

CRITICAL OBSERVATIONS ON THE  
PHYLOGENY OF THE  
RHINOCEROSES

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Study of a series of skulls and skeleton material of the rhinoceros *Aphelops* from the Texas Pliocene has made necessary various comparisons with the later Tertiary American rhinoceroses and with those of the Old World. There is much diversity of opinion among authorities as to the relationship and phylogeny of the Old World rhinoceroses and their affinity to the American genera. In my view insufficient weight has been given to the generally recognized Holarctic origin of the family, the living members, all in the outlying regions, being persistently primitive survivors little changed from ancestral stages which inhabited Holarctica in the Miocene and Pliocene. In the accompanying diagram the principal living and extinct types are arranged in accordance with the outstanding distinctive characters in horns, tusks, and hypsodonty of the cheek teeth. The tentative phyletic arrangement indicated is based upon these and various other distinctive characters.

Two early side branches of the family appear in the Oligocene and early Miocene, the *Baluchitheres* and *Diceratheres*, the latter group, however, closely related to the main stock. The remainder of the *Rhinocerotidae* are a rather nearly related but divergent group characterized by cheek teeth progressively hypsodont, more so in some than in others; with nasal horns or frontal horns or both or neither. In the African group two horns are developed, nasal and frontal, the skull is long and both upper and lower tusks are lost. The Sumatran rhinoceros is a primitive member of this group, in which the horns are still rudimentary, the teeth are still quite short crowned, and the tusks have not yet been lost (although they are considerably reduced). The two African rhinoceroses are more progressive, have developed the horns and lost both tusks; in the Black



Rhinoceros the cheek teeth are moderately high-crowned, in the White Rhinoceros more decidedly so with a somewhat different and peculiar pattern. The rhinoceroses of the Pleistocene of Palaeartica carry these two types a stage farther, developing a bony partition between the nares, which serves to strengthen the front horn and enable it to shift a little further forward; they are also a bit more hypsodont. Another less known Pleistocene Palaeartic genus of this group, *Elasmotherium*, has developed the frontal horn greatly, but lost the nasal horn, the pattern of cheek teeth seems to be a further specialization of that seen in the white and woolly rhinoceroses. The skeleton of this genus however is unknown, and very little as to its ancestry, so that its position is still provisional, but the recent recognition of related and resembling forms in the Pliocene of China and Persia throw some light on its affinities.

A second group, represented by the Indian rhinoceros, develops a powerful nasal horn but no frontal horn and retains both upper and lower tusks. The modern Javan rhinoceros is a somewhat more primitive stage of this group and various species of the Tertiary and Pleistocene of the Old World belong to it. The short-legged rhinoceroses of the Holarctic Tertiary may be more or less related to this group, accord well with it in horn and tusk development and in the detail construction of the cheek teeth, but whether they constitute a distinct phylum as Osborn supposed or are a number of independent short-legged specializations, is not so clear. *Teleoceras* of the American Pliocene has nothing especially in common with *Brachypotherium* of the European Miocene excepting the short legs. The skull is of very different form, the specializations of its cheek teeth are in no way foreshadowed in any of the *Brachypotherium* group; the feet although short are not much alike in details. In any event they do not need to be placed in a separate subfamily. *Teleoceras*, the most specialized of the short-legged rhinoceroses, has enlarged hypsodont molars and much reduced premolars; this specialization is unique among the true rhinoceroses.

A third group represented by *Aphelops* of the Nearctic and *Chilotherium* of the Palaeartic Mio-Pliocene, is hornless, with degenerate upper tusks but powerful lower tusks. The upper tusks are vestigial in *Aphelops*, wholly absent in *Chilotherium* and *Peraceras*; the nareal notch is retracted, approaching the tapir construction in some degree; the nasals are reduced to a varying extent. As in other rhinoceroses the latter specialized members are usually more hypo-

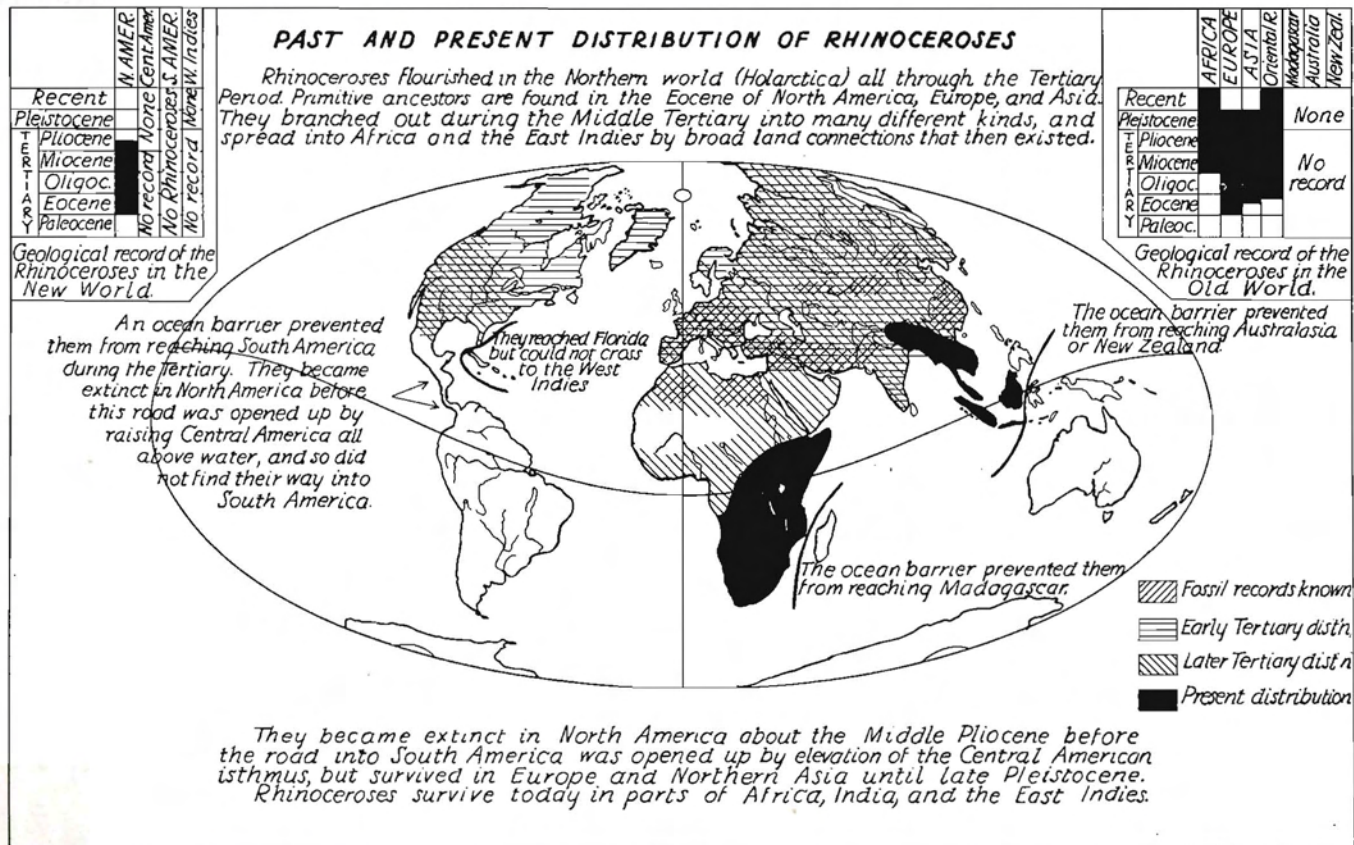


Fig. 1.



dont. *Peraceras* however remains subbrachydont. This group varies rather widely in length of skull, form, and reduction of nasal bones, but species otherwise closely related differ so much in these respects that the character cannot be given much taxonomic value. The retraction of the nareal notch on the other hand is fairly constant throughout. Various Old World species which have been mistakenly referred to *Teleoceras* or the "Teleoceratinae" so called, appear to belong in the *Aphelops* group.

*Aceratherium* of the European Miocene appears to be a primitive stage of this Aphelopine phylum, still retaining upper canines and comparatively brachydont cheek teeth but showing its affinities in the retracted nareal notch, powerful lower tusks, etc. But some of the species which have been referred to this genus should be otherwise assigned.

The common ancestry of all these later rhinocerotid groups is to be seen in the Oligocene group of *Caenopus* and its allies, small, hornless long-skulled types with unreduced nasals, unretracted nares, quite brachydont teeth of simple pattern, good-sized upper and lower tusks and some vestiges of the other front teeth. The limbs and feet are more slender, the construction of carpals and tarsals much more primitive in this group; they have not taken on the numerous peculiar details of construction seen in the later rhinoceroses, but are in nearly the same stage of adaptive specialization seen in the modern tapirs. Numerous intermediate stages between this group and the specialized rhinoceroses of the later Tertiary are to be found in the older Miocene of Europe and North America; but they are not sufficiently known or critically studied to prove whether they are genetic intermediates or parallel specializations. The American members of this group have recently been revised by H. E. Wood. I am in agreement with most of Dr. Wood's conclusions as to apparent relationships but disposed to a more conservative expression of them both in the separation of genera and species and the value attached to detail phylogenies supported by inadequate evidential data.<sup>1</sup>

The European members of this *Caenopus* group have been split up into a number of genera by Abel, and three or four genera have been

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<sup>1</sup> Constructing detailed phylogenies upon inadequate evidence with few or no independent data to check the correctness of conclusions is a favorite occupation of many paleontologists. Such provisional arrangements have their value, but they should not be classed with the sound and well proved conclusions of our science, nor used as a basis for taxonomic and nomenclatorial work. The result of doing so is to obscure and reduce the importance of the well proved and major distinctions and groupings.

proposed by various American paleontologists, but a comprehensive revision of the group based upon teeth, skulls, and skeleton characters is still to be made.<sup>2</sup>

Ancestral to the *Caenopus* group stands the genus *Trigonias*, admirably represented now by the fine series of skulls and partly associated skeletons obtained by the Denver Museum from a single fossil quarry in the Chadron beds of Weld County, Colorado. There is every reason to believe on ecologic and other grounds that this series represents one genus and one species thereof, the wide range of variation in structure of the cheek teeth illustrating how little value should be attached to the complex detailed phylogenies with numerous species and many so-called genera, that have been built up on the comparison of numerous fragmentary specimens from various localities.

Such genealogies I regard as largely illusory, resulting from failure to envisage and appreciate the real scope of a species as it exists in nature, constituted of a large number of interbreeding strains, of more or less differing heredity. The interbreeding ranges all the way from continuous to occasional; its results are seen in characters of individual variation, sometimes intergrading, often intermingling though not intergrading. It is not reasonably probable that a large number of nearly related individuals living in the same locality, watering at the same pool, similar so far as we have any indications, in habits and environment would fail to interbreed. It is wholly improbable that any infertility existed to prevent it. And so long as they habitually or frequently interbreed, directly or indirectly, they are *not* distinct species. There is abundant evidence that all species in nature are thus variable. The variability seems often to be thought of as the result of hybridizing of originally pure strains. But this is not so. The species never were pure. They always have consisted of a complex of interbreeding strains. Environmental pressure, bringing about selection, change of geographic range, creation of new

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<sup>2</sup> The group includes *Subhyracodon* Brandt, *Anchisodon* Cope, *Caenopus* Cope, *Leptaceratherium* Osborn, *Amphicaenopus* Wood, *Metacaenopus* Cook (= ? *Menoceras* Troxell), *Praeaceratherium*, *Protaceratherium*, *Epiaceratherium*, *Meninatherium* Abel, *Paracaenopus* Breuning, *Eggysodon* Meyer, *Pleuroceros* Roger, *Menoceras* Troxell, *Diceratherium* Marsh, probably other names. The last two represent a distinct side branch, although still nearly related to the central group. The others have been variously treated by Osborn, Abel, Peterson, Cook, Troxell, Wood, and others. In my judgment the majority of the species that have been proposed rest upon individual variation—well known to have wide range in the rhinoceroses, both in number and structure of the teeth as well as in skull proportions, horns, and skeletal characters—and that the majority of the genera proposed could be cashiered to advantage or reduced to the rank of subgenera at most.



“mutations,” (DeVriesions), elimination of old ones, bring about continual changes in the composition of this band of anastomosing lines. Isolation, divergence of groups into progressively different adaptations or environment may result in a practical cessation of interbreeding, followed, if it continues long enough, by progressive lack of fertility between one and another group, resulting in the emergence of distinct species, which once wholly infertile, can never reunite.<sup>3</sup> From that stage onward, but not previously, we deal with parallel evolution. The attempt to extend parallel evolution backward into interbreeding races is, we believe, illusory.

I regard the variation seen in numerous specimens of a race found together in a single fossil quarry as being individual variation. It has been so regarded by most paleontologists.<sup>4</sup> Many, however, fail to use that standard of the range of individual variation when dealing with a variety of specimens from different localities. They substitute for these practical standards certain theoretical concepts of several parallel lines of closely related “species” evolving side by side but distinct, and presumably not interbreeding, although no adequate evidence is offered that they were so distinct, and only rarely is there sufficient comparative material available to prove it. In absence of such evidence the range of variability of the well-known “quarry” species ought to be our guide, supplemented by the range of variability shown in large series of living related species.

These standards have been often cited but seldom used. If applied systematically the majority of described “species” would be relegated to synonymy. The inevitable result of such unnatural splitting of species is a correspondingly fine splitting of genera and of larger groups, resulting in a complicated taxonomy that has no real necessity, and elaborate “polyphyletic” phylogenies that have no real foundation in fact. The overemphasis of minor groups serves merely to obscure the real divergence of major groups. To split the Rhinocerotidae into a dozen “subfamilies” serves to obscure the fact of the striking divergence of one group (*Baluchitheres*) from all the rest, and to place each of the others upon a systematic parity with such far more distinct groups as the subfamilies of *Mustelidae*, each

<sup>3</sup> But upon this point, see Matthew, *Bull. Geol. Soc. Am.* 1913, p. 284.

<sup>4</sup> The practical test of it lies in the fact that a large series of specimens show the differences in characters either *intergraded* or *intermingled*—i.e., even though certain characters do not intergrade, yet they are so distributed among the specimens that these cannot be divided into groups separable by several independent characteristic and constant distinctions.



of which includes types quite as fundamentally diverse as the whole group of the later Tertiary and modern rhinoceroses.

The *primitive* characters of the Oligocene and Lower Miocene rhinoceroses may be held to justify their being placed in a distinct subfamily, ancestral to the rest (except for Baluchitheres).

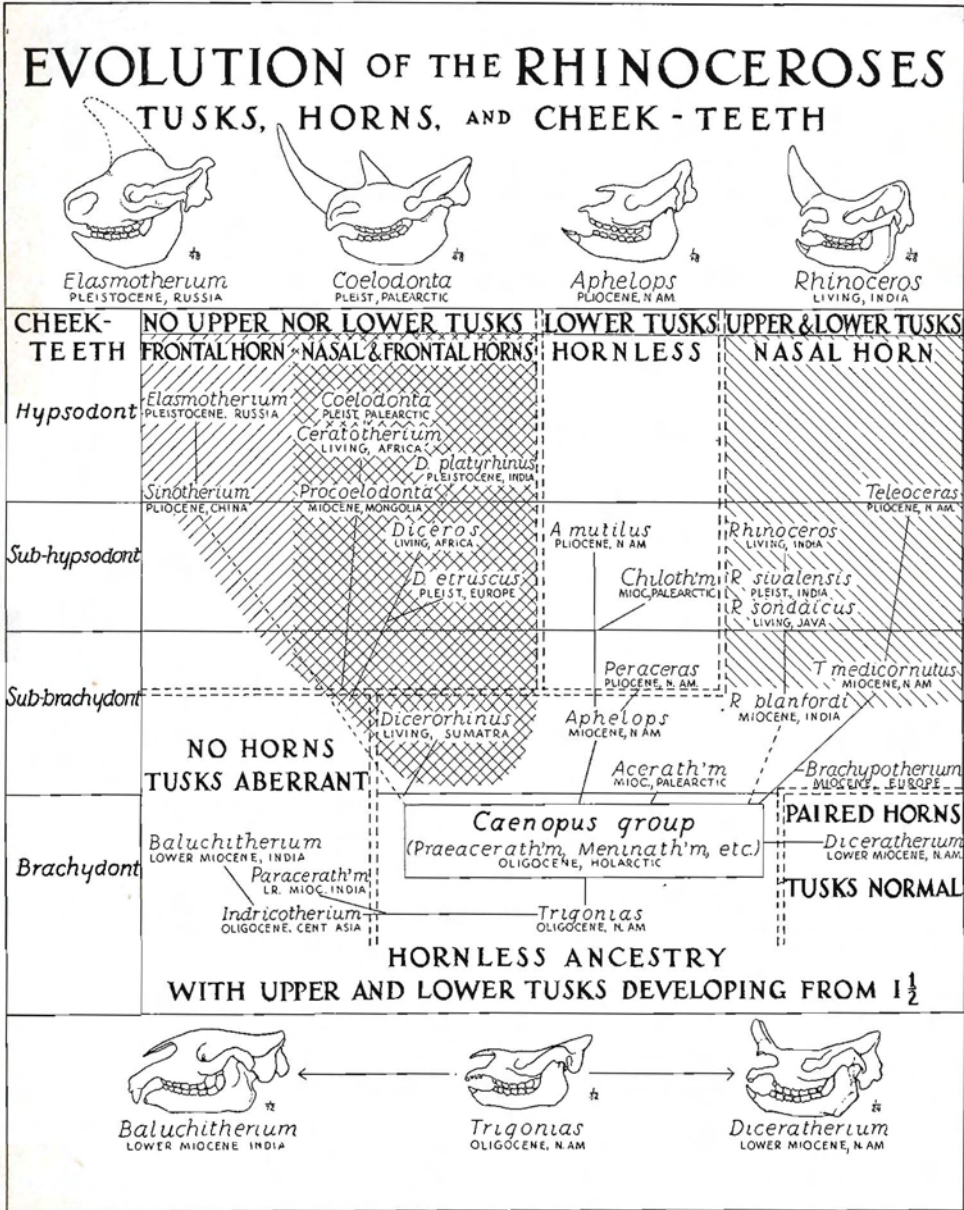


Fig. 2.

## KEY TO THE GENERA

RHINOCEROTIDAE.  $I_{\frac{1}{2}}$  enlarged as tusks, one or both tusks subsequently lost in specialized types.  $M^2$  with ectoloph not extended behind metaloph but forming a continuous crest. Muzzle narrowed anteriorly with a pointed lip in front, the superior outline more or less concave. Fifth digit of manus reduced, mostly vestigial or wholly lost, remaining digits of manus and the three digits of pes mostly tending to be subequal, short and stout.

- A. BALUCHITHERIINAE. Upper tusk subcircular, blunt-pointed; lower tusk decumbent conical. Hornless with elongate skull, brachydont cheek teeth. Rectigrade limbs, elongate feet, tridactyl but lateral digits reduced, appressed, phalanges very short, unguals very wide forming a subcircular line of hoof.

*Baluchitherium*, Lower Miocene Baluchistan and adjacent parts of India. May prove to be a synonym of *Paraceratherium*, same formations and locality.

*Indricotherium*, Oligocene of Turkestan and Mongolia, has not been clearly distinguished from the preceding, but may probably be generically distinct.

- B. DICERATHERIINAE. Upper tusk short, trilobate, lower tusk upcurved or partly procumbent, forming an elongate lanceolate trigonal blade like crown. One or more of smaller anterior teeth retained. Cheek teeth brachydont, premolars more or less molariform, molars with little or no development of the accessory crests. Skull long, muzzle pointed, superior outline slightly to moderately concave in cranial region and with little convexity in frontal region. Limbs comparatively slender, tapiroid, carpal and tarsal bones relatively high and narrow throughout, much as in modern tapirs. Ancestral to later rhinoceroses and connected with them by many intermediate types.

*Trigonias*. Usually  $I \frac{1.2.3}{1.2.(3)}$  C, 5th digit complete, premolar construction simpler. Lower Oligocene.

*Caenopus* group.<sup>5</sup> Usually  $I \frac{1.2.(3)}{1.2}$ , 5th digit vestigial premolars somewhat more complex. Oligocene.

*Diceratherium*.  $I \frac{1}{1.2}$ , 5th digit vestigial, premolars more complex, accessory crests often appear on molars. Paired horns on nasals of male, skull more concave superiorly with broader muzzle and flanged angle on jaw.

<sup>5</sup> Wood is disposed to recognize several genera in the *Caenopus* group, partly for the purpose of validating Cope's name, anticipated by the unfortunate name of *Subhyracodon*. A better method would be to get it on the list of "nomina conservanda" with Leidy's classic species as type and the fine skeleton in the American Museum as the neotype of the species. Wood is disposed to doubt the need of separating *Menoceras* from *Diceratherium*; it seems to me quite unnecessary.



- C. RHINOCERINÆ. Cheek teeth higher crowned, subbrachydont to hypsodont, front teeth specialized or lost, horns if present median on nasals or frontals or both. Larger animals with massive limbs broadened feet and foot-bones modified in numerous details.
- I. Nasal horn only. Upper and lower tusks retained.
1. Short legs and feet, rudimentary horn.
    - a. Brachydont, premolars unreduced, short concave skull. *Brachypotherium*.
    - b. Subhypsodont, premolars reduced, medium skull little concave. *Teleoceras*.
  2. Normal legs and feet, well developed horn.
 

a. Subbrachydont	}	<i>Rhinoceros</i> .
b. Subhypsodont		
- II. Hornless, retracted nares. Lower tusks large, upper mostly vestigial to absent.
1. Brachydont, upper tusks little reduced. *Aceratherium*.
  2. Subbrachydont to subhypsodont, upper tusks vestigial to absent.
    - a. Skull short, teeth subbrachydont, no upper tusks. *Peraceras*.
    - b. Skull medium to long, teeth subbrachydont to subhypsodont, upper tusks vestigial or absent. *Aphelops*.
    - c. Skull medium, teeth subhypsodont, no upper tusks. *Chilotherium*.
- III. Nasal and frontal horns.
1. Subbrachydont, tusks retained. *Ceratorhinus*.
  2. Subhypsodont, tusks lost. *Opsiceros*.
  - 2a. With ossified nasal septum. (*O. etruscus*, etc.).
  3. Hyposodont, tusks lost. *Ceratotherium*.
  - 3a. With ossified nasal septum. *Coelodonta*.
- IV. Frontal horn only. Hyposodont with crenulate enamel.<sup>6</sup>
1. *Sinotherium*.
  2. Hyposodont. Tusks lost. Septum. *Elasmotherium*.

<sup>6</sup> Ringström holds the last group as a separate family. Wood comments as to this, that, according to that scale, one would have to rank *Baluchitherium* in a distinct order. Ringström in fact brings out one very strong point against his own view, in showing that the peculiar tooth pattern of *Sinotherium* and *Elasmotherium* is combined in "*Rhinoceros*" (*Iranotherium*) *morgani* with a skull which is a typical two-horned rhinoceros. Evidently the connection is not so very remote with such hypsodont two-horned types as *Ceratotherium* and *Coelodonta*.