ON THE EXTINCT AMERICAN RHINOCEROSES AND THEIR ALLIES.[1]

BY E. D. COPE.

TWELVE species of mammals which may be called rhinoceroses, have been defined from materials obtained from the Tertiary formations of North America; and five additional species have been distinguished, which may be regarded as more or less nearly allied to that family. A few additional names have been proposed for supposed species whose characters are not yet established. In the corresponding formations of Europe and Asia, the fossil remains indicate a still larger number of species. The forms included in the family, first appear in both continents in the Lowest Miocene or Oligocene epochs; that is, in North America in the White River formation. The family still exists in Asia and Africa, but in Europe it disappeared during the glacial epoch. In North America it became extinct at a still earlier period, no remains of rhinoceroses having been found in beds of later age than the Loup Fork, or Upper Miocene period.

The genus *Hyracodon* (Leidy) which has a full series of incisor teeth, was formerly included in this family, and it agrees with the various genera in the structure of the molar teeth of both jaws. But I have ascertained that it differs so widely from them in some other respects, that it became necessary to regard it as the type of another family, the *Hyracodontidæ*. The mastoid bone forms part of the external wall of the skull as in tapirs, and the neck is quite elongate. It fact the *Hyracodon arcidens* must have had the proportions of some of the horses in this respect. There is also no posterior tuberosity of the mandibular condyle, so conspicuous in the rhinoceroses.

The following table explains the relations of the two families:

IV. Anterior exterior crescent of superior molars much reduced; inferior molars with cross-crests; superior molars and premolars alike, with cross-crests.

6. Mastoid bone forming part of the external wall of the skull; no postcotyloid tuberosity of the mandible; neck elongate..... *Hyracodontidæ*

7. Mastoid bone excluded from the walls of the skull by the contact of the occipital and squamosal; a postcotyloid tuberosity of the mandible; neck short..... *Rhinoceridæ.*

The genera of *Rhinoceridæ* differ from each other as follows:

I. Four anterior digits.

Incisors $\frac{2}{1}$; canine $\frac{0}{1}$; no horn; posttympanic bone distinct..... *Aceratherium.*

[1]Adapted from a paper published in the Bulletin of the U. S. Geol. Surv. Terrs., Vol. v, No. 2, 1879.

II. ? Digits.

Incisors $\frac{2}{1}$; canine $\frac{0}{1}$; posttympanic bone distinct; an osseous tuberosity on each side the muzzle..... *Diceratherium.*

III. Three anterior digits.

Incisors $\frac{?-?}{1}$; canines $\frac{0}{1}$; no horn; posttympanic bone distinct..... *Aphelops.*

Incisors $\frac{1}{1}$; canines $\frac{0}{1}$; a dermal horn; posttympanic distinct... *Ceratorhinus.*

Incisors $\frac{3}{2}$; canines $\frac{0}{1}$; a dermal horn; posttympanic?..... *Zalabis.*

Incisors $\frac{1}{1}$; canines $\frac{0}{1}$; a dermal horn; posttympanic process coössified with postglenoid process; no nareal septum..... *Rhinocerus.*

Incisors $\frac{0}{0}$; canines $\frac{0}{0}$; a dermal horn; posttympanic process not united with postglenoid; no nareal osseous septum..... *Atelodus.*

Incisors $\frac{0}{0}$; canines $\frac{0}{0}$; a dermal horn; posttympanic coössified with postglenoid; an osseous septum dartum..... *Cœlodonta.*

My catalogue of species of the above genera contains twenty-eight names, of which six belong to living species. The latter are *Ceratorhinus sumatranus* Cuv.; *C. lasiotis* Scl.; *Rhinocerus unicornis* L.; and *R. sondaicus* Cuv., all from Asia and Malaysia; and *Atelodus bicornis* L. and *A. simus* Burch., of Africa. It is possible that a species of *Aphelops* still exists in some of the Indian islands, in the *Rhinocerus inermis* Less. There are probably several distinct fossil species not in the list; but their characters have not yet been sufficiently made known to enable me to refer them to their proper places. It will be observed that eight species have been found in North American formations, ten in European, and three in those of Hindostan. It appears also that no extinct species of the true genus of *Rhinocerus* has yet been found in North America or Europe, and that no extinct rhinoceros of North America which is known, possessed a median dermal horn.

It can readily be seen that the genera above defined form a graduated series, the steps of which are measured principally by successive modifications of four different parts of the skeleton. These are, first, the reduction of the number of the toes of the anterior foot; second, the reduction in the number and development of the canine and incisor teeth; third, the degree of closure of the meatus auditorius externus below; and fourth, in the development of the dermal horns of the nose and its supports. While these characters have the tangible and measurable quantities which render them available for generic diagnosis, there are others which possess a similar significance, and which I now notice, so far as they are observable in the extinct species of North America.

I premise by observing that the *Aceratheria* and *Diceratheria* of this continent have only been found in the eastern and western divisions of the White River formation, while the species of *Aphelops* are confined, so far as is known, to the Upper Miocene or Loup River formation.

The posttympanic process is, it is well known, well separated from the postglenoid process in the tapir, so as to leave the auditory meatus widely open below. The arrangement is similar in *Hyracodon*. In *Rhinocerus*, as shown by Flower, the meatus is closed below by the coössification of the two processes. In the oldest genus of the family *Aceratherium*, the relations of the parts are as in *Hyracodon*. In *Aphelops* the two processes approach each other, but do not come in close contact as in the genus *Ceratorhinus*.

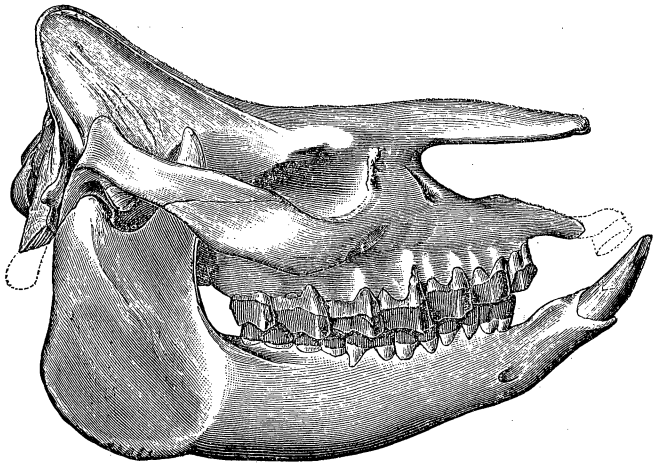


FIG. 1.—*Aphelops megalodus* Cope, one-sixth natural size. Loup Fork beds, Colorado.

The postglenoid process is low and transverse in the tapirs; in *Rhinocerus* it is long and has a triangular section. In some species of American *Aceratheria* its form is much like that of the tapirs (*A. mite*, *A. occidentale*); while in *Diceratherium pacificum* and in the species of *Aphelops*, the form of this process is as in *Rhinocerus*.

In the tapirs, the foramina sphenoörbitale and rotundum are distinct. They are also distinct in *Aceratherium mite*. In *D. pacificum* they are confluent, but the walls of their orifice present two opposite projections, which are the rudiments of a dividing septum. In *Aphelops* these foramina are one as in *Rhinocerus*. At the same time, the external wall of the alisphenoid canal is shorter and thinner in the *Aceratheria* than in the *Aphelopes*.

In the older types of *Perissodactyla*, e. g., *Symborodon*, the foramen ovale is situated well in advance of the foramen lacerum medius, and is separated from it by a considerable space of the sphenoid bone. The same structure is seen in *Hyracodon* and in

Aceratherium. In *Aphelops*, the foramen ovale approaches near to the f. lacerum, so as to be separated by a narrow bridge only in *A. megalodus*, which is wanting on one side in a specimen of *A. malacorhinus*. In the genus *Rhinocerus*, these foramina are not divided.

In the structure of the teeth, the same serial order is to be observed. Commencing with the incisors $\frac{3}{3}$ in the tapiroid types and *Hyracodon*, and canine $\frac{1}{1}$, we find $\frac{3}{2}\ \frac{0}{1}$ in *Zalabis*; $\frac{2}{1}\ \frac{0}{1}$ in *Aceratherium*; $\frac{2-1}{1}\ \frac{0}{1}$ in *Aphelops*; $\frac{1}{1}\ \frac{0}{1}$ in *Ceratorhinus* and *Rhinocerus*, to $\frac{0}{0-1}\ \frac{0}{0}$ in *Atelodus* and *Cœlodonta*. As to the molars, in those of the upper jaw the series of modifications consists of successive complication of the transverse crests. In *Hyracodon*, as in the tapiroid genera, the external wall of the posterior molar is

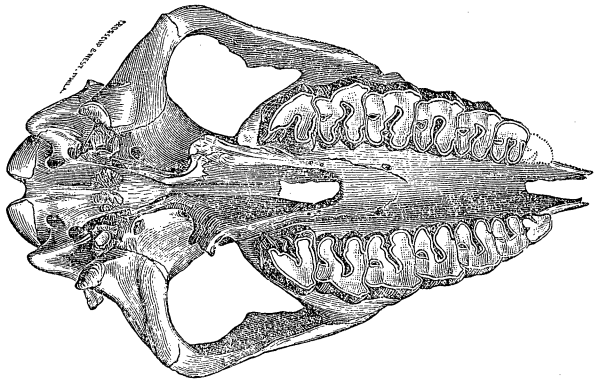


FIG. 2.—*Aphelops megalodus* Cope, inferior view of cranium represented in Fig. 1.

continued beyond the posterior cross-crest; in the *Rhinocerida*, generally the external wall is not continued beyond this crest, but is in line with the posterior cross-crest. In a specimen of *Aceratherium occidentale*, the posterior superior molar of one side is like that of *Hyracodon*, while that of the other side is like that of *Rhinocerus*. The cross-crests in *Aceratherium* are quite simple, having slight bulges into the median valley. In the species of *Aphelops* these bulges are more prominent, especially that of the posterior crest, which is more externally situated than that of the anterior cross-crest, so that the fundus of the valley is turned abruptly backwards. In several of the existing species, this bulge becomes an antero-posterior crest, and the fundus is further divided by other crests from the outer wall and elsewhere. The cingula become so elevated as to cause an isolation of the valleys as fossæ at a comparatively early stage of wear. This

state of things commences in the extinct species of Kansas, the *Aphelops fossiger.*

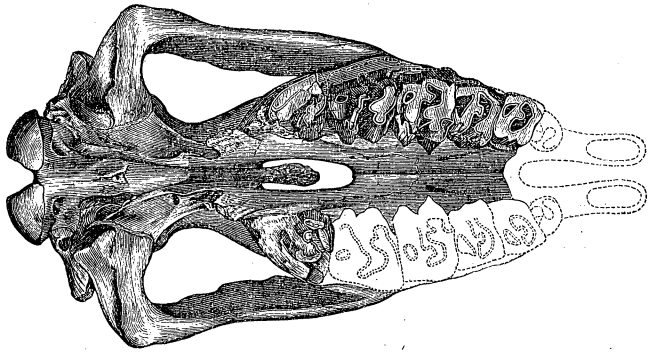
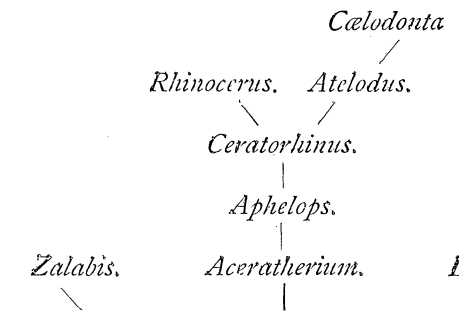


FIG. 3.—*Aphelops fossiger* Cope, skull from below, one-sixth natural size. Loup Fork beds of Kansas.

In the bones of the skeleton, modifications accompanying those of the cranium and dentition may be observed. The femur of the species of the earlier formations may be readily distinguished from that of those of the later Tertiaries by the forms of both the extremities. In the *Aceratheria* this bone resembles that of the tapirs in the form of the great trochanter. This process is produced at its external border, has a recurved apex, and encloses a deep trochanteric fossa. In *Aphelops* it is precisely as in *Rhinocerus*, obliquely truncate externally, without prominent apex or well marked fossa. In the *Aceratheria* the inner crest of the rotular groove is but moderately prominent; in *Aphelops* and *Rhinocerus* it is greatly developed.

The succession of development of the line of the *Rhinoceridæ* is now not difficult to trace, and I give the following diagram in explanation of it.



It is evident that the descent diverged at a comparatively late period of geological time into two lines, which are represented at the present day by the African and Indian species respectively.

The earliest species of the toothless or African series is the *Atelodus pachygnathus* of Wagner, whose characters have been so well worked out by Gaudry in his great work on the Fossil Fauna of Attica. That species sometimes presents a single small incisor or canine tooth in the mandible.[1] From what has preceded it is also apparent that the generally most specialized type of rhinoceros, the genus *Cœlodonta*, has become entirely extinct. Its three species yet known, were confined to Europe and Northern Asia, and the most formidable of them extended its range with the hairy mammoth within the Arctic circle. The *Cœlodonta antiquitatis* (the wooly rhinoceros) was evidently the most effectively armed of the family, as it had two horns, which, judging from the character of the surface of the skull to which they were attached, must have been of unusual size. To provide further against the shocks incident to their use in combat, the nareal septum was ossified, thus becoming a solid support to the nasal bones, etc., on which they stood.

It remains to look backwards, and to discover, if possible, the probable origin of the family in that of its earliest known genus, *Aceratherium*. A late survivor of this ancestral type is seen in the genus *Zalabis* Cope, of which one species, the *Z. sivalensis*, has been discovered by Cautley and Falconer in the late Tertiary of Hindostan. In this form, according to Falconer, there are $\frac{3}{2}$ incisors and $\frac{0}{1}$ canines. The early type, which corresponds most nearly with this genus, and which preceded the *Aceratheria* in time, is the genus *Amynodon* Marsh, which has left a species in the Uinta or Upper Eocene of Utah. Here the incisors are $\frac{2}{2}$ and the canines $\frac{1}{1}$. This formula is intermediate between that of *Aceratherium* and that of the Eocene tapirs, where the normal numbers $\frac{3}{3}$ $\frac{1}{1}$ prevail. According to Marsh, *Amynodon* further differs in the primitive condition of the premolars above, which, as in the *Lophiodontidæ*, differ from the molars in their greater simplicity. Thus it is probable that tapiroid animals, probably *Lophiodontidæ*, gave origin to the *Rhinoceridæ*, as Marsh has suggested. And it is further altogether probable that the general type of dentition presented by the *Rhinoceridæ*, *Lophiodontidæ*, etc., which I have named the palæotheriodont, took its origin from the type which is intermediate between it and the bunodont, viz: the symborodont, as I have pointed out in an essay on this subject.[2]

[1] The large tooth of the mandible described by the older authors as an incisor, has been regarded as a canine by Gervais. Subsequently Marsh adopted the same view.

[2] The Homologies and Origin of the Molar Teeth of Mammalia, etc. Journal Academy Nat. Sciences, Philada., 1874, pp. 13–14.

The first appearance of dermal horns was apparently in a pair placed transversely on the nasal bones, in species of Eocene *Lophiodontidæ*, of the genus *Colonoceras*. The same character has been observed by Duvernoy in species of the Lower Miocene, which belong to the true *Rhinocerida*, and which Marsh has called *Diceratherium*. This genus appears to have terminated the line exhibiting this structure, and the family in North America remained without horn. As we have seen, the types possessing the median horn arose in Europe, in the *Ceratorhinus schleiermacheri* of the Middle Miocene, and still survives.

It may be observed in conclusion, that a successive increase of size in the species of this line has taken place in North America with the advance of geologic time. Thus, their probable ancestors of the genus *Hyrachyus* were the least of all. The *Aceratheria* of the White River formation were larger, the oldest, *A. mite*, being the smallest. The *Diceratheria* of Oregon were larger still. The species of the Loup River or Upper Miocene formation were larger, and nearly equal to the large existing species.

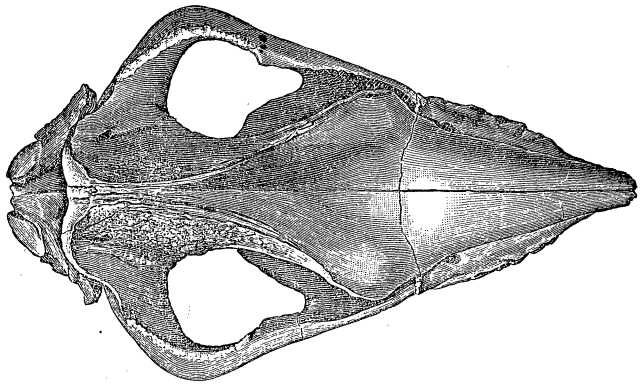


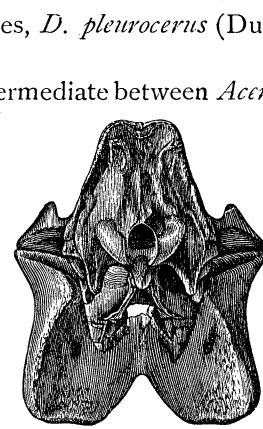
FIG. 4.—*Aphelops megalodus* Cope, skull from above (same as FIG. 1), one-sixth natural size.

Aceratherium Kaup. is characteristic of the Miocene or Middle Tertiary formations of Europe, and is the primitive form of the true rhinoceroses. Its four anterior digits relate it to the lower or more generalized perissodactylous types of the same and of older geological horizons, which are equally allied to the tapirs. The dentition differs from that of the genus *Rhinocerus* in the presence of two superior incisors, but agrees with it in the existence of one incisor and one canine on each side below, and in the forms of the premolar teeth. The species display great simplicity in the character of the crests of the molars. They also possess

the tapiroid feature of the non-closure of the auditory meatus below by the posttympanic process; and the postglenoid process is generally more like that of the tapirs than are those of the later genera *Aphelops* and *Rhinocerus*. The form of the femur is also quite characteristic, presenting tapiroid characters again in the shape of the great trochanter. This process is not flat and obliquely truncated as in the genera above named, but is horizontal proximally, and with a produced recurved apex and posterior crest, which bound a large fossa. The species are the smallest of the family, the *A. mite* having the dimensions of the Malayan tapir.

In the species of *Diceratherium* (Marsh) the cranium and limb bones present the characters above ascribed to the *Aceratheria*. In size they are intermediate between the latter and the *Aphelopes*. The two American species are known from the beds of the Truckee epoch of Oregon; a third species, *D. pleurocerus* (Duv.) has been found in France.

Aphelops (Cope) occupies a position intermediate between *Aceratherium* Kaup and *Rhinocerus* Linn. It agrees with the former in the presence of incisor and canine teeth, and in the absence of indication of a nasal horn, but differs from it in lacking the fifth digit of the anterior foot. In the last respect it is identical with the genus *Rhinocerus*, differing from it in characters already mentioned, in which it agrees with *Aceratherium*. From *Atelodus* Pom. it differs still more widely, as that genus wants incisor and canine teeth.



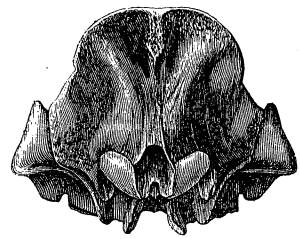


FIG. 5.—*A. megalodus* figured above, posterior view of skull.

FIG. 6.—*A. fossiger*, skull figured in Fig. 3, one-sixth natural size.

The evidence on which this genus rests is furnished by two species, the *Aphelops megalodus*, and the *A. fossiger*. In both of these animals, the number of anterior digits is known to be only three and in the former the inferior canines and alveoli for incisors can be seen in the specimens. In two other species provisionally referred to the same genus, the *A. crassus* and *A. malacorhinus*, the digits and incisor teeth are unknown but the last named species was certainly hornless, and it is supposed that the first named was

so also. Of the many mandibular symphyses from the Loup Fork formation which I have seen, none lack the canines and incisor teeth, so that it is probable that this character belonged to the two species above mentioned. A fifth species, the *A. meridianus* Leidy, I have provisionally referred here, on account of the similar character of the mandibular dentition; but its nasal bones and feet are unknown. Still another species, the *A. jemezanus* Cope, has been referred here, but on no other ground than that it is found in the same formation as the others.

Specific characters.—The species above named all present well-marked cranial or dental characters, or both. But it is important to take into consideration the general structure of the skeleton. I am in position to do this with three of the species named, the

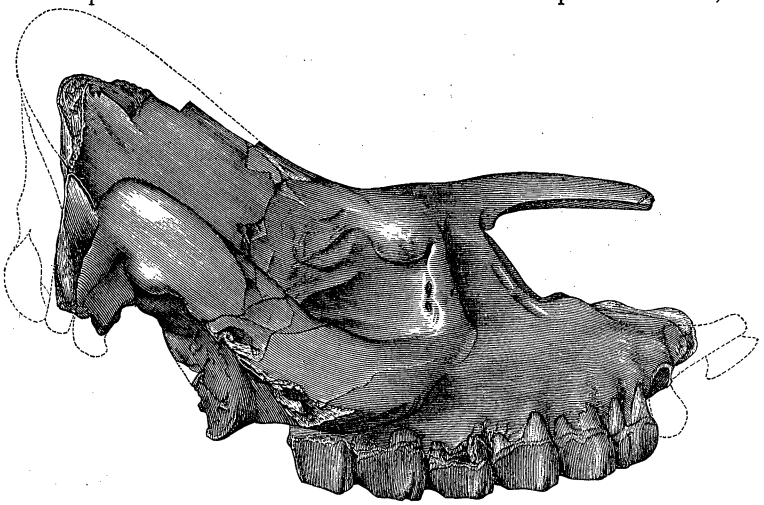


FIG. 7.—*Aphelops malacorhinus* Cope, skull one-sixth natural size, restored behind from another cranium.

A. megalodus, the *A. fossiger* (of this paper), and the *A. malacorhinus* and find distinctive characters present in nearly all their bones which I have observed. The *A. malacorhinus* is a comparatively long-limbed animal, and its apparent elevation was increased by the shortness of the body, and especially of the neck. There was probably a great development of the upper lip, or snout, and the face was concave in profile. The *A. megalodus* was somewhat intermediate in proportions between this species and the *A. fossiger* Its limbs were shorter than in the *A. malacorhinus*, and the neck was longer. The feet were more slender. The *A. fossiger* had still shorter legs, and the length of the neck was about as in *A. malacorhinus*. In its form it must have been like a *Hippopotamus*. Its limbs, and especially the feet, were very robust.

Position.—The longest known species, the *A. crassus*, was found by Dr. Hayden on the Niobrara River, Nebraska. Teeth presenting the same characters have been found in Northern Kansas and Eastern Colorado. The other species are more restricted geographically. A considerable exploration in the Loup Fork beds of North-eastern Colorado, conducted by myself in 1873, yielded four individuals of *A. megalodus*, but no fragments referable to the other species. Explorations in Northern Kansas by Russell S. Hill, of Philadelphia, produced five individuals of *A. fossiger* and five of *A. malacorhinus*, but not a fragment of *A. megalodus*.

History.—In my original definition of this genus, I relied on

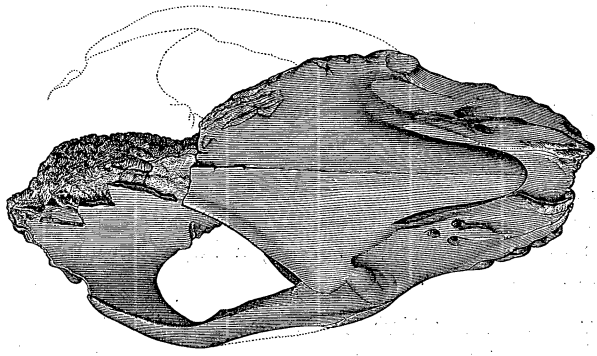


FIG. 8.—*A. malacorhinus* skull, represented in Fig. 7 from above, one-sixth natural size.

the number of premolars in distinguishing it from *Rhinocerus*, as well as on the absence of the horn. These teeth are generally $\frac{3}{3}$ in *Aphelops*, and are said to be $\frac{4}{4}$ in *Rhinocerus*, in most works on the subject. These numbers are not constant; on one side of both jaws in *Aphelops* from Colorado, I have observed a first premolar, and on one side of the upper jaw of *A. malacorhinus* there are four premolars; the other side is injured. In several species of *Rhinocerus*, three premolars only are usually found in the mandible. I may add that Lesson and Peters[1] have described a *Rhinocerus inermis* Less., which is found living on some of the islands at the mouth of the Ganges. The only known specimens are the skulls, with portions of the skin, of a female and young. These are hornless, and in general structure allied to the *R. sondaicus*, yet presenting some important differences.[2] Should the characters of this form prove to be specific, and the male be found to lack the horn, it must be regarded as a species of *Aphelops*.

[1] Monatsberichte Berlin. Akademie, 1877, p. 68, pl. 1–2.

[2] Peters represents the posttympanic as not coössified below the meatus as in *R. sondaicus*.