta should prove to have been ancestral to the Xenarthra the ultimate derivation of the latter from forms with simple tritubercular upper and tuberculo-sectorial lower molars would be almost demonstrated (*cf.* Osborn, 1907, 154–6). But even if the Ganodonta be not ancestral, any evidence tending to show that the Xenarthra at one time had a dental formula of $\frac{3.1.4.3}{3.1.4.3}$ would tend also to indicate that their upper molars were once tritubercular; because many other groups in which the formula is derived from $\frac{3.1.4.3}{3.1.4.3}$ have also passed through the tritubercular stage.

Resemblances to the Insectivora are usually obscured by marked difference in habits, but *Peltephilus* suggests the primitive Insectivore type in its projecting muzzle, overhanging upper incisors, and low mandibular condyle, while certain of the primitive mammalian characters of the Xenarthra are preserved also among the Insectivora (*e. g.*, low brain, traces of scales). In possessing a well developed entotympanic (van Kampen, 1905, p. 498) the Xenarthra recall the Menotyphla and Carnivora.

Resemblances to the Rodentia also appears to be due largely to the retention of primitive Placental characters. The astragalus of certain Miocene Armadillos (Scott, 1905, pll. xiv) strongly suggests the Rodent type.

Conclusion. The balance of evidence appears to indicate that the existing Xenarthra, like the Tubulidentata, the Pholidota and perhaps the Rodentia, are the highly modified descendants of some Mesozoic Placentals, which branched off before the differentiation of Insectivores, Creodonts and Protungulates.

CHAPTER IX. GENETIC RELATIONS OF THE UNGULATA AND SIRENIA.

Analysis.

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I. Outline History of the Ordinal Classification.

The systematic history of the term "Ungulata" and its correlative, "Unguiculata," may be said to begin in 1696 when Ray employed these terms in his dichotomous table of the hairy viviparous quadrupeds (*cf.* p. 18 above). Linnæus emended the terms in 1766 by transferring *Camelus* and *Elephas* from the Unguiculata, where Ray had placed them, to the Ungulata. At the same time he erected the coördinate division "Mutica" to include the Cetaceans. With more or less varying content "Unguiculata," and "Ungulata" were used by many subsequent authors (*e. g.*, Storr, Blumenbach, Owen, Cope) down to the present time.

It was early realized that "Unguiculata," covering Monotremes Marsupials and unguiculate Placentals (including the Primates) was in its original signification an unnatural assemblage, and by many authors (*e. g.*, Blumenbach, Illiger, de Blainville) it was not used in a systematic sense. In modern times it has been tacitly recognized by many that even after the restriction of the term to include only the unguiculated Placentals it is still only a partly natural residuum, since it embraces such widely removed orders as the Edentates, Bats, Carnivores, etc. The following studies tend to the conclusion that the term "Ungulata" likewise includes a group of

orders of rather diverse origin, and more particularly that the so called "Ungulata Vera," embracing the Artiodactyla and Perissodactyla is almost as unnatural an assemblage as "the Pachydermes" of Cuvier, and that in brief many of the resemblances between the Artiodactyla and Perissodactyla are due to convergent evolution.

The more important classifications of the Ungulate orders are summarized below.

1693. Ray (p. 18), adopts the following division (here condensed):

Ungulata.
- I. Solidipeda. [Equus.]
- II. Bisulca.
  - 1. Ruminantia. a. Bos, Ovis, Capra.
    b. Cervus.
  - 2. Non-ruminantia. Sus.
- III. Quadrisulca.
  Rhinoceros, Hippopotamus, etc.

Unguiculata.
- 1. Bifido, Camelus
- 2. Multifido.
  - a. Digitis indivisis. Elephas.
  - b, c, etc. [typical unguiculates].
- 3. Anomala. Echinus terrestris, Tatou sive Armadillo, Talpa, Mus araneus, Tamandua, Vespertilio, Ai sive Ignavus [Bradypus].

Noteworthy features of the preceding are: (1) the classification in accordance with the number of digits, implied in the terms Bisulca, Quadrisulca; (2) the correct association of *Sus* with the other Artiodactyls; (3) the clear separation of the solid-horned (*Cervus*) from the hollow-horned Ruminants; (4) the correct division into ruminant and non-ruminant forms.

In general this classification was far better than many later ones.

1735. Linnæus groups all non-ruminant ungulates under the order "Jumenta" (*Equus, Hippopotamus, Elephas, Sus*). The ruminants were included under the order "Pecora."

1758. Linnæus (p. 29).

Ordo Bruta. Elephas, Trichechus, Bradypus, Myrmecophaga, Manis.
" Bestiæ. Sus, Dasypus, Erinaceus, Talpa, Sorex, Didelphis.
" Glires. Rhinoceros, Hystrix [etc., other Rodents].
" Pecora. Camelus, Moschus, Cervus, Capra, Ovis, Bos.
" Belluæ. Equus, Hippopotamus.

Thus Linné's arrangement of the Ungulata was much better in the first edition than in the tenth.

1766. Linnæus.

Ordo II. Bruta. Elephas, Bradypus, Myrmecophaga, Manis, Dasypus.

" V. Pecora. [vide supra.]

" VI. Belluæ. Equus, Hippopotamus, Sus, Rhinoceros.

1771. Thomas Pennant (see p. 51 above).

Hoofed Quadrupeds.

1. Whole hoofed. Horse.
2. Cloven hoofed. Ox, sheep, goat, giraffe, antelope, deer, musk, camel, hog, rhinoceros, hippopotame, tapir, elephant.

1780. Storr (p. 50 above).

Cohors II. Mamalium, Pedatorum, Ungulatorum.

Ordo I. Jumenta. Equus.

Ordo II. Pecora. Camelus, Giraffa, Aries, Antilope, Taurus Cervus, Moschus.

Ordo III. Belluæ. Sus, Hydrochoerus, Rhinoceros, Elephas Hippopotamus.

The "Belluæ" of Storr thus includes the same assemblage as the "Pachydermes" of Cuvier.

1779. Blumenbach (p. 46, above) distributes the ungulates in the orders Solidungula, Bisulca, Belluæ.

1792. Vicq d'Azyr (p. 55 above) dividing the mammalia into 15 "primordial groups," distributes the ungulates as follows:

9. Chevaux d'eau. *Hippopotamus.*
10. Elephans.
11. Tapiriens.
12. Porcini.
13. Ruminans.
14. Solipèdes.

1795. Geoffroy and Cuvier (p. 58 above).

Ordre X. Pachydermes. Elephantus, Rhinoceros, Hippopotamus, Tapir, Sus.

Ruminans. [The Ruminants.]

Solipèdes. Equus.

This seems to be the first use of the term "Pachydermes," which, as noted above, is practically synonymous with Storr's usage of "Belluæ."

1800. Cuvier (p. 66 above). In this classification the *number of digits* is again emphasized as a basis of classification.

Mammiferes à Sabots.
- Les Pachydermes. Plus de deux doigts, plus de deux sabots. Éléphans, Tapirs, Cochons, Hippopotame, Daman, Rhinoceros.
- Les Ruminans. Deux doigts, deux sabots. Chameaux, Chevrotains, Cerfs, Giraffe, Antilopes, Chèvres (Capra), Brevis, Boeufs.
- Les Solipèdes. Un seul doigt, un seul sabot. Cheval.

1811. Illiger (p. 70 above).

Multungula.		
Familia	Lamnunguia.	Hyrax and a Marmot.
"	Proboscidea.	Elephas.
"	Nasicornia.	Rhinoceros.
"	Obesa.	Hippopotamus.
"	Nasuta.	Tapirus.
"	Setigera.	Sus.
Solidungula.		
Bisulca.		
Familia	Tylopoda.	Camelus, Auchenia.
"	Devexa.	Camelopardalis, Capreoli, Cervus, Moschus.
"	Cavicornia.	Antilope, Capra, Bos.

1816. De Blainville (p. 78 above).

V. Degré ou Ordre Gravigrades. Éléphans.
VI. Degré ou Ordre Ongulogrades.
- Normaux.
  - doigts
    - impairs.
      - Pachydermes,
      - Solipèdes
    - pairs.
      - Non-Ruminans ou Brutes,
      - Ruminans.
- Anomaux.
  - pour nager.
    - Les Lamantius.

The Gravigrades were placed after "les Rongeurs" ("Celerigrades").

Here for the first time *Equus* is closely associated with the other Perissodactyls ("Pachydermes"), and the number of digits adopted as the chief criteria (*cf.* Cuvier's classification of 1800). See also de Blainville's later classification given below (1834).

1817. Cuvier.

Pachydermes.
(1) Proboscidiens. Elephans, Mastodontes.
(2) Pachydermes ordinaires. Hippopotames, Cochons, Anoplotherium, Rhinoceros, Daman [Hyrax], Palaeotherium, Tapirs.

(3) Solipèdes. Chevaux.
Ruminans.
(a) Sans cornes. Chameaux, Chevrotains.
(b) Avec cornes. Cerfs, Giraffes, Antilopes, Chèvres [Goats], Moutons, Boeufs.

In this classification there is a closer association of the various ungulate groups than in the classification of 1800.

The anatomical relationships of the horses with the tapirs and Palæotheres is recognized.

1821. Gray, J. E.[1]

Ungulata.
Ord. Tardigrada [Sloths.]
Oligodontae. Dasypus, Orycteropus.
Edentulae. Myrmecophaga, Manis, Tamandua, Cyclopes.
Proboscidiae. [Proboscideans.]
Tesserachenae. Hippopotamidæ, Suidae.
Trichenia. Rhinoceridae, Hyracidæ, Tapiridae.
Monochaena. Equus.
Hydrophora. Camelidae.
Ruminatia.

Gray regarded the Edentates as allied to the Ungulates.

1830. Wagler. [2]

Order Scrofae. [Suina, Elephas, Rhinoceros].
Hyraces, Hyrax.
Cameli [Tylopoda and Giraffe].
Equi.

(Hyraces given ordinal rank.)

1834. De Blainville (*cf.* p. 83).

V. Gravigrades.
Normaux terrestres. Proboscidei. Elephans.
Anomaux pour nager. Sirenei. Lamantins.
VI. Ongulogrades.
à doigts
impairs
3 doigts. Pachydermes.
1 doigt. Solipèdes. Cheval.
pairs
4 doigts. Brutæ. Cochon, etc.
2 doigts. Ruminantia.

[1] Medical Repository, 1821, p. 304.
[2] Naturl. System. Amphibien, 1830, quoted by Gray.

In his 'Ostéographie' de Blainville intimates that future palæontological discoveries will more completely bridge over the gaps between these subdivisions of "les Ongulogrades."

1840–45. Owen ('Odontography').

Ungulata
1. Isodactyle, as Ox, Hog, Peccary, and Hippopotamus.
2. Anisodactyle, as Horse, Tapir, Rhinoceros.
3. Proboscidians.

De Blainville's terms "à doigts pairs" and "à doigts impairs" are here rendered into "Isodactyle" and "Anisodactyle." De Blainville's arrangement is improved by the closer association of the Horse with the Tapir and Rhinoceros.

1847. Owen.[1]

Ungulata
Artiodactyla.
1. Ruminantia.
2. Non-ruminantia.
Perissodactyla.
Proboscidia.

Here the groups formerly characterized as Isodactyle and Anisodactyle are given the ordinal names "Artiodactyla," "Perissodactyla."

1855. Wagner.[2]

Ruminantia.
I. Fam. Cervina Moschus, Cervus, Camelopardalis.
II. " Cavicornia. [Sheep, Goats, Antelopes, Oxen.]
III. " Tylopoda. [Camels.]
Solidungula. Equus.
Pachydermata. Hippopotamus, Sus, etc., Tapirus, Hyrax, Rhinoceros, Elephas.

This classification differed but little from that of Cuvier in 1800 and was thus about half a century behind the times. Illiger's terms "Cavicornia," "Tylopoda" are used.

1858. Owen establishes the order Toxodontia.

1866. Haeckel places the "ordo Ungulata" (Perissodactyla, Artiodactyla) together with the "ordo Cetacea" (including Sirenians and cetaceans) as a second sublegion of the legion "Indeciduata," the first sublegion comprising the Edentates. *Hyrax*, Toxodonts, *Dinotherium* and the

[1] Quar. Jour. Geol. Soc., pt. IV for 1847.
[2] In Schreber's 'Säugethiere.'

elephant constitute so many suborders of the order "Chelophora," which forms the first sublegion "Zonoplacentalia," of the legion "Deciduata." It will be noted that the main criteria of classification are the modes of placentation.

1868. Owen.[1]

Ungulata.
- Order Artiodactyla.
  - Suborder Ruminantia. Family names listed: Bovidae, Moschidae (including Tragulus, Moschus), Cervidae, Camelidae.
  - Suborder Omnivora. Merycopotamus, Dichodon, Xiphodon, Anoplotherium, Microtherium, Entelodon, Hippopotamus, etc., Suidae.
- Order Perissodactyla. Coryphodon, Pliolophus, Hyracotherium, Lophiodon, Palaeotherium, Paloplotherium, Macrauchenia, Elasmotherium, Rhinoceros, etc., Hyrax, Anchitherium, Hipparion, Equidae, Tapirus, Toxodon, Nesodon.

This classification is actually inferior to that of de Blainville of thirty-four years earlier date (1834).

1864 to 1872. Huxley.[2]

Ungulata.
- Order Perissodactyla.
  - Families Equidæ, Rhinocerotidæ, Tapiridæ, Palæotheridæ, Macrauchenidæ.
- Order Artiodactyla.
  - Non-Ruminantia. Families Suidæ, Hippopotamidæ, Anoplotheridæ.
  - Ruminantia Divisions Tragulidæ, Cotylophora (Cervidæ, Bovidæ, Giraffidæ, Antilocapridæ), Camelidæ.
- Order Toxodontia.
- " Proboscidea.
- " Hyracoidea.

Note: (1) the close association of the families listed under "Cotylophora" and the emphasis upon placental characters implied in this term. (2) The separation of the orders Hyracoidea Huxley, Toxodontia Owen. Huxley (1872, p. 292) doubted the naturalness of the group Ungulata, saying that "it may be open to question whether the group thus named represents a single order, or more than one."

[1] Zool. Index to his Comp. Anat., Vol. III, pp. 839 et seq.).
[2] Medical Times and Gazette, 1864.

1872. Gill.

Order Ungulata.
- Suborder Artiodactyla.
  - Superfamily Chalicotheroidea (Artiodactyli ? Incertæ sedis).
  - Pecora.
    - Superfamily Cameloidea. Fam. Camelidæ.
    - Superfamily Giraffoidea. Fam. Giraffidæ.
    - Superfamily Boöidea. Fam. Saigiidæ, Bovidæ (Subfam. Bovinæ, Ovibovinæ, Antilopinæ, Caprinæ, Ovinæ), Fam. Antilocapridæ, Cervidæ (subfam. Cervinæ, Cervulinæ, Moschinæ).
    - Superfamily Traguloidea. Fam. Tragulidæ.
    - Superfamily ? Sivatheroidea. Fam. Sivatheriidæ.
    - Superfamily ? Helladotheroidea. Fam. Helladotheriidæ.
    - Superfamily Oreodontoidea. Fam. Oreodontidæ. (Subfam. Oreodontinæ, Agriochœrinæ.)
    - Superfamily Anoplotheroidea. Fam. Anoplotheriidæ, Dichobunidæ (Cænotherium, Dichobune, Xiphodon).
  - Omnivora.
    - Superfamily Merycopotamoidea. Fam. Merycopotamidæ, Hippopotamidæ (Subfam. Hippopotaminæ, Chœropsinæ).
    - Superfamily Setifera. Fam. Phacochœridæ, Suidæ, Dicotylidæ.
    - Superfamily Anthracotheroidea. Fam. Anthracotheriidæ (Subfam. Hyoptaminæ, Anthracotheriinæ).
    - Extinct Omnivora ? Incertæ sedis. Chœropotamus, Palæochœrus, Chœromorus, Entelodon, Heterohyus, Acotherulum, Chœrotherium = Tetraconodon.
  - Suborder Perissodactyla.
    - Superfamily Anchippodontoidea. Fam. Anchippodontidae (Anchippodus = Trogosus).
    - Superfamily Solidungula. Fam. Equidæ (Equus, Asinus (Asinus sensu strictu, Hippotigris)). Anchitheriidæ (Anchitherium, Hypohippus, Parahippus, Anchippus).
    - Superfamily Pliolophoidea. Fam. Pliolophidæ (Hyracotherium).
    - Superfamily Rhinocerotoidea. Fam. Rhinocerotidæ [African and Asiatic rhinoceroses separated generically (following Gray).] Macraucheniidæ, Palæotheriidæ (Palæotherium, Paloplotherium, etc.).
    - Superfamily Lophiodontoidea. Fam. Tapiridæ (Elasmognathus, Tapirus, Rhinochœrus). Lophiodontidæ (Lophiodon, Coryphodon, Listriodon, Pachynolophus, Lophiotherium, Tapirulus Anchilopus).
  - Perissodactyli Incertæ sedis. Fam. Elasmotheriidæ.
  - Ungulata ? Incertæ sedis Stereognathus Owen.
- Order Toxodontia.
  - Fam. Nesodontidæ, Toxodontidæ.
- Order Hyracoidea. Fam. Hyracidæ.
- Order Proboscidea. Fam. Elephantidæ (Subfam. Elephantinæ, Mastodontinæ) Dinotheriidæ.

This very elaborate classification (which is founded in part on the systems of Cuvier, Owen and Huxley) presents the following noteworthy features:

(1) It is based on the principle that analysis should precede synthesis and therefore sets apart many groups which later researches have joined together.

(2) It raises certain previously accepted genera to subfamily rank, certain subfamilies to families and families to superfamilies. In this manner it magnifies the taxonomic value of observed resemblances and differences and thus invites renewed analysis and synthesis.

(3) It is based on the "totality of characters drawn from all parts of the organism" and therefore avoids the errors of those systems which are founded upon single characters or upon a correlated series of characters; but on the other hand it is inferior to that of Huxley in many points.

(4) It recognizes more fully the great complexity and extent of the problems of mammalian taxonomy.

(5) It attempts to make classification express consistently corresponding degrees of homological resemblances and differences.

(6) By the use of the superfamily division it facilitates the expression of affinity and separation between families.

1891. Flower and Lydekker.

Order Ungulata.
- Ungulata Vera.
  - Suborder Artiodactyla.
    - Suina. Fam. Hippopotamidæ, Suidæ, Dicotylidæ, "Extinct Transitional Artiodactyls" (Chœropotamidæ, Anthracotheriidæ, Cotylopidæ [Oreodontidæ], Anoplotheriidæ, Cænotheriidæ, Dichodontidæ).
    - Tylopoda. Fam. Camelidæ.
    - Tragulina. Fam. Tragulidæ.
    - Pecora. Fam. Cervidæ (Subf. Moschinæ, Cervinæ (Plesiometacarpalia. Cervulus, Elaphodus, Cervus; Telemetacarpalia. Rangifer, Alces, Cervalces, Capreolus, Hydropotes, Cariacus, Pudua.) Fam. Giraffidæ, Antilocapridæ, Bovidæ.
  - Suborder Perissodactyla. Fam. Tapiridæ, Lophiodontidæ, Palæotheriidæ, Equidæ, Rhinocerotidæ, Lambdotheriidæ, Chalicotheriidæ, Titanotheriidæ, Macraucheniidæ, Proterotheriidæ.
- Subungulata.
  - Suborder Hyracoidea. Fam. Hyracidæ.
  - Suborder Proboscidea. Fam. Elephantidæ, Dinotheriidæ.
  - Suborder Amblypoda (not divided into families).
  - Suborder Condylarthra.
  - Suborder Toxodontia.

This classification was on the whole not only the best up to that date but also far more natural than several later ones. With some emendations it has been very widely accepted. It is evidently founded on practical knowledge and discriminating judgment. It erred chiefly in including the Macraucheniidæ and Proterotheriidæ in the suborder Perissodactyla.

1891, 1898. Cope.

Order Ancylopoda (under Unguiculata). Fam. Chalicotheriidæ.
Ungulata.
Order Taxeopoda.
Suborder. Condylarthra. Fam. Periptychidæ, Phenacodontidæ, Meniscotheriidæ.
Litopterna. Fam. Proterotheriidæ, Macraucheniidæ, Astrapotheriidæ.
Hyracoidea. Hyracidæ.
Daubentonioidea. Fam. Chiromyidæ, (Mixodectidæ [1898]).
Quadrumana. Fam. Mixodectidæ [1891], Adapidæ, Anaptomorphidæ, Tarsiidæ, Lemuridæ, Hapalidæ, Cebidæ, Cercopithecidæ.
Anthropomorpha. Fam. Simiidæ, Hominidæ.
Order Toxodontia. (Typotheria [1898]): Fam. Atryptheriidæ, Interatheriidæ, Protoxodontidæ, Nesotheriidæ, Xotodontidæ, Toxodontidæ.
Order Proboscidea. Fam. Dinotheriidæ, Elephantidæ.
Order Amblypoda.
Suborder Taligrada. Fam. Pantolambdidæ.
Pantodonta. Fam. Coryphodontidæ.
Dinocerata. Fam. Uintatheriidæ.
Order Diplarthra.
Suborder Perissodactyla. Fam. Lophiodontidæ, Triplopidæ, Cænopidæ, Hyracodontidæ, Rhinoceridæ, Tapiridæ, Lambdotheriidæ, Menodontidæ [Brontotheriidæ], Palæotheriidæ, Equidæ.
Suborder Artiodactyla. Fam. Pantolestidæ [Trigonolestidæ], Eurytheriidæ, Anoplotheriidæ, Dichobunidæ, Cænotheriidæ, Anthracotheriidæ, Xiphodontidæ, Suidæ, Hippopotamidæ, Merycopotamidæ, Dichodontidæ, Oreodontidæ, Poëbrotheriidæ, Protolabididæ, Camelidæ, Eschatiidæ, Tragulidæ, Moschidæ, Bovidæ, Cervidæ.

Cope's classification appears to be in a considerable degree unnatural and founded upon supposed principles of the evolution of the carpus and tarsus which subsequent research has largely discredited (p. 452).

The order Ancylopoda, instead of being independently derived from an unguiculate stock, as maintained by Cope, is almost certainly a division of the Perissodactyla (see p. 400).

The order Taxeopoda seems to be a very artificial assemblage, held together chiefly by a more or less negative character of the carpus and tarsus. To judge from the arrangement of its "suborders," the Chiromyidæ are no more nearly related to the Lemuridæ than they are to the Hyracoidea.

The distribution of the families of Primates seems very bad. The Primates are unjustifiably grouped with the Condylarths and Litopterns. The Litopterns are widely separated from their relatives, the Toxodonts. The order Diplarthra is shown below to be an unnatural group (see pp. 385, 400). The division of the Artiodactyla is confused and open to criticism in many respects.

Several classifications of the Ungulates as a whole appeared between that of Cope and that of Weber in 1904. The classification embodying the most novel features was that of Ameghino in 1905, 'Recherches de Morphologie Phylogenétique sur les Molaires superieures des Ongulés' (1904, pp. 511–526). Many of Dr. Ameghino's families are founded upon very imperfect material especially teeth not associated with skulls or limbs. One of the negative results of modern studies is that such material in many instances serves rather to raise new, than to settle old, questions of relationship. Even in groups in which the entire skeleton and soft anatomy is fully known (*e. g.*, Tubulidentata, Pholidota, Hyracoidea, Sirenia) it is sometimes very difficult to settle positively the precise relationships with other orders; while in many cases surprising similarities in the dentition (*e. g.*, between *Notoryctes* and *Chrysochloris*), do not prove ordinal kinship (*cf.* p. 108 above). For these and similar reasons phylogenetic conclusions and classifications which are based either upon superficial similarity in molar patterns or upon equally adaptive features of the skull and limbs are apt to lack certainty and permanence.

The labors of Marsh, Cope, Osborn, Scott, Schlosser, Wortman, Depéret, Stehlin and others upon different groups of Ungulates, in so far as they have affected the general classification, are reflected in the following scheme given by Weber (1904).

1904. Weber.

Ungulata [term used in a superordinal sense].
Diplarthra.
I. Ordn. Perissodactyla.[1]
Titanotheroidea. Palaeosyopidae, Titanotheriidae.
Hippoidea. Equidae, Palaeotheriidae.
Tapiroidea. Tapiridae, Lophiodontidae.
Rhinocerotoidea. Hyracodontidae, Amynodontidæ, Rhinocerotidae.

[1] Classification after Osborn, 1898.

II. Ordn. Artiodactyla.
  A. Nonruminantia.
    1. Unterordn. Suoidea. Hippopotamidae, Suidae, Elotheriidae.
  B. Ruminantia.
    2. Unterordn. Tylopoda. Camelidae, Oreodontidae, Homacodontidae.
    3. Unterordn. Pecora. Cervidae, Bovidae, Giraffidae.
    4. Unterordn. Traguloidea. Tragulidae.
    5. Unterordn. Dichobunoidea. Anoplotheriidae, Dichobunidae (Subfam. Xiphodontinae, Caenotheriinae).
    6. Unterordn. Anthracotheroidea. Anthracotheriidae.

III. Ordn. Condylarthra. Phenacodontidae, Meniscotheriidae, Mioclaenidae.

IV. Ordn. Ancylopoda. Chalicotheriidae, ? Homalodontotheriidae.

V. Ordn. Litopterna. Proterotheriidae, Macrauchenidae, ? Astrapotheriidae.

VI. Ordn. Amblypoda.
  1. Subordn. Taligrada (Cope) Osborn. Periptychidae, Pantolambdidae.
  2. Subordn. Pantodonta Cope. Coryphodontidae.
  3. Subordn. Dinocerata Marsh.

VII. Ordn. Toxodontia. Typotheriidae, Toxodontidae, Protypotheriidae, Hegetotheriidae.

VIII. Ordn. Hyracoidea.

IX. Ordn. Proboscidea. Dinotheriidae, Elephantidae.

This classification is wisely conservative in spirit but is probably susceptible of improvement in the following details:

(1) The group Diplarthra is very likely unnatural, even in a superordinal sense (p. 400).

(2) The Ancylopoda are probably closely related to the Perissodactyla and not related to *Homalodontotherium* (pp. 397, 399).

(3) The Anthracotheroidea are probably related more nearly to the Suina than to the Ruminantia.

(4) The Litopterna are probably related superordinally to the Toxodontia (p. 378).

The classification adopted in the present work is given on pages 464–466.

II. The Condylarthra.

Phenacodus and *Euprotogonia.*

The famous *Phenacodus primævus* of the Lower Eocene was described and figured by Cope (1884, pp. 435–463, pll. lvii b *et seq.*) and by Osborn (1898, pp. 159–164, pl. xii). It was at first regarded as the "five-toed atavus" of the Perissodactyls and especially as ancestral to *Hyracotherium* and the Equidæ; but Matthew (1897, pp. 309–310) and Osborn (1898, pp. 163–164) showed that *Phenacodus* and even its more generalized Basal Eocene ancestor *Euprotogonia* were only indirectly related to the ancestors of the Perissodactyla and were in fact a cursorial hoofed offshoot of a common Condylarth-Creodont stock.

The derivation of *Phenacodus* and *Euprotogonia* from the ancestors of the Insectivore-Creodont group is indicated by many primitive characters, as follows:

(1) The dental formula $\frac{3.1.4.3.}{3.1.4.3.}$, is especially characteristic of the Insectivore-Creodont stock and its descendants.

(2) The upper molars are derived from the tritubercular type by the addition of the hypocone, the lower by the reduction of the paraconid. In *Euprotogonia* the derivation of the molars (figured by Osborn, 1907, p. 169) from a tritubercular type analogous to that of the supposed Insectivore *Hyopsodus laticuneus* (Osborn, *l. c.*, p. 149) is very obvious. In the Basal Eocene genus *Protogonodon* Scott, the hypocone is only incipient and the molars are tritubercular (see Osborn, *l. c.*, p. 169, fig. 148).

(3) The skull in *Phenacodus* and *Euprotogonia* resembles the primitive Creodont type in its heavy muzzle, small brain case, long low sagittal crest and rather slender zygomata. An alisphenoid canal, into which, as in the dog, the foramen rotundum opened, was present. Derivation from Insectivorous ancestors may also be indicated by the rather short erect canines, elongate premaxillaries and slightly procumbent lower incisors (*P. wortmani*).

(4) The brain (Cope, 1884, pl. lvii *b*) was of a very low type, with large olfactory lobes, and small smooth cerebra which probably left the corpora quadrigemina and cerebellum uncovered.

(5) The skeleton, which has been figured by Cope (1884) and Osborn (1898) also retains many archaic Insectivore-Creodont features, such as the long tail, arched back, hatchet-shaped spine of axis, entepicondylar foramen, large shaft of the ulna, third trochanter on the femur, pentadactyl manus and pes, etc. There were 20–21 dorso-lumbar vertebræ (Osborn), *i. e.*, very near the characteristic Creodont number of 20. The "serial" arrange-

ment of the carpal bones is no longer thought to be primitive (see below and p. 446).

The small *Euprotogonia puercensis* (Cope), the Basal Eocene (Torrejon) forerunner of *Phenacodus*, was described by Matthew (1897, pp. 305–310) and by Osborn (1898, pp. 163–164). It approached nearer to the Insectivore-Creodont type in many characters, including the following:

(1) In the dentition the molar pattern is less removed from the tritubercular type than is the case in *Phenacodus* (*vide supra*).

(2) *Euprotogonia* was only about half the size of *Phenacodus primævus*, *i. e.*, about nine inches high at the withers.

(3) In the carpus the magnum and trapezoid are small and the lunar retains a little of its primitive contact with the unciform (Matthew, 1897, p. 320, *infra*, p. 446).

(4) The astragalus retains a distinct astragalar foramen (lost in *Phenacodus*) and shows a decided approach to the Creodont astragalus, *e. g.*, as represented by *Sinopa*.

(5) The hind foot was probably semiplantigrade (Matthew).

(6) The ungual phalanges are narrower than in *Phenacodus*, "intermediate between claws and hoofs" (Osborn).

The more precise derivation of the Euprotogonia-Phenacodus line is unknown.

Meniscotherium.

Presumably specialized characters.— This Lower Eocene genus (figured in Cope's 'Tertiary Vertebrata,' plates xxv f and g) appears to be an isolated form widely removed from *Phenacodus* by the possession of many specializations. Its buno-lopho-selenodont upper molars (figured by Osborn, 1907, p. 184, fig. 183) are remarkably elaborate in pattern for a Lower Eocene Holarctic Ungulate. The main external cusps and the large protoconule are crescentic, the metaconule obliquely lophoid and confluent with the large hypocone, the para- and mesostyles well developed. The fourth upper premolar and the third molar are like m^1 and m^2 except that they lack the postero-internal cusp. The fourth lower premolar is molariform and the metaconid on the lower molars is reduplicate. The third lower molar lacks the third lobe. The incisors and canines are reduced in size. The skull is brachycephalic, and very broad across the orbits, which are large. The brain case is relatively wider than in *Phenacodus*. The long flattened femur has the large third trochanter well down on the shaft and continuous with a ridge running down to the external condyle, *i. e.*, much as in *Pantolambda*. The calcaneum is large and has a long tuber calcis; the small, wry-necked astragalus is figured as being without an astragalar foramen.

Along with these peculiar specializations some *primitive features* also survive: The dental formula is $\frac{3.(?)1.4.3.}{3.\ 1.4.3.}$; the nasals spread somewhat posteriorly (*fide* Cope's figure), there is a long low sagittal crest and the orbit is broadly continuous with the temporal fossa; the tibia also is long and slender, distally acuminate, the head flares widely on the fibular side. The tibia seems to represent an exaggeration of the type seen in the Creodont *Sinopa* (*cf.* Matthew, 1906, p. 227, fig. 19). Resemblances to the Creodonta are seen in the large lumbar vertebræ, the long slender humerus with a very large sub-globular head, a supratrochlear and an entepicondylar foramen, a long deltoid crest and a large great tuberosity. The astragalus approximates the *Sinopa* type; the carpus retains a free centrale and a lunar-unciform contact (p. 447).

In short, *Meniscotherium* appears to be an advanced, early derivative of the Insectivore-Creodont-Condylarth stock, allied remotely to the Phenacodontidæ. It resembles the short footed orders Hyracoidea, Proboscidea and others in the length of its humerus and femur, in the small size of the lunar-unciform facet and consequent tendency for the carpus to become serial, and in its relatively short metacarpals. Its cheek teeth, however, have too complex a pattern to be prototypal to those of any later order. It parallels *Hyrax* in some inconclusive features (p. 362) but it distinctly resembles some of the extinct South American ungulates (*e. g., Trigonostylops*) in the characters of the astragalus and calcaneum (*cf.* p. 384).

III. Genetic Relations of the Condylarthra, Taligrada, and Amblypoda.

The Eocene order Amblypoda as defined by Cope (1884, pp. 600–601, 514–517) included the suborders Taligrada Cope (Pantolambdidæ), Pantodonta Cope (Coryphodontidæ) and Dinocerata Marsh (Uintatheriidæ). Osborn (1898, pp. 169–218), who elucidated the evolution of the order and gave evidence of its derivation from the Creodont stock, revised the classification of the Taligrada and Pantodonta and added to the former the family Periptychidæ Cope (*cf.* Osborn and Earle, 1895, pp. 52–64) which Cope had placed in the Condylarthra. Matthew (1897, pp. 294–299) revised the Periptychidæ but regards them as properly falling under the definition of the order Condylarthra.

The morphological relations of these two orders may be indicated briefly as follows. (The Mioclænidæ (Osborn and Earle, *l. c.*, pp. 48-52), which are doubtfully referred to this group are not discussed.)

Order CONDYLARTHRA Cope.

Family PHENACODONTIDÆ. Examples: Basal Eocene *Euprotogonia*, Lower Eocene *Phenacodus*. Progressively cursorial, manus and pes becoming tridactyl by reduction of digits I and V; lunar-unciform contact decreasing (Matthew), carpals flattening and carpus becoming serial; centrale not free (*Phenacodus*), magnum large. Humerus with moderate entocondyle and entepicondylar foramen. Scapula rounded superiorly, coracoid process small. Astragalus with well developed trochlear keels; not touching cuboid; foramen early reduced or wanting. First and second upper molars quadrate, *i. e.*, with well developed hypocone; cusps bunoid. P^4 triangular, with tritocone. M_3 with small hypoconulid.

Family MENISCOTHERIIDÆ. Lower Eocene, *Meniscotherium*. Ambulatory; tridactyly less pronounced. Lunar-unciform contact not large, carpals flattening (sub-serial), centrale free. Humerus with moderate entocondyle and entepicondylar foramen. Coracoid process small. Astragalus not touching cuboid, trochlear groove slight, neck slender; astragalar foramen variable. M^1, m^2 quadrate, with well developed hypo-, para- and metacones and large protoconule, all crescentic; metaconule confluent with hypocone. P^4 triangular, with tritocone; protocone, tritocone and protoconule crescentic. M_3 without hypoconulid; metaconids on m_1–m_3 reduplicate.

Order TALIGRADA (Cope).

Family PERIPTYCHIDÆ.[1] Basal Eocene (*e. g.*, *Anisonchus, Haploconus, Conacodon, Periptychus*). Ambulatory; pes (*Periptychus*) fully pentadactyl (digits I and V hardly if at all reduced); manus not known. Humerus with very stout entocondyle and large entepicondylar foramen (*Periptychus*). Scapula pointed superiorly; coracoid process large. Astragalus broadly touching cuboid, trochlea very broad and convex, with broad neck; or trochlea broad with low keels (*Hemithlæus kowalevskianus cf.* Matthew, 1897, p. 297), large astragalar foramen. M^1, m^2 triangular; an anterior and a posterior basal cingulum sometimes rising into distinct cusps; main cusps conic. P^4 bicuspid, tritocone wanting. M_3 with or without hypoconulid.

Family PANTOLAMBDIDÆ. Basal Eocene (Torrejon) *Pantolambda*. Ambulatory; digits rather short, I and V not reduced; lunar-unciform contact broad, centrale separate, magnum small. Humerus with stout entocondyle and entepicondylar foramen. Scapula pointed superiorly; coracoid process

[1] Regarded by Matthew as Condylarthra.

large (?). Astragalus broadly touching cuboid, trochlea broad, with low keels; an astragalar foramen. M_1, m_2 triangular (without hypocone), with small anterior and posterior cingula; para- and metacone strongly V-shaped, mesostyle very prominent. P^4 bicuspid, external cusp V-shaped, tritocone wanting. M_3 without third lobe. Size not large, skull hornless, with sagittal crest.

Order AMBLYPODA Cope.

Family CORYPHODONTIDÆ. Lower Eocene (chiefly *Coryphodon*). Ambulatory; all digits very short, II–IV very broad, phalanges very short; lunar-unciform contact retained; unciform spreading upon digit III, pushing magnum over on digit II. Humerus with entocondyle relatively reduced and without entepicondylar foramen. Scapula pointed superiorly but postspinous fossa produced backward. Astragalus very broad, trochlear surface extending down on front of neck, astragalus spreading over on cuboid; astragalar foramen wanting or greatly reduced. M_1, m_2 sub-triangular, a prominent protoloph formed of the protocone and parastyle, paracone small, conic, metacone V-shaped. M_3 without hypoconulid. Size large, skull hornless (incipient frontal tuberosities in *Coryphodon wortmani, fide* Osborn). Sagittal crest widening into a flat vertex. Canines elongate.

Family UINTATHERIIDÆ. Middle Eocene (*e. g., Uintatherium, Loxolophodon*). Ambulatory; limb characters of the Coryphodontidæ all further developed. Upper molars with strong protoloph (formed as in Coryphodontidæ) and metaloph (probably representing a displaced paracone, mesostyle and metacone—*fide* Osborn, 1907, p. 167). M_3 without hypoconulid. Size very large, skull top finally with three pairs of bony protuberances on nasals, frontals and occiput respectively. Upper canines sabre-like.

The preceding brief analysis is sufficient to indicate that the Pantolambdidæ, Coryphodontidæ and Uintatheriidæ form an ascending series and that the Periptychidæ are connected on the one hand with this series at its base and on the other hand with the Condylarth families Phenacodontidæ and Meniscotheriidæ. Osborn, who favors the phylogenetic, or vertical, system of classification, observing that *Periptychus* resembles the Amblypoda rather than the Condylarthra in the possession of an astragalo-cuboid contact and of "strictly trigonal molars" (*l. c.*, p. 181) added the family to the Taligrada and placed the latter with the Amblypoda as already stated.

More in detail, apparent reasons for this phylogenetic grouping may be stated as follows:

CONDYLARTHRA (including only the Phenacodontidæ and Meniscotheriidæ).

Feet more slender, tridactyly progressive. Astragalus with slender neck; trochlea keeled. Lunar-unciform facet becoming reduced, carpals becoming serial. M^1, m^2 early becoming quadrate, with large hypocone. Premolars triangular, with tritocone.

AMBLYPODA (Cope) Osborn. (Including the Periptychidæ, Pantolambdidæ, Coryphodontidæ, Uintatheriidæ).

Digits becoming stout and short, pentadactyly unreduced. Astragalus with neck progressively broadening and trochlea flattening; with cuboid contact.

Lunar-unciform facet broad, carpals becoming displaced toward the ulnar side (*Pantolambda*). M^1, m^2 persistently trigonal, protocone remaining central, hypocone small. Premolars bicuspid, without tritocone.

Matthew (*l. c.*, p. 295) having in mind on the one hand the great structural interval between *Periptychus* and the highly specialized Amblypods and on the other the resemblance of the smaller Periptychidæ (Anisonchinæ) to the Condylarthra, placed the family in the latter order and showed that the two orders were so closely connected in the Basal Eocene that the systematic position of the Periptychidæ is largely a question of definitions.

The Basal Eocene families of the Condylarthra and "Taligrada" seem in fact to be not widely removed from each other, and there is evidence that the broad "horizontal" group of which they were doubtless a small part had about the same relation to certain of the more highly specialized ungulate orders that the most primitive Creodonta (including the Miacidæ) had to the later Creodonta, Fissipedia and Pinnipedia. These "protungulates" retained very many Creodont characters in the skull and skeleton and were separated from that group chiefly by the greater elaboration of the molar teeth.

Probably the most primitive members of the series are the smaller Periptychidæ, especially *Haploconus lineatus* Cope (1884, pl. xxv e, figs. 1–4) the dentition of which exhibits the following interesting features:

The premaxillaries may have been prolonged as in Insectivores, the canines are not large. The bicuspid p^4 is larger than the small narrow tritubercular molars. The internal basal apex of the molars is a prominent hypocone spur (*cf.* certain Zalambdodont Insectivores). The chin is shallow, the lower premolars are narrow, the lower molars lack the paraconid. The palate is broad and well ossified.

This small species, the teeth of which were no larger than those in *Dasyurus viverrinus*, may have been omnivorous to insectivorous-carnivorous in diet. It is allied with the much larger *Periptychus* by way of *Conacodon* (*cf.* Osborn, 1907, p. 165). Osborn and Earle (1895, p. 63) suggested that the

smaller members of the family may have been arboreal; and there is considerable evidence (pp. 288, 307) for regarding their arboreal adaptations (*e. g.*, divergent hallux, astragalo-cuboid contact) as primitive Placental characters. Other primitive features are: the entepicondylar foramen on the humerus the third trochanter on the femur, the dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$; so that in case the skull and skeleton are more fully made known some of the smaller Periptychidæ may prove to stand almost as near to the generalized Placental prototypes as do any known Creodonts, Primates or Insectivores (including *Hyopsodus*). In this connection it is interesting to note that Matthew (1909, p. 512) has recently noted many resemblances between the Eocene Insectivore *Hyopsodus* and the Mioclænidæ, which latter are probably of "protungulate" affinities. The astragalus of the Periptychidæ (*cf.* p. 454 *Ectoconus*) approaches the Marsupial type in several characters: *e. g.*, the slight development of the trochlear ridges, the broad surface for the internal malleolar region of the tibia, the relations of the sustentacular facet. In other respects it approaches the Creodont type.

IV. The Hyracoids.

The small modern Hyraces present a confusing mixture of characters: some quite unique among mammals, others primitive, others recalling such diverse groups as Rodents, the Meniscotheres, Santa Cruz "Protypotheres." Embrithopoda, Proboscidea, Horses and Rhinoceroses. Although the correct phylogenetic evaluation of these characters is by no means easy, the following principles may assist to some extent.

(1) It is obvious that some differences between modern and Eocene or Miocene forms may be divergent adaptations, and a small number of distinctive or even primitive characters in common may be of great significance in indicating interordinal affinities, which may be obscured by a large number of more recently acquired specializations. For example, in "*Hyrax*" the dental formula (which is a direct derivative of $\frac{3.1.4.3}{3.1.4.3}$), the complete milk dentition, the possession of an alisphenoid canal, the independent optic foramen, the retention of interparietals, of a third trochanter on the femur, a free os centrale carpi, abdominal testes, uterus bicornis, structure of the endoturbinals, etc., collectively prove that we are dealing with a primitive Placental and more particularly with an offshoot of the stock which gave rise to the Insectivores, Creodonts, Condylarths, Periptychids, etc.; and these few characters outweigh any number of peculiar specializations which distinguish the Hyracoidea from all other Placentals.

(2) The greater the number of homoplastic resemblances to different orders the more probable is it that the remote ancestors of the Hyracoidea

resembled the remote ancestors of those other orders, at least in its "potential of evolution."

A very comprehensive description of the chief characters of the Hyracoidea is given by Weber (1904, p. 707) so that what follows is merely an analysis of the more important characters.

A few of the *peculiarities of the Hyracoidea which distinguish them from all other ungulates and point to a long phylogenetic independence* are as follows: The proximal end of the colon gives off a pair of cœcal diverticula which are unknown in other mammals; the arrangement of the cerebral sulci is peculiar (Weber, 1904, p. 710) and likewise many of the details of the vascular and reproductive systems.

The skeleton too abounds in specialized characters, some of which are unique. A process from the parietal reinforces the postorbital process of the frontal; the malar extends backward into the glenoid fossa; The hyoid arch is "unlike that of any other mammal" (Flower and Lydekker); the scapula is V-shaped and lacks the acromion; the slender humerus has lost the entepicondylar foramen; the clavicle is lost; the radius and ulna tend to ankylose, likewise the tibia with the proximal end of the fibula; the third trochanter of the femur is reduced; the inner side of the astragalus has a deep step-like articulation for the tibial malleolus; the dorso-lumbar formula of D. 20–21 + L 7–9 is much higher than in any other primitive mammal; the number of sacrals, 5–7, is also very high, while the caudals are reduced to 4–8, facts suggesting that the sacrum has been pushed backward along the caudal series.

Resemblances to members of other orders.

The above mentioned mixture of characters in *Hyrax* is well illustrated in the characters of the eye as viewed under the ophthalmoscope. According to Lindsay Johnson (1901) the fundus oculi of *Hyrax* retains two marked and presumably primitive features in common with Rodents and Marsupials: *viz.*, it presents an aster-like radiation of nerve fibres and the pale reddish brown fundus shows traces of choroid vessels. On the other hand it shows a general resemblance to the fundi both of the Elephants and of the Perissodactyls, since it has a large round disc, a uniform field with bacillary markings and small radiating retinal vessels. Finally the fundus of *Hyrax* resembles that of the Artiodactyls in the development of a projection from the iris, the umbraculum, which is highly contractile and serves to screen the iris from strong light. Similarly also in regard to the arrangement of the azygos veins Beddard (1907, p. 219) speaks as follows: "... the position and number of these veins in *Hyrax* are of particular interest. In this 'subungulate,' admittedly primitive, and standing nearer to the

base of the Ungulate series than any other living form, except the Elephant, there is as it were a hesitation to adopt definitely the form of the azygos veins to be seen in either Artiodactyle or Perissodactyle."

The Hyraces resemble the *Rodentia* chiefly in the purely adaptive character of the enlarged incisors and diastema and in the above noted characters of the fundus oculi. They resemble the *Amblypoda* and *Proboscidea* in the width of the vertebral centra, arched back, high number of dorsals, flattened ilium (which might give rise to the spreading type), long humerus and femur, stout ulna, partial crossing of the radius and ulna, short digits and flattened carpals. They further resemble the *Proboscidea* in certain characters of the fundus oculi, in the zonary placenta, in the flat nail-like characters of the hoofs, in the small lachrymal, in the extension of the malar to the glenoid fossa, in the lack (*cf.* Insectivores) of posterior clinoid processes in the pituitary fossa (Flower), and finally in the reduction of the floccular fossa of the petrosal (Flower). Special resemblances to *Mœritherium* are noted below (p. 368).

These resemblances are consistent with the hypothesis that the Hyracoidea and Proboscidea, together with certain other groups (p. 110) have been derived from unknown basal members of the Condylarth-Amblypod stem.

Resemblances to different *Perissodactyla* are numerous. The Perissodactyl features of the fundus oculi have been noted above. The ossicula auditus suggest those of the horse (Doran, 1879), and so also the Eustachian tube, especially the peculiar diverticulum from it (Weber, 1904, p. 711). The mastoid portion of the periotic is reduced and the molar pattern, which is buno-lopho-selenodont, has a Perissodactyl-like facies, especially in *Megalohyrax minor* (Andrews, 1906, pl. vii, fig. 1) in which the true molars suggest those of *Palæosyops*. The premolars also tend to become like the molars, but differ in details from those of any known Condylarth or Perissodactyl. The lower molars of *Megalohyrax* (Andrews, *op. cit.*, pll. vi, vii) have a reduplicate metaconid, as in *Meniscotherium, Eohippus, Lambdotherium,* etc., and the hypoconulid is small. The digits are reduced to four in the manus (a reduced hallux sometimes persists) and three in the pes, as in Lower Eocene Perissodactyls. All the foregoing characters as well as the arrangement of the chief cranial foramina, seem consistent with remote relationships with the Perissodactyla.

Resemblances to *Meniscotherium* (p. 355) are seen in the general form of the skull, large orbits, breadth across the orbits, long humerus and femur and largely serial carpus (p. 447). The centrale is likewise still separate, the proximal row of carpals relatively small and the trapezoid large. The magnum in *Hyrax*, however, is very broad and quadrate. The metacarpals

do not overlap any more than they do in *Meniscotherium*. The reduction of the digits to 4–3 is already suggested in *Meniscotherium*. The astragalus, as in Condylarths, usually lacks the cuboid facet (at least in *Procavia capensis*), the cuboid lying below the level of the head of the astragalus, but in *Dendrohyrax arboreus* an astragalo cuboid contact occurs (Osborn, 1889, pp. 537–538). The step-like articulation for the internal malleolar extension of the tibia on the astragalus, already noted, may have been initiated from conditions similar to those in *Meniscotherium* in which the tibia articulated chiefly with the internal side of the astragalus. The peculiar conditions in *Hyrax* are possibly connected with its plantigrade habits and with the development of adhesive plantar pads for running up smooth steep surfaces (Dobson, 1876). On the whole, however, the resemblances to *Meniscotherium* do not appear to be of the same phylogenetic value as the resemblances to the Proboscidea (p. 362).

The Hyraces resemble *Protypotherium* of the Patagonian Miocene in the general form of the skull, short premaxillaries excluded from contact with the frontals, backward prolongation of the malars, broad frontals which strongly resemble those of the Eocene *Saghatherium* (see Andrews, 1906, pl. vii, fig. 5), high position of the squamosal root of the zygoma, cancellous dilation of the squamoso-periotic, tubular upwardly directed auricular meatus, shape of the posterior border of the palate and of the ectopterygoid fossæ, carotid canal united with foramen lacerum posterius [not true of *Hegetotherium* and *Pachyrukhos* (Sinclair)], canine more or less premolariform. The mandible also deepens posteriorly and was drawn from behind upward, slightly forward and sharply inward.

These resemblances, which do not obtain to so great a degree between *Hyrax* and other Santa Cruz Typotheres are all regarded as secondary by Sinclair (1908), who points out that they are associated with important differences in the skull, in the pattern of the molars and in the carpus and tarsus (see p. 376). Nevertheless the resemblances between *Hyrax* and *Protypotherium* are so extraordinary that one can scarcely help feeling that they may after all outweigh the well marked differences above cited.

That Dr. Andrews is right in referring to the order Hyracoidea the Eocene Egyptian genera *Megalohyrax* and *Saghatherium* appears to be indicated by the following facts:

(1) In *Pliohyrax* (Osborn, 1898), *Megalohyrax*, *Saghatherium*, the canines are premolariform, the premolars very advanced in type, the molars agree in essentials with those of *Hyrax* as figured by Osborn (1907, p. 185); the posterior crescent of the lower molars touches the anterior crescent at a point just external to the posterior metaconid spur (metastylid). In all three genera the inner upper incisor (i^1) is enlarged pointed, triangular in section, as in *Hyrax*.

(2) In both groups, according to Granger (quoted by Sinclair, 1908, p. 77), the base of the coronoid process shows a peculiar perforation which is a separated portion of the dental canal.

The idea that the Eocene Hyracoids may be related to the Artiodactyls, which might be suggested by the general similarity of the upper and lower molar teeth of *Megalohyrax* to those of *Ancodus gorringei* (*cf.* Andrews, *op. cit.*, pl. xviii, figs. 1–3), seems to be negatived by the differences in the premolars, which in *Megalohyrax* are much more molariform than in any Artiodactyl.

In conclusion, out of all the divergent resemblances cited above, the writer is inclined to regard those indicating remote affinity with the Proboscidea as having the most weight, and this too in spite of the great differences in the dentition (*cf.* p. 107). This conclusion appears to be strengthened by the evidence for common ancestry of the Hyracoidea and Embrithopoda, the latter in turn showing many underlying features (p. 366) with the Proboscidea and Amblypoda. Finally the existence of so many "cross-resemblances" between the Proboscidea and the Perissodactyla by way of *Hyrax* seem more consistent with the hypothesis that all these now very divergent orders have been derived from a common protungulate stock, than with the hypothesis that all the resemblances are due to convergent evolution.

V. The Embrithopoda (Barypoda).

In discussing the affinities of *Arsinoïtherium*, the gigantic Eocene pachyderm of the Fayûm, Dr. Andrews (1906, p. 63) says: "Comparison with the Hyracoidea is very difficult on account of the small size of the modern representatives of the group and our complete ignorance of the skeleton of the large extinct forms. In the early Hyracoidea there is a tendency for the anterior teeth (incisors, canine, and premolars) to form a continuous series, the anterior pair of incisors being more or less enlarged and separated from one another in the middle line by a short interval, as in *Arsinoïtherium*. The molars are brachyodont, but their pattern is such that if there were an increase in height accompanied by an increasing infolding of the outer wall, they might give rise to a type of tooth very similar to the molars of *Arsinoïtherium*, as was explained above. Since, however, these early brachyodont Hyraces are contemporaries of *Arsinoïtherium*, it is not suggested that they are closely related; but the circumstance that they both seem to have originated in the same region lends some probability to the belief that they may have had a common ancestry in the late Secondary or earliest Tertiary period." Dr. Andrews also refers the Embrithopoda, along with the

Proboscidea, Hyracoidea and Amblypoda to the Subungulate section of the Ungulata and expresses the opinion that most of the similarities in the skeleton between *Arsinoïtherium* and *Elephas* and the Amblypoda are probably parallel modifications due to great size and weight in the two groups.

The following observations based on a comparison of Dr. Andrew's excellent figures with specimens of *Hyrax* seem to lend additional support to his conclusions:

(1) The upper premolars of *Arsinoïtherium* are derivable (in accordance with the analogy furnished by the Rhinoceroses) from the type represented in *Megalohyrax*. The little worn upper premolar of *Arsinoïtherium* (*l. c.*, pl. v, fig. 2) differs from the corresponding premolar of *Megalohyrax* (*l. c.*, pl. vi, fig. 2) chiefly in the hypsodonty and flattening of the ectoloph, development of the parastyle, anterior cingulum and postero-internal cingulum cusp (tetartocone). In both types the metaconule is absent and there is a prominent median valley just posterior to the protoloph. In fact it may confidently be stated that in respect to the unworn premolars *Arsinoïtherium* offers a closer comparison with *Megalohyrax* than with any known Amblypod, Condylarth, Perissodactyl or other ungulate.

(2) The lower cheek teeth of *Arsinoïtherium* likewise appear to be hypsodont modifications of the type seen in *Megalohyrax*. The fourth lower premolar (*l. c.*, pl. iv, fig. 3) retains evidence of the reduplicate metaconid (metastylid) which is so conspicuous an element in *Meniscotherium* and *Hyrax* (but which appears also among the Perissodactyla). The unworn lower molars, however (*l. c.*, pl. iv, fig. 1) suggest those of the Amblypod *Coryphodon*. The third lower molar lacks the third lobe (hypoconulid) as in *Meniscotherium*, *Hyrax* and other forms. In general, the dentition of *Arsinoïtherium* differs from the contemporary Hyracoids chiefly in the kind of features which in other cases distinguish highly specialized from primitive forms.

(3) The architecture of the young skull of *Arsinoïtherium* (*l. c.*, pl. iii) differs from that of the Dinocerata (Marsh, 1884, pl. ii) in several characters, apart from the more obviously adaptive differences; *e. g.*, the lachrymal in *Arsinoïtherium* is practically vestigial and apparently without a canal; in *Dinoceras* it is very large and spreading and is pierced by the large lachrymal foramen.

In underlying features *Arsinoïtherium* exhibits a much closer resemblance with *Hyrax*. The premaxillaries, lachrymals, nasals and frontals have essentially similar relations and differ chiefly in proportions; the malar extends back to the anterior edge of the glenoid fossa; the dorsal ridge of the zygoma is continued above the auricular meatus, (*op. cit.*, pl. iii, figs. 1, 2)

the mastoid is not exposed externally in *Arsinoïtherium* and is barely so in *Hyrax*. In *Arsinoïtherium* the post-glenoid and post-tympanic form a tubular meatus which might readily be derived from the conditions in *Hyrax*. In both genera there is an alisphenoid canal and the condyles are widely separated.

Arsinoïtherium resembles the contemporary Proboscidea in the following features:

(1) The premaxillaries are excluded by the nasals from contact with the frontals.

(2) The lachrymals are widely separated from the nasals by the frontals.

(3) The post-tympanic and post-glenoid processes tend to bridge over the auditory meatus.

(4) The paroccipital process is closely appressed to the post-tympanic.

(5) There is no condylar foramen.

(6) An alisphenoid canal is present.

(7) The fore arm and manus parallel those of *Elephas* closely in many details and leave little doubt that both have been derived from forms having a serial type of carpus, with a tendency toward reduction of the radius and enlargement of the ulna, and with a correlated tendency toward reduction of the scaphoid and broadening of the cuneiform.

Arsinoïtherium resembles the Dinocerata chiefly in the ectal spreading of the astragalus over the cuboid and under the fibula, and in the consequent reduction of the calcaneum. This very likely indicates that in the remote and small ancestors of *Arsinoïtherium* the astragalus had a considerable cuboid facet and that the foot as a whole was not very different from that of *Pantolambda*.

In short *Arsinoïtherium* appears to be related to the Hyracoidea on the one hand and to the Proboscidea on the other, and more remotely to the stem forms of the Amblypoda, *i. e.*, to the Pantolambdidæ or Periptychidæ.

VI. The Proboscidea.

The derivation of the later Proboscidea from forms resembling *Palæomastodon* of the Lower Oligocene of the Fayûm, Egypt, has been demonstrated by Andrews (1903, 1906) and calls for no comment in this work; but the position of *Mœritherium* (also from the Fayûm — Upper Eocene and Lower Oligocene) with reference to the later Proboscidea and Sirenia may be discussed briefly. The following analysis of the characters of *Mœritherium* is based on Dr. Andrews's excellent figures and descriptions (1906) of the type and referred species.

I. *Evidence for relationship with the stem of the Proboscidea*:

(1) $I\frac{2}{2}$ enlarged as in *Palæomastodon* ($I\frac{1}{1}$ enlarged in Sirenia) (*cf. Eosiren, Eotherium*). Mandibular symphysis approaching the Proboscidean rather than the Sirenian type.

(2) Cheek teeth of Proboscidean rather than Sirenian appearance (*cf.* special resemblances to *Palæomastodon* in *Mœritherium lyonsi.*

(3) Partial closure of the external auditory canal in palatal view by a backward prolongation of the postglenoid, which in *Eotherium* is widely open. The meatus in side view appears as a circular opening situated above the level of the zygoma, as in *Palæomastodon.*

(4) Confluence of condylar foramen with the foramen lacerum posterius (Condylar foramen distinct in *Eotherium*).

(5) Malar extending very far backward: *viz.*, back of glenoid (contrast *Eotherium*, Andrews, *op. cit.*, figure on p. 205).

(6) Large fossa for an anterior slip of the masseter, below the orbit (as in *Palæomastodon*).

(7) In occipital view squamosal very large (larger than in *Eotherium*; *cf. Palæomastodon*).

(8) A small tubercle on the lachrymal (Andrews, p. 103). The latter however differs from that of *Palæomastodon* in having no lachrymal foramen.

II. *Evidence for relationship between Mœritherium and the Stem of the Sirenia.*

(1) In palatal view general similarity between *Mœritherium* and *Eotherium* very striking.

(2) Extreme anterior position of orbits (noted by Andrews and by Osborn).

(3) "Upper posterior angle of the squamosal [in *Eotherium*] shut off from contact with the supraoccipital by a narrow posterior prolongation of the parietal which is wedged in between the two bones as in *Mœritherium*" (Andrews, *op. cit.*, p. 205).

(4) General similarity in the occipital view between *Mœritherium* and *Eotherium.*

(5) Certain resemblances in pelvis (noted by Andrews) between *Mœritherium* and *Eotherium.*

(6) Scapula of *Mœritherium* (*op. cit.*, pl. xi, fig. 5) resembling the Sirenian type in the backward sweep of the superior part of the blade.

(7) Strong resemblances between *Mœritherium* and *Eotherium* shown in the brain casts (Andrews).

III. *Characters in which Mœritherium differs from the Proboscidea.*

(1) All those mentioned above under II.

(2) Long tubular midcranial region, as in primitive Insectivores, Creodonts, *Pantolambda*, etc. Primitive.

(3) Diploë of the skull not markedly inflated. Primitive.

(4) Narrow supraorbital region. Primitive.

(5) Naso-premaxillary and palatal regions very different in *Mœritherium* and *Palæomastodon*.

(6) Neck longer in *Mœritherium*; atlas with peg-like odontoid (Andrews). Primitive.

(7) Dorso-lumbars (Andrews) at least 23 (D. 19, L. 4, S 4), *i. e.* more or less intermediate in number between Proboscidea (D. 19–20, L. 4–5, S 4) and Sirenia (D. 17–19, L 2–5).

(8) Referred humerus (*op. cit.*, pl. xi) somewhat more primitive than that of *Palæomastodon* in smaller supinator crest and larger internal condyle (*cf.* Taligrada).

(9) Referred femur lacking third trochanter (retained, low down on shaft, in *Palæomastodon*).

Conclusion in regard to Mœritherium. The genus represents a very primitive offshoot from the Proboscideo-Sirenian stock. Its dentition and certain other characters indicate a nearer alliance with the Proboscidea than with the Sirenia, but it is far more primitive than any other known representative of either order.

Points of similarity to the Hyraces also are not lacking, especially the detailed relations of the premaxillaries, maxillaries, nasals and frontals, the areas for the insertion of the masseter muscle, the backward extension of the malar, reduction of the mastoid, general shape of the lower jaw, shape of the ilium and other characters.

Genetic Relations of the Proboscidea.

Assuming that *Mœritherium* is a relatively primitive offshoot of the Proboscidea, allied also to the Sirenia, and perhaps more remotely to the Hyracoidea what light does it seem to throw on the derivation of these orders?

There can be no question of the derivation of *Mœritherium* from typical Placentals with a dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$, a normal milk dentition (retained in *Mœritherium*, *cf.* Andrews, p. 111), and normal cranial foramina. The premolars could not have been molariform and p^4 was probably bicuspid (*cf. Mœritherium*). The premolars seem to suggest the quadrate contour of the premolars of *Megalohyrax*. The upper molars were derived from a quadritubercular, incipiently bilophodont type in which the proto- and metaconules were ridged transversely.

The pentadactyl manus may have resembled that of *Hyrax* in a general way and also in certain detailed relations of the carpals (p. 448). The pes was probably not dissimilar to that of *Pantolambda* (p. 358). With the

phyletic increase in body size the humerus early lost the entepicondylar foramen and reduced the entocondyle; the femur originally may have had the third trochanter nearly half way down the shaft (*Palæomastodon, cf. Pantolambda*) but in the *Mœritherium* line the third trochanter was lost.

The family of perhaps Basal Eocene protungulate mammals having the above-mentioned combination of characters would be hard to classify under any known order and would probably be rather remotely related in various degrees to the Meniscotheres, Phenacodonts, Mioclænids, Periptychids, and Pantolambdids.

VII. The Barytheria (Incertæ Sedis).

The remains of *Barytherium grave* Andrews (1906, pl. xvii, figs. 4–9) from the Qasr el Sagha (Upper Eocene) beds of the Fayûm, Egypt, are too incomplete to afford decisive evidence as to the relationships of the order Barytheria of Andrews with other orders. The molars are bilophodont and in the worn dentition of the type, p $\frac{3-4}{3-4}$ also may have been bilophodont (*cf. Mœritherium*). The coronoid process of the mandible is very broad, anteroposteriorly rectangular at top and extended forward externally to m_3 (*cf. Mœritherium*). The anterior incisors are much enlarged and procumbent, and the scapula, also as in *Mœritherium*, has a large coracoid process. The humerus however is rather analogous with that of *Dinoceras*, though differing in the great development of the internal crest (Andrews). The radius also resembled the Dinoceratoid type in its general form and in the proportions of the scaphoid and lunar facets (Andrews). *So far as it goes* the material tends to confirm the hypothesis that the Proboscidea, Amblypoda and certain other orders have had a common origin. Ameghino's suggestion that *Barytherium* is related to *Pyrotherium* has been disputed with cogent evidence by Gaudry (1909, pp. 27, 28).

VIII. The extinct South American groups Homalodotheria, Astrapotheria, Toxodontia, Typotheria, Litopterna.

Recent Classifications.

1891–1893. Zittel.

[Order] Ungulata.

[Suborder] Toxodontia. Fam. Homalodontotheridae, Astrapotheridae Nesodontidae, Toxodontidae.

[Suborder] Typotheria. Fam. Protypotheridae, Typotheridae.

[Suborder] Perissodactyla. Fam. Equidae, Proterotheridae, Macrauchenidae, Tapiridae, Rhinoceridae, Titanotheridae, Chalicotheridae.

1893. Lydekker.

Order Ungulata.

Suborder Toxodontia. Fam. Pachyrucidæ, Typotheriidæ, Toxodontidæ.

Suborder Astrapotheria [subord. nov.] Fam. Homalodontotheriidæ, Fam. Astrapotheriidæ.

Suborder Litopterna. Fam. Proterotheriidæ, Fam. Macraucheniidæ.

". . . . phylogenetically the Toxodonts may apparently be regarded as related to the Perissodactyla, but as retaining certain features now common to the Artiodactyla which have probably been inherited from common Condylarthrous ancestors. The structure of the carpus precludes the inclusion of the group in the Subungulata, among which it has been placed [by Flower and Lydekker] and indicates that the Toxodonts must occupy a position of equal rank with the Artiodactyla and Perissodactyla. . . . " (p. 3).

As regards the Litopterna the author states (p. 56) that the group "appears to hold a somewhat intermediate position between the Astrapotheria and the Perissodactyla, although the peculiar character of the cervical vertebræ indicate that it cannot in any way be regarded as ancestral to the latter suborder."

1903. Roth.

[Order Ungulata.]

[Suborder] "Notoungulata (los géneros Toxodon, Nesodon y Typotherium). . . . . los tipos del grupo Notoungulata muestran una particularidad en la construcción de los huesos temporales que no existe en ningún otro suborden de los Ungulados." The author here refers to the peculiar construction of the temporal region in the above mentioned group and speaks of it as "un carácter típico y constante, como lo es, por ejemplo, el ángulo mandibular invertido en los Marsupiales. . . . " Consequently the author meant to exclude from this group the Astrapotheres and Litopterns, which are said to lack this character.

1904. Scott.

Notoungulata.

I. Toxodontia.

1. Toxodonta.
2. Typotheria.
3. Homalodotheria.

II. Litoptema [misprint for Litopterna].

III.? Astrapotheria.

The author states that although the Litopterna and Astrapotheria lack the peculiar structure of the periotic region referred to by Roth, yet on the other hand "all of the orders, including at least the Litoptema [Litopterna], have certain constant characteristics, such as the extensive articulation between the fibula and calcaneum, the convex distal end of the astragalus, which does not rest upon the enboid, and some peculiarities in the form of the teeth. The limb and foot bones of the Astrapothina [Astrapotheria] are not yet known, and their systematic position is, therefore, still a matter of conjecture. There is a striking similarity between the dentition of these animals and that of the northern genera, *Cadureotherium* [*Cadurcotherium*] and *Metamynodon*, but the form of the skull is so radically different as to make it probable that the resemblance in dentition is analogical only.

"It seems likely, therefore, that Roth's term, 'Notoungulata' may properly be extended to include all of the Santa Cruz hoofed animals, and that all of the groups which agree in the structure of the periotic region, already alluded to, should be regarded as sub-orders of the Toxodontia. This conception is shown in the following provisional table [given above]. . . . "While these South American ungulates are singularly different from those of the Northern Hemisphere, it does not seem at all likely that they originated altogether independently of the latter. Ameghino has described a number of genera from pre-Patagonian formations which, though incompletely known, appear to be referable to the Condylarthra, the parent stock of the northern Ungulates. Very probably an early Eocene or late Mesozoic migration brought the Condylarthra into South America, and there, in almost complete isolation, they gradually gave rise to the various peculiar orders and suborders of the Notoungulata. The possibility of such migration is shown by the discovery of an armadillo in the Middle Eocene of North America" (*op. cit.*, p. 590).

1904. Ameghino. In the "Liste des Figures distribuées par Ordres et par Familles" (p. 511) the following arrangement is adopted:

Ord. Protungulata. Fam. Caroloameghinidae [?Polyprotodont Marsupials].

Ord. Lemuroidea. Fam. Archaeopithecidae, Notopithecidae, Henricosbornidae, Adapidae, Microchœridae.

Ord. Simioidea. Fam. Homunculidae, Cebidae, Cercopithecidæ, Simiidae.

Ord. Hyracoidea. Fam. Acoelodidae, Archaeohyracidae, Adiantidae.

Ord. Typotheria. Fam. Protypotheriidae, Hegetotheriidae.

Ord. Toxodontia. Fam. Nesodontidae, Toxodontidae.

Ord. Hippoidea. Fam. Notohippidae, Equidae.

Ord. Condylarthra. Fam. Phenacodontidae [Didolodus, Notoprotogonia, Lambdaconus, etc.], Periptychidae [Argyrolambda, Josepholeidya, etc.], Pantolambdidae [Ricardolydekkeria, Guilielmofloweria, etc.]

Ord. Perissodactyla. Fam. Hyracotheriidae [Hyracotherium, Ectocion, Proectocion, etc.], Palaeotheriidae [Palaeotherium, Paloplotherium, Victorlemoineia, Anchitherium, Parahippus, Hypohippus, etc.], Proterotheriidae [Proterotherium, Thoatherium, Diadiaphorus etc.], Macrauchenidae [Theosodon, Scalabrinitherium, Macrauchenia etc.], Rhinoceridae, Tapiridae.

Ord. Artiodactyla. Fam. Suidae, Camelidae, Cervidae, Bovidae.

Ord. Proboscidea. Fam. Carolozittelidae, Pyrotheriidae.

Ord. Amblypoda. Fam. Pantostylopidae [Pantostylops, Hemistylops etc.] Trigonostylopidae [Trigonostylops etc.], Albertogaudryidae [Albertogaudrya etc.] Coryphodontidae [Coryphodon], Astrapotheriidae [Astrapotherium, Astrapothericulus, Astraponotus, etc.], Uintatheriidae [Uintatherium].

Ord. Ancylopoda. Fam. Isotemnidae [Isotemnus, Pleurostylodon etc.], Leontiniidae [Leontinia, Colpodon etc.], Homalodontotheriidae [Homalodotherium, Asmodeus etc.].

Ord. Tillodonta. Fam. Notostylopidae [Notostylops etc.], Tillotheriidae [Tillotherium], Exthonychidae [Exthonyx].

It is only gradually coming to be realized that parallel and convergent evolution have been largely influential in bringing about resemblances in the dentition and skeleton between the extinct South American hoofed mammals and those of the northern world. As shown in the classification quoted above Ameghino refers the Archæohyracidæ to the Hyracoidea, the Notohippidæ to the "Hippoidea," the Proterotheriidæ and Macrauchenidæ to the Perissodactyla, the Astrapotheriidæ to the Amblypoda etc. But the investigations of Lydekker, Roth, Gaudry (1906–1909), Scott, Sinclair and others have made it appear very probable: first that the extinct South American hoofed mammals belonged to peculiar southern groups which followed their own lines of evolution independently of the mammals of the rest of the world; secondly that in becoming adapted to a herbivorous diet they often "paralleled" the northern ungulates in many characters; thirdly that such adaptive characters are never associated in exactly the same combinations in northern and southern groups.

The memoirs by Professor Scott and Dr. Sinclair, now in progress, on the material collected by Hatcher in the Santa Cruz (?Miocene) beds, may be expected to deal definitively with many of the systematic and genetic problems of the South American ungulates; but meanwhile, for the purposes

of the present work, it seems advisable to attempt a preliminary brief review of the available evidence of their relationships with each other and with other orders. Among the sources of evidence on this subject examined by the writer may be mentioned: first a series of excellent casts representing many Santa Cruz and pre-Santa Cruz ungulates, which has been presented to the American Museum by the Museo Nacional de Buenos Aires through the courtesy of Dr. Fl. Ameghino; secondly the figures given especially by Ameghino, Lydekker, Roth, Scott and Sinclair; thirdly the observations and conclusions of these authors.

South American Condylarths (?) and Taligrada (?).

Resemblances between the dentition of different forms of unknown ordinal affinities are frequently apt to be misleading, as elsewhere noted (p. 108); but they are not always misleading and in the case of *Didolodus* and certain other genera (*e. g., Giulielmofloweria, Ricardolydekkeria*) from the Notostylops Beds, described by Ameghino (1904), the resemblances to the Condylarths and Taligrada of the northern hemisphere extend to certain details which seem to indicate affinity; and this indication is strengthened by considerable indirect evidence: *e. g.*, (1) the several plans of limb structure in the Toxodonts, Typotheres and Litopterns seem derivable (pp. 377, 379) from the conditions seen in the Condylarthra; (2) the skull of the primitive Litopterns suggests that of *Meniscotherium*; (3) the astragalus and calcaneum of *Trigonostylops* (Gaudry, 1906.1, fig. 48, p. 28) is of the Meniscothere type; (4) the astragalus and calcaneum of all the extinct South American ungulates seem to be modifications either of the typical Condylarth or of the Taligrade types.

The simple, sexitubercular bunodont upper molars of the ?Basal Eocene *Didolodus* and its allies may at first appear to bear little relation to the complex hypsodont molar patterns of the Santa Cruz ungulates, etc.; but an examination of the casts and figures already referred to shows that there are several morphological if not genetic intermediates between the two extremes, and that, as noted in detail below (pp. 376, 379), the molar patterns of Litopterns, Homalodotheres, Astrapotheres, Toxodonts and Typotheres may be analysed with some degree of confidence in accordance with the nomenclature of trituberculy (*cf.* Osborn, 1907, pp. 189–190). And it may be well to state in this connection that the writer does not give assent to the theory of trituberculy in certain of its implications; but nevertheless, after returning to test certain basal assumptions he feels convinced that all the extinct South American ungulate groups have been derived from forms in

which the upper molars still retained clear traces of the trigonal pattern, while the lower molars retained equally clear traces of the tuberculo-sectorial pattern.

Relations of the Homalodotheres and Astrapotheres.

As shown above Lydekker grouped "*Homalodontotherium*" and *Astrapotherium* in a single suborder and in support of this procedure there seems to be considerable evidence: *e. g.*, (1) Ameghino has figured a number of genera (*e. g., Albertogaudrya, Astraponotus, Astrapothericulus*) in which the upper molar pattern appears to connect the Homalodotheres with the Astrapotheres. (2) The hypsodont lower molars of *Albertogaudrya* have the trigonid short and the talonid long anteroposteriorly, and they suggest a common origin of the Homalodothere and Astrapothere types. (3) The upper molars of the Homalodotheres, Astrapotheres, Toxodonts and Typotheres are all broadly of the Rhinocerotic type, *i. e.*, with flattened ectoloph and large protoloph, no mesostyle, a crista. They also have a strongly developed protostyle and hypostyle. (4) The astragalus referred by Ameghino to *Albertogaudrya* is of the flattened type, which Gaudry (1906.1, p. 19) assigns also, on other grounds to *Astrapotherium.*

Against the association of Astrapotheres and Homalodotheres in a single suborder the following objections might be raised: (1) *Astrapotherium* is said to lack the dilated condition of the squamoso-periotic region; but even if it be shown that in *Homalodotherium* this region is slightly dilated, this will not prove that the two groups are very widely separated; and, partly on account of the variability of such inflation between different families in Marsupials and Rodents, the writer suspects that Dr. Roth has overestimated its significance in the South American ungulates. (2) In *Astrapotherium* the limbs are thought by Gaudry (1906. 1, p. 19) to have been rectigrade, whereas in *Homalotherium,* as figured by Ameghino (1898, p. 175), the feet end in large fissured ungues and were probably semi-plantigrade. But such differences, in the case of the Marsupials (compare *Diprotodon* and *Phalangista*) and of the Perissodactyls and Ancylopoda, are not inconsistent with ordinal relationships.

The astragalus of *Albertogaudrya* resembles the Amblypod type in so far as it has suffered a shortening of the neck, which has ended in the virtual disappearance of the latter and the bringing of the navicular facet below the tibial facet or trochlea; but this is probably an indication, not of ordinal affinity with the Amblypoda, but simply of the assumption of the rectigrade pose of the limbs, which in *Pyrotherium,* according to Gaudry (1909) likewise has resulted in the astragalus assuming the general type seen in the

Amblypods and Proboscideans. The astragalus of *Albertogaudrya* may thus have been derived as above described, from the type retained in the Miocene *Homalodotherium*, which in turn seems to be derived from the Condylarth, or in respect to its dorsal portion from the Periptychid, type.

The Homalodotheres probably represent a very old branch of the South American ungulate group, as suggested by the following considerations: (1) The oldest Patagonian formations (?Basal Eocene) yield certain genera, which are in some respects already highly specialized, but which, as argued above, probably belong to this group. (2) The Miocene (?) *Homalodotherium* retains the complete Placental formula in the dentition, and five digits in the manus and pes, at a time when most of the allied groups had undergone various reductions in the number of the teeth and feet.

The ungues of *Homalodotherium* (*cf.* Ameghino, 1898, figures on p. 175 *et seq.*) are large, compressed and clawlike, recalling those of the Ancylopoda, and also tending, as in that group to coalesce with the second row of phalanges. Apparently upon these grounds Ameghino (1898) refers *Homalodotherium* to the Ancylopoda; but evidence is adduced below (p. 399) to show that the resemblances in question probably indicate convergent evolution; and certainly in the palatal aspect the skull of *Homalodotherium segoviæ*, as figured by Ameghino (1898, p. 173, 1906, p. 317, fig. 134) differs in very important details from the skulls of the Ancylopod genera *Chalicotherium* and *Moropus*.

The Notostylopidæ.

The genus *Notostylops* of Ameghino gives its name to the oldest mammal-bearing horizon of the Patagonian series. Ameghino (1906) places this formation in the Middle Cretaceous but other eminent palæontologists (*e. g.*, Gaudry, 1908) are inclined to regard it as not older than Basal Eocene. As figured by Ameghino (1906, p. 346) *Notostylops* is seen to be specialized in respect to its enlarged median incisors (i^1), reduced i^2, i^3 and canine, and molariform p^3, p^4. The upper molars are becoming hypsodont; they have a flat ectoloph, a median valley, a more or less central protocone continuous with the protoconule, and a hypocone continuous with the metaconule; both conules in the slightly worn tooth connect with the ectoloph. These details are more clearly shown in certain less specialized molars of the same general type from the same beds (*e. g.*, *Acœlodus* Ameghino, 1906, p. 311). They have evidently been derived from a trigonal type possibly resembling in a general way that of the smaller Periptychidæ.

The pterygoid, glenoid and squamosal regions recall those of *Hyrax* and *Protypotherium*, the bullæ were much inflated. On the ground of very

superficial resemblances in the dentition Ameghino places the Nothstylopidæ near the Esthonychidæ, in the order Tillodontia; but it appears much more likely that they are connected more or less closely with the Albertogaudryidæ or Homalodotheriidæ.

The genera *Henricosbornia, Trigonostylops* and *Leontinia,* which are the types of as many families, are referred by Ameghino to different orders: the first (1904, p. 511) to the Lemuroidea, the second (1904, p. 523) to the Amblypoda and the third (1904, p. 525) to the Ancylopoda; but there seems to be some reason for suspecting that all are more or less nearly related to the common stem of the Homalodotheres and Astrapotheres.

The Typotheres and "Protypotheres."

The Santa Cruz forerunners (Interatheriidæ, Hegetotheriidæ) of the Pampaean Typotheres have been monographed recently by Sinclair (Mem. Princeton Expedition to Patagonia, Vol. VI, Pt. I, 1909), whose main results were published in 1908 (*op. cit.*). The frequently assumed relationship with the Rodents is shown by Sinclair (1908, pp. 75-76) to rest on probably convergent resemblances in the skull and dentition and to be associated with many deep seated differences. Sinclair also shows that the families in question differ radically from the Hyracoidea especially in the details of the carpus and astragalus, and it may be assumed provisionally that the points of resemblance to *Hyrax* are the result of parallel evolution, like the resemblances of Litopterns and Toxodonts to hippoids and rhinocerotoids; but at the same time it seems likely that in both cases the resemblances were conditioned by the fact that Hyracoids, Perissodactyls and South American ungulates were all alike derived from one order of protungulates (*cf.* pp. 410-411).

In the preliminary report Dr. Sinclair does not discuss further the relationships of the forms in question, but presents the data for the following observations and conclusions:

(1) *Protypotherium, Interatherium* and *Hegetotherium* preserve the complete Placental dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$.

(2) The pattern of the unworn upper molar of *Protypotherium* Sinclair (*op. cit.*, p. 73) is seen to be a hypsodont, antero-posteriorly elongate modification, of a simpler pattern, *e. g.*, such a one as is represented roughly in some of the older (Notostylops Beds) genera figured by Ameghino (*e. g., Acælodus oppositus,* 1906, p. 311). The protocone is connected with the parastyle, the protoconule with the "crista," which as in the Rhinoceroses (*cf. Hyrachyus*) is merely the constricted inner face of the paracone; the hypocone, metaconule and metacone form the "postero-internal crescent,"

while the hypostyle forms the "posterior pillar." The *Acœlodus molar* has in turn the familiar elements which appear in their simplest expression in *Hyracotherium* and *Ectocion*. This fact, with others, indicates that all the elements of the complex hypsodont molars of Typotheres and Toxodonts may be homologized with those of the Eocene Perissodactyls and Condylarths.

(3) In the unworn lower molars of *Protypotherium* (Sinclair, *op. cit.*, p. 74) the anterior limb of the posterior crescent lies externally to the posterior (metastylid) extension of the anterior crescent, as it does in *Hyrax*. In both cases the lower molar pattern while differing in proportion is fundamentally identical with the *Meniscotherium* type.

(4) The manus of *Protypotherium*, as figured by Sinclair (*op. cit.*, p. 71) is already specialized in the loss of the pollex, reduction of digit V and enlargement of digit II. It is, however, functionally tridactyl. The carpus differs from that of *Meniscotherium* in that the centrale is no longer free but is probably represented in the internal process of the scaphoid; the lunar has a broad contact with the unciform so that the cuneiform is widely separated from the magnum; the latter is small and polygonal in front view (it is large and quadrate in *Hyrax* and Condylarths). The emphasis of the interlocking features (p. 449) in the carpus may be connected with the hypertrophy of the second digit. The carpus as a whole is not high as it is in early Perissodactyls, but low and broad and in so far agrees with that of *Meniscotherium*. The ungual phalanges are dorsally compressed but expand somewhat on the plantar surface, much less so however than in *Meniscotherium*.

(5) The tarsus of *Protypotherium* (Sinclair, *op. cit.*, p. 70) is paraxonic, probably in correlation with cursorial habits; while that of the saltatorial *Hegetotherium* (*op. cit.*, p. 72) was markedly mesaxonic (Sinclair; compare the mesaxonic pes of the saltatorial *Dasyprocta*). In both families, however, the astragalus is weakly attached to the calcaneum, the neck diverging and the head widely separated by the navicular from contact with the cuboid. The latter feature is also seen in the Litopterns and may be an inheritance from the Condylarth conditions. The trochlea is narrow and very large in proportion to the neck. The fibula articulates with the calcaneum, as it does also in Litopterns. The navicular has a decided postero-internal prominence, analogous to that in many Rodents and Marsupials.

Conclusions. The evidence available from Sinclair's contributions permits us to infer with considerable probability some of the leading characters of the common ancestors of the Toxodonts, Typotheres, Interatheres and Hegetotheres. These were primitive Placentals with a complete dental formula, a clavicle, third trochanter, entepicondylar foramen and penta-

dactyl manus and pes. The general proportions of the skull were about as in *Meniscotherium, i. e.,* with face of medium length, large orbits, broad interorbital region and deep lower jaw. The palate probably terminated posteriorly in a pair of processes analogous to those in *Hyrax.* The tympanic very early became inflated and prolonged into a tubular meatus; the squamoso-periotic region also became inflated. The upper molars, at first brachyodont, with six cusps, and with prominent anterior and posterior cingula, became hypsodont and compressed; the premolars tended to become molariform; the anterior incisors became hypsodont, the lateral incisors and canines either became like the adjacent teeth or tended to disappear. The mandible originally had a moderately deep angle (*cf. Meniscotherium*) a feature emphasized with the increasing hypsodonty of the teeth, and procumbency of the incisors. To this factor may be ascribed: (1) the progressive increase of the antorbital slip of the masseter (*cf. Hyrax*), (2) the deepening and backward projection of the malar, (3) the broadening of the palate.

The cervical vertebræ had flattened articular faces on the centra. The dorsolumbar vertebral formula (20 in *Toxodon*) originally approached the Condylarth type (15 + 5) but secondarily rose to 15 + 7 (*Interatherium*) and 15 + 8 (*Pachyrukhos*). The tail was long and heavy (*cf. Protypotherium, Interatherium*) and the true sacrals were three in number. The carpus early lost the free centrale (which may have fused with the scaphoid) and widened the lunar-unciform contact (p. 449). The tarsus in general resembled the Condylarth type but very early developed the fibulo-calcaneal contact and lost the astragalar foramen. Such a family of mammals would fall under the Condylarthra as here understood (p. 383), but would probably be separated from *Meniscotherium* by the non crescentic character of the protoconule, from *Phenacodus* and *Euprotogania* by the more advanced condition of the molars.

The Litopterna.

Some of the smaller Litopterna such as *Diadiaphorus* and *Proterotherium* resemble the three-toed and one-toed horses not only in the general form of the skull and molar teeth but also in the predominance of the middle digit (III) and reduction or disappearance of the lateral digits. But in spite of these resemblances it seems highly probable that the Litopterns are only very remotely related to the Perissodactyls, for the following reasons: (1) the cervical vertebræ, in retaining flat terminal faces resemble the Typothere-Toxodont rather than the Perissodactyl type (Lydekker, 1893, p. 57); (2) in the detailed relations of the carpals and tarsals (pp. 449, 379) the Litop-

terns disagree radically with the Perissodactyls; (3) the premolars are simpler than in the contemporary hippoids and the molars retain clearer indications of derivation from the trigonal type.

The Litopterns appear to be separated subordinally from the Toxodont-Typothere group: (1) by the detailed characters of the carpals and tarsals; (2) by the characters of the molars, which are of hippoid rather than rhinocerotoid type and have a prominent mesostyle; (3) by the lack of inflation in the squamoso-periotic region.

More in detail, the evidence for the preceding conclusions in regard to the relationships of the Litopterna is as follows: (1) *Dentition.* In the most primitive dentition, that of *Proterotherium* sp. (figured by Osborn, 1907, p. 189) the molars have the familiar elements of the *Hyracotherium* molar, but differ from those of Eocene Perissodactyls in significant details, especially the lack of union of the proto- and metaconules with the ectoloph. The protocone also is centro-internal, as in the Periptychidæ. The Miocene Litopterns were thus less progressive in molar evolution than the Lower Eocene Hippoids. (2) *Feet.* The feet of the Litopterns, as figured by Ameghino (1898, pp. 162, 165) parallel those of the Equidæ in the reduction of the digits, first to three and then to one; but ordinal relationship with the Perissodactyla is excluded by the following detailed characters of the carpus and tarsus: In the tridactyl manus of *Theosodon* (*op. cit.*, p. 162) the carpus is serial, but of a peculiar type, inasmuch as the cuneiform touches the magnum, the lunar being thus separated from the unciform; all the bones are relatively wide and flat. In the tarsus the astragalus is widely separated from the small cuboid and the calcaneum has a large ridge for the fibula, both of which characters are seen also in the Typotheres. In the monodactyl *Thoatherium* (*op. cit.*, p. 165) one of the typical Litoptern "pseudo-horses," all the peculiarities of the carpus and tarsus of *Theosodon* are emphasized. The lunar is now widely separated from the unciform, while in the tarsus the navicular is widely separated from the cuboid, which is greatly reduced in size; the fibular facet on the calcaneum is pronounced. In all these features the "pseudo-horses" contrast with the Equidæ. Thus the characters of the carpus and tarsus in no case appear to indicate direct relationship with the Perissodactyla, and they are without doubt of higher phylogenetic significance (p. 110) than resemblances either in the number of digits and axis of symmetry or in the dentition.

The preceding conclusions might be criticised on the ground that while the "serial" tarsus and carpus of the Litopterns is held to disprove relationship with the Perissodactyls, the interlocking carpus of the early Typotheres is yet held to be consistent with derivation from the serial Condylarths. But this apparent inconsistency seems to be necessitated by the evidence.

The interlocking narrow carpus of the Perissodactyls, as we know them, is a very constant character (p. 393), while there is some reason to suppose that in the Condylarths the differentiation of the serial and interlocking types was at first almost nil, and long remained inconstant. It is of course understood that when the Typotheres, Litopterns, etc., are hypothetically derived from the Condylarthra it is meant only that the supposed common ancestors of the South American series would probably resemble *Euprotogonia* in some respects, *Meniscotherium* in others, and would thus fall within the order Condylarthra.

The Pyrotheria[1] (*Incertæ Sedis*).

Pyrotherium is not the least puzzling of the curious extinct Patagonian Ungulates. Its upper and lower cheek teeth are of the bilophodont type, that is, with two straight cross crests, and they are at first sight so much like those of the Miocene proboscidean *Dinotherium* of Europe that Dr. Fl. Ameghino (*e. g.*, 1902, pp. 223–224), the original describer of *Pyrotherium*, has regarded it as an ancestral proboscidean. It has also a single pair of procumbent lower incisor tusks which grew continuously and had the enamel band confined to the anterior surface, as in rodents and early proboscideans; while the manus ascribed to it by Ameghino, but later declared by M. Tournouër to belong to *Astrapotherium*, certainly resembles in most characters the proboscidean type.

Fragmentary remains of the genus under consideration are characteristic of the so-called "*Pyrotherium* beds" of Chubut and Deseado. The age of these beds is very differently estimated by the leading authorities. Ameghino places them in the uppermost Cretaceous, but the majority of northern paleontologists, including M. Gaudry, are unwilling to concede that the *Pyrotherium* beds are older than the Middle Eocene.

M. Gaudry's material, although by far the most complete so far collected, still leaves us with a very imperfect knowledge of the skull and feet; but it includes specimens in an excellent state of preservation of the following parts: the upper and lower jaws, with the milk and permanent dentitions, the atlas, axis, a cervical vertebra, a lumbar, a caudal, the lower part of the scapula, and a part of the ilium, a sternal bone, and fore and hind limbs complete except for the manus and pes, which are represented only by a lunar, cuneiform carpi, astragalus and cuboid.

M. Gaudry's observations upon the special characters of *Pyrotherium* may be summarized briefly as follows: The dentition differs in important

[1] The following section is partly quoted from a review by the writer (1909) of the late Professor Gaudry's memoir on *Pyrotherium* (1909).

details from the proboscidean types (including *Mœritherium*): for instance, the mode of wear of the cheek teeth is entirely different, the premolars are different, the milk teeth are different, the section of the procumbent lower tusks shows no suggestion of the peculiar proboscidean "engine turning." The palate is very narrow, the orbit is placed above the fourth premolar. The atlas and axis differed widely from the proboscidean type, the atlas not being pierced by the vertebral artery and having a prominent median hypapophysis, the odontoid of the axis being very large and short and supported on the enormous anterior border, while the neural tunnel in both bones is very circumscribed. The head was probably pointed downward and M. Gaudry ventures the hypothesis that the beast had the proportions of a gigantic cavy with bent fore limbs, but post like hind limbs. A cervical vertebra is flattened, as in *Arsinoitherium* and the Proboscidea, but the lumbar vertebræ differ from the latter type. The most striking contrast with the Proboscidea lies in the forearm. The scapula has the spine turned forward instead of backward, the coracoid process is very long and prominent, the glenoid greatly extended. The massive humerus is extremely broad with very stout ento- and ecto-condylar and deltoid crests, large tuberosities and an enormous head. The radius and ulna are very stout but absurdly short. M. Gaudry concludes from a study of the muscular attachments that the very powerful forearm may have been used in digging. The lunar and pyramidal (cuneiform) resemble those of *Elephas*, but are narrower. The acetabulum, as in the elephants, faced downward rather than outward. The straight hind limb had a long femur held almost in line with the tibia; the astragalus was greatly flattened and the navicular facet was directly below the tibial facet, and this indicates that the foot was strictly rectigrade, *i. e.*, with the digits in line with the tibia. To compensate for the relative immobility of the pes the knee joint could double up at a very sharp angle.

Upon this material M. Gaudry bases the important conclusion that *Pyrotherium* is not an ancestral proboscidean, and that all its resemblances to members of that order result from the assumption of bilophodont cheek teeth and post-like, rectigrade hind limbs; that these resemblances are accompanied by more numerous and fundamental differences, and that, in brief, *Pyrotherium* is not closely related to any other of the great "pachyderms" of different orders, such as *Astrapotherium, Dinoceros, Arsinoitherium, Brontotherium* etc., and does not fit into any known order.

The supposed relationship of *Pyrotherium* with the Proboscidea being thus at least temporarily disposed of, it seems not impossible that the most likely point of origin lies somewhere near the Homalodotheria, or rather in the protungulate ancestry of that group. To judge by analogy with

many similar cases *Pyrotherium* has been derived from smaller forms with tapiroid molars (*cf. Carolozittelia* Ameghino), and such tapiroid molars in several other cases (*cf.* Gregory, in Osborn, 1907, p. 171, footnote) have been evolved from quadritubercular molars with transversely ridged proto- and metaconules, *i. e.*, from a type nearly realized in the Patagonian protungulate genus *Didolodus*. The flat Amblypod-like astragalus of *Pyrotherium* is more or less closely paralleled by that of *Albertogaudryia, Asmodeus* and several other Patagonian genera which the writer regards (p. 384) as belonging in the suborder Astrapotheria. The peculiar form of the distal end of the humerus is to some extent suggested in the more normal humerus of *Homalodotherium* (*cf.* Gaudry, 1906.1, p. 36, figs. 23, 24).

The extinct South American Ungulate groups not related to the Rodentia, Artiodactyla, etc.

The Condylarthra or Condylarthra + Taligrada appear, in short, to be the only probable known source for the orders in question. Relationship of the Protypotheres with the Rodents appears to be extremely remote (Sinclair), notwithstanding the Hare-like adaptations of some of the "Protypotheres" (*e. g., Pachyrukhos*). Relationship even with the earliest known Primates appears to be excluded by obvious differences in the skull, dentition and limbs. While remote relationship with some of the Paratheria (Edentates) is not definitely contradicted, derivation from that group appears highly improbable.

Finally, near relationship with the Artiodactyla appears to be negatived by the following considerations: (1) The earliest known Typotheres differ radically from the Artiodactyla in the characters and relations of the astragalus. In the Litopterna the astragalus of the typical forms is, as stated above, very widely separated from the cuboid; however the astragalus ascribed to *Thoatherium minusculum* by Ameghino (1906, p. 342) has a narrow facet in the position of the cuboid facet.

Some at least of the Nesodonts, as figured by Gaudry (1906.1, p. 29), developed a large cuboid facet on the astragalus, but since this character appears late among the South American orders, it may be regarded as an instance of convergent resemblance to the Artiodactyla and Rhinoceroses. The Typotheres and Litopterns are likewise distinguished by the precocious molarization of the premolars, in wide contrast to the very delayed and imperfect molarization of the premolars in Artiodactyls.

Assuming the correctness of the view that the extinct South American hoofed mammals are not directly related to the Perissodactyls, Hyracoids,

Proboscidea, Amblypoda, etc., and have been derived independently of these but from the same ancestral order of protungulates, it follows that the numerous resemblances in special characters between southern and northern forms are due to similar adaptations occurring in the divergent descendants of similar and more closely related ancestors. This confusing mixture of homological and analogical resemblances deprives of permanent value all attempted classifications and phylogenetic conclusions which are based upon isolated points of resemblance between northern and southern groups, in respect either to the dentition or to the feet.

Summary.

The foregoing views on the interrelationships of the extinct South American ungulates are summarized in the subjoined table, which is doubtless very imperfect, since it deals only with the better known forms; but it may, perhaps, serve as a trial hypothesis.

I. Order PROTUNGULATA (Condylarthra). Upper molars bunodont, sexitubercular, with mesostyle. Paracone and metacone rounded externally. Astragalus and calcaneum, so far as known, approximating to the Euprotogonia (Phenacodont) type.
   1. Quadrangular arrangement, hypocone very prominent, *e. g.*, *Didolodus, Notoprotogonia.* (?Condylarthra).
   2. Triangular arrangement, hypocone and protostyle subequal, *e. g.*, *Guilielmofloweria, Ricardolydekkeria* (?Taligrada, *i. e.*, Peripty-chidæ or Pantolambdidæ.)

II. Order NOTOUNGULATA. Upper molars when known more or less rhinocerotic: *i. e.*, progressively hypsodont, with flattened ectoloph, a long protoloph, smaller metaloph, a crista, proto- and hypostyles, no mesostyle. Lower molars with talonid typically much longer than trigonid. Carpus (when known) alternating (*i. e.*, lunar touching unciform). Structure of limbs and feet various.
   1. Suborder Homalodotheria. Astragalus (*Homalodotherium*) retaining distinct neck and rounded head, trochlea flattened not compressed; digits (*Homalodotherium*) 5–5. Complete Placental dentition ($\frac{3.1.4.3}{3.1.4.3}$) in typical forms. Incisors and canines (when known) subequal.
      ?*a*. Size small; molars brachyodont; protoloph well developed, metaloph beginning, hypocone prominent, *e. g.*, *Henricosbornia.* (Referred by Ameghino to the Lemuroidea.)
      ?*b*. Size medium; molars subhypsodont, roundly trigonal, ectoloph flat, rather straight, protoloph prominent. Astragalus

and calcaneum approximating the *Meniscotherium* type (in *Trigonostylops*). *e. g., Trigonostylops, Notostylops.*

c. Size large; molars subtriangular. Astragalus with trochlea flattened but wide, head small, convex, neck oblique. Ungues compressed, fissured. *Homalodotherium.*

?*d.* Molars more quadrangular, partly suggesting those of *Astrapotherium. Leontinia.*

?*e.* Molars approximating the *Leontinia* type; astragalus and calcaneum approximating the Nesodont type, *Colpodon.*

2. Suborder Astrapotheria. Astragalus probably flattened, *i. e.*, losing head and neck. Fibular facet on calcaneum probably reduced (Gaudry). Limbs rectigrade (Gaudry). Squamoso-periotic region not inflated; zygomatic arch not extending to top of occiput. ? Canines enlarged.

?1. Molars moderately hypsodont, suggesting partly the Homalodothere type: *e. g., Albertogaudrya.*

2. Molars approximating the *Astrapotherium* type: *e. g., Astraponotus.*

3. ?Canines tusk-like, molars very hypsodont, premolars small. *Astrapotherium.*

3. Suborder Toxodontia. Astragalus with distinct neck and convex head, trochlea more or less compressed. Fibular facet on calcaneum prominent. Squamoso periotic region inflated. Zygomatic arch extending backward to top of occiput. Median incisors often enlarged as cropping teeth, canines often reduced, never tusk-like. Premolars well developed. Upper molars curving more or less inward above and outward below; with strong crista and large protostyle and hypocone, flanking the centrally placed protocone.

1. Digits 4–4. Interatheriidæ, Hegetotheriidæ.

?2. " ?–? Archæohyracidæ.

3. " 5–4. *Typotherium.*

4. " 3–3. Nesodontidæ, Toxodontidæ.

III. Order LITOPTERNA (?derived from I). Upper molars more or less hippoid, *i. e.* buno-lopho-selenodont, with mesostyle; brachyodont to hypsodont. Lower molars with subequal trigonid and talonid. Feet unguligrade. Carpus a modification of the serial type (lunar separated from unciform by cuneiform-magnum contact). Tarsus with distinct fibulo-calcaneal facet; astragalus becoming hippoid, *i. e.*, with broad transversely convex head (navicular facet). Digits long, tri- to monodactyl. Squamoso-periotic region not inflated; zygomatic arch not extending on top of occiput. Fam. Proterotheriidæ, Macraucheniidæ.

IV. Order PYROTHERIA. Molars bilophodont, tapiroid to Dinotheroid. Limbs rectigrade. Astragalus greatly flattened.
1. Molars tapiroid. *Carolozittelia.*
2. " Dinotheroid. *Pyrotherium, Propyrotherium.*

IX. THE PERISSODACTYLA.

The question of the derivation of the Perissodactyls as an order and of their relationship to the Condylarthra is still open. Cope saw in *Phenacodus* the atavus of practically all the hoofed orders. Osborn holds the contrary opinion that *Phenacodus* is a hoofed offshoot of the Creodonta and a member of the Meseutheria, or small brained Cretaceous-Basal Eocene orders, and that the Perissodactyls have sprung from some entirely unknown "Cæneutheria" (p. 457).

Still another view may be adduced: that although neither *Phenacodus* nor *Euprotogonia* were the ancestors of the Perissodactyla yet they resemble those forms more nearly than do any other known mammals; and that the Basal Eocene ancestors of the Perissodactyla would, if discovered fall under the superorder Protungulata as defined above (p. 383).

Supposed relations with the Artiodactyla.

The frequently assumed relationship of the Perissodactyla with the Artiodactyla is treated in a general way in the section on the Artiodactyls (p. 400) but it seems desirable to touch here upon a particular phase of the question, namely, the supposed Artiodactyl characters of the Oligocene Titanotheres. These characters were noted by Osborn (1893, p. 94 and 1895, p. 350) as follows: (1) the dorso-lumbar formula of 20 (Osborn); (2) the four-toed manus, which superficially resembles that of *Hippopotamus*; (3) the buno-selenodont molars which, especially in some genera of the Palæosyopidæ resemble those of the Artiodactyl *Anoplotherium.* To these may be added: (4) the large size of the cuboidal facet of the astragalus; and (5) the reduction of the third trochanter of the femur.

Now that the general phylogeny of the Titanotheres has been cleared up by Osborn in various publications (1896, 1902, 1908) it is plain that the characters given above, with the exception of the first, have all been acquired within the Titanothere phylum and therefore constitute no evidence of close relationship with the Artiodactyls.

(1) The 20 dorso-lumbars may be simply a primitive Placental character which only the Titanotheres among the Perissodactyls have retained

Moreover in the Oligocene Titanotheres the number of dorsals, 17, is much higher than in typical Artiodactyls (12–14), and in the Upper Eocene *Dolichorhinus* (Osborn, 1908, p. 612) the number seems to be 15, as in *Phenacodus*.

(2) The broad, spreading, four-toed manus is an adaptation to great weight, as it is also in *Hippopotamus*. The spreading of the digits and of the carpals, especially of the magnum, may be traced with considerable probability within the Titanothere phylum. The detailed characters of the carpals in the side and back view is very different in Titanotheres and Artiodactyls.

(3) The large size of the cuboid facet of the astragalus is another progressive Titanothere character, and is equally an adaptation to weight, which never attains the development that it does in the Artiodactyls.

(4) The reduction of the third trochanter is likewise progressive, and it is concomitant with the lengthening of the femur and relative shortening of the tibia and fibula.

(5) The simple buno-selenodont molars alike in Titanotheres and Artiodactyls result from the reduction and final disappearance of the proto- and metaconules. This character is accompanied by radical differences between the two orders in the premolars, which are often better indicators of ordinal separation than the molars.

Relatively close relationships of the Lower Eocene Titanotheres to other Perissodactyls.

The general relationship of the Titanotheres to other Perissodactyl phyla and the relatively close interrelationship of all the Perissodactyl families in the Lower Eocene may be made clear in the following remarks on the Lower Eocene (Wind River) genus *Lambdotherium* Cope, the systematic position of which was long in doubt. Osborn and Gregory (in Osborn, 1909, p. 599) have shown: (1) that this animal (which was about the size of a coyote), was an early member of the family Titanotheriidæ, (2) that in many features it is prototypal to the later Titanotheres, with which it is linked structurally through the genera *Eotitanops* and *Mesatirhinus* of Osborn.

As compared with other Eocene Perissodactyls its Titanothere affinities are revealed in the following characters:

(1) Its skull, judging from the lower jaw, must have been larger and heavier than that of the earliest representatives of the Tapiridæ, Equidæ or Rhinocerotidæ.

(2) The canines were relatively stout (*cf.* Palæosyopinæ).

(3) The upper premolars, especially p^4, are of the *Mesatirhinus* type

and differ in significant details from those of other contemporary Perissodactyls.

(4) The upper molars, as compared with those of the contemporary Perissodactyls, approach those of *Eotitanops* in respect to the strong development of the mesostyle, the V-shaped paracone and metacone, and the separation of the protoconule ridge from the protocone.

(5) The lower premolars and molars are of the Palæosyopid type, the molar cusps being arranged in a M, from which they differ only in more primitive characters; and they also contrast in details with those of the other Perissodactyls.

(6) The humerus, radius and ulna, so far as known, agree in essentials with those of *Eotitanops*.

(7) The manus is like that of *Eotitanops*, only still narrower. It differs from the manus of *Eohippus* in the relative height of the carpals, prominence of the hook of the scaphoid, wedge-shaped lunar, broader unciform, relatively smaller digit III, etc. It differs from the manus of *Heptodon, Hyrachyus*, etc., in other details.

Nearly all the known characters in which *Lambdotherium* differs from the later Titanotheres serve to ally it with the Lower Eocene forerunners of the Equidæ, Tapiridæ and Rhinocerotidæ. For example, the incisors are compressed antero-posteriorly, the jaw is constricted back of the canines, and the premolars and molars approach the Lower Eocene Perissodactyl type in respect to the relatively large size and incipiently ridged condition of the proto- and metaconules and in the form of all the remaining cusps. The forearm and manus, which are the chief remaining parts known, were also of the Lower Eocene Perissodactyl type, which is clearly distinguishable from that of contemporary Condylarths and Artiodactyls. From certain fragments of the skull, and from the known characters of *Limnohyops priscus* Osborn (1909, p. 601), a primitive Middle Eocene Titanothere, it is legitimate to infer that *Lambdotherium* shared with other early Perissodactyls (*e. g., Eohippus, Systemodon, Isectolophus*) the following skull characters: very broad forehead; large face; small cranium with postorbital constriction; high narrow occiput with low sagittal crest; nasals pointed, not reaching to end of premaxillaries.

Principal characters of the stem Perissodactyla.

The phylogeny and natural classification of the various families of Tertiary and Recent Perissodactyls is better known than is the case in many other orders; first, because the principal evolution of the group took place during the Tertiary period; secondly, because its center of dispersion lay

in some unknown region, whence a long series of forms were driven into the localities in Europe and North America where conditions for preservation and discovery have been most favorable. The numerous lower Tertiary forms have been described chiefly by Cuvier, de Blainville, Owen, Leidy, Cope, Marsh, Osborn and Wortman and form the basis of many important evolutionary writings. The evolution of the Tapiridæ has been treated by Wortman (1893) and Hatcher (1896), of the Lophiodontidæ by Stehlin (1903–1906) and Depéret (1901) who have also revised the European Eocene hippoids and Palæotheres (Depéret, 1901) while Wortman (1896) and Granger (1908) have revised the American Eocene hippoids. The evolution and phylogeny of the Rhinoceroses (including the Amynodonts and Hyracodonts) have been treated in a series of studies by Osborn (*e. g.*, 1898, 1900), who also has long been engaged in monographic revision of the Titanotheres and Horses. The interrelations of the families themselves have been treated principally by Kowalevsky (1873), Schlosser (1886) and Osborn (1898) and the superfamily classification adopted by the latter author has been widely accepted (*cf.* Weber, 1904, pp. 614–615).

All these researches have supplied abundant data for a reconsideration of the genetic relations of the order as a whole. The published figures and descriptions show that the Lower Eocene representatives of the Tapirs, Horses, Palæotheres, Titanotheres, Lophiodonts and Rhinoceroses had not gone very far in acquiring the special characteristics of their descendants. At any rate, the differences, for example, between *Systemodon*, of the Tapiridæ, *Heptodon* of the Lophiodontidæ, *Lambdotherium* of the Titanotheriidæ and *Eohippus* of the Equidæ are *relatively* small and indicate that the various Perissodactyl families could not have been distinguished in the Upper Cretaceous. If then the chief characters of these unknown stem Perissodactyls may be inferred from those of their Lower Eocene descendants, the question of the genetic relations of the order will be greatly simplified.

This problem has long engaged the attention of the writer who has had the pleasure of assisting Professor Osborn in the investigation of the Titanotheres, and in that connection has studied the authors cited above as well as the described Perissodactyl material which is on exhibition in the American Museum of Natural History. Special attention has been given to the genera *Eohippus, Palæotherium, Systemodon, Lambdotherium, Eotitanops, Isectolophus, Trilopus, Hyrachyus, Heptodon* and *Lophiodon,* which are all primitive in some characters and which are represented by fairly adequate material. By projecting backward the known trends of evolution in the different families from the vantage ground furnished by the above mentioned genera, we can assign certain characters to the unknown stem Perissodactyls with considerable assurance of probability, as follows:

Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$ Preserved in most Lower Eocene Perissodactyls. Taken in connection with the form of the teeth and many other characters it is a significant indication of derivation from the stock which gave rise also to the Insectivores, Creodonts and Condylarths.

Canine stout, piercing; *incisors* in a transverse or partly elongate row: crowns convex anteriorly, flattened posteriorly. Indicates derivation from omnivorous Creodont-Condylarths; canines possibly preserved as fighting weapons.

Premolars similar to the *Euprotogonia* type, namely: p^4 triangular; with proto-, deutero- and tritocones, protoconule, metaconule and strong surrounding cingula; p^3 simpler, p^2 compressed, p^1 conic.

Upper molars similar to the *Euprotogonia* type but protoconule and metaconule becoming lophoid, paracone and metacone rounded (*cf. Hyracotherium leporinum*).

Lower cheek teeth much as in *Euprotogonia* but with the paraconid smaller.

The dentition of the stem Perissodactyl thus resembled the *Euprotogonia* type more closely than any other and taken in connection with so many other characters throughout the skeleton this dental resemblance to *Euprotogonia* is significant of common origin.

Diet. Possibly succulent tender herbage, berries, tubers, etc. Some vestiges of the former animalivorous habits may have persisted. Even the modern Peccaries, while relying chiefly on fruits and roots, "are by no means adverse to varying their diet with carrion, worms, or insects" (Lydekker).[1]

Brain case intermediate in width between that of *Euprotogonia* and that of *Eohippus*. Because the brain of even the oldest Perissodactyls was larger than that of the Condylarths, it might be objected that the former were therefore derived from some entirely unknown relatively large brained "Cæneutherian" stock (p. 458); but the remarks made above (p. 310) touching the increase in size in the brain in the Carnivores seem to apply equally well here. The large brained Perissodactyls are known to run back into much smaller brained forms in the Lower Eocene and the Basal Eocene Perissodactyls may reasonably be inferred to have had still smaller brains, but for lack of material this cannot be stated positively. Even among the Condylarths there was considerable variation in the size of the brain, the brain case of *Meniscotherium* being relatively broader than that of *Phenacodus*. It is not denied that the ancestral Perissodactyl had a larger brain case and better brain than *Euprotogonia*. It is merely inferred that there was a considerable variation in brain characters in the Condylarthra and that the Perissodactyls sprang from some unknown, possibly Asiatic, larger

[1] The New Natural History. Vol. II, p. 443.

brained form, which in all its dental and skeletal characters would fall under the Condylarthra as here defined.

Muzzle heavy, forehead very broad. This is a universal character of the Lower Eocene Perissodactyls and is a direct inheritance from the Condylarth condition.

Post-orbital constriction rather marked. Another very primitive (Condylarth) and strongly marked character (seen especially in *Eohippus*). Its meaning is that the small brain was still largely confined to the parietal segment and that the anterior portion of the cerebrum, *i. e.* the frontal lobes, had not yet broadened and pushed forward against the anterior wall of the brain case.

Face larger than cranium. Seen in *Eohippus, Isectolophus, Hyrachyus* and others (*cf.* Condylarthra).

Skull moderately dolichocephalic, i. e., about as in *Eohippus* and *Isectolophus* (*cf.* Condylarthra).

Occiput high and narrow. Seen in *Eohippus, Heptodon* and others. Occipital crest slender not flaring (*cf. Phenacodus wortmani*).

Zygomata slender (as in *Eohippus*) (*cf. Phenacodus wortmani*). The very stout zygomata, high sagittal crest and flaring occipital crest in the Middle Eocene *Palæosyops* are possibly a secondary result of extreme brachycephaly and heavy jaws and canines. Zygomatic process of maxillary extending outward below malar.

Orbit bounded by small post-orbital processes both on frontals and malars.

Proportions and relations of *premaxillaries, maxillaries, lachrymals, nasals* and *frontals* probably much as in *Euprotogonia.* In the orbital region, maxillaries overlapping nasals and overlapped by frontals and lachrymals; in the lateral aspect, a slight anterior narial sinus above maxillaries. Nasals not reaching forward quite as far as the premaxillaries (*Eohippus, Isectolophus,* the most primitive Titanotheres, etc.), *cf. Phenacodus wortmani.* Lachrymal with small tubercle, spreading out on the orbit internally, partly extending on face, duct marginal to internal.

Ascending ramus of mandible and coronoid, large; areas for temporal and masseter muscles relatively large (*cf.* Condylarthra).

Cranial foramina conforming strictly to the Condylarth-Creodont plan: *i. e.,* optic and rotund foramina distinct from the foramen lacerum anterius; an alisphenoid canal; large foramen ovale piercing alisphenoid at some little distance back of the alisphenoid canal and just internal to the glenoid fossa; postglenoid foramen not conspicuous; sphenopalatine foramen normal; median and posterior lacerate foramina confluent, owing to the small size of the petrosal and tympanic, which had not coälesced. Osseous au-

ricular meatus (arch) wide and well defined by large *postglenoid* and *post-tympanic processes* of the squamosal; the latter confluent with the downward extension of the mastoid and this in turn with the downwardly directed paroccipital process of the exoccipital. *Mastoid* a wedge-like bone showing on the oblique postero-external corner of the occiput. Post-mastoid foramen present.

The preceding skull characters may confidently be assigned to the stem Perissodactyl and are all inherited from an Insectivore-Creodont-Condylarth plan.

Vertebræ in essentials similar to those of *Phenacodus*. Atlas with parapophysis pierced by vertebraterial artery. This character is lost in the Oligocene Titanotheres (Osborn). Axis with peg-shaped odontoid. Pleurapophysial flange of sixth cervical vertebra very broad, obliquely placed. Lumbars with transverse processes directed slightly forward. Sacrals at first probably of Creodont-Condylarth type, namely, transverse process of anterior sacral widely expanded and forming the chief support of the pelvis, those of second and third sacrals rapidly narrowing. Later the second and third sacrals became broader and shared in the iliac attachment, at the same time the transverse process of the fourth, fifth and sixth sacrals broadened but in decreasing degrees, producing the characteristic Perissodactyl type of sacrum. Dorso-lumbar formula possibly 20 or 21 (15 or 16 + 4–6). In correlation with the increasing size of the viscera and thorax, the number of rib-bearing vertebræ increase. The primitive Condylarth number (19–20) is retained only in the early Titanotheres (Osborn), in the remaining families the number has increased as follows: *Tapirus* 18 + 5, *Rhinoceros* 19 or 20 + 3, *Equus* 18 + 5—19 + 6 (Flower, p. 83). Tail very early becoming lighter than in the Condylarth-Creodont stem.

Scapula rather high and narrow, round topped, prespinous fossa narrow at top, anterior border above neck with sharp convexity. This type is readily derived from the scapula of *Phenacodus*. It gives rise to various modifications, in the horses paralleling the Artiodactyl type, in the Titanotheres the Proboscidean type.

The *humerus* has progressed beyond that of any known Condylarth in its cursorial adaptations. Even in the earliest Perissodactyls there was no entepicondylar foramen and the entocondyle itself was reduced, the supinator crest small, the capitellum for the radius transversely extended (more than in *Phenacodus*) and the radio-ulna trochlea flatly convex. The head of the *radius* was transversely expanded and there was a decreasing power of supination, the hand becoming more sharply pronated, even when extended forward.

Pelvis. The ilium, even in the Creodonts, had already lost its primitive

trihedral character by the outgrowth of its external ridge and the flattened spatulate character of its postero-superior glutæal surface. In *Phenacodus* this external ridge was already produced into a long sickle-shaped surface. In the ancestral Perissodactyl the ridge was probably not pointed at the tip but slightly expanded and flattened while the internal superior border of the ilium was produced inward and upward above the level of the sacrum. These two ridges, the internal and the external, caused the ilium in oblique postero-superior view to be ⅂-shaped, the antero-superior border being concave. This type of ilium is preserved in the primitive cursorial types *Eohippus* and *Hyrachyus* but is lost in the very heavy slow moving types. The pubo-ischiadic part of the pelvis was somewhat smaller than in *Phenacodus* and much shorter and less stout than in the Mesonychidæ and Artiodactyla.

Femur. The shaft was slightly flattened and retained a moderate third trochanter, which was perhaps placed higher up on the shaft than in *Phenacodus.*

The *manus and pes* of the ancestral Perissodactyl had already advanced beyond the Condylarth stage. In the manus the pollex was much reduced, in the pes the hallux disappeared very early and the fifth digit was greatly reduced. The functional digital formula was thus 4–3, as it is in all Lower Eocene Perissodactyls. The middle digit was the longest, especially in the pes, the proportions of the several digits were approximately as in *Tapirus* but the manus was very likely narrower. The manus in all known Lower Eocene Perissodactyls was very narrow, with a rather high carpus and there is good reason to believe that this is an inheritance from unknown small sized cursorial ancestors. No truly cursorial Creodont or Condylarth known has a broad manus. The broad manus of later Titanotheres, Palæotheres, Lophiodonts, Rhinoceroses, etc., is very probably a progressive adaptation to increasing weight.

The Perissodactyl character of the feet may be more directly derived from the Condylarth than from the Creodont condition. In none of the Creodonts does the tendency to tridactylism become nearly as pronounced as it does in *Phenacodus,* where both in manus and pes the digits are symmetrically arranged on either side of the third. *Phenacodus* itself, of course, is not ancestral to the Perissodactyls and may be more Perissodactyl-like than its own ancestors; but the development of perissodactylism in both orders argues a similar type of foot in the ancestors of each, a type of foot which is not reached in the more remotely ancestral Insectivore-Creodont stock. The perissodactylism of the Litopterns offers no obstacle to this reasoning, for they themselves were probably also derived from Condylarthra (p. 448).

The *carpus* (see also p. 450) of the ancestral Perissodactyl differed sharply from that of *Phenacodus* in that it was not altogether serial but *partly* displaced or interlocking in type: *i. e.*, with the scapho-centrale touching the small magnum, the lunar resting not only on the magnum but *partly* on the unciform (see p. 446). This condition is shown in all the known manus of Eocene Perissodactyls, representing the earlier types of each family. Formerly when *Phenacodus* itself was held to be ancestral to the Perissodactyls it was easy to believe that the so called displaced type of carpus in the early Perissodactyls was secondary. But evidence was adduced by Matthew (see p. 446 below) that the serial carpus of *Phenacodus* is itself secondary, since the manus of *Euprotogonia* retains the lunar-unciform contact; and in the present work it is shown (pp. 442–446) that the lunar-unciform and scapho-centrale-magnum contacts are characteristic of many of the lowest pentadactyl unguiculates and persist into the orders Creodonta, Amblypoda, Primates, Artiodactyla, Litopterna, etc.

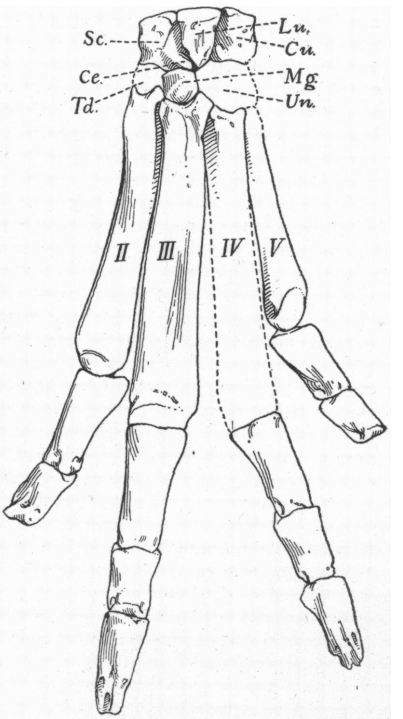

Fig. 23. Left manus of a Lower Eocene Tapiroid (Lophiodont) *Heptodon calciculus* Cope (Amer. Mus. No. 294). *Ce.*, hook of the scaphoid, formed by the coalesced centrale. In the back view the lunar is seen to rest almost equally on the magnum and unciform × ⅔.

It is not intended to imply that the carpus in the ancestral Perissodactyl was of the fully "displaced" type (p. 451). In the Lower Eocene "Lophiodont" *Heptodon calciculus* (Fig. 23) the lunar-unciform contact, while very considerable in front view, is narrower in rear view; and in the Rhinoceros line it is easy to follow the progressive broadening of the scapho-centrale-magnum and lunar-unciform contacts, through *Hyrachyus* and *Cœnopus* to the widely displaced type in *Rhinoceros*.

The *magnum* of the ancestral Perissodactyl in front view was small and compressed but in side view was large and shaped like a shoe, the toe pointing downward, the sole backward (Fig. 24). The strong flexor carpi muscles were attached to the sole of this shoe, while the rand or part above

the heel was keeled for the support of the lunar on one side and of the scapho-centrale on the other. These characters of the magnum are strongly marked in all the Lower Eocene Perissodactyls examined and sharply separate the latter from *Phenacodus* in which the toe of the magnum is at most represented by a blunt low process. Most of the later Perissodactyls retain this "toe" in a more or less modified condition, but in *Lophiodon* as figured by Depéret (1903) it is wanting. It is also developed to some extent in the Artiodactyla (*e. g., Oreodon*) but is there shaped quite differently.

The *unciform* was inclined somewhat upward and this condition in-

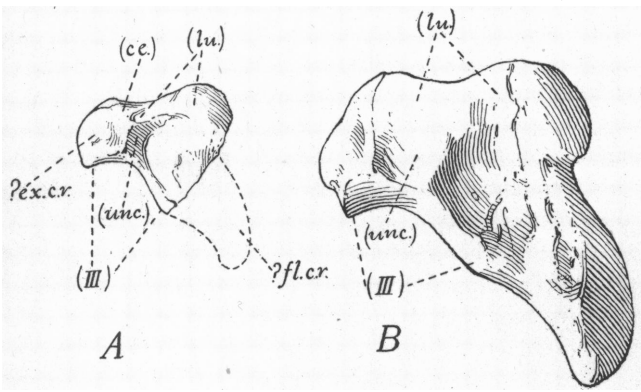

Fig. 24. Left magnum of two Lower Eocene Perissodactyls, *Heptodon calciculus* (Cope) Amer. Mus. No. 294, × ⅔ and *Eotitanops borealis* (Cope) Amer. Mus. No. 296. × ⅔. The small end faces anteriorly, the bones are seen from the outer side.

? ex. c. r., tuberosity for ? extensor carpi radialis.
?fl. c. r., " " ? flexor " "
(*ce.*), facet for hook of the scapho-centrale.
(*lu.*), " " lunar.
(*unc.*), " " unciform.
(III) " " metacarpal III.

creased with the broadening of the lunar-unciform contact; the unciform had a prominent process on its postero-external face.

The *lunar* was wedge-shaped distally, with an oblique anterior facet for the magnum. The centrale was very early fused with the scaphoid, forming the so called "hook of the scaphoid" in Rhinoceroses.

The successive overlap of the *metacarpals* II–IV on the external proximal ends was an inheritance from the Insectivore-Creodont stock and due originally to the fact that the magnum and trapezoid were shallow small bones which caused their attached metacarpals III and II to appear as if thrust up into the carpus above the lower level of the unciform and trapezium. The distal ends of the metacarpals were without keels and were neither

globular nor flatly-covex but perhaps more or less intermediate in character. The *ungual phalanges* were depressed, pointed and slightly fissured distally.

From the preceding notes it appears that even in the stem Perissodactyls the lunar (since its bluntly wedge-shaped distal end received the thrust of both unciform and magnum, and its sides received the thrusts of the scaphoid and cuneiform), formed the main keystone of the carpus (Fig. 25). The interlocking carpus of any ungulate consists, in fact, of a complex series of keystones which receive the weight and impact from the fore arm above and the ground below.

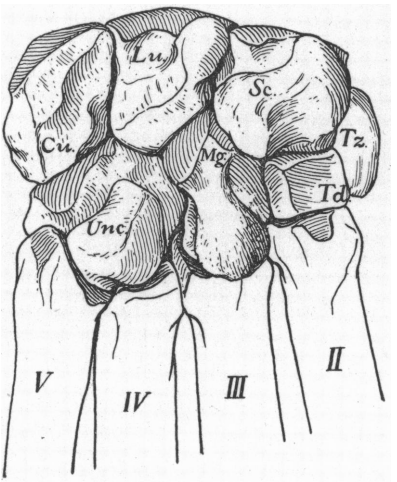

Fig. 25. Back view of the carpus of an Eocene Titanothere, *Mesatirhinus petersoni* Osborn. The lunar rests almost equally on the magnum and unciform. × ⅔

The *astragalus* in the ancestral Perissodactyl differed from that of *Phenacodus* in the following characters:

(1) The internal keel of the trochlea was better developed. (2) The neck of the astragalus was more nearly parallel to the calcaneum and did not diverge distally from it. (3) The head or condyle of the astragalus was transversely broader and flatter and its distal facet (for the navicular) was warped in two planes, *i. e.*, convex anteroposteriorly and very slightly concave transversely, in contrast to the simple ovoid astragalar condyle of *Phenacodus*. (4) The cuboid just touched the head of the astragalus along a very narrow facet on its external angle. In *Phenacodus* the cuboid is separated from the astragalus by the navicular, but this may be secondary, because in Periptychids and some Creodonts the cuboid touches the astragalus. (5) In the back view of the astragalus there was a small "distal facet" (Osborn, 1889) by which the astragalus gained additional contact with the calcaneum. This is absent in *Phenacodus* — apparently by reason of the lateral divergence of the astragalar head from the calcaneum. (6) The sustentacular facet, instead of being a broad median oval, was narrow, and located more on the external border; it formed with the distal facet a ⌋. These characters of the astragalus may be seen in any Lower Eocene Perissodactyl and sharply separate them from all known Condylarths.

Conclusion.

The ancestral Perissodactyl as thus conceived resembled the more primitive Condylarths such as *Euprotogonia* in many features. It had the same dental formula, the same kind and arrangement of incisors, canines and premolars, its sexitubercular upper molars were essentially similar in the relative positions of the cusps to those of *Euprotogonia*, and differed only in their somewhat better adaptations to a herbivorous diet. The architecture of the skull, the arrangement of the cranial foramina and the dorso-lumbar vertebral formula were about the same as in *Phenacodus*, while the peculiarities of its scapula and pelvis (p. 391) are not of a radical nature. The manus and pes, in spite of the differences noted below, retained clear traces of derivation from a pentadactyl incipiently mesaxonic type, and in so far are similar to those of Condylarths.

The known Lower Eocene Perissodactyls had, as stated above, a larger brain than *Phenacodus* but reasons have been given (p. 389) for regarding this as a not insuperable objection to the supposed Condylarth affinities of the stem Perissodactyl.

Most of the differences between the stem Perissodactyl and the known Phenacodonts may be regarded as more *advanced adaptations to cursorial habits.* Under this heading may be cited the changes in the scapula and ilium, the strengthening of the sacrum and, in the humerus, the total loss of the entepicondylar foramen, the reduction of the entocondyle, the flattening of the capitellum and widening of the radio-ulnar trochlea, and the early reduction of the digital formula to 4–3. The differences between the serial manus of *Phenacodus* and the interlocking or displaced manus of Perissodactyls are probably the result of divergent adaptations from a more central type (p. 451). The complex form and function of the magnum in the earliest Perissodactyls demand a much simpler form in their remote predecessors, and this condition is retained in *Euprotogonia.* The difference in the astragalus in the two types, while very radical, is doubtless also an expression of improved cursorial powers in the Perissodactyls. In the Condylarths and earliest Amblypods the diverging distal end of the astragalus (doubtless a Creodont and remotely arboreal inheritance) exposes the head of the astragalus in the rear view and makes a relatively movable but unstable joint between the astragalus and calcaneum. By a development of the external (calcaneal) side of the neck or by a twisting of the trochlea, the head of the astragalus was finally brought downward and outward into contact with the distal end of the calcaneum. The "distal facet" thus established, together with the cuboid facet thus made possible, greatly

strengthened the connection but limited the mobility, between the astragalus and the calcaneum. The sustentacular and ectal facets at the same time formed the peculiar ⌋-shaped facet described above (p. 395). The narrowing of the sustentacular facet is foreshadowed to some extent in *Phenacodus wortmani*. After examining considerable material, the writer ventures to assert that in the characters of the astragalus the Phenacodont-Condylarthra approach the Perissodactyl type somewhat more nearly than do the known Eocene representatives of any other order.

To conclude, the derivation of the Perissodactyl order from the general Insectivore-Creodont-Condylarth group of Placentals seems fairly well established. There is no reason to suspect *direct* derivation from either of the two lower orders of this group (Insectivora, Carnivora), because a comprehensive study of the osteology reveals nothing in support of the hypothesis, but shows on the contrary that the stem Perissodactyl had already attained relatively advanced cursorial and herbivorous adaptations which are not foreshadowed in those orders. On the other hand, genetic derivation from any well known Condylarths (*Phenacodus, Euprotogonia, Meniscotherium*) is almost equally improbable. But with regard to many important dental and osteological features it is obvious also that *Euprotogonia* and *Phenacodus* bridge over the structural gap between the Perissodactyls and the lower unguiculate orders, and in brief, that the stem of the Perissodactyls would very likely fall under the Condylarthra, as re-defined by Matthew (1895).

The Ancylopoda (Chalicotheroidea).

The deeply fissured ungues impressed all earlier writers on the "clawed" ungulate *Chalicotherium* of the European Miocene and its allies and led Cope to disregard the numerous ungulate features in the rest of the skeleton in favor of the view that *Chalicotherium* must have been derived from some primitive unguiculate. He therefore (1889, p. 153) made the Chalicotheridæ the type of a distinct order, the Ancylopoda.

Depéret (1892) saw its prevailing resemblance to "les Pachydermes"; but the inclusion of *Anoplotherium* in that group somewhat confused the issue.

Osborn (1893, pp. 118–133) came to the conclusion that the Ancylopoda were intermediate between *Meniscotherium* of the Condylarthra on the one hand and the Perissodactyls on the other. He later (1898) included the Chalicotheroidea as an aberrant superfamily of the Perissodactyls. This view has recently been supported with fresh evidence by Peterson (1907, pp. 733–752) who, in describing the skeleton of *Moropus*, points out many peculiar

resemblances to the Horse, to *Aceratherium* and to *Titanotherium*.[1] Among the chief Perissodactyl resemblances cited by Peterson are the following: The general similarity of both deciduous and permanent cheek teeth to those of *Titanotherium*; the curiously horse-like character of the condylar foramen and paroccipital process and of many features in the neck vertebræ: the Perissodactyl facies of the sacrum; the resemblance of the scapula and pelvis to that of *Aceratherium*; the possession of four digits in the manus and three in the pes, the third digit being the longest in both, all as in Eocene Perissodactyls; the general resemblance of the humerus, radius and ulna, femur and pes to those of *Titanotherium*. To this evidence may be added the following considerations:

(1) The dentition of *Schizotherium* Gervais,[2] a European Oligocene Chalicothere, shows evidence of derivation from an Eocene Perissodactyl type. The premolars must have passed through a stage illustrated in *Lambdotherium*. The molars have been evolved from a buno-lopho-selenodont form not unlike that of the Palæotheres. They must have attained their definitive form through combined lengthening and compression, the inner and outer cusps being brought nearer, even more than in the Upper Eocene Titanothere genus *Dolochorhinus*, this causing the connecting cross crests to be very oblique.

(2) A very suggestive Perissodactyl feature is the funnel shaped fossa running backward and inward from a point just internal to the postglenoid process to the petrosal region. This curious fossa is very characteristic of the horses and Titanotheres and is thought by Dr. C. S. Mead to have lodged the internal extension of the meniscal cartilage.

(3) The foramen ovale is large and situated near the internal confines of the glenoid surface, as in Titanotheres.

(4) The carpus which is of the "displaced" type, retains as many primitive features as could be expected in view of the great difference in function between this heavily clawed digging manus and the normal Perissodactyl type. It might be derived either from the Perissodactyl type represented in *Palæosyops* or from the Artiodactyl type represented in *Ancodus* but the height of the carpals favors the former view. In correlation with the hypertrophy of the internal digit (II), the trapezium is unusually large but its scaphoid surface is still convex as in Perissodactyls and Artiodactyls. The internal process of the scaphoid (representing the centrale) is very broad, as in many Perissodactyls, the lunar has a nearly vertical magnum facet and an oblique unciform facet as in both Perissodactyls and

[1] The valuable figures of the skull and skeleton of *Moropus* given by Barbour (1908) point to the same conclusion.

[2] Represented in the American Museum by casts showing the upper and lower cheek teeth

Artiodactyls. The magnum of Chalicotheres, although highly modified in form, is fundamentally similar to that of *Palæosyops* and its allies. Every facet in the more primitive type is represented in distorted form in the Chalicotheres, while the posterior hook or toe of the magnum, a frequent Perissodactyl feature, is represented by the whole posterior part of the bone in the Chalicotheres. This comparison of the magnum with that of *Palæosyops* is however not altogether convincing, since the Chalicothere magnum might have been derived independently from that of *Euprotogonia*.

(5) As stated above (p. 375) Ameghino associates with the Ancylopoda the genus *Homalodotherium* of the Santa Cruz beds (Miocene) of Patagonia, apparently because the latter has deeply fissured claw-like ungues and the first and second phalanges tend to coalesce, as in Chalicotheres. But this is the kind of adaptive resemblances to other groups which the extinct South American orders so frequently present and it is accompanied by important differences throughout the skeleton. The second metacarpal of *Moropus* and the corresponding ungual phalanx are greatly hypertrophied, but according to Ameghino's figures, no trace of this peculiar feature is seen in the five-toed *Homalodotherium*. The carpus of *Moropus* is high, as in Perissodactyls, that of *Homalodotherium* broad as in *Protypotherium* (figured by Sinclair, 1908, p. 71) among the Typotheres. The astragalus of *Homalodotherium* as figured by Gaudry (1906.1, p. 28, fig. 47) is widely different from that of *Moropus* and the same is true of the humerus (which retained an entepicondylar foramen. *Cf.* Gaudry, *l. c.*, p. 9, fig. 8).

(6) The astragalus of *Moropus*, while superficially resembling that of *Titanotherium*, differs in this important respect, that as noted by Peterson, it has no contact whatever with the cuboid. As the astragalo cuboid contact is a progressive feature in the Titanotheres and Rhinoceroses, this joins with other evidence to show that the Chalicotheres probably diverged from the other Perissodactyls before the astragalo-cuboid contact became fixed, *i. e.*, probably much before the Middle Eocene.

(7) The Chalicotheres resemble the Lower Eocene Condylarth *Meniscotherium* in a number of characters enumerated by Osborn (1893, pp. 118–133), especially in the form of the top of the skull and the characters of the dentition. In both groups the molars are buno-lopho-selenodont, the metaconule ridge is confluent with the hypocone, both lack the third lobe on m_3, both have reduplicate metaconids. However, there are also important differences: *e. g.*, the proto- and metaconules in *Meniscotherium* show no tendency to join the ectoloph as they do in all the Chalicotheres, the protoconule in *Meniscotherium* is V-shaped, not lophoid; the reduplication of the metaconid is equally characteristic of *Lambdotherium* and *Eohippus*; in fact, the Chalicothere dentition may be derived as well from the Lower

Eocene Perissodactyl as from the Meniscotheroid type. The third lobe of m_3 is lost, in correlation with the atrophy of the posterior part of m^3, in both groups. The manus of *Meniscotherium* has no suggestion of the Chalicothere type, the carpus being of the incipiently serial type. The astragalus of *Meniscotherium* resembles that of the Chalicotheres in the absence of a cuboid contact, but this was equally true of *Phenacodus* and probably of the remote ancestors of the Perissodactyls (p. 396).

Conclusions.

The numerous resemblances of the Chalicotheres to different Perissodactyls in the skull, dentition and skeleton can hardly all be set down as convergent, though many of them may be homoplastic as that term is used by Osborn, *i. e.*, independently evolved from a common ancestor. Osborn and Peterson seem justified in concluding that the Chalicotheres are an aberrant family of the Perissodactyls. It seems probable that the affinity is nearer to the Palæothere-Horse-Titanothere division than to the Tapir-Lophiodont-Rhinoceros group and the Chalicotheres may be an offshoot from some Lower Eocene forms resembling *Paloplotherium.* The deeply cleft ungues are of course secondary — an intensification of the slightly cleft ungues of Lower Eocene Perissodactyls. The resemblances to *Homalodotherium* are entirely convergent. The resemblances to *Meniscotherium* are chiefly primitive characters inherited from Lower Eocene Perissodactyls which still retained many Condylarth characters (p. 396).

X. The Artiodactyla.

The Artiodactyla are often grouped with the Perissodactyla under the term "Ungulata Vera" in contrast to the Hyracoidea, Proboscidea, Amblypoda, Toxodontia, etc., which are collectively called "Subungulata." Cope applied the term "Diplarthra" to the "Ungulata Vera," apparently because both Artiodactyla and Perissodactyla are distinguished first by the contact of the astragalus with the cuboid as well as with the navicular, and secondly by the interlocking character (*i. e.*, the double set of facets) in the carpus.

Aside from the characters of the feet, the Artiodactyla and Perissodactyla possess very few characters in common and these are of a very inconclusive nature (*e. g.*, placenta non-deciduate, uterus bicornuate, testes descending into a scrotum, os penis absent. Flower and Lydekker, 1891, p. 275).

The points of resemblance between the two orders in the limbs are sometimes very striking. In the most generalized Artiodactyl manus known, that of the Oligocene *Ancodus,* as described by Scott (1894), the

carpus (Fig. 26, *A'*) shows the same elements, arranged in much the same manner, as in the oldest Perissodactyl. It is alternating in type, the centrale is fused with the scaphoid, and the lunar has a broad contact with the unciform; the third digit also is considerably longer than its fellows. Again in the Tertiary Equidæ the fore limb resembles that of the Ruminants in the humerus and in the V-shaped scapula, vestigial ulna shaft and long cannon bone; and in certain Miocene horses the proportions of the limbs closely paralleled those of *Odocoileus* (Gidley, 1903). The so called Artiodactyl characters of *Titanotherium* are discussed below (p. 385), as well as the general resemblance in the manus between *Metamynodon* and *Hippopotamus* (p. 109).

Yet in spite of these resemblances the evidence indicates that the Diplathra or Ungulata Vera is a wholly unnatural group, that the Artiodactyla and Perissodactyla have been derived from very different sources, and that the resemblances are either primitive protungulate characters or of an entirely convergent nature.

The differences between the oldest Eocene Perissodactyls and most Artiodactyls are very striking. In the earliest Perissodactyls, *e. g.*, *Eohippus*, *Heptodon*, and *Eotitanops*, the third digit of the manus is markedly longer than its fellows and digits II and IV tend to be subequal; in the oldest Artiodactyl type the third digit is indeed longer than the fourth, but digits II and V tend to become subequal. In the pes the difference between the two orders is still more pronounced. In all known Perissodactyls the pes is functionally tridactyl and mesaxonic, the middle digit being much the longest; in the most primitive Artiodactyls the pes is tetradactyl and paraxonic. In the Lower Eocene Perissodactyls (*e. g.*, *Eohippus*, *Heptodon*, *Lambdotherium*, *Eotitanops*) the cuboid facet of the astragalus is represented by a very thin limited surface, the navicular facet is gently convex, and the narrow sustentacular facet lies on the inner posterior border. In the oldest Artiodactyls the astragalus has a very broad contact with the cuboid, the navicular facet is sharply convex and the sustentacular facet is broadly oval and more central in position. These characters were certainly established by the Middle Eocene (Bridger).

In the dentition the contrasts are equally marked. Even in the oldest Perissodactyls the posterior premolars are already relatively large and complex and rapidly assume the molar pattern; the molars also are quadrangular, the protocone being at the antero-internal corner of the crown and the hypocone well developed. The lower molars are already acquiring well developed proto- and metalophids or two subequal V's. In the Artiodactyla the premolars are from the first retarded in their development, p^4 is at most bicuspid, p^2 is compressed, the molars are still triangular and tritubercular

(*e. g., Leptochœrus*), the lower molars were not far from the tuberculo-sectorial type. Even the earliest known selenodont Artiodactyl skulls (from the Upper Eocene) differ from the Lower Eocene Perissodactyl type in many details (apart from the dentition) which suggest a wide separation of the two groups, while the primitive Artiodactyl *Achœnodon* presents only a very superficial resemblance in its skull to the Perissodactyl *Palœosyops*.

A comparison of recent material naturally reveals still wider differences between the two orders both in the skeleton and in the soft parts (Weber, 1904, pp. 597–690).

In the structural details of the fundus of the eye, the Perissodactyls are very sharply separated from the Artiodactyls (Johnson, 1901), while as regards the azygous veins Beddard states (1907, p. 219) that "....the Perissodactyles have their own plan of azygosus tructure, which happens to agree with that of some Cervidæ, but distinguishes the Suborder from the Pigs and hollow-horned Ruminants."

The Perissodactyla, it is suggested (p. 396), were probably derived from some unknown family of Condylarths in which the premolars and molars resembled those in *Euprotogonia*, the manus and pes were becoming mesaxonic, the head of the astragalus had begun to flatten and the sustentacular facet to become J shaped. There is little or no evidence that the Artiodactyla were derived from such a source. From what source then did they originate?

Certain conditions of the hypothetical prototype of the Artiodactyla seem to be realized in the dentition of the Basal Eocene Mioclænidæ (*cf.* Osborn, 1907, figs. 147, 148, 152, 157). These have been thought to be Condylarths and may also be allied to the supposed Insectivore *Hyopsodus* (Matthew, 1909, p. 512). Earle (1893, pp. 377–379) has suggested that *Protogonodon* may hold the same relationship to the Artiodactyla that *Phenacodus* was supposed to hold to the Perissodactyla, but in the absence of skeletal remains such comparisons are very indecisive and Matthew (1897, p. 302) has adduced evidence to show that *Protogonodon* is related to *Euprotogonia* rather than to the Artiodactyla.

Hemithlœus kowalevskianus, a Basal Eocene Periptychid figured by Osborn (1907, p. 165), in its tritubercular molars and bicuspid premolars also fulfills nearly all the desired conditions for the Artiodactyl prototype (except the loss of the paraconid) and further resembles the Artiodactyla in the early development of a broad contact between the astragalus and the cuboid (*cf.* Matthew, 1897, p. 297, fig. 11); but in other features the astragalus is very different from that of the Artiodactyls.

There are also some suggestions of relationship between the Artiodactyla and early Tertiary Insectivores and Primates. In *Poëbrotherium* a primi-

tive Tylopod of the Upper Eocene (figured by Wortman, 1898, p. 111, fig. 7) the premaxillary is elongate, the small incisors are arranged in a longitudinal series, the lower incisors are procumbent and the canines are small and incisiform. The skull also has weak zygomata, an elongate muzzle, a post-orbital ring, a delicate mandible, etc., all features which are seen also among the Insectivora. But here the analogy ends for both the upper molars and the limbs of *Poëbrotherium* are fully Artiodactylous. Even stronger general resemblances to the Lemuroid-Insectivore type are exhibited in the skull of the small *Dichobune leporina* as figured by Stehlin (1906, fig. lxxi). There are also marked analogies in the dentition and skull between the earliest Artiodactyls and the Upper Eocene Lemuroids. But again the objection against deriving the Artiodactyls from the Primates is the radical difference in the character of the tarsus. In the Lower Eocene Artiodactyl genus *Trigonolestes* the astragalus is of the typical Artiodactyl type, while on the other hand in the Middle Eocene Primate *Notharctus* (now known from excellent material in the American Museum) all the limb bones including the astragalus are of characteristically Primate type and show no significant resemblances to the Artiodactyla.

These comparisons of Artiodactyls with Insectivores and Primates are also weakened by the entirely different facies of the skull of *Achœnodon robustus* a Middle Eocene Suilline described by Osborn (1883, pp. 23–35, pl. vi).

This important skull is full of Creodont resemblances. The stout incisors are arranged in a transverse series, the canines are very stout and of the bluntly caniniform long-rooted type; the lower premolars are large and conical, the upper fourth premolar bicuspid; the zygomata are very heavy and there is a high sagittal crest, the glenoid facets for the mandibles are set well back as in the Mesonychids and are equally prominent and transversely extended; the nasals spread proximally as in Mesonychidæ (Matthew) the lachrymal is large, the postorbital process of the frontal is stout, the postorbital constriction marked. It is not stated whether the alisphenoid canal is lacking as in recent Artiodactyla, but if so this fact would not constitute an important objection to the derivation of the Artiodactyla from the Creodonta, since in certain Creodonts (p. 306) the alisphenoid canal is known to be variable (p. 430). The mandible also is very heavy but differs from the Mesonychid type in the high position of the condyle and in the broad angle. The quadritubercular upper molars are a bunodont modification of the tritubercular type; the lower molars show no characters that are inconsistent with derivation from a tuberculosectorial type much like that of *Triisodon*. These observations are in line with Matthew's suggestion (1909, p. 485) that the Artiodactyla have been derived from unknown Creodonts allied to the Mesonychidæ.

A brief review of the limb structure and general skeletal characters of the Mesonychids may therefore be useful at this point.

The manus of *Dromocyon* (Fig. 26, B^1), a Middle Eocene Mesonychid, as figured by Wortman (1902) resembles in many points that of *Ancodus*, a primitive Oligocene Anthracothere figured by Scott (1895) (*cf.* Fig. 26 A^1). The third and fourth digits in *Mesonyx* are subequal and longer than digits II and V; proximally the metacarpals overlap each other from digit II to digit IV. The centrale is appressed to the scaphoid and forms the connection between the scaphoid and the magnum; the magnum is much smaller than the lunar and articulates with metacarpals II and III, the centrale, the lunar and the unciform. The scaphoid and lunar have convex surfaces for the radius, the lunar is broad and rests subequally on the magnum and unciform, the cuneiform is shallow and concave superiorly. The pes (Fig. 26, B^2) is paraxonic: digits III and IV are paired and subequal and the same is true of digits II and V; digit I is represented only by the entocuneiform. The astragalus has a well keeled trochlea, the navicular facet is transversely extended and convex antero-posteriorly, and the astragalo-cuboid contact, although small, is distinct. The sustentacular facet as in Artiodactyls is broadly oval. The cuboid is high, the tuber of the calcaneum long. Thus in the pes every prototypal feature of the Artiodactyla is fulfilled. The analogy also holds in the remaining limb bones. The humerus (*Harpagolestes*) has lost the entepicondylar foramen, the radio-ulnar facet is broad and very Artiodactyl-like, the deltoid is a high ridge terminating in a prominent great tuberosity, the radius is long and straight and proximally flattened and the olecranon is compressed and high. In the femur the third trochanter is reduced and long, the great trochanter is prominent, the distal end is very deep antero-posteriorly with very large condyles and well defined intercondylar notch and rotular groove. The tibia and fibula suggest the Artiodactyl type in the downward extension of the internal malleolar ridge, and in the marked expansion of the distal end of the fibula which is closely appressed to the tibia; the fibula did not however touch the calcaneum (Wortman). According to Wortman the dorso-lumbars numbered 19 (D 12, L 7) in *Dromocyon*, as in Artiodactyla (D 12–13, L 6–7). The anterior sacral vertebra was expanded and alone bore the ilium as in the Artiodactyls and certain other groups. The pubo-ischiadic region was relatively heavier than in Perissodactyls and more as in Artiodactyls; the ilium moreover was expanded as in the Oligocene Artiodactyls.

The foregoing comparisons are by no means made with the object of showing that the Mesonychidæ are ancestral to the Artiodactyla, but, taken in connection with other evidence (p. 401), they appear to indicate that in spite of the similarity in the carpus the Artiodactyla are widely removed

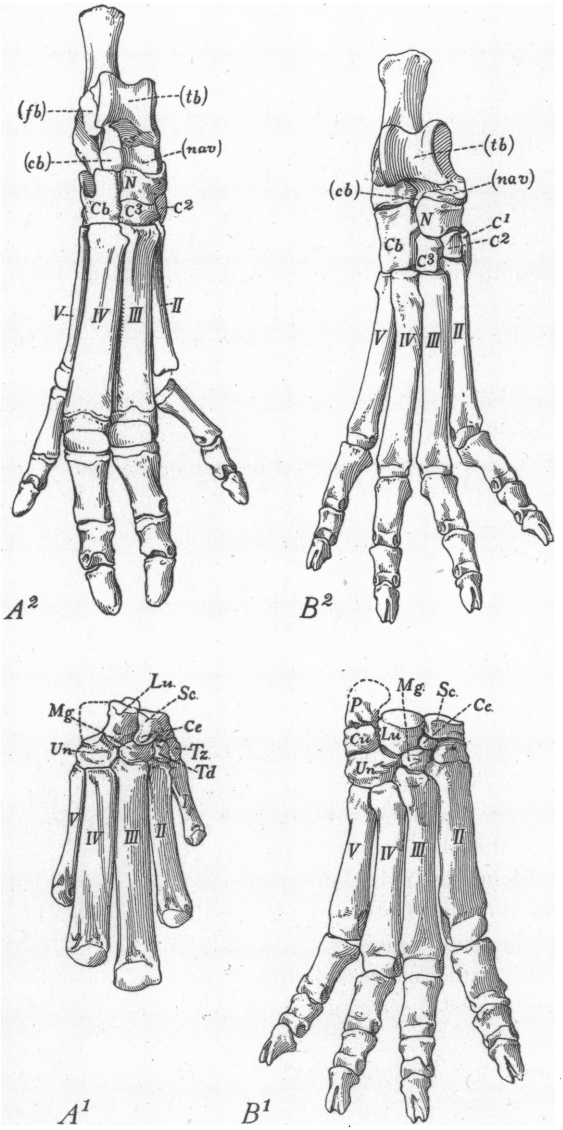

Fig. 26. Comparison of the fore and hind feet of a primitive Artiodactyl (*Ancodus*) with those of a cursorial Creodont (*Dromocyon*).

A^1, right manus of "*Hyopotamus* "(*Ancodus*) sp. After Scott. × $\frac{1}{4}$.

A^2, right pes of *Ancodus brachyrhynchus*. After Scott. × $\frac{1}{4}$.

B^1, right manus of *Dromocyon vorax*. After Wortman. × $\frac{3}{8}$.

B^2, right pes of same. After Wortman. × $\frac{3}{8}$. Abbreviations as in Fig. 19, p. 250.

from the Perissodactyla; that their ancestry is probably not to be sought in the known Condylarthra; and that the principal peculiarities of the skull and dentition and especially of the limbs and feet were already foreshadowed in the Creodonta, from unknown Basal Eocene members of which they may possibly have sprung.

Affinity with the Carnivores is also indicated by certain features of recent Artiodactyls. In the cerebrum the Sylvian fossa is surrounded by 3 concentric gyri, the sylvian, suprasylvian and marginal (Weber, 1904, p. 126). The ossicula auditus are very different from those of the Perissodactyla and are distinguished by the frequent recurrence of the broadly laminate form of malleus which prevails among the fissipede Carnivora (Doran, 1879, p. 421).

At the same time the Lemuroid-Insectivore facies of the skull of *Dichobune* and other Eocene Artiodactyls suggests the possibility that not all Artiodactyls have been derived from a pro-Creodont source.

XI. The Sirenia.

Historical Notes.

A summary of the early history of discovery is given by Gervais (1835, p. 331).

According to Ray (1693, p. 194) the Manatee was described by the Spaniards as *Manati* "quod posterioribus pedibus careat." Ray placed the Manatee after the Walrus under the "Quadrupeda vivipara unguiculata, multifido, carnivora majora, capite longiore, seu Caninum genus."

By nearly all the earlier systematists the Sirenia were affiliated with the Cetacea. De Blainville (1816), the great innovator in classification, boldly separated them from the Cetacea and placed them with "les monodelphes Ongulogrades" in a grand division "anomaux" of that order. Later (1834), relying upon the numerous resemblances between the Proboscideans and Sirenians he associated these two groups in "les Gravigrades," a group of superordinal rank.

Later authors simply assigned the Sirenia separate ordinal rank and gradually gave up the idea of close relationship with the Cetacea.

The most notable of the numerous known fossil Sirenia are: (1) *Halitherium* from the Oligocene of Europe, described in detail by Kaup in the first half of the nineteenth century (1838–1855). Kaup (1855, pp. 9, 10) at first regarded this genus as an ally of *Dinotherium*, and like de Blainville pointed out the resemblances between Proboscidea and Sirenia, regarding the Proboscidea are representing the "Primatentypus" of the Sirenia.

Halitherium was monographed by Lepsius in 1881. (2) *Prorastomus* Owen 1855 from the Eocene of Jamaica, a primitive Sirenian with the complete Eutherian dental formula. (3) *Eotherium* Owen (non Leidy) 1875 from the Upper Eocene of Cairo Egypt, described more fully by Abel (1904) and by Andrews (1906). This genus retained a well developed pelvis and femur and together with *Eosiren* Andrews from the neighboring Fayûm enabled Andrews in 1906 to state new evidence (see below) in support of the theory that the Sirenia are related to the Proboscidea.

Genetic relations.

The theory of the relationship of the Sirenia and Proboscidea which was held by de Blainville has been strengthened by the discoveries of Andrews and Beadnell in the Upper Eocene of Egypt. Several remarkable points of resemblance in the soft anatomy of recent Elephants and Sirenians are cited by Dr. Andrews (1906, p. xxi) in the following words:

"(1) pectoral mammæ, (2) abdominal testes, (3) a bifid apex of the heart, (4) bilophodont molars with a tendency to the formation of an additional lobe from the posterior part of the cingulum. [5] The peculiar mode of displacement of the teeth from behind forwards in some members of both groups may perhaps indicate a relationship, although in the case of the Sirenia the replacement takes place by means of a succession of similar molars, while in the Proboscidea the molars remain the same numerically, but increase greatly in size and number of transverse ridges. [6] Dr. Chalmers Mitchell has lately shown (Trans. Zool. Soc., Vol. XVII, 1905, pp. 464–7) that the Sirenia and Proboscidea resemble one another in the arrangement of the intestinal tract and that in neither group is there any trace of the Ungulate specialization: it is also significant that he states that *Hyrax* likewise approaches the Sirenia in this respect. In a former paper (Phil. Trans., Vol. 196B (1903), p. 116) it was stated that the possession of a non-deciduate zonary placenta was common to the two groups in question, but it has been pointed out by Messrs. Assheton and Stevens (Quart. Journ. Micr. Sci., Vol. XLIX, 1905, p. 1) that this is an error, and that as a matter of fact in the Proboscidea the placenta is deciduate. At the same time, these writers show that in both groups the placenta, in addition to the short villi, also possesses a number of larger and longer villi, which deeply penetrate the maternal tissue and seem to be torn off at parturition. Although these points of similarity, taken separately, may be of no great value, together they supply a very strong argument in favor of the close relationship of the two orders."

In his description of *Mœritherium* and *Eosiren* Dr. Andrews cites much further evidence for the unity of origin of the two orders. For example, in speaking of the brain of *Eosiren* (1906, p. 202) he says: "The chief interest of the brain.... lies in its remarkable similarity with that of *Mœritherium*.... In both animals the hemispheres are divided in a quite similar way by the pseudosylvian depression and the cerebellum is relatively small. In *Mœrithe-*

rium as might be expected in a land animal, the olfactory lobes are more developed than in *Eosiren*.... It is interesting to note further that in the Middle Eocene forms of both these orders [Proboscidea and Sirenia] the brain is relatively large for mammals of that early date."

The scapula of *Mœritherium* (Andrews, *op. cit.*, pl. xi, fig. 5) resembles that of *Eosiren* (pl. xx, fig. 3) in the backward prolongation of the top of the blade, obliquely placed spine and large prespinous fossa (aquatic adaptations). In both genera the humeri although of very different proportions present points of similarity in the form of the distal trochlea and inner condyle; in both the deltoid ridge continues down to a point near the internal condyle, and both lack the entepicondylar foramen. The pelvis of *Eotherium* as noted by Andrews (*op. cit.*, p. 214) is in many respects intermediate in character between those of the Sirenian *Halitherium* and the supposed Proboscidean *Mœritherium*. The ilium of *Mœritherium* is not expanded as in Proboscidea but trihedral, with an ileo pectineal tubercle at its base, the ischial tuberosity is very broad, the thyroid fenestra relatively small and the posterior part of the pubic bar slender; these characters, with some changes in proportion, are also seen in *Eotherium*; the acetabulum of which is well developed, proving that in this most primitive Sirenian the hind limb was still functional. The skull of *Eotherium* (Andrews, *op. cit.*, p. 205) while already much modified in the Sirenian direction tends on the whole to confirm the view that the Sirenia, Proboscidea and Hyracoidea are divergent offshoots from a single stock.

Among the characters which the skulls of *Eotherium* and *Mœritherium* exhibit in common some may be conceived to have developed more or less independently, such as: (1) The retraction of the nasals (very early reaching an extreme in the Sirenia): (2) the enlargement of one pair of incisors (i^1 in *Eotherium*, i^2 in *Mœritherium* and the Proboscidea); (3) the prolongation of the palate and straightness of the tooth row; (4) the development of bilophodont molars; (5) the broadening of the coronoid, the anterior edge of which is external to the posterior molars. The skulls however show further resemblances which are less obviously adaptive, *e. g.*, (1) the extremely forward position of the orbits, a point emphasized by Osborn (2) the resemblances in the occipital aspect of the skull; the mastoid being entirely concealed in *Mœritherium* and nearly so in *Eotherium*; while the upper posterior angle of the squamosal in "*Eotherium* is shut off from contact with the supra-occipital by a narrow posterior prolongation of the parietal which is wedged in between the two bones somewhat as in *Mœritherium*" (Andrews, *op. cit.*, p. 205). (3) The base of the cranium is rather similar in the two forms. *Eotherium*, however, retains a condylar foramen, unlike the Proboscidea and Embrithopoda, in which the condylar foramen is generally confluent with the foramen lacerum posterius.

In consideration of the differences in habits between *Mœritherium* and *Eotherium* which are implied by the possession in the former of a well developed, in the latter of a reduced, femur, it is evident that the possession of so many characters in common constitute strong evidence of community of origin; even although some of these characters may have been independently developed in the two forms. When it is further realized that apart from *Mœritherium* there is no known Artiodactyl, Perissodactyl, or representative of any other order that approaches *Eotherium* in nearly so many points, and that even between existing Sirenia and Proboscidea many peculiar features not obviously due to any similarity of habits are retained in common, it then becomes clear that the evidence for relatively close relationship between the Proboscidea and the Sirenia is very strong. Lydekker (1892) notes that in certain Sirenia the last milk molar is molariform and shows certain additional resemblances to the last milk molar of certain bunoselenodont Artiodactyls. But such isolated points of similarity in the dentition have often proved to be very deceptive when interpretated as indications of relatively near relationship.

XII. General Conclusions.

As shown in the preceding sections the various suborders of hoofed mammals are connected by a tangled web of resemblances, a web which early caused the "order" Ungulata to be regarded as a natural group — as natural as, for example the Primates. It is only rather recently that it has been suspected that this general stock of resemblances may have been built up to a considerable extent by the processes of convergent and parallel evolution. Indeed it seems almost as if certain authors had not yet become aware of this possibility, for they continue to base classifications and phylogenetic conclusions upon adaptive resemblances, in a manner recalling the methods of Blumenbach and Cuvier.

The present problem in regard to the Ungulates is not whether they form a wholly natural group, but rather to determine how far convergent evolution has proceeded, to decide how many different primary stocks have contributed to this composite "order" and especially to locate the time and place, when and where these primary stocks became differentiated from lower Placental orders.

Among the provisional conclusions to which the writer has been led may be mentioned the following:

(1) The Artiodactyla are widely removed not only from the Perissodactyla but also from all other ungulate groups. They may well be,

according to certain evidence, an offshoot from ancestors of the Creodont Mesonychidæ (as first suggested by Matthew) but the alternative possibility of relationship with some Lemuroid-Insectivore group has certain points in its favor. Perissodactyls occasionally parallel Artiodactyls in some features, but the Lower Eocene Artiodactyls and Perissodactyls are widely separated in many seemingly deep seated characters. Certain resemblances to Condylarths are simply primitive Placental characters.

(2) All the remaining ungulate suborders may be conceived to trace their ancestry back to a varied order of Cretaceous Protungulates. These were primitive Placentals of small size, related to the Creodont-Insectivore stock but probably falling under the original definition of the Condylarthra. There are various possible reasons why such forms have not yet been discovered. They may have dwelt in some boreal Holarctic centre as yet unknown; or they may have inhabited the same lands as did the known Cretaceous mammals and dinosaurs, but, being forest dwellers and possibly in part arboreal, they escaped preservation, whereas the known Cretaceous mammals may have dwelt near the swamps or on the plains.

(3) By Basal Eocene times the Protungulates had spread into North America, South America, and Europe and had already split up into a number of well separated families. In North America (Puerco and Torrejon) we find Phenacodonts, Meniscotheres, Periptychids and Pantolambdids. In Europe Condylarths (*Euprotogonia*) and Amblypods (*Coryphodon*) are recorded by Depéret (1908, p. 111) in the Thanetian stage. In South America, the Notostylops Beds of Patagonia (which according to all authorities are at least not later than Basal Eocene) contain ?Condylarths (*e. g., Didolodus*), ?Periptychids (*e. g., Guilielmofloweria*) and early specialized members of the Homalodotheria or related groups.

(4) From different families of this widely distributed Upper Cretaceous-Basal Eocene protungulate order arose in different continents the various groups known as Amblypoda, Proboscidea, Hyracoidea, Perissodactyla, Notoungulata, etc. The Amblypoda may have sprung from North American Pantolambdids; the Hyraces, Embrithopods, Barytheres and Proboscidea may trace their origin to a common Lower Eocene African stock which also gave rise to the Sirenia; the Perissodactyls and Chalicotheres may have been derived from Holarctic Condylarths allied to the Phenacodontidæ; one of the South American orders (the Litopterna) may have been derived from South American representatives of the Meniscotheriidæ, others (Homalodontheres and Astrapotheres, Toxodonts and Typotheres) from small protungulates allied to *Henricosbornia* and the ancestors of the Notostylopodiæ; while from related forms with more distinctly bilophodont molars arose the Pyrotheria.

(5) The confusing web of cross resemblances, *e. g.*, of Litopterns to Perissodactyls, of Hyracoids to Protypotheres and Perissodactyls has been conditioned by the facts: (*a*) that the several orders have been derived from related families of protungulates having a similar "potential of evolution"; (*b*) that these protungulate families inherited in common a great number of primitive Placental characters which they distributed in various combinations to their several lines of descendants; (*c*) that many of the characters which have been used to unite very different groups (*e. g.*, the interlocking carpus of Artiodactyls and Perissodactyls) were at first less defined and more plastic but later became fixed ordinal characters.

CHAPTER X. GENETIC RELATIONS OF THE CETACEA.

Historical Notes.

A. On the Zeuglodontia.

1670. Agostino Scilla describes and figures a fossil tooth of the animal later known as *Zeuglodon*. Scilla's figure is reproduced in de Blainville's 'Ostéographie' (tom. ii, "Phoca.").

1834. Harlan applies the term "*Basilosaurus*" to certain fragmentary vertebræ belonging to the genus now commonly known as *Zeuglodon*.

1836. Agassiz examines Scilla's fragment and in his 'Poissons fossiles' refers to it as "une espèce remarquable du genre Phoca qui differe sensiblement de tous nos Phoques vivans." He later calls it *Phocodon* (Palmer, 1904).

1839. Owen having determined the mammalian nature of "Basilosaurus" proposes to substitute the name *Zeuglodon*.

1840. Grateloup describes certain remains as "*Squalodon*," supposing them to be saurian in nature (Palmer). H. von Meyer refers these remains to the Cetacea.

1840. De Blainville refers Scilla's original fragment to the Pinnipedia and distinguishes it from *Squalodon*, since in Scilla's specimen the teeth had two roots, in *Squalodon* only one. De Blainville calls it "Phoca melitensis antiqua."

1849. J. Müller monographs the group, which he considers Cetacean in the broad sense, intermediate between the Pinnipedia and the Cetacea proper, but occupying an order by itself.

1872. Gill applies the term "Zeuglodontia" to a suborder of the order "Cete."

1889. D'Arcy Thompson adduces evidence to prove that the Zeuglodonts are nearly allied to the Pinnipedia, rather than to the Cetacea.

1904. Fraas describes the genera *Protocetus* and *Mesocetus* from the middle Eocene near Cairo, Egypt, both of which are very primitive Zeuglodonts and are believed by him to demonstrate the connection of that group with the Creodonta. He proposes to reduce the rank of the Zeuglodontia, regarding them as an aquatic section of the Creodonta, and denying their supposed connection with the Cetacea.

1906. Andrews describes the genus *Prozeuglodon* from the Upper Eocene of the Fayûm, Egypt, which is intermediate in character between *Protocetus* and *Zeuglodon*.

B. Historical notes on the Cetacea in General.

Some idea of the extent of the early literature of Cetology may be had from the figures given by Dr. J. A. Allen in his remarkable 'Bibliography of Cetacea and Sirenia' (1881, pp. 399–562). For the period from 1495 to 1758 Allen lists 276 titles of works dealing with this subject, the total number of titles up to the end of 1840 being *one thousand and thirteen.*

1692. Sibbald (quoted by Gray, 1850) classifies the whales as follows: "I. The small Whales with teeth in both jaws, of which he notices three: [probably the Killer, the Beluga and the Porpoise]. II. The larger Whales with teeth in the lower jaw: 1, the Sperm Whale and 2, the Blackfish [*Globiocephalus*]. And III, the Whalebone Whales of which he describes three specimens" (Gray). The arrangement he used was the one followed by Gray in 1850, and Gray's terms "Denticete," "Mysticeti" possibly refer to Sibbald's characterizations. Sibbald's work "forms the ground work of all that was known on the larger Cetacea up to the Linnæan time."

1693. Ray recognizes the true nature of the Cetacea ("Pisces cetacei seu Belluæ marinæ," "animalia vivipara pilosa") especially in the following passages (transl.): "For except as to the place in which they live, the external form of the body, the hairless skin, and the progressive or swimming motion, they have almost nothing in common with fishes, but in remaining [characters] agree with the viviparous quadrupeds." And again "The Whales breathe like quadrupeds with lungs, copulate, bear living young and suckle them with milk, and agree with them [the quadrupeds] in the structure and function of almost all the internal organs."

1735. Linnæus classifies the Cetacea among the fishes.

1758. Linnæus groups the Cetacea with the hairy quadrupeds under the class name "Mammalia."

1754. Brisson makes a separate class of the Cetacea coördinate with the other Mammalia.

1779. Blumenbach places the order Cetacea at the end of the Mammalia, following the aquatic or semiaquatic "Palmata."

1780. Storr gives the Cetacea subclass rank in the "phalanx Pinnata."

1795. Geoffroy and Cuvier group "les Cétacées" with other aquatic mammals under the order "Amphibies."

1800. Cuvier excludes the seals from "les Cétacés," which now embraces only Sirenians and Cetaceans; the two great "familles" forming a grand division of the mammals ("les mammifères à pieds en nageoire").

1816. De Blainville suggests that the Cetacea represent an anomalous modification of the edentate type. He divides the "ordre Édentés?" into two groups: "Normaux, Édentés" and "Anomaux, Cétacés?".

1817. Cuvier divides "les Cétacés" into two sections, I° "Herbivores" [Sirenians], 2° "Ordinares" (true Cetaceans). The latter he subdivides into: 1° those "*à petite tête*" ("Dauphins, Narvals") and 2° those "*à grosse tête* ("Cachalots, Baleines").

The idea that the Cetacea and Sirenia were allied persisted for a long time, Owen in 1866 still grouping the two orders in a division "Mutilata" coördinate with the "Unguiculata."

1826–1866. Gray clears the ground for further work by careful descriptions of actual material and by correctly grouping the genera into families.

?1849 (or earlier). Eschricht (quoted by Gray), one of the great names in Cetology, in his *Nordischen Walthiere* proposes the following interesting partition of the order:

"1. Sarcophagen: *Orca.*

2. Teuthophagen: *Physeter, Rhynchotocete* (*Hyperodontina* Gray), *Monodon, Beluga, Globioceps.*

3. Ichthyophagen: *Phocæna, Delphinus, Ogmobalæna,* [= *Balænoptera*].

4. Pteropodophagen: Leiobalæna Eschricht [= *Balæna*]."

He further proposes to separate these groups into

I "Zahnwalle," namely, groups 1–3 except *Ogmobalæna.*

II "Bartenwalle," Balænoids, including *Ogmobalæna* (*Balænoptera*).

1864. Gray proposes the subordinal terms "Denticete," "Mysticete."

1861–1882. Van Beneden publishes a series of important memoirs on the fossil Cetaceans of Belgium. He groups the genera *Squalodon, Stenodon* and *Zeuglodon* into an order "les Zeuglodontes" parallel to the Sirenians and "Cetedontes" as a division of the "Thallasothériens."

1864–1891. Flower makes many contributions to Cetology. In 1891

he summarizes the evidence bearing on the origin of the order with negative results, emphasizing, however, the resemblances to the Ungulata Suina in the larynx, stomach, liver, reproductive organs, and fœtal membranes.

1866. Haeckel groups the "order" Cetacea (including the suborders "Phycoceta" or Sirenia and" Autoceta (Balænia)") with the order Ungulata (Perissodactyla and Artiodactyla) as a second sublegion "Pycnoderma" of the "Indeciduata," the first sublegion comprising the Edentata.

1867–1890. Cope contributes a series of papers to Cetology: describing several genera of fossil Platanisidæ from the United States, emphasizing the primitive characters of that family, describing also several Miocene Balænids which were more primitive than existing forms. He also contributes to the development of the classification.

1880. Van Beneden and Gervais publish the 'Ostéographie des Cétacés vivants et fossiles'.

1893. Lydekker describes the fossil genus *Physodon* from Patagonia, a generalized ally of *Physeter*, with teeth in both jaws; also the fossil genus *Argyrocetus* from the Argentine Republic, a primitive Platanistid.

1900. Beddard reviews the natural history and anatomy of the Cetacea in his 'Book of Whales.'

1901–02. Abel describes many Miocene Platanistids of Europe and contributes much to the knowledge of the phylogeny and evolution of the Cetacea. In 1905 he describes as the "stem form of the Delphinidæ" a small genus, *Palæophocæna*, from the Miocene of Germany.

1902. Beddard adduces new evidence in support of de Blainville's idea that the Cetacea are related to the Edentata.

1904. Weber's clear review of the Cetacea leaves little doubt as to the following conclusions: (1) the derivation of the group from quadrupedal Placental mammals; (2) the unity of origin of the two orders Odontoceti and Mystacoceti; (3) the probable relationship of the higher orders with the Zeuglodontia.

Genetic relations of the Cetacea.

To those capable of appreciating the force of anatomical evidence and especially the meaning of vestigial structures, the proof that the Cetacea have been derived from four-footed land-living mammals is cumulative and wholly convincing. The facts are very clearly presented by Weber (1904, pp. 580–582) who cites among other evidences: (1) the vestigial "sinus hairs" analogous to the bristles of a hog; (2) the vestigial skin glands, especially the conjunctival gland; (3) the vestigial ear muscles pointing to the former existence of external ears; (4) the presence of the three mammalian

auditory ossicles and of an internal ear, which all become profoundly modified for aquatic life; (5) the vestiges of the pelvis and hind limbs; (6) the indications that the testes were formerly extra-abdominal and have been withdrawn secondarily into the body cavity in adaptation to aquatic habits; (7) the significant vestiges of the naso- and ethmoturbinals which indicate that the reduction of the olfactory organs is only an extreme adaptation to aquatic life, a process seen in less advanced stages among the Sirenia and Pinnipedia.

Hardly less clear, as Weber says (1904, p. 581), is the evidence that the terrestrial quadrupedal forefathers of the Cetacea were true Placentals.

The Cetacea not related to the Sirenia. The nearer affinities of the Cetacea can best be treated after the claims of the Sirenia and Pinnipedia to this relationship have been shown to be based upon purely convergent adaptations. It would hardly be necessary to refer at this date to the old idea that the Cetacea are genetically related to the Sirenia if it had not been defended by two such eminent naturalists as Dr. Theodore Gill (1873, pp. 272–273) and Professor Haeckel (quoted by Beddard, 1902, p. 120). Even if there were no palæontological data bearing on the subject, the thorough review of the morphology of the existing Cetacea and Sirenia given in Weber's 'Säugetiere' (pp. 552–580, 727–738) offers convincing evidence that the marked resemblances between the two orders are entirely adaptive. Even aside from the very conspicuous differences in the dentition and digestive apparatus, the two orders are separated by profound differences in the whole architecture of the skeleton, especially in the skull, lower jaw, scapula and fore-limb bones; while equally striking differences (Weber, 1904, p. 739) obtain in the brain, male organs, teats, etc.

Dr. Gill holds that the detailed relations of the vestiges of the hind limbs and tail in the two groups are so distinctly similar that they must imply a relatively near kinship, because they can scarcely be conceived as being altogether the result of convergent evolution. But in view of the cumulative evidence against such a genetic relationship, that is precisely the conception we are constrained to adopt. The "amphibiotic" ancestors of both Sirenia and Cetacea doubtless had long and very heavy tails and small hind legs, and as each group became more thoroughly aquatic the tail increased still more and the hind limbs grew smaller and sank deeper into the integument. The caudal "flukes" are in each case purely dermal appendages and bear of course no homological relation whatever to the somewhat similarly appearing hind flippers of the most advanced Pinnipedia. And when the palæontological record is appealed to it is seen that the Sirenia (p. 407) appear to approach the Proboscidea, while the Cetacea (as shown below) approach the Insectivore-Carnivore series.

Resemblances to the Pinnipedia. Convergent evolution is also responsible for the points of resemblance wherein those most advanced Pinnipeds, the Sea-Elephants (*Macrorhinus*), approach the Cetacea. Aquatic adaptation has proceeded so far in the Sea-Elephants that it is expressed not only in the general form of the body, flippers, etc., but even in certain Cetoid features of the base of the cranium,[1] of the enlarged periotic bones and of the auditory ossicles (*cf.* Doran, 1879). But even in regard to these structures *Macrorhinus* is clearly only a development of the normal Phocid type and is separated from the Cetacean type by a host of significant differences.

Resemblances to the Edentates. The claims of the Edentates to relationship with the Cetacea rest upon characters which are less obviously adaptive and are therefore entitled to more serious consideration. They were first advocated by de Blainville (p. 76) and recently by Beddard (1902, p. 120). The latter author cites the following characters:

"(1) the existence of traces of a hard exoskeleton of which vestiges remain in the Porpoise; (2) the double articulation of the rib of the Balænopterids to the sternum, with which compare the conditions obtaining in the Great Anteater; (3) the concrescence of some of the cervical vertebræ; (4) the share which the pterygoids may take in the formation of the hard palate; (5) the fact that in the Porpoise, at any rate, as in many Edentates, the vena cava, instead of increasing in size as it approaches the liver, diminishes."

The Cetacea further resemble the Armadillos in the multiplication and cylindrical character of the cheek teeth.

These interesting resemblances are rather strengthened by other occasional features, such as the carrying back of the palate in *Myrmecophaga*, or the frequent presence of retia mirabilia in both groups, which seem to point toward potential similarities between the remote ancestors of the two orders; but these resemblances are not numerous enough to be at all convincing and are not supported by what is known of the palæontological record, so that the case for the Edentate affinities of the Cetacea can scarcely be regarded as anything more than a possible hypothesis.

Relations of the typical Cetacea to the Zeuglodontia. The problem of the origin of the typical Cetaceans rests largely upon the question whether the Zeuglodonts are genetically true Cetaceans or whether the resemblances between *Zeuglodon* and *Squalodon* may be regarded as convergent. Dr. True (1908) has reëxamined the question of the relationships of the Cetacea with the Zeuglodonts and reaches a negative conclusion. He states that the humerus of *Microzeuglodon* (a genus which was formerly thought to

[1] The skull of *Macrorhinus* (= *Mirounga*) is figured in Elliot's 'Mammals of Middle America and the West Indies.'

bridge over the gap between the Zeuglodontia and Odontoceti) is decidedly of the longer, or Zeuglodont type and that therefore the supposed connection of Zeuglodonts and Odontocetes breaks down at this point. He is inclined to agree with Gill (1873) that the Cetacea are an extremely ancient branch of the mammalian stem which cannot be connected with any known group of land animals. Coming from an eminent cetologist, this conclusion will be likely to carry great weight, but a quite different interpretation of the facts seems permissible. It is of course not at all necessary to suppose that any known Zeuglodont is directly ancestral to *Squalodon* and the Odontocetes. Indeed, the relatively large size and comparatively late appearance of all known Zeuglodonts raises a strong presumption against that idea; but the hypothesis that the known Zeuglodonts are rather closely allied to the ancestors of the Odontocetes and that these ancestors when discovered will fall under a properly constructed definition of the suborder Zeuglodontia has much evidence in its favor.

Morphologically the Zeuglodonts realize many conditions which may confidently be looked for in the ancestors of the Odontocetes. The earliest Odontocetes must certainly have had an elongate premaxillo-maxillary rostrum, retracted symmetrical nasals, a skull top sloping anteriorly, strong post-orbital constriction, prominent post-orbital processes, small orbits placed very low on the side of the face, slender jugals, a backwardly produced palate in which the pterygoids shared, inflated petro-tympanic, condyles less sessile and nearer to the median line, coronoid process of jaw broad not hooked, condyle of jaw placed below level of cheek teeth, etc. With respect also to the form of the limb bones, the Zeuglodonts are morphologically intermediate between the Odontocetes on the one hand and normal placental unguiculated quadrupeds on the other. The Zeuglodont humerus shows, it is said, a curious mingling of Pinniped with Cetacean characters (Lucas, 1895), but this neither proves that the Zeuglodonts are related to the Pinnipeds nor casts any just suspicion upon their relationships with the Cetacea, since the latter is probable on other grounds. A very striking fact is that the scapula of *Zeuglodon* is of the Cetoid type (Lucas, 1895) in which the prespinous fossa is rudimentary or absent, the acromion very large and situated on the anterior border, and the coracoid prominent. Neither in the Pinnipedia nor in the Sirenia has adaptation to aquatic habits produced this peculiar type of scapula, which is common to the Zeuglodonts and to the Cetaceans.

The brain cast of *Zeuglodon*, according to Elliot Smith (1903, pp. 322) reveals no features that are inconsistent with Cetacean affinities, but it resembles the Cetacean type in two important characters, namely, the great breadth of the cerebrum, and the peculiar elongation of the olfactory peduncles beyond the anterior extremities of the hemispheres.

The teeth of *Squalodon* are morphologically intermediate between those of the Odontocetes and those of the Zeuglodonts. So far as the form of the teeth is concerned, analogy with the Phocidæ would indicate that the cylindrical teeth of the Odontocetes are a secondary adaptation to marine piscivorous habits. The great variability in the characters of the teeth among the Odontocetes and among the Pinnipeds indicates that in both groups rapid evolutionary changes in the dentition have been in progress at a relatively recent date. In the ancestors of the Odontocetes probably the form of the teeth may have been rather diverse: some types may have been derived from the *Squalodon* type, others more directly from the *Protocetus* type.

We may, in short, readily agree with Dr. True that the known Zeuglodontia differ from the known Odontoceti in many characters, notably in the greater length of the humerus and in the retention of a distinct radio-ulnar trochlea, but if the Cetacea have been derived from land mammals these very characters must be looked for in their immediate, less completely aquatic ancestors. And before the Zeuglodontia as an order are proved to be morphologically not ancestral to the Cetacea it would be necessary to cite evidence to show that the Cetacea had been derived from some very different type of mammals, say for example the Sirenia.

Assuming then that the Zeuglodontia are offshoots of the ancestral Cetacean stock, the next question is, from what orders of terrestrial quadrupeds are the Zeuglodonts in turn derived? The discovery of the remarkably primitive species *Protocetus atavus* led Professor Fraas (1904) to infer that the ancestors of *Protocetus* must have been Creodonts. To this view Dr. Matthew, in conversation with the writer, at once took exception, on the ground that the characters of the *Protocetus* skull might be derived as readily from the Eocene Insectivore type represented by *Pantolestes* as from the Creodont type. Among the facts which tend to support Dr. Matthew's view the following may be mentioned:

(1) The elongate rostrum of *Protocetus* is more readily derived from the Insectivore type, with the incisors arranged in an antero-posterior series, than from the Creodont type. The elongate rostrum and antero-posterior arrangement of the incisors are exceedingly characteristic of the Cetacea. If the latter had been derived from the Creodont type having a transverse incisor series it is likely that *Protocetus* would have showed some traces of this arrangement, and that the end of the snout would have been analogous to that in the Gavial.

(2) The sharply triangular outline of the skull in palatal view, together with the relatively weak malar bones is more consistent with derivation from an Insectivore type than from a Creodont type. The very large attachments

for the temporal, and weak attachments for the masseter muscles in *Zeuglodon* also favor this view.

(3) No Creodonts are known in which the petrotympanic bullæ are expanded as they are in *Protocetus*. This however is an aquatic adaptation seen also in the Pinnipedia, and like the backward prolongation of the palate (which is a point of resemblance to the Creodont *Hyænodon*) it may be of little phylogenetic significance.

(4) The marked post-orbital constriction is no necessary indication of Creodont affinity. In the Seals and probably in *Protocetus* this is largely secondary and due apparently to the reduction of the olfactory parts of the brain. In the Creodonts themselves it is due not to any actual narrowing but to the very rapid broadening of the muzzle and zygomata in adaptation to carnivorous habits. In all three cases it is readily derivable (p. 267) from the tubular postorbital region represented in the Zalambdodont *Microgale*.

(5) It is a very surprising fact that the skull of the little Zalambdodont genus *Hemicentetes* presents a superficial analogy to that of the Zeuglodonts in a number of points, such as the great elongation of the muzzle, the low anterior position of the orbits, the shape of the lower jaw, etc., and in the cheek teeth the reduction of the inner part of the crown and the elongation of the outer part. Together with the marked aquatic modifications of the limbs in the Eocene *Pantolestes*, these curious resemblances indicate that the Insectivora did occasionally develop features which might be thought at first to be entirely distinctive of the Zeuglodontia.

(6) The true molars of *Protocetus* present only a superficial resemblance to those of any Hyænodont. The reduction of the inner side of the molar crown has been effected independently also in the Pinnipedia and, as stated above, in *Hemicentetes*. The relatively small size of the canine and the very large size of the third premolar also tend to remove *Protocetus* from the Creodonts.

The Cetacea not of Mesozoic origin. Evidence in contradiction of the view that the Cetacea are an extremely ancient (*i. e.*, Mesozoic) branch of the Mammalia is furnished by the reproductive organs. The reproductive organs seem to have been affected relatively little by the process of adaptation for aquatic life which has so profoundly changed the entire skeleton and the digestive, respiratory and vascular systems. The uterus is two horned, as in many Monodelphia of high type (*e. g.*, Carnivora, Artiodactyla, Perissodactyla), the yolk sack is rudimentary (contrast most primitive Placentals). The penis (in contrast with that of Rodents and Edentates) is also of high type (Weber, 1909, p. 571).

In the highly convoluted brain (see Weber, 1909, pp. 126, 562) the three concentric gyri which surround the Sylvian fissure are characteristic of the

Cetacea, Carnivora and Ungulata. The larynx, according to Flower (Flower and Lydekker, p. 233) resembles that of *Hippopotamus*. The prolongation of the larynx into the posterior nares may be regarded as an aquatic development of the retrovelar larynx of Insectivores. The marked aquatic modifications in the petro-tympanic region are readily derivable from normal Placental conditions as exemplified in the Carnivora and Ungulata (Boenninghaus, quoted by van Kampen, 1905, p. 653).

Conclusion.

The resemblances of the Cetacea to the Suilline Artiodactyls which was emphasized by Flower, may possibly be connected with the derivation of the Artiodactyls from Creodonts (p. 403). Aside from the evidence (p. 416) cited by Beddard for relationship with the Edentata the prevailing resemblances of the Cetacea (including the Zeuglodontia) seem to be with the Insectivore-Creodont group, rather than with the Ungulates, Rodents, and Edentates. It would not be surprising to find true Odontocetes in the Eocene, since so many other Placental orders were already differentiated at that time, but no good evidence of an especially great antiquity of the order or of relationship with Marsupials or pre-Placentals has been advanced.

The hypothesis that the resemblances between Odontocetes and Mystacocetes are largely of a convergent character (Kükenthal) has been cogently disputed by Weber (1904, pp. 583–584).

CHAPTER XI. OSTEOLOGICAL MISCELLANIES.

The need of a new osteology of the Mammalia.

In preceding chapters the object has been to review and interpret evidence bearing on the genetic interrelations of the mammalian orders. Osteological characters of living and fossil mammals have naturally entered largely in this attempt, but attention has been centered on questions of phylogeny rather than upon osteology itself as a method of inquiry. The present chapter is designed to introduce to the student a few of the problems of modern osteological research, to assist him in tracing the probable history of certain parts of the skeleton in the more primitive orders, and finally to express the present need for a new general treatise on the osteology of living and fossil mammals.

Recorded observations of osteological characters furnish of course the

raw material for phylogenetic conclusions; but in the leading existing text books on vertebrate osteology this raw material seems to have been assimilated and wrought into permanent philosophical results only to a very limited extent.

To the student of phylogeny the problem of the relative antiquity of different characters may be said to involve all the other general problems of palæontology and mammalogy, and especially such questions as the following: What is the taxonomic rank or extension of the character in question? Is it a class character, a subclass, ordinal, superfamily, family, subfamily, generic, or only a specific character? Does it depend upon age or sex? How far is it "cænotelic," *i. e.*, of recent origin and related to particular habits and habitat? Does it depend upon mere size, or weight, or upon strength of muscular pull? Or is it a fundamental and universal character like the foramen magnum, a character which conditions survival in any group whatever? At what stage of its phyletic development does the character stand? How far is it correlated with other characters and how far are other characters correlated with it?

The solution of such questions, so far as it has progressed, naturally has been largely by means of the "guess-try-guess-again" method, but the point to be noted here is that basal assumptions and postulates should be re-tested in order to make further advance sure. In the present state of phylogenetic research the need for new material is no greater than the need for the reëxamination of old material. A new and comprehensive treatise on the osteology of living and fossil mammals is, in fact, urgently needed. For although Flower's 'Osteology of the Mammalia' and Reynold's well arranged text book on the 'Vertebrate Skeleton' have proved continuously useful, yet these works contain no real clue to the interpretation of the facts they record, so that the student in attempting to compare one form with another is lost in the bewildering maze of analogical and homological resemblances.

Like the above mentioned works the new osteology also should be primarily an "osteography," abounding in good figures. It would of course include living and fossil mammals; perhaps two or more representatives of all the well known families. It would devote much more space to the more ancient and generalized forms than to the more specialized and usually better known forms. The forms should be arranged as far as possible in accordance with the most nearly phylogenetic classification, and while this feature would cause the work to become "out of date" to the degree that the phylogenetic classification of the mammals became modified by the progress of the science, yet such an arrangement would be the best means of testing certain theories of relationship and of showing the relative phylogen-

etic significance of different kinds of characters in different orders. The work might begin with a series of side views of the skeleton as a whole, accompanied by a very brief tabulated statement of the mode of progression, nature of the food, etc., of each animal figured. This would be followed by side views of the skull, palatal views showing especially the foramina, which should be carefully identified, top views and back views; longitudinal sections, details of the skull such as composition of the auditory bulla, form of the auditory ossicles, etc. A series showing the throat bones would come next. The vertebral column with the ribs on the further side only would follow, then a ventral view of the thorax showing the sternum and shoulder girdle. The fore and hind limbs would be figured as a whole in side view, the separate parts in front view. Special attention would be paid to both front and back views of the carpus and tarsus, especially the astragalus.

Doubtless such a work would be far beyond the resources of most investigators and could only be accomplished adequately by the application of modern coöperative methods to the science of osteology. But M. Edmond Hue's 'Musée Osteologique' (1908), with its 2187 careful drawings of the bones of recent and quaternary mammals, indicates what may be accomplished in that direction by even a single investigator.

Another requisite for the testing of hypotheses of relationship among primitive orders is a thorough re-study and careful figures of the osteology of such very primitive mammals as the insectivorous Dasyurids, various species of the smaller Didelphids and Phalangers, and of the more primitive Insectivores such as *Microgale, Geogale, Ericulus, Hylomys, Anurosorex, Uropsilus, Tupaia, Ptilocercus, Rhynchocyon.* Among the Viverridæ, *Eupleres, Nandinia, Galidictis, Cynogale,* might be refigured to advantage. All these forms have been figured before but what is needed are more figures of young skulls showing the limits of all the bones and the location of the principal foramina. Parker's invaluable work on the development of the skull in the Edentates and Insectivores (1885–86) sets an example in this respect. The certain identification of the foramina requires in some instances the dissection of representative types.

Since the skeleton is the framework for the muscles, a thorough knowledge of the former would be possible only to one who understood well the origin, insertion and action of the muscles. The subject of comparative myology appears to be still largely in the descriptive stage,[1] but there is urgent need of more studies of the kind typified by Gaudry's memoir (1906.1) upon the attitudes of certain extinct Patagonian ungulates.

In studying the orders of mammals the student should look for "palæo-

[1] The important researches of Messrs. Windle and Parsons cited below (pp. 478, 504) offer a decided exception to this statement.

telic" or so called "morphological" characters in order to strengthen the theory (*cf.* pp. 111–112) that such characters preserve evidences of interordinal kinship and separation better than "adaptive" or cænotelic characters. The auditory ossicles for example, as figured by Doran (1879), show that animals having approximately the same life-habits and which are outwardly similar, such as the Wolf and the Thylacine, may yet possess very different ossicles, which conform in each case to a recognizable ordinal type. In certain cases, however, the differences in the auditory ossicles between forms that are nearly related and of similar habits are so pronounced that the question is raised whether an abnormal range of variation may not sometimes occur in these palæotelic characters (p. 423). Many characters of this class require reëxamination. What for example is the phylogenetic or the adaptive meaning of the fact recorded below that Insectivores contrast both with the Marsupials and with many Placental orders in the slight extent of the vertical plate of the palatine?

Such in brief appears to be some of the problems and requirements of the study of osteology, if that study be approached not as a descriptive catalogue of unmeaning facts but as a vital element of the science of mammalian evolution.

Notes on the mammalian skull.

The general characteristics of the skull in Monotremes and Marsupials has been described above (pp. 155, 217–225). The skull of the ancestral Placentals doubtless resembled that of the Marsupial *Marmosa* in all those characters relating directly to minute size and insectivorous habits, such as the relatively large brain case, triangular, rather brachycephalic skull, pointed muzzle, elongate row of incisors, small canines, pointed premolars, sharp-cusped triangular upper molars, etc. But the ancestral Placental skull at a very early date became different from the ancestral Marsupial skull in many characters which have been listed above (pp. 253, 279) as "primitive Placental characters." From such a minute insectivorous type of skull, with a diphyodont dentition and a dental formula of $\frac{3.1.4.3.}{3.1.4.3.}$, the various types that are characteristic of the most primitive representatives of all the Placental orders may have been derived, in the manner outlined in preceding chapters.

A few notes upon some of the principal elements of the skull in the more primitive mammals may now be given.

Premaxillæ. Derived from the pointed type seen in *Galesaurus*. Surrounding the anterior palatine foramina, which appear to be continuous with the primitive reptilian choanæ. Ascending process originally far removed from frontals. In Rodents secondarily extending backward and

upward to meet frontals — perhaps correlated with backward growth of rootless incisors. Internal horizontal process homologous with the dumbbell bone of *Ornithorhynchus.*

Maxillæ. Overlapping premaxillæ and nasals; in contact internally with vertical plate of palatine; overlapped by palatines, jugals and lachrymals, finally gaining broad contact with frontals.

Palatines. Vertical plate pierced or notched by the sphenopalatine foramen. Vertical plate more or less extensive in Marsupials, Carnivores, Rodents, Primates, Ungulates and Edentates, reduced in Insectivores.

Palatal vacuities. In the Marsupials may be partly secondary, partly a result of the primitively imperfect development of the secondary palatal plates of the maxillaries and palatines. In the Insectivora palatal vacuities may well be secondary (*cf.* pp. 220, 286).

Pterygoids. Derived from pterygoids of Cynodonts, possibly in the manner suggested on page 120. Primitively consisting of thin lamellæ, articulating with basisphenoid and posterior extension of vertical plate of palatines, and closely appressed to pterygoid wing of alisphenoids. Often becoming reduced to a thin strip (*e. g., Equus*).

Pterygoid fossæ. Formed by the insinking of the ectopterygoid muscles which are originally (*e. g., Microgale, Arctomys*) fastened on top of the combined pterygo-alisphenoid ridge but gradually separate this ridge into its two components, so that the (ecto) pterygoid fossæ become bounded internally by the pterygoids (which are sometimes produced into a long hamular process), externally by the pterygoid wing of the alisphenoid (*e. g., Erinaceus, Lepus, Canis, Homo*).

Nasals. Distal end originally terminal and pointed. Proximal end spreading widely (*e. g., Didelphis, Meniscotherium, Mesonyx*) and almost excluding the maxillary from contact with the frontals. By the upgrowth of the maxillary the proximal expansion of the nasals becomes overlapped so that finally only the internal mesial fork of the proximal end remains exposed to view (*e. g., Erinaceus, Canis, Lemur*). Sometimes the external proximal portion of the nasals is overgrown by a forward process of the frontals (*e. g., Ursus*).

Lachrymals. Overlapping maxillaries, frontals and vertical plate of palatines, articulating with malars, usually pierced by lachrymal duct. Absent in Monotremes. Orbital portion large in Marsupials, with marginal foramen. Lachrymal becoming extended anteriorly with the prolongation of the face in Creodonts and certain Ungulates. In Insectivores becoming reduced, dorsally displaced and overlapped by alveolar portion of maxillary.

Frontals. Originally very small and anteriorly placed (Monotremes), covering chiefly the ethmoids and rhinencephalon; always forming dorsal

border of orbit. Spreading forward over nasals and maxillaries, encroaching posteriorly on orbitosphenoids and alisphenoids, becoming expanded transversely by the forward growth of the cerebrum. (The postorbial constriction (see p. 419) is also gradually widened by the growth of the frontal lobes.) Originally without postorbital processes, which appear to be related in the Metatheria to the postorbital bar of the Cynodonts, but in the Eutheria to the necessity for a strong ridge adapted not only for the attachment of the anterior portion of the temporal muscle but also to shield the nerves and muscles of the orbit from the disturbing action of the temporal muscle.

Interparietals. The paired interparietals of *Solenodon* (p. 242) and the unpaired interparietal of Marsupials, Rodents, *Orycteropus, Galeopithecus,* Ungulates, etc. (p. 242) may be homologous with the large "parietale mediale" described by Van Bemmelen in *Ornithorhynchus;* while the parietals of normal mammals may possibly be homologous with the "parietalia lateralia" of the same form. The interparietals may share in the formation of the tentorial plate (Weber). A large interparietal appears in *Oudenodon* (Broom).

Supraoccipital. The supraoccipital, which is a cartilage bone is usually unpaired, but it is paired in *Echidna* (Van Bemmelen), and it arises from paired centers in *Tatusia, Erinaceus* and the Cetacea (Weber, 1904, p. 49).

Orbitosphenoids. Preformed in cartilage. Very large in Prototheria, reduced in many Theria. Probably not pierced originally by optic foramen; overlapped on the internal surface of the brain case by the backward extension of the ethmoid. Marsupial and Placental types compared above (p. 245).

Alisphenoids. Preformed in cartilage. Large in Monotremes and Marsupials, reduced in Placentals. In Marsupials entering the glenoid, forming part of the bulla and extending well up on the side of the brain case.

Basioccipital. Exceedingly short in Cynodonts. Short in Marsupials and Insectivores. Progressively lengthening in Creodonts and Carnivores.

Basisphenoid. The pituitary fossa in Marsupials and certain Insectivores has the posterior clinoid process reduced or wanting (p. 245).

Squamosal. Primitively separated from the brain case by a post-temporal canal (Monotremes, Theriodonts). Glenoid fossa perhaps originally located about as in *Marmosa,* assuming a relatively posterior position by the forward extension of the mid-cranial region in *Didelphis* and *Thylacynus* (see above, p. 218); assuming a relatively anterior position by the backward extension of the base of the cranium in Placental Carnivores, Primates and primitive Ungulates.

Postglenoid process. In Cynodonts, in certain Mesozoic Marsupials

and in *Peltephilus* among Edentates extending below the level of the cheek teeth; in Marsupials and most Placentals above that level. In Insectivora the postglenoid process appears to have been originally of small size, and continuous with the "tympanic" ridge of the alisphenoid which runs inward and joins the pterygoid ridge of the alisphenoid (p. 244); by the reduction of this ridge and of the process itself (in *Macroscelides* and *Ptilocercus*) the glenoid fossa becomes more or less elongate and makes some approach toward the conditions seen in Rodents (p. 331). In certain Rodents (*e. g., Lepus*) the glenoid region shifts dorsally until finally (*Ochotona*) it almost usurps the position usually held by the postorbital process of the frontals. On the other hand, by the transverse growth of the postorbital ridge the familiar conditions in Carnivores and primitive Ungulates is produced.

Post-tympanic process of the squamosal. Apparently indicated in Cynodonts (p. 121), well defined in primitive Marsupials. Fused with the mastoid in *Erinaceus* (p. 261).

Paroccipital processes. Absent in Cynodonts, absent or feebly developed in the most primitive insectivorous Marsupials and Placentals; backwardly produced in *Erinaceus* and certain Creodonts (*e. g., Sinopa agilis*); progressively developing in many Carnivores and Ungulates.

Mastoid portion of periotic. Very large in Monotremes, conspicuous in Marsupials and primitive Placentals becoming reduced in size in Fissipede Carnivores and Ungulates. In *Hyrax* only the upper portion of the mastoid is exposed. In *Arsinoïtherium* it appears to be covered entirely.

Tympanic. The mammalian tympanic, according to Broom, has been derived from a certain element preserved in the skull of *Oudenodon, Dicynodon* and other mammal-like reptiles (p. 121). The primitive position of the ring-shaped tympanic was probably oblique to horizontal (*cf.* Monotremes p. 151, *Microgale* p. 246). As shown by the thorough researches of van Kampen (1905) the tympanic frequently offers characters of importance in phylogeny, *e. g.*, in the case of the Menotyphlous Insectivores (p. 274), Dermoptera (p. 317), Chiroptera, Lemuroidea (p. 326), Arctoid and Æluroid Carnivora.

Auditory Ossicles. The several possible homologies and modes of derivation of these ossicles are discussed on pages 125–143. Some of the phylogenetic results of Doran's important researches on the mammalian ossicula (1879) have been mentioned above under the various orders. It seems possible that an extension and thorough restudy of Doran's admirable work might lead to new evidence regarding certain theories of relationship. The form of the ossicula should be considered carefully with reference to function. How do aquatic, fossorial, arboreal and other habits affect the ossicula? How far are they influenced by the form or condition of the

surrounding parts? Until such problems are to some extent understood it will be difficult to judge for example of the phylogenetic significance of the imperforate columnar stapes of the Sloths and of *Manis* (p. 338). Is this truly a persistent primitive character? Is it an indication (possibly like the embryonic characters of the male organ in Sloths) of arrested development? Or is it a merely secondary loss (as in the Pinnipedia) of the stapedial perforation? What is the significance of the sudden departures from type observable in the ossicula of certain genera?

Ethmoturbinal complex. Paulli's researches (quoted by Weber, 1904) show that the characters of the olfactory bones confirm as far as might be expected the hypotheses of relationship developed in the preceding chapters. As indicated in the subjoined table, the Insectivora seem to be a central Placental type and to have transmitted their olfactory characters with little change to the Chiroptera, Lemuroidea, Rodentia, Carnivora and Hyracoidea. In the macrosmatic *Echidna*, Ungulata and Edentata, in which the rhinencephalon is very large the number of ethmoturbinals has considerably increased. In *Ornithorhynchus*, the Anthropoidea and Cetacea, which are microsmatic, the number is greatly reduced. The theory of the derivation of the Pinnipedia from the Arctoid Carnivora is strengthened.

The number and characters of the turbinals in the various orders may be summarized as follows:

	Number of endoturbinals exclusive of the nasoturbinal.	Number of olfactory scrolls.	*Remarks.*
Monotremata.			
Echidna.	7	7	Parallels *Orycteropus* in backward extension of endoturbinal series below cribriform plate, from which the scrolls project vertically.
Ornithorhynchus	3	4	Fenestræ cribrosæ represented by a single opening. Aquatic adaptation?
Marsupialia.	5	5	Mesethmoid well ossified, ends abruptly in middle of nasal cavity.
Insectivora.	4	5	Endoturbinals very generalized. Mesethmoid ends abruptly much as in Marsupialia (at least in *Solenodon, Centetes, Erinaceus*). In *Centetes* it grows upward between the frontals. (Beddard, 1901).
Chiroptera.	4	5	

	Number of endoturbinals, exclusive of the nasoturbinal.	Number of olfactory scrolls.	*Remarks.*
Lemuroidea.	4	5	Closely resembles Insectivore type. In correlation with reduced rhinencephalon: olfactory scrolls simple, cribriform plate narrow, with few perforations.
Anthropoidea.			Progressive reduction of turbinals and rhinencephalon (microsmatism).
Rodentia.	4	5	Closely similar to Insectivora (Paulli).
Hystrix.	4	6	
Carnivora.			Primitively very similar to Insectivora (Paulli).
Æluroidea.	4	5	*Epimycteri* Cope (Æluroidea plus primitive Arctoidea): maxilloturbinal doubly wound, not excluding nasoturbinal and second olfactory scroll from anterior nares. *Hypomycteri* Cope (*e. g.*, Ursidæ, Mustelidæ): maxilloturbinal branched and very large, excluding nasoturbinal etc. from anterior nares.
Canidæ.	4	5	
Remaining Fissipeds.	4	6–7	
Pinnipedia.	4	6	Hypomycterous condition carried to an extreme (p. 314) (Aquatic adaptation for warming inspired air).
Hyracoidea.	4	5	Closely similar to Insectivora (Paulli).
Proboscidea.	5	7	
Perissodactyla.			Macrosmatic. Ectoturbinals highly developed Perissodactyla and Artiodactyla. Ungulata in parallel Edentata in secondary increase of number in turbinals.
Equus	6	6	
Rhinoceros.	6	8	
Tapirus	7	8	
Artiodactyla.			
Tylopoda, Pecora.	5	6	
Suina.	5	8	
Tubulidentata.	9	11	Highest number among mammals (extreme macrosmatism).
Xenarthra. (except Sloths.)	8	9	Nasoturbinal very large, as in *Orycteropus.*
Sloths.	8	7	In *Cholœpus* mesethmoid well ossified and ending abruptly, much as in Marsupialia.
Cetacea.			
Balœnoptera.	3	3	Extreme reduction, anosmatism.

The Cranial Foramina.

Most of the cranial foramina are pretty constant in position throughout the Theria (except in the Cetacea). But certain foramina that are variable either in presence or position afford distinctive ordinal characters, so that many orders and often certain families, may be distinguished by one or more foraminal characters (*cf.* Monotremata, p. 150; Marsupialia p. 222; Insectivora pp. 253, 285, Rodentia, p. 329, Creodonta p. 306, Condylarthra p. 354, Proboscidea p. 367, "Protypotheres," Primates p. 321, etc.). For the convenience of the student a brief review of the cranial foramina is given below:[1]

I. Foramina for the cranial nerves.

Fenestræ cribrosæ. Nerve I. Lacunæ left in the cribriform plate; rarely (*Ornithorhynchus, Tarsius*) confluent into one or two openings.

Optic foramen. Nerve II. Apparently this nerve originally issued through the sphenorbital fissure (foramen lacerum anterius) (*cf.* Monotremata, Marsupialia, *Sorex*). It later pierced the orbitosphenoid (most Placentals).

Sphenorbital foramen (foramen lacerum anterius). Nerves III, IV, V_1, VI, and sometimes II. Constant. Opposite foramina lacera anterius confluent in Marsupials.

Foramen rotundum. Nerve V_2. Nerve originally issued through sphenorbital fissure (Monotremes). In Marsupials generally a prominent opening some distance behind the foramen lacerum anterius. In Placentals the alisphenoidal partition separating it from the foramen lacerum anterius is often poorly developed (*e. g., Arctomys*), this causing more or less confluence with the foramen lacerum anterius. In the Placentals the flange of the alisphenoid which is external to the foramen rotundum often grows forward and forms a common arcade into which the rotundum and foramen lacerum anterius open.

Foramen ovale. Nerve V_3. Originally issuing through the foramen lacerum medius but enclosed by the progressively increasing alisphenoid (Weber). The foramen ovale always looks toward the inner face of the mandible, since it gives exit to the mandibular branch of the trigeminus nerve. In Marsupials it is generally in or near that portion of the alisphenoid which extends on to the glenoid fossa. In Placentals it is sometimes secondarily confluent with the foramen lacerum medium (*e. g., Rhinoceros, Equus,* many Rodents, Cetacea).

[1] A very clear treatment of the foramina in the Dog is given in Reynold's 'The Vertebrate Skeleton,' pp. 399–402. Weber (pp. 47–52) reviews the mammalian foramina in general.

Infraorbital foramen. Nerve V_2. Constant in Theria (? Cetacea). Foreshadowed in the Cynodont skull (?). Must have been originally dorsal to the maxillary. ? Prototheria.

Ethmoid foramen, for the *entry* of the nasal nerve (a branch of V_1) and ethmoid artery. ?Constant in Theria.

Internal orbital (sphenopalatine) foramen. Nerve V_2. Constant in Theria. Always pierces or notches the vertical plate of the palatine. ?Prototheria.

Anterior palatine foramina. Nerve V_2. Constant (?Cetacea).

Posterior palatine foramina. Nerve V_2 (and blood vessels). Variable in position, often piercing the palatine, sometimes represented by vacuities (Marsupialia, certain Insectivores).

Internal auditory meatus (in petrosal). Nerves VII, VIII. Constant. The facial nerve (VII) passes through the petrosal and leaves the skull by the stylomastoid foramen.

Stylomastoid foramen (VII). Constant. "Lies between the tympanic bulla, the paroccipital process and the mastoid portion of the periotic" (Reynold's, *l. c.*, p. 400; *cf. supra*, p. 224).

Foramen lacerum posterius. Nerves IX, X, XI. Constant?

Condylar foramen. Nerve XII. Sometimes double (*e. g.*, Marsupials, *Ursus, Tapirus, Lepus*) or even triple (*Arctomys*, p. 329). Absent (confluent with for. lac. post.) in *Arsinoïtherium,* Proboscidea.

II. Foramina for blood vessels.

The location of the foramina for the two main branches of the carotid artery is of great importance.

Alisphenoid canal. For the external carotid. Posterior opening in front of foramen ovale; tunnels or grooves alisphenoid and, running forwards, sometimes becomes confluent with the foramen rotundum (*e. g., Canis*) but sometimes opens separately (Rodents). Absent in Monotremes, Marsupials, usually present in Insectivores, Creodonts (sometimes absent, p. 306); affording family distinctions in the Fissipedia; present in Condylarthra, Amblypoda, Hyracoidea, Arsinoitheria, Proboscidea, Perissodactyla; absent in Artiodactyla.

Foramen lacerum medium (Flower,= foramen lacerum anterius Weber). In the Dog the internal carotid runs forward through an entocarotid canal lying between the tympanic bulla, the petrosal and the basisphenoid, and enters the cranium through the foramen lacerum medium. In the Polyprotodonts (Figs. 1, 16) a similar canal (probably for the posterior branch of the entocarotid) pierces the basioccipital. In *Cœnolestes* (Fig. 15) this canal runs forward to the "carotid foramen" of the basisphenoid (see below).

In the Insectivora there are two main branches of the internal carotid as described above (p. 247). The course of these branches in the different families and orders has been carefully described by Winge and others and is noticed especially by Matthew (1909, p. 350).

"Carotid foramen" of Marsupials, etc. The internal carotids pierce the basisphenoid on either side in Monotremes and Marsupials (except *Acrobates*, p. 223). This condition may be foreshadowed in the Cynodontia[1] (Fig. 1*B*). A similar arrangement is reported in the Cetacea but in view of the strongly preponderating evidence for Placental affinities this condition in the Cetacea is very likely secondary. The internal carotid occasionally pierces the basisphenoid in certain other Placentals noted by van Kampen (1905, p. 383: *Erinaceus, Centetes*, Vespertilionidæ, *Orycteropus*, Herpestinæ.)

The *posterior palatine* and *infraorbital* foramina also serve to transmit blood vessels. So also the *suboptic* foramina (characteristic of Insectivores only ?). There are a number of foramina that have some relation to the *transverse sinus and jugular vein* which are described above (pp. 224, 248).

The *transverse canal* (venous) pierces the basisphenoid in Marsupials and Rodents.

The Vertebræ.

The vertebræ have so far yielded relatively few characters of much interordinal genetic importance, among which may be cited the following:

(1) Retention of distinct cervical ribs in Cynodonts and Monotremes, and on the axis of *Parameles* (p. 152).

(2) Retention of "intercentra" below the lumbars of certain Insectivora (p. 265) and below the cervicals of the embryonic *Bos*. The homology of these elements with the intercentra of reptiles is doubted by Weber (1904, p. 86).

(3) Frequency of the dorso-lumbar formula of 19–20 (D 13–15, L 7–5) among Monotremes, Marsupials and primitive Placentals (p. 275). The dorso-lumbar formula of Artiodactyls (*typically* D 13, L 6) contrasts with the formulæ of most Perissodactyls (D 18–20, L 6–3).

(4) Secondary increase in the number of vertebræ, *e. g.*, in the cervicals of Sloths, in the dorso-lumbar region of many Placentals (*e. g.*, Perissodactyls), in the caudal region of *Manis* and *Microgale*. In certain instances (*e. g., Galeopithecus*) this increase may be due to the shifting of the sacrum. Bateson (1894, pp. 106–123) has shown that where an abnormal increase or decrease in the number of vertebræ occurs the vertebræ that find themselves

[1] That is, if the deep fossa between the alisphenoid and basisphenoid in *Cynognathus* (Fig. 1*B*) really ended in a foramen.

in new positions take on the functions and appearance of the vertebræ whose position they have usurped.

(5) The perforation of the transverse process of the seventh cervical by the vertebral artery in Marsupials. This very rarely (*e. g., Lepus*) happens in Placentals.

(6) The large size of the proximal caudal vertebræ and of the root of the tail in many primitive mammals.

(7) The preservation of lumbar parapophyses in arboreal and cursorial forms and the loss of them in fossorial forms.

The "preaxial" and " postaxial" borders of mammalian limbs.

The conception of what constitutes the "preaxial" and "postaxial" borders of the parts of the limbs, as worked out by Huxley and Flower (1885, pp. 361–373) appears *in certain respects* to be artificial and incorrect. It was founded in part on erroneous notions of the phylogenetic relations of the Chelonia, "Enaliosauria" and Cetacea to the lower Mammalia. Flower's diagrams imply that the ancestral mammals had slender limbs resembling the highly modified type realized in the Primates. His theory starts with the limbs "extended at right angles to the axis of the trunk" in a horizontal plane. It assumes that the limbs were "parallel to each other" and more or less completely homodynamous. Concurrent evidence from many lines shows that these assumptions are both unnecessary and incorrect. In regard to the ultimate derivation of the primitive cheiropterygium from the pterygium of unknown Crossopterygians or Proto-Amphibians it is not necessary at present to make any assumptions. Neither do we know the *actual* genetic series which led from Carboniferous Amphibians to early Permian Cotylosaurs and thence from late Permian Therocephalians to early Triassic Cynodonts, Triassic Monotremes and Metatheria and perhaps Jurassic and Cretaceous Eutheria. But so many collateral offshoots of the direct series, representing different stages in the evolution of the limbs are known that the interpretation of "pre-" and "post-axial" above referred to requires considerable modification.

The subject may be introduced conveniently by a consideration of the shoulder girdle in primitive Placentals. The shoulder girdle in certain embryonic and adult Rodents and Insectivores retains in a more or less reduced condition certain bilaterally paired structures called by Gegenbaur "præclavia (*cf.* Weber, 1904, p. 94), which are doubtfully homologized by some authors with the procoracoids of Monotremes. In the adult *Microgale* (p. 237), as recorded by Leche, these structures appear as two large plates which dorsally overlap the sternum in the middle line. This, joined

to the evidence of the former large size of the coracoid in Edentates (Weber) and Rodents (Howes) suggests that the scapula of Placentals may have passed through a stage retained in the adult Monotreme. This hypothesis is somewhat strengthened by the great depth of the spina scapulæ and the small size of the prespinous fossa in the most primitive Insectivores; for according to the theory mentioned on p. 152, the border of the spine in Placentals and Marsupials is homologous with the anterior (acromial) border of the scapula in Monotremes, and the prespinous fossa is a neomorph. Since the Placentals and Marsupials are believed to be related and the Marsupials stand on a lower plane with respect to many characters, the occurrence of a Monotreme stage in the development of the shoulder girdle of Marsupials (p. 157) strengthens the inference that the Marsupio-Placental stem also passed through this stage. Finally, this conclusion is supported by the clear conception of the homologies of the borders and surfaces of the scapula in Prototheria and Theria which was worked out by means of a thorough study of the musculature by Wilson and McKay (1893), and by Broom (1899). Thus the Monotremes, in respect to the shoulder girdle as well as to the reproductive apparatus and functions and many details of the brain and vascular system are *morphologically ancestral to the higher mammals.*

From all this it follows that the blade of the scapula in the ancestral Marsupio-Placental (p. 226) was not reflected back over the ribs but was held in a nearly vertical position (Broom); the glenoid facet also must have been elongate and the head of the humerus flattened, with the shaft of the humerus running *backward,* but perhaps not so sharply outward as it does in Monotremes. This agrees perfectly with the evidence offered by the scapula and humerus of Cynodonts, which also show other ancestral Marsupial characters (pp. 119–120).

The humerus of the ancestral mammal must furthermore have resembled that of the Cynodonts, *i. e.,* it had very strong crests, a very broad heavy entocondyle ("entepicondyle" Owen), and a very large entepicondylar foramen.

The radius was very probably antero-internal to the ulna, *i. e.,* with reference to the humerus and partly to the anteroposterior axis of the body. This condition is preserved in Stegocephalia (*e. g., Eryops*), Cotylosauria (*e. g., Labidosaurus, Pareiasaurus*), Pelycosauria (*e. g., Naosaurus*), Rhynchocephalia (*e. g., Sphenodon*), Monotremata, and to a very large extent in all primitive Marsupials and Placentals. The idea that the proximal end of the ulna originally had a considerable share in the internal *anterior* face of the humeral trochlea (Flower) apparently is based on the conditions in Man and other highly specialized mammals. The flattened internal

part of the humeral trochlea in primitive mammals on its *posterior* face receives the internal process of the ulna. In many forms this internal process gradually extends forward on to the anterior face of the trochlea, and in Man causes the radial capitellum to be shifted to the extreme outer side of the humerus. This conception is directly in contradiction to that of Flower, who says (*l. c.*, p. 269) that in the "primitive or unmodified condition" the "radius articulates above with the preaxial (external) side of the humerus, the ulna with the postaxial (internal) side of the humerus." To him the primitive relations are "best illustrated in the fore-limb of the Cetacea" where the radial or preaxial border is "external," the ulnar postaxial border "internal." But the "Cetoid nature of the promammalia" (Albrecht) is a thoroughly discredited theory (p. 414), and as stated above, the evidence from many lower vertebrates shows that the primitive position of the ulna with respect to the humeral trochlea is wholly behind, and not side by side with, the radius. In brief, the *preaxial border* in the mammalian fore limb includes the following elements which on the theory that the humerus originally pointed backward and outward (see above) were all primitively more or less *antero-internal* with respect to the axes of the body:

Digit I.

Scaphoid.

"Front" face of radius (contrast Flower, fig. 133, p. 364.)

" " " humeral trochlea (contrast Flower, fig. 133, p. 364).

" " " humerus, including the deltoid crest (contrast Flower, fig. 133, p. 364).

Thus the entocondyle and ectocondyle were neither preaxial nor postaxial (contrast Flower's diagram, *l. c.*, p. 364) but in a plane nearly at right angles to the plane of the radius and ulna.

The "postaxial" (postero-external) border included the following elements:

Digit V.

Cuneiform.

Ulna.

Anconeal fossa.

"Back" (dorsal) face of humerus (contrast Flower, p. 365, fig. 134 G.).

The "preaxial" border of the scapula was antero-external in position, and was homologous with the spine and acromion of the scapula in higher mammals. The "postaxial" border of the scapula was posterior or postero-internal in position.

The evolution of the fore limb from the Prototherian to the Metatherian stage may possibly have been conditioned by the assumption of arboreal habits (*cf.* p. 226). It involved chiefly the following factors: (1) the back-

ward rotation of the scapula, (2) the drawing in of the elbows, (3) the movement of the glenoid fossa away from the sternum. This caused the humerus to assume a more erect position and to face forward rather than inward.

Flower's view (*op. cit.*, p. 269–270) that the permanent pronation of the manus in quadrupedal mammals is altogether a "very modified and adaptive position" appears very improbable. The manus was very likely turned *forward* as well as outward to a considerable degree even in *Pareiasaurus* (Broom, 1903.4) and certainly is so held in *Ornithorhynchus*. In fact, the pose of the manus may have remained relatively fixed as compared with the rapidly changing pose of the elbow, humerus and scapula. In the standing pose of the limb in Monotremes the ulna is largely *external* to the radius with respect to the body, but *posterior* to the radius with respect to what was later the front of the humerus. When the elbow was drawn inward the olecranon would become *posterior* to the radius with respect to the long axis of the body and would also retain its *posterior* relation to the radius with respect to the "front" face of the humerus. But the lower end of the ulna, being attached to the external part of the carpus in the relatively fixed pose of the manus, would always remain *external* to the radius. This, and not the *pronation* of the manus, may be the principal cause of the slight crossing of the long axes of the radius and ulna which is observed even in very primitive mammals. The *extreme* crossing of these bones in Man and the Elephant is a secondary condition.

The Pelvis and Scapula.

Flower also assumed the more or less complete homodynamy and serial homology of the parts of the scapula and pelvis and of the fore and hind limbs; his diagrams (*op. cit.*, p. 364) are in fact suggestive of Owen's "archetypal" homologies. But even in the Palæozoic Crossopterygian fishes we do not find any such correspondence. In the Permian Stegocephalia, Cotylosauria, Therapsida and Pelycosauria the scapula and pelvis were radically different and lend no support to the proposition that in every mammal "both scapula and ilium may be resolved into rods or bars of three sided prismatic form" (Flower, p. 369). The primitive form of the scapula has already been discussed (p. 432). If the mammals are derived from unknown Cynodonts, then the trihedral ilium of *Didelphis* must be derived from the flattened triangular ilium of the *Diademodon* type by the atrophy of the posterior angle and hypertrophy of the anterior border (Broom, 1905.4). Remains of this posterior border are preserved in *Orycteropus* (Broom). The ilium in very small primitive insectivorous forms like *Marmosa, Microgale,* and *Tupaia* is not trihedral but varies from a small

out-curved rod with a knob at the top (*Microgale*) to a spatulate form with rounded upper border (*Tupaia*).

The humerus.

The series of humeri figured herewith (Fig. 27) brings out many interesting facts, especially the following: The humerus of *Echidna* is seen to be a modified form of that foreshadowed in the Anomodontia, as represented (Fig. 27, no. 1) by the American Triassic genus *Eubrachiosaurus* Williston. Noteworthy features are the very broad entocondyle, the large greater and lesser tuberosities, the globular capitellum, and relatively weak ectocondyle; the ulna apparently took no part in the front face of the trochlea. The Marsupial type (Fig. 27, nos. 6–10) is directly derivable from the type seen in the Cynodont *Gomphognathus* (*cf.* p. 119). The Marsupials seem to be characterized by the prominence of the supinator crest which in many primitive Placentals (*e. g.*, Fig. 27, nos. 11–18) is less developed. The entepicondylar foramen has its primitive elongate character in several Marsupials, Edentates, *Periptychus*, etc. Very noteworthy is the loss of the entepicondylar foramen in *Castor*, *Arctomys*, and *Erinaceus*, as well as in all but the most generalized ungulates.

The primitive form of the humeral capitellum appears to be globular. In the ambulatory and cursorial forms (Fig. 27, nos. 7, 12, 16, 18) it becomes transversely cylindrical. The internal part of the trochlea was perhaps at first not very wide and served only for the radius (*cf.* p. 433). The humeri of *Myrmecophaga* and the Sloths are very peculiar (Nos. 3, 5). The very wide entocondyle and entepicondylar foramen, joined with the globular capitellum, may possibly be primitive features. Analogies with the Monotremes on the one hand and with *Castor* on the other are evident.

The series furnishes an instructive example of the manner in which palæotelic and cænotelic features are mingled in the humerus of every type. When classified in accordance with the supposed habits of the animals the humeri would be grouped about as follows:

Arboreal.	*Semi-fossorial.*	*Ambulatory.*	*Cursorial.*
Didelphis (6).	Echidna (2).	Arctocyon (11).	Viverravus (12).
Phalanger (10).	Eubrachiosaurus (1).	Solenodon(15).	Euprotogonia (18).
? Hapalops (5).	Myrmecophaga (3).	Periptychus (17).	Thylacynus(7).
	Dasypus (4).	Arctomys (14).	
	Phascolomys (8).	Erinaceus (16).	
	Castor (13).		

The brackets indicate close resemblances.

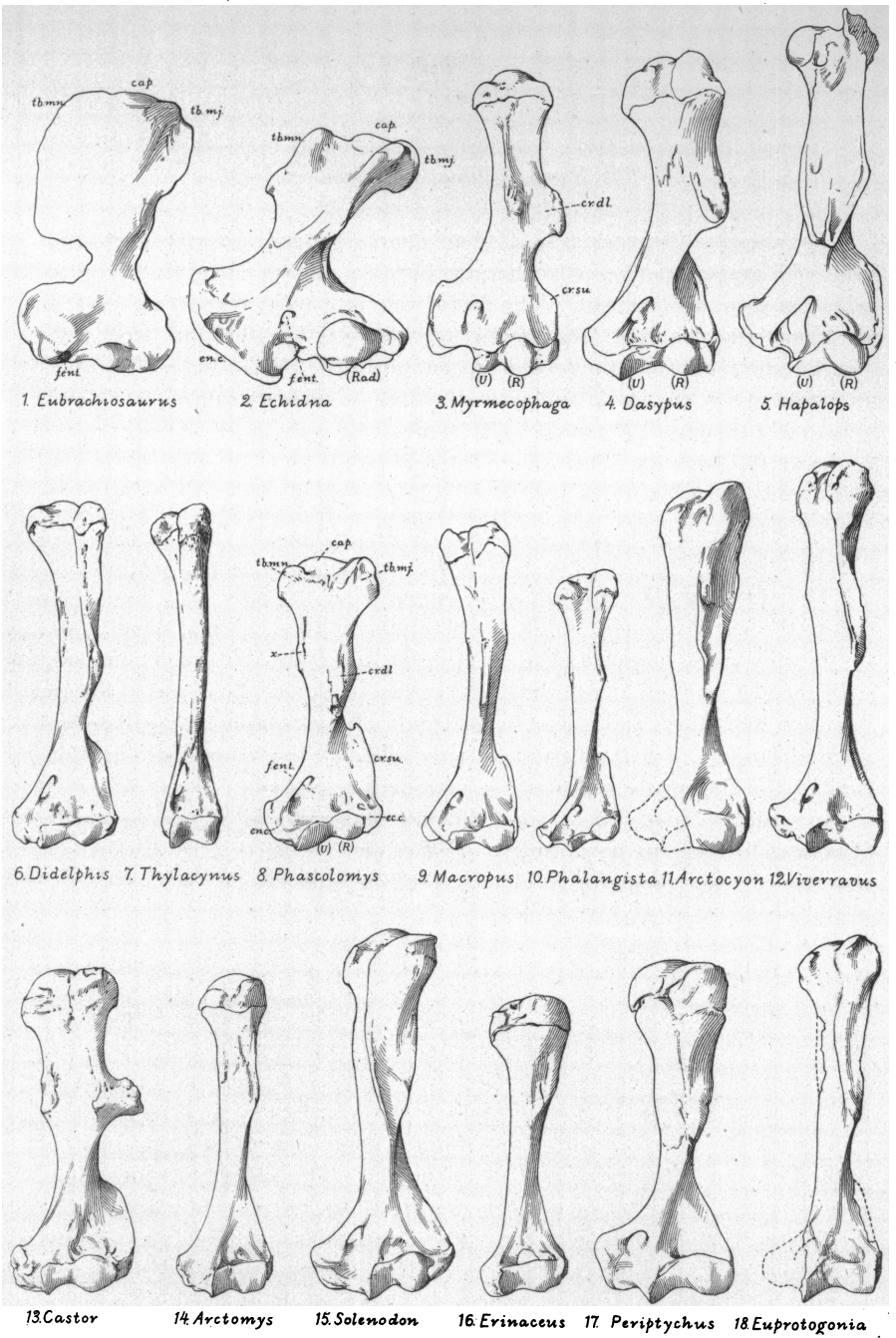

Fig. 27. Morphology of the mammalian humerus (p. 436). Scale various.

No. 1. *Eubrachiosaurus*, an Anomodont from the Upper Trias of Wyoming. After Williston. No. 5. *Hapalops* a Santa Cruz Gravigrade. After Scott. Other figures from specimens in the American Museum.

Abbreviations. *cap.*, head; *tb. mj.*, great tuberosity; *tb. mn.*, lesser tuberosity; *cr.dl.*, deltoid ridge; *x.*, tuberosity for the deltoid; *cr. su.*, supinator ridge; *ec. c.*, ectocondyle, or ectepicondyle; (*R*)., capitellum (facet for radius); (U)., trochlea (facet for ulna); *en.c.*, entocondyle, or entepicondyle; *f.ent.*, entepicondylar foramen.

The Femur, Tibia and Fibula.

The ancestral femur (p. 118) probably had a flattened expanded proximal end, with greater and lesser trochanters forming a continuous ridge, between which lay the sessile head. The femur was probably pointed outward, as in Monotremes (p. 154), the patellar trochlea was flat, the third trochanter not differentiated from the second trochanter ridge. The tibia was much as in Monotremes, the fibula ended proximally in a wide expansion (*cf.* Monotremes, Marsupials, *Microgale*). The pes was very likely turned partly outward, the first digit being antero-internal (*cf.* p. 435).

Evolution of the manus and pes.

The very important researches of Broom (1904.1) on the structure of the feet in the Permian and Triassic mammal-like reptiles and of Emery (1901) on the embryonic manus and pes of *Echidna* and *Didelphis,* when compared with the descriptions of the feet of Eocene mammals by Cope, Osborn, Matthew and others and also with the feet in all the existing unguiculate and ungulate orders, together furnish a fairly adequate basis for a review of the evolution of the carpus and tarsus in mammals.

In order to make clear what follows, the valuable figures given by Broom and Emery are here brought together and arranged in such a manner that they all now represent specimens from the same side.

A. The Carpus.

Permian Amphibians and Therapsidans.— The prototypal form of the mammalian carpus is more or less completely realized (Fig. 28, *2–4*) in the carpus of the Permian Anomodonts *Opisthoctenodon* and *Oudenodon* and the lower Triassic Dromasaurian *Galechirus,* as figured by Broom. This type is readily derived in turn from the still more generalized one realized in the Permian Stegocephalian *Eryops* (no. 1). The orders to which these genera belong are certainly much nearer to the ancestral mammals than is the Water Tortoise (*Chelydra serpentina*), the manus of which was selected by Gegenbaur (*cf.* Flower, 1885, p. 281) as being prototypal to that of mammals. Perhaps the most noticeable feature of the manus of *Eryops* is its more or less fin-like, or paddle-like, character, but it shows practically no feature in common with the largely hypothetical "cheiropterygium" and "archipterygium" of Gegenbaur (1895), and it cannot be compared with the paired fins of any known Devonian Dipnoans or Crossopterygians. It

is, however, analogous *in certain respects* with the posterior *dorsal* fin of the Devonian Crossopterygian *Holoptychius leptopterus* (*cf.* Woodward, 1898, fig. 19, p. 22). The metacarpals of *Eryops* are suggestive of the radial cartilages of the pectoral fins of *Polypterus*; its radius and ulna recall the pro- and metapterygia of that form; while the mass of carpals might correspond with the mesopterygium. The suggestion is that the proto-Amphibian or Crossopterygian ancestors of the land living vertebrates had paddle-like fins in which the bony elements, arising from the concentration of the basals and radials, became widely extruded from the body wall. Be that as it may, the manus of *Eryops*, as fully shown by Broom, certainly foreshadows the type seen in the Anomodonts.

The most striking feature of the manus of *Oudenodon* (Fig. 28, no. 2) is the retention of a more or less paddle-like character. The metacarpals are very short, much as in *Eryops*, and all the carpal elements of that genus are represented. In comparison with the carpus of mammals, that of *Oudenodon* retains two elements which are never found free in mammals, namely, the second centrale (c^2) and the fifth distal carpale. The manus of the Endothiodont genus *Opisthoctenodon* (no. 3) retains the so called "præpollex" which seems to persist in the embryo *Didelphis* (no. 9) and in certain Insectivores and Rodents. The importance of this structure has been emphasized by Bardeleben (1889). Whether it be called a digit or not is of little moment; its presence in the Permian Anomodonts and in certain modern orders is the important point. Moreover, as regards its status as a digit, there is no *convincing* evidence that it was not present in the Amphibian ancestors of the Anomodonts. The four fingered *Branchiosaurus* and the five fingered *Keraterpeton* probably do not stand very near to the direct ancestors of the Anomodontia. The præpollex is, however, not known in *Eryops* nor in the Dromasaurian *Galechirus*, but it is figured in the Therocephalian (?) *Theriodesmus* (Fig. 28, no. 5). As observed by Broom (*op. cit.*) the manus of *Galechirus* (no. 4) compares on the one hand with that of such typical reptiles as *Sphenodon* and on the other with that of *Theriodesmus*. The manus of *Theriodesmus*, which is possibly a Therocephalian, as reconstructed by Bardeleben and Broom (Fig. 28, no. 5), shows a decided progress toward the mammalian type, when compared with that of *Oudenodon*. The metacarpals are more slender and the oblique arrangement of the carpus is replaced by a more horizontal arrangement, betokening perhaps a more advanced pronation of the manus and better running powers. The radiale, intermedium, ulnare and pisiform distinctly foreshadow the scaphoid, lunar, cuneiform and pisiform respectively of mammals. The second centrale is reduced in size, the fifth distal carpale is apparently absent, and the fourth which is enlarged and, like its homologue the unciform of mam-

CARPI

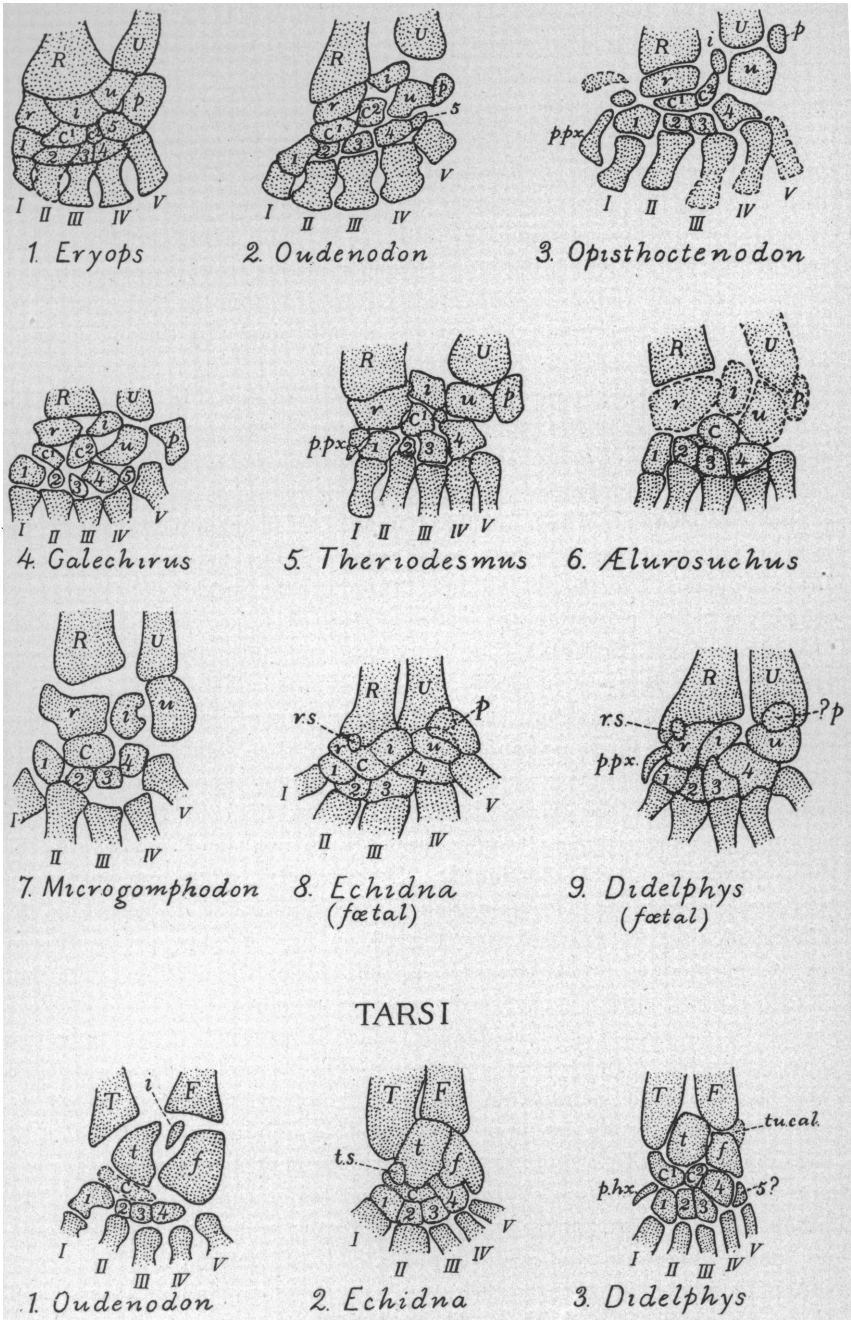
1. Eryops
2. Oudenodon
3. Opisthoctenodon
4. Galechirus
5. Theriodesmus
6. Ælurosuchus
7. Microgomphodon
8. Echidna (fœtal)
9. Didelphys (fœtal)
TARSI
1. Oudenodon
2. Echidna
3. Didelphys

Fig. 28.

Fig. 28. Carpus and tarsus of Permian genera in comparison with those of the embryonic *Echidna* and *Didelphis*.

Carpi: Nos. 1–6 after Broom, 7 after Seeley (specimen distorted), 8–9 after Emery.

Tarsi: No. 1 after Broom, nos. 2 and 3 after Emery.

Abbreviations: Carpus.

R., radius.
U., ulna.
r., radiale (scaphoid of mammals).
i., intermedium (lunar).
u., ulnare (unciform).
C^1, C^2 centrale (one or both together homologous with the centrale of mammals).
p.px., "prepollex."
1, carpale 1 (trapezium).
2, " 2 (trapezoid).
3, " 3 (magnum).
4, " 4 (unciform).
5. " 5 (disappears or fuses with no. 4).
I–V, metacarpals.

Abbreviations: Tarsus.

T, tibia.
F, fibula.
t, tibiale (astragalus).
t.s., tibial sesamoid.
i, intermedium.
f., fibulare (calcaneum).
C^1, centrale 1 (navicular).
C^2, " 2.
p.hx., "prehallux."
1, tarsale 1 (entocuneiform).
2, " 2 (mesocuneiform).
3, " 3 (ectocuneiform).
4, " 4 (cuboid).
5, " 5.
I–V, metatarsls.

mals, bears digits IV and V. The trapezium (1) is also much larger than the trapezoid (2), the second metacarpal is thrust up slightly between metacarpal 1 and metacarpal 3 as in primitive mammals (Osborn). The relations of the radiale, intermedium and centrale 1 precisely foreshadow the coalesced scapho-lunar-centrale of the embryonic *Echidna* (Fig. 28, no. 8). Centrale 1 occupies the position which it does in the manus of Eocene Creodonts, *Pantolambda,* recent Insectivores, Rodents, etc. By the absorption or disappearance of the minute centrale 2, the lunar (intermedium) would be brought into contact with the unciform (4) and thus *the alternating and falsely called "displaced" type of carpus is foreshadowed* even in the Triassic.

The manus of the Cynodontia (reptiles which as shown above resemble the carnivorous Marsupials in many characters) is unfortunately not well known. Broom has figured the lower part of the carpus with the metacarpals of *Ælurosuchus* and Seeley (1895, pl. i, fig. 7) figures the imperfect manus of *Microgomphodon* (Fig. 7). The "thrust up" position of digit II is again noticeable. Otherwise there are no very important differences from the type represented in the supposed Therocephalian *Theriodesmus.* No trace of the "præhallux" appears.

The above described manus of Permian and Triassic Therapsids might be expected to confirm or disprove the following ingenious suggestions, the arguments for which have been summarized by Matthew (1904, pp. 814–815): first that the trapezoid of mammals, which is unusually large in certain Eocene Creodonts, may be the serial homologue not of its fellow the trapezium, but of the metacarpals; secondly that the so called metacarpal of the first digit is really a modified proximal phalanx. This would explain first, the occurrence of only two phalanges on the first digit, secondly, the exceptional relations of the metacarpal and phalangeal epiphyses of digit I, thirdly, the anomolous arrangement of the muscles (Matthew). It cannot be said, however, that distal carpale 1 (the homologue of the trapezium) in either *Eryops, Galechirus, Opisthoctenodon, Ælurosuchus, Theriodesmus* or *Microgomphodon,* any more than in the embryonic *Echidna* and *Didelphis,* is of such a form as to give definite support to the hypothesis that it is the homologue of metacarpal II, although in *Oudenodon* it does suggest such a comparison. Broom (1906) has explained the anomolous relations of the epiphyses in digit I on mechanical (adaptive) grounds.

Monotremes.— The manus of the embryonic *Echidna* (Fig. 28, no. 8), as figured by Emery shows the following very interesting features:

(1) The distal end of the radius and ulna are now in contact, whereas in all the Therapsida they are separated. This condition was foreshadowed to some extent in *Oudenodon* (Fig. 28, no. 2) in which the radius had begun to overlap the intermedium and in which (as in *Echidna*) the ulna was also in

contact with the intermedium. Digit V in *Oudenodon* is nearly in contact with the ulnare (cuneiform); in the embryo *Echidna* it actually touches it.

(2) The whole manus is spreading and fan-like, suggesting that of *Oudenodon* and digits I and V likewise diverge sharply. The divergence of digit I and the spreading character of the hand in *Oudenodon* and the embryo *Echidna* as well as in the embryos of many higher mammals is especially interesting because it shows that the hand of the ancestral mammals had the potentiality of adaptation into either (*a*) the digging and swimming type or (*b*) the climbing and grasping type or (*c*) the ambulatory and finally cursorial types.

(3) In other characters the manus of the embryo *Echidna* is more like that of *Theriodesmus* (Fig. 28, no. 5). The scapho-lunar-centrale complex might be derived from the arrangement of the radiale, intermedium and centrale 1 in that genus; centrale 2 might have coalesced with the unciform (4). The intermedium (lunar) in *Echidna* articulates chiefly with the radius, a mammalian character, wheras in Therapsids it occupies the space between the radius and ulna.

(4) A radial sesamoid (Fig. 28, no. 8) which occurs also in the embryo *Didelphis* and in many higher mammals, is present.

Didelphis.— The manus of the embryonic *Didelphis* figured by Emery (Fig. 28, no. 8) is of a somewhat more normal mammalian type, but none the less is clearly derivable from the type seen in *Theriodesmus*, which it resembles in the relations of the præhallux (Fig. 28, no. 5) and of the distal carpalia 1–4. The intermedium (lunar) is now entirely overspread by the radius and has possibly united with centrale 2. Centrale 1 may have united with the scaphoid or with the lunar but at any rate it is never free in Marsupials. In the Marsupials also the magnum and unciform are generally larger than the lunar and cuneiform, whereas in most primitive Placentals the reverse is the case.

The lunar in *Didelphis* is in broad contact with the unciform, as is the case in the great majority of the primitive mammalian types. As compared with the embryonic manus of *Echidna*, that of *Didelphis* shows how readily the grasping-climbing type may be derived from the primitive fan-shaped paddle-like type.

Ancestral Placentals.— No mammalian manus is known before the Basal Eocene; consequently the morphological gap between the manus of the Therapsida and the manus of early Placentals has not yet been bridged over by discovery. We may feel certain, however, that the pentadactyl manus of the ancestral Placental must have had a more or less divergent pollex, a large trapezium, a free centrale, and a relatively small magnum, because these characters are preserved not only in the Basal Eocene Creo-

donts, in *Pantolambda* and in *Euprotogonia*, but also in all the more primitive existing Insectivores and Rodents. The ancestral Placental probably had another character of the greatest importance: namely, the lunar in the front view rested on the centrale, on the magnum and perhaps partly on the unciform.

The contact between the lunar and unciform may have been established as far back as the Triassic, as already noted. In varying degrees it persists in the majority of the Marsupials, Edentates, Rodents, Insectivores, Creodonts, Fissipedes, Tillodonts, Primates, Condylarths (*Euprotogonia*), Amblypods (*Pantolambda*), Notoungulata, Perissodactyla, Artiodactyla, Sirenia and Cetacea. The principal orders in which the lunar-unciform contact is greatly reduced or absent are the Tubulidentata, Hyracoidea, Embrithopoda and Proboscidea and it is very probable that its reduction in these orders is secondary (see below). The lunar-unciform contact and the existence of a separate centrale produces the alternating or interlocking arrangement, as first noted by Matthew (1897, pp. 299, 308). The idea that this interlocking arrangement in the Unguiculates is largely secondary arose from the unwarranted extension to the carpus of Unguiculates of Cope's famous but untenable theory of the evolution of the carpus of Ungulates (*cf.* pp. 449, 451).

The truly primitive nature of the so called displaced carpus of the Creodonts was first pointed out by Matthew (1897, pp. 308–309) who also advanced the theory (1904, pp. 811–814) that the primitive Placentals had been derived from pentadactyl forms in which the pollex and hallux were divergent and more or less grasping in function. The evidence for the *primitive nature of the interlocking carpus* in the various orders of Placentals may be reviewed briefly.

Insectivora. It has already been shown that the Insectivora as an order are exceedingly primitive in many ways. The lunar-unciform contact and a free centrale are preserved in the majority of the forms. Among the Zalambdodonta, *Centetes* and *Ericulus* show these characters, but in the otherwise primitive *Microgale* (figured by Leche, 1907, p. 80) the scaphoid, lunar and centrale coalesce and the internal inferior angle of the cuneiform is thrust in between the lunar and the unciform. In *Oryzoryctes* this tendency is greatly emphasized so that the scapho-lunar-centrale is widely separated from the unciform. In all these Zalambdodonts the trapezium is relatively large, as it is in Creodonts, and the pollex is more or less divergent. The carpus of Zalambdodonts is reviewed more in detail above (pp. 241–251). In the Eocene and Oligocene Leptictidæ the manus is not known. In *Erinaceus* and *Gymnura* the lunar-unciform contact is preserved. In *Talpa*, perhaps owing to the necessity for a compact and strong carpus, the interlocking features are emphasized in the oblique facets, and the

lunar-unciform contact becomes broad. In *Blarina*, on the contrary, in which the manus is very slender the carpals are flatter and the lunar-unciform contact slight. In *Tupaia*, which retains many primitive characters throughout the skeleton, the centrale remains free, the lunar-unciform contact is of moderate size, and the pollex is partly divergent. The scaphoid however, is fused with the lunar. In the terrestrial *Rhynchocyon*, as figured by Peters (1852, pl. xxiii, fig. 2), digit I is lacking, the carpals are flattened and the lunar-unciform contact (at least in front view) is very slight. In the allied *Petrodromus* (*l. c.*, pl. xxiii, fig. 6) digit I is reduced, the magnum is relatively large and separates the lunar from the unciform, but in the back view (*l. c.*, fig. 6a) the lunar-unciform contact appears to be well developed.

The ancestral Insectivores certainly had a free centrale. If they were arboreal or semi-arboreal forms with more or less spreading feet as suggested above (p. 288), then they very likely had at least some contact between the lunar and the unciform.

Rodentia. The carpus in forms with spreading digits (*e. g.*, *Fiber*, *Castor*) has oblique carpal facets and a broad lunar-unciform contact. In the forms with narrow feet of ambulatory type (*e. g.*, *Mus*, *Lepus*) the carpals are broad and flat and the lunar-unciform contact is small. The centrale is usually free but the scaphoid is often fused with the lunar. In *Mus* the front view of the centrale shows it as a very small round bone, but dissection of the carpus shows that the centrale is really broad and much flattened.

Tillodontia. The details of the carpus of the Lower Eocene *Esthonyx acutidens* are very suggestive of the Creodont type. The trapezium is large, the scaphoid shallow, the centrale occupies the same position as it does in Creodonts, the magnum is keeled on top, the unciform is high, and the cuneiform is shallow. The lunar rests about equally on the centrale, magnum and unciform.

Creodonta. The manus of the Basal Eocene forms is partly known in *Dissacus carnifex* (figured by Osborn and Earle, 1895, p. 33) a primitive member of the Mesonychidæ; and in *Clænodon corrugatus* (figured by Matthew, 1901, p. 14), a member of the Arctocyonidæ. The manus is also known in *Dromocyon* (Fig. 26, p. 405) and *Mesonyx*, in *Hyænodon*, *Sinopa*, *Oxyæna*, *Patriofelis* and others. The primitive features of all these forms may conveniently be summarized in the accompanying generalized scheme of the Basal Eocene Creodont manus (Fig. 29). The most noteworthy features are the large trapezium and divergent pollex, the large free centrale, small trapezoid, magnum smaller than lunar, lunar resting almost equally on centrale, magnum, and unciform. In regard to the digits, D. I is divergent, D. II overlaps III and III overlaps IV. This overlapping was formerly regarded as an evidence of marked "displacement" but it is much more

probably merely an emphasis of conditions partly foreshadowed in the Permian *Theriodesmus*.

From this primitive type the carpus of *Clænodon* (p. 304) may be derived by the fusion of the centrale and scaphoid, the close appression of the lunar to the scapho-centrale and the broadening of the lunar-unciform contact; that of *Dromocyon* may be derived by the suppression of digit I, the increase in size in digit II, the broadening of the lunar-unciform contact. It should not be forgotten that the known Creodont manus pertained to animals that were already several times larger than the small insectivorous forms from which they were probably descended. The manus in the primitive Oxyclænidæ is unfortunately not known; but it appears probable that the minute insectivorous ancestors of the Creodonts had a rather slender hand, with flattened carpals, a large trapezium, free centrale, a small lunar-unciform contact, and a slightly divergent hallux.

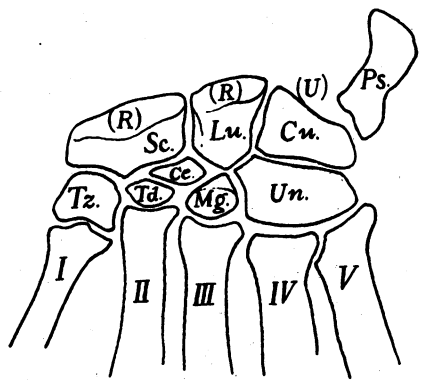

Fig. 29. Generalized scheme of the Basal Eocene Creodont carpus; based on a study of the carpus of *Clænodon*, *Triisodon*, *Sinopa*, *Oxyæna*, etc. Many features of this type were foreshadowed in the manus of Permian Therapsids (p. 434), and according to the writer's view it is itself prototypal to the carpus of all the Placental orders.

Fissipede Carnivores. Matthew (1909, p. 388) has shown that the ancestral type of manus is realized in the Miacidæ, in which the scaphoid, lunar and centrale, although closely appressed, are not yet fused into a single bone. The hand was primitively of the grasping type and the lunar-unciform contact is always broad.

Condylarthra. All authorities now agree that the famous *Phenacodus primævus* of Cope is less primitive as regards size and characters of the dentition than its small Basal Eocene forerunner and presumable ancestor *Euprotogonia puercensis*. As regards the carpus, Matthew (1897, pp. 308–309) has shown that *Euprotogonia* has an alternating, not serial, carpus, in which there was a distinct oblique lunar-unciform contact, the magnum had "a comparatively small upper surface" and was "extended proximally into a keel separating two nearly equal facets, one for the lunar, the other supporting the scaphoid, or as may be suspected, a centrale." After showing that in many characters *Euprotogonia* was intermediate between the later *Phenacodus* and the Basal Eocene Creodonts, Matthew concluded that the

alternating carpus of *Euprotogonia* as well as that of the Basal Eocene *Pantolambda* was also an inheritance from the Creodonts and that therefore the serial carpus of *Phenacodus* was probably secondary. This important generalization receives strong additional support from the fact already noted that the most essential features of the interlocking carpus were foreshadowed as far back as the Triassic and are still preserved in varying degrees in the more primitive pentadactyl unguiculates of every order. Matthew's conclusion opened the way for a recognition of the possibility that the Perissodactyla and Artiodactyla may have been derived from forms with a carpus resembling that of the oldest Creodonts, and at the same time it implied that *Phenacodus* in respect to its carpus was very far from being the "atavus" of all the Ungulates. Matthew also concluded that the carpal pattern of *Phenacodus* was probably derived from that of *Euprotogonia*: (1) by the flattening of all the elements, (2) by the reduction of the centrale and its fusion with the antero-external angle of the scaphoid, (3) by the broadening and flattening of the magnum; this caused the reduction of the lunar-unciform facet which however persists in a reduced condition in some specimens.

Meniscotherium. This Lower Eocene Condylarth is relatively highly specialized in the degree of complication of its cheek teeth, and belonging as it does to an order in which the carpals showed great variation, it would not be surprising if its carpus also had undergone considerable modification. As provisionally reconstructed by Matthew, the five toed manus appears to lack the free centrale, and all the carpals are considerably flattened. The trapezium is large. The lunar is suggestive of that of *Hyrax*. The magnum is flattened but is much smaller than in *Hyracops socialis*, as figured by Marsh (Matthew doubts the accuracy of this figure). A small lunar-unciform contact is retained. In brief, the carpus of *Meniscotherium* is becoming serial like that of its contemporary *Phenacodus*, perhaps in adaptation to exclusively ambulatory, as opposed to grasping, functions (*cf. Hyrax*).

Taligrada. The carpus of *Pantolambda* (figured by Osborn, 1898, p. 187), a genus which in many characters is structurally ancestral to the Amblypoda, is strongly interlocking and directly derivable from the Creodont type. As noted by Matthew, the centrale occupies its primitive position which is also the position of the internal hook of the scaphoid in Perissodactyls, *i. e.* it articulates with the magnum, trapezoid, lunar and scaphoid. The trapezium is very large (as in Creodonts) and the pollex rather divergent. The lunar-unciform contact is broad. This may be partly secondary and a result of the progressive widening of the unciform which is characteristic of the order. The manus of *Periptychus* is not known, but judging from the close resemblance of its pes to that of *Pantolambda*, its manus was probably of the interlocking type.

Amblypoda.— In *Coryphodon*, as noted by Osborn (1889, p. 539) *pari passu* with the increasing weight of the body and with the widening of the distal end of the ulna, the carpus becomes very broad, the unciform grows toward the inner side, overspreading the third metacarpal and broadening the lunar-unciform contact; the magnum also spreads in the same direction, the lunar widens and causes the reduction of the scapho-centrale-magnum contact. In *Uintatherium* these tendencies are carried to an extreme (*cf.* p. 358).

Hyracoidea. The carpal facets are more or less horizontal, so that the proximal row articulates with the distal row by a horizontal and very convex joint. The magnum is relatively large, the lunar partly overspreads the trapezoid and centrale; the lunar-unciform contact is variable but it is very evident in the back view at least in the specimens examined by the writer.

Embrithopoda. The carpus is very similar to that of *Elephas*, while the tarsus resembles the *Coryphodon* type. This may imply that *Arsinoitherium* has been derived from a short footed form with a carpus resembling those of *Meniscotherium* and *Hyrax* and a tarsus like that of *Pantolambda*.

Proboscidea. The evolution of the manus in the Proboscidea has been traced by Osborn (1889, p. 564, diagram 8) and by Weithofer (1890). In correlation with the growth of the ulna and the reduction of the radius, the cuneiform and especially the lunar, become very broad, the lunar overspreading the trapezoid and causing the reduction of the scaphoid.

Pyrotheria. As shown by the casts in the American Museum of Natural History, the manus ascribed to *Pyrotherium* is very Proboscidean in general appearance, and differs from the manus of *Mastodon* chiefly in the extension of the lunar over the unciform. According to Gaudry (1909) however the reference of this manus to *Pyrotherium* may be incorrect, and Gaudry states that Tournouër has suggested that it pertains to *Astrapotherium*.

In brief, the manus in the Condylarthra, Taligrada, Amblypoda, Hyracoidea, Embrithopoda, and Proboscidea is either progressively serial or at least flattened. All exhibit a tendency for the carpals to change the oblique into horizontal facets, so that the first row articulates with the second row by more or less horizontal joints which extend across the carpus on about the same level. The lunar is always broad and tends to spread inward over the trapezoid, the scaphoid often loses contact with the magnum and the scapho-centrale hook is reduced or absent. The lunar-unciform contact usually becomes reduced (except in Taligrada and Amblypoda).

Notoungulata. The carpal types of the Homalodotheria (p. 449), Typotheria (p. 376), Toxodontia (p. 109), and Litopterna (p. 379) are very diverse and include extreme interlocking types and peculiar forms of the serial type, but in no case do they show any features that seem inconsistent

with the theory that these orders have been derived from different families of the Condylarthra. The strongly interlocking types represented in *Homalodotherium* and the Typotheres have doubtless been evolved by a progressive increase in the obliquity of the facets and by the broadening of the lunar-unciform and scapho-centrale-magnum contacts. In the larger Toxodontia, as in the Perissodactyls, this is associated with a marked tendency toward mesaxonic tridactyly. In the Litopterns the carpals have flattened down and the lunar-unciform contact has been disrupted (p. 379).

Artiodactyla. The theory that the Artiodactyla (p. 403) have been derived from relatives of the Mesonychid Creodonts, and the Perissodactyla (p. 396) from relatives of the stem of the Condylarthra is supported in large measure by the nature of the resemblances and differences between the manus of Artiodactyls and that of Perissodactyls. The manus of Artiodactyls has been derived from a progressively paraxonic, functionally tetradactyl type with interlocking carpus, more or less resembling the manus of *Dromocyon* (p. 404); the manus of Perissodactyls has been derived from a mesaxonic progressively tridactyl type more or less like that of *Euprotogonia*; but in this type the carpus, while interlocking, was narrower and higher than was the case in the Artiodactyla. In both orders digit III was originally the largest but in the ancestral Artiodactyl its superiority over digit IV was less than was the case in the ancestral Perissodactyl. The general resemblance of the carpus of *Ancodus*, a primitive number of the Anthracotheriidæ to that of *Dromocyon* has already been noted above. Nor can there be any doubt that the carpus of *Ancodus* is approximately prototypal to that of all higher Artiodactyla; for it compares with those of the hippopotamus and pig on the one hand, while on the other by further emphasis of its didactylism it would lead into the carpus of the larger Anthracotheres, and of the Oreodontidæ, Hypertragulidæ, Camelidæ, Cervidæ, Bovidæ, etc. The unity of derivation of all the more modified types of carpus in the Artiodactyla and the contrast in important details with all other ordinal types of carpi, becomes plain from a study of the Tertiary Artiodactyls exhibited in the American Museum of Natural History and from the figures given by Kowalevsky (1873), Scott (1895) and others. From all this it is evident that it is misleading to say as Cope did that the "carpus of Artiodactyls is of the highly displaced type." In the oldest and indeed in all Artiodactyla the lunar-unciform contact is broad and the scapho-centrale process or hook is in contact with the magnum. Very probably the lunar-unciform contact and the scapho-centrale-magnum contact were narrower in the ancestral Artiodactyls than they were in later Artiodactyls, but the interlocking arrangement is no more a true "displacement" in the Artiodactyla than it is in the Basal Eocene Creodonts or in *Euprotogonia* or *Pantolambda*.

Perissodactyla. According to Cope's original view, the characteristic arrangement of the carpals in Perissodactyls, in which the scaphoid in front view rests largely on the magnum, the lunar on the unciform, was derived from the serial condition of *Phenacodus* and was produced by the shifting or displacement of the proximal row upon the distal row. Osborn, in his study on the 'Evolution of the Ungulate Foot' (1889, pp. 560–569) took the more correct view that this "displacement" was brought about by metatrophic growth in response to certain mechanical requirements, the theory of which he developed at length. But both Cope and Osborn took the serial carpus of *Phenacodus* as the starting point. From what has already been said, however, it will be clear that this assumption is not in accordance with the present evidence. A reëxamination of the carpus of the known Eocene Perissodactyla and of the trend of evolution in the various families leads to the following conclusions:

(1) So far as present evidence indicates, in the ancestral Perissodactyl the manus was narrow, more like that in *Heptodon* (Fig. 23), and not broad like that in *Palæosyops*. Reasons:

(*a*) Small light-bodied primitive forms often have a narrow manus, especially cursorial forms (*e. g.*, cursorial Polyprotodonts, Creodonts, Fissipedes and Rodents (Agutis)).

(*b*) The manus of *known* Lower Eocene Perissodactyls, representing the principal families, are all relatively narrow.

(*c*) Several families exhibit an *apparent* progression from narrow footed cursorial to broad footed slow moving forms.

Compare *Lambdotherium* and *Eotitanops* with *Palæosyops* and *Titanotherium.*

Compare *Heptodon* with *Lophiodon.*
" *Paloplotherium* " *Palæotherium.*
" *Hyrachyus* " *Metamynodon* and *Teleoceras.*

(2) In the ancestral Perissodactyl the middle digit was already in the ascendant but perhaps to a less degree even than in *Heptodon*; for

(*a*) The manus is already mesaxonic in *Meniscotherium* and *Pantolambda,* and even in the Artiodactyls digit III was primitively longer than digit IV (*cf.* p. 405).

(*b*) Digit III is somewhat longer than its fellows in the majority of the Unguiculates.

(3) In the ancestral Perissodactyl the magnum in front view was small. This is supported by:

(*a*) The progressive *widening* of the magnum in Titanotheres, Horses, Amynodonts, and Lophiodonts.

(*b*) The small size of the magnum in the Lower Eocene *Heptodon, Lambdotherium,* and *Eotitanops.*

(*c*) The small size of the magnum in *Euprotogonia*, *Pantolambda*, Creodonts and many lower Unguiculate orders.

(4) In the ancestral Perissodactyl the lunar in back view rested on both magnum and unciform (*cf.* Fig. 25). This condition is preserved in all Perissodactyls and is a direct inheritance from the unguiculate orders.

(5) In the ancestral Perissodactyl the proximal row of carpals were vertically deeper than the distal row, for:

(*a*) This is so in the Lower Eocene forms.

(*b*) It seems to be a primitive character in Creodonts and other Unguiculates.

(6) Even the oldest known Perissodactyls had already attained the ordinal characters in the astragalus and in the reduced number of digits, and since the manus had already lost digit I, it is probable that the carpus also had advanced considerably in the Perissodactyl direction.

(7) If the carpus had advanced considerably in the Perissodactyl direction, then in the light of the foregoing considerations, in its earlier state it must have approached the unguiculates in the following characters, in comparison with those of *Heptodon* (Fig. 23, p. 393):

(*a*) Magnum small in front view (about as in *Heptodon*).

(*b*) Smaller lunar-unciform contact.

(*c*) Smaller scapho-centrale-magnum contact.

(*d*) Larger trapezium and digit I.

(*e*) Relatively smaller digit III, with narrower proximal abutment on the unciform.

(*f*) Unciform more horizontal.

(*g*) Carpal facets less oblique.

In other words, the carpus of the ancestral Perissodactyl was less completely interlocking, and somewhat more "serial," than that of *Heptodon* which appears to the writer to be on the whole the most primitive Perissodactyl manus so far discovered.[1]

(8) From this point of view Cope and Osborn were justified in regarding the carpus of later Perissodactyls as "displaced" only in so far as the scapho-centrale-magnum and lunar-unciform contacts became secondarily widened, but it is very probably incorrect to state that in the ancestral Perissodactyl the "scaphoid rested solely on the trapezoid and the lunar on the magnum."

Ancylopoda. The carpus of *Moropus* and *Chalicotherium* is characterized by: (*a*) the extreme convexity of the proximal facets, (*b*) the backward extension of the superior and inferior facets on the magnum, so that

[1] In *Eohippus* the scapho-centrale-magnum contact is very broad, the magnum is broad and digit III is very broad.

the posterior hook or toe of the magnum becomes part of the articular surface for digit III, (*c*) the broad overlapping of the metacarpals, etc. But all these and other peculiarities present nothing inconsistent with derivation from the carpus of Lower Eocene Perissodactyls (p. 398).

Sirenia. The carpus in *Manatus* contains the principal elements, with the exception of the centrale. The lunar rests mainly on the magnum but retains the connection with the unciform.

Cetacea. The carpus in *Globiocephalus* retains elements which are interpreted by Flower as scaphoid, lunar, cuneiform, trapezium (?), trapezoid and unciform. The lunar-unciform connection is retained.

Summary in regard to the carpus: The principal conclusions of the preceding section are as follows:

(1) The structural prototype of the mammalian carpus is realized in the Permian and Triassic Therapsida in which the carpus differs from that of mammals chiefly in retaining two elements (centrale 2, and distal carpale, 5) which afterward disappeared at least as separate elements.

(2) The essential features of the interlocking type, namely the scapho-centrale-magnum and lunar-unciform contacts are present in many Unguiculate orders and are probably a primitive mammalian character.

(3) In Unguiculates the retention of the grasping function, and of a divergent pollex, favors the development of oblique facets and of a strongly interlocking carpus (*e. g., Didelphis, Talpa,* Creodonts, Primates).

(4) The loss of a divergent pollex and the development either of ambulatory and cursorial habits or of great weight often favors the flattening of the carpal facets in horizontal planes and the development of the serial carpus (*e. g.*, certain Insectivores, Rodents, *Hyœnodon, Hyrax,* Proboscidea, etc.).

(5) The Perissodactyl and Artiodactyl manus have both been derived from different varieties of the incipiently interlocking type. In both also the interlocking features became emphasized, the serial features more or less suppressed.

(6) The observed and inferred modes of evolution of the carpus in mammals suggests first the complexity of the factors that have contributed to the results and secondly the apparent inadequacy of explanations which take into account only natural selection on the one hand and adaptive fitness on the other. For example, it might be assumed that the rectangular character of the carpals in the Proboscidea was largely an adaptation to great weight, but since the carpals are almost equally rectangular in the small-bodied *Hyrax,* it is quite possible that in the Proboscidea this condition was established before great weight had been acquired.

(7) In the different orders different elements of the carpus seem to be

the dominant factors and to have as it were, greater growth vigor to crowd and modify their fellows. As shown by Weithofer (1888) and Osborn, (1889, p. 539) in the Proboscidea the ulna and the lunar are in the ascendant, the scaphoid is literally crowded out; in the Amblypoda the unciform and digit III broaden, in the Hippoids it is digit III and the magnum; in *Macrauchenia* and the Litopterns the cuneiform acquires a broad contact with the magnum, widely disrupting the former lunar-unciform contact.

Conceivably the active or dominant features may have been "unit characters" or orthogenetic characters which were not divided in crossing, while the elements which appear to be passive may have been more subject to fluctuating variation and to division. The evolution of the carpals furnishes a good illustration of the very obvious principle that there is a strong analogy between the evolutionary relations of parts to each other and of parts to environment.

The Hind foot.

1. The astragalus.

Oudenodon. The pes of *Oudenodon* figured by Broom (Fig. 28, no. 2) indicates that the true "tibiale tarsi" is not the sesamoid so named by Baur (1885) in Rodents, *Galeopithecus*, etc., but the astragalus itself, the intermedium being a greatly reduced element.

The astragalus and calcaneum of *Oudenodon* are prototypal in form to those of mammals, because they are very simple in shape and the astragalus is not differentiated into trochlea, neck and head, nor the calcaneum into tuber, sustentaculum, etc. The other elements of the pes are homologous with those in mammals. Most of the elements of the pes correspond in position with those in the manus, but the lunar (intermedium) of the manus, which was destined to increase in size, corresponds with the intermedium in the pes which was destined to disappear as a separate element; hence in the mammals the correspondence between the manus and pes is never complete (see below, page 455).

Monotremes. The pes is described on page 154.

Marsupials. The astragalus and calcaneum of the ancestral Marsupials (as described below) are adapted to a divergent hallux and more or less arboreal habits. As observed in the smaller Marsupials these bones are especially interesting because they are morphologically intermediate between the Therapsid and Monotreme types on the one hand and the Placental types on the other. For example, in the astragalus of *Didelphis* (Fig. 30, *A*) the trochlea is very broad, with a very indistinct groove while the neck is feeble and not differentiated from the head, the sustentacular facet is in the middle

part of the back and not separated from the navicular facet. The navicular facet, in correlation with the spreading character of the pes extends up on the inner side of the neck. The tuber of the calcaneum is pointed downward as well as backward and the foot is entirely plantigrade. In *Phascolomys*, representing the Diprotodontia, the ectal, sustentacular and navicular facets are quite continuous, and the sustentacular is still near the outer border of the back (Fig. 30, *B*). Just internal to the ectal-sustentacular facet is a deep groove;[1] a similar groove in *Ectoconus*, *Patriofelis*, etc., lies *between* the ectal and sustentacular facets and terminates in the astragalar foramen. In an

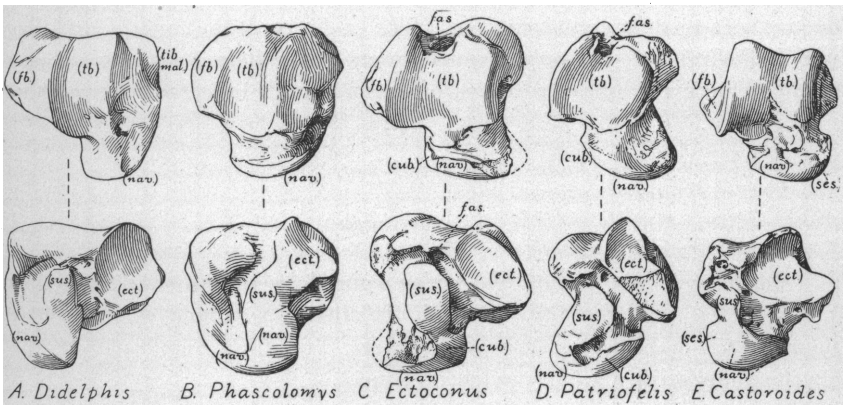

Fig. 30. Morphology of the astragalus in Marsupials etc. From specimens in the American Museum. Scale various.

(*tb.*), tibial facet.
(*fb.*), fibular "
tib. mall., surface for malleolar portion of tibia.
(*ect.*), ectal facet.
(*sus.*), sustentacular facet.
(*nav.*), navicular "
(*cb.*), cuboid "
(*ses*), facet for tibial sesamoid.
f.astr., astragalar foramen.

astragalus of *Ectoconus* (Amer. Mus. No. 3036) a Periptychid, wrongly ascribed by Cope to the Basal Eocene *Polymastodon* (p. 169), we find a clear foreshadowing of the Placental type, in so far as regards the better development of the trochlear ridges, the separation of the neck from the trochlea, the angulation of the internal inferior region of the neck, the presence of an astragalar foramen, the beginning of the separation of the sustentacular and navicular facets, and the more central position of the sustentacular facet.

The most distinctive features of the primitive Marsupial astragalus thus appear to be:

[1] Possibly lodging a branch of the peroneal artery (Matthew, 1909, p. 451).

(1) Its oblique position on the side of the calcaneum.

(2) Its very broad trochlea, with poorly defined condylar ridges.

(3) Its short neck, not produced inferiorly, especially at the infero-internal angle.

(4) The relatively external position of the sustentacular facet and its continuity with the navicular facet.

(5) The absence of a cuboid facet.

Placentals. There is some doubt as to which is the most primitive type of astragalus known among Placentals but the type with very broad trochlea, short neck and convex head [1] seen in the most ancient Rodents, Edentates, Basal Eocene Periptychids and *Homalodotherium* appears to be morphologically nearer the Marsupial type than does the relatively long narrow astragalus, with narrow trochlea and slender neck seen in the smaller Creodonts, Condylarths (*Euprotogonia*) and certain Insectivores (*e. g., Microgale,* [Fig. 19, C^3, p. 250] *Sorex, Tupaia*).

Rodents and Edentates. In these orders, as well as in some of the Notoungulata (*e. g., Homalodotherium*) the astragalus usually has a very wide low-keeled trochlea a short oblique neck and a very convex or even globular head, and the ectal and sustentacular facets are more or less parallel, oblique, and separated by a deep groove which sometimes (*e. g., Orycteropus Homalodotherium*) ends in an astragalar foramen.

The cuboid contact is variable but usually absent. The astragalus of the Eocene Rodent *Paramys* (p. 327) approaches the Insectivore type.

Insectivores. In the more primitive Lipotyphla (pp. 252, 254) the astragalus, as stated above, is primitively long and slender, at least in certain Zalambdodonta (Fig. 19, p. 250), Erinaceidæ and Soricidæ; but has a wide trochlea and short neck in *Pantolestes* (Matthew). The trochlear crests are developed to a varying extent but the inner is often subequal with the outer one. A vestige of the astragalar foramen appears to be present in *Erinaceus* (p. 252).

Creodonta. In this group the trochlear ridges are variable; in *Patriofelis* the ridges are but faintly expressed, in *Hyænodon* and the Mesonychidæ they become very pronounced. The astragalar foramen is usually present but is lost in the Mesonychidæ; it appears to have resulted from the bridging over of a notch in the postero-superior rim of the trochlea, which notch was probably continuous with the groove between the ectal and the sustentacular facets (see above, p. 454). An astragalo-cuboid contact appears to be a primitive character for the Creodonta (as it is also for the Taligrada), since

[1] The extension of the antero-dorso-internal part above the trochlear facet appears to be another primitive character seen especially in Periptychids, early Creodonts and more ancient Patagonian Ungulates.

it is present in *Clænodon,* the Oxyænidæ, *Sinopa,* and the Mesonychidæ. It seems to be correlated with the spreading of the digits and oblique position of the cuboid.

The partial *homodynamy and correspondence between the manus and pes* appears very clearly in *Clænodon,* as figured by Matthew (1901, pp. 14–15, figs. 6, 7). The entocuneiform is large and its digit (I) divergent, as is the case with the trapezium of the manus; the mesocuneiform is small, like the trapezoid, and digit II is "thrust up"; the ectocuneiform corresponds to the magnum; the oblique cuboid, with its astragalo-cuboid contact, to the unciform with its lunar-unciform contact. The navicular is analogous with the centrale. But here the strict analogy ends, for the calcaneum performs the functions of the cuneiform plus pisiform, while the astragalus corresponds to both the scaphoid and lunar.

The primitive Creodont astragalus would appear to have been one with a rather narrow trochlear facet, with low tibial and high fibular-keel, astragalar foramen, head flattened anteroposteriorly but very convex transversely, neck twisted so that the long axis of the head is directed obliquely backward; an astragalo-cuboid contact. The fibular surface always makes a sharp angle with the trochlea and never a gentle angle with it as it does in primitive Marsupials. Strong resemblances to the Periptychid type.

Fissipedia. The astragalus may be derived from the type seen in *Clænodon: i. e.,* with low rounded trochlear keels, rather narrow trochlea, an astragalar foramen (preserved in certain Mustelidæ), and a small astragalocuboid contact.

Condylarthra. The astragalus in *Euprotogonia* is not essentially different from the Creodont type; it retains the slender neck, the astragalar foramen, the convex head, and apparently a slight cuboid contact, etc. The name Condylarthra was given in allusion to the characters of the head of the astragalus which distinguish the order from that of the later and more specialized Ungulate orders but not from many Unguiculate orders nor from early members of the Typotheria. The Condylarthra are rather exceptional in the lack of an astragalo-cuboid contact and it is by no means evident that Cope was correct in assuming this condition to be primitive.

Taligrada. In the very primitive families Periptychidæ and Pantolambdidæ the cuboid was large and had a broad contact with the astragalus. It appears to the writer very misleading and unwarranted to speak of this as the "displaced" condition, or to say, for example, that the "astragalus is widely displaced upon the cuboid," as is frequently done. On the contrary, the very primitive characters of *Anisonchus, Periptychus, Pantolambda* and the Creodonts raise a presumption that the astragalo-cuboidal contact is primitive, at least for those orders. An astragalar foramen was present

in *Anisonchus* (Matthew, 1897, p. 297, fig. 11), *Periptychus* (Osborn, 1898, p. 181) and *Pantolambda* (Osborn, 1898, p. 188). The evolution of the pes in the Amblypoda has been described above (pp. 357–358).

Artiodactyla. The derivation of the Artiodactyl astragalus from the type seen in the Mesonychid Creodonts was described above (p. 404). This was from the first a strictly cursorial type, since motion was limited to the fore and aft plane, not only by the sharp trochlear keels but also by the transverse flattening and antero-posterior convexity of the navicular facet. The presence of the astragalo-cuboid facet in addition to the navicular facet gave rise to Cope's term "Diplarthra." By false analogy with the interlocking carpus, which was again falsely thought to be an entirely secondary arrangement, the doubly unwarranted conclusions were reached that "diplarthrism" is a wholly secondary acquirement in both Artiodactyls and Perissodactyls, and further, that it is an indication of close relationship between those two orders. As it appears to the writer, the Artiodactyls were essentially diplarthrous long before they became Artiodactyls, although of course the astragalo-cuboid facet widened progressively. An essential feature of the Artiodactyl astragalus is the very large flattened sustentacular facet on the back, which is foreshadowed in the Mesonychidæ.

Perissodactyla. In this order the astragalo-cuboid contact may at first have been almost or entirely absent; it was absent or at most exceedingly narrow in all the Lower Eocene Perissodactyls; it widened progressively, especially in Rhinoceroses and Titanotheres but never became as extensive as in the Artiodactyls; the navicular facet generally became flatter; the sustentacular facet formed a reversed L (⌋), a distal calcaneal facet also developed (p. 395).

2. The Calcaneum.

In the Monotremes, which are entirely plantigrade, the tuber of the calcaneum is pointed downward. In the most primitive Polyprotodont Marsupials and Insectivores, the heel is slightly raised from the ground and the calcaneum points backward and slightly downward. In the digitigrade and unguligrade mammals the tuber is elongate and points backward and upward.

CHAPTER XII. CONCLUSIONS.

I. Genetic Relations of the "Meseutheria" and "Cæneutheria."

Cope believed that the Basal Eocene (Puerco and Torrejon) fauna was directly ancestral to the Lower Eocene Wasatch fauna and various writers selected different members of the Taligrada, Condylarthra, Creodonta and Tillodontia as ancestral respectively to the Artiodactyla, Perissodactyla, Fissipedia, Pinnipedia, and Rodentia; but Osborn[1] in 1894 (pp. 234–237) advanced the hypothesis that the ""Mesoplacentalia," later called "Meseutheria," typified by the Amblypoda, Condylarthra, Creodonta and Tillodontia, were not ancestral to the "Cænoplacentalia" (Cæneutheria), typified by the Proboscidea, Diplarthra (Artiodactyla and Perissodactyla), Fissipedia and Rodentia, but were the dying members of a great Mesozoic Placental radiation; that the Meseutherian orders became extinct on account of "their stationary brain development and comparatively defective tooth and foot structure," while the Cæneutherian radiation, appearing in the Lower Eocene, began "from some comparatively unspecialized spurs of the dying Mesoplacental group" and was characterized by a "rapidly progressive development of the brain, dentition and feet."

In so far as this hypothesis implies that the *specialized* genera of the Meseutheria (*e. g., Palæonictis, Patriofelis, Arctocyon, Periptychus, Phenacodus, Meniscotherium*) were not ancestral to the Cæneutherian orders it has been fully confirmed by all subsequent research by Osborn and others. But the hypothesis has been extended by its author so that, if the writer correctly understands Professor Osborn, it now means: (1) that the Cæneutherian orders have been derived from some wholly unknown potentially large brained stock; (2) that no Creodonts were ancestral to the Fissipedia, no Condylarths to the Perissodactyla, no Amblypods or Condylarths to the Hyracoidea, Embrithopoda, Proboscidea or Notoungulata.[2]

The conclusions which seem to be indicated by the evidence now available are as follows:

(1) The large brained "Cæneutheria" have been derived from forms in which the brain was of the Meseutherian type. Unless the evidence of

[1] Trans. N. Y. Acad. Sci., Vol. XIII, 1894.

[2] Professor Osborn has kindly stated his present view in the following words:

"My point has always been: 1) *that the known Meseutheria are not an ancestral but a dying out group*, 2) that small brained forms elsewhere—with *a potential of brain development* — gave rise to the rapidly progressive Ceneutheria. Such forms may come within our definition of Creodonta but more likely within that of Insectivora."

comparative anatomy and embryology is at fault all forms with large well furrowed cerebra and relatively small rhinencephalon must have been derived from forms with smooth small cerebra, large rhinencephalon and large fully exposed cerebellum — a type of brain preserved in the more primitive Insectivores, in the Meseutheria and in the earliest forerunners of the Carnassident Carnivores (*Didymictis protenus*; *cf.* p. 310).

Upon such differences in brain structure Bonaparte divided the Mammalia into the Ineducabilia and Educabilia, and Owen placed mankind in a separate grand division, the "Archencephala."

If these quantitative differences in brain type imply divergence in origin rather than differences in degree of development, they ought to be accompanied by widely divergent non-adaptive characters in various parts of the organism.

(2) The ancestors of the Fissipedia (Carnassidentia) had all the ordinal characters of the Creodonta. The Eocene Miacidæ (Viverravidæ) as described by Matthew (1909) are prototypal (p. 309) to the Fissipedia in the dentition and in the characters of the skull, cranial foramina, manus and pes, etc. If the Miacidæ are to be regarded as Creodonts then at least one Meseutherian group is shown to be prototypal to a Cæneutherian group. If on the contrary the Miacidæ are regarded as Cæneutherians, then it is shown that among the earliest Cæneutherians were forms (*Didymictis protenus*) which had a brain case no bigger than that of *Arctocyon*, a typical Meseutherian. Further, Matthew (1909, pp. 399–400) has shown: first, that certain Miacidæ (*Palæarctonyx*) closely resembled the Arctocyonidæ in all the parts known, namely the dentition, humerus and terminal phalanges; secondly, that both in the manus and pes the Arctocyonid genus *Clænodon*, foreshadowed the Miacid-Fissiped group in many significant details (p. 310).

(3) Unless convergent evolution is again deceiving us, the ancestors of the Cæneutherian order Perissodactyla seem to have been related to the ancestors of the Meseutherian Condylarth genus *Euprotogonia*, because the latter is approximately prototypal to the Perissodactyls in the dentition, carpus and tarsus and all other parts of the skeleton (p. 396).

(4) The ancestors of the Cæneutherian orders Hyracoidea, Embrithopoda, Pyrotheria, Proboscidea, and Notoungulata were probably small-brained Meseutherian protungulates (pp. 369, 382, 410, 411), which were probably rather nearly related in various ways to each other.

(5) The ancestors of the Cæneutherian order Artiodactyla (p. 404) may be related to the ancestors of the Meseutherian Creodonta-Mesonychidæ, because the latter are approximately prototypal to the former in many details of the skull, dentition, limbs and feet, carpus and tarsus.

(6) The Cetacea are certainly typically Cæneutherian, both in respect to their extraordinarily progressive brain and their post-Basal-Eocene radiation. But the collateral ancestors of the Cetacea, namely the earliest Zeuglodonts, have a low type of brain (p. 417) and are probably derived from some Meseutherian Insectivore-Creodont family.

(7) The Anthropoidea are typical Cæneutheria but there can be little doubt that they have been derived from Eocene Lemuroidea of some kind. This is indicated not only by the fundamental resemblances between existing members of the two suborders and the union of certain of their most distinctive characters (p. 321) in the genus *Tarsius,* but also by the existence of Lower Eocene Primates (Notharctidæ) which are classed by some authors as Lemuroids, by others as early Anthropoids. The Lemuroidea were placed by Osborn (*l. c.*, p. 236) among the Meseutheria. Certain forms (*e. g.*, Indrisinæ) have a richly convoluted cerebrum (Weber, 1904, p. 748); the more primitive ones have a relatively low brain type: the olfactory parts of the brain and the ethmoturbinal complex (p. 428) clearly indicate derivation from macrosmatic animals with a brain of the typical Meseutherian type. The Lemuroidea have very probably been derived from progressive Insectivores with relatively large brain, analogous to *Tupaia* (p. 321).

Hence, whether the Lemuroidea be regarded as Meseutheria or Cæneutheria, it follows that the order Primates has been derived from a Meseutherian source but not necessarily from any well known Basal Eocene genera.

(8) The Rodentia are not known until the Lower Eocene and are therefore classed by Osborn as Cæneutheria (*l. c.*, 1909, p. 33) but even in the existing families the brain in the more primitive forms is of very low type, the hemispheres being small and smooth and not overlapping the cerebellum (Weber, p. 478), while the rhinencephalon is large; in the characters of the ethmo-turbinal complex, and in all the characters of the skeleton the Rodentia retain traces of derivation from some unknown Basal Eocene or Upper Cretaceous, insectivorous Meseutheria.

(9) The Insectivora (especially the Zalambdodonta) are typically Meseutherian in brain structure and in whatever "incapacity for progressive evolution" may be implied in the retention of a large number of extremely primitive characters in the existing forms. But as noted by Osborn, the Leptictidæ, which are approximately ancestral to the Erinaceidæ, appear to have come in with the Lower Eocene "Cæneutheria," while certain Insectivores (*Tupaia*) have a relatively large brain case. The Insectivore-Creodont group also appears in fact to be largely prototypal (p. 253) to both the Meseutherian and Cæneutherian orders.

(10) The Edentates are left "Incertæ Sedis" in the original description of the Meseutheria and Eutheria. The Edentata-Tæniodonta (Gano-

donta) were later (1909, p. 33, footnote *c*) referred to the Meseutheria. Whether or not the Tæniodonts are structurally ancestral to the Xenarthra, all the Edentate orders exhibit indications of derivation from some Mesozoic order (p. 341).

If the foregoing conclusions be correct the more general conclusions in regard to the status of the conception designated by the terms Meseutheria and Cæneutheria appear to be as follows:

(1) The idea is valuable in so far as it centers attention upon the following inferences: (*a*) the existence of a great Mesozoic mammalian radiation, (*b*) the extinction of the majority of the Mesozoic families, (*c*) the retarded development of the brain especially in the Amblypoda and the lowly character of the brain in all the Meseutheria; (*d*) the non-derivation of the Lower Eocene families from the more specialized Basal Eocene predecessors; (*e*) the inference that as a whole the Lower Eocene fauna of Western North America represents a fresh immigration from the north; while the Basal Eocene fauna in part moved southward, in part lingered on in competition with the higher invading types, and in part gave rise to other higher types.

(2) On the other hand it would appear inadvisable to apply the terms Meseutheria and Cæneutheria in a systematic sense, for the following reasons:

(*a*) The names virtually stand for the inferred relations of two limited faunas and do not represent systematic groups which can be properly defined. Neither of the groups are held together by characters drawn from various parts of the organism and are as originally stated by their author "very heterogeneous." They are separated (incompletely) chiefly by their position in time and by an assumed difference "in the capacity for progressive evolution."

(*b*) If understood in a systematic sense the two groups Meseutheria and Cæneutheria appear to overlap each other at many points, both structurally and phylogenetically.

(*c*) The division would thus be largely "horizontal" in character, analogous to Bonaparte's Ineducabilia and Educabilia, only not as well defined, since the Ineducabilia included all the macrosmatic, small brained modern groups.

(*d*) Such a division would obscure the fact that the large brained forms must have been derived from small brained forms, and that the ancestors of the Insectivore-Creodont group were also the ancestors of many if not all of the higher orders.

II. A Classification and Provisional Phylogeny of the Orders and Suborders of Mammals.

In the preceding chapters the writer has endeavored to collate and interpret the work of many authors, to add his quota of new observations and to develop therefrom a general hypothesis of interordinal relationships. This is summarized in the present chapter, first in the form of a classification of the orders and suborders, secondly in the form of a phylogenetic tree (Fig. 32, 33). The classification is founded, so far as possible, upon a consideration of the "totality of characters drawn from various parts of the organism" (Gill), and thus contrasts, for example, with Cope's classification of the Ungulates, which was founded upon practically a single character of the carpus and tarsus. As other principles of classification followed in the present work were discussed in the writer's review[1] of the phylogeny of the Teleostomous fishes (1907, pp. 440–444), the only matter here requiring discussion is the use of the superorder.

The orders of mammals have probably been fairly well determined in the majority of instances. It is not likely, for example, that the Perissodactyla will ever be split up into several orders, at least if the term "order" is to retain its historical meaning. Consequently the orders are capable of exact definition, that is, the ordinal characters apply to all members of the order. The superorder, on the contrary, as here used, stands only for an hypothesis of common origin; its definition describes the *group* from which two or more parallel or divergent orders were derived but whose ancestral characters are lost in varying degrees in the actual orders. Consequently the superorder is usually a more elastic and indefinite conception than the order. The superordinal grouping here proposed may in several cases prove erroneous, but the abandonment of the names and the bringing together of new groups should not cause confusion, whereas the abandonment of any of the well established ordinal names and groups would be justifiable only after the discovery of a most convincing accumulation of evidence. The history of classification warns us against taking superordinal groupings too seriously. They are bound to expand and divide and recombine to some extent, because it may be assumed that the palæontological record will always remain very imperfect and classification must, therefore, remain a compromise between the "vertical" and "horizontal" factors, *i. e.*, it must be an expression of the mingled results of heredity on the one hand and of parallel and convergent evolution on the other. In view of the more or less hypothetical character of the superordinal groupings here adopted, the writer therefore does not expect to see all of them gain very wide acceptance, and

[1] Ann. N. Y. Acad. Sci., Vol. XVII, pt. ii, no. 3, pp. 437–508.

some of them may not withstand the destructive criticism which will be raised by new discoveries or a more extended analysis.

One advantage of the use of the superorder is that it permits the breaking up of unnatural sequences. Juxtaposition and sequence are inseparable features of all classification, but since it is impossible to represent branching kinship in a linear sequence of names, some authors have gone to the other extreme and failed to adopt definite rules of sequence. For instance, in a linear arrangement of the orders the Edentates must come in somewhere, but wherever we put them they are bound to stand next to some order to which they are but very remotely related. On the other hand, if juxtaposition is to mean nothing, if we are to understand a " Da Capo " sign in front of every order, we then lose sight of the fact that some orders (*e. g.*, Dermoptera, Chiroptera) do not run back independently to the beginning but seem to be rather closely related.

The classification given below usually passes from the older and more generalized to the newer and more specialized. It is intended to express first degrees of homological resemblances, secondly, degrees of kinship, and thirdly, successive grades of specialization.

A difficult question for the taxonomist is how far morphological differences are to be neglected in favor of expressing linear derivation, *i. e.* of grouping ancestral and derived divisions together. For example, if the Ancylopoda are to be grouped in the same suborder with the Perissodactyla, why not unite the Sirenia with the Proboscidea, the Bats with the Insectivora? The obvious answer is that the systematist has generally given due weight to the magnitude of the morphological resemblances and differences, and has tried to express *grades of specialization*, as in the terms Prototheria, Metatheria, and Eutheria; although, of course, it is impossible to be thoroughly consistent, especially in assigning a position to the Edentate orders, and any classification requires some arbitrary decisions and artificial sunderings.

One other general principle here adopted is that truly convergent resemblances between members of widely removed orders are accompanied by fundamental differences which may usually be discovered upon close examination of adequate material. If, for example, the resemblances in the dentition, skull and limbs between the Eocene Miacidæ and the Oligocene Canidæ are convergent to the same degree that the resemblances between *Notoryctes* and *Chrysochloris* are convergent, then almost all phylogenetic speculation from existing material is useless. But as a matter of experience the kind of characters separating *Chrysochloris* from *Notoryctes* are found to be of a very different nature from the kind of characters (primitive) separating the Miacidæ from the Oligocene Canidæ.

Thus a crucial problem raised by the present work is whether convergent

evolution has been a well nigh universal or only a frequent phenomenon. In the former then such superordinal groups as the Cetacea may prove to be unnatural, but in view of the net work of resemblances (p. 420) connecting the different orders of the superorder with each other, it seems to be only a conservative application of generally accepted principles to assume that these resemblances imply derivation from a common source, and that in general similar adaptations are most likely to arise in the descendants of similar ancestors.

A Classification of the Orders and Suborders of Mammals.

Class Reptilia.
- Order Therapsida Broom.
  - Suborder Dromosauria Broom.
  - Suborder Therocephalia Broom.
  - Suborder Anomodontia Owen.
  - Suborder Cynodontia (Owen) Broom.

Class Mammalia Linn.
- ?Subclass Promammalia Haeckel.
  - Order Protodonta Osborn.
- Subclass Prototheria Gill, Huxley.
  - Order Monotremata Geoffroy.
- Subclass Theria Parker & Haswell (= Eutheria Gill).
  - I. Infraclass Metatheria Huxley.
  - Order Triconodonta Osborn.
  - ? Order Trituberculata Osborn (= Pantotheria Marsh, in part).
  - Order Marsupialia Illiger.
    - Suborder Allotheria Marsh (Multituberculata Cope).
    - Suborder Diprotodontia Owen.
    - Suborder Paucituberculata Ameghino (Cænolestoidea).
    - Suborder Polyprotodontia Owen.
  - II. Infraclass Eutheria Huxley (Monodelphia Blainv., Placentalia auct.).
    - Superorder Therictoidea.[1]
      - Order Insectivora (Gray).
        - Suborder Lipotyphla Hæckel.
          - Section ———. Fam. Pantolestidæ.
          - Section Zalambdodonta Gill. Fam. Centetidæ Potamogalidæ, Solenodontidæ, Necrolestidæ, Chrysochloridæ.
          - Section Erinaceomorpha. Fam. Leptictidæ, Erinaceidæ, Dimylidæ.

[1] Θήρ wild beast ἴκτις "weasel" (insectivore), εἰδή form.

Section Soricomorpha. Fam. Soricidæ, Talpidæ.

Suborder ———. Fam. Hyopsodontidæ.

Order Feræ Linn. (1758). Carnivora auct.

Suborder Creodonta Cope.

Suborder Fissipedia (Blumenbach). Carnassidentia Wortman (in part).

Suborder Pinnipedia (Storr) Illiger.

Superorder Archonta [1]

Order Menotyphla Hæckel. Fam. Tupaiidæ, Macroscelididæ.

Incertæ Sedis. Fam. Mixodectidæ.

Order Dermoptera Illiger. Fam. Galeopithecidæ.

Order Chiroptera Blumenbach.

Suborder Frugivora Gill (Megachiroptera Dobson).

Suborder Animalivora Gill (Microchiroptera Dobson).

Order Primates (Linn.).

Suborder Prosimiæ Milne Edwards

Section Lemures.

Section Tarsii.

Suborder Anthropoidea Mivart.

Section Platyrrhina Owen (*ex* Blainv.).

Section Catarrhina (Owen) (*ex* Blainv.). Fam. Cercopithecidæ, Hylobatidæ, Simiidæ, Hominidæ.

Superorder Rodentia Vicq d'Azyr.

Order Glires Linn.

Suborder Duplicidentata Illiger.

Suborder Simplicidentata Lilljeborg.

? Superorder Edentata Vicq d'Azyr (Paratheria Thomas).

? Order Tæniodonta Cope (Ganodonta Wortman).

? Order Tubulidentata Huxley.

? Order Pholidota Weber.

Order Xenarthra Gill.

Suborder Anicanodonta Ameghino (Pilosa Flower).

Suborder Hicanodonta Ameghino (Loricata Flower).

[1] See p. 322

Superorder Paraxonia Marsh.
- Order Artiodactyla Owen (*ex* Blainv.).
  - Suborder Non-ruminantia (auct.). Fam. Trigonolestidæ, Dichobunidæ, Anthracotheriidæ, Hippopotamidæ; Achænodontidæ, Entelodontidæ; Dicotylidæ, Suidæ.
  - Suborder Ruminantia (auct.). Fam. Camelidæ, Oreodontidæ, Anoplotheriidæ, Hypertragulidæ, Tragulidæ, Cervidæ, Merycodontidæ, Antilocapridæ, Giraffidæ, Bovidæ.

Superorder Ungulata (Linn.).
- Order Protungulata (auct.).
  - Suborder Taligrada (Cope) Osb. Fam. Periptychidæ, Pantolambdidæ.
  - Suborder Condylarthra (Cope). Fam. Meniscotheriidæ, Phenacodontidæ.
- Order Amblypoda Cope. Fam. Coryphodontidæ, Uintatheriidæ.
- Order Barytheria Andrews.
- Order Sirenia Illiger.
- Order Proboscidea Illiger.
- Order Hyraces Wagler.
- Order Embrithopoda Andrews.
- Order Notoungulata (Roth) Scott.
  - Suborder Homalodotheria (Scott). Fam. ? Notostylopidæ, ?Henricosbornidæ, Homalodotheriidæ.
  - Suborder Astrapotheria. Fam. ?Albertogaudryidæ, ?Isotemnidæ, Astrapotheriidæ.
  - Suborder Toxodontia Owen. Fam. Nesodontidæ, Toxodontidæ, Archæohyracidæ, Protypotheriidæ, Interatheriidæ, Typotheriidæ.
  - ? Suborder Pyrotheria. Fam. Pyrotheriidæ.
  - Suborder Litopterna (Ameghino). Fam. Proterotheriidæ, Macraucheriidæ.
- Order Mesaxonia (Marsh).
  - Suborder Perissodactyla Owen.
  - Suborder Ancylopoda Cope.

Superorder Cetacea Linn.
- Order Zeuglodontia Gill (Archæoceti Zittel).
- Order Odontoceti (Gray).
- Order Mystacoceti (Gray).

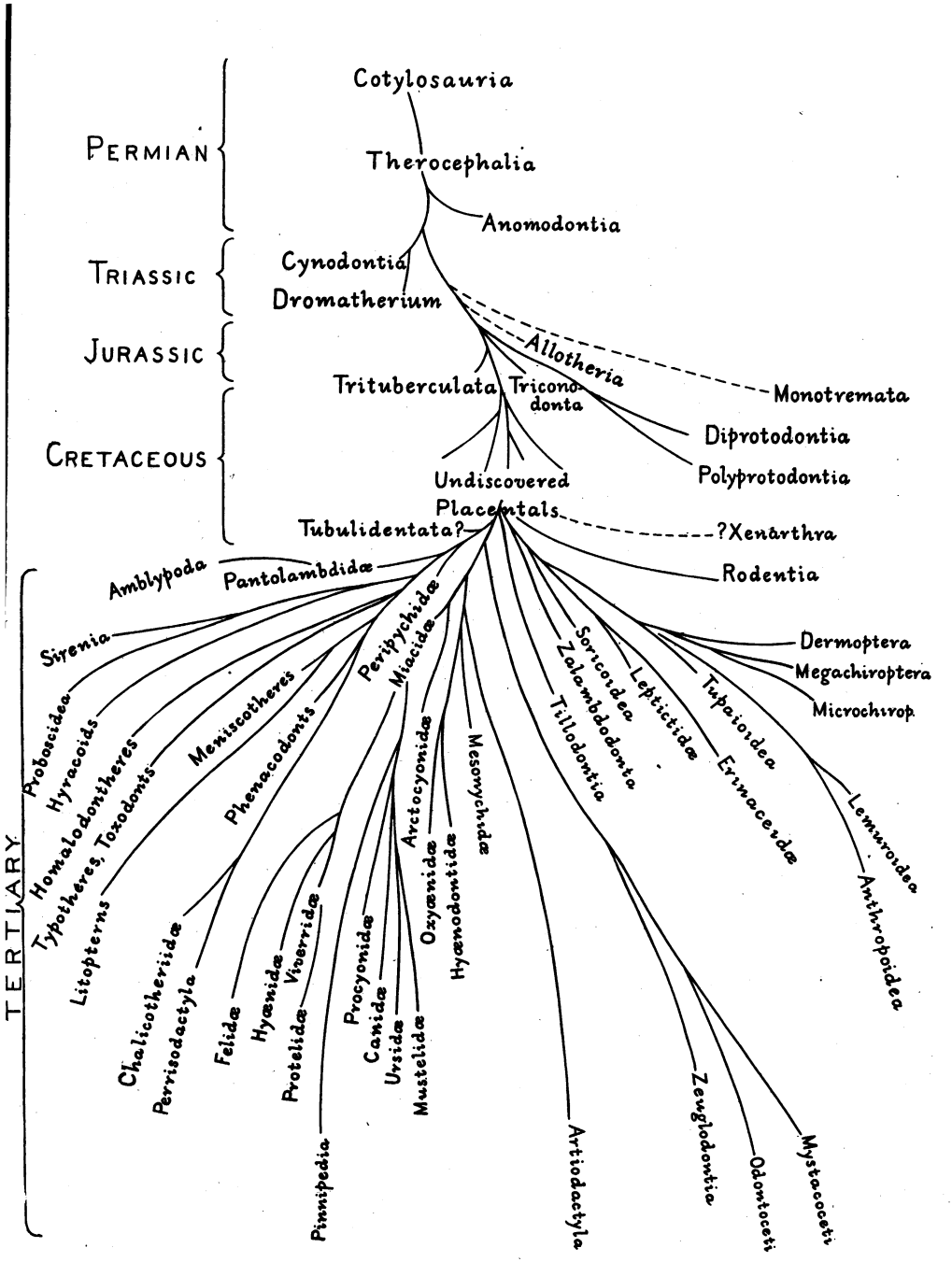

Fig. 31. Genetic relations of the orders, suborders and principal families of mammals according to the author's interpretation of the evidence adduced in this work.

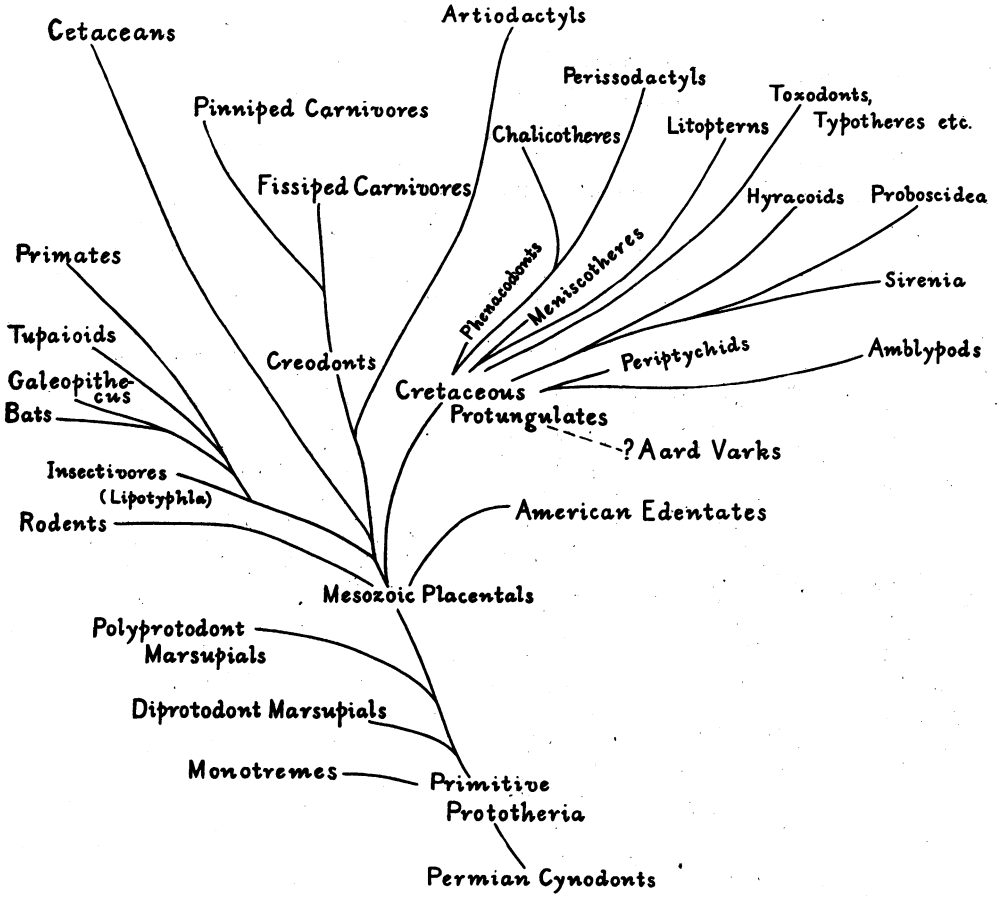

Fig. 32. Genetic relations of the orders and suborders of mammals according to the author's interpretation of the evidence adduced in this work.

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