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ON THE
PRIMITIVE TYPES
OF THE
Orders of Mammalia Educabilia.

BY
PROF. E. D. COPE.

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ON THE PRIMITIVE TYPES OF THE ORDERS OF MAMMALIA EDUCABILIA.

BY PROF. E. D. COPE.

(*Read before the American Philosophical Society, April 18, 1873.*)

In the Proceedings of the American Philosophical Society, 1872, p. 554, the writer described a species of Quadrumanous Mammal under the name of *Anaptomorphus æmulus*, comparing its dental and other characters with *Simia* and *Homo*.^{*} In the American Journal of Science and Arts for November,† 1872, Prof. O. C. Marsh announced that he believed that three genera previously described by him, viz., *Thinolestes*, *Limnotherium* and *Telmatolestes*,‡ were referable to the Quadrumana, saying that they “have the principal parts of the skeleton much as in some of the lemurs.” Prior to either of these determinations, the author de-

^{*} Published October 12th, 1872.

† Published October 8th, 1872.

‡ Published August 7th, 1872.

scribed a new genus and species as allied to *Notharctus*, Leidy, under the name of *Tomitherium*,* but made no suggestion as to its ordinal position.

On a re-examination of the last-named genus, I am satisfied that it also should be referred to the *Quadrumana*, and describe it as follows:

TOMITHERIUM. Cope.

Dental formula $\frac{2222}{2143}$, in an uninterrupted series. Last molars with five tubercles, others with four; all low and slightly alternating, the outer wearing into crescents. Canines quite small. Incisors very prominent, the median pair with transverse cutting edges. Symphysis coössified, projecting in front. In the molars, the adjacent horns of the two outer crescents unite with the anterior outer tubercle; the posterior outer is insignificant. There is a projection but no tubercle in front of the outer anterior tubercle. The premolars present but a single compressed conic crown; the posterior, however, widened behind, and with a low tubercle. The first and second premolars are one-rooted (not entirely a generic character).

I base the distinction between this genus and *Notharctus* on the small canine, and the sub-horizontal position of the incisors; believing that when other portions of the skeleton are studied, other differences will appear.

The portions of the skeleton of the type species preserved are: the entire dentition of the lower jaw minus the crowns of the outer incisor, canine and first premolar; the left ramus nearly complete, the extreme angle being wanting: the right humerus complete, with right ulna and radius, the latter lacking the distal extremity; a large part of the left ilium; the right femur nearly entire; part of the left humerus, metatarsals, etc.

The mandibular rami are quite stout, but not very deep; the symphyseal portion long and oblique, and the coronoid and condylar portions elevated, with axis at right angles to that of the horizontal portion. The condyle is well elevated, and the coronoid process small; the dental foramen is half way between the margins of the ascending ramus, and opposite the bases of the crowns of the molars. The inferior margin of the jaw shows no tendency to inflection at a point immediately below this foramen, where it is broken off. The mental foramen is divided, the exits being at points opposite those between the premolars 1-2 and 2-3.

The humerus has a round head directed backwards and a little outwards. The tuberosities are rather small, of about equal size, and obtuse; they enclose a short bicipital groove. The bicipital crests are very largely developed, and extend to the middle of the shaft enclosing an open groove between them. The external is narrow and most

* Published August 7th, 1872.

elevated, the internal more obtuse and directed inwards. The shaft is thus sub-triangular in section. The distal extremity is nearly at right angles to the axis of the proximal and is much expanded transversely. A large part of this expansion is caused by the truncate internal tuberosity, and by the less prominent external one. The latter is continued in a thin ala which only sinks into the shaft at its middle. The condyles are small, the external the most prominent. There is a shallow olecranon fossa, and no coronoid, and hence no supercondylar foramen. There is an arterial foramen above the internal tuberosity.

The *ulna* is compressed, and contracts rapidly to the extremity. The olecranon is broad and obtuse and the humeral cotylus oblique to the long axis. The coronoid process is low. The shaft is remarkably curved from right to left (inwards). The *radius* has a discoidal head with central depression, and it was evidently capable of complete rotation. It exhibits a tuberosity and slight flexure below the head. The distal extremity has a horizontal triangular section with the apex internal and truncate; the shaft near it is quite flat.

The left *ilium* is obspatulate and flat, widest at the convex crest, and slightly concave on the outer side. It is rather thin, and the impression for the sacral diapophyses is elongate. The inferior border thickens gradually to the acetabulum; the superior is excised so as to form an open concavity.

The right *femur* is remarkable for its length. Its shaft is flattened from before backwards, and without flexure. The great trochanter is large, and embraces a deep in-looking fossa. There is a flat tuberosity looking outwards just below, and the little trochanter is a little below opposite to it. The condyles are sub-similar in size, the trochlear surface wide, but not flat, and the inner border thickened and considerably elevated. The femur is 1.75 times as long as the humerus; it was scarcely longer, though a small piece is wanting from the shaft of our specimen.

Remarks. Having described the more important parts of the skeleton preserved, I now proceed to consider its systematic position, and the order to which it should be referred.

The first impression derived from the appearance of the lower jaw and dentition, and from the humerus, is that of an ally of the coati (*Nasua*). The humerus indeed is almost a fac-simile of that of *Nasua*, the only difference being a slight outward direction of the axis of the head. The same bone resembles also that of many marsupials, but the flat ilium, elevated position of dental foramen, and absence of much inflection of the angle of the lower jaw, etc., render affinity with that group highly improbable. The length of the femur indicates that the knee was entirely free from the body as in the quadrumana, constituting a marked distinction from anything known in the *Carnivora*, including

Nasua. The round head of the radius indicates a complete power of supination of the fore foot, and is different in form from that of *Carnivora* including *Nasua*; and finally, the distal end of the radius is still more different from that of *Nasua*, and resembles closely that of *Semnopithecus*.

We have, then, an animal with a long thigh free from the body, a foot capable of complete pronation and supination, and a form of lower jaw and teeth quite similar to that of the lower monkeys. The form of the humerus and its relative length to the femur are quite as marked as in some of the lemurs. The most marked difference is seen in the increased number of teeth; but in this point it relates itself to the other *Quadrumanæ*, as the most ancient types of *Carnivora* and *Ungulates* do to the more modern; e.g., *Hyænodon* to the former and *Palæosyops* to the latter. In its special dental characters it shows a close resemblance to small types of the Eocene, which have been regarded as low Perissodactyles, as *Hypopsodus*, etc.

TOMITHERIUM ROSTRATUM. Cope.

Proceedings of the American Philosophical Society, 1872, p. 470. - 471

This species was about the size of the prehensile tailed-monkey, so frequently seen in shows. The first and second premolar have but one root, the base of the second being about the size of the base of the canine. The latter are cylindric at base. The incisors form a parabolic outline, and have entire edges, the middle pair transverse ones. Enamel generally smooth, premolars somewhat striate; an indistinct inner cingulum.

M.

Length of entire dental series (straight).....	0.044
“ symphysis mandibuli.....	.020
Depth ramus at second molar.....	.010
Length crown of “ “	.006
Width “ “ “	.0045
“ between two “ “	.014
“ “ canines.....	.005
“ of ascending ramus above dent. foramen.....	.016
Length of humerus.....	.083
Diameter of head.....	.013
Diameter of shaft at middle.....	0.0085
“ “ distal end, transverse.....	.023
“ “ “ antero-posterior.....	.0078
Depth of olecranon.....	.009
“ “ ulna at coronoid	.010
Diameter extremity of radius, proximally.....	.009
“ “ “ distally.....	.010
Length of ilium from acetabulum	.042
Width near crest	.017
Length of femur preserved.....	.137

	M.
Width just below neck.....	.017
“ at middle.....	.011
“ “ extremity.....	.019
“ of trochlea.....	.009
Longest chord of condyles and trochlea.....	.019

The remains of this species were found together by the writer in the Bridger beds on Black's Fork, Wyoming.

ANAPTOMORPHUS. Cope.

Proceedings of the American Philosophical Society, 1872, p. 554. -

This genus is represented by the left ramus mandibuli of a single species. The posterior portion is broken away, and the teeth remaining perfect are the P. M. 2, and M. 1 and 2. The ramus, though small, is stout, and deeper at the symphysis than at the last molar. What appears to be the dental foramen is nearly opposite the bases of the crowns of the molars. The mental foramen issues beneath the first premolar.

Dentition of the *ramus mandibuli*, In. 2, C. 1, P.M. 2, M. 3, total, 16. It differs in many respects from these; there is no interruption in the series near the canine, and the symphysis, though massive, is not coössified. Further details are, the last molar is three-lobed and elongated behind. The composition of the crowns of the preceding molars consists of four opposed lobes, which are very stout, and connected transversely by a thin ridge behind, or in close contact in front. The premolar tooth which is best preserved, is a perfect second, which, while having two roots, possesses a crown which stands almost entirely on the anterior, presenting a curved sectorial crest forwards and upwards.

The dentition is more decidedly quadrumanous in this genus than in the last, and it might be referred decidedly to *Lemuridæ* were it not for the unossified symphysis. It no doubt represents a distinct group or family from *Tomitherium*, and one more nearly related to the existing types of Madagascar and South Africa.

ANAPTOMORPHUS ÆMULUS. Cope, loc. cit.

This species was about as large as a marmoset or a red squirrel. The enamel of the teeth is entirely smooth.

Measurements.

	M.
Length dental line.....	0.0148
“ of last molar.....	.0030
“ “ ante-penult.....	.0025
Width “ “	.0020
Length of three molars preserved.....	.0070

From the Bridger Beds of the upper valley of Green River.

On the Phylogeny of the Mammalian Orders. So much light is thrown on this subject by the researches into the structure of the fossil mammalia of the Eocene formation, that it seems opportune to call attention to the subject. I deem it demonstrated to a certainty, that the case with the mammals of this formation is the same as with the reptiles of the Trias, *i.e.*, that the family types are all more generalized, and the orders not nearly so widely distinguished as in later periods of the world's history.

- The succession of forms which has terminated in the horse, has been clearly pointed out by Prof. Huxley, as well as the line which has given the world the beautiful order of the *Artiodactyla*; but the approximate lineal predecessors of the *Proboscidea*, of the Ungulate animals as a whole, of the *Quadrumania* (including man), and of the *Carnivora*, have not been clearly pointed out.

The genus *Eobasileus* has been shown* to be a Proboscidian which combines some important features of the *Perissodactyla* with those of its own order, thus standing in antecedent relation to the elephants, etc., of the present day. The number of such characters was shown to be somewhat increased in *Bathmodon*, which therefore stands still nearer to the common point of departure of the two orders. This point is to be found in types nearer the clawed orders (*Unguiculata*), in the number of their digits (4-5), and in which the transverse and longitudinal crests of the molar teeth are broken up into tubercles more or less connected, either type of dentition being derived according as such tubercles are expanded transversely or longitudinally. We have several genera which answer this description so far as the teeth are concerned, but unfortunately the digits are unknown; such are *Oligotomus*, *Orotherium*, etc.

The type of *Tomitherium* already described, evidently stands between Lemurine monkeys and such small allies of *Paleotheriidae*, with conic-tubercular teeth, and which abound in the Eocenes of Wyoming and France. The dentition of the two types is indeed but little different in the Quadrumanous and Ungulate types respectively, being a continuous series of I. 2 or 3; C. 1, P.M. 3-4; M. 3; the canines but moderately developed.

A comparison with *Nasua* reveals no distant affinity. As above remarked, the fore-limb presented a great similarity in this genus and *Tomitherium*. The teeth, though less numerous, in the molar series have the cutting type anterior and tubercular posterior, in both genera. *Notharctus*, Leidy, resembles *Nasua* still more than does *Tomitherium*, and occurs in the same Eocene strata. Prof. Leidy originally regarded it as a Carnivore, and subsequently (Hayden's Survey Montana, 1871) placed it among Ungulates. He was probably nearly correct on both occasions, and that only a technical line will ultimately decide whether it be not a monkey.†

* On the Short-footed Ungulata of Wyoming, page 3.

† Dr. Lockwood, of Rutgers's College, in a recent number of the Popular Science Monthly, expressed serious suspicions of the Quadrumanous relationships of the Coati, little thinking at the time that the specimens to confirm his view were at that moment in the hands of palæontologists.

But the genus which associates more definitely the orders *Carnivora* and *Quadrumania*, is the *Cercoleptes*, which F. Cuvier* placed between the two. Its two cutting premolars and three true molars, with the co-ossified rami of the mandible are truly Quadrumanous features, although it should on other grounds be regarded as a plantigrade carnivore. Several of the extinct genera of the Wyoming Eocene will prove to be allied to this form.

Cercoleptes does not, however, present us with the *ultimate* original type of the *Carnivora*. Such a type must also generalize the seals, with their longitudinal, cone-bearing molars, and flat, fissured claws. Some of the seals also unite the scaphoid and lunar bones later in life than other *Carnivora*, hence we would reasonably look for the division of these bones in their predecessors. The flat-clawed genera of Wyoming† answer these demands. The genera *Mesonyx* and *Synoplotherium* presents us with a series of molar teeth which repeat each other in form, are compressed below, and bear conical cusps. The jaws in the latter genus are slender, and the canines tend to the great development seen in many seals; but principally, the scaphoid and lunar bones are distinct, and the claws flat and widely fissured. The tympanic bone is more like that of the bear, and some seals, than that of the digitigrade *Carnivora*. These genera, though probably good swimmers, were well removed from the seals in the structure of the long bones of the limbs, and were probably remote in their ancestry.

In *Oligotomus*, *Orotherium*, *Hyopsodus* and similar forms, the conic tubercles of the lower molars have a slight alternation, and the posterior, which has a crescentoid section in wearing, inclines to connection with both the inner conic tubercles by low ridges. These ridges are fully developed in *Palæosyops* so that we have a dental crest of two Vs, in the inferior molars. This in wearing produces the two crescents of *Palæotherium*. The addition of two tubercles on the inner side takes place in the higher forms, which terminates in the four crescent-bearing molars of the Ruminants. How this is done is proven later by examples from the maxillary teeth. In *Orotherium vasacciense* there is a tendency for the conic tubercles to be connected in pairs by low cross ridges. These ridges fully developed produce the two cross-crests of *Hyrachyus* and *Tapirus*. In *Rhinoceros* the outer portion retains a crescentoid form, giving rise to an L-shaped crest. In *Bathmodon* diagonal ridges appear which would result in two Vs, as in *Palæosyops*, were it not that both transverse and oblique elements of the posterior V disappear, leaving but one such in the middle and posterior part of the mandibular series. In *Uintatherium* the diagonal from the posterior crest never appears, leaving a transverse crest and a V on the true molars.

In the superior molar series the flattening of the outer tubercles may

* Dentes des Mammifères, p. 31.

† See the Flat-clawed *Carnivora* of Wyoming, by E. D. Cope, April, 1873.

proceed so far as to produce on wearing a confluence of the crescentoid surfaces. This is the case in *Orotherium sylvaticum* in the mandibular series. In both *Palæosyops* and *Hyrachyus* those tubercles of the upper molars are confluent into two Vs (more or less open, when unworn). In the former the inner tubercles retain their primitive conic tubercular form, but in *Palæotherium*, *Rhinoceros*, *Lophiodon*, *Hyrachyus* and *Tapirus* they elongate transversely so as to meet the corresponding outer tubercles (now crests) forming the familiar cross-crests of those genera. If the tubercles are alternate, they produce the oblique crest of *Palæotherium*, if opposite, the cross-crest of *Tapirus*.

If on the other hand the inner tubercles flatten like the outer, on wearing, we have the quadricrescentoid type of *Anoplotherium* and the Ruminants.

But it is important to observe, that the lower types of *Quadrumania* and *Carnivora* present the quadrituberculate crown with tendency to flattening of the outer tubercles, as seen in these lowest *Ungulata*. In the *Carnivora* the sectorial tooth is produced by the greater flattening and partial confluence of the outer tubercles, and the entire loss of the inner, the "heel" being in the dogs and cats, *e. g.* their only representative. In the *Quadrumanous* families, including man, the primitive quadrituberculate type of molars is preserved, the flattening of the outer tubercles being finally lost.

It is to be observed that the lines of *Ungulata*, *Quadrumania*, and *Carnivora*, originate in plantigrade types, a state of things quite predominant among the lower series, or *Lissencephala*. It is universal in *Edentata* and very usual in *Rodentia* and *Insectivora*. The lower forms of *Marsupialia* and all of the *Monotremes* present it. In the Marsupials, Rodents, Ungulates, and Carnivores we have series whose highest expression is in the most highly digitigrade genera.

The accompanying diagram is designed to express to the eye more clearly the propositions made above. By comparing it with a similar table published by Prof. Gill (Proceedings of the American Association for the Advancement of Science for 1871, p. 295), a close resemblance between the two may be observed, as well as certain differences.

I wish to be understood that the genera named in it as ancestors, are to be regarded in the light of types of groups. There is no other mode of explaining the facts, than that in accordance with the law of "homologous groups," *i. e.* that several genera of one group have undergone similar modification into corresponding ones of a second group.*

* See Origin of Genera, page 79, Prop. V.

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